OXYCLINE CHARACTERISTICS AND SKIPJACK TUNA DISTRIBUTION IN THE SOUTHEASTERN TROPICAL ATLANTIC

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ABSTRACT

A shallow layer of low oxygen concentration, containing minimum values frequently less than 1.0 ml/l and a strong oxycline, was measured on two cooperative cruises in the southeastern tropical Atlantic Ocean and found to be consistent with previous portrayals and hypotheses based on fragmentary data. The low-oxygen layer was in the form of a thick wedge off the southwestern coast of Africa, extending from about lat. 18° to 3° S. The oxycline overlying the low-oxygen layer was generally coincident with a pycnocline and was found at depths of 20-50 m in most of the area surveyed, as revealed by the topography of the 3.5 ml/l iso-oxygen surface. It is believed that a shallow oxycline has a strong influence on the distribution and availability of skipjack tuna schools. The hypothesis was tested by overlaying school sighting positions on the 3.5 ml/l topography. The association between sightings and oxycline depth was further defined by developing a linear "equation" relating the two variables as follows: $s = 23.15 - 0.59z$, where s is the number of school sightings, z is the depth of the 3.5 ml/l surface, and 23.15 and 0.59 are constants. A similar correlation was attempted with school sightings and habitat layer thickness, but the results were less systematic and convincing than the oxycline correlation.

A shallow oxycline containing low values of dissolved oxygen concentration should serve as a lower boundary of the environment habitable by surface schooling tunas. In a study of the relationship of thermocline depth to success of purse seining of tuna in the tropical Pacific, Green (1967) stated that an oxycline approximately coincident with the thermocline could play a major role in restricting the fish to near surface waters. Work on the oxygen requirements of captive skipjack tuna in the Southwest Fisheries Center Honolulu Laboratory[3] by R. M. Gooding and W. H. Neill indicated a 4-h TL_m (median tolerance limit) between 2.4 and 2.8 ml O_2/l, and in experiments with gradually declining oxygen concentrations an alarm threshold was found near 3.5 ml/l. If we regard the 3.5 ml/l iso-oxygen surface to be the "floor" of habitable environment of surface schooling tunas in tropical waters, then the topography of this surface becomes significant in describing their environment.

The shoaling of the oxycline, the floor of the habitable environment, may serve not only to crowd the skipjack tuna schools to the surface, but also to influence the lateral distribution of the fish schools through other ecological factors associated with the shoaling. The oxycline is imbedded in the thermocline, which is brought up to or near the sea surface under conditions of upwelling which seasonally occur off the southwestern coast of Africa. Such conditions, when well developed, will lead to the development of fronts, which tend to concentrate forage, and higher rates of primary and secondary productivity to sustain larger forage populations; both processes tending to concentrate predators such as tunas, as described by Blackburn (1965).

BACKGROUND INFORMATION ON OXYGEN MINIMA IN THE SOUTHEASTERN ATLANTIC

The oxygen minima in the Atlantic have been studied since the early part of this century. These studies have not, however, resulted in a definitive explanation of the mechanisms of formation of these low-oxygen layers. While many theories have been proposed to explain the origin of these layers, the mechanisms generally cited as being most significant are either an extremely high biochemical oxygen consumption or low rates of oxygen replenishment by mixing processes. Some recent papers have dealt with a synthesis of these

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processes in an attempt to give a more complete explanation of the observed patterns (Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968).

Proponents of the first mechanism argue that an oxygen minimum layer is formed as a result of biochemical oxidation of organic matter that has accumulated at intermediate depths due to specific gravity relationships between seawater and sinking detritus (Seiwell 1937; Miyake and Saruhashi 1956). Those supporting the second mechanism suggest that an oxygen minimum will be formed at the relatively still boundary between circulating water masses where replenishment of oxygen will be minimal. This view was first advanced by Jacobsen in 1916 and was later supported by Dietrich and Wüst (Richards 1957).

More recent studies (Redfield 1942; Wyrtki 1962; Bubnov 1966, 1972; Menzel and Ryther 1968) have stressed the importance of advective processes in the formation of oxygen minimum surfaces. Redfield (1942) hypothesized that the deep oxygen minimum of the Atlantic could be formed by advection along isentropic surfaces of water carrying a heavy load of organic detritus and solutes from high latitude convergence areas. Subsequent oxidation of the organic load forms a minimum. Wyrtki (1962), Menzel and Ryther (1968), and Bubnov (1966, 1972) considered high oxygen consumption as necessary for initial formation of low-oxygen water with advective and mixing processes controlling its position and movement. Wyrtki (1962) contended that oxidation occurring in the layer of least advection results in formation of an oxygen minimum, which can spread by mixing into other water masses. Menzel and Ryther (1968) and Bubnov (1966, 1972) argued that oxygen depleted water will form in specific areas due to high biochemical oxygen consumption and that these waters are then spread by advection and turbulent diffusion.

