CONTRIBUTION TO THE POPULATION DYNAMICS OF ATLANTIC ALBACORE WITH COMMENTS ON POTENTIAL YIELDS¹

GRANT L. BEARDSLEY²

ABSTRACT

Length-frequency data on Atlantic albacore from the Bay of Biscay surface fishery and the Atlantic longline fishery were analyzed. Lengths at age were estimated and the von Bertalanffy growth parameters were calculated: K = 0.141, $L_{\infty} = 140$ cm, and $t_0 = -1.63$ years. Instantaneous rates were computed on an annual basis. The total instantaneous mortality coefficient was estimated as 0.96 for albacore in the Bay of Biscay fishery and 0.79 in the longline fishery. Analysis of catch and effort data suggested that greater yields are available from the North and South Atlantic longline stocks though stock identification in the South Atlantic is not clear. Estimates of population structure in the North Atlantic were made by utilizing total instantaneous mortality rates of 0.50, 0.96, and 1.40 and an instantaneous natural mortality rate of 0.23. The population based on a total mortality coefficient of 0.96 appeared to be the most reasonable.

The albacore. Thunnus alalunga, has become increasingly important to the Atlantic tuna fisheries in recent years. From 1956 to 1961 the Japanese longline fishery in the Atlantic was primarily directed at yellowfin tuna, T. albacares, but rapidly declining catch rates for vellowfin soon forced a shift of fishing into primarily albacore areas (Wise, 1968). As a result of decreased vellowfin catches and a corresponding shift in fishing toward albacore, the average number of albacore caught yearly by the Japanese in the Atlantic increased from 228,000 in the years 1956-61 to 1,332,857 in the years 1962-68. The percentage of albacore in the combined catch of albacore and yellowfin in the Atlantic by the Japanese rose from an average of about 18.7% in 1956-61 to 67.7% in 1962-68 (Figure 1).

Since 1965 the Japanese have significantly curtailed their longline fishing in the Atlantic. From a high of almost 100 million hooks in 1965, they set slightly over 30 million hooks in 1967 and again in 1968. This decrease, however, has been offset by the entry of China (Taiwan) and South Korea into the fishery as well as small amounts



FIGURE 1.—Total number of albacore caught and the percentage of albacore in the combined yearly albacoreyellowfin tuna catch by Japanese longliners in the Atlantic Ocean, 1956 through 1968.

¹ Contribution No. 203, National Marine Fisheries Service, Southeast Fishery Center, Miami, Fla. 33149. ² National Marine Fisheries Service, Southeast Fish-

ery Center, Miami, Fla. 33149.

Manuscript accepted June 1971. FISHERY BULLETIN: VOL. 69, NO. 4, 1971

of fishing by Cuba and Venezuela. In 1968 the combined landings of albacore by China and South Korea were about 15,500 metric tons, which was only 1000 tons less than the Japanese catch for 1968. Recent estimates have placed the Atlantic albacore catch for 1969 by China and South Korea at 19,300 metric tons.

Worldwide demand for tuna is increasing every year, and there is growing concern over the condition and well being of Atlantic tuna stocks. Catch rates of yellowfin tuna in the longline fishery suffered severe declines in the 1960's. Wise (1968), Food and Agriculture Organization (1968), Wise and Fox (1969), Hayasi and Kikawa (1970), and others have examined the problem and have concluded that the longline stocks of yellowfin tuna have been fished beyond their maximum capacity.

This paper is an analysis of some aspects of the population dynamics of Atlantic albacore with comments on potential yields and stock size.

AGE AND GROWTH

There have been few studies on the age and growth of Atlantic albacore. Distinct modes appear in length-frequency distributions of albacore samples from the Bay of Biscay surface fishery, and these modes probably represent agegroups. There is considerable disagreement, however, over the assignment of absolute ages to Atlantic albacore (Table 1).

Le Gall (1949, 1952) worked with length frequencies from the Bay of Biscav. He stated that age-group I was less than 48 cm in length. and that the first group that appeared in the fishery was age-group II (56 cm). Figueras (1957) used vertebrae from 67 fish in his analvsis and concluded that 56- to 57-cm albacore were 4 years old and that 17- to 18-cm albacore were 1 year old. Yang (1970) estimated that 56-cm albacore were approximately 3 years old based on results of his analysis of annular markings on scales. Otsu and Uchida (1959b), however, concluded from their study of vertebrae, scales, and other hard parts of Pacific albacore that there were no markings that could be considered age marks.

I used data from the Bay of Biscay for 1967, 1968, 1969, and 1970 (Allain and Aloncle, 1968; Philippe Serene and Jean-Claude Dao, Centre National pour l'Exploitation des Océans, personal communication) (Figure 2) as well as longline data (Figure 3) and estimated lengths at age for Atlantic albacore (Table 1).

