



REVIEW

Pelagic predator associations: tuna and dolphins in the eastern tropical Pacific Ocean

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ABSTRACT: The association of yellowfin tuna and pantropical spotted dolphins in the eastern tropical Pacific Ocean (ETP) has been exploited by tuna fishermen and has intrigued scientists for decades, yet we still have questions about what the benefits of the association are—whether the association is obligatory or facultative, why the tuna are most often found with spotted dolphins, and why the species associate most strongly in the ETP. We review the hypotheses that have been proposed to explain the bond and present results from 3 studies conducted to address these hypotheses: a simultaneous tracking study of spotted dolphins and yellowfin tuna, a trophic interactions study comparing their prey and daily foraging patterns, and a spatial study of oceanographic features correlated with the tuna–dolphin association. These studies demonstrate that the association is neither permanent nor obligatory and that the benefits of the association are not based on feeding advantages. These studies do support the hypothesis that one or both species reduce the risk of predation by forming large, mixed-species groups. The association is most prevalent where the habitat of the tuna is compressed to the warm, shallow, surface waters of the mixed layer by the oxygen minimum zone, a thick layer of oxygen-poor waters underlying the mixed layer. The association has been observed in other oceans with similar oceanographic conditions, but it is most prevalent and consistent in the ETP, where the oxygen minimum zone is the most hypoxic and extensive in the world.

KEY WORDS: Spotted dolphin · Yellowfin tuna · Tuna–dolphin bond · Spinner dolphin · ETP · Purse-seine fishery · Food habits · Tagging

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INTRODUCTION

In the eastern tropical Pacific (ETP), large mixed-species aggregations of dolphins, tunas, and seabirds are common. Central to these aggregations are pantropical spotted dolphins *Stenella attenuata* and yellowfin tuna *Thunnus albacares*. Tuna fishermen have exploited this association for many decades because the dolphins are easier to sight at a distance and make the tuna swimming beneath them easier to follow and catch. In the years following World War II, baitboat fishermen would sight dolphin herds, cued

often by the presence of seabirds overhead, and then chum the water with live baitfish to attract tuna to the surface and catch them with hook-and-line gear. By the mid 1960s, however, the baitboat fishery had largely been transformed into a purse-seine fishery, and the dolphins were no longer used just to find the tuna, but were actively chased and encircled to catch the tuna (Perrin 1968, Green et al. 1972). Despite the long history of fishing tunas associated with dolphins and the intensive management-oriented research on the 2 species, there are still questions about the biological basis for the association.

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This paper reviews what is known about the association and the hypotheses that have been proposed to explain the association, and presents results from 3 studies that could support or contradict these hypotheses. We know that the association between tuna and dolphins is much more prevalent in the ETP than in other oceans (Joseph & Greenough 1979, Scott et al. 1999). Early oceanographic studies recognized several distinctive features of the ETP: warm surface waters, a shallow thermocline (usually less than 60 m deep), and a thick oxygen minimum zone just below the thermocline (Wyrтки 1964, reviews by Fiedler & Lavín 2006, Fiedler & Talley 2006). These features have been thought to enhance fishing success by limiting the vertical distribution of the yellowfin tuna to the warm mixed layer near the surface (Green 1967) and promoting the tuna–dolphin association (Perrin et al. 1973, 1976, Au & Perryman 1985). Fishermen were quick to determine that tuna were found most reliably with spotted dolphins, although they were also sometimes caught with other dolphin species such as spinner dolphins *Stenella longirostris* and short-beaked common dolphins *Delphinus delphis*.

Yellowfin and skipjack *Katsuwonus pelamis* tunas are schooling species that are frequently found in large aggregations and we know that the tuna–dolphin association is one of 3 modes of tuna aggregation in the ETP. Aggregations of the smaller yellowfin, skipjack and bigeye tuna ('logfish') are also commonly found in association with natural floating objects such as logs or with manmade fish aggregating devices (FADs) seeded by the fishermen to catch tunas more efficiently. In addition, tuna aggregations are often found as free-swimming schools ('schoolfish') that are not associated with either dolphins or floating objects. Purse-seine fisheries around the world typically catch schoolfish and logfish, but in the ETP, catching tuna associated with dolphins is common, and it has been suggested that the tuna–dolphin association may be an extension of the tendency of small tuna to associate with floating objects (Hall et al. 1999). The association with dolphins occurs when the yellowfin tuna become large enough to keep pace with the more mobile dolphins (Edwards 1992).

A number of hypotheses have been suggested to explain why tuna and dolphins associate (see reviews by Hammond 1981, Stuntz 1981, Allen 1985, Fréon & Misund 1999, Fréon & Dagorn 2000). After many years of observation and research, however, 2 main hypotheses have emerged to explain the association: (1) one or both species may gain direct or indirect foraging benefits from the association, and (2) one or both species may reduce their risk of predation.

Foraging benefits

One potential benefit of the association is that it improves foraging success. One or both species may benefit because their large moving aggregation may flush prey (such as flyingfish), tuna may benefit from the dolphins' ability to echolocate prey at a distance, while dolphins may benefit from the tuna's superior sense of smell (Norris 1978, Norris & Dohl 1980a, Au 1991, Pryor & Kang-Schallenger 1991, Edwards 1992, Norris et al. 1994). The association occurs where the thermocline is shallow (Au & Pitman 1986, Edwards 1992, Norris et al. 1994, Hall et al. 1999), and an energetics model (Edwards 1992) predicts that the association, if based on feeding, would most likely occur where prey is distributed in rare, but rich, patches. The association may be involuntary for the dolphins because large tuna can swim faster than the dolphins (Pryor & Kang-Schallenger 1991, Edwards 1992).

Temporary feeding aggregations on a common prey by tunas and dolphins have been observed in other waters. Near the Azores, large yellowfin and bluefin *Thunnus thynnus* tunas (>100 kg) are thought to gain advantages when feeding with common dolphins *Delphinus* spp. and Atlantic spotted dolphins *Stenella frontalis* (Clua & Grosvalet 2001). The dolphins foraged by herding prey fishes into a tight ball near the surface, but the tunas tended to break up the ball, scattering both prey and dolphins. Groups of yellowfin tuna and spinner dolphins also have been observed foraging together off Brazil (Sazima et al. 2006). In neither of these areas, however, have the tunas and dolphins been observed in more than temporary feeding aggregations.

An alternative idea, that dolphins may gain feeding advantages by associating with the tuna was proposed by Au & Pitman (1986, 1988). Tunas are known to drive prey to the surface and many seabirds are strongly dependent on this source of prey (Ashmole & Ashmole 1967). The feeding advantages that seabirds gain from associating with the tuna, it is argued, could be gained by the dolphins as well.

Protection from predators

One benefit of travelling in large groups of fish or mammals is to reduce an individual's risk of predation (see reviews by Brock & Riffenburgh 1960, Hamilton 1971, Jarman 1974, Partridge 1982, Inman & Krebs 1987). Reduced risk may be due to the dilution effect (whereby the risk is lessened by spreading

it over a larger number of individuals), the confusion effect (whereby predators have increased difficulty in tracking a potential target within a large group of similarly colored and rapidly moving individuals), the encounter effect (whereby a single predator would be less likely to encounter prey that is concentrated in a few large groups rather than dispersed in many smaller groups), and the vigilance effect (whereby predators can be detected more readily by integrating the senses of a large number of individuals). Large sharks and billfishes are commonly caught in association with tunas in the ETP (Au 1991, Hunsicker et al. 2012), and are known both to prey on tunas and dolphins and to compete with them for the same prey (Leatherwood et al. 1973, Scott & Cattanach 1998, Galván-Magaña 1999, Heithaus 2001, Acevedo-Gutiérrez 2002, Maldini 2003, Santos-Monteiro et al. 2006, Bocanegra-Castillo 2007, Felando & Medina 2011, Hunsicker et al. 2012). False killer whales *Pseudorca crassidens* and killer whales *Orcinus orca* are also known predators (Perrin & Hohn 1994, Pitman et al. 2003). Au et al. (1999) noted that yellowfin tuna would stop feeding to follow spotted dolphins that were attempting to avoid their research ship and suggested that 'fleeing with dolphins would be advantageous to tuna if, as a general tactic, it results in escaping predators most of the time'. Scott & Cattanach (1998) argued that, because spotted dolphins and yellowfin tuna have many of the same potential predators, dolphin herds in the ETP increase during the daytime to reduce the risk of predation, and schools of large yellowfin tuna increase as well due to their association with the dolphins.

Exploring the hypotheses

We conducted 3 studies in the ETP to provide information that could support or contradict these hypotheses. The first was a simultaneous tracking study that used pressure-sensitive sonic transmitters on tuna and radiotags and time-depth recorders (TDRs) on dolphins to record movements and diving patterns. The second was a trophic interactions study that examined the stomach contents of dolphins and tunas captured together in purse-seine nets. The third used information collected by observers aboard tuna purse seiners on the spatial extent of the tuna–dolphin association in relation to oceanographic features. The results from these and previous studies could answer pivotal questions about the tuna–dolphin association: whether the association is oblig-

atory for either species, which species initiates the association, what the benefits of the association are for one or both species, why the association primarily occurs between large yellowfin and spotted dolphins, and why the species associate so strongly in the ETP and not elsewhere.

