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PARKINSON'S PETREL DISTRIBUTION AND FORAGING ECOLOGY IN THE EASTERN PACIFIC: ASPECTS OF AN EXCLUSIVE FEEDING RELATIONSHIP WITH DOLPHINS[1]

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Abstract. During 28 research vessel cruises in the eastern tropical Pacific Ocean from 1976 through 1990, Parkinson's Petrels (*Procellaria parkinsoni*) were observed near shore from southern Mexico (ca. 15°N) to northern Peru (ca. 5°S), and along a broad seaward extension that continued west of the Galápagos Islands to 110°W. Parkinson's Petrels regularly associated with dolphins: of the 618 petrels observed, 469 (76%) were associated with 10 species of dolphins, on 55 occasions, with 1 to 300 petrels present. They occurred mostly with two rare dolphin species: the melon-headed whale (*Peponocephala electra*) and the false killer whale (*Pseudorca crassidens*). This appeared to be a largely obligatory foraging relationship for Parkinson's Petrels. Associations with other dolphin species occurred primarily when those species also associated with melon-headed and false killer whales. Parkinson's Petrels avoided a common and widespread, multi-species feeding assemblage which consisted of a diverse, fast-moving group of seabirds, spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*), and tuna, all of which feed on live prey forced to the surface. The lumbering Parkinson's Petrels appeared ill-equipped to take such prey. In contrast, melon-headed and false killer whales apparently fed by dismembering large prey below the surface and so, provided feeding opportunities for a scavenging bird with diving capabilities. Among eastern tropical Pacific (ETP) seabirds, Parkinson's Petrels alone are adapted for recovering food scraps well below the surface. Parkinson's Petrels appear to be more dependent on marine mammals for foraging than any other species of seabird studied and feed diurnally more than was previously thought.

Key words: Parkinson's Petrel; Procellaria parkinsoni; *feeding ecology; tropical seabirds; dolphin associations; scavenging.*

INTRODUCTION

Seabirds are widely known to associate with subsurface predators in order to feed on prey forced to the surface. Fish have been the predators most often identified, especially in the tropics where surface-feeding tunas are of major importance to foraging birds (Ashmole and Ashmole 1967, Erdman 1967, Colblentz 1985, Au and Pitman 1988, Hulsman 1988, Safina 1990). Similarly, marine mammals, especially cetaceans, have been shown to provide feeding opportunities for seabirds (Rumboll and Jehl 1977, Würsig and Würsig 1980, Evans 1982, Hoyt 1983, Blaber 1986, Enticott 1986, Martin 1986, Au and Pitman 1988, Pierotti 1988).

Evans (1982) reviewed seabird/cetacean interactions and concluded that seabirds' feeding with cetaceans is largely opportunistic or incidental, but now there is evidence to the contrary. For example, Obst and Hunt (1990) found that gray whales (*Eschrichtius robustus*) provided a significant amount of food for seabirds foraging in the Bering Sea: up to 87% of the Red Phalaropes (*Phalaropus fulicarius*) and Black-legged Kittiwakes (*Rissa tridactyla*) they observed in the Chirikov Basin foraged in gray whales' mud plumes (see also Harrison 1979). Martin (1986) suggested that prey made available by Atlantic spotted dolphins (*Stenella frontalis*) was the most important source of food for Cory's Shearwaters (*Calonectris diomedea*) and Great Shearwaters (*Puffinus gravis*) foraging around the Azores Islands. Dusky dolphins (*Lagenorynchus obscurus*) foraging off Argentina reportedly drove anchovies to the surface where thousands of seabirds sometimes gathered to feed for hours (Würsig and Würsig 1979, 1980). In the eastern tropical

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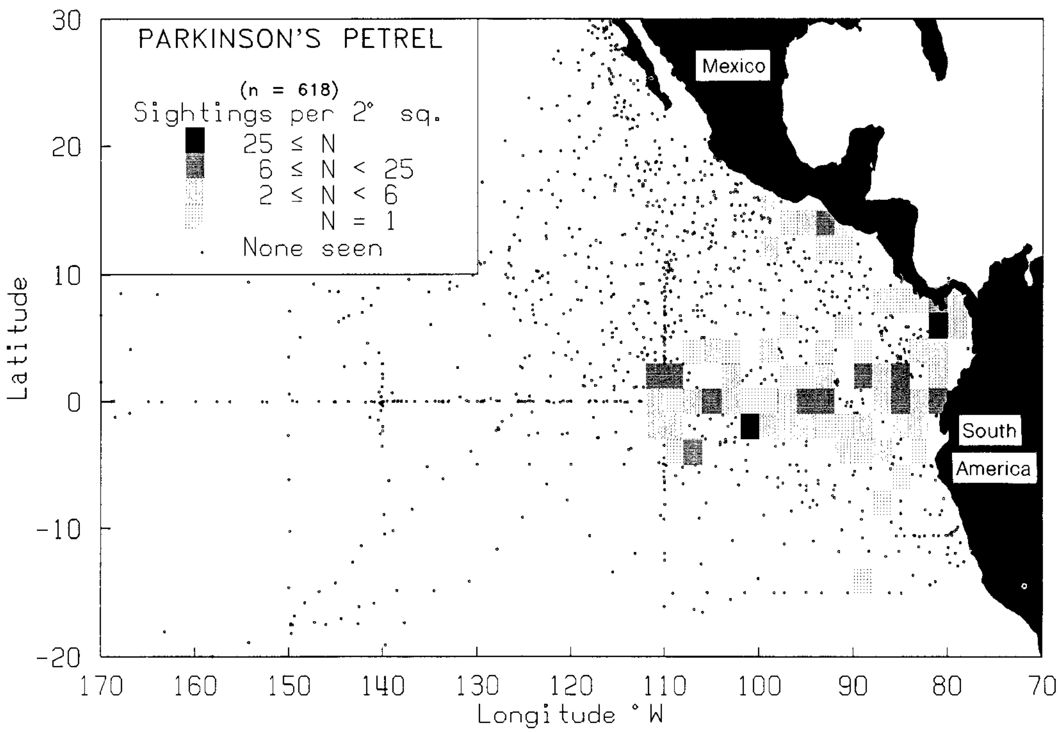

FIGURE 1. Sightings of Parkinson's Petrel in the eastern tropical Pacific, 1976–1990. Shaded areas represent total number of sightings per 2° square; dots represent noon vessel positions for days on which no petrels were observed.

