North Pacific Albacore Ecology and Oceanography

R. MICHAEL LAURS and RONALD J. LYNN

Southwest Fisheries Science Center National Marine Fisheries Service, NOAA La Jolla, California 92038

ABSTRACT

Albacore, *Thunnus alalunga*, is a wide-ranging tuna species occurring between latitudes 10° and 50° N in the North Pacific Ocean. Albacore are a resource which supports important U.S. and Pacific-nation commerical fisheries and U.S. recreational fisheries. There is a growing body of evidence that there are two subgroups of albacore that have different migratory patterns, modal sizes, growth rates, and spawning periods, although they do not appear to be genetically distinct. Pre-spawning albacore, two to five years old, are highly migratory and conduct well-defined, trans-Pacific migrations. The spawning adults are generally confined within the subtropical and tropical zones of the central North Pacific. Their distribution and migration are markedly influenced by the marine environmental conditions associated with the waters of the North Pacific transition zone and its frontal boundaries. The subarctic and subtropical fronts are regions of large gradients in temperature and salinity which lie in bands across much of the North Pacific. The dynamic processes that maintain these gradients influence the nutrient and biomass distribution. The major centers of albacore catch are found about these fronts and within the transition zone waters that lie between them.

Introduction _____

Albacore, Thunnus alalunga, is a wide-ranging tuna species occurring between latitudes 10° and 50° N in the North Pacific Ocean. There is a general geographical separation by age, spawning adults occurring mostly in the central waters between latitudes 10° and 20° N and pre-spawning juveniles making extensive migrations between latitudes 30° and 50° N. The resource supports important U.S. commercial and recreational fisheries and several foreign fisheries. The distribution, availability, and migration of the albacore, as well as its vulnerability to capture, are markedly influenced by marine environmental conditions. A general review of the ecology, biology, and fisheries operating on the resource are discussed in this report with emphasis on the physical oceanographic regimes associated with the North Pacific transition zone.

North of the subarctic front the waters are cold and have low salinity. South of the subtropical front waters are warm and have high salinity. The waters between these large water masses are transitional in characteristics and are termed the North Pacific transition zone. The narrow zones where the changes in properties are abrupt are termed fronts. The schematic representation of ocean fronts presented in Figure 1 is a simplification of the complex features found.

Fisheries Harvesting North Pacific Albacore _____

Japan and the United States account for the majority of the catches of North Pacific albacore, catching approximately 72% and 26%, respectively, from 1965 through 1985. Canada, Korea, and Taiwan each land about 0.5% to 1% of the total catch. Historically, the Japanese have had two fisheries that harvest North Pacific albacore, a pole-and-line surface fishery operating during spring and summer and a longline subsurface fishery operating during winter. In 1978, a third Japanese fishery gained importance with the



Schematic representation of the major fronts in the temperate zone of the North Pacific based upon numerous individual observations (dots). The transition zone lies between the fronts.

dramatic expansion of summer gillnet fishing targeting albacore.

For several decades the pole-and-line (bait boat) fishery extended from near the coast of Japan eastward to about 150° E. In the early 1970's, the fishery was expanded further eastward within the Kuroshio extension waters to near the dateline. However in the mid-1980's, it was contracted back to about the same distribution as earlier. The Japanese longline fishery is conducted across much of the North Pacific, and by 1981, gillnet fishing operations had also spread almost entirely across the North Pacific, mostly within the North Pacific transition zone waters. The major centers of catches of the Japanese pole-and-line and longline fisheries are shown in Figure 2A and the distribution of the gillnet fishery in 1981 in Figure 2B.

The U.S. North Pacific albacore fishery, which began in the early 1900's, uses surface trolling and pole-and-line fishing gear (Dotson 1980). The fishery takes place during summer and autumn, and for many decades has operated in waters within a few hundred miles of the coast between northern Baja California, Mexico, and British Columbia, Canada. In 1975, the U.S. troll fleet began a broad westward extension of its operating range (Laurs and Nishimoto 1979). Beginning by the late 1970's, 35 to 50 vessels would start to fish near the date line in about May, and progress eastward across the mid-North Pacific in transition zone waters, ending the fishing season in autumn in California Current waters off the west coast of the United States. The main centers of catches of the U.S. fishery are shown in Figure 2A.

Major geographical variations in the location of the U.S. coastal fishery occur; during some periods it is centered in waters off the Pacific Northwest, during others, off southern-central California (Laurs et al. 1976). These geographical shifts in the location of the fishery have been linked to variations in largescale environmental conditions (Clark et al. 1975).

The U.S. albacore industry through the cooperation of American Fishermen's Research Foundation¹ and NOAA/NMFS scientists has conducted numer-

¹ The American Fishermen's Research Foundation is an albacore fishing industry non-profit organization funded by assessments imposed by the industry on landings of albacore caught by U.S. fishermen. The funds are used for research and education purposes.



