# 5

# Seabird Relationships with Tropical Tunas and Dolphins

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Flocks of seabirds accompanying surface-schooling tunas are characteristic of tropical seas, but are especially notable in the eastern tropical Pacific (ETP) where the birds also associate with dolphins. We recently described these species interactions (Au and Pitman 1986) from extensive ship surveys that entailed the examination of cetacean schools, particularly those associated with birds and tuna. Our observations enabled us to form an ecological perspective of species behaviors and interrelationships. There have been few other studies on the oceanic ecology of ETP seabirds, although the birds are much watched by fishermen as indicators of fish and fishing conditions. King (1970, 1974a) and Gould (1971) presented the first comprehensive descriptions of tropical central and eastern Pacific birds at sea, but as their observations were primarily from ships conducting oceanographic surveys, they had limited opportunities for closeup observations of feeding flocks and were not able to study the relationships with cetaceans.

In this essay we review the relationships between seabirds, tuna, and cetaceans as observed in the ETP and describe the ecological role of tunas. We will explain how the organization of, and interactions within, the apex pelagic community might depend upon forage and foraging tactics, especially that of the tunas—perhaps the key top predators of tropical seas. Our inferences will be based largely upon the behavior of the birds and dolphins, as the tuna were seldom directly observable.

## Data and Methods

Observations on birds, tuna, and cetaceans were obtained from both biological census and oceanographic ship surveys. Most important were the Southwest Fisheries Center (SWFC) dolphin surveys of 1976, 1977, 1979, and 1980, designed to assess the distributions and abundances of dolphins involved in the "porpoise-tuna" fishery of the eastern Pacific. These surveys provided information over a broad area overlapping the tuna fishing grounds. In addition to our participation on these biological surveys, Pitman studied birds, tuna, and cetaceans from ships conducting physical oceanographic studies in the central and eastern Pacific.

The search and much of the observations were conducted through twenty or twenty-five power binoculars, generally mounted both port and starboard on or above the flying bridge of each survey ship. We usually searched between 6 A.M. and 6 P.M., using two teams of observers. The high powered binoculars proved indispensable for closeup observations and for minimizing the overlooking of bird flocks and cetacean schools. On the dolphin surveys, most mammal schools were approached closely after initial detection for better observations (often within a hundred meters), as were bird flocks if they appeared to be associated with cetaceans. Flocks and schools were usually not approached on the oceanographic surveys. On all surveys, species were identified whenever possible, and numbers estimated for all flocks and mammal schools. We took notes on any tuna seen, but direct observations or measurements of these fish schools were not feasible.

Noon positions from the above cruises, shown in figure 5.1, illustrate survey coverage. The concentrations of survey days along certain lines is due to repeated hydrographic transects on the oceanographic cruises. Though there were surveys during every month, about 63 percent of the observations took place during January through March; there is thus a seasonal bias in our data. A monthly breakdown of observations is given by Pitman (1986), and a more detailed description of the dolphin surveys by Au and Perryman (1985).

## Flock Characteristics

We defined a flock as an aggregate of ten or more birds. We did not include storm-petrels, phalaropes, tropic birds, or the occasional gulls, as they feed largely independently of fish schools in pelagic waters and rarely occur with either tuna or cetaceans. The 1977, 1979, and 1980 dolphin surveys provided the most representative and accurate subset of our observations; these data are summarized in table 5.1 (flock associations) and table 5.2 (flock composition) by 5° latitude intervals and according to eastern and western sectors. We sighted a total of 637 flocks in the eastern sector, and 125 flocks in the western sector (table 5.1). Overall, few (25 percent) of these flocks were with cetaceans, although the association rates were high in certain areas (see below). If we assume that flocks of ten or more birds are associated with tuna, most tuna schools, then, were not with cetaceans.

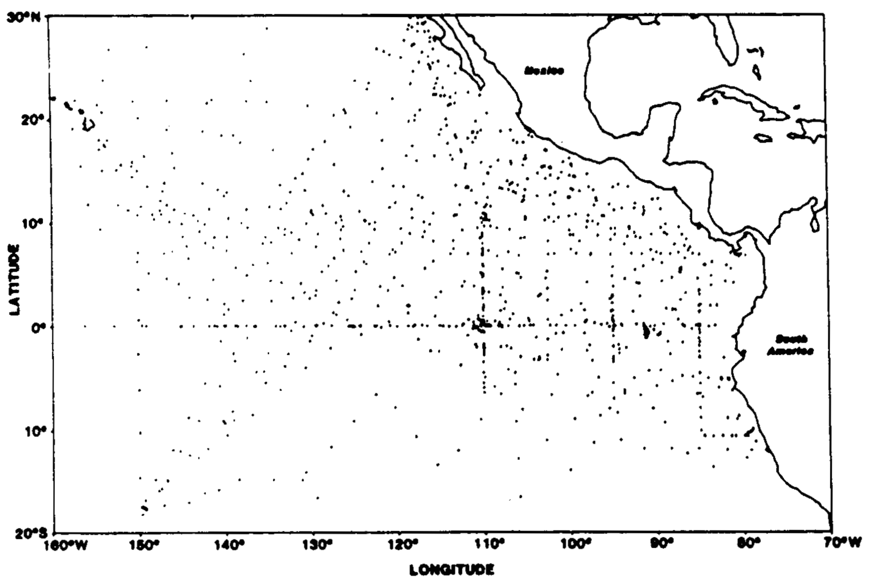


Figure 5.1. Noon positions of sea days during which a seabird watch was maintained.

Table 5.1. Percentage of seabird flocks associated with whale or delphinid cetaceans by area.

| Center of 5° Latitude Intervals | EASTERN SECTOR (COAST-125°W) | | | | WESTERN SECTOR (> 125°W–155°W) | | | |
|---|---|---|---|---|---|---|---|---|
| | Days observed | No. flocks | Pct. flocks with whales | Pct. flocks with delphinids | Days observed | No. flocks | Pct. flocks with whales | Pct. flocks with delphinids |
| 25°N | 16 | 6 | 0 | 0 | | | | |
| 20°N | 14 | 11 | 0 | 73 | 21 | 7 | 0 | 0 |
| 15°N | 35 | 104 | 0 | 68 | 15 | 19 | 0 | 0 |
| 10°N | 54 | 133 | 2 | 35 | 27 | 23 | 0 | 30 |
| 5°N | 49 | 126 | 2 | 27 | 22 | 51 | 0 | 8 |
| 0° | 38 | 108 | 2 | 4 | 11 | 13 | 0 | 0 |
| 5°S | 14 | 80 | 0 | 5 | 7 | 6 | 0 | 0 |
| 10°S | 11 | 69 | 1 | 7 | 8 | 5 | 0 | 0 |
| 15°S | — | — | 0 | 0 | 5 | 1 | 0 | 0 |
| Total | 231 | 637 | 1 | 27 | 116 | 125 | 0 | 9 |

NOTES: Flocks are defined as ≥ 10 birds; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded; each latitude interval is defined by its center latitude ± 2.5°.

Table 5.2. Species composition and species diversity of flocks by area.

| Sector | Center of 5° Latitude Intervals | Total Birds | PERCENT SPECIES COMPOSITION: boobies | sooty tern | WTSW | jaeger | frigate birds | LPT | other terns | other shear-waters | other petrels | SPECIES DIVERSITY: $\frac{1^a}{\Sigma Pi^2}$ | Spp. per[b] Flock |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Eastern (From Coast to 125°W) | 25°N | 151 | | | | 1 | 10 | | | 68 | 21 | 1.96 | — |
| | 20°N | 1,279 | 15 | 3 | 8 | 1 | + | 2 | 22 | 46 | 3 | 3.46 | 4.4 |
| | 15°N | 13,035 | 50 | 4 | 30 | 11 | 2 | + | 1 | 1 | + | 2.80 | 4.0 |
| | 10°N | 6,852 | 14 | 28 | 32 | 13 | 8 | 1 | 1 | 2 | + | 4.40 | 4.2 |
| | 5°N | 9,358 | 42 | 20 | 13 | 2 | 5 | + | 17 | + | + | 3.75 | 3.3 |
| | 0° | 4,092 | 7 | 90 | 1 | + | + | + | 1 | + | | 1.22 | 1.2 |
| | 5°S | 3,696 | + | 94 | | + | 2 | | 4 | | + | 1.12 | 1.3 |
| | 10°S | 5,366 | 6 | 47 | | 1 | 1 | 2 | 43 | | + | 2.43 | — |
| | 15°S | | | | | | | | | | | | |

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Western (From > 125°W to 155°W) | 25°N | | | | | | | | | | | | |
| | 20°N | 100 | 2 | 76 | | | 9 | 13 | | | | 1.66 | |
| | 15°N | 1,076 | + | 64 | 16 | 6 | | 10 | 1 | 3 | 1 | 2.23 | — |
| | 10°N | 3,355 | + | 69 | 8 | 2 | | 19 | + | 1 | + | 1.92 | 3.0 |
| | 5°N | 2,439 | + | 68 | 7 | 1 | | 15 | + | 1 | 7 | 2.02 | 2.7 |
| | 0° | 4,239 | | 88 | 4 | + | | 4 | 1 | 1 | 2 | 1.29 | 2.3 |
| | 5°S | 6,983 | 1 | 97 | 1 | + | 1 | | | | 1 | 1.07 | 2.2 |
| | 10°S | 2,576 | + | 52 | 1 | | 2 | + | 40 | + | 4 | 2.29 | — |
| | 15°S | 1,538 | + | 40 | | | 1 | | 57 | + | 2 | 2.07 | — |

NOTES: Flocks are defined as ≥ 10 birds; flocks were evaluated whether or not cetaceans were present; data from January–February cruises, 1977, 1979, 1980; percentages have been rounded: each latitude interval is defined by its center latitude ± 2.5°.