Lengths at ages 1, 2, 3, and 4 were estimated by modes in length-frequency histograms from Bay of Biscay samples. The first mode distinguishable in the length frequencies (Figure 2, 1968) is at approximately 44 cm, and I assume that it represents age-group I. There is support in the literature for the assignment of this approximate length to 1-year-old albacore. Otsu and Uchida (1963) indicated that 30- to 35-cm

Investigator		Method Sample size	Age (years)									
	Method		1	2	3	4	5	6	7	8	9	10
Priol (1944)	Scales (total length)	50	 50-58	<u> </u>	74-86	 86-94	94-98	m	 			
Le Gall (1949)	Length frequencies (total length)		<25	25-46	46-60	60-74	74-88					
Le Gall (1952)	Length frequencies (total length)	50,000	<48	56	68	81-82	>93					
Figueras (1957)	Vertebrae (total length)	67	17-18	31-32	44-45	56-57	69-70	81-82	91-93			~-
Yang (1970)	Scales (fork length)	159	20.3	39.6	56.1	71.2	80.9	90. 3	98.1			
Beardsley (present study)	Length frequencies (fork length)	62,602	44	55	64	75	87	95	100	104	108	112

TABLE 1.—Summary of age and growth investigations on Atlantic albacore.



FIGURE 2.—Albacore length-frequency distributions from the Bay of Biscay surface fishery, 1967-70. Estimated ages in years are shown above the histograms.



FIGURE 3.—Albacore length-frequency distribution from the Atlantic longline fishery, several years combined. Estimated ages in years are shown above the histograms.

albacore occasionally appear in the Japanese livebait fishery in spring, and they assume that these fish are approximately 1 year old. On this basis they assign 2, 3, and 4 years of age to 55-, 65-, and 76-cm albacore respectively in the United States west coast fishery. Yoshida (1968) studied age and growth of juvenile albacore based on 35 specimens recovered from stomachs of billfishes in the Pacific. He derived a hatching date of May 1 based on a regression analysis of length of the juveniles against month of capture and concluded that 1-year-old albacore are approximately 38 cm standard length. Although I have assigned a length of 44 cm to age-group I, a more practical approach would probably be to accept Le Gall's (1952) statement that 1-yearold albacore are "less than 48 cm in length."

Longline length frequencies were used to estimate ages 5 and older (Figure 3). The assignment of ages beyond age 5 is somewhat subjective. I assigned ages 7 and 8 to the modes appearing at 100 to 101 and 104 to 105 cm. Other ages were assigned mostly by extrapolation. My estimates agree in most cases with those made for Pacific albacore by Otsu and Uchida (1963). No attempt was made to assign ages beyond age 10 although undoubtedly some albacore in the Atlantic live to be older than 10.

The two modes which correspond to ages 3 and 4 in the longline samples (68-69 and 78-79 cm) are located at a length of 3 to 6 cm greater than the same age in the Bay of Biscay samples. Yang (1970) stated that ring formation on albacore scales occurred in February-March for North Atlantic albacore. The Bay of Biscay samples were taken in summer, and the albacore had completed approximately a half year's growth. Most 3- and 4-year-old albacore captured by longliners are taken in winter when they are first recruited to the fishery. These 3- and 4vear-old fish are at the end of a year's growth or just beginning a new year's growth, and the disparity in the position of the modes between the longline samples and the Bay of Biscay samples represents growth during the period between the summer fishery and the winter fishery.

GROWTH PARAMETERS

I constructed a Walford line (Figure 4) using the lengths at age from this study (Table 1) and took the intercept of the 45° diagonal as an initial trial value for L_{∞} in the expression for growth (von Bertalanffy, 1938):

$$\log_e (L_{\infty} - L_t) = \log_e L_{\infty} + Kt_0 - Kt.$$

A best fit was obtained with $L_{\infty} = 140$ cm. K was calculated as 0.141, and t_0 was -1.63 years. Yang (1970) found $L_{\infty} = 135$ cm and K = 0.19



FIGURE 4.—Walford transformation of length in centimeters at age t + 1 against length at age t for Atlantic albacore.

from his analysis of albacore growth. The growth curve based on my calculations is shown in Figure 5.



FIGURE 5.-Growth curve for Atlantic albacore.

LENGTH-WEIGHT

De Jaeger (1963), de Jager, Nepgen, and van Wyk (1963), van den Berg and Matthews (1969), and Nepgen (1970) published information on the length-weight relation of Atlantic albacore. All gave separate equations for males and females although de Jaeger (1963) was unable to detect any significant differences in his samples. I combined data from the longline fishery and the Bay of Biscay fishery and calculated a length-weight equation for both sexes combined since sex information was not available for most of the samples at the smaller sizes:

$$W = 6.303 \times 10^{-6} \times L^{3.28253}.$$

Weight is in kilograms and length is fork length in centimeters (Figure 6).



