A THEORETICAL EXAMINATION OF SOME ASPECTS OF THE INTERACTION BETWEEN LONGLINE AND SURFACE FISHERIES FOR YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

This paper explores several aspects of a dual fishery (surface and longline) on yellowfin tuna, *Thunnus albacares*. The work is exploratory in nature and results, though indicative, are not conclusive for any specific fishery. Our results indicate that the yield per recruit is higher for the longline fishery than for surface gear if all fish are available to both gears and higher for the combined gears than for either gear fishing alone. The effect of fishing by one gear on yield to the other gear and the effect of the fishery on stock fecundity is shown to be greater for the often assumed 1:1 sex ratio than for the ratios usually observed. A simulation model was used to examine the interrelations of pattern of movement of fish, pattern of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either only along the coast or throughout the fishing area. The results indicated that either of these patterns of recruitment could allow for increased catch as the surface fleet moved offshore. However, location or pattern of recruitment is shown to be important when measuring natural mortality and for examining the potential of a localized fishery, primarily on younger fish, relative to a fishery exploiting the full range of the stocks or to one taking primarily older fish. Tagging and fecundity studies are suggested for further investigation of the questions examined in this paper.

An unsolved problem common to many of the tuna fisheries of the world is the nature of the interaction between longline and surface (i.e., seining, pole and line, and occasionally trolling and shallow handline) fisheries for the same species. Fisheries for yellowfin tuna, *Thunnus albacares;* albacore, *T. alalunga;* bluefin tuna, *T. thynnus;* southern bluefin tuna, *T. maccoyii;* and bigeye tuna, *T. obesus,* are prosecuted by both types of gear in the Pacific, Atlantic, and Indian Oceans. Although there can be considerable overlap of sizes of fish taken by the two types of gear, in general, longline gear takes larger (older) fish. Exploitation of a tuna stock by the two types of gear presents management with the problems of determining the effect of various combinations of fishing effort by the two gears on both yield per recruit to the two gears and recruitment to the stocks. In order to make these determinations, it is necessary to estimate 1) availability of the stock at each age to each of the two gears [The available portion of the stock is subject to both other mortality (any mortality not caused by gear of concern) and fishing mortality caused by the gear of concern. The unavailable portion of the stock is subject only to other mortality.], 2) fishing mortality of the available portion of the stock caused by each gear, 3) natural mortality, 4) growth, 5) fecundity, and 6) the relationship between egg production and recruitment.

The aim of this paper is to examine the interactions between longline and surface fisheries for yellowfin tuna and to determine the impact such interactions may have on the assumptions often made in assessment of yellowfin tuna fisheries and thus on the assessment calculations themselves. The paper is divided into three major sections. The first section examines the relationship between availability of the stock(s) of yellowfin tuna to surface and longline fishing and yield per recruit to the two gears. This is an important, and to our knowledge unexamined, aspect of all tuna fisheries exploited by both types of gear; the subsequent sections examine two asepcts of the biology of tuna that can affect the catch by each type of gear. The second section examines the effect of age specific sex ratios of yellowfin tuna on yield per recruit to the two types of gear and on egg production. The third section examines the effect of

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random migration or dispersal and location of recruitment of yellowfin tuna on estimates of mortality and yield per recruit to each gear. We have restricted our analysis to yellowfin tuna but believe that the concepts that we develop apply to the other species as well.

MATERIALS AND METHODS

While stocks of yellowfin tuna are subjects of important fisheries in all tropical oceans, information on vital parameters is sketchy and nonuniform. For example, tagging information available in the Pacific is lacking for the Atlantic stocks. On the other hand, regulation of the Pacific fishery makes interpretation of the catch information more difficult. Hence it is necessary to pick and choose from the available information that which is most relevant to the problems at hand. Although the parameters are likely to differ for fish from different oceans, if not fish from different areas of the same ocean, few studies have conclusively demonstrated that such differences exist. In addition, several (e.g., Lenarz et al. 1974) have found that conclusions from studies such as described in this paper are often insensitive to the likely range of values of parameters such as natural mortality, fishing mortality, and growth. In the first and second sections, we have used data primarily from the eastern Atlantic because historically catches have been more equally shared by longline and surface fisheries than in the eastern Pacific; in the third section we have modelled the eastern Pacific since information on migration patterns is more extensive. In both instances, the results are intended to be general rather than specific. Data extracted from one area and used in another is thought to be the best available and the question of real differences is left for further investigation.

With a noted exception, the growth equation $L = 194.8 \times (1 - e^{-0.42(t-0.67)})$ estimated by Le Guen and Sakagawa (1973) and length-weight equation $W = 0.0000214L^{2.9736}$ estimated by Lenarz (1974) are used for yellowfin tuna where L is fork length in centimeters, t is age in years, and W is weight in kilograms. Unless otherwise stated, we assumed that the annual instantaneous coefficient of natural mortality (M) is 0.8 (Hennemuth 1961). We estimated age-specific fecundity from two indices derived by Hayasi et al. (1972) (Table 1). Their index I was obtained from longline data and their index II was obtained from surface data. The fecundity indices were calculated by Hayasi et al. (1972) for fish caught in the Pacific by multiplying mean ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish. For much of our work, we used estimates of the 1967-71 average size (age) composition of the Atlantic yellowfin tuna fishery made by Lenarz et al. (1974) (Table 2). Use of length-age key assumes that length and age are equivalent. Sex composition shown in Table 2 is based on data from the Pacific.

TABLE 1.—Indices of fecundity of yellowfin tuna as interpolated from Hayasi et al. (1972), for fish caught in the Pacific calculated by multiplying average ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish.

Midpoint of size interval (cm)	Fecundity index I	Fecundity index II
80	0.04	0.07
85	0.04	0.14
90	0.05	0.21
95	0.08	0.27
100	0.15	0.36
105	0.23	0.42
110	0.33	0.51
115	0.42	0.61
120	0.55	0.70
125	0.70	0.81
130	0.88	0.92
135	1.12	1.04
140	1.40	1.15
145	1.80	1.26
150	2.30	1.37
155	2.77	1.50
160	3.20	1.62
165	3.57	1.76
170	4.05	1.91
175	4.42	2.06
180	4.82	2.23
	5.01	2.43

Estimates of the size- (age-) specific instantaneous coefficient of fishing mortality (F_t) on an annual basis were made using the Gulland (1965) and Murphy (1965) method. The computer program COHORT, written by W. W. Fox, Jr., of the Southwest Fisheries Center, was used to obtain estimates of F_t for each 5-cm size interval, beginning at 32.5 cm. The estimation procedure was initiated with a trial value of F_t for the largest size interval (Input F).

Estimates of F_t were obtained from the average 1967-71 catch composition data (Table 2) as was done by Lenarz et al. (1974). When feasible it is more desirable to estimate F_t from individual cohorts. This was not done because of the small number of years in the data series and belief that estimates from the average composition would adequately reflect conditions of the fishery. In a latter study, Fonteneau and Lenarz (1974) estimated F_t for individual cohorts from a longer time

TABLE 2.—Composite catch in numbers of yellowfin tuna by gear, sex, and size. Length composition by gear is based on data from Lenarz et al. (1974) on the Atlantic fishery. Sex composition is based on data from the Pacific (Murphy and Shomura 1972).

Age at beginning of interval (yr)	Midpoint of size interval (cm)	Male			Female		
		Surface	Longline	Total	Surface	Longline	Total
1.0579	35	1,179	0	1,179	1,179	0	1,179
1.1325	40	14,528	0	14,528	14,528	0	14,528
1.2039	45	61,563	0	61,563	61,563	0	61,563
1.2888	50	186,611	4	186,615	186,611	4	186,615
1.3710	55	237,622	11	237,633	237,622	11	237,633
1.4562	60	210,711	226	210,937	210,711	226	210,937
1.5445	65	121,824	324	122,148	121,824	324	122,148
1.6363	70	137,389	1,076	138,465	137,389	1,076	138,465
1.7317	75	102,046	2,718	104,764	102,046	2,718	104,764
1.8310	80	90,710	2,847	93,557	90,710	3,847	93,557
1.9348	85	67,060	6,013	73,073	67,060	6,013	73,073
2.0432	90	52,541	6,525	59,066	52,541	6,525	59,066
2.1568	95	51,366	5,833	57,199	51,366	5,833	57,199
2.2761	100	56,714	7,537	64,251	56,714	7,537	64,251
2.4017	105	52,752	17,036	69,788	52,752	17,036	69,788
2.5343	110	51,497	20,105	71,602	51,497	20,105	71,602
2.6748	115	35,981	22,017	57,998	35,981	22,017	57,998
2.8240	120	26,167	21,430	47,597	26,167	21,480	47,597
2.9832	125	30,779	28,679	59,458	30,779	28,679	59,458
3.1538	130	26,001	29,272	55,273	26,001	29,272	55,273
3.3376	135	21,975	22,345	44,320	21,975	22,345	44,320
3.5368	140	16,749	26,035	42,784	16,749	26,035	42,784
3.7542	145	26,919	38,782	65,701	11,661	16,800	28,461
3.9935	150	31,942	36,099	68,041	8,450	9,549	17,999
4.2595	155	24,727	33,933	58,665	3,767	5,170	8,937
4.5590	160	18,701	22,644	41,345	1,524	1,845	3,369
4.9017	165	14,497	13,140	27,637	573	519	1,092
5.3021	170	5,621	6,162	11,783	94	103	197
5.7838	175	3,703	240	3,943	21	1	22
6.3883	180	1,836	55	1,891	3	0	3
Total		1,781,711	371,093	2,152,804	1,679,858	254,020	1,933,878

span and obtained results similar to Lenarz et al. (1974).