Abbreviations: WTSW = wedge-tailed shearwater; LPT = large pterodroma: Juan Fernandez/white-necked/dark-rumped petrels; + = small percent < 1.0.

[a] Simpson's Index.

[b] Mean spp. per flock weighted by flock size; dash indicates unreliable data; for dolphin-associated flocks, mean spp./flock was 4.4 (s = 2.0) in eastern sector and 1.9 (s = 1.2) in western sector (Au and Pitman 1986).

## *Dichotomy in the Pelagic Community*

Two distinct faunal communities involving seabird flocks occur in the ETP, and suggest a strong, regional change either in prey or in the responses of predators to prey. The dichotomy separates multispecies flocks often associated with delphinid cetaceans from virtually single-species flocks seldom with delphinids (i.e., dolphins and other small, toothed "whales"). This separation occurs between latitudes 0° and 5°N and approximately corresponds with the oceanographic division between the permanently warm (> 25°C) and low salinity (< 34°/p.p.t.) Tropical (Surface) Water and the Equatorial (> 34°/p.p.t.) and Southern Subtropical (> 35°/p.p.t.) waters (see Wyrtki 1966; Ashmole 1971).

### *Northern (Tropical Water) Flocks*

The Northern, or Tropical Water, flocks in the eastern sector were notable for frequently being with delphinid cetaceans: 68 percent and 73 percent of flocks from the 15°N and 20°N (± 2.5°) latitude intervals, respectively, were with delphinids (table 5.1). Associations with whales in these latitudes were infrequent (0–2 percent). These flocks (table 5.2) were typically multispecies aggregates of boobies—primarily red-footed *(Sula sula)*, masked *(S. dactylatra)*, and brown *(S. leucogaster)*—and wedge-tailed shearwaters *(Puffinus pacificus)*, sooty terns *(Sterna fuscata)*, and jaegers *(Stercorarius* spp.) (see appendix 5.1 for a list of species names). Boobies were most abundant, composing 42 percent and 50 percent of individuals in flocks in the latitude intervals centered at 5°N and 15°N. Their reduced importance about the 10°N interval was due in part to sampling near the Costa Rica Dome, a localized upwelling regime (Wyrtki 1964) that does not normally produce good catches of yellowfin tuna (the significance of which will be explained below).

In the western sector the northern flocks were associated with delphinids mainly within the 10°N interval (a much narrower zonation than seen to the east) where the association rate was 30 percent. As in the east, whales appeared unimportant to seabirds; none were seen with flocks. The species composition of these flocks was different from that of flocks farther to the east, and thus comprised a second type of multispecies community consisting mainly of sooty terns and Juan Fernandez/white-necked petrels (*Pterodroma externa externa/cervicalis*—subspecies that are difficult to separate in the field).

*Southern (Equatorial and Southern Subtropical Water) Flocks*

South of the 5°N latitude interval, in Equatorial and Southern Subtropical waters, but primarily the latter, flocks in the eastern sector occurred infrequently with delphinid cetaceans (table 5.1), in sharp contrast to the northern multispecies flocks. The southern flocks were clearly dominated by sooty terns (table 5.2) which composed 90 percent or more of birds in flocks in the 0° and 5°S latitude intervals, mainly in the areas away from islands.

In the west none of the southern flocks encountered were associated with either delphinids or whales. The sooty tern was still the most abundant species, up to 97 percent of the birds in all flocks. White terns *(Gygis alba)* and noddy terns (*Anous* spp.) were an increasing component of the flocks in the far southern latitudes; the latter terns were especially abundant near islands.

## *Species Diversity Differences*

The transition and difference between the northern and southern seabird communities are reflected in latitudinal changes in species diversity. Values of Simpson's Dominance Index $\frac{1/\Sigma p_i^2}{p_i^2}$ where $p_i$ is the fraction of total birds that are species i) and of the average number of species per flock are given in the last two columns of table 5.2. Here the index could vary between 1.0 for flocks completely dominated by one species to 9.0 for flocks with individuals evenly divided among all nine categories of species. Simpson's Index is one of the more useful and easily understood measures for describing species in communities (Hill 1973) and shows that flocks in the northern latitude intervals, 20°N to 5°N, were on average 3.1 to 1.7 times more diverse than were flocks in the intervals 0° and 5°S, in the eastern and western sectors respectively. The southern flocks had index values close to 1.0 due to dominance by sooty terns. Data in the species per flock column suggest a decline in the average number of species from northern to southern latitudes (from ca. 4 to 1 spp./flock), at least in the eastern sector. Although there were difficulties in observing and identifying species from non–dolphin-associated flocks, this measure indicates areawide changes in diversity similar to those shown by Simpson's Index.

■

## Seabirds and Cetaceans

As a group, seabirds associate only with specific cetaceans, a fact reflecting an underlying, probably feeding, relationship. This is shown in table 5.3, a summary of schooling and bird association characteristics of ETP whales and delphinids, again mainly from the more representative 1977, 1979, and 1980 dolphin surveys. Study of this table will give the reader an appreciation of the structure of the pelagic community under discussion, including the relative abundance of the different Cetacea and the likelihood (percent occurrence) of finding particular bird species in the associated flocks. In judging relative abundance, however, one should remember that different species vary in their detectability according to their size (school and individual) and behavior (including association with birds).

### *Associations with Dolphins*

Of all Cetacea, spotted *(Stenella attenuata)* and spinner *(S. longirostris)* dolphins are associated most often with birds: 74 percent and 78 percent, respectively, of these species' schools were with flocks (table 5.3: first two species, col. 6). A high percentage of these schools included other cetaceans, 79 percent in the case of the spinner dolphin (col. 5). Most of this mixing involved these two species themselves: of the 113 spinner dolphin schools, 67 percent were mixed with spotted dolphins and of 206 spotted dolphin schools, 37 percent were mixed with spinner dolphins. Both of these dolphins occurred in large schools, averaging 150 and 133 individuals respectively (col. 3), and were associated with large flocks averaging 121 and 147 birds respectively (col. 7). The standard deviations (s) of these measures were large relative to the means, due to size distributions skewed toward the larger sizes. The bird species most likely present (high percent occurrence) in flocks with these dolphins were boobies (*Sula* spp.), frigate birds (*Fregata* spp.), wedge-tailed shearwaters, and jaegers, generally in that order. Spotted and spinner dolphins are diurnally active—i.e., fast swimming ("porpoising"), leaping often—and are frequently associated with yellowfin tuna. Both are pursued by purse seiners in "porpoise-tuna" fishing, a technique in which tuna are first caught with dolphins, then retained as the mammals are subsequently released.

Table 5.3. Summary of cetacean species encountered and their associations with seabirds: Characteristics of schools and flocks.

| SPECIES | SCHOOLS | | | | | ASSOCIATED FLOCKS | | | COMMENTS |
|---|---|---|---|---|---|---|---|---|---|
| | *n* | $\bar{x}$ | *s* | *Pct. mixed*[a] | *Pct. with flocks* | $\bar{x}$ | *s* | *Spp. of > 50% occur*[b] | |
| Spotted dolphin *(Stenella attenuata)* | 206 | 150 | 177 | 40 | 74 | 121 | 219 | booby –82%<br>frigate –70<br>WTSW–57<br>jaeger –53 | Main target of "porpoise-tuna" fishing; diurnally active (leaping, fast swimming) sp.; mixed schools usually with spinner dolphin. Frequently with flocks; epipelagic prey (Perrin et al. 1973). |
| Spinner dolphin *(Stenella longirostris)* | 113 | 133 | 207 | 79 | 78 | 147 | 258 | booby –73%<br>frigate –69<br>jaeger –62<br>WTSW–54 | Second most important dolphin in "porpoise-tuna" fishing; diurnally active, usually mixed with spotted dolphins; frequently with flocks. Epi- and mesopelagic prey (Perrin et al. 1973). |
| Common dolphin *(Delphinus delphis)* | 62 | 129 | 176 | 6 | 39 | 38 | 46 | booby –70% | Less involvement in "porpoise-tuna" fishing; often escapes with tuna from nets; very active diurnally; third most frequent dolphin with flocks. May feed on deep prey (Fitch and Brownell 1968). |

