

Apex Predation by Yellowfin Tuna (*Thunnus albacares*): Independent Estimates from Gastric Evacuation and Stomach Contents, Bioenergetics, and Cesium Concentrations

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Three approaches for estimating predation by yellowfin tuna (*Thunnus albacares*) were compared: (1) stomach analysis adjusted for gastric evacuation; (2) food energy required as a function of swimming speed in yellowfin tracked at sea; and (3) food intake needed to maintain observed cesium concentrations. Gastric evacuation data from captive yellowfin were best fit by linear functions of time for four foods. Fish with high lipid content (mackerel, *Scomber japonicus*) were evacuated at a slower rate (proportion per hour) than smaller fish (smelt, *Hypomesus pretiosus*), squid (*Loligo opalescens*), and small fragile fish (nehu, *Stolephorus purpureus*), all of which had lower lipid contents. Tuna captured in the eastern Pacific had daily rations averaging 3.9% of body mass based on stomach contents and gastric evacuation rates, 5.2% based on bioenergetics estimates, and 6.7% based on the cesium estimate. Swimming costs accounted for one-third to one-half of the energy budget. Annual predation by the eastern Pacific yellowfin population averaged 4.3–6.4 million metric tons during 1970–72, depending on the method used for estimating ration; 34% was frigate tunas (*Auxis* spp.). High growth and turnover rates (*P/B* ratios) of tropical tunas in contrast with low conversion and trophic transfer efficiencies suggest a trophic structure that differs from more productive ecosystems.

Les auteurs comparent trois méthodes pour l'estimation de la prédation par l'albacore à nageoires jaunes (*Thunnus albacares*): 1) l'analyse du contenu stomacal corrigé en fonction de l'évacuation gastrique; 2) l'énergie alimentaire nécessaire présentée comme une fonction de la vitesse de nage d'albacores dont les déplacements ont été relevés en mer; et 3) l'ingestion alimentaire nécessaire au maintien des concentrations de césium observées. Les données sur l'évacuation gastrique d'albacores gardés en captivité étaient le mieux représentées par des fonctions linéaires temporelles, ceci pour quatre aliments. Les poissons à forte teneur en lipides (maquereaux, *Scomber japonicus*) étaient évacués plus lentement (proportion par heure) que des poissons plus petits (éperlans, *Hypomesus pretiosus*), des calmars, *Loligo opalescens* et un petit poisson fragile (néhu, *Stolephorus purpureus*), tous à teneur en lipides moins élevée. La ration quotidienne des albacores capturés dans l'est du Pacifique s'élevait en moyenne à 3,9% de la masse corporelle, sur la base du contenu stomacal et des taux d'évacuation gastrique, de 5,2%, sur la base des estimations bioénergétiques, et de 6,7%, sur la base des concentrations de césium. L'énergie consacrée à la nage représentait du tiers à la demie du bilan énergétique. La prédation annuelle de la population d'albacores de l'est du Pacifique s'est élevée en moyenne à 4,3–6,4 millions de tonnes métriques au cours de la période 1970–1972, tout dépendant de la méthode utilisée pour l'estimation de la ration; 34% de celle-ci était composée de thazards (*Auxis* spp.). La croissance rapide et les taux de renouvellement élevés des thons tropicaux comparativement aux faibles efficacités de conversion et de transfert trophique, portent à croire à l'existence d'une structure trophique différente de celle des écosystèmes plus productifs.

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Yellowfin tuna (*Thunnus albacares*) are abundant and ubiquitous in tropical regions of the world's oceans. Tunas are opportunistic, generalist predators (Alverson 1963; Blackburn 1968; Magnuson and Heitz 1971). Metabolic rates of tunas greatly exceed those of cold-bodied fishes (Stevens and Dizon 1982) due to their obligate con-

tinuous activity (Magnuson 1978) and high "standard" metabolic rates (Brill 1979; Gooding et al. 1981). Estimates of food consumption and an understanding of energy partitioning are needed to explain the ecological strategy of this high-cost mode of living (Stevens and Neill 1978; Kitchell 1983). The large energy requirements of yellowfin, their abundance, and their broad diet make this species useful for estimating pelagic productivity at the intermediate trophic levels occupied by their prey.

Several methods for estimating daily rates of food con-

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sumption in fishes have been employed. Direct methods entail quantifying the amount of food in the stomachs of wild-caught fish and adjusting for the gastric evacuation rate determined by laboratory experiments (Elliott and Persson 1978; Jobling 1981a). Indirect methods include constructing energy and nutrient budgets (Davis and Warren 1971; Mann 1978). Both approaches have drawbacks. Direct methods are laborious and provide infrequent point estimates of in situ feeding rate. Bioenergetics modeling of food consumption can be biased by errors in parameter estimation (Bartell et al. 1986) but are useful for evaluating the effect of temperature, body size, and activity of a predator on its food resource (Kitchell 1983). Comparing estimates of food consumption from direct and indirect methods can provide valuable independent validation of laboratory-measured bioenergetics parameters (Rice and Cochran 1984).

In our study, three independent approaches were taken to estimate the flux of energy through a tuna population. In the first, stomach analysis on thousands of field-caught yellowfin tuna was combined with laboratory determinations of gastric evacuation rates for mixed meals of different food items to estimate the daily ration of yellowfin at sea and to estimate predation rates on various prey organisms. The second approach was to employ a model derived from energy expenditures in yellowfin as a function of size and swimming speed in the laboratory (Boggs 1984). This model was applied to swimming speeds measured by acoustic telemetry of yellowfin at sea (Carey and Olson 1982) to estimate typical energy and food requirements. In the third approach, previous determinations of trophic level and cesium concentration in yellowfin and their prey (Mearns et al. 1981) and residence time of cesium in tuna tissue (Folsom et al. 1967) were used to estimate the amounts of prey consumed by yellowfin.

This diversified investigation of food consumption by yellowfin allows for comparison and corroboration of methods, and thus overcomes some of the inadequacies of each approach. The objective was to determine if food consumption by yellowfin in nature was consistent with laboratory results showing a very high energy demand. Validation of laboratory results was sought to increase the credibility of "top-down" trophic models that use bioenergetics parameters such as predation rate (Laevastu and Larkins 1981; Polovina 1984), gross conversion efficiency (Longhurst 1983), or trophic transfer efficiency (Adams et al. 1983) of major predators to describe the trophic system at lower levels. We estimated these parameters for yellowfin tuna, a dominant apex predator in the eastern tropical Pacific Ocean, and used them to estimate the minimum production rate of a variety of prey types.

Materials and Methods

Gastric Evacuation Experiments

Experimental yellowfin were caught by pole-and-line boats using live bait. They were delivered to the Kewalo Research Facility (Nakamura 1972) of the National Marine Fisheries Service in Honolulu, Hawaii, within 2–6 h and placed in 40- or 700-m³ outdoor tanks. Ambient temperature ranged from 23.5 to 25.5°C. All experiments were conducted within 45 d of capture. Yellowfin exhibit the least degenerative physiological change of any tuna species in captivity. Individuals have been maintained for several years and have gained mass up to 50 kg (C. H. Boggs, pers. obs.).

Sixty-nine yellowfin averaging 36.2 cm in fork length (range = 23.6–45.1 cm) and 973 g (range = 220–1756 g, excluding stomach contents) were individually tagged (with color codes) for easy recognition and were trained to accept mixed meals of dead mackerel (*Scomber japonicus*), squid (*Loligo opalescens*), smelt (*Hypomesus pretiosus*), and nehu (*Stolephorus purpureus*). The foods were selected based on their taxonomic and/or gross morphological similarity to important yellowfin prey in the eastern Pacific (Alverson 1963; Anonymous 1984). Red crabs (*Pleuroncodes planipes*), an important prey, were offered but not eaten by the captive yellowfin.

All food species were acquired frozen, thawed in air, blotted, and weighed to the nearest 0.01 g. Some of the larger mackerel and squid were cut in half to allow ingestion by the yellowfin. Samples of each food type were dried at 60°C to a constant mass to determine water content. Replicate subsamples of dried specimens were analyzed for lipid content using a Soxhlet apparatus (Joslyn 1950) and chloroform–methanol, 2:1 by volume.

The yellowfin were not fed for 24 h prior to experimental feedings, allowing enough time to clear their guts. Although Noble (1973) found that fish may process food more slowly after a moderate period of food deprivation than when feeding continuously, a fairly high frequency of empty stomachs suggests that intervals without food are typical for tunas (Alverson 1963). Mixed meals of the four food organisms were offered, one food particle at a time. The time that each preweighed food particle was eaten by each individually recognized (tagged) fish was recorded to the nearest minute. Feeding continued until the tuna were satiated. The elapsed time from ingestion of each food particle to the time the fish were killed was recorded. Freshly killed fish were weighed to the nearest gram, and fork length was measured to the nearest millimetre. Hemostats were used to ligate the alimentary canal at the esophagus and pyloric sphincter. The stomach was removed from the yellowfin, slit, and the food remains removed, sorted by species, blotted, and weighed to the nearest 0.01 g. The elapsed time from handling the fish to weighing the stomach contents was about 5 min. Stomach contents were oven dried at 60°C to a constant mass at 0.01 g accuracy.

