

AN ENERGETICS MODEL FOR THE EXPLOITED YELLOWFIN TUNA, *THUNNUS ALBACARES*, POPULATION IN THE EASTERN PACIFIC OCEAN

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ABSTRACT

An energetics model (ENSIM) for the exploited yellowfin tuna, *Thunnus albacares*, population in the eastern Pacific Ocean is developed. Hydrodynamic properties and respiration-swimming work theory are combined to describe the energy expenditure due to swimming as a function of length for tunas. Growth and maintenance energetics are estimated and incorporated into a simplistic three process model. This model is interfaced with a population simulator (TUNPØP) and minimal energy requirements for the exploited yellowfin tuna population are derived for the simulated fishing years 1964-72. A theoretical unexploited population simulation is made, and the energy requirements by this population are compared with primary productivity rates and minimum micronekton (forage) standing stock availability. No obvious food limitation is indicated for yellowfin tunas greater than 40 cm, particularly since the exploited population is at a level of, at most, 50% of the unexploited biomass estimates. Population limitation processes are examined and indications that the recruitment rates are independent of exploited biomass are discussed.

The intent of studies of the population dynamics of exploited populations is the determination of the numbers, biomass, age structure, and potential yield from a population in order that rational management decisions can be made about the manner and rate of exploitation in order to insure efficient utilization of the resource. The validity of the resulting estimates of numbers, biomass, and potential yield is of concern to all those involved with the resource. Underestimations generally result in conservative efforts which are "safe" but not necessarily efficient. Overestimations can result in reduced profit margins or, in the extreme case, decimation of the resource.

Since the implementation of the program for conservation of yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific in 1966, a series of complex changes in the fishery have occurred which make production model results less and less comparable between years (Inter-American Tropical Tuna Commission Annual Reports). Attempts to account for multiple changes in the effort variables and corresponding but independent changes in the exploited population have resulted in serious interpretation problems as to the relative status of the exploited stock.

The economic and temporal problems inherent in the collection and analysis of biological data and the difficulties in representation of the biological processes in a useful mathematical manner has served to hinder utilization in the management procedures of what sparse physiological and ecological information is available.

In this report, an energy budget model is developed for the exploited yellowfin tuna population in the eastern Pacific Ocean within the Inter-American Tropical Tuna Commission's Yellowfin Regulatory Area (CYRA). The model will be used to assess the energy flow through the exploited yellowfin tuna population and also to compare the estimated utilization of energy by yellowfin tuna with the estimated primary productivity in the CYRA. Comparisons will be made using simulations of the population under both exploited and unexploited conditions.

The energy budget estimates are interfaced with an age dependent population simulation model (TUNPØP) (Francis 1974) resulting in a model of the energy utilization by semiannual recruitment cohorts. This model is referred to as ENSIM. The model incorporates the population parameter estimates and variables of TUNPØP and the empirical and estimated size dependent relationships for the major energy consuming processes, resulting in estimates of energy utilization rates. The development of the empirical

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relationships and the resulting formulations are presented so as to encourage research in the area so that improvements on this crude model can be made in the future.

THE MODEL

Population Dynamics

In an attempt to produce a new, more detailed method for evaluating the population or stock status it was decided that the development of TUNPOP, a biologically oriented population simulator, would be appropriate. The only available population data which are collected on a routine basis from within the fishery are length-frequency information from commercial catches. These data are collected according to criteria which require that the several time-area strata be sampled regularly and multiply, whenever possible (Hennemuth 1961). Data from the period 1963-72 have been analyzed and processed in the following manner.

The 12 existing sampling areas in the CYRA were reassembled into three major areas: N—North of lat. 10°N except east of long. 95°W; 5—North of lat. 5°N to the boundary of area N; S—all the CYRA south of the boundary of area 5 (see Figure 1). The areas N and S tend to have separable length-frequency distributions during any given time interval. Area 5 tends to have unique components as compared to N and S, but also contributions from both the other areas can be observed in the data from area 5. (This phenomenon is typically nonseasonal or noncyclic with respect to the fishing year and is probably related to population and environmental pressures within the separate areas.) In all three areas, recruitment components of a semestral nature are evidenced. The apparent relative abundance of these components within the areas changes seasonally and also between years (Table 1). Analysis of this phenomenon has made the separation of the semestral cohorts seem the first logical step when the available genetic, morphometric, and length-frequency data are considered.

The catch data associated with each length-frequency sample were obtained. The individual sample sets were then given relative values proportional to the contributions of the catches (in weight) from which they were drawn. From this basic processing of all the length-frequency data,

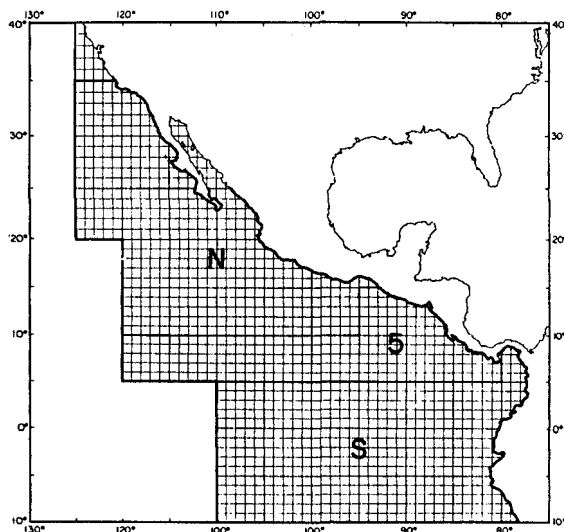


FIGURE 1.—The study area CYRA (Commission Yellowfin Regulatory Area) used in the simulations is enclosed in the dark outline. Three subareas were used in the preliminary population dynamics work in estimating cohort strength from the length-frequency and catch and effort data appropriate to these areas. N = North of lat. 10°N except inside of long. 95°W; 5 = North of lat. 5°N to boundary of N; S = all CYRA South of boundary of subarea 5.

estimates of the catch composition with respect to size-age for each fishing area were made and a growth curve was determined for each of two semestral cohorts. The two curves were essentially identical and warrant no further discussion here other than to say that from 40 to 145 cm fork length it is possible to give relative monthly ages to all individuals, given a length and corresponding date of capture. The labeling problem was handled such that any fish that was 40 cm from 1 January to 30 June is labeled S_A and correspondingly 40-cm recruits from 1 July to 31 December are labeled S_B . The cohorts are identified in relation to their recruitment year when they are 40 cm, not their spawned year. For example, a 40-cm fish caught in February 1969 is attributed to the cohort labeled S_A , 1969; and a 40-cm fish caught in October 1968 is attributed to the semester cohort labeled S_B , 1968. The two semestral groups can be treated as independent units in the population and provide a biological basis in assessment of population size with respect to size-age classes within the fishing year. The annual growth increment in the most often encountered cohort classes (40-140 cm) in the fishery appears to be about 32 cm/yr; therefore,

TABLE 1.—For the years 1964-71 the data are presented for the catch in short tons by semestral cohort in the three areas (N, 5, S) within the CYRA. Also given are the percent of the total catch ($S_A + S_B + \text{Big}$) by cohort within the areas. The category, Big, represents the fish of length \bar{l} greater than 145 cm which we feel are not ageable under the present system. The percent of the individual semestral cohorts (S_A or S_B) caught in the three areas is also given. Note the erratic shifting of the cohort dominance (S_A or S_B) in the catch as well as the distribution of the cohorts between areas.