(A) Major centers of catch for Japanese Pole-and-line, longline, and U.S. jigboat fisheries. The contoured and shaded regions represent approximately 75% of total annual average for the years indicated for each fishery. The contoured regions having finer hatching (Japanese baitboat and U.S. jig and baitboat only) indicate areas of highest concentrations of catch. (B) Distribution of the Japanese drift gill-net fishery for North Pacific albacore in 1981, indicated by the shaded area.



Figure 3

Annual catches of North Pacific albacore by country and year for 1955–1983 (from A. Coan, G. Rensink, C. Perrin, and F. Miller, NMFS SWFSC Adm. Rep. LJ-90-21, "Summary of the 1989 North and South Pacific albacore fisheries data" 1990).

ous research operations, including a series of exploratory fishing and research operations to evaluate the feasibility of establishing a winter U.S. longline fishery for albacore in the eastern Pacific (Laurs and Dotson 1983). The results of the experiments are encouraging, and while a number of fishermen have expressed an interest in participating in this winter expansion of the U.S. albacore fishery, none are doing so at this time.

Annual catches of North Pacific albacore by country and gear type are given in Figure 3 for years 1955–1989 and in Table 1 for years 1952–1988. Fishing effort and catch in both the Japanese baitboat and U.S. surface fisheries have declined beginning in the early 1980's. In contrast, recent landings and effort in the Japanese longline fishery have been relatively constant and there has been a rapid development of Asian gillnet fisheries that take large numbers of albacore in the North Pacific.

There are a number of factors which are associated with the decline in the traditional North Pacific albacore surface fisheries, but the relative importance of these factors is unknown. Parrish et al. (1989) discuss trends and status of the fisheries and the North Pacific albacore population.

Stock Structure _

There is a growing body of evidence (Brock 1943; Laurs and Lynn 1977; and Laurs and Wetherall 1981) that the population of North Pacific albacore is not as homogeneous as has been assumed (Clemens 1961; Otsu and Uchida 1963). Results from tagging studies suggest that there are two subgroups of albacore which have different migratory patterns (Laurs 1983), modal sizes (Brock 1943; Laurs and Lynn 1977; Laurs and Wetherall 1981), growth rates (Laurs and Wetherall 1981), and peak spawning periods (Wetherall et al. 1987). Off the coast of North America, the boundary between the two subgroups appears to be situated near 40° N. Although the proposed subgroups are differentiated by geographic dissimilarities in biological or fishery statistic criteria, they do not appear to be genetically distinct (Graves and Dizon 1989).

Migration _

North Pacific albacore are one of the most highly migratory species of tuna. The extent and degree of migration are most expansive in pre-adult ages between about 2 and 5 years. Fish of these ages may conduct trans-oceanic migrations or migrations across broad regions of the North Pacific, mostly within transition zone waters. The migration habits of the spawning adults, six years of age and older, are much more limited and are confined mostly within the subtropical and tropical zones of the central North Pacific.

Tagging results show that albacore that had been tagged and released in coastal waters off North America north of lat. 40° N have a different migration pattern than those tagged south of 40° N. For example, for fish that had been tagged and released in the northern area and had been at liberty for up to 5 years, 28 percent were recovered in the same general area as release, 54 percent west of long. 180°, 13 percent in coastal waters off North America south of 40° N and about 5 percent in the central eastern Pacific or unknown area of recovery (Fig. 4A). In contrast, for fish that had been tagged and released

