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SKIPJACK TUNA, *KATSUWONUS PELAMIS*, HABITAT BASED ON TEMPERATURE AND OXYGEN REQUIREMENTS

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ABSTRACT

The habitat of skipjack tuna, *Katsuwonus pelamis*, has generally been assumed to be the warm surface layers of tropical and subtropical ocean, where most of these fish are seen and caught. But experiments with captive Hawaiian skipjack tuna imply that their habitat is more restricted, with boundaries defined by both temperature and dissolved oxygen. The lower temperature limit appears to be about 18° C. The upper temperature limit apparently varies with size of the fish, from 30° C or more for small individuals to as little as 20° C for the largest. Skipjack tuna also require water with unusually high concentrations of dissolved oxygen, at least 3.0-3.5 ml/l (4-5 ppm), for long-term survival. If our Laboratory findings with captive skipjack tuna accurately define their natural habitat, only the smallest of these animals can inhabit the warm surface waters of the tropics; those larger than 4-5 kg must inhabit the thermocline. Our hypothesis, which can be tested, explains many features of the known distribution of skipjack tuna in the eastern and central Pacific Ocean.

For skipjack tuna, *Katsuwonus pelamis* (Linnaeus), the question "Where are the fish?" is particularly hard to answer. Their habitat is known only in the most general terms. These fish are found in tropical and subtropical waters of all oceans, at surface temperatures between 15° and 30° C. Because they are caught most frequently by methods such as trolling, purse seining, and pole-and-line fishing, it is generally assumed that skipjack tuna inhabit the surface mixed layer. Japanese longline gear, which fishes well below the sea surface, catches very few skipjack tuna, and then only on the hooks which fish nearest the surface (Yabe et al. 1963). In a review of the literature on this species, Matsumoto and Skillman[3] pointed out that the sea-surface temperature range where most skipjack tuna are caught varies from one fishery to another. Off Tasmania and southeast Australia, the range is 15° to 18° C. Off Japan and South America, the range appears to be 20° to 24° C, while the fishery off southern India operates in water of 28° to 29° C. The Hawaii fleet fishes skipjack tuna all year, in water with surface temperatures ranging from 23° to 27° C, with the majority of catches in the warm, summer months.

Because studies of the occurrence of wild skipjack tuna in relation to sea-surface temperature yield such disparate results from one area to another, and because the total temperature range, 15° to 30° C, includes more than half of the surface area of the world's oceans, we have worked with captive animals in a series of experiments intended to define more precisely their physiological requirements. Results of three of these studies (Neill et al. 1976; Dizon et al. 1977; Gooding and Neill[4]) provided information on the skipjack tuna's temperature and dissolved oxygen requirements which, taken together, appear to define the actual habitat of this species in nature.

We present here a summary of the physiological studies and their results, which suggest specific temperature and dissolved oxygen values that define the spatial limits of the skipjack tuna habitat. With the resultant temperature and dissolved oxygen values, we have mapped the habitat of the skipjack tuna using averaged oceanographic data from the eastern Pacific Ocean.

These habitat maps present our hypothesis in a testable form. If skipjack tuna in nature have the same requirements as those studied in captivity, their distribution should, on average, correspond

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[3]Matsumoto, W. M., and R. A. Skillman. Synopsis of biological data on skipjack tuna, *Katsuwonus pelamis* (Linnaeus). Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

[4]Gooding, R. M., and W. H. Neill. Respiration rates and low oxygen tolerance limits in skipjack tuna, *Katsuwonus pelamis*. Manuscr. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

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with the habitat volume shown on the maps. If, under normal oceanographic conditions, they occur in significant numbers well outside of the mapped habitat volume the hypothesis is invalid, and we should look for evidence of adaptations (behavioral, physiological, and genetic) which were not evident in our work with captive fish. If the distribution of skipjack tuna is more restricted than our habitat maps would indicate, we should look for factors in addition to temperature and dissolved oxygen (e.g., turbidity) which might further limit the habitat. Salinity is not apt to be one of these factors, however, since captive skipjack tuna do not respond to rather drastic changes in this variable (Dizon 1977).

More immediate and definitive tests of the hypothesis can be made by tagging wild skipjack tuna of various sizes with tags capable of sensing and telemetering depth, temperature, and dissolved oxygen.

TEMPERATURE AND OXYGEN REQUIREMENTS

Lower Temperature Limit

Dizon et al. (1977) determined that 15°C was the lower lethal temperature limit for skipjack tuna. They subjected recently caught, apparently healthy individual fish to water temperatures which decreased 1° or 5°C/day, starting at ambient temperature (about 24°C), with other skipjack tuna held continuously at ambient temperature as controls. All seven of the test animals survived and fed until temperature had declined to 18°C; at 17°C all but one fish stopped eating, and one fish died. None of the fish survived 15°C for more than a few hours. Accordingly, we have selected 18°C as the lowest water temperature which Hawaii skipjack tuna can withstand for prolonged periods of time without significant increases in mortality.