The computer program MGEAR, written by W. H. Lenarz, was used to obtain estimates of yield per recruit using the Ricker (1958) yield equation. A description and listing of MGEAR is available from its author. The program was slightly modified to calculate indices of egg production using the following equation

$$E_{t_1,t_2} = 0.5\,(t_2 - t_1)\,N_{t_1}\,(FI_{t_1} + FI_{t_2}e^{-(F_{t_1} + M_{t_1})(t_2 - t_1)})$$

where E_{t_1,t_2} = index of egg production between age t_1 and t_2,
FI_{t_1} = index of fecundity for age t_1,
N_{t_1} = number of females in population of age t_1,
F_{t_1} = coefficient of instantaneous fishing mortality between age t_1 and age t_2, and
M_{t_1} = coefficient of instantaneous natural mortality between age t_1 and age t_2.

For this equation it is assumed that the estimates of FI are proportional to egg production per female, which is assumed to be continuous, and that the rate of egg production is linear over the interval (t_1, t_2).

A computer program MIGR was written by J. R. Zweifel to perform the calculations used for the third section of this paper. Since new methodology is developed, a description of the calculations will be given in that section.

AVAILABILITY OF THE STOCK(S) OF ATLANTIC YELLOWFIN TUNA TO SURFACE AND LONGLINE GEAR

In previous works on yield per recruit, yellowfin tuna of all ages in either the entire Atlantic (e.g., Hayasi and Kikawa 1970; Wise 1972; Hayasi et al. 1972; Lenarz et al. 1974), or in the eastern Atlantic (e.g., Fonteneau and Lenarz 1974) were assumed to be equally available to both longline and surface gear. However, since the surface fishery for yellowfin tuna occurs very close to the west African coast (Fox and Lenarz 1973) while the longline fishery for yellowfin tuna is distributed throughout the tropical Atlantic, it seems possible that the longline fishery is exploiting some fish that are not available to the surface fishery. It is

also possible that some stock(s) which are available to surface fishing are never available to the longline fishery. Since significant tagging efforts have begun only recently in the Atlantic and the results of these studies have not been published, data are not available to evaluate the availability of yellowfin tuna to both gears.

However, there is evidence from the Pacific that yellowfin tuna are not equally available to longline and surface gears. With the permission of W. H. Bayliff of the Inter-American Tropical Tuna Commission (IATTC), we examined yellowfin tuna tag return data from the eastern Pacific during 1963-66 in an attempt to evaluate the availability of fish to both gears in that area. We tabulated the number of tag returns for fish larger than 100 cm at return by 10-cm size groups (Table 3). All of the fish had been at liberty for at least 10 mo. Although all of the tagged fish were measured when released, not all were measured when recovered. Bayliff recommended the relationship

$$L = 167\,(1 - e^{-0.6(t-0.833)})$$

estimated by Davidoff (1963) for growth of yellowfin tuna in the eastern Pacific as the best equation to estimate the size of unmeasured fish. All of the returns were surface-caught fish, even though longliners captured a considerable number of yellowfin tuna in the eastern Pacific (east of long. 130°W) (Kume and Joseph 1969). In fact for many of the 10-cm size groups, the longliners caught more yellowfin tuna than the surface gear operators (Table 4).

TABLE 3.—Number of returns of tagged yellowfin tuna from the eastern Pacific Ocean by size interval and year (W. H. Bayliff, pers. commun.).

Size interval (cm)	1963	1964	1965	1966
101-110	2	16	3	3
111-120	1	7	1	1
121-130	2	0	2	0
131-140	0	0	0	1
141-150	0	0	0	0
151-160	0	0	1	0

Again at the suggestion of Bayliff, we estimated the expected return of tags from longline-caught fish when all fish are equally available to both gears. Assuming tag recoveries were independent of each other, recovered tags were reported at the same rate by both components of the fishery, and tagged fish were equally available to both gears: then the expected returns of tagged fish of size i by gear j in year k is given by

$$E(R_{ijk}) = R_{i\cdot k}N_{ijk}/N_{i\cdot k} \qquad (1)$$

$$i = \begin{cases} 1, \text{ when size is between 101 and 110 cm} \\ \cdot \\ \cdot \\ \cdot \\ 6, \text{ when size is between 151 and 160} \end{cases}$$

$$j = \begin{cases} 1, \text{ when fish are caught by surface gear} \\ 2, \text{ when fish are caught by longline gear} \end{cases}$$

$$k = \begin{cases} 1, \text{ when fish are caught in 1963} \\ 2, \text{ when fish are caught in 1964} \\ 3, \text{ when fish are caught in 1965} \\ 4, \text{ when fish are caught in 1966} \end{cases}$$

where R_{ijk} = number of returns and
N_{ijk} = number of fish caught.

A dot in the position of a subscript signifies summation of the variable over the subscript, e.g., $X_{i\cdot k} = \sum_{j=1}^{2} X_{ijk}$.

Forty fish were returned by the surface gear during 1963-66 (Table 3). Using the statistics of Tables 3 and 4 and the three assumptions, a return of 5.4 of these tags would have been expected from the longline fishery and 34.6 from the surface fishery. The chi-square value, corrected for discontinuity, for the observed and expected returns (Equation 1) is 5.13, with probability slightly less than 0.025. The power of the test of the hypothesis of independence, equal reporting rate, and equal availability was reduced because we combined the year and size strata to avoid

TABLE 4.—Catch of yellowfin tuna from the eastern Pacific Ocean (east of long. 130°W) in hundreds of fish by size and gear (Kume and Joseph 1969).

Size interval (cm)	1963		1964		1965		1966	
	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear
101-110	653	336	4,082	173	3,386	30	2,926	54
111-120	473	455	2,245	465	2,211	93	2,044	116
121-130	508	390	720	1,078	1,895	444	1,312	304
131-140	237	751	448	804	905	758	718	515
141-150	240	541	320	469	498	466	536	575
151-160	212	144	102	104	194	205	204	200

strata with low expected values. The probability under Equation (1) of a returned tag being from a surface-caught fish (P_{i1k}) is

$$P_{i1k} = N_{i1k}/N_{i\cdot k} \ . \qquad (2)$$

The exact probability of all returns during the 1963-66 period being from surface-caught fish, given the distribution of returns among year and size categories, is

$$P_{.1.} = \prod_{i=1}^{6} \prod_{k=1}^{4} (P_{i1k})^{R_{i\cdot k}} \ . \qquad (3)$$

Our estimate of $P_{.1.}$ is 0.00152, which is very low and indicates that Equation (1) does not hold. Thus we may conclude that 1) tag returns are not independent (e.g., fish that were captured from a school and tagged may remain in the same school until recaptured), and/or 2) longline recoveries are reported at lower rates than surface recoveries, and/or 3) the fish were not equally available to both gears. Since all fish were at liberty for more than 10 mo before being recovered, the assumption of tag returns being independent seems likely to be valid. The independence of tag returns would seem to be a desirable subject for further research since the assumption is so often made in analyses of tag returns. A considerable number of southern bluefin tuna have been recovered and returned by longliners (Shingu 1970), indicating longline fishermen do cooperate in tagging programs. During the period of the study, the surface fishery was only beginning to move offshore (Calkins and Chatwin 1971), while the longline fishery was distributed throughout the area (Kume and Joseph 1969). Also, the fish that were released were caught by surface gear, tagged, and released in nearshore areas. Thus, tagged fish were probably more representative of fish exploited by the surface fishery than those that were exploited by the longline fishery, if two groups of fish existed. Thus it seems plausible that the tagged fish were not equally available to longline and surface gears.

This is further evidence of unequal availability of yellowfin tuna to the two gears in the Pacific. Previously, Hisada (1973) showed that yellowfin tuna caught near the surface using handlines were of the same size as those caught by longliners at the same time and in the same area of the western Pacific. However, the surface-caught fish tended to be more sexually mature except in areas in which the 26°C isotherm occurred at depths fished by longliners. He attributed this phenomenon to a preference for warmer waters by sexually mature fish and noted that larvae of yellowfin tuna tend to be found at water temperatures exceeding 26°C. Thus, some yellowfin tuna evidently behave in a fashion that makes them available to surface fishing but not to longline fishing. Further evidence along these lines is provided by Shingu and Tomlinson (Patrick K. Tomlinson, Inter-American Tropical Tuna Commission, La Jolla, Calif. Pers. commun., 1974) who found that the length-weight relationship estimated by Lenarz (1974) for surface-caught yellowfin tuna in the Atlantic was more representative of the longline catch in the eastern Pacific than was the relationship estimated by Chatwin (1959) for surface-caught yellowfin tuna in the eastern Pacific.

With the above in mind, we considered three hypothetical stock structures for the Atlantic yellowfin tuna fishery: 1) the same stock(s) are equally available to both gears, 2) half of the catch of the longline fishery comes from stock(s) not available to the surface fishery, and 3) the entire catch of the longline fishery comes from stock(s) not available to the surface fishery. The effects of the three hypotheses on estimates of fishing mortality and yield per recruit to the gear were examined.

