

Abstract. – The basis for the curious association between yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* in the eastern tropical Pacific Ocean has never been explained. Consideration of the bioenergetics of the associated tuna and dolphins suggests that the association may be based on the combined effects of a shallow thermocline, overlapping size (length) ranges of associated yellowfin and young dolphins, congruent diets, hydrodynamic constraints on swimming speeds of dolphin schools, and social (care-giving) behavior of dolphins. Insights developed during construction and exercise of comparative bioenergetics models for the tuna and dolphin suggest that tunas are more likely to follow dolphins than dolphins to follow tunas, and that the strength of the association in a given area may be related to oceanographic conditions affecting prey distribution and abundance.

Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: A basis for the bond

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In the eastern tropical Pacific Ocean, yellowfin tuna *Thunnus albacares* and spotted dolphin *Stenella attenuata* form an association strong enough that the fish can be captured by capturing the associated dolphins (e.g., Orbach 1977). The dolphins, easier to locate than the tuna, form the sighting cue for locating tuna schools. Despite chases lasting on average about half an hour (and occasionally as long as 2–3 hours) the fish tend to remain with the dolphins throughout. Eventually the dolphins tire and can be encircled, along with the associated tunas, with a purse-seine net.

Although the subject of substantial conjecture (e.g., Perrin 1969, Orbach 1977, Au and Pitman 1986, Au 1991), no definitive explanation exists for the association, perhaps in part because conjectures to date have been qualitative rather than explicitly quantitative. Quantifying the advantages or disadvantages of the association in terms of the energetics of its component groups holds promise for helping understand the bond, because such quantification can more readily expose conceptual errors, lead to unexpected insights, and form the basis for testable hypotheses. Expressing relationships in terms of energy flow (e.g., cost of finding food, cost of reproduction, feeding requirements, etc.) has often proved a useful format for developing understanding of biological phenomena. Following this precedent, I present here bioenergetics models for both tunas and dolphins in a “typical”

association in the eastern tropical Pacific Ocean. I use these models to estimate feeding rates of tuna and dolphins, and discuss implications concerning the ecological advantage to tuna (or dolphins) when associated with dolphins (or tuna).

Estimates of forage requirements predict that tuna and dolphins should experience severe competition under some circumstances of prey distribution and abundance, but perhaps not under others. Observations of overlaps in sizes between associated tuna and dolphins and of morphological similarities between the animals have implications for the importance of swimming energetics to the association.

These estimated forage requirements and considerations about swimming energetics are discussed in terms of their implications for determining which component (tuna or dolphins) controls the association, how the competition might be mitigated, when the association might be more likely to occur, and how these factors might be used to locate large yellowfin tuna unassociated with dolphins. The last point is important in relation to current interest in eliminating the practice of “dolphin-fishing” in the eastern tropical Pacific Ocean. “Dolphin-fishing” involves location and capture of tuna schools by locating and capturing associated dolphin schools; as air-breathers, the dolphins are more easily sighted than the tuna due to the dolphin’s surface activity. Other explanations for the bond, and poten-

tial conflicting evidence, are discussed briefly as they relate to the energetics models and results presented here.

Methods: Model development and description

The tuna-dolphin association

The tuna-dolphin association occurs in the eastern tropical Pacific Ocean (ETP) in a triangular region roughly the size of the continental United States (~ 10 million km^2), extending along the western coast of the Americas from the tip of Baja California ($\sim 20^\circ\text{N}$) south to Peru ($\sim 20^\circ\text{S}$) and seaward to $\sim 140^\circ\text{W}$ (Fig. 1). Total productivity in this area tends to be low relative to all other oceans, but high relative to other tropical oceans. Ocean currents and winds generate a typical pelagic environment in which areas of high productivity are distributed in dynamic, nonrandom, complex patterns (Fiedler et al. 1990, Fiedler 1992).

The ETP is characterized by an exceptionally shallow surface mixed layer. In contrast to other areas of the equatorial Pacific where the thermocline is generally 150–200 m deep (Kessler 1990), the depth of the thermocline layer throughout much of the ETP extends only 50–100 m below the surface (Fig. 1). Water temperatures in this wind-mixed layer are quite warm ($25\text{--}30^\circ\text{C}$) and oxygen concentrations are high (Wyrski 1966 and 1967, Fiedler et al. 1990, Fiedler 1992). Below this layer, water temperatures fall relatively rapidly (from ~ 27 to $\sim 15^\circ\text{C}$) through the thermocline (usually 5–25 m vertical extent), stabilizing again below the thermocline (Fiedler et al. 1990). Oxygen concentrations also decrease relatively rapidly through the thermocline, increasing again in cold water at greater depths.

Strong dependence on warm water and on high concentrations of oxygen apparently force both tuna and dolphins into this unusually shallow mixed layer. Tuna must swim more or less constantly both to provide an adequate flow of sufficiently-oxygenated water over their gills and to locate adequate food supplies (e.g., Magnuson 1978, Olson and Boggs 1986). Yellowfin tuna would likely have difficulty maintaining an adequate energy balance swimming in the colder waters below the mixed layer, nor can they afford being caught for long in the oxygen minima characteristic of the thermocline.

Dolphins are constrained to reside near the ocean surface in order to breathe. Only temporary excursions below the mixed layer are tolerable, both because of this requirement for gaseous oxygen and because the blubber layer of the tropical dolphins involved in the tuna-dolphin association is too thin to maintain thermo-

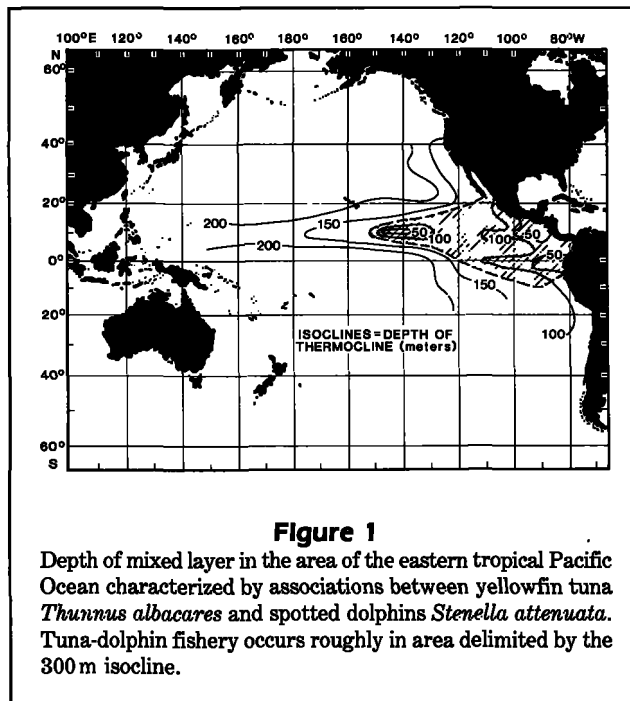


Figure 1

Depth of mixed layer in the area of the eastern tropical Pacific Ocean characterized by associations between yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata*. Tuna-dolphin fishery occurs roughly in area delimited by the 300 m isocline.