This preliminary estimate of the lower temperature limit is essentially identical with the value obtained by Williams (1970) from a comparison of fishery catch data with sea-surface temperatures in the eastern Pacific. Williams found that most skipjack tuna were caught in water with temperatures between 29° and 20°C, with diminishing catches down to temperatures between 18° and 17°C, and no catches in colder waters.

Three large (ca. 70 cm) Hawaiian skipjack tuna released with tags that telemetered swimming depth were found to spend >85% of their time in water warmer than 20°C and <10% in water colder than 18°C (Dizon et al. in press).

In the western South Pacific, skipjack tuna have been caught in water near 15°C, off Tasmania (Robins 1952) and off eastern Australia (G. I. Murphy, Division of Fisheries and Oceanography, CSIRO, New South Wales, Australia, 1977, pers. commun.). These fish probably belong to a different subpopulation (Fujino 1972) than fish found in Hawaii.

Lower Dissolved Oxygen Limit

Gooding and Neill (see footnote 4) examined the effects of low dissolved oxygen concentrations on skipjack tuna. Their animals, habituated in open tanks with circulating, essentially saturated seawater (4.5 ml O_2/l, or 6.4 ppm), were transferred to tanks in which the concentration of dissolved oxygen could be maintained at a preselected constant subsaturation level. Temperatures in both sets of tanks were ambient, 23° to 24°C. Dissolved oxygen concentrations down to 1.0 ml/l (1.4 ppm) were used. Resistance times and swimming speeds were measured, and general behavior was observed for up to 4 h in each experiment. Under their experimental conditions, Gooding and Neill concluded that hypoxic stress was first manifest, through changes in swimming behavior and speed, at about 2.8 ml/l (4.0 ppm), a value fairly typical for fish. Lethal oxygen levels, leading to death in 4 h or less, were found to be higher than those for any other freshwater or marine fish thus far studied. Only one fish (out of six) survived 4 h at 2.5 ml/l (3.5 ppm), and none survived as long as 2 h at still lower concentrations. At higher oxygen values, above 2.5 ml/l, all skipjack tuna tested in this study survived at least 4 h.

Because we sought to estimate the lowest dissolved oxygen concentrations that skipjack tuna can tolerate indefinitely without significant stress, we have chosen a conservative value of 3.5 ml/l (5 ppm) as the lower limit to the skipjack tuna's habitat, where temperature and other variables are not limiting.

Upper Temperature Limit

The case for an upper temperature limit to the skipjack tuna's habitat is somewhat less direct. Three small (30-35 cm) individual skipjack tuna maintained in water warmed 1°C/day survived until the temperature reached 33° C, when two died; the other lived until the water reached 34° C (Dizon et al. 1977). Skipjack tuna have a high metabolic rate and a countercurrent heat exchanger in their circulatory system which dramatically restricts heat loss through the gills. This accounts for the fact that freshly caught wild skipjack tuna can have red muscle core temperatures as high as 11° C above that of the surrounding water (Stevens and Fry 1971).

Temperature excesses of this magnitude could lead to dangerously high muscle temperatures if they occur in the warmer parts of the ocean. To examine this possibility we use a heat balance model developed for skipjack tuna by Neill et al. (1976) which yields an estimate of temperature excess in the red muscle core as a function of size and metabolic activity (Figure 1a). Actual muscle core temperatures are found by adding the values shown in this figure to the temperature of the surrounding water, for any given size fish. Clearly, large skipjack tuna in surface waters of the tropics must either tolerate high muscle core temperatures, or reduce their metabolic activity substantially below the 3 mg O_2 g^{-1} h^{-1} level.

But skipjack tuna appear to avoid heating their muscle tissue much above 35° C (Stevens and Fry 1971). This upper limit must place a similar upper limit on the water temperatures which skipjack tuna can inhabit, unless they can thermoregulate physiologically or behaviorally. In Figure 1b, 35°C is taken as the upper limit for the red muscle core, and temperature excesses of Figure 1a are subtracted from that value to arrive at an estimate of the upper temperature limits for the habitat of skipjack tuna, as a function of size. If the values thus obtained are valid, these fish should be able to live anywhere in the ocean when they are small, but they should be limited to lower and lower environmental temperatures as they grow. The largest known skipjack tuna, weighing approximately 16 kg, would—if active enough—be confined to water temperature near 18°C, which is also their approximate lower limit.

SKIPJACK TUNA HABITAT HYPOTHESIS

We hypothesize that skipjack tuna of the central and eastern Pacific Ocean occupy a primary habitat—a volume of water whose properties they can tolerate indefinitely—which is 18°C or warmer, but cooler than the upper limits for normally active animals shown in Figure 1b, provided that the dissolved oxygen concentration is at least 3.4 ml/l (5 ppm). Skipjack tuna can presumably