The evacuation data were analyzed separately by food species. Evacuation functions² were fitted using wet-mass data, since wet mass was the quantity measured during stomach analysis, and we wished to calculate daily ration on a wet-mass basis. Some data were eliminated prior to curve fitting to correct for a significant bias in this type of data (Olson and Mullen 1986). The problem becomes important when the duration of gastric evacuation experiments is long enough that at least some test individuals empty their stomachs. Empty stomachs must be omitted during data analysis because the exact time they became empty cannot be determined. Prior to the time when the fastest digestors in a sample begin to empty their stomachs, the data include the full range of intraspecific variability expected. But subsequent to that time, an ever-increasing proportion of the sample representing the faster digestors is eliminated from the distribution. Thus, as postprandial time increases, the distribution becomes constricted by the time axis. Olson and Mullen (1986) showed conclu-

²Functions actually represent gastric retention, but we follow convention in calling them gastric evacuation functions.

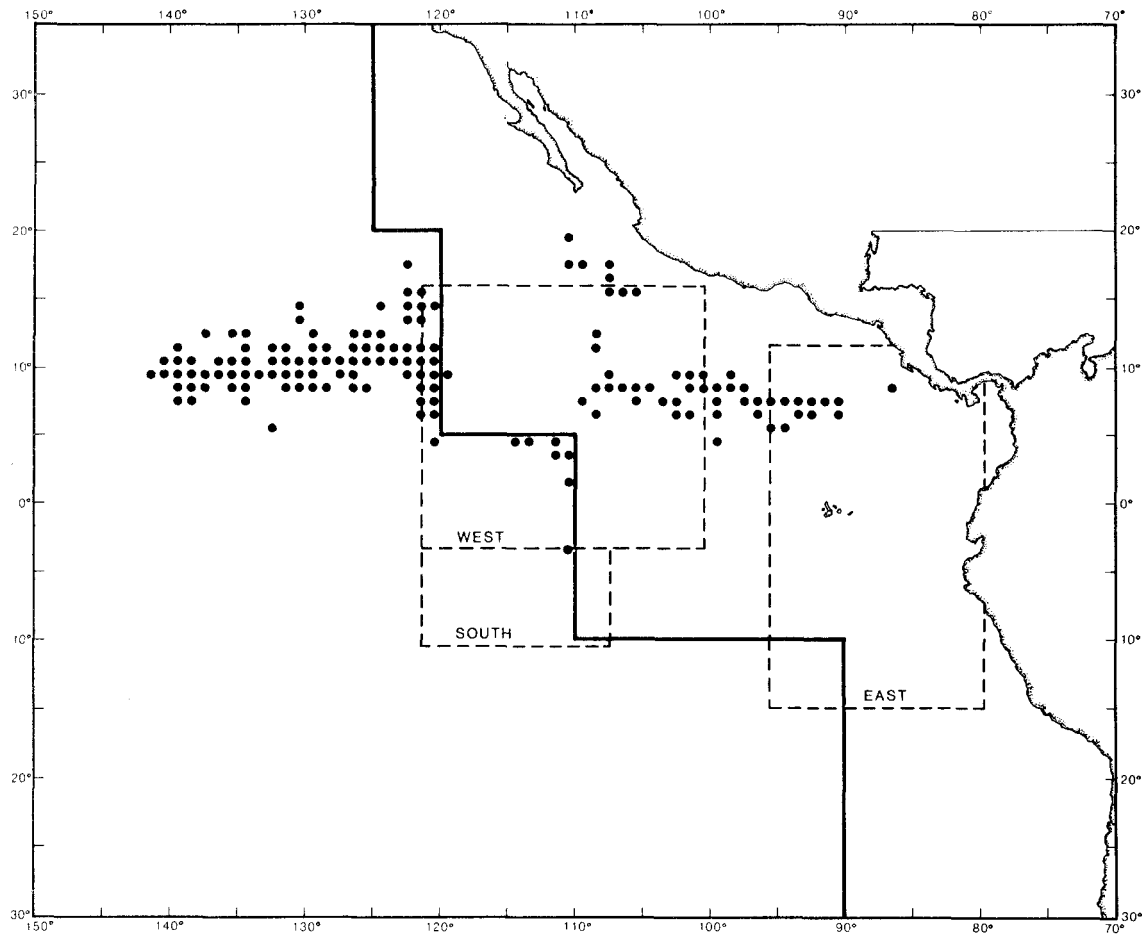


FIG. 1. Sampling locations in the eastern tropical Pacific from which stomachs of yellowfin tuna were collected during 1970–72. The western boundary of the regulated fishing area (bold line) encloses $1.696 \times 10^{11} \text{ m}^2$ (Sharp and Francis 1976). The broken lines enclose three sampling areas of the EASTROPAC oceanographic expedition (Blackburn et al. 1970).

sively that "constricted" data distributions can cause serious bias in evacuation rate estimates and a false indication or exaggeration of curvature. Therefore, the data were truncated prior to curve fitting to eliminate those points associated with postprandial times when empty stomachs appear. A simple procedure for choosing points of truncation was explained by Olson and Mullen (1986).

The gastric evacuation data were fitted to linear, square root, and exponential models and the fits evaluated using residual mean squares and statistical procedures of residual analysis, including tests for normality (Filliben 1975), homoscedasticity, and autocorrelation (Wesolowski 1976). The Y_i values (proportion of initial amount recovered from the stomach) were transformed as $\ln(Y_i + 1.0)$ and $\sqrt{Y_i + 0.5}$ for the exponential and square root models, respectively (Zar 1974). An arcsine transformation was attempted, but did not improve the approximation of this proportion data to normality. The data were analyzed for the effect of food type, meal size, yellowfin size, mixed meals, partial food particles, and food composition on evacuation rates using analysis of covariance (Dixon and Massey 1957).

Stomach Samples

Yellowfin stomach samples from fish captured by the eastern tropical Pacific purse-seine fishery during 1970–72 (Fig. 1) were collected by scientific technicians at tuna canneries in San Diego and San Pedro, California. These yellowfin were captured during daylight hours, and most often in schools associated with dolphins (*Stenella attenuata* and *S. longirostris*). Fork length of sampled fish was measured to the nearest millimetre and the stomachs were preserved by freezing.

Stomach contents were identified to the lowest possible taxa, counted, and weighed to the nearest 0.1 g. After removing the food, the stomachs were weighed to the nearest 1.0 g. This was used to adjust for the often missing anteriormost portion of the stomachs due to the canneries' method of eviscerating tuna. A relationship between complete empty stomach mass and yellowfin fork length was determined from an independent sample of 95 yellowfin which we eviscerated. In partially filled complete stomachs the contents were distributed fairly evenly throughout the stomach. Thus, it seemed reasonable that the proportion of each prey category in the stomach contents (if any) missing from each sample was proportional to the weight

of the stomach missing.

A second adjustment was made to account for reduced stomach contents due to gear retention and disturbance, since feeding presumably ceases when dolphins and associated yellowfin are chased and while enclosed in a purse seine, but digestion continues at least until death or freezing. The average duration of pursuit and enclosure was determined for fishing operations in the early 1970's and used in conjunction with evacuation rates to adjust upward the weight of stomach contents at time of gut removal.

Stomach contents data were stratified into arbitrary age-classes based on yellowfin fork length. Age-class subdivisions were selected to approximate the sizes of yellowfin upon completing their first, second, and third years based on yellowfin otolith increment counts (A. Wild, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA, pers. comm.).

In representing the relative biomass of prey types consumed, the contribution of each prey to the daily meal was determined by accounting for differences in evacuation rate of each prey. The components of the diet were expressed as proportions of the daily meal.

Ration Estimates

Since preliminary analysis indicated that the evacuation data were poorly fitted by an exponential function, even before data were omitted as described above, an alternative to those methods for calculating daily ration which require an a priori assumption of exponential gastric evacuation (e.g. Elliott and Persson 1978) was needed. A method (Robson 1970) that is appropriate for a variety of evacuation functions was described in detail by Olson and Mullen (1986). The model predicts feeding rate (\hat{r} , grams per hour) by dividing the mean stomach contents per predator (\bar{W} , grams) by the integral (A , proportion \times hours = hours) of the function that best fits experimental gastric evacuation data. A represents the average amount of time required to evacuate the average proportion of all meals present in the stomach at any instant in time. For a predator that consumes a variety of prey organisms which are evacuated at different rates:

$$(1) \hat{r} = \sum_{i=0}^I \frac{\bar{W}_i}{A_i}$$

where subscripts i refer to each of the I prey types. Daily meal is calculated by multiplying \hat{r} by 24 h, and daily ration is daily meal expressed as a percent of body mass.