FIGURE 6.—Length-weight relation of Atlantic albacore, both sexes combined.

SEX RATIO

Five hundred ninety-eight albacore were measured and sexed at canneries located in Puerto Rico from December 1969 to September



FIGURE 7.—Length-frequency distribution of 598 male and female albacore measured at canneries in Puerto Rico from December 1969 to September 1970. All were caught in the Atlantic by longline gear.

1970. Males constituted 61% of the samples and were more abundant at the larger sizes (Figure 7). Few females appear to attain a length of much over 100 cm. This dominance of males both in numbers and at the larger sizes has been reported for Pacific albacore by Otsu and Uchida (1959a, 1959b) and Otsu and Hansen (1962) and for Atlantic albacore by de Jaeger (1963) and Talbot and Penrith (1963).

MORTALITY

There have been no mortality estimates for Atlantic albacore that I am aware of. Suda (1963) stated that the total instantaneous mortality coefficient of North Pacific albacore is probably around 0.4. He later estimated that the natural mortality coefficient for the same stock is about 0.2 (Suda, 1966). I estimated the total instantaneous mortality coefficient (Z) for Atlantic albacore using Bay of Biscay length frequencies (Figure 2) and longline length frequencies (Figure 3). All mortality rates in the following discussion are instantaneous rates unless specifically designated as annual.

BAY OF BISCAY

If we assume that the 1967, 1968, 1969, and 1970 samples from the Bay of Biscay are reasonably representative of the total catch which is in turn an accurate estimator of the true relative abundance of the different age groups in the fishery, we can calculate a total mortality coefficient from the decline in abundance of a given year class from one year to the next, beginning with the first year it is fully recruited (age 3). This method requires weighting the frequencies by catch per unit of effort (CPUE). Accurate estimates of CPUE for the entire Bay of Biscay fishery are not available, although recent research suggests that a slight decline in CPUE has occurred at selected ports in France in the late 1960's (Jean-Claude Dao, personal communication). I have assumed a constant CPUE over the 4 years in question for the purpose of this analysis since complete figures are not available.

I have also assumed equal recruitment for ages 3 and 4 though this is not likely. Any mortality estimates based on the relative abundance of ages 3 and 4 in the fishery will be affected by relative differences in recruitment. Some 3-year-old albacore and many 4-year-olds are recruited to the winter longline fishery in the North Atlantic: however, for the 4 years, 1965-68, the average number of 4-year-old albacore caught in the North Atlantic winter fishery was only about 40,000. This is a relatively insignificant number when compared with the total number of 4-yearolds available in the Bay of Biscay fishery. It is not known if all the survivors return to the Bay of Biscay the following summer although it is probable that most of them do. If 4-year-old albacore do not all return to the Bay of Biscay from the winter longline grounds then mortalities will be slightly overestimated.

Mortality coefficients were calculated from the decline in abundance from age 3 to age 4 only, and the frequency polygons were divided in the following manner. Where there was an obvious null between age classes, for example at 70 to 71 cm in the 1967 plot, the number of fish in that length group were evenly divided, half were assigned to the age above and half to the age below. Where there was no obvious null, as between ages 2 and 3 in the 1969 plot and between ages 4 and 5 in almost all the plots, the dividing point was placed at a length approximately half way between the assigned lengths at age obtained from Table 1. Using this method I obtained the following values of Z:

		Year	clas	s		\underline{Z}
1964	(3	years	old	in	1967)	0.73
1965	(3	years	old	in	1968)	1.04
1966	(3	years	old	in	1969)	1.12

The average total mortality coefficient over the 3 years was estimated to be 0.96.

LONGLINE FISHERY

A total mortality coefficient was calculated for albacore in the longline fishery using a formula derived by Beverton and Holt (1956):

$$Z = \frac{K (L_{\infty} - \bar{L})}{\bar{L} - L_{r}}$$

where \overline{L} is the average length of the fish in the catch that are as large as or larger than the first fully recruited length, L_r .

Using: $L_{\infty} = 140 \text{ cm}$ K = 0.141 $\bar{L} = 94.2 \text{ cm}$ $L_r = 86 \text{ cm}$

then:

$$Z = 0.79$$

The total mortality coefficient is not incompatible with the average Bay of Biscay estimate if we consider that the longline is probably relatively inefficient compared with surface gear; hence fishing mortality in the longline fishery and consequently total mortality (assuming natural mortality stays nearly the same throughout the life span of the fish) is probably less than in the surface fishery.

The albacore samples used to estimate mortality in the longline fishery were taken over several years from different areas in the Atlantic. It is very likely, however, that the composite length-frequency distribution in Figure 3 is not a completely accurate picture of the length composition of albacore in the Atlantic. Size distribution in the winter fishery, for example, is entirely different from that in the summer fishery, and suitable samples from each fishery would have to be taken to ensure a representative picture over the entire ocean.