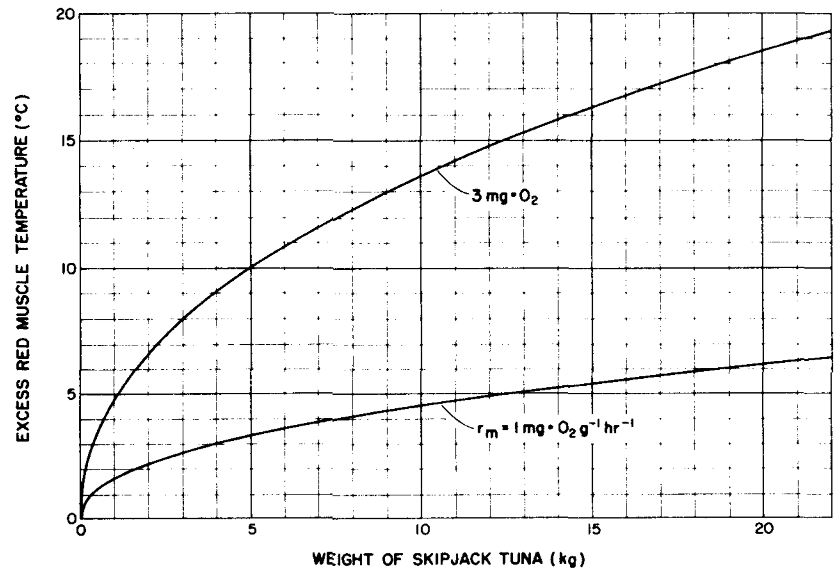

FIGURE 1a.—Calculated excess of internal temperature, over that of the surrounding water, in red muscle for skipjack tuna of all known sizes. Values are shown for a measured minimum (anesthetized) level of metabolic activity (lower line) and our estimate of the mean metabolic activity for normally active animals (upper line), triple the minimum level. (From Neill et al. 1976.)

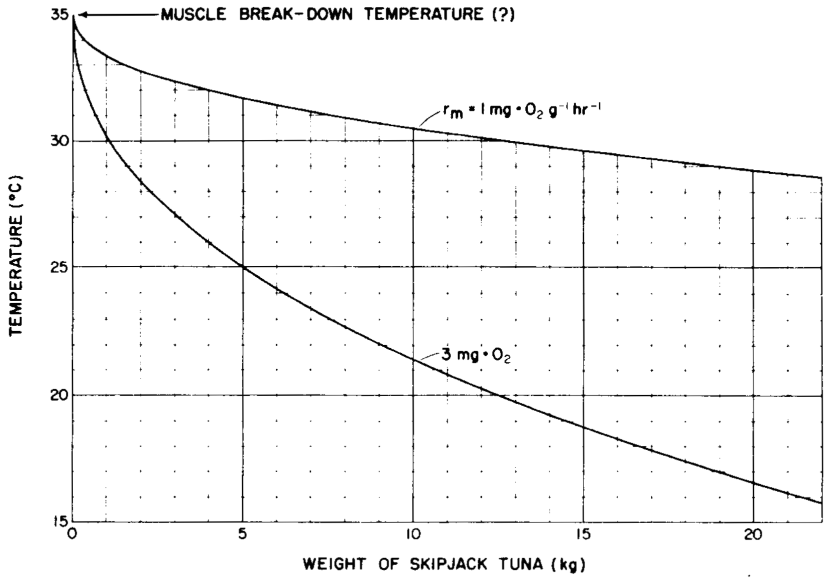

FIGURE 1b.—Maximum tolerable water temperature for skipjack tuna as a function of size for the same two rates of metabolic activity illustrated in Figure 1a. Based on calculated internal temperature excesses and the assumption that damage to red muscle tissue occurs above 35°C.