Pacific (ETP), spotted dolphins (*Stenella attenuata*) and, to a lesser extent, spinner dolphins (*S. longirostris*) are part of a persistent and widespread feeding assemblage that includes large and diverse bird flocks and schools of surface-feeding tunas (Au and Pitman 1986, 1988). To this growing list we add a previously undescribed foraging relationship between two species of dolphins in the eastern Pacific and the little-known Parkinson's Petrel (*Procellaria parkinsoni*).

Parkinson's Petrel breeds on two islands off northern New Zealand where a remnant population of approximately 3,000–4,000 birds has been seriously threatened by introduced cats and other predators (Imber 1987). It nests during the austral summer (November–June), then migrates to the ETP to spend its non-breeding season (Loomis 1918, Murphy 1936, Jehl 1974, Imber 1976, Stiles and Smith 1977, Arnbom 1986, Ridgely and Gwynne 1989, this study). Because of this species' small population size and pelagic habits, little is known about its foraging ecology or distribution at sea. In this paper we present information on Parkinson's Petrel distribution, feeding habits, and foraging associations in the ETP.

STUDY AREA

Our study area covered more than 10 million km^2 of open ocean between San Diego, California, and Lima, Peru, extending west roughly to the longitude of Hawaii, at approximately 155°W (Fig. 1). Two major surface currents are particularly relevant to this study: the South Equatorial Current, and the Equatorial Countercurrent (Wyrtki 1966). The South Equatorial Current is derived mainly from the cold Peru Current, which flows north along western South America, veers away from the northern coast of Peru at about latitude 5°S, and crosses the equator east of the Galápagos Islands before heading west between 1° and 3°N. To the north of this, the Equatorial Countercurrent, nominally between 4° and 10°N, flows east and is considerably warmer and less saline (i.e., more tropical). The boundary between these currents forms the Equatorial Front, an area of increased abundance of surface organisms (Wyrtki 1966, Pak and Zaneveld 1974).

METHODS

We recorded observations of Parkinson's Petrel during 28 research cruises from 1976 to 1990. Our survey effort of 1,687 days at sea was distributed fairly evenly throughout the study area (Fig. 1), during all months.

Research cruises were of two types: those designed to assess the status of dolphin stocks in the ETP and those designed to collect oceanographic information. The oceanographic cruises followed pre-determined tracks, with stops to collect data at pre-determined locations. The dolphin cruises also followed pre-determined tracks but diverted towards dolphin herds to identify species, estimate herd size, and count associated birds. On both cruise types, one or two observers scanned the ocean during most daylight hours when underway, using 20× or 25× mounted binoculars, and censused mammals using standard line-transect methods (see Holt and Sexton 1989 for details). We recorded *all* sightings of Parkinson's Petrels and seabird flocks (see below), regardless of distance from the ship, and noted any associated marine mammals and fishes. We also recorded the behavior of Parkinson's Petrel. One specimen was collected as it foraged among dolphins on 11 February 1977 at 5°52′S, 82°50′W (Los Angeles County Museum No. 85145).

To examine distribution, we plotted all Parkinson's Petrels seen per 2° latitude-longitude block regardless of whether seen while conducting survey or not (e.g., we included sightings at dawn and dusk or during bad weather). We did not plot sightings standardized for survey effort, but used the larger data set, because Parkinson's Petrel was rarely seen.

We analyzed Parkinson's Petrel associations with each cetacean species (some related taxa were lumped when there were no associations with them, e.g., *Balaenoptera* spp. and *Megaptera novaeangliae* were combined into the single category of "rorquals"). We also compared associations with distinct dolphin groups: (1) spotted and spinner dolphins, and (2) all the remaining dolphin species (see Au and Pitman 1986, 1988).

To characterize the relative abundance and species composition of the ETP cetacean community, we analyzed a detailed subset of data collected during four, four-month cruises from 1986 through 1989: 3,866 sightings of 23 cetacean species sighted throughout the study area. Similarly, to describe seabird flocking associations with cetaceans and schooling fishes in the ETP, we used detailed flock data from the same 1986–1989 cruises: counts of 1,062 separate seabird flocks. When no Parkinson's Petrels were present, we defined a flock as five or more birds, but, to quantify all Parkinson's Petrel associations with other species, any group of two or more birds which contained Parkinson's Petrel was also defined as a flock.

To investigate foraging associations with subsurface predators, flocks were carefully scrutinized for associated marine mammals and schooling fishes (mainly tunas). Because dolphins must break the surface to breathe, few herds associated with birds were probably missed. Tunas, on the other hand, often stayed below the surface and were undoubtedly often overlooked; the number of times we observed tuna schools occurring with seabird flocks represents only a minimum value.

RESULTS

DISTRIBUTION AND OCCURRENCE IN THE ETP

We recorded 618 Parkinson's Petrels in the ETP (Fig. 1). They occurred near shore from at least southern Mexico (ca. 15°N) to northern Peru (ca. 5°S), and broadly seaward roughly on the equator or equatorial front, through the Galápagos Islands to at least 110°W.

We recorded Parkinson's Petrel in the ETP in all months except January; presumably some nonbreeding birds can be found there year-round.

MARINE MAMMAL ASSOCIATIONS

Parkinson's Petrel regularly associated with herds of 10 species of delphinid cetaceans (some of the larger dolphins in the family *Delphinidae* are referred to by their common names as "whales"): 469 (75.9%) were associated with dolphins on 55 occasions (Table 1); the remaining 149 (24.1%) were single birds or flocks not associated with cetaceans. When occurring with dolphins, numbers ranged from 1 to 300 birds, with a mode of 1 (Fig. 2). Thirty Parkinson's Petrels (54.5% of sightings) were present as lone birds with dolphins, but single birds accounted for only 6.4% of the total number of associated petrels.