| | North Pacific albacore workshop, May 18–19, 1989" 1989). | | | | | | | | | | | | | | | | | |
|-------------------|--|----------------------------|--------------------------|---------------|------------|---------------|--------------------------|--------|----------------------------|--------------------------|---------------|------------------|--------------|-------|-------------|---------------------|-------|----------------|
| | Japan | | | | Taiwan | | | Korea | | | United States | | | | | Canada | | |
| Year | Pole and line ^a | Long- line ^b | Gill net ^c | Othe: gear | r Total | Long- line | Gill net ^d | Total | Long- line ^e | Gill net ^d | Total | Pole and line | d Troll f | Sport | Gill net | Total | Troll | Grand Total |
| 1952 | 41,786 | 26,687 | | 237 | 68,710 | | | | | | | | 23,843 | 1,373 | | 25,216 | 71 | 93,997 |
| 1953 | 32,921 | 27,777 | | 132 | 60,830 | | | | | | | | 15,740 | 171 | | 15,911 | 5 | 76,746 |
| 1954 | 28,069 | 20,958 | | 38 | 49,065 | | | | | | | | 12,246 | 147 | | 12,393 | | 61,458 |
| 1955 | 24,236 | 16,277 | | 136 | 40,649 | | | | | | | | 13,264 | 577 | | 13,841 | | 54,490 |
| 1956 | 42,810 | 14,341 | | 57 | 57,208 | | | | | | | | 18,751 | 482 | | 19,233 | 17 | 76,458 |
| 1957 | 49,500 | 21,053 | | 151 | 70,704 | | | | | | | | 21,165 | 304 | | 21,469 | 8 | 92,181 |
| 1958 | 22,175 | 18,432 | | 124 | 40,731 | | | | | | | | 14,855 | 48 | | 14,903 | 74 | 55,708 |
| 1959 | 14,252 | 15,802 | | 67 | 30,121 | | | | | | | | 20,990 | 0 | | 20,990 | 212 | 51,323 |
| 1960 | 25,156 | 17,369 | | 76 | 42,601 | | | | | | | | 20,100 | 557 | | 20,657 | 5 | 63,263 |
| 1961 | 18,636 | 17,437 | | 268 | 36,341 | | | | | | | 2,837 | 12,061 | 1,355 | | 16,253 | 4 | 52,598 |
| 1962 | 8,729 | 15,764 | | 191 | 24,684 | | | | | | | 1,085 | 19,760 | 1,681 | | 22,526 | 1 | 47,211 |
| 1963 | 26,420 | 13,464 | | 218 | 40,102 | | | | | | | 2,432 | 25,147 | 1,161 | | 28,740 | 5 | 68,847 |
| 1964 | 23,858 | 15,458 | | 319 | 39,635 | 26 | | 26 | | | | 3,411 | 18,392 | 824 | | 22,627 | 3 | 62,291 |
| 1965 | 41,491 | 13,701 | | 121 | 55,313 | 16 | | 16 | | | | 417 | 16,545 | 731 | | 17,693 | 15 | 73,037 |
| 1966 | 22,830 | 25,050 | | 585 | 48,465 | 16 | | 16 | | | | 1,600 | 15,342 | 588 | | 17,530 | 44 | 66,055 |
| 1967 | 30,481 | 28,869 | | 520 | 59,870 | 17 | | 17 | | | | 4,113 | 17,826 | 707 | | 22,646 | 161 | 82,694 |
| 1968 | 16,597 | 23,961 | | 1,109 | 41,667 | 15 | | 15 | | | | 4,906 | 20,444 | 951 | | 26,301 | 1,028 | 69,011 |
| 1969 | 32,107 | 18,006 | | 1,480 | 51,593 | 21 | | 21 | | | | 2,996 | 18,839 | 358 | | 22,193 | 1,365 | 75,172 |
| 1970 | 24,376 | 15,372 | | 956 | 40,704 | 23 | | 23 | | | | 4,416 | 21,041 | 822 | | 26,279 | 354 | 67,360 |
| 1971 | 53,198 | 11,035 | | 1,262 | 65,495 | 24 | | 24 | | | | 2,071 | 20,537 | 1,175 | | 23,783 | 1,587 | 90,889 |
| 1972 | 60,762 | 12,649 | 1 | 921 | 74,333 | 25 | | 25 | | | | 3,750 | 23,608 | 637 | | 27,995 | 3,558 | 105,911 |
| 1973 | 69,811 | 16,059 | 39 | 1,883 | 87,792 | 35 | | 35 | | | | 2,236 | 15,667 | 84 | | 17,987 | 1,270 | 107,084 |
| 1974 | 73,576 | 13,053 | 224 | 1,065 | 87,918 | 40 | | 40 | | | | 4,777 | 20,187 | 94 | | 25,058 | 1,207 | 114,223 |
| 1975 | 52,157 | 10,060 | 166 | 402 | 62,785 | 28 | | 28 | 319 | | 319 | 3,243 | 18,975 | 640 | | 22,858 | 101 | 86,091 |
| 1976 | 85,336 | 15,896 | 1,070 | 1,394 | 103,696 | 37 | | 37 | 971 | | 971 | 2,700 | 15,932 | 713 | | 19,345 | 252 | 124,301 |
| 1977 | 31,934 | 15,737 | 688 | 1,039 | 49,398 | 61 | | 61 | 65 | | 65 | 1,497 | 10,005 | 537 | | 12,039 | 53 | 61,616 |
| 1978 | 59,877 | 13,061 | 4,029 | 3,209 | 80,176 | 53 | | 53 | 174 | | 174 | 950 | 16,682 | 810 | | 18,442 | 23 | 98,868 |
| 1979 | 44,662 | 14,249 | 2,856 | 1,280 | 63,047 | 81 | | 81 | 27 | | 27 | 303 | 6,801 | 74 | | 7,178 | 521 | 70,854 |
| 1980 | 46,743 | 14,743 | 2,986 | 1,516 | 65,988 | | | | 15 | | 15 | 382 | 7,574 | 168 | | 8,124 | 212 | 74,339 |
| 1981 | 27,426 | 18,020 | 10,348 | 959 | 56,753 | | | | 600 | | 600 | 748 | 12,694 | 195 | | 13,637 | 200 | 71,190 |
| 1982 | 29,615 | 16,762 | 12,511 | 1,054 | 59,942 | | | | 1,070 | | 1,070 | 425 | 6,661 | 257 | | 7,343 | 104 | 68,459 |
| 1983 | 21,098 | 15,103 | 6,884 | 471 | 43,556 | | | | 1,233 | | 1,233 | 607 | 9,512 | 87 | | 10,206 | 225 | 55,220 |
| 1984 | 26,015 | 15,111 | 10,569 | 3,898 | 55,593 | | | | 2,708 | | 2,708 | 1,030 | 9,378 | 1,427 | | 15,563 ^g | 50 | 73,914 |
| 1985 | 20,714 | 14,320 | 13,132 | 1,940 | 50,106 | | | | 5,447 | | 5,447 | 1,498 | 6,431 | 1,176 | 2 | 9,109 | 56 | 64,718 |
| 1986 | 16,096 | 12,945 | 9,749 | 2,192 | 40,982 | | | | | | | 432 | 4,708 | 196 | 3 | 5,339 | 30 | 46,351 |
| 1987 ^h | 19,091 | 14,642 | 7,617 | 1,394 | 42,744 | | | | | | | 158 | 2,766 | 74 | 5 | 3,003 | 104 | 45,851 |
| 1988 ^h | 7,000 | | | | 12,000 | | 11,000 | 11,000 | | | | 598 | 4,212 | 64 | 15 | 4,889 | 85 | 27,974 |