Year	North A	5 A	South A	Total A	North B	5 B	South B	Total B	Total A + B	Big
1964	27,452	9,401	5,209	42,062	33,561	5,881	17,515	56,957	99,019	2,921
% total A + B	26.9	9.2	5.1	41.2	32.9	5.8	17.2	55.9		2.9
% total A or B	65.3	22.4	12.4		58.9	10.3	30.8			
1965	18,967	13,512	6,406	38,885	24,064	14,164	8,386	46,614	85,499	4,543
	21.1	15.0	7.1	43.2	26.7	15.7	9.3	51.8		5.0
	48.8	34.7	16.5		51.6	30.4	18.0			
1966	7,769	23,128	20,176	51,073	10,292	11,394	14,771	36,457	87,530	3,626
	8.5	25.4	22.1	56.0	11.3	12.5	16.2	40.0		4.0
	15.2	45.3	39.5		28.2	31.3	40.5			
1967	20,699	9,564	7,664	37,927	29,482	8,572	11,867	49,921	87,848	1,802
	23.1	10.7	8.5	42.3	32.9	9.6	13.2	55.7		2.0
	54.6	25.2	20.2		59.1	17.2	23.8			
1968	16,361	23,921	13,552	53,834	33,917	22,132	3,128	59,177	113,011	1,602
	14.3	20.9	11.8	47.0	29.6	19.3	2.7	51.6		1.4
	30.4	44.4	25.2		57.3	37.4	5.3			
1969	22,437	20,034	9,030	51,501	34,887	29,587	5,648	70,122	121,623	4,888
	17.7	15.8	7.1	40.7	27.6	23.4	4.5	55.4		3.9
	43.6	38.9	17.5		49.8	42.2	8.1			
1970	39,197	15,942	10,529	65,668	43,476	13,257	11,125	67,858	133,526	9,176
	27.5	11.2	7.3	46.0	30.5	9.3	7.8	47.6		6.4
	59.7	24.3	16.0		64.1	19.5	16.4			
1971	12,372	18,719	14,453	45,544	17,357	25,283	15,712	58,352	103,896	9,277
	10.9	16.5	12.8	40.2	15.3	22.3	13.9	51.6		8.2
	27.2	41.1	31.7		29.7	43.3	26.9			

the mean lengths and modes of the two semestral cohorts are separated by approximately 16 cm (Tomlinson and Sharp work in progress). A significant number of animals may shift from the leading edge of one labeled distribution into the trailing edge of the other, but we are assuming that countershifts are equally as probable and both are irreversible. An effect of shortening the sampling "season," since the implementation of regulations, has been to distort the apparent abundance of the two groups and merge the modal distributions into a single amorphous distribution (Figure 2).

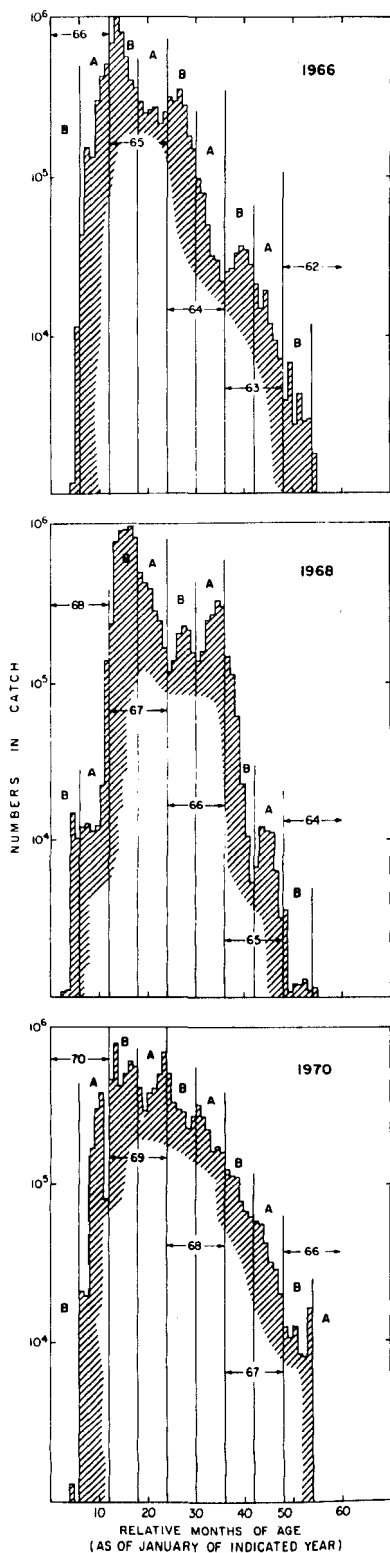
The cohorts are treated independently by the model. Each cohort is considered to have a unique effect in the analysis of the net biomass and numbers estimates for a given fishing year. Differential exploitation of these cohorts can be determined from the catch-effort length-frequency data and as such warrants this disintegration technique as opposed to treating the year class as a single unit. We have, however, decided not to present in this report the area breakdown results in the simulations. When the cohorts are separated, it is possible to construct a catch table for each from the length-frequency sample data from the fishery. With this catch table and the catch data (yield) it is possible to determine the relative mortality (F) attributable

to fishing, by assuming a constant natural mortality (M), a necessary, but perhaps poor assumption in the case of tunas due to the inherent rapid changes in ecological status as they grow. The Murphy cohort analysis procedure (Murphy 1965; Tomlinson 1970) was used for estimation of recruitment at first availability to the fishery (N_{40}). Using this approach we have generated the underlying population structure for the historical series we wish to represent.

Energetics

The energetics parameters for free-swimming predatory species such as the tunas must be size-related functions due to the broad range of sizes commonly encountered in the fishery; 1.3 kg to greater than 62 kg, or 40 cm to greater than 145 cm. In no case for fish has anyone measured physiological parameters from such a range of sizes.

Magnuson (1973) discussed the effect of gas bladders and lift surfaces on the velocity of obligatory swimmers such as the tunas. He determined the relationships between size and minimum velocity for maintenance of hydrostatic equilibrium for several scombrid species, including skipjack tuna, *Katsuwonus pelamis*, and *Thunnus albacares*. This work has provided a



basis for determining some of the relative energy expenditures in the population simulation study.

The energy utilization which is simulated in ENSIM is that attributable to 1) maintenance of metabolic stasis, 2) growth, and 3) swimming. Each is calculated independently and summed with the others to give an estimate of the total minimum energy utilized on a daily basis. No attempt has been made to evaluate energy expenditures due to gonad maturation or migratory behavior beyond the daily forage or flight behavior levels because of the inherent void in our knowledge of these processes in tunas.

Metabolic maintenance of stasis energy requirements (E_m) are difficult to assess under optimum conditions and are typically derived from extrapolation of O_2 consumption versus activity relationships to a zero activity level. The magnitude varies greatly between species and in general is a tenuous function of size and physiological state. It is essentially impossible to directly measure the stasis energy requirements of tunas due to their continuous swimming behavior. Estimates of E_m should not include the energy expenditures due to even minimum swimming activity if it is to be useful in the determination of energy expenditures due solely to swimming work.

The respiration rate attributable to tissue stasis can be estimated from the metabolic weight (W_{met}) of fish of length \bar{l} from the equation:

$$E_m = 24 k W_{met} \text{ (modified from Winberg 1960)}$$

where $W_{met} = (M_f)^{0.8}$,

and

$$M_f = 1.858 \times 10^{-2} (\bar{l})^{3.021} \text{ (grams) (Chatwin 1959)}$$

and where k is estimated to equal 1 cal/g h from data and estimates for other highly active fishes (Fry 1957; Winberg 1960). Therefore

$$E_m = 4.46 \times 10^{-1} (\bar{l})^{3.021} \text{ cal/day.}$$

FIGURE 2.—The numbers of fish caught in the fishing years 1966, 1968, 1970, as a function of their recruitment month, and age, relative to the fish of the year are graphically represented. Semestral (A, B) and annual cohort labeling is as indicated. Note the central tendency of the peaks within the semestral limits in the years 1966 and 1968. In these years the fishing "season" was quite long (>6 mo) as compared to 1970 (<3 mo), which combined with cyclic migratory behavior and subsequent availability of cohorts probably results in the drastic change from multimodality to the amorphous distribution seen in the 1970 data.

