Abstract.– Yellowfin tuna *Thunnus albacares* are commonly found associated with other species, especially sharks, birds, and dolphins, in the eastern tropical Pacific. Data from the purse seine fishery there, collected during 1974 and 1975, indicate that sharks occurred with tuna in 40% or more of the purse seine sets made around floating logs. Most other species, including rays, billfish, and small tunas, usually occurred in less than 10% of the sets. The association rate of these bycatch species declined progressively from log- to school- to porpoise-associated sets. This, together with their behavior as understood, suggests that at least some of these species stay with the tuna as much as they can. Such behavior would be like that of polyspecific associations in which two or more species travel together for foraging and protective advantages.

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Polyspecific Nature of Tuna Schools: Shark, Dolphin, and Seabird Associates

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Tuna are often found associated with other species, a behavior that is also seen among other schooling, herding, or flocking animals. While it is often convenient to think of any of these species as being effectively monospecific (single species) in behavior, there is growing awareness that polyspecific, enduring assemblages are common among higher animals. Such associations, comprised of several species that feed, interact, and travel together for periods of time, are not merely aggregations of animals along routes or points of common attraction. The specific interactions involved are not well understood, even though field observations have been intensive in some cases.

Mixed-species schools of fishes are frequently observed and caught. While usually seen as chance associations (e.g., Itzkowitz 1977), some species in these schools may obtain enhanced protective and foraging benefits (Ehrlich and Ehrlich 1972, Barlow 1974, Wolf 1987). Many such schools may therefore be polyspecific, and represent purposeful interactions.

Polyspecific bird flocks are common (Moynihan 1962; Morse 1970, 1977; Munn and Terborgh 1979). In some cases, over a dozen species move together through different environments with the composition of individuals and species apparently changing little (Hutto 1987). Diamond (1981) pointed out that polyspecific flocks often consist of similar core species that stay together, perhaps for years, maintaining flock characteristics and holding group territories. There are leader species, which are usually conspicuous, and follower species (Caldwell 1981, Greig-Smith 1978).

Mammals, with even more complex behaviors, abound with examples of polyspecific associations. Such associations have been noted in bats, cetaceans, often in ungulates, and particularly in the behaviorally versatile primates. Among the latter, species pairs of certain cercopithecid monkeys may be together 50% of the time, and it often appears that one species initiates and terminates the association, and uses the other to better discover food and detect danger (Struhsaker 1981, Cords 1987). Locally, these polyspecific associations are species-specific; other sympatric monkeys are apparently ignored and always by themselves (Gautier-Hion et al. 1983). This suggests that benefactor species are actively searched for by follower species. These associations, which vary in species composition by area, may last for days or months. Group territories may be defended. Similar behaviors have been observed in cebid monkeys, some of whose polyspecific associations appear to be permanent (Terborgh 1983). Interestingly, monkey species that appear to initiate and benefit from the polyspecific associations can be observed sometimes in front, sometimes at the rear, of traveling groups.

In general, polyspecific associations seem to form when social species of similar foraging ecology join to form larger groups to increase feeding success and to better avoid predators. The former may be ascribed to facilitation of feeding or to greater access to resource information (Clark and Mangel 1984). An additional benefit might be a lessening of intragroup competition (relative to monospecific groups of the same size). The enhanced safety could result from more effective vigilance (Pulliam 1973) or to the "convoy" effect (Olson 1964). It seems that the behaviorally more versatile species often exploit other species' behaviors, although there appear to be mutual benefits as well. For the most part, these polyspecific associations seem loosely coupled; the overt interspecies behaviors are circumstantial rather than obligatory, and generally agonistic. Species appear to join and leave the groups mainly in response to foraging situations; accordingly, they may be together for hours or days, sometimes months or even years.

In this paper I describe species found with tuna in the eastern tropical Pacific (ETP) and propose that tuna schools have a polyspecific nature. What this implies about tuna biology, especially that of the yellowfin *Thunnus albacares*, is discussed.

Data and methods

I used data collected by Southwest Fisheries Science Center (SWFSC) observers placed aboard U.S. tuna purse seiners. Such data have been available since 1966, but the records have not always been consistent or extensive with respect to other species caught with tuna (except for dolphins). The reasons include the pressure of observers' duties and the proprietary nature of fishing operations. After 1975, some kinds of bycatch information were no longer collected at all, and only abbreviated codes for certain other associated species were recorded.

The earlier, pre-1976 observer records, however, contain many candid notes on bycatches and other tuna associates, although even then the logs required only generic, not comprehensive, descriptions. Fortunately, some observers clearly were interested in tuna-associated fauna, and they frequently recorded detailed descriptions of what they saw.

I therefore selected records from the more information-rich 1974–75 database on purse seine sets (a "set" is a launch and retrieval of a purse seine net) for information on species that occur with tuna. I compiled a list of 22 observers personally known by myself or other SWFSC workers to have been reliable or to have had keen interest in pelagic fauna, and obtained pertinent information from their original logsheets. These logsheets constituted the set records of each of their 33 fishing trips. The trips occurred during all months except December, with 90% of the data collected between January and mid-June.