SIMULTANEOUS TRACKING

Methods

The simultaneous tracking study was conducted during a 30 day research cruise in November to December 1993 aboard the NOAA RV 'McArthur' and the chartered purse seiner 'Convemar'. Details of the capture, tagging, and tracking of the dolphins are described by Scott & Chivers (2009). In summary, tuna–dolphin aggregations were encircled by the purse seiner. The dolphins were caught by swimmers inside the net, placed in a raft, outfitted with radio transmitters, and released back inside the net so that the entire aggregation could be released from the net together. Transmitters were mounted on plastic saddles that were attached to the dorsal fin with Delrin pins secured by corrodible magnesium nuts; TDRs were also incorporated into most of the dolphin transmitter packages. TDRs recorded the time and the depth of the package every 5 s, and the data were recovered when the dolphin was recaptured and the package removed.

The tuna were tagged with sonic transmitters attached to flat dart heads. Three types of transmitters were used: one type gave only horizontal movement information (Model V3: 71 kHz, range 0.5–0.75 nautical miles (n miles), VEMCO), while the other 2 also transmitted the ambient pressure to monitor the animals' swimming depth (Models V7P: 50 kHz, range 0.75–1.0 n miles, and V3P: 60 kHz, range 0.5–0.75 n miles, VEMCO). The transmitters had nominal longevities of 8 to 13 days. Swimmers used lances to implant the dart tips into the dorsal musculature of the yellowfin tuna as they were being released from the net. We attempted to tag 2 tuna per set, a primary focal animal with the longer range V7P tag, and a backup animal in case the primary animal could not be released. We attempted to release all the dolphins and tuna together, either by the normal backdown release procedure (Coe & Sousa 1972) or by releasing one end of the net ('dropping the ortza') from the boat, creating an opening for the animals to escape.

Two tracking boats (5 to 9 m long) were rigged with sonic- and radio-tracking gear to track both

dolphins and tuna. A receiver and hydrophone (Models VR-60 receiver and VH-65 hydrophone, VEMCO) were mounted on the tracking boats using a system described by Holland et al. (1985). When sonic tracking, the pulse repetition rate of the pressure-sensitive sonic transmitter was recorded and decoded, and the position of the tracking boat, and the time and depth of the tuna were recorded approximately every 5 s. Radiotracking receivers were also mounted on the RV 'McArthur' and the purse seiner. When radio-tracking from any of the vessels, the position, time, heading of the vessel, bearing to the dolphin, and signal strength were recorded every 15 min. The purse seiner's helicopter allowed us to observe the behavior of the dolphins and tuna and monitor changes in herd size and composition of the aggregation.

A SEACAT mini-CTD (Sea-Bird model SBE 19) or an expendable bathythermograph (XBT) was deployed to measure depth and temperature from the RV 'McArthur' approximately every 4 h to a depth of at least 200 m. A shipboard environmental data acquisition system (SEAS) collected and processed these data. Of particular interest was the correlation of the swimming depths of the dolphins and tuna with the depth of the thermocline.

Results

Five dolphins were tracked during the study from 1 to over 4 d during 1993 (Scott & Chivers 2009), and 3 focal tuna were tracked for 1, 8, and 31 h. Table 1 provides details of the capture and tracks made when both dolphins and tuna were tagged. These tracks allow us to compare the horizontal and vertical movements of the 2 species.

The longest simultaneous track involved Dolphin D8 and Tuna T1. These 2 animals were released from the net together, along with about 60 spotted dolphins and about 100 yellowfin tuna, at 11:20 h on 21 November 1993 (Fig. 1). The tuna and dolphin separated 2.5 h later and did not rejoin during the rest of the track but remained within 15 n miles of each other. The

tuna came within 400 m of several other dolphin herds the following day, including one herd accompanied by feeding seabirds, but it did not join these herds. The dolphin milled over the continental slope and 15 n miles offshore of the coast over the next 4 d. After excluding the first 2 h of data after release from the net, the dolphin's average travelling speed was 9.8 km h^{-1} (= 6.7 knots [kn] or 2.7 m s^{-1} ; Scott & Chivers 2009). The tuna travelled at an average speed of 7.4 km h^{-1} (= 4.6 kn or 2.1 m s^{-1}) along the continental slope to the northwest before milling in an area about 15 n miles away from the dolphin. Even though Dolphin D8 and Tuna T1 were separated for most of their tracks, their diving histories were recorded simultaneously (Fig. 2).

Dolphin D9 and Tuna T3, along with about 120 spotted dolphins and a few tuna, were released together at 09:46 h on 26 November 1993, but the tuna was tracked for only 1 h due to a malfunctioning tracking boat. Dolphin D11 and Tuna T5 were captured together; D11 was released at 12:45 h on

Table 1. *Stenella attenuata* and *Thunnus albacares*. Summary of sets and tagging and tracking operations during 1993. VHF: 148–150 MHz radio transmitter only; TDR: VHF transmitter plus a time-depth recorder; V7P: 50 kHz pressure-sensitive sonic transmitter; V3P: 60 kHz pressure-sensitive sonic transmitter, V3: 71 kHz sonic transmitter

Date	Position captured	Dolphins tagged	Tuna tagged	Comments
19 Nov	17°48'N, 103°30'W	D7 (TDR) 191 cm male		D7 tracked for 19 h
20 Nov	17°21'N, 103°54'W			D7 recaptured
21 Nov	18°34'N, 103°57'W	D8 (TDR) 198 cm female with ~1 yr calf	T1 (V7P) ~25 kg T2 (V3P) ~25 kg	D8 tracked for 49 h T1 tracked for 31 h T2 not tracked
23 Nov	18°37'N, 104°02'W			D8 recaptured
26 Nov	18°28'N, 104°14'W	D9 (TDR) 196 cm female	T3 (V7P) ~30 kg T4 (V3P) ~25 kg	D9 tracked for 102 h T3 tracked 1 h T4 not tracked
29 Nov	18°23'N, 104°04'W	D10 (TDR) 200 cm male		D10 tracked 32 h
30 Nov	18°21'N, 104°12'W	D11 (VHF) 175 cm male	T5 (V7P) ~10 kg T6 (V3) ~10 kg	D11 tracked 11 h T5 tracked 8 h T6 not tracked
30 Nov	18°17'N, 104°16'W			Recaptured D9

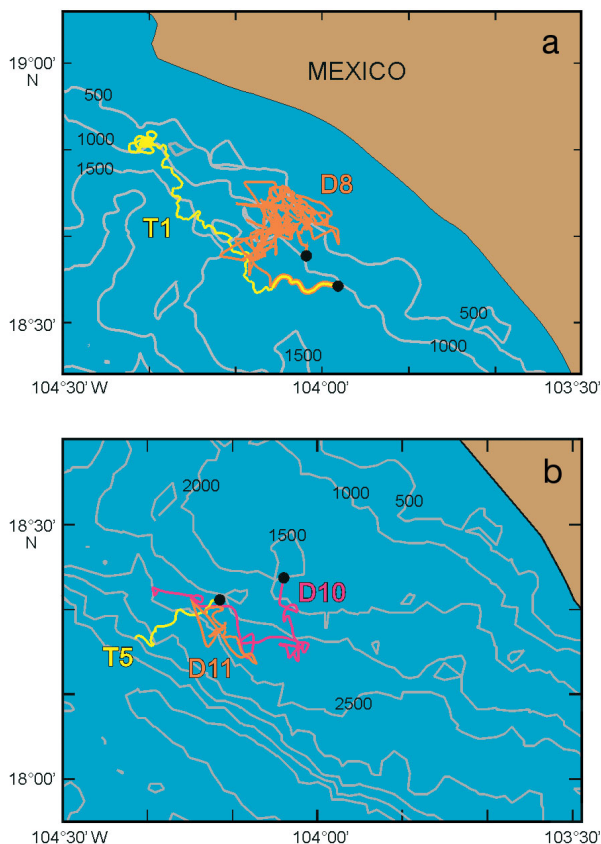


Fig. 1. *Stenella attenuata* and *Thunnus albacares*. (a) Movements of Dolphin D8 and Tuna T1 tracked simultaneously during 21 to 23 November 1993 off the Pacific coast of Mexico and (b) movements of Tuna T5 and Dolphins D10 and D11 tracked during 29 November to 1 December 1993. T5 and D11 were captured together off the Pacific coast of Mexico but released 15 min apart; D10 was tagged and released the previous day. Bottom contours shown in meters. Capture locations are indicated by black circles

30 November (Fig. 1), but T5 could not be backed out of the net with the dolphins and had to be released 15 min later. The dolphin was released with 29 spotted and 21 spinner dolphins, and the

tuna was released with about 600 tuna. The tuna did not rejoin the original dolphin herd, but was close to a group of dolphins from 19:00 to 22:00 h, as evidenced by the echolocation sounds heard through the tracking hydrophone and the visual observations of rapidly swimming and jumping dolphins. The tuna's signal was lost at about 22:00 h when the weather worsened and the tuna's speed increased. The average speed of Dolphin D11 was 9.3 km h^{-1} ($= 5.8 \text{ kn}$ or 2.6 m s^{-1} ; Scott & Chivers 2009) and the average speed of Tuna T5 was 5.1 km h^{-1} ($= 3.2 \text{ kn}$ or 1.4 m s^{-1}). The difference in travelling speeds may be due to the relatively small size of Tuna T5 ($\sim 10 \text{ kg}$) compared to the tuna normally associated with dolphins.

The dolphins and tuna showed different swimming patterns. The dolphin usually travelled during the day at a depth of 15 to 20 m, in the mixed layer above the thermocline. The characteristics of the daytime dives (i.e. no rapid 'wiggles' or fluctuations at depth) suggested the dolphins were not feeding (Bengtson & Stewart 1992, Testa et al. 1993, Scott & Chivers 2009). The dolphins dove deeper at night, often below the thermocline, apparently to feed on organisms associated with the deep scattering layer until dawn (Scott & Chivers 2009). The deepest dive was to 121 m.