Table 1 Catches of North Pacific albacore in metric tons by fisheries, 1952-1988 (from N. Bartoo and Y. Watanabe, NMFS SWFSC Adm. Rep., "Report of the eleventh

^a Japanese pole-and-line catches include fish caught by research vessels. ^b Japanese longline catches for 1952–60 exclude minor amounts taken by vessels under 20 tons. Japanese longline catches from 1958–68 were readjusted in 1988. Longline catches in weight are estimated by multiplying annual number of fish caught by average weight statistics.

^c Japan gillnet catches include south Pacific catches.

^d Taiwanese and Korean gillnet catches are missing or incomplete. ^e Korean longline catches calculated from FAO statistics and Korean catch/effort data.

J U.S. troll catches from 1952-60 include fish caught by baitboats, from 1961-85 include fish landed in Hawaii. U.S. jig (troll) catches (1984-88) include gillnet catches.

g U.S. total for 1984 includes 3,728 mt caught by purse seines.

^h Figures for 1987–88 are preliminary.

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(A) Percent of total recoveries of tagged albacore for fish released in coastal waters off North America north of 40° N. Release area is indicated by hatching. (B) Percent of total recoveries of tagged albacore for fish released in coastal waters off North America south of 40° N. Release area is indicated by hatching.



Figure 5

(A) Positions of release (dots) and recovery (arrowheads) of tagged albacore which were recovered within the season of release during 1972. (B) The same as A except for recoveries in the subsequent fishing season, 1973.

in the southern area, 78 percent were recovered in the same general area as release, 10 percent west of 180° , 8 percent in coastal waters off North America north of 40° N, and about 4 percent in the central eastern Pacific or unknown area of recovery (Figure 4B).

The tagging results suggest that the northern subgroup of albacore is primarily exploited by the Japanese surface fishery in the western Pacific, the Asian longline fishery and the portion of the North American fishery operating north of about 40° N. The southern subgroup appears to be harvested mainly by the North American surface fishery operating south of about 40° N and the Asian longline fishery, and only limitedly by the Japanese pole-andline fishery.

Release and recovery locations for tagged albacore that were recovered by U.S. fishermen within the same fishing season as release and the fishing season following release are shown in Figure 5, A and B, respectively. These results reveal that the movement patterns of albacore are highly directed, that the fish follow well-defined routes during intra- and inter-fishery migrations. Further evidence for this is indicated by the relatively high proportion of tagged fish that have been recovered within 150 miles of where they were released off the coast of North America after being at liberty for one to three fishing seasons (Laurs and Nishimoto 1974). Presumably these fish had migrated seasonally between coastal waters off North America and the central or western Pacific. For example, one tagged fish was recovered only 39 miles from where it had been tagged nearly two years earlier. Tagged albacore recoveries made by the Japanese pole-and-line fishery also show a pattern indicative of a directed, well-defined migration route (Laurs and Nishimoto 1974).