I examined the data pooled over all fishing trips and also by individual trip, since the quality of the records varied among observers. The data from one T.M. Duffy (TMD) is presented separately in the analysis below (TMD sets cf. the regular fleet sets) to illustrate how the actual observations of a particular observer could differ from the overall, pooled results. Duffy recorded information copiously and was an experienced and interested observer.

The data were divided into two areas and according to how the tuna were caught. The areas, delimited by latitudes 15°S and 25°N, were from the Central American coasts westward to 100°W ("off Central America") and from 100°W out to 135°W ("off Mexico") (see Figure 1). The first area contained sets mainly off the Central American coasts and southwestward to the Galapagos Islands; this is an important area for fishing both free-swimming and log-associated tuna, and also dolphin-associated tuna (explained below). The second area had sets mainly between southern Mexico and Clipperton Island, where much dolphin-associated tuna is taken. The tuna sets were further partitioned according to whether they were made around floating logs ("log-fish" sets), on free-swimming tuna ("school-fish" sets), or on dolphin-associated tuna ("porpoise-fish" sets). These are the terms used by the fishermen for the variously caught tuna, i.e., for different set types. The porpoise-fish sets refer to tuna caught usually with spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris* (called "porpoise"). Table 1 gives the numerical breakdown of the 1762 purse seine sets I examined according to the above categories.

The purse seine sets in each area and set-type category were examined for frequency of different associated species to obtain a profile of the multispecies composition of the tuna schools. For each of certain species—actually grouped species because identifications were inexact—this frequency was expressed as the fraction (p) of the pertinent sets in which the species was caught. For comparison, I calculated both overall fractions considering all sets from all trips and arithmetic means of the fractions for individual trips. The latter fractions were computed only where fishing trips had more than ten sets in the category of interest. Binomial 95% confidence limits of the overall fractions were determined in accordance with the number of sets involved (n). Ranges were determined for the trip fractions. These latter fractions were statistically heterogeneous among trips, at least for log-fish and porpoise-fish sets. Thus the overall fractions probably best reflect the polyspecific composition of schools.

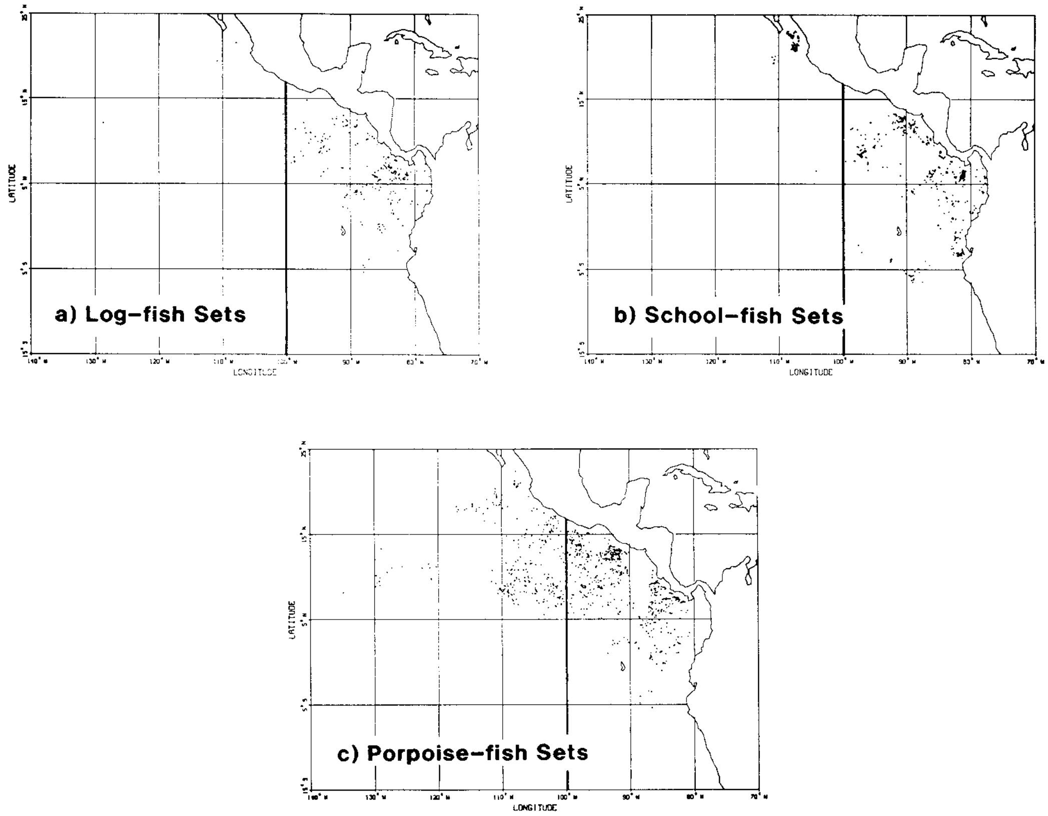

Figure 1

Locations of (a) log-fish sets, (b) school-fish sets, and (c) porpoise-fish sets inspected. Data were examined separately to the east ("off Central America") and west ("off Mexico") of longitude 100°W.