When estimates of the true stasis energy relations are finally available, they can be easily incorporated into the model.

Probably the most difficult process to define, estimate, and measure is that of growth. The energy requisite to growth (E_g) can be estimated minimally as the biomass gain per time period as converted to calories. This is a highly unsatisfactory method because of the many energy requiring steps between ingestion of a food organism and the consequential deposition of the materials assimilated into the living biomass of the growing organism (Phillips 1969).

One slight change in the accepted methodology of bioenergetic accounting which we will make is in our definition of specific dynamic action (SDA). If one is willing to accept that the SDA contributed little other than heat to the feeding organism, then it can be defined as the loss of energy due to the inefficiency of the digestive processes, including cost of transport, deamination, biosynthesis, and related processes. The rate of inefficiency (percent of SDA energy with respect to total ingested energy) is variable in most animals studied as a function of feeding level (Warren and Davis 1967) and environmental conditions (Warren 1971). In our definition of SDA we do not include the unavailable portion of foodstuffs.

For our purposes we will assume that growth of yellowfin tuna in the CYRA is relatively continuous with respect to season or environmental state. There are several assumptions involved in this basic tenet which require some discussion. Tunas are highly endothermic animals, and Carey and Teal (1966) have shown the presence of a relatively high efficiency heat exchange (conservation) mechanism in tunas. This suggests that tunas are likely to be somewhat independent of ambient temperatures in that the temperature variability encountered within the core of these fishes is likely less than the ambient variability. Their large mass (>1 kg) would contribute to thermal stability over a wide ambient change (Neill and Stevens 1974).

Observations of temperature dependent activity indicate a lower activity as temperature decreases in small yellowfin tuna (<50 cm, <2.5 kg) at a Q_{10} of near 2 (Neill, pers. commun.). This size of yellowfin tuna is rarely encountered in the CYRA at temperatures below 23°C and is found aggregated on the warm side of the north-south surface temperature cline including this tempera-

ture, indicating some preference for temperatures near 23°C. Preliminary studies of effects of the environmental characteristics on the abundance and availability of 40- to 70-cm yellowfin tuna in the CYRA indicate a direct relationship between the 23°C isotherm depth of the average number of fish per school, and the overall availability of these fish to surface fishing gear (Inter-American Tropical Tuna Commission 1975).

All this is emphasized to indicate the limited range of temperatures likely to be affecting the metabolic rates of yellowfin tuna as compared to that affecting smaller species without the complex stabilization mechanisms (heat exchangers, etc.) as is the typical situation in fishes.

The relative activity, mobility, and distribution with respect to temperature of yellowfin tuna can be used as supportive background for assuming a relatively stable growth energy availability as they developed, bringing us to the conclusion that a first approximation of the SDA can be made with respect to the energy equivalent to the biomass change on a daily basis. From studies discussed by Paloheimo and Dickie (1966) and Warren and Davis (1967) on several species and estimates by Kitchell et al.² for *K. pelamis*, it appears that SDA probably accounts for 30-40% of the total consumed calories which could be part of the growth process. We have, therefore, assumed that E_g is going to equal the equivalent caloric value of the tissues plus the SDA which will be given by the relation

$$\text{SDA} = \frac{\text{(Biomass change in grams per day)}}{2}$$

where, if 1 g is calorically equivalent to 1.46 kcal (Kitchell et al. see footnote 2) then

$$\begin{aligned} E_g &= \frac{3}{2} \text{Biomass change (grams)(1.46 kcal/g)} \\ &= 2,190 \text{ kcal/kg growth.} \end{aligned}$$

Smit (1965) has provided the mathematical basis for our determinations of energy output and caloric requirements due to swimming. He shows that:

$$\text{Power} = \frac{(M_c g S) (143 \times 10^3)}{3,600} \frac{g \text{ cm}^2}{s^3} \quad (1)$$

²Kitchell, J. F., W. H. Neill, and J. J. Magnuson. Bioenergetics of skipjack tuna, *Katsuwonus pelamis*. Manuscr.

where M_e is the efficiency of the muscle tissue when converting chemical energy to mechanical work; S is the respiration due to activity in mg O_2/h ; and g is the acceleration due to gravity (981 cm s^{-2}). The propulsion efficiency is assumed to be 0.90 (Lighthill 1970) and is included in the resulting muscle efficiency figure.

For our purposes we assume M_e to be 0.18. Therefore from Equation (1)

$$S = \frac{(\text{Power}) (3,600 \text{ s/h})}{(0.18) (143 \times 10^3 \text{ g cm}) (981 \text{ cm/s}^2)} \text{ mg } O_2/h. \quad (1A)$$

From the hydrodynamics theory (Streeter 1962)

$$\text{Power} = \frac{\rho}{2} A V^3 C_d \frac{\text{g cm}^2}{\text{s}^3}$$

where ρ = the density of seawater (1.025 g/cm^3)

$A = 0.4(\bar{l})^2$ from Bainbridge (1961) (cm^2)

V = is derived from Magnuson's empirical relationships between \bar{l} and species velocity \bar{V} (cm/s)

C_d = the coefficient of total drag of the fish, which is derived from an empirical relation including the results of studies by Pyatetskiy (1971).

We can therefore rewrite the equation so that respiration due to swimming is equal to

$$S_s = \frac{\rho A \bar{V}^3 C_d}{2 (7,017.66)} \\ = 2.59 \times 10^{-5} (\bar{l})^2 (\bar{V})^3 C_d \text{ mg } O_2/h. \quad (2)$$

We now have an Equation (2) of three elements for which we have solutions for two (\bar{V} and C_d) as functions of the third (\bar{l}) given below.

\bar{V} Determination

From Magnuson (1970), the relation for the minimum velocity (V_{100}) for sustained hydrostatic equilibrium by tunas is given as

$$V_{100} = \left[\frac{L_t}{\frac{\rho}{2} (C_{L_f} A_{f_t} + C_{L_k} A_k)} \right]^{1/2} \quad (3)$$

where C_{L_f} = the coefficient of lift for the pectoral fins

A_{f_t} = the total lifting area of the pectoral fins (cm^2), $\log A_{f_t} = -1.2154 + 1.87 \log \bar{l}$

C_{L_k} = the coefficient of lift of the keel

A_k = the lifting area of the keel (cm^2), $\log A_k = -2.7033 + 2.26 \log \bar{l}$ (cm^2)

L_t = the total weight of the fish in seawater (dynes). (L_t values are obtained by multiplying M_f values by appropriate constants as provided by Magnuson (1973) by species and weight class.)

M_f = mass of the fish = $1.858 \times 10^{-2} (\bar{l})^{3.021}$ (grams).

Determination of the Coefficient of Total Drag C_d

The relation between the total drag coefficient (C_d) and the Reynolds number (Re) for Atlantic bonito, *Sarda sarda*, reported by Pyatetskiy (1971) is taken to be representative in form for scombriform fishes. $Re = \frac{\bar{l} \bar{V}}{\nu}$, where ν is the kinematic viscosity of seawater or $0.01 \text{ cm}^2/\text{s}$; \bar{l} is the fish fork length in centimeters; and \bar{V} is the fish velocity in centimeters per second.

An analytical expression was derived for estimating the C_d values in the following manner: R. Gooding (Gooding et al. 1973) of the National Marine Fisheries Service Honolulu Laboratory, Honolulu, Hawaii reported respiration rates for unfed *K. pelamis* from 32 to 36 cm fork length, swimming at or near minimum velocities (V_{100}). From these data it was possible to calculate C_d given the observed respiration rate (S_{total}) was $431.5 \text{ mg } O_2/\text{kg h}$ and $\bar{l} = 35 \text{ cm}$. The minimum velocity (V_{100}) = 59.1 cm/s and $Re = 2.07 \times 10^5$ at this velocity.