The tuna showed a different pattern. During the day, the tuna swam in the mixed layer to about the depth of the thermocline at 35 to 40 m, below the typical swimming depths of the dolphins. After dusk, when the dolphins began to dive deeper, the tuna ascended to depths of about 25 m or less. Near dawn, the 2 species showed strikingly different changes in swimming depths. As the dolphins resumed their daytime swimming depth nearer the surface, the tuna descended toward the thermocline. The greatest swimming depth of the tuna was 110 m.

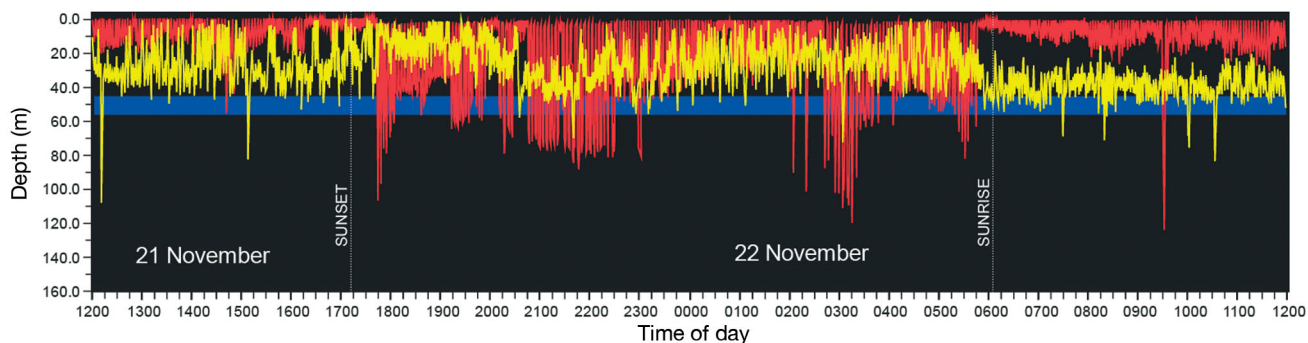


Fig. 2. *Stenella attenuata* and *Thunnus albacares*. Sample of vertical movements of Tuna T1 (yellow) and Dolphin D8 (orange) simultaneously tracked during 21 to 22 November 1993. The depth of the thermocline is represented as a blue band

TROPHIC INTERACTIONS

Methods

Stomachs from dolphins and yellowfin tuna were sampled at sea by observers of the Inter-American Tropical Tuna Commission (IATTC) during 1992 to 1994. The tuna and dolphins were caught by tuna purse-seiners of the international fleet. For dolphin sets in which 3 or more dolphins were sampled (to ensure a large enough sample size of prey items eaten by the dolphins in that herd), samples were taken from up to 25 dolphins and 25 yellowfin tuna. Each animal was measured, the sex determined, and the stomach and a core of dorsal muscle were collected and frozen for food habits and for stable isotope analysis (Román-Reyes 2005), respectively. On occasion, the tunas were marked immediately after capture, placed in the vessels' fish holds, and sampled after unloading.

In the laboratory, the stomach samples were thawed, and stomach fullness, as a percentage of stomach capacity, was estimated visually. The stomach contents were identified to the lowest taxon possible, weighed, and counted (Galván-Magaña 1999), and degree of digestion was determined (Olson & Galván-Magaña 2002). The data were stratified by the local time of day that the sets began: 06:00–08:59 h, 09:00–11:59 h, 12:00–14:59 h, and 15:00–18:00 h. Within each time stratum, the percent occurrence of prey items that were fresh or in intermediate digestion state ('Recent,' digestion states 1 and 2 defined by Olson & Galván-Magaña 2002) was calculated. Two stomach fullness strata were calculated for each time period. The 'Full' category comprised the percentage of predators whose stomachs were estimated to be 50 to 100% full of food, and the 'empty' category comprised the percentage of predators that had empty stomachs or contained only residual hard parts that could have been consumed on a previous day.

Prey composition in stomach contents was analyzed both by prey weight and prey occurrence because these diet indices emphasize different information about the diet of predators (Chipps & Garvey 2007). For each predator species (dolphins or tuna), the proportional composition by weight of each prey type in each individual was computed and averaged for each prey type over all individuals with food remains in the stomachs during the entire day, as:

$$MW_i = \frac{1}{P} \sum_{j=1}^P \left(\frac{W_{ij}}{\sum_{i=1}^Q W_{ij}} \right) \quad (1)$$

where MW_i is mean proportion by weight for prey item i , W_{ij} is the weight of prey item i in stomach j , P is the number of individuals with food in their stomachs, and Q is the number of prey types in the sample (Chipps & Garvey 2007). Digestion-resistant hard parts (squid mandibles and fish otoliths) were disregarded to ensure that only recent prey items were included. The occurrence-based prey composition (percentage of all individuals sampled whose stomachs contained a particular prey species) included residual hard parts to provide a longer-term view of the diet, although this may include periods of time when the tuna and dolphins were not associated. The prey were grouped into categories according to their taxonomy and whether the species remained in the epipelagic zone day and night or migrated vertically into the zone at night.

Results

Data were analyzed from the 73 sets that had a sample size of at least 3 yellowfin tuna stomachs and at least 3 spotted and/or spinner dolphin stomachs. The 73 sets provided samples from 218 spotted dolphins, 172 spinner dolphins, and 1523 yellowfin tuna that were spatially distributed across the geographical range of the fishery (Fig. 3). Sets were made during daylight, with the earliest set at 07:55 h and the latest set at 18:06 h. Prey remains, excluding residual hard parts, were found in the stomachs of 23% of the spotted dolphins, 17% of the spinner dolphins, and 64% of the yellowfin tuna. The principal taxa are listed in Table 2.

The daily trends in digestion state and stomach fullness illustrate the difference in the feeding times of the dolphins and the tuna (Fig. 4). Most of the spotted and spinner dolphins had full stomachs when caught during the early morning, but the percentages with full stomachs and recently eaten prey declined and percentages with empty stomachs increased throughout the day (Fig. 4). Full stomachs and signs of recent feeding were rare in the afternoon for both dolphin species. The yellowfin tuna, however, showed signs of recent feeding and full stomachs throughout the daytime, with the greatest percentage of empty stomachs occurring in tuna caught in early morning sets (06:00–08:59 h). Thus, the digestion and fullness data indicate that the dolphins feed mainly at night and in the early morning, whereas the tuna feed throughout the daylight hours but less at night.

Differences in the mass of prey in the stomachs confirmed that the dolphins fed primarily at night.

The prey weights per stomach sampled were (mean ± SE) 29 ± 6 g for spinner dolphins, 101 ± 12 g for spotted dolphins, and 254 ± 11 g for yellowfin tuna. The observed prey weights for the spotted dolphins were only 1 to 8% of what would be expected; an energetics study (Edwards 1992) estimated that the foraging requirement of spotted dolphins is 5 to 10 times that of yellowfin tuna. This large discrepancy between the observed prey weights for spotted dolphins and that expected based on the Edwards energetics model indicates that daytime sampling underestimates their prey consumption.

The weight-based measure of prey composition indicated that spotted dolphins consumed most of their daily rations during the night and early morning. Forty-three percent of the food in the stomachs of spotted dolphins during the entire daytime was from animals captured between 06:00 and 08:59 h. Prey composition was dominated by vertically migrating cephalopods and epipelagic flyingfishes, scombrids, nomeids, and crustaceans (Fig. 5). Spinner dolphins fed mainly on vertically migrating myctophid fishes (Fig. 5). Daytime feeding by spinner dolphins was rare; 81% of the food in spinner dolphins' stomachs during the entire daytime was from animals captured between 06:00 and 08:59 h. In contrast, yellowfin tuna preyed largely on epipelagic fishes; prey that vertically migrates to near-surface waters at night comprised only minor percentages of the diet. Scombrids, particularly frigate tunas *Auxis* spp., dominated the fresh food remains during the daytime (Fig. 5).

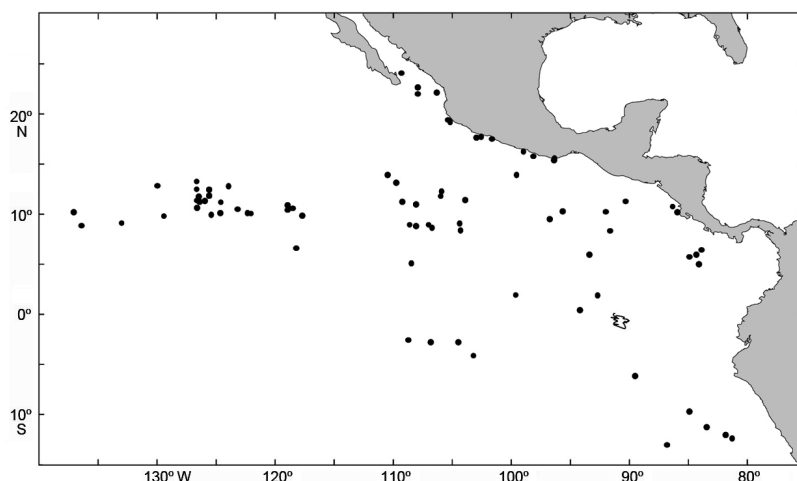


Fig. 3. *Stenella attenuata*, *S. longirostris*, and *Thunnus albacares*. Locations where stomach samples were collected by IATTC observers aboard purse seiners during 1992 to 1994