YIELD ESTIMATES

There are five major areas in the Atlantic where longliners concentrate on albacore. I have designated these areas A through E in Figure 8 and for ease of discussion will subsequently refer to these areas by their letter designation. Areas A, B, C, and D were described by Beardsley (1969) and Koto (1969) as major fishing areas. Area E off the coast of Argentina, Uruguay, and southern Brazil has only recently developed into a relatively major albacore fishing area. Of the four areas discussed by Beardsley and Koto, only area C has shown a decline over the years in catch rate (Figure 9). Areas A and D produce fish that are relatively small for longline fish and presumably are recruits to the longline fishery. Recent size data obtained from albacore landed in Puerto Rico and caught in area E reveal that small albacore are also a large part of the catch in this area.



FIGURE 8.—The major longline fishing areas for albacore in the Atlantic Ocean.



FIGURE 9.—Total longline effort and catch per unit of effort (CPUE) for the five major albacore fishing areas in the Atlantic Ocean, 1956-68.

NORTH ATLANTIC

The North Atlantic supports two different albacore fisheries, the longline fishery and the Bay of Biscay surface fishery, while the South Atlantic has only the longline fishery. The Bay of Biscay fishery, conducted primarily by the French and Spanish, has yielded about 45,000 metric tons annually since 1963. The fishery catches primarily 3- and 4-year-old albacore before they are fully recruited into the longline fishery.

There is evidence that albacore stocks in the North and South Atlantic are separate (Beardsley, 1969; Koto, 1969; Yang, Nose, and Hiyama, 1969). Koto indicates, however, that there may be some mixing of immature albacore between the South Atlantic and Indian Oceans. I combined catch and effort data from the two major albacore fishing areas in the North Atlantic and from the three areas in the South Atlantic and treated each group as separate stocks.

From 1957 through 1965 I used only Japanese data (Shiohama, Myojin, and Sakamoto. 1965: Fisheries Agency of Japan, 1966, 1967a, 1967b) since the longline fishery during those years was almost exclusively Japanese. For 1966, 1967. and 1968 Lused Japanese data (Fisheries Agencv of Japan, 1968, 1969, 1970) as well as estimated Chinese and Korean catch data (Wise, 1970). Catch per unit of effort (CPUE) in this discussion is the number of albacore caught per hundred hooks fished. CPUE was calculated by summing the number of albacore caught in a given area in a given year, multiplying by 100, and dividing by the number of hooks fished in that area during the year. Only the catch data were available from the Chinese and Korean fishery. Total Chinese and Korean fishing effort for 1966, 1967, and 1968 was obtained by using Chinese and Korean albacore landings and Japanese CPUE and back calculating to the number of hooks fished. This procedure assumes that CPUE for the Chinese and Korean fleets was the same as for the Japanese fleet. This is probably not true; however, the difference is not likely to be large. The Chinese and Korean fishing effort in the Atlantic was not great until 1968 and by then their fishing efficiency was probably comparable to that of the Japanese.

One of the more common mathematical models used to express yield from a stock of fish is the equilibrium-yield model used by Graham (1935). Schaefer (1954, 1957), and others. One of the major advantages of this type of model is that it requires only catch and effort data. Assuming a fishery that has attained equilibrium conditions, a plot of CPUE against effort should show a linear decline which will produce a parabolic curve of yield when plotted against effort. Fox (1970) has argued that the relationship between CPUE and effort is more nearly exponential than linear. Both models, however, predict almost identical yields for the ascending limb of the vield curve. The major difference in the two models occurs after theoretical maximum vields have been exceeded. I chose to limit my analysis to the linear model. The Atlantic longline fishery, however, has never been under equilibrium conditions. I adjusted for this by using a method suggested by Gulland (1961) whereby effort is an average of the current year's effort (X_i) and the effort from some number of preceding years $(X_{i-1}, X_{i-2}, X_{i-3}...)$, depending on the average number of years a year class is available to the fishery. I used for North Atlantic albacore an average of effort in the current year and the two preceding years:

$$ar{X} \;=\; rac{X_i \;+\; X_{i-1} \;+\; X_{i-2}}{3}$$

The results (Figure 10) show that in the North Atlantic there has been only a slight decline in CPUE over the history of the fishery. When actual catch and effort data are plotted on the predicted yield curve, only in 1964 did yield exceed even 50% of the predicted maximum. It is likely, therefore, that an analysis using an equilibrium-yield model for the North Atlantic albacore longline fishery is not feasible since the population abundance (as represented by CPUE) has apparently not declined sufficiently to effectively describe the dynamics of the stock in relation to fishing. Consequently, maximum sustainable yield from the North Atlantic longline fishery is not estimable at this time. It appears, however, that increased fishing will result in increased yield with no major decline in CPUE.