Parkinson's Petrel consistently associated with two species of dolphin: the melon-headed whale (*Peponocephala electra*) and the false killer whale

TABLE 1. Mean number (±SD) of Parkinson's Petrels present per dolphin herd for herds with associated Parkinson's Petrels. Means are given for single-species herds and for mixed-species herds with and without false killer and melon-headed whales. (*n*) = number of herds with associated Parkinson's Petrels.

Dolphin species	Species composition of dolphin herds: Single-species herds	Mixed-species herds including False Killer Whale	Mixed-species herds including Melon-headed Whale	Mixed-species herds except those including False Killer Whale or Melon-headed Whale
Melon-headed whale *Peponocephala electra*	9.5 ± 13.8 (4)	–	–	–
False killer whale *Pseudorca crassidens*	4.0 ± 3.3 (9)	–	–	–
Killer whale *Orcinus orca*	1.5 ± 1.0 (4)	–	–	1.5 ± 1.0 (4)
Pilot whale *Globicephala macrorhynchus*	1.7 ± 0.6 (3)	14.0 (1)	–	1.9 ± 1.3 (10)
Common dolphin *Delphinus delphis*	1.5 ± 0.6 (6)	–	–	1.5 ± 0.6 (6)
Bottlenose dolphin *Tursiops truncatus*	1.7 ± 1.6 (6)	105.3 ± 168.6 (3)	10.0 (1)	1.7 ± 1.4 (16)
Risso's dolphin *Grampus griseus*	–	300.0 (1)	–	1.0 (1)
Spotted dolphin *Stenella attenuata*	1.0 ± 0.0 (2)	–	–	1.0 ± 0.0 (5)
Striped dolphin *Stenella coeruleoalba*	1.0 ± 0.0 (2)	–	–	1.0 ± 0.0 (2)
Spinner dolphin *Stenella longirostris*	–	–	–	1.0 ± 0.0 (3)

(*Pseudorca crassidens*) (Fig. 3). We analyzed the 1986–1989 marine mammal sightings data for associations with Parkinson's Petrel and rejected the null hypothesis that Parkinson's Petrel associated randomly with cetacean species in the ETP ($\chi^2 = 845.2$, df = 16, $P = 0.00$). Although melon-headed whales and false killer whales were rarely seen in the ETP (0.4% and 0.9% of the

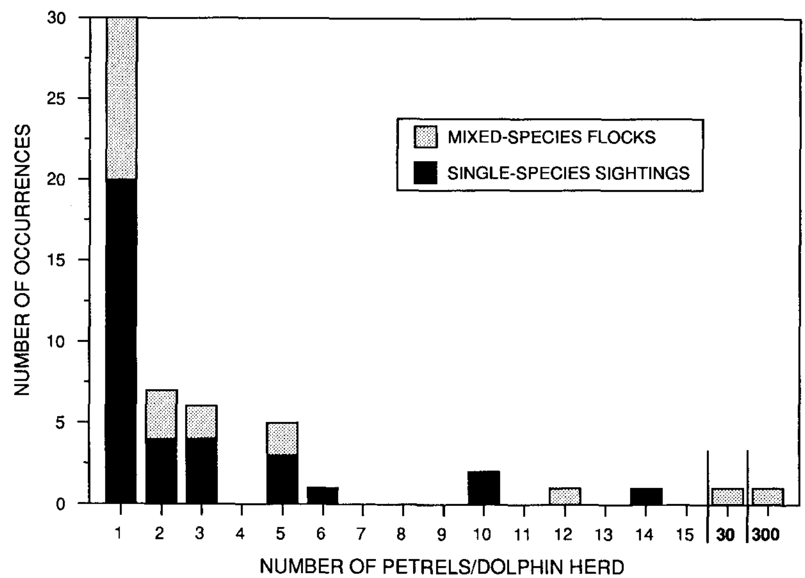

FIGURE 2. Frequency histogram of number of Parkinson's Petrels per herd for all dolphin herds with associated Parkinson's Petrels ($n = 55$ herds). Results are shown for single-species sightings (only Parkinson's Petrel present) and mixed-species flocks.

