TUNAS AND THEIR ENVIRONMENT IN THE PACIFIC OCEAN: A REVIEW

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INTRODUCTION

Fifteen years ago, the late Harold Barnes invited one of us to review relations between tunas and their oceanic environment in this Annual Review Series (Blackburn, 1965). Recent advances in that field prompted the U.S. National Marine Fisheries Service to commission the writing of an updated review for the benefit of investigators in all countries. The present paper is the result of that work. Tunas are of increasing interest to marine scientists in a number of ways: as food resources, as pelagic organisms with immense but well-described distributions, as apex predators in oceanic ecosystems, and as a group of fishes with unique anatomy, biochemistry and physiology. These interests have led to the mounting of oceanographic expeditions and the founding of scientific organizations, many of them multi-disciplinary or international. From those and other efforts, tuna ecology has progressed from the descriptive to the explanatory phase, although much work of both kinds still remains to be done. Designed experiments have become frequent. The making and testing of fairly complex models has begun. This progress is summarized and reviewed here. Probably no group of oceanic animals has been the subject of such comprehensive ecological research on a world scale, except perhaps cetaceans. Many valuable contributions to the main-stream of oceanography have resulted from tuna-ecological programmes, although they are not within the scope of this review. Examples include the discovery of the Pacific Equatorial Undercurrent (Cromwell, Montgomery & Stroup, 1954), and the development of a method for the continuous

measurement of *in vivo* chlorophyll concentration (Lorenzen, 1966). At present work continues notably in the areas of physiology, behaviour, biochemistry, genetics, stock identification, and fluctuations in distribution and abundance, as well as on refinement of recent definitions of species habitat.

Major compilations of information on tuna ecology have been made. Of particular note are the works collected in the Symposium on Scombroid Fishes, Parts 1–4, Mandapam Camp, India (Anonymous, 1962); the Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, Vols. 1–4, FAO Fisheries Report No. 6 (Rosa, 1963); Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu, U.S.A. (Manar, 1966); and the review mentioned above (Blackburn, 1965). We intend not to consider the material covered in these works in detail, but rather to concentrate on reviewing the progress made in understanding tuna-environment interrelationships since then. The greater part of this review relates to six tunas (yellowfin, skipjack, bigeye, albacore, bluefin, and southern bluefin) and to one ocean, the Pacific. References to other species and oceans are restricted to those most necessary for the understanding of the subject. In our discussions of the impact of the environment on the tunas we shall confine our remarks mostly to the influence of features on distribution, and not on abundance. Real abundance cannot be determined at this time, and descriptions of stocks and changes in their condition (abundance) are speculative.

NOMENCLATURE

The six species selected for primary consideration in this paper are the tunas which have been exploited commercially. Because of their commercial importance they have been subjects of research investigations to varying degrees. All species discussed are in the family Scombridae, which was reviewed by Collette & Gibbs (1963), and commonly are called tunas in the English vernacular. More recently Klawe (1977) summarized the classification of the family and discussed the common and scientific nomenclature. Sharp & Pirages (1978) discussed the phylogenetic relationships among the tunas. In this paper references to the six principal tunas will be made according to:

Scientific Nomenclature	Vernacular Nomenclature
Thunnus alalunga (Bonnaterre)	Albacore
Thunnus albacares (Bonnaterre)	Yellowfin
Thunnus maccoyii (Castelnau)	Southern bluefin
Thunnus obesus (Lowe)	Bigeye
Thunnus thynnus orientalis (Temminck and Schlegel)	Bluefin: Northern (Pacific)
Katsuwonus pelamis (Linnaeus)	Skipjack

Other species are named where they occur in the text.

AREAL DISTRIBUTION OF PACIFIC TUNAS

Our knowledge of geographical ranges of the principal tuna species now appears to be almost complete in all oceans. Few large extensions of range have been reported during the past fifteen years. Here we summarize information on areal distribution of adult tunas, as distinct from that of tuna larvae. We consider as adults all ontogenetic stages at which the fish resemble adults morphologically, regardless of size or sexual condition. There is not much information about such stages at sizes below 30 cm, which are known mostly from stomach contents of larger fish (Yoshida, 1971; Mori, 1972).

The principal sources of information on adult distribution are records of commercial fisheries and fishery research surveys. The latter are important sources in areas where fisheries have not developed. Commercial fisheries are of three main types, surface hooking (mostly pole-and-line fishing, trolling), surface netting (mostly purse-seining), and subsurface hooking (pelagic long-lining); or more simply of two types, surface and subsurface. Surface fisheries are more restricted in area than subsurface, partly because they need high concentrations of visible fish and also because of special conditions such as bait supply, weather, and market demand. They can expand when the special conditions change or are overcome, as has recently occurred with the introduction of larger and faster vessels to fish yellowfin and skipjack in the eastern tropical Pacific. Individuals of a particular species caught in surface
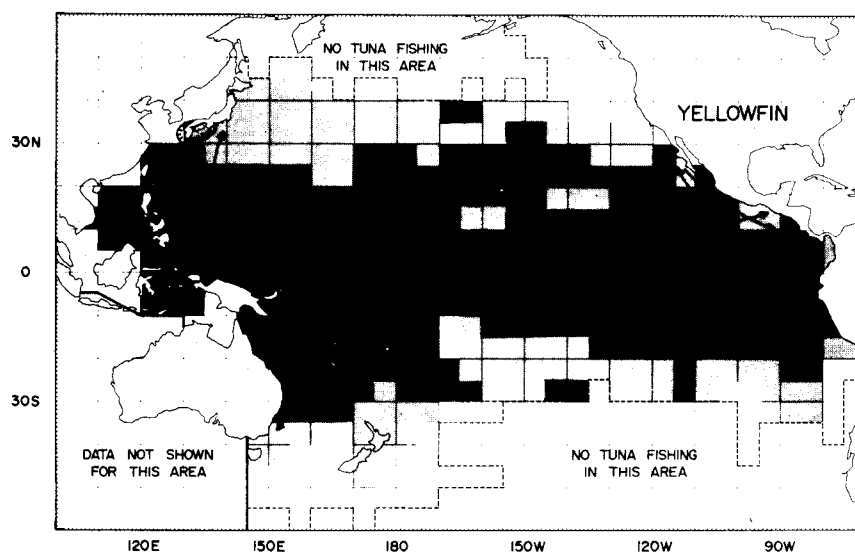

Fig. 1.—Distribution and movements of yellowfin tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, heavy shading shows 5-degree rectangles in which the longline catch of yellowfin was $\geqslant 0.5$ fish per 100 hooks in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch; hatched lines are approximate boundaries of surface fishing areas for yellowfin, which are explained further in the text; arrows (schematic) show major movements of tagged and recaptured yellowfin.
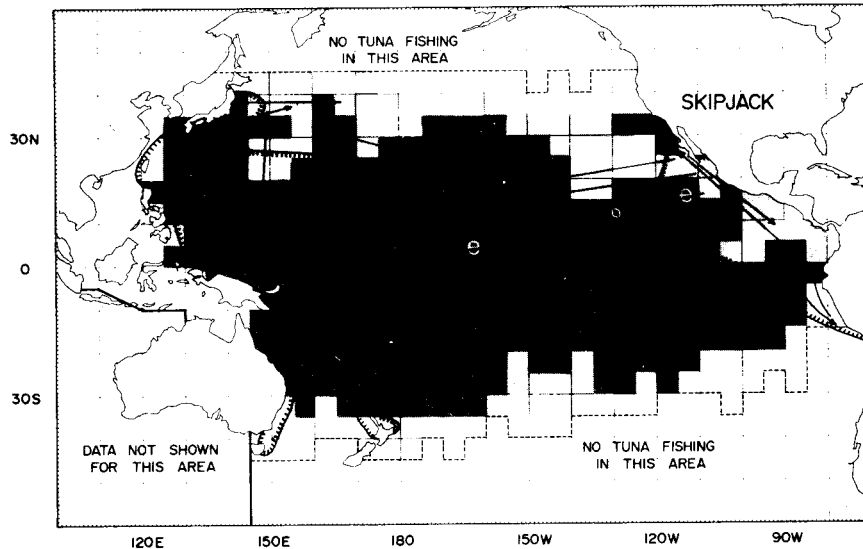
Fig. 2.—Distribution and movements of skipjack tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1964–1967; within that area, heavy shading shows 5-degree rectangles in which the number of skipjack caught per 100 hooks was two or more times the average for the whole area, in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch (from Matsumoto, 1975); hatched lines are approximate boundaries of surface fishing areas for skipjack, which are explained further in the text; arrows (schematic) show most extensive movements of tagged and recaptured skipjack; note arrow (ee) indicating movement from approximately 110° W: 15° N to 167° W:3° N is in error and should be disregarded (W. Bayliff, pers. comm.).

fisheries tend to be smaller than in subsurface fisheries. Higgins (1966) summarized data on that subject for yellowfin, bigeye, and albacore, and Robins (1963) gave similar information for southern bluefin. Skipjack are caught only incidentally in subsurface fishing, but large skipjack are possibly more common below than at the surface (see p. 485).

Figures 1 to 5 show the limits of range in the Pacific of yellowfin, skipjack, bigeye, albacore, and bluefin from the records of the Japanese long-line fishery, and Figure 6 shows worldwide limits for southern bluefin from the same fishery. Except for skipjack these charts are based upon records published by the Research Division, Fisheries Agency of Japan, for the years 1971 to 1977, which are the latest available. The charts for skipjack are based upon records for the years 1964 to 1967, assembled by Matsumoto (1975). Areas where there was no long-line fishing in any of those years are indicated. In Figures 1 to 4, areas of higher and lower relative abundance, measured by catch per unit of fishing effort, are distinguished. Figures 1 to 6 also show approximate boundaries of areas of surface fishing, based on information from the following sources: for yellowfin, Schaefer, Broadhead & Orange (1963) and Suzuki, Tomlinson & Honma (1978); for skipjack,
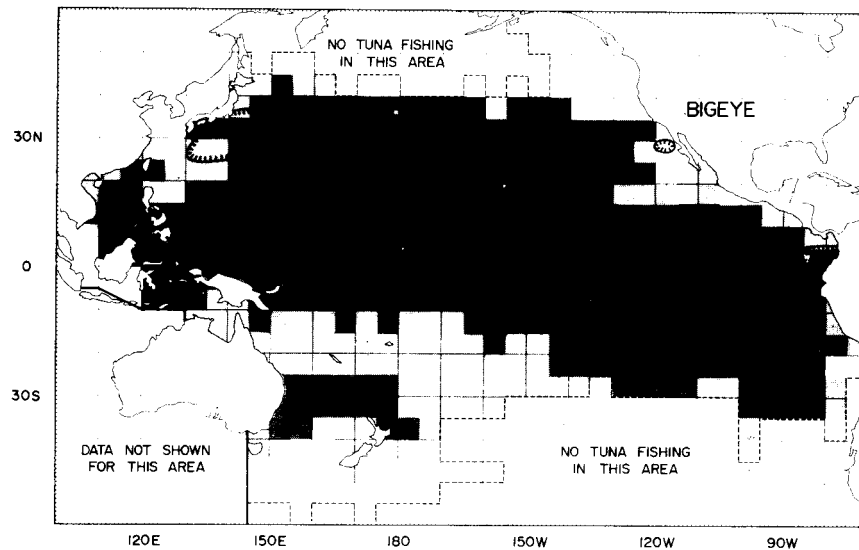
Fig. 3.—Distribution of bigeye tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, heavy shading shows 5-degree rectangles in which the longline catch of bigeye was $\geqslant 0.5$ fish per 100 hooks in any quarter-year; light shading indicates a catch rate lower than that; open areas indicate zero catch; hatched lines are approximate boundaries of surface fishing areas for bigeye; the arrow (schematic) shows the most extensive movement of a tagged and recaptured bigeye.

Matsumoto (1975), Otsu (1975), and Inter-American Tropical Tuna Commission (1978); for bigeye, Barrett & Kume (1965) and Kume & Morita (1967); for albacore, Yoshida & Otsu (1963); for bluefin, Bell (1963, unpubl.), Yamanaka & staff (1963), I. Yamanaka (pers. comm.), and Bayliff & Calkins (1979); and for southern bluefin, Robins (1963). We have also referred to Joseph, Klawe & Murphy (1979).

Yellowfin, skipjack, bigeye, and albacore are similar in their total range in the long-line fishery, namely about 40° N to 40° S in the Pacific (Figs 1 to 4). Comparing distributions at two levels of relative abundance shows, however, important differences between some of these species. Yellowfin is the most tropical of the four species, being most abundant between 30° N and 30° S. Skipjack and bigeye are relatively abundant from the Equator to about 35° or 40° in each hemisphere. Albacore has a comparatively low relative abundance in equatorial waters, and its poleward limits are at slightly higher latitudes than bigeye. All four species are relatively scarce in certain parts of the eastern tropical Pacific, for reasons discussed later (see pp. 480–487) under temperature and oxygen. Bluefin (Fig. 5) occur principally at about 25° to 35° in the North and South Pacific and also in equatorial waters of the western Pacific. Except for the surface fishery area off the Californias, the species seems less common east than west of 155° W, especially in the tropical region. Individuals have been recorded as far north as 57° N in the Pacific. Bluefin extend as far south as 15° to 20° S in the western Pacific (Shingu,
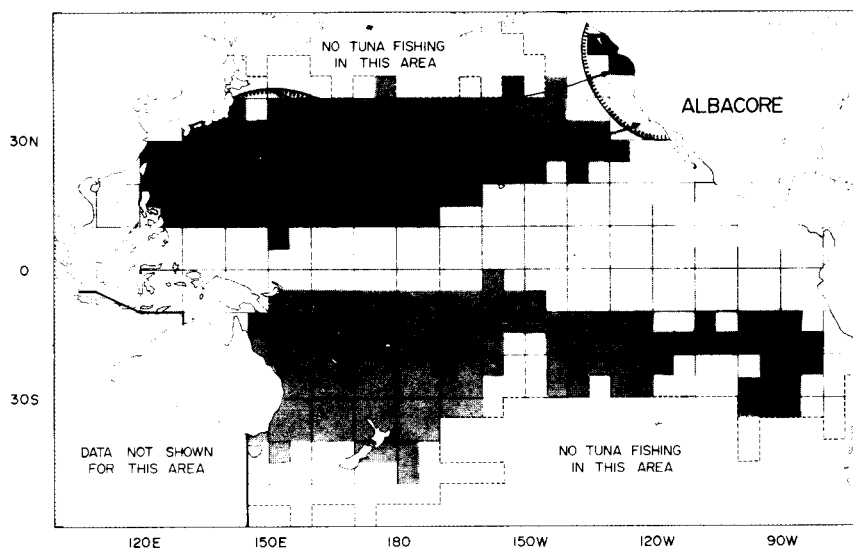
Fig. 4.—Distribution and movements of albacore tuna in the Pacific Ocean:
broken lines shown are extreme poleward boundaries of the Japanese longline
fishery in the years 1971–1977; within that area, heavy shading shows 5-degree
rectangles in which the longline catch of albacore was ≥ 0·5 fish per 100 hooks
in any quarter-year; light shading indicates a catch rate lower than that; open
areas indicate zero catch; hatched lines shown are approximate boundaries
of surface fishing areas for albacore; arrows (schematic) indicate generalized
movements of tagged and recaptured albacore.

Warashina & Matsuzaki, 1974), and longline records show the apparent
occurrence of bluefin in the area of 5° to 15° S, 90° to 135° W (Fig. 5). Long-
line records also indicate their occurrence from 20° S to 50° S off eastern
Australia, New Zealand, and from 25° to 35° S off Chile. The point has been
made that these fish may instead be southern bluefin, but Japanese fishermen
are considered to be accurate in separating the two bluefin species (in view
of the significant difference in market value). Southern bluefin (Fig. 6)
occurs between 10° and 55° S overall, and abundantly from 25° to 50° S in
the Pacific. The apparent gap in its distribution in the South Pacific, between
100° and 155° W, may reflect the lack of any fishing in that region. The range
of this species in other oceans is similar, except in the eastern Indian Ocean
where it is also abundant from 5° to 25° S.

The surface fishing areas fall within the ranges for the long-line fishery
except for certain coastal waters. Those for some species require comment.
The surface fishery for yellowfin and skipjack in the eastern Pacific now
extends nearly half way across the ocean (Figs 1 and 2), but until 1968 it
operated only within a relatively narrow band, up to 500 km wide, adjacent
and parallel to the American coast. Most of the catch taken west of 115° W is
yellowfin, which is the higher-priced species and the easier species to take by
purse-seining because of its association with porpoise (Calkins, 1975; Perrin,
1975; Suzuki *et al.*, 1978). The range of surface yellowfin in the eastern and
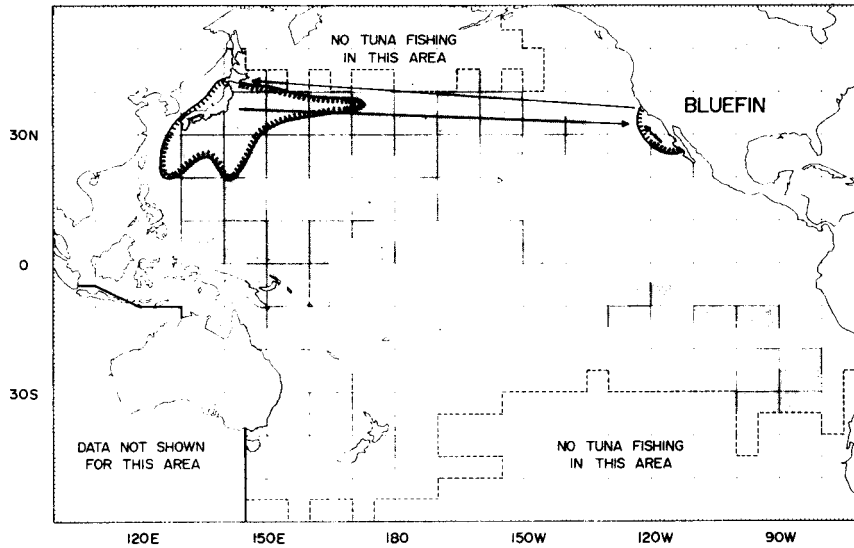central tropical Pacific is more extensive than shown, because the species

Fig. 5.—Distribution and movements of bluefin tuna in the Pacific Ocean: broken lines shown are extreme poleward boundaries of the Japanese longline fishery in the years 1971–1977; within that area, shading shows 5-degree rectangles in which any bluefin were taken; hatched lines shown are approximate boundaries of surface fishing areas for bluefin; arrows (schematic) indicate generalized movements of tagged and recaptured bluefin.

has been taken by trolling and seen in schools during research cruises in several other areas, especially near islands. The same cruises likewise demonstrated a much wider distribution of skipjack than the surface fishing areas shown. The skipjack were less confined to island regions than yellowfin, and were more abundant than yellowfin except near certain islands (Murphy & Ikehara, 1955; Murphy & Shomura, 1972; Blackburn & Williams, 1975). Some of the skipjack surface fisheries in the western tropical Pacific
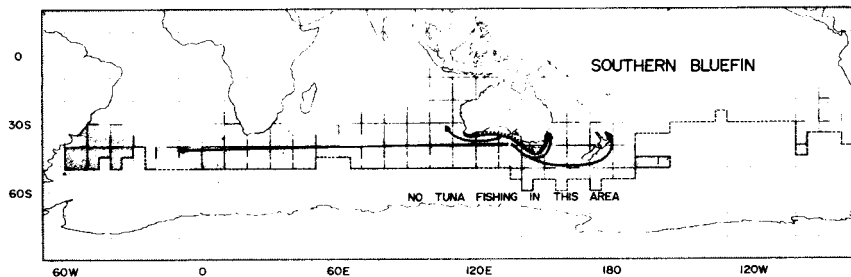
Fig. 6.—Distribution and movements of southern bluefin in all oceans: broken line shown is the extreme southern boundary of the Japanese longline fishery in the years 1971–1977; within that area, shading shows 5-degree rectangles in which any southern bluefin were taken; hatched line shown is the approximate boundary of the surface fishing area for southern bluefin; arrows (schematic) show major movements of tagged and recaptured southern bluefin.

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have recently extended their range (Otsu, 1975). The area shown off eastern Australia in Figure 2 is the known range of surface skipjack in coastal waters, not of the fishery which is very small because of low demand locally (Blackburn & Serventy, in press). The area shown off New Zealand is according to Habib (1976). Surface fishing areas for bigeye are quite restricted (Fig. 3) and only small catches are made there.

The distributions shown in Figures 1 to 6 are discussed later (see pp. 480–500) in relation to particular ocean conditions that may determine them. At this point, however, it is of interest to compare them with a series of biotic provinces recognized in the Pacific by McGowan (1974). These provinces are not based primarily on currents, water masses, or ocean properties, although they obviously are related to some of these. They were recognized empirically by classifying charted distributions of many species of pelagic organisms into a small number of distinct but overlapping patterns. Most of the organisms were zooplankton but some were nekton and phytoplankton. The provinces are Subarctic and Subantarctic (poleward of 40° N and S), North and South Transition (30° to 45° in each hemisphere), North and South Central (10° to 35° in each hemisphere, but tending to join across the Equator in the western Pacific), Equatorial (between 25° N and 25° S), and Eastern Tropical Pacific (between 20° N and 20° S in the eastern Pacific). In addition to the eight faunas respectively characteristic of these provinces, a Warm Water Cosmopolite fauna, ranging from about 40° N to 40 S, was recognized. The boundaries given apply to the areas in which over 60% of the species in the faunas occurred.

The distributions of albacore and northern bluefin show a reasonable congruence with the North and South Central provinces. The yellowfin distribution is somewhat like the Equatorial province but extends more poleward, whence this species could also be considered a Warm Water Cosmopolite. The area of the present surface fishery for yellowfin and skipjack in the Eastern Tropical Pacific is similar to McGowan's Eastern Tropical Pacific province. Southern bluefin occur mainly in the South Transition province but to some extent in subtropical and tropical waters as well. Skipjack and bigeye are clearly Warm Water Cosmopolites. Tunas have much greater mobility than the other organisms on which McGowan's scheme is based, so one would not necessarily expect them to conform to that scheme unless they were prey-selective for particular province faunas. In fact, they are opportunistic feeders (see p. 490).

The distributions of tunas or any pelagic species are, of course, contained within fluctuating natural boundaries and not by latitude and longitude. McGowan's (1974) paper is valuable in specifying a number of these natural faunal boundaries, although for various reasons, such as indicated later for the tunas, these boundaries will not apply to all species.

BATHYMETRIC DISTRIBUTION OF PACIFIC TUNAS

Information on the vertical distribution of tunas is based mostly upon estimates of depth of capture in commercial and/or research fishing operations. A few observations have been made by use of depth-indicating sonic tags, by maximum–minimum depth or temperature sensors, and by echo sounding.

On one occasion, observations were made from a submarine vehicle. It has been estimated that most hooks on a commercial longline hang at depths between 80 and 140 m (Yabuta & Ueyanagi, 1953), and a mean depth of 100 m has been assumed for certain purposes in this paper. Lines set in strong currents will not fish so deeply. Tuna can be caught while the line is sinking, at rest, or being retrieved.

The surface fisheries generally take smaller fish than those caught on longlines. In pole-and-line operations, and sometimes in trolling and purse seining, the fish appear at the sea surface. The deepest purse-seines, however, are effective at depths to 50–80 m and yellowfin are known to escape under such nets.

The depth range of a tuna species is not the same in all regions. For example, Hanamoto (1974) found that bigeye catch rates as a function of depth varied with latitudinal zones in the eastern tropical Pacific. He considered this variation to be related to zonal currents. Depths of capture for the different zones were:

Latitudinal Zone	Capture Depth
9° N–3° N	90–140 m
3° N–3° S	50–150 m
3° S –9° S	110–160 m
9° S –13° S	120–160 m

Longline catches vary in species composition depending on area and season, and it is shown later that some of these differences can be explained from vertical distributions of temperature and dissolved oxygen concentration.

Japanese workers have made several valuable observations on bathymetric distributions of Pacific tunas in recent years. Saito (1973) and Saito & Sasaki (1974) used special very deep lines, with depth recorders at the hooks, in an area west of Fiji. They obtained yellowfin, bigeye, and albacore down to 380 m, which was the greatest depth fished. The yellowfin and albacore seemed to be approaching the bottom of their range at 380 m, since they were most abundant at depths less than 300 m. On the other hand, the bigeye were most abundant at depths over 300 m. Suzuki, Warashina & Kishida (1977) compared catches of the regular longline, fishing to about 130 m, and of another type that fished to about 260 m. The ratios of mean catches by number of fish, deep:regular, were as follows:

yellowfin	0.73
albacore	0.82
bigeye	1.79

These observations indicate that abundance of bigeye increases below the depth of regular commercial longlines, whereas abundance of the other two species does not. Similarly, Hanamoto (1976) found that more bigeye were caught on the deepest hooks (160 m) of the regular longline than on the shallower hooks, which took more yellowfin. It is clear that we cannot yet specify the maximum depth of occurrence of bigeye with any certainty.

No similarly detailed bathymetric data are available for bluefin or southern bluefin, which are taken by longline as well as in surface fishing. The deepest

records of skipjack are 185 m from a submersible (Anonymous, 1965) and 263 m from sonic tracking (Dizon, Brill & Yuen, 1978) (see Fig. 15). It is shown later that large skipjack are probably most abundant at subsurface levels.

MOVEMENTS AND SEASONAL DISTRIBUTION OF TUNA STOCKS

Tuna biologists have long suspected that some species are not homogeneous populations, but are groups of relatively independent sub-populations or stocks. The recognition of these stocks has begun in some species but is not complete in any. Stock definition is important for the management of fisheries, and tuna biologists are increasingly active in this field. Each stock is expected to occupy a definable area although the areas may overlap. The principal methods of stock recognition are tagging and statistical analysis of differences between measurable hereditary characters in samples of fish from different areas. Other biological observations can provide indications of the existence of separate stocks. For instance, the two spawning areas of albacore in the Pacific (Fig. 12) suggest reproductive isolation of northern and southern hemisphere stocks within that species.

Tuna schools or individual tuna move within the area of their stock. Tagging is the best source of information about these movements. some of which have been called migrations. Some authors (*e.g.*, Jones, 1968; Jones, Walker & Arnold, 1978) have defined migrations, as distinct from other movements of fishes. It is not easy, however, to apply their criteria to some of the movements that tunas have been found to make. As a result some tuna biologists have used the word "migration" quite loosely. In this paper we prefer the word "movement", and use "migration" only where necessary to agree with a cited author's use.

