

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<sup>2</sup> 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<sup>2</sup> 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  $\pm 1$  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 pelicaniforms.

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

TABLE 6. PRINCIPAL COMPONENT ANALYSES BY EIGHT GROUPS OF PREY IN THE DIETS OF ETP SEABIRDS.

PC	Eigenvalue cumulative proportion	Prey group <sup>a</sup>	Eigenvector loadings	
			PC1	PC2
1	0.23	gono/ster/phot	0.26	-0.13
2	0.45	myctophid	0.55	0.26
3	0.60	breg/dire/mela	0.38	0.26
4	0.74	hemi/exoc	-0.50	-0.19
5	0.87	cara/scom/gemp	-0.13	0.03
6	0.96	epipelagic ceph	-0.46	0.48
7	1.00	mesopelagic ceph	0.01	0.09
8	1.00	misc. invertebrate	0.10	-0.76

<sup>a</sup> Prey groups: gono = gonostomatids, ster = sternoptychids, myctophids, phot = photichthyids, breg = bregmacerothids, dire = directmids, mela = melamphids, hemi = hemirhamphids, exoc = exocoetids, cara = carangids, scom = scombrids, gemp = gempylids, ceph = cephalopods.

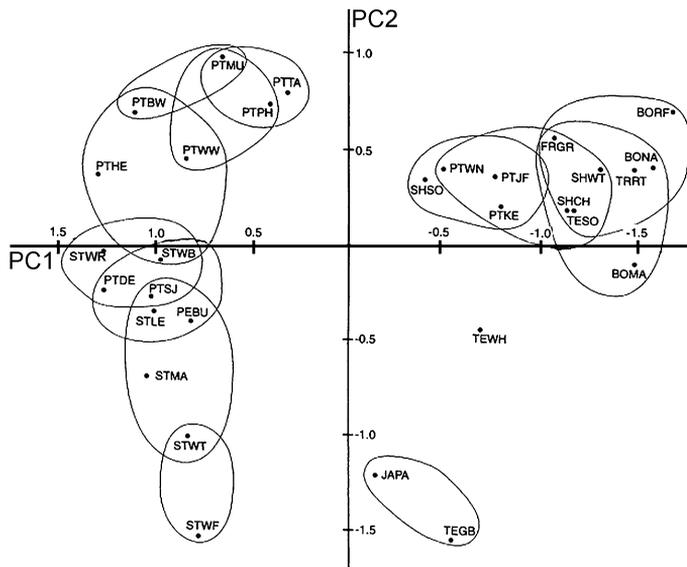


FIGURE 3. Results of the PCA comparing diets among 30 species of seabirds from the ETP. Diets of species enclosed in the same circle were not significantly different (Sidak multiple comparison tests,  $P > 0.05$ ). BORF = Red-footed Booby (*Sula sula*), BOMA = Masked Booby (*S. dactylatra*), BONA = Nazca Booby (*S. granti*), FRGR = Great Frigatebird (*Fregata minor*), JAPA = Parasitic Jaeger (*Stercorarius parasiticus*), PEBU = Bulwer's Petrel (*Bulweria bulwerii*), PTBW = Black-winged Petrel (*Pterodroma nigripennis*), PTDE = DeFilippi's Petrel (*Pterodroma defilippiana*), PTHE = Herald Petrel (*Pterodroma arminjoniana*), PTJF = Juan Fernandez Petrel (*Pterodroma externa*), PTKE = Kermadec Petrel (*Pterodroma neglecta*), PTMU = Murphy's Petrel (*Pterodroma ultima*), PTPH = Phoenix Petrel (*Pterodroma alba*), PTSJ = Stejneger's Petrel (*Pterodroma longirostris*), PTTA = Tahiti Petrel (*Pterodroma rostrata*), PTWN = White-necked Petrel (*Pterodroma cervicalis*), PTWW = White-winged Petrel (*Pterodroma leucoptera*), SHCH = Christmas Shearwater (*Puffinus nativitatus*), SHSO = Sooty Shearwater (*Puffinus griseus*), SHWT = Wedge-tailed Shearwater (*Puffinus pacificus*), STMA = Markham's Storm-Petrel (*Oceanodroma markhami*), STWR = Wedge-rumped Storm-Petrel (*Oceanodroma tethys*), STLE = Leach's Storm-Petrel (*Oceanodroma leucorhoa*), STWB = White-bellied Storm-Petrel (*Fregata grallaria*), STWF = White-faced Storm-Petrel (*Pelagodroma marina*), STWT = White-throated Storm-Petrel (*Nesofregatta fuliginosa*), TEGB = Gray-backed Tern (*Onychoprion lunatus*), TESO = Sooty Tern (*Onychoprion fuscatus*), TEWH = White Tern (*Gygis alba*), TRRT = Red-tailed Tropicbird (*Phaethon rubricauda*).

differentiated it from all other species except the White-throated Storm-Petrel (*Nesofregatta fuliginosa*), which also fed predominantly on miscellaneous invertebrates. For the Tahiti Petrel, its separation from other species positively loaded on the PC1 axis was related primarily to an

extensive use of epipelagic cephalopods, which in conjunction with a high use of myctophids resulted in nearly neutral placement on that axis. The diet of this species was similar only to that of the Murphy's Petrel (*Pterodroma ultima*) and Phoenix Petrel, which also fed heavily on

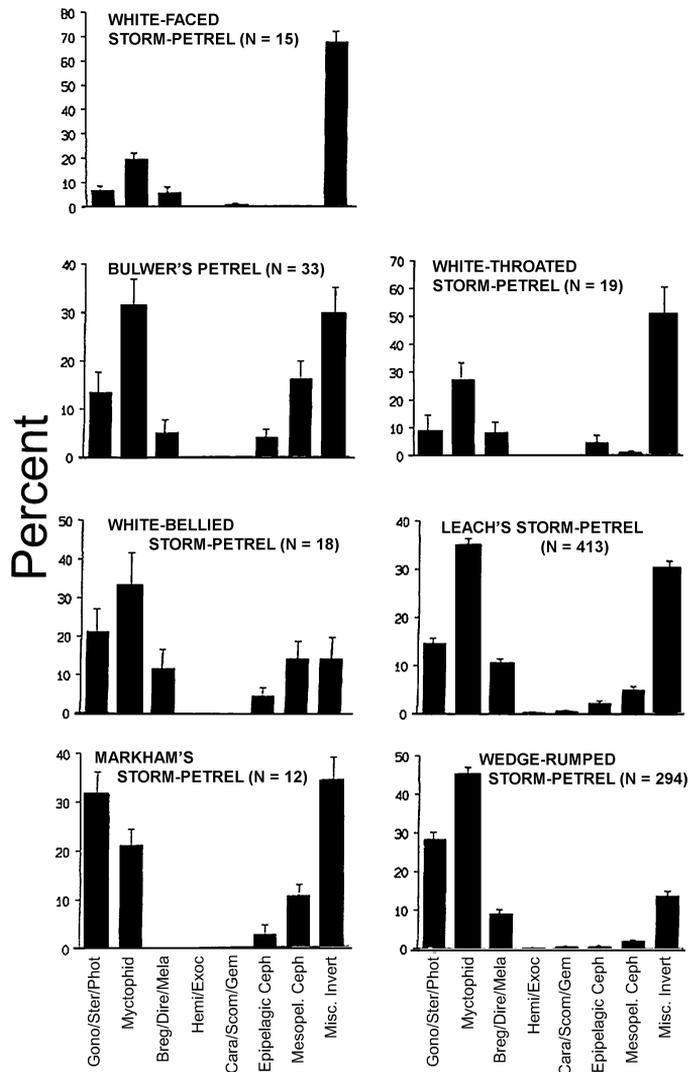


FIGURE 4. Percent of each of eight prey groups in the diet of seven smaller species of petrels, which feed solitarily in the ETP. Percent was calculated as the total number of prey representing a given prey group divided by the total number of prey summed across all eight prey groups in a given seabird species' diet. Values of N (in parentheses) are the number of birds containing at least one prey item. Error bars denote the standard error. See Methods for details on classification of the eight groups of prey species, and Appendices 3-9 for detailed prey lists.