Table 5.3. (continued)

| SPECIES | SCHOOLS | | | | | ASSOCIATED FLOCKS | | | COMMENTS |
|---|---|---|---|---|---|---|---|---|---|
| | *n* | $\bar{x}$ | *s* | *Pct. mixed*[a] | *Pct. with flocks* | $\bar{x}$ | *s* | *Spp. of > 50% occur*[b] | |
| Striped dolphin (*Stenella coeruleoalba*) | 139 | 54 | 62 | 9 | 7 | 15 | 24 | | Common, diurnally very active species in relatively small schools; seldom with birds or tuna. May feed on mesopelagic prey (Miyazaki et al. 1973). |
| Bottlenose dolphin (*Tursiops truncatus*) | 119 | 25 | 59 | 41 | 13 | 11 | 12 | | Often with *Globicephala*, *Grampus*, *Steno*; sometimes with *Stenella*; often approaches ships; not with large flocks. |
| Risso's dolphin (*Grampus griseus*) | 106 | 11 | 18 | 20 | 3 | 16 | 17 | | Often with *Tursiops*, *Globicephala*, traveling slowly. Seldom with birds. |
| Pilot whale (*Globicephala macrorhynchus*) | 98 | 14 | 12 | 37 | 4 | 11 | 11 | | Often with *Tursiops*, *Grampus*; appears to be resting much of the time. Seldom with birds. |
| Rough-toothed dolphin (*Steno bredanensis*) | 54 | 12 | 10 | 15 | 35 | 12 | 15 | booby –72%<br>frigate –72 | Sluggish behavior; often near flotsam; sometimes with *Tursiops*, *Globicephala*, *Grampus*; fourth most frequent dolphin with birds. |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Melon-headed whale *(Peponocephala electra)* | 4 (42 | 194 | 151 | 75 17 | 25 7)[c] | 1 | — | Diurnally active; often in large, dense schools with *Lagenodelphis*. Seldom with birds. |
| Fraser's dolphin *(Lagenodelphis hosei)* | 10 (23 | 391 | 576 | 40 44 | 20 13)[c] | 2 | — | Often in large, densely packed, fast-moving schools with *Peponocephala*. Schools often execute coordinated turning and diving. |
| Pygmy killer whale *(Feresa attenuata)* | 9 | 37 | 18 | 0 | 0 | — | — | Appears to rest during the day; may approach ships. Seldom with birds. |
| False killer whale *(Pseudorca crassidens)* | 19 | 13 | 13 | 26 | 10 | 12 | 5 | Sometimes with *Tursiops*; will approach ships at high speeds; not with large flocks. |
| Killer whale *(Orcinus orca)* | 8 | 7 | 4 | 12 | 12 | 20 | — | Small schools, usually loosely aggregated; not with large flocks. |
| Rorquals (baleen whales)[d] | 94 | 2 | 1 | 3 | 3 | 43 | 27 | Generally feed near surface on small fish and crustaceans; seldom with birds. |
| Ziphiids (beaked whales) | 85 | 2 | 2 | 1 | 0 | — | — | Deep feeder; shy and inconspicuous. Not with birds. |
| Sperm whale *(Physeter macrocephalus)* | 63 | 8 | 7 | 8 | 2 | 2 | — | Deep feeders; sometimes in large aggregations. Rarely with birds. |
| Dwarf/pygmy sperm whale *(Kogia spp.)* | 30 | 2 | 1 | 0 | 0 | — | — | Difficult to see except in calm seas. Not with birds. |

NOTES: Numbers in table rounded for greater clarity; standard deviations not calculated for $n < 10$; birds counted regardless of flock size; n = number of schools, $\bar{x}$ and s refer to school or flock size.

Abbreviations, *see* table 5.2.

[a] i.e., school mixed with other cetacean sp.

[b] Listed here are bird spp. and their percentage occurrence in flocks associated with the given cetacean sp., provided the percentage was ≥ 50 and flocks ≥ 10 birds. WTSW = wedge-tailed shearwater.

[c] From larger sample from all research ship observations, and also including *Feresa* schools.

[d] Mostly Bryde's whale.

The common dolphin *(Delphinus delphis)* was the third most frequent species of dolphin found with bird flocks, although the percentage of its schools found with flocks was much lower (39 percent). This species also forms large ($\bar{x}$ = 129), actively porpoising schools. Boobies, and also wedge-tailed shearwaters and frigate birds, often occurred in flocks associated with this dolphin. Fishermen do not regularly catch tuna with the common dolphin.

The last of the more frequently encountered, active delphinids, the striped dolphin *(Stenella coeruleoalba)*, is seldom found with birds. It usually occurred in fast-moving and often high-leaping, relatively small, unmixed schools ($\bar{x}$ = 54) that were without indications of associated tuna. It is seldom deliberately fished on by purse seiners.

With two exceptions (see below) the remaining delphinids occur in small schools that are seldom with birds, and perhaps never with large flocks. Except for the false killer whale *(Pseudorca crassidens)*, all are relatively slow moving. And although the sluggish-behaving rough-toothed dolphin *(Steno bredanensis)* would seem to be an exception in that 35 percent of its schools were recorded with birds, we saw no evidence to indicate that this or any other other of these remaining dolphins occurred with tuna.

The melon-headed whale *(Peponocephala electra)*—sometimes called the electra dolphin—and Fraser's dolphin *(Lagenodelphis hosei)* are also seldom with birds, but yet they are like the bird-associated spotted and spinner dolphins in being diurnally active, fast moving, and in large schools ($\bar{x}$ = 194 and 391, respectively), often mixed together. A sample from all research ship sightings between 1976 and 1981 that included all schools that were at least very likely either *Peponocephala* or *Feresa attenuata* (pygmy killer whale)—two species difficult to distinguish—gave twenty-three *Lagenodelphis* schools, of which only 13 percent were with bird flocks, and forty-two either *Peponocephala* or *Feresa* schools, of which only 7 percent were with birds (see bracketed results in table 5.3). It is clear, therefore, that birds are not strongly associated with any of these three dolphins.

### *Associations with Whales*

We sighted many species of whales, and found they are generally not associated with birds (table 5.3). The rorquals we observed included blue *(Balaenoptera musculus)*, minke *(B. acutorostrata)*, sei *(B. borealis)*, and Bryde's *(B. edeni)* whales; these occurred singly or in small groups, all rarely with flocks. The ziphiid, or beaked whales, were also in small groups and were never seen with birds. Sperm whales *(Physeter macrocephalus)*, occasionally in large groups, were only rarely with birds. The related pygmy/dwarf sperm whales (*Kogia* spp.) were not seen with birds.

## Seabirds, Dolphins, and Yellowfin Tuna

### *The Predominance of Spotted/Spinner Dolphins with Seabirds*

Clearly, only spotted and spinner dolphins in the ETP are commonly associated with seabirds, an indication of underlying behavioral interactions that are very species specific. This predominance is made clear in figure 5.2, which shows the percentage of schools of the different dolphins that were with flocks, as well as the percentage of all associated flocks occurring with each dolphin species. Separate histograms are given for latitudes 5°N to 30°N (Tropical Water) and < 5°N to 12°S (Equatorial and Southern Subtropical waters). Among the spotted and spinner dolphins, in mixed or in pure schools, schools with spotted dolphins were usually most often with birds, particularly in the 5°N to 30°N Tropical Water.

The relationship of birds to spotted dolphins appears to be stronger than that of birds to spinner dolphins. Of the 242 flocks in table 5.3, 63.2 percent were associated with at least some spotted dolphin as opposed to 43.0 percent with at least some spinner dolphin. Also, 34.7 percent of these flocks were with unmixed spotted dolphin but only 10.3 percent with unmixed spinner dolphin schools. Most spinner dolphin schools associated with birds (78 percent of 113 = 88 schools; table 5.3) were also with spotted dolphins (76.1 percent of 88). Flocks were less likely to be with unmixed spinner dolphin schools in northern tropical waters and more likely in waters to the south (figure 5.2). This was because most bird-associated spinner schools in the northern waters were also with the spotted dolphin.

While this strong relationship of seabird flocks to spotted and spinner dolphins is characteristic of the Tropical Water habitat north of the equator, and also of the area south of the Galapagos Islands during the southern summer (December to February), these dolphins are relatively infrequently with birds elsewhere (compare the two latitude intervals in figure 5.2). This is so particularly in areas southwest of the Galapagos Islands, in spite of the abundance of flocks there. Table 5.4 shows the reduction in equatorial and southern latitudes of both the schools of these two dolphins and the percent of these schools that were associated with flocks of more than ten birds.

### *The Yellowfin Tuna Link*

*Tuna Under Flocks*

Seabirds in flocks appear to feed mainly on prey driven to the surface by tunas, which are the only sizable pelagic fishes known to form abundant and large surface schools in the tropical ocean. Not infrequently we have been able to identify the predatory fish under

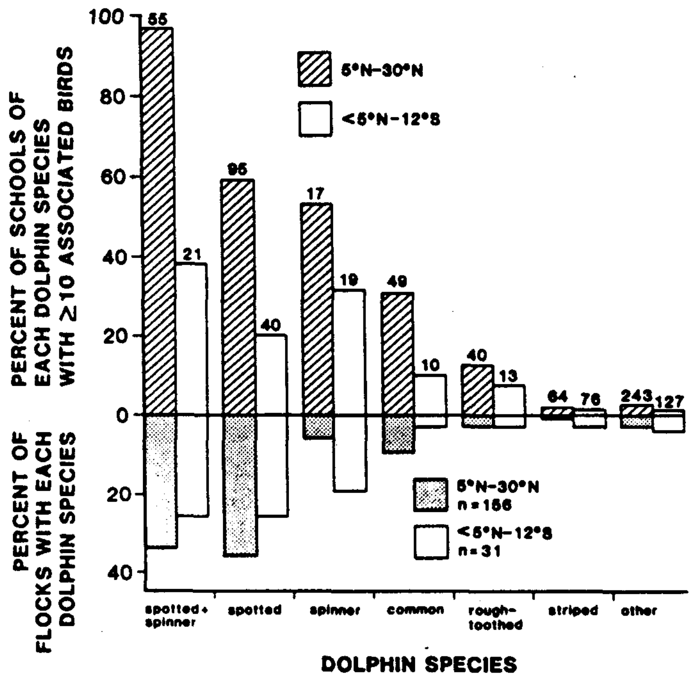


Figure 5.2. The rate of association of different dolphins with bird flocks (above) and the percent of these dolphin-associated flocks with each dolphin species (below). Numbers over the bars are the schools examined.