Nakamura (1954, 1969) hypothesized that tunas make two kinds of movements, which he called migrations: "One is assumed to be a rather passive movement within a certain habitat in response to a change in the conditions of the habitat, and the other as an active movement between habitats following a change in the physiological or ecological requirements of the fish." By habitat he meant a particular current system, usually zonal, as he considered that different species have their centres of distribution in different currents. His "migrations between habitats" were mostly meridional in direction, and seasonal in the examples given. Some of the "migrations within habitats", of which few examples were given, were also seasonal. Nakamura's central idea of characteristic habitats in different current systems has been criticized, as mentioned elsewhere, but there is direct and indirect evidence that tunas move zonally or meridionally or in both ways, seasonally in some instances.

There certainly is partitioning of energy in tunas between migration and spawning. Sharp (1978) defines several types of migrations, all related to feeding or reproduction. The first two types, short-term short-distance and long-term long-distance migrations. are facilitated by ocean currents or minor directed movements. They do not require much above basic energy needs and may represent the types which produce the spare energy needed

for the subsequent spawning mode. The third type, short-term long-distance migrations, require the most energy (Sharp & Dotson, 1977), but may be the type which subsequently allows the very rapid growth needed for juveniles and pre-spawners. Sharp's classification does not include the case in which tunas move out of an area which is becoming unsuitable (such as by seasonal cooling). Seckel (1972) considered migration in a mechanistic sense. He described it as a combination of the movement of fish by virtue of their being carried by the current plus the movement of fish relative to the current. Seckel's hypothesis is further discussed in this section under Skipjack and on p. 489.

YELLOWFIN

Yellowfin movements in the Pacific have been demonstrated from tagging (Fig. 1 and Bayliff, 1979) and the distribution of fish contaminated by radioactivity, and inferred from changes in catch per unit of fishing effort between areas and seasons (Suzuki et al., 1978). The latter changes are not large and probably indicate movements due to currents within the gyres, or perhaps changes in fish concentration. The yellowfin movements are apparently less than ocean-wide in scale. Sharp (1972 and pers. comm.) biochemically recognized a lack of homogeneity within yellowfin of the eastern Pacific based on genetic disparities within some areas among age-cohorts. The longest predominantly zonal movement of a tagged yellowfin was about 3000 km (Bayliff & Rothschild, 1974; see large east to west arrow in Fig. 1). Meridional movements occur in the Kuroshio and California Currents (Suzuki et al., 1978 and references; Fink & Bayliff, 1970). They are seasonal, poleward in summer, with the Kuroshio and against the California Current. The movement in the California Current follows a shift in the 20 C surface isotherm, north in summer and south in autumn (Blackburn, 1969a). There is no evidence that any of these movements are for spawning. Spawning areas are widespread in the entire central area of adult yellowfin distribution, as shown in Figures 1 and 9.

SKIPJACK

Skipjack adults occur in most tropical waters right across the Pacific (Fig. 2). The spawning region is likewise tropical but less extensive, mostly west of 130° W (Fig. 10). Tagging has demonstrated that substantial movements should occur in a zonal direction between the American coastal region and the spawning areas (Fig. 2). A total of 24 fish tagged in the eastern Pacific have been recaptured in the central Pacific, including one that travelled at least 9000 km (Anonymous, 1979a). Other zonal movements of tagged skipjack have been observed within the central Pacific (Anonymous, 1979a). Tagging has also demonstrated meridional movements along the American coasts and in the Kuroshio Current (Fink & Bayliff, 1970; Anonymous, 1979a). Skipjack tagging programmes are operated by the Inter-American Tropical Tuna Commission, the South Pacific Commission, and various fishery organizations in Japan. Figure 2 shows the principal results. Some of the movement along the coast of North America is seasonal, the boundary of skipjack range moving first north and then south in step with the 20 C surface isotherm (Blackburn, 1969a; Williams, 1970). A similar seasonal

change of range occurs off eastern Australia in conjunction with the 15 °C surface isotherm (Robins, 1952; Blackburn & Serventy, in press). The northward movement in the Kuroshio occurs through spring and summer (Kawai & Sasaki, 1962; Matsumoto, 1975 and references).

Population structure in Pacific skipjack has been studied from genetic analyses of blood group and serum group systems (Fujino, 1970a,b, 1972, 1976; Sharp, 1978). Fujino recognized two stocks or sub-populations, western and central-eastern, incompletely separated at about 160° to 170° E. Sharp recognized at least five overlapping stocks as shown in Figure 7, and more recently stated (pers. comm.) that there is evidence for at least one additional stock in the western Pacific. Tagging results do not contradict either of these systems. Kearney (1978) considered that Fujino's two stocks also differed in the rate of growth of the fish.

Matsumoto (1975) used catch per unit effort data from the longline fishery to suggest patterns of skipjack movement in the Pacific. Positions of high catch per effort per quarter-year were charted and schematically connected in time sequence, on the assumption that the changes in position indicated movements of groups of fish. The charted connections took tagging and other biological information, and surface currents which were assumed to facilitate the movement, into account. This very detailed study suggested the existence of 14 "groups" of skipjack, each characteristic of a large area of the Pacific and moving in a circular pattern in that area during each year. Matsumoto stated that these groups were not necessarily sub-populations, and not
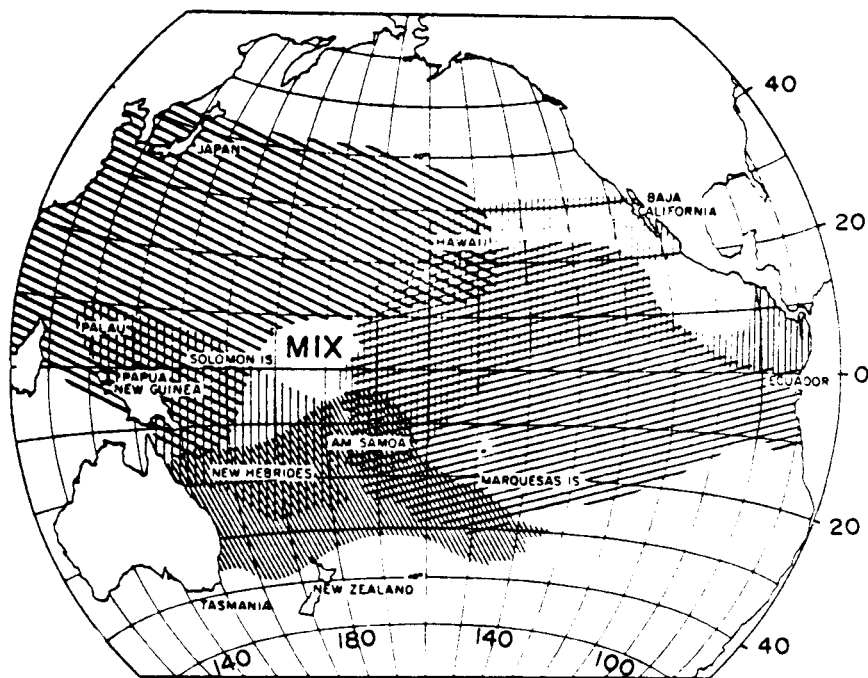

Fig. 7.—The approximate ranges of five populations of skipjack tuna in the Pacific Ocean: from Sharp, 1978.

independent. He noted that the postulated circular movements could be reconciled with zonal and meridional movements known from tagging studies assuming, however, that individuals could transfer between adjacent groups. The need for validation of this scheme of movements was emphasized.

Seckel (1972) considered the migration path to consist of two parts: (1) the distance a fish, or school, is carried by the current, and (2) the distance a fish, or school, swims relative to the moving water or current. He then asked what contribution the current made to skipjack migrating from the eastern to the central Pacific. This was answered by modelling the drift of a floating object under the influence of the geostrophic flow and surface wind drift. Results showed that the time of drift from the eastern Pacific to Hawaiian waters was about the same as that of skipjack tagged in the eastern Pacific and recovered in the Hawaiian fishery. Seckel hypothesized that one of the possible modes of migration for skipjack recovered in Hawaii could be fish randomly swimming in search of food while being carried by the ocean current. Most authors agree that this westward movement from the eastern Pacific is made by young adults in order to reach the central Pacific spawning areas. These fish must originally have moved eastward from the central Pacific, probably as larvae or juveniles, and Williams (1972) suggested three possible modes of movement. All three assumed some kind of active or passive orientation to surface currents, and all are plausible. Field observations are, however, still inadequate to indicate which—if any—of these models is correct.

BIGEYE

Tagging observations on movements of bigeye are very scarce and do not suggest a pattern. The greatest distance travelled by a tagged and recaptured fish is about 1500 km, from west to east as shown in Figure 3 (Kume, 1967; Anonymous, 1979a). No definite information exists about sub-populations. Catch per unit fishing effort varies with season in some areas, but these changes are not well understood (Alverson & Peterson, 1963; Shingu, Tomlinson & Peterson, 1974). Kume (1967) considered that the changes indicate movement from west to east during the life of the fish. There must be considerable meridional movement of bigeye, because spawning areas are known only between 25° N and 15° S (Fig. 11), whereas the species is quite abundant poleward of those latitudes in each hemisphere (Fig. 3). Abundance to the north of 25° N is greater in winter than in summer (Kume, 1967). Nakamura (1969) presented a diagram of distribution and migration which distinguished ontogenetic stages and areas, but not seasons. West-to-east movements of adults were shown in addition to the meridional movements mentioned above. The need for more information, which might lead to a revision of the scheme, was emphasized.

ALBACORE

The northern and southern hemisphere albacore are believed to be distinct stocks or sub-populations. Available data indicate: (1) that albacore do not migrate across the equator in any season; (2) that the areas occupied by the

albacore in the two hemispheres are roughly symmetrical (Nakamura, 1969; also see Fig. 4); and (3) that there are separate and distinct spawning grounds and times in the two hemispheres (Fig. 12). The seasons of spawning are in the respective warm (summer) seasons of each hemisphere (Nishikawa, Kikawa, Honma & Ueyanagi, 1978). We concur that there are two distinct hemispheric populations and will discuss them separately.

North Pacific Albacore

Results from tagging studies (Laurs, 1979) suggest that there are at least two sub-stocks of albacore that comprise the North Pacific population, and that these sub-stocks have different migratory patterns. Fish of the northern sub-stock make trans-Pacific migrations between the eastern and western North Pacific, resulting in an exchange of fish between the area of the U.S. surface fishery north of about 40° N and the Japanese surface fishery, and the longline fishery west of 180°. The southern group of fish have a different migration scheme and appear to enter the U.S. fishery south of about 40° N and the longline fishery east of 180°. Only a small proportion of the southern group appear to migrate between the eastern and western Pacific and enter the Japanese surface fishery. During a given season there is also very little exchange of albacore in the U.S. fishery between the northern and southern sub-stocks.

The two surface fisheries, off Japan and North America, are supported by young fish. It still is unknown at which stage of maturity and where, the albacore change their habits and enter the subsurface longline fishery. Hypotheses proposed by Otsu & Uchida (1963) and by Rothschild & Yong (1970) offer different interpretations. The former suggest that the fish move sequentially from the North American fishery through the longline fishery to the Japanese surface fishery, based on the timing of exploitation among these fisheries. On the other hand, the latter authors state that the fish move from the American into the Japanese surface fishery and finally into the longline fishery. They postulated that the fish pass between the peripheral surface fisheries *via* the longline area, but are not vulnerable to the longline gear at those times. The Rothschild & Yong hypothesis is founded upon size distribution, growth rates, and times of fisheries, apparent abundance and some tagging data.

Kikawa, Shiohama, Morita & Kume (1977) and Kikawa (in Anonymous, 1977) hypothesized that four-year old fish migrate from the Japanese surface fishery to the United States surface fishery. Recently, Japanese-tagged fish from the surface fishery in the western North Pacific were all reported to have been recovered during the same season east of their release locations. Some fish were recovered in subsequent seasons to the west of the release sites. Two recoveries have been made off the Columbia River in late September and early October 1974 of fish tagged by Japanese scientists in mid-June 1974 in the Emperor Seamount chain near 34° N: 171° E. General results from western Pacific tagging indicate that albacore move eastward across the Pacific during spring and summer months, and that those from the western side near the Emperor Seamount can migrate to the American fishery area by early fall of the same year (Anonymous, 1978, and Fig. 4).

Western Pacific albacore, taken on longlines in the Philippine Sea in December, are pre-spawners. They move out from there in February and March to the spawning grounds (see Fig. 12). Other pre-spawners occur in the North Pacific Current (see Fig. 8) (winter longline grounds). They may pass through the Philippine Sea or disperse directly from the North Pacific Current to the spawning grounds (Otsu & Uchida, 1963), penetrating a wide area of the Subtropical Convergence (region in which converging currents are present; see Sverdrup, Johnson & Fleming, 1942, p. 140). The latter conclusion is supported by large fish occurring along the southern fringe of the longline grounds in numbers which increase progressively from west to east.

Young albacore of about age 1 year (30 cm) are present in Japanese coastal waters in spring and summer. These are considered to have moved in from the North Equatorial Current spawning ground and to have entered the North Pacific Current area via Japanese coastal waters (Nakamura, 1969). One-year olds also occur occasionally in North American coastal waters.

The albacore taken in the North American surface fishery align into three major modal groups at approximately 55, 65, and 75 cm fork length (ages 2, 3, and 4 years, respectively). Fish in the northern portion of the fishery are 2–3 cm smaller at a given mode than those in the southern part (Laurs & Lynn, 1977). These fish all are sexually immature.

Laurs & Lynn (1977) and Anonymous (1977) present evidence for two groups (see p. 456 and Laurs, 1979) taking separate routes of entry into the North American surface fishery. Their interpretation differs from that of Clemens (1961), who postulated a single group which varies in latitude of entry in accordance with variations in environmental factors and travels up
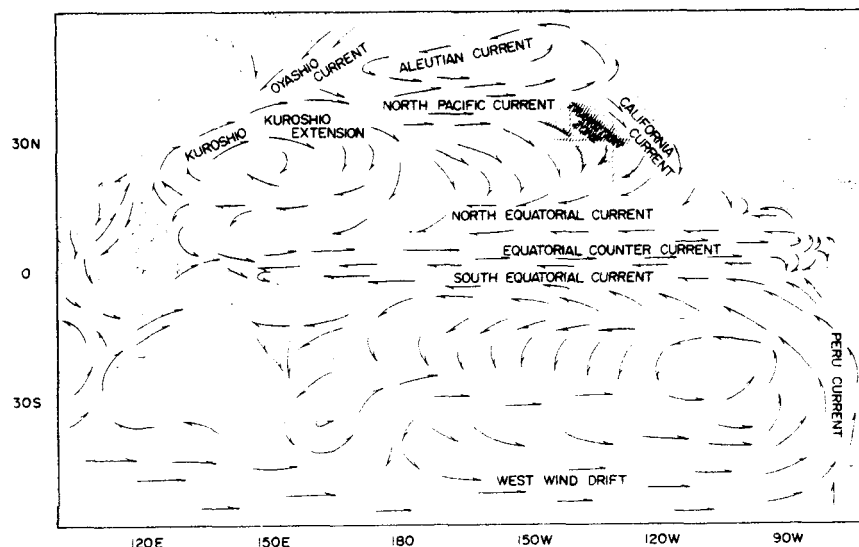

Fig. 8.—Major features of surface circulation: shaded area is the Transition Zone.

the coast as the season progresses. Support for the proposed division of route pattern is found in the length–frequency distribution of the catch. Size compositions recorded during 1972–1974 show different modes in sizes of fish caught off California from those taken off the states to the north (see above). The smaller fish in the northern area presumably convert less energy into growth and more into ocean-wide migration than the fish in the southern area, which are thought not to have moved so far between their passes through the American fishery. Sizes of fish taken offshore from the fishing grounds and south of 35° N indicate that those fish are the ones that move into the southern portion of the fishery. Additional evidence to support this hypothesis has been based on radioactive cobalt fallout data by Krygier & Pearcy (1977). Those investigators also propose one group entering north of 35 N and the other to the south. The division and its location may be modelled in response to the environmental conditions prevailing at the time. Furthermore, Laurs (in Anonymous, 1977) presented evidence that the northern group moves trans-Pacific, while the southern group migrates between the eastern and central Pacific areas. He postulates some degree of intermixing among the two groups.

According to Laurs & Lynn (1977), the general pattern by which the albacore seasonally migrate into the United States surface fishery proceeds in three stages, regardless of which of the two sub-stocks is considered. (1) They migrate eastward from the central North Pacific and form centres of relative abundance within the eastern section of the Transition Zone (Sverdrup *et al.*, 1942, p. 714 and Fig. 8) approximately 1000 to 1600 km off the United States coast in late May and June. (2) They move towards the American coastal regions as nearshore warming occurs; catches during this time indicate that the fish are scattered. (3) By mid-July, concentrations of fish are evident near the coast, often in the vicinity of fronts at the edges of coastal upwellings. Clemens & Craig (1965) reported concentrations of albacore off southern California in June in a number of years.

The eastward migration from offshore central ocean waters to the nearshore area appears to continue throughout the summer. Variation in the migration pattern has been interpreted as responses to variation in surface temperature and other environmental variables (Craig & Graham, 1961; Graham & Craig, 1961; Craig & Caneday, 1962; Craig & Dean, 1968). Laurs & Lynn (1977) concluded that the eastward migration of albacore is linked to the Transition Zone and that variations in the pattern of migration occur in response to variations in the character and development of the Transition Zone and its frontal structure. They believe that when the Transition Zone is narrow and the fronts well defined, the migration is well defined; when weakly developed, the migration is less well defined. The albacore migration is confined to temperatures of about 16° to 19 °C; speed of the fish is about 50 km/day for 78–80 cm fish (see also Clemens, 1961); and forage availability is a factor which influences the migratory route. It also is believed that the spring migration is markedly influenced by frontal boundaries and the temperature preference of the fish. Temperature appears to be limiting at the northern boundary of the Transition Zone. At the southern limit of the route, the major limiting factor may be forage availability since this drops off sharply near the southern boundary of the zone. Some foraging is done *en route*, particularly in areas associated with the Transition Zone fronts

where the fish may feed for up to several weeks. Since these fish are immature, fat is utilized for migration rather than for reproduction (Sharp & Dotson, 1977).

South Pacific Albacore

Overall, the distributional aspects of the North and South Pacific populations are roughly symmetrical across the Equator. Nakamura (1969) summarized the study of South Pacific albacore made by Kamimura & Honma (1959). Briefly stated, the longline fishing ground is located between 10° and 30° S, and seasonal variations in hook rates are not evident. Segregation of feeding and spawning in the South Pacific is not obvious, although Nakagome (1959) stated that there were southern and northern groups, each of which migrate north in autumn and south in spring; and he assumed the northern group to be spawners and the southern group to be composed of feeding individuals. Various workers have identified oceanographic structures (e.g. convergences) which are potentially of ecological significance to the fish (Koto & Hisada, 1967; Yamanaka, 1956).

Taking the minimum size at maturity as being around 90 cm, Ueyanagi (1955, 1957), and Otsu & Hansen (1962) consider those fish in waters north of 30° S latitude to be spawners. The latter authors, however, point out differences in degree of sexual maturity between the fish on either side (north and south) of about 20° S latitude. Size differences noted and indications of a discontinuity structure at that latitude may be evidence of a habitat border in that area (Honma & Kamimura, 1957; H. Nakamura, 1965). Other workers (e.g. Hidaka, 1955; Yamanaka, 1956; Koto, 1966; Yamanaka, 1978) indicate a relationship between fish distribution and ocean structure. Zones of fish concentrations are considered to coincide with discontinuities, current rips, and tropical fronts.

Kume & Schaefer (1966) identified separate latitudinal zones occupied by spawners at 15° to 20° S, and by feeding fish at 25° to 32° S. There is evidence of size segregation of albacore in the South Pacific (Saito, 1973) which at times is closely related to ocean structure. The structure of the South Pacific is not as distinct as that in the North Pacific, perhaps because of the less clearly differentiated water masses in the southern ocean.

Not enough information is available to construct a migration model for South Pacific albacore, even though some similarities to the northern pattern are emerging in the New Zealand and Australian areas. An interesting gap in the story is the apparent lack of a habitat corresponding to the one occupied by young fish along the North American coast. There are no surface fisheries of consequence in the South Pacific.

BLUEFIN

Yamanaka & staff (1963) and Bell (1963) reviewed existing knowledge of the distribution and movements of western and eastern North Pacific bluefin, which were then considered as separate species (*Thunnus orientalis* and *T. saliens*, respectively). Later, evidence of trans-Pacific migrations of bluefin in both directions (Orange & Fink, 1963; Flittner, 1966; Clemens & Flittner,

1969) showed that the supposed two species were the same. Much useful information of a general biological nature is also given for bluefin by Bayliff & Calkins (1979) in a paper discussing stock assessment.

On the basis of larval distribution the bluefin appears only to spawn in a single area of the western Pacific, east of Taiwan, although Okiyama (1974, 1979) indicated some isolated spawning in the eastern Sea of Japan in recent years (Fig. 13). Movements of bluefin, after the postlarval stage, are recognized from analysis of fishery statistics, biological information such as length and weight frequencies, and tagging studies. Distribution and movements of the small fish (<20 cm) are unknown but are considered to be gradually northwards in the warm waters of the Kuroshio Current and its branches; however, there may also be some movement southwards as suggested by Bayliff & Calkins (1979). Subsequently, young-of-the-year (zero age class) fish of 20–30 cm (< 1 kg) begin to appear off the southern coast of Japan in summer (July); fish in the 2·3–8·3 kg range (age 0+ to 1+) can be found in these same waters during most of the year. These small fish then move northwards with the warm waters of the Tsushima Current into the Sea of Japan, and with the Kuroshio Current into the coastal waters of eastern Japan, where they form the basis for different types of surface fisheries, each with distinct seasonal peaks.

At age 1+, or even younger, most of the fish disappear from Japanese coastal waters although some 2 to 3-year olds are found in the Sea of Japan and off northeast Honshu (Sanriku ground). Many of the small fish migrate into the eastern Pacific where they appear some 12 months later, at lengths of 55–65 cm. Certainly other age classes are involved in the migration, as up to five age classes but usually three (ages 1–3) are represented in the eastern Pacific catch. The bluefin may then leave the American coast after one year or remain for as long as two or three years (as determined by tagging); a small group is found year-round in the neighbourhood of Guadalupe Island, Baja California. Recently, mature fish about 30 kg (age 3+) were reported by Yorita (1976) from fishes caught by set net on the west coast of Hokkaido in July to August, 1972 and 1975. Bluefin appear to re-enter the fishing grounds off Japan (Sea of Japan or east coast) at age three to five years; some are older than this when recaptured, but actual dates of return to these areas are unknown. Relative abundance of fish of age two to five years varies according to the occurrence of dominant year classes. The fish returning from the eastern Pacific join the other immature adults on the Sanriku and Sea of Japan grounds in the summer (tagging data). The age and size of bluefin at first maturity appears still to be in doubt, but is probably 5+ (>140 cm) or older, except in pen-cultured fish (Yamanaka & staff, 1963; Hirota & Masaichi, 1976).

During November and December bluefin off Japan show a general southward movement. By spring (April–June) small and medium size fish (age 4+ to 7) are found on the longline ground immediately to the south of Japan, but not on the more southerly spawning grounds where sexually mature fish (age 6+ to 7+ or older) occur. Subsequently, medium and large fish (immatures and adults) from both these longline grounds move for feeding into the Sea of Japan (mainly caught by set nets and seines) or, more usually, to the Sanriku grounds off northeast Honshu where they are mainly caught by longliners and purse seiners in early summer; they move onto the

offshore longline grounds east of Japan in late summer. Bluefin can also be found in waters off Hokkaido and Sakhalin in late summer.

Bell (1963) indicated that commercial production of bluefin off the coast of North America is restricted to the area from 23°–34° N, within 160 km of the coast and usually in the upper 100 m of the water column. Smith & Clemens (1973) stated that the initial approach to land is made in the southerly part of the fishery area, off Baja California, in April–June, with the fish subsequently moving north into southern California waters in July–August as the water temperature increases northwards. Remnants of the population which overwinter in the region are found well to the south in Baja California waters. The occurrence of the bluefin in the eastern Pacific is at much the same time as that of albacore tuna.

Shingu, Warashina & Matsuzaki (1974) reviewed the 1960–1967 longline catches of bluefin in the northern and southern hemispheres from 120° E–160° W. They indicated that, despite the widespread distribution of bluefin, the major longline grounds are near the continents, except east of Japan and near the Equator, where they extend considerable distances eastward. The authors confirmed and strengthened earlier descriptions of the migration routes in the northwest Pacific. Recently, Bayliff and Calkins (1979) presented a model of bluefin migrations which, in addition to North Pacific movements mentioned previously, took into account those bluefin found in the equatorial western Pacific as well as further to the south. The distribution of small surface-caught (by bait boats) bluefin south of 20° N in 1972–1976 suggested that at least some of the fish caught by longline south of the single known spawning ground are the result of larvae, postlarvae, and juveniles moving south from the spawning ground or young fish moving south from Japan.

The western Pacific bluefin fishery is characterizea by year classes of varying strength (Yamanaka & staff, 1963; Nakamura, 1969). Prior to 1938 small bluefin were very common off Japan but in the period 1938–1949 were extremely scarce, then again after 1950 became much more abundant as in the pre-1937 era (Yamanaka, 1959; Uda, 1973). Abundance of bluefin in the Sea of Japan fell after 1949 (Uda, 1973). Uda (1957, 1973) has stated that periodic, major changes in the bluefin population off Japan are caused by major oceanographic events such as the abnormal intrusion of cold Oyashio Current water (as in 1941–1945) and subsequent warming periods with a strengthened Kuroshio Current, i.e., when its meandering was reduced (as in 1949–1950). Yamanaka (1978) reported the advent of a strong year class of bluefin tuna a few years after the occurrence of upwelling off the eastern coast of the Philippines. Movements of small fish in Japanese coastal water appear to be related to northward increasing surface temperatures in summer, whilst the larger sized fish offshore appear to stay near the boundaries of cooler water (18–21 °C) or eddies caused by localized upwelling (Uda, 1973). The eastern Pacific bluefin fishery is similarly characterized by varying number and size of the length frequency groups for the years 1951–1978 (Bell, unpubl.; Schultze & Collins, 1977; Anonymous, 1979a), although Bayliff & Calkins (1979) have pointed out the difficulty of assigning ages to length modes. That distribution, movement, and perhaps availability of bluefin is dependent (directly or indirectly) on water temperature is supported by the fact that the fishery was best off southern California in the warm-water years of 1957, 1958, and 1959, and poorest in the cold-water years of 1954.