epipelagic cephalopods and myctophids, but which avoided miscellaneous invertebrates. Indeed, the latter three gadfly petrels were the most positively loaded on the PC2 axis. This was due to avoidance of miscellaneous invertebrates in lieu of myctophids, bregmacerotids, diretmids, and melamphids as well as epipelagic cephalopods.

Among the 15 seabirds occurring on the positive side of the PC1 axis, the nine species occurring on the negative side of the PC2 axis

and the six species occurring on the positive side were almost completely separated (Fig. 3). Only one species, the White-bellied Storm-petrel (*Fregetta grallaria*), essentially neutral on that PC2 axis, differed insignificantly among three of the species on the positive side (Herald Petrel [*Pterodroma arminjoniana*], White-winged, and Black-winged petrels) and five of the species on the negative side (Leach's and Wedge-rumped storm-petrels; Stejneger's, DeFilippi's [*Pterodroma defilippiana*] and Bulwer's petrels).

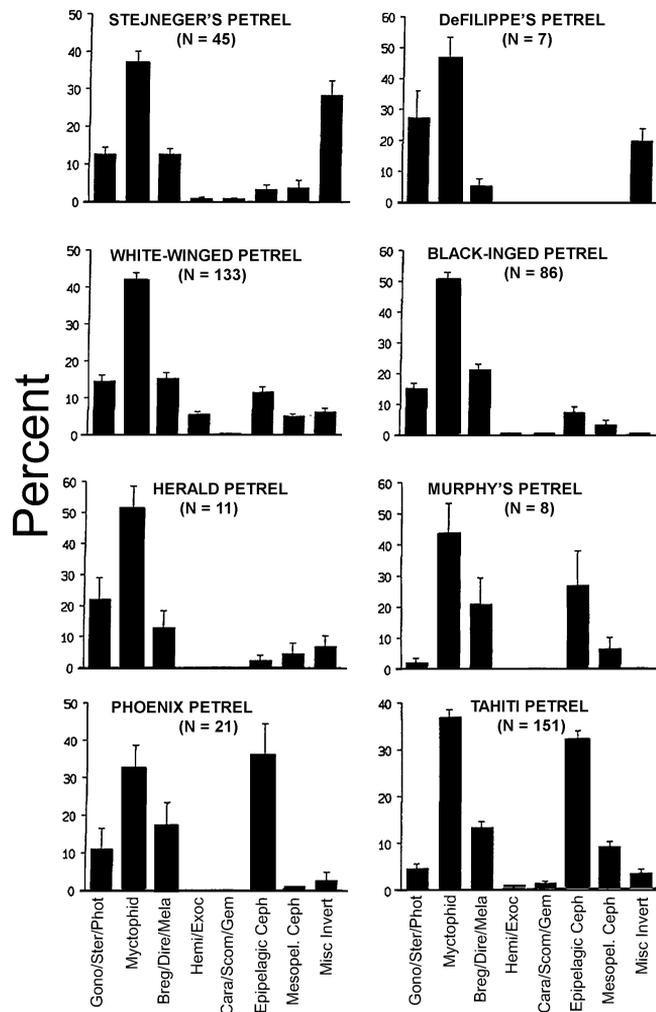


FIGURE 5. Diet composition of the eight medium-sized petrels, most of which feed solitarily in the ETP. For each seabird species, percent was calculated as the total number of prey representing a given prey group divided by the total number of prey summed across the eight prey groups in a given seabird species' diet. Values of N (in parentheses) are the number of birds containing at least one prey item. Error bars denote the standard error. See Methods for details on classification of the eight groups of prey species, and Appendices 10-17 for detailed prey lists and predator sample sizes.

This was primarily due to the lower intake of miscellaneous invertebrates by the White-bellied Storm-Petrel (Figs. 4, 5).

Interestingly, the Wedge-rumped Storm-Petrel, one of the species on the positive side of the PC1 axis, also consumed a low proportion of invertebrates and was also nearly neutral on the PC2 axis (Figs. 3, 4). In fact, the diet of this species was significantly different from that of the Leach's Storm-Petrel, with whom it associated spatially in the ETP. The very large sample sizes for each of the two species notwithstanding, this difference in diet resulted primarily from

the higher proportion of myctophids and lower proportion of miscellaneous invertebrates in the diet of the Wedge-rumped Storm-Petrel. Indeed, among all species, this storm-petrel was surpassed only by the DeFilippi's Petrel in the proportion of gonostomatids, sternoptychids, and photichthyids (primarily the photichthyid, *Vinciguerria lucetia*, see Appendix 2), and was surpassed in the proportion of myctophids in its diet only by the Black-winged and Herald/Henderson petrels (Figs. 4, 5). The latter species were separated from the Wedge-rumped Storm-Petrel due to differences on the PC2 axis

resulting from the lower proportion of miscellaneous invertebrates in their diets.

The diets of the Stejneger's and DeFilippi's petrels were also significantly different from the other two closely-related Cookilaria (small *Pterodroma*) petrels (Fig. 3). This was mostly due to the higher proportion of miscellaneous invertebrates in the diet of the former (Fig. 5). Among the four Cookilaria, the diet of the White-winged Petrel was noteworthy because of the larger proportions of hemirhamphids, exocoetids, and epipelagic cephalopods compared to the other three.

As noted above, occurring on the negative side of the PC1 axis were seabirds having a high proportion of hemirhamphids, exocoetids, and epipelagic cephalopods and low proportions of myctophids in their diets. Twelve of the 15 species (details on the three exceptions below) occurred in a tight group (Fig. 3). Significant differences consisted only for diets of the Sooty Shearwater (*Puffinus griseus*), and Juan Fernandez, White-necked (*Pterodroma cervicalis*), and Kermadec (*Pterodroma neglecta*) petrels compared with the Red-tailed Tropicbird, and Masked, Nazca, and Red-footed boobies (*Sula sula*). In fact, the Sooty Shearwater's diet differed significantly from all species except the three large *Pterodroma*. These differences resulted from the nearly complete dependence by the four pelecaniforms, the Christmas (*Puffinus nativitatus*) and Wedge-tailed shearwaters and Sooty Tern on hemirhamphids, exocoetids, and epipelagic cephalopods compared to the more diverse diets among the Sooty Shearwater and three large *Pterodroma* (Fig. 6). Indeed, for the PC1 axis, the boobies, tropicbird, and Wedge-tailed Shearwater had the highest negative loadings of the 30 predator species, although the Sooty Tern, Christmas Shearwater, and Great Frigatebird (*Fregata minor*) were not significantly different (Fig. 3). Among the boobies, the diet of the Red-footed Booby differed from that of the Masked Booby primarily because of differences on the PC2 axis resulting from the nearly complete use of epipelagic squid by the former in comparison to the much higher proportion of exocoetid/hemirhamphids in the diet of the latter (Fig. 6).