Bubnov (1972) stated that the main factors controlling the formation of an oxygen minimum are the rate of biochemical oxidation, the density stratification of the water, and the supply of oxygenated water to bottom layers. In the southeastern tropical Atlantic the presence of one or more of these factors results in highly favorable conditions for the formation of an oxygen minimum. The coastal region off South-West Africa has strong upwelling conditions which result in high organic production and subsequent high oxygen consumption (Hart and Currie 1960). Though the coastal waters are weakly stratified in comparison with the region of the Congo River effluent, there is, nonetheless, a well-developed pycnocline which inhibits downward-mixing of highly oxygenated surface waters (Visser 1970; Bubnov 1972). In addition, the deep waters of the Angola Basin are somewhat lower in oxygen than those of the western basin of the South Atlantic. This reduces the amount of oxygen which will be mixed into the upper layers by upwelling or turbulent diffusion (Bubnov 1972). Taft (1963) and Visser (1970) suggested that the waters to the north of lat. 20°S off the coast of South-West Africa may be isolated from the highly oxygenated deepwater masses formed at high latitudes, thus inhibiting the renewal of oxygen from this source.

Because of the favorable conditions for the formation of low-oxygen water in the coastal region of South-West Africa, it has been suggested that this area is a source for much of the water that forms the oxygen minimum surfaces in the South Atlantic. Taft (1963) plotted the oxygen and salinity distributions on surfaces of constant potential specific volume anomaly for the South Atlantic. On the 125, 100, and 80 cl/t surfaces (σ_θ 26.81, 27.07, and 27.49 g/l, respectively), the isopleths of both oxygen and salinity are zonal at lat. 20°S. The areas of lowest oxygen concentration are located just north of lat. 20°S off the coast of South-West Africa, strongly suggesting that this region serves as a source area for low-oxygen water which is then transported westward to form the primary minimum at 300-600 m in the study area).

In a study by Menzel and Ryther (1968), the concentration of dissolved organic carbon in the South Atlantic was found to be essentially constant below 400-500 m while the oxygen content varied. Based on this finding, they concluded that oxygen concentrations in the minimum layer will not be further reduced by in situ decomposition of organic matter. They suggest that low-oxygen water is formed off South-West Africa and is then distributed horizontally along isentropic surfaces to form the primary oxygen minimum layer. Changes in the oxygen content occur by mixing with water masses of higher oxygen content, resulting in the increase of oxygen concentrations as the water moves farther from its source.

Bubnov (1972) identified three areas off South-West Africa where waters of very low oxygen content are formed (see Figure 1): 1) the shelf region to the south of lat. 17°S, 2) the coastal region extending from long. 8°-10°E to the shelf, and from lat. 7°-9°S to 17°-18°S, and 3) the region of the quasi-stationary cyclonic gyre to the west of long. 6°E.

In the shelf region south of lat. 17°S, water with extremely low-oxygen content (<1 ml/l) forms in the near-bottom layer (80-150 m) and spreads northward and westward beneath the warmer, less dense surface water by advection and turbulent diffusion. This water forms the shallow minimum layer that is characteristic of this region, extending westward to about long. 0° where it loses its identity due to mixing.

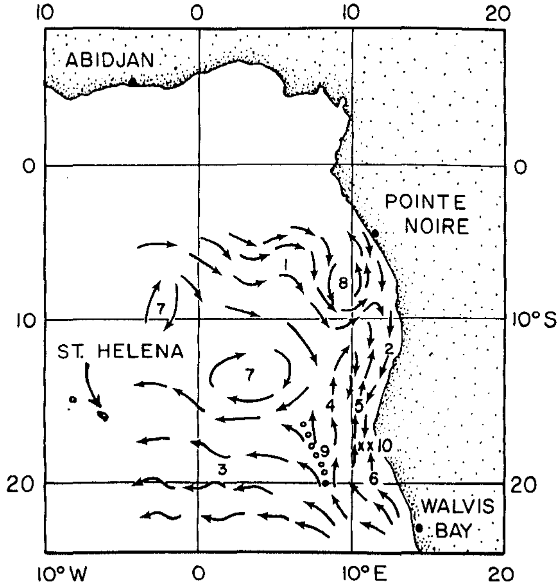

FIGURE 1.—Diagram of geostrophic water circulation in the 0 to 100 m layer. 1) South equatorial countercurrent; 2) Angola Current; 3) west (main) branch of Benguela Current; 4, 5, 6) north branches of Benguela Current; 7) eddies in inner region of cyclonic gyre; 8) anticyclonic curl; 9) Benguela divergence; 10) merging zone of Angola Current and north littoral branch of Benguela Current. From Moroshkin et al. (1970).