Bioenergetics Model

Energy requirement calculations were based on a separate study by Boggs (1984) wherein mass and energy content of starved yellowfin were compared with controls to estimate metabolic rates following the approach described by Brett (1973). The method of estimating metabolic rates from starved fish can be used to estimate rates in the field by adjusting for mass, length, and speed and by including the increase due to SDA. Brett (1973) and Boggs (1984) did not find that starvation per se reduced metabolic rate in the highly active fishes studied. The lack of postprandial metabolic increment (SDA), reduced activity, and mass loss during starvation does reduce metabolic rate (Beamish 1964; Glass 1968; Jobling 1980a). However, nonfeeding, mass-specific, speed-specific metabolic rates are not reduced by starvation (Jobling 1980a). In Boggs's

(1984) experiments the volitional speeds maintained by tuna differed between individuals, and other individuals were forced to swim fast by altering buoyancy and lift (Magnuson 1970, 1973, 1978). The effects of mass, speed, and length on the metabolic rates of 21 yellowfin were used by Boggs (1984) to fit a model for standard metabolism (\dot{E}_0 , joules per gram per day) plus swimming work (\dot{E}_V , joules per gram per day) where

$$(2) \dot{E}_0 = aM^\beta$$

$$(3) \dot{E}_V = fV^\gamma L^\delta$$

where M is wet mass (grams), V is speed (centimetres per second), L is fork length (centimetres), and a , β , f , γ , and δ are empirically determined constants.

Horizontal and vertical movements of four yellowfin were tracked by Carey and Olson (1982) using acoustic telemetry. The vertical vector of the movements was ignored, since calculations indicated that horizontal movements accounted for almost 100% of distance covered. Swimming speeds were grouped in increments of 0.5 body lengths $\cdot s^{-1}$, and the average speed (centimetres per second) and total tracking duration (hours) in each increment were calculated. Then, equation 3 was used to calculate the cost of locomotion (\dot{E}_V) for the mean speed in each increment for the four tracked yellowfin.

The sum of locomotory costs at each speed increment was added to standard metabolism (\dot{E}_0). Growth rates (grams per day) for eastern Pacific yellowfin of the sizes tracked by Carey and Olson (1982) were calculated based on a size-time relationship determined from recent yellowfin otolith increment counts (A. Wild, pers. comm.) and a previous tetracycline increment validation study (Wild and Foreman 1980). Growth (grams per day) was transformed into joules per day (\dot{E}_G) assuming a caloric density of $6.03 \times 10^3 J \cdot g^{-1}$ for wild yellowfin (Boggs 1984). Energy losses due to excretion, egestion, and food assimilation were assumed to account for 35% of the energy consumed in food (Kitchell et al. 1978). Thus, total energy requirements (joules per gram per day) were estimated at

$$(4) \frac{\dot{E}_0 + \dot{E}_V + \dot{E}_G}{1 - 0.35}$$

Cesium Budget

The rate of cesium intake was assumed to balance the rate of cesium loss and to maintain the measured cesium concentration in yellowfin (Mearns et al. 1981) during growth. The rate of loss in yellowfin was assumed to be comparable with the biological half-life of cesium in albacore, *Thunnus alalunga* (Folsom et al. 1967; Young 1970), which is similar to that in other marine fishes (Baptist and Price 1962). A 50% decrease in concentration over 53 d (Folsom et al. 1967) is equivalent to an exponential decline ($C_{S_{out}}$) in total cesium content of about $1.3\% \cdot d^{-1}$. Growth (G) was estimated at 0.63% wet mass $\cdot d^{-1}$ (=percent cesium content per day) for the average-sized yellowfin measured by Mearns et al. (1981). A reasonable value (0.8) (Isaacs 1972) was assumed for cesium assimilation efficiency. Yellowfin cesium concentration (C_{SY} , micrograms per kilogram wet mass) was several times greater than prey cesium concentration (C_{SP}) (Mearns et al. 1981). Thus, food intake (F , percent body mass per day) was calculated as

$$(5) F = \frac{(C_{S_{out}} + G) C_{SY}}{(0.8)C_{SP}}$$

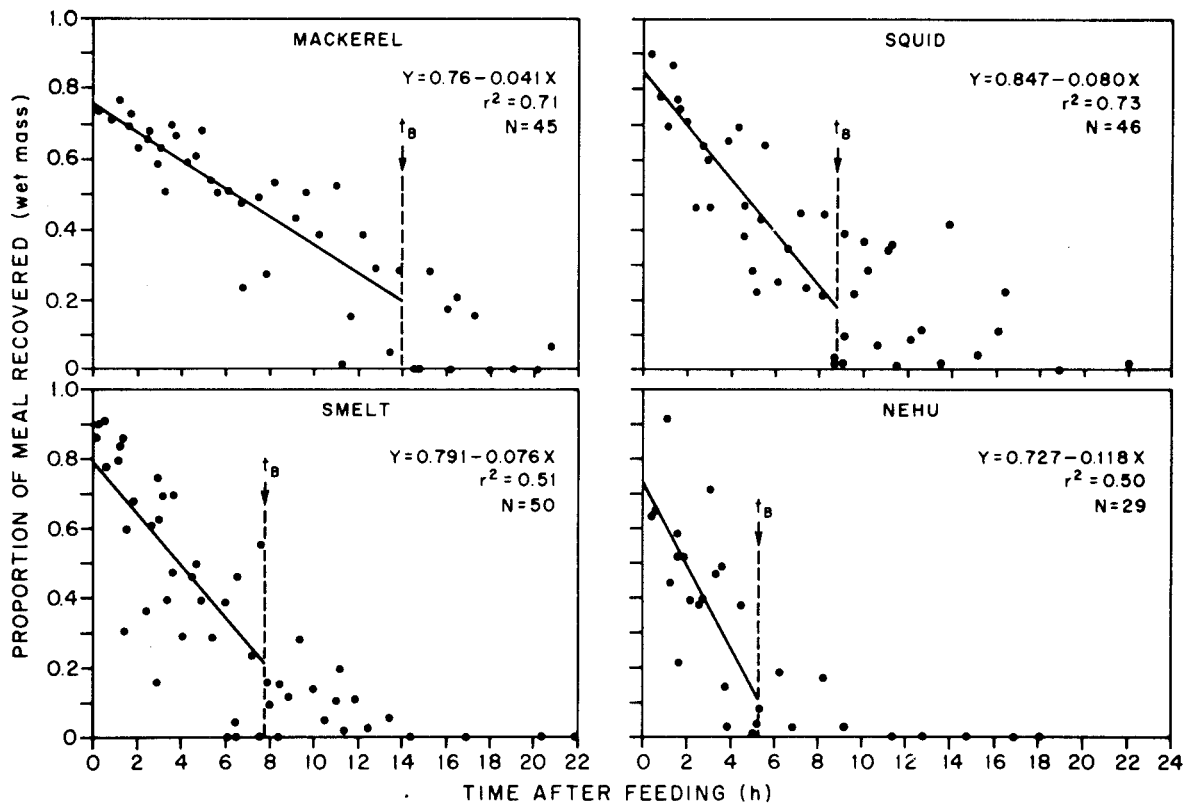


FIG. 2. Proportion of initial wet mass of four experimental foods recovered from the stomachs of captive yellowfin versus time after feeding. T_B is the point beyond which data were omitted prior to curve fitting (see text).

The total cesium concentration in the diet was determined from the values given by Mearns et al. (1981) using the proportions of different prey in the diet of age-class 1 and 2 yellowfin in this study. The cesium concentration of squid was used for cephalopods and other invertebrates and that for frigate tuna (*Auxis thazard*) was used for scombrids. The cesium concentration of flyingfish was used for all other fishes. This latter value was assumed, since these other fishes were generally smaller and thus were probably at a trophic level closer to that of flyingfish than that of frigate tuna.

Results and Discussion

Gastric Evacuation

The experimental yellowfin became satiated after about 30 min of feeding. Mean sizes of the four food organisms and the various combinations in which they were consumed are presented in Tables 1 and 2, respectively. Wet mass of the experimental meals averaged 77.1 g ($N = 69$, $\sigma = 36.4$ g, range = 15.8–164.8 g) and was positively correlated ($r = 0.424$, $P < 0.001$) with predator wet body mass (less food mass in the stomach). Relative meal size averaged 8.53% of wet body mass ($\sigma = 3.88\%$, range = 1.31–18.31%) and was negatively correlated ($r = -0.438$, $P < 0.001$) with wet body mass. Subtracting mean water content per food type (Table 1) resulted in a mean experimental meal of approximately 18.9 g ($\sigma = 8.9$ g, range = 3.8–40.2 g) dry mass.

TABLE 1. Mean size, water content, and lipid content of four experimental foods used in the gastric evacuation experiments (standard deviation in parentheses).

Food species	Mean mass (g)	Mean length (mm) ^a	% water	% lipid		N
				Dry mass	Wet mass	
Mackerel	62.9	188	73.7	30.7(2.2)	8.1(0.6)	7
Squid	53.2	160 ^b	76.8	19.1(1.0)	4.4(0.2)	4
Smelt	17.8	126	76.5	23.6(1.1)	5.5(0.3)	5
Nehu	0.4	40	76.2	18.0(1.2)	4.3(0.3)	4

^aFork length.

^bLength excludes tentacles.

Amounts of the four food types (proportion of initial wet mass) recovered from the yellowfin stomachs as a function of time after feeding are presented in Fig. 2. Prior to curve fitting, the data were truncated at postprandial times marked t_B (Fig. 2) to avoid a serious bias resulting from distributions constricted by the X-axis ($Y = 0$) (Olson and Mullen 1986). For data with variance comparable with that of Fig. 2, Olson and Mullen (1986) found, using Monte Carlo simulations, that data constriction causes the slope to be biased by about $18\% \pm 9\%$ (mean ± 1 SD). This can cause the illusion of a tail (reduced slope) at later stages of digestion, which may partly explain why curvilinear functions are commonly used with this type of

TABLE 2. Mixed meal combinations of mackerel (M), squid (Sq), smelt (Sm), and nehu (N) ingested by the experimental yellowfin. Individual food particles were numbered, weighed, and fed in order to individually color-code tagged yellowfin.