Two species occurring on the negative side of the PC1 axis, the Gray-backed Tern (*Onychoprion lunatus*) and Parasitic Jaeger (*Stercorarius parasiticus*), were distinct from all other species due to high negative loading on the PC2 axis and nearly neutral loading on the PC1 axis (Fig. 3). For the tern, the cause of divergence was its unique diet consisting almost solely of approximately equal proportions of hemirhamphids/exocoetids and miscellaneous invertebrates (primarily *Halobates* spp.; Fig. 6).

Similarly, the diet of the jaeger consisted of 70% miscellaneous invertebrates (primarily barnacles [*Lepas* spp.]) and exocoetid egg bunches, with the remainder being an assortment of small fish and squid (the latter taken mostly by scavenging). Indeed, the proportion of miscellaneous invertebrates in the diet of these two species was similar only to that of the White-faced and White-throated storm-petrels, although the latter had no hemirhamphids/exocoetids in their diets (Fig. 4).

#### TEMPORAL AND SPATIAL ASPECTS OF DIET

Results of the PC analysis comparing temporal/spatial patterns among diets of the 10 most abundant seabird species were similar to those comparing diets among the remaining 30 abundant species. For the former, the first and second PC axes explained 40% of the variance in prey species intake (Table 7). Similar to the previous analysis, the most important prey groups on the PC1 axis were the positive loading of myctophids, and the negative loadings of hemirhamphids/exocoetids and epipelagic cephalopods. The most important prey groups on the PC2 axis were the miscellaneous invertebrates with negative loadings, and the myctophids with positive loadings. Thus, myctophids had a major effect on both axes, although not nearly as great as miscellaneous invertebrates on the PC2 axis.

Diets of none of the 10 seabirds differed significantly when compared between sexes and seasons (Figs. 7, 8). Similarly, the diet of only one of the 10 species, the Stejneger's Petrel, differed significantly when the 10 species' diets were compared between the SEC and NECC (Fig. 9). This was due to differences primarily on the PC2 axis reflecting a considerably higher intake of invertebrates and lower intake of myctophids in the NECC compared to the SEC (Fig. 10).

The diets of three of nine species differed significantly between the eastern and western waters (Fig. 11). Bulwer's Petrel was excluded because of a small sample in the eastern section. The differing species included Stejneger's Petrel, Leach's Storm-Petrel, and Sooty Tern. The differences occurred primarily on the PC2 axis for Leach's Storm-Petrel and Stejneger's Petrel and on the PC1 axis for Sooty Terns. For the first two species this was mostly due to a higher intake of invertebrates and lower intake of myctophids in the east (Fig. 10). For the Sooty Tern, this was due to a considerably higher intake of gonostomatids, sternoptychids, and photichthyids (particularly *Vinciguerria lucetia*) and lower intake of hemirhamphids/exocoetids and epipelagic cephalopods in the east.

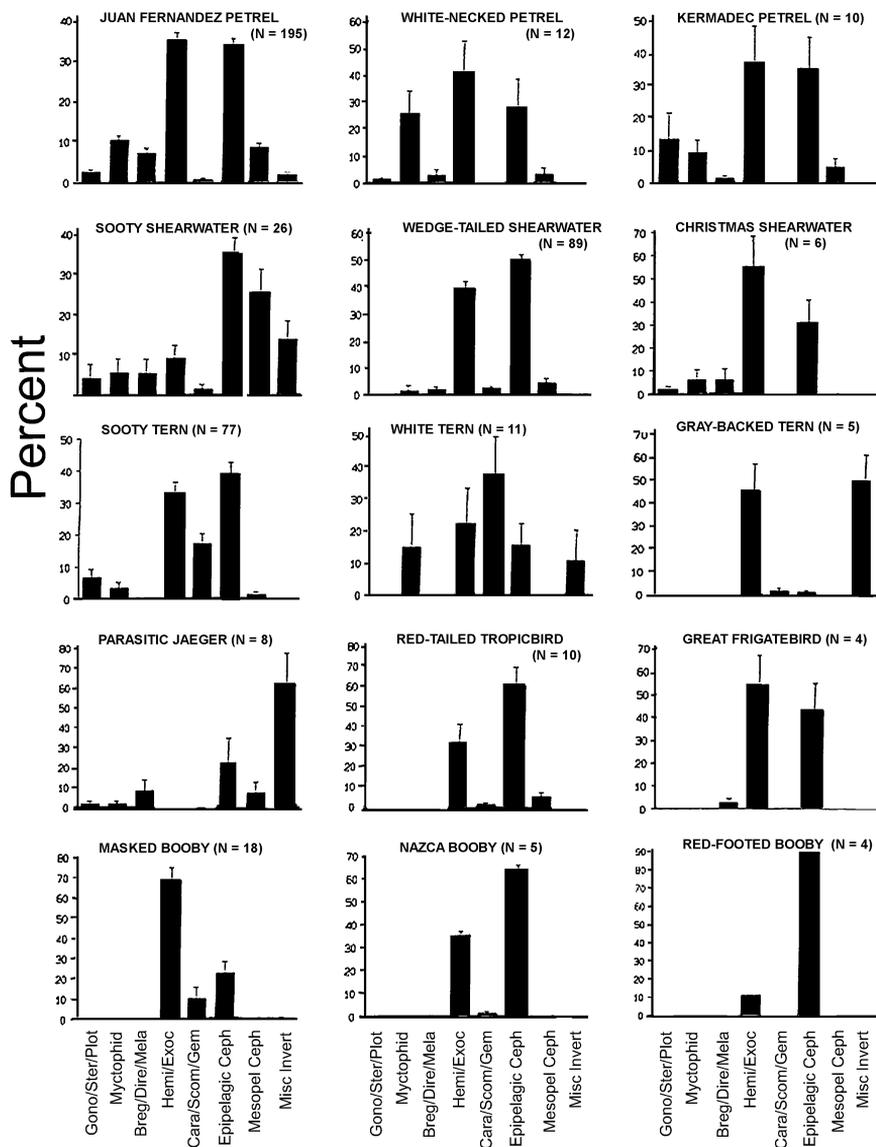


FIGURE 6. Diet composition of the 15 species of birds that generally feed over surface-foraging tuna in the ETP. For each seabird species, percent was calculated as the total number of prey representing a given prey group divided by the total number of prey summed across the eight prey groups in a given seabird species' diet. Values of N (in parentheses) are the number of birds containing at least one prey item. Error bars denote the standard error. See Methods for details on classification of the eight groups of prey species, and Appendices 18–32 for detailed prey lists and predator sample sizes.