Using the data in Table 2, we estimated the vector F of size-specific instantaneous mortality rates F_t under the three hypotheses which are identified by the proportion ϕ of the longline catch which comes from the stocks exploited by the surface fishery as ϕ = 1.0, 0.5, and 0.0 respectively. For ϕ = 1.0, all of the data in Table 2 was used to estimate the F vector. For ϕ = 0.5, the surface catch plus 50% of the longline catch was used and for ϕ = 0.0 only the surface catch was used for estimating F. When ϕ = 0, an additional F vector was estimated for a longline fishery operating without the presence of a surface fishery by using only the longline catch. The F vectors were then used to calculate yield per recruit to the two gears. Estimation of a vector of size-specific F requires an estimate of natural mortality and size-specific F for one size category. In all instances, we chose to use an estimate of size-specific F for the fish >177.5 cm. This estimate will be referred to as Input F. The final value of size-specific F was set at 0.2 following Lenarz et al. (1974). The estimates (Figure 1) indicate that values of F for large fish are directly related to the portion of the longline catch that comes from the stock(s) exploited by the

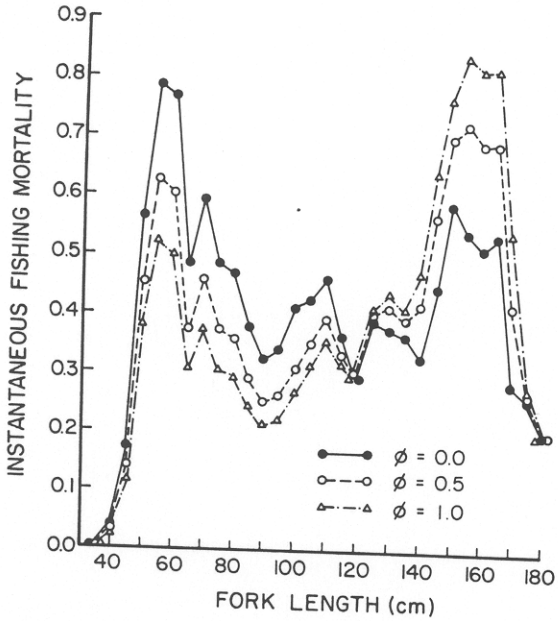


FIGURE 1.—Estimates of size-specific fishing mortality of Atlantic yellowfin tuna as a function of porportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery.

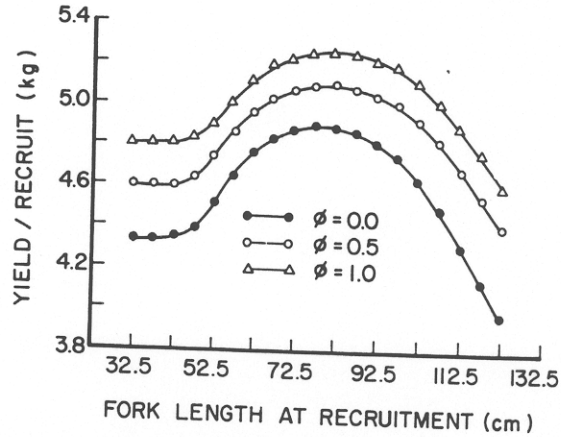


FIGURE 2.—Yield per recruit (kilograms) of Atlantic yellowfin to surface and longline gear as a function of size at recruitment and proportion of catch (ϕ) by the longline fishery that comes from stock(s) exploited by surface fishery. The vector of fishing mortality is equal to the value at the time of study.

surface fishery. The relative values of yield per recruit within a hypothesis are not significantly affected by the portion of the longline catch that comes from the stock(s) exploited by the surface fishery (Figure 2). Therefore, the three hypothetical stock structures do not seem to have much bearing on decisions concerning minimum size regulations.

Estimates of yield per recruit were also plotted as functions of fishing effort (mortality), size at recruitment, and portion of longline catch that comes from stock(s) exploited by the surface fishery. Again the relative values of the results are not significantly influenced by the stock structure (Figure 3a, b). We note that Figure 3 is in agreement with the conclusion of Fox and Lenarz (1974), ". . . that the Atlantic yellowfin fishery is approaching or has obtained a plateau where substantially increased sustainable average yield of yellowfin tuna will not be obtained by increasing fishing effort without some concomitant change in the constitution of the fishery. . . ." They used the production model approach under the alternative assumptions that either the longline or surface gear exploits the same or separate stock(s).

The effect of the surface fishery on the longline fishery was examined by estimating yield per recruit to the longline fishery in the presence and in the absence of a surface fishery (Figure 4). The results suggest that if the two gears exploit the same stock(s), the surface fishery reduces the potential yield per recruit to the longline fishery by about twofold at the position of the fishery during the study period (i.e., multiplier of effort = 1) and about fivefold for a threefold increase in effort. The same procedure was used to examine the effect of the longline fishery on the surface fishery (Figure 5). The results indicate that at the level of fishing effort at the time of study, the yield per recruit to the surface fishery would be increased by 25% if the longline fishery ceased.

Although the presence of each fishery reduces the yield per recruit of the other, the yield per

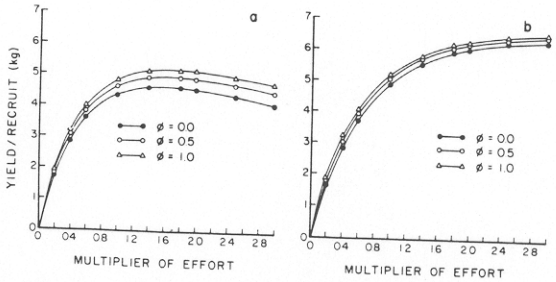


FIGURE 3.—Yield per recruit of Atlantic yellowfin tuna as a function of fishing effort and proportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery: (a) size at recruitment is 32.5 cm, (b) size at recruitment is 77 cm.

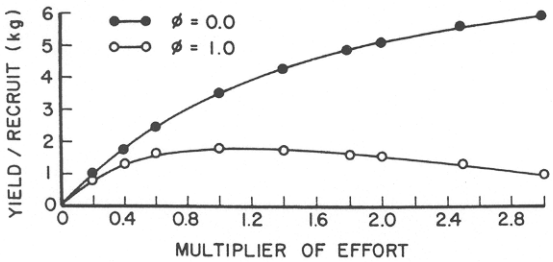


FIGURE 4.—Estimates of yield per recruit of Atlantic yellowfin tuna to the longline fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of a surface fishery.

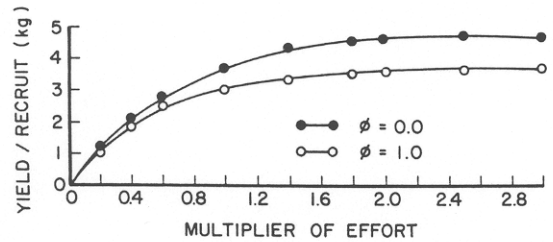


FIGURE 5.—Estimates of yield per recruit of Atlantic yellowfin tuna to the surface fishery as a function of effort and presence (ϕ = 1.0) or absence (ϕ = 0.0) of longline fishery.

recruit of the combined fisheries is higher than the yield per recruit of either fishery alone. The results suggest that if a catch quota system is imposed on the Atlantic yellowfin tuna fishery, all components should be included unless it is shown that different stock(s) are being exploited by the gear.

The above results (Figures 4, 5) suggest that a stock of yellowfin tuna will produce a potentially higher yield per recruit to a longline fishery than to a surface fishery, if the fish are equally available to the two gears. However, until the question of availability is settled, it is not possible to predict the potential production to the two gears. We point out here that gear-specific availability is not well known for any tuna fishery and would be difficult to determine. Thus, we are faced with the prospect of probably being forced to determine empirically the production potential for each gear in each fishery. After a fishery is established, an analysis of the type conducted on the Atlantic yellowfin tuna fishery could be used to examine the effects of availability to the two gear types, and a tagging study could be designed to provide the required answers.

EFFECTS OF AGE-SPECIFIC SEX RATIOS OF ATLANTIC YELLOWFIN TUNA ON YIELD PER RECRUIT TO THE TWO TYPES OF GEAR AND STOCK FECUNDITY

While a number of authors have noted that the ratio of females to males appears to be less than 1:1 for catches of larger tunas, none to our knowledge has incorporated these observations into calculations of yield per recruit or stock fecundity. Beardsley (1971) reported that the ratio of female to male Atlantic longline-caught albacore was 233:365 during the December 1969-September 1970 period. Males increasingly dominated at sizes >100 cm. Females slightly outnumbered males between 92 and 100 cm. One explanation for the catch curves estimated by Beardsley is a 1:1 sex ratio at small sizes, a slightly slower growth for females for fish >90 cm, and beyond 100 cm, either a higher rate of natural mortality for females or a change in behavior that makes females less available than males to longline fishing. Other explanations exist, e.g., a combination of low sex ratio and slow growth of females throughout their life. Sakamoto (1969) noted for Atlantic bigeye tuna, ". . . males predominated in areas of higher water temperature. Proportion of females increase as the water temperature gets lower." His data indicate that as size increases the proportion of females decreases and females may grow slower than males in waters between lat. 30° to 50°N, but not in equatorial waters. Data presented by Kikawa (1964) indicate that southern bluefin tuna >150 cm are predominantly males, while females often outnumber males at smaller sizes. Thus, female southern bluefin tuna may grow more slowly than males.