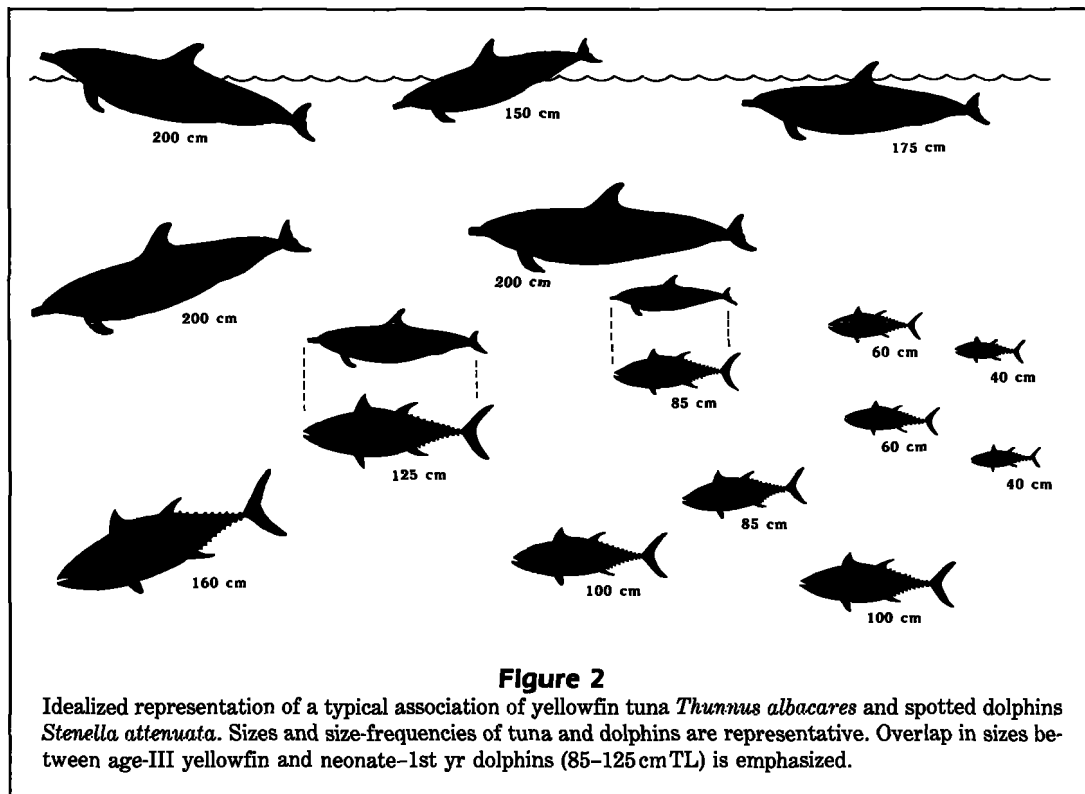
neutrality in waters much colder than that in the mixed layer (unpubl. estimates). This is not necessarily a disadvantage, as the major prey for associated tuna and dolphins (small fish and squid; Perrin et al. 1973) also tend to concentrate in this upper mixed layer, at least periodically throughout a 24-hour day.

Although any individual tuna-dolphin association is doubtless dynamic in the details of its spatial configurations and component individuals, the association in general can be envisioned as a loose aggregation of animals characterized by dolphins swimming relatively near the ocean surface, separated vertically from the tuna swimming below by only a few meters (Fig. 2).

Although several species of dolphins and two species of tuna have been found to associate in the ETP, one species of dolphin (spotted dolphin *Stenella attenuata*) and one species of tuna (yellowfin *Thunnus albacares*) comprise the majority ($>80\%$) of the associations (e.g., Orbach 1977, IATTC 1989). The remainder of this paper assumes the "tuna-dolphin association" includes only these two groups.

Energetics models

Both models followed the same format, using the standard bioenergetics approach of balancing food requirements against estimated energy costs for metabolism and energy savings as growth in biomass (University of Wisconsin Sea Grant 1989). The Wisconsin bioenergetics model derives estimates of consumption by



iteratively fitting an energetics equation for growth in body weight over time, to observed growth-rate curves derived from field samples of the organism in question. When the model growth curve simulates well the observed growth curve, the other fluxes estimated by the model are presumed to be reasonably accurate.

Specific rates (calories of flux · calories of animal⁻¹ · day⁻¹) of energy flux were estimated based on data derived from various sources for individual tunas and dolphins as a function of size. Rates of energy flux for schools of dolphins and tuna were estimated as the sum of weight-specific estimates for individuals in each group.

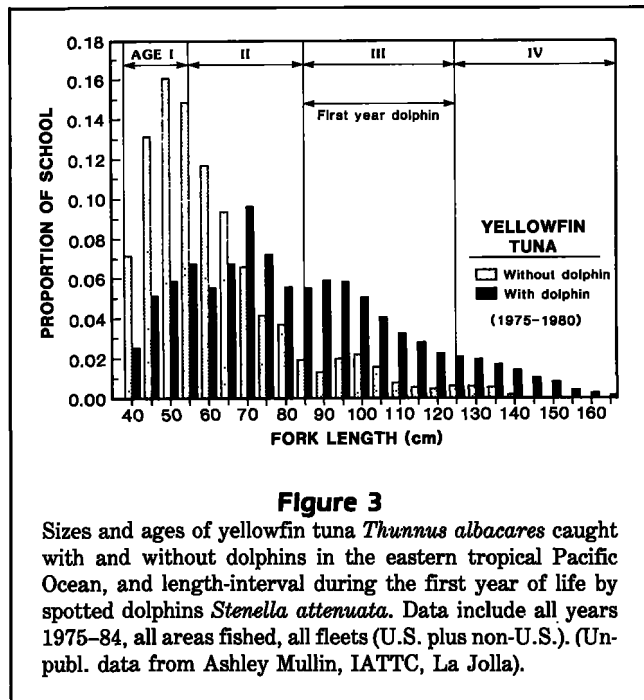
Costs of reproduction were ignored for both yellowfin and spotted dolphins; in the yellowfin model because the model focuses on the sizes of yellowfin associated with dolphins, which tend to be relatively immature fish. Spawning activity in yellowfin does not occur in fish much smaller than 80 cm, and increases slowly to the maximum activity in fish larger than ~150 cm (Joseph 1963). Energy costs of reproduction for spotted dolphins were omitted because the fraction of pregnant, lactating, or pregnant and lactating females in a typical school at any time is relatively small (~25%; see School composition).