SOUTH ATLANTIC

The albacore longline fishery in the South Atlantic is concentrated in three main areas (Figure 8). During the late 1950's and early 1960's fishing was excellent in area C and fishing effort increased rapidly to a peak of about 22 million hooks in 1964. CPUE declined sharply, however, from a high of 10.0 albacore per hundred hooks, and in recent years has stabilized at about 2.5. In 1961 the Japanese fished in area D for the first time, and this area quickly became the major producer of albacore in the South Atlantic. Fishing is excellent almost year round, and CPUE has remained fairly constant at about 8.0 albacore per hundred hooks over the past 5 years. Area E has recently developed as a good



FIGURE 10.—Linear relation between catch per unit of effort (CPUE) and effort (upper panel) and theoretical equilibrium yield curves (lower panel) predicted for the North Atlantic albacore longline fishery. The effort figures in the upper panel are means of the current year's effort and the two preceding year's effort. Effort figures in the lower panel are actual yearly values.

albacore area although effort is still relatively low.

I combined catch and effort data from the Japanese, Chinese, and Korean longline fishery and plotted CPUE against effort in the same manner as for the North Atlantic (Figure 11). The decline in CPUE is more pronounced than for the North Atlantic. The yield curve indicates a theoretical maximum yield of about 1,100,000 albacore from an effort of about 32 million hooks. This yield was equaled in 1964 and surpassed in 1966 and 1968 with an effort of about 25 million hooks.

The South Atlantic albacore fishery has undergone two rather separate and distinct phases. The first phase was from 1956 to 1964 when most fishing effort was in area C. This area produced excellent catches for several years; then catch rates declined rapidly. In 1965 the Japanese increased their fishing in area D in response to excellent catch rates in this area.



FIGURE 11.—Linear relation between catch per unit of effort (CPUE) and effort (upper panel) and theoretical equilibrium yield curves (lower panel) predicted for the South Atlantic albacore longline fishery. The effort figures in the upper panel are means of the current year's effort and the two preceding year's effort. Effort figures in the lower panel are actual yearly values.

When the data are combined from areas C, D, and E, a decline in CPUE is evident to about 1963 (Figure 11). This decline is primarily in area C. From 1963 to 1968 a steady increase in CPUE is evident which represents the decrease in effort in area C and the increase in effort in area D where excellent catches were being made. It appears from the overall picture of CPUE versus effort that the albacore population in the South Atlantic has declined only slightly in relative abundance as a result of longline fishing.

This may be misleading. I suggested (Beardsley, 1969) that the small albacore in area D formed the recruitment to the South Atlantic population. This hypothesis was based on size differences between the two areas; albacore from area D were small, often averaging as little as 10 to 12 kg, while those caught in area C usually averaged 18 to 20 kg or larger. The monthly distribution of catch rates also indicated seasonal movement between the two areas.

Recent size information obtained from albacore landed in Puerto Rico and caught in area E show that small albacore are a large part of the catch. Recruitment to the South Atlantic population may take place in this area. Koto's suggestion that small albacore move between the Indian and South Atlantic Oceans lends support to this hypothesis. The small albacore in area D may well be transients in the South Atlantic, and any population analysis would have to treat them as a separate stock.

Until the problem of stock identification in the South Atlantic is resolved, any estimates of yield are to be considered tentative. Consistently high CPUE values in area D over the past 5 years suggest that even greater yields are possible from this area. The pronounced decline in CPUE in area C demonstrates a significant response of the population to heavy longline fishing pressure, and any large increase in fishing effort probably would not result in a significant increase in yield.

POPULATION ESTIMATES

I obtained the approximate average number of albacore caught from each age-class in the Bay of Biscay from 1963 through 1968 in the following manner.

Each length-frequency sample from the Bay of Biscay (Figure 2) was separated into agegroups in the same manner as described earlier. The number of albacore in each age-group was then divided by the total number of fish in the respective sample to obtain the percentage contribution of each age-group to the sample. This percentage was considered as being representative of the contribution of that age-group to the total catch for that year. An average percentage contribution over the 4 years, 1967-70, was then calculated for each age-group (Table 2).

I then calculated the total weight of a cohort of 1000 albacore using weights at age (Figure 5) and average percentages obtained above (Table 3). The average annual catch from the Bay of

TABLE 2.—Percentage contribution (in number of fish) of each age-group in the Bay of Biscay from 1967 through 1970.

Age-group					
	1967	1968	1969	1970	Mean
1	00.0	01.1	00.0	00.0	00.3
2	01.9	05.6	03.9	32.5	11.0
3	78.0	54.9	74.6	34.7	60.5
4	16.3	37.5	19.5	24.3	24.4
5	03.8	00.9	02.0	08.5	03.8
					100.0

TABLE 3.—Calculated numbers of fish and corresponding weights for a cohort of 1,000 albacore and estimated average annual catch in number and by age groups from 1963 through 1968 from the Bay of Biscay. See text for explanation of procedures.