1955, and 1956. The extensive movements of Pacific bluefin, Atlantic bluefin (Rivas, 1978), and the southern bluefin (see below), all in waters with temperatures from 4°–31 °C, are somewhat similar; each species has localized spawning grounds in the tropics and makes very long zonal migrations of a feeding nature at various developmental stages.

On pp. 460 and 469 it is reported that there is at present only a single known spawning area for the Pacific bluefin tuna (Yabe, Ueyanagi & Watanabe, 1966; Ueyanagi, 1969b; Nishikawa *et al.*, 1978). Little genetic work has been done on the Pacific bluefin except for electrophoretic studies of soluble eye lens proteins from specimens from the California fishery (Smith, 1962, 1966, 1971; Smith & Clemens, 1973) and haemoglobin comparisons by Sharp (1973). Results indicate that the fish show remarkable homogeneity of electrophoretic patterns, even from year to year, and suggest the fish belong to a single North Pacific population exhibiting some local genetic differences on the fishing grounds. Bayliff & Calkins (1979) added, however, that the alternative to a single population might be several sub-populations represented by the various migratory groups: Japan, North America, southwest Pacific. It would be useful to understand this from the point of view of stock assessment.

SOUTHERN BLUEFIN

The distribution and movements of southern bluefin around Australia were reviewed by Robins (1963), whilst Shingu (1967) presented the first comprehensive statement on the species covering most of its geographic range as then known. Subsequently, Hynd (1969), Nakamura (1969), and Shingu (1970) presented rather similar hypotheses of migration routes of southern bluefin, based on commercial fisheries statistics, tagging data, morphometric studies, and oceanographic data. These hypotheses clearly showed the relationship of life history or developmental stages of the species to various oceanographic regimes, including the transition of young surface dwelling fish of coastal waters to the larger immature and adult stages at subsurface levels and the expansion of habitat area with increasing size of the fish.

The species appears only to spawn on the "Oka" ground (Yabe *et al.*, 1966; Ueyanagi, 1969b; Nishikawa *et al.*, 1978; see p. 470 and Fig. 14) in the tropical eastern Indian Ocean south of Java. The movement of the young fish (< 1 year old) is unknown but is probably slowly southwards until they appear in substantial numbers as 1 to 2-year olds in neritic waters of Western Australia. (Ages of southern bluefin have not been determined with certainty.) The hypotheses then indicate movement around into southern and southeastern Australian waters (excluding Bass Strait) where the catch is mainly of 2 + to 4 + -year old juveniles (Robins, 1963; Hynd, Kesteven & Robins, 1966; Hynd, 1969). This largely eastward movement is progressive with time and is accompanied by an increase in average weight of the fish. These fish form the basis of the Australian coastal surface fisheries for southern bluefin in the southern summer off South Australia and in the southern spring off New South Wales. At 4 + years the fish leave the surface fishery for subsurface levels and become subject to longlining. As 5 to 6-year olds they are found further offshore at greater depths and lower temperatures. Distribution of these sub-adults apparently is controlled by seasonal oceanographic condi-

tions. They move northwards to as far as 30° S (in the western Tasman Sea and off the east coast of New Zealand) in winter and southwards (West Wind Drift; see Fig. 8) south of 40° S in warmer months.

By the time maturity is reached at 7 to 8 years old, the fish almost exclusively inhabit the region of the West Wind Drift. The sexually maturing fish (pre-spawners) then migrate to the "Oka" spawning ground through the "Oki" fishing ground west of Australia in the region of 20–30° S: 90–110° E; the returning spent fish also pass through the "Oki" ground. The work of Mimura (1962) and Kikawa (1964) showed that both pre-spawners and spent fish were found on the "Oki" ground from September to April. Gonadal studies by the same authors also confirmed the "Oka" ground as the spawning area from August to March. From the "Oki" ground the spent fish move back to the richer feeding grounds of the West Wind Drift, with some specimens being found on the longline grounds of the Tasman Sea and off New Zealand. The spawning migration (from the West Wind Drift to the "Oka" ground and return) is a meridional movement in what is otherwise a markedly zonal distribution and movement. The authors of the migration models—Hynd, Nakamura, Shingu—and in particular Hynd, showed, from tagging results, the extensive zonal migrations of southern bluefin of.at least up to 7200 km, *e.g.* from off South Australia to southeast of Cape Town, South Africa (see Fig. 6). Thus, there is apparently only one stock or population of southern bluefin, with a single tropical spawning area and an immense circumpolar range in temperate waters.

It should be noted, however, that no juvenile southern bluefin tagged in neritic waters (or elsewhere) have yet been recaptured on the "Oka" spawning grounds. An interesting and unusual indirect confirmation of the seasonal meridional spawning movement of adult southern bluefin was provided by Warashina & Hisada (1974), who looked at the temporal and spatial occurrence of "fat" (red meat) and "lean" (brown meat) condition in fish over 130 cm (spawning size). The results showed good agreement with proposed times and routes to and from the "Oka" spawning ground. Hynd (1965) suggested that three separate groups of fish spawn there within the extensive overall spawning season from September to March and all three are later represented in catches of juveniles in Australian coastal waters. Initial surveys of southern bluefin off the Cape of Good Hope (Jager, Nepgen & Wyk, 1963) showed catches were composed of fish about 4 years old or older, suggesting that there was no spawning group in the South African region.

The original hypothesis that all juvenile southern bluefin must migrate through Australian coastal waters was questioned by Hynd (1969), F.A.O. (1975), and Hynd & Lucas (1975). Murphy (1977) has pointed out that Japanese longline catches of 61–80 cm southern bluefin (2¾ to 4 years old) off South Africa are in total as large as, if not larger than, those caught on the longline grounds off Australia. The occurrence in numbers of these sizes of fish simultaneously in both areas suggested that large numbers of juveniles must move from the "Oka" spawning grounds to the longline grounds without passing through Australian neritic waters. Tagging evidence also supports this argument.

Knowledge of the migratory movements of southern bluefin was most helpful in the introduction in 1969–1970 of voluntary restrictions by the Japanese industry of longline fishing effort because of apparent over-fishing

of the stocks (Anonymous, 1972; Hayashi [Hayasi], Shingu & Hisada, 1972; Hayashi [Hayasi], 1974; Warashina & Hisada, 1974).

As mentioned, one spawning area ("Oka" ground) is known for the southern bluefin tuna. More than one spawning group may, however, be involved in that area (Hynd, 1965, 1969; Shingu, 1967, 1970). Whether there are any genetic differences in these spawning groups is unknown. Shingu & Warashina (1965) indicated that morphometric studies of southern bluefin from Australia and New Zealand waters showed no separation of stocks. Similarly, blood samples analysed for this purpose at the then U.S. Bureau of Commercial Fisheries Laboratory in Honolulu, Hawaii showed no differences (Hynd, 1969). In fact, tagging studies indicate positive mixing of fish from the Indian and western Pacific Oceans (Hynd, 1969; Murphy, 1977). All these observations indicate that the southern bluefin from all known areas comprise a single stock.

LARVAL DISTRIBUTION, SPAWNING AREAS, AND SEASONS OF TUNAS

Spawning areas of the various tuna species have been defined primarily by capture of larvae and juveniles and by the occurrence of sexually mature adults. The larvae are collected in plankton, nekton, and neuston nets, by dip-netting at the sea surface at night—usually near a light set out for that purpose, and by examination of stomach contents of piscivores (Klawe, 1963). Juvenile tunas have been observed in samples taken by trawls and in the contents of bird and fish stomachs (Higgins, 1970). The occurrence of running ripe adults or adults with high gonad indices (weight of ovaries divided by cube of fish length; see Orange, 1961; Shingu, Tomlinson & Peterson, 1974; Naganuma, 1979 for example) are noted in the course of research or exploratory fishing expeditionary activities and, on occasion, during commercial fishing operations. The vertical distribution of tuna larvae has been examined by comparison of net tows made at the surface with tows made at or through various depth strata. Conclusive evidence is not available, but the consensus of opinion is that the larvae are concentrated above the thermocline, although some have been taken within and below that layer (Matsumoto, 1958; Strasburg, 1960; Klawe, 1963; Ueyanagi, 1969b). There is some evidence that suggests diurnal vertical migration within the upper 50 m (Matsumoto, 1958; Strasburg, 1960). Rarely have enough data been collected to describe definitively any seasonal variation in spawning activity; however, a notable effort in this regard is the atlas derived from Japanese research vessel surveys, 1956–1975, compiled by Nishikawa *et al.* (1978). Their atlas includes charts of the annual and quarterly distributions of the larvae of 14 species of tunas and billfishes and related forms based on about 6000 net tow samplings taken from two research vessels. Another article of major importance is that of Ueyanagi (1969b), which includes some of the same data as in the atlas of Nishikawa *et al.* combined with information from other research vessels. The atlas of Nishikawa *et al.* has a limited areal coverage, especially in the second and third quarters of the year; Ueyanagi summarizes the data into two halves of the year but does not treat them with regard to density of occurrence (Ueyanagi, pers. comm.). Other

summary reports of general note are in the Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, Vols 1–4, F.A.O. Fisheries, Report No. 6 (Rosa, 1963), and the Proceedings of the Governor's Conference on Central Pacific Fishery Resources, Honolulu, U.S.A. (Manar, 1966).

YELLOWFIN, Figure 9

The warm tropical region centred around the Equator is the area in which yellowfin tuna larvae are abundant. Suzuki, Tomlinson & Honma (1978) identified three high density areas of yellowfin larval abundance (western, central, and eastern Pacific). This was not taken as evidence of the existence of separate stocks or sub-populations but as possible evidence of quasi-independent stocks in the three areas. Periods of spawning in offshore and coastal areas within the eastern tropical Pacific surface fishery area were discussed by Knudsen (1977). Coastal yellowfin of two recruitment groups showed sporadic spawning. In some years there were two peak periods but activity varied from year to year. Offshore fish did not exhibit this variable pattern and spawning periods lasted longer.
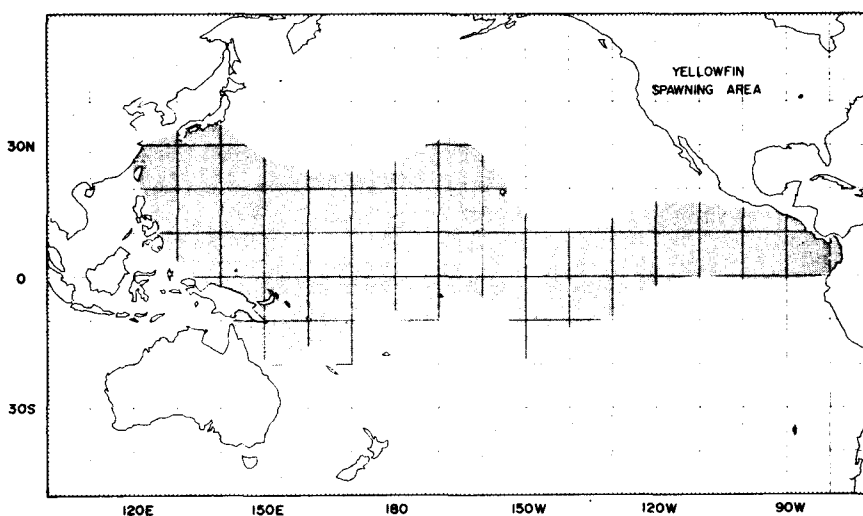

Fig. 9.—Spawning area of yellowfin tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

Comments regarding seasonal variability of larval occurrence should be taken with some reservation because of time and space limitations of sampling (see above; Ueyanagi, pers. comm.). Throughout this present paper the quarters of the year are: first, January–March; second, April–June; third, July–September; fourth, October–December. During the second quarter yellowfin larvae occur only in the western side of the Pacific between the Equator and 30° N latitude. Spawning is scattered from 130° E to 160° W at 15° N to 35° N and is of low intensity in the third quarter. In the fourth

quarter larval occurrences are numerous within 15° north and south of the Equator in the Indo-Pacific with scattered occurrences elsewhere across the entire Pacific within this band of latitude. The first quarter shows some spawning throughout the range from 10° S to about 20° N.

The north–south range in the eastern Pacific around 120° W (0–15° N) is narrower than in the west at 170° E (20° S–25° N), which limitation seems to be in alignment with the temperature field because the isotherms in the east converge towards the Equator from both the north and south. Klawe, Pella & Leet (1970) reported a marked increase in the proportion of net tows containing larvae of yellowfin at stations near the Gulf of California where the surface temperature exceeded 26 or 27 °C. Richards (1969) recorded yellowfin larvae only in waters above 27 °C in the eastern tropical Atlantic.

Collections of larvae taken at the surface and at depths of 20–30 m both conform to the general distribution stated above (Nishikawa *et al.*, 1978).

SKIPJACK, Figure 10

Skipjack tuna larvae have been found over wide areas in all major oceans (Klawe, 1963, 1970, 1972a,b; Nakamura & Matsumoto, 1967; Ueyanagi, 1969b; Mori, 1972; Richards & Klawe, 1972; Chen & Tan, 1973; Matsumoto & Skillman, in prep.). In the western Pacific the known distribution of skipjack larvae extends from about 35° N off Japan to about 35° S off southeastern Australia. The latitudinal range narrows in the central ocean to a band about 15–20° north and south of the Equator; and east of approximately 120° W it is mostly restricted to the strip between the Equator and 10° N. The distribution coincides closely with the area delineated on the north and south by the 24 °C isotherm (Ueyanagi, 1969b).
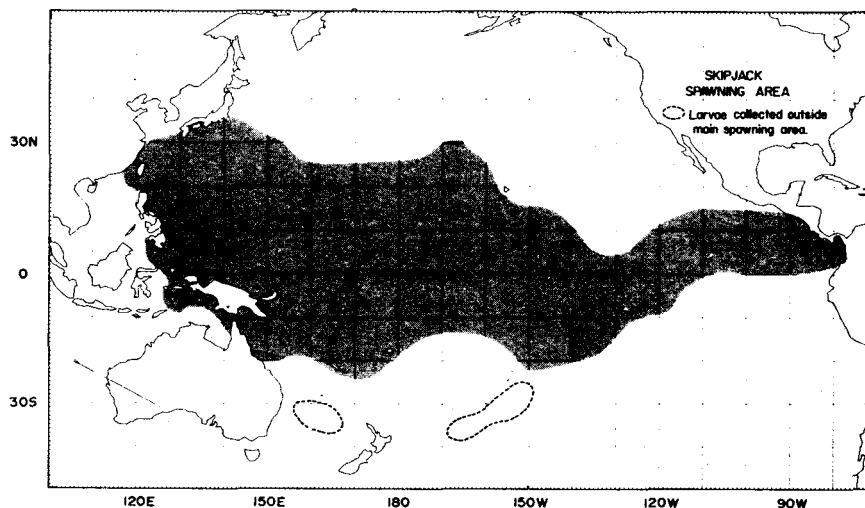

Fig. 10.—Spawning area of skipjack tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

Spawning activity seems most intense in the western Pacific in the second quarter of the year. The spawning area spreads east and south in the third and fourth quarters, and is diffuse in the first quarter (Nishikawa *et al.*, 1978). Density of larvae increases to the west (Ueyanagi, 1969b).

According to Ueyanagi (1969b) skipjack larvae in the Indo-Pacific are scarce at the surface in daytime, and most were collected in tows in the 20–30 m layer. Night samples showed less variance between the towing depths, but there are still higher numbers of larvae at deeper levels.

Naganuma (1979) consolidated much of the available information on skipjack reproduction in the western Pacific. Spawners range from 40 to 80 cm, occurring widely between 35° N and 24° S. In the North Pacific there is a size segregation in the spawning season such that the larger the fish, the earlier in the year they spawn. Skipjack of 40 to 50 cm size constitute the spawners in the South Pacific. In any area, the spawning that does take place occurs in the warmest season.

It was observed that skipjack larval abundance was highly and positively correlated with high sea surface temperature (Inter-American Tropical Tuna Commission (IATTC), 1973). This led to the hypothesis that warm years in the Central Pacific might lead to higher abundances of adults in the eastern tropical Pacific fishery. Correlation tests indicated that about 50% of the variation in the catch index was attributable to temperature variations although the causal factors are unknown. Attempts have been made to predict abundance about one year in advance based on temperature and atmospheric changes in selected equatorial areas (IATTC, 1973, 1974, 1975). These predictions have, however, often failed (IATTC, 1975). Investigation into the relationships between environmental indices, spawning success and larval survival, and year class abundance in the fishery are continuing.

We wish to point out an apparent contradiction. The spawning and survival of larvae of skipjack apparently is related, positively, to high sea surface temperatures. But physiological studies (see p. 482) suggest that large skipjack—spawners—are adversely affected by high temperatures. Thus, large spawners should not occur in areas in which larvae are found; this, of course, cannot be true. This apparent dilemma can be resolved if the spawning adults occur at depths with cooler temperatures (within the thermocline), if spawning takes place at those depths, and if the eggs float to the surface layer where their survival is enhanced. The young then would be separated from their parents, who are a major predator upon them. On the other hand, there are large adults in Fijian and Tahitian surface fisheries when the surface water is very warm, about 30 °C (Sharp, pers. comm.).

BIGEYE, Figure 11

The entire equatorial region of the Pacific is a spawning ground for bigeye tuna (Kume, 1969). Spawning occurs largely in the warm, low latitude areas on the eastern (0°–10° N) and western (10° S–15° N) sides of the ocean. More larvae have been collected at the surface than at 20–30 m.

Gonad development of adults is at a very high level on the average, with marked seasonal variation in the eastern area. The season of greatest spawning is during the fourth quarter in the equatorial Pacific to the northwest and southeast of New Guinea, in the Hawaiian Islands, and along an equatorial
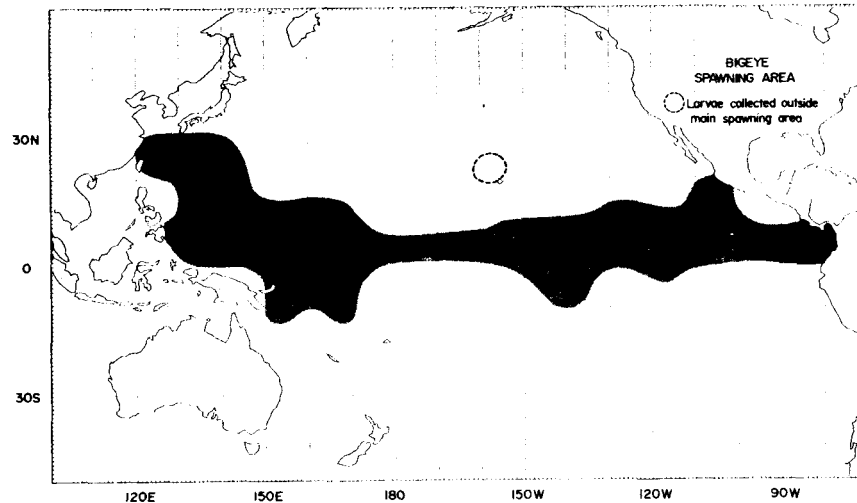

Fig. 11.—Spawning area of bigeye tuna: shading indicates areal extent of accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

band extending between Ecuador and about 115° W. There is scattered activity primarily in the western Pacific in other seasons (Nishikawa *et al.*, 1978). Kume (1969) suggested that sexually developed individuals occur in the cooler waters of the eastern part of the range.

Kikawa (1957) reported that the ocean currents in the western Pacific have a definite ecological significance. Bigeye in the North Pacific Current are in a resting stage; those in the North Equatorial Current comprise recruits of the spawning group, and the most mature individuals are dominant in the Equatorial Countercurrent, so that the bigeye spawning area aligns with this current.

ALBACORE, Figure 12

The centres of distribution of albacore larvae are at about 20° N and 15° S; larvae are not found in equatorial waters. The areas of occurrence correspond approximately with the western halves of the subtropical gyres (Ueyanagi, 1969b; Nishikawa *et al.*, 1978). Each range expands meridionally during the warm season and contracts in the cold. Thus, the North and South Pacific spawning areas are assumed to be separate. The spawning grounds are characterized by surface layer (to 50–60 m) temperatures over 24 °C, and no strong thermocline above approximately 250 m (Ueyanagi, 1969b). The possibility of spawning has been reported off Baja California, Mexico, in the vicinity of Guadalupe Island (Clemens, 1961), and fish as small as 30 and 40 cm have been reported in the American coastal fishery (Clemens, pers. comm.; Laurs, pers. comm.).

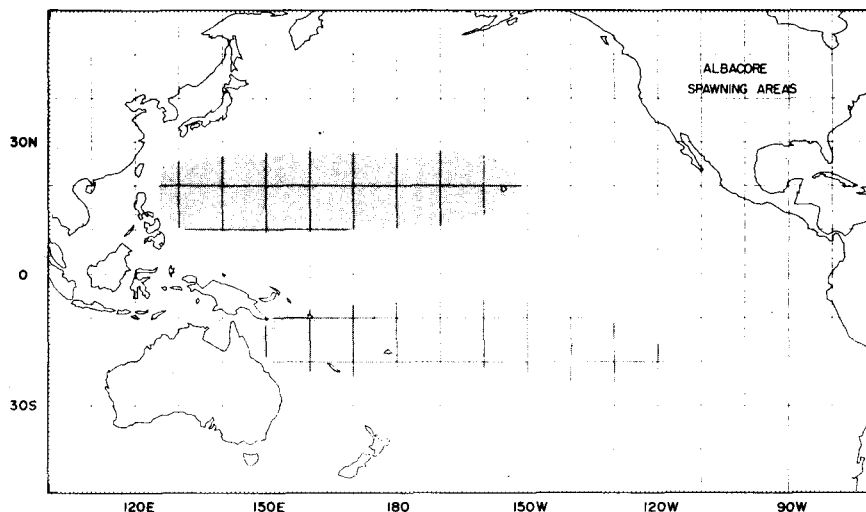The peak spawning season in the North Pacific is in summer, broadly

Fig. 12.—Spawning areas of albacore tuna: shading indicates areal extent of accepted and known spawning grounds; these do not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

speaking, with some activity evident throughout the year in areas south of 20° N. Larval occurrences in daytime net tows at 20–30 m are greater than in tows at the surface, but the tendency is less marked than in some tunas, e.g. skipjack (Ueyanagi, 1969b). Numbers taken in night tows at the two levels are similar.

BLUEFIN, Figure 13

According to Nishikawa et al. (1978) bluefin spawning occurs only in a limited area off the Asian mainland between 20° and 30° N and extending east to 150° E. The area corresponds to a zone occupied by the Kuroshio Current and the Kuroshio Countercurrent. The known spawning area is rather confined relative to the distributional range (compare Figs 5 and 13) of this species (Yabe et al., 1966). All spawning occurs in April–July. Most larvae were captured at the surface, both during the day and night.

Okiyama (1974) reported the capture of post larval bluefin in waters off Niigata, Japan, and concluded that they were spawned in the Japan Sea. He noted that the ocean conditions at the time (August 1972) were unusually warm and that the occurrence was a rarity. Okiyama (1979) has, however, reported on the occurrence of additional postlarvae off Niigata in August 1974 (14 individuals) and in August 1978 (1 individual). In view of this and previous occurrences, he speculated on the presence of an isolated spawning group of bluefin in the Sea of Japan, which spawns later than the main body of fish to the south, i.e., to the east of Taiwan in April to June. Okiyama commented on this in relation to Kawana's (1935) implication of spawning in the Sea of Japan in years of peak abundance of the species which, of course,
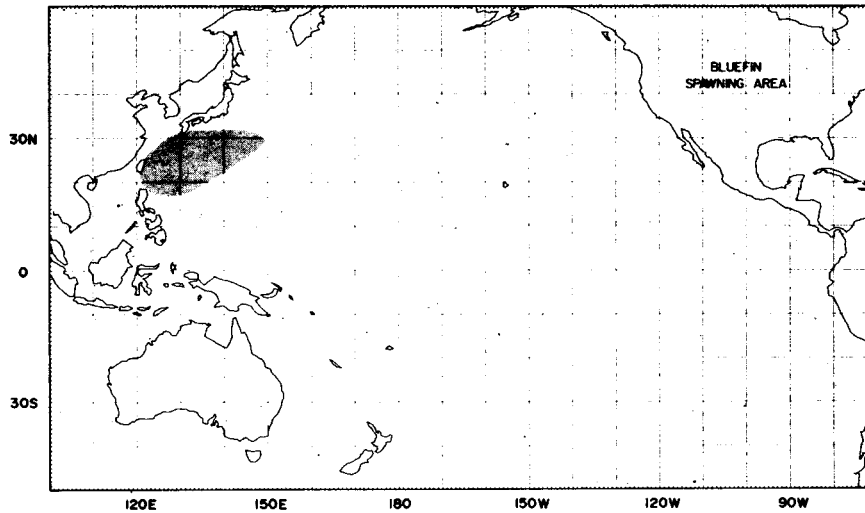
Fig. 13.—Spawning area of bluefin tuna: shading indicates areal extent of the accepted and known spawning ground; this does not necessarily encompass every location from which larvae were collected or sexually mature adults were captured.

may be related to environmental events. Okiyama also reported the appearance of large numbers of juvenile bluefin (zero year class) along the Sea of Japan coast, including Hokkaido, in recent years.

SOUTHERN BLUEFIN, Figure 14

Yabe et al. (1966) and Ueyanagi (1969a) found larvae present from October to March. The area of spawning is in a relatively confined part of the eastern Indian Ocean between the Sunda Islands and Australia (Ueyanagi, 1969a,b; Nishikawa et al., 1978). Larvae of southern bluefin are unknown from other oceans. Almost all specimens were collected at or near the surface.

FRIGATE AND BULLET TUNA

Larvae of Auxis thazard and A. rochei occur largely on the eastern and western sides of the Pacific, extending from 20° S to 30° N on the west and 5° S to 20° N on the east. Some occurrences in mid-ocean have been recorded. In the eastern Pacific most spawning occurs in the fourth and first quarters with no activity in the intermediate period. In the west, most spawning occurs in April to June in the north (20°–30° N) and in October to December in the south and equatorial areas (10°–20° S) (Nishikawa et al., 1978).