Some of the energetics parameters reported here for spotted dolphins are based on morphological measure-

ments from 4 dolphin specimens from the ETP; 3 spotted dolphins measuring 81-189 cm total length (TL), plus 1 spinner dolphin *Stenella longirostris* 114 cm in length. The 81 cm individual was a very late-term fetus carried by the 189 cm animal. Although this sample is very small, all morphological measurements from these 4 animals fall well within the bounds of size-related regressions of morphological characteristics derived subsequently for a sample of 34 spotted dolphins measuring 74-215 cm TL (tip of rostrum to fluke notch) (unpubl. data).

School composition The yellowfin model addresses only those sizes of yellowfin found associated with dolphins (relatively large age-II and age-III fish, 55-125 cm TL; Fig. 3). Based on catch records from the fishery, an "average" association was assumed to include 500 yellowfin with an age composition of 65% age-II and 35% age-III fish per school (Ashley Mullin, IATTC, c/o Scripps Inst. Oceanogr., La Jolla; unpubl. data from commercial fishery).

Dolphin school composition was assumed to reflect the apparent age distribution of the spotted dolphin population, which in turn was assumed to appear as the length (age) distribution of dolphins collected during purse-seining operations in the ETP (Smith 1979, Barlow and Hohn 1984; A. Hohn, NMFS Southwest



Fish. Sci. Cent., La Jolla, unpubl. data). Proportions of nursing calves (ages 0-2 yr), adolescents (ages 3-14 yr), sexually adult males (ages 15 and up), and sexually adult females (ages 11 and up) in an average school were 0.05, 0.40, 0.25, and 0.30, respectively. Proportions of adult females not pregnant or lactating, lactating, pregnant, and pregnant and lactating animals were 0.05, 0.15, 0.08, and 0.02, respectively.

Weight-length conversions The tuna model used, as the calibration growth curve, the Gompertz fit derived by Wild (1986) for yellowfin tuna from the ETP. When necessary, body fork lengths in centimeters (cmFL) were converted to wet weights in grams (WW_g) using the length-weight relationship (Alex Wild, IATTC, La Jolla, unpubl. data for yellowfin tuna from the ETP)

$$FL = e^{((\ln(WW_g/1000) + 11.184)/3.08612)}$$

The calibration growth curve for expected size-at-age in spotted dolphins was derived from equations and figures in Hohn and Hammond (1985) and unpublished data (A. Hohn, Southwest Fish. Sci. Cent., La Jolla). Weight-length conversions assumed the relationship

$$WW_{kg} = 1.4 \cdot 10^{-5} \cdot TL^{2.95}$$

where WW_{kg} is wet weight in kilograms, and TL is total length (tip of rostrum to fluke notch) in centi-

meters, based on weight-length measurements from a sample of 50 spotted dolphins ranging in size from 82 to 210 cm TL.

Equations Each model included equations for specific rates of consumption (C_{sp}), respiration (R_{sp} ; including both swimming activity ACT_{sp} , and standard metabolism STD_{sp}), heat of digestion (specific dynamic action, SDA_{sp}), and waste losses (excretion plus egestion; WL_{sp}). Specific rate of growth is estimated simply as the difference between consumption and the sum of energy expenditures.

The form of the equation for each specific rate was the same for both models, with the exception of R_{sp} , which was estimated for yellowfin using Boggs' (1984) experimental results. R_{sp} was estimated for dolphins following Magnuson's (1978) procedure for estimating cost of swimming by carangiforms.

No effect of water temperature on consumption or respiration rates appears in either model. Ambient water temperature was assumed to be constant at 27°C, as most of the tuna-dolphin habitat occurs in waters of this temperature.

Consumption Specific rate of consumption (C_{sp} ; calories food consumed · calories of animal⁻¹ · day⁻¹) was estimated as

$$C_{sp} = \text{CONS}_{cal} / \text{CAL}_{an}$$

CAL_{an} is total caloric content of an individual yellowfin or spotted dolphin, estimated as a function of wet weight in grams,

$$\text{CAL}_{an} = \text{CD} \cdot \text{WW}_g$$

where CD is caloric density (cal/g wet wt) of yellowfin tuna¹ or spotted dolphins².

CONS_{cal} is total calories consumed per individual per day, estimated as

$$\text{CONS}_{cal} = \text{CONS}_{ind} \cdot \text{CD}_f$$

where CD_f is caloric density of food (cal/g wet wt) for

¹ 1440 cal/g wet wt (Boggs 1984).

² $\text{CD}_d = 1860$ cal/g wet wt; average caloric density of four dolphins measuring 81-189 cm TL. Caloric density of each animal was determined as the sum of calories contained in blubber, muscle, viscera, and bone divided by total animal wet weight in grams. Average caloric density of individual dolphins ranged from 1985 cal/g wet wt in the 81 cm animal, to 1760 cal/g wet wt in the large adult female (189 cm TL). Assuming constant energy density for spotted dolphins is acceptable, as spotted dolphins do not appear to exhibit any significant seasonal, and little age-related, changes in thickness of their blubber layer.

yellowfin tuna³ or spotted dolphins⁴, and $CONS_{ind}$ is wet weight in grams of food consumed, estimated as

$$CONS_{ind} = C_{max} * P_{val} * WW_g,$$

where C_{max} is maximum possible consumption (expressed as a fraction of wet weight) for the largest yellowfin or dolphin, estimated as

$$C_{max} = C_a * WW_g^{C_b},$$

where ${}^5C_a = 1.2$ and ${}^6C_b = -0.22$ for yellowfin, or ${}^7C_a = 3.98$ and ${}^8C_b = -0.29$ for spotted dolphins.

P_{val} is an iteratively fitted unitless value in the range 0–1 that, when “correct,” results in the simulated growth curve matching the observed growth curve (University of Wisconsin Sea Grant 1989), and WW_g is body wet weight in grams.

Respiration (yellowfin tuna) Specific rate of respiration (R_{sp} ; calories respired · calories of animal⁻¹ · day⁻¹) for yellowfin tuna was estimated as

$$R_{sp} = (STD_w + ACT_w) * (20650/CD),$$

with energy costs of standard (STD_w) and active (ACT_w) metabolism expressed in watts. The factor

³Energy density of yellowfin food was based on an assumed diet of 70% fish, 20% squid, and 10% invertebrates (Olson and Boggs 1986), with undigestible fractions of 0.124, 0.066, and 0.025, and caloric densities of 1440, 1260, and 1000 cal/g wet wt, respectively. Average ingested energy density (including the undigestible fraction) is 1380 cal/g wet wt.

