None of these questions can be addressed without studies of seabirds at sea. Therefore, we examined niche partitioning by collecting and analyzing data on the species and size of prey taken, and preference for use of the four feeding strategies, including timing of feeding. To do this we examined (1) the effects on diet and its diversity in relation to season, current system, interannual environmental variability (El Niño Southern Oscillation [ENSO] phase), sex, body condition, and predator mass (2) the propensity of the migratory, temperate component of the ETP avifauna to feed in tropical waters rather than merely passing through, and (3) effects on diet due to preferential use of different species of tuna. We were also interested in comparing diets and feeding strategies of seabird species that specialize by foraging in flocks over large aquatic predators vs. birds that feed solitarily, and we were interested in making comparisons to the analogous study we completed in the Southern Ocean (Ainley et al. 1992, 1993, 1994), realizing that we would learn much about the structuring of both communities based on how they differed.

METHODS

Data Collection

Specimens

Beginning in the autumn 1983, seabirds were collected during spring and autumn of each year through 1991. To do this, we participated in 17 cruises designed to study spatial and temporal marine climate variability of the ETP by deploying, retrieving and maintaining weather and ocean buoys as well as obtaining comparative, real-time ocean data (Table 1). Each cruise, sponsored by the U.S. National Oceanographic and Atmospheric Administration (NOAA) lasted 2–3 mo. At locations where an inflatable boat (5-m long with 20–35 hp motor) could be deployed, bird sampling was conducted using a shotgun. These locations included recovery/deployment sites of NOAA buoys and deep CTD (conductivity-temperature-depth) stations (Fig. 1), operations that required most of a day. Sampling in which at least one bird was collected occurred at 96 different locations on 264 d. Thirty-four of the sites were sampled on multiple days (2–29 d/site), but no site was sampled more than once/season/year. Between ocean stations, we conducted surveys to collect data on species composition, at-sea densities, and foraging behavior (Ribic and Ainley 1997, Ribic et al. 1997, Spear et al. 2001).

During each of the 264 sample days, an attempt was made to collect five or six birds of each avian species present in the area. Bird collecting was conducted using two methods. The first was to drive the inflatable boat 2–3 km from the ship where the motor was stopped and a slick was created by pouring fish oil on the water. The slick was freshened periodically by the addition of oil, about every 1–2 hr depending on wind speed (and our drift), which was the primary factor causing the oil slick to break up and disperse. The scent of the oil attracted mainly storm-petrels and gadfly petrels, but generally not shearwaters, larids, or pelecaniforms. Secondly, we also watched for feeding flocks while positioned at slicks. When one was sighted, the boat was moved to the flock where an attempt was made to collect a sample of birds. This allowed us to collect species not attracted to the oil slicks and also to determine the diet of seabirds that foraged over tuna. When at the flocks, we also attempted to determine the species of tuna that were forcing to the surface the prey on which the birds were feeding. We collected 85 birds (Table 2) from 11 flocks foraging over yellowfin (*Thunnus albacares*) and 46 birds from five flocks foraging over skipjack tuna (*Euthynnus pelamis*).

Table 1. Sample sizes, by season and year, of seabirds collected in the ETP and that contained prey[a].

Year	Spring–summer	Autumn–winter	Total
1983	0	74	74
1984	81	57	138
1985	39	91	130
1986	31	144	175
1987	128	211	339
1988	126	229	355
1989	75	115	190
1990	58	207	265
1991	100	55	155
Total	638	1,183	1,821

[a] Shown with respect to season (spring–summer [March–August] and autumn–winter [September–February]) and year; 30 species represented (See Table 3).

TABLE 2. BIRDS COLLECTED IN ASSOCIATION WITH YELLOWFIN AND SKIPJACK TUNAS[a].

Collected over yellowfin tuna		Collected over skipjack tuna	
Juan Fernandez Petrel (*Pterodroma externa*)	26	Sooty Tern (*Onychoprion fuscata*)	24
Wedge-tailed Shearwater (*Puffinus pacificus*)	26	White Tern (*Gygis alba*)	7
Sooty Tern (*Onychoprion fuscata*)	12	Gray-backed Tern (*Onychoprion lunatus*)	4
Phoenix Petrel (*Pterodroma alba*)	4	Black Noody (*Anous tenuirostiris*)	3
Christmas Shearwater (*Puffinus nativitatus*)	3	Blue-gray Noody (*Procelsterna cerulean*)	3
Sooty Shearwater (*Puffinus griseus*)	3	Wedge-tailed Shearwater (*Puffinus pacificus*)	1
Kermadec Petrel (*Pterodroma neglecta*)	2	Flesh-footed Shearwater (*Puffinus carneipes*)	1
Stejneger's Petrel (*Pterodroma longirostris*)	2	Phoenix Petrel (*Pterodroma alba*)	1
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	2	Great Frigatebird (*Fregata minor*)	1
Masked Booby (*Sula dactylatra*)	1	White-tailed Tropicbird (*Phaethon lepturus*)	1
Buller's Shearwater (*Puffinus bulleri*)	1		
Herald Petrel (*Pterodroma arminjoniana*)	1		
White-winged Petrel (*Pterodroma leucoptera*)	1		
Pomarine Jaeger (*Stercorarius pomarinus*)	1		

[a] Species listed in order of decreasing sample size.

All collected birds were immediately placed in a cooler with ice in plastic bags. Towels covering the ice kept birds dry to facilitate accurate determination of body mass once we returned to the ship. During 1987–1991, the hour of day during which each specimen was collected was recorded.

Once back at the ship, before removing stomachs, birds were weighed (nearest gram for birds <250 g, nearest 5 g for larger birds) and measured. We did not weigh birds that had become wet below the contour (outer) feathers (i.e., had significant water retention). Mean bird-mass values reported are the average mass of each species after having subtracted the mass of the food load (details below: stomach fullness).

One of us (LBS) also examined most individuals to determine sex, breeding status, and fat load. Sex and breeding status were determined by examining gonads. Females were classed as having bred previously (laid an egg) if their oviduct was convoluted as opposed to uniform in width (Johnston 1956a). Testis width of males not having bred previously was considerably smaller than those having bred, because testes do not recede to the original width once an individual has bred (when the testes expand several orders of magnitude; Johnston 1956b). The difference between breeder vs. non-breeder testis width is ≥2 mm among smaller petrels and larids, and ≥3 mm among larger petrels, shearwaters, and pelecaniforms (Johnston 1956b; Spear, unpubl. data). Birds of fledgling status can also be identified during the post-breeding period by their fresh plumage and complete absence of molt compared to older birds that then exhibit considerable flight feather and/or body molt.