LITTLE TUNA

Spawning areas of Euthynnus affinis and E. lineatus are limited mainly to peripheral areas of the Pacific. Occurrences of larvae are restricted to the
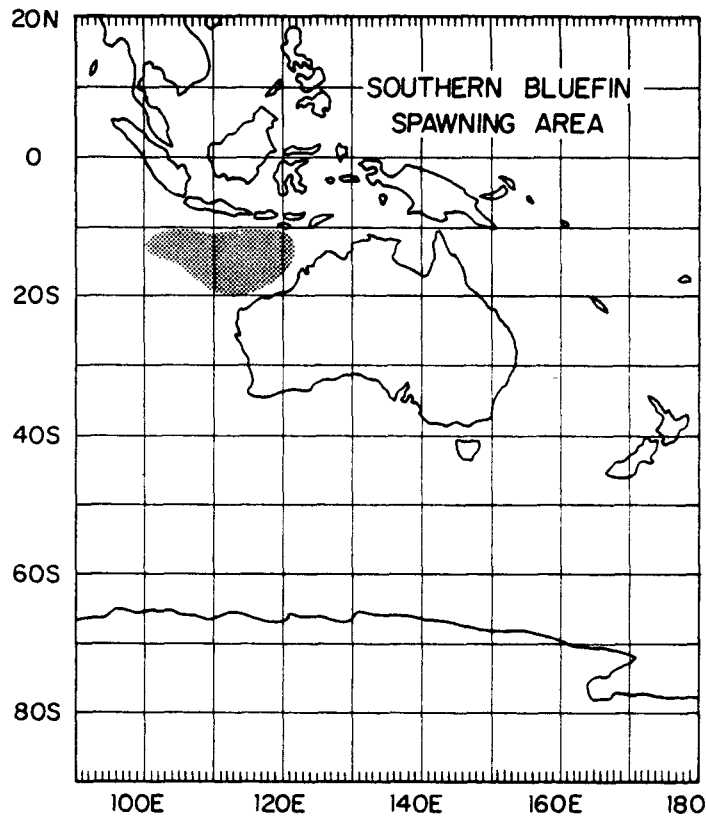
Fig. 14.—Spawning area of southern bluefin tuna: shading indicates areal
extent of the accepted and known spawning ground.

first quarter in the eastern tropical Pacific, and to the fourth and first quarters
in the western Pacific (Nishikawa *et al.*, 1978).

SLENDER TUNA

The larvae of *Allothunnus fallai*, described by Watanabe, Yukinawa, Naka-
zawa & Ueyanagi (1966), occur over a wide area of the Indian and South
Pacific Ocean in temperate latitudes (20°–30° S). In the South Pacific they
were found mostly in November and December, so that spawning is assumed
to be a late southern spring event. The area of spawning is in southern waters
slightly colder than, but contiguous with, those of the albacore. Of all the
tunas, the slender tuna appears to spawn in the coldest waters.

INDO-PACIFIC DOGTOOTH TUNA

All recent collections of larvae and juveniles of *Gymosarda unicolor* were
made in the tropical and subtropical western Pacific. An advanced larva was
identified in the "Dana" collection from the easternmost Indian Ocean.

Collections range over a wide area of the tropical and subtropical western Pacific, from approximately 10° N to 20° S. Concentrations occur near the shallow seas along island clusters such as the Carolines, Solomons, and New Hebrides. All specimens were taken at the surface and subsurface to 20–30 m, with higher numbers in the deeper net hauls. There is evidence of vertical diurnal migration by at least the advanced larvae. Water temperatures at the collection sites were around 27 °C, or higher. The data indicate spawning activity throughout most of the year (Okiyama & Ueyanagi, 1977).

INFLUENCE OF THE OCEAN ENVIRONMENT ON LARVAE

The major and most obvious influences exerted by the ocean on larvae are: (1) provision of conditions suitable for spawning and subsequent survival of larvae, and (2) drift or transport of larvae to areas with beneficial conditions of adequate food and physical well being.

We have seen that two primary types of spawning activity exist: (1) broad activity (*e.g.*, yellowfin, skipjack, bigeye) over extensive areas and times, and (2) activity confined to specific areas and times. The latter type is particularly remarkable because it is exhibited by the most migratory species such as bluefin and southern bluefin. The evolutionary trends in the physiology of these species have allowed penetration into cooler temperate ocean areas, but the requirement for spawning in warmer tropical waters has remained. The detailed mechanisms by which adults of these latter species navigate extensive distances to the relatively small areas in which they spawn, remain unknown, although there apparently is some form of genetic imprintation.

A series of related questions pertain to whether the fish are "active" ("directed") in their migrations or movements or whether "passive" or random movements can account for them. A combination of "active" and "passive" situations (Williams, 1972) is, of course, possible which could account for changes in behaviour with age, physiological state, *etc.* Furthermore, the environmental stimuli to which the fish respond in these behaviours are almost totally undefined (see p. 452), although one might speculate that they may be related to cyclical endocrine changes (Williams, 1972, 1976). Models such as Seckel's (1972) skipjack drift hypothesis account for at least major portions of the time–place movements, but do not explain such events as repetitive return of adults to limited spawning areas within limited time frames.

RÔLE OF TEMPERATURE IN TUNA SPAWNING ACTIVITY

Numerous authors cited elsewhere in this review have stated that temperature is in some way related to the distribution of adults and to the spawning of tunas and survival of the larvae. The analyses concerning larvae, however, have often been superficial and the relationships break down when it is attempted to apply them over wide areas or extensive times (*e.g.*, IATTC, 1973, 1974, 1975). Klawe *et al.* (1970) concluded that there is little, if any, influence of surface temperature, surface salinity, and seasons on the distribution and abundance of most larval tunas. Temperature, however, was shown clearly to be an important variable for *Auxis* sp., a curvilinear relationship being demonstrated, with optimum temperature near 27 °C.

The authors found a marked increase in the proportion of net tows containing larval *Thunnus albacares* and *Euthynnus lineatus* at stations where surface water temperatures exceeded 26 or 27 °C. As noted below temperatures of 26 °C or higher seem to be required for hatching of yellowfin larvae in captivity.

No other environmental variable has been conclusively shown to influence spawning or larval survival. Data on the water quality or conditions in experiments and culture operations wherein tunas have been reared are given below. Hydrographic data on the physical and chemical properties of water observed quasi-synoptically with larva collections have not been successfully evaluated regarding any meaningful relationships. The lack of any relationship between zooplankton and capture of larval *Auxis* sp. has been documented by Strasburg (1960), Nakamura & Matsumoto (1967), and Klawe *et al.* (1970). Salinity likewise proved ineffective in explaining variations in *Auxis* catches, and it was suggested that the range of salinity values of the waters encountered are unimportant in affecting its distribution.

OCEANOGRAPHY AND THE CULTURE OF TUNAS

Since 1970 there has been considerable effort in Japan devoted to the culture of tunas (Ueyanagi, 1978). The coordinated Japanese plan had two objects which formed the basis for two research projects: (1) to develop rearing techniques for larvae and juveniles resulting from artificially fertilized eggs, and (2) to develop rearing techniques for young tunas caught at sea. The projects have been described in some detail by Ueyanagi (1978 and references therein) and Anonymous (1973, 1979b). The matter of interest for our purposes is the environmental conditions which were found to be suitable or unsuitable for the fish.

With regard to the first project (culture *per se*), comment is limited here to aspects with ecological–oceanographic implications (for discussion of technical details of rearing see original publications). Yellowfin tuna was the target species for experiments from 1970–1976 and artificially fertilized eggs were hatched and the larvae grew to 4 cm length in 28 days. Maximum survival was 38 days, by which time the remaining larva had reached the juvenile stage and was 5·1 cm and weighed 1·35 g. Successful hatching was achieved in the temperature range 26–30 °C. Ueyanagi (1978) considered that the major impact of the work was (1) verification of the identification of yellowfin larvae made by other means and (2) confirmation that yellowfin spawning grounds may be delineated by the 26–30 °C isotherms and that 26 °C is probably the lower limiting temperature for spawning. Much of the success with the yellowfin was considered to be due to the earlier rearing and larval feeding work carried out with the frigate tunas, *A. thazard* and *A. rochei*, and the bonito, *Sarda orientalis*. Ueyanagi stressed the importance of the right type (quality) and size of food for the yellowfin larvae at critical developmental stages, *i.e.*, 7 mm, 10 mm. The high mortality of tuna larvae in nature presumably occurs at times when there is a change in food preference and hence relates to the density of available, suitable food organisms during these critical periods.

In the second research project, the target species was the bluefin tuna. Young bluefin of 0·25–2·0 kg, caught in set nets and by trolling, were reared in floating pens (similar to those used for the yellowtail, *Seriola quinqueradiata*) in sheltered coastal waters, mainly in southern Japan. Considerable mortality was caused initially by the capture, transportation, and transfer of the fish to the pens, and also by the abrasive action of the pen walls on the fish. It is important, however, to consider the causes of mortality other than those mechanical ones for which remedies are being developed. The most important of the environmental conditions affecting the bluefin appeared to be heavy rainfall, which caused rapid lowering of salinities; high levels of sedimentation and pollution, either directly from the land or from river run-off (free swimming tunas might be expected to avoid or leave such areas); and the increase in light intensity following changes in netting in the pens. The disadvantages of locating the rearing pens in coastal waters were off-set by the plentiful supply of natural food in such sheltered areas, good water exchange, and ease of logistical support for the facilities.

After acclimatization, the daily feeding rate of young bluefin was about 10% of body weight during periods of high water temperature. The rate decreased rapidly with decreasing water temperature to about 3% of body weight in mid-winter. Bluefin tuna grown in pens showed that they could survive winter water temperatures down to 12 C but, as reported by Hirota & Masiachi (1976), growth (and survival) the following year was normal only if the winter temperatures were 15 C or above. Initial experiments showed growth of bluefin cultured in pens was rapid, from 0·25 to 0·30 kg in mid-August to 2·5 to 3·0 kg in December, a ten-fold increase in just four months. After the winter in which growth was nil, growth re-started in April of the following year. In later successful long-term experiments, bluefin showed growth from 0·14 kg in July–August 1972 to 4·5 kg in March 1973; to 15–17 kg in March 1974; to about 30 kg in March 1975; and to 50 kg in October 1975. Recently, Anonymous (1979b) has reported that Dr Harada and his group at Kinki University had achieved the first successful artificial fertilization and hatching (June 1979) of bluefin tuna eggs spawned naturally by pen-raised fish which were then 5 years old at about 100 kg and 1·9 m in length. Temperature was held at 22–24 C in the well-oxygenated water in the hatchery tanks; larvae were fed *Chlorella* and grew 4 mm in 4 days.

There is only fragmentary information on pen culture of other tunas. In the dogtooth tuna, *Gymnosarda unicolor*, feeding and growth were normal at temperatures of 18 °C and above, but feeding stopped at 16 C and death occurred at 14 °C. On the other hand, the bonito, *Sarda orientalis*, survived winter water temperatures as low as 14 C and exhibited no subsequent growth problems. In 1978 Harada and his group were able to rear bonito larvae from fertilized eggs collected from fish grown in holding pens.

PHYSIOLOGY AND BEHAVIOUR IN RELATION TO TUNA HABITAT

It is only in the last few years that it has become possible to specify some of the habitats of tunas from experimental data, instead of relying entirely upon comparison of distributions of tunas from catch data and environ-

mental variables observed at sea. Much of the experimental work has been done in Hawaii, and owes much to early encouragement by A. L. Tester and later directors of the Honolulu laboratory of the National Marine Fisheries Service. The 1960s saw the perfecting of techniques for handling and holding small tunas at the Service's Kewalo Research Facility at Honolulu (Naka-mura, 1960, 1962, 1964, 1966, 1972; Magnuson, 1965). Many of the studies of sensory and auditory physiology, chemoreception, general physiology, and behaviour which took place in the 1960s and early 1970s (Dizon & Sharp, 1978) were directed at understanding responses to fishing gear and improving harvesting techniques. These gave rise to more sophisticated experimental and theoretical studies in physiology, biochemistry, and hydro-dynamics, dating from the mid-1970s to the present, which were reviewed in detail by Sharp & Dizon (1978), Magnuson (1978), Stevens & Neill (1978), and Dizon & Brill (1979). More attention has been paid to skipjack than any other species.

Studies of the physiological ecology of tunas have progressed to the point where possible evolutionary trends can be related to distribution in the ocean. Sharp & Pirages (1978) compared morphological characteristics such as distribution of red muscle, development of cutaneous vasculature, and development of central vasculature and associated retia, together with biochemical characteristics such as electrophoretic mobility of proteins, in several species of scombroids. They suggested that these characteristics indicate the temporal order of events in the colonization of habitats in the oceans. Earlier, Sharp & Francis (1976) showed that, based on energy expenditure and growth energetic studies of exploited stocks of yellowfin in the eastern tropical Pacific, morphological and physiological characteristics changed considerably with life history stage and that these related to their oceanic distribution. The two muscle types (red and white) and the vascula-ture are especially adapted to the respiratory and energetic requirements of tunas with different habits and habitats. In particular, the internalization of red muscle is found in the larger tunas which are widely distributed in the oceans, and has progressed farthest in the species which have extended into temperate waters—albacore and especially bluefin and southern bluefin. Sharp and Pirages concluded that tunas were originally inshore tropical fishes (as some still are) which through biochemical and morphological adaptations extended their ranges, made themselves less dependent upon environmental fluctuations, and reduced their competition. The extreme case is that of albacore, bluefin, and southern bluefin which spread to tem-perate ocean waters and make long migrations there. Yellowfin and skipjack are intermediate between the temperate and the coastal-tropical tunas (e.g. Euthynnus affinis) of today. Yellowfin and skipjack are warm-water cosmo-politan forms with complex population structure which do not make such long migrations as the temperate species. That the tunas indeed had a tropical origin is confirmed by the apparent need of their larvae for very warm condi-tions (see pp. 464–473).

One of the most interesting features of tunas is that they cannot be strictly classified as either poikilotherms or homeotherms and, unlike other teleosts, are "thermoconserving" fishes (Dizon & Brill, 1979), meaning that they maintain muscle temperatures above ambient. Sharp & Vlymen (1978) tabulated observations by various authors on the differences between tuna

body temperatures and ambient temperatures and these ranged from 1°–21 °C. Stevens & Neill (1978) have reviewed in detail the thermo-conserving mechanism, which is the countercurrent rete (heat exchanger) of the vascular system to the trunk musculature in the true tunas (tribe Thunnini), first pointed out by Kishinouye (1923).

There has been considerable discussion regarding whether or not tunas can regulate their body temperature, with particular reference to the skipjack (Dizon, Brill & Yuen, 1978; Stevens & Neill, 1978) and the Atlantic bluefin (Carey & Teal, 1969; Carey & Lawson, 1973; Neill & Stevens, 1974; Stevens & Neill, 1978). More recently, Dizon & Brill (1979) have presented an excellent detailed account of thermoregulation in tunas. They considered that the thermoregulatory options of tunas are: (A) behavioural thermoregulation represented by (i) environmental (habitat) selection and (ii) control of activity-dependent heat production; (B) passive thermoregulation (which stabilizes muscle temperature and requires no central nervous system (CNS) intervention) represented by (i) water temperature-related and swimming speed-related heat production, (ii) thermal inertia, and (iii) swim velocity-related heat dissipation; (C) physiological thermoregulation (requiring ability of the CNS to alter the effectiveness of thermo-conserving mechanisms). Dizon & Brill (1979), based on their analysis of previous work and their own experimental observations, concluded that tunas are capable of some degree of physiological thermoregulation, in addition to behavioural and passive thermoregulation. Physiological thermoregulation mechanisms are indicated by the labile and independent nature of excess muscle temperatures with respect to swimming speed and hence heat production. In addition, high speed swimming requires mechanisms to dissipate rather than concentrate the almost cubic increase in heat production. The physiological processes which could serve to adjust heat dissipation rates per degree of driving gradient are alterations in (i) circulatory patterns to change the effectiveness of the heat exchangers and (ii) the relative contribution of the red and white muscle fibre systems to propulsion.

Several authors, such as Dizon et al. (1978), have emphasized the advantages to tunas of warm body temperatures and large thermal inertia. Brill's (1978) experiments with skipjack white muscle showed that elevated muscle temperatures are related to increased swimming speed, but he did not know which caused which. Similarly, Bone (1978) suggested that the advantage of high muscle temperature lies in the greater power available from a given muscle mass rather than in the possibility of operating at more or less constant muscle temperature in waters of differing ambient temperature. Stevens & Neill (1978) pointed out that after severe exercise, warmth (high body temperature) is of adaptive value, promoting rapid recovery and thus permitting more frequent feeding frenzies. Recently, Dizon & Brill (1979), Guppy, Hulbert & Hochachka (1979) and Hulbert, Guppy, Murphy & Hochachka (1979) and references therein have indicated that tuna white muscle fibres can function at speeds only slightly above basal rates. Because much of the blood supply of the white muscle by-passes the heat exchangers, aerobically generated heat is not retained and is dissipated at the gills and skin in the usual teleost fashion.

Neill, Chang & Dizon (1976) thought the value of thermal inertia would lie in making tunas relatively independent of changes in water temperature

encountered when moving between the upper mixed layer and the thermocline. Graham & Diener (1978) agreed, citing observations on skipjack and *Euthynnus*. Skipjack are oceanic and may penetrate into cooler waters of thermoclines as deep as 200 m (Fig. 15) on a more regular basis than the more coastal *Euthynnus* spp. during foraging and in escaping from predators. The larger and more efficient heat exchangers in the skipjack enable it to go deeper and stay there longer, because reduced heat loss and large thermal inertia prevents the adverse effects from rapid changes in ambient temperature at the thermocline. Thermal inertia may also permit or enhance detection of weak temperature gradients in the sea (Neill *et al.*, 1976). Core temperature changes slowly, so that differences between core and ambient temperature could increase to the point where they are detectable by the fish. Such a mechanism might explain some observed relations between tuna distribution and weak horizontal temperature gradients. Perception would be of the same order as open ocean gradients: $0.0001°$ to 0.001 °C/m (Stevens & Neill, 1978).
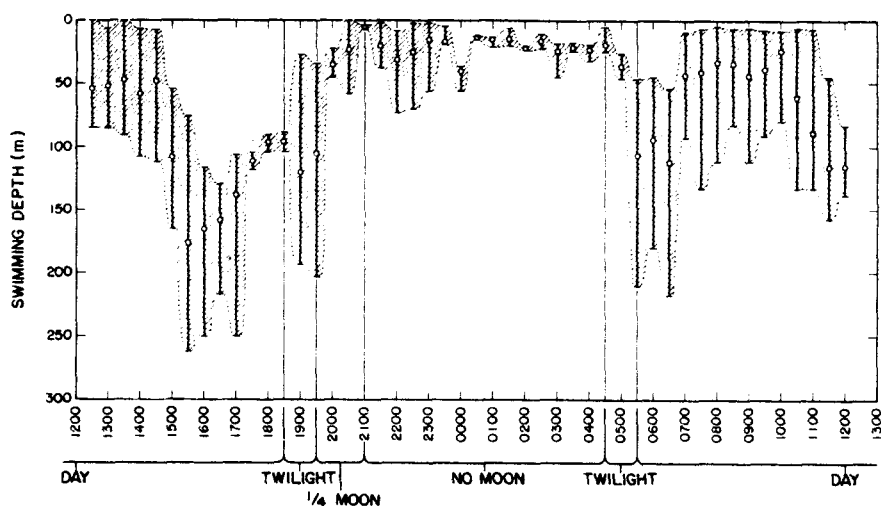

Fig. 15.—Swimming depths of skipjack tuna near Hawaii marked with sonic tags: after Dizon, Brill & Yuen, 1978.

The effects of variations in important ocean properties (temperature, salinity, and dissolved oxygen) have been determined experimentally, mainly for small skipjack, yellowfin, and kawakawa (*Euthynnus affinis*). Dizon, Neill & Magnuson (1977) found that, for skipjack (30–60 cm) and kawakawa (44–50 cm), the lower and upper lethal temperatures were 15 and 33 °C, respectively. All fish stopped feeding within 1 to 2° of the lethal limits. The same work, and that of Stevens & Fry (1971), showed no increase in swimming speed of those species with increase in ambient temperature. Dizon *et al.* (1978), however, in an extensive series of experiments with skipjack, noted slightly higher swimming speeds at higher temperatures. Behavioural responses were also noted in skipjack when tank water was cooled to 20 °C; the fish began to show stress reactions or would not enter the cool water. This work by Dizon *et al.* supported the results of field observations on tracked tagged skipjack by the same authors and by Yuen (1970).

Dizon (1977) showed experimentally that young skipjack and yellowfin exhibit no response to alterations in salinity between 34 and 29‰. Hence, the relatively small salinity changes encountered in the ocean by those and other species are unlikely to regulate their behaviour or habitat. On the other hand, behavioural responses to low oxygen levels were dramatic in experiments on small skipjack (Dizon, 1977; Gooding & Neill, in prep.). An initial reduction from oxygen saturation levels to 2·8 ml/l produced no change in swimming speed or survival time. Below that level swimming speed and mortality increased rapidly at successively lower oxygen concentrations. Only three out of eight skipjack survived at 1·8 ml/l, even for short periods. The increase in swimming speed seems not to be for increase in ram jet ventilation, and is probably an escape response to an unfavourable habitat. Other experiments indicated that oxygen levels as low as 1·4 ml/l were tolerated by yellowfin without signs of stress (Dizon, 1977), and by kawakawa for short periods when searching for food. We discuss on pp. 481–487 the conclusions that authors have drawn from these experiments at different levels of temperature, salinity and dissolved oxygen, regarding the areal and vertical extent of suitable habitat for tunas in the Pacific.

Neill *et al.* (1976) showed from observations on captive skipjack that the thermal inertia is dependent upon fish weight, so that large skipjack would overheat in warm waters if they were as active as small skipjack. It should be pointed out, however, that the value of basing future work on body temperature-limited activity in skipjack has been questioned by Dizon & Brill (1979). Dizon & Brill 'force-swam' skipjack in 30 °C water and observed that excess body temperatures actually decreased or remained constant even though heat production was markedly increased. Assuming that the highest observed muscle temperatures (35 °C) are the highest at which the fish can live, Neill *et al.* (1976) used their data to estimate upper limits of environmental temperature at a normal level of activity. Examples are mentioned on pp. 482–485. Kitchell, Neill, Dizon & Magnuson (1978) suggested that energetic limitations vary according to body weight in skipjack and yellowfin. Growth in fish less than 7 to 10 kg appears limited by food availability, but the growth in fish weighing more than 7 to 10 kg is probably limited by their ability to consume and process available food. The risk of overheating core tissue may restrict activity, and thus the amount of food that can be gathered, in skipjack at the observed maximum weight of 22 to 25 kg. For a variety of reasons the authors have less confidence in explaining the much greater maximum weight of yellowfin (about 182 kg) in the same way.

Sharp & Dizon (1978) have pointed out the results of the deviation of the tunas from the biochemical and respiratory norm of the teleosts. First, these adaptations in tunas result in the high speed, continuous swimming behaviour (Magnuson, 1970, 1973, 1978) necessitated by lack of, or reduction in, the swim bladder (at least in specimens less than 60 kg) and resultant drag, as well as the need for continuous passage of large volumes of water over the gills. Magnuson (1978) indicates that in an evolutionary sense these changes probably took place to permit increased vertical mobility, especially near the sea surface, which is important for food capture and escape from predators. A new hypothesis advanced by Magnuson is that the negative buoyancy (causing the need for continuous swimming) makes possible gliding and soaring in internal waves near the surface of the thermocline. Under these

conditions, horizontal motion in the sea would be nearly effortless under certain circumstances. At this time, however, there is little evidence in support of this idea. Secondly, the adaptations in tunas account for the bulk of caloric expenditure, and hence their high daily food requirements (Sharp & Francis, 1976).

Some of the experimental and field work on the limits of tuna habitat imposed by temperature and oxygen has application also to the tuna's vulnerability to fishing gear in different regions, although few published studies are available. Vertical thermal structure is important to longline fishing success, which is less directed as to species than is surface gear. Long-line catches are typically multi-species, whereas surface catches are of only one or two species. Using vertical longlines, Saito (1973) and Saito & Sasaki (1974) demonstrated distinct vertical stratification of tunas, as well as high availability, at depths much greater than those normally fished. That lower oxygen tolerances are of considerable potential importance to longline fishing was illustrated by Hanamoto's (1975) work. He showed a decrease in catch success for bigeye tuna when the oxygen concentration at 100 m was less than 1 ml/l. Similarly, where bigeye and albacore distributions over-lapped, the albacore catch declined before bigeye presumably because of the lower oxygen values, even when temperatures were satisfactory for albacore. In the eastern Pacific yellowfin fishery Green (1967) demonstrated a signifi-cantly greater success of capture by purse-seine net where the thermocline was shallow (less than 20 m below surface) and the mean vertical thermal gradient sharp (greater than 0.55 °C/m). The effects of these two features were additive. The interpretation was that the yellowfin would have to descend into unsuitably cold water in order to escape under the net before it was pursed. Green believed that the vertical distribution of dissolved oxygen also affected the success of purse-seining in the same way, but he gave no data. This work was extended by Sharp (1978) who analysed data on catches from successful purse-seine sets as a function of time of day, depth of the mixed layer, and depth of the 23 and 15 °C isotherms over a period of six months. The work showed (at least for 1973–1974) that the productive area of the purse-seine fishery for yellowfin in the Pacific could be described exclusively as the area where the 23 °C isotherm is less than 50 m below the surface, and the 15 °C isotherm no deeper than 80 m below surface. Based on the criteria mentioned above, Sharp presented charts for each month showing areas where yellowfin are expected to be most vulnerable to purse-seining. He emphasized that his criteria would not predict occurrence of yellowfin or fishing success in optimal habitat areas.

Sharp (1978) attempted a similar treatment for skipjack in the Pacific, with a series of monthly charts showing areas of presumed highest skipjack vulnerability to surface fishing. The areas were based upon the depth of the 15 °C isotherm, the surface temperature, and the depth of the 2.5 ml/l value of dissolved oxygen. The central Pacific provides the most suitable habitat for skipjack which probably is the reason why the species spawns there with movement to the more productive, peripheral areas of the ocean for feeding and subsequent maturation of the gonads. There are, however, at least five genetic units of skipjack in the Pacific which overlap geographically to varying extents (Fig. 7); and Sharp (1978) cautions the extrapolation of data from specimens of one sub-population to the others because of the

difference which might be expected in physiology and behaviour. He points out that, in the genetic sense, morphological and biochemical patterns have a probable rôle in the skipjack coping successfully with the diverse environments of the differing Pacific geographic regions. Physical factors, such as high ambient temperature, are very important to rapid growth and development. In areas with very high sea temperatures (greater than 28 C) over most of the year, migration activity can be expected to be slight because of the high respiratory rate needed in warm water. This probably accounts for the reported slow rate of growth of skipjack in the Papua-New Guinea region. Behaviour is probably similarly determined, as shown by the data in Table I on schooling activities in various areas of the Pacific.