⁴Energy density of spotted dolphin food changes with age (size). Spotted dolphins nurse throughout their first year (Perrin et al. 1976). They do not begin to ingest solid food until their second year, and they do not stop nursing entirely until their third year when they are ~145 cm in length. In this simulation, dolphins up to 1 yr of age were assumed to consume only milk (2855 cal/g wet wt) (Pilson and Walker 1970). Diet during the second year was assumed to be the same as that for yellowfin tunas, with an ingested energy density (CD_r) of 1380 cal/g wet wt.

⁵Based on the assumption that maximum specific feeding rate for very large yellowfin tunas (95000 g wet wt) would not exceed 10%/day, then solving for the intercept C_a (i.e., $C_a = 0.10/(95000^{-0.22})$) yields $C_a = 1.2$. In practice, the exact value chosen for C_{max} is flexible, as higher values simply reduce the fitted value of P_{val} , and vice versa.

⁶By analogy to walleye *Stizostedion vitreum* (Kitchell et al. 1977).

⁷Assuming maximum possible ration for adult spotted dolphins (~75 kg) would not exceed 15% of body weight/day (Sergeant 1969), and with $C_{max} = 0.15$, $WW_g = 85000$ g, and $C_b = -0.29$, then $C_a = 3.98$.

⁸As a compromise between the unresolved arguments of Kleiber (1961; $C_b = -0.25$) and Heusner (1982; $C_b = -0.33$) for scaling of metabolic rate with size in mammals. This compromise was chosen because consumption is not strictly a metabolic rate. While Huesner's argument for metabolic rate is supported by data for metabolic rate changes with size (see formulation for dolphin respiration), no such data exist for consumption rates.

20650 converts watts to cal/day. Dividing by caloric density of the animal (CD) produces the specific rate.

Weight-specific energy cost of standard metabolism for yellowfin was assumed constant for all sizes of yellowfin (Boggs 1984) as

$$STD_w = 0.464 \text{ watts/g wet weight.}$$

Energy cost of active metabolism (watts/g wet wt) was estimated using Boggs' (1984) equations and data for energy costs of activity in yellowfin,

$$ACT_w = F * VL^G * FL^H,$$

where VL is velocity in cm/sec and $F (= 1.59 \text{ E}^{-4})$, $G (= 1.64)$, and $H (= -1.28)$ are fitted parameters derived from Boggs' (1984) laboratory studies on yellowfin energetics.

Yellowfin were assumed to swim at length-specific optimum-sustained cruising speeds, with velocity scaling to fish length as

$$VL = VL_a * FL^{VL_b},$$

where ${}^9VL_a = 20.6$, and ${}^{10}VL_b = 0.4$.

Respiration (spotted dolphins) Specific rate of respiration (R_{sp} ; calories respired · calories of animal⁻¹ · day⁻¹) for spotted dolphins was estimated as

$$R_{sp} = (ACT_{sp} + STD_{sp} + HL_{rsp}),$$

where ACT_{sp} is specific rate of swimming activity, STD_{sp} is specific rate of standard (basal) metabolism, and HL_{rsp} is specific rate of residual heat loss.

Specific rates of swimming activity and standard metabolism are estimated as

$$ACT_{sp} = ACT_{cal}/CAL_{an}$$

and

$$STD_{sp} = STD_{cal}/CAL_{an}.$$

Caloric cost of **standard metabolism** was estimated as

$$STD_{cal} = S_a * WW_g^{S_b},$$

⁹Intercept estimate based on 100 cm FL yellowfin swimming on average 130 cm/sec *in situ* (Holland et al. 1990).

¹⁰Slope estimate based on theoretical and empirical studies by Weihs (1973, 1981).

where $^{11}S_a = 1380$, and $^{12}S_b = 0.67$.

Caloric cost of activity¹³ was estimated as

$$ACT_{cal} = PWR * 20650,$$

where 20650 converts watts to calories/day. Power required to swim (PWR) was estimated as

$$PWR = MP / (ME * PE),$$

where MP is mechanical power required to overcome drag, ME is mechanical efficiency,¹⁴ and PE is "propeller efficiency" (efficiency of propulsion by flukes)¹⁵. MP (in watts) was estimated as a function of total drag (D_t ; in dynes) and velocity (VL; in c/sec) as

$$MP = (D_t * L) / 10^7,$$

where the factor 10^7 converts the product $D_t * L$ to watts.

¹¹ S_a was assumed constant for all sizes of spotted dolphins. Given an observed rate of $0.45 \text{ mg O}_2 \cdot \text{g wet wt}^{-1} \cdot \text{hr}^{-1}$ for a spinner dolphin *Stenella longirostris* weighing 68000 WW_g (Hampton and Whittow 1976) and assuming 3.25 cal/mg O_2 (Elliot and Davidson 1975), then $2,386,800 (0.45 * 3.25 * 68000)$ calories are expended daily in standard metabolism, and $S_a = 1380 (2,386,800 / 68,000^{0.67})$. The observed resting rate of oxygen consumption is consistent with the range of resting rates ($0.3\text{--}0.6 \text{ mg O}_2 \cdot \text{g wet wt}^{-1}$) reported for bottlenose dolphins under various conditions (Hampton et al. 1971, Karandeeva et al. 1973, Hampton and Whittow 1976).

¹² Heusner (1982) presents convincing statistical arguments that intra-specific relationships between basal (standard) metabolism and body weight in adult mammals are better described by the 2/3 power than the 3/4 power proposed by Kleiber (1961). Heusner's argument is based on observed differences between adults of similar species (e.g., breeds of dog); but Huesner's curve is also more realistic because it predicts a relatively higher weight-specific rate in smaller (younger) animals of a given species. This is more consistent with Kleiber's (1961) observation that younger animals tend to have elevated weight-specific metabolic rates compared not only with adults of the same species, but with small adults of similar species. In young marine mammals, weight-specific standard metabolic rate is often at least twice the standard rate of adults (Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982). The parameterization above results in weight-specific estimates of S that are 2.3–1.3 times higher in dolphins measuring 80–140 cm TL than in adult dolphins (~190 cm TL). This differs by 0–11% (increasing with increasing size) from basal metabolic rates of juvenile through adult seals of similar weight (Ashwell-Erickson and Elsner 1981).