Combination No.	Food species	Number that ate meal combination
—	M	2
—	Sq	2
—	Sm	2
—	N	1
1	M, Sq	10
2	M, Sm	3
3	M, N	4
4	Sq, Sm	10
5	Sq, N	1
6	Sm, N	2
7	M, Sq, Sm	11
8	Sq, Sm, N	6
9	M, Sm, N	9
10	M, Sq, Sm, N	6

data. The only option to circumvent this problem was to omit some data.

Several different mathematical models have been utilized to describe the time course of stomach emptying in fishes, including a linear model (e.g. Swenson and Smith 1973; Jones 1974), an exponential model (e.g. Elliott and Persson 1978), and a square root model (e.g. Jobling 1981a). The four data sets (Fig. 2, $X_i < t_{1/2}$) were fitted to these three models. For all four food types, residual mean squares (untransformed) of the three fits were homogeneous (F_{\max} -test, $P > 0.05$, Sokal and Rohlf 1969). Therefore, residual analysis was used to evaluate the fits. For all four food species, residual analyses indicated that the linear model gave a superior fit, and these regressions (Fig. 2) were accepted to represent gastric evacuation rates in yellowfin.³ The data for dry mass recovered from the stomachs also appeared to be linear. For comparison purposes, Olson and Mullen (1986) fitted the complete unedited data sets (less empty stomachs) to the same three functions. Again, residual mean squares failed to indicate a superior fit to any of the functions (F_{\max} -test, $P > 0.05$, Sokal and Rohlf 1969). Residual analysis showed that the linear model gave the best fit for three of the four foods. The squid data were best described by the square root function. Although the exponential model is conceptually more satisfying than the linear model, consensus shows that linear gastric evacuation is plausible for piscivorous fishes that eat large prey (Simenstad and Cailliet 1986). Previous work substantiates this (Swenson and Smith 1973; Diana 1979; Adams et al. 1982).

It is noteworthy that the intercepts of the regression lines fall considerably below 100% (Fig. 2). Wet mass of the food in the stomachs a few minutes after feeding was considerably less than the wet mass of food prior to feeding. Magnuson (1969) found the same phenomenon when feeding smelt to skipjack tuna (*Katsuwonus pelamis*). In Magnuson's experiments, an average of 17.3% of the wet mass of smelt was lost from the

³For calculating daily ration, another equation representing the evacuation rate for mackerel in small meals was used (equation 7). See discussion of the effect of meal size and daily ration based on stomach analysis.

food within a few minutes after ingestion. In our experiments, 20.9% of the wet mass of smelt was quickly lost. Magnuson theorized that this loss was equal to the mass of water absorbed by the food during the process of thawing in fresh water. In the present experiments, all food items were air-thawed. Nevertheless, the most plausible explanation for this sudden decrease in food mass is water loss, as there were no visible signs of digestive action on the food particles removed from fish killed within a few minutes after eating. Tuna stomachs may rapidly express water from the food, resulting in a rapid initial loss of mass (Fig. 2). Subsequently, food appears to gradually rehydrate with digestive fluids to facilitate mechanical breakdown. Significant positive correlations between percent water in food removed from stomachs and time after feeding were obtained for squid ($P < 0.001$) and nehu ($0.05 > P > 0.02$); correlations were positive but not significant for mackerel and smelt ($0.20 > P > 0.10$).

Factors Affecting Evacuation Rates

The type of prey organism ingested affects significantly the rate at which food is passed from the stomachs of fishes (Windell 1978; Fänge and Grove 1979). In yellowfin, significant differences in evacuation rate occurred among the four food types (ANCOVA, $P < 0.0005$). Mackerel were evacuated at a significantly slower rate than squid, smelt, and nehu (t -tests for slopes, $P < 0.01$, Zar 1974), which were evacuated at about equal rates (ANCOVA, $P > 0.25$). However, intercepts of the regression lines for squid, smelt, and nehu were significantly different ($P < 0.0005$), and thus a common regression line was not adequate to describe these three data sets.

The evidence for an effect of meal size on gastric evacuation rate of fishes is equivocal. Large meals may take longer to be totally eliminated from the stomach than small meals (Barrington 1957; Steigenberger and Larkin 1974; Jones 1974). However, the amount of food digested during a given time (grams per hour) may increase in proportion to meal size (Hunt 1960; Kitchell and Windell 1968; see review by Windell 1978). In the latter case, the percentage of the meal evacuated per unit time remains constant, and thus the time required to evacuate a meal remains approximately the same regardless of food volume (Magnuson 1969; Tyler 1970; Elliott 1972; Bagge 1977).

The yellowfin gastric evacuation data for each food type were subdivided into three groups according to relative meal size (below 8.0%, between 8.1 and 11.5%, and above 11.6% of body mass). The results of analyses of covariance performed on the subgroups indicated that relative meal size had a significant effect on the evacuation rate of mackerel ($P < 0.0005$), but not on those of squid, smelt, and nehu. Small meals of mackerel were evacuated significantly faster than medium and large meals of mackerel (t -tests for slopes, $P < 0.002$). Therefore, the gastric evacuation rate for mackerel in yellowfin appears to be consistent with the hypothesis of more rapid digestion of small meals, while those for squid, smelt, and nehu seem to follow the alternative hypothesis of a constant percentage per unit time.

Mackerel are larger and appear to be considerably more digestion resistant than the other three food types. The musculature of mackerel is compact, while that of smelt and nehu tends to fall apart in the stomach, providing increased surface area for digestive activity to take place. Squid also have dense musculature; however, the body cavity is more accessible and

TABLE 3. Observed and adjusted stomach contents (% of body mass) and size characteristics of four age-classes of yellowfin tuna from which stomach samples were taken in the eastern Pacific Ocean. Adjustments for partial stomachs and gear disturbance are described in the text.

Age-class	Fork length (mm)	Body mass (g)			Observed stomach contents			Adjusted stomach contents		
		Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean
1	≤550	968	3 255	2 629	0	4.98	0.31	0	5.97	0.39
2	551–865	3 310	13 140	8 603	0	3.31	0.48	0	5.55	0.62
3	866–1220	13 187	37 914	22 655	0	4.64	0.38	0	5.50	0.52
4+	>1220	38 010	95 415	53 411	0	2.99	0.39	0	5.46	0.57

the body wall is thinner than in mackerel. These results suggest that two or more models of gastric evacuation may be applicable in a single predator, depending on prey type.

Body size is recognized as one of the principal factors which can influence gastric motility in fishes (Windell 1978; Fänge and Grove 1979). However, within the size range of yellowfin in this study, analysis of covariance showed that evacuation rates were not significantly influenced by yellowfin size ($P > 0.05$).

Whether foods that are evacuated at distinctly different rates retain their distinct evacuation rates when fed in mixed meals is unknown. Windell (1967) and Elliott (1972) reported that mixed meals of organisms that have similar evacuation rates in bluegill sunfish (*Lepomis macrochirus*) and brown trout (*Salmo trutta*) were evacuated at the same rate as the organisms separately. In the present study, no indication was found to suspect that measuring evacuation rates of food organisms in mixed meals influenced the rate determinations for each food type. For example, evacuation rates (slopes) for mackerel by yellowfin which ate meal combinations 1, 2, 3, 7, 9, and 10 (Table 2) were not significantly different (ANCOVA, $P > 0.05$).

To analyze the effect of cutting some food items into pieces, analysis of covariance was conducted on the data for each food type grouped by whole food specimens, anterior halves, posterior halves, and mixed anterior and posterior halves. Low F -ratios resulted ($P > 0.25$), indicating that the practice of cutting food items did not significantly affect the evacuation rates in these experiments.

Previous workers using prepared foods have demonstrated that low-energy foods are emptied from the stomach more rapidly than foods of high caloric content (Grove et al. 1978; Flowerdew and Grove 1979; Jobling 1981b). Elevated energy levels in natural organisms are commonly related to increased quantities of lipids in the tissues, and the presence of lipids, particularly when in excess of 15% of dry mass (Windell 1978), appears to have a retarding effect on gastric evacuation (Quigley and Meschan 1941; Windell 1967; Fänge and Grove 1979). This is generally attributed to a feedback mechanism, possibly triggered by a hormone similar to enterogastrone in mammals (Hunt and Knox 1968) produced in response to the presence of lipids or the digestive products of lipids in the duodenum (Windell 1967; Hunt 1975; Jobling 1980b).

In yellowfin, gastric evacuation rates (regression coefficients, Fig. 2) were correlated with total lipid content (Table 1) (lipid as percent wet mass: $r = 0.885$, $N = 20$, $P < 0.001$; lipid as percent dry mass: $r = 0.888$, $N = 20$, $P < 0.001$) and calories per gram of wet mass ($r = 0.983$, $N = 20$, $P < 0.001$) of the food. It appears, then, that the relationships between caloric content, total lipid content, and evacuation rate found

for prepared foods hold true for the natural food organisms tested here. Thus, the high lipid content of mackerel could explain its slow evacuation rate in yellowfin.