For skipjack tuna of $\bar{l} = 35 \text{ cm}$, $W_{\text{met}} = 200.5 \text{ g}$, so that

$$S_m = 60.0 \text{ mg } O_2/h$$

$$S_{\text{total}} - S_m = S_s = 371.5 \text{ mg } O_2/h.$$

From Equation (2) it is now possible to determine that

$$C_d = \frac{371.5}{2.59 \times 10^{-5} (35)^2 (59.1)^3} = 0.057.$$

This value of C_d was related to the values graphically displayed by Pyatetskiy (1971) and what was assumed to be a good approximation

of the total drag on the test animals was derived relative to his graphed observations as a function of Re . From Re , one can determine the approximate coefficient of total drag (C_d) from the relation:

$$C_d = 0.262 e^{-4.805 \times 10^{-6} Re} \quad (4)$$

Gooding also reported respiration data for skipjack, ranging from 45 to 53 cm, swimming at or near \bar{V}_{100} where $S_{total} = 1,403$ mg O_2 /h. These test animals had also been deprived of food for 24 h. Assuming $\bar{l} \cong 50$ cm:

$$W_{met} = 523.5 \text{ g}; V_{100} = 70.5 \text{ cm/s};$$

$$Re = 3.525 \times 10^5;$$

$$S_m = 156 \text{ mg } O_2/\text{h};$$

$$C_d = 0.262 e^{-4.805 \times 10^{-6} (3.525 \times 10^5)} = 0.048.$$

$$\therefore S_s = 2.59 \times 10^{-5} (50)^2 (70.5)^3 (0.048) \\ = 1,233 \text{ mg } O_2/\text{h}.$$

$$S_s + S_m = S_{total} = \{1,233 + 156\} \text{ mg } O_2 \\ = 1,389 \text{ mg } O_2/\text{h}, \text{ (expected)}$$

$$\text{where } S_{total} = 1,403 \text{ mg } O_2/\text{h}, \text{ (observed)} \\ \text{leaving } 14 \text{ mg } O_2/\text{h}, \text{ (difference).}$$

The Relation (4) we have used for C_d as a function of Re appears to be adequate for our purposes.

Within the factors M_e and C_d there are an inseparable pair of modifying effects which must be accounted for, but which are essentially indeterminate at the present state of the art. One is the mechanical propulsion efficiency, and the other is the effect of the short-term flux of the rates of acceleration due to caudal fin position and velocity within a single tail beat cycle on the "average" calculations of M_e and C_d . The M_e and C_d values are continuous variables within the tail beat cycle and are inextricably bound together. Where in the integration and estimation of these two values the trade off is made is inconsequential due to the equal and direct effect of the estimate of one on the other value. Until either value is measured and fixed, the other coefficient is relative and therefore not necessarily realistic.

The effect of velocity on propulsion efficiency is probably great in tunas (and other large organisms) due to several processes, including local heating phenomena and subsequent contraction rate increases of the muscle fibers

(Walters 1962; Sharp and Vlymen³). The graded increase in utilization of white muscle fibers as velocity is increased should result in generalized heating and increased overall efficiency of the energy conversion processes in the muscles. This and other effects may indeed account for the considerable efficiency changes in work done as compared to respiration rate when extended periods of white muscle utilization are monitored (Kutty 1968).

The higher scombrids (*Auxis*, *Euthynnus*, *Katsuwonus*, and *Thunnus*) have incorporated, in various designs, a subcutaneous vascular system which is the distribution mechanism for transport of arterial and venous blood to and from the warm swimming musculature (Kishinouye 1923). The direct transport of "warm" venous blood to the fish's surface probably affects the hydrodynamics of the fish and contributes to the dynamic flux of the C_d value. Since no data are available for these phenomena, they have to be ignored in this treatment of the swimming energetics, but future laboratory studies should not ignore or delete these potential effectors.

Considering the range of possible error in estimating both muscle efficiency and/or the coefficient of total drag, the close agreement between observed and expected respiration rates indicates that we have useful estimates of energy requirements.

The only available respiration-activity data from tunas is for *K. pelamis*. Assuming that Magnuson's (1973) empirical relations and density multipliers are representative of the relative hydrodynamic status of the several species, these relations should give a similarly good approximation of energy consuming processes in *T. albacares* as they appear to give for *K. pelamis*.

The three continuous energy consuming processes are, therefore, roughly accountable using the previously described relations. The conversion of oxygen consumption to caloric utilization is made on the basis that 3.359 cal are available from 1 mg O_2 . Apparently the major energy consumption process is swimming, including feeding and flight behavior. The energy expended is a function of the velocity \bar{V}_{typ} which is

³Sharp, G. D., and W. J. Vlymen III. The relation between heat generation, conservation and the swimming energetics of tunas. Manuscr.

in turn a function of the length of the individuals (see Figure 3). In Magnuson's (1973) relationships the variables necessary for a solution for the minimum velocity are \bar{l} and the density of the fish. Magnuson (1973) provided data for fish density (in the form of empirically derived multipliers) by weight class for several species including yellowfin tuna. We have extrapolated his data to fit our size distribution with an asymptotic lower limit of fish density at 1.06 g/cm³ reached by 120-cm fish.

We are assuming that the animals have their pectoral fins 75% extended all of the time that they are in nonfeeding-flight behavior, hence $C_{L_f} = 0.75$, and that the keel surface is 85% effective so that $C_{L_k} = 0.85$. This results in a fish that is swimming somewhat faster on the average than its V_{100} or minimum velocity. These values are "best guess" estimates and as such, represent only minor changes in the appropriate direction as opposed to using absolute minimum energy utilization in the population simulation. Magnuson's V_{100} for a 50-cm yellowfin tuna is 50.91 cm/s. Solving for the "typical" velocity under our "best guess" conditions results in a \bar{V}_{typ} of 58.29 cm/s.

We have set a "typical" feeding-flight speed at 3 m/s. This is an integrated average that includes all velocities above \bar{V}_{typ} and includes the burst speed forays. Since the energy required for different speeds is proportional to a cubic function of the velocities, it should be noted that the most probable velocity is less than 2 m/s, since the energy requirements for a few short bursts of up to 10 body lengths/s rapidly increase the overall energy utilization. With this in mind,

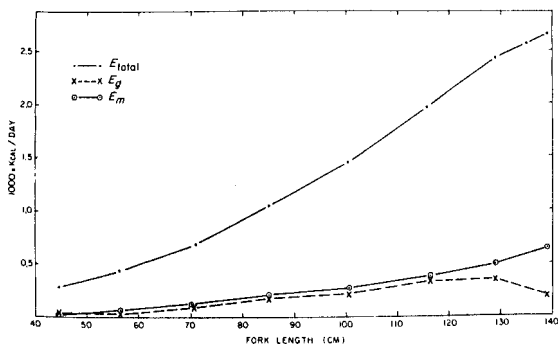


FIGURE 3.—The energy utilization (in kcal/day) for growth (E_g), maintenance (E_m), and the total ($E_g + E_m + E_s = E_{total}$) energy utilization are portrayed as functions of length \bar{l} .

we have attributed 95% of the day or 22.8 h of the day to \bar{V}_{typ} requirements and 5% or 1.2 h to \bar{V}_{feed} behavior. This is not to say that the fish are limited to 1.2 h/day of feeding but that on the average the increased velocity due to external stimuli are exhibited for this period. One suspects that the feeding of large and small tuna is entirely different in nature, but for simplicity and since no data are available, it is not unreasonable to assume that the relative effectiveness of feeding is somewhat similar over the life history of the animals. Based on these estimates we hope to have contrived a "reasonable" fiction for use in our model. The need for better estimates is obvious.