**Table 5.4. Areawide differences in the percentage of spotted and spinner dolphin schools with bird flocks.**

| Center of Latitude Intervals | COAST TO 125°W | | | > 125°W TO 155°W | | | TOTALS | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Schools with flocks | | | Schools with flocks | | | Schools with flocks | |
| | Schools | n | % | Schools | n | % | Schools | n | % |
| 20°N | 9 | 3 | 33 | | | | 9 | 3 | 33 |
| 15°N | 76 | 51 | 67 | | | | 76 | 51 | 67 |
| 10°N | 50 | 33 | 66 | 11 | 5 | 46 | 61 | 38 | 62 |
| 5°N | 67 | 32 | 48 | 3 | 3 | 100 | 70 | 35 | 50 |
| 0° | 28 | 3 | 11 | 3 | 1 | 33 | 31 | 4 | 13 |
| 5°S | 15 | 3 | 20 | 1 | 0 | 0 | 16 | 3 | 19 |
| 10°S | 6 | 5[a] | 83 | 3 | 0 | 0 | 9 | 5 | 56 |
| Total | 251 | 130 | | 21 | 9 | | 272 | 139[b] | |

NOTES: Data from research cruises in 1976, 1977, 1979, 1980; some schools near land are deleted; flocks are of size ≥ 10 birds. Each latitude interval is defined by its center latitude ± 2.5°.

[a]These associated flocks were encountered south of the Galapagos Islands and west of Peru, where the porpoise-tuna fishery extends during the southern summer.

[b]58.8% of schools in latitude intervals ≥ 5°N (± 2.5°) were with flocks of size ≥ 10; only 21.4% of schools in latitude intervals < 5°N (± 2.5°) were with such flocks. This differential is significant ($X^2$, $P < 0.005$).

a feeding flock as tuna (see also Murphy and Ikehara 1955; Ashmole and Ashmole 1967). The strongest evidence linking birds and dolphins to tuna is the existence of the "porpoise-tuna" fishery of the eastern Pacific, in which purse seiners catch yellowfin and to a lesser extent skipjack *(Katsuwonus pelamis)* tuna that swim with dolphins. These tuna, and the associated dolphins, are found mainly by searching the horizon for birds. Spotted, spinner, and common dolphins (ranked by importance) are the primary cetaceans involved in that fishery (Hammond 1981; Smith 1979). These are the same species, and order of importance, of dolphins that are associated with bird flocks, indicating that birds and dolphins are associated because of a tuna relationship.

*The "Porpoise-Tuna" Fishery*

The extent of the fishing grounds for surface-caught yellowfin is shown in figure 5.3 with the distribution of sightings of spotted dolphin superimposed (the distribution of spinner dolphin is nearly the same). The similarity of these distributions indicates an intimate species interaction, although such a result could be an artifact of joint fishing on both species by the purse seiners that supplied the data to the SWFC. However, the general pattern of the dolphin distribution has been confirmed by fishery-independent surveys (Au and Perryman 1985). Dolphin-associated yellowfin tend to be large ($\bar{x} = 120$ cm, $s = 22$ cm, years 1981–85) (see also Allen 1985) with sizes overlapping into the range of smaller yellowfin not caught with dolphins and of larger, deep-dwelling yellowfin that are caught by longline gear. Appendix 5.2 shows the relationship between tons of yellowfin caught and sizes of the associated dolphin schools on the purse seine grounds. The porpoise-tuna fishery indicates that seabirds and dolphins are linked via a relationship (probably feeding) with large yellowfin tuna.

■

## The Ecology of Flocks

### *Species in Dolphin-Associated Flocks*

*Composition*

The species composition of dolphin-associated flocks shows the same regionwide differences among flocks in general. The important bird species that make up flocks associated with spotted and spinner dolphins are shown in figure 5.4, where again the histogram is separated for latitudes 5°N to 30°N and 5°N to 12°S. As in table 5.2, boobies, wedge-tailed shearwaters, jaegers, sooty terns, and frigate birds were numerically most important, in that order, in the dolphin-associated flocks from the northern Tropical Water habitat (5°N–30°N).

In the southern waters (< 5°N–12°S) boobies and sooty terns predominated; however, they were not usually in the same flocks. Boobies occurred mainly in flocks not too distant from coasts, while the sooty tern—more usually in virtually single-species flocks not with dolphins—was characteristic of the far offshore flocks (tables 5.1, 5.2).

*Species Associations*

Boobies, wedge-tailed shearwaters, jaegers, and frigate birds were found to be positively associated in dolphin-associated flocks from the Tropical Water purse seine fishing grounds, while frigate birds and sooty terns were positively associated in mainly the outer areas

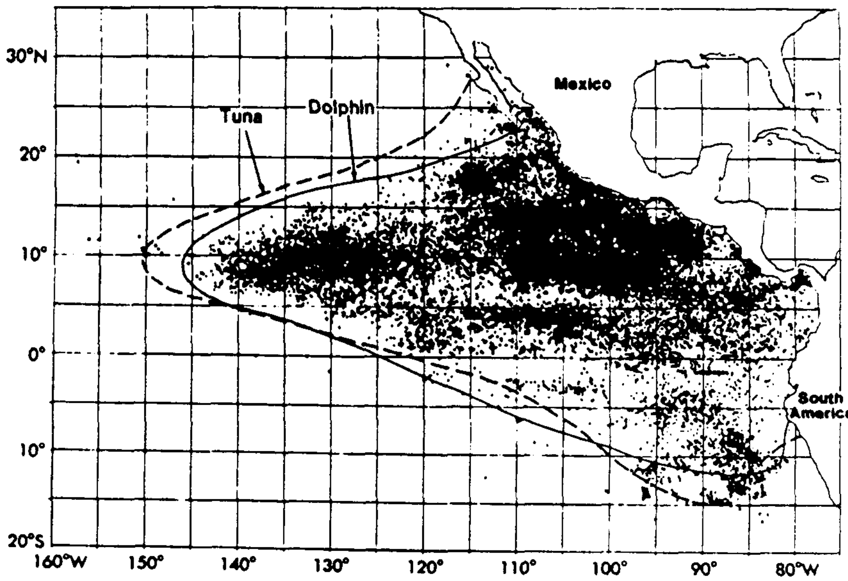


**Figure 5.3.** The distribution of records of spotted dolphins (dots and solid boundary, after Perrin et al. 1983) in relationship to the yellowfin tuna purse seiner grounds (dashed boundary, after Calkin's (1975) map of areas that produced 25+ tons of yellowfin catch).

of that habitat (Au and Pitman 1986). Table 5.5 is an extract of that analysis, showing percent co-occurrence of different bird species both in those flocks in which the species occurred, and in all flocks. The significant positive associations are also indicated. A schematic interpretation of this association complex is given in figure 5.5, where two measures of strength of association between species pairs are presented: Cole's (1949) coefficient and Yule's contingency index (see Pielou 1969:164). Our data indicate that none of the associations are very strong. The figure suggests that frigate birds are positively associated with other species in all habitats. The simplest explanation of these positive associations is attraction to common feeding opportunities.

### *Feeding Tactics/Strategies*

*Multispecies Flocks and Facultative Commensals*

Within multispecies flocks, simultaneously different, species-specific feeding behaviors suggest prey aggregations that are diverse

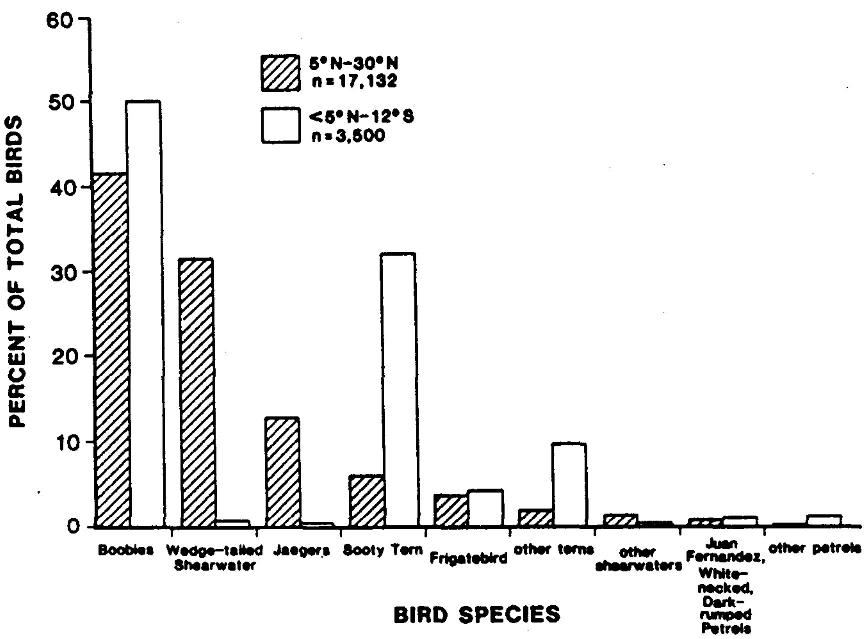


Figure 5.4. Likelihood (percentage frequency) of finding bird species in flocks associated with spotted and spinner dolphins.