Related data gleaned from the records were summarized. These included information on size, abundance, and actual species composition within the species groups.

The species composition of bird flocks occurring with the tuna was described after ordering the (n) reported species in each flock according to (1 to n) decreasing ranks of abundance (again, the species were actually grouped species). This was done to circumvent differences in the accuracy with which different observers estimated species' flock sizes. The fraction of total flocks in which a bird species ranked at least 2 (i.e., was at least second most-abundant) was regarded as that species' importance value. When that value was 50% or more of the flocks in a category, that species was considered dominant for that set-type category. Several species could be "dominant" according to this criterion.

Both yellowfin, and skipjack *Katsuwonus pelamis*, tuna are sought by purse seiners, although yellowfin is usually preferred. Overall, yellowfin was captured in 78% of the log-fish sets, 57% of school-fish sets, and 99% of porpoise-fish sets examined (including sets capturing both tunas). The mean tonnages of yellowfin caught per set, based on "successful sets," are given in Table 1. Successful sets are those catching more than 1 ton of yellowfin and/or skipjack tuna.

Tunas from the different set types are likely to behave differently, since younger yellowfin tend to associate with floating logs in nearshore waters while older, larger fish tend to be with dolphins farther offshore (Greenblatt 1979). Therefore, the species associations

Table 1
Characteristics of yellowfin tuna sets examined for other-species associations according to log-fish, school-fish, and porpoise-fish set types.

		Off Central America			Off Mexico		
		Log	School	Porpoise	Log	School	Porpoise
Fleet data	Total sets	185	438	540	2	104	220
	SS Ratio[1]	0.69	0.61	0.80	—	0.54	0.92
	YF tons[2]	6.5	6.8	8.9	—	5.7	8.2
	(n)	102	145	379	—	51	192
	2 SE[3]	1.3	1.2	1.1	—	1.5	1.2
TMD[4] data	Total sets	58	65	78	1	1	70
	SS Ratio	0.74	0.57	0.85	—	—	0.83
	YF tons	6.0	7.5	11.8	—	—	7.4
	(n)	34	22	49	—	—	60
	2 SE	1.4	1.7	1.3	—	—	1.3

[1]The Successful Set (SS) Ratio = fraction of total sets catching more than 1 ton of yellowfin and/or skipjack tuna. On porpoise-fish sets, the SS Ratio pertains to sets on *Stenella* dolphins only.
[2]Geometric mean short tons of yellowfin tuna (YF) per set, based on successful sets only; n is the size of the sample. Not all successful sets caught yellowfin.
[3]The multiplication-division factor for mean YF tons/set giving its 95% confidence interval.
[4]Observer T.M. Duffy (fleet data exclude these data).

with tuna, as seen in this study, will be discussed in terms of the ontogeny of yellowfin behavior.

Results

The fractions (p) of purse seine sets measuring the association rates of different (grouped) species are given in Table 2 (off Central America) and Table 3 (off Mexico). These fractions (expressed as percentages) are for the fleet sets, and they are summarized graphically in Figure 2. Figure 3 shows the association fractions for the T.M. Duffy (TMD) sets. In the tables, those species whose association rates differed significantly (χ^2, $P<0.05$) among set types are indicated by asterisks. For these, one can determine which of the set types was actually different by noting which of the mean rates occurred outside the 95% confidence intervals for the other set types.

Sharks clearly stood out among the fishes found associated with tuna. Overall, 40% of log-fish tuna sets took sharks. There was a progressive decline in this percentage to 10%, from log- to school- to porpoise-fish sets. Off Mexico, however, porpoise-fish sets may have been more likely to catch sharks (lower graphs in Figures 2 and 3). How commonly sharks may associate with tuna is emphasized by the TMD data (Fig. 3); individual fishing trips, of which this data from a single observer are an example, can experience shark occurrence rates of up to 90% on log-fish sets. The silky shark *Carcharhinus falciformis* was the most commonly reported species (25.2%) (Table 4). These sharks averaged 29.2 individuals in sets that caught them. However the range was large, from 1 to 500 per set. Other carcharhinids recorded were each under 10% of the identified sharks. Of these, the whitetip shark, frequently recorded with porpoise-fish sets (especially off Mexico), was most likely the oceanic whitetip *C. longimanus*, (R. Rasmussen, SWFSC, pers. commun.). Other less-common sharks included the whale shark *Rhincodon typus*. This species can be locally common off Baja California, where it is often associated with skipjack tuna. Sizes of the sharks caught with yellowfin were seldom recorded; however, it is known that medium- to large-sized specimens that are considered dangerous are often caught. The few sizes recorded ranged from 1.7 to 2.1 m. Many were simply described as "large." Others, described as "small" or comprising "25 tons" of catch, were probably all small-sized.