The diets of two species—Stejneger's and Bulwer's petrels—differed significantly when compared between the El Niño vs. La Niña phases of ENSO (Fig. 12). This was related mostly to a higher proportion of non-cephalopod invertebrates in the diet of Bulwer's Petrels during El Niño, and in the diet of Stejneger's Petrels during La Niña (Fig 10). The latter also had a

much higher proportion of myctophids in their diet during El Niño than La Niña.

#### DIET DIVERSITY

Diet diversity ( $H'$ ) averaged  $2.60 \pm 0.62$  ( $N = 23$  seabirds species with sample sizes  $\geq 9$ ) and ranged from a high of 3.553 for White-

TABLE 7. PRINCIPAL COMPONENT ANALYSES FOR TEMPORAL/SPATIAL COMPARISONS BY EIGHT GROUPS OF PREY IN THE DIETS OF 10 ETP SEABIRDS.

PC	Eigenvalue cumulative proportion	Prey group <sup>a</sup>	Eigenvector loadings	
			PC1	PC2
1	0.21	gono/ster/phot	-0.21	0.27
2	0.40	myctophid	-0.58	-0.39
3	0.57	breg/dire/mela	-0.31	-0.21
4	0.71	hemi/exoc	0.40	-0.13
5	0.83	cara/scom/gemp	0.21	-0.14
6	0.90	epipelagic ceph	0.55	0.26
7	0.96	mesopelagic ceph	0.07	0.28
8	1.00	misc. invertebrate	-0.03	0.74

<sup>a</sup> Prey groups: gono = gonostomatids, ster = sternoptychids, myctophids, phot = photichthyids, breg = bregmacerotids, dire = directmids, mela = melamphoids, hemi = hemirhamphids, exoc = exocoetids, cara = carangids, scom = scombrids, gemp = gempylids, ceph = cephalopods.

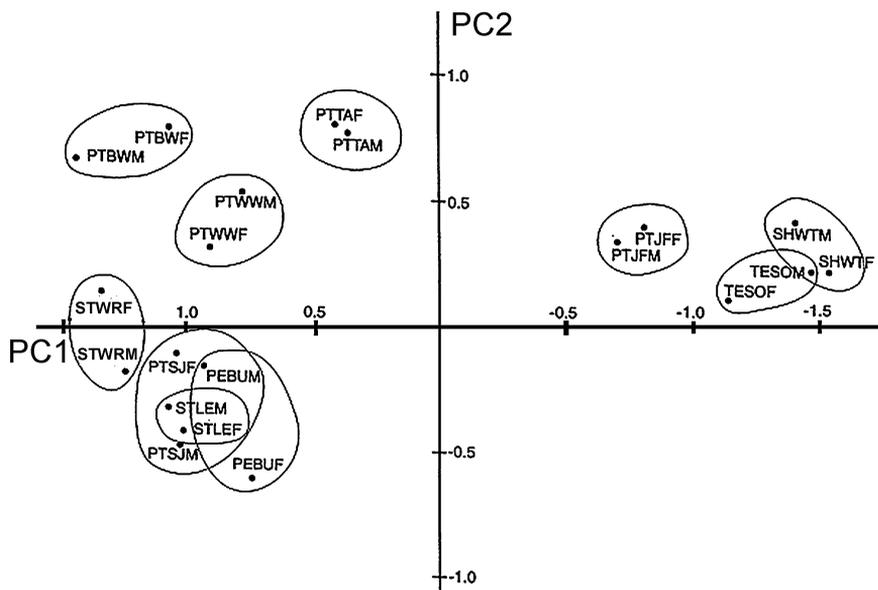


FIGURE 7. Results of the PCA to compare diets between sexes for each of 10 species of seabirds in the ETP. See Fig. 3 for species codes (first four letters). The fifth letter in the code designates female (F) or male (M). Diets of species enclosed in the same circle did not differ significantly between sexes (Sidak multiple comparison tests, all  $P > 0.05$ ). Difference among species are not shown (see Fig. 3 for those results).

winged Petrels to a low of 1.296 for Red-tailed Tropicbirds (Fig. 13a). Solitary feeders (storm-petrels and certain procellariids) had significantly higher  $H'$  values than flock-feeding species (flocking procellariids, larids, and pelecaniforms; Sidak tests, all  $P < 0.025$ , Fig. 13b). Within the latter, flocking procellariids had significantly higher  $H'$  values than pelecaniforms (Sidak test,  $P < 0.001$ ), but not larids ( $P = 0.3$ ). There was an insignificant tendency for predator mass to be negatively correlated with  $H'$  in solitary and flock-feeding groups (flocking species,  $r = -0.503$ ,  $df = 15$ ,  $P = 0.06$ ; solitary species,  $r = -0.499$ ,  $df = 13$ ,  $P = 0.06$ ; Table 4).

#### PREY SIZE

Prey size was estimated using fish otolith and cephalopod beak lengths. The multiple regression conducted to examine factors related to prey size (otolith/beak length = dependent variable) among two storm-petrels, two small *Pterodroma* and one large *Pterodroma* representing the more abundant solitary feeders (all fed extensively on myctophids and other small fishes), explained 74% of the variance in prey size (Table 8; see Table 9 for mean standard lengths of these prey species). Significant main effects (other than prey species) were seabird species, sex, and body mass. Thus, sizes of the

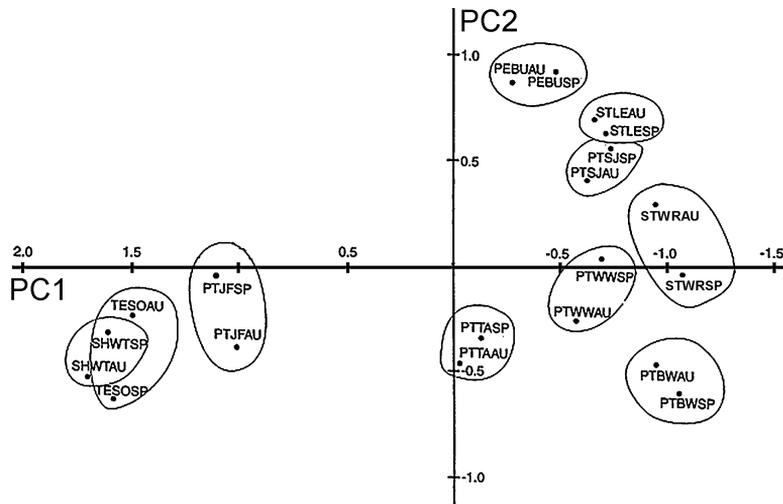


FIGURE 8. Results of the PCA to compare diets between spring and autumn for each of 10 species of seabirds in the ETP. See Fig. 3 for species codes (first four letters). The fifth and sixth letters in the code designates spring (SP) and autumn (AU). Diets of species enclosed in the same circle did not differ significantly between seasons (Sidak multiple comparison tests, all  $P > 0.05$ ). Difference among species are not shown (see Fig. 3 for those results).