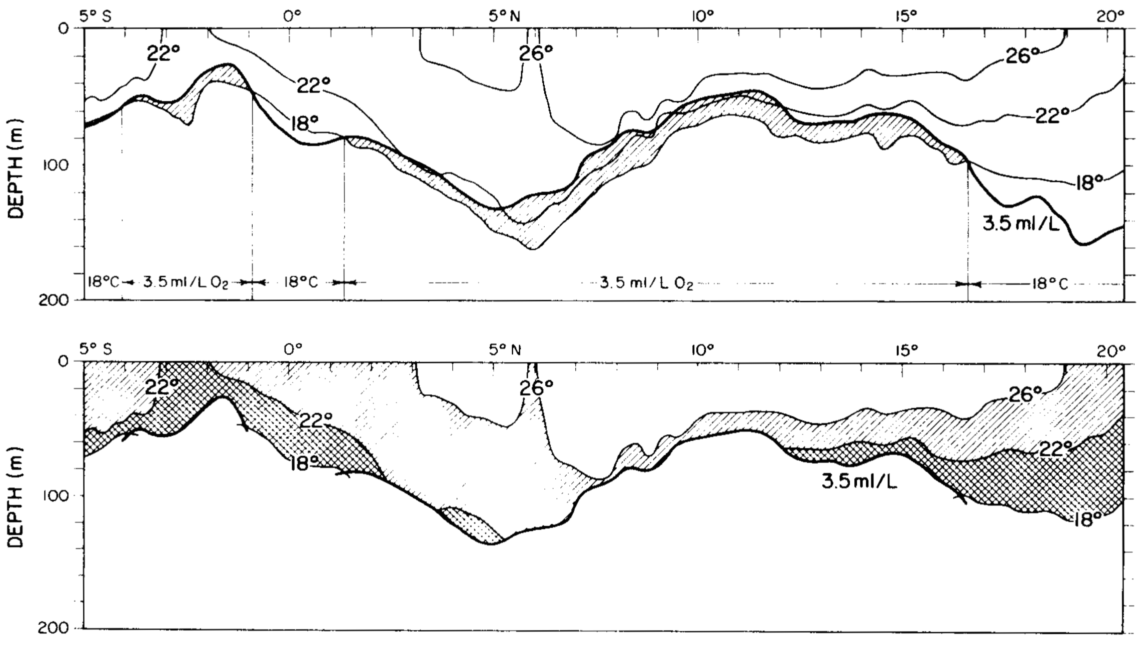

FIGURE 2.—Upper panel: Temperature and dissolved oxygen (selected isopleths only) along long. 119° W, eastern Pacific Ocean, August 1967 (Love 1972). Lower limits of the skipjack tuna habitat are assumed to be either 18° C or 3.5 ml/l dissolved oxygen, as indicated. The hatched layer should be warm enough 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.

leave their primary habitat only for limited periods of time without suffering thermal or oxygen stress. Prolonged excursions to colder water would require increased activity and thus more dissolved oxygen and food. Skipjack tuna could stay in the warm upper layers only if they would reduce their physical activity, or tolerate overheating. Hypothetical consequences of these conditions are illustrated in Figure 2 which shows the hypothetical layers along long. 119° W for skipjack tuna of two sizes. The 4-kg fish are those most abundant in catches by the eastern Pacific fishery; 9-kg fish are the largest normally found there, and then only in certain areas such as the Revillagigedo Islands (ca. lat. 17° N, long. 112° W).

The deeper limit of the habitat should be the same for skipjack tuna of all sizes. The upper limit is deeper and more restrictive for larger fish, which find essentially no habitable water between lat. 5° and 12° N, a distance of more than 700 km or 400 n.mi. Larger fish also have much less continuous access to the sea surface than those weighing 4 kg. Only skipjack tuna of the smallest size commonly found in this area (<4 kg) could inhabit all of the water above the lower limits in Figure 2.

Figures 3 to 6 are maps of a hypothetical skipjack tuna habitat for the entire central and eastern Pacific Ocean, based on oceanographic station data used in preparing the Oceanographic Atlas of the Pacific Ocean (Barkley 1968). For these maps,