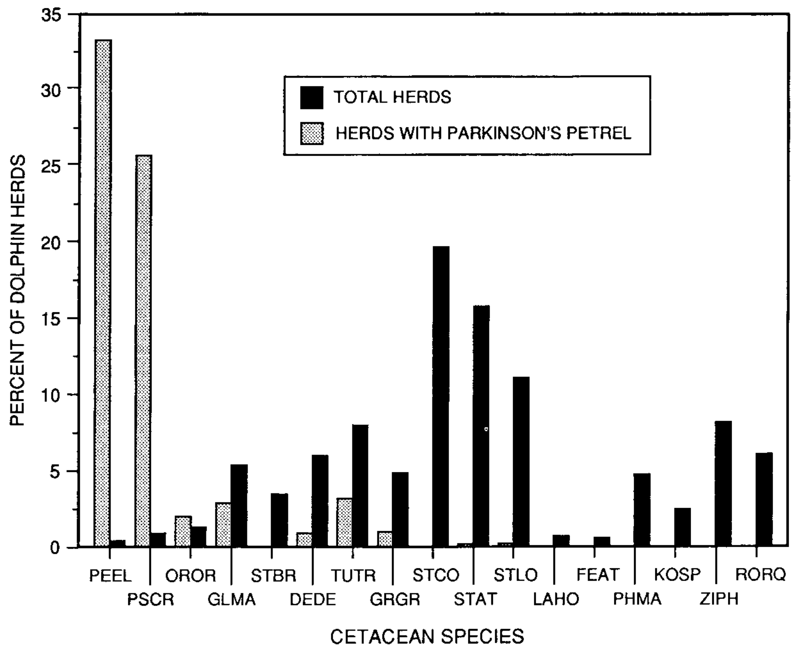

FIGURE 3. Relative sighting frequency of cetacean species (or species groups) recorded during 1986–1989 survey cruises and frequency of association with Parkinson's Petrels. (Example, 0.4% of all cetacean herds were PEEL, while 33.3% of all PEEL herds were with associated Parkinson's Petrels.) Species codes: PEEL—*Peponocephala electra,* melon-headed whale (*n* = 15 herds); PSCR—*Pseudorca crassidens,* false killer whale (*n* = 35 herds); OROR—*Orcinus orca,* killer whale (*n* = 50 herds); GLMA—*Globicephala macrorhynchus,* short-finned pilot whale (*n* = 209 herds); STBR—*Steno bredanensis,* rough-toothed dolphin (*n* = 135 herds); DEDE—*Delphinus delphis,* common dolphin (*n* = 231 herds); TUTR—*Tursiops truncatus,* bottlenose dolphin (*n* = 309 herds); GRGR—*Grampus griseus,* Risso's dolphin (*n* = 190 herds); STCO—*Stenella coeruleoalba,* striped dolphin (*n* = 764 herds); STAT—*S. attenuata,* spotted dolphin (*n* = 613 herds); STLO—*S. longirostris,* spinner dolphin (*n* = 431 herds); LAHO—*Lagenorhynchus hosei,* Fraser's dolphin (*n* = 26 herds); FEAT—*Feresa attenuata,* pygmy killer whale (*n* = 25 herds); PHMA—*Physeter macrocephalus,* sperm whale (*n* = 184 herds); KOSP—*Kogia* spp., dwarf and pygmy sperm whales (*n* = 97 herds); ZIPH—Ziphiidae, beaked whales (*n* = 316 herds); RORQ—*Megaptera novaeangliae* and *Balaenoptera* spp., rorquals (*n* = 236 herds).

total cetacean sightings, respectively), these two species had by far the highest incidences of association with Parkinson's Petrel: 33.3% of melon-headed whale herds and 25.7% of false killer whale herds were accompanied by petrels. In contrast, Parkinson's Petrel occurred with less than 3.5% of herds of each of the remaining cetacean species.

Melon-headed whales and false killer whales also had the highest average number of associated Parkinson's Petrels per attended single-species herd with 9.5 and 4.0 petrels, respectively (Table 1). The remaining species each averaged less than 2.0 petrels per single-species herd. The eight flocks containing the largest number of Parkinson's Petrels, including every aggregation of over five individuals, were with herds that had either melon-headed or false killer whales present. The largest flock of Parkinson's Petrels, estimated at 300 birds, was associated with a mixed herd of false killer whales, bottlenose dolphins (*Tursiops truncatus*), and Risso's dolphins (*Grampus griseus*). This flock alone may have contained nearly 10% of the world population of this species!

We recorded high numbers of Parkinson's Petrels with other species of dolphins only when they occurred as mixed-species herds containing melon-headed or false killer whales (Table 1). Thus, the bottlenose dolphin, pilot whale (*Globicephala macrorhynchus*), and Risso's dolphin were important largely when they also associated with melon-headed and false killer whales. All other cetacean species were unimportant or completely ignored, although many were abundant in the study area (Fig. 3).

TABLE 2A. Mean number (±SD) of Parkinson's Petrels in single-species sightings (i.e., Parkinson's Petrel was the only seabird present). 2B. Mean number of birds (±SD) in mixed-species flocks containing Parkinson's Petrel. Means are given for three categories of dolphin associations.

	Dolphin association		
Bird species	No dolphins present	Dolphin species other than Spotted or Spinner	Only Spotted or Spinner present
A: Single-species sightings	(n = 112)	(n = 34)	(n = 1)
Parkinson's Petrel *Procellaria parkinsoni*	1.0 ± 0.1	2.7 ± 3.1	1.0
B: Mixed-species flocks	(n = 4)	(n = 15)	(n = 4)
Parkinson's Petrel *P. parkinsoni*	1.0 ± 0.0	24.6 ± 76.6	1.0 ± 0.0
Galápagos Storm-Petrel *Oceanodroma tethys*	13.3 ± 18.8	36.4 ± 64.0	—
Unidentified storm-petrel *Oceanodroma* sp.	—	9.8 ± 9.5	—
Unidentified frigatebird *Fregata* sp.	—	2.7 ± 1.5	—
Tahiti Petrel *Pterodroma rostrata*	1.2 ± 0.0	—	—
Markham's Storm-Petrel *O. markhami*	1.0 ± 0.0	0.1 ± 0.0	—
Wedge-tailed Shearwater *Puffinus pacificus*	—	0.1 ± 0.0	142.0 ± 127.4
Juan Fernandez Petrel *Pt. externa*	—	—	47.5 ± 38.9
Masked Booby *Sula dactylatra*	—	0.1 ± 0.0	18.8 ± 14.1
Red-footed Booby *S. sula*	—	—	8.7 ± 9.9
Pink-footed Shearwater *P. creatopus*	—	0.1 ± 0.0	7.5 ± 5.2
Arctic Tern *Sterna paradisaea*	—	2.7 ± 2.1	4.0 ± 4.2
Pomarine Jaeger *Stercorarius pomarinus*	—	—	4.0 ± 1.4
Unidentified shearwater *Puffinus* sp.			
Christmas Island Shearwater *P. nativitatus*	—	0.1 ± 0.0	—
Dark-rumped Petrel *Pt. phaeopygia*	0.8 ± 0.0	—	0.2 ± 0.0
White-bellied Storm-Petrel *Fregetta grallaria*	—	0.2 ± 0.0	—
Unidentified booby *Sula* sp.	—	0.1 ± 0.0	—
Magnificent Frigatebird *F. magnificens*	—	0.1 ± 0.0	—
Unidentified jaeger *Stercorarius* sp.	—	0.3 ± 0.0	—
Parasitic/Long-tailed Jaeger	—	—	0.2 ± 0.0
S. parasiticus/longirostris	—	—	0.2 ± 0.0

MARINE BIRD ASSOCIATIONS

We observed Parkinson's Petrel associated with a total of 15 species of marine birds on 23 separate occasions. Sightings consisted of both single-species (only Parkinson's Petrel present; Table 2A) and mixed-species flocks (Table 2B), with or without dolphins present.

Flocks without dolphins. We saw Parkinson's Petrels in mixed-species flocks without dolphins on only four occasions and in each case only one petrel was present (Table 2B). In each of the four cases the total flock size was small ($\bar{x}$ = 13.0 birds of other species; SD = 14.8), with few species ($\bar{x}$ = 1.5 other species, SD = 0.6), and all the birds appeared to be scavenging (i.e., we saw something floating on the surface that the birds were picking at). Galápagos Storm-Petrels (*Oceanodroma tethys*) constituted 77% of the individuals of the associated other species.