The occurrence-based measure of prey composition also indicated different feeding times for the dolphins and tuna. Stomachs from both dolphin species largely contained the remains of vertically migrating prey at all times of the day. The vast majority of these prey remains were digestion-resistant squid mandibles and fish otoliths, which accumulate in the stomachs. For spotted dolphins, the diurnal pattern of prey occurrence supported the weight-based data in that the high prey diversity, which included epipelagic taxa in the early morning, declined in the afternoon. For spinner dolphins, virtually all occurrences of cephalopods and fishes in the stomach contents were animals eaten earlier and already digested, with only hard parts remaining. For yellowfin tuna, epipelagic prey were important in occurrence throughout the day, although mesopelagic

Table 2. *Stenella attenuata*, *S. longirostris*, and *Thunnus albacares*. Categories of prey remains in the stomach contents of spotted dolphins (Sa), spinner dolphins (Sl), and yellowfin tuna (Ta), and the principal prey based on percent mass in each category

Category	Order (O) or Family (F)	Species	Common name	Predator
Vertical migrating				
Cephalopods	Ommastrephidae (F)	<i>Dosidicus gigas</i>	Jumbo or Humboldt squid	Ta, Sa
Fishes	Phosichthyidae (F)	<i>Vinciguerrria lucetia</i>	Lightfish	Ta, Sl
Epipelagic				
Cephalopods	Teuthoidea (O)	<i>Thysanoteuthis rhombus</i>	Diamondback squid	Ta
	Argonautidae (F)	<i>Argonauta</i> spp.	Argonauts	Ta
Exocoetids	Hemiramphidae (F)	<i>Oxyporhamphus micropterus</i>	Bigwing halfbeak	Ta, Sa
	Exocoetidae (F)	<i>Exocoetus volitans</i>	Tropical two-wing flyingfish	Sa, Ta
Scombrids	Scombridae (F)	<i>Auxis</i> spp.	Frigate and bullet tunas	Sa, Ta
Nomeids	Nomeidae (F)	<i>Cubiceps pauciradiatus</i>	Driftfish	Ta, Sl, Sa
Other epipelagic fishes	Ostraciidae (F)	<i>Lactoria diaphanum</i>	Boxfish	Ta
Crustaceans	Galatheididae (F)	<i>Pleuroncodes planipes</i>	Pelagic red crabs	Ta
	Portunidae (F)	<i>Euphylax robustus</i>	Swimming crabs	Ta

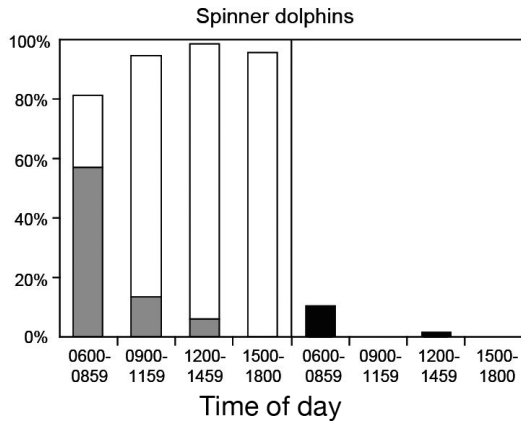
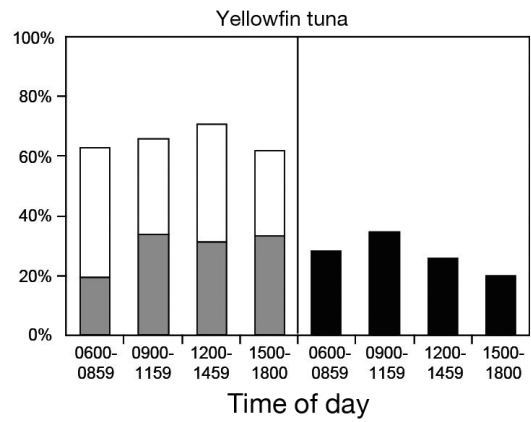
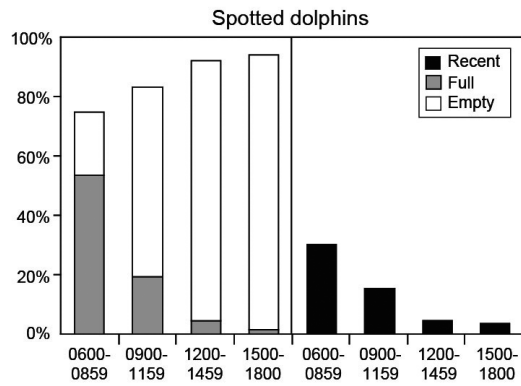


Fig. 4. *Stenella attenuata*, *S. longirostris*, and *Thunnus albacares*. Percentages of predators whose stomachs were estimated to be 50 to 100% full ('Full') and stomachs that had no fresh remains ('Empty'), and percent occurrence of all prey items, including residual hard parts, in digestion states 1 and 2 ('Recent'). The data were stratified by time of day that the sets were initiated: 06:00–08:59 h (10 sets), 09:00–11:59 h (14 sets), 12:00–14:59 h (28 sets), and 15:00–18:00 h (21 sets). The sum of the percentages of Full and Empty stomachs is less than 100% because those with fullness >0 to 49% are not displayed

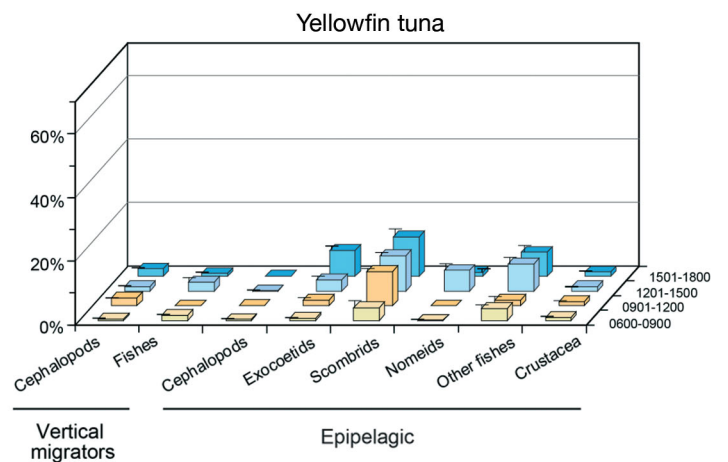
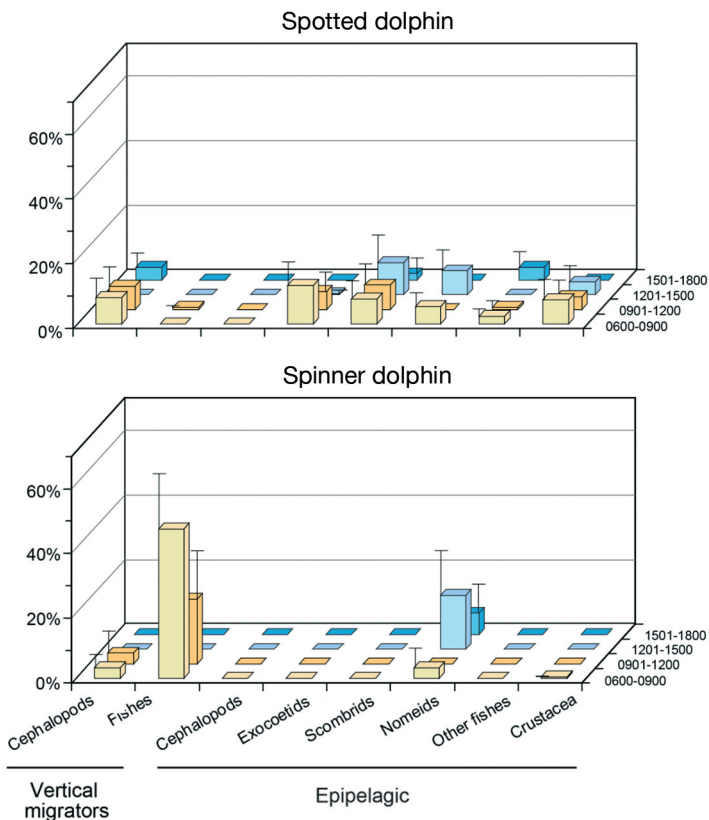


Fig. 5. *Stenella attenuata*, *S. longirostris*, and *Thunnus albacares*. Percentage composition by weight (see Eq. 1) of each prey type in each individual tuna or dolphin averaged for each prey type over all tuna or dolphins with food remains in the stomachs during the daytime (06:00–18:00 h). Error bars are 2 SE from the mean. The data for residual hard parts were omitted

cephalopods were also high in occurrence during the daytime after 09:00 h, which is likely due to residual mandible retention (81 to 94 % of the records were hard parts).

SPATIAL ASSOCIATIONS

Methods

IATTC or national observer programs have monitored virtually 100 % of the large tuna purse-seiners fishing in the ETP since 1992. These observers collect information on dolphin sightings, tuna catches, mortalities of dolphin and other bycatch species, and other data (Bayliff 2001). Dolphin sighting and dolphin set data from 1995 to 2005 were stratified by 5° quadrat for pure herds of spotted and spinner dolphins and mixed-species herds of these 2 species. Data were included only if the purse-seiner had made at least one dolphin set during the cruise. The data base included trips monitored by observers from the IATTC (all years) and the national programs of Venezuela (2000 to 2005), Ecuador (2001 to 2005), and Colombia (2005). Data from the Mexican national program that monitors half of the Mexican fleet were, however, not available for this study.

The percentage of sets-to-sightings was used as an index of the prevalence of the tuna-dolphin association. Sightings included those made and identified as pure and mixed herds of offshore spotted and spinner dolphins by either the observer, or the ship-board or helicopter crew members.