¹³ Dolphins were assumed to swim steadily far enough below the surface to eliminate the effects of surface drag (e.g., Hertel 1969). This formulation ignores the costs of surfacing to breathe, and the attendant increase in total distance swum to follow a sinusoidal rather than a straight path through the water. Preliminary estimates of these additional costs for individual dolphins of several sizes, for reasonably realistic depths of dive and distance between surfacings, ranged from 10 to 25% of steady swimming costs. As this cost is relatively low, the dolphin model was not reformulated to include these added costs of surfacing.

¹⁴ ME = 0.20, by analogy to observed muscle efficiencies of terrestrial mammals.

¹⁵ PE = 0.85 by analogy to tunas (Magnuson 1978).

Total drag was estimated as a function of drag due to body, fins, and movements by flukes as

$$D_t = (0.5 * N * VL^2 * S_w * C_t) / (1.0 - FID),$$

where N is density of seawater (1.025 g/cm^3), S_w is wetted surface area of the body, C_t is coefficient of total drag, and FID is (fin + induced) drag. FID¹⁶ is expressed here as the fractional increase in estimated total drag due to adding the effects of fins and moving flukes.

S_w is wetted surface area of the body, excluding flippers, dorsal fin, and flukes, estimated as¹⁷

$$S_w = 0.1636 * TL^{2.14}.$$

Surface areas of fins are excluded from this calculation because fin drag is incorporated into the equation for total drag as an increase of 21% over drag estimated from body dimensions alone.

C_t was estimated from the formula for drag of submerged streamlined bodies moving with constant velocity

$$C_t = C_f * [1 + (1.5 * (D_a / TL)^{3/2}) + (7 * (D_a / TL)^3)]$$

(Hoerner 1965, Webb 1975). C_f is the coefficient of friction drag, and D_a is the maximum body diameter (cm; derived from girth at axilla (G_a)) where

$$G_a = G_{aa} * WW_{kg}^{G_{ab}},$$

with $G_{aa} = 25$ and $G_{ab} = 0.28$, based on measurements of 50 spotted dolphins measuring 82–210 cm TL.

C_f was estimated from the equation for streamlined bodies moving submerged at constant velocity in turbulent flow as

$$C_f = 0.072 R_L^{-1/5},$$

where R_L is Reynolds number, estimated here as

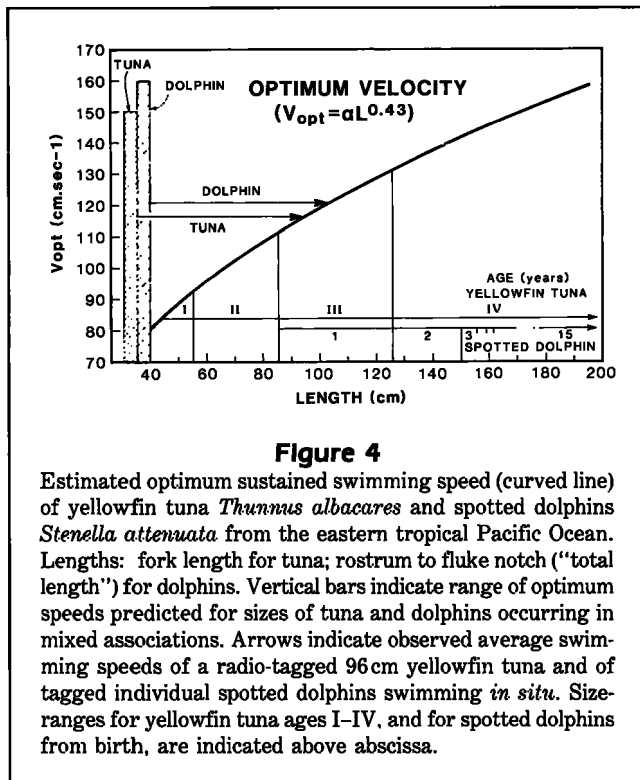
$$R_L = (TL * VL) / v,$$

where v is kinematic viscosity (= 0.01 Stokes) assuming turbulent flow at the boundary layer (Webb 1975), and VL is velocity (cm/sec), estimated as

$$VL = VL_a * TL^{VL_b},$$

¹⁶ FID was assumed = 0.21, based on the fraction of estimated total (body + fin + induced) drag accounted for by (fin + induced) drag in the 4-dolphin sample.

¹⁷ Based on measurements of wetted surface area in the 34-dolphin sample.



where $VL_a = 20.6$ and $VL_b = 0.43$, assuming swimming velocity scales with length in the same manner for both spotted dolphins and yellowfin tuna (Fig. 4). Using the same formula and parameters to predict velocity as a function of length in both the tuna and dolphin models maintains comparability between results from the two models. As geometrically similar swimmers, hydrodynamic constraints should be approximately the same for both tuna and dolphins.

Specific rate of residual heat loss (HL_{rsp} ; calories heat lost in excess of that generated by active and standard metabolism, and specific dynamic action · calories of animal⁻¹ · day⁻¹)¹⁸ was estimated as

$$HL_{rsp} = HL_{usp} - (ACT_{sp} * (1.0 - ME) + STD_{sp} + SDA_{sp}),$$

where $HL_{rsp} > 0$, otherwise $HL_{rsp} = 0$.

¹⁸Because spotted dolphins are warm-blooded relative to their environment and because their blubber layer is not a perfect insulator, they will constantly lose heat to surrounding water. If the sum of estimated heat production generated by muscle activity, standard metabolism, and specific heat of digestion equals or exceeds this unavoidable passive loss, the term has no effect. Otherwise, the additional heat loss was added to the animal's energy cost. In practice, the influence of the term was negligible, as differences between H_a and the sum of STD , ACT , and SDA were <10%.

The term $(1.0 - ME)$ in conjunction with ACT_{sp} expresses the fraction of total active metabolism that is dissipated as heat, rather than converted to mechanical energy. The term H_{rsp} was taken to be zero when the estimate of H_{rsp} yielded a negative result. In this case, all passive losses were more than offset by heat generated by metabolism.

Specific rate of unavoidable passive heat loss (HL_{usp} ; calories lost passively as heat · calories of animal⁻¹ · day⁻¹) was estimated following Brodie's (1975) procedure for passive losses in large whales,

$$HL_{usp} = \frac{((21.18/BD_a) * (37.0 - T_a) * S_m / 10000.0) * 24}{WW_g * (CD_d / 1000.0)},$$

where $^{19}BD_a$ is average blubber depth, CD_d is caloric density of spotted dolphins, 37.0 ($^{\circ}C$) is the assumed core temperature for spotted dolphins (Hampton and Whittow 1976), T_a is ambient temperature (assumed constant at $27^{\circ}C$), 21.18 is the conductivity factor for whale blubber (Brodie 1975), and $^{20}S_m$ is metabolic surface area, estimated as

$$S_m = 0.84 * S_w.$$

Unavoidable heat loss from fins and head is assumed negligible, as blood flow to these areas can be adjusted to minimize or maximize heat loss, as needed.