The amount of fat covering the pectoral muscles, abdomen and legs was examined, and fat load was scored as 0 = no fat, 1 = light fat, 2 = moderate fat, 3 = moderately heavy fat, and 4 = very heavy fat (validation of this method in Spear and Ainley 1998).

Stomach processing and prey identification

We removed the stomach and gizzard from each bird and sorted fresh prey, otoliths, squid beaks, and non-cephalopod invertebrates. First, an incision was made in the bird's abdomen to expose the stomach. Using tweezers (0.1–0.4 m depending on bird size), a wad of cotton was inserted in the mouth and through the esophagus to the opening of the stomach to make sure that all food items were within the

latter. The esophagus was then pinched with two fingers placed just above the cotton wad and was cut just above that point, as was the small intestine at a point just below the gizzard. This procedure allowed the stomach and gizzard to be removed intact.

The stomach was weighed, placed in a pan (the bottom of which had been painted black) and then cut open from one end to the other, so that only the gizzard was left intact. The stomach contents were dumped into the pan and the stomach wall was rinsed clean with water from a squirt bottle and massaging with the fingers. Whole fish and cephalopods, as well as pieces of large cephalopods were rinsed, weighed, and placed in plastic bags with a light covering of water, and then frozen. Otoliths and beaks were removed from partially digested fishes and cephalopods. Some partial fish and cephalopods were also saved in plastic bags and some were discarded after otoliths and beaks had been removed. Loose pieces of flesh left in the pan were covered with a shallow layer of water, massaged into smaller pieces, and, with the pan in hand, swirled around to allow even the tiniest (white) fish otoliths to be seen as they moved over the surface of the black pan. Non-cephalopod invertebrates were measured (total length recorded in mllimeters), weighed, and identified to highest taxon possible. When all non-cephalopod invertebrates, otoliths and visible cephalopod beaks had been removed, pan contents were dumped into a second, white-bottomed pan. The procedure was repeated to find (dark) squid beaks not detected in the black-bottomed pan. Otoliths were saved in slide containers and squid beaks in small plastic bottles with 50% ethanol. After the stomach contents were sorted and saved, the gizzard was cut open with care being taken not to damage the contents (otoliths and squid beaks) with the scissors. The gizzard was rinsed, and all otoliths and beaks were sorted and saved in the manner noted above for specimens from stomachs.

After finishing each cruise, all whole fish and cephalopods (and saved flesh parts) as well as otoliths and squid beaks were identified, enumerated, and measured by one of us (WAW). Measurements of fish were that of the standard length (SL, from the snout to the end of the vertebral column); those of squid were dorsal mantle length (DML). For each bird specimen containing prey, prey number was recorded to the most specific possible taxon for all whole prey, scavenged cephalopod remains, otoliths, and beaks. The minimum number of each cephalopod taxon was determined by the greater number of upper or lower beaks present. Prey size estimates were determined by measuring the lower beak rostral length (squid) or lower beak hood length (octopods), and then applying regression equations. For each bird stomach, the number of teleost prey was determined from the greater number of left or right saggital otoliths. Exceptions to this were when it was obvious that due to differences in otolith size, the left and right otoliths of a given species were from two different individuals. Hereafter, when we refer to otolith and/or beak number, it must be kept in mind that one otolith refers to one fish individual, and one beak refers to one cephalopod individual.

All beaks and otoliths were measured in millimeters; otoliths also were classified into four categories of erosion: (1) none, (2) slight, (3) moderate, and (4) severe. Condition categories scored for cephalopod beaks included: (1) no wear, beak wings and lateral walls (terminology of Clarke 1986) in near perfect condition, often with flesh attached; (2) no flesh present with beaks demonstrating little wing and lateral wall erosion; (3) beak wings absent with some erosion of lateral wall margins; and (4) severe erosion of beak; lateral wall edges ranging from severely eroded to near absent. To avoid positive bias in the importance of cephalopods by the fact that beaks are retained much longer than fish otoliths (Furness et al. 1984), we considered only those beaks of condition 1 and 2 as representing prey ingested within 24 hr of collection. Because an attempt was made to identify all cephalopod beaks to species, regardless of condition, enumeration of cephalopods in the diets of seabirds includes individuals represented by beaks of condition 3 or 4. However, beaks of condition 3 and 4 were not measured and, therefore, were not included in the analysis of prey size/mass and overall contribution to diets.

The sample of 2,076 birds that comprises the basis for the diet analysis in this study is composed of the 30 most abundant species found in the ETP study area (King 1970, Brooke 2004; Table 3). Hereafter, we refer to the 30 species collectively as the ETP avifauna. These birds contained a total of 10,374 prey (Appendix 1). Voucher specimens of prey, their otoliths and beaks were retained by WAW at the NOAA National Marine Mammal Laboratory in Seattle, WA. Seabird specimens were either prepared as study skins or frozen; tissue samples from many were given to Charles Sibley for DNA analyses. All bird skins and skeletons were given to the Los Angeles County Museum or U.S. National Museum.

Feeding behavior

We determined the tendency of birds to feed in flocks as opposed to feeding solitarily. To do this

TABLE 3. COLLECTION DETAILS FOR THE 30 MOST-ABUNDANT AVIAN SPECIES IN THE ETP.