Rapid Evacuation Rates in Tunas

This study provides evidence that yellowfin evacuate food from the stomach faster than most other fishes studied, and at about the same rate as skipjack tuna. Magnuson (1969) found that only 1 of 12 species of carnivorous fishes he reviewed had a higher rate of emptying than skipjack. Yellowfin and skipjack emptied their stomachs of smelt in an average of 10.4 and 12 h (Magnuson 1969), respectively. Other piscivores of similar body length reviewed by Magnuson required four to five times longer than skipjack to evacuate a meal. Experiments by Steigenberger and Larkin (1974) on northern squawfish (*Ptychocheilus oregonensis*) were conducted on fish similar in size to our yellowfin, at the same water temperature, and using fish as experimental food. The squawfish required almost 2 h more to empty their stomachs of 3- to 6-cm juvenile rainbow trout (*Salmo gairdneri*) than it took the yellowfin to evacuate nehru, a comparably sized food.

Tunas are a highly specialized group of fishes that must swim continuously to maintain hydrostatic equilibrium and to ventilate their gills (Magnuson 1973; Roberts 1978). Energy expenditures for both "standard" metabolism (Brill 1979) and the metabolic work required for swimming (Gooding et al. 1981; Graham and Laurs 1982; Boggs 1984) are substantially higher than those typical of most other fishes (e.g. Brett 1972). Yet, yellowfin and skipjack are abundant in tropical seas where primary production is purported to be low (but see Kerr 1983) and the food distributions are known to be patchy (Blackburn 1968). It is advantageous for the tropical tunas to have the ability to process large amounts of food in a short time when food is available. The more rapidly food is digested and evacuated from the stomach, the more food a tuna can acquire from what may be very short-lived aggregations of prey. Any excess energy that is left after meeting metabolic demands is used for growth or stored as body lipids for reproduction and migration (Sharp and Dotson 1977).

Consumption Estimates

Stomach contents and gastric evacuation

Total adjustments of prey mass for partial stomachs and gear disturbance by age-class in the 1970–72 stomach samples amounted to increases of 26–46% of the mean observed stomach contents (Table 3). A relationship between complete empty stomach mass (Y , grams) and yellowfin fork length (X , millimetres) was used to adjust for partial stomachs:

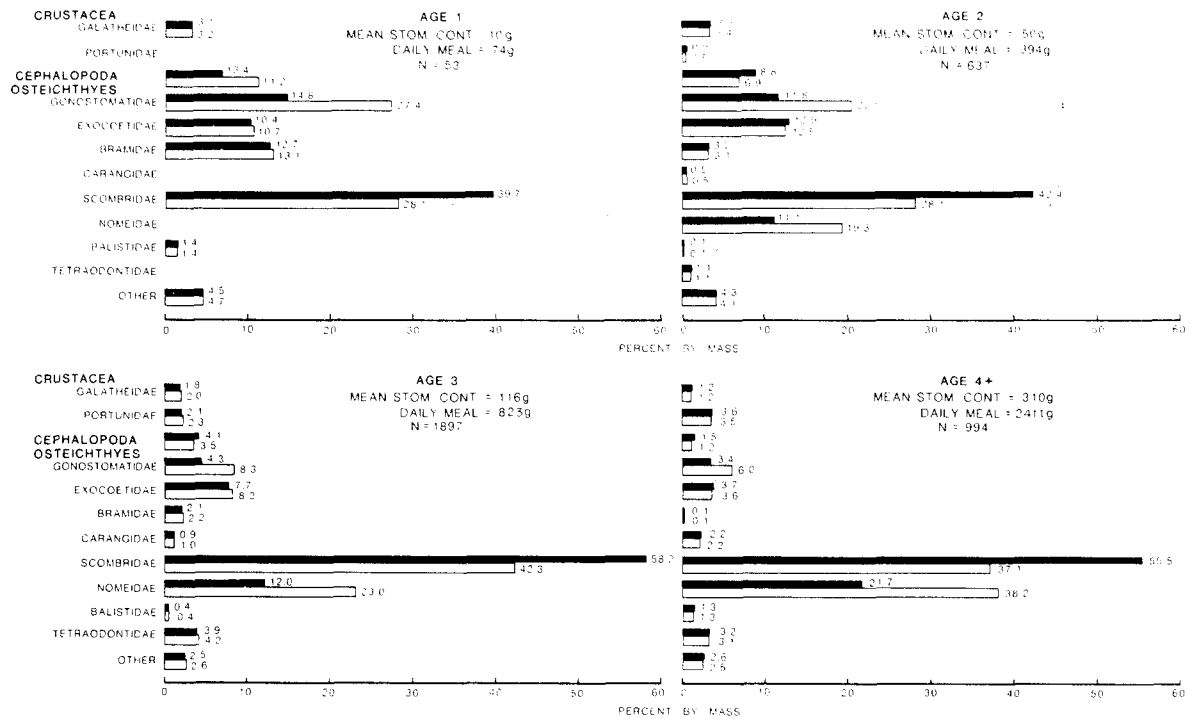


FIG. 3. Percent by mass of adjusted stomach contents (black bars) and of daily meal (white bars) for prey found in yellowfin stomachs sampled during 1970-72.

$$(6) \ln Y = -12.61 + 2.59 \ln X \quad (r^2 = 0.968).$$

The average duration of pursuit and gear enclosure by purse seiners in the early 1970's (2.25 h) and the gastric evacuation functions (Fig. 2) were used to calculate adjustments for reduced stomach contents due to fishing gear disturbance. The effect of this adjustment was to increase ration by about 25%.

Mean adjusted stomach contents pooled ranged between 0.39 and 0.62% and maximum adjusted amounts between 5.46 and 5.97% of wet body mass (Table 3). Yellowfin prey were matched with the most similar food organisms tested in the gastric evacuation experiments (Table 4). We assume that the evacuation functions for mackerel, squid, and nehu in small captive yellowfin approximate those of frigate tunas, cephalopods, and gonostomatids/nomeids, respectively, in wild yellowfin. The mean gastric evacuation rate and intercept for the four experimental food organisms (Table 4) were assumed to approximate those of all other prey in yellowfin stomachs. The error created by application of the mean rate to organisms with chitinous exoskeletons is probably not too important to the total ration estimate because crustaceans represented only 3.1-4.8% by mass of the stomach contents (Fig. 3). Since the stomach contents indicated that small meals are common, and meal size had an effect on the evacuation rate of mackerel, the regression equation (from ANCOVA above) for mackerel in small meals was used to calculate A_i for the Scombridae:

$$(7) Y = 0.856 - 0.0693X \quad (r^2 = 0.925).$$

Estimates of average hourly feeding rate, \hat{r} , for eastern Pacific yellowfin were calculated from equation 1 using values

TABLE 4. Yellowfin prey categories, corresponding gastric evacuation rates (b_1) and intercepts (b_0) from linear regressions fit to evacuation data for mackerel in small meals^a (M), squid (Sq), and nehu (N) (Fig. 2), mean b_1 and b_0 of M, Sq, N, and smelt (Sm) regressions, and A 's used in the food consumption model (equation 1). A 's were calculated as the area (integral) under the evacuation function: $A = |b_0^2/2b_1|$ (hours).

Prey	Experimental food species	Regression values		
		b_1	b_0	A
Scombridae	M	-0.0693 ^a	0.856 ^a	5.29
Gonostomatidae	N	-0.1182	0.727	2.24
Nomeidae	N	-0.1182	0.727	2.24
Cephalopoda	Sq	-0.0800	0.847	4.48
Others	Mean of M, Sq, Sm, N	-0.0859	0.805	3.77

^aFrom equation 7.

for \bar{W}_i and of A , from data in Fig. 3 and Table 4, respectively. Empty stomachs were included for calculating \bar{W}_i , since they, as well as full stomachs, reflect the natural feeding condition of the population. Yellowfin are known to feed in the daytime as well as at night (Watanabe 1958; Kume and Morita 1966). Lacking quantitative evidence for diel differences in feeding rate, we have assumed a daily feeding period of 24 h (steady state), recognizing that under some circumstances, nighttime feeding may decline or not occur, which would reduce ration estimates by as much as 50%. Daily meal, then, is assumed to be $24\hat{r}$. Daily rations are the daily meals expressed as a percent of mean mass of yellowfin sampled in each age-class (Table 3).

The initial reduction of wet mass immediately following ingestion in yellowfin is not accounted for in calculating \hat{r} from equation 1. This phenomenon probably occurs with prey in nature as well as in the laboratory. Thus, in calculating daily rations for yellowfin in the eastern Pacific, \hat{r} values were increased by the difference between 100% and the intercept for each food type (Table 4).

Mean daily rations were 2.8, 4.6, 3.6, and 4.5% of body mass per day for age-classes 1, 2, 3, and 4+, respectively. The expected decrease in daily ration with increased size (Kitchell et al. 1978) was not observed. Perhaps the ration of the smallest age-class was poorly represented through some selectivity in the catch. Although the estimated rations are similar to daily rations calculated for small fishes using field data (Seaburg and Moyle 1964; MacKinnon 1973a, 1973b; Swenson and Smith 1973; Lane 1975; Thorpe 1977; Diana 1979; Lane et al. 1979), they are larger than expected for fish of this size.