Specific dynamic action Specific rate of specific dynamic action (SDA_{sp} ; calories lost as heat of digestion · calories of animal⁻¹ · day⁻¹) was estimated as

$$SDA_{sp} = SDA * C_{sp},$$

where SDA (the fraction of consumption converted to heat energy during digestion) = 0.15 for both yellowfin tuna²¹ and spotted dolphins²².

Waste losses Specific rate of waste losses (WL_{sp} ; calories lost as feces or urine · calories of animal⁻¹ · day⁻¹) were estimated as the sum of fractional losses to egestion (F_a) and excretion (U_a)

¹⁹ $BD_a = 0.65$ cm, based on measurements of blubber depth at maximum girth for a sample of 72 spotted dolphins measuring 80–190 cm TL.

²⁰ S_m is the surface area of the body beneath the blubber layer. S_m averaged 84% of S_w in the 4-dolphin sample.

²¹Reflecting the relative high-protein low-carbohydrate diet ingested by yellowfin tunas (Olson and Boggs 1986).

²² SDA is primarily a function of the protein content of ingested food, and is ~15% for a variety of carnivores, including sea otters eating clams and squid (10–13%, Costa and Kooyman 1984), harp seals eating fish (17%, Gallivan and Ronald 1981), and various terrestrial mammals fed a mixed diet (Kleiber 1961).

$$WL_{sp} = (F_a + U_a) * C_{sp},$$

where $^{23}F_a = 0.20$ and $^{24}U_a = 0.07$ for yellowfin tuna; $F_a = 0.125$ and $U_a = 0.07$ for spotted dolphins²⁵.

Growth Specific rate of growth (calories available for growth · calories of animal⁻¹ · day⁻¹) was estimated as

$$G_{sp} = C_{sp} - (R_{sp} + SDA_{sp} + WL_{sp}).$$

Total calories available for growth (G_{cal}) is

$$G_{cal} = G_{sp} * CAL_{an}.$$

Total grams wet-weight biomass available for growth (G_{wwg}) is then

$$G_{wwg} = G_{cal} / CD.$$

The formulas and parameter values presented above produce reasonable model estimates of the various energy fluxes for both yellowfin tuna and spotted dolphins (Edwards 1992).

Results: Estimated consumption

Despite the apparent similarity between yellowfin tuna and spotted dolphins in food composition (prey type and size²⁶), estimated food requirements for tuna and dolphins differ considerably. Estimated food requirements for individual tuna and dolphins imply that each dolphin requires 5–10 times more food per day than each yellowfin tuna, depending on the sizes of the tuna and dolphin being compared (Fig. 5). In a “typical” association of 200 dolphins and 500 tuna, total dolphin requirements are still 2–5 times higher than total tuna requirements per time-period (Fig. 6), despite the greater number of tuna than dolphins.

²³Based on the relative assumed nondigestible portions of tuna diet items by analogy to similar items (Cummins and Wuycheck 1971).

²⁴Based on measurement of non-fecal excretion by carnivorous fish (Brett and Groves 1979).

²⁵Together these processes probably account for 15–20% of ingested food energy in spotted dolphins, as found for other small marine mammals eating fish (Shapunov 1973, Ronald et al. 1984, Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982, and references therein.)

²⁶Diet is undoubtedly an important factor in the tuna-dolphin association, as associated yellowfin tuna and spotted dolphins apparently have nearly identical feeding preferences (Perrin et al. 1973). Stomach contents of co-occurring tuna and spotted dolphins consisted primarily of small pelagic schooling fish (e.g., mackerel *Auris thazard*) and squid of similar types and sizes.

Discussion: Model implications

The strict “result” of exercising the models is estimation of food consumption by yellowfin tuna and spotted dolphins of various sizes. This information alone is not particularly helpful in furthering our understanding of the tuna-dolphin bond. However, the process of model

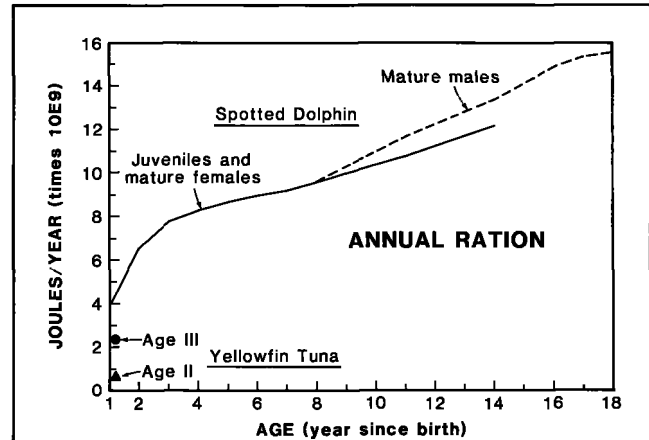


Figure 5

Estimated annual ration for individual spotted dolphins *Stenella attenuata* ages birth–18 yr, and yellowfin tuna *Thunnus albacares* ages II–III, occurring in mixed associations in the eastern tropical Pacific Ocean.

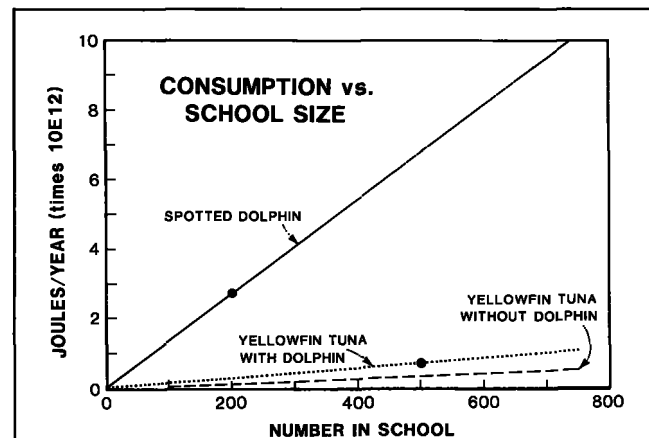


Figure 6

Estimated annual ration for schools of yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* occurring in mixed associations in the eastern tropical Pacific Ocean (ETP). Solid circles indicate number of individual dolphins and individual tuna in a typical mixed association. Ration estimates for schools were based on average observed size-frequency distributions of tuna and dolphin in the ETP.

development and comparisons of similar energy fluxes in the completed models generated several interesting observations with potentially significant implications.