When not associated with dolphins *or* other species of birds, of Parkinson's Petrels not initially sighted as ship followers, 110 (98%) were single birds and the remaining two (2%) were a lone pair.

Flocks with dolphins. Most flocks containing Parkinson's Petrels occurred with dolphin herds, including 15 of 16 (94%) single-species flocks and 19 of 23 (83%) mixed-species flocks. Parkinson's Petrels were also more numerous in flocks associated with dolphins: the mean number of petrels per sighting with dolphins other than spotted/spinner herds, was significantly higher than without dolphins, for both single- and mixed-species flocks (Mann-Whitney U = 1,066.0, P = 0.00; Mann-Whitney U = 10.0, P = 0.03, respectively; Table 2A, B).

Parkinson's Petrel was often the only bird species present when it occurred with dolphins (Fig. 2). Of the 55 times we recorded it with dolphins, it was the only species present on 35 occasions (64%). The number of Parkinson's Petrels present in single-species flocks with dolphins ranged from 1 to 14 with a mode of 1. When Parkinson's

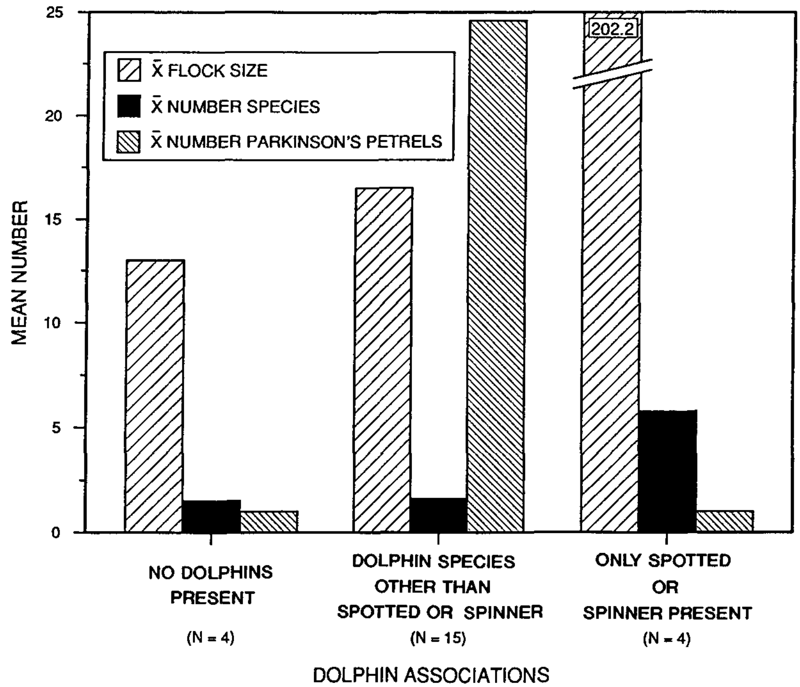

FIGURE 4. Associations between seabird flocks containing Parkinson's Petrels and dolphin herds. Shown are mean flock size (less Parkinson's Petrel), mean number of bird species (less Parkinson's Petrel), and mean number of Parkinson's Petrels for each of three categories of dolphin associations: a) flocks not associated with dolphin herds, b) flocks associated with herds other than spotted/spinner dolphins, and c) flocks associated with spotted/spinner herds only.

Petrels did occur in mixed-species flocks, there were usually very few individuals of other bird species present. For example, on 6 of the 19 occasions when Parkinson's Petrel occurred in mixed-species flocks with dolphins, only one bird of another species was present.

Mixed-species flocks containing Parkinson's Petrels and associated with spotted and spinner dolphins (Table 2B, Fig. 4) were large ($\bar{x} = 202.2$ birds of other species, SD = 139.6), diverse ($\bar{x} = 6.0$ other species, SD = 0.8), and had only single Parkinson's Petrels. These were dominated by a different group of bird species: the Wedge-tailed Shearwater (*Puffinus pacificus*), Juan Fernandez Petrel (*Pterodroma externa*), and Masked and Red-footed boobies (*Sula dactylatra* and *S. sula*). Flocks with Parkinson's Petrels but associated with dolphin species other than spotted and spinner dolphins, were relatively small ($\bar{x} = 17.5$ birds of other species, SD = 37.8), had few species ($\bar{x} = 1.7$ other species, SD = 0.8), but typically had a large number of Parkinson's Petrels ($\bar{x} = 24.6$, SD = 76.6) and storm-petrels (see the first group of six taxa in Table 2B). Of the 255 birds of nine species that comprised this flock category, 182 (71%) were Galápagos Storm-Petrels (*Oceanodroma tethys*), the only seabird that regularly occurred with Parkinson's Petrel. We recorded 1,062 seabird flocks during 1986–1989; of these 217 (20.4%) were associated with spotted and spinner dolphins but only a single Parkinson's Petrel was present.

SCHOOL FISH ASSOCIATIONS

Unlike many other species of ETP seabirds, Parkinson's Petrel almost never foraged in association with surface-feeding tunas: only four (0.6%) individuals, all singles, were so observed, and spotted or spotted and spinner dolphins were also present. We never observed tunas present when Parkinson's Petrel was with any other species of dolphin.

Among 1,062 bird flocks recorded in 1986–1989, a minimum of 192 (18.1%) were associated with tuna, and, of these, 125 (65.1%) were also associated with spotted and/or spinner dolphins, but we recorded only one Parkinson's Petrel with them.

FORAGING BEHAVIOR

We observed three types of potential foraging by Parkinson's Petrel in the ETP. In increasing order of observed importance they were: scavenging dead prey (0.5% of the total individuals observed), following ships to pick through garbage and offal (8.0%), and associating with dolphin herds (75.9%). The remaining individuals (15.6%) were unassociated traveling birds.

Scavenged natural prey appeared to be primarily floating dead squid and was the least important food source we identified, as only single birds fed on it and then only rarely.