The tendency to overestimate ration by the assumption of a 24-h feeding period may be offset due to negatively biased stomach samples. Sampling difficulties and an unknown rate of regurgitation during capture would reduce the apparent food mass in stomach samples. Also, gastric motility presumably ceases at death, but digestion is a chemical process that may continue at a reduced rate until the stomach is frozen (Eggers 1977) and after thawing.

Average daily food consumption by eastern Pacific yellowfin appears to be a small fraction of the maximum possible rate, as evidenced in the laboratory and in the field. Assuming that fish with full stomachs could have continued feeding on the same prey at a rate sufficient to maintain that quantity in the stomachs for 24 h, maximum daily rations would average about 40% of body mass. This is higher, but not double, the maximum rations determined for 1.4-kg skipjack fed small food particles ad libitum for a 12-h daylight period (28–35% of body mass) (Kitchell et al. 1978).

Estimates from bioenergetics

The mass-specific rate of "standard" metabolism in skipjack tuna was found to decrease significantly with increasing mass in spinalectomized skipjack by Brill (1979). This decrease ($\beta = -0.44$, equation 2) was greater than in other fishes. By extrapolating from swimming metabolism to zero speed, Gooding et al. (1981) found that standard metabolism increased significantly with mass ($\beta = 0.19$). No significant effect of mass on standard metabolism (determined by extrapolation) was found by Boggs (1984). These contradictory results may be related to a small range in mass in the latter two studies. The mean value for standard metabolism (\dot{E}_0) determined by Boggs (1984) for yellowfin was $38.4 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ ($a = 38.4$, $\beta = 0$, equation 2).

Boggs (1984) found that mass-specific swimming metabolism (\dot{E}_s) of yellowfin had a length exponent (δ) of -1.28 , a speed exponent (γ) of 1.64, and a coefficient (f) of 13.7. The speed exponent (γ) was lower than the 2.5–2.8 predicted by hydrodynamic theory (Wu and Yates 1978) but similar to the exponent (1.9) resulting from reanalysis of data on salmon (Wu and Yates 1978; Boggs 1984). In general, the effect of speed on metabolic rate in fishes (Beamish 1978) is less than that predicted by hydrodynamic theory.

Daily swimming costs (Table 5) calculated using equation 3 accounted for one-third to one-half of the energy budget (Table 6) of the four yellowfin tracked by Carey and Olson (1982). The mean swimming cost (weighted by the duration of

each track) amounted to $100 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$. The most frequently recorded speeds of the four tracked yellowfin were less than $100 \text{ cm} \cdot \text{s}^{-1}$ (less than one body length per second for these fish, Table 5), but faster speeds were common, and speeds as high as $300\text{--}400 \text{ cm} \cdot \text{s}^{-1}$ were maintained for over half an hour. These short times spent at high speeds contributed substantially to the total estimated cost of swimming (Table 5). Daily swimming costs varied by a factor of 4 among the four tracked yellowfin. There was a trend for speeds and locomotory costs to be low in the two fish that were tracked for a full day or longer (Table 5).

Estimates of total energy consumption ranged from 175 to $441 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (Table 6). When total energy requirements were converted into a daily ration using a caloric equivalent of $4.60 \text{ kJ} \cdot \text{g}^{-1}$ for food (Kitchell et al. 1978), the mean ration for 87- to 98-cm yellowfin was equivalent to about 5.2% of wet body mass per day. This was about 1.1–1.4 times the estimates from stomach contents and gastric evacuation rates for similarly sized yellowfin (age-classes 2 and 3). This suggests that the energy requirements we estimated were reasonable and that extrapolation of the empirical model for swimming costs (equation 3) did not result in values that were unrealistically low.

Sharp and Francis (1976) estimated a mean energy requirement of $319 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for 12.6-kg yellowfin based on a hydrodynamic model for power output and assuming that yellowfin swim at $300 \text{ cm} \cdot \text{s}^{-1}$ for 1.2 h per day and at near minimum speeds (Magnuson 1973) the rest of the day. Sharp (1984) used the same hydrodynamic model to estimate an average energy requirement of $232 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ for two yellowfin tracked by Carey and Olson (1982). Both of these estimates (Sharp and Francis 1976; Sharp 1984) are within the range of total energy expended estimated using equation 4 (Table 6). Sharp and Francis's (1976) model includes the effects of transition between laminar and turbulent boundary layer conditions. If the velocity exponent does increase radically at Reynold's numbers above about 10^6 (Sharp and Francis 1976), then the values given in Tables 5 and 6 could be underestimates.

Energy can be supplied from stored reserves of fat as well as from food consumption. Thus, bioenergetics estimates of required energy may exceed actual consumption over a short term. Of course, fat reserves are ultimately derived from surplus energy intake, but the feeding conditions that permit such fat storage are probably not represented by the average stomach contents observed in the field. It is clear from our laboratory studies that yellowfin can eat much more than the overall average rates indicate, and it is clear from field studies that fat content in tunas is highly variable and can increase dramatically in certain areas (Dotson 1978; Vlieg et al. 1983). Tuna bioenergetics may be pictured as "speculative" (Stevens and Neill 1978) in the sense that tuna may exhaust their energy reserves in migrating hundreds of kilometres (Sharp and Dotson 1977) to reach good foraging habitats. This gamble must succeed frequently enough to permit rapid rates of growth among survivors, but the gamble must sometimes fail, resulting in energy depletion, disease, and vulnerability to predation. This would help explain the high natural mortality rates of tuna (Murphy and Sakagawa 1977). Depletion of fat reserves during reproduction would increase the potential for severe energy depletion and might explain reports that sex ratios are skewed strongly towards males in very large yellowfin (Cole 1980; Anonymous 1983). Further investigation of fat dynamics could suggest patterns in foraging behavior,

TABLE 5. Speeds and swimming costs of four yellowfin tuna tracked by Carey and Olson (1982). Observed speeds were grouped by 0.5 body lengths (bl) · s⁻¹ increments. The average speed and the total time spent in each increment were used to calculate swimming costs.

Fish ID No. (fork length)	Speed interval (bl · s ⁻¹)	Mean speed (cm · s ⁻¹)	Power output (J · g ⁻¹ · h ⁻¹)	Duration (h)	Swimming cost (J · g ⁻¹)	Daily swimming cost (J · g ⁻¹ · d ⁻¹)
2 (87 cm)	0-0.5	40	0.8	0.4	0.3	
	0.5-1.0	77	2.4	2.1	5.1	
	1.0-1.5	118	4.9	2.0	9.7	
	1.5-2.0	152	7.4	1.5	11.4	
	2.0-2.5	189	10.6	1.4	14.5	
	2.5-3.0	236	15.3	0.7	11.4	
	3.0-3.5			0	0	
	3.5-4.0	274	19.6	0.3	5.9	
	4.0-4.5	377	33.1	0.4	14.3	
	4.5-5.0	396	36.8	0.4	15.5	
			Total	9.3	88.2	228
3 (89 cm)	0-0.5	38	0.7	4.9	3.9	
	0.5-1.0	67	1.9	19.4	36.1	
	1.0-1.5	115	4.6	11.1	50.6	
	1.5-2.0	150	7.1	9.8	69.6	
	2.0-2.5	186	10.1	0.7	7.0	
	2.5-3.5			0	0	
	3.5-4.0	316	24.0	0.2	4.0	
			Total	46.1	170.9	89
4 (98 cm)	0-0.5	34	0.6	2.1	1.1	
	0.5-1.0	70	1.8	5.9	10.5	
	1.0-1.5	120	4.3	4.9	21.1	
	1.5-2.0			0	0	
	2.0-2.5	219	11.6	1.4	16.8	
	2.5-3.0	294	18.8	0.5	10.0	
	3.0-3.5	295	19.0	0.2	3.5	
	3.5-4.0	370	27.5	0.5	14.2	
			Total	15.5	77.3	120
5 (96 cm)	0-0.5	31	0.5	11.2	5.4	
	0.5-1.0	66	1.6	7.2	11.8	
	1.0-1.5	117	4.3	3.6	15.4	
	1.5-2.0	177	8.4	0.7	6.2	
	2.0-2.5	214	11.5	0.3	3.5	
	2.5-3.5			0	0	
	3.5-4.0	354	26.3	0.6	14.5	
			Total	23.6	56.7	58
			Grand total	94.5	393	

energy utilization, and movements of tunas.