Rays occurred mainly in school-fish and porpoise-fish sets, the former more often. The records indicate that most were medium- to large-sized manta rays (Mobulidae). They occurred in groups of 1 to 2 on average, though up to 12 were recorded in some sets (Table 4).

Billfish (Istiophoridae) co-occurred with tuna in about 9% of the sets overall and more often off Central America than off Mexico. The association rates were similar among all set types, except for the TMD data

Table 2

Fraction (p) of purse seine sets (n) having various associated "species," off Central America (coast to 100°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	n	95% CI[3]	p (%)	n/T	Range (%)[3]	Comments
Birds	L	83*	185	76–89	79	144/8	36–100	Birds very common with schools. Virtually all porpoise-fish sets are with birds.
	S	80	438	75–84	82	404/13	43–100	
	P	98	540	96–99	98	497/17	89–100	
Sharks	L	40*		32–48	37		21–77	Sharks common to very common with log-fish sets, but decreasingly so from log- to school- to porpoise-fish sets.
	S	21	″	17–26	20	″	0–61	
	P	13		10–17	13		0–36	
Rays	L	1*		0–3	1		0–7	Rays more often with school-fish sets than with porpoise-fish; rather seldom with log-fish.
	S	10	″	7–13	10	″	2–18	
	P	5		3–8	4		0–18	
Billfish	L	8		5–13	7		0–25	Billfish sometimes more frequent with log-fish sets, otherwise, similarly frequent among all school types.
	S	9	″	6–12	11	″	3–35	
	P	9		6–12	7		0–23	
Bullet tuna	L	10*		6–16	8		0–23	Bullet tuna often with logs; decreasingly so with school- and porpoise-fish sets.
	S	4	″	2–6	4	″	0–17	
	P	1		0–3	<0.5		0–5	
Black skipjack	L	12*		7–18	15		0–40	Black skipjack more often with log-fish sets; not with porpoise-fish.
	S	5	″	3–8	5	″	0–19	
	P	0		0–1	<0.5		0–2	
Turtle	L	3*		1–7	4		0–9	Turtles infrequent and without trend among the different tuna set types.
	S	5	″	3–8	4	″	0–13	
	P	1		0–3	1		0–6	
Dolphinfish	L	24*		18–31	27		0–50	Dolphinfish mainly with log-fish sets.
	S	7	″	5–10	7	″	0–26	
	P	2		1–4	3		0–23	
Yellowfin and skipjack tuna	L	66*	127	57–74	62	78/5	27–82	Skipjack common with school- and especially log-fish sets; seldom with porpoise-fish.
	S	40	266	34–46	45	225/10	8–63	
	P	3	392	1–6	2	325/12	0–8	

[1] Fleet sets are the data without T.M. Duffy sets; see text.
[2] Set types are log-fish (L), school-fish (S), and porpoise-fish (P) types.
[3] 95% CI of p's are from the binomial distribution. Trip fractions (n/T) are n sets from only those T trips having ≥10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

which showed billfish significantly more frequent in log-fish sets (Fig. 3). Those rates ranged from 20% to 43% on different fishing trips. Sailfish *Istiophorus platypterus* comprised 31.4% of the billfish, the remainder being marlin. Several of the latter were identified as striped marlin *Tetrapturus audax* and black

Table 3
Fraction (p) of purse seine sets (*n*) having various associated "species," off Mexico (100–135°W).

		Fleet sets[1]						
		Overall fraction			Mean of trip fractions			
Associated spp.	Set type[2]	p (%)	*n*	95% CI[3]	p (%)	*n*/T	Range (%)[3]	Comments
Birds	L	—*	—	—	—	—	—	Birds very common with schools; virtually all porpoise-fish sets are with birds.
	S	77	104	68–85	72	80/4	50–100	
	P	98	220	93–100	98	169/6	91–100	
Sharks	L	—*		—	—		—	Sharks may be less frequent with school- than with porpoise-fish sets; cf. Table 2.
	S	6	″	2–12	3	″	0–11	
	P	13		7–21	14		0–43	
Rays	L	—		—	—		—	Rays similarly frequent with school- and porpoise-fish sets.
	S	9	″	4–16	8	″	0–18	
	P	5		2–11	5		0–8	
Billfish	L	—		—	—		—	Billfish relatively infrequent with both school- and porpoise-fish sets.
	S	4	″	1–10	5	″	0–9	
	P	3		1–8	5		0–23	
Bullet tuna	L	—		—	—		—	Rare in all set types.
	S	1	″	0–5	1	″	0–3	
	P	0		0–4	0		0–0	
Black skipjack	L	—		—	—		—	Not recorded.
	S	0	″	0–4	0	″	0–0	
	P	0		0–4	0		0–0	
Turtle	L	—		—	—		—	Relatively rare in all sets.
	S	3	″	0–8	1	″	0–3	
	P	3		0–8	4		0–9	
Dolphinfish	L	—*		—	—		—	Dolphinfish more often with school- than porpoise-fish sets.
	S	14	″	8–22	14	″	0–32	
	P	1		0–5	2		0–8	
Yellowfin and skipjack tuna	L	—*		—	—		—	Skipjack more often with school- than porpoise-fish sets; cf. Table 2.
	S	36	56	27–45	22	33/2	0–43	
	P	12	202	6–20	14	153/5	0–39	