Age	Co	phort	Estimates for an average year's catch			
	Fish	Weight	Fish	Weight		
	#0.	kg	no.	metric tons		
1	3	5.4	21,327	34.1		
2	110	363.0	781,999	2,580.6		
3	605	3,267.0	4,300,992	23,225.4		
4	244	2,196.0	1,734,615	15,611.5		
5	38	554.8	270,145	3,944.1		
Total	1,000	6,386.2	7,109,078	45,394.7		

Biscay from 1963 through 1968 was 45,400 metric tons (data from Food and Agriculture Organization, 1969). I assumed that the average percentages obtained for 1967 through 1970 were also representative of the years 1963 through 1968.

I used proportion to estimate the average annual catch from the Bay of Biscay in number of fish using the total weight of the cohort, the number in the cohort, and the average annual weight of the Bay of Biscay catch. This total was then separated into age-groups (Table 3) using the percentages in Table 2.

I used these figures to reconstruct three theoretical albacore populations in the North Atlantic based on total mortality coefficients of 0.50, 0.96 (determined from length frequencies), and 1.40 (Tables 4, 5, and 6). In each case I began the calculations using the estimated number of 3year-old albacore landed. I assumed a natural mortality coefficient (M) of 0.23 and obtained the fishing mortality coefficient (F) by subtraction. I used the number of 3-year-olds landed (L_3), fishing mortality (F), and total mortality

TABLE 4.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 0.50 from age 3 through 5. See text for procedures.

Age	Number of fish	Z	Total deaths	Natural deaths	Fishing deaths (surface only)
1	thousands 33,372			iousands of	fish — —
2	26.514	0.23	6,858	6,837	21
3	20.241	0.27	6,273	5,491	782
4	12 276	0.50	7,965	3,664	4,301
5	7 445	0.50	4,831	3,096	1,735
		0.50	2,930		270

TABLE 5.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 0.96 from age 3 through 5. See text for procedures.

Age	Number of fish	z	Tot al deaths	Natural deaths	Fishing deaths (surface only)
1	thousands 15,578		t/	ousands of	fish — —
2	12,377	0.23	3,201	3,180	21
3	9,169	0.30	3,208	2,426	782
4	3.510	0.96	5,659	1,358	4,301
5	1.344	0.96	2,166	431	1,735
		0.96	830		270

TABLE 6.—Theoretical albacore population in the North Atlantic, ages 1 through 5, based on a total mortality coefficient (Z) of 1.40 from age 3 through 5. See text for procedures.

Age	Number of fish	Z	Total deaths	Natural deaths	Fishing deaths (surface only)
1	thousands 11,841	•	tl	ousands of	fish
2	9,408	0.23	2,433	2,412	21
3	6,831	0.32	2,577	1,795	782
4	1,685	1.40	5,146	845	4,301
5	416	1.40	1,269		1,735
		1.40	313		270

(Z) to determine the number of 3-year olds that died (D_3) :

$$D_3 = \frac{L_3 \times Z}{F}$$

Simple back calculation using the annual mortality rates gave the original number of 3-yearolds present. I was then able to work forward and backward from this figure to obtain estimates at other ages.

Adjustments were necessary, however, in order to obtain reasonable estimates. I used much lower total mortality coefficients for 2-year-olds, for example, than for 3-year-olds. Two-yearolds were not fully recruited, and they constitute only about 10% of the total catch. I also assumed total mortality for 1-year-olds was equal to natural mortality since very few 1-year-olds are captured.

Only one of the total mortality coefficients proved to be completely unreasonable. The estimated number of 4-year-olds present was less than the estimated annual catch of 4-year-olds when Z = 1.40, which is obviously an impossible situation. In estimating the other two populations. Z = 0.96 appeared to be more reasonable than Z = 0.50. When the number of 4-year-old albacore that die of natural causes is obtained by subtracting the estimated fishing deaths from the estimated number of total deaths the result corresponds to an M of 0.20 when Z = 0.96, which is close to the assumed natural mortality coefficient of 0.23 (based on Suda's (1966) estimate) estimated for ages 1 through 3. When Z = 0.50, the number of natural deaths of 4year-olds corresponds to an M of 0.32.

If we use the figures in Table 5 and apply a total mortality coefficient of 0.96 from age 5 to age 6 and 0.79 (from longline data) from age 6 through age 10, we can reproduce what theoretically occurs in the North Atlantic longline fishery in an average year. Table 7 shows that the longline fishery should capture about 718,000 albacore, ages 5 through 10, in the North Atlantic each year. The actual average number of albacore captured annually from 1963 through 1968 is estimated at 513,000 (data from Wise, 1970). This difference is large, but a relatively

TABLE 7.—Theoretical yields from ages 5 through 10 based on the population in table 5 with natural mortality coefficient 0.23, and total mortality coefficient 0.96 from age 5 to age 6 and 0.79 from age 6 to age 10.