Ship-following may have been a more dependable food source for Parkinson's Petrel. A total of 49 birds joined our vessel, with a maximum of nine at any one time. This represents 8.0% of the total number of petrels seen and 38.0% of the birds not associated with other birds or dolphins (only unassociated birds came over to our vessel). We observed ship-followers picking through garbage and scavenging bait and discarded fishing offal. Ship-following was especially common near shore: we had up to five petrels at a time in our wake off the Azuero Peninsula, Panama, where Panama Canal traffic was always heavy.

Associating with dolphins was the most common type of foraging we observed. On 11 February 1977 at 11:30 hr, Pitman observed a lone Parkinson's Petrel associated with a herd of bottlenose dolphins. Each time the dolphins surfaced from a dive, the petrel flew over to them, landed with its wings held high and partially extended, and put its head underwater. This was the normal searching mode we observed when Parkinson's Petrels associated with dolphins, except that on other occasions we often saw birds dive from the surface. Pitman collected this bird subsequent to these observations. Its stomach contained the remains of a recently ingested squid, identified to family *Octopoteuthidae,* probably *Octopoteuthis* sp. by D. Au (pers. comm., SWFSC, La Jolla, CA).

Parkinson's Petrel is a capable diver. On 15 May 1986, a pair of petrels associated with a herd of pilot whales came close to our stopped vessel and Pitman attracted them with pieces of squid. The squid sank but the birds were able to dive from the surface and stay submerged for up to 20 seconds before surfacing with the bait. It was difficult to judge how deep they went, but they almost disappeared in clear blue water and Pitman estimated they were going down at least 10 m.

DISCUSSION

DISTRIBUTION

Along the coast of the Americas, Parkinson's Petrels appeared to concentrate adjacent to areas of upwelling associated with the Gulf of Tehuantepec (surrounded by the northernmost cluster of sightings in Fig. 1; Blackburn 1962) and Gulf of Panama (Forsbergh 1963). The southernmost limit of distribution along the mainland coast was at about 5°S where the cooler water of the Peru current veers west from the coast of Peru at the equatorial front. This front continues west, out beyond Galápagos, and may have formed the physical axis and biological basis for the westward extension of the range of Parkinson's Petrel in the ETP.

The location of the equatorial front is somewhat variable and fluctuates according to seasonal changes in the intensity of the Peru Current (Wyrtki 1966), and in response to longer term oceanographic variability. The only occurrence known to us of Parkinson's Petrel south of latitude 6°S in the ETP was a specimen found on the beach near Lurin, Peru (12°16′S), in February 1983 (identified by G. Watson from a photograph, specimen not saved; M. Plenge, in litt.). This was when the pronounced 1982–1983 El Niño was transporting warm tropical water and associated organisms farther south than normal along the coast of South America (Barber and Chavez 1983, Velez et al. 1984), including, apparently, Parkinson's Petrel.

Why should Parkinson's Petrel restrict its nonbreeding range to the ETP when all of the dolphin species it associates with are pan-tropical? The ETP is characterized by having a permanent shallow thermocline which is related to its unusually high productivity (Wyrtki 1966). The ETP is also the only place in the world where large yellowfin tuna (*Thunnus albacares*) and spotted and spinner dolphins are known to regularly occur together and to feed at the surface (Au and Perryman 1985). It has been suggested that this shallow thermocline may constrain, or allow, large tunas to forage at or near the surface in the highly productive mixed layer (Au and Perryman 1985). It is possible that this feature also allows other predators, such as melon-headed and false killer whales, to feed closer to the surface—close enough for the relatively shallow-diving Parkinson's Petrel to successfully interact with them.

FORAGING ECOLOGY

Jackson's (1988) suggestion that "a natural tendency to exploit the feeding activity of whales may account for the propensity of White-chinned Petrels [*Procellaria aequinoctialis*] to scavenge behind fishing vessels" applies equally well to Parkinson's Petrel, and may account for its ship-following and trash-picking habits in general. But our observations suggest that associating with dolphins is the main food source for Parkinson's Petrel in the ETP, where we think they feed mainly by scavenging.

The seabird/dolphin/tuna assemblage that Parkinson's Petrel ignored involves seabirds taking live prey forced to the surface by tunas and dolphins (Au and Pitman 1986, 1988). Spotted and spinner dolphins and tuna are swift predators and in most of the hundreds of feeding bouts we have observed, fleeing prey were conspicuous, often leaping or flying out of the water to avoid predation. The prey, often flying fish and flying squid, were typically small: birds caught them live and swallowed them whole. Not surprisingly, seabirds that worked these aggregations were highly mobile; they tended to be plunge divers (boobies) or high-speed aerialists (terns, frigatebirds, shearwaters, *Pterodroma* petrels), and most were adept at aerial feeding (Gould 1971, Pitman, pers. observ.). In these situations, dolphins and tunas acted as "beaters" for foraging birds as described by Diamond (1981).

In contrast, we think that Parkinson's Petrel feeds mainly by diving under the surface and retrieving sinking scraps of large prey dismembered by larger, generally slower-swimming species of dolphins feeding below the surface. We base our conclusion on several pieces of evidence. First, we have observed the four dolphin species that Parkinson's Petrel associated with most often (false killer whale, melon-headed whale, pilot whale and bottlenose dolphin) on many occasions in the ETP and we have never seen prey visible at the surface when these animals appeared to be feeding. Second, of the many times we observed Parkinson's Petrels in the company of these dolphins, we never saw the birds feeding at the surface, although we saw them dive below the surface on many occasions. Finally, the diving capability that we observed and the heavy, hooked bill of Parkinson's Petrel makes it well suited for scavenging prey below the surface. Also, it seems unlikely that Parkinson's Petrel would have the speed underwater to catch live prey in relatively clear tropical water.

There are several published accounts of dolphins making food available for scavenging seabirds. Martin (1986) reported that Cory's Shearwaters and Great Shearwaters feeding among herds of Atlantic spotted dolphins took mainly scraps or wounded fish, and only occasionally took whole, live prey. Seabirds have often been seen feeding on offal left by killer whales (e.g., Lillie 1955, Jacobsen 1986, Rice and Saayman 1987, Reeves and Mitchell 1988, Wenzel and Sears 1988), and on two occasions in the ETP we have seen birds collect around dolphin entrails floating at the surface after killer whale attacks. Seabirds are also reported to feed on squid remains vomited by sperm whales (*Physeter macrocephalus*) (Clarke et al. 1981).