[1] Fleet sets are the data without T.M. Duffy sets; see text.
[2] Set types are log-fish (L), school-fish (S), and porpoise-fish (P) types.
[3] 95% CI's are from the binomial distribution. Trip fractions (*n*/T) are *n* sets from only those T trips having ≥10 sets. Asterisks indicate statistical significance among set types ($P \leq 0.05$).

marlin *Makaira indica* (Table 4). The blue marlin *M. nigricans* was not present on the records examined, but occurs in the area. Usually 1 or 2 marlin were captured. Records of measured or estimated sizes show that some fish were large, e.g., a 3.2 m sailfish and a 4.4 m (total length) marlin. A swordfish *Xiphius gladius* was also recorded in one of the sampled sets.

"Bullet" tuna (*Auxis* sp.) and black skipjack *Euthynnus lineatus* are small tunas often taken in large numbers—but usually recorded in tons—in log-fish sets off Central America. Bullet tuna and black skipjack were very seldom in porpoise-fish sets. The association rate for bullet tuna was 10% for fleet log-fish sets and 41% for TMD log-fish sets (Table 2; Figs. 2, 3).

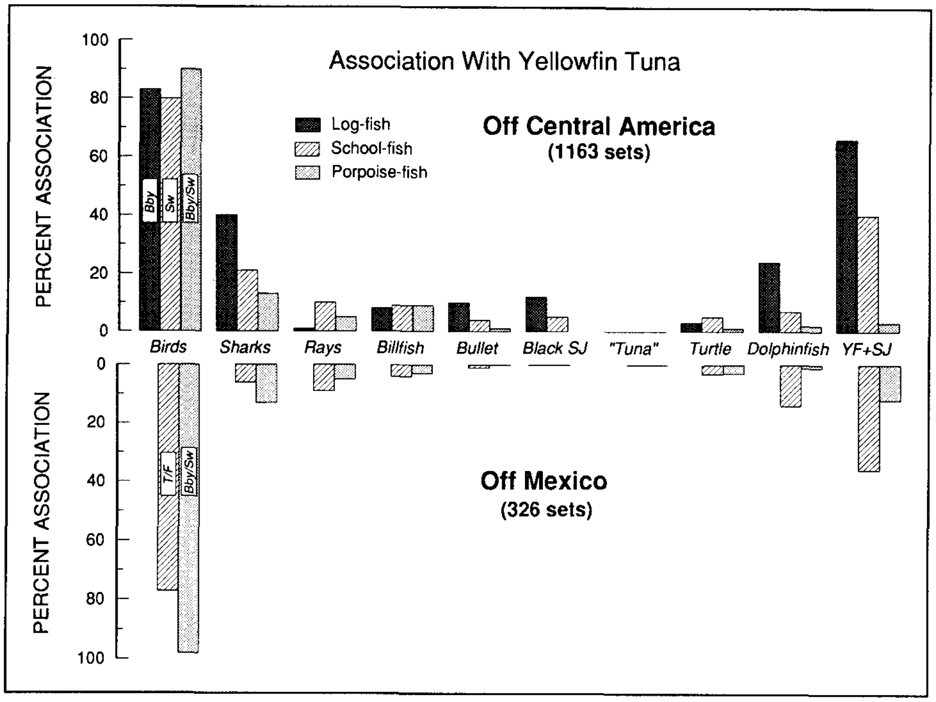

Figure 2
Percent association of different "species" with yellowfin tuna in fleet samples. Bby = boobies, Sw = shearwaters, T = terns, F = frigatebirds, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