Hydrodynamics and body length

Length frequencies of the tuna and dolphins in a typical association show a surprisingly strong overlap between age-III yellowfin and neonate-1st yr dolphins. Both animals begin their respective years at ~ 85 cm TL, and complete the year at ~ 125 cm TL (Fig. 4). This is significant for two reasons. First, this size range comprises the majority of the yellowfin tuna found associated with dolphins (Fig. 3)²⁷. Second, both animals have relatively stiff torpedo-shaped bodies with stiff fins and carangiform swimming behavior. Because theory predicts that optimum swimming speeds (the speed at which the least energy is consumed for a given distance covered) of geometrically-similar swimmers will be comparable (Weihs 1973, Webb 1975), the similar body forms and swimming behaviors of the tuna and the dolphins imply that optimum swimming speeds will also be similar for either animal of a given length.

Swimming speeds of sonic-tagged yellowfin tuna measured *in situ* show that individual undisturbed yellowfin, of the size most often found associated with dolphins, choose in their natural environment to swim on average at their predicted optimum cruising speed (e.g., yellowfin 90–100 cm FL swim at 100–130 cm/sec; Holland et al. 1990). Because yellowfin tuna tend to associate in schools of like-sized individuals, the expected speed of the tuna group is similar to the expected speed of the individuals involved.

In contrast, tracking studies (Perrin et al. 1979) of spotted dolphins in the ETP indicate that dolphin schools swim on average not the speed most efficient for the majority of the individuals in the school (i.e., ~ 160 – 170 cm/sec for large adults) but the speed most efficient for the neonate-1st yr animals (~ 120 cm/sec; Fig. 4).

These observations imply that yellowfin associating with dolphin schools may do so at little or no added hydrodynamic cost. The associated fish, unlike larger or smaller sizes of yellowfin, need swim neither faster nor slower than their apparently preferred optimum in order to maintain an association with dolphins.

The observation that associating with dolphins may cost tuna little does not explain *why* the tuna par-

ticipate. The similarity in feeding preferences and probable similarity in feeding behaviors provides one explanation and suggests that tuna are more likely to follow dolphins than the reverse.

Who follows whom

The higher forage requirements of dolphins both individually and as an association imply that dolphins following tuna, particularly single dolphin schools following single tuna schools, would fall far short of meeting their daily energy requirements. Dolphin schools might avoid this energy deficit by switching from one tuna school to another, but they would have to switch consistently from recently-successful to soon-to-be-successful schools of foraging tuna. This frequent switching could be difficult because it would likely involve periods of searching at speeds greater than sustainable by the young dolphins, in order to find new tuna schools (and new patches of forage) faster than the patches could be found by the current tuna school.

Measurements of muscle mass and estimates of power-time curves for various sizes of spotted dolphins imply that the relatively small muscle mass of neonate-1st yr dolphins probably cannot sustain speeds much faster than their predicted optimum for any extended length of time (unpubl. data). If searching for new schools of tuna requires sustained accelerated swimming, the young dolphins could have trouble keeping up with the rest of the school. Because it is unlikely that dolphins, as nursing mammals and highly social animals, would simply leave their young behind, switching frequently from one tuna school to another may not be a practical option.

The disparity in feeding requirements implies that, while dolphins would probably be disadvantaged by having to rely upon tuna to locate sufficient prey, the tuna could recognize an advantage by following dolphins. The fish would then be associating with another predator that is searching for the same prey, but which must encounter that prey either more often or in considerably larger patches than required by the tuna, per time period.

However, the greater need of the dolphins for food implies concomitantly that competition for resources, if those resources are limited, could be fierce. The schooling characteristics of the predators and prey, coupled with feeding behaviors and differing sizes of the predators, provide one possible explanation for the ability of the smaller yellowfin tuna under some circumstances to persist in this potentially competitive association despite the dolphin's greater size, and need for food.

²⁷ Figure 3 includes fish from all areas of the fishery, not just the offshore areas where most dolphin fishing occurred during the years these data were collected, causing dolphin-fish distribution to be skewed to left.

WHEN SHOULD TUNA ASSOCIATE WITH DOLPHIN?				
PREY ABUNDANCE:	LOW		HIGH	
	RARE LARGE	FREQUENT SMALL	RARE LARGE	FREQUENT SMALL
ABILITY TO LOCATE PREY:				
D > T	<u>YES</u>	NO	<u>YES</u>	NO
D = T	NO	NO	NO	NO
D < T	NO	NO	NO	NO

Figure 7
Decision table predicting conditions under which yellowfin tuna *Thunnus albacares* and spotted dolphins *Stenella attenuata* should (or should not) associate.

Avoiding competition for food

As is characteristic of pelagic ocean systems, both predators and prey in the ETP occur in clumped distributions. Individuals occur in schools or aggregations separated by (often vast) distances devoid of other individuals. The prey, like the yellowfin tuna, will tend to occur in schools of like-sized individuals with similar swimming speeds. Aggregations of tuna and dolphins will typically consist of dolphins of assorted sizes accompanied by tuna of approximately one size. The feeding strategy of the predators will involve searching for a clump of prey, simultaneous (or nearly so) arrival at the prey patch by both tuna and dolphins, and repeated incursions by individuals of both predator groups into the clump of prey wherein prey are seized and swallowed whole individually.

Associated yellowfin tuna may be able to mitigate this direct competition with dolphins for food on the basis of the difference in size between the fish and the feeding adult dolphins (~100 cm vs. 200 cm TL). Because the tuna are smaller, they have smaller maximum stomach capacity (~400 g wet wt for age-2 yellowfin, ~1100 g wet wt for age-3 yellowfin; Olson and Boggs 1986) compared with spotted dolphins (~2000 g wet wt in adults; Bernard and Hohn 1989). Even if the smaller, presumably more-agile tuna could seize individual prey only as fast as the dolphins and no faster, they would satiate more quickly than the dolphins.

As both groups would begin feeding at the same time, when the prey concentration was maximum, the tuna at any time would be relatively closer than the dolphins to satiation, given the observed (average) relative proportions of tunas and dolphins in a typical association.

The tuna would be filling their stomachs while the prey were still relatively dense. Depending on the size of the prey patch, dolphins might never succeed in satiating, even though the tuna had their fill. Even if the prey patch was sufficiently limited that neither group achieved satiation, the tuna would always be relatively more full at any given time. Thus, although the dolphins require more prey overall, the tuna could succeed competitively by satiating sooner (being relatively more successful) during any given prey encounter.

However, it may not always be to the tuna's advantage to associate with dolphins, even given this scenario. The benefit (or not) can be assessed by evaluating the relative advantages of associating or not, given the range of possibilities for prey spatial distribution and abundance.