Because data requiring identification of dolphin species by crew members were used in these calculations, only the 2 species that the crews were most familiar with, spotted and spinner dolphin, were considered. There are also caveats about the use of the index. The index likely overestimates the prevalence of the association because some dolphin sightings by the crew may not have been reported to the observer when no tuna were present, and this bias may have increased somewhat since the 1980s (Lennert-Cody et al. 2001). Another potential cause of overestimation is that small herds of dolphins are less likely to be detected and less likely to carry tuna than larger herds. However, we found no significant inter-annual differences in the index for the 1995 to 2005 time period chosen. We included only those quadrats where sightings of either of the 2 dolphin species were recorded by the purse-seiner observers, indicating that the quadrat was within the distributional ranges of both the dolphins and fishery.

Using a linear regression, the tuna-dolphin association index for each 5° quadrat was modeled as a function of the 1995 to 2005 average mixed-layer depth for the corresponding quadrat. The mixed layer depth (the depth at which temperature equals the sea surface temperature minus 0.8°C) was calculated from the Simple Ocean Data Assimilation model (Carton et al. 2000) and served as a proxy for both the depth of the thermocline and the upper boundary of the oxygen minimum zone. The annual average mixed-layer depth was used for most quadrats, but for some quadrats, where the fishery only occurred in a few months of the year, 1 or 2 quarterly averages were used instead to match the months in which the dolphin sightings were recorded.

Results

The percentage of single-species sightings that led to sets (indicating tuna were likely present) was 42 % for spotted dolphins (39 593 sets in 94 202 sightings); the percentage ranged as high as 73 % but declined to less than 30 % where the mixed layer depth deepened to over 40 m. The average for spinner dolphins was only 20 % (3159 sets in 15 888 sightings); the percentage ranged as high as 46 % but declined to 15 % or less where the mixed layer depth deepened to over 30 m. Mixed herds of spotted and spinner dolphins had the highest percentage with 54 % (32 094 sets in 59 778 sightings). The higher percentage for mixed herds is likely due to these herds tending to be larger than single-species herds and larger herds tending to be more attractive to fishermen because they yield larger catches of yellowfin tuna (Scott & Cattanch 1998, Perkins & Edwards 1999).

The mixed layer is very shallow in the eastern tropical Pacific, but deepens to the west (Fig. 6). A linear regression of the association index on mixed layer depth showed significant trends for pure herds of spotted ($p < 0.01$) and spinner dolphins ($p < 0.01$), and for mixed spotted-spinner dolphin herds ($p = 0.01$). The association between tuna and dolphins increased as the mixed-layer depth shallowed.

For spotted dolphins, the association is most prevalent in waters where the depth of the mixed layer is about 45 m or less (Figs. 6 & 7), and the oxygen concentration below the mixed layer is extremely low. The spatial pattern of mixed spotted-spinner herds was similar to that of spotted dolphins. Pure spinner dolphin herds are not thought to normally carry tuna (unless spotted dolphins are also present). However, there are areas where the association with tuna is

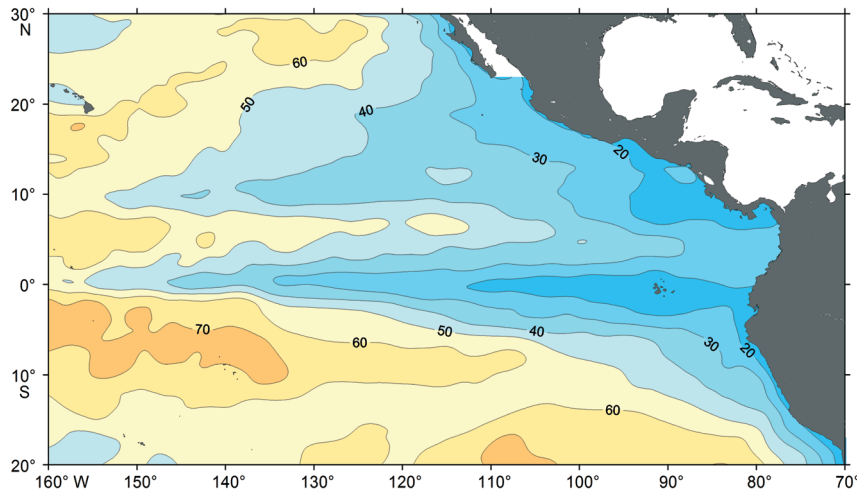


Fig. 6. Average annual mixed layer depths (in m) during 1995 to 2005 (adapted from Fiedler & Talley 2006). Note that the depth of the mixed layer, representing the top of the thermocline, is shallowest (blue) in the eastern tropical Pacific and deepens to the west (yellow)

relatively strong—areas where the depth of the mixed layer is about 25 m or less (Figs. 6 & 8), with a hypoxic oxygen minimum zone below.

Distribution plots of sets on tuna associated with spotted and spinner dolphins show that the spatial extent of the tuna–dolphin association changes seasonally. For the spotted dolphin, there are areas along the northern and southern margins of the distribution where the association is prevalent only in the summer (Fig. 7), while for the spinner dolphin, a southern cluster of sets is present only in the austral summer (Fig. 8). This expansion in the distribution of dolphin sets coincides with the summer shallowing of the mixed layer, particularly north of 20° N and south of 15° S (Fiedler 1992). This seasonal pattern is illustrated in a 5° quadrat (85 to 90° W, 10 to 15° S) where the seasonal differences in dolphin sets were particularly dramatic; sets occurred only when the average depth of the mixed layer was at a minimum (Fig. 9).

DISCUSSION

Tunas are known to associate often with floating objects, whale sharks, whales, and dolphins (see reviews in Scott et al. 1999). In the ETP, small tunas are commercially caught in association with floating objects or as free-swimming (unassociated) schools, but large yellowfin tuna are usually caught in association with dolphins. A ‘meeting place’ hypothesis has been proposed that links the associations of small tunas and floating objects and large yellowfin tuna with dolphins by arguing that tunas have a genetic predis-

position to associate with objects. This could serve as a mechanism to increase their own encounter rates and facilitate school formation (Fréon & Misund 1999, Fréon & Dagorn 2000). These authors have suggested that tuna–dolphin aggregations may represent a specific version of the ‘meeting point’ phenomenon whereby the dolphin school, while mobile, provides a cue that allows yellowfin tuna to aggregate into larger schools.

Two main hypotheses to explain why tuna and dolphins associate propose (1) benefits due to increased foraging efficiency, or (2) benefits from reduced risk of predation. To fully explain the association we must determine which species initiates the association and whether the association is obligatory or facultative for one or both species. The hypothesis must explain not only the benefits of the association, but why yellowfin tuna associate primarily with spotted dolphins, to a lesser extent with spinner dolphins and common dolphins, and rarely, if ever, with the several other species of dolphins occurring in the ETP; why this association involves primarily large yellowfin tuna and not small yellowfin or other tunas; and why dolphins and tuna associate in the ETP and only to a much a lesser degree, if at all, in other oceans.

Which species follows the other?

This is not as simple a question as it may appear because there are no obvious ‘leaders’ or ‘followers’ in the spatial sense—one species or one individual is not always in front of the aggregation and the species that initiates the association may not be obvious. In the constantly shifting aggregations of tuna and dolphins, individuals or species in front of the aggregation at one moment will find themselves on the flank or rear of the aggregation when it changes direction. Early observations by baitboat fishermen (Silva 1941) suggested the tuna followed the dolphins, but others (Godsil 1938) suggested the opposite. Most fishermen, however, have come to believe that the tuna follow the dolphins (National Research Council 1992, Felando & Medina 2011). They consistently observed that if the dolphins moved away from the baitboat, the tuna would follow, even while the fishermen were chumming the water with live baitfish. When the purse-seine fishery began, the fishermen ob-