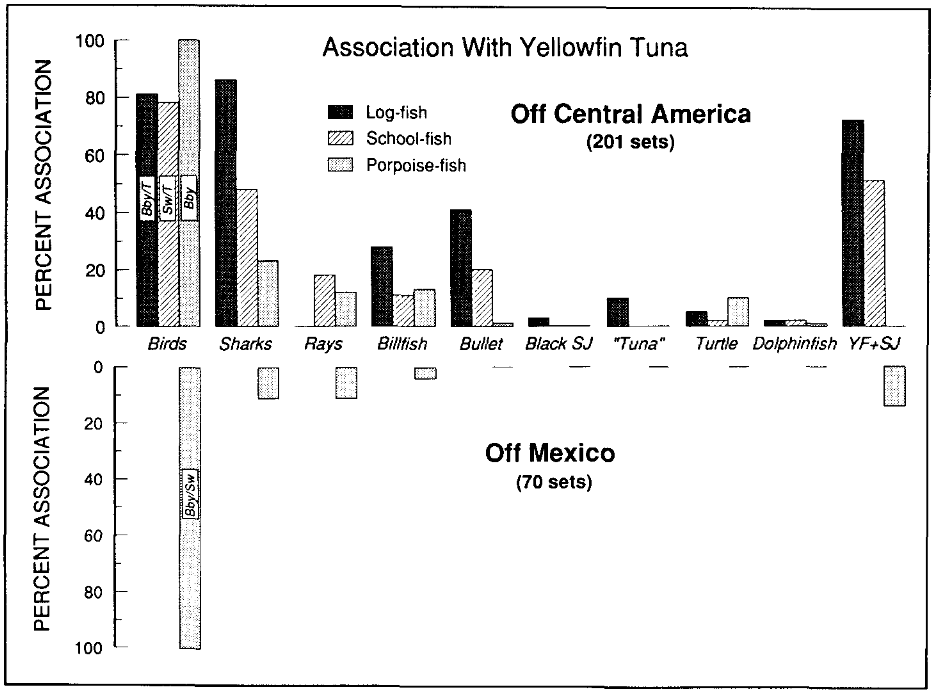

Figure 3
Percent association of different "species" with yellowfin tuna in T.M. Duffy samples. Bby = boobies, T = terns, Sw = shearwaters, "Tuna" = unspecified tuna species, YF = yellowfin tuna, SJ = skipjack tuna.

Table 4
Characteristics of tuna-associated species.

Species	Species[1] percent	Numbers of individuals/set[2] Mean	Range
Shark or "carcharhinid"	49.1	23.4	1–350
Silky (*Carcharhinus falciformis*)	25.2	29.2	1–500
Whitetip (*C. longimanus*)	9.0	5.1	1–39
Other carcharhinids (bull, "requiem," "brown," blacktip, gray)	6.1	11.6	1–80
Hammerhead (*Sphyrna* spp.)	3.9	2.3	1–7
Thresher (*Alopias* spp.)	3.2	3.6	1–28
Mackerel/Mako/White (Lamnidae)	2.4	8.3	1–40
Blue (*Prionace glauca*)	0.5	1.0	—
Whale (*Rhincodon typus*)	0.5	1.0	—
All (*N* 409)	(100.0)		
Ray	15.0	1.1	1–2
Manta (Mobulidae)	75.0	1.6	1–12
Others (Sting, bat, skate)	10.0	1.1	1–2
All (*N* 118)	(100.0)		
Swordfish (*Xiphias gladius*)	—	1.0	—
All (*N* 1)	(100.0)		
Billfish (Istiophoridae)			
Marlin (*Tetrapturus audax, Makaira indica*)	68.6	1.3	1–5
Sailfish (*Istiophorus platypterus*)	31.4	1.4	1–6
All (*N* 159)	(100.0)		
"Turtle" or Ridley (*Lepidochelys olivacea*)	87.5	1.4	1–4
Others (leatherneck, green)	12.5	2.5	1–3
All (*N* 24)	(100.0)		
Dolphinfish[3] (*Coryphaena hippurus*)	63.2	6.0	1–200
Amberjack/yellowtail (*Seriola* spp.)	30.5	11.8	1–100
Pompano (*Trachinotus*?, Kyphosidae?)	6.2	22.5	1–100
All (*N* 144)	(100.0)		
Wahoo (*Acanthocybium solandri*)	76.2	2.9	1–25
Spanish mackerel/mackerel (*Scomberomorus, Trachurus*?)	23.8	17.8	1–50
All (*N* 42)	(100.0)		
Ocean sunfish (*Mola mola*)	—	1.7	2–3
All (*N* 3)	(100.0)		

[1] From all data. Refers to species composition among individuals that could be identified or categorized.
[2] In sets that caught the species.
[3] Not including dolphinfish reported with other species absent.

Turtles were relatively infrequent in the tuna purse seine sets, at rates generally less than 5% overall and without evident pattern among the three set types. Most (21 of 24) were recorded as "turtle" or identified as Ridley turtles *Lepidochelys olivacea*, as probably most were (pers. observ.) (Table 4). A few leatherback turtles *Dermochelys coriacea* and green turtles *Chelonia mydas* were also identified.