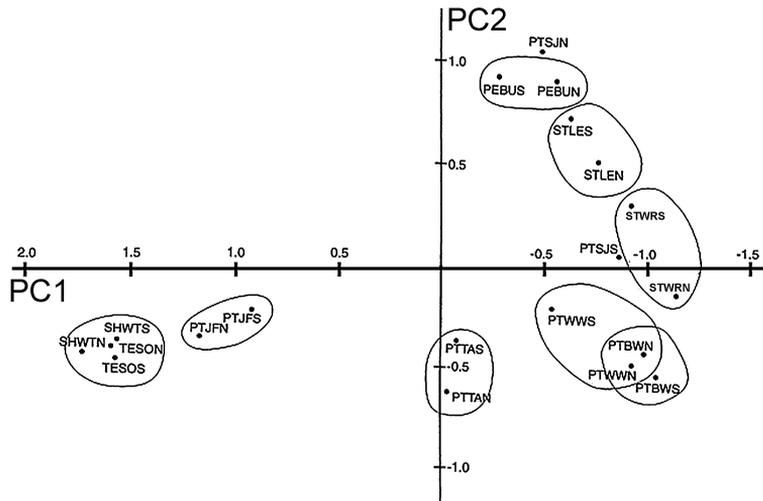


FIGURE 9. Results of the PCA to compare diets of 10 species of seabirds between the South Equatorial Current and North Equatorial Countercurrent. See Fig. 3 for species codes (first four letters). The fifth letter in the code designates current system; S = South Equatorial Current, or N = North Equatorial Countercurrent. Diets of species enclosed in the same circle did not differ significantly between current systems (Sidak multiple comparison tests, all  $P > 0.05$ ). Difference among species are not shown (see Fig. 3 for those results).

prey representing each prey species differed significantly, and size of prey eaten by a given predator species differed when compared to the size of prey eaten by other petrel species (when controlling for within-predator effects of body mass and sex). In addition, females of a given predator species and of given mass, ate larger prey than males and, for a given predator species and sex, individuals of larger mass ate

larger prey. Each of these effects was independent from the others.

An interaction was also found between predator species and prey species (Table 8). However, the difference in prey sizes was apparent in only five of the 10 prey species: *Myctophum aurolaternatum*, *Ceratoscopelus warmingii*, *Diaphus parri*, *Diaphus schmidti*, and *Lampanyctus nobilis* (Fig. 14a), and were

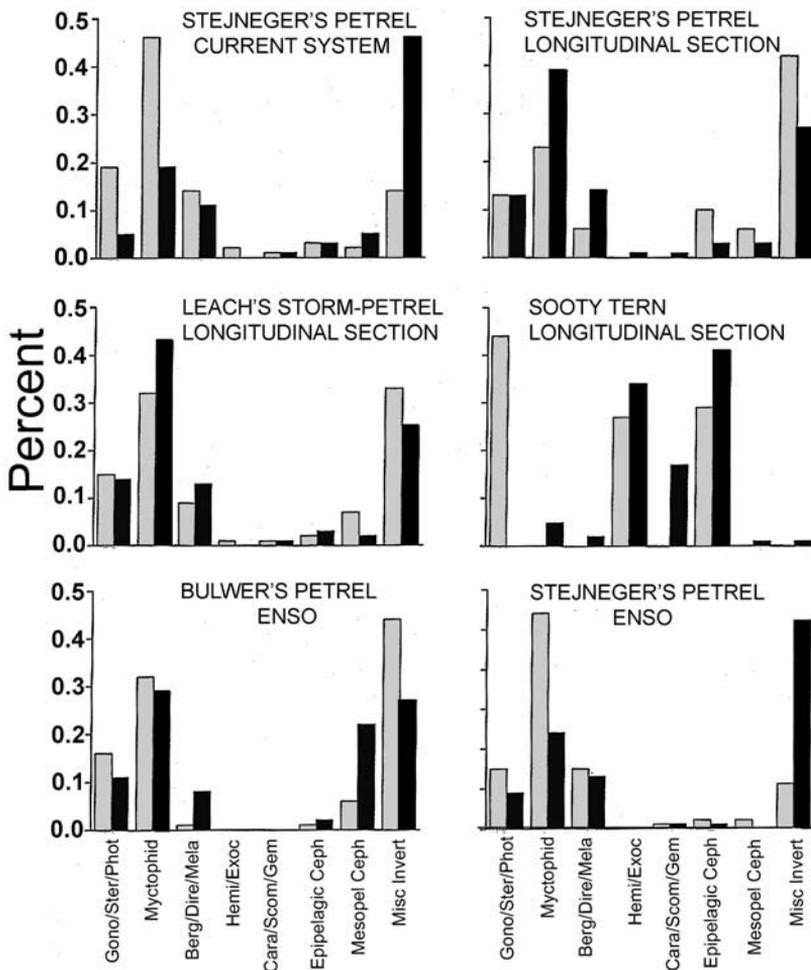


FIGURE 10. Percent of eight different categories of prey in the diets of different species of seabirds occurring within different current systems, longitudinal sections, or during La Niña vs. El Niño. See Methods for details on divisions for these waters or temporal periods. For current system, longitudinal section, and ENSO phase, the light bars designate the SEC, East, and El Niño, respectively; and the dark bar designates the NECC, West, and La Niña.

primarily because Wedge-rumped Storm-Petrel (the smallest species) ate smaller prey than did the other four seabird species. The Tahiti Petrel (the largest of the five predators) ate the largest individuals among five of the 10 prey species.

The multiple regression analyses to examine factors related to prey size among one larid, two procellariids, and three pelicaniform species representing those predators that feed in multispecies flocks and that primarily ate *Exocoetus* spp., *Oxyporhamphus micropterus* and *Sthenoteuthis oualaniensis*, explained 78% of the variance (Table 10; see Table 11 for average prey lengths of these prey species). Other than prey species, significant main effects were seabird

species, sex, and fat load. Thus, for a given prey, the six seabird species ate individuals that were of significantly different sizes when controlling for within-predator effects of sex and fat load. In contrast to the solitary petrel group feeding on smaller prey, males ate larger prey than females and, for a given predator species and sex, individuals of lower fat load ate larger prey. Each of these effects was independent from the others.

Five significant interactions were found, including those of seabird species with prey species and seabird mass, sex, and fat load, as well as sex with mass (Table 10). The interaction between predator and prey species reflected the fact that, for a given prey, the size of individuals

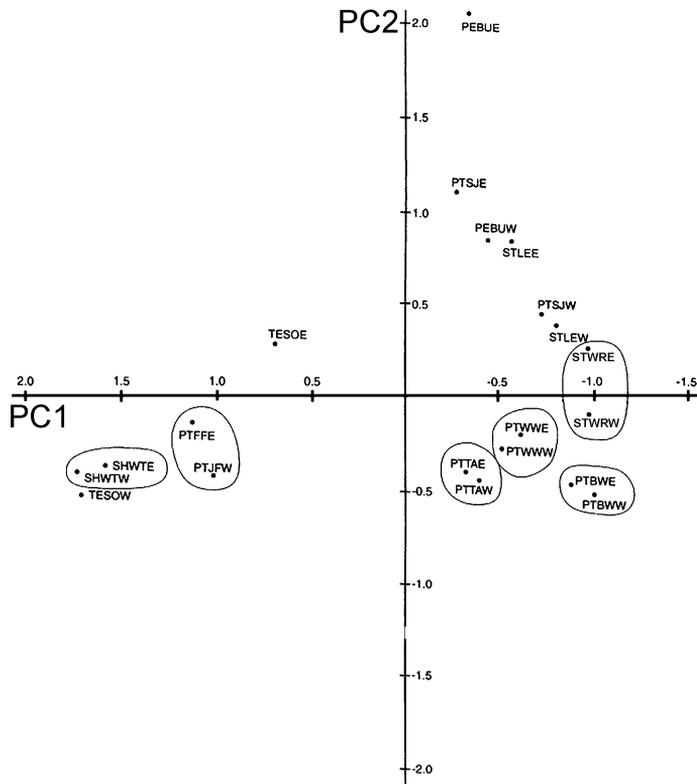


FIGURE 11. Results of the PCA to compare diets between east and west longitudinal portions of the ETP for each of 10 species of seabirds. See Fig. 3 for species codes. The fifth letter in the code designates east (E) or west (W). Diets of species enclosed in the same circle did not differ significantly between longitudinal sections (Sidak multiple comparison tests, all  $P < 0.05$ ). Differences among species are not shown (see Fig. 3 for those results).