Species	Number collected	Birds w/prey N	Birds w/prey %	Prey/bird $\bar{x}$ ± SD	Sampling episodes[a]
Hydrobatidae					
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	503	433	86.1	4.4 ± 5.2	143
Wedge-rumped Storm-Petrel (*O. tethys*)	411	308	74.9	2.2 ± 2.6	128
Markham's Storm-Petrel (*O. markhami*)	15	12	80.0	2.5 ± 4.7	8
White-throated Storm-Petrel (*Nesofregetta fuliginosa*)	22	19	86.4	4.0 ± 4.5	16
White-bellied Storm-Petrel (*Fregetta grallaria*)	22	20	90.9	2.6 ± 1.7	16
White-faced Storm-Petrel (*Pelgaodroma marina*)	15	15	100.0	21.5 ± 15.3	10
Procellariidae					
Sooty Shearwater (*Puffinus griseus*)	43	31	72.1	2.5 ± 5.5	25
Christmas Shearwater (*Puffinus nativitatis*)	7	7	100.0	5.4 ± 3.6	7
Wedge-tailed Shearwater (*Puffinus pacificus*)	112	95	84.8	4.7 ± 5.5	40
Juan Fernandez Petrel (*Pterodroma externa*)	214	204	95.3	6.1 ± 13.4	70
White-necked Petrel (*Pterodroma cervicalis*)	14	12	85.7	2.4 ± 2.6	9
Kermadec Petrel (*Pterodroma neglecta*)	12	11	91.7	3.6 ± 3.0	9
Herald/Henderson Petrel (*P. heraldica/atrata*)[b]	5/8	5/8	100.0	2.5 ± 4.9	4/5
Phoenix Petrel (*Pterodroma alba*)	21	21	100.0	5.4 ± 5.1	11
Murphy's Petrel (*Pterodroma ultima*)	8	8	100.0	4.6 ± 7.2	7
Tahiti Petrel (*Pterodroma rostrata*)	156	154	98.7	6.8 ± 6.5	74
Bulwer's Petrel (*Bulweria bulwerii*)	43	34	79.1	2.9 ± 3.5	29
White-winged Petrel (*Pterodroma leucoptera*)	139	135	97.1	8.0 ± 6.6	56
Black-winged Petrel (*Pterodroma nigripennis*)	89	88	98.9	7.6 ± 5.2	36
Stejneger's Petrel (*Pterodroma longirostris*)	48	46	95.8	8.0 ± 5.7	26
DeFilippi's Petrel (*Pterodroma defilippiana*)	7	7	100.0	17.6 ± 15.0	3
Pelecaniformes					
Red-tailed Tropicbird (*Phaethon rubricauda*)	11	10	90.9	7.6 ± 6.7	9
Red-footed Booby (*Sula sula*)	5	4	80.0	20.2 ± 12.2	3
Masked Booby (*Sula. dactylatra*)	18	18	100.0	8.0 ± 5.1	10
Nazca Booby (*Sula granti*)	5	5	100.0	24.3 ± 14.5	1
Great Frigatebird (*Fregata minor*)	4	4	100.0	6.5 ± 3.3	4
Laridae					
Parasitic Jaeger (*Stercorarius parasiticus*)	9	9	100.0	5.6 ± 3.6	5
Sooty Tern (*Onychoprion fuscata*)	93	82	88.2	4.3 ± 5.6	35
Gray-backed Tern (*Onychoprion lunatus*)	5	5	100.0	10.0 ± 3.5	2
White Tern (*Gygis alba*)	12	11	91.7	4.9 ± 5.4	8
Totals	2,076	1,821	87.7	5.0 ± 7.5	264

Notes: See Appendices 3–32 for prey numbers for each species.

[a] Sampling episodes refer to the dates on which the species was collected, but many sites were visited on more than one date. Therefore, an episode refers to both the date and place of sampling.

[b] The Henderson and Herald petrels were combined into one group because of their close taxonomic and morphological relationships (Brooke et al. 1996, Spear and Ainley 1998), and because of the small sample sizes for those two species.

we used observations gathered during surveys conducted in the ETP when vessels were underway between stations (Fig. 2). These surveys were conducted using 600-m wide transects (details in Spear et al. 2001), in which we recorded 92,696 birds representing the ETP avifauna (69,246 after counts were corrected for the effect of bird flux through the survey strip [Spear et al. 1992]; flight speeds from Spear and Ainley [1997b]). Of the 92,696 birds, 9,472 were recorded in flocks over surface-feeding fishes, and thus, were stationary; these counts required no correction for movement. Other than flock-feeding birds that passed within the survey strip, we also counted those in flocks that would have passed through the survey strip if they had not moved outside of it to avoid the approaching ship when it was within 1 km of the flock (Spear et al. 2005).

We defined a feeding flock as a group of three or more birds milling, or foraging over, surface-feeding fishes (mean flock size was 24.1 ± (SD) 27.7 birds, N = 457 flocks; some flocks contained species other than those of the ETP avifauna). We did not consider a group of birds as having been in a flock if they were in transit, sitting on the water resting, or scavenging (e.g., eating a dead squid). Although we recorded another 57 birds (<0.1% of the flock count) feeding in flocks over cetaceans where no fishes were observed, we excluded these because cetaceans are not important to tropical seabirds (Ballance and Pitman 1999) and because we did not collect any birds over feeding cetaceans. On this basis, we scored a flock index (Fl = the tendency to feed in flocks over piscine predators) for each species. Fl for each species was calculated as the

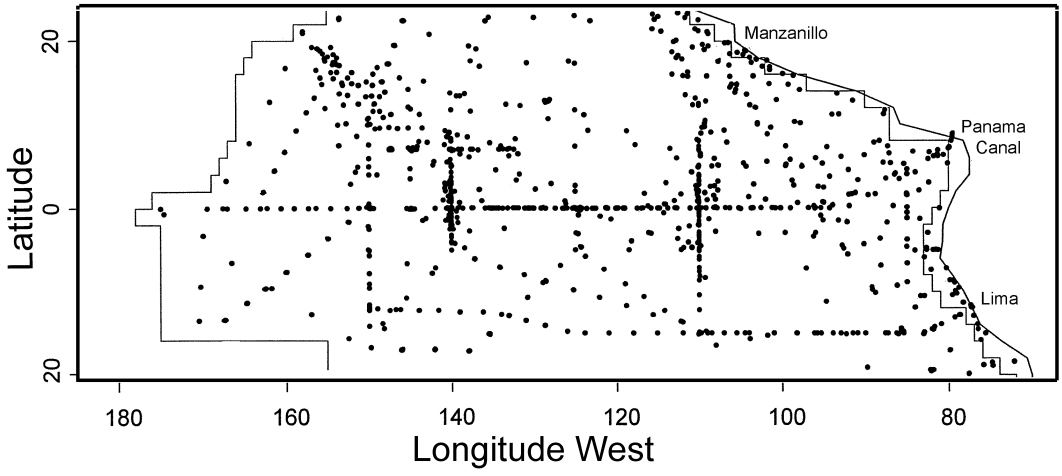

FIGURE 2. The distribution of at-sea survey effort of seabirds in the eastern Pacific Ocean (1983–1991). Each dot represents one noon ship position. The staircase line effect along the coast on the east side of the study area denotes the boundary separating pelagic waters to the west and coastal waters to the east.

number of birds of a given species observed in predatory fish-induced feeding flocks divided by the total number recorded (all behaviors), multiplied by 100, and therefore, is specific to those birds forming flocks over surface-feeding fishes.