The "eastern coastal region" and the region of the cyclonic gyre are areas where low-oxygen water (<1 ml/l) forms at "intermediate" depths (Bubnov 1972). These waters apparently are advected and mixed to the west, forming the primary oxygen minimum in the eastern South Atlantic. These observations provide further evidence to support the hypothesis that the coastal waters off Southwestern Africa are a source for much of the low-oxygen water that forms the oxygen minima in the South Atlantic.

RESULTS OF JISETA CRUISES

In 1968 the National Marine Fisheries Service, then Bureau of Commercial Fisheries, joined with the U.S. Coast Guard and the Missao de Estudos Bioceanologicos e de Pescas de Angola in the Joint Investigation of the Southeastern Tropical Atlantic (JISETA); an oceanographic and biological investigation in the coastal waters of southwestern Africa. Distribution of tunas and oceanographic conditions from the Equator to lat. 18°S were investigated on cooperative cruises of the RV *Undaunted,* the USCGC *Rockaway*, and the RV *Goa* during February through April and September through December 1968.

Low-Oxygen Layer

Vertical sections of dissolved oxygen concentration developed from the JISETA data (Cook et al. 1974) characteristically showed a layer of low oxygen concentration, including a minimum which frequently was <1.0 ml/l and occasionally <0.5 ml/l in concentration. The minimum values were not well defined because of the means of sampling employed: 1 cast of 10 Niskin bottles spaced throughout the upper 1,000 m of the water column at each station. However, the samples were spaced well enough to portray the layer of low concentration and the sharp oxycline which formed its upper boundary.

The transects obtained in March 1968 (Figures 2, 3) showed a layer of oxygen concentration <1.0 ml/l of variable thickness (50-450 m) extending from lat. 15° to 18°S in the upper 500 m of the water column. In the southern portion of the area the layer was thicker and nearer the sea surface.

In the October-November transects (Figures 4, 5) a thick layer of water containing <1.0 ml/l dissolved oxygen was found to extend from lat. 17° to 7°S in the upper 600 m of the water column. Once again the layer was thicker (up to 550 m) and nearer the surface in the southern portion of the area. In the northern portion it thinned to <100 m and was detected at about 300-400 m depth at the outer stations, about n.mi. (180 km) offshore.

The form of the layer of very low oxygen concentration (<1.0 ml/l) observed in October-November 1968 (Figure 6) appears to be consistent with Bubnov's (1972) contention that the source of the layer is located in coastal waters between lat. 18° and 23°S, from which it is advected northward by the northern branches of the Benguela Cur-

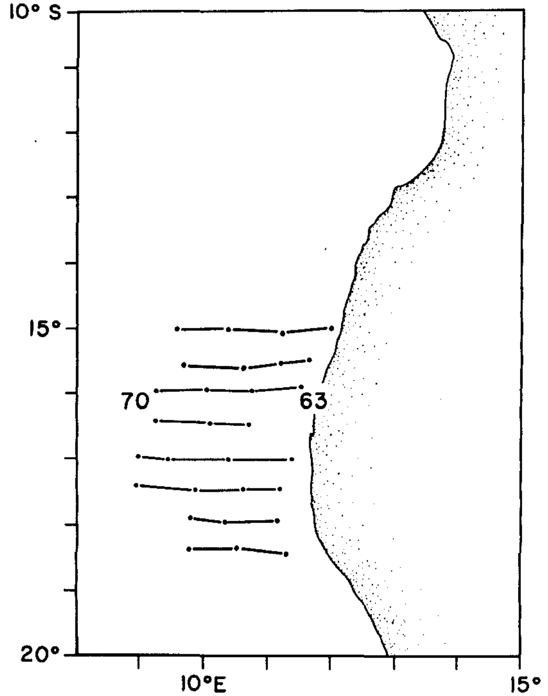

FIGURE 2.—Locations of transects of dissolved oxygen concentration conducted by *Undaunted* during 8-16 March 1968. From Cook et al. 1974.