Physiological Ecology and Habitat Definition

Most of the present understanding of albacore habitat has been gained through studies at sea following multi-disciplinary approaches including physical and biological oceanography, satellite oceanography, acoustic tracking, and physiological ecology research. The latter investigations have shown that the albacore is a highly advanced teleost with many specialized adaptations. It is a thermo-regulating endotherm (Graham and Dickson 1981), has a high metabolic rate (Graham and Laurs 1982), an advanced cardio-vascular system (Breich et al. 1983; Lai et al. 1987), specializations in the circulatory system and blood/gas exchange system (Laurs et al. 1978; Alexander et al. 1980; Cech et al. 1984; Graham et al. 1989), distinctive enzyme and complement systems (Morrison et al. 1978; Giclas et al. 1981; Dyke et al. 1987; Dickson 1988), and high energetic costs for migration (Sharp and Dotson 1977), which may be partly met by utilization of stored fat (Dotson 1978).

Recent research refutes earlier published information on temperature preference, which was based on the belief that albacore were confined to the upper mixed layer and that the thermocline formed a barrier to their vertical distribution (Clemens 1961). Based on these assumptions, modal sea surface temperatures (SST) measured where highest troll catches were made, generally between 16° and 19° C (e.g., Clemens 1961), were thought to represent the temperature preference for pre-adult albacore in the eastern Pacific. However, acoustic tracking of freeswimming albacore and concurrent measurement of ocean vertical thermal structure (Laurs et al. 1980; Laurs and Dotson, in prep.) have demonstrated that 3 to 5 year-old albacore spend most of their time swimming in or near the thermocline. The fish spend small amounts of time in the upper mixed layer, presumably only when enticed there to feed. The tracked fish moved through waters with a temperature range of about 10° to 19° C and spent most of the time in waters with temperatures much cooler than those originally thought to be their optimal range.

The tracked fish also exhibited marked vertical excursions in depth; the range generally was larger during the day than at night when in California Current waters (Fig. 6). However, two fish tracked in offsore waters, which are believed to have been actively migrating, showed larger depth excursions during the night, which often brought them up into the lower portion of the mixed layer. When making vertical excursions, albacore pass through large temperature gradients, routinely 4° to 6° C and up to 10° C, within about twenty-minute periods.

Based on the acoustic tracking results that albacore seldom enter into waters cooler than 10° C and the finding of Graham and Dickson (1981) that thermoregulation processes begin to fail at temperatures below 10° C, it appears that this temperature is the lower limit of the preferred temperature range. At this point of our understanding, we believe that the normal habitat of albacore is within a temperature range of about 10° to 20° C, in waters with a dissolved oxygen saturation greater than 60 percent (Graham and Laurs 1982). However, the SST range of 16° to 19° C still has value in fishing operations.

There is ample evidence that the migration, distribution, availability, and vulnerability of albacore are markedly influenced by oceanographic conditions in the North Pacific Ocean, notably fronts. Albacore





A time plot of the vertical movements of an acoustically tracked albacore in California Current waters. Vertical temperature field is based upon concurrent XBT casts.

fishing grounds in the western Pacific have been linked to oceanic fronts (Uda 1973). Also, the seasonal migration of albacore into North American coastal waters has been found to be associated with the North Pacific transition zone waters and its frontal zone boundaries (Laurs and Lynn 1977). Oceanographic conditions also play important roles in the local concentrations and movements of albacore in coastal waters off North America. Albacore tend to aggregate on the warm side of upwelling fronts and to move away from the locations where the fronts occurred when upwelling breaks down (Laurs et al. 1977). Satellite images of ocean color and SST and concurrent albacore catch data also clearly show that the distribution and availability of albacore in nearshore waters off California are related to coastal upwelling fronts. Albacore are most abundant in warm, clear, blue oceanic waters adjacent to the temperature and color fronts which form the seaward boundary of the relatively cool, turbid coastal water masses (Laurs et al. 1984). Laurs et al. (1984) found that, in waters beyond about 500 miles from the coast, fishing success was related to the productivity of the waters. Ocean boundaries associated with the Columbia River plume also appear to be important in the aggregation of albacore (Pearcy and Mueller 1970).

It is presumed that albacore aggregate in the vicinity of upwelling fronts to feed on forage organisms that are plentiful in these areas (Blackburn 1969; Laurs et al. 1977). Yet, it remains unclear what physical factors prevent albacore from penetrating these fronts in order to reach what would likely be the highest potential forage biomass (Blackburn 1969). Because tuna can perceive temperature gradients as small as 0.1° C (Steffel et al. 1976), thermal-physiological mechanisms have been thought to be the main limitation to tunas crossing sea surface temperature gradients into cooler waters. Neill (1976) postulated that tunas utilize frontal gradients for behavioral thermoregulation. Past studies have also stressed confinement to physiological optimal temperature range (Thompson 1917; Clemens 1961; Sund et al. 1981). However, the findings that albacore can regulate their body temperatures over a relatively broad range and that they may routinely pass through vertical temperature gradients of up to 10° C, clearly substantiate that the aggregation of albacore on the warm, clear side of SST fronts is not related to thermal-physiological mechanisms.