**Table 5.5. Percentage of co-occurrence of species pairs in flocks.**

| | | *Boobies* *n* = 111 | *Frigate Birds* *n* = 90 | *WTSW* *n* = 82 | *Large Pterodromas* *n* = 18 | *Jaegers* *n* = 80 |
|---|---|---|---|---|---|---|
| Sooty tern | % n | 45 | 53* | 49 | 56 | 46 |
| | (% total) | (38) | (37)* | (31) | ( 8) | (28) |
| Boobies | % n | | 90* | 90* | 44 | 92* |
| | (% total) | | (62)* | (56)* | ( 6) | (56)* |
| Frigate birds | % n | | | 72 | 50 | 75 |
| | (% total) | | | (45) | ( 7) | (46) |
| WTSW | % n | | | | 50 | 74* |
| | (% total) | | | | ( 7) | (45)* |
| Large Pterodromas | % n | | | | | 11 |
| | (% total) | | | | | ( 7) |

NOTES: From $n$ = 131 flocks associated with spotted or mixed spotted and spinner dolphin schools in latitudes 5°N–30°N in the eastern Pacific; example: sooty terns co-occurred with boobies in 45 percent of the 111 flocks containing boobies, and in 38 percent of all 131 flocks; * indicates a significant positive association between the species pair (by $X^2$, $P < 0.05$); there were no significant associations detectable among the thirty-three spotted/spinner dolphin–associated flocks from latitude < 5°N.

WTSW = wedge-tailed shearwater.

with respect to behavior, distribution in the water column, size, or species composition (we will refer to this diversity as prey "configuration"). Boobies, flying rapidly back and forth, especially over the advancing front of a tuna school, wheel and plunge after their prey or make midair captures. Wedge-tailed shearwaters seemingly race with the boobies, but at lesser heights, and then drop to the water in surface plunges or for contact dipping or surface seizing of prey that appear available for at least several seconds. Jaegers, taking prey by aerial pursuit and dipping, and occasionally by piracy, add to the scene of frantic activity (feeding methods are defined by Ashmole [1971]). By rapidly covering the school, birds of each species increase their encounter rate with unpredictably available and fleeting prey. Sooty terns employ another tactic—they watch widely and deep into the water for developing feeding opportunities from positions high above. Their prey appear to be grouped, for the entire

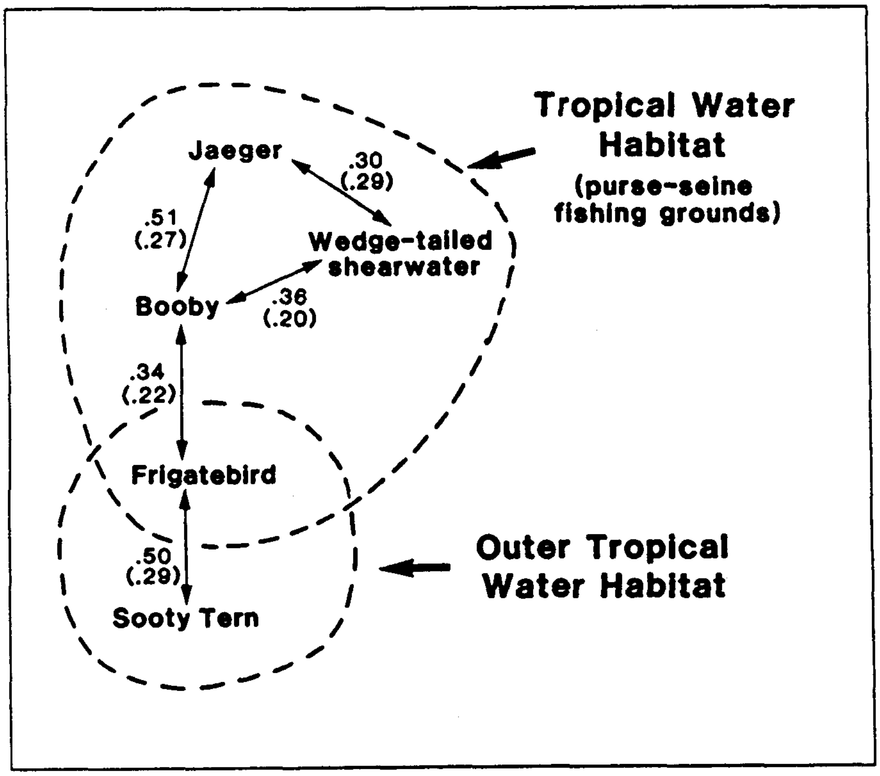


Figure 5.5. Positive species-association links within flocks, with strength-of-association coefficients (Cole's and Yule's [in parentheses] coefficients) shown.

flock will swoop down synchronously. Frigate birds soar high above the feeding melee and swoop down at opportune moments after individual prey that are likely larger than that of the terns.

Except for sooty terns and frigate birds, most birds that occur in these multispecies flocks are facultative commensals with tuna. When feeding independently, these birds occur singly or in small groups, and aerial feeding is rarely seen. Petrels and shearwaters, for example, then rely more on scavenging or preying upon free-floating organisms such as *Velella* (Pitman personal observations). Boobies, however, appear to feed independently of tuna the least, and their distribution most closely coincides with that of the yellowfin tuna fishery (cf. figures 5.3 and 5.6, considering also the low-density, westward extension of booby habitat [below]). Boobies are both the most abundant of birds in flocks over tuna and dolphins (figure 5.4) and the most abundant of seabirds in the northern Tropical Water (Pitman 1986), with colonies in the eastern Pacific that are probably the world's largest (Nelson 1978). The abundance of boobies is likely a direct consquence of their strong association with yellowfin.

*"Obligate" Commensals*

In contrast to the facultative commensals, sooty terns and frigate birds are almost never seen feeding independently of tuna in oceanic

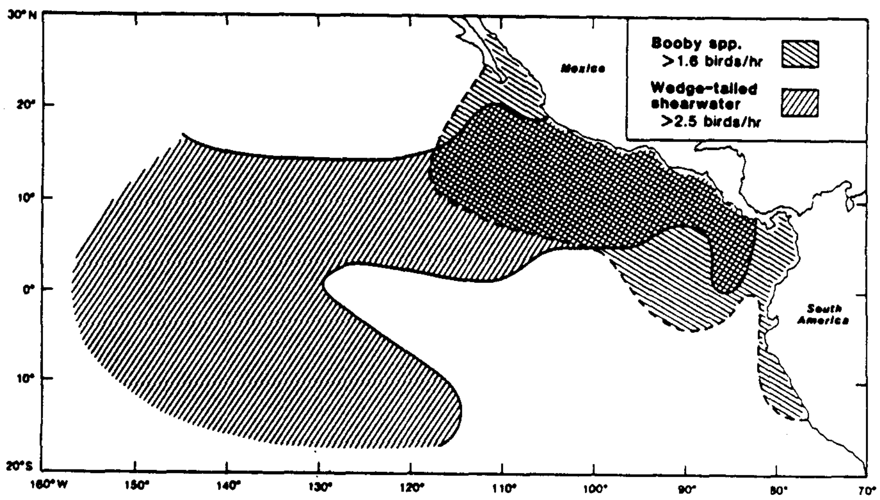


Figure 5.6. Booby and wedge-tailed shearwater habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

areas; they appear to be near-obligate commensals with these fish. The sooty tern, in particular, is most abundant beyond the yellowfin fishing grounds, where the tuna it feeds with are generally small, probably skipjack (Hida 1970), but possibly also frigate mackerel (*Auxis* spp.; see Olson and Boggs 1986) or small yellowfin and bigeye tuna *(Thunnus obesus)*. It is the most abundant seabird of the southeastern and central Pacific (Pitman 1986; Gould 1974). In the former area, there is apparently little opportunity for feeding independently of tunas; facultative commensals (i.e., most other birds) are virtually excluded from those waters, apparently being unable to feed either with sooty terns or independently (table 5.2 and below). The obvious ecological success of the sooty tern probably stems from its ability to follow and feed with the small tuna.