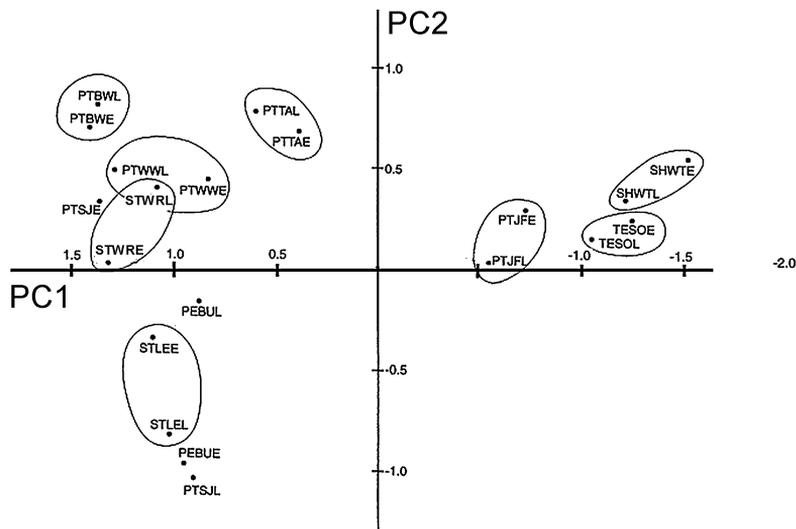


FIGURE 12. Results of the PCA to compare diets between El Niño and La Niña for each of 10 species of seabirds in the ETP. See Fig. 3 for species codes. The fifth letter in the code designates El Niño (E) or La Niña (L). Diets of species enclosed in the same circle did not differ significantly between the two ENSO phases (Sidak multiple comparison tests, all  $P < 0.05$ ). Difference among species are not shown (see Fig. 3 for those results).

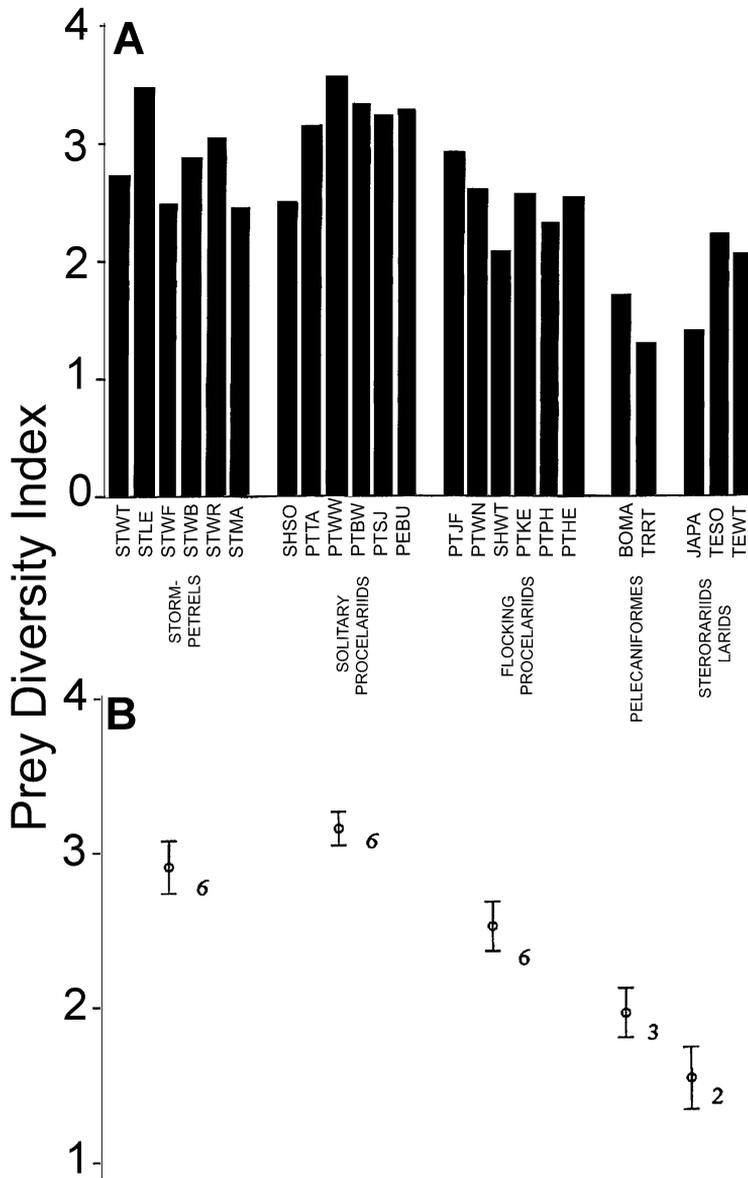


FIGURE 13. (A) Shannon-Wiener diet-diversity indices ( $H'$ ) for species of seabirds in the ETP having sample sizes (number of birds containing prey)  $\geq 9$ . See Table 3 for species' sample sizes; Fig. 3 for species code definitions. (B) Mean  $H' \pm SD$  among six groups of ETP seabirds.

eaten increased with predator body mass among the four smaller predators (Sooty Tern, Wedge-tailed Shearwater, Juan Fernandez Petrel, and Red-tailed Tropicbird (given in increasing mass)). This interaction was less apparent, and differed in intensity among the three largest predators (Red-tailed Tropicbird, and Nazca and Masked boobies, given in increasing mass; Fig 14b).

The interaction between predator species and predator mass was due to a significant increase in prey size with increase in predator mass among the petrel and shearwater, but not in the tern, tropicbird, or boobies (Table 10). The interaction between seabird species and sex reflected the significantly larger prey taken by males representing the petrel and shearwater, compared to no sex-related prey size differences within

TABLE 8. REGRESSION ANALYSES FOR THE RELATIONSHIP BETWEEN PREY SIZE AND VARIOUS INDEPENDENT VARIABLES.