Recent research involving acoustic telemetry of free-swimming albacore, satellite measurements, and oceanographic sampling indicate that water clarity as it affects the ability of albacore to detect prey may be the causal mechanism underlying the aggregation of albacore on the warm, clear sides of upwelling fronts (Laurs, in prep.). In offshore regions, the distribution of albacore in relatively productive waters of the transition zone is believed to occur because relatively higher amounts of food organisms are present than in the Central Pacific gyre waters, yet the waters are clear enough for the albacore to see their prey.

Food Habits of Albacore in Transition Zone Waters

Information is very limited about the food habits of albacore in the central North Pacific. However, they appear to be opportunistic carnivores, as they are in other areas (e.g., McHugh 1952).

Iverson (1962) reported on the stomach contents of 79 albacore caught by trolling and 87 caught by gill net in the area bounded by longitudes 140° W and 180° and latitudes 32° and 47° N. The fish ranged in fork length from 51 to 85 cm and were caught on research cruises conducted between 1950 and 1957. The average displacement volume of food per stomach in troll-caught fish was 15.1 mL and in gillnet-caught fish was 9.8 mL. The author speculated that there was less food in the stomachs of the gillnetcaught fish because the fishing was done at night and albacore are not known to feed at night, and because the fish may have vomited excessively while struggling in the net. Laurs and Nishimoto (1973) and Nishimoto and Laurs (1974) reported on the stomach contents of 33 and 75 albacore caught in the transition zone area between 130° and 140° W during May of 1973 and 1974, respectively. Stomachs were examined in both years from fish ranging in size from 50 to 85 cm FL. Food was found in all stomachs and averaged 16.3 mL displacement volume for fish examined in 1973, and was found in 88 percent of the stomachs and averaged 13.3 mL for fish examined in 1974.

Variations are apparent in the frequency of occurrence and percent volume of the major food groups found in the albacore stomachs in the studies reported above (Table 2). Cephalopods had the greatest biomass in two of the analyses and saury the greatest in the other two. For all the analyses combined, cephalopods occurred in nearly 57 percent of the stomachs examined and comprised approximately 38 percent of the food by volume. Fishes (other than saury) and crustaceans were found in nearly the same number of stomachs, about 48 and 42 percent, respectively, but contributed only about 14 and 11 percent of the volume of food, respectively.

| Food Crown | Gillnet caught ^a | | Gillnet caught ^b | | Gil cau | lnet ght ^c | Gil cau | lnet ght ^d | All studies combined % occur/vol. | |
|---------------------------|--------------------------------|---------|--------------------------------|------|------------|--------------------------|--------------|--------------------------|---|------|
| rood Group | % οςςι | ar/vol. | % occur/vol. | | % осс | ur/vol. | % occur/vol. | | | |
| Saury | 11.5 | 26.5 | 25.3 | 61.5 | 10 | 38.2 | 10 | 0.3 | 14.2 | 31.6 |
| Other fish | 10.3 | 8.0 | 31.6 | 16.9 | 80 | 18.0 | 65 | 14.8 | 46.7 | 14.4 |
| Cephalopods | 28.7 | 62.1 | 53.1 | 11.3 | 70 | 20.1 | 75 | 59.1 | 56.7 | 38.2 |
| Crustacea | 5.7 | 1.2 | 41.7 | 6.5 | 60 | 16.7 | 60 | 19.5 | 41.8 | 11.0 |
| Others and Unidentifed | _ | 2.1 | _ | 3.8 | 35 | 7.0 | 25 | 6.3 | _ | 4.8 |

Table 9

^{*a*} Iverson (1962) n = 87; mean volume = 9.8 mL.

^b Iverson (1962) n = 79; mean volume = 15.1 mL.

^c Laurs and Nishimoto (1973) n = 33; mean volume = 16.3 mL.

^d Nishimoto and Laurs (1974) n = 75; mean volume = 13.3 mL.

Because of their large size, saury, which occurred in only about 14 percent of the stomachs examined, composed nearly 32 percent of the biomass of food found in the stomachs.