An additional way that dolphins might make prey available to scavenging seabirds comes from Clarke et al. (1988). While investigating the feeding habits of sperm whales captured off Peru and Chile, they noticed that there were many more squid bodies than squid heads in the whales' stomachs. From this they hypothesized that captured squid often cling to the outside of the whale's head with their tentacles and when the whale swallows the bodies the decapitated heads later drop off and are lost. Although the heads probably sink when they fall off (Clarke et al. 1979), a diving bird such as Parkinson's Petrel might have a chance at retrieving these parts. Currently, the only direct evidence we have that this kind of feeding may happen comes from Roberson (pers. comm.), who observed a White-chinned Petrel diving among pilot whales off northern Peru and reported that "one appeared to actually strike the head of one surfacing pilot whale."

Although there is little specific information available on the feeding habits of the false killer whale, it is known to take large prey which could provide feeding opportunities for scavengers. Perryman and Foster (1980) described instances of false killer whales attacking dolphins during tuna purse seine fishing operations in the ETP and Hoyt (1983) reported an attack on a humpback whale calf. Watson (1981) observed several members of a group of feeding false killer whales each carrying a single large fish crosswise in its mouth. He also described captive false killer whales shaking large fish until the head and entrails fell free, then peeling off the skin before swallowing the fillet.

Almost nothing is known about the food or feeding habits of the melon-headed whale. Mead et al. (cited in Perryman et al., in press) examined the stomach contents of a herd of melon-headed whales that stranded on the Pacific coast of Costa Rica. They found large numbers of ommastrephid squid beaks (primarily *Dosidicus gigas*), and, based on the squid beak measurements, they postulated that melon-headed whales were taking larger squid than were spotted and spinner dolphins in the same area.

Evidence suggests that all *Procellaria* petrels feed as scavengers, at times in association with dolphins. The Grey Petrel (*P. cinerea*) is a proficient diver (Brothers 1991:259) and has been observed foraging with cetaceans (Rumboll and Jehl 1977, Blaber 1986). Little is known about the foraging habits of the Westland Petrel (*P. westlandica*), except that it readily takes offal from fishing boats (Bartle 1985). The White-chinned Petrel readily takes fishing vessel offal when it is available (Jackson 1988); it is able to "dive well below the surface" (Murphy 1936:647), and Enticott (1986) found that it was more commonly associated with cetaceans than any other species of southern seabird in his study. Ridoux (1987) reported White-chinned Petrels followed killer whales even when the whales were not feeding, apparently in anticipation of feeding opportunities and we have seen Parkinson's Petrels in the ETP following false killer whales, possibly for the same reason. Our results suggest that Parkinson's Petrels, at least while in the ETP, has expanded this foraging relationship and become more dependent on cetaceans than has been suggested for any other seabird species to date.

A final point concerns the extent to which Parkinson's Petrel feeds at night. Imber (1976) studied Parkinson's Petrel diet in New Zealand during the breeding season and suggested that it is predominantly a nocturnal feeder because its diet consists largely of prey items, mainly squid, that he believed are present at the surface only at night because they might migrate to deeper water during the day. He also noted that bioluminescent forms predominate in the diet, which he argued was further evidence for nocturnal feeding. Our observations indicate that Parkinson's Petrels, at least while in the ETP, are more diurnal in their foraging than Imber (1976) has suggested. A habit of foraging with deep-diving dolphins during the daytime might also explain a diet of prey not normally expected to be available to a diurnal seabird. Although our observations do not preclude nocturnal feeding, they do indicate a need for additional study.

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LITERATURE CITED

ARNBOM, T. A. 1986. Seabirds off the Galápagos Islands. (Abstract). Pacific Seabird Group Bulletin 13:99–100.

ASHMOLE, N. P., AND M. J. ASHMOLE. 1967. Comparative feeding ecology of seabirds of a tropical oceanic island. Bull. Peabody Mus. Nat. Hist. 24: 1–131.

AU, D.W.K., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. Fish. Bull. 83:623–643.

AU, D.W.K., AND R. L. PITMAN. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. Condor 88:304–317.

AU, D.W.K., AND R. L. PITMAN. 1988. Seabird relationships with tropical tunas and dolphins, p. 174–212. *In* J. Burger [ed.], Seabirds and other marine vertebrates. Columbia Univ. Press, New York.

BARBER, R. T., AND F. P. CHAVEZ. 1983. Biological consequences of El Niño. Science 222:1203–1210.

BARTLE, J. A. 1985. Westland Black Petrel, p. 91. In *The Complete Book of New Zealand Birds.* Reader's Digest, Sydney.

BLABER, S.J.M. 1986. The distribution and abundance of seabirds south-east of Tasmania and over the Soela Seamount during April 1985. Emu 86: 239–244.

BLACKBURN, M. 1962. An oceanographic study of the Gulf of Tehuantepec. U.S. Fish. Wildl. Serv. Spec. Sci. Rep., Fish. No. 404.

BROTHERS, N. 1991. Albatross mortality and associated bait loss in the Japanese longline fishery in the southern ocean. Biol. Conserv. 55:255–268.

CLARKE, M. R., E. J. DENTON, AND J. B. GILPIN-BROWN. 1979. On the use of ammonium for buoyancy in squids. J. Mar. Biol. Ass. 59:259–276.

CLARKE, M. R., J. P. CROXALL, AND P. A. PRINCE. 1981. Cephalopod remains in regurgitations of the Wandering Albatross *Diomedea exulans* L. at South Georgia. Bull. Br. Antarct. Surv. 54:9–21.

CLARKE, R., O. PALIZA, AND A. L. AGUAYO. 1988. Sperm whales of the southeast Pacific, part 4: fatness, food and feeding. Investigations on Cetacea 21:53–195.

COLBLENTZ, B.E. 1985. Mutualism between Laughing Gulls *Larus atricilla* and epipelagic fishes. Cormorant 13:61–62.

DIAMOND, J. M. 1981. Mixed-species foraging groups. Nature 292:408–409.