TABLE I

Data on schooling activities of skipjack in different areas of the Pacific Ocean (after Sharp, 1978, Table VII)

Exploited group	Average school size (tons)	Bait fishing method	Mixed layer depth in fishing areas	Optimum temperature range of commercial activity
Northeastern Pacific	5-25	stop schools with bait	30-100 m	20-26 °C
Southeastern Pacific	1-25	walking schools	20-100 m	20-28 °C
New Zealand	10-30	stop schools with bait	20-90 m	17-23 °C
Papua New Guinea, Solomon Is.	10-15 (?)	drift into schools	100-300 m	28-30 °C
Northwestern Pacific	3-10	walking schools	50-200 m	20-28 °C (?)

In a relative sense, smaller schools of skipjack tuna are found in areas where the mixed layer is very deep compared with those from areas with more compressed mixed layers. In the latter situations there will be more schools in a smaller volume, hence they will be more likely to aggregate; this also leads to heterogeneity in the population.

TUNA DISTRIBUTIONS IN RELATION TO THE ENVIRONMENT

TEMPERATURE

Blackburn (1965) considered that the following temperatures directly limit the range of adult yellowfin areally and bathymetrically: 18 to 31 C for all occurrences and 20 to 30 C for occurrences in abundance. Two references to occurrence at 15 C, including one for surface fish, were omitted (Bini, 1952; Uda, 1957). The principal evidence of temperature-limitation was that the range of surface yellowfin expands and contracts at its periphery in the same way as the area in the stated isotherm range at the sea surface, in areas with good time series of data (Blackburn & associates, 1962; Broadhead & Barrett, 1964). Such data were not available for subsurface fish, for which

depth of capture was not precisely known. Blackburn (1965) assumed a mean capture depth of 100 m (see p. 451) and noted that temperatures there were generally not below 20 °C in areas where yellowfin were taken in abundance.

Subsequent surface observations confirmed the congruence of yellowfin areas and areas over 20 °C off Baja California (a fringe area for yellowfin), except for one situation when the fish occurred at 17 °C. On that occasion 17 °C was the highest temperature at which yellowfin could find abundant food in the area (Blackburn, 1969a).

Bathymetric data on yellowfin were summarized earlier (see p. 451). Yellowfin occur as deep as 380 m. They may even occur deeper, since 380 m was the maximum fishing depth, but the numbers taken declined below 300 m. This work was done west of Fiji, where the mean temperature at 400 m is 13 to 14 °C (Muromtsev, 1958). In a comparison of mean yellowfin catches using the regular longline, fishing to about 130 m, and of another type that fished to about 260 m, the ratio, deep/regular, was 0·73. From this and other information it was concluded that subsurface yellowfin are generally above the thermocline, as hypothesized earlier by Suda & Schaefer (1965), although the above-mentioned findings at Fiji indicate some occurrence in the thermocline as well. In the eastern tropical Pacific, a sharp oxycline accompanies the thermocline. This would further tend to limit the depth range of tunas in that area, as is mentioned later. Temperatures at the top of the thermocline are almost always over 20 °C in the areas where yellowfin are taken most abundantly by longline, which are mostly very near the Equator (Robinson, 1976; Suzuki et al., 1978). The equatorial mixed layer is generally thicker than 100 m in the western Pacific but much thinner, frequently less than 30 m, in the eastern Pacific (Robinson, 1976; Wyrtki, 1964). Thus, if mean hook depth for the regular longline is 100 m, most hooks would hang in waters much colder than 20 °C in the eastern equatorial Pacific. Then if temperatures below 20 °C are unsuitable, longline fishing for yellowfin should be much less successful in the east than in the west, which is the case (Suzuki et al., 1978). Surface yellowfin, however, are more abundant, or at least more vulnerable to capture, in the east (see p. 446 and p. 448). The elevated thermocline may concentrate them near the surface. Small yellowfin (40–70 cm) are found at current boundaries where the sea surface temperature is greater than 23 °C but rarely below that level. This is because they are more sensitive than are large yellowfin (greater than 70 cm) to colder than optimal water, and because of the greater thermal inertia in large specimens (Neill & Stevens, 1974).

Thus the previous hypothesis that the range of yellowfin in abundance is directly limited by a water temperature about 20 °C, both in the horizontal and vertical planes, remains plausible. The species occurs occasionally in deep waters as cold as 14 °C, however, and in surface waters as cold as 15 °C. The large subsurface yellowfin may tolerate slightly lower temperatures than the smaller surface fish.

There is general agreement that certain temperatures likewise limit horizontal and vertical distributions of skipjack, but these temperatures can vary by region and by size of fish. Limits of surface range of skipjack in the eastern Pacific have been compared with contemporaneous surface temperatures by several authors. The limiting temperatures are about 17 to 30 °C for all occurrences and 20 to 29 °C for occurrences in abundance (Broadhead &

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Barrett, 1964; Blackburn, 1965, 1969a; Williams, 1970). In Japanese waters,
skipjack occur between 18 and 30 °C (Uda, 1957). Off eastern Australia,
however, the lower temperature limit for all occurrences is 15 °C, and the
upper limit may also be lower than in the eastern Pacific and Japan (Robins,
1952; Blackburn & Serventy, in press). This may represent a difference
between sub-populations. Skipjack was seen at 185 m (temp. not < 17 °C;
Anonymous, 1965) and a sonically tagged one was tracked at 200 m (temp.
12–14 °C but little time spent at < 18–20 °C; Dizon *et al.*, 1978); both cases
were off Hawaii.

Captive skipjack in Hawaii were subjected to gradually lowered and in-
creased temperatures with the following results: of seven fish, one died at
17 °C and none survived at 15 °C more than a few hours; of three fish, two
died at 33 °C and one at 34 °C (Dizon *et al.*, 1977; Barkley, Neill & Gooding,
1978). These results on skipjack temperature tolerance support the field
observations from the eastern Pacific, but not those from Australia.

Thermal inertia in skipjack depends upon weight (see p. 478). Neill *et al.*
(1976) estimated possible upper limits of environmental temperature for
skipjack as a function of weight at a normal level of activity. For example,
4 kg and 9 kg skipjack can live in water as warm as 26 ° and 22 °C, respec-
tively, and only fish of less than 1 kg can tolerate temperatures over 30 °C.
Using these estimates and those on the lower temperature limit, Barkley *et
al.* (1978) prepared sections and maps of the eastern and central Pacific
showing areas and layers suggested as suitable habitats for skipjack of differ-
ent sizes. They took the limiting concentrations of dissolved oxygen into
account as discussed later. They concluded that surface tropical (mixed
layer) waters are not a good environment for adult skipjack except at small
sizes, and that the normal habitat of large skipjack is the upper thermocline,
where it is not oxygen-deficient. They emphasized the need for field testing
of their hypothesis. According to Sharp (pers. comm.), skipjack of greater
than 1 kg are common in 30 °C waters in some areas, *e.g.*, Papua–New Guinea.

The range of temperature at which bigeye occur was given as 11 to 29 °C
by Uda (1957) and 13 to 29 °C by Alverson & Peterson (1963). The higher
temperatures represent occurrences in the relatively small surface fishing
areas, and the lower temperatures refer to the more extensive range in the
longline fishery. Hanamoto (1975) recorded bigeye from 12 to 27 °C,
principally in and below the thermocline, in the southern region of the eastern
tropical Pacific. This distribution in relation to the thermocline had previous-
ly been proposed by Suda, Kume & Shiohama (1969). As shown earlier (see
p. 451), bigeye tend to occur deeper than other tunas. The deep longline
caught 1·79 times as many bigeye as the regular longline, confirming other
indications that abundance increases below the regular longline depth. Bigeye
were caught down to 380 m near Fiji and catches in general were higher
below 300 m than above. It is clear that the bathymetric limit and hence the
lower temperature limit are not yet known for bigeye; it is not known if
temperature limits their range.

Much field work has been done to identify range-limiting temperatures
for albacore in surface fishing areas of the Pacific. The fish occurrences vary
geographically in much the same way as areas of water within a certain
temperature range. The lower and upper temperatures suitable for any alba-
core are about 14 ° and 23 °C, and the corresponding limits for abundant

albacore are 15 and 21 C, in surface waters (Laevastu & Rosa, 1963; Blackburn, 1965; Laurs & Lynn, 1977, and references). In experimental longlining west of Fiji, Saito (1973) found albacore over the whole range of tested depth, 80 to 380 m. They were most abundant between 200 and 260 m, within the thermocline, where temperatures ranged from 17 to 21 °C. The range of temperature at all depths of capture was 13·5 to 25·2 °C. Other work p. 451) has shown that the vertical distribution of albacore is in general like that of yellowfin, whereas bigeye extend deeper. The deep longline to regular longline catch ratio in albacore is 0·82. It seems, therefore, probable that albacore, like yellowfin, do not occur much deeper than they have already been found. Then the lowest temperature for subsurface albacore may be taken, from Saito's observations, as 13 °C; because this is almost the same as the limiting lower temperature for surface fish it may also be limiting in the horizontal plane. The upper limiting temperature seems to be 25 °C from Saito's data, not 23 °C as found in the temperate-water surface fisheries. Ranges of temperature for the smaller surface albacore and the larger deeper ones appear to be very similar.

The relatively low abundance of albacore along the Equator can be explained, largely, from the range of temperatures in which albacore are abundant. All surface equatorial waters are warmer than 21 °C, except in some areas east of 110° W for a few months of the year. All equatorial waters close to the mean hook depth are either above 21 °C or no higher than 15 °C, except during part of the year between 115° and 140° W (Wyrtki, 1964; Robinson, 1976). Thus the equatorial area is unsuitable or marginally suitable for albacore throughout the year as far as temperature is concerned. Low abundance or absence of albacore in many areas of the eastern tropical Pacific can be explained similarly.

Bluefin in the Pacific have been recorded between 12 and 21 °C, most abundantly between 14 and 19 °C (Uda, 1957; Bell, 1963; see also p. 474). Most of these data are from surface fisheries. We know of no observations on depths or temperatures at which bluefin occur in the longline fishery. Probably the poleward edge of the range of abundant bluefin is temperature-limited, because the species was plentiful farther north than usual along the North American coast during the warm years 1957 to 1959 (Radovich, 1961).

Southern bluefin occur between 10·5 and 21 °C (Robins, 1963), although catches have been made in the northern parts of the West Wind Drift where surface water temperatures reach as low as 8 °C. In the Australian surface fishery almost all the catch is made between 17 and 20 °C, although warmer and cooler waters occur within range of the fishermen (Hynd & Robins, 1967; Williams, 1977).

The foregoing information shows that certain temperatures coincide with and probably determine the limits of the geographical range of certain tunas, including at least yellowfin, skipjack, and albacore. Temperature possibly influences the bathymetric limits in the same species. It is possible, however, that some fish move beyond these limits for short periods. The evidence of limitation by temperature is particularly strong in the case of skipjack, where experimental data confirm the local field observations. These direct effects of temperature upon tuna distribution are confined to determination of range, however, as several authors (e.g., Nakamura, 1951, 1969; Blackburn, 1965, 1969b) have pointed out. Within the range limits of

a species, its distribution varies from zero to high abundance in ways that are not related to contemporaneous distributions of temperature as a variable (*e.g.*, Broadhead & Barrett, 1964). As shown later there can be associations between tuna and features of thermal structure such as fronts, but the attractive property of the front is probably biological. Possible causes of patchy tuna distributions in waters of suitable temperature are discussed later (see pp. 490–500).

OXYGEN

Barrett & Connor (1962) suggested that dissolved oxygen concentrations might not greatly exceed the requirements of tunas in warm waters, even at the surface. Blackburn (1965) remarked that dissolved oxygen might limit bathymetric ranges of tunas in some areas where concentrations are very low in the upper 150 m, such as in the eastern tropical Pacific. Experimental data are now available to confirm these ideas for skipjack, which are stressed at concentrations below 2·8 ml/l. Yellowfin, however, are not stressed at 1·4 ml/l (see p. 478). Hanamoto (1975) compared bigeye catches in areas of differing oxycline depth in the eastern Pacific, and concluded that bigeye can tolerate concentrations down to 1·0 ml/l.

Sharp & Francis (1976) presented an equation to estimate the rate of oxygen consumption due to swimming. The swimming rate used in the equation was the minimum required to maintain hydrostatic equilibrium, which was assumed to be the least demanding rate energetically. It varies by species and fish size, and can be estimated for different tunas from data given by Magnuson & Weiniger (1978). Thus, Sharp (1978) could estimate relative rates of oxygen consumption for different species and sizes of tuna and, from the experimental data on lowest tolerable oxygen concentration for skipjack, could estimate such concentrations for other species. The estimated lowest concentrations, varying with fish size, are listed in Table II. These figures for yellowfin and bigeye are, respectively, higher and lower than those obtained from sources mentioned earlier, *i.e.* 1·4 and 1·0 ml/l. The differences are, however, not large and appear quite reasonable in view of the various methods employed.

TABLE II

Estimated oxygen tolerances for tunas of different sizes (after Sharp, 1978, Table V)

Species	Fork length (cm)	Estimated lower oxygen tolerance, 10 min levels (ml O_2/l H_2O)
Katsuwonus pelamis	50	2·45
(skipjack)	75	2·89
Thunnus albacares	50	1·49
(yellowfin)	75	2·32
T. obesus	50	0·52
(bigeye)	75	0·65
T. alalunga	50	1·67
(albacore)	75	1·39

The specified limiting concentration for skipjack would confine the fish to fairly shallow layers in some tropical areas, but temperatures in some of those layers might be unsuitably high for the larger fish. Barkley *et al.* (1978) specified areas and layers that would constitute suitable habitats for skipjack of various sizes in the eastern and central Pacific, assuming a limit of 3·5 ml/l of oxygen and the size-dependent temperature limits mentioned earlier. An example of their findings is reproduced in Figure 16, which represents a meridional section along 119° W in August. Almost all waters above 22 °C have enough oxygen, and are cool enough for skipjack weighing less than 9 kg. Those above 26 °C would be suitable only for skipjack of under 4 kg. The layer between 22 and 18 °C would be suitable for skipjack of all sizes with regard to temperature, but deficient in oxygen at most latitudes. The layer below 18 °C is too cold for skipjack and is also mostly oxygen-deficient. Thus skipjack over 9 kg would find suitable habitat only in the cross-hatched parts of the section (Fig. 16), most of which are subsurface. On the other hand, fish under 4 kg have a much larger habitat available, both in area and depth.

Subject to fuller validation, this hypothesis is useful in explaining and predicting certain features of skipjack distribution. For instance Barkley *et al.* drew attention to large areas west of Mexico and Peru where no suitable habitat for large skipjack could exist. The movement of such fish from coastal waters to the spawning region would then be confined to pathways
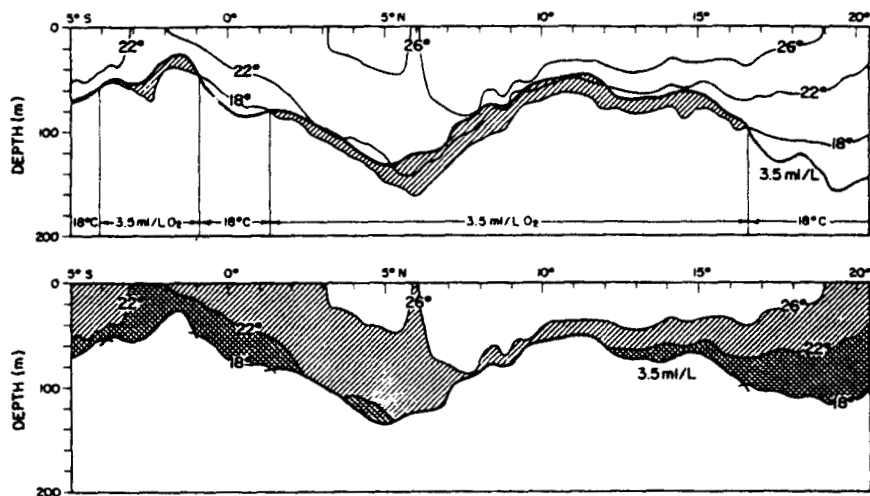

Fig. 16.—Upper panel: temperature and dissolved oxygen (selected isopleths only) along 119° W, eastern Pacific Ocean, August 1967. Lower limits of the skipjack tuna habitat are assumed to be either 18 °C or 3·5 ml/l dissolved oxygen, as indicated; the hatched layer should be warm enough for these fish, but oxygen deficient. Lower panel: hypothesized habitat layers for skipjack tuna of two sizes, 4 kg (entire hatched area) and 9 kg (cross hatched area only) in the same section; fish <4 kg could presumably live anywhere between the sea surface and the lower limits, 18 °C or 3·5 ml/l of dissolved oxygen; from Barkley *et al.*, 1978.

between those areas. Any search for the migrating skipjack should be concentrated in those pathways. The restriction of habitat suitable for large skipjack in the eastern Pacific may explain why the fish caught in the surface fishery near the Americas are generally small, although quite numerous, and why the principal spawning areas are in the central and western Pacific. The depth of the limiting property measurement (temperature or oxygen concentration) is within 50 m of the surface in many parts of the eastern tropical Pacific. Observations by Ingham, Cook & Hausknecht (1977) in the southeastern tropical Atlantic Ocean indicate that oxygen limits the bathymetric distribution of skipjack in other areas besides the Pacific. They found that surface schools of skipjack occurred where the 3·5 ml/l oxygen level was less than 50 m below the surface, with most schools occurring where it was less than 30 m below the surface. This was interpreted as a crowding of fish upwards by the oxygen-poor layer.

Sharp (1978) discussed the question of suitable habitat for both skipjack and yellowfin. For skipjack he recognized the limiting rôles of both temperature and oxygen, in much the same way as Barkley *et al.* (1978). On the other hand, Sharp considered yellowfin habitat to be determined by temperature, since that species can tolerate lower oxygen concentrations (2 ml/l or less) than skipjack. This seems probable to us from the following observations. Mean hook depth in the longline fishery is about 100 m. Yellowfin should become scarce in that fishery where (a) mean temperature at 100 m is below 20 °C or (b) mean oxygen concentration at 100 m is below 2 ml/l. The yellowfin catch per unit fishing effort in the longline fishery is, in general, highest in equatorial waters, but declines in those waters from west to east, starting at about 150° or 140° W (Suzuki *et al.*, 1978). Temperatures and oxygen concentrations at 100 m fall close to the values in (a) and (b) at about those longitudes, and then further decline towards the east as the thermocline and oxycline ascend in the water column. Condition (a) is generally encountered west of (b) at a given latitude, however, because the 2 ml/l level is deeper than the 20 °C isotherm (Muromtsev, 1958; Wyrtki, 1964; Barkley, 1968; Robinson, 1976; Reid *et al.*, 1978). Thus, temperature appears to exclude yellowfin in some situations where oxygen concentration would be suitable. In other situations in the far eastern tropical Pacific, temperature and oxygen are both unsuitable at mean longlining depths.

Bigeye can tolerate 1 ml/l of dissolved oxygen. Concentrations less than that occur at 100 m in several parts of the eastern tropical Pacific where bigeye are hardly ever caught, especially west of southern Mexico and Peru (Wyrtki, 1967; Barkley, 1968; Shingu, Tomlinson & Peterson, 1974; Reid *et al.*, 1978). Oxygen may limit the occurrence of bigeye in those areas, as Hanamoto (1975) suggested. Temperatures at 100 m in the same areas are above 11 °C, which bigeye can tolerate. Some higher temperature may be limiting for bigeye in abundance, but that value is not known. Curiously, yellowfin are taken by longlining in greater quantities than bigeye in some of the areas mentioned, although yellowfin is less tolerant of low temperature and oxygen. The explanation may be that yellowfin are more available than bigeye at hooking depths less than 100 m, as was indicated in the study of bathymetric distribution.

The minimum oxygen concentration for albacore is probably like that for yellowfin, about 2 ml/l, according to the values in Table II. Going from west

to east along the Equator, where albacore are scarce, lower oxygen concentrations are encountered at 100 m in some areas east of 130° W (Reid *et al.*, 1978), but at 100 m temperatures are unsuitable for albacore almost everywhere in equatorial waters, as shown earlier. An example of an area with no albacore catch is 10° N: 95° W (Fig. 4). The presumed oxygen limit and the temperature limit for any albacore (13 to 14 °C) are both at about 100 m (Wyrtki, 1964, 1967; Barkley, 1968; Robinson, 1976). There is a layer about 30 m thick within the thermocline where temperature and oxygen both would be suitable, but this habitat may be too restricted for the species to occur abundantly. If it were to occur, it would not often be taken on the longline because few hooks would hang in such a shallow layer. We wish to emphasize a point made elsewhere: that because oxygen and temperature values are suitable does not mean that tunas will be present. Absence of favourable water properties does mean exclusion of the fish, but presence of favourable waters does not mean presence of fish.

No information on oxygen requirements of bluefin or southern bluefin is available. We conclude that the known bathymetric ranges of the other four species, and thus some features of their geographic ranges in the subsurface fishery, can be explained from vertical distributions of temperature or dissolved oxygen or both. The clearest cases are for skipjack, where both properties set the range limits, and yellowfin, where temperature alone does so.

SALINITY

Atlantic bluefin tuna (*Thunnus thynnus thynnus*) occur in waters with salinity ranging from 18 to 38‰ in the Mediterranean and Black Seas (Tiews, 1963). This is almost the entire range of salinity in the world oceans. Except for the report of Laurs, Yuen & Johnson (1977) on ultrasonic tracking experiments with albacore noting that a change in the orientation of albacore was observed at a weak salinity front, other comparisons of salinity and tuna distributions suggest a lack of relation. Scarcity of tuna near river mouths might be explained by turbidity. Blackburn (1965) considered that salinity by itself has no direct effect upon tuna distributions at or within the range limits, and that statement has not been challenged. Salinity also seems not to determine distributions of other pelagic oceanic animals (Kinne, 1971; Holliday, 1971). Barkley (1969) noted that adult skipjack occur in areas of the Pacific where there is a shallow salinity maximum permanently or seasonally, or where the salinity maximum is at the sea surface. The two kinds of areas together cover the entire tropical and subtropical Pacific. It was not claimed that the actual salinities or the maximum were directly related to the skipjack distribution. Donguy, Bour, Galenon & Gueredrat (1978) and Bour & Galenon (1979) noted a strong correlation between the catch of surface tunas and salinity in the western Pacific. Dizon (1977) observed no changes in swimming speed or in any other behaviour of captive young skipjack and yellowfin as salinities were reduced from 34 to 29‰.

Seckel (1963, 1972) found an association between salinity and skipjack at Hawaii, the fish being most abundant when salinity is below 34·8‰. These lower salinities are an indicator of water of the California Current Extension, which is a tributary of the North Equatorial Current. Migrating skipjack

from the east approach Hawaii in the North Equatorial Current, as mentioned elsewhere. In winter, and in summer of some years, this low-salinity water does not reach Hawaii and skipjack are scarce there. The salinity does not determine the distribution of skipjack at Hawaii but it is a useful indicator of the current, which does.

TRANSPARENCY

Tunas locate food objects principally by vision, and perhaps also by olfaction (Magnuson, 1963, and references; Nakamura, 1962). Turbid waters should, therefore, be rather unsuitable for them, although extremely clear waters would contain little food. Reid *et al.*, (1978) gave a map of Secchi disc depths in the equatorial and North Pacific, based on data from Frederick (1970) and other authors. It shows that Secchi depths in the geographic range of tunas (*i.e.*, to 40° N) are generally between 15 and 50 m, with the highest readings in the anticyclonic gyre of the central North Pacific. North of 40° N the waters are less clear with Secchi depths generally below 15 m. Secchi depths under 15 m indicate high concentrations of terrigenous or phytoplanktonic particles near the sea surface. Where these particles are phytoplanktonic, the chlorophyll concentrations are over 0.8 mg/m^3 (Forsbergh, 1969). Such chlorophyll concentrations in tropical and subtropical waters are virtually confined to coastal upwelling areas, which are frequently too cold for tunas as shown later in this section. If low transparency of water directly restricts the habitat of tunas, it is probably in coastal areas that are kept turbid with particles washed or blown from the land, and such processes as waves and tides which stir up shallow water. There are such areas where tunas are absent or rare, although other conditions such as temperature and food appear satisfactory for them. Bass Strait, between the Australian mainland and Tasmania, is an example (Blackburn & Serventy, in press).

CURRENTS

It was suggested by Nakamura (1954) that different tuna species have their centres of distribution or characteristic habitats in different currents. The idea arose from earlier studies of variations in apparent abundance of species in the Japanese longline fishery, especially in the western Pacific where that fishery originated. The examples most commonly mentioned were yellowfin and bigeye, considered to be most abundant in the South Equatorial Current and North Equatorial Countercurrent, respectively. The idea appeared less satisfactory as the fishery spread across the Pacific and into other oceans; the known ranges of the species were extended considerably northwards and southwards, and overlapping was seen between areas of maximum abundance for different species. In addition, it was not clear why the postulated relations with the currents should be expected. Doubts about the suggestion were expressed by Blackburn (1965). Nakamura (1969) replied to the objections, and appeared to concede that the species were indeed distributed more broadly and in a less segregated way than he had originally suggested. He described more instances of tuna migrations between currents than within them.

Blackburn (1965) also noted that several other authors had written rather casually about relations between tunas and currents, without specifying what the relations were. He thought some of the tuna distributions in the Kuroshio Current and Gulf Stream might be determined by temperature instead of by the current. He also pointed out that tunas exhibit swimming speeds in the range of 15 to 50 km/day (Clemens, 1961; Anonymous, 1977; Laurs et al., 1977; see also Dizon, Brill & Yuen, 1978), which would enable them to move independently of currents or with them (Sharp & Vlymen, 1978).

Seckel (1972) took a mechanistic approach when discussing the relationship between migration and currents in that the term migration means simply that a fish is in one location at one time and in another location at another time. He expressed this relationship as follows. The distance covered by the fish or schools, S, during a time interval Δt is $\Delta S = V \Delta t$, where V is the velocity of the fish. The velocity of the fish is the velocity of the water (W) carrying the fish (current) plus the velocity of the fish (F) swimming relative to the water, that is

$$V = (V_W + V_F).$$

Thus, the distance covered becomes

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

Over a period of time, the migration distance is the sum of these elements

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

In short, all fish migrations contain these elements and, therefore, currents are a part of all migrations except when $V_W = 0$, a rare occurrence.