An estimate from cesium concentrations

The proportions of food in the diet (stomach contents adjusted for differential rates of gastric evacuation) of age-class 1 and 2 yellowfin (white bars, Fig. 3) were used to represent those of a typical yellowfin in the size range used by Mearns et al. (1981) in their measurements of cesium concentrations. Thus, approximately 28% of the diet (by wet mass) was frigate tunas and other scombrids, 12% was squid and other invertebrates, 12% was flyingfish, and 48% was other fishes (34% gonostomatids and nomeids). Assigning these proportions (Materials and Methods) to the cesium concentrations of prey given by Mearns et al. (1981) resulted in an estimate of total dietary cesium concentration (Cs_p) of about 21.8 µg · wet kg food⁻¹. Yellowfin cesium concentration (Cs_y) was given as

60.5 µg · wet kg⁻¹. Thus, from equation 5 the estimated daily ration is 6.7% of body mass per day. This is 2.4 and 1.5 times higher than the estimates from gastric evacuation rates and stomach contents for yellowfin of similar size (age-classes 1 and 2, respectively). The greatest difference is due to the anomalous low ration estimate from stomach contents of age-class 1. The cesium budget estimate is 29% higher than the ration estimate from energy requirements (mean ration, Table 6). The cesium estimate was made for smaller fish than the bioenergetics model estimate, and a larger ration is expected in smaller yellowfin (Kitchell et al. 1978).

The data on cesium concentrations were limited, and the assumptions required to translate these into a ration are crude. This approach may be the least accurate of the three. However, the consistency of results from the cesium approach and the bioenergetics approach implies that stomach analysis under-

TABLE 6. Daily ration estimates (% body mass · d⁻¹) for four yellowfin tuna tracked by Carey and Olson (1982) based on energy expenditures for swimming, standard metabolism, growth, excretion, egestion, and food assimilation.

Fish ID No.	Fork length (cm)	Mass (kg)	Energy expended (J · g ⁻¹ · d ⁻¹)					Total consumed	Ration (% · d ⁻¹)
			Swimming cost (T _{swim})	Standard metabolism (E ₀)	Growth (E _G)	Excretion, egestion, and assimilation			
2	87	13.4	228	38	21	155	441	9.6	
3	89	14.3	89	38	20	79	226	4.9	
4	98	19.3	120	38	18	95	270	5.9	
5	96	18.1	58	38	18	62	175	3.8	
Mean			100 ^a	38	19		241 ^b	5.2 ^c	

^aWeighted mean from grand total in Table 5.

^bFrom equation 4 using weighted mean swimming costs of 100 J · g⁻¹ · d⁻¹.

^cBased on total of 241 J · g⁻¹ · d⁻¹.

estimates the true amount of food in stomachs of yellowfin at sea, especially in smaller fish. For comparable age-classes, the bioenergetics estimate (5.2%) averaged 1.3 times higher (ages 2 and 3) and the cesium estimate (6.7%) averaged 1.8 times higher (ages 1 and 2) than the direct estimates from stomach contents and gastric evacuation rates. Together, the indirect estimates averaged 1.5 times the results from the direct method.

Apex Predation and Trophic Relations

It is difficult to estimate biomass or production at intermediate trophic levels in pelagic marine ecosystems by direct sampling. As an alternative, bioenergetics models combined with estimates of apex predator biomass from fisheries statistics, tag and recapture studies, or surveys can be used to estimate the rate of prey production required to balance consumption by predators (Laevastu and Larkins 1981; Polovina 1984). This trophic approach can be extended down through the food web to estimate production and biomass at lower levels. The trophic model inputs are predation rates determined from studies like this one, and turnover rates determined from studies of age structure (Allen 1971) and natural mortality (Pauly 1980) or from other estimates of annual production to annual mean biomass (*P/B*) ratio (Banse and Mosher 1980; Adams et al. 1983; Longhurst 1983; Polovina 1984).

Total predation by yellowfin in the eastern tropical Pacific depends on the number of yellowfin in that region. Cohort analysis has been used to estimate the size of the exploited yellowfin population (Anonymous 1983) in the regulated area shown in Fig. 1. The average of estimates for 1970–72 is 4×10^7 individuals (3×10^8 kg). This population was subdivided among the four age-classes used to stratify the stomach contents data (Table 3) according to average size composition of the catch (Anonymous 1983, p. 87). Dividing the numbers and biomass of yellowfin in each age-class by the area of the regulated fishery (Sharp and Francis 1976) (Fig. 1) results in estimates of yellowfin density (Fig. 4).

Predation rates on each prey type can be estimated from their proportion in the diet. Proportions of prey in the stomach contents (black bars, Fig. 3) do not adequately represent relative biomass of prey types consumed due to differential rates of digestion and gastric evacuation (Hess and Rainwater 1939; Macdonald et al. 1982). Although Persson (1984) recommended otherwise, stomach contents were adjusted for dif-

ferential rates of gastric evacuation (white bars, Fig. 3). This adjustment substantially reduced the proportion of Scombridae in the diet compared with the proportion found in stomach samples. Nevertheless, in the offshore areas (Fig. 1), scombrids (almost entirely frigate tunas, *Auxis* spp.) were the most important prey by mass in all age-classes except 4+. Small epipelagic and mesopelagic fishes, Nomeidae (mostly *Cubiceps pauciradiatus*), and Gonostomatidae (mostly *Vinciguerria lucetia*), respectively, were either first, second, or third most important prey by mass in the diet of each age-class. Exocoetidae (flyingfish) and cephalopods (mostly squids) were also important by mass. The food habits of yellowfin inhabiting inshore and island areas differ from this pattern (King and Ikehara 1956; Alverson 1963).

Total annual predation by the yellowfin population was divided into predation on each major prey type using the adjusted proportions in the diet (Fig. 4). Assuming that a long-term equilibrium exists, the energy passed from prey trophic levels to the predators represents production rather than a decline in standing stock of prey. Under this assumption, predation rates of yellowfin tuna represent minimum rates of production, and in many cases, the only estimates of production for these pelagic animals. Actual predation rates may be about 1–1.5 times higher than these estimates, since the consumption estimates based on energy requirements and cesium concentrations were about 1.5 times the consumption estimates based on stomach contents. This range (1–1.5 times) is incorporated in the following estimates.

The annual production of frigate tunas in the regulated fishing area (Fig. 1) during 1970–72 must have amounted to at least 1.4–2.1 million metric tons (*t*). This amount was calculated by multiplying the predation rate on Scombridae (Fig. 4) by the area of the regulated fishing region (Fig. 1) and the range in the ration estimates (1–1.5 times). This production is more than the average annual world catch of all tunas during those years (1.2 million *t*, FAO 1974). It amounts to about 11–17 times the average biomass of yellowfin caught in this area annually during those years (Anonymous 1983). Frigate tunas are important prey of other apex predators that inhabit the region (Uchida 1981), so these figures underestimate total production of frigate tunas. Possible interaction between frigate tunas and young stages of other tunas could have important implications on the tuna stocks. If frigate tunas prey on larval or postlarval yellowfin, then increasing the commercial harvest of yellowfin, resulting in larger standing stocks

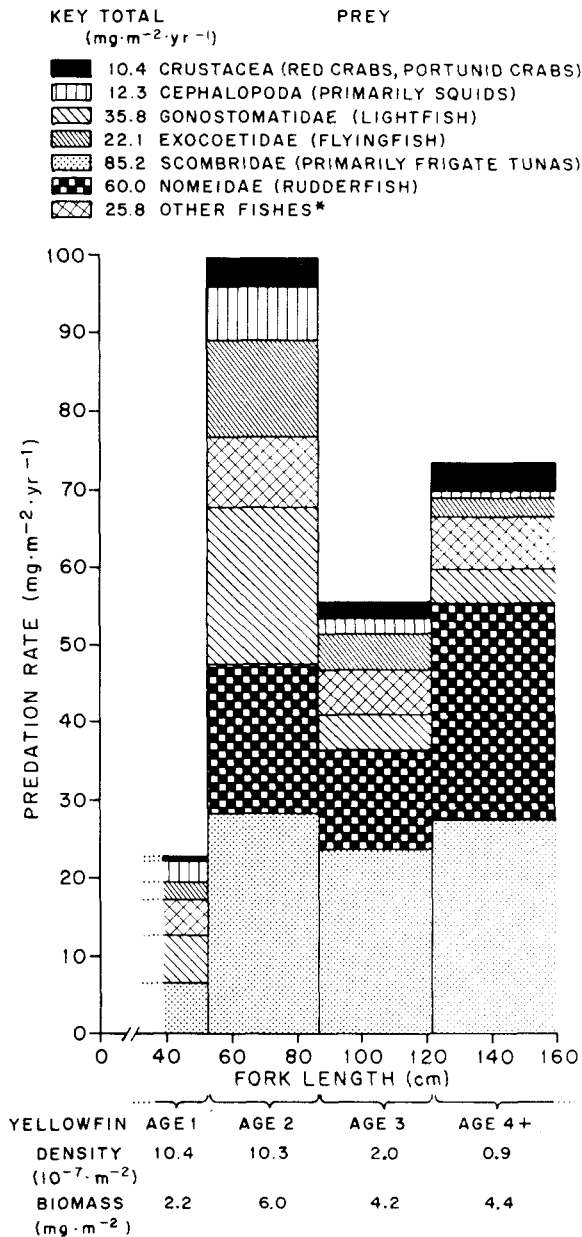


FIG. 4. Total prey biomass ($\text{mg} \cdot \text{m}^{-2}$) consumed per year by the yellowfin population in the eastern tropical Pacific Ocean in 1970–72 based on stomach contents and gastric evacuation rates. Yellowfin density and biomass are given at the bottom for each age-class. *The "other fishes" category was composed primarily of Bramidae, Carangidae, Balistidae, and Tetraodontidae.

of yellowfin prey, might have a deleterious effect on yellowfin recruitment. Previous to this study there were no estimates of standing stock or production for the frigate tunas. These species are largely unexploited in the eastern tropical Pacific.