We classified the ETP avifauna into two groups—solitary-feeders, those that feed predominantly alone; and flock-feeders, those that feed predominantly in multi-species flocks over surface-feeding fishes. We defined the cutoff between the two groups based on the hiatus in Fl values that occurred between species seldom seen in flocks (Fl = 0.0–4.7) and those regularly seen in them (Fl = 11.0–72.1; Table 4).

We used an adaptation of the feeding methods defined by Ashmole and Ashmole (1967) to classify the primary feeding method of each member of the ETP avifauna observed during our at-sea surveys (Table 4). Feeding methods are: (1) plunging that involves using gravity and momentum to reach a prey that is well beneath the surface, (2) plunging pursuit that involves plunging and then pursuing prey using underwater wing propulsion, (3) surface plunging that rarely involves becoming submerged, (4) contact dipping or swooping, in which only the bill touches the water, (5) aerial pursuit in which volant prey is captured, (6) surface seizing that involves eating dead or live prey while sitting on the water, (7) pattering on ocean surface or briefly stopping—only the feet, bill, and sometimes the breast and belly touch the water, and (8) kleptoparasitizing prey from other birds.

Data Analysis

Comparison of diets

Principal component (PC) analysis in conjunction with ANOVA was used to assess diet differences. For these analyses, the most abundant prey species were grouped into eight categories based on similarities in taxonomy and behavior (Appendix 1): (1) gonostomatids, sternoptychids, and photichthyids, (2) myctophids, (3) bregmacerotids, diretmids, and melamphaids, (4) hemirhamphids and exocoetids, (5) carangids, scombrids, and gempylids, (6) epipelagic cephalopods, (7) mesopelagic cephalopods, and (8) miscellaneous invertebrates (all non-cephalopod) and eggs.

These eight groups made up 90.4% of the prey sample (Appendix 1) with the majority (6.8%) of the remainder being fishes and cephalopods unidentifiable to family level. Thus, only 2.8% of the prey sample was miscellaneous identified fishes. After exclusion of seabirds that did not contain at least one prey item representing the eight prey groups, the sample size was 1,817 birds, or 87.5% of the original sample of the 2,076 birds (Table 3).

For the PC analysis, each bird record was weighted by 1/N, where N was the sample size of the species to which that bird belonged. This was required to control for unequal sample sizes and thus give equal importance to each seabird species in the statistical outcome. For each bird specimen we also converted the prey number it contained to the proportion representing each of the eight prey groups by dividing the number

TABLE 4. FLOCK INDEX, PRIMARY FEEDING METHOD, MEAN MASS (G ± SD), AND PREY-DIVERSITY INDEX (*H'*) FOR THE 30 MOST ABUNDANT AVIAN SPECIES OF THE ETP.

	Flocking index	Primary feeding method	Mean mass	Prey-diversity index (*H'*)
Flock feeders				
Masked Booby (*Sula dactylatra*)	15.9 (546.3)	1	1,633 ± 75 (16)	1.708 (18)
Nazca Booby (*Sula granti*)	15.9	1	1,487 ± 110 (5)	1.096 (5)
Great Frigatebird (*Fregata minor*)	73.1 (101.3)	4, 5, 8	1,355 ± 59 (4)	1.808 (4)
Red-footed Booby (*Sula sula*)	19.9 (706.7)	1	1,169 ± 145 (5)	0.554 (4)
Juan Fernandez Petrel (*Pterodroma externa*)	16.1 (5,636.4)	5, 3	427 ± 42 (208)	2.919 (204)
White-necked Petrel (*Pterodroma cervicalis*)	11.5 (208.9)	5, 3	414 ± 29 (12)	2.603 (12)
Wedge-tailed Shearwater (*Puffinus pacificus*)	24.8 (5,965.6)	3	381 ± 38 (99)	2.081 (95)
Kermadec Petrel (*Pterodroma neglecta*)	15.4 (149.3)	3, 6, 8	369 ± 34 (12)	2.545 (11)
Parasitic Jaeger (*Stercorarius parasiticus*)	11.0 (481.1)	6, 8	367 ± 81 (6)	1.404 (9)
Christmas Shearwater (*Puffinus nativitatus*)	42.8 (144.9)	2, 3	316 ± 18 (6)	2.148 (7)
Phoenix Petrel (*Pterodroma alba*)	16.7 (131.8)	3, 5	287 ± 34 (19)	2.323 (21)
Herald/Henderson Petrel (*Pterodroma heraldica/atrata*)	21.6 (85.5)	3, 5	280 ± 26 (13)	2.539 (13)
Sooty Tern (*Onychoprion fuscata*)	44.0 (12,744.4)	3, 4	184 ± 14 (68)	2.226 (82)
Gray-backed Tern (*Onychoprion lunatus*)	28.3 (60.0)	3, 4	124 ± 10 (5)	1.370 (5)
White Tern (*Gygis alba*)	44.5 (883.6)	3, 4	97 ± 6 (8)	2.055 (11)
Solitary feeders				
Sooty Shearwater (*Puffinus griseus*)	0.4 (8,642.8)	2, 3	771 ± 85 (36)	2.495 (31)
Red-tailed Tropicbird (*Phaethon rubricauda*)	0.0 (170.3)	3	742 ± 101 (9)	1.296 (10)
Tahiti Petrel (*Pterodroma rostrata*)	3.3 (716.6)	6, 3	413 ± 40 (140)	3.142 (154)
Murphy's Petrel (*Pterodroma ultima*)	1.9 (53.5)	6	374 ± 29 (7)	2.496 (8)
White-winged Petrel (*Pterodroma leucoptera*)	4.2 (1,525.3)	3, 5	160 ± 16 (136)	3.553 (135)
Black-winged Petrel (*Pterodroma nigripennis*)	3.2 (2,104.1)	3, 6	154 ± 12 (78)	3.325 (88)
DeFilippi's Petrel (*Pterodroma defilippiana*)	0.2 (405.9)	3, 6	154 ± 8 (7)	1.792 (7)
Stejneger's Petrel (*Pterodroma longirostris*)	4.7 (569.1)	3, 6	145 ± 10 (47)	3.226 (46)
Bulwer's Petrel (*Bulweria bulwerii*)	2.0 (543.6)	6, 7	94 ± 11 (41)	3.268 (34)
White-throated Storm-Petrel (*Nesofregetta fuliginosa*)	1.8 (56.1)	7, 6	63 ± 3 (18)	2.725 (19)
Markham's Storm-Petrel (*Oceanodroma markhami*)	0.0 (2,338.9)	7, 6	51 ± 4 (15)	2.452 (12)
White-bellied Storm-Petrel (*Fregetta grallaria*)	0.5 (187.5)	7, 6	46 ± 3 (19)	2.872 (20)
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	0.3 (13.986.7)	7, 6	41 ± 3 (413)	3.465 (433)

TABLE 4. CONTINUED.