When V_W is much less than V_F, V_W may possibly be ignored. When the migration time is long, however, even if V_W is much less than V_F, $V_W \Delta t$, the distance the fish is carried by the water, may not be negligible. Therefore, it is not unreasonable to have a first impression such as that of Nakamura. Subsequent spread of the fishery illustrates that the additional component V_F is also present. One also might consider the fact that current speeds and direction at the ocean surface are not necessarily the same as at depth, particularly at the depths occupied by deep swimming bigeye.

As mentioned on p. 455, Seckel (1972) and Williams (1972) invoked currents to account for movements of skipjack between the eastern and central Pacific. Seckel concluded that the movement of adults from the eastern Pacific to Hawaii could be explained by random swimming and drifting in the North Equatorial Current. He said, "An attractive aspect of the drift hypothesis is its simplicity. Skipjack while in the North Equatorial Current need not do, know, or remember anything other than to search for food." These westward-moving fish do not, as far as is known, return later to the eastern Pacific. Movement from the central to the eastern Pacific is thought to occur only when skipjack are very young, and Williams (1972) has considered ways in which it could take place. His three models assume either a passive drift with currents or an active movement against them.

In addition to the direct effects of currents on the distribution of tunas, currents affect the distribution of prey and the distribution of temperature and thermocline topography and, therefore, indirectly affect the distribution of tunas. Hanamoto (1974) considered that the Equatorial Undercurrent affects the apparent abundance of bigeye in the far eastern Pacific by preventing longline hooks from sinking to normal depths.

WATER MASSES

A few authors have attempted to explain geographical distribution of tunas from distributions of water masses (bodies of water characterized by specific temperature-salinity relations), but none have been very successful. Yamanaka, Morita & Anraku (1969) considered that Pacific bluefin and albacore were distributed according to water masses at particular stages of their life history, but not in the same way at all stages. At times when tunas do appear to show close association with water masses, it is quite likely that some other property or feature of the water actually determines the tuna's occurrence. For instance, Laurs & Lynn (1977) considered that temperature and food conditions in the Transition Zone actually determine the uneven occurrence of the albacore.

FOOD AND FOOD CHAINS

Thus far, we have identified properties that limit the total range of tunas, by area (temperature and possibly transparency) and depth (temperature and oxygen). These properties do not account for differences in abundance of adults within the ranges. It seems likely that some major differences of that kind are due to tuna travelling in particular current systems, but even those systems are very large and tuna do not occur uniformly within them. It has often been suggested that tuna tend to be most abundant where their food is concentrated, within areas of suitable temperature. Blackburn (1965, 1969b) strongly supported this view.

The food of tunas in nature has been much studied from stomach contents, with very consistent results. It consists in general of active pelagic animals measuring from about 1 to 10 cm: fishes, molluscs, and crustaceans. Micronekton is a convenient term for this group, although some of the organisms, such as euphausiids, are generally considered as plankton. Much of the literature on tuna food up to 1963 was cited by Blackburn (1965). Important later papers include Williams (1966), Dragovich (1969), Dragovich and Potthoff (1972), and Legand *et al.* (1972). The first of these deals with Indian Ocean yellowfin and the next two deal with Atlantic tunas.

The tunas do not, however, eat all kinds of micronekton that are within their ranges. Two major groups by biomass that are little consumed are the mesopelagic fishes which migrate from deeper waters towards the surface at night, especially Myctophidae and Gonostomatidae, and euphausiids. An exception to the first is the gonostomatid genus *Vinciguerria*, which is eaten significantly (Alverson, 1963; Legand *et al.*, 1972). Probably the tunas cannot see prey well at night. *Vinciguerria* moves upwards at night, but lives within the vertical range of tunas in the daytime (Legand *et al.*). Another exception is the significant eating of certain euphausiids by skipjack in some

areas, such as off Ecuador (Alverson, 1963) and Tasmania (Blackburn &
Serventy, in press). Skipjack may be better than other tunas at sensing,
catching, and retaining euphausiids. The mean gillraker gap is smaller in
skipjack than in several other species (Magnuson & Heitz, 1971). Cushing
(1976) cited myctophids → tuna and euphausiids → tuna as steps in food
chains in the tropical and subtropical ocean, and gave no other examples
at those trophic levels. These statements describe exceptional rather than
typical cases and therefore, are misleading.

In general, then, tunas eat epipelagic fishes, molluscs, and crustaceans,
including the larvae of those groups. They are opportunistic feeders, swallow-
ing whatever moving small objects they can see (Blackburn, 1968). It is not
clear how they sense and take dead bait in longlining operations at depths
greater than 300 m, where very little light is available. Olfaction is possibly
involved in that case.

The distribution of micronekton has been little studied quantitatively in
the ocean. Estimates of standing stock can be obtained, with difficulty, from
catches made in various large nets in a few parts of the Pacific (King &
Iversen, 1962; Vinogradov, 1968; Blackburn, Laurs, Owen & Zeitzschel,
1970; Legand et al., 1972). With euphausiids included, values in the 0–200 m
layer are approximately 0·6–1·0, 0·3, and 0·6 g/m² in tropical, subtropical,
and subarctic waters, respectively (Blackburn, 1977). These estimates must
be too low, because it has been found repeatedly that nets do not capture
most epipelagic fishes and molluscs efficiently, except as larvae. King &
Iversen (1962), Blackburn (1968), and Legand et al. (1972) all noted that
those groups were much better represented in tuna stomachs than in net
catches—presumably because they can avoid nets. The nets appeared good
only for catching mesopelagic fishes, crustaceans, and larvae. We have no
reliable biomass estimates of the part of the micronekton not taken by the
nets. Thus the concentrations estimated from the nets include much that
tuna do not eat and omit much that they do eat. Laurs & Nishimoto (in
prep.) found a direct relationship between the displacement volume of food
in the stomachs of albacore and the biomass of micronektonic animals taken
with the Isaacs–Kidd Midwater Trawl in the same area, although the species
composition in the stomachs and net hauls were different.

It seems certain, however, that the general ocean-wide distribution of
micronekton is broadly similar to that of nutrients (Reid, 1962), phyto-
plankton (Koblentz-Mishke, Volkovinsky & Kabanova, 1970), and zoo-
plankton (Bogorov et al., 1968); that is, high in subpolar and upwelling
regions, moderate in other coastal and equatorial regions, and low in the
anticyclonic gyres. The agreement between these steps in the food chain
probably holds within these parts of the ocean as well as between them. In
the eastern tropical Pacific, standing stocks of net-caught micronekton and
zooplankton are positively correlated (in logarithms and with the micro-
nekton measured four months later; Blackburn, 1973). In the waters where
most tunas live, biological productivity ranges from moderate to low. Regions
of high productivity tend to be too cold for them, except in equatorial and
other tropical upwellings.

On the other hand, tunas are fairly heavy feeders. Captive skipjack fed to
satiation ate 15% of their body weight per 12 h day (Magnuson, 1969).
Feeding experiments with other fish species, mostly fed to excess, indicated

daily rations generally less than 10% of body weight, although up to 24%
was noted in the scombroid *Pneumatophorus japonicus* (Conover, 1978). A
similar tendency is evident from published estimates of rations, based on
bioenergetic demand. Sharp & Francis (1976) estimated the required daily
ration as 10% of body weight for yellowfin 45 cm long, declining gradually
to 3% for the same species at 140 cm. Other tunas under 40 cm can eat more
than 30% of body weight per day (Sharp, pers. comm.). By contrast, the
estimated daily rations for the pelagic fish community of a coastal upwelling
area, predominantly planktivorous carangids and clupeoids, ranged from
4-8% of the body weight (Mathisen, Thorne, Trumble & Blackburn, 1978).

Despite the high daily food requirements of tunas, the migratory life style
of these fishes is obviously very successful even in the open ocean where there
is a highly patchy distribution of forage at all trophic levels (Magnuson &
Heitz, 1971; Kitchell *et al.*, 1978). Magnuson & Heitz (1971) also commented
on the occurrence in a given habitat of a resident population(s) present
throughout the year, and a seasonal influx of other individuals and species.
The resident population is supported by the lowest expected level of produc-
tivity, whereas the seasonal influx is synchronous with seasonal productivity
resulting from variable oceanographic phenomena such as upwelling.
Sharp & Francis (1976) and Kitchell *et al.* (1978) have emphasized this
'bottleneck' of lowest expected productivity and how it may affect, in par-
ticular, the early stages of tunas. The pre-spawners of many tunas are highly
migratory and hence oceanographic events can have major effects on stocks,
such as growth rates. Dotson (1978), in his work on north Pacific albacore,
has shown the fluctuations of fat content in tunas and how, they are
associated with different behavioural patterns or stages in the life history.
Kitchell *et al.* (1978) were unsure that the attainment of the "maximum daily
ration" in tunas is quite so spectacular as implied by their habitation of one
of the most unproductive environments—the epipelagic zone of the tropical
seas, given the broad feeding habits of tunas, the amount of food which
they can take in a given period, and the inaccuracy of estimates of potential
forage based on trophic relationships.

It seems likely, therefore, that movements into relatively productive areas
may have survival value for tunas, and that they probably aggregate at any
rich patches of food that they find in waters of suitable temperature. The
next two sections of our review give some support for these ideas, based upon
observations in the field. To make a more definite statement about tunas'
food requirements in relation to the food available in a given area, the
following kinds of information would be needed: (i) biomass of tunas;
(ii) biomass of all other animals, such as certain billfishes and porpoises, that
eat the same kinds of food as tunas; (iii) amount of food required per day by
all those animals; and (iv) daily production of the food organisms. None of
this information exists at present. Sharp & Francis (1976) attempted to
solve the problem in the eastern tropical Pacific. They estimated (i) and
thence (iii) for yellowfin only, ignoring all other tunas, billfishes, *etc.* Item
(iv) was not specifically estimated, but the authors considered it was higher
than their (iii). It is not quite clear how they reached that conclusion, but it
was apparently based upon the biomass of net-caught micronekton and
some unspecified estimate of its turnover rate. Such biomass measurements
are unreliable as measures of tuna forage, for reasons already stated. This

work is, therefore, unconvincing. By contrast, in the above-mentioned study of a fish community made by Mathisen *et al.* (1978), it was found possible to measure the total fish biomass (equivalent to (i) plus (ii)) acoustically, thence estimate (iii), and to estimate (iv) from the measured biomass of zooplankton together with production/biomass ratios taken from literature. In that case (iv) exceeded (iii), as might be expected in a coastal upwelling area, but one could not assume that result for tuna habitats in general. Similar studies on tunas should be continued as adequate measurements or estimates become available for the biomass of the tunas, their competitors, and their prey.

UPWELLING AND VERTICAL MIXING

Physical processes that may enrich near-surface waters with nutrients are considered here. They include wind-induced upwelling (coastal and equatorial), geostrophic upwelling, and vertical mixing by wind. The enrichments will lead to the appearance of higher than average standing stocks of micronekton, either at or downstream from the upwelling or mixing site. Tuna are expected to be plentiful in those areas because of the micronekton, unless the waters are too cold or turbid.

In a non-tropical upwelling situation the rich forage (food supply) should
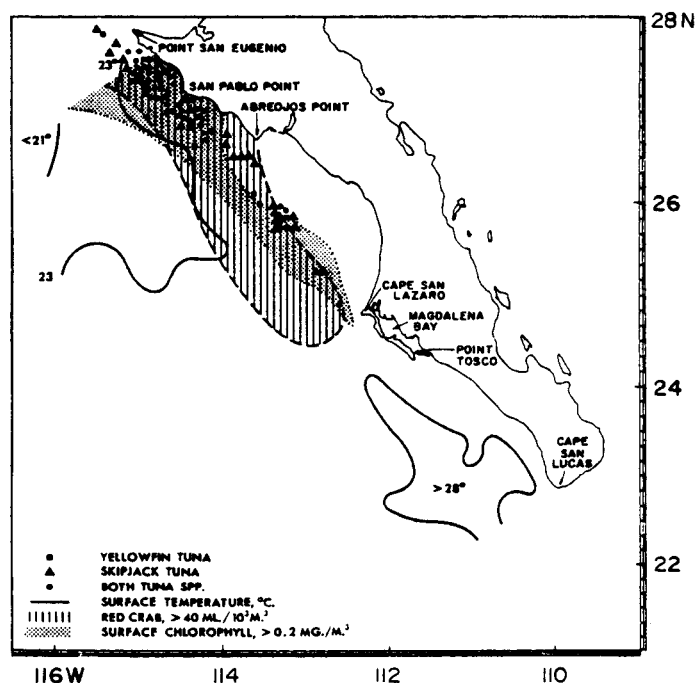

Fig. 17.—Distributions of surface temperature, surface chlorophyll *a*, and red crabs in September, 1965 and locations of contemporaneous tuna catches; from Blackburn, 1969.

attract tunas, but the low temperatures may exclude them from it. This was shown well in studies made at different stages of the coastal upwelling off western Baja California (Blackburn, 1969a). Advantage was taken of the fact that yellowfin and skipjack in that area eat predominantly one species, the red crab, *Pleuroncodes planipes*, which can be sampled quantitatively with micronekton nets. The crab, a herbivore, is most abundant in the upwelling areas where the highest phytoplankton stocks occur. When the upwelling is strong, surface temperatures in those areas are below 20 °C and the tunas can, at best, reach only the fringes of the high crab concentrations. The fish aggregate at these fringes, obtaining some food at temperatures they can tolerate. As the upwelling regime decays, the food-rich areas become warm enough for the tunas to penetrate them. The distributions of tuna, crab, and phytoplankton then tend to become congruent in the former upwelling areas (Fig. 17, from Blackburn, 1969a). Finally, the same three distributions become uniform over most of the area west of southern Baja California, until the normal seasonal cooling drives the tunas southwards.

Similarly, albacore in the northeast Pacific approach the edges of coastal upwelling areas, presumably to feed, but they avoid the upwelled water where it is colder than 15 °C (Laurs *et al.*, 1977). Farther offshore, they are confronted with the same problem of forage-rich waters tending to be too cold. They apparently avoid Subarctic water, where food is plentiful (from vertical mixing) but temperature is too low, and also Central water, where food is scarce and temperature varies from too high to suitable. The Transition Zone between the two types of water contains food at an intermediate level of abundance, and has suitable temperatures in the albacore season, and it is there that most albacore are found (Laurs & Lynn, 1977; Fig. 18).
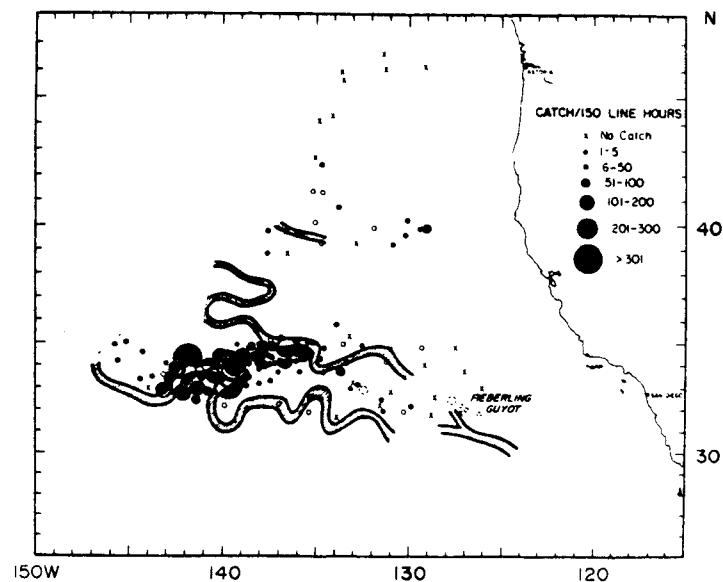

Fig. 18.—Albacore catch per 150 line-hours by charter fishing vessels and locations of fronts delineating the Transition Zone waters during June, 1973; from Laurs & Lynn, 1977.

In tropical upwellings, temperatures at the surface are usually suitable for tunas. Blackburn (1962, 1963) described the upwelling situation (although he did not call it that) in the Gulf of Tehuantepec. Yellowfin abundance increased three months after the upwelling, the lag being attributed to the production of an increased biomass of micronekton. Forsbergh (1969) investigated the upwelling in the Gulf of Panama and the apparent relation of yellowfin and skipjack to it. He considered the conditions to be practically the same as in the Gulf of Tehuantepec.

The distribution of subsurface yellowfin in relation to the equatorial upwelling in the Pacific has been discussed by several authors including Sette (1955), and reviewed again by Murphy & Shomura (1972). The fish are more abundant between 1° and 6° N than at the Equator where the upwelling is centred. The explanation given is that the major drift of newly upwelled water is towards the northwest. Organisms develop in this water, those at successively higher trophic levels reaching their biomass maxima at successively longer intervals of time. The biomass maximum of the micronekton tuna should be, therefore, a few degrees north of the Equator, with tuna aggregated on the forage. This expected forage maximum was found (King, 1958; King & Iversen, 1962).

Blackburn & Laurs (1972) suggested that skipjack might also be related to the equatorial upwelling through their food. These authors charted the distribution of total biomass of all skipjack prey organisms, which were sorted from micronekton net catches made on several cruises in the offshore waters of the eastern tropical Pacific. Three zonal maxima were noted, the one just north of the Equator already mentioned, another just south of the Equator, and a third in the latitudes of the North Equatorial Countercurrent. The first maximum was much better defined than the others. The second was assumed to be formed in the same way as the first but under conditions of southwesterly drift. The third was thought to result from vertical mixing over a ridge in the thermocline along the north edge of the Countercurrent. Two cruises were made to test the hypothesis that skipjack would be most abundant in those areas (Blackburn & Williams, 1975). On the cruise both skipjack and its forage were most abundant just north of the Equator and no other zonal maximum of either was seen. On the other cruise skipjack were more abundant north of the Countercurrent than near the Equator, but the forage distribution was the reverse.

FRONTS

Fronts are boundaries between waters of different densities, recognizable by strong gradients of temperature and/or salinity. Fronts at the sea surface may also at times be recognized by differences in colour or turbulence between the waters and by lines of flotsam. They have important effects on tuna distribution. A knowledge of fronts is valuable to fishermen in the surface tuna fisheries, probably more so than any other kind of oceanographic information except surface temperature. Some fronts, really frontal systems, are a few hundred kilometres wide. Examples are the Transition Zone in the northeast Pacific, previously discussed in relation to albacore, and the corresponding zone between the Kuroshio and Oyashio Currents in the northwest Pacific, which is also an important area for tunas (Uda & Ishino, 1958).

Other fronts vary in width from a few tens of kilometres to tens of metres. The smaller they are, the less permanent and more variable in position they tend to be.

When a temperature front contains the isotherm that limits a tuna's range, the front constitutes a simple barrier. This occurs at times in the Cape San Lucas front off Baja California (Blackburn, 1969a) and in 'upwelling fronts' along the offshore boundary of coastal upwelled water (Laurs *et al.*, 1977). On the other hand, it is common to find tuna aggregated at a front, under conditions in which the range of temperatures in the general area is suitable (*e.g.*, Williams, 1977). The question in that case is, what causes the tuna to be abundant at the front? Investigators believe food is responsible, being more abundant at the front than elsewhere. Dufour & Stretta (1973) pointed out that this could occur in three ways: mechanical accumulation of plankton because of convergence at the front, higher biological production because of divergence near the front, and higher production because of the mixing of waters with complementary characteristics.

Few attempts have been made to demonstrate the expected high abundance of tuna prey in fronts. The best instances known to us concern the Cape San Lucas front in the eastern Pacific (Griffiths, 1965; Blackburn, 1969a) and the Cape Lopez front in the eastern Atlantic (Dufour & Stretta, 1973). Each front is on the order of tens of kilometres wide. Chlorophyll *a*, zooplankton, and micronekton (taken in nets) were sampled during synoptic crossings of each front: on the warm side, on the cool side and in the middle. At the Cape San Lucas front chlorophyll and some kinds of zooplankton were most abundant as biomass in the middle of the front. Micronekton biomass was highest on the warm side, except at a part of the front where the cool side was upwelled and had the most micronekton. Yellowfin tuna, when present near the front at the times of these observations, were on the warm side; temperatures in the front and on the cool side were too low for them. At the Cape Lopez front, chlorophyll showed a gradual decline across the front region from the cool to the warm side. Zooplankton (by numbers, mostly copepods) were most abundant in the middle. Micronekton were most abundant by numbers in the middle, but by biomass they were slightly more abundant on the cool side than in the middle. Yellowfin and skipjack were most abundant in the front, although temperatures on both sides of it were also suitable.

The above-mentioned differences in chlorophyll, zooplankton, and micronekton across each front were not large, seldom more than half or double, and could therefore be questioned. More observations are desirable. It appears significant to us that zooplankton, the animals most likely to be mechanically accumulated, were most abundant in the middle of each front. Micronekton, being stronger swimmers, are less likely to be concentrated in the same way. They could be attracted to the front by the zooplankton, but perhaps not all of them at the same time. It must also be remembered that micronekton nets are poor samplers of tuna forage. The data available do not show beyond doubt that tuna forage is more abundant in fronts than in adjacent waters, although Dufour & Stretta's (1973) observations give indications that it is.

Laurs *et al.* (1977) described movements of three albacore which were tagged and tracked with ultrasonic equipment. It appeared that the fish

remained close to 'upwelling fronts' when they existed, but moved away from the area where the front was located when upwelling ceased and the front was no longer apparent at the surface. The fish avoided temperatures of less than 15 °C. There was an interesting indication that the fish tended to move slowly when crossing fronts. A deliberate response of that kind to the temperature gradient is possible, because tunas can perceive changes as small as 0·1 °C (Steffel, Dizon, Magnuson & Neill, 1976). The response also could have been to food organisms, if any were present.

ISLANDS AND BANKS

Surface-swimming tunas are often more abundant around these features than elsewhere in the same part of the ocean. It has generally been assumed that more food is available on or around the banks and islands, or in associated fronts and eddies. Some attempts have been made to demonstrate such distributions of food, with mixed results. Blackburn (1965) briefly reviewed some of the literature. Although the food hypothesis is reasonable, it may not explain all cases. In the central tropical Pacific the association between tuna and islands is much more obvious for yellowfin than for skipjack (Murphy & Ikehara, 1955; Murphy & Shomura, 1972). The occurrence of skipjack at the Hawaiian Islands can be explained partly by their arrival in a current, as mentioned earlier. Japanese tuna fishermen note that fishing grounds form on the upstream side of banks and sea mounts (I. Yamanaka, pers. comm.). Tuna fishing off Baja California is often particularly successful at banks, but Blackburn (1969a) showed that some of these instances could be explained by food-rich upwelled water (when not too cold) enveloping the banks. It is also possible that islands and banks are attractive to tunas as points of orientation.

PORPOISES

In the offshore waters of the eastern tropical Pacific surface fishery, co-occurrence of porpoise and tuna is considered vital to fishing success. Purse-seine fishermen use the sighting of birds as an indication of the presence of tuna. At times porpoise are also present, and if so they are surrounded and both the porpoise and tunas are captured. The porpoise then are liberated and the tunas brought aboard the boat. There are instances that porpoise are observed without the presence of birds, and they are also checked for the presence of tunas, and the operation is similar if fish are present.

Two species of porpoise, *Stenella attenuata* and *S. longirostris*, are especially important in the tuna fishery. The cause of the tuna–porpoise association and why the association appears to vary in strength between species and years is unknown. Yellowfin and *S. attenuata* eat many of the same kinds of food and may feed together, but the diet and feeding habits of *S. longirostris* are different (Perrin, Warner, Fiscus & Holts, 1973). The area of the porpoise–tuna association in the eastern tropical Pacific is essentially coincident with that of the yellowfin surface fishery. Many of the environmental features that appear important to yellowfin appear similarly important to these porpoise. The habitat of the porpoise extends beyond the area of the surface fishery, but the porpoise–tuna association is primarily in the latter area where

environmental features such as temperature and oxygen may result in feeding interactions near the surface between porpoise, yellowfin, and birds (Au, Perryman & Perrin, 1979).

PREDATORS

Apart from man, the only known predators of large adult tunas in nature are billfishes, especially blue marlin (*Makaira mazara*) and black marlin (*M. indica*) (Royce, 1957). Sharks and killer whales (*Orcinus orca*) eat tunas that have been caught or injured in fishing operations. Tuna larvae and juveniles are eaten by billfishes, adult tunas, and probably many other animals. Skipjack larvae and young juveniles are a significant part of the diet of adult skipjack in some regions (E. L. Nakamura, 1965; Kearney, 1978).

ENVIRONMENTAL REQUIREMENTS OF TUNA LARVAE AND JUVENILES

It was shown previously that the patchy distribution of adult tunas within a suitable habitat is probably related very largely to forage, whose distribution can be explained in relation to physical features such as upwellings and fronts. Another possible determinant of adult tuna distribution, during spawning seasons, is the needs of their larvae.

Very little information exists on larval requirements. As mentioned earlier (see pp. 465–472) the spawning areas of most investigated tunas are in near-surface tropical waters, and tuna larvae are most abundant at the high end of the species' temperature ranges. The warm waters appear most suitable for larvae, but must often be relatively poor in food for adults. Adults will not always be found in the most forage-rich areas. They must sometimes leave them in order to reproduce effectively. In the case of southern bluefin, the tropical spawning area is far removed from the high-latitude waters which seem to constitute the principal habitat of the adults.

With skipjack and albacore the areas of highest larval abundance are only in certain areas of the tropical Pacific, for instance, not in the eastern Pacific for skipjack (although temperatures suitable for larvae are available) and not in equatorial waters for albacore. These areas with few or no larvae are physically unsuitable for the parent fish (large adults of skipjack, all adults of albacore) as shown earlier.

No investigator has yet successfully described the vertical distribution of young stages of tunas. These distributions are probably not uniform, and as has recently been learned for coastal pelagic fishes (Lasker, 1978), the survival of larvae and juveniles is largely dependent on their distribution being coincident with that of patches of their food. Seckel (1969) showed the presence of a layer of high oxygen concentrations, which is probably of biological importance, at depths of around 50 to 100 m in the North Pacific. This layer is in the upper thermocline, and is likely to be formed as a consequence of high productivity. High zooplankton and micronekton concentrations would also be expected in nearby layers, but would not be detected by the usual sampling method of obliquely hauled nets. In fact, detection of layers or patches of concentrated plankton has been, and is, a persistent problem in marine biological investigations.