Turnover rates for frigate tunas can be approximated using an equation relating the P/B ratio to body mass (Banse and Mosher 1980) and from the natural mortality rate ($P/B = M$,

Allen 1971). Average mass at maturity (400 g) and von Bertalanffy growth parameters ($L_{\infty} = 53 \text{ cm}$, $K = 0.4$) were estimated from the sparse data summarized by Uchida (1981). The body mass relationship implies an annual P/B ratio of 0.5, but Banse and Mosher's (1980) equation was derived from data on small, temperate fishes. Empirical relationships between P/B ratios and body mass should be interpreted cautiously (McLaren and Corkett 1984). Longhurst (1983) discussed the reasons for larger P/B ratios for marine fishes in the tropics. Pauly's (1980) formula for natural mortality (M) as a function of L_{∞} , K , and mean environmental temperature (25°C) suggests a P/B ratio of 0.8 for frigate tunas. Fishing mortality (F) in the eastern tropical Pacific is negligible (Anonymous 1983). Based on our production estimate, this would indicate a standing stock of at least 1.7–2.6 million t of frigate tunas in the regulated fishing area (Fig. 1).

The turnover rate for the yellowfin tuna population can be approximated as the total mortality rate ($P/B = Z = M + F$). Fishing mortality averaged 0.44 during 1970–72, and natural mortality was estimated at 0.8 (Anonymous 1983). Thus, P/B was about $1.2 \cdot \text{yr}^{-1}$. In contrast, Banse and Mosher's (1980) equation gives an estimate of only 0.2 for an average mass at maturity of 30 kg (Cole 1980). Some estimates for tropical marine fishes range as high as 3.4–4.5 (Longhurst 1983). The P/B for skipjack tuna in the Pacific Ocean is about 5.3 at MSY (R. F. Francis, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, 2725 Montlake Blvd East, Seattle, WA 98112, pers. comm.).

High P/B ratios could result from an abundant food supply, a high trophic transfer efficiency, or both. Using our estimate of food consumption by yellowfin tuna, we can proceed to make a direct estimate of gross conversion efficiency and trophic transfer efficiency. The average food consumption for an individual yellowfin tuna estimated from bioenergetics was $241 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ whereas growth was estimated at only $19 \text{ J} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ (Table 6), indicating a gross conversion efficiency of only 8%. Annual yellowfin production was about 1.2 times the standing stock of yellowfin whereas annual consumption by yellowfin was estimated at 15–22 times the standing stock of yellowfin (Fig. 4), indicating a trophic transfer efficiency of only 8–5%. These efficiencies seem low compared with those in more productive ecosystems (Kozlovsky 1968; Adams et al. 1983; Longhurst 1983; Polovina 1984).

The availability of food is difficult to address without a more complete trophic analysis. Primary production and standing stocks of phytoplankton, zooplankton, crustacean micronekton, and fish–cephalopod micronekton in the eastern tropical Pacific were measured by the EASTROPAC oceanographic expedition (Owen and Zeitzschel 1970; Blackburn et al. 1970). These studies examined areal and seasonal variations over a year (1967–68) in a comprehensive survey of a magnitude that is unlikely to be repeated. They found that the average standing stock of fish–cephalopod micronekton in the western region (Fig. 1) was about $3 \text{ mL} \cdot \text{m}^{-2}$ or about $3 \text{ g} \cdot \text{m}^{-2}$ for a 200-m water column (Blackburn et al. 1970). This is only twice as much as would be consumed annually by the estimated standing stock of frigate tunas if they ate 4% of their body mass per day.

Only 2.8% or $0.08 \text{ g} \cdot \text{m}^{-2}$ of the fish–cephalopod standing stock measured by Blackburn et al. (1970) consisted of epipelagic fishes whereas 90% ($0.23\text{--}0.35 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) of predation by yellowfin in the offshore regions (Fig. 1) was on

epipelagic fishes, predominantly frigate tunas, nomeids, and exocoetids (Fig. 4). These estimates are not strictly comparable, since some of the prey consumed by yellowfin were larger than micronekton (1–10 cm), but they suggest some degree of scarcity and/or a high annual turnover rate for the epipelagic forage fishes.

Sharp and Francis (1976) estimated that daily consumption by the yellowfin population was small compared with the standing stocks measured by Blackburn et al. (1970). They considered the relative effective productivity at different size-related trophic levels as well as the underestimation of the standing stocks of the more mobile tuna forage species, and argued that yellowfin with fork length greater than 40 cm were not food limited. Of course, the forage available to yellowfin should be based on the productivity of their forage rather than standing stock, but Sharp and Francis were not confident that the available information from the EASTROPAC files was adequate regarding the standing stock figures beyond an absolute minimum estimation (G. D. Sharp, P.O. Box 12294, Gainesville, FL 32607, pers. comm.). One should consider that a proportion of the yellowfin forage comprises organisms larger than micronekton, and these prey would be less abundant and less productive than the micronekton. Also, the importance of foraging by other apex predators must be considered.

The population of four dolphin species (*Stenella* spp. and *Delphinus delphis*) is estimated at 7–8 million individuals (R. S. Holt, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.), and the food consumption of the spotted dolphin (*S. attenuata*) population (3.1–3.5 million individuals) is estimated to be roughly equivalent to that of the yellowfin population (E. F. Vetter, National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, pers. comm.). Thus, food consumption by all four dolphin species could amount to 2 times that of the yellowfin population. Dolphins consume many of the same types of prey as yellowfin (Perrin et al. 1973). We estimate prey consumption by yellowfin to represent less than 33% ($100\% \times (1/(1 + 2))$) of the apex predation in this community. The predation rates of other tuna species, billfishes (Istiophoridae and Xiphiidae), dolphinfish (Coryphaenidae), sharks, and seabirds require further investigation before concluding that the food supply is more than adequate.

Conclusions and Implications

The estimates of daily ration for yellowfin tuna derived from the bioenergetics model and tracking study were median among the three independent estimates, lending validity to the use of such models in trophic analyses. The differences between our direct and indirect estimates imply that ration estimates derived from gastric evacuation rates and stomach contents data were too low or that the bioenergetics and cesium budget estimates were too high. The possibility that the bioenergetics model overestimates tuna energy requirements deserves consideration. Metabolic rates of tunas are reported to be 2–3 times higher than in other active fishes swimming at similar speeds (Gooding et al. 1981; Stevens and Dizon 1982; Boggs 1984). Perhaps these findings are due to some bias in the measurement of tuna metabolic rates (due to capture stress, confinement, handling, poor nutrition, starvation, etc.). The independent estimate of energy requirements from stomach contents and gastric evacuation rates indicates that the bio-

energetics model could be positively biased by about 30%. This is not enough to account for the major difference between tunas and equally active, cold-bodied fishes. In contrast, the other independent estimate (from cesium concentrations) suggests that the bioenergetics model is not positively biased.

Ration estimates for dominant apex predators and estimates of trophic transfer efficiency are the raw materials required for "top-down" trophic models that can provide estimates of production and biomass for animals at lower trophic levels. Our independent estimates of ration varied above and below the bioenergetics estimate by less than 30%. Direct sampling of forage biomass at sea may be much less precise than estimates based on the "top-down" approach. Direct standing stock estimates such as those of Blackburn et al. (1970) are hampered by gear inadequacies, time limitations, and increasing costs of ship time. Increased understanding of patchy distributions (Fasham 1978; Wormuth and Roper 1983), gear avoidance, and gear selectivity (Kashkin and Parin 1983; Percy 1983) suggests that the estimates of Blackburn et al. (1970) may be least accurate for the highly mobile types of prey consumed by yellowfin. Direct sampling must be repetitive to provide more than point estimates whereas trophic models can be dynamic and descriptive of changes at lower levels as a function of the bioenergetics and food habits of the apex predators (Laevastu and Larkins 1981; Stewart et al. 1981). Major apex predators are much more effective than research vessels as samplers of production at intermediate trophic levels.

The "top-down" trophic approach in our study reveals a huge unexploited resource in the form of the frigate tunas in the eastern tropical Pacific. The relationship between frigate tuna production and yellowfin tuna production requires further examination. A more complete trophic analysis could indicate the presence or absence of a food surplus for yellowfin tuna. Such a model will require inputs for the other predators. If adequate estimates for the prey are also found, the analysis can be extended down to the level of primary production and compared with independent estimates, which was done by Adams et al. (1983), Longhurst (1983), and Polovina (1984). At present, there is no compelling evidence for or against food limitation of yellowfin tuna.

The low trophic transfer efficiency between ingestion and production by yellowfin in contrast with their high growth rate, mortality rate, and production to biomass ratio suggests a trophic structure that differs from that of more productive ecosystems. A high production to biomass ratio could be maintained without a high transfer efficiency as long as the ratio between the production of forage and the standing stock of predators is large. In this situation the predator population puts a higher proportion of energy into turnover and maintains a smaller standing stock. This may be characteristic of many tropical pelagic predators that grow rapidly in spite of high metabolic rates in an oligotrophic habitat.

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