Aga	Numbe r of físh	Total deaths	Natural deaths	Fishing deaths	
			- thousands of	fish	
5	1,344				
		829	199	360 (longline)	
6	515			270 (surface)	
		281	82	199	
7	234				
		127	37	90	
8	107	59	17	41	
0	40	50	17	41	
,		27	8	10	
10	22	27	0	.,	
		12	3	9	
Total	2.271			718 (longline only)	

small adjustment in the number of recruits at age 5 would bring the figures closer together. For example, by decreasing the number of recruits to 1,100,000 the potential longline catch was calculated as 533,000 fish, much closer to the 6-year average of 513,000.

ACKNOWLEDGMENTS

Jean-Claude Dao and Philippe Serene, Centre National pour l'Exploitation des Océans, France, supplied length-frequency data from the Bay of Biscay fishery. John A. Gulland, Food and Agriculture Organization, Rome, Italy, and Ralph P. Silliman, National Marine Fisheries Service, Seattle, Wash., critically reviewed the manuscript, and I am grateful for their suggestions.

LITERATURE CITED

- ALLAIN, C., AND H. ALONCLE.
- 1968. Migrations du germon en fonction des variations thermiques du milieu entre le secteur Portugais et le SO de l'Irlande. Sci. Pêche 176, 15 p.
- BEARDSLEY, G. L., JR.
 - 1969. Proposed migrations of albacore, *Thunnus* alalunga, in the Atlantic Ocean. Trans. Am. Fish Soc. 98: 589-598.
- BERG, R. A. VAN DEN, AND J. P. MATTHEWS.
 - 1969. A preliminary investigation of the tuna resources off the South West African coast. South West Afr. Mar. Res. Lab., Invest. Rep. 15, 39 p.

BERTALANFFY, L. VON.

1938. A quantitative theory of organic growth. Hum. Biol. 10(2): 181-213.

BEVERTON, R. J. H., AND S. J. HOLT.

1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Cons. Perm. Int. Expor. Mer, Rapp. P.-V. Réun. 140, Part I, p. 67-83.

DE JAEGER, B.

1963. Synopsis of biological data on bluefin tuna Thunnus thynnus orientalis (Temminck and Schlegel) 1842, longfin tuna Thunnus alalunga (Bonnaterre) 1788, yellowfin tuna Thunnus albacares (Bonnaterre) 1788, and bigeye tuna Thunnus obesus (Lowe) 1839 (South Africa). In H. Rosa, Jr. (editor), Proceedings of the world scientific meeting on the biology of tunas and related species, p. 588-607. FAO Fish. Rep. 6.

DE JAGER, B. VAN D., C. S. DE V. NEPGEN, AND

1963. A preliminary report on South African west coast tuna. S. Afr. Div. Sea Fish., Invest. Rep. 47, 40 p.

1957. Datos sobre le edad y crecimiento de la albacora (*Germo alalunga*, Bonnaterre). Invest. Pesq. 9: 27-31.

FISHERIES AGENCY OF JAPAN.

- 1966. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1963. Fish. Agency Jap., Res. Div., 322 p.
- 1967a. Annual report of effort and catch statistics by area on Japanese tuna long line fishery, 1964. Fish. Agency Jap., Res. Div., 379 p.
- 1967b. Annual report of effort and catch statistics by area on Japanese tuna long line fishery, 1965. Fish, Agency Jap., Res. Div., 375 p.
- 1968. Annual report of effort and catch statistics by area on Japanese tuna long line fishery, 1966. Fish. Agency Jap., Res. Div., 299 p.
- 1969. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1967. Fish. Agency Jap., Res. Div., 293 p.
- 1970. Annual report of effort and catch statistics by area on Japanese tuna longline fishery, 1968. Fish. Agency Jap., Res. Div., 283 p.

FOOD AND AGRICULTURE ORGANIZATION.

- 1968. Report of the meeting of a group of experts on tuna stock assessment. FAO Fish. Rep. 61, 45 p.
- 1969. Catches and landings, 1968. FAO Yearb. Fish. Stat. 26, 318 p.

Fox, W. W., Jr.

1970. An exponential surplus-yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99: 80-88.

GRAHAM, M.

1935. Modern theory of exploiting a fishery, and

application to North Sea trawling. J. Cons. 10: 264-274.

- GULLAND, J. A.
 - 1961. Fishing and the stocks of fish at Iceland. Fish. Invest. Minist. Agric. Fish. Food, Ser. II 23(4), 52 p.

HAYASI, S., AND S. KIKAWA.