The number of albacore stomachs that were examined in the investigations discussed above was relatively small, and care must be exercised in drawing conclusions concerning the feeding habits of albacore in the transition zone waters. However, some trends are evident and it is possible to make tentative comparisons with the results of investigations of feeding habits of albacore caught in waters closer to shore in the California Current (McHugh, 1952; Pinkas et al. 1971; Bernard et al. 1985). Larval fishes from several families, juvenile lanternfishes, and often times small-eye squaretail (Tetragonurus cuvieri), carangid fishes, and amphipods are more important in the diet of albacore in the offshore transition zone waters than in those caught closer to shore in the California Current. In the latter region, saury or anchovy (or both) and euphausiids or sergestid shrimps are generally more important. Squids are important in both regions, but the species composition is different. While the composition of the food in the stomachs is different between inshore and offshore, the average volume of food in stomachs from the two regions is similar. For example, in an examination of 262 stomachs of albacore caught by trolling in waters along the Pacific coast of the United States within a few hundred miles of shore, the volume of food averaged 15.0 mL displacement volume per stomach (Laurs and Nishimoto, in prep.). This compares with displacement volumes ranging between 13.3 mL and 16.3 mL for albacore caught by trolling in the Transition Zone (Table 2).

North Pacific Albacore in Relation to Transition Zone Oceanography_

North Pacific transition zone waters lie between the cool, low salinity Pacific Subarctic waters to the north and the warm, saline North Pacific Central waters to the south and have temperatures and salinities characteristic of a mixture of these two water masses (Sverdrup et al. 1942). Transition zone waters are found in a band across the North Pacific middle latitudes within the North Pacific Current and are bounded by sharp discontinuities in temperature and salinity at the surface, extending to depths of about the halocline (McGary and Stroup 1956; Roden 1975; and Lynn 1986). These bounding gradient regions are often times referred to as the subarctic front at the north and the subtropical front at the south (Fig. 1), and each may comprise a complex series of fronts. The dynamic processes which produce and maintain these gradients also enrich these waters (McGary and Stroup 1956).

The association of albacore with transition zone waters in the central North Pacific was initially suggested by Shomura and Otsu (1956), Graham (1957) and McGary et al. (1961). These authors reported on the results of a two-year program, 1954 and 1955, in which a series of eight exploratory fishing surveys in various seasons and three oceanographic surveys were conducted in the central temperate North Pacific. The fishing methods used were longlining, trolling, and a brief experiment with gill netting. Although catches were small, there was a clear association with the oceanographic regime of the transition zone and a significant latitudinal shift with season.





(A) Jig-boat catches of albacore and oceanic fronts for June 1973 (from Laurs and Lynn 1977). (B) Jig-boat catches of albacore and oceanic fronts for June 1974 (from Laurs and Lynn 1977).

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Vertical sections of temperature and salinity along 137°30' W for June 1973 (from Lynn 1986).

Based on extensive oceanographic sampling and concurrent albacore fishery data in the eastern North Pacific, Laurs and Lynn (1977) demonstrated that the distribution, relative abundance, and seasonal migration of albacore in the eastern Pacific are related to the transition zone waters. In a series of late spring surveys conducted in 1972 through 1976, albacore were caught by chartered commercial fishing boats, while a research vessel made detailed oceanographic measurements. The summaries of re-



Figure 9 Selected isolines of the salinity distribution at 300 feet (90 meters) (from Robinson 1976).

sults for June 1973 and June 1974 are given in Figure 7, A and B. The shaded bands indicate oceanic fronts in plan view, at which there were strong horizontal gradients of temperature and salinity. The solid circles show albacore daily catch rates, using a scale given in the legend. There was a well-defined relationship between high albacore catch rates and fronts. In 1973 the fronts were strong and catches were confined between them. In 1974 the fronts were weak and diffuse, and catches were spread over a greater region and showed considerable movement over short periods during the month. Despite the weaker development of the ocean fronts, there was still a clear association of albacore with the fronts.

Vertical sections of salinity and temperature along a meridian for 1973 show the water masses and the fronts that define their boundaries (Fig. 8). The definition is clearest in the salinity structure. Water having its source in the subarctic is low in salinity (hatched) and that from the subtropics is high in salinity (shaded). Although there is a great deal of variability, these fronts are semi-permanent and quasi-continuous across the North Pacific. Specific isohalines are traditionally associated with each front (e.g., Roden 1980; Lynn 1986). The average salinity: contours at 90 m (Robinson 1976) for the North Pacific are roughly zonal (Fig. 9) and show some curvature similar to the large-scale pattern of the North Pacific current field. The 33.8 isohaline is found in the subarctic front. The 34.6 isohaline is located in the Kuroshio Extension front and in the northern subtropical front in the eastern North Pacific. The 34.8 isohaline is situated in the subtropical front. The meanders in the 34.6 isohaline coincide with major bathymetric features, the Shatsky Rise, the Emperor Seamounts, and the Hess Rise (Fig. 10), showing the strong influence that these major features have upon surface currents and distributions (see Roden and Taft 1985). The schematic of the frontal system in the temperate zone (Fig. 1) was drawn using this smoothed version of salinity and a large number of specific observations of fronts from research cruises (most conducted by the International North Pacific Fisheries Commission, the University of Washington [G. Roden] and the Southwest Fisheries Center). This is not unlike a similar schematic developed by Roden (1975). It does, however, add the northern subtropical front first identified by Lynn (1986). For a major portion of the year, these fronts apparently are an important mechanism for increasing biological productivity in the central portions of the North Pacific Ocean, which lead to higher levels of forage organisms for albacore.