	Flocking index	Primary feeding method	Mean mass	Prey-diversity index (*H′*)
White-faced Storm-Petrel (*Pelagodroma marina*)	0.4 (552.4)	7, 6	40 ± 3 (15)	2.487 (15)
Wedge-rumped Storm-Petrel (*Oceanodroma tethys*)	0.3 (9,614.3)	7, 6	25 ± 2 (330)	3.039 (308)

Notes: See Methods for calculation of flock index, species' mass, prey diversity index (*H′*), and definitions of feeding methods. Peculiarities as follows: flocking index (values in parenthses = total number of birds recorded, corrected for effect of flight movement); mean mass (values in parenthses = sample size); prey diversity index (values in parenthses = sample size). Species with flock index <11.0 were considered to be solitary. Species with samples size of collected birds <9 are not considered in subsequent analyses of *H′*. Species in each group (flocking and solitary) are listed in order of decreasing mass. Nazca and Masked boobies were distinguished during surveys in only two of our 17 cruises (1983–1991); herein we have assumed that their flocking indices are the same.

of prey representing each group by the total number of prey summed across all eight prey groups, multiplied by 100. The purpose of this was to avoid biases such as that due to larger seabirds being capable of containing larger numbers of prey.

To test for significant differences in diet, we used two one-way ANOVAs (i.e., Sidak multiple comparison tests, an improved version of the Bonferroni test; SAS Institute 1985). In the first, we tested for differences among the PC1 scores of the individuals representing the species composing the ETP avifauna; in the second we compared PC2 scores among those individuals. We considered diet differences between two species to be significant if either or both of their respective PC1 or PC2 scores differed significantly.

Only the first two PC axes were used to assess outcomes of this and the following PC analyses. Although the third and fourth axes explained up to 15% of the variance in PC analyses, our reasoning for using only the first two axes is that they usually explained about 50% of the variance in diet composition, and for presentation of plots, using more than two axes is difficult.

Analysis of temporal, spatial, and demographic factors

PC analyses were also used to compare temporal, spatial, and demographic effects on diet. Because this required sub-sampling, we used only the 10 most abundant avian species representing the ETP avifauna, represented by 1,516 individuals. Included were three species of piscivores that, based on prey size (average >20 g), were subsequently shown to be at or near the top of the trophic scale among ETP seabirds: Juan Fernandez Petrel (*Pterodroma externa*), Wedge-tailed Shearwater (*Puffinus pacificus*), and Sooty Tern (*Onychoprion fuscata*); four that were of intermediate trophic level (prey mass >7 g and <20 g): Tahiti Petrel (*Pterodroma rostrata*), White-winged Petrel (*Pterodroma leucoptera*), Black-winged Petrel (*Pterodroma nigripennis*), and Stejneger's Petrel (*Pterodroma longirostris*); and three that were of lower trophic level (prey mass <7 g): Leach's Storm-Petrel (*Oceanodroma leucorhoa*), Wedge-rumped Storm-Petrel (*Oceanodroma tethys*), and the Bulwer's Petrel (*Bulweria bulwerii*). Diets of each of the 10 species were compared between seasons (spring [March–August] vs. autumn [September–February]); current systems (South Equatorial Current [SEC] vs. the North Equatorial Countercurrent [NECC], where the division between the two systems was assumed to be 4° N; Wyrtki 1966); longitudinal sections (where west was designated as those waters between 135° W and 165° W and east was those waters east of 135° W to the Americas); and ENSO phase. ENSO phases include El Niño, neutral, and La Niña, and were scored by year and season following the guidelines of Trenberth (1997), as 1, 2, and 3, respectively (Table 5). For the PC analysis examining ENSO period, we compared diets of birds collected during El Niño vs. La Niña, and excluded those collected during the neutral phase. We also compared diets between the two sexes.

Prey groups designated for these analyses were the same eight groups as those defined above. Following the PC analysis, one-way ANOVAs also were used to test for significant differences in among species' PC1 and PC2 scores generated in the PC analysis to model diet among individuals of the 10 bird species. Using the one-way ANOVAs, we tested for differences in species' PC1 and PC2 scores compared between two ENSO periods (El Niño vs. La Niña), seasons (spring vs. autumn), current systems (SEC vs. ECC), longitudinal sections (west vs. east), and sexes. In order to examine season, ENSO, current system, longitude, and sex-related effects, data for each of these four environmental, temporal, and sex variables were included in the PC data set, but

TABLE 5. SEASON AND YEAR OF THE OCCURRENCES OF EL NIÑO, NEUTRAL, AND LA NIÑA PHASES OF THE EL NIÑO SOUTHERN OSCILLATION [a].

	Spring–summer (March–August)	Autumn–winter (September–February)
El Niño	1987, 1991	1986, 1987, 1991
Normal	1984, 1986, 1990	1983, 1985, 1989, 1990
La Niña	1985, 1988, 1989	1984, 1988, 1998

[a] Data from Trenberth (1997); for La Niña 1998, see Legeckis (1999).

not included (analyzed) as independent (prey group) variables in the initial PC analysis. Thus, the independent variable in one-way ANOVAs comparing PC scores among species with respect to diet composition was the PC value and the independent variable was bird species. Each ANOVA was constrained to summarize results pertaining to one of the two seasons, ENSO periods, current systems, or sexes.

Multiple regression analyses

With the exception of the use of generalized additive models to estimate the size of the ETP seabird population, most of the analyses summarized below were conducted with ANOVA—either one-way ANOVA (Sidak multiple-comparisons tests) or multiple linear regression (STATA Corporation 1995). The latter was performed using a hierarchical stepwise approach (dependent and independent variables summarized below). For each analysis we confirmed that residuals met assumptions of normality (skewness/kurtosis test for normality of residuals, $P > 0.05$), and in some cases log-transformation of the dependent variable was required to achieve that.

Diet diversity

Diet diversity of each seabird species was examined using the Shannon-Weiner Index (Shannon 1948; $H' = -\sum p_i \log p_i$, where p_i represents the proportion of each species in the sample). After calculating the index, we used a one-way ANOVA to compare diet diversity among three feeding guilds: (1) small hydrobatids (storm-petrels) that feed solitarily, (2) solitary-feeding procellariids, and (3) procellariids, larids, and pelecaniforms that feed in flocks over predatory fish.