## *Feeding Regimes*

### *Species Distribution*

Distinctly different distributions of four birds that occur in flocks illustrate how the community dichotomy is formed from seabirds that seem to feed differently. The distributions are depicted in figures 5.6 and 5.7, where a single contour is used to enclose areas of higher population density of each species. These were derived from distribution and relative abundance studies by Pitman (1986). Each species' contour approximately delimits areas where densities were greater than that species' median sighting rate (birds per hour). Figure 5.6 shows boobies and wedge-tailed shearwaters inhabiting the Tropical Water north of the equator, but seldom occurring in a large area of the southeastern tropical Pacific west of the Peru Current. The habitat of the wedge-tailed shearwater extends into the eastern Pacific from broad areas to the west, while that of boobies extends from the east, westward with the yellowfin tuna fishing grounds. The lower-density (less than median sighting rate) habitat of boobies (primarily the masked booby) extends far west of Clipperton Island—at 10°N, 109°W (Pitman 1986) (this is not shown clearly in figure 5.6 because areas of greater than median sighting rate of boobies, especially the red-footed booby, are compressed toward the American coasts). Figure 5.7 shows an extensive high-density area of the sooty tern habitat in the central Pacific, extending into the Subtropical Water of the southeastern Pacific, the area with a dearth of boobies and wedge-tailed shearwaters. The high-density areas of this tern are sparse in the Tropical Water north of the equator. Finally, Juan Fernandez/white-necked petrels occur in a band about latitude 10°N, especially to the west of longitude 110°W.

Not shown is the jaeger habitat, mainly within a thousand-kilometer-wide band along the coast of Middle America, and the fact that the larger seabirds are relatively uncommon along the equator, being replaced there by plankton-feeding storm petrels. The distributions of the seabirds also vary seasonally; in particular, sooty terns probably extend farthest into the southeastern Pacific during the southern summer.

*Regional Prey Differences*

The northern (Tropical Water) and the southern (Equatorial and Southern Subtropical waters) habitats of the ETP thus appear to have different prey characteristics or configurations that require different foraging tactics, as indicated by community differences in seabird species and their interactions. In the northern Tropical Water, prey patches appear to be relatively large and to have diverse kinds of prey. Once found, hundreds of birds and dolphins (see table 5.3) and yellowfin (e.g., 10 tons of fish 60 lbs or greater; see IATTC 1984 and appendix 5.2) may feed upon the patch. Feeding many continue for some time (we have watched this activity for nearly an hour before continuing on). Under such conditions, satiated birds, e.g.,

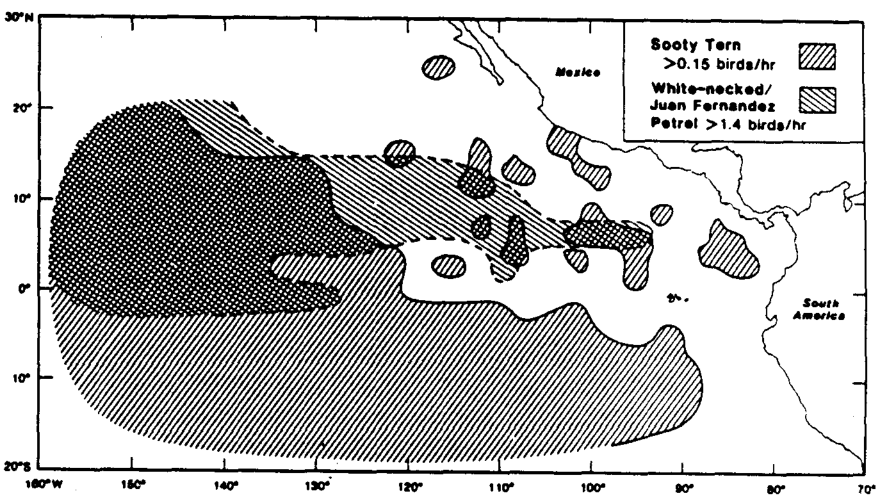


Figure 5.7. Sooty tern and white-necked/Juan Fernandez petrel habitats. Each shaded area delimits regions of greater than median sighting rate of the species (birds/hour). After Pitman 1986.

boobies, petrels, and especially shearwaters, may rest upon the water while others continue to feed (personal observation). In contrast, prey in the less productive southeastern and central Pacific appear to be in small, ephemeral, and thinly scattered patches of simple configuration, judging by the behavior and composition of feeding flocks. The buoyantly flying sooty tern especially, which is unable to rest long, or at all, upon the water, is evidently adapted for exploiting such prey, whose availability appears to change quickly, lending few opportunities for heavy feeding. These habitat differences probably reflect dissimilarities in biological productivity. The northern Tropical Water is richest because of its proximity to land and mechanisms that carry nutrients across its strong, shallow thermocline (Brandhorst 1958; Wyrtki 1966).

*Pertubations*

If prey characteristics select for particular bird-tuna-dolphin interactions, environmental perturbations could alter these behaviors through effects on forage. During the 1982–83 El Niño warming event in the Pacific (Philander 1983), fishermen experienced a 25 percent reduction in the yellowfin tuna catch (IATTC 1984) and reported fewer porpoise-tuna schools. Because El Niño episodes usually result in reduced biological production and a deepened thermocline (see Barber and Chavez 1983), a weakened tuna-dolphin association might be expected, as is characteristic of the deep-thermocline and less productive southeastern and central Pacific. We looked for such effects in the characteristics of flocks recorded off Middle America (from Baja California to the equator) in 1979, 1980, and 1983. Records of all flocks and of flocks associated with spotted, spinner, and common dolphins were examined. These data, summarized in table 5.6, suggest that flock density was similar over the years, as was species composition: boobies and wedge-tailed shearwaters were always most abundant. However, flock size, dolphin school size, the percent of dolphin schools with birds, and the ratio of size of dolphin-associated flocks to that of all flocks were all much reduced in 1983. Although the 1983 sample was probably too small to be representative, these reduced percentages in 1983 are consistent with the idea that decreased food production or availability near the surface results in tuna feeding more independently of dolphins and in ways that are less useful to birds.

## General Discussion

It is curious that the association of seabirds, yellowfin tuna, and dolphins is so specific to spotted and spinner dolphins; the birds essentially ignore the twenty or so other species of Cetacea in the eastern Pacific. This is somehow related to the conspicuous partitioning of the eastern tropical Pacific (ETP) into distinct epipelagic communities of differently interacting predators.

### *Foraging Tactics and Species Interactions*

*Tuna Strategy and Consequences*

To begin understanding oceanic species interactions, it is useful to consider the behavior of the surface-schooling tunas. Tuna behavior exemplifies a strategy for exploiting the relatively sparse prey of tropical seas. Tropical tunas feed on epipelagic fish, squids, and crustaceans, whose distributions are undoubtedly very patchy with low overall densities (Blackburn 1968). To ensure a sufficient capture rate of such prey, tunas search by extensive ranging in the horizontal dimension, an energetically demanding tactic. Norberg (1977) postulated that as prey density decreases, the search method required of a predator increasingly becomes both more energy consuming and more efficient. Thus tunas have evolved into perhaps the most streamlined of fishes; their whole morphology and physiology appear designed for fast, sustained swimming with metabolic rates probably higher than those of all other fishes (see Sharp and Dizon 1978 for descriptions of energetics and hydrodynamics). High energy expenditure to obtain moderate energy returns from low-density prey must constrict the tunas' positive energy balance, narrowing the scope, or margin, between energy gained from food and energy consumed (see Warren and Davis 1966). Constriction of this energy margin increases vulnerability to natural mortality; for their size and speed, tropical tunas are remarkably short-lived, living probably less then ten years on the average (Beverton and Holt 1959).

These costs notwithstanding, the efficacy of the tunas' feeding strategy is evident; they are the dominant pelagic fishes of the tropical ocean, supporting extensive bird populations and productive fisheries. During the period 1974 to 1981 (between major El Niño events) an average of 196,000 metric tons of yellowfin tuna was harvested annually from the ETP, virtually all from surface or near-surface schools (IATTC 1984), approximately half of which were dolphin-associated (Allen 1985). In the same period, skipjack tuna produced an average annual catch of 122,000 metric tons, mainly from "schoolfish," i.e., surface schools without dolphins.

*Feeding with Tuna*

Seabirds that feed with surface tunas exploit the tunas' tactic for finding prey and their habit of driving it to the surface. This role was recognized by Ashmole and Ashmole (1967) and is the basis for fishermen's reliance on birds to locate these fish. The degree to which tuna schools are accompanied by flocks, however, is difficult to estimate, as most schools are detected only if associated with birds. Appendix 5.3 shows that whereas most schools fished ~~by~~ seiners were with birds (as expected), schoolfish tuna were both less often and more variably with birds (29 percent to 77 percent overall depending upon area).

Dolphins that associate with yellowfin tuna also may have a feeding relationship with these fish. The prey of the spotted dolphin is similar to that of yellowfin, both feeding diurnally upon epipelagic fishes and squids (Perrin et al. 1973; Reintjes and King 1953). Seabirds feed on much the same kinds of prey (Harrison, Hida, and Seki 1983; Diamond 1983). Spinner dolphins feed more on mesopelagic animals and may be less directly linked to tuna (Perrin et al. 1973). The ecological success of spinner and especially spotted dolphins in the eastern Pacific, which may be appreciated by comparing the numbers and average sizes of their schools with that of the

**Table 5.6.** Comparison of flock characteristics and interactions off middle America during three years.

| *Year* | TOTAL *Flocks* | TOTAL *Birds* | *Hours observed* | *Flocks per hour* | *% Flocks with dolphins* |
|---|---|---|---|---|---|
| 1979 | 136 | 10,366 | 270.0 | 0.5 | 27 |
| 1980 | 73 | 3,721 | 191.6 | 0.4 | 45 |
| 1983 | 25 | 800 | 49.0 | 0.5 | 28 |

NOTE: Dolphins referred to are spotted, spinner, and common dolphins.
WTSW = wedge-tailed shearwater.

other cetaceans (table 5.3), is likely due to a considerable advantage gained from feeding with yellowfin tuna.