ENTICOTT, J. W. 1986. Associations between seabirds and cetaceans in the African Sector of the Southern Ocean. S. Afr. J. Antarct. Res. 16:25–28.

ERDMAN, D. S. 1967. Sea birds in relation to game fish schools off Puerto Rico and the Virgin Islands. Carib. J. Sci. 7:79–85.

EVANS, P.G.H. 1982. Associations between seabirds and cetaceans: a review. Mammal Rev. 12:186–206.

FORSBERGH, E. D. 1963. Some relationships of meteorological, hydrographic, and biological variables in the Gulf of Panama. Inter-Amer. Trop. Tuna Comm., Bull. 8:3–109.

GOULD, P. J. 1971. Interactions of seabirds over the open ocean. Ph.D.thesis, Univ. Arizona, Tucson.

HARRISON, C. S. 1979. The association of marine birds and feeding gray whales. Condor 81:93–95.

HOLT, R. S., AND S. N. SEXTON. 1989. Monitoring trends in dolphin abundance in the eastern tropical Pacific using research vessels over a long sampling period: analyses of 1986 data, the first year. Fish. Bull. 88:105–111.

HOYT, E. 1983. Great winged whales: combat and courtship rites among humpbacks, the ocean's not-so-gentle giants. Equinox 10:25–47.

HULSMAN, K. 1988. The structure of seabird communities: an example from Australian waters, p. 59–91. *In* J. Burger [ed.], Seabirds and other marine vertebrates. Columbia Univ. Press, New York.

IMBER, M. J. 1976. Comparison of prey of the black *Procellaria* petrels of New Zealand. N. Z. Journal of Marine and Freshwater Res. 10:119–130.

IMBER, M. J. 1987. Breeding ecology and conservation of the Black Petrel (*Procellaria parkinsoni*). Notornis 34:19–39.

JACKSON, S. 1988. Diets of the White-chinned Petrel and Sooty Shearwater in the southern Benguela region, South Africa. Condor 90:20–28.

JACOBSEN, J. K. 1986. The behavior of *Orcinus orca* in the Johnstone Strait, British Columbia, p. 135–185. *In* B. C. Kirkevold and J. S. Lockard [eds.], Behavioral biology of killer whales. A. R. Liss, New York.

JEHL, J. R., JR. 1974. The nearshore avifauna of the Middle America west coast. Auk 91:681–699.

LILLIE, H. R. 1955. The path through penguin city. Ernest Benn Ltd., London.

LOOMIS, L. M. 1918. A review of the albatrosses, petrels, and diving petrels. Proc. Calif. Acad. Sci. Vol. 2, Ser. 4, Pt. 2, p. 1–187.

MARTIN, A. R. 1986. Feeding association between dolphins and shearwaters around the Azores Islands. Can. J. Zool. 64:1372–1374.

MURPHY, R. C. 1936. Oceanic birds of South America. Amer. Mus. Nat. Hist., New York.

OBST, B. S., AND G. L. HUNT, JR. 1990. Marine birds feed at gray whale mud plumes in the Bering Sea. Auk 107:678–688.

PAK, H., AND J.R.V. ZANEVELD. 1974. Equatorial front in the eastern Pacific Ocean. J. Phys. Oceanogr. 4: 570–578.

PERRYMAN, W. L., D.W.K. AU, AND S. LEATHERWOOD. In press. Melon-headed whale, *Peponocephala electra* (Gray, 1846). *In* S. H. Ridgway and R. Harrison [eds.], Handbook of marine mammals. Vol. 5. Academic Press, London.

PERRYMAN, W. L., AND T. C. FOSTER. 1980. Preliminary report on predation by small whales, mainly the false killer whale, *Pseudorca crassidens,* on dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA, NMFS, Southwest Fisheries Center Admin. Rept. No. LJ-80-05.

PIEROTTI, R. 1988. Associations between marine birds and mammals in the northwest Atlantic Ocean, p. 31–58. *In* J. Burger [ed.], Seabirds and other marine vertebrates. Columbia Univ. Press, New York.

REEVES, R. R., AND E. MITCHELL. 1988. Distribution and seasonality of killer whales in the eastern Canadian Arctic. Rit Fiskideildar 11:136–160.

RICE, F. H., AND G. S. SAAYMAN. 1987. Distribution and behavior of killer whales (*Orcinus orca*) off the coasts of southern Africa. Investigations on Cetacea 20:231–250.

RIDOUX, V. 1987. Feeding association between seabirds and killer whales, *Orcinus orca,* around subantarctic Crozet Islands. Can. J. Zool. 65:2113–2115.

RIDGELY, R., AND J. A. GWYNNE, JR. 1989. Birds of Panama with Costa Rica, Nicaragua and Honduras. Princeton Univ. Press., Princeton, NJ.

RUMBOLL, M.A.E., AND J. R. JEHL, JR. 1977. Observations on pelagic birds in the south Atlantic Ocean in the austral spring. Trans. San Diego Soc. Nat. Hist. 19:1–16.

SAFINA, C. 1990. Bluefish mediation of foraging competition between Roseate and Common Terns. Ecology 71:1804–1809.

STILES, F. G., AND S. M. SMITH. 1977. New information on Costa Rican waterbirds. Condor 79: 91–97.

VELEZ, J., J. ZEBALLOS, AND M. MENDEZ. 1984. Effects of the 1982–83 El Niño on the fishes and crustaceans off Peru. Tropical Ocean-Atmosphere Newsletter 28:10–12.

WATSON, L. 1981. Sea guide to whales of the world. E. P. Dutton, New York.

WENZEL, F., AND R. SEARS. 1988. A note on killer whales in the Gulf of St. Lawrence, including an account of an attack on a minke whale. Rit Fiskideildar 11:202–204.

WÜRSIG, B., AND M. WÜRSIG. 1979. Day and night of the dolphin. Nat. Hist. 88:60–67.

Würsig, B., and M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus,* in the south Atlantic. Fish. Bull. 77:871–890.

WYRTKI, K. 1966. Oceanography of the eastern equatorial Pacific Ocean. Oceanogr. Mar. Biol. Annu. Rev. 4:36–68.