MODELING RESULTS

The model ENSIM computes the caloric requirement of each semestral cohort in the exploited population, by quarter of the fishing year. Summary data are listed after each quarterly output which differentiate the semester A cohort caloric expenditure from that of the semester B cohort, and a composite total expenditure is listed (see Table 2). An annual summary for 1972 is also generated and an example is presented in Table 3.

Initial biomass and numbers, yield in weight and numbers, gross growth, and average biomass are tabulated for each quarter, and summary tables are generated for the individual semestral cohorts as well as composite values. The biomass of food ingested per day is generated for each cohort, assuming 1.00 kcal (Paloheimo and Dickie 1966) are available per gram food ingested. The minimum percent biomass ingested per day with respect to the cohort biomass is also calculated for each cohort (see Figure 4). The caloric requirements for maintenance, swimming (at \bar{V}_{typ} , \bar{V}_{feed}), and growth are tabulated by size of the average animal in each cohort in the simulation by quarter (see Table 4).

We have simulated the fishing years 1964-72 and included the best available estimates for cohort strength, fishing effort, and availability parameters. We have also simulated a nonexploited population which was recruited at the average level for the data from the last 5 yr which includes all the population indicated or expected from inside our study area (see Figure 5). From Figure 5, the plot of the average annual biomass estimate, one can readily see the effect of fishery

TABLE 2.—ENSIM output for quarter three of the 1972 simulation is presented. The calculated kilocalories expended by each cohort (age-class) in the exploited population is given. The appropriate averages (N_i , weight (kg) and \bar{l}) are also listed for each cohort. Summary data are given by cohort and for both cohorts summed together.

Age	Maintenance	Swimming V_{typ}	Swimming V_{feed}	E_g	E_{total}	N_i	Weight (kg)	\bar{l}
1	.634079E+11	.640848E+11	.280680E+12	.377884E+11	.445961E+12	.186707E+08	.176060E+01	.444182E+02
2	0.	0.	0.	0.	0.	0.	0.	0.
3	.889373E+11	.776321E+11	.354145E+12	.431443E+11	.563858E+12	.141776E+08	.379126E+01	.572565E+02
4	0.	0.	0.	0.	0.	0.	0.	0.
5	.501222E+11	.307991E+11	.185411E+12	.264195E+11	.292751E+12	.521301E+07	.646561E+01	.683217E+02
6	0.	0.	0.	0.	0.	0.	0.	0.
7	.463850E+11	.196178E+11	.157393E+12	.237458E+11	.247142E+12	.292458E+07	.120872E+02	.840421E+02
8	0.	0.	0.	0.	0.	0.	0.	0.
9	.352487E+11	.120881E+11	.111902E+12	.138239E+11	.173063E+12	.151084E+07	.195812E+02	.985929E+02
10	0.	0.	0.	0.	0.	0.	0.	0.
11	.176499E+11	.514907E+10	.528273E+11	.601945E+10	.816457E+11	.537688E+06	.300053E+02	.113553E+03
12	0.	0.	0.	0.	0.	0.	0.	0.
13	.928307E+10	.302828E+10	.263712E+11	.297797E+10	.416605E+11	.208937E+06	.438055E+02	.128704E+03
14	0.	0.	0.	0.	0.	0.	0.	0.
15	.465814E+09	.166772E+09	.128095E+10	.796327E+08	.199317E+10	.868343E+04	.554414E+02	.139141E+03
16	0.	0.	0.	0.	0.	0.	0.	0.
17	.695863E+09	.256764E+09	.189348E+10	.249005E+08	.287100E+10	.122020E+05	.598477E+02	.142709E+03
18	0.	0.	0.	0.	0.	0.	0.	0.
Total A	.153438E+12	.102566E+12	.565646E+12	.729892E+11	.894639E+12			
Total B	.158758E+12	.110257E+12	.606257E+12	.810347E+11	.956307E+12			
Total	.312196E+12	.212823E+12	.117190E+13	.154024E+12	.185095E+13			

TABLE 3.—The 1972 annual summary data are listed which give the yield in number and weight for each of the semestral cohorts as well as the kilocalories utilized in the year by the cohorts and the combined sum.

	Yield numbers	Yield weight (metric ton)	Kilocalories utilized
Total S_A	0.491282 E + 7	0.653748 E + 5	3.85 E + 12
Total S_B	0.534418 E + 7	0.640257 E + 5	2.28 E + 12
Total $S_A + S_B$	0.102570 E + 8	0.129427 E + 6	7.13 E + 12

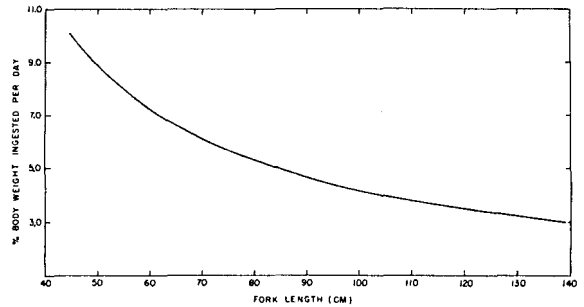


FIGURE 4.—The amount of food required per day is given in percent body weight of the individual yellowfin tuna of length \bar{l} .

TABLE 4.—The estimates of the daily energy utilization (in kcal/day) for maintenance, swimming at V_{typ} and V_{feed} , growth, and the total daily energy utilized due to all these activities is provided for the average individual of length \bar{l} and weight W for each cohort in the population during each quarterly time period. The average number of individuals present in each cohort is given in the column headed N . The semestral cohorts are separated (Total A or Total B) and the energy utilization estimates summed and listed for each. The composite estimates ($S_A + S_B$) are also listed (Total).

Age	Maintenance	Swimming V_{typ}	Swimming V_{feed}	E_g	E_{total}	N	W	\bar{l}
1	.377346E+02	.381374E+02	.167035E+03	.224882E+02	.265395E+03	.192145E+08	.176060E+01	.444182E+02
2	0.	0.	0.	0.	0.	0.	0.	0.
3	.667851E+02	.604781E+02	.267903E+03	.225852E+02	.417752E+03	.125166E+08	.359406E+01	.562530E+02
4	0.	0.	0.	0.	0.	0.	0.	0.
5	.116280E+03	.663364E+02	.423896E+03	.451705E+02	.651683E+03	.863385E+07	.718813E+01	.707599E+02
6	0.	0.	0.	0.	0.	0.	0.	0.
7	.181619E+03	.751903E+02	.613072E+03	.902863E+02	.960167E+03	.562388E+07	.125513E+02	.850967E+02
8	0.	0.	0.	0.	0.	0.	0.	0.
9	.271052E+03	.911480E+02	.853897E+03	.112988E+03	.132909E+04	.387916E+07	.207038E+02	.100429E+03
10	0.	0.	0.	0.	0.	0.	0.	0.
11	.381489E+03	.112386E+03	.113300E+04	.169496E+03	.179638E+04	.252689E+07	.317387E+02	.115684E+03
12	0.	0.	0.	0.	0.	0.	0.	0.
13	.497444E+03	.162886E+03	.141127E+04	.180946E+03	.225255E+04	.174290E+07	.442248E+02	.129111E+03
14	0.	0.	0.	0.	0.	0.	0.	0.
15	.596227E+03	.213496E+03	.163949E+04	.101935E+03	.255115E+04	.113565E+07	.554626E+02	.139159E+03
16	0.	0.	0.	0.	0.	0.	0.	0.
17	.639329E+03	.236943E+03	.173697E+04	.340073E+02	.264725E+04	.783083E+06	.605190E+02	.143236E+03
18	0.	0.	0.	0.	0.	0.	0.	0.
Total A	.156184E+04	.595451E+03	.459307E+04	.395600E+03	.714596E+04			
Total B	.122612E+04	.461550E+03	.365347E+04	.384302E+03	.572544E+04			
Total	.278796E+04	.105700E+04	.824654E+04	.779903E+03	.128714E+05			