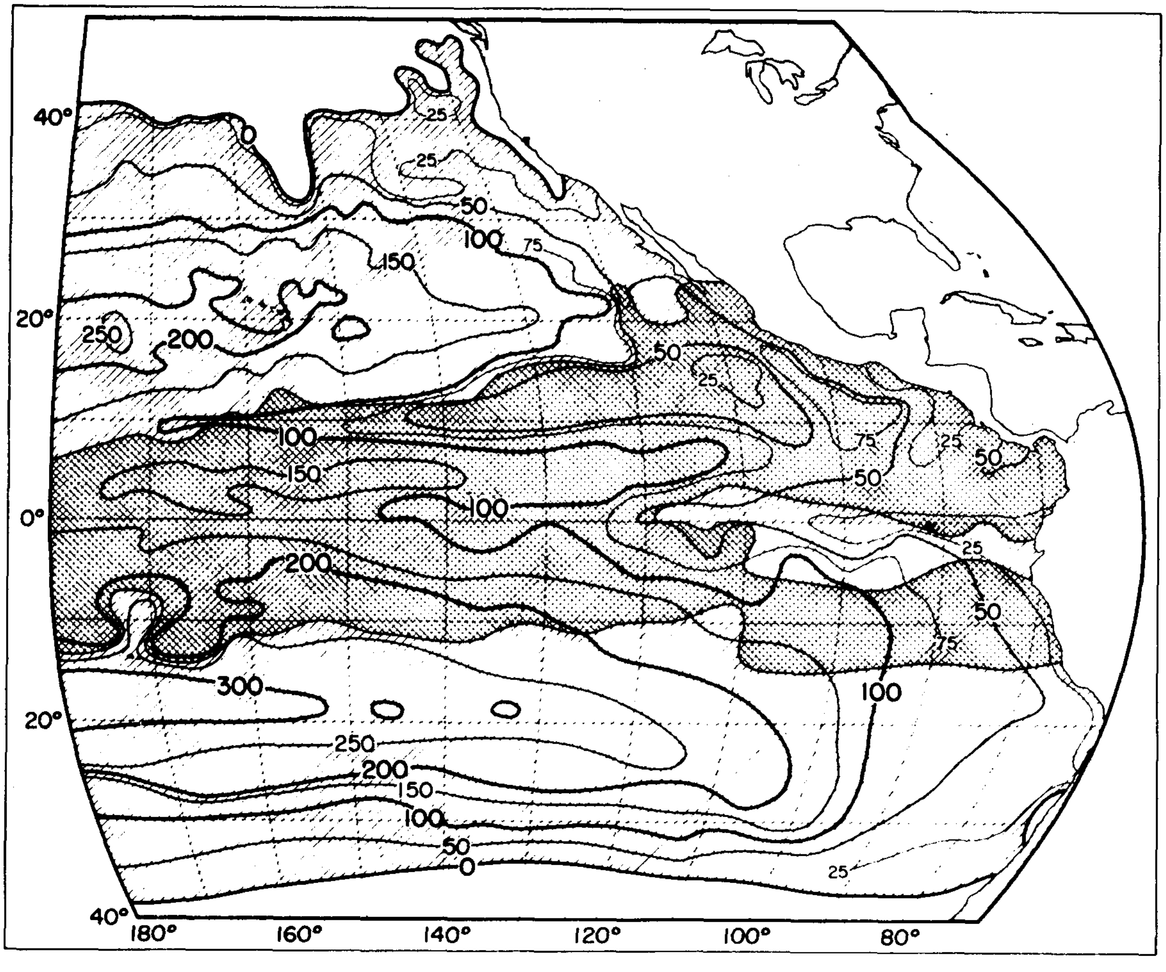

FIGURE 3.—Hypothetical maximum depth (meters) of the skipjack tuna habitat in the eastern Pacific Ocean, as determined by the depth of the 18°C isotherm (hatched area) or the 3.5 ml/l (5 ppm) isopleth of dissolved oxygen (cross hatched area). Contour interval is 50 m except for a few areas near the coast, where a 25-m contour interval is used.

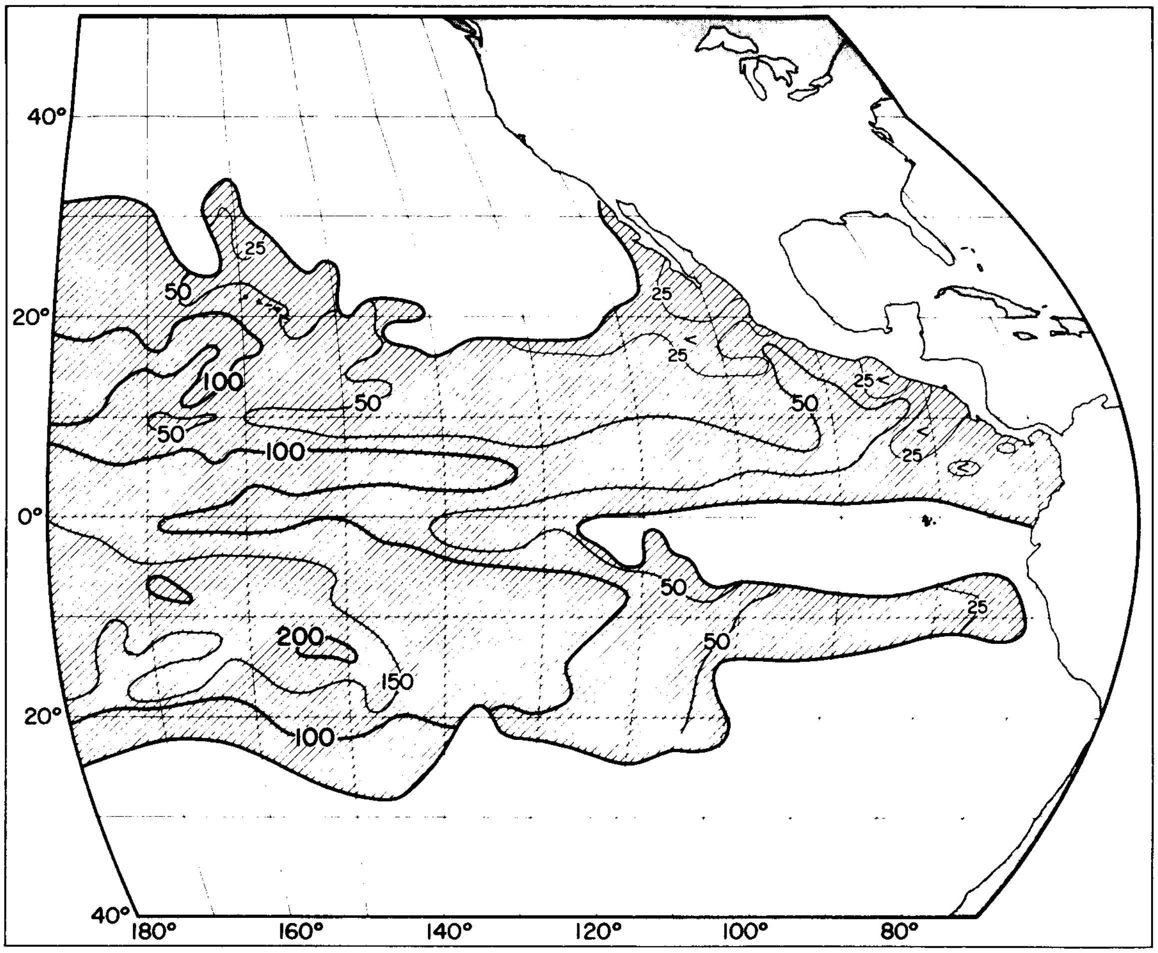

FIGURE 4.—Hypothetical minimum depth of the skipjack tuna habitat in the Pacific Ocean east of long. 180°, for fish weighing about 6.5 kg (14 lb) which are limited to water cooler than 24° C. Contours show the depth, in meters, of the 24° C isotherm.

station data were averaged within 2° areas of latitude and longitude, for all months, to approximate annual mean conditions.

Figure 3 shows the hypothetical "floor" of the skipjack tuna habitat, i.e., maximum depths (in meters) for this species. In Figure 3, the unhatched areas off the Pacific coast of the Americas, and at latitudes higher than about 40° in both hemispheres, indicate water which, at all depths, is colder on average than 18° C; presumably skipjack tuna would not normally be present.

Figure 4 shows the minimum habitat depth or ceiling for 6.5-kg fish. Outside of the hatched area annual mean surface temperatures are <24° C, and 6.5-kg fish would normally have access to all of the water column above the habitat floor (Figure 3), up to and including the sea surface.

Figure 5 shows the hypothesized habitat layer thickness for 6.5-kg skipjack tuna. In some areas, there is no water cooler than 24°C with more than 3.5 ml/l dissolved oxygen, so in these areas there is no habitat for 6.5-kg or larger fish; such areas are double hatched on Figure 5. Extensive regions around these areas have habitat layer thickness of 10 m or less, and large areas of the equatorial Pacific Ocean have <25 m of habitat layer thickness. This rather thin layer can lie beneath as much as 150 m of water warmer than 24° C (at lat. 4° N, long. 170° W, e.g.). North of the Hawaiian Islands, the opposite situation is present: a 150-m thick habitat layer lies under 25 to 50 m of water

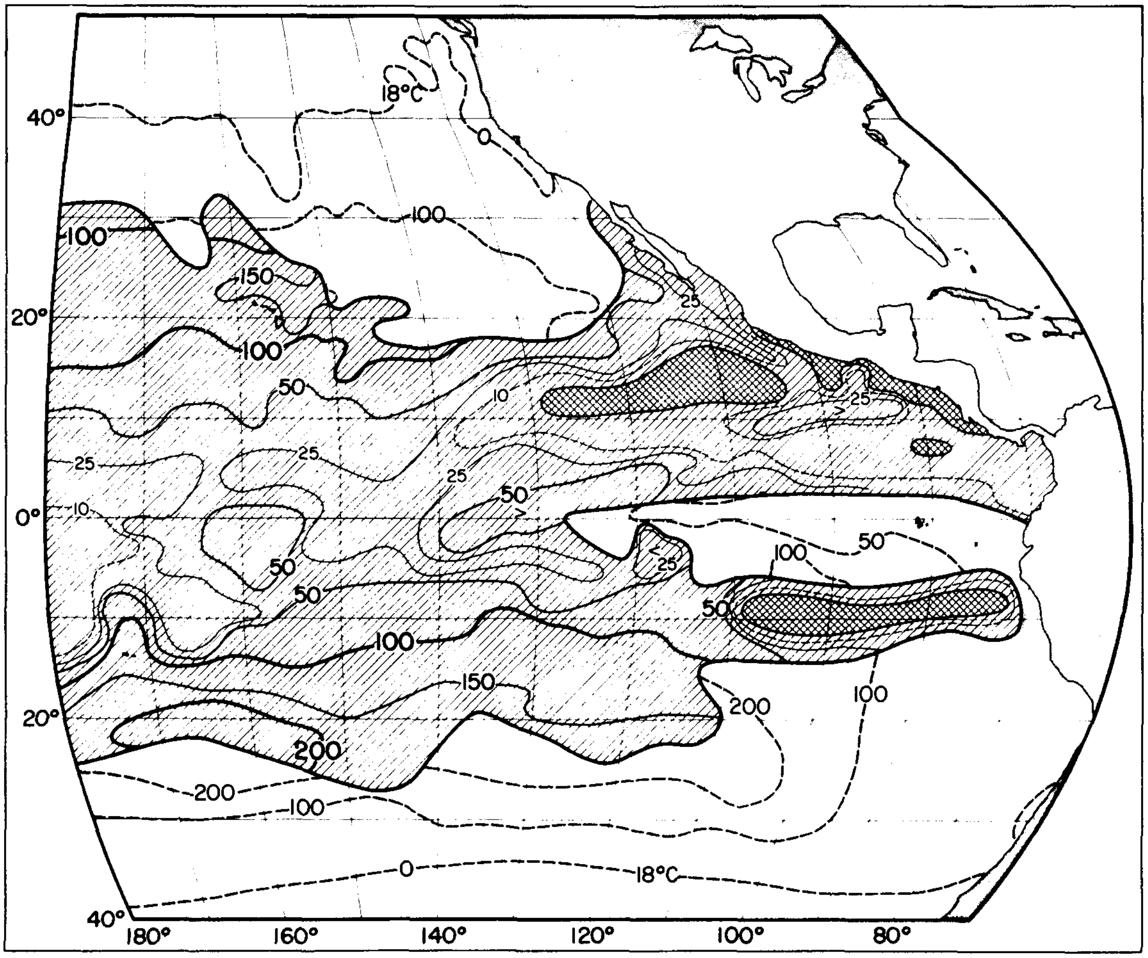

FIGURE 5.—Thickness of the hypothetical habitat layer (meters), for 6.5-kg skipjack tuna in the eastern and central Pacific Ocean. Contours were obtained by subtracting depths of the upper habitat limit (Figure 4) from the lower one (Figure 3). In the crosshatched areas off Mexico and Peru, there should be no habitat suitable for fish of this or larger sizes. In the hatched area, water warmer than 24°C is present above the habitat layer. Immediately beyond this area the habitat (dashed depth contours) extends to the sea surface. Outside of the 18°C surface isotherm, the water is probably too cold for skipjack tuna.

warmer than 24°C. Clearly, the South Pacific Ocean offers the roomiest habitat to large skipjack tuna, and in fact some of the largest known individuals of this species were caught slightly south of Tahiti (lat. 17°S, long. 150°W), according to catch records of longline fishing boats (R. A. Skillman, Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, 1977, pers. commun.).

An interesting feature of the habitat map for 6.5-kg fish (Figure 5) is a channel of relatively cool and adequately oxygenated water some 200 km off the coast of Mexico. This channel should allow skipjack tuna as large as 6.5 kg to pass from the Baja California fishery to the equatorial fishery, or vice versa, when fish as small as 4 kg would find stressful conditions for hundreds of kilometers on either side of that channel. Seasonal and year-to-year closure or shifting of this channel could readily explain puzzling variations in the distribution of skipjack tuna catches in the eastern Pacific.

Figure 6 shows areas of presumably stressful environment (zero habitat thickness) in the eastern tropical Pacific for fish of various sizes and therefore temperature limitations. Skipjack tuna >11 kg should find no habitat at all within the shaded area. Fish 4 kg in size would find no habitat within the smallest contour (temperatures above

26° C). Fish weighing <4 kg should find some thickness of habitable water, within and just below the upper mixed layer, everywhere in the eastern tropical Pacific.

DISCUSSION

Although we anticipate that temperature and dissolved oxygen will prove to be primary determinants of the habitat of skipjack tuna in all oceans, it is possible that limiting values of these variables may differ from one population or region to another. The lowest temperature (ca. 15° C) at which skipjack tuna are caught in Australian waters (Robins 1952) is considerably lower than in the eastern Pacific. The fish caught off Australia may also differ in their ability to tolerate warm or low-oxygen water.

The gross features of the distribution of skipjack tuna in the eastern tropical Pacific, where only small skipjack tuna are found in large numbers (Williams 1970), agree with the hypothesis. Those areas where large skipjack tuna do occur (Matsumoto 1975) are outside of the hatched area in Figure 6; the Revillagigedo Islands, e.g., are just north of the hatched area, and Tahiti is well south of it.

The hypothetical habitat proposed here explains why skipjack tuna leave the northern fishery of the eastern Pacific when they reach a certain size. To find cooler, better oxygenated water as they grow, these fish must move out of the eastern tropical Pacific toward higher latitudes in the central Pacific. Also, they must then spend less time at or near the sea surface, since the thermocline, where they live, is generally much deeper in the central Pacific, and the water above the thermocline is too warm to permit normal activity. This size-specific movement in response to the environment is consonant with Rothschild's (1965) migration model for the eastern Pacific skipjack tuna population. It also suggests a mechanism for the evolution of migratory processes, an important topic in marine ecology.

For several reasons, existing fishery data are inadequate for making a refined judgment of our skipjack tuna-habitat hypothesis: 1) Commercial fishery data generally include neither information

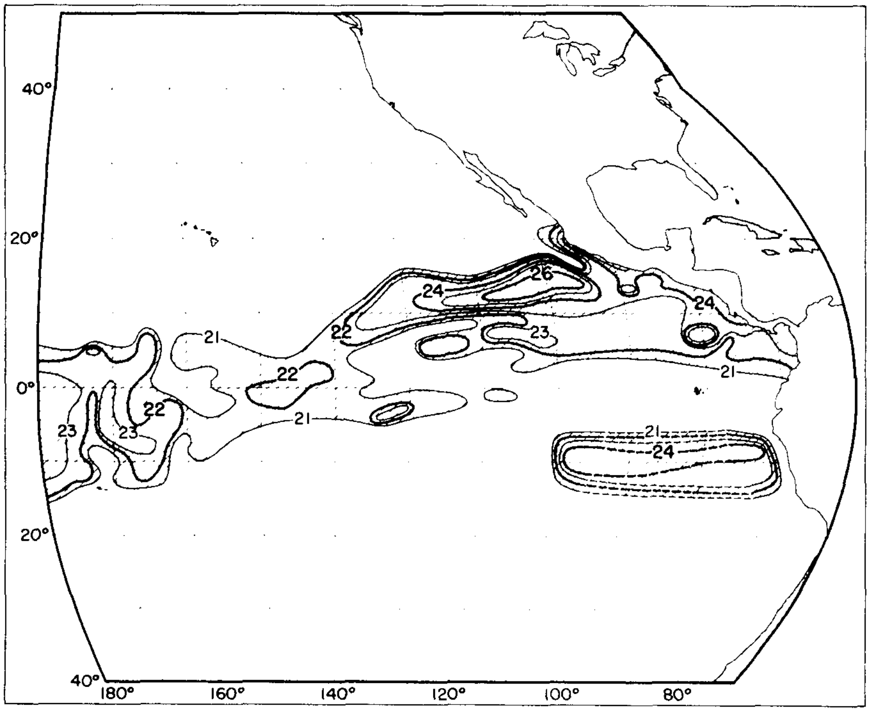

FIGURE 6.—Average water temperature in the eastern Pacific Ocean at those depths where the concentration of dissolved oxygen is 3.5 ml/l. Deeper water is cooler and lower in oxygen, shallower water is warmer and has more oxygen. See Figure 1b for the relationship between skipjack tuna size and upper temperature limits.

on individual sizes of skipjack tuna composing the catch nor synoptic information on the vertical distribution of temperature and dissolved oxygen in the fishing area. 2) The degree to which catch per unit effort measures fish abundance may vary greatly with gear type, fish size, and environmental conditions. For example, the habitat hypothesis implies that purse seines (which fish the upper 50 m or so of the water column) should be most effective in those parts of skipjack tuna habitat with a shallow floor. In fact, the eastern Pacific purse seine fishery operates almost entirely in waters with a skipjack tuna habitat-floor at depths of 50 m or less (c.f. our Figure 3 and fig. 1 of Matsumoto 1975). Efforts to catch skipjack tuna by purse seining in Hawaiian waters—where the habitat-floor lies at depths near 200 m (Figure 3)—have been ineffectual (Murphy and Niska 1953). Green (1967) reported strong positive correlations between the success of purse seining for eastern Pacific skipjack tuna and yellowfin tuna, *Thunnus albacares*, and the presence of shallow ($\leqslant$60 m to top), steep ($\geqslant$0.55°C cm^{-1}) thermoclines. 3) Commercial fishermen naturally fish only where they expect to find and catch fish; thus, fishing effort tends to be very unevenly distributed.

A partial test of the habitat hypothesis might be achieved through experimental fishing in and near the hatched areas of Figure 6; fishing effort, the sizes of captured skipjack tuna, and vertical distributions of temperature and dissolved oxygen would need to be measured at each fishing location. But, experimental fishing—even if conducted in a thorough and systematic fashion—might not yield a conclusive test of the hypothesis, because there would still be no guarantee that catch per unit effort accurately reflected fish abundance (reason 2 above).

We advocate, instead, the application of ultrasonic telemetry to test the skipjack tuna-habitat hypothesis. Because skipjack tuna tagged with ultrasonic transmitters tend to stay with their school (Yuen 1966) and because skipjack tuna schools tend to be homogeneous with respect to fish size (Brock 1954), the track of a single tagged fish could be taken as representative of a large number of normally behaving, similarly sized fish. Pressure-sensitive ultrasonic transmitters (like that described by Luke et al. 1973) would permit continuous monitoring of fish position in all three spatial dimensions through time. Spatial-temporal coordinates of fish could then be compared with synoptic data on vertical distributions of temperature and dissolved oxygen. A few dozens of such comparisons, for fish of various sizes in waters with diverse vertical distributions of temperature and dissolved oxygen, would constitute a valid and sufficient test of the habitat hypothesis. Toward this end, preliminary telemetry work is now underway at this Laboratory.

SUMMARY

Work with captive skipjack tuna at this Laboratory has yielded information on the temperature and dissolved oxygen requirements of this species. If these laboratory results apply to skipjack tuna in nature, they provide new insight into the evolution of migration in skipjack tuna populations, make it possible to account for the geographic distribution of skipjack tuna on the basis of environmental conditions, and provide means for predicting their movements in major fisheries such as those of the eastern tropical Pacific.

In particular, we suggest that only young skipjack tuna can inhabit tropical surface waters, and that the habitat of adult skipjack tuna in the tropics is the thermocline and not the warmer surface layer, as has generally been thought. Since the thermocline in many areas is too oxygen-poor to support these active fish and the well-oxygenated surface layer is too warm for adult skipjack tuna, only heat-tolerant young skipjack tuna can live in those areas. As they grow, these fish are forced to move into areas where well-oxygenated water of the proper temperature is more readily available.

Up to now, it has not been possible to trace the movements of migrating skipjack tuna largely because they move through areas of many millions of square miles, at unknown depths. Knowledge of their temperature and dissolved oxygen requirements dramatically reduces the scope of the problem: the fish should be in a well-defined layer of water, of directly and easily measured thickness, whose geographic extent can be sharply defined with either historical or current oceanographic observations.

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