Since there is considerable evidence for age-specific changes in the sex ratio of tunas, we believe that the effects of such changes on estimates of yield per recruit to each gear type and fecundity should be investigated. We have assumed sex ratios to be the same as with Pacific yellowfin tuna because no extensive studies of age-specific sex ratios for Atlantic yellowfin tuna have been published. We used results from a study by Murphy and Shomura (1972), who found that beyond 140 cm male yellowfin tuna greatly outnumbered females (Figure 6). The data in Figure 6 do not show a large excess of females in any size interval and thus no evidence of sex-specific growth is exhibited. Using their data and the age-length

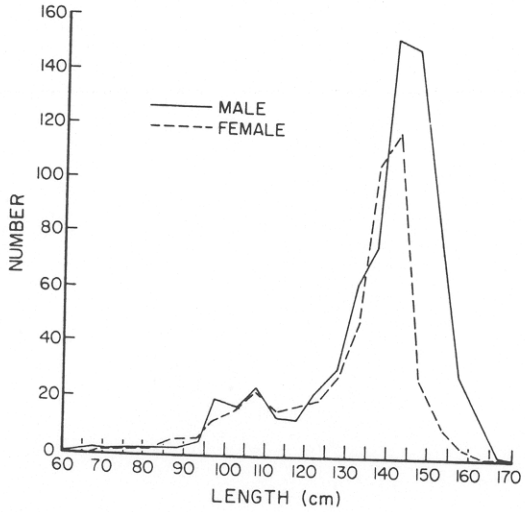


FIGURE 6.—Length distribution by sex of longline-caught yellowfin tuna in the central Pacific Ocean (Murphy and Shomura 1972).

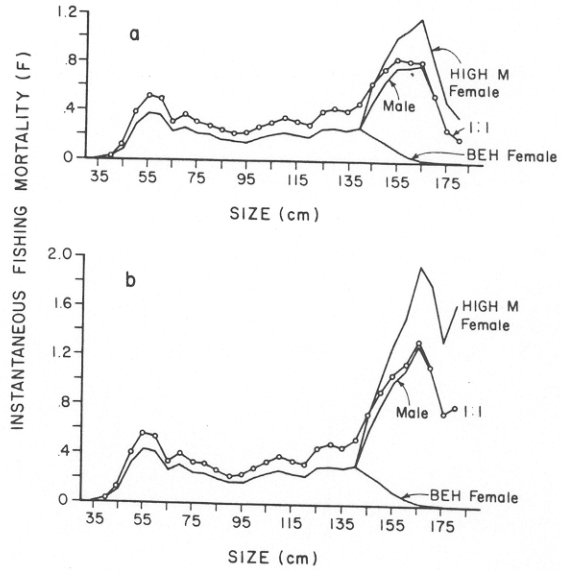


FIGURE 7.—Estimates of size and sex specific coefficient of instantaneous fishing mortality on annual basis (F) for Atlantic yellowfin tuna for 1:1, BEH and HIGH M hypotheses (see text): (a) low Input F, B) high Input F.

relationship of LeGuen and Sakagawa (1973), we estimated that beyond 140 cm

$$\ln R = 6.74 - 1.96t \qquad (4)$$

where R = ratio of females to males
t = age in years.

One interpretation of the above result (assuming that males have a coefficient of instantaneous natural mortality of 0.8 on an annual basis as do all fish <145 cm) is that female yellowfin tuna >140 cm have a coefficient of apparent natural mortality of 2.76. Assuming that the results of Murphy and Shomura apply to the Atlantic and that all yellowfin tuna are equally available to both gears, we separated the catch of yellowfin tuna into males and females using Equation (4) and Table 2, and estimated F for the males using Input F values of 0.2 and 0.8 for fish >177.5 cm (Lenarz et al. 1974). An alternative method would be to use the same Input F for the three hypotheses at the smallest size interval. This was attempted and resulted in either estimates of F_t which, based on the results of other studies, appeared to be too low under the 1:1 hypothesis or too high under the other hypotheses. The estimates of size-specific F are similar except for very large yellowfin tuna (Figure 7). Since the deviations in sex ratio from 1:1 occurs only at large sizes, we used both sets of estimates of F.

For females, three hypotheses were examined for estimating F: 1) the observed differences in sex ratios are artifacts, and consequently females have the same values of F and M as males (denoted 1:1); 2) females >140 cm have a higher natural mortality rate than males but are exploited at the same rate as males for all sizes (denoted as HIGH M); and 3) females have the same natural mortality rate as males but become less subject to fishing mortality beyond 140 cm (denoted as BEH for behavior changes). Under the BEH hypothesis, F_t for females >140 cm is equal to the ratio of the catch of females to the catch of males times F_t estimated for males. The alternative hypotheses considerably affected the estimates of size-specific F (Figure 7).

In the following analyses, we found that the BEH and HIGH M hypotheses produce similar results. To save space, we refer to only the one hypothesis that produced results which showed the greatest difference from the 1:1 hypothesis. Also, when not specifically indicated, size of recruitment and effort are assumed to be those at the time of the study, i.e., 1967-71 where the multiplier of effort is equal to unity.

Estimates of yield per recruit as a function of fishing effort are shown in Figure 8. The choice of Input F has little effect on the relative values of

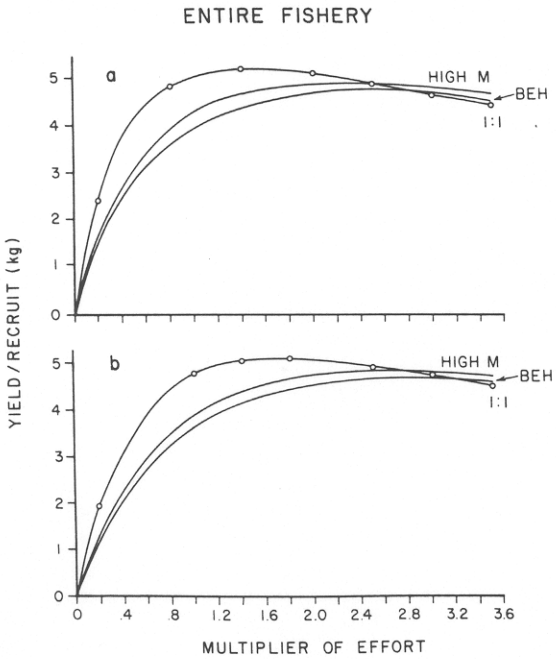


FIGURE 8.—Estimates of yield per recruit of Atlantic yellowfin tuna at size of recruitment at time of the study as a function of fishing effort and sex hypothesis: (a) high Input F, (b) low Input F.

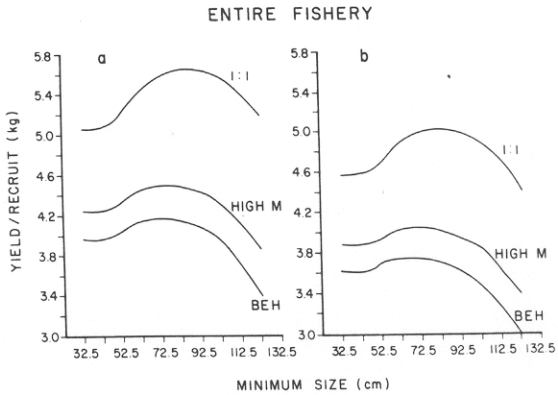


FIGURE 9.—Estimates of yield per recruit of Atlantic yellowfin tuna at level of fishing effort at the time of the study for 1:1, BEH and HIGH M hypotheses as a function of size at recruitment: (a) high Input F, (b) low Input F.

yield per recruit. Yield per recruit is closer to the maximum under high Input F than low Input F. The curves are considerably more dome-shaped when a 1:1 sex ratio is assumed than under the other two hypotheses. Under high Input F and the 1:1 hypothesis only a 3% increase in yield per recruit could be obtained by increasing fishing effort. Under the BEH hypothesis, a 20% increase in yield per recruit could be obtained by doubling the effort.

Estimates of yield per recruit as a function of size at recruitment are shown in Figure 9. Again the choice of Input F has little effect on the relative values of yield per recruit. A slightly greater dependence of yield per recruit on minimum size is obtained when the high Input F is used. Under high Input F, and the 1:1 hypothesis a 10% increase in yield per recruit could be achieved by increasing size at recruitment. Under the BEH hypothesis, only a 5% increase would occur. Eumetric fishing occurs when size at recruitment is raised from the current 32.5 to 82.5 cm under the 1:1 hypothesis and 72.5 cm under the BEH hypothesis.

Estimates of yield per recruit as a function of fishing effort were also calculated for each gear (Figure 10). The results show that the curves are more dome-shaped for the longline fishery than for the surface fishery under all three hypotheses. Furthermore, the longline fishery is more sensitive to fishing effort under the 1:1 hypothesis than under the other two. The curves for the surface fishery are dome shaped under the 1:1 hypothesis, but appear to approach an asymptote under the other two.

We also estimated yield per recruit for each gear when the other gear is not exploiting the stock (Figure 11). A comparison of Figures 10 and 11 reveals that yield per recruit to the longline fishery would increase by about 115% if surface fishing were eliminated under high Input F and the 1:1 hypothesis and 76% under high Input F and the BEH hypothesis. Yield per recruit to the surface fishery would increase by about 30% if the longline fishery were eliminated under high Input F and the 1:1 hypothesis and 22% under the BEH hypothesis. Thus, the nature of age-specific sex ratio has a greater effect on that of the longline fishery than on the relative success of the surface fishery. The curves for a longline fishery in the presence of a surface fishery are dome-shaped (Figure 10), while the curves in the absence of a surface fishery are not (Figure 11). This again points out the importance of not treating the two fisheries as separate entities unless it is shown that they exploit separate stocks.