It is a characteristic of tunas of many species that up to 40–70 cm in length they school together in surface waters. At this size range the juveniles attain the morphological and physiological adaptations which result in ecological stratification and the constituent species of the mixed schools rapidly disperse to their respective adult strata. There is little information on the location of juvenile tunas, especially those less than 40 cm. The problems of field sampling to define their distribution become obvious when one considers that a 50 cm specimen of even the slowest swimming tuna must travel the equivalent of 27 km per day for hydrodynamic equilibrium, and a skipjack about 60 km per day. Migratory behaviour of pre-spawners in general, and their occurrence in areas of high productivity and high vulnerability, indicates an ability to sense and perhaps 'climb' environmental gradients (Neill et al., 1976) and food gradients (Williams, 1972). Such behaviour may prove useful in future attempts to define their distributions in more detail than is at present possible.

AGGREGATION OF TUNA AROUND FLOATING OBJECTS

Tuna fishing in the immediate vicinity of anchored or free-floating objects has gone on for many years. Occasionally, large catches have been made in the proximity of floating objects using surface gear. Bamboo rafts are used in Japanese waters, vertical arrays of palm fronds are set out in the Philippines and Indonesia, and cork slabs are used in the Mediterranean Sea. Japanese fishing vessels are at times reported to transport floating materials to the fishing grounds of the western tropical Pacific and to set them adrift there for the purpose of attracting tunas for capture. The new purse-seiners from Japan set their nets around floating logs or other objects whenever such are available in the western Pacific. Experiments were conducted during 1972 and 1974 in Papua–New Guinea waters on the attraction of artificial floating objects to skipjack (Yamanaka, Yukinawa & Morita, 1977). Floating objects encountered by the surface tuna fleet in the eastern Pacific have long been routinely investigated for the presence of fish (Greenblatt, 1979). In the past few years, the National Marine Fisheries Service Honolulu Laboratory has conducted experiments in Hawaiian waters on the attraction of anchored floating 'buoys' to tunas.

Reports have been published on the sequential occurrence of fishes of numerous kinds and their behaviour under floating, drifting rafts and objects (e.g., Kojima, 1956; Hunter & Mitchell, 1967, 1968; Wolf, 1974). Attempts to observe and explain events related to tuna behaviour and to the attractiveness of various floating object configurations have been made and reported on by Gooding & Magnuson (1967), Hunter & Mitchell (1967, 1968), and Inoue, Amano, Iwasaki & Yamauti (1968). Hypotheses advanced to explain the accumulation of fishes around inanimate floating objects include the following: (1) fish seek shelter from predators; (2) larger fish gather to prey upon concentrations of smaller fish; (3) fish feed on algae and decaying material from the 'raft'; (4) fish seek shade under the object; (5) fish use floating objects as a substratum on which to lay their eggs; (6) the shadow of the objects makes zooplankton (forage) more visible to fish; and (7) floating objects are cleaning stations.

Gooding & Magnuson (1967) considered these hypotheses and concluded

that no single one could explain the occurrence of fishes around floating objects at sea. They thought that the shelter hypothesis (1) was the best substantiated of those listed. Obviously, some of them cannot pertain to tunas (*e.g.*, 3, 5, and perhaps 7). Wolf (1974) observed that the "attraction of fish appears to be due to random encounter with the drifting object and while chances of such encounters may be slightly increased by an increase in the size of the surrounding fish aggregation, the removal of some fish does not seem to affect the overall attractiveness of the object". Hunter & Mitchell (1967) also remarked on the mechanism of encounter, stating that most naturally occurring objects did have fish around them and were located in areas of current convergence. These two latter observations bring to mind important questions which remain unanswered with respect to tunas and free-floating objects: (1) whether the objects and the tunas move together with the currents and accumulate (passively) in areas such as convergences (Seckel, 1972; Williams, 1972), or (2) whether the tunas seek and encounter the objects and thus accumulate (actively) in their proximity? The latter possibility would apply to anchored objects as well (Klima & Wickham, 1971). Further testing of the hypotheses seems feasible in the near future through application of available technology involving radio and satellite tracking of fish and drifting objects.

RECENT ADVANCES IN PRACTICAL APPLICATION OF TUNA OCEANOGRAPHY TO FISHING AND IN THE USE OF REMOTE SENSING FOR COLLECTION OF THE NEEDED OCEANOGRAPHIC DATA BASE

Scientific and technological observations on the environment and the behaviour of tuna (or other fishes) and hypotheses on their interdependence are of direct value to fishermen, but are rarely available to them. Such information is worked-up by fisheries environmental services into various more suitable formats for transmission to the fishing fleets (and industry generally, *e.g.*, processors) so as to assist in the development and optimal utilization of their resources. The data base for such advisory services is increasingly being supplemented by oceanographic information derived from remote sensing techniques (using aircraft or satellites as observation platforms). To date, most services have exclusively attempted to relate fish distribution and water temperature (Tomczak, 1977); given the importance of water temperature to tunas, it is not surprising that many of the fishery environmental services have been developed for tuna fisheries. The fisheries environmental services usually are of two kinds (Tomczak, 1977): (a) analyses and short-term forcasts for tactical use by fishing fleets, and (b) medium to long-term forecasts for strategic use.

There are at least six fisheries environmental services dedicated (or partly so) to supporting tuna fisheries and most are concerned with short-term tactical forecasts. Two services are operated for the eastern Pacific Ocean by the National Marine Fisheries Service, La Jolla, California. These are as follows.

(1) In the surface purse-seine fishery for yellowfin and skipjack many tactical fishing decisions are made, based in part, on daily charts of weather

and sea state and weekly charts of sea surface temperature and mixed layer depths transmitted by radio facsimile (see Evans, 1977, for details). The information is from analyses based on mixed source data bases, including remote sensing (meteorological satellites), and marine weather and temperature at depth (from expendable bathythermographs) direct from the fishing fleets.

(2) Similarly, in the northeast Pacific albacore fishery, daily and biweekly advisory forecasts are made to the boats with information on fishing activity and location, surface and subsurface temperatures, marine weather, *etc.*, which can be used for tactical advantage. In addition, a pre-season forecast is made of the expected geographic distribution of the albacore along the coast from Mexico to Canada (Laurs, 1977) and this has proved of strategic value in the choice of location of the vessels prior to the opening of the season.

Brief details of the other four services are given after Tomczak (1977).

(3) For the Australian seasonal coastal fishery for southern bluefin, the product is a chart of schools of fish sighted and sea surface isotherms based on airborne radiometry from spotter aircraft.

(4) In the French northeast Atlantic albacore fishery, information on temperature, mainly from research and fishing vessels and aircraft, is used to produce charts of sea surface temperature. Predictions of sea state and weather from meteorological satellites, are also transmitted to the fishing fleet.

(5) In the Gulf of Guinea, airborne radiometry has been used on a limited time and space scale to assist in the forecasting of suitable fishing zones for surface yellowfin and skipjack.

(6) The Japanese Fisheries Environmental Information Services Center is well established and for some time has been providing a large variety of information in many formats to all segments of the Japanese fishing industry, both ashore and afloat. Support is provided for the seasonal coastal fisheries for albacore, skipjack, and bluefin through forecasts of temperature conditions, currents, marine weather, and also at the strategic level through advance predictions of long-term trends of abundance in certain pelagic fisheries such as skipjack.

The use of remote sensing techniques from aircraft in support of fisheries research was discussed in some detail by Stevenson & Pastula (1971) and Joseph & Stevenson (1974). In tuna fisheries the value lies in the use of airborne radiometry from spotter aircraft for detection of surface temperature fields, visual observations of current–water mass boundaries indicated by colour, slicks, weed lines, *etc.*, as well as the sighting of tuna schools. Obviously these techniques are mainly limited to fisheries within range of land-based aircraft, *e.g.* coastal Australian southern bluefin fisheries. The authors listed above also speculated on the use of remote sensing of the ocean from spacecraft in support of fisheries and this subject was reviewed (for the entire marine science field) by Szekielda (1976). In particular, Joseph & Stevenson (1974) stressed the importance, especially for tuna, of information on sea surface temperature, water masses, currents, surface fronts, thermocline depth, and gradients. Such information concerning the thermocline can be derived from models involving sea surface temperature, wind intensity, direction and duration, and cloud cover.

Data derived from satellites dedicated to meteorology and oceanography,

e.g., United States GOES, NIMBUS, NOAA, TIROS series and European METEOSAT already are being used by the National Environmental Satellite Service, Office of Sea Grant, National Weather Service, and National Marine Fisheries Service on a routine basis in formulation of products for fisheries environmental services as well as in support of fisheries research projects. The future will certainly bring about an increasing use of available equipment and techniques to allow full use of infra-red, visible, and multispectral data to provide temperature and other oceanographic information mentioned in the preceding paragraph. Many problems relate to the processing of the remote sensing data from the various satellite sources (*e.g.*, uncertainties of radiation temperatures in the tropics; Barnett, 1977), acquisition of ground (sea) truth data, the subsequent integration with concurrently available data on the tuna fishery in question, and in some cases the method of transmission to the users (fishermen). In addition, especially in coastal upwelling zones, there may be problems because of persistent cloud cover and the transient nature of the oceanographic features. An understanding of the formation, movements, gradients, and persistence of fronts in relation to tuna distribution and abundance will probably be of the most immediate value to the tuna fishing industry. This probably means application at the scale of 1–100 km, and possibly up to the mesoscale of 100–1000 km. Of course, the real problem remains: that of finding a linkage mechanism between tuna and the environment. Remote sensing will probably serve in a supplementary manner in fishing industry operations; it has yet to be proved of value in management.

CONCLUDING REMARKS

It has been our purpose to review critically information on the apparent relationships between the tunas and their environment. What becomes evident from our review is essentially a detailed 'habitat description'. The next critical accomplishment by tuna researchers must be the gaining of an understanding of the dynamics of the tuna populations—their reproduction, rates of growth, migrations and concentrations, all of which are influenced by the dynamic and varying properties of the habitat. For instance, virtually nothing is known about how spawning success and subsequent year-class strength are affected by environmental factors. Such information should be included in the population dynamics models by which management is attempted. Nelson, Ingham & Schaaf (1977) indicated the importance of this in the case of the Atlantic menhaden (*Brevoortia tyrannus*). They were able to show that 84% of the variation from the Ricker spawner-recruit curve for the species was due to zonal Ekman transport, the mechanism by which larvae are transported from offshore spawning grounds to inshore nursery grounds. For the Pacific mackerel (*Scomber japonicus*) in the California Current, Parrish & MacCall (1978) dramatically demonstrated, through increased understanding of variations in recruitment, the informative and explicit value of including environmental factors in stock management models.

An understanding of the causal relations between environmental forcing processes and biological responses is important in designing an investigation

of the effects of environment upon a species or stock. For example, Laurs *et al.* (1977) showed that the apparent relationship of North Pacific albacore to coastal upwelling fronts is, in fact, a response of the fish to the distribution of their forage, and not the thermal gradient itself. The forage, in turn, is responding to changes in plankton abundance associated with the front and not to the physical field. It may, however, be operationally easier to relate temperature and albacore than forage and albacore, in terms of management strategy, forecasting, or fishing operational considerations.

We expect that more work will be done, that our understanding will improve, and that managers of the fisheries resources and directors of fisheries research will increasingly recognize the rôle of the environment in the ecology of the fish and in the operation and management of the fisheries, and thus will be able to act with wisdom on behalf of both man and resource. It would be prudent now to test a number of the hypotheses that have been set forth. Some suggested areas of future investigation are enumerated briefly here.

(1) Many hypotheses about the effects of environmental variables in determining tuna occurrence have been put forward, but few have been adequately tested in the field. For instance, it has been argued that certain areas and water layers are suitable habitats for skipjack of only certain sizes because of temperatures and oxygen concentrations, but no adequate attempts to verify this proposition have been made. Also, the assumed relations between aggregations of tunas and their prey have not been verified sufficiently in the ocean. Such hypotheses should be tested in selected oceanic areas at appropriate periods. We recognize that field work in oceanic waters is expensive, but nevertheless, more of such work is needed. Furthermore, one should not overlook the fact that recent advances with multi-spectral visible and infrared sensors, and concomitant processing techniques give us the opportunity to use satellite remote sensing for comprehensive and synoptic monitoring of surface features and events over large ocean areas.

(2) The biological processes which have the greatest potential for elucidating cause and effect relationships with climatic factors are: (a) survival and growth of larval stages, and (b) predation. The breeding pattern for most species of tuna, and especially the more tropical ones, is to spawn large numbers of eggs throughout much of the year over large oceanic areas. By this tactic, adverse environmental conditions encountered by larvae and juveniles appear to be minimized and chances for survival enhanced. The larval period is short and growth is rapid, which further reduces adversity from environmental conditions, cannibalism, and predation. Thus, the Cushing & Dickson (1976) match–mismatch theory of spawning and environmental events should not become a major factor for survival. In the case of bluefin and southern bluefin tunas with relatively discrete spawning areas and short spawning seasons (see pp. 469–470) following long migrations, the match–mismatch theory may be more relevant. The early stages in the life history of tunas (larvae to juveniles) still probably are the most important with regard to the influence of environmental factors on survival and recruitment to fishable stocks. It is these early stages about which little is known concerning their distribution and abundance, physiology, behaviour, and general ecology. The requirements of young tunas also may determine

some features of the distribution of adult tunas. Studies should be intensified to fill this gap in our information even although development of new techniques and gear may be required.

(3) Indices of environmental phenomena that appear causally related to tunas should be specified and methods of measuring some of them (*e.g.* their food supply) should be improved. These should then be used to improve the basic data collected for scientific and management objectives. When a relationship is finally established between a tuna's distribution or behaviour and some aspect of its environment, useful short-term information for the fishery can be provided by monitoring those aspects, as is the case now with the environmental services mentioned earlier (pp. 500–503). Long-term forecasting, on the order of six months or more, would have greater value. This will not be possible, however, until much more is known of the processes and rates by which the important environmental features develop. Satellite remote sensing of oceanic conditions may prove to be valuable in this regard.

It behoves those interested in tuna forecasting to make their special interests better known to others in the oceanographic community, and to co-operate with them in the necessary work. It should not be overlooked that some marine scientists who were not formerly interested in fish populations are now becoming so, recognizing the rôle of those populations in ecosystem structure.

(4) Changes over time in size, integrity, and gene pool composition of tuna schools should be observed to learn the make-up of the basic school unit, how and under what circumstances the school grows and the dynamics of that growth, and how the school's composition (inter- and intraspecific) changes over time. Observations should also be made of any alteration of behaviour of the individuals in the school as the school size and structure change. In this respect, the theoretical study of Clark & Mangel (1979) on aggregation and fishery dynamics using schooling and the purse-seine tuna fisheries is of interest because of the implications for fisheries management.

(5) The hypotheses on migration and movement by 'active' and 'passive' means (Seckel, 1972; Williams, 1972) should be tested while being aware of the possibility that the two modes may each play a rôle to varying degrees, depending on the stage in the life history of the fish.

(6) Tunas should be tracked with acoustic tags to record their small-scale behaviour of movement. General patterns, if any, should be specified and attempts made to explain them in terms of contemporaneous environmental observations.

(7) Investigations of the methodology of defining tuna stocks, and of measuring changes in their condition over time should be continued.

(8) Additional information of many kinds is needed on many of the tuna species. For example, relatively little is known about the biology of bigeye tuna, even though it is a major, highly desired resource. In addition, some advances in fishing technology may be needed to exploit the relatively deep-dwelling adults of this species more effectively.

This general lack of knowledge is certainly true of many of the species at present of minor market value; *e.g. Auxis, Euthynnus, Sarda, Allothunnus,* *etc.* The frigate or bullet tunas of the genus *Auxis* are a worldwide under-utilized resource with a potential production of greater than one million metric tons (Gulland, 1971). Our overall knowledge of the biology of frigate

tunas and relationships to their habitat is, however, still very weak (Uchida, in press) and their importance as major components of the food chain of apex predators such as other tunas, billfishes, and sharks is virtually unknown. In addition, the market demand, in terms of the global tuna industry, for this small, dark-meat tuna apparently is not large. This may not be the case, however, in the lesser developed nations of the world desirous mainly of increasing total available fish catch.

(9) Porpoise–tuna interactions should be observed under various environmental and behavioural conditions in order to develop explanations of why the porpoise–tuna association varies in strength between species and between years. Environmental conditions extant in these various circumstances should be monitored for possible influences of the environment on the association.

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REFERENCES

Alverson, F. G., 1963. *Bull. inter-Am. Trop. Tuna Commn*, **7**, 295–396.

Alverson, F. G. & Peterson, C. L., 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 482–514.

Anonymous, 1962. *Mar. Biol. Ass. India*, Mandapam Camp, 1–4.

Anonymous, 1965. *Comm. Fish. Rev.*, **27** (12), 29–30.

Anonymous, 1972. *Far Seas Fish. Res. Lab.*, S Series 6, 1–83.

Anonymous, 1973. *Far Seas Fish. Res. Lab.*, S Series 8, 165 pp.

Anonymous, 1977. Rep. Sec. No. Pac. albacore workshop, Shimizu, Japan, 17–18th May, 1977. *Far Seas Fish. Res. Lab.* (Shimizu), 19 pp.

Anonymous, 1978. Director's Rep. 30th Tuna Conf. *NOAA, Nat. Mar. Fish. Serv. Southwest Fish Cent. Admin. Rep.* LJ-79-12 (*mimeo*), 39 pp.

Anonymous, 1979a. *U.S. Tuna Foundation*, San Diego, 39 pp.

Anonymous, 1979b. Bluefin tuna spawn in captivity—world's first record of artificial fertilization and hatching of bluefin tuna. *Sōgō* (Japan), 27th June, 1979. (Translation no. 37 [2 p] by Tamio Otsu, NOAA-NMFS Honolulu Laboratory, Honolulu, Hawaii 96812, July, 1979.)

Au, D. W. K., Perryman, W. L. & Perrin, W. F., 1979. NOAA, *Nat. Mar. Fish. Serv., Southwest Fish Cent. Admin. Rep. LJ-79-43,* 59 pp.

Barkley, R. A., 1968. *Oceanographic Atlas of the Pacific Ocean. University of Hawaii Press,* Honolulu, 172 pp.

Barkley, R. A., 1969. In, *Perspectives in Fisheries Oceanography, Jap. Soc. Fish. Oceanogr.,* Tokyo, 243–248.

Barkley, R. A., Neill, W. H. & Gooding, R. M., 1978. *Fishery Bull., NOAA,* 76, 653–662.

Barnett, T. P., 1977. *J. phys. Oceanogr.,* 7, 633–647.

Barrett, I. & Connor, A. R., 1962. *Bull. inter-Am. Trop. Tuna Commn,* 6, 233–280.

Barrett, I. & Kume, S., 1965. *Calif. Fish. Game,* 51, 252–258.

Bayliff, W. H., 1979. *Bull. inter-Am. Trop. Tuna Commn,* 17, 447–506.

Bayliff, W. H. & Calkins, T. P., 1979. *Inter-Am. Trop. Tuna Commn, Internal Report,* No. 12, 78 pp.

Bayliff, W. H. & Rothschild, B. J., 1974. *Bull. inter-Am. Trop. Tuna Commn,* 16, 1–64.

Bell, R. R. 1963. *F.A.O. Fish. Rep.,* No. 6, 2, 380–421.

Bini, G., 1952. *Boll. Pesca Piscic. Idrobiol.,* 7, 11–60.

Blackburn, M., 1962. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish.,* No. 404, 28 pp.

Blackburn, M., 1963. *F.A.O. Fish. Rep.,* No. 6, 3, 1557–1582.

Blackburn, M., 1965. *Oceanogr. Mar. Biol. Ann. Rev.,* 3, 299–322.

Blackburn, M., 1968. *Fishery Bull. Fish Wildl. Serv. U.S.,* 67, 71–115.

Blackburn, M., 1969a. *Fishery Bull. Fish Wildl. Serv. U.S.,* 68, 147–176.

Blackburn, M., 1969b. In, *Perspectives in Fisheries Oceanography, Jap. Soc. Fish. Oceanogr.,* Tokyo, 221–225.

Blackburn, M., 1973. *Limnol. Oceanogr.,* 18, 552–563.

Blackburn, M., 1977. In, *Oceanic Sound Scattering Prediction,* edited by N. R. Anderson and B. J. Zahuranec, Plenum Press, New York, 283–299.

Blackburn, M. & Associates, 1962. *Spec. Sci. Rep. U.S. Fish Wildl. Serv. Fish.,* No. 400, 48 pp.

Blackburn, M. & Laurs, R. M., 1972. *NOAA Tech. Rep. NMFS SSRF-649,* 16 pp.

Blackburn, M., Laurs, R. M., Owen, R. W. & Zeitzschel, B., 1970. *Mar. Biol.,* 7, 14–31.

Blackburn, M. & Serventy, D. L., in press. *Fishery Bull. NOAA.*

Blackburn, M. & Williams, F., 1975. *Fishery Bull. NOAA,* 73, 382–411.

Bogorov, V. G., Vinogradov, M. E., Voronina, N. M., Kanaeva, I. P. & Suetova, I. A., 1968. *Dokl. Akad. Nauk SSSR,* 182, 1205–1207.

Bone, Q., 1978. In, *The Physiological Ecology of Tunas,* edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 183–205.

Bour, W. & Galenon, P., 1979. *S. Pac. Comm., Occas, Pap.,* No. 12, 33 pp.

Brill, R. W., 1978. In, *The Physiological Ecology of Tunas,* edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 277–283.

Broadhead, G. C. & Barrett, I., 1964. *Bull. inter-Am. Trop. Tuna Commn,* 8, 419–473.

Calkins, T. P., 1975. *Bull. inter-Am. Trop. Tuna Commn,* 17, 3–116.

Carey, F. G. & Lawson, K. D., 1973. *Comp. Biochem. Physiol.,* 44A, 375–392.

Carey, F. G. & Teal, J. M., 1969. *Comp. Biochem. Physiol.,* 28, 205–213.

Chen, S. & Tan, T., 1973. *Rep. Inst. Fish. Biol. Min. Econ. Aff. Nat. Taiwan Univ.,* 36, 158–172.

Clark, C. W. & Mangel, M., 1979. *Fishery Bull. NOAA,* 77, 317–337.

Clemens, H. B., 1961. *Calif. Fish. Game, Fish. Bull.,* No. 115, 128 pp.

Clemens, H. B. & Craig, W. L., 1965. *Calif. Dept Fish Game, Fish. Bull.,* No. 128, 301 pp.

Clemens, H. B. & Flittner, G. A., 1969. *Calif. Fish Game,* 55, 132–135.

Collette, B. B. & Gibbs, Jr, R. H., 1963. *F.A.O. Fish. Rep.,* No. 6, 1, 23–32.

Conover, R. J., 1978. In, *Marine Ecology, Volume 4*, edited by O. Kinne, Wiley, Chichester, 221–499.

Craig, W. L. & Caneday, R. H., 1962. *Calif. Fish Game*, **48**, 172–198.

Craig, W. L. & Dean, E. K., 1968. *Undersea Technol.*, May 1968, p. 60 *et seq.*

Craig, W. L. & Graham, J. J., 1961. *Calif. Fish Game*, **47**, 73–85.

Cromwell, T., Montgomery, R. B. & Stroup, E. D., 1954. *Science*, **119**, 648–649.

Cushing, D. H., 1976. In, *The Ecology of the Seas*, edited by D. H. Cushing and J. J. Walsh, Blackwell Scientific Publications, Oxford, 317–340.

Cushing, D. H. & Dickson, R. R., 1976. *Adv. Mar. Biol.*, **14**, 1–122.

Dizon, A. E., 1977. *Fishery Bull. NOAA*, **75**, 649–653.

Dizon, A. E. & Brill, R. W., 1979. *Am. Zool.*, **19**, 249–265.

Dizon, A. E., Brill, R. W. & Yuen, H. S. H., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 233–259.

Dizon, A. E., Neill, W. H. & Magnuson, J. J., 1977. *Environ. Biol. Fishes*, **2**, 83–92.

Dizon, A. E. & Sharp, G. D., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 451–458.

Dizon, A. E., Stevens, E. D., Neill, W. H. & Magnuson, J. J., 1977. *Comp. Biochem. Physiol.*, **49A**, 291–299.

Donguy, J. R., Bour, W., Galenon, P. & Gueredrat, J. A., 1978. *Cah. O.R.S.T.O.M. sér Océanogr.*, **16**, 309–317.

Dotson, R. C., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 343–355.

Dragovich, A., 1969. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish.*, No. 593, 21 pp.

Dragovich, A. & Potthoff, T., 1972. *Fishery Bull. NOAA*, **70**, 1087–1110.

Dufour, P. & Stretta, J. M., 1973. *Doc. Sci., Cent. Rech. Océanogr., Abidjan*, **4**, 99–142.

Evans, R. H., 1977. In, *Environmental Analysis in Marine Fisheries Research; Fisheries Environmental Services*, edited by G. H. Tomczak, *F.A.O. Fish. Tech. Pap.*, No. 170, 98–109.

F.A.O., 1975. Report on the second session of the IPFC/IOFC *ad hoc* working party of scientists on stock assessment of tuna. Nantes, France, 16–18th September, 1974. *F.A.O. Fish. Tech. Pap.*, No. 152, 1–18.

Fink, B. D. & Bayliff, W. H., 1970. *Bull. inter-Am. Trop. Tuna Commn*, **15**, 1–227.

Flittner, G. A., 1966. Proc. Vol. 7, 11th Pacific Science Congress, Tokyo, Japan, abstr. p. 3 only.

Forsbergh, E. D., 1969. *Bull. inter-Am. Trop. Tuna Commn*, **14**, 49–385.

Frederick, M. A., 1970. M.S. thesis, U.S. Naval Postgraduate School, Monterey, California, 179 pp.

Fujino, K., 1970a. *Trans. Am. Fish. Soc.*, **99**, 152–178.

Fujino, K., 1970b. In, *The Kuroshio. A Symposium on the Japan Current*, edited by J. C. Marr, East-West Center Press, Honolulu, 385–393.

Fujino, K., 1972. In, *Proceedings of the Second Symposium on the Results of the Co-operative Study of the Kuroshio and Adjacent Regions*, edited by K. Sugawara, Saikow Publishing Co., Tokyo, 373–384.

Fujino, K., 1976. *Bull. Jap. Soc. scient. Fish.*, **42**, 1229–1235.

Gooding, R. M. & Magnuson, J. J., 1967. *Pacif. Sci.*, **21**, 486–487.

Graham, J. J. & Craig, W. L., 1961. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish.*, No. 386, 31 pp.

Graham, J. B. & Diener, D. R., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 113–133.