Term	Coefficient sign	F-value	P-value	df
<b>Main effects</b>				
Predator species	-	3.48	<0.01	4
Prey species	-	343.48	<0.0001	9
Sex	(+)	4.15	<0.05	1
Body mass	(+)	14.25	<0.001	1
<b>Interactions</b>				
Predator sp. X prey sp.	-	4.02	<0.0001	36
<b>Rejected terms</b>				
Fat load	ns	0.02	0.9	1
Prey species X sex	ns	1.10	0.4	9
Prey species X fat load	ns	1.54	0.12	9
Prey species X mass	ns	1.35	0.2	9
Predator species X mass	ns	0.50	0.7	4
Predator species X sex	ns	0.59	0.7	4
Predator species X fat load	ns	0.59	0.7	4
Mass X sex	ns	0.01	0.9	1
Mass X fat load	ns	0.11	0.7	1
Sex X fat load	ns	0.27	0.6	1

Notes: Otolith length = dependent variable; See Methods; independent variables include predator species, mass, sex, and fat load among the five more abundant seabirds that feed solitarily on small fishes (Leach's Storm-Petrel [*Oceanodroma leucorhoa*], Wedge-rumped Storm-Petrel [*O. tethys*], White-winged Petrel [*Pterodroma leucoptera*], Black-winged Petrel [*P. nigripennis*], and Tahiti petrel [*P. rostrata*]). Sample size was 1,449 prey items. Prey size pertains to the 10 more abundant prey species common to the diets of each predator (See Methods, Appendices). Prey species was controlled for in these analyses to control for differences in size. Predator and prey species were analyzed as categorical; sex, mass, and fat load as continuous. A negative coefficient for sex indicates larger otolith size among males than females. Two terms separated by an asterisk indicate an interaction between respective terms. Model  $F_{[51, 1397]} = 79.57$ , 73.6% of variance explained.

TABLE 9. STANDARD LENGTHS OF PHOTICHTHYIDS AND MYCTOPHIDS EATEN BY CERTAIN ETP SEABIRDS.

	Wedge-rumped Storm-Petrel ( <i>Oceanodroma tethys</i> )	Leach's Storm-Petrel ( <i>O. leucorhoa</i> )	Black-winged Petrel ( <i>Pterodroma nigripennis</i> )	White-winged Petrel ( <i>P. leucoptera</i> )	Tahiti Petrel <i>P. rostrata</i>
<i>Vinguerria lucetia</i>					
$\bar{x} \pm sD$	32 ± 7 (182)	31 ± 6 (204)	30 ± 4 (48)	33 ± 6 (87)	34 ± 2 (9)
Range	19–51	15–53	25–38	19–44	31–39
<i>Myctophum aurolaternatum</i>					
$\bar{x} \pm sD$	42 ± 10 (32)	41 ± 14 (70)	38 ± 12 (13)	41 ± 16 (20)	49 ± 11 (13)
Range	23–60	15–80	21–55	16–75	36–73
<i>Symbolophorus evermanni</i>					
$\bar{x} \pm sD$	39 ± 8 (8)	56 ± 11 (30)	55 ± 8 (10)	50 ± 5 (7)	55 ± 11 (9)
Range	25–64	28–69	43–62	44–59	46–70
<i>Ceratoscopelus warmingii</i>					
$\bar{x} \pm sD$	39 ± 14 (20)	48 ± 11 (74)	51 ± 9 (48)	45 ± 11 (27)	51 ± 7 (10)
Range	17–60	19–67	27–67	24–60	36–69
<i>Lampanyctus nobilis</i>					
$\bar{x} \pm sD$	42 ± 9 (4)	54 ± 10 (7)	91 ± 16 (5)	86 ± 36 (7)	93 ± 24 (10)
Range	30–52	46–75	46–104	28–140	64–134

Notes: Prey sample sizes are given in parentheses. Predator species are given in order of increasing mass. See Appendix 2 for regressions used to calculate standard lengths (in millimeters) from otolith lengths (in millimeters).

the other four seabirds. The interaction between seabird species and fat load occurred because the petrels and shearwaters with a lower fat load ate significantly larger prey than those with a heavy fat load. No such relationship existed among the terns, and for tropicbirds and boobies fat loads did not vary enough to be compared. The interaction between sex and mass reflected a significant increase in prey size with increase in mass among female, but not among male seabirds (Table 10).

#### SCAVENGING

Species of cephalopods that were scavenged (M. Imber, pers. comm.) were larger individuals of mesopelagic-bathypelagic species—*Octopoteuthis deletron*, *Histioteuthis hoylei* and *H. corona*, *Megalocranchia* sp., *Taonius pavo*, *Galiteuthis pacifica* and *Alloposus mollis* (Table 12). We consider all individuals of smaller size as well as all other species of cephalopods recorded in this study to have been eaten

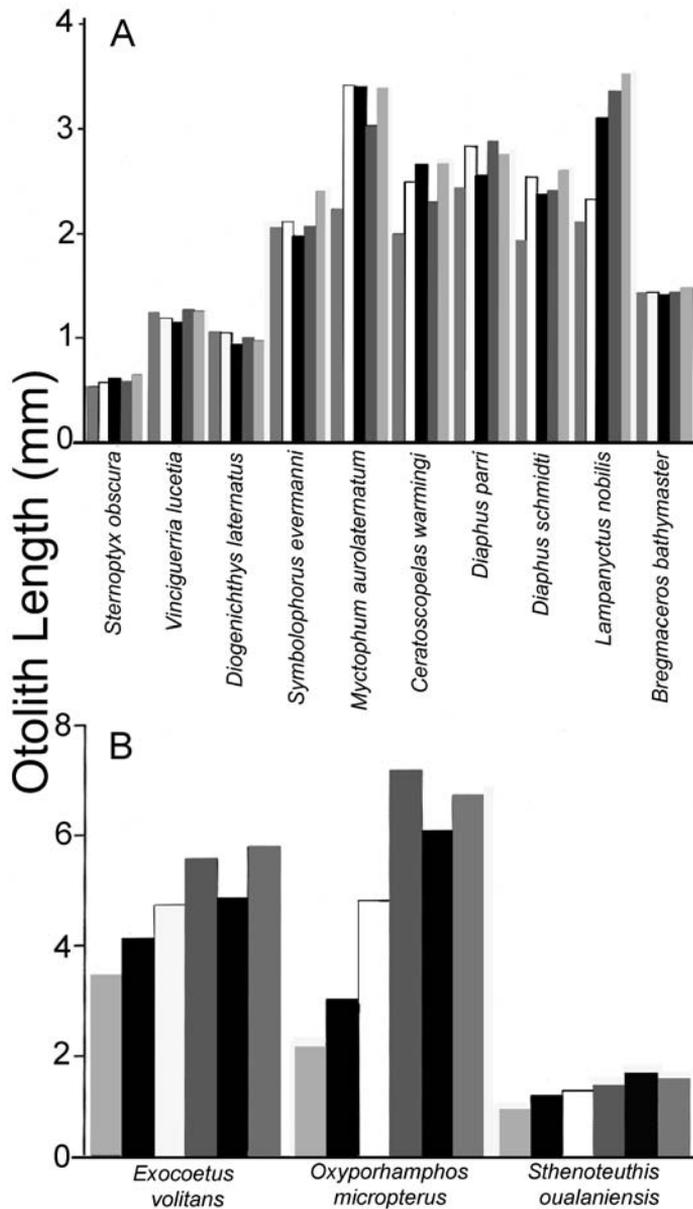


FIGURE 14. (A) Average otolith length (millimeters) of 10 species of prey taken by five species of seabirds that feed on smaller fishes. Predator species' bars for each prey species are from left to right (in order of increasing predator mass): Wedge-rumped Storm-Petrel (*Oceanodroma tethys*), Leach's Storm-Petrel (*O. leucorhoa*), Black-winged Petrel (*Pterodroma nigripennis*), White-winged Petrel (*P. leucoptera*), Tahiti Petrel (*P. rostrata*). (B) Average otolith or beak length (millimeter) of three species of prey taken by six species of seabirds that feed on larger prey. Predator species' bars are from left to right (in order of increasing mass): Sooty Tern (*Onychoprion fuscata*), Wedge-tailed Shearwater (*Puffinus pacificus*), Juan Fernandez Petrel (*Pterodroma externa*), Red-tailed Tropicbird (*Phaethon rubricauda*), Nazca Booby (*Sula granti*), Masked Booby (*Sula dactylatra*). See Appendices for prey sample sizes.