*Seabirds' Relationship to Cetaceans*

In spite of the strong association of spotted and spinner dolphins with birds, our observations indicate that cetaceans themselves have little role in making prey available to seabirds. It is the tuna, primarily, that appear to drive prey to the surface, whether or not dolphins are present; foraging birds are almost always most active where the tuna are feeding, which often is at the leading edge of the school. This has been seen from ships (personal observation) and from helicopters (Au and Perryman 1982; Hewitt and Friedrichsen ms.). Thus spotted and spinner dolphins are commonly with birds because they swim with tuna with which the birds feed. And the common dolphin is relatively infrequently found with flocks because its association with tuna is similarly infrequent. Though the rough-toothed dolphin is not uncommonly associated with small flocks, it was probably the flotsam (and associated fish) near which this species was often encountered, rather than tuna or the mammals, that attracted the birds. Tropical seabirds thus appear to strongly associate only with those dolphins that swim and feed with tuna, dolphins that, like the tuna, are fast traveling and in large, diurnally active schools. Even so, these tuna and birds appear to feed independently of dolphins much of the time, as indicated by the delphinid association rate of flocks: between latitudes 2.5°N and 22.5°N, 58 percent of flocks (presumably with tuna) were not with dolphins (data for table 5.1, Eastern Sector). The tuna-dolphin association is

| PERCENT SPP. COMPOSITION OF FLOCKS | | | | | | | | FLOCK SIZE | | DOLPHIN SCHOOLS | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Boobies* | *Sooty tern* | *Other tern* | *WTSW* | *Other shear-waters* | *Jaegers* | *Frigate birds* | *Other birds* | *All* | *With dolphins* | *Size* | *Pct. With birds* |
| 38 | 13 | 3 | 34 | 1 | 8 | 2 | 1 | 76.2 | 159.8 | 297.9 | 75 |
| 23 | 17 | 12 | 15 | 1 | 11 | 7 | 3 | 51.0 | 88.4 | 149.2 | 76 |
| 16 | 1 | 10 | 66 | 2 | 4 | 2 | 0 | 32.0 | 21.7 | 115.2 | 29 |

clearly not obligatory; it seems rather to indicate an intersection or overlap of certain foraging tactics adopted by these species to exploit local prey configurations.

*Communities and Foraging Requirements*

The foraging tactics required in a particular environment seem to shape communities by placing stringent demands upon the behavioral or energetic capabilities of predators, especially in biologically sparse waters. Thus while spotted and spinner dolphins regularly associate with large yellowfin tuna on the purse seine fishing grounds of the Tropical Water habitat, these tuna are largely unable to forage in the surface layer beyond those grounds, perhaps in part due to physiological needs (see Sharp 1978 for a detailed discussion), and the dolphins there seem unable to feed with the skipjack or other small tuna that replace the yellowfin. The multispecies flocks of both facultative and obligatory commensals that feed with yellowfin on the purse seine grounds are reduced to mainly sooty terns and wedge-tailed shearwaters in the biologically sparse waters of the central Pacific and to virtually sooty tern–only flocks, obigatorily commensal on small tuna, in the Southern Subtropical Water. Like other facultative commensals, wedge-tailed shearwaters, so widespread in the central Pacific (Pitman 1986; King 1974b), are apparently unable to assume the required feeding tactics and to penetrate the Southern Subtropical Water of the eastern Pacific (figure 5.6).

## *Who Follows Whom?*

It is clear that seabirds follow and benefit from feeding with tuna, but where these tuna are also associated with certain dolphins, does either the tuna or dolphin provide benefit to the other? This question is pertinent to understanding the role of dolphins in bird-tuna-dolphin associations. A widely held view is that tuna follow dolphins in foraging. Tuna evidently do follow dolphins that are chased by purse seiners and are eventually captured with these schools. Mullen (1984) showed how two potentially competing predators could theoretically and stably coexist in a commensal relationship and suggested that the tuna were commensals on the dolphins. But perhaps tuna, and pelagic schooling fishes in general, obtain protection from pursuing predators by crowding under objects they normally encounter, both animate and inanimate—as when a predacious marlin approaches, skipjack will hide under the boat fishing them (D. Correa, personal communication). We suggested (Au and Pitman 1986) that spotted and spinner dolphins follow yellowfin in jointly foraging schools, inferring this mainly because seabirds are often seen feeding at the front of such schools in immediate association with the tuna rather than the dolphins. We note that the tuna-dolphin association breaks down outside the ETP purse seine grounds, where large yellowfin no longer commonly school at the surface (the dolphins must continue to do so, though they are no longer often with birds), and that a large tuna school, searching in three-dimensional space and perhaps using olfactory cues, could be more efficient than dolphins in locating prey.

In retrospect, it seems unlikely that a simple answer, either the dolphins or the tuna following the other to food, could be satisfactory. Neither is it likely that the tuna-dolphin-bird association merely results from the convergence of predator species upon the same food patches, for the association is too species specific, and tunas and dolphins appear to travel together, even while not actively feeding. Finally, no explanation can be satisfactory unless it also explains why the dolphin-tuna association is not characteristic of the eastern tropical Atlantic (Levenetz, Fonteneau, and Regalado 1980; Stretta and Slepoukha 1986), where a large purse seine fishery for surface yellowfin and skipjack tuna also exists, and dolphins similar to that of the ETP occur (Leatherwood, Caldwell, and Winn 1976).

## *A Feeding Tactics Hypothesis*

### *Hypothesis*

We propose a hypothesis that particular prey configurations or arrangements that are a function of productivity shape species interactions through the foraging tactics required to exploit that prey. The resulting explanation of species interactions is as follows: In low productivity waters, low-density prey are exploited by skipjack or similar small-sized tuna that are specialists at surviving on small prey from highly dispersed, relatively small patches. These patches are sufficiently encountered only through the most rapid and energetically expensive, wide-ranging search. Under such conditions smaller, rather than larger, predators are at an advantage (Norberg 1977). In accordance with foraging theory (Charnov 1976), these tuna employ, in effect, hit-and-run tactics on patches not much more profitable than from average searching between patches. Ecologically successful seabirds in such areas would be those capable of keeping up with these fast tuna, there being little food available independent of the fish.

In areas of intermediate food productivity, such as along oceanic boundary zones, food patches and prey are larger, though still best discovered by extensive horizontal ranging. Once found, these patches often provide for relatively long feeding bouts. Large yellowfin tuna and similarly foraging spotted and spinner dolphins find and exploit this prey, often jointly. When doing so, the tuna may be the primary predator, and they may drive some prey to the surface. Many birds take advantage of these enhanced feeding opportunities, forming multispecies flocks; however, most species in these flocks can also supplement their food by also feeding independently of tuna.

In still higher-productivity waters, such as coastal areas, prey is more diverse, the food encounter rate is high, prey patches are large and more predictable, and the advantage of the wide-ranging foraging tactic of tunas is lessened. It may sometimes be advantageous for tunas to forage passively—for example by waiting for prey under objects. The richer and less clumped food resources would enable the different predators to specialize and to feed more independently.

*Extensions*

The hypothesis would predict that reductions in food productivity would reduce the participation of all species involved in joint feeding, as suggested for 1983 in table 5.6 (this would not be expected if there were an obligate commensal relationship between tuna and dolphins). Moreover, the switching of feeding tactics and hence changes in community interactions might be the mode of response to such changes. Such a mechanism may have been involved in the massive population failure of seabirds from Christmas Island during the last El Niño (see Schreiber and Schreiber 1984).

The hypothesis suggests that intermediate productivity would be most conducive to the formation of multispecies interactions involving birds, tuna, and dolphins. In fact, the most extensive porpoise-tuna fishing areas in the eastern Pacific are not the rich coastal and upwelling-influenced waters off Central America, but the warm, stable waters off southern Mexico and the waters west of Clipperton Island. Areas where two-thirds or more of purse seine operations are on dolphin-associated yellowfin begin about 600 kilometers offshore (see Allen 1985), except off southern Mexico, where the fishing comes close to shore. Could it be that yellowfin tuna in the eastern tropical Atlantic are seldom associated with dolphins because waters there are not sufficiently intermediate in productivity to develop the right prey configuration? That fishery is located mainly in the Equatorial Counter and Guinea currents within 500 kilometers of the southern West African coast, an environment more similar to Pacific waters west of Panama and Colombia than to the ridged thermocline (Cromwell 1958), offshore porpoise-tuna grounds west and southwest of southern Mexico (see Merle 1978).