1970. Comments to rational utilization of the yellowfin tuna in the Atlantic Ocean. In Resources and fisheries of tunas and related fishes in the Atlantic Ocean, p. 73-96. Far Seas Fish. Res. Lab. (Shimizu), S Ser. 3.

Кото, Т.

1969. Studies on the albacore-XIV. Distribution and movement of the albacore in the Indian and the Atlantic Oceans based on the catch statistics of Japanese tuna long-line fishery. [In Japanese, English summary.] Bull. Far Seas Fish. Res. Lab. (Shimizu) 1: 115-129.

LE GALL, J.

- 1949. Germon. Résumé des connaissances acquises sur la biologie du germon. Rev. Trav. Off. Sci. Tech. Pêches Marit. 15: 1-42.
- 1952. La constitution du stock de germons sur les pêcheries du Golfe de Gascogne et de la Mer Celtique. Off. Sci. Tech. Peches Marit., Bull. Inf. Doc., Nouv. Ser. 64, 3 p.
- NEPGEN, C. S., DE V.
 - 1970. Exploratory fishing for tuna off the South African west coast. S. Afr. Div. Sea Fish., Invest. Rep. 87, 26 p.

OTSU, T., AND R. J. HANSEN.

- 1962. Sexual maturity and spawning of the albacore in the central South Pacific Ocean. U.S. Fish Wildl. Serv., Fish Bull. 62: 151-161.
- OTSU, T., AND R. N. UCHIDA.
 - 1959a. Sexual maturity and spawning of albacore in the Pacific Ocean. U.S. Fish Wildl. Serv., Fish Bull. 59: 287-305.
 - 1959b. Study of age determination by hard parts of albacore from central North Pacific and Hawaiian waters. U.S. Fish Wildl. Serv., Fish Bull. 59: 353-363.
 - 1963. Model of the migration of albacore in the North Pacific Ocean. U.S. Fish Wildl. Serv., Fish Bull. 63: 33-44.
- PRIOL, E. P.
- 1944. Observations sur les germons et les thons rouges capturés par les pêcheurs Bretons. Rev. Trav. Off. Sci. Tech. Pêches Marit. 13: 387-439. SCHAEFER, M. B.
 - 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries, [In English and Spanish.] Inter-Am. Trop. Tuna Comm., Bull. 1: 27-56.
 - 1957. A study of the dynamics of the fishery for yellowfin tuna in the eastern tropical Pacific Ocean. [In English and Spanish.] Inter-Am. Trop. Tuna Comm., Bull. 2: 247-285.

R. J. VAN WYK.

FIGUERAS, A.

SHIOHAMA, T., M. MYOJIN, AND H. SAKAMOTO.

1965. The catch statistic data for the Japanese tuna long-line fishery in the Atlantic Ocean and some simple considerations on it. Rep. Nankai Reg. Fish. Res. Lab. 21, 131 p.

SUDA, A.

- 1963. Catch variations in the North Pacific albacore IV. The survival-rate in the fishing ground of the North West Pacific. [In Japanese, English summary.] Rep. Nankai Reg. Fish. Res. Lab. 17: 103-110.
- 1966. The trend and present status of important stocks. In Symposium on tuna fisheries. Part II. Stock assessment (T. Kamimura, coordinator) [In Japanese]. Bull. Jap. Soc. Sci. Fish. 32: 756-779.

TALBOT, F. H., AND M. J. PENRITH.

1963. Synopsis of biological data on species of the genus *Thunnus* (Sensu lato) (South Africa). In
H. Rosa, Jr. (editor), Proceedings of the world scientific meeting on the biology of tunas and related species, p. 608-646. FAO Fish. Rep. 6.

WISE, J. P.

1968. The Japanese Atlantic longline fishery, 1964,

and the status of the yellowfin tuna stocks. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 568, 5 p. 1970. Preliminary effort and catch estimates for Atlantic longline fisheries, 1956-68. Int. Comm. Conserv. Atl. Tunas, ICCAT/CON/70/26, 17 p.

WISE, J. P., AND W. W. FOX, JR.

1969. The Japanese Atlantic longline fishery, 1965, and the status of the yellowfin tuna and albacore stocks. U.S. Fish Wildl. Serv., Spec Sci. Rep. Fish. 582, 7 p.

YANG, R.-T.

1970. Studies of age and growth of Atlantic albacore and a critical review on the stock structure. [In Chinese, English summary.] China Fish. Mon. 213: 3-16.

YANG, R.-T., Y. NOSE, AND Y. HIYAMA.

1968. Morphometric studies on the Atlantic albacore and yellowfin tuna. Bull. Far Seas Fish. Res. Lab. (Shimizu) 2: 23-64.

YOSHIDA, H. O.

1968. Early life history and spawning of the albacore, *Thunnus alalunga*, in Hawaiian waters. U.S. Fish Wildl. Serv., Fish Bull. 67: 205-211.