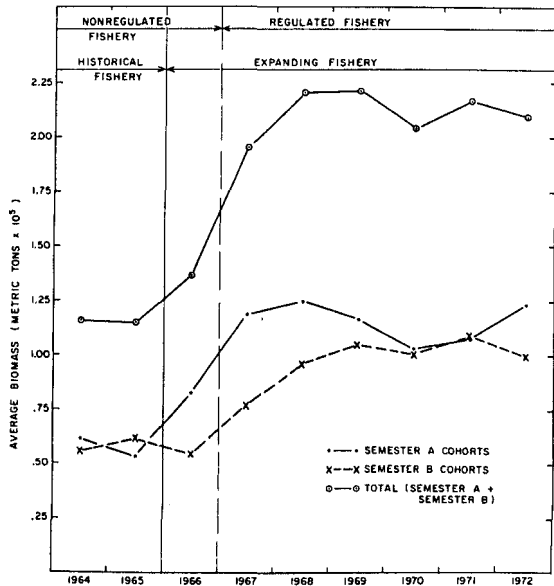


FIGURE 5.—The average biomass estimate of the exploited yellowfin tuna population in the CYRA is shown. The historical fishery label indicates the coastal fishery which operated prior to 1965; the expanded fishery indicates the process of seaward areal expansion which dramatically changed the estimates of exploited biomass from 1966 until approximately 1968. Fishery regulation was implemented in September 1966. The simulation of the unexploited populations yielded estimates of the average biomass for the two cohorts to be $S_A = 282,400$ metric tons; $S_B = 272,700$ metric tons; $S_A + S_B = 555,100$ metric tons. Recruitment was assumed to be consistent with recent levels.

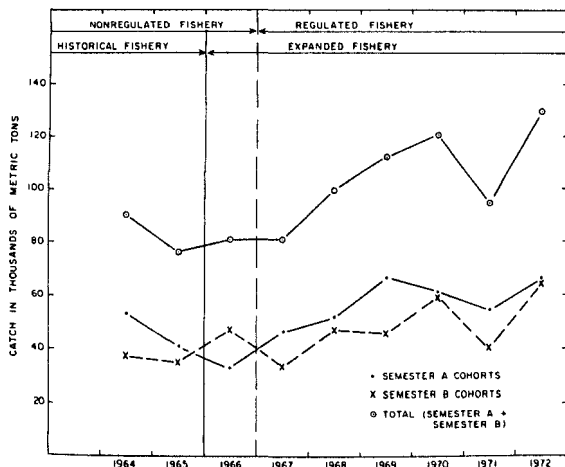


FIGURE 6.—The catch in metric tons of yellowfin tuna from the CYRA is shown for the study period. The cohorts and total catch are indicated by symbols as in Figure 5.

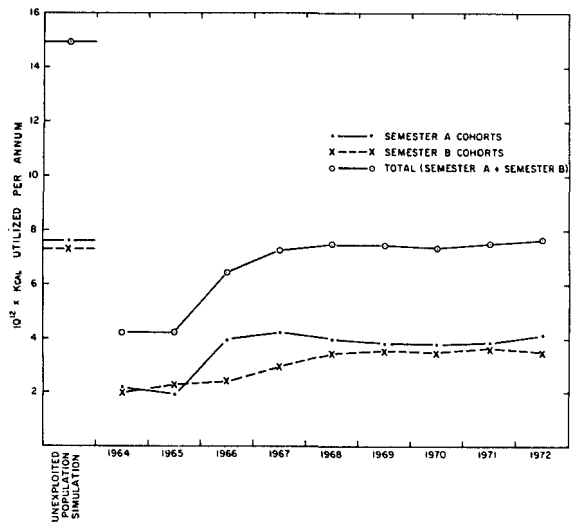


FIGURE 7.—Estimates from ENSIM of the kilocalories used per year by yellowfin tuna in the exploited CYRA population for the 1964-72 period.

growth (areal expansion) on population size estimates. From Figures 6 and 7 it is obvious that the catch has great fluctuations (e.g., 1971) but the energy flow seems to have stabilized in the exploited population estimates. This may be artificial but we think it may be significant to attempt interpretation.

The ratio of yield in weight to gross growth is another interesting indicator (Figure 8). Note the differential rate of exploitation of the semestral cohorts through time prior to 1967. The S_A and S_B cohorts became approximately equally exploited in this respect about 1967 or at about the end of the changes in fishery strategy and when

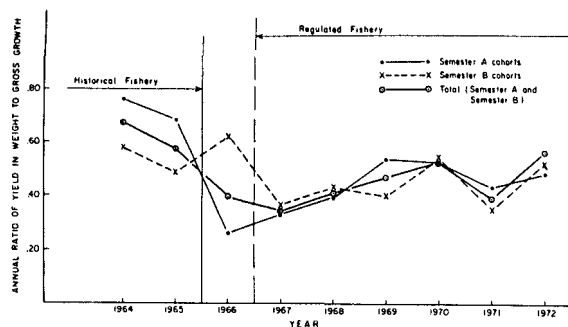


FIGURE 8.—The ratio of the yield in weight (catch) to gross growth for the years 1964-72. Note the relative similarity of the levels of the cohorts respective ratios in the regulated years as compared to the preregulated years.

regulation occurred. The indication is that since approximately 1969, the biomass and exploitation levels on the semestral cohorts have somehow paralleled a somewhat uniform energy utilization by the two cohorts, whereas from 1966 until 1969 a larger semester A biomass was under exploitation compared to the semester B cohort. The large discrepancies in biomass caught as compared to gross growth in the early data (1964-65) compared to the recent data (1969-72) may be an indicator of the relative health of the stocks under exploitation in recent years in contrast to the preregulatory years.

SPECULATIONS

The utility of simulation studies lies in the process of linking together observations, using generalized principles where possible, to generate testable hypotheses which ultimately lead to resolution of cause and effect relationships. As examples, from the results of the simulation model ENSIM, hypotheses were conceived concerning the relative importance of forage organisms, primary productivity and the size of the animals with respect to recruitment limitations.

Food as a Population Regulator

The availability of food is classically attributed the role of limiting population size. We do not intend to assail this premise, but intend only to show that the most probable source of limitations is at very early ages in tunas (<40 cm), and not on the late juvenile or adult population.

Forage for tunas is generally considered to be in the micronekton size range (1-10 cm). It probably extends upwards to 30 cm or more in length for larger sizes of tunas (Magnuson and Heitz 1971; Perrin et al. 1973). Tunas eat largely crustaceans, fishes, and cephalopods in most regions (Alverson 1963; Magnuson and Heitz 1971; Perrin et al. 1973). These organisms are poorly sampled by micronekton sampling devices.

The EASTROPAC cruises sampled from our study area over the year 1967 and early 1968. Productivity, micronekton, and most physical and chemical properties which are linked to biological productivity were sampled. EASTROPAC data (Blackburn et al. 1970) indicate that the average minimum micronekton night haul contained 5 ml of micronekton per 10^3 m³ of

water sampled. The samples represent a 200-m water column.