TABLE 10. REGRESSION ANALYSES FOR THE RELATIONSHIP BETWEEN PREY SIZE AND VARIOUS INDEPENDENT VARIABLES.

Term	Coefficient sign	F-value	P-value	df
Main effects				
Predator species	-	25.71	<0.0001	5
Prey species	-	388.46	<0.0001	2
Sex	(-)	4.17	<0.05	1
Fat load	(-)	22.50	<0.0001	1
Interactions				
Predator sp. X prey sp.	-	7.09	<0.0001	10
Predator sp. X mass	-	3.60	<0.01	5
Red-tailed Tropicbird ( <i>Phaethon rubricauda</i> )	ns	0.59	0.5	1
Nazca Booby ( <i>Sula granti</i> )	ns	1.73	0.2	1
Masked Booby ( <i>Sula dactylatra</i> )	ns	0.86	0.4	1
Sooty Tern ( <i>Onychoprion fuscata</i> )	ns	0.08	0.8	1
Juan Fernandez Petrel ( <i>Pterodroma externa</i> )	(+)	6.06	<0.02	1
Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	(+)	4.19	0.05	1
Predator sp. X sex	-	2.45	<0.05	5
Red-tailed Tropicbird	ns	0.04	0.9	1
Nazca Booby	ns	1.18	0.2	1
Masked Booby	ns	0.16	0.7	1
Sooty Tern	ns (-)	2.21	0.14	1
Juan Fernandez Petrel	(-)	4.87	<0.03	1
Wedge-tailed Shearwater	(-)	8.56	<0.01	1
Predator sp. X fat load	-	9.37	<0.0001	5
Red-tailed Tropicbird (dropped from model; all fat scores = 1)				
Nazca Booby (dropped; all fat scores = 0)				
Masked Booby (dropped; all fat scores = 0)				
Sooty Tern	ns	0.03	0.5	1
Juan Fernandez Petrel	(-)	5.08	<0.025	1
Wedge-tailed Shearwater	(-)	17.04	<0.0001	1
Sex X mass	-	10.62	<0.01	1
Males	ns	0.31	0.6	1
Females	(+)	6.21	<0.01	1
Rejected terms				
Mass	ns	0.63	0.6	1
Fat load X sex	ns	2.13	0.15	1
Mass X fat load	ns	1.64	0.2	1
Prey sp. X fat load	ns	1.82	0.2	2
Prey sp. X mass	ns	1.72	0.2	2
Prey sp. X sex	ns	0.99	0.4	2

Notes: Otolith length = dependent variable; independent variables include: predator species, mass, sex, and fat load among six of the larger seabirds (Sooty Tern, Wedge-tailed Shearwater, Juan Fernandez Petrel, Red-tailed Tropicbird, Nazca Booby, and Masked Booby) that fed in multispecies flocks and preyed on similar species of prey. Sample size was 567 prey items. Prey size pertains to the three more abundant prey species (see Methods); prey species was controlled for in these analyses to control for differences in size; see Table 9 for further details. Model  $F_{[35, 530]} = 59.44$ , 78.3% of variance explained.

when alive (Roper and Young 1975; M. Imber, pers. comm.). We estimate that about 70%, 21%, and 15% of the squid eaten by Tahiti and Black-winged petrels and Sooty Shearwaters, respectively, were obtained by scavenging. Other procellariids including Stejneger's, Juan Fernandez, White-winged petrels, and Wedge-tailed Shearwaters scavenged 1.8–10.5% of the cephalopods they consumed. All other members of the ETP avifauna consumed 0–1.5% of the cephalopods they ate while scavenging and are not presented in Table 12.

#### STOMACH FULLNESS

Stomach fullness (SF), a measure of the propensity of different species of seabirds to feed while in the ETP, averaged  $4.43 \pm 5.58\%$  ( $N = 1,784$  birds; Nazca Booby excluded; Fig. 15). Stomach fullness was significantly different when compared among species ( $F_{[26, 1757]} = 6.26$ ,  $P < 0.0001$ ). This difference was primarily due to very low mean SF among four species, which, from the lowest, were the Parasitic Jaeger (SF =  $1.26 \pm 1.12\%$ ,  $N = 9$ ), White-necked Petrel ( $1.95 \pm$

TABLE 11. MEAN ( $\pm$  SD) AND RANGE FOR STANDARD LENGTHS OF THE MORE ABUNDANT PREY CONSUMED BY CERTAIN ETP SEABIRDS THAT FEED IN MULTISPECIES FLOCKS.

	<i>Exocoetus</i> spp.	<i>Oxyporhamphus</i> <i>Micropterus</i>	<i>Sthenoteuthis</i> <i>oualaniensis</i>
White-winged Petrel ( <i>Pterodroma leucoptera</i> )	63 $\pm$ 10 (18) 53–88	– –	51 $\pm$ 17 (25) 32–70
Sooty Tern ( <i>Onychoprion fuscata</i> )	51 $\pm$ 27 (25) 25–135	85 $\pm$ 17 (17) 46–108	54 $\pm$ 14 (49) 25–84
Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	73 $\pm$ 32 (74) 28–167	103 $\pm$ 27 (39) 52–155	62 $\pm$ 9 (46) 38–102
Juan Fernandez Petrel ( <i>Pterodroma externa</i> )	110 $\pm$ 44 (59) 30–196	120 $\pm$ 21 (50) 133–163	67 $\pm$ 19 (81) 29–117
Red-tailed Tropicbird ( <i>Phaethon rubricauda</i> )	153 $\pm$ 14 (9) 130–173	139 $\pm$ 8 (4) 133–144	71 $\pm$ 12 (13) 54–118
Nazca Booby ( <i>Sula granti</i> )	124 $\pm$ 38 (18) 75–180	126 $\pm$ 20 (29) 87–171	77 $\pm$ 12 (59) 48–102
Masked Booby ( <i>Sula dactylatra</i> )	148 $\pm$ 20 (54) 91–195	145 $\pm$ 9 (8) 133–175	91 $\pm$ 5 (7) 81–121

Notes: Sample sizes are given in parentheses; ranges are given below means. Predator species are given in order of increasing mass. See Appendix 2 for regressions used to calculated standard lengths (in millimeters).