Dolphinfish (*Coryphaena* spp.) were most frequent (24%) in log-fish sets and progressively rarer in school-fish and porpoise-fish sets. Individual fishing trips had log-fish sets with association rates ranging from zero to 50%. Considering that dolphinfish are frequently associated with flotsam and are not strong

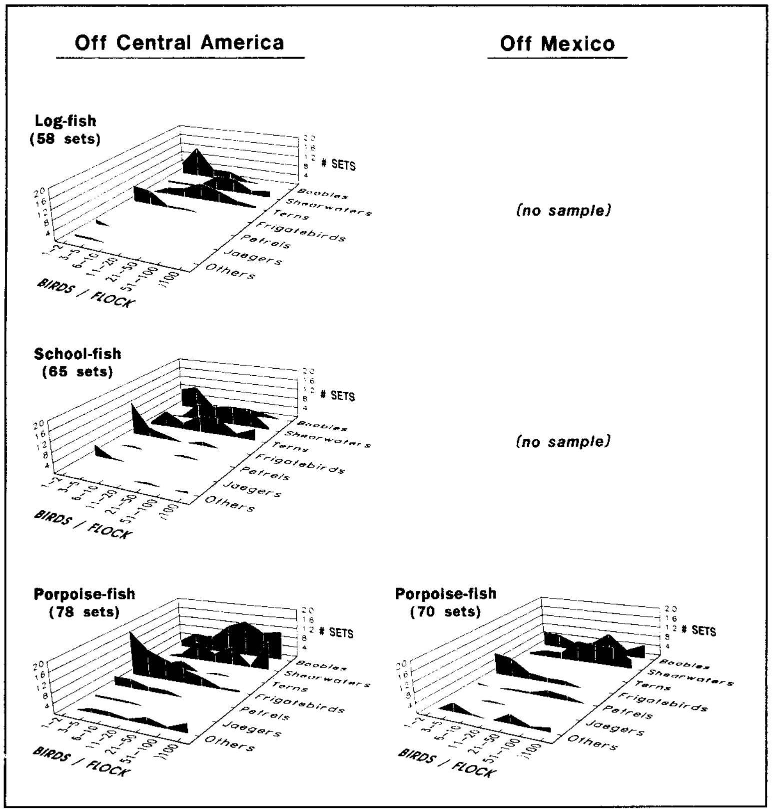

Figure 4
Histogram envelopes of bird flock sizes off Central America and off Mexico according to log-fish, school-fish, and porpoise-fish set types. Each histogram plots frequency (# SETS) against the species' abundance in the flocks (BIRDS/FLOCK). T.M. Duffy samples only.

swimmers like tuna, those trips with low occurrence rates may represent separation of this species from tuna during capture. When captured together with tuna, and with other associated fishes as well, dolphinfish averaged 6 individuals per set, with the range from 1 to 200 (Table 4).

Several other miscellaneous fishes were caught rather persistently, especially in log-fish sets. Notable among these were yellowtail or amberjack (*Seriola* sp.) and wahoo *Acanthocybium solandri* (Table 4). Others, such as triggerfish (Balistidae) were common and were probably associated with the flotsam near which the tuna were caught; these small fish are frequently seen under such objects (pers. observ.).

The fraction of successful (not total) purse seine sets that took both yellowfin and skipjack tuna measures the likelihood of these two tunas being associated. Yellowfin and skipjack were together in nearly 70% of successful log-fish sets. This fraction declined markedly in school-fish sets and even more so in the porpoise-fish sets, i.e., to 3% or less (Table 2).

The largest category of other animals associated with tuna was seabirds (Figs. 2, 3). Birds have a close relationship to tuna (and tuna fishing to birds), and observers usually record some aspect of their presence. Approximately 80% of log-fish and school-fish sets were in company with birds, and birds were present with virtually all porpoise-fish sets, regardless of area. The dominant bird species, as identified by the importance-ranking criterion, were usually boobies (*Sula* spp.) or boobies and shearwaters (*Puffinus* spp.) with log- and porpoise-fish sets; in the school-fish sets, the dominants were shearwaters or shearwaters and terns, *Sterna* especially (labeled histograms in Figures 2 and 3). The distribution of flock sizes of component species from the single-observer TMD data (Fig. 4) shows an increase in flocks and flock sizes of frigatebirds (*Fregata* spp.) and especially boobies in porpoise-fish sets relative to the other set types. Also, large tern flocks occurred primarily with school-fish sets. There was a shift toward larger shearwater flocks in the porpoise-fish sets off Mexico; the identifications indicate these were wedge-tailed shearwaters *Puffinus pacificus*.

Discussion

As yellowfin tuna grow, they become involved in changing species associations, some of which are polyspecific in nature, i.e., like the associations studied elsewhere that seem situation-dependent, opportunistic, and often casual. This is reflected in the changing pattern in the association rates (p) from log-fish to school-fish to porpoise-fish sets on tuna; it is this pattern, rather than the actual rate values, that is of significance. The rates themselves should be used cautiously as they are derived from data affected by observer interest and from samples that were not large.