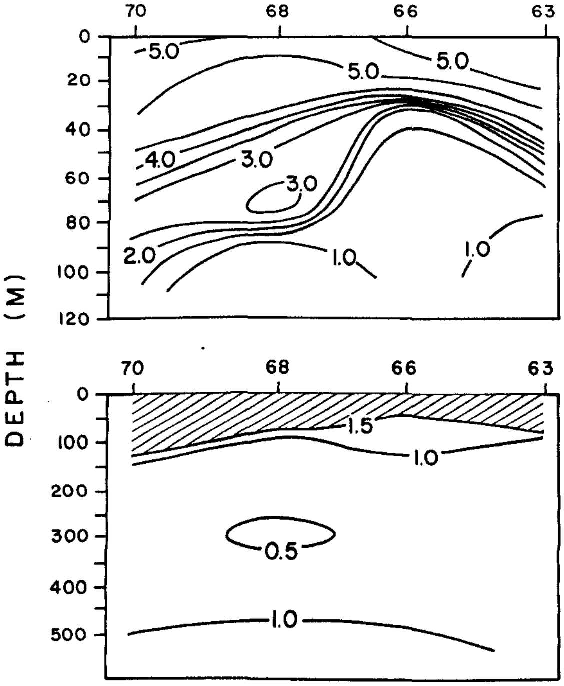

FIGURE 3.—One of the transects of dissolved oxygen concentration (milliliters per liter) produced from *Undaunted* data (8-16 March 1968). From Cook et al. 1974.

rent. The apparent divergence of the layer from the coast shown in the onshore-offshore transects north of lat. 9°S (Cook et al. 1974) also is consistent with the general direction of flow given for the extension of the current.

Although a subsurface oxygen minimum was found throughout the area surveyed from lat. 18°S to the Equator, the layer of very low oxygen concentrations (<1.0 ml/l) extended northward only as far as lat. 7°-8°S. The increase in oxygen concentration northward from those latitudes is the result of either westward turning of the northward currents carrying the low oxygen concentrations as suggested by Bubnov (1972) or increased mixing rates attenuating the oxygen minimum.

Oxycline

Overlying the layer of low oxygen concentration throughout its extent was an intense oxycline. The range of concentrations in the oxycline usually was from 2.0 to 4.0 ml/l, but was found to be as great as from 1.0 to 5.0 ml/l in the southern portion of the surveyed area. The oxycline thickness ranged from about 40 m to 10 m, producing intense vertical gradients when thinnest. The most intense gradients were found on the shoreward ends of the transects and in the southern portion of the surveyed area.

The 3.5 ml/l iso-surface was selected to portray oxycline topography because it was found in the upper oxycline throughout the area surveyed (lat. 18°S-Equator) and because this oxygen concentration has been found to be significant in the physiology and distribution of skipjack tuna in the eastern tropical Pacific (Neill see footnote 3; Barkley et al.[4]). The resulting topographies for the February-April and October-November periods (Figures 7, 8) were generally of low relief and shallow (<50 m) except at the seaward end of transects south of lat. 16° S in March and north of lat. 2°-3° S in October-November. Two large areas of shallow depths (<25 m) to the oxycline were found in the October-November data field, from lat. 10° to 16°S and from lat. 5° to 7°S. Due to the

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[4] Barkley, R. A., W. H. Neill, and R. M. Gooding. 1977. Skipjack tuna habitat based on temperature and oxygen requirements. Unpubl. Manuscr. 12 p. Southwest Fish. Cen. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, P.O. Box 3830, Honolulu, HI 96812.

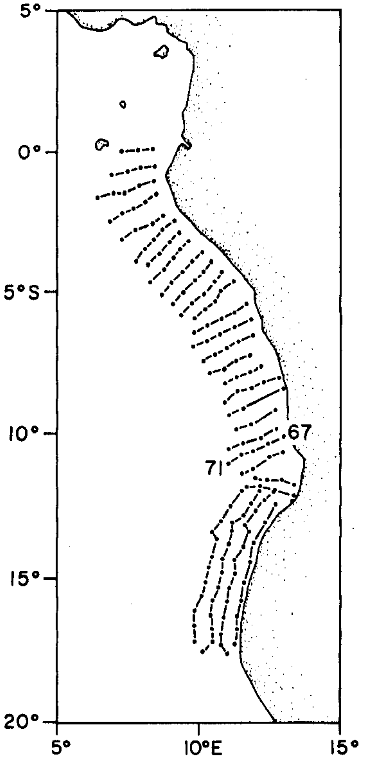

FIGURE 4.—Location of transects of dissolved oxygen concentration by *Undaunted* and *Rockaway* 15 October-21 November 1968. Derived from Cook et al. 1974.

relatively incomplete sampling grid in the February-April period, little can be learned from any attempts to compare the results of the two periods.