Stock fecundity (egg production per recruit) relative to an unfished stock was estimated as a function of fishing effort. Stock fecundity was considerably affected by the choice of fecundity index

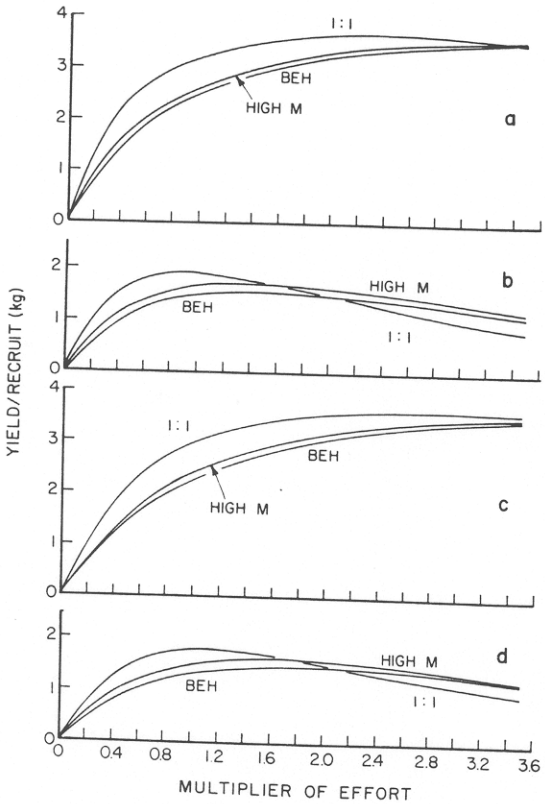


FIGURE 10.—Estimates of yield per recruit of Atlantic yellowfin tuna when both gear fish at size of recruitment at the time of the study as a function of sex ratio hypothesis, fishing effort, and gear: (a) surface gear with high Input *F*, (b) longline gear with high Input *F*, (c) surface gear with low Input *F*, and (d) longline gear with low Input *F*.

and sex ratio hypothesis but only slightly affected by the choice of Input *F* (Figure 12). At the level of fishing effort at the time of the study under high Input *F* and 1:1 hypotheses, the relative fecundity is 0.28 when the fecundity index I is used and 0.39 when fecundity index II is used. Under the HIGH *M* hypothesis, relative fecundity is 0.55 when fecundity index I is used and 0.61 when fecundity index II is used. Thus, at the level of fishing effort at the time of the study, the choice of fecundity has a 10 to 30% effect on estimates of relative fecundity, while the choice of sex ratio hypothesis has a 30 to 50% effect. The two choices, fecundity index and sex ratio hypothesis, also have considerable effect on relative fecundity when plotted as a function of size at recruitment (Figure 13).

The relationship between stock fecundity and recruitment has not been demonstrated for any tuna. As shown above, one of the difficulties in demonstrating such a relationship is obtaining a reasonably accurate estimate of stock fecundity. Even if stock fecundity could be accurately determined, the recruitment process is likely to be so complex that much more research would be required before a reliable predictor of recruitment could be developed.

It is interesting to note that similar estimates of yield per recruit and relative fecundity are obtained under the HIGH *M* and BEH hypotheses. Thus it appears that research should be directed toward determining whether or not the 1:1 hypothesis or one of the other two are valid rather than distinguishing between the HIGH *M* and BEH hypotheses. This research should be a fairly simple matter. The choice of fecundity index is also of significance for estimating relative fecundity. The difference between the two indices is caused mainly by different maturity schedules (Hayasi et al. 1972). The surface-caught fish appeared to mature at an earlier age than longline-caught fish, and could be an artifact related to the phenomenon noted by Hisada (1973); i.e., mature fish tend to prefer warm water. It should also be a fairly simple matter to determine the cause of the difference between the two indices.

SIMULATION MODEL OF PATTERNS OF DISPERSAL AND RECRUITMENT OF YELLOWFIN TUNA

Factors that could cause groups of tuna to not be available to all components of a fishery include nonrandom movements, random movements but nonrandom distribution of fishing gear or effort, and recruitment that is nonrandom in a geographical sense.

Extensive tagging experiments have not produced any clear-cut evidence of a definite migration pattern for yellowfin tuna in the eastern Pacific. Bayliff and Rothschild (1974) recently found evidence for both random dispersal and directed movements. They were not able to remove the effects on their data of lack of fishing effort in some time-area strata and of the coastal boundary. The evidence for directed movements indicated that such movements were generally parallel to the coast, suggesting that the presence of the coast influenced their results. Fink and Bayliff (1970), in a synthesis of extensive tagging data, proposed that recruitment to the nearshore surface fishery is not random in a geographical sense, but tends to take place off Mexico and in the Panama Bight.

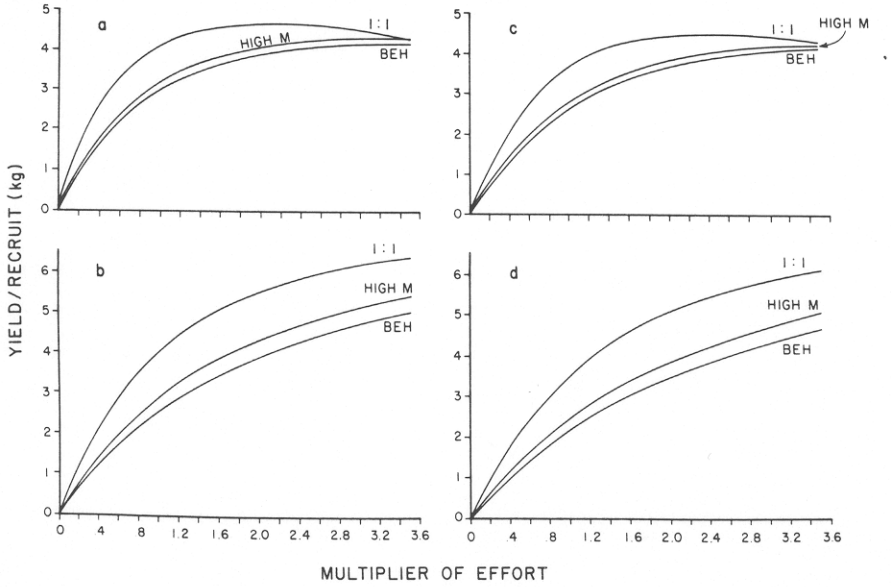


FIGURE 11.—Estimates of yield per recruit at size at recruitment at the time of the study as a function of fishing effort, sex ratio hypothesis, and fishing gear when only one gear is fishing: (a) high Input F and surface gear, (b) high Input F and longline gear, (c) low Input F and surface gear, and (d) low Input F and longline gear.

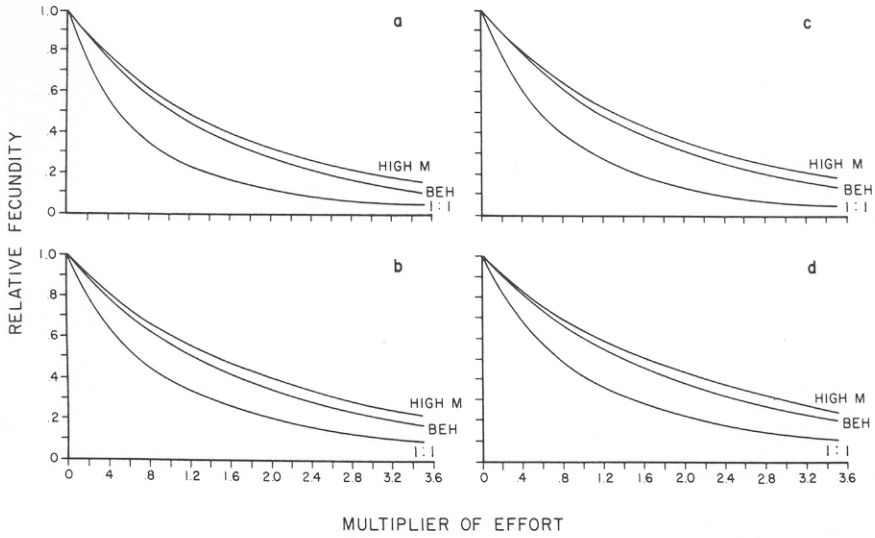


FIGURE 12.—Estimates of relative stock fecundity at size at recruitment at the time of the study as a function of fishing effort, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity Index II, (c) low Input F and fecundity index I, and (d) low input F and fecundity index II.

With the above results in mind, we developed a computer simulation model to examine the interrelationships of: 1) patterns of movement of fish; 2) patterns of recruitment (i.e. by area), and 3) fishing strategy for two gear types (surface and longline) fishing alone or together on the same population.

The model is general in that it allows the user to

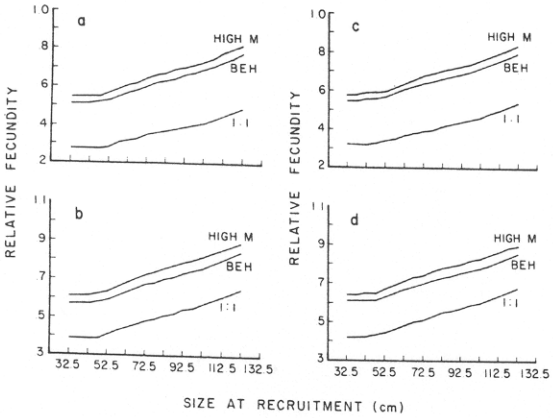


FIGURE 13.—Estimates of relative stock fecundity at level of fishing effort at the time of study as a function of size at recruitment, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity index II, (c) low Input F and fecundity index I, and (d) low Input F and fecundity index II.