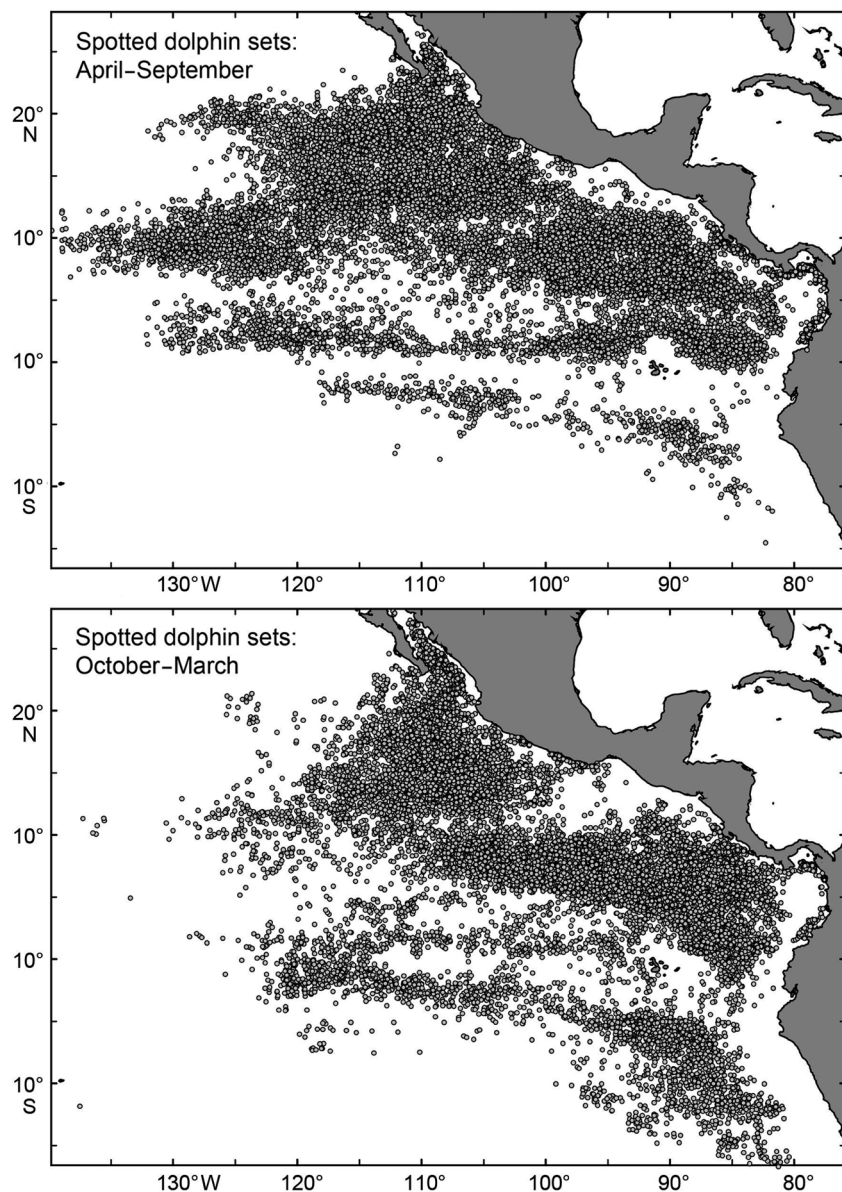


Fig. 7. *Stenella attenuata* and *Thunnus albacares*. Sets on tuna associated with pure herds of spotted dolphins from 1995 to 2005 during April to September and October to March

served that successfully herding the more-visible dolphins reliably yielded catches of tuna, whereas when even a small part of the dolphin herd escaped, the tuna often followed them out of the net and escaped as well (National Research Council 1992).

Researchers have also proposed different ideas about which species initiates the association. Au & Pitman (1986, 1988) suggested that the tunas' ability to drive prey to the surface attracts seabirds and could attract the behaviorally adaptable dolphins as well, while Norris et al. (1994) argued that it would be advantageous for the tuna to exploit the dolphins'

ability to echolocate and find prey patches at a distance. Scientists observing underwater behavior inside the purse-seine net suggested that the tuna follow dolphins (Norris et al. 1978, Pryor & Kang 1980). Mathematical population models have indicated that the species with the shorter lifespan, the tuna, must benefit if the association is to remain stable (Mullen 1984). Comparative bioenergetics models suggested that it is unlikely that dolphins initiate the association because the dolphins have greater foraging requirements (Edwards 1992).

Is the association obligatory or facultative?

Yellowfin tuna and spotted dolphins are both found throughout the tropics but only have a persistent, spatially extensive association in the ETP, so it is not likely that the association is obligatory for either species. The tracking results supported this: even though Tuna T1 and Dolphin D8 were caught and released together, they separated shortly afterwards and T1 did not join other dolphin herds that were sighted about 400 m away. A previous tracking study of yellowfin tuna in the ETP also showed that tagged tuna sometimes joined nearby herds of spotted dolphins and at other times did not (Carey & Olson 1982). A study of dolphin and tuna group sizes found that spotted and spinner dolphin herds and yellowfin tuna schools all increased in numbers during the day and fragmented at

night (Scott & Cattanach 1998). The nighttime fragmentation of both dolphin and tuna aggregations led the authors to suggest that the tuna–dolphin association weakened at night as well.

What are the benefits of the tuna–dolphin association?

In the light of the results of our 3 studies, we re-examine the 2 hypotheses put forward previously. It has often been suggested that there is not a

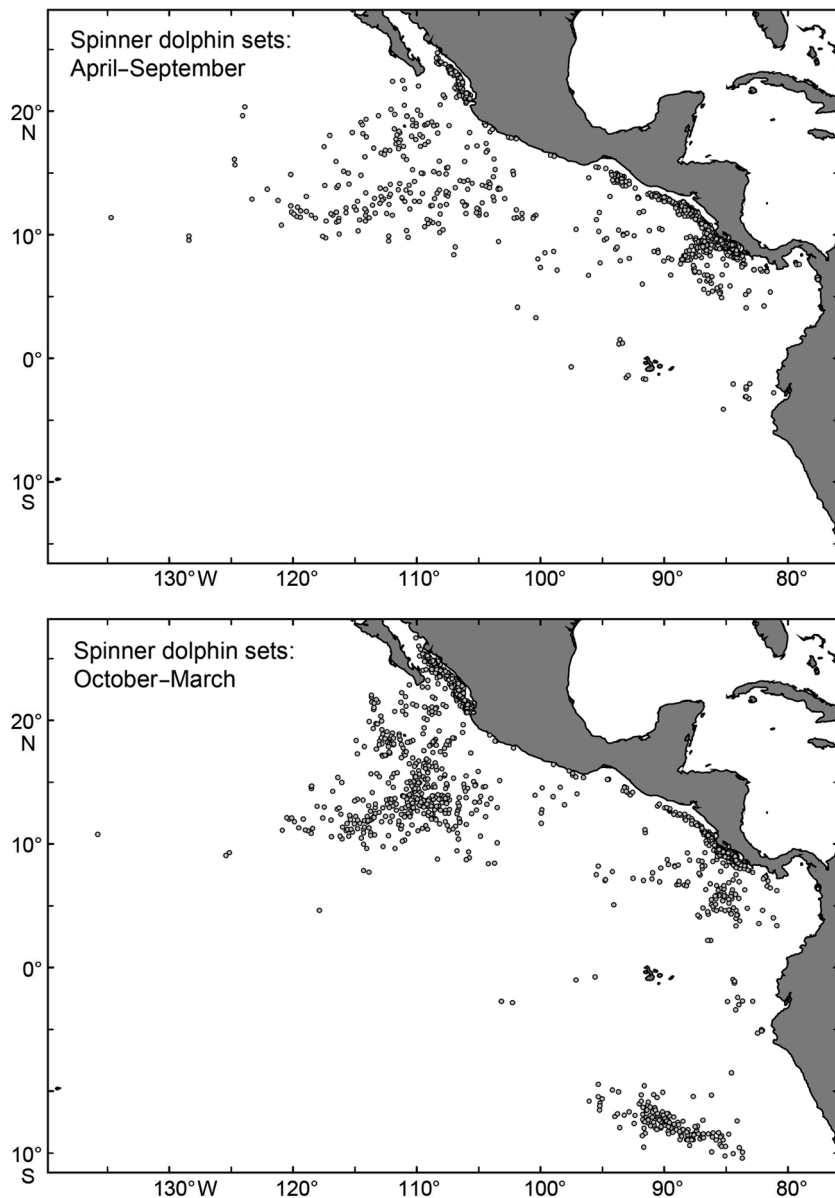


Fig. 8. *Stenella longirostris* and *Thunnus albacares*. Sets on tuna associated with pure herds of spinner dolphins from 1995 to 2005 during April to September and October to March

single cause for the tuna–dolphin association, but rather a combination of factors (Hammond 1981, Au & Pitman 1988, Scott & Cattanach 1998, Fréon & Dagorn 2000). As with conspecific schools, the size of a mixed-species group is likely a result of the dynamic balance between the risk of predation tending to increase group size for protection, and prey distribution tending to limit groups to a size that can be sustained by the available resources (Jarman 1974, Janson & Goldsmith 1995, Scott & Cattanach 1998).

Foraging benefits

The results of Perrin et al.'s (1973) food-habits study not only indicated that there was overlap in the prey species eaten by spotted dolphins and yellowfin tuna, but provided evidence of prey species specialization as well. Spotted dolphins and yellowfin tuna were thought to feed primarily on epipelagic prey, while spinner dolphins fed primarily on mesopelagic prey (see also Fitch & Brownell 1968, Morán-Angulo et al. 1995). The observation that tuna associate more readily with spotted dolphins than with spinner dolphins led other authors to suggest that the similarity in food habits is the basis of the tuna–dolphin association and that one or both of the species gains feeding benefits from the association (Norris 1978, Norris & Dohl 1980a, Au & Pitman 1986, 1988, Pryor & Kang-Schallenberg 1991, Au 1991, Edwards 1992, Norris et al. 1994). However, the sample size (5 sets from which both dolphin and tuna stomachs were examined) in Perrin et al.'s (1973) study was too small to detect feeding differences between yellowfin tuna and spotted dolphins by time of the day.

Food habits data collected in our study from 73 sets in which tuna and dolphins were caught together do not support the feeding hypothesis. The tuna–dolphin association is primarily a diurnal one (Scott & Cattanach 1998) and if the association was based on feeding benefits, one would expect both dolphins and tuna to feed primarily in the daytime. In the ETP, however, yellowfin tuna are primarily daytime feeders, while spotted and spinner dolphins are primarily nighttime or crepuscular feeders (Reintjes & King 1953, Alverson 1963, Shomura & Hida 1965, Fitch & Brownell 1968, Perrin et al. 1973, Ortega-García et al. 1992, Buckley & Miller 1994, Perrin & Hohn 1994, Richard & Barbeau 1994, Roger 1994, Robertson & Chivers 1997, Fiedler et al. 1998, Scott & Cattanach 1998, Galván-Magaña 1999, Román-Reyes 2005, this study). While yellowfin tuna may also feed at night and both dolphin species feed occasionally during the day, daytime feeding is clearly

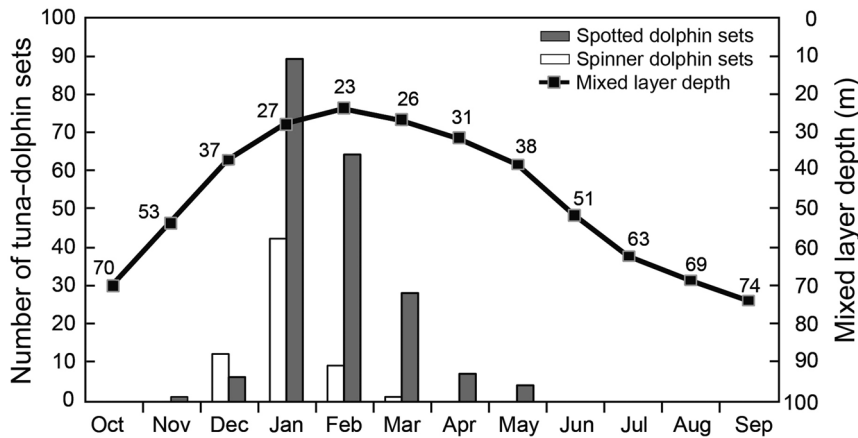


Fig. 9. *Stenella attenuata*, *S. longirostris*, and *Thunnus albacares*. Number of sets from 1995 to 2005 made on tuna associated with pure herds of spotted and spinner dolphins by month in one 5° quadrat (85 to 90° W, 10 to 15° S). Overlaid is the average mixed layer depth for that same quadrat by month

more important for the tuna and nighttime feeding is more important for the dolphins.