The surface area of the CYRA is estimated to be 5,012,643 sq nautical miles or 1.696×10^{13} m². The minimum available forage is therefore

$$(1.696 \times 10^{13} \text{ m}^2) (200 \text{ m}) \left(\frac{5 \text{ ml forage}}{10^3 \text{ m}^3} \right) \\ = 1.696 \times 10^{13} \text{ cc.}$$

If 1 cm² forage has approximately 1 g or 1.25 kcal caloric equivalency, then one should expect that there is a minimum forage availability of 1.25 kcal/m² or assuming 80% utilization efficiency of these calories by predators (Winberg 1960), 1.0 kcal/m² are present for metabolic utilization.

Owen and Zeitzschell (1970) in their analysis of EASTROPAC data also show that the primary productivity averages 169 mg carbon m⁻² day⁻¹ over long. 119°-112°W, 219 mg carbon m⁻² day⁻¹ at long. 105°W, and 282 mg carbon m⁻² day⁻¹ along long. 98°W. They also indicate coastal effects as being the probable cause of the eastward increase in productivity. The average productivity over the entire study area was 205 mg carbon m⁻² day⁻¹.

The energetic equivalent value for 1 mg carbon fixation is 11.4 cal (Platt and Erwin 1973), so that the average caloric productivity is 2,340 cal/m² day (or 2.34 kcal/m² day).

We have seen that the minimum estimate of the micronekton standing stocks caloric value is 1,250 cal/m², indicating that the probable daily turnover rate is less than 125 cal/m² so that maintenance of this stock is not unreasonable if the primary production is 2,340 cal/m² day.

The yellowfin tuna population simulation procedure based on average Murphy recruitment estimates of the 1966-71 S_A and S_B cohorts indicates that an unfished population (exhibiting a stable age structure) would have the biomass of 600,000 metric tons (6.0×10^{11} g). Assuming that the yellowfin tuna (YF) are distributed proportionally over the forage:

$$\frac{6.0 \times 10^{11} \text{ g YF}}{1.696 \times 10^{13} \text{ m}^2} = 3.54 \times 10^{-2} \text{ g YF/m}^2 \\ = 35.4 \text{ mg YF/m}^2;$$

$$35.4 \text{ mg YF/m}^2 \times 1.2 \text{ cal/mg YF} = 42.5 \text{ cal/m}^2.$$

Assuming the average caloric consumption by the yellowfin tuna population per day to be 10% of its caloric biomass, a somewhat higher than realistic estimate, daily utilization in calories would be 4.25 cal/m² day. The results of the ENSIM estimates of the total calories utilized per year for the unexploited population was 14.96 × 10¹⁵ cal/annum, so that the resulting utilization per square meter day is given by:

$$\frac{14.96 \times 10^{15} \text{ cal/annum}}{(365 \text{ day/annum}) (1.696 \times 10^{13} \text{ m}^2)} = \frac{2.5 \text{ cal}}{\text{m}^2 \text{ day}}$$

The results of the simulations of the exploited fishery for the years 1964-72 yield estimates of less than 50% of this figure as the energy utilization by the yellowfin tuna population. One would expect the true values of caloric utilization to lie somewhere in the range from approximately 1.5 cal/m² day to the upper value of 4.25 cal/m² day.

With the primary productivity estimated to be at an average level of 2.34 kcal/m² day and forage standing stock utilizable caloric values averaging at a minimum of 1.00 kcal/m², it seems hardly likely that yellowfin tuna are food limited from the 40-cm recruitment size.

This brings up the problem of how the eastern tropical Pacific yellowfin tuna population is limited. This, of course, is best taken in perspective. Population limitation examples are typically taken from terrestrial populations and extrapolations made to ecosimilar strategies in closed systems such as lakes and estuaries where primary productivity is greatly affected by season, and indeed can be determined to be the limiting factor in population numbers and biomass.

In those marine animals where density dependent growth functions are evidenced there is generally a two-dimensional limitation imposed such that crowding is likely to affect each individual. For filter-feeding organisms, such as herring and menhaden, the density dependent function is easily conceptualized.

One needs only to examine the relative abundance of food available to highly mobile predatory species which feed opportunistically on organisms ranging in size from 1 to 30 cm, which are available on a relatively continuous basis in a tropical system, to see that dogma general to terrestrial, estuarine, limnetic, two-dimensional substrate tied, or filter-feeding animal

ecology does not generally apply to the 40- to 140-cm yellowfin tuna.

There are, however, several possibilities concerning the survival of yellowfin tuna from larvae to 40 cm which would certainly fit into the schemes which typically limit species. Since they are probably particulate feeders (e.g., do not undergo ecometamorphoses at early ages from filter feeders to predators), it can easily be seen that they are victims of the availability of concentrations of food at smaller sizes because of their relative lack of mobility. If a 40-cm tuna requires 10-20% of its body weight per day to maintain, as compared to 3-5% in large yellowfin tuna, then one can hypothesize that the smaller predators must consume even greater amounts due to the pressures of very rapid growth, feeding activity, and competition with peers, indicating that they are more likely severely affected by density of both conspecifics and food than are the larger sized fish.

Another consideration is the size distribution of the forage organisms. It is obvious that there are considerably larger amounts of the smaller food organisms than the bigger sizes, which would perhaps indicate that the real density competition pressures are on the intermediate sizes (vis. 10-40 cm) as compared to the postlarval sizes. This brings us to the next important process, larval survival.

Spawning Survival Versus Population Biomass

For our hypothesized unexploited population of 600,000 metric tons of individuals from 40 to 140 cm fork length, we can calculate the requisite number of postlarval survivors which must be generated each year to maintain this stock at equilibrium. Assuming 40-cm yellowfin tuna are approximately 7 mo of age and that the survival rate is constant for all ages after postlarval transformation and is approximately equal to $e^{-0.8}$ on an annual basis (Hennemuth 1961), the number of postlarval survivors each year is given by the relation

$$N_s = N_{40} e^{0.8 \left(\frac{7}{12}\right)}$$

If N_{40} is approximately 2.12×10^7 individuals per year in cohort S_A , and 2.06×10^7 in cohort S_B , then there are approximately 6.67×10^7 survivors/yr. If we assume that they are aggregated

spatially but not temporally (there are two cohorts of 3.33×10^7 postlarvae spread approximately evenly over the year), approximately 9.13×10^4 postlarvae enter the system daily. (This is the equivalent of nearly 1% reproductive success of either one 155-cm female or five 87-cm females.)

The relative fecundity of yellowfin tuna is given by Joseph (1963) to the following:

$$\text{Number of eggs} = 8.955 \times 10^{-3} l^{2.791}$$

where l is the fork length of the fish in mm.

If we assume the average spawning female to weigh 25 kg and we estimate the presence of 175,000 metric tons of females of reproductive age in our unexploited population, then the equivalent number of reproductive females is approximately equal to 7×10^6 . These females would be an average of 107 cm in length and therefore:

$$\begin{aligned} &(8.955 \times 10^{-3}) (1,070^{2.791}) (7 \times 10^6 \text{ females}) \\ &= 1.79 \times 10^{13} \text{ eggs produced.} \end{aligned}$$

So if 6.67×10^{-7} postlarvae start the process we need invoke only 3.72 postlarval survivors per million eggs spawned. This estimate is conservative due to the assumption that females only spawn once per year, whereas they could spawn more often. (No evidence for or against multiple spawnings is in existence for yellowfin tuna.) It does, however, seem likely that spawning success (survival to postlarvae) is greater than 3.72 individuals per million eggs produced (Sette 1943; Farris 1961). It is also important to mention that all attempts at relating spawning biomass to recruitment estimates for yellowfin tuna in the CYRA have been futile. This could be due to error in either, or both, estimates of spawning biomass and recruitment and/or the possibility that environmental conditions indeed override any obvious relationships.