Preliminary analyses demonstrated a significant positive correlation between bird species' sample size (N) and H' ($r = 0.538$, $df = 28$, $P < 0.01$; Table 4), indicating that H' was underestimated among species with smaller sample sizes. This problem has been dealt with elsewhere (Hurtubia 1973, Baltz and Morejohn 1977) using accumulated prey diversity index curves in which H' is computed for increasing N until, at H'_N, an asymptote is reached at which a further increase in N is not expected to cause a change in H'. However, because we had a relatively large number of seabird species, we were able to use an alternative method. In our case, we regressed the predator N on H' to determine what sample size was required to obtain an insignificant ($P > 0.05$) relationship between H' and N. The predator N required for an insignificant relationship was N = 9. Therefore, we did not calculate H' for predators with N <9, and considered H'-values of predators with N >8 as realistic estimates. To further adjust for the relation between predator N and H', we controlled for predator N in the multiple regression that examined the relationship between H and variables potentially affecting H'.

Prey size

We compared prey size among two species-groups of seabirds. The first group included the five most abundant seabird species that prey solitarily on smaller fishes at night and are, in order of increasing mass, Wedge-rumped and Leach's storm-petrels, and Black-winged, White-winged, and Tahiti petrels (Table 4). Ten prey species most abundant, by number, as well as common to each of these predators, were *Sternoptyx obscura, Vinciguerria lucetia, Diogenichthys laternatus, Symbolophorus evermanni, Myctophum aurolaternatum, Ceratoscopelus warmingii, Diaphus parri, Diaphus schmidti*, *Lampanyctus nobilis*, and *Bregmaceros bathymaster* (see Appendix 1).

The second group included the six flock-feeding seabird species that were either very abundant and/or contained large numbers of prey; each preyed to a large extent on *Exocoetus* spp., *Oxyporhamphus micropterus*, and *Sthenoteuthis oualaniensis*. These predators were, in order of increasing mass, the Sooty Tern, Wedge-tailed Shearwater, Juan Fernandez Petrel, Red-tailed Tropicbird (*Phaethon rubricauda*), Nazca Booby (*Sula granti*), and Masked Booby (*S. dactylatra*). All but the tropicbird are flock-feeders (Table 4).

We used separate multiple regression analyses to examine prey size among the bird species

representing each of the two predator groups. The dependent variable was otolith or beak length of prey; beak and otolith lengths are highly correlated with prey size (Appendix 2), and thus, are very reliable for estimating the latter. Independent variables in the regression analyses were predator species, and predator sex, mass, and fat score. We also included prey species in these analyses to control for prey-related differences in otolith or beak length.

In addition, when not known from measurements of intact prey, we calculated standard lengths and mantle lengths for fishes and *Sthenoteuthis oualaniensis*, respectively. We calculated these values only for prey species for which allometric equations were available for conversion of otolith or beak lengths to respective body lengths (Appendix 2). The mean ± SD for these values are presented for the primary prey of the predators listed above.

Scavenging

Most squid are semiparous, short lived and die after spawning (Clarke 1986). Many species that die after spawning float to the ocean surface (Rodhouse et al. 1987, Croxall and Prince 1994). Procellariiforms take advantage of this by scavenging their carcasses (Imber 1976, Imber and Berruti 1981, Croxall and Prince 1994); these birds have strongly hooked beaks for ripping flesh and a well developed sense of smell (Bang 1966, Nevitt 1999). Scavenging of dead cephalopods too large to be swallowed whole consists of eating the parts that are easiest to tear loose: eyes, tentacles, buccal structure including the beak, and then pieces of the mantle if the animal has become decomposed enough so that the mantle is flaccid and can be ripped apart (Imber and Berruti 1981; Spear, pers. obs.).

Cephalopod parts obviously torn from large individuals were considered to have been scavenged. Yet, these parts could usually not be identified to species if only scavenged flesh with no beaks was present in a bird's stomach. Therefore, it was necessary to estimate the proportional number of individual cephalopods of each species scavenged from the total number of lower rostral beaks of condition 1 or 2, representing squid that had been eaten within 24 hr. Thus, beaks of condition 3 and 4 were excluded. To determine if a cephalopod represented by its lower beak had been scavenged, we estimated cephalopod size using lower rostral length applied to allometric equations (Appendix 2), and information provided by M. Imber (pers. comm.) regarding beaks of smaller juveniles and subadults not likely to have had die-offs, and therefore, probably taken alive. Thus, individuals were considered to have been scavenged only if their beaks were too large to represent individuals that could have been swallowed whole. All of these were mesopelagic-bathypelagic species of cephalopods.

Because various amounts of dead cephalopod individuals were eaten by scavenging seabirds, we could not calculate the mass consumed directly from the size of scavenged beaks. We therefore used another method to calculate cephalopod mass consumed by scavenging birds.

Stomach fullness

We consider stomach fullness (SF) as an index for the propensity of a seabird species to feed while in the ETP study area. We calculated these indices as the mass of food in the stomach divided by the mass of the bird multiplied by 100. Mass for each individual was calculated as mass at the time of collection, minus the mass of food in the stomach. Mass of food in the stomach was calculated by subtracting the average mass of empty stomachs from that of the mass of the stomachs containing food. Thus, SF for each bird is the percent of that bird's unfed mass that the mass of food in the stomach represents. In cases when stomachs contained non-food items (e.g., pebbles or plastic), those items were excluded from calculations of food mass. We compare SF among the ETP avifauna except the Nazca Booby. We excluded this species from these analyses because we did not consider our sample as random. All Nazca Boobies were collected as they returned to the Malpelo Island colony, and, not surprisingly, each stomach was very full (SF mean = 26.6%, range = 18–35%).

We used multiple regression analyses to examine factors related to SF using the 10 more abundant seabird species but also included the Phoenix Petrel because of the paucity (three) of flock-feeding species among the 10. The sample unit was one bird. Thus, the analysis for SF included four flock-feeding species and seven solitary-feeding species.

It was necessary to exclude the less-abundant species from these analyses because many were lacking data for the different current systems, ENSO periods, seasons, and/or ETP longitudinal sections. The effects of the latter four variables, as well as sex, age, status, fat load, and mass, were examined (as independent variables) in these regression analyses; SF was the dependent variable and was log transformed so that residuals met assumptions of normality (skewness/kurtosis test, $P > 0.05$). We controlled for species' differences and weighted

analyses by the inverse of species N so that outcomes reflect the average effect among species.