Green, R. E., 1967. *Fish. ind. Res*, **3** (1), 29–45.

Greenblatt, P. R., 1979. *Fishery Bull. NOAA*, **77**, 147–155.

Griffiths, R. C., 1965. *U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish.*, No. 499, 54 pp.

Gulland, J. A., 1971. Editor, *Fish Resources of the Ocean*. Fishing News (Books) Ltd, West Byfleet, Surrey, England, 255 pp.

Guppy, M., Hulbert, W. C. & Hochachka, P. W., 1979. *J. exp. Biol.*, **82,** 303–320.

Habib, G., 1976. In, *Proceedings of the Skipjack Tuna Conference*, Occas. Publ. No. 11, Fish, Res, Div., New Zealand, 40–48.

Hanamoto, E., 1974. *La mer (Bull. Soc. Fr.-Jap. océanogr.)*, **12,** 128–136.

Hanamoto, E., 1975. *La Mer (Bull. Soc. Fr.-Jap. océanogr.)*, **13,** 58–71.

Hanamoto, E., 1976. *Bull. Jap. Soc. Fish. Oceanogr.*, **29,** 41–44.

Hayashi [Hayasi], S., 1974. *Bull. Far Seas Fish Res. Lab. (Shimizu)*, **11,** 51–65.

Hayashi [Hayasi], S., Shingu, S. & Hisada, K., 1972. *Far Seas Fish. Res. Lab.*, S Series 6, 63–88.

Hidaka, K., 1955. *Kairyu (Ocean Currents)*. Iwanami Book Store, Tokyo, 291 pp.

Higgins, B. E., 1966. In, *Proceedings of the Governor's Conference on Central Pacific Fishery Resources*, edited by T. A. Manar, State of Hawaii, Honolulu, 169–195.

Higgins, B. E., 1970. *Trans. Am. Fish. Soc.*, **99,** 60–69.

Hirota, H. & Masaichi, M., 1976. *Bull. Jap. Soc. scient. Fish.*, **42,** 939.

Holliday, F. G. T., 1971. In, *Marine Ecology, Volume 1*, edited by O. Kinne, Wiley-Interscience, London, 997–1033.

Honma, M. & Kamimura, T., 1957. *Rep. Nankai reg. Fish. Res. Lab.*, **6,** 84–90.

Hulbert, W. C., Guppy, M., Murphy, B. & Hochachka, P. W., 1979. *J. exp. Biol.*, **82,** 289–301.

Hunter, J. R. & Mitchell, C. T., 1967. *Fishery Bull. Fish Wildl. Serv. U.S.*, **66,** 13–29.

Hunter, J. R. & Mitchell, C. T., 1968. *J. Cons. perm. int. Explor. Mer*, **31,** 427–434.

Hynd, J. S., 1965. *Aust. J. mar. freshw. Res.*, **16,** 25–32.

Hynd, J. S., 1969. *Aust. Fish.*, **28** (5), 26–30.

Hynd, J. S., Kesteven, G. L. & Robins, J. P., 1966. *Food Technol. Aust.*, **18,** 190–194 & 274–276.

Hynd, J. S. & Lucas, C., 1975. Proc. 15th session Indo-Pacific Fish. Counc., Section III, Symposium on coastal and high seas pelagic resources, 424–435.

Hynd, J. S. & Robins, J. P., 1967. *C.S.I.R.O., Aust., Div. Fish. Oceanogr., Tech. Pap.*, No. 22, 53 pp.

Ingham, M. C., Cook, S. K. & Hausknecht, K. A., 1977. *Fishery Bull. NOAA*, **75,** 857–865.

Inoue, M., Amano, R., Iwasaki, Y. & Yamauti, M., 1968. *Bull. Jap. Soc. scient. Fish.*, **34,** 288–294.

Inter-American Tropical Tuna Commission, 1973. *Ann. Rep.* for 1972, 166 pp.

Inter-American Tropical Tuna Commission, 1974. *Ann. Rep.* for 1973, 150 pp.

Inter-American Tropical Tuna Commission, 1975. *Ann. Rep.* for 1974, 169 pp.

Inter-American Tropical Tuna Commission, 1978. *Ann. Rep.* for 1977, 163 pp.

Jager, B. Van D. de, Nepgen, C. S. de V. & van Wyk, R. J., 1963. *Rep. S. Afr., Div. Sea Fish., Investigational Rep.* No. 47, 40 pp.

Jones, F. R. H., 1968. *Fish Migration*. St Martin's Press, New York, 325 pp.

Jones, F. R. H., Walker, M. G. & Arnold, G. P., 1978. In, *Advances in Oceanography*, edited by H. Charnock and Sir George Deacon, Plenum Press, New York, 185–207.

Joseph, J., Klawe, W. L. & Murphy, P., 1979. *Tuna and Billfish—Fish Without A Country*. Inter-Am. Trop. Tuna Comm., La Jolla, California, 46 pp.

Joseph, J. & Stevenson, M. R., 1974. In, *COSPAR, Approaches to Earth Survey Problems through use of Space Techniques*. Proc. Symp. held at Constance, F.R.G., 23–25th May, 1973, edited by P. Bock, Akademie-Verlag, Berlin, 75–100.

Kamimura, T. & Honma, M., 1959. In, *Nankai Regional Fisheries Research Laboratory* (editor), 1958 ed., Fed. Jap. Tuna Fish. Coop. Ass., Tokyo, 308–352.

Kawai, H. & Sasaki, M., 1962. *Bull. Tohoku reg. Fish. Res. Lab.*, **20,** 1–27.

Kawana, T., 1935. *Suisan Kenkyu Shi*, **30,** 8–10.

Kearney, R. E., 1978. *South Pacific Commn, Noumea, Occ. Pap.*, No. 7, 23 pp.

Kikawa, S., 1957. *Rep. Nankai reg. Fish. Res. Lab.*, **5,** 145–157.

Kikawa, S., 1964. *Rep. Nankai reg. Fish. Res. Lab.*, **20,** 37–58.

Kikawa, S., Shiohama, T., Morita, Y. & Kume, S., 1977. *Bull. Far Seas Fish. Res. Lab.* (*Shimizu*), **15**, 101–113.

King, J. E., 1958. *Proc. Ninth Pacif. Sci. Congr.*, **16**, 98–107.

King, J. E. & Iversen, R. T. B., 1962. *Fishery Bull. Fish Wildl. Serv. U.S.*, **62**, 271–321.

Kinne, O., 1971. In, *Marine Ecology, Volume 1*, edited by O. Kinne, Wiley-Interscience, London, 821–995.

Kishinouye, K., 1923. *J. Coll. Agric. imp. Univ. Tokyo*, **8**, 293–475.

Kitchell, J. F., Neill, W. H., Dizon, A. E. & Magnuson, J. J., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 357–368.

Klawe, W. L., 1963. *Bull. inter-Am. Trop. Tuna Commn*, **6**, 449–540.

Klawe, W. L., 1970. In, *Eastropac Atlas*, edited by C. M. Love. Vol. 4, Circ., U.S. Nat. Mar. Fish. Serv., **330**, figs 20–FS, 20–FA, 30–FS, and 30–FA, pp. 1–12+unpaginated section.

Klawe, W. L., 1972a. In, *Eastropac Atlas*, edited by C. M. Love, Vol. 4, Circ., U.S. Nat. Mar. Fish. Serv., **330**, figs 40–FS and 40–FA, pp. i–vi+unpaginated section.

Klawe, W. L., 1972b. In, *Eastropac Atlas*, edited by C. M. Love, Vol. 2, Circ., U.S. Nat. Mar. Fish. Serv., **330**, figs 10–FS and 10–FA, pp. i–vii+unpaginated section.

Klawe, W. L., 1977. *Mar. Fish. Rev.*, **39**, 1–4.

Klawe, W. L., Pella, J. J. & Leet, W. S., 1970. *Bull. inter-Am. Trop. Tuna Commn*, **14**, 507–544.

Klima, E. F. & Wickham, D. A., 1971. *Trans. Am. Fish. Soc.*, **100**, 86–99.

Knudsen, P. F., 1977. *Bull. inter-Am. Trop. Tuna Commn*, **17**, 119–169.

Koblentz-Mishke, O. J., Volkovinsky, V. V. & Kabanova, J. G., 1970. In, *Scientific Exploration of the South Pacific*, edited by W. S. Wooster, National Academy of Sciences, Washington, 183–193.

Kojima, S., 1956. *Bull. Jap. Soc. scient. Fish.*, **21**, 1049–1052.

Koto, T., 1966. *Rep. Nankai reg. Fish. Lab.*, **23**, 43–54.

Koto, T. & Hisada, J. K., 1967. *Rep. Nankai reg. Fish. Lab.*, **24**, 15–20.

Krygier, E. E. & Pearcy, W. G., 1977. *Fishery Bull. NOAA*, **75**, 867–870.

Kume, S., 1967. *Rep. Nankai reg. Fish. Res. Lab.*, **25**, 75–80.

Kume, S., 1969. *Bull. Far Seas Fish. Res. Lab.*, **1**, 77–98.

Kume, S. & Morita, Y., 1967. *Rep. Nankai reg. Fish. Res. Lab.*, **25**, 81–90.

Kume, S. & Schaefer, M. B., 1966. *Bull. inter-Am. Trop. Tuna Commn*, **11**, 103–170.

Laevastu, T. & Rosa, H., 1963. *F.A.O. Fish. Rep.* No. 6, **3**, 1835–1851.

Lasker, R., 1978. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, **173**, 212–230.

Laurs, R. M., 1977. In, *Environmental Analyses in Marine Fisheries Research—Fisheries Environmental Services*, edited by G. H. Tomczak, F.A.O. Fish. Tech. Pap., No. 170, 110–119.

Laurs, R. M., 1979. *NOAA Nat. Mar. Fish. Serv. Southwest Fish Cent. Admin. Rep. LF-79-17*, 10 pp.

Laurs, R. M. & Lynn, R. J., 1977. *Fishery Bull. NOAA*, **75**, 795–822.

Laurs, R. M., Yuen, H. & Johnson, J. J., 1977. *Fishery Bull. NOAA*, **75**, 347–355.

Legand, M., Bourret, P., Fourmanoir, P., Grandperrin, R., Gueredrat, J. A., Michel, A., Rancurel, P., Repelin, R. & Roger, C., 1972. *Cah. ORSTOM, sér. Océanogr.*, **19**, 303–393.

Lorenzen, C. J., 1966. *Deep-Sea Res.*, **13**, 223–227.

Magnuson, J. J., 1963. *F.A.O. Fish. Rep.*, No. 6, **3**, 1057–1066.

Magnuson, J. J., 1965. *Progve Fish Cult.*, **27**, 230–233.

Magnuson, J. J., 1969. *Trans. Am. Fish. Soc.*, **98**, 379–392.

Magnuson, J. J., 1970. *Copeia*, 1970, 56–85.

Magnuson, J. J., 1973. *Fishery Bull. NOAA*, **71**, 337–356.

Magnuson, J. J., 1978. In, *Fish Physiology, Vol. VII Locomotion*, edited by W. S. Hoar and D. J. Randall, Academic Press, New York, 239–313.

Magnuson, J. J. & Heitz, J. G., 1971. *Fish. Bull. NOAA*, **69**, 361–370.

Magnuson, J. J. & Weiniger, D., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 293–311.

Manar, T. A., 1966. Editor, *Proceedings of the Governor's Conference on Central Pacific Fishery Resources*. Bur. Comm. Fish., Honolulu, Hawaii, 266 pp.

Mathisen, A. O., Thorne, R. E., Trumble, R. J. & Blackburn, M., 1978. In, *Upwelling Ecosystems*, edited by R. Boje and M. Tomczak, Springer-Verlag, Berlin, 111–123.

Matsumoto, W. M., 1958. *Fishery Bull. Fish Wildl. Serv. U.S.*, **58**, 31–72.

Matsumoto, W. M., 1975. *NOAA Tech. Pap.*, NMFS SSRF–695, 30 pp.

McGowan, J. A., 1974. In, *The Biology of the Oceanic Pacific*, Oregon State University Press, Corvallis, Oregon, 9–28.

Mimura, K., 1962. *Occ. Rep. Nankai reg. Fish. Res. Lab.*, No. 1, 15–22.

Mori, K., 1972. *Bull. Far Seas Fish. Res. Lab.*, **6**, 111–157.

Muromtsev, A. M., 1958. *The Principal Hydrological Features of the Pacific Ocean*. Gimiz, Leningrad, in Russian; (Engl. transl. 1963, Israel Program for Scientific Translations, Jerusalem, 417 pp.).

Murphy, G. I., 1977. *Aust. Fish.*, **36**, 2–6.

Murphy, G. I. & Ikehara, I. I., 1955. *Spec. scient. Rep. U.S. Fish Wildl. Serv., Fish.* No. 154, 19 pp.

Murphy, G. I. & Shomura, R. S., 1972. *Fishery Bull. NOAA*, **70**, 875–913.

Naganuma, A., 1979. *Bull. Tohoku reg. Fish. Lab.*, **40**, 1–13.

Nakagome, J., 1959. *Bull. Jap. Soc. scient. Fish.*, **24**, 957–960.

Nakamura, E. L., 1960. *Proc. Hawaii Acad. Sci.* 35th ann. meet., 1959–1960, 24–25.

Nakamura, E. L., 1962. *Copeia*, 1962, 499–505.

Nakamura, E. L., 1964. *U.S. Bur. Sports Fish Wildl. Res. Rep.*, **63**, 169–172.

Nakamura, E. L., 1965. *Trans. Am. Fish. Soc.*, **94**, 236–242.

Nakamura, E. L., 1966. *Progve Fish Cult.*, **28**, 60–62.

Nakamura, E. L., 1972. In, *Behavior of Marine Animals, Volume 2*, edited by H. E. Winn and B. L. Olla, Plenum Press, New York, 245–277.

Nakamura, E. L. & Matsumoto, W. M., 1967. *Fishery Bull. U.S. Fish Wildl. Serv. U.S.*, **66**, 1–12.

Nakamura, H., 1951. *Rep. Nankai reg. Fish. Res. Lab.*, **1**, 144 pp. (Engl. transl. 1954, In, *Spec. scient. Rep. U.S. Fish Wildl. Serv. Fish.* No. 112, 168 pp.).

Nakamura, H., 1954. *Suisan Kaguku*, **14**, 9–17.

Nakamura, H., 1965. *Nihon Suisan Shinen Kyokai, Suisan Kenkyu Sosho*, **10**, 64 pp.

Nakamura, H., 1969. *Tuna Distribution and Migration*. Fishing News (Books) Ltd, London, 76 pp.

Neill, W. H., Chang, R. K. C. & Dizon, A. E., 1976. *Environ. Biol. Fishes*, **1**, 61–80.

Neill, W. H. & Stevens, E. D., 1974. *Science*, **184**, 1008–1010.

Nelson, W. R., Ingham, M. C. & Schaaf, W. E., 1977. *Fishery Bull. NOAA*, **75**, 23–42.

Nishikawa, Y., Kikawa, S., Honma, M. & Ueyanagi, S., 1978. *Far Seas Fish. Res. Lab., S Series*, **9**, 1–99.

Okiyama, M., 1974. *Bull. Jap. Sea reg. Fish. Res. Lab.*, **25**, 89–97.

Okiyama, M., 1979. *Proc. 7th Japan-Soviet Joint Symp. Aquaculture, Sept. 1978, Tokyo*, 1979, 223–233.

Okiyama, M. & Ueyanagi, S., 1977. *Bull. Far Seas Fish. Res. Lab.*, **15**, 35–49.

Orange, C. J., 1961. *Bull. inter-Am. Trop. Tuna Commn*, **5**, 457–526.

Orange, C. J. & Fink, B. D., 1963. *Calif. Fish Game*, **49**, 307–309.

Otsu, T., 1975. *NOAA Tuna Newsletter*, **31**, 5–9.

Otsu, T. & Hansen, R. J., 1962. *Fishery Bull. Fish Wildl. Serv. U.S.*, **62**, 151–161.

Otsu, T. & Uchida, R. N., 1963. *Fishery Bull. Fish Wildl. Serv. U.S.*, **63**, 33–44.

Parrish, R. H. & MacCall, A. D., 1978. *Calif. Fish Game, Fish. Bull.*, No. 167, 110 pp.

Perrin, W. F., 1975. *J. Fish. Res. Bd Can.*, **32**, 1059–1067.

Perrin, W. F., Warner, R. R., Fiscus, C. H. & Holts, D. B., 1973. *Fishery Bull. NOAA*, **71**, 1077–1092.

Radovich, J., 1961. *Fish. Bull. Sacramento*, No. 112, 62 pp.

Reid, J. L., 1962. *Limnol. Oceanogr.*, **7**, 287–306.

Reid, J. L., Brinton, E., Fleminger, A., Venrick, E. L. & McGowan, J. A., 1978. In, *Advances in Oceanography*, edited by H. Charnock and Sir George Deacon, Plenum Press, New York, 65–130.

Richards, W. J., 1969. *Cah. ORSTOM. Sér. Océanogr.*, **7** (3), 3–7.

Richards, W. J. & Klawe, W. L., 1972. *NOAA Tech. Rep. NMFS SSRF* No. 652, 107 pp.

Rivas, L. R., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 369–393.

Robins, J. P., 1952. *Aust. J. mar. freshwat. Res.*, **3**, 101–110.

Robins, J. P., 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 562–587.

Robinson, M. K., 1976. *Naval Oceanogr. Off. Ref. Pub.*, **2**, Washington.

Rosa, H., 1963. Editor, *F.A.O. Fish. Rep.*, No. 6, 1–4.

Rothschild, B. J. & Yong, M. Y. Y., 1970. *Spec. scient. Rep. U.S. Fish Wildl. Serv. Fish.*, **623**, 37 pp.

Royce, W. F., 1957. *Fishery Bull. Fish Wildl. Serv. U.S.*, **57**, 497–554.

Royce, W. F., 1964. *Fishery Bull. Fish Wildl. Serv. U.S.*, **63**, 395–443.

Saito, S., 1973. *Mem. Fac. Fish. Hokkaido Univ.*, **21**, 107–182.

Saito, S. & Sasaki, S., 1974. *Bull. Jap. Soc. scient. Fish.*, **40**, 643–649.

Schaefer, M. B., Broadhead, G. C. & Orange, C. J., 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 538–561.

Schultze, D. L. & Collins, R. A., 1977. *Calif. Dept Fish Game, Mar. Res. Tech. Pap.*, No. 38, 44 pp.

Seckel, G. R., 1963. *F.A.O. Fish. Rep.*, No. 6, **3**, 1201–1208.

Seckel, G. R., 1969. *U.S. Fish Wildl. Serv., Circ.* No. 323, 11 pp.

Seckel, G. R., 1972. *Fishery Bull. NOAA*, **70**, 763–787.

Sette, O. E., 1955. *J. mar. Res.*, **14**, 398–414.

Sharp, G. D., 1972. Doctoral dissertation, Scripps Institution of Oceanography, 75 pp.

Sharp, G. D., 1973. *Comp. Biochem. Physiol.*, **44B**, 381–388.

Sharp, G. D., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 397–449.

Sharp, G. D. & Dizon, A. E., 1978. Editors, *The Physiological Ecology of Tunas*. Academic Press, New York, 485 pp.

Sharp, G. D. & Dotson, R. C., 1977. *Fishery Bull. NOAA*, **75**, 447–450.

Sharp, G. D. & Francis, R. C., 1976. *Fishery Bull. NOAA*, **74**, 36–50.

Sharp, G. D. & Pirages, S., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 41–78.

Sharp, G. D. & Vlymen III, W. J., 1978. In, *The Physiological Ecology of Tunas*, edited by G. D. Sharp and A. E. Dizon, Academic Press, New York, 213–232.

Shingu, C., Tomlinson, P. K. & Peterson, C. L., 1974. *Bull. inter-Am. Trop. Tuna Commn*, **16**, 67–230.

Shingu, C. & Warashina, I., 1965. *Rep. Nankai reg. Fish. Res. Lab.*, **22**, 85–93.

Shingu, C., Warashina, Y. & Matsuzaki, N., 1974. *Far Seas Fish Res. Lab. Bull.*, **10**, 109–140.

Shingu, S., 1967. *Rep. Nankai reg. Fish. Res. Lab.*, **25**, 19–35.

Shingu, S., 1970. *Far Seas Fish. Res. Lab., Bull.*, **3**, 57–113.

Smith, A. C., 1962. *Calif. Fish Game*, **48**, 199–201.

Smith, A. C., 1966. *Am. Zool.*, **6**, 577 only.

Smith, A. C., 1971. *Comp. Biochem. Physiol.*, **39B**, 719–724.

Smith, A. C. & Clemens, H. B., 1973. *Trans. Am. Fish. Soc.*, **102**, 578–583.

Steffel, S., Dizon, A. E., Magnuson, J. J. & Neill, W. H., 1976. *Trans. Am. Fish. Soc.*, **105**, 588–591.

Stevens, E. D. & Fry, F. E. J., 1971. *Comp. Biochem. Physiol.*, **38A**, 203–211.

Stevens, E. D. & Neill, W. H., 1978. In, *Fish Physiology, Volume VII. Locomotion*, edited by W. S. Hoar and D. J. Randall, Academic Press, New York, 315–359.

Stevenson, W. H. & Pastula, E. J., 1971. *Comm. Fish. Rev.*, **33**, 9–21.

Strasburg, D. W., 1960. *Fishery Bull. Fish Wildl. Serv. U.S.*, **60**, 231–255.

Suda, A., Kume, S. & Shiohama, T., 1969. *Bull. Far Seas Fish. Res. Lab. (Shimizu)*, **1**, 99–114.

Suda, A. & Schaefer, M. B., 1965. *Bull. inter-Am. Trop. Tuna Commn*, **9**, 305–462.

Suzuki, Z., Tomlinson, P. K. & Honma, M., 1978. *Bull. inter-Am. Trop. Tuna Commn*, **17**, 277–441.

Suzuki, Z., Warashina, Y. & Kishida, M., 1977. *Bull. Far Seas Fish. Res. Lab. (Shimizu)*, **15**, 51–90.

Sverdrup, H. U., Johnson, M. W. & Fleming, R. H., 1942. *The Oceans. Their Physics, Chemistry and General Biology.* Prentice-Hall, New York, 1060 pp.

Szekielda, K.-H., 1976. *Oceanogr. Mar. Biol. Ann. Rev.*, **14**, 99–166.

Tiews, K., 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 422–481.

Tomczak, G. H. (Ed.), 1977. *F.A.O. Fish. Tech. Pap.*, No. 170, 141 pp.

Uchida, R. N., (in press). *NOAA Tech. Rep. N.M.F.S. Circ.*

Uda, M., 1957. *Bull. Jap. Soc. Scient. Fish.*, **23**, 368–372.

Uda, M., 1973. *J. Fac. Mar. Sci. Technol., Tokai Univ.*, **7**, 245–266.

Uda, M. & Ishino, M., 1958. *J. Tokyo Univ. Fish.*, **44**, 105–129.

Ueyanagi, S., 1955. *Bull. Jap. Soc. scient. Fish.*, **20**, 1030–1053.

Ueyanagi, S., 1957. *Rep. Nankai reg. Fish. Res. Lab.*, **6**, 113–124.

Ueyanagi, S., 1969a. *Bull. Far Seas Fish. Res. Lab. (Shimizu)*, **1**, 1–4.

Ueyanagi, S., 1969b. *Bull. Far Seas Fish. Res. Lab (Shimizu)*, **2**, 177–219.

Ueyanagi, S., 1978. *5th int. Ocean Dev. Conf. Preprints (I)*, Sept. 25–29, 1978, Tokyo, 23–30.

Vinogradov, M. E., 1968. *Akad. Nauk SSSR*, Moscow, in Russian; (Engl. Trans. 1970, Israel Program for Scientific Transl., Jerusalem, 339 pp.).

Warashina, K. & Hisada, K., 1974. *Bull. Far Seas Fish. Res. Lab. (Shimizu).*, **10**, 193–220.

Watanabe, H., Yukinawa, M., Nakazawa, S. & Ueyanagi, S., 1966. *Rep. Nankai reg. Fish. Res. Lab.*, **23**, 85–94.

Williams, F., 1966. *E. Afr. Agric. ror. J.*, **31**, 374–382.

Williams, F., 1970. *Bull. inter-Am. Trop. Tuna Commn*, **15**, 229–281.

Williams, F., 1972. *Fishery Bull. NOAA*, **70**, 741–762.

Williams, F., 1976. *Bull. mar. Sci.*, **26**, 18–26.

Williams, K. F., 1977. In, *Environmental Analyses in Marine Fisheries Research*, F.A.O. Tech. Pap., No. 170, 38–55.

Wolf, S., 1974. *Mar. Fish. Rev.*, **36**, 78–87.

Wyrtki, K., 1964. *Ergänzungsh. Deutsch. Hydrog. Zeitschrift*, Reihe A6, 84 pp.

Wyrtki, K., 1967. *Int. J. Oceanol. Limnol.*, **1**, 117–147.

Yabe, H., Ueyanagi, S. & Watanabe, H., 1966. *Rep. Nankai reg. Fish. Res. Lab.*, **23**, 95–129.

Yabuta, Y. & Ueyanagi, S., 1953. *Contr. Nankai reg. Fish. Res. Lab.*, **1** (28), 8 pp.

Yamanaka, H., 1956. *Bull. Jap. Soc. scient. Fish.*, **21**, 1187–1193.

Yamanaka, H., 1959. In, *Average Year's Fishing Condition of Tuna Longline Fisheries*, Tokyo, Japan Fishermen's Cooperative Associations, 153–204.

Yamanaka, H., Morita, J. & Anraku, N., 1969. *Bull. Far Seas Fish. Res. Lab. (Shimizu)*, **2**, 257–273.

Yamanaka, H. & Staff, 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 180–217.

Yamanaka, H., Yukinawa, M. & Morita, J., 1977. *Agric. Forestry and Fish Res. Counc. Jap., Result of Study*, **94**, 6–32.

Yamanaka, I., 1978. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer.*, **173**, 203–211.

Yorita, T., 1976. *Mon. Rep. Hokkaido Fish. Exp. St.*, **33** (3), 2–10.

Yoshida, H. O., 1971. *Fishery Bull. NOAA*, **69**, 545–554.

Yoshida, H. O. & Otsu, T., 1963. *F.A.O. Fish. Rep.*, No. 6, **2**, 274–318.

Yuen, H. S. H., 1970. *J. Fish. Res. Bd Can.*, **27**, 2071–2079.