Pycnocline

The density field of the upper waters off southwestern Africa is determined mostly by temperature, except in the area influenced by the effluent of the Congo River (Bubnov 1972). Results of the JISETA cruises support this contention, showing a well-developed thermocline throughout the area.

During the October-November period thermocline gradients increased from south to north with the most intense gradients found off the Congo River. The sea-surface temperature ranged from <17° C in the south (lat. 18° S) to >26° C near the Equator. In the February-April period the thermocline appeared to be more intense than during the October-November period but generally con-

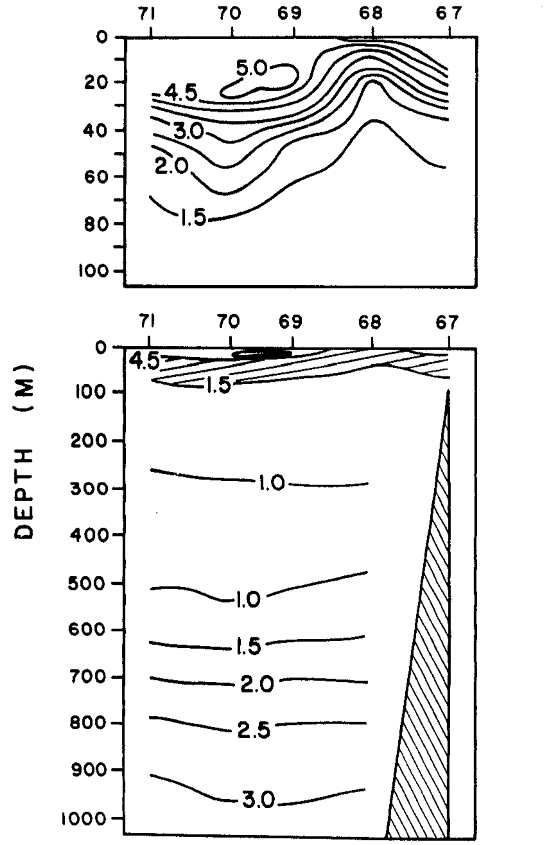

FIGURE 5.—One of the transects of dissolved oxygen concentration (milliliter per liter) produced from *Undaunted* data (22-23 October 1968). From Cook et al. 1974.

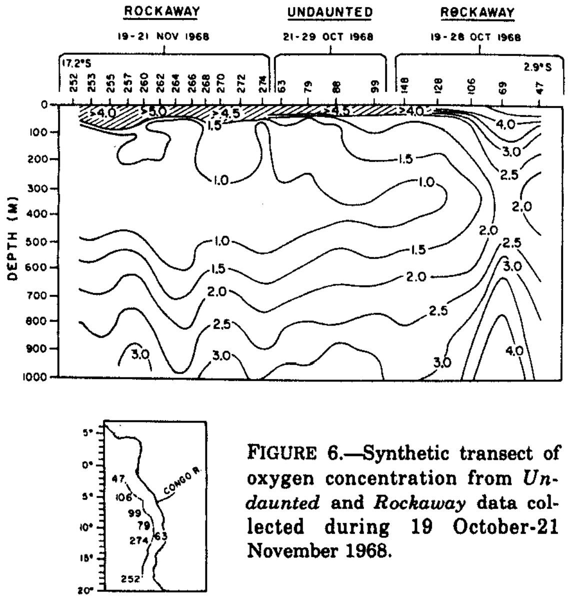

FIGURE 6.—Synthetic transect of oxygen concentration from *Undaunted* and *Rockaway* data collected during 19 October-21 November 1968.

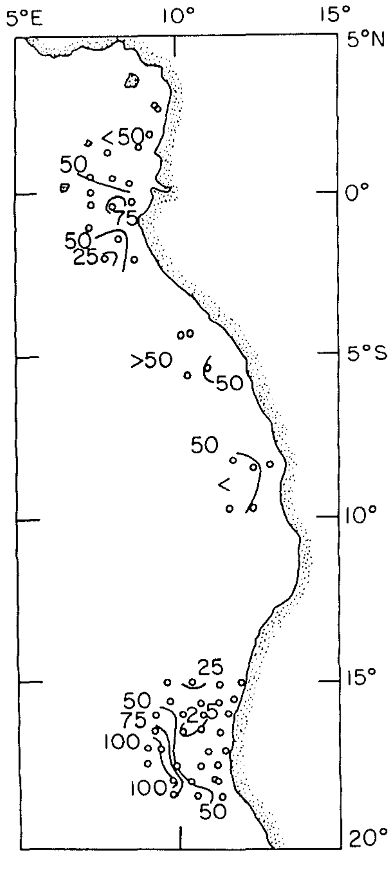

FIGURE 7.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* data, February-March 1968.