The food-habits study found that, while there is some overlap in the diets of spotted dolphins and yellowfin tuna, the prey resources were largely partitioned by time of day, prey species, and size (Galván-Magaña 1999). Stable isotope analysis performed on muscle samples from a subset of the predators analyzed for food habits (Román-Reyes 2005) revealed trophic overlaps of about 78% between yellowfin and spotted dolphins and between spotted and spinner dolphins, but only 57% between yellowfin and spinner dolphins. Despite similarity among $\delta^{15}\text{N}$ values of the predators, trophic-level overlap only requires feeding on prey from overlapping trophic levels, and can occur without sharing any of the same prey species. The tracking data also suggested that the yellowfin tuna and spotted dolphins feed at different depths.

Although the hypothesis that the association is largely food-based is not supported by current evidence, there may still be a foraging benefit. Both dolphin and tuna groups disaggregate during the night, beginning at dusk when dolphins begin to feed (Scott & Cattanch 1998, Scott & Chivers 2009). The feeding times of the spotted dolphins and yellowfin tuna overlap in the dawn hours, however, and early morning feeding bouts on multi-species concentrations of prey may draw tunas, dolphins, and other predators into proximity, and thus serve as a catalyst in the creation of the association.

Protection from predators

Travelling in groups provides more protection from predation than travelling alone. This advantage can

extend to multi-species aggregations, whereby the combined number of individuals of all species dilutes the risk of predation to individuals. Mixed-species aggregations comprised of different species with different sensory capabilities may also detect predators more efficiently than either species could provide alone (e.g. Diamond 1988).

Spotted dolphins and yellowfin tuna are of a similar size and have the same potential predators (Scott & Cattanch 1998). The predation risk may be particularly high for the yellowfin tuna because sharks and billfishes are significant predators that are commonly caught with tunas (Au 1991, Hunsicker et al. 2012). Hunsicker et al. (2012) found that

even large yellowfin tuna were prey for large sharks, particularly in the ETP, and they suggested that yellowfin tuna should more properly be considered a mesopredator rather than an apex predator.

Rare observations of shark attacks on spotted dolphins illustrate how vulnerable dolphins may be when the protection provided by being part of a herd is disrupted. Leatherwood et al. (1973) reported observations of shark predation on spotted dolphins after the herd's structure had been disrupted by fishing operations in the ETP. Maldini's (1993) observation of an attack of a tiger shark *Galeocerdo cuvier* on a juvenile spotted dolphin off Hawaii illustrated the high predation risk faced by calves and juveniles and the vulnerability of dolphins when they stray outside the envelope of the herd. Successful attacks by sharks were typically ambushes initiated from behind and below the dolphin.

Our results are in line with the expectations of the 'meeting point' hypothesis proposed to explain the schooling of pelagic tunas (Fréon & Misund 1999, Fréon & Dagorn 2000). The mobile dolphin herds may serve as a cue that allows tunas to aggregate into larger schools. At the same time, the benefit of 'safety in numbers' is accentuated by the combined group size of 2 or more similarly sized species. Scott & Cattanch (1998) noted that predation pressure need not be high to promote these aggregations, only that the risk of predation should be less than that incurred by an alternate strategy, such as forming small groups or straying from the group in the presence of predators.

Large sharks are not only potential predators, but competitors as well (Leatherwood et al. 1973, Compagne 1984, Heithaus 2001, Acevedo-Gutiérrez 2002,

Maldini 2003). Pelagic sharks would be attracted to the same prey patches as the dolphins and tuna, and habitat compression would likely increase their encounters. By monitoring each others' alarm responses, the dolphins and tuna could both gain from the association. The dolphins can echolocate or hear predators at a distance, allowing them, and the associated tuna, to avoid or monitor the predators. Because dolphins are most vulnerable to shark attacks coming from behind and below (Cockcroft et al. 1989, Mead & Potter 1990, Scott & Cattanach 1998), any alarm responses by deeper-swimming tuna could alert the dolphins to predators beneath them. Similarly, the surface-swimming spinner dolphins, which have been hypothesized to seek out spotted dolphin herds to increase protection from predation (Norris 1978, Norris & Dohl 1980b, Norris et al. 1994, Cramer et al. 2008, Kiszka et al. 2011), could also be alerted by the deeper-swimming spotted dolphins (discussed below).

Why does this association primarily involve spotted dolphins, much more so than other dolphin species?

If the predation hypothesis is valid, it would require an explanation for why, if tuna join dolphin herds seeking safety in numbers, do they associate mainly with spotted dolphins, even though other species, particularly spinner and common dolphins, form large herds that would provide protection as well.

The weaker association between yellowfin tuna and common dolphins can be explained by their different habitats. Yellowfin tuna are found primarily in tropical waters, while common dolphins tend to inhabit cooler, upwelling-modified waters (Au & Perryman 1985, Reilly 1990, Fiedler & Reilly 1994, Reilly & Fiedler 1994, Ballance et al. 2006).

Spinner dolphins, however, inhabit tropical waters and associate with yellowfin tuna, but generally as part of a mixed-species spotted-spinner dolphin herd. Spotted and spinner dolphin herds coalesce throughout the mornings such that, by mid-day, 87% of all spinner dolphin sightings are in mixed-species herds associated with spotted dolphins (Scott & Cattanach 1998). The apparent weaker association between yellowfin tuna and spinner dolphins may be explained, in part, because tuna encounter pure spotted dolphin herds and mixed spotted-spinner dolphin herds more frequently than pure spinner dolphin herds. Thus, even when tuna join pure spinner dolphin herds in the early morning, it is likely that those herds will soon coalesce with herds of spotted dolphins.

The tuna's apparent preference for spotted dolphins can also be explained by their swimming depths. The foraging depths of yellowfin tuna are restricted by low dissolved oxygen concentrations, and they cannot swim for long in waters where the concentrations are less than 2.0 ml l^{-1} without resorting to 'bounce diving' (Schaefer et al. 2009). Tracking studies (Carey & Olson 1982, Holland et al. 1990, Block et al. 1997, Schaefer et al. 2007, 2009, this study) have shown that yellowfin tuna are typically found during the daytime near or slightly above the thermocline (20 to 60 m deep in the ETP areas where the association is most often observed and exploited by the fishermen). Aerial photogrammetry studies have observed that spinner dolphins are easier to photograph than spotted dolphins (Cramer et al. 2008) because spinner dolphins swim near the surface while spotted dolphins swim deeper (W. Perryman & M. D. Scott pers. obs.); the TDR data confirmed that the spotted dolphins swim at depth, travelling 15 to 20 m below the surface during the daytime. Radio-tracking and aerial photogrammetry data also indicate that common dolphins, like spinner dolphins, are also surface swimmers during the day (Evans 1974, W. Perryman & M. D. Scott pers. obs.). Thus, the depth at which spotted dolphins typically swim is much closer to the typical swimming depth of the yellowfin tuna than that of the spinner and common dolphins. It would be easier for the tuna, swimming just above the thermocline, to maintain an association with the deeper-swimming spotted dolphins than the surface-swimming spinner dolphins.

If differences in swimming depth were indeed influencing the formation of the tuna–dolphin association, then one might expect tuna to associate with spinner dolphins where the mixed layer was the shallowest and the oxygen minimum zone just below the mixed layer was most hypoxic. Comparison of the mixed layer depth (Fig. 6) to the distribution of sets on tuna associated with pure herds of spinner dolphins (Fig. 8) and with spinner dolphins in southern areas during summer when the mixed layer depth is shallower (Fig. 9) suggests that this is so.

Why does this association involve primarily large and not small tunas?

The yellowfin tuna caught by purse seines in association with floating-object sets are small (averaging 2.6 to 4.6 kg, modal fork length [FL] ~45 cm, depending on area), those caught in unassociated schools are larger (8.7 to 11.2 kg, modal FL ~70 cm), and

those caught in association with dolphins are the largest (13.5 to 37.3 kg, modal FLs >90 cm; IATTC 2004). Edwards (1992) argued that it would not be energetically efficient for small yellowfin tuna or skipjack to travel with dolphins until they reached at least the same length of a newborn spotted dolphin (about 85 cm, Hohn & Hammond 1985; or a weight of about 12.9 kg, Wild 1986). Otherwise, Edwards (1992) argues, smaller tunas would have to travel faster than their optimum cruising speed to keep up with the dolphins, which is energetically unsustainable. When small tunas are associated with dolphins, they do comprise a small proportion of the catch, likely because they may not be able to keep pace during the high-speed chase that usually precedes a dolphin set.