Timing of feeding

To determine the time of day when birds were feeding, we regressed the hour-of-day that birds were collected on the condition of otoliths found in their stomachs. We examined feeding time among four groups: (1) storm-petrels, (2) solitary procellariids, (3) flock-feeding procellariids, and (4) all flock-feeding species combined (see Table 3 for species included in each group). For groups 1–3, we examined timing of feeding on myctophids. For all flocking species, we examined timing of feeding on exocoetid and/or hemirhamphids. For these analyses we included several bird specimens representing species within the storm-petrel, larid, and pelecaniform groups that were not included in other analyses. Among storm-petrels we also included eight Wilson's (*Oceanites oceanicus*) and nine Band-rumped storm-petrels (*Oceanodroma castro*); additional larids included two Pomarine Jaegers (*Stercorarius pomarinus*), four Black Noddies (*Anous minutus*), two Brown Noddies (*A. stolidus*), and six Brown Boobies (*Sula leucogaster*).

It should be noted that determination of the proportion of live cephalopods that are taken during the night vs. day is difficult because of confounding caused by occurrence at the surface during the day due to being forced there by tuna vs. occurrence at the surface at night as the result of vertical migration. Because tuna feed during the day, and the only cephalopods eaten by seabirds feeding over them were epipelagic species, we considered all of the latter eaten by flock feeders to have been consumed during the day. However, many of the cephalopods (including epipelagic, mesopelagic, and bathypelagic species) are represented by juveniles and sub-adults that perform vertical migrations to the surface at night (Roper and Young 1975; M. Imber, pers. comm.). Therefore, we considered these smaller mesopelagic-bathypelagic cephalopods found in seabird stomachs to have been consumed at night. We assumed that epipelagic cephalopods consumed by solitary feeders were also eaten at night.

Mass of prey consumed in relation to foraging strategy

We calculated mass of prey consumed as a function of each of the four feeding strategies. Thus, four different complexes of prey were consumed, one complex representing each of the four feeding strategies. The four prey groups were classified based on prey behavior (Weisner 1974, Nesis 1987, Pitman and Ballance 1990; M. Imber, pers. comm.), and the results of this study for timing of feeding and flock composition and prey of birds feeding over tuna. The four groups are: (1) prey eaten by seabirds feeding in association with large aquatic predators during the day—hemirhamphids, exocoetids, carangids, scombrids, gempylids, coryphaenids, nomeids, and epipelagic cephalopods found in seabirds feeding over tuna; (2) prey eaten by seabirds feeding solitarily at night—crustaceans, gonostomatids, sternoptychids, myctophids, bregmacerotids, diretmids, melamphaids, crustaceans, and mesopelagic-bathypelagic cephalopod individuals too small to have been scavenged, (3) live prey eaten by seabirds feeding solitarily during the day—photichthyids, fish eggs, and non-cephalopod invertebrates except crustaceans; and (4) dead cephalopods that were scavenged (i.e., mesopelagic-bathypelagic cephalopods too large to have been eaten whole). We excluded miscellaneous families of fishes as well as fishes and cephalopods unidentified to family level (9.4% of the prey sample; Appendix 1).

Based on these classifications and the diets observed during this study (Appendices 3–32), we estimated the mass of prey consumed using each of the four feeding strategies during one day of foraging by one individual bird representing each of the 30 ETP seabird species. From these values, we could estimate the percent of the daily prey mass consumed when using each of the four feeding strategies.

Calculation of consumption rate for different prey groups

Otolith condition and temporal occurrence of hemiramphid/exocoetid prey indicated that 37.9% of all such otoliths present in seabird stomachs at 0800 H on a given day had actually been eaten between 1600 and 1900 H of the previous day although, due to progressive otolith digestion, the birds eliminated these otoliths by 1200 H the following day. Therefore, we adjusted values for number of hemiramphid/exocoetid prey by multiplying numbers of otoliths of these fish by 0.621 for those in birds collected at 0800, by 0.716 for those collected at 0900, 0.811 for 1000, and 0.906 for 1100 H, and assumed that no otoliths eaten between 0700 and 1800 H had been eliminated before 1800 H. We then calculated mass of hemiramphid/exocoetids using equations for *Exocoetus* spp. and *Oxyporhamphus micropterus* (Appendix 2) applied to all species of respective families of prey. We also used regression equations to calculate biomass of non-scavenged

cephalopods (Appendix 2, Clarke 1986) that represented beaks.

Except for whole fishes representing photichthyids, carangids, coryphaenids, scombrids, nomeids, and gempylids, we calculated average mass of these fishes using the average mass of individuals of respective fishes found whole, or nearly so, in seabirds. For the carangids, coryphaenids and *Auxis* spp., we used masses of 25 g, 15 g, and 35 g for individual prey found in large procellariiforms, larids, and pelecaniforms, respectively; for gempylids these values were 12 g, 10 g, and 15 g; and for juvenile *Euthynnus*, 6 g, 6 g, and 7 g. Mean mass of the photichthyid, *Vinciguerria lucetia*, was 1.4 g, and the mass of the nomeid, *Cubiceps carnatus*, was 4.0 g, based on the mass of whole individuals found in bird stomachs and the fact that the otolith lengths of these species were similar among the birds containing them (sample sizes in Appendix 1).

Essentially, all otoliths of prey group 2 (gonostomatids, sternoptychids, myctophids, bregmacerotids, diretmids, and melamphaids) that were identifiable to family level (hereafter = identifiable) were eliminated by seabirds within 24 hr after being consumed. Based on otolith wear, we determined that these otoliths were obtained during the earlier hours of night, and that the proportion remaining in the stomach decreased with hour in such a way that only about 63% of the identifiable otoliths present at about 2000 H the previous night remained at 0800 H the next day, and only about 4% remained in the stomach at 1800 H.