At any particular time and place, the fronts associated with the transition zone may have large



Figure 10 Bathymetric features of the North Pacific as given by the 2000 fathom isobath.



Distribution of the 20-year average sea surface bands of temperature between 16 and 18° C for February, May, and August.



Figure 12 Vertical sections of temperature for a great circle path between Honolulu and San Francisco for four periods between April and July 1972. 84

meanders, be split into multiple fronts, or be dissipated. The schematic in Figure 1 is meant to describe a base pattern that may not be evident at the surface at all times, but likely can be found in the upper 100 or so meters. The surface mixed layer undergoes strong seasonal changes in temperature. In particular, during late summer and fall the surface may not reflect the deeper frontal structure. During winter, cooling and deep mixing reestablish the fronts in the surface layer.

Peak catches of albacore in the U.S. surface fisheries generally occur where SSTs are between 16° and 19° C (Clemens 1961). Plots of surface temperatures within this latter temperature range for February, May, and August show the seasonal progression of warming (Fig. 11). In some seasons and some regions this temperature range coincides with the oceanic fronts; in other seasons and regions they are greatly separated. For instance, in the western Pacific in May, the temperature range coincides with the Kuroshio Extension front and, in the eastern Pacific during summer, it falls well to the north and east of the fronts associated with the transition zone.

The seasonal warming of the surface layer and the development of the summer thermocline is shown in a series of panels of temperature versus depth along a great circle route between Honolulu and San Francisco for April through July, 1972 (Fig. 12); temperatures between 16° and 19° C are shaded. In April there is a deep mixed layer and winter thermocline. The surface warming indicated in the subsequent panels, forms a shallow surface layer in which the waters characteristic of albacore surface fisheries advance toward the California coast. This development is coincident with the local development of the U. S. troll fishery.

Catches and Ocean Features _

The center of the largest catches by the Japanese longline fishery based on 5° square data summaries falls in a band of latitude between 25° and 35° N, and extends from Japan to the dateline (Fig. 2A). A second band is found north of Hawaii between 30° and 35° N. The largest catches are coincident with the estimated mean position of the subtropical front, 30° to 31° N (Fig. 1). Winter surface temperatures at these locations are higher than 15° C; hence, a layer of water that has temperatures that include the upper end of the "favored" range lies above the deep winter themocline (Fig. 12). The zonal division in longline catches in the area located at 170°W to 180°, appears well documented in the data records. It appears to be related to a downstream effect of major bathymetric features (Fig. 10) upon the current field and oceanic

structure. This division in catches may offer an explanation for the development of subgroups of North Pacific albacore. If large-scale oceanic structure divides the wintering habitat, separate migration paths and related consequences may be the result.

The center of the largest catches of the Japanese pole and line fishery progresses from near the coast of Japan during April to 175° E by June (Fig. 2A). The large catch nucleus is found within the Kurshio extension front (Fig. 1) and follows the northward advance of warming, which forms a shallow surface layer over the transition zone waters north of the Kuroshio front (Fig. 11). The core of high catches near 170° E is probably related to events controlled by the bathymetry of the rises and seamounts.

The U.S. jig surface fishery starts in May near the Hess Rise, centered at about 180° and 35° N (Fig 2A). The appropriate surface temperatures coincide with the northern subtropical front, or eastward continuation of the Kuroshio extension front. Subsequently, the surface warming and the fishery shift northward as the migration of albacore continues eastward. By July the seasonal warming creates favorable temperatures north and east of the subarctic front. A fishery subsequently develops offshore of coastal upwelling regions off the coast of North America.

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NOAA Technical Report NMFS 105

Biology, Oceanography, and Fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone

Papers from the North Pacific Transition Zone Workshop Honolulu, Hawaii 9–11 May 1988

Jerry A. Wetherall (editor)

Sponsored by

Honolulu Laboratory Southwest Fisheries Science Center National Marine Fisheries Service National Oceanic and Atmospheric Administration 2570 Dole Street Honolulu, HI 96822 and NOAA/University of Hawaii Joint Institute for Marine and Atmospheric Research 1000 Pope Road University of Hawaii Honolulu, HI 96822

December 1991



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