Foraging associates

Logs, or other floating objects, seem to provide opportune sites for development of species associations. Not only can logs attract prey and predators, but they can also drift to convergences where species gather. The behavior of predators feeding near flotsam is not simple, however. If the arrival rate of prey should decrease sufficiently, a passively feeding predator may switch to active, wide-ranging foraging (see Gerritsen 1984).

The very common association of sharks with tuna and the strong decrease in this association from log- to school- to porpoise-fish sets suggest that sharks mostly encounter tuna near flotsam. Then, like gray reef sharks (carcharhinidae) that follow feeding carangid fish for leftovers (Enewetak Is., pers. observ.), these sharks might follow the yellowfin as both scavengers and predators. Such behavior is probably of decreasing advantage as the tuna grow and forage more widely and at faster speeds. The tuna themselves, in some situations, may be attracted to sharks, as they are to whale sharks (Stretta and Slepoukha 1986).

The overall association rate for most other species with yellowfin tuna averaged in the 10% range, including that of billfish, rays, turtles, and smaller tunas. The marlins probably follow tuna both as parasitic foragers and as predators; they share many prey species with tunas and also eat tunas, especially the smaller specimens (see Shomura and Williams 1975). Unlike the sharks, however, these powerful fish appear to have little difficulty keeping up with fast-moving tuna; their association rates did not appear different among set types. Manta rays and turtles probably represent the opposite situation, where the tuna initiate and maintain the associations, perhaps as an extension of their proclivity to investigate flotsam. This may be why rays tended to be taken more often in the school-fish sets. The large schools of black skipjack, bullet, and skipjack tunas that are frequently taken with log-associated yellowfin may be obtaining feeding and protective advantages, but these benefits likely decrease as the yellowfin grow. The smallest tunas would find it increasingly difficult to swim at the speed of the yellowfin, and the danger of predation by the larger fish would also increase. It is first the black and bullet tunas that decrease in school-fish sets; finally even skipjack become scarce in the sets on the large, porpoise-associated yellowfin.

The most conspicuous and strong association with tuna is that of seabirds. Most bird species can feed independently of tuna, but they feed closely with these fish at every opportunity. The flocks of terns and smaller shearwaters that feed with free-swimming tuna of school-fish sets suggest that these fish of mainly nearshore waters feed on abundant, smaller prey. The larger, more mature tuna are farther offshore, feeding on sparser but evidently still-rich food patches. Dolphins and the larger seabirds, i.e., boobies and wedge-tailed shearwaters, feed with them (see also Au and Pitman 1986). The dominating importance of boobies in both porpoise-fish and log-fish sets suggests they forage by a wide and fast-ranging search for all discontinuities at the sea surface, including that of surface-schooling tuna and dolphins. Such foraging would be particularly effective offshore, for the yellowfin there have been found to prey more on fish (i.e., on larger but likely more patchily distributed prey) and less on crustaceans than do nearshore-caught yellowfin (Olson and Boggs 1986).

The porpoise-fish sets are themselves a category of species association, although not treated above as such. The highly mobile dolphins and the tuna of these sets appear to feed actively together; they share many of the same prey species (Perrin et al. 1973).

Enhanced foraging may be the main advantage of polyspecific associations involving the larger, more mobile species of tropical, pelagic seas; this may stem from converging foraging tactics among these animals. Just as boobies and shearwaters race about over a feeding tuna school to maximize interceptions of fleeting and unpredictably surfacing prey, yellowfin and other large species, on a larger scale, should range rapidly over large expanses to find sparse and unpredictable, yet relatively rich, prey patches. Food overlap would be increased by such nomadic foraging (see Huey and Pianka 1981), and strong patchiness of prey should itself reduce the tendency of each species to exploit different spatial intervals of the spectrum of prey distribution (see Terborgh and Stern 1987).

Polyspecific tuna and dolphins

The tuna–dolphin association of the ETP is the association most similar to the polyspecific associations studied among primates and terrestrial birds, in that specific species appear to forage together without strong or obvious interactions. However, virtually all porpoise–fish sets are attended by birds that appear to be closely following the feeding tuna (Au and Pitman 1986). That and the high 80–90% successful set ratio of these sets compared with the other set types (Table 1) suggest that dolphins do not commonly feed with birds that are not also with tuna. These specific dolphins that feed with tuna are ecologically successful (i.e., abundant, especially relative to other non-tuna-associated dolphin species; Au and Pitman 1988). And since these dolphins are largely found within the habitat of surface-schooling yellowfin in the ETP (see Allen 1985 for distributions), and not the converse, it could be that dolphins exploit the feeding behavior of tuna more often than the reverse. If so, this would agree with what seems typical in polyspecific associations, that it is the behaviorally more-adaptive species that takes advantage. Considering further the opportunistic, casual nature typical of polyspecific associations, one should not be surprised that tuna and dolphins are not intimately associated in many other seas and even in certain areas within the ETP. Moreover, if either the tuna or the dolphins were to be overexploited where they are associated, dire (or propitious) consequences to the other of the pair need not be expected.

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