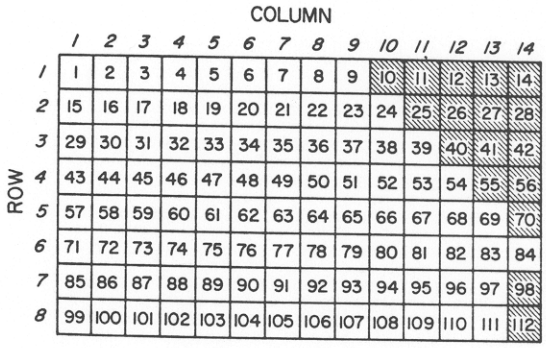


FIGURE 14.—Representation of eastern Pacific Ocean. Each cell represents a 5° square area. Hatched cells represent land. Column 1 is western boundary and Column 14 is eastern boundary. Row 1 is northern boundary and row 8 is southern boundary.

specify the nature of movements, locations of recruitment, parameters of growth, and natural fishing mortality.

We crudely represented the eastern Pacific Ocean with the grid of 5° square areas shown in Figure 14. The number of fish of a specific age in each cell at time t is given by the vector

$$N_t = AS_tN_{t-1} \tag{5}$$

where N_t (112 × 1) has elements $(n_i)_t$ equal to the number of fish in cell i at time t, S_t (112 × 112) is a diagonal matrix with elements $(s_{ii})_t$ equal to the survival rate of fish in cell i from time $t - 1$ to time t, A(112 × 112) is a probability transfer matrix with elements (a_{ij}) equal to the probability of a fish in cell j moving to cell i, and where N_0(112 × 1) has elements $(n_i)_0$ equal to the number of recruits in cell i. Five consecutive year classes are in the system at a time.

For our work we specified A, the transfer matrix, by the assumption that for any cell the probabilities of fish remaining stationary and moving to each of eight adjacent cells is the same, i.e., 1/9. Any other transfer has zero probability. This general rule is modified as follows:

1) Probabilities of remaining stationary in cells adjacent to the shore are augmented by the sum of probabilities of those movements which would otherwise put fish on land and the probability of occurrence on land is zero.

2) Probabilities projecting beyond the northern and southern edges are similarly absorbed on the boundaries.

3) In cells of rows 2 and 7, probabilities of moving toward rows 1 and 8 are decreased by half with the probability of remaining stationary increased by a like amount. This is an attempt to simulate a stock encountering increasingly marginal conditions as the northern and southern boundaries are approached.

4) Probabilities of remaining stationary on the western edge are augmented by the probability of returning from beyond the boundary in a single time interval. The remainder of the fish that move beyond the western boundary are lost to the system.

The speed of dispersion is controlled both by A and the time interval. The time interval was 3 mo for this study. The combination of A as defined and time interval of 3 mo allows a fish to travel a maximum of 1,200 mi in a year. Only 1 out of 820 surviving fish that begin the year in the center of the grid travel 1,200 mi in a year. These relatively slow random movements seemed reasonable, based on the results shown in Bayliff and Rothschild (1974) and recent results of IATTC tagging studies (Inter-American Tropical Tuna Commission[3]).

Two alternative recruitment models were examined. For the first, denoted as inshore re-

[3]Cited with permission of M. Clifford Peterson, Acting Director of the Inter-American Tropical Tuna Commission. From the Inter-American Tropical Tuna Commission Bi-monthly Report, March-April 1976:8-13.

cruitment, recruits are divided equally among the five cells 51, 52, 69, 83, and 84, which resemble the recruitment areas proposed by Fink and Bayliff (1970). For the other alternative, denoted as uniform recruitment, recruits are divided equally among all cells except those on the boundaries or on land. Total annual recruitment is 100 fish. We assumed 1) that fish are 1 yr old when recruited, 2) growth proceeds according to the von Bertalanffy curve of LeGuen and Sakagawa (1973), and 3) the coefficient of instantaneous natural mortality is 0.8 on annual basis and is independent of time and location. Fish >6 yr old (175 cm) were removed from the system. Consequently, under constant conditions the fishery reaches equilibrium in 5 yr. The system was always run for 5 yr before an experiment was begun.

We first examined the effects of sampling location, dispersal, and location of recruitment on age distribution and the resulting apparent rate of natural mortality obtained from unbiased samples from an unfished population. Mortality was estimated with the standard linear regression model ($\ln N_t = \ln N_0 - Mt$) from the age distribution of fish in each cell. It is assumed that mortality is constant after full recruitment, and that the modal age represents first age of full recruitment. The results reveal that M is usually overestimated as would be expected when fish emmigrate from a sampled area (Figure 15). Estimates of M tend to be relatively high near areas of spawning with inshore recruitment. In the case of uniform recruitment, estimates of M tend to be highest on the western boundary where fish are lost to the system. Modal age tends to increase in a westerly direction for inshore recruitment and stay relatively constant for uniform recruitment (Figure 15). The modal size of actual catches of surface-caught yellowfin tuna in the eastern Pacific increases in a westerly direction (Figure 16). Although the surface fishery probably does not take an unbiased sample of the size distribution of the population, the data are suggestive of reduced recruitment in the western areas.

We simulated a 20-yr hypothetical yellowfin tuna fishery to examine interactions among a longline fishery, inshore surface fishery, ocean-wide surface fishery, and ocean-wide surface fishery that does not heavily exploit young fish as follows:

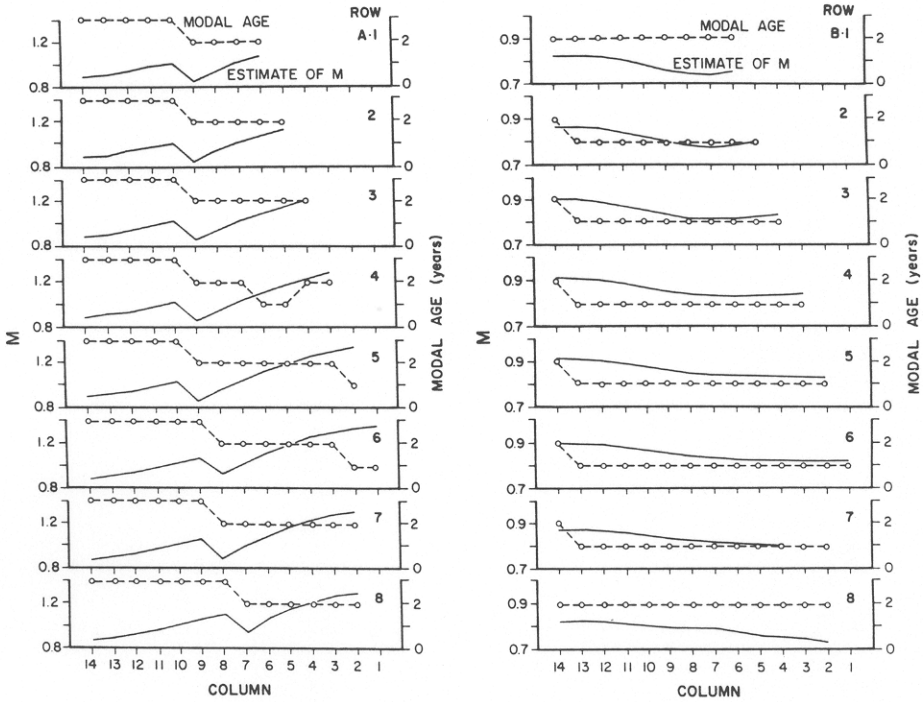
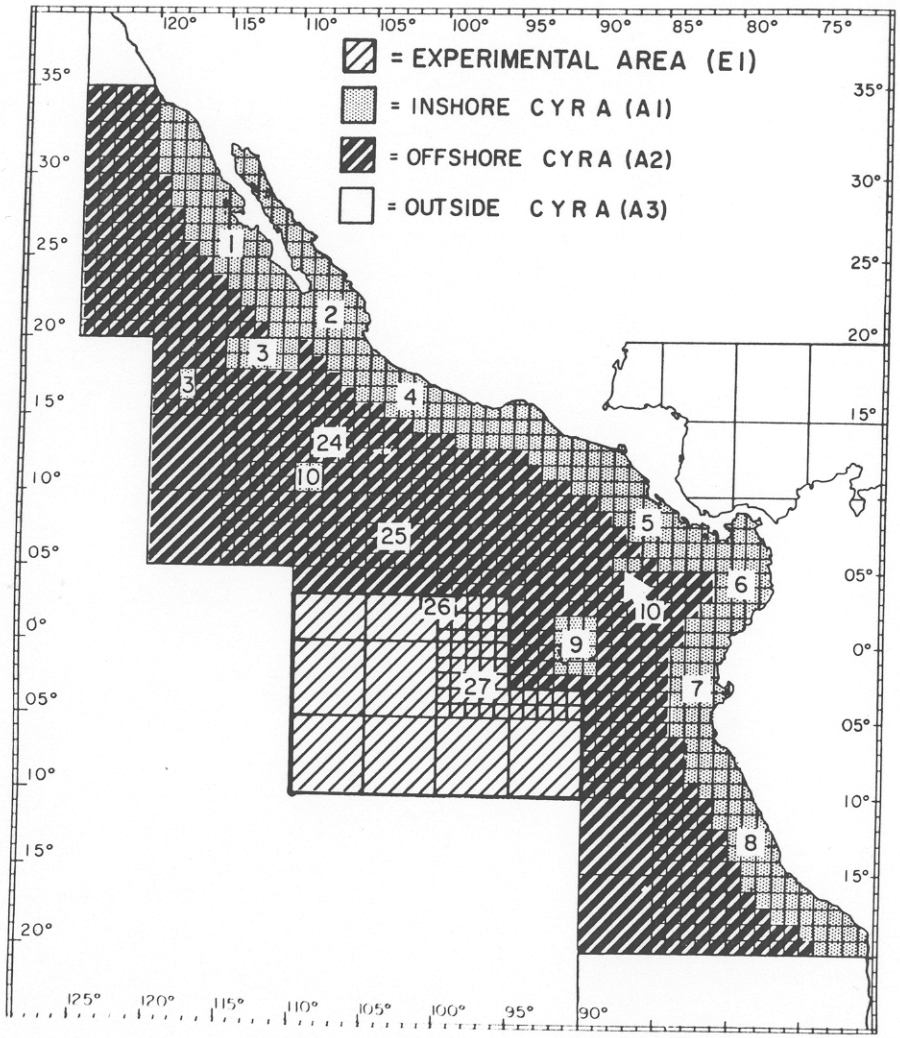


FIGURE 15.—Estimates of coefficient of instantaneous natural mortality on annual basis (M) and modal age of yellowfin tuna by row and column: (A) inshore recruitment, and (B) uniform recruitment.