Thus, to estimate the proportion of identifiable prey group 2, otoliths remaining in the stomachs of procellariiforms (essentially the only seabirds to feed on group 2 prey) at different hours of the day (all of those birds collected between 0800–1800 H), we used the regression relationship [Y = a + b (x)] between otolith condition in prey group 2 and hour of day. Hence, we calculated the proportion of identifiable otoliths in group 2 (Y) present in the stomach during the hour that birds were collected as:

$$Y = (1.46 + 0.133\ (\text{hour}/100))/4,$$

where 1.46 is the constant (a), 0.133 is the regression coefficient (b), (hour/100) is (x) (e.g., 0800 H/100 = 8), and 4 = condition of a highly worn (unidentifiable and unmeasured) otolith. We then adjusted prey group-2 otolith values in the stomach samples to estimate the true number eaten in a given night of feeding by multiplying values for number of group-2 otoliths found in bird stomachs in a given hour by the inverse of Y. We calculated mass for all group-2 prey for which we had regression equations relating otolith length to fish mass (Appendix 2). To calculate the mass of group-2 prey for which no regression equations were available, we averaged the mass across all species for which we had regression equations and used that value to estimate the mass of the other group-2 prey species. That is, we assumed that the average mass was similar across all group-2 prey for those in which we could not calculate mass from regression equations.

To calculate the mass of non-cephalopod invertebrate prey, first we calculated the average mass of different species of whole prey weighed during sorting. We then estimated the mass of invertebrate prey species that we did not weigh (either because of time constraints or because they were not whole) by multiplying the counts of these prey by the average values of mass of whole conspecifics. We divided these prey into two groups depending on whether caught at night or during the day (all others). Crustaceans contributed 16% of the prey mass among non-cephalopod invertebrates consumed, and were included with the prey acquired by birds feeding nocturnally.

Because various amounts of dead cephalopod individuals were eaten by scavenging procellariiforms, we could not calculate the mass consumed directly from the size of scavenged beaks. Therefore, to calculate the average mass of prey consumed by each scavenging seabird species, we averaged the mass of animal tissue in the stomachs of individual birds that had been scavenging shortly before being collected (i.e., containing torn off pieces of cephalopods showing little evidence of digestion). The average mass of cephalopod tissue present was 36.1 g for scavenging birds of mass >300 g (N = 41 birds having recently scavenged), 12.3 g for birds <300 g and >100 g (N = 19), and 4.6 g for those <100 g (N = 12). Using these values, we assigned the appropriate mass to the scavenged proportion of the diet of each bird determined to have recently scavenged.

The proportional amount of prey obtained during a 24-hr period when using each of the four foraging strategies was preliminarily estimated for each bird representing each species by: (1) summing prey mass across all prey species representing respective strategies, and (2) dividing the mass estimated to have been obtained when using each strategy by the total prey mass for the four strategies.

Estimation of total prey mass consumed

Estimating the total mass of prey consumed by the ETP avifauna per day first required an

estimate of the number of birds representing each of the 30 seabird species present in the study area. To accomplish this, we used generalized additive models (GAMs; Hastie and Tibshirani 1990) and the software and analytical procedure of Clarke et al. (2003) implemented using S-Plus (S-Plus 1997). Inference from model-based methods such as GAMs, unlike sample-based methods, is not dependent on a random survey design and therefore is suited to data from at-sea seabird surveys. GAMs have been used in place of stratified analytical procedures to estimate abundance of marine biota with substantial improvements in precision (Swartzman et al. 1992, Borchers et al. 1997, Augustin et al. 1998). The gains arise because GAMs capture non-linear trends in density while using few parameters. The data used in the GAM for this study were those obtained during the survey portion of cruises. These data included 5,599.8 hr of seabird surveys over 82,440.3 km^2 of ocean surface within the study area (Fig. 2). The 30 species made up 97.3% of the seabirds recorded during the surveys. As explained above, bird counts were corrected for the effects of bird flux. The sample unit was one survey-day and independent variables were latitude, longitude, ocean depth, and distance to mainland. After excluding 20 d when <10 km^2 of ocean area was surveyed (low survey-effort-d can easily result in erroneous densities), the sample size was 807 survey days.

Using the population estimate for all 30 species combined, we then estimated the abundance of each species within the study area by multiplying the total by the percent contribution of a given species, as determined during the corrected survey counts. Using the estimated abundance for each bird species, we then calculated total biomass of each bird species by multiplying the estimated abundance for that species by its respective mean mass as determined in this study (Table 4).

To estimate the mass of prey consumed in one 24-hr period for a given species, we assumed that non-migrant species (species residing in the study area during the breeding season and/or non-breeding season) consumed 25% of their respective mass each day (Nagy 1987). The four species that fed opportunistically while migrating through the ETP were classified as opportunist migrants for this analysis. Because stomach fullness of these species was 50% of that of residents, we assumed a consumption rate of 12.5% of body mass, instead of the 25% used for residents.

Estimated values of average prey mass consumed, using analyses of mass of prey consumed per feeding strategy by each species in a given day, generally yielded masses lower than expected if residents consumed 25% of their mass per day (and migrants 12.5%), we used a second method to estimate the total mass consumed by the ETP avifauna. For the second analysis, we estimated the total mass of prey consumed per species per day by multiplying total bird species mass by 0.25 for resident species and 0.125 for migrants. To estimate the total mass of prey consumed using each foraging strategy for a given species we multiplied the total prey mass consumed by the percent obtained using each strategy calculated using the method described above. Total prey mass consumed by the ETP avifauna was estimated by summing total prey mass across the 30 most-abundant ETP seabird species.

Statistical conventions

Unless otherwise noted all means are expressed with ± 1 SD.

RESULTS

Comparison of Seabird Diets

The prey mass consumed by the ETP avifauna consisted of 82.5% fishes (57% by number), 17.1% cephalopods (27% by number), and 0.4% non-cephalopod invertebrates (16% by number). Fish predominated in the diet of procellariiforms and larids, but both fish and cephalopods were consumed about equally by pelecaniforms.

The first and second PC axes explained 45% of the variance in prey species taken (Table 6). The most important prey groups on the PC1 axis were myctophids with positive scores, and the hemirhamphids/exocoetids and epipelagic cephalopods with negative scores. The 15 seabird species that fed predominantly on myctophids were positioned on the positive side, and those that fed on the others were positioned on the negative side (Fig. 3). The most important prey groups on the PC2 axis were the negatively loaded miscellaneous invertebrates, and the positively loaded epipelagic cephalopods (Table 6).

Species locations on the PC1 axis indicated two distinct feeding groups. The 15 birds on the myctophid side included the six species of storm-petrels, Bulwer's Petrel (Figs. 3, 4), and the eight species of small- to moderately sized *Pterodroma* spp. (Figs. 3, 5). Among these, the White-faced Storm-Petrel (*Pelagodroma marina*) and Tahiti Petrel were the most unique. The storm-petrel was unique due to its more extensive use of miscellaneous invertebrates, which