When should the association occur?

The possibilities can be summarized in a simple decision table (Figure 7). At the extremes, prey abundance may be either low or high and any given abundance may be either homogeneously distributed (frequent) or clumped (rare). The possibilities for locating prey are that (1) dolphins are more adept than tuna, (2) both are equally adept, or (3) dolphins are less adept than tuna. The advantages for tuna to associate with dolphins can be assessed for each cell in the table.

Consideration of each cell in the table suggests that tuna may benefit from associating with dolphins only when (1) prey are distributed in rare patches and (2) dolphins are more adept than the tuna in finding these patches. This would be true regardless of prey concentration within the patches, because whenever tuna and dolphin associate they will compete for food. If tuna are more adept than dolphins at finding food, then there will be no foraging-related advantage for the tuna to associate with their competitors. The tuna would be able to find food more easily on their own than by following dolphins, and would not have to risk sharing these resources once located. If the tuna and dolphins are equally adept, there is still no advantage, for the same reason.

If the prey are distributed in relatively small but numerous patches, there is still no advantage for tuna to associate with dolphins, again because the spatial frequency of schools would produce a relatively high probability of tuna encountering the food on their own without risk of sharing with their competitor. In addition, when patches are small, the tuna would be especially disadvantaged by having to compete with dolphins because the presence of dolphins could prevent the tuna from satiating, despite the fact that the tuna would still be relatively more full than the dolphins when the patch had been exhausted.

But when the prey are distributed in rare patches and the dolphins are more adept than the tuna at locating these patches, then tuna could benefit from associating with dolphins because the fish could encounter food more often than if they were not associated. This will be true regardless of the density of the prey patch.

It is never the case that dolphins benefit energetically from depending entirely on tuna for finding prey, because dolphin forage requirements are so much higher than tuna requirements.

These conclusions lead to the hypothesis that tuna-dolphin associations should be more prevalent in areas where oceanic conditions encourage strong clumping of prey, and less prevalent when conditions encourage a more homogeneous distribution of prey. I am currently exploring, with a simulation model of tuna, the movements of dolphin and prey in response to environmental characteristics of the ETP (work in progress). Further studies correlating oceanic environmental characteristics with catches of various size-classes of tuna are planned but not yet underway. If the suggestions described above are borne out, it may be possible to identify areas of the ETP where large yellowfin tuna could be captured without having to rely on dolphin-associated fishing.

Caveats

This study assumes that average size of dolphin schools remains constant at about 200 animals. This is the average school size for spotted dolphins observed during dolphin survey research cruises in the ETP. In fact, neither school size nor school composition are constant. Observers on both research and commercial vessels report school sizes ranging from a few animals to many hundreds. Scott (1991) reports diel changes in sizes of schools sighted by tuna fishermen in the ETP.

However, these inconsistencies may not significantly affect the implications of the energetics estimates presented here. Average sizes of dolphin schools captured with tuna in the ETP are considerably larger (400–600 animals) than the average school size observed during research surveys because the fishermen preferentially search and capture large schools of dolphins, which tend to carry more tuna. Estimates concerning the relative importance of tuna and dolphins to energetics of the association are probably reasonably similar for both large and small associations, because in both cases the proportions of tuna and dolphins tend to be similar (i.e., as the number of dolphins increases, in general the number of associated tuna increases). The study of diel differences (Scott 1991) shows that school sizes of dolphins sighted in association with tuna vary from a morning low to a late-afternoon high, but

the change is relatively small, from ~450 to ~600 animals on average.

Other explanations for the bond

Other hypotheses have been proposed to explain the tuna-dolphin association. The two most-often suggested are the possibility that tuna perceive dolphin schools as FADs (fish aggregating devices) or as protection from sharks. Both of these factors may well contribute to the strength of the bond; neither precludes the energetics results discussed above.

The propensity for fish to collect around floating objects is well known, although the reasons are not yet understood. Presumably, floating objects provide a reference point for the aggregating tuna and in some way increase foraging success, perhaps by concentrating prey items or by tracking convergence areas where prey densities may be higher than elsewhere.

The FAD hypothesis has merit for the sizes of tuna actually found with dolphins in the ETP, for two reasons in particular. First, associating with dolphins may increase foraging success for the associated tuna because both tuna and dolphins are apparently seeking the same prey and dolphins may be more adept at finding it. Thus, tuna are associating with a FAD that does not simply attract appropriate prey passively, but actively searches and finds it. Second, tuna are required to swim constantly in order to ventilate their gills. It appears convenient that the average observed speed of dolphin schools is also the optimum speed of the sizes of tuna usually found associated with these schools. Rather than circling a stationary FAD, tuna associated with dolphin schools will cover a much larger area while moving at their most efficient cruising speed, and will cover that area in the presence of a sentient foraging FAD.

The shark protection hypothesis derives from a common perception that dolphins actively protect their young by driving sharks from their vicinity. If this is so, tuna associating with dolphins may be associating with the best of all possible FADs; a floating object that moves at the tuna's optimal speed, moves in search of the same prey the tuna would like to find, is probably at least as adept as the tuna at finding that preferred prey, and which provides protection against, rather than increased risk of, predation (FADs of course concentrate not only fish, but also their predators).

Both the FAD and shark hypotheses assume that tuna follow dolphins. Not all hypotheses assume that tuna are the followers. Au and Pitman (1986) and Au (1991) suggest, for example, that dolphins follow tuna in order to take advantage of tuna foraging in conjunction with bird flocks. This would be an advantage for dolphins during the actual feeding event. However, it

does not solve the problem that dolphins apparently must locate not only the same type of prey as large yellowfin tuna, but quite a bit more of it during any given time-period. Following tuna does not appear adequate to fulfill dolphin schools' energy requirements.

This fundamental difference in food energy requirements may be the single most important biological factor underlying the association. Oceanographic conditions (the shallow mixed layer) set the stage; energetics requirements (hydrodynamics and foraging patterns) appear to constrain the roles. Although the definitive answer has yet to be demonstrated quantitatively, the energetics-based hypotheses presented here are at least consistent with currently available data. The tuna-dolphin association may be a consequence of a combination of oceanography, hydrodynamics, foraging energetics, and life-history characteristics, i.e., a consequence of the ecology of the association's components.

Acknowledgments

This study could not have been completed without generous sharing of data, time, and constructive advice by helpful individuals from, but not limited to, the National Marine Fisheries Service, Southwest Fisheries Science Center, and the Inter-American Tropical Tuna Commission. This work was completed while the author was a National Research Council PostDoctoral Research Associate at the Southwest Fisheries Science Center, La Jolla, CA.

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