Why is the association of dolphins and tuna such a predominant feature in the ETP, but not in most other oceans?

It has long been suggested that the unusual oceanographic features of the ETP—the high surface temperatures, shallow thermocline (<60 m deep), and the thick oxygen minimum zone—promotes the association of tuna and dolphins (Green 1967, Perrin et al. 1976, Au & Perryman 1985, Edwards 1992, Norris et al. 1994). Oxygen is depleted in warm waters of the mixed layer due to high phytoplankton production, and the stable thermocline prevents oxygenation of the cooler waters below, producing the characteristic thick oxygen minimum zone (see review by Fiedler & Talley 2006). The oxygen minimum zone in the ETP ‘includes a greater body of almost oxygen-free water than any other region in the world’s oceans’ (Knauss 1963). To the west, the thermocline deepens to about 150 m and the oxygen minimum zone thins markedly (Knauss 1963, Sprintall & Cronin 2001, Tomczak 2001), and the tuna–dolphin association becomes uncommon. Tuna purse seiners in the western Pacific rarely set on dolphins (Donahue & Edwards 1996, Hall 1998, Hampton & Bailey 1999, WCPFC 2011).

The combination of a shallow thermocline and a thick layer of cold hypoxic water just below is thought to restrict the vertical movements of tunas (Edwards 1992, Brill 1994, Prince & Goodyear 2006). Although yellowfin tuna may make occasional dives down into very cold water (Carey & Olson 1982, Block et al. 1997, Dagorn et al. 2006), their vertical range appears to be limited by temperatures that are about 8°C less than the surface temperatures (Brill & Lutcavage 2001) and by an oxygen content of about

3.5 ml l⁻¹ or 152 µmol kg⁻¹ (Cayré 1991, Cayré and Marsac 1993, Brill 1994, Graham & Dickson 2004, Prince & Goodyear 2006).

This compresses the yellowfin tuna habitat to the surface waters of the mixed layer and allows the tuna–dolphin association to occur. Yellowfin tuna tend to swim just above the thermocline, with frequent excursions upward within the mixed layer (Carey & Olson 1982, Holland et al. 1990, Block et al. 1997, Brill et al. 1999, this study); the air-breathing spotted dolphins are obviously tied to the surface, and spend most of their time in the mixed layer travelling and foraging. The shallow thermocline also promotes propagation of dolphin sounds, and yellowfin tuna may detect these sounds at distances of several hundred meters (Finneran et al. 2000, Schaefer & Oliver 2000). The deeper the thermocline, however, the greater the vertical distance there is between the 2 species, and the more difficult it would be to maintain the association. This would explain why the association is so prevalent in the ETP and then becomes progressively rarer farther to the west. It may also explain the effects on tuna catches during some El Niño years. During the severe 1983 El Niño, for example, the mixed layer in the ETP deepened over a wide area, and likely as a result, made the tuna–dolphin association more difficult to maintain, which likely explains the greatly reduced number of dolphin sets and tuna catches in that year (Fig. B-4 in IATTC 2004).

The association between dolphins and tuna is not entirely unique to the ETP, however. Tuna associate with dolphins around many islands: the Maldives (Anderson & Shaan 1999), Sri Lanka (de Silva & Boniface 1991, Leatherwood & Reeves 1991), Fernando de Noronha Archipelago (Sazima et al. 2006), the Azores (Clua & Grosvalet 2001, Silva et al. 2002), Hawaii (Shallenberger 1981), and the Philippines, Indonesia, and New Guinea (Dolar 1994, Hampton & Bailey 1999, WCPFC 2011). These associations may be promoted by the shallower thermocline in the lee of some islands (e.g. McManus et al. 2008). Dolphins and tuna are also known to associate, to a much lesser extent than in the ETP, in the tropical waters of the western Indian and the eastern Atlantic Oceans (Simmons 1968, Levenez et al. 1980, Pereira 1985, Donahue & Edwards 1996, Ballance & Pitman 1998, Hall 1998, Ariz-Telleria et al. 1999, Van Waerebeek et al. 1999, Felando & Medina 2011). These ocean regions contain areas with a shallow thermocline and a marked oxygen minimum zone (Fig. 10), although these areas are not as expansive nor is the oxygen minimum zone as hypoxic as in the ETP (Tomczak

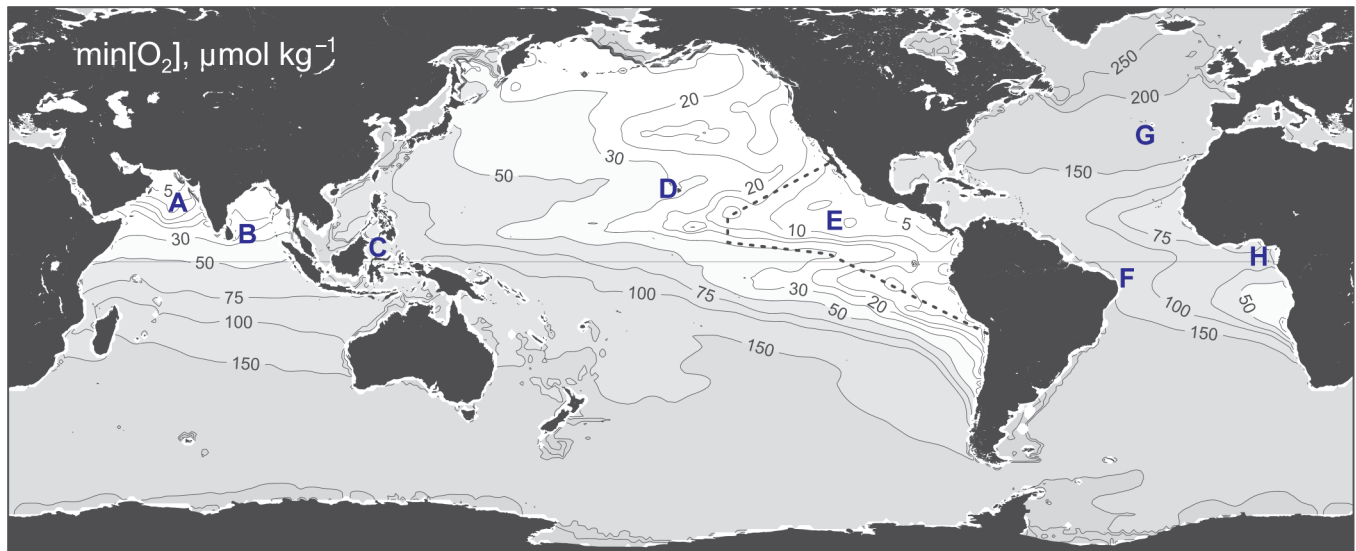


Fig. 10. Global minimum dissolved oxygen concentration ($\mu\text{mol kg}^{-1}$) from World Ocean Atlas 2001 (adapted from Fiedler & Talley 2006). Letters indicate approximate areas where published accounts refer to a tuna–dolphin association: (A) Gulf of Oman and Arabian Sea: Van Waerebeek et al. (1999), Ballance & Pitman (1998); (B) Sri Lanka: de Silva & Boniface (1991), Leatherwood & Reeves (1991); (C) Archipelagic waters of Indonesia, Philippines, and New Guinea: Dolar (1994), Hampton & Bailey (1999), WCPFC (2011); (D) Hawaiian Islands: Shallenberger (1981); (E) Eastern tropical Pacific: Figs. 7 & 8; (F) Fernando de Noronha archipelago: Sazima et al. (2006); (G) Azores Islands: Clua & Grosvalet (2001), Silva et al. (2002); (H) Gulf of Guinea: Simmons (1968), Levenez et al. (1980)

2001, Prince & Goodyear 2006, Prince et al. 2010). Only in the ETP is the association strong enough and reliable enough for a pelagic commercial purse-seine fishery to take advantage of the association consistently (Donahue & Edwards 1996, Hall 1998, Scott et al. 1999).

CONCLUSIONS

The ‘meeting point’ hypothesis (Fréon & Misund 1999, Fréon & Dagorn 2000) proposes that tuna have a genetic tendency to associate with floating objects, dolphins, whales, or whale sharks. Observations by fishermen and studies by researchers have provided evidence that it is the yellowfin tuna that initiates the association with dolphins. Our results, however, suggest that the tuna–dolphin association is neither an obligatory nor a permanent one. It involves mainly large yellowfin tuna, and not small yellowfin or skipjack tunas, likely due to energetic constraints on small tunas (Edwards 1992). It involves mainly spotted dolphins, and only to a lesser extent other dolphin species, due to the closer match in habitat and traveling depths of the spotted dolphins with the yellowfin tuna. The association is most common in the ETP because this large region is characterized by warm waters and a shallow thermocline overlaying a thick

hypoxic oxygen minimum zone that compresses the habitat for the tuna (Prince & Goodyear 2006). The shallower the thermocline and the more hypoxic the waters below the thermocline, the more likely it is that the association will occur.

The results of our studies support the hypothesis that the formation of large, mixed-species groups of spotted dolphins and yellowfin tuna reduces the risk of predation for one or both species. Both species show increased group sizes during the day, likely for the same reason, as both are potential prey for large sharks and small whales (Scott & Cattanch 1998). The habitat compression that promotes the tuna–dolphin association may also increase the number of encounters with sharks. Large sharks are both potential predators on and competitors with dolphins and tuna. All of these species are likely attracted to the same prey patches, particularly during early morning feeding bouts. The dolphin–tuna association may then be maintained throughout the day because of the threat sharks pose as potential predators.

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