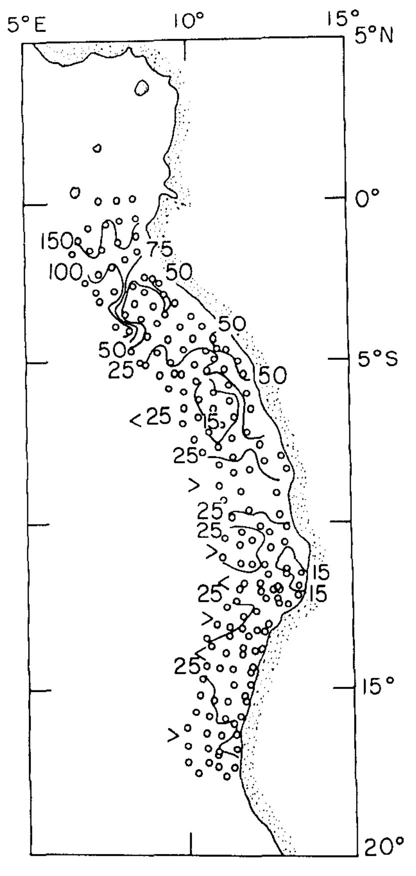

FIGURE 8.—Depth (meters) to the 3.5 ml/l iso-oxygen surface from *Undaunted* and *Rockaway* data, October-November 1968.

stant throughout the limited area surveyed. The sea-surface temperature ranged from 22°C in the south (lat. 18°S) to 29°C in the north (lat. 2°N).

In order to portray the pycnocline topography and minimize the differences in surface heating in the two periods, an isopycnal surface found near the bottom of the thermocline, the $\sigma_t = 26.0$ surface, was chosen (Figures 9, 10). Comparison of the vertical sections of density and oxygen from the JISETA cruises (Cook et al. 1974) shows that the 26.0 iso-σ_t surface parallels the oxycline and is found in its lower levels. Therefore the topography of the isopycnal surface also should reflect geostrophic circulation patterns in the lower oxycline.

During the October-November 1968 period the 26.0 g/l topography (Figure 10) deepened nearshore north of lat. 10°S, but was shallow and irregular south of there. The topography north of lat. 10°S indicates a general southward flow in the upper layer from about lat. 4° to 10°S, corresponding with the southward Angola Current described by Moroshkin et al. (1970), but not extending as far south as they portray it (Figure 1).

RELATIONSHIP BETWEEN OXYCLINE DEPTH AND SKIPJACK DISTRIBUTION

Variations in the thickness of the habitable environment of skipjack tuna, bounded beneath by the oxycline, should strongly inflence the distribution and availability of surface schooling tunas. To test this contention, the positions of sightings of skipjack schools during the October-November 1968 cruise period were plotted on a map of oxycline (3.5 ml/l) topography (Figure 11). A cursory study of this plot reveals that the fish were generally sighted where the oxycline was <50 m deep, and over 80% of the schools were seen where it was <30 m deep.

An apparent relationship between school distribution or availability and oxycline depth can

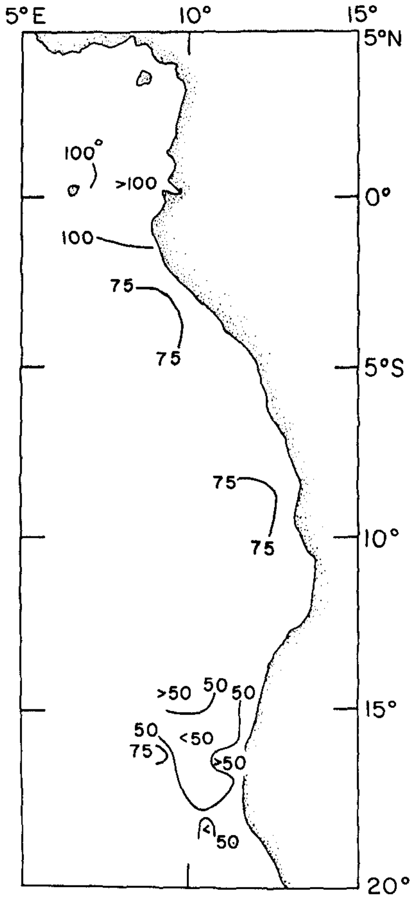

FIGURE 9.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* data, February-April 1968.