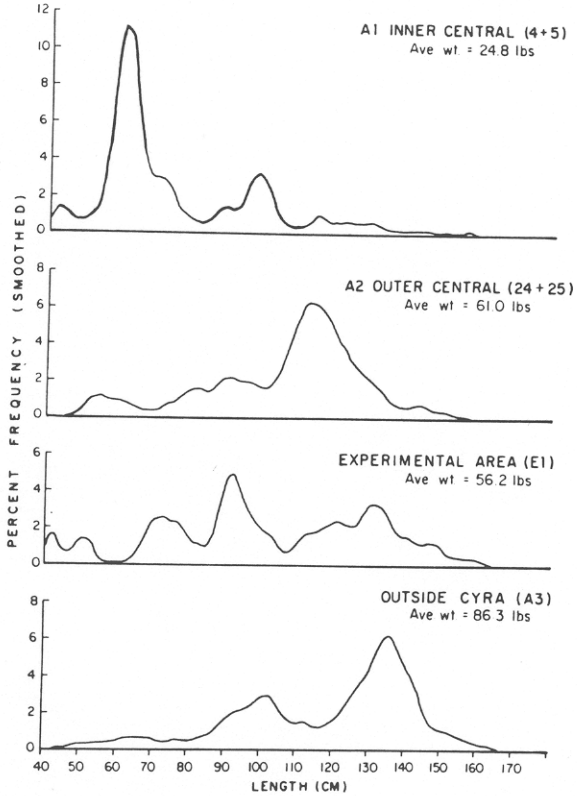


FIGURE 16.—Taken from the Inter-American Tropical Tuna Commission (1974): (a) the eastern Pacific Ocean showing areas A1, A2, and A3. The numbers within the areas designate subareas used for size composition studies, and (b) length-frequency distribution of yellowfin tuna in the inner area (areas 4 and 5), the outer area (areas 24 and 25) of the central region of the CYRA (Commission Yellowfin Regulatory Area), in the experimental area (E1), and in the area to the west of the CYRA (A3).

1) For the first 5 yr only longliners fished and only in rows 5 to 8.

2) For the next 5 yr, this longline fishery was augmented with surface gear in all cells adjacent to the coast.

3) Next, exploitation by the surface gear was expanded to include all cells for 5 yr.

4) Finally, for the last 5 yr, age specific surface fishing mortality was reduced by 75% for fish <2.5 yr of age because much of the surface catch of yellowfin tuna in offshore areas of the eastern Pacific comes from schools associated with porpoise. Typically, porpoise schools contain few yellowfin tuna <2.5 yr of age (Calkins 1965).

Steps 1, 2, and 3 resemble the sequence of events in the eastern Atlantic fishery for yellowfin tuna. Yellowfin tuna first were exploited in a significant fashion by longliners in a 10° band along the equator, then a nearshore surface fishery became significant, and in recent years some exploitation by surface gear in offshore areas has occurred. To our knowledge, step 4 has not occurred in the Atlantic. Age-specific fishing mortality rates similar to those by surface gears estimated by Lenarz et al. (1974) for the Atlantic yellowfin tuna fishery were used (Table 5). The Ricker yield equation was used to calculate yield for each time-area stratum.

Total yields per recruit were calculated and are shown in Figure 17. Yields per recruit are quite similar for both recruitment models except near shore, where yield per recruit was considerably higher for the inshore recruitment model than for the uniform recruitment model. The difference in yield per recruit between the two models decreases slightly as time increases. Yield per recruit closely approached equilibrium yield within 3 yr after a change was made in the fishery. Total equilibrium yield per recruit with an inshore surface fishery

TABLE 5.—Estimates of age-specific F on an annual basis used as baseline for simulation. See text for modifications of mortality rates during simulation.

Age (yr)	Longline gear	Surface gear	Surface gear with reduced F
1.0	0.00	0.30	0.08
1.5	0.00	0.30	0.08
2.0	0.05	0.22	0.06
2.5	0.15	0.20	0.20
3.0	0.25	0.18	0.18
3.5	0.35	0.30	0.30
4.0	0.45	0.35	0.35
4.5	0.40	0.42	0.42
5.0	0.40	0.27	0.27
5.5	0.20	0.20	0.20
6.0	0.05	0.15	0.15

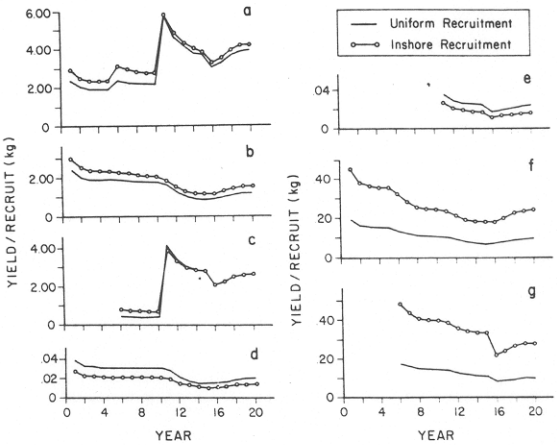


FIGURE 17.—Yield per recruit of hypothetical yellowfin tuna fishery: (a) total, (b) longliners in all areas, (c) surface gear in all areas, (d) longliners in cells 71 and 85, (e) surface gear in cells 71 and 85, (f) longliners in cells 69, 84, and 97, and (g) surface gear in cells 69, 84, and 97.

and longline fishery was about 17% higher than with a longline fishery alone, 54% higher with a uniform surface fishery than with only a longline and inshore surface fishery, and increased by 9% when F for small fish was reduced by 75%. Under the assumption that the catchability coefficient is independent of area, the surface fishery increased its equilibrium yield per recruit about fourfold by increasing its effort about 12-fold when it expanded into offshore waters. The same action decreased yield per recruit to the longliners by about 55%.

We next examined the potential yield per recruit to longliners in rows 5, 6, 7, and 8 by starting a longline fishery with the age-specific F vector multiplied by the scalar 0.3 and then multiplying by 1.3 each year afterward. Yield per recruit appears to approach an asymptote of about 6 kg for inshore recruitment and 5 kg for uniform recruitment (Figure 18). The reduction in catch per recruit per effort by fishing is not significantly affected by choice of recruitment model. Even though catch per recruit per effort at high levels of effort was only about 20% of that at the beginning of exploitation, overfishing in a yield-per-recruit sense did not occur. Average size of fish in the catch was not significantly affected by the recruitment model, and decreased from about 50 to 30 kg with increased fishing effort (Figure 18).

A simulation for an inshore surface fishery indicated an asymptotic production curve with a

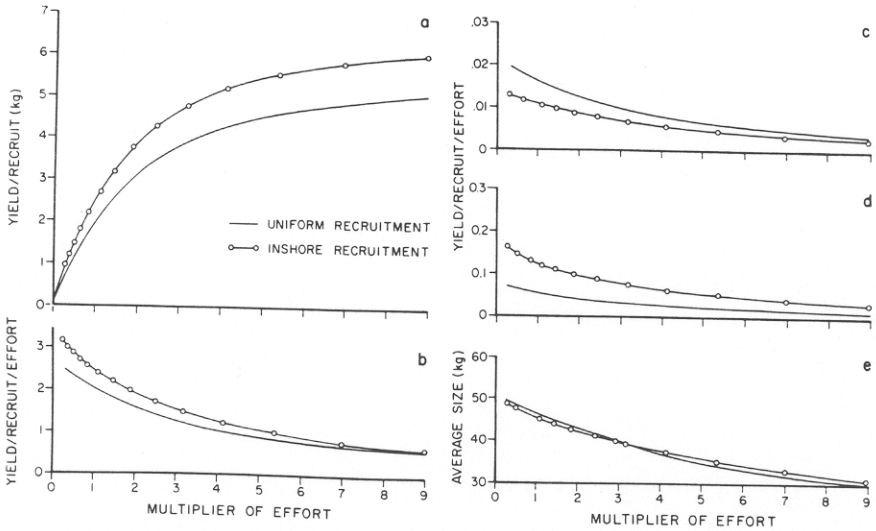


FIGURE 18.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical longline fishery: (a) total yield per recruit, (b) total yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size in all squares.

maximum yield per recruit of about 1.4 kg for uniform recruitment and 2.2 kg for inshore recruitment (Figure 19). Catch per recruit per effort was reduced by about 75% under both alternatives. The ratio of maximum yield per recruit for a longline fishery to an inshore surface fishery was about 2.7 for inshore recruitment and 3.4 for uniform recruitment. Average size of fish in the catch was about 2 kg higher for uniform recruitment than for inshore recruitment and decreased from 16 or 18 kg to 8 or 11 kg with increased fishing effort (Figure 19).