These comments are presented to point up the likelihood that the density dependent factors for limiting yellowfin tuna abundance are probably more effective on the egg to larvae to juvenile stages than at 40 cm or more. The larvae to 40-cm fish are likely very narrowly distributed in the water column (approximating a two-dimensional distribution) due to thermal and energetic requirements. The recruitment at 40 cm in the

highly productive regions such as the periphery of the Costa Rica Dome and the Panama Bight-Ecuador coastal regions can perhaps be best explained by the high productivity levels in these regions which ranges from 500 to 700 mg carbon $m^{-2} \text{ day}^{-1}$ as compared to the 205 mg carbon $m^{-2} \text{ day}^{-1}$ average CYRA carbon fixation rate, in conjunction with the relatively shallow oxygen minimum and thermal optima which probably act to compress the available habitat toward the surface. If one could invoke the ability of yellowfin tuna to climb a food gradient, a simple volume change in the preferred thermal-oxygen regime combined with a negatively correlated food gradient could result in the observed coastal "emergence" of recruits, which "grow out" of their previous thermal-oxygen limitations as they develop, and exploit a significantly wider niche than they could as relatively poikilothermal entities at sizes below 40 cm.

To summarize, larval tunas are relatively immobile and for survival are probably dependent on aggregations of food resources. The ability of tunas, particularly postlarval sizes, to detect food gradients is unknown, but may indeed account for the easterly trend in abundance of recruits. The wider distributions of larger fish (postrecruits) probably is a response to competitive feeding problems and changing physiological capabilities. These larger fish are increasing their daily demands but are gaining in adaptive physiological and morphological characteristics which widen their niche as compared to smaller sizes. Their mass and mobility insure their ability to move rapidly from low to high availabilities of food resources, in response to seasonal and areal fluctuations in productivity, perhaps accounting for the cyclic migratory behavior observed in their first few years in the fishery. The relative offshore surface distribution of the larger fish (>40 cm) may be roughly correlated with the depth distribution of the 22°-23°C isotherms, a relationship which we are now starting to study. As the larger fish grow in mass, they can afford deeper and longer forays into colder than optimal zones with low O_2 availability to obtain larger and more calorific food sources; and by thus increasing the maximum excursion depth, competition is likely to be less severe. The disaggregation of larger sized fish into smaller schools (number of individuals) may be accounted for by these effects. The large yellowfin tuna in the offshore areas are certainly concentrated at the surface

over highly productive regions where their main sources of competition are probably porpoise and bigeye tuna, *Thunnus obesus*. The porpoise-tuna composite likely indicates the optimum availability of fish and squid in the eastern tropical Pacific. It is obvious from the Perrin et al. (1973) studies that the two *Stenella* species and tunas coexist but tend to feed differentially. The tuna diet shares most of the organisms found in both species indicating that they are less selective and/or feed throughout the water column.

No data support the concept of food limitation for population size in yellowfin tuna in post-recruit sizes and in most cases the arguments tend toward the opposite conclusion. Since no stable relationship can be found to exist between recruitment and spawning biomass, it is unlikely that reproductive success is affected by spawning biomass at the population levels we are experiencing. More probable is that the environmental parameters are more important in regulating the absolute numbers of surviving larval or juvenile yellowfin tuna which are recruited to the fishery.

In the future, we plan to incorporate the available productivity and environmental data (temperature, oxygen, etc.) with a more complete version of this model. We hope to determine the environmental correlates with the fluctuations in the catch, effort, and length-frequency data generated from the fishery on yellowfin tuna. Preliminary studies have been encouraging (Inter-American Tropical Tuna Commission 1975) and point up the need for data on the thermal preferences (perhaps indicating energetic optima) and the levels of environmental variability which can be sensed and therefore compensated for by the several tuna species at the various developmental stages in their life cycles. Also obvious is the need to work with smaller areas and corresponding population segments rather than assuming "average" conditions in environmental and population parameters. The ultimate goal of these studies is the development of predictive tools for use in assessing likely catch conditions as well as the basic distributional properties of the tunas. The use of unsupported guesses based on overviews which integrate vast areas with significant oceanographic and population structure differences may do little more than obscure the existing relationships which are important to this goal. The application of the crude model we

have described in this study will depend upon the development of better estimates of the physiological parameters and appropriate use of the areal breakdown in the population simulator. Studies of trophic dynamics and competition interactions would help complete the picture necessary to "efficiently" manage a dynamic resource. We hope to generalize, where possible, the relationships which arise from these analyses in order to provide a useful descriptive tool as well as a hypothesis testing device for studying the occurrence, abundance, and availability of tunas in the world ocean.

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APPENDIX.—GLOSSARY OF TERMS

- A = wetted surface area of the fish.
 A_{ft} = the total lifting area of the pectoral fins.
 A_k = the total lifting area of the keel.
 C_{L_f} = the coefficient of lift of the pectoral fins.
 C_{L_k} = the coefficient of lift of the keel.
 C_d = coefficient of total drag of fish of length \bar{l} which includes an inseparable efficiency term involving acceleration processes during continuous swimming.
 E_g = the daily caloric expenditure of fish of length \bar{l} attributable to growth in the form of positive changes in mass.
 E_m = the daily caloric expenditure of fish of length \bar{l} to maintain metabolic stasis.
 E_s = the daily caloric energy expenditure of fish of length \bar{l} utilized by swimming work, a function of swimming velocity (\bar{V}_{real}).
 F = the instantaneous mortality rate due to fishing.
 g = acceleration due to the force of gravity.
 k = the rate of oxygen consumption due to metabolic stasis of 1 g of respiring tissue, not doing external work.
 l = the length of a fish from snout to fork of tail in millimeters.
 \bar{l} = the fork length of a fish in centimeters.
 L_t = the total weight of a fish in seawater of density ρ , in dynes.
 M = the instantaneous natural mortality rate.
 M_e = the efficiency of muscle when converting chemical energy to mechanical work.
 M_f = mass of the fish in grams where for yellowfin tuna: $M_f = 1.858 \times 10^{-2} (\bar{l})^{3.021}$ (Chatwin 1959).
 $N_{\bar{l}}$ = the estimated number of individuals of length \bar{l} .
 N_s = the number of postlarval survivors from a spawning.
 N_{40} = the number of recruits at 40 cm.
 Re = the Reynolds number.
 ρ = the density of seawater, in this work $\rho = 1.025 \text{ g/cm}^3$.
 S = the rate of oxygen consumption due to swimming activity, from the power equation of Smit (1965).
 S_A = recruitment cohort label for all individuals that attain 40 cm fork length from 1 January to 30 June of each year.
 S_B = recruitment cohort label for all individuals that attain 40 cm fork length from 1 July to 31 December of each year.
 S_m = the oxygen consumption rate of fish of length \bar{l} attributable to metabolic stasis.
 S_s = the oxygen consumption rate of a fish of length \bar{l} attributable to swimming energy expenditures.
 $S_{total} = \frac{S_m + S_s}{M_f \times 10^{-3}}$ = respiration rate attributable to swimming and metabolic stasis energy expenditures.
 ν = the kinematic viscosity of seawater.
 V = the constant velocity of a fish, in centimeters per second.
 \bar{V} = the estimated integrated velocity of a fish of length \bar{l} used in determining Re and C_d , and in the estimation of S .
 V_{100} = the minimum swimming speed of a fish of given species and \bar{l} for maintenance of hydrostatic equilibrium (Magnuson 1973).
 \bar{V}_{typ} = the velocity which is "typical" of the swimming speed of a fish of length \bar{l} .
 \bar{V}_{feed} = the velocity which is meant to integrate all energy expenditures due to fish swimming faster than \bar{V}_{typ} , including short bursts in feeding or flight behavior (assumed to be 3 m/s).
 \bar{V}_{real} = the average daily velocity of a fish of length \bar{l} , $= 0.95 \bar{V}_{typ} + 0.5 \bar{V}_{feed}$.
 W_{met} = the metabolic weight of a fish, in grams (Winberg 1960).