*Background*

This idea, that the resource base in different environments controls species interactions through the tactics required for its exploitation, is patterned after the concepts developed by Crook (1965) in a study on birds and as applied in comparative behavior studies of primates (Crook 1970; Clutton-Brock and Harvey 1977). These authors explained how the social organization and behavior of species are shaped by the availability of food and sites for reproduction. Smith et al. (1986), noting that common dolphins tended to occur in large, mobile schools in oceanic waters off California, while Dall's porpoise *(Phocoenoides dalli)* occurred in small, relatively sedentary schools in chlorophyll-rich, coastal waters, suggested that the behavioral and population differences were due to feeding strategies required of each species in the different environments. Differences in feeding behaviors of seabirds from Antarctic to tropical seas were explained by Ainley and Boekelheide (1983) as adaptations to regional differences in prey density and patchiness, as well as to the presence of subsurface competitors and predators. Wiens (1984) reviewed the importance of resources in the organization of avian populations and communities, noting how little direct evidence there was of resource limitation. He cautioned against imposing possibly preconceived processes, such as competition, on the analysis of relationships. However, Safina and Burger (1985) thought that terns in coastal waters could compete with bluefish by pursuing the same individual prey. We have not directly considered competition as a mechanism in our hypothesis. Until demonstrated, Schoener's hypothesis (1982) of predator convergence onto locally abundant prey patches, with little interspecies competition, seems more likely. Ours is an attempt to explain the existence in the eastern tropical Pacific of distinct pelagic communities, not separated by physical barriers, and composed of specific assemblages of highly mobile species with specific behavioral interactions.

## Summary

Two distinct faunal communities involving seabirds may be recognized in the eastern tropical Pacific. One, characteristic of the Tropical Water habitat mainly north of latitude 5°N, consists of multispecies flocks of primarily boobies, wedge-tailed shearwaters, jaegers, and sooty terns. These flocks are frequently associated with large yellowfin tuna and dolphins. Of the dolphins, the spotted and spinner species predominate (ca. 75 percent of dolphin-associated flocks involve these two species). These dolphins appeared to be linked to birds because both feed with large yellowfin tuna wherever the latter forage close to the surface. The other community occurs primarily in Subtropical Water to the south and consists of virtually single-species flocks of sooty terns. These flocks are associated with small tuna but seldom with dolphins. We propose that the different kinds of species associations seen in the eastern Pacific are manifestations of different foraging tactics required of pelagic predators in the different areas, and that the intersection of such tactics could explain the bird-tuna-dolphin association.

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Appendix 5.1. Common and scientific names of species mentioned in text.

| | |
|---|---|
| TUNAS | |
| Yellowfin | *Thunnus albacares* |
| Bigeye | *T. obesus* |
| Skipjack | *Katsuwonus pelamis* |
| Frigate mackerel | *Auxis* spp. |
| BIRDS | |
| Boobies | |
| Red-footed | *Sula sula* |
| Masked | *S. dactylatra* |
| Brown | *S. leucogaster* |
| Wedge-tailed shearwater | *Puffinus pacificus* |
| Sooty tern | *Sterna fuscata* |
| Jaegers | *Stercorarius* spp. |
| Juan Fernandez petrel | *Pterodroma externa externa* |
| White-necked petrel | *Pterodroma externa cervicalis* |
| Dark-rumped petrel | *Pterodroma phaeopygia* |
| White tern | *Gygis alba* |
| Noddy terns | *Anous* spp. |
| Frigatebirds | *Fregata* spp. |
| Phalaropes | (Phalaropodidae) |
| Storm-petrels | (Hydrobatidae) |
| Gulls | *Larus* spp. |
| Tropic birds | *Phaethon* spp. |
| CETACEANS | |
| Delphinids | |
| Spotted dolphin | *Stenella attenuata* |
| Spinner dolphin | *S. longirostris* |
| Striped dolphin | *S. coeruleoalba* |
| Common dolphin | *Delphinus delphis* |
| Bottlenose dolphin | *Tursiops truncatus* |
| Risso's dolphin | *Grampus griseus* |
| Pilot whale | *Globicephala macrorhynchus* |
| Rough-toothed dolphin | *Steno bredanensis* |
| Melon-headed whale | *Peponocephala electra* |
| Fraser's dolphin | *Lagenodelphis hosei* |
| Pygmy killer whale | *Feresa attenuata* |
| False killer whale | *Pseudorca crassidens* |
| Killer whale | *Orcinus orca* |
| Dall's porpoise | *Phocoenoides dalli* |
| Whales | |
| Rorquals | |
| Blue | *Balaenoptera musculus* |
| Minke | *B. acutorostrata* |
| Sei | *B. borealis* |
| Bryde's | *B. edeni* |
| Ziphiids (beaked) | *Mesoplodon* spp.; *Ziphius cavirostris* |
| Sperm | *Physeter macrocephalus* |
| Dwarf/pygmy sperm | *Kogia* spp. |

5.3

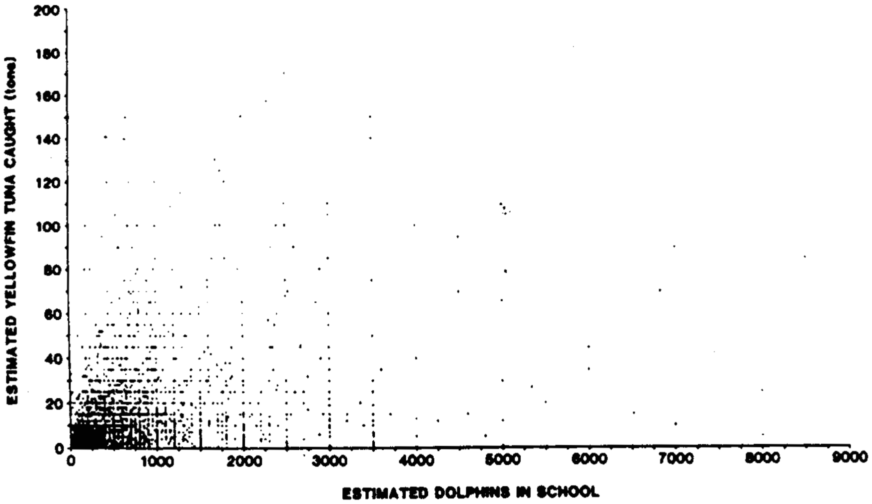
**Appendix 5.2.** Relationship between dolphin school size (numbers) and the catch (in short tons) of associated yellowfin tuna. Data collected by SWFC observers abroad U.S. purse seiners, 1981 through 1985.

| | COAST—110°W LONGITUDE | | | | | | 110°W—140°W LONGITUDE | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Porpoise fish*[a] | | *School fish*[b] | | *All* | | *Porpoise fish*[a] | | *School fish*[b] | | *All* | |
| YEAR | *n* | *(%)* | *n* | *(%)* | *n* | *(%)* | *n* | *(%)* | *n* | *(%)* | *n* | *(%)* |
| 5°N–25°N Latitude | | | | | | | | | | | | |
| 1981 | 374 | (97.6) | 102 | (79.4) | 476 | (93.7) | 328 | (95.7) | 78 | (24.4) | 406 | (82.0) |
| 1982 | 378 | (98.4) | 67 | (80.6) | 445 | (95.7) | 179 | (96.6) | 74 | (33.8) | 253 | (78.3) |
| 1984 | 173 | (95.4) | 1 | (–) | 174 | (95.4) | 153 | (94.8) | 2 | (–) | 155 | (93.5) |
| 1985 | 728 | (93.0) | 24 | (–) | 752 | (91.8) | 157 | (99.4) | 0 | (–) | 157 | (99.4) |
| 1981–85 | 1,653 | (95.5) | 194 | (76.8) | 1,847 | (93.6) | 817 | (96.4) | 154 | (28.6) | 971 | (85.7) |
| 5°N–15°S Latitude | | | | | | | | | | | | |
| 1981 | 44 | (75.0) | 122 | (33.6) | 166 | (44.6) | 43 | (81.4) | 0 | (–) | 43 | (81.4) |
| 1982 | 166 | (87.4) | 55 | (38.2) | 221 | (75.1) | 68 | (83.8) | 4 | (–) | 72 | (83.3) |
| 1984 | 27 | (92.6) | 0 | (–) | 27 | (92.6) | 1 | (–) | 0 | (–) | 1 | (–) |
| 1985 | 11 | (–) | 0 | (–) | 11 | (–) | 0 | (–) | 0 | (–) | 0 | (–) |
| 1981–85 | 248 | (86.3) | 177 | (35.0) | 425 | (64.8) | 112 | (83.0) | 4 | (–) | 116 | (82.8) |

NOTES: These 1981–85 data are of sets (= purse seine launches) during a period straddling the 1982–83 El Niño event and during which time fishermen have often checked tuna schools *for* size *before* setting on the school. The data were collected by SWFC technicians aboard U.S. purse seiners. % = percentage of *n* tuna school set upon by the seiners that were with birds. (–) indicates unreliable percentage because of small sample size. There is no data for 1983.

[a]"Porpoise fish" = tuna schools associated with dolphins.

[b]"School fish" = not associated with dolphins.




Appendix 5.3. The percent of yellowfin tuna schools (n) (set upon by purse seiners) that were with birds, according to area and whether schools were with dolphins ("porpoise fish") or not ("school fish").