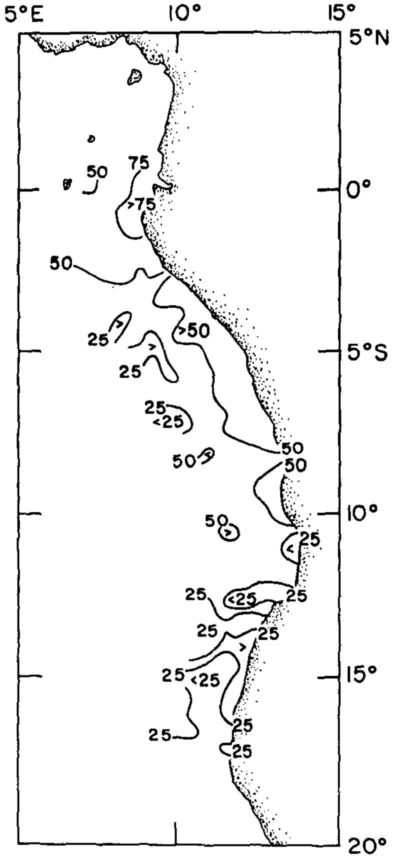

FIGURE 10.—Depth (meters) to the 26.0 g/l σ_t surface from *Undaunted* and *Rockaway* data, October-November 1968.

best be demonstrated with the data collected in October-November, involving 49 sightings with relevant oxygen data. After grouping the oxycline depth measurements into 5-m classes and plotting a sighting versus depth-frequency bar graph (Figure 12), it appears that a smooth inverse relationship exists for depths >10 m. By assigning the central value of each depth class to each sighting in the class, a least squares linear "equation" can be obtained for sighting frequency as a function of oxycline depth in the form:

$$s = a + mz \qquad (1)$$

where s = the number of sightings
z = the depth of the 3.5 ml/l surface
a and m = constants, in this case, equal to 23.15 and −0.59, respectively, leading to

$$s = 23.15 - 0.59z \qquad (2)$$

as the "equation." Note that the equation is defined only over the range of depths from 11 to 40 m. At depths greater than this, school sightings may be difficult to make and at depths less than this the fish may avoid the thin habitable layer.

Although the relationship portrayed in the bar graph appears to be nonlinear, the errors introduced by interpolation between sampling bottle depths and the arbitrary assignment of central values to the frequency classes make any attempts to obtain a best-fit, nonlinear "equation" unwarranted. The linear relationship shown above is about all the sophistication the data will bear, particularly in view of the small number of fish school sightings.

To further pursue the role of environmental conditions in influencing the distribution of skipjack tuna, we considered the concept of habit layer

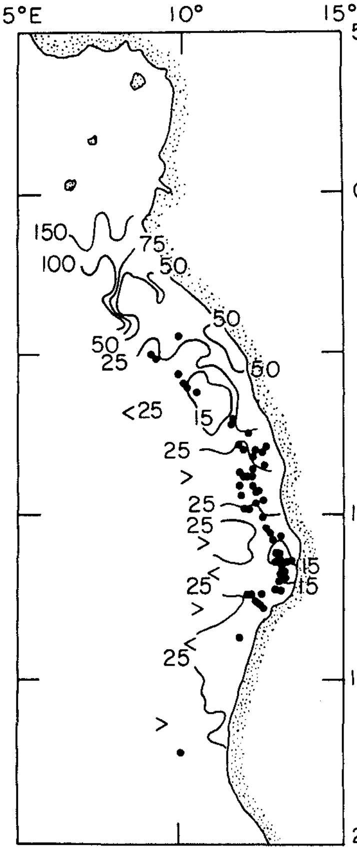

FIGURE 11.—Location of sightings of schools of skipjack tuna during October-November 1968 plotted on the observed ocycline (3.5 ml/l) topography.

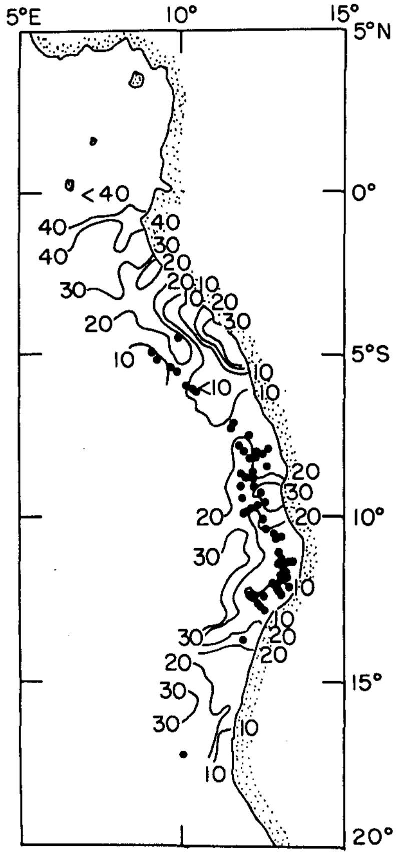

FIGURE 13.—Location of sightings of schools of skipjack tuna (dots) and habitat thickness (meters) from *Undaunted* and *Rockaway* data, October-November 1968.