Simulation of a uniform surface fishery revealed that choice of recruitment model had an insignificant effect on yield per recruit, catch per recruit per effort, and average size of catch, except that catch per recruit per effort in the nearshore area was relatively high for inshore recruitment (Figure 20). A 75% reduction in F for fish <2.5 yr old had considerable effect on the results. Maximum yield increased from about 5.1 to 6.9 kg when F was reduced. Both yield curves are dome-shaped. Catch per recruit per effort became relatively higher at high levels of effort when F was reduced. As expected, average size was considerably higher for reduced F.

With inshore recruitment, maximum yield per recruit changes from about 2.2 kg for an inshore fishery (Figure 19) to about 5.1 kg for a uniform

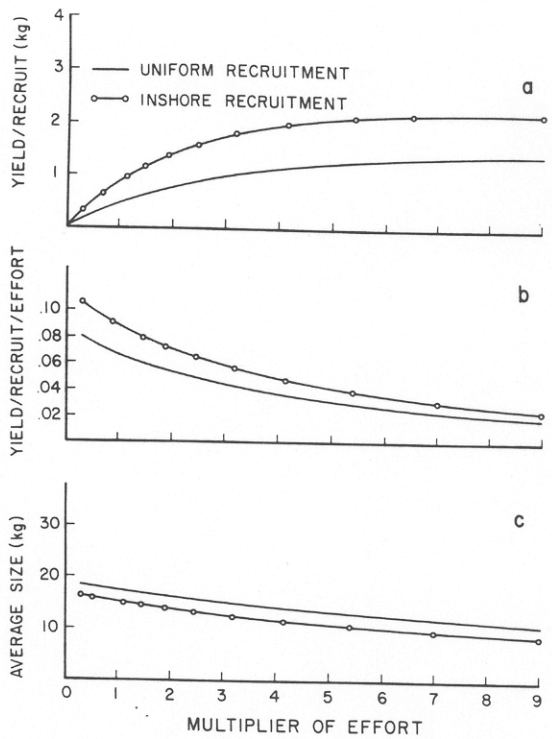


FIGURE 19.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical inshore surface fishery: (a) yield per recruit, (b) yield per recruit per effort, and (c) average size of fish in catch.

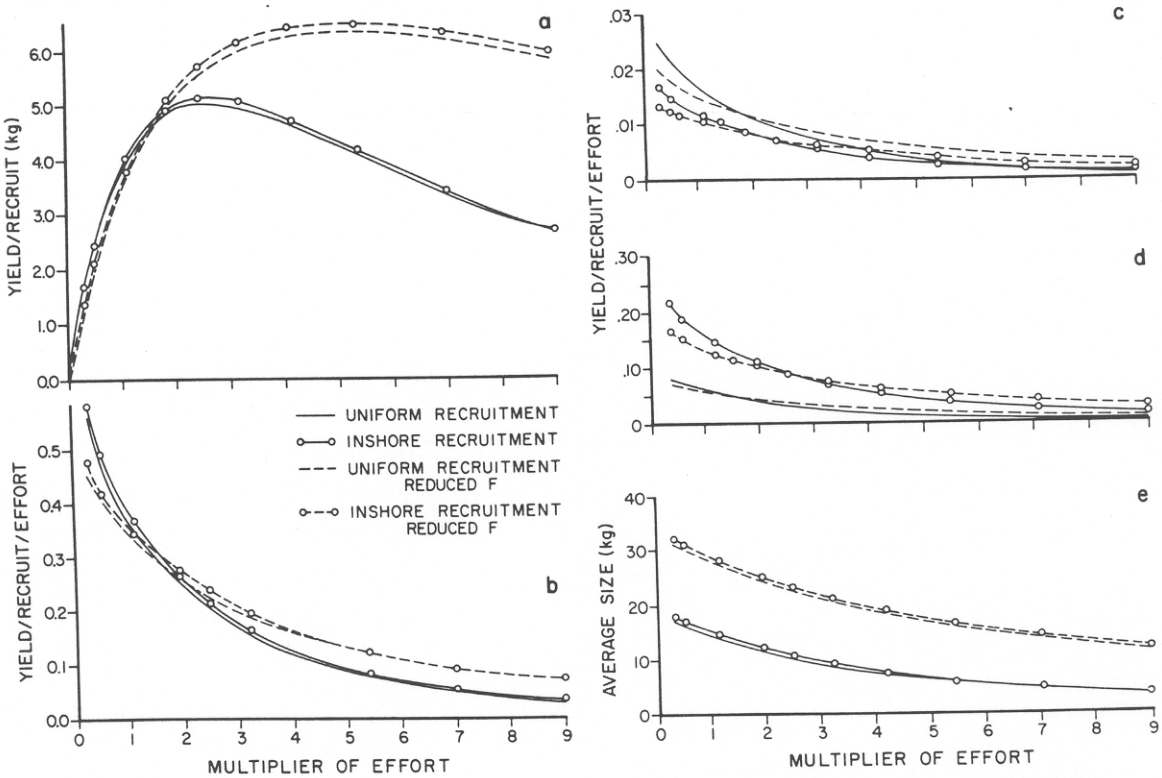


FIGURE 20.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical uniform surface fishery: (a) yield per recruit, (b) yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size of fish in catch.

fishery (Figure 20). With uniform recruitment, maximum yield per recruit changes from about 1.4 kg for an inshore fishery to about 5.0 kg for a uniform fishery.

The results of this section indicate that the pattern of recruitment is primarily of interest for examining the potential of a nearshore surface fishery to a surface fishery that exploits the entire area or a longline fishery. The presence of some small yellowfin tuna in length-frequency data for offshore areas from the eastern Pacific fishery (Figure 17) reveals that some recruitment occurs offshore. Recruits apparently are not highly available to surface fishing offshore because most yellowfin tuna are caught in schools associated with porpoise. Such schools normally contain only low percentages of small yellowfin tuna. A well-designed tagging study could provide estimates of the exploitation rate by size for yellowfin tuna in the offshore areas. Until the pattern of recruitment is determined, it will be necessary to continue estimations of relative production to longliners, inshore surface gear, and offshore surface gear in an empirical fashion.

We examined only one reasonable example of an infinite number of possible configurations of the transfer matrix A and time interval. Further use of the model should include a sensitivity analysis of the results to choice of A and number of cycles per year.

SUMMARY AND CONCLUSIONS

This paper examines three aspects of dual fisheries (surface and longline) on yellowfin tuna. Models of yellowfin tuna fisheries are developed to evaluate possible effects of unknown components of the biology and behavior on the fisheries. The results, while not conclusive because of insufficient knowledge, indicate the magnitude of the effects of those factors which were examined.

We present evidence that not all yellowfin tuna are equally available to longline and surface fisheries in the Pacific Ocean. We show that three

models of availability of yellowfin tuna to the two types of gear in the Atlatnic Ocean do not have much effect on decisions concerning minimum size regulations. If fish are equally available to both gear types, yield per recruit is higher to a longline fishery than to a surface fishery, but is higher for the combined gears than to either gear fishing alone.

We also note that there is considerable evidence that large females of all commercially important *Thunnus* are caught in fewer numbers than large males. The effect of this phenomenon on yield per recruit and relative stock fecundity was examined for Atlantic yellowfin tuna. When plotted against fishing effort, yield per recruit is more dome-shaped when the sex ratio is 1:1, as is usually assumed, than when the sex ratio is as observed. Changes in size at recruitment also have a greater effect on yield per recruit when the sex ratio is 1:1 than when the sex ratio is as observed. Competition between longline and surface fishing is more intense when the sex ratio is 1:1 than otherwise. The fishery has a greater effect on stock fecundity if the sex ratio is 1:1 instead of that observed.

Tagging studies of yellowfin tuna in the eastern Pacific indicate that movements are fairly slow compared with more highly migratory species such as albacore and bluefin tuna and have not produced any clear-cut evidence of a definite migration pattern. Size composition of the catch suggests that recruitment to the fishery occurs mainly along the coast of Central America. A simulation model was developed for the eastern Pacific to examine the interrelationships of patterns of movements of fish, patterns of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either along the coast or throughout the eastern Pacific. The results indicate that either pattern of recruitment could allow the increased catch observed in the Pacific as the surface fleet moved offshore. However, the pattern of recruitment does affect the potential yield per recruit of a nearshore surface fishery relative to a surface or longline fishery that exploits the entire area. Both choices of recruitment models resulted in an asymptotic relationship between yield per recruit and effort for a longline fishery over the range of effort examined. Overfishing in a yield per recruit sense did not occur, even though catch per effort decreased by 80%. Approximately the same results were obtained for an inshore surface fishery. However, curves of yield per recruit plotted against effort for a surface fishery that exploits the entire area are dome-shaped.

The study reveals several biological and behavioral parameters which, because of lack of knowledge or information, are rarely considered but do appear to have a significant effect on some aspects of the dynamics of yellowfin tuna fisheries. Tagging and fecundity studies are suggested in order to fill these gaps. Perhaps as important, other aspects of the dynamics of yellowfin tuna fishing appear to be insignificantly affected by the examined parameters.

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