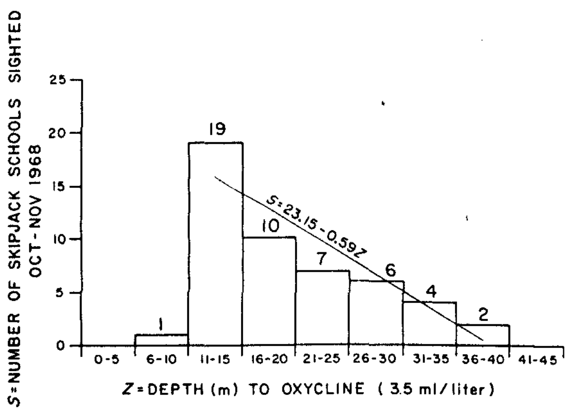

FIGURE 12.—Relationship between skipjack school sightings and oxycline depth from *Undaunted* and *Rockaway* data for October-November 1968.

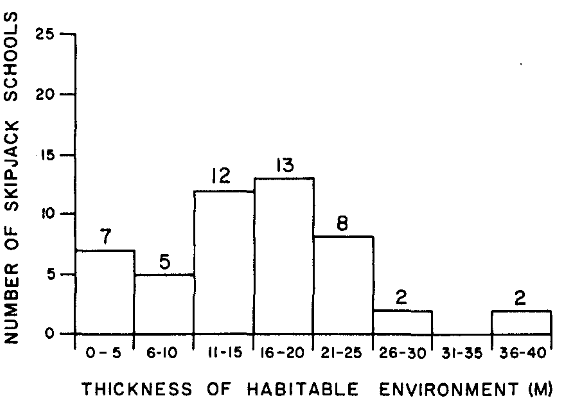

FIGURE 14.—Relationship between skipjack school sightings and habitat thickness from *Undaunted* and *Rockaway* data for October-November 1968.

developed by Barkley et al. (see footnote 4). They defined the habitat of adult skipjack to be bounded above by the sea surface or 22°-26°C (for 9- to 4-kg fish) and below by 18°C or 3.5 ml/l oxygen concentration, whichever is shallower. We plotted the skipjack tuna school sightings on a horizontal chart of habitat layer thickness (using 24°C) for the October-November cruise period (Figure 13). The distribution of school sightings at various habitat layer thicknesses (Figure 14) is considerably different from that at various oxycline depths. Many points in the school sightings versus oxycline depth plot (Figure 12) have shifted to shallower classes in the school sighting versus habitat thickness plot, including seven observations in habitat thicknesses of 5 m or less. This shift is the consequence of regarding the 18°C isothermal surface as the floor of the habitat when it is shallower than the oxycline and assuming that it has a constraining effect equal to that of the 3.5 ml/l oxygen surface. The validity of this assumption is unknown, but comparison of the two distributions (Figures 11, 13) suggest that the 3.5 ml/l oxygen surface has a stronger effect on the skipjack tuna than the 18°C isothermal surface.

The question of whether it is school distribution or availability (to a fishing method) which has been related to oxycline depth cannot be resolved without an independent assessment of tuna school distribution by a different method. 'The means used to locate tuna schools is essentially that employed by crews of purse seiners and live-bait boats; a watch is maintained for bird activity above feeding or "breezing" schools. This technique reveals only those schools which are available to seines or pole-and-line fishing methods, hence it would be more accurate to consider the factor portrayed in Equation (2) as availability rather than distribution. Those fish not closely approaching the surface would not be detected and would not be available to these harvesting methods.

The pragmatic significance of the relationship between skipjack tuna school availability and oxycline depth lies in its use by fishermen and fishery scientists, the former for more efficient harvest strategy and the latter for more accurate resource assessment. The coincidence of the oxycline and thermocline should provide a very strong lower barrier to downward excursions of tropical tunas, perhaps even strong enough to prevent an encircled school from escaping by sounding before the seine is pursed. If this were true, the efficiency of capture by purse seine would be greater in waters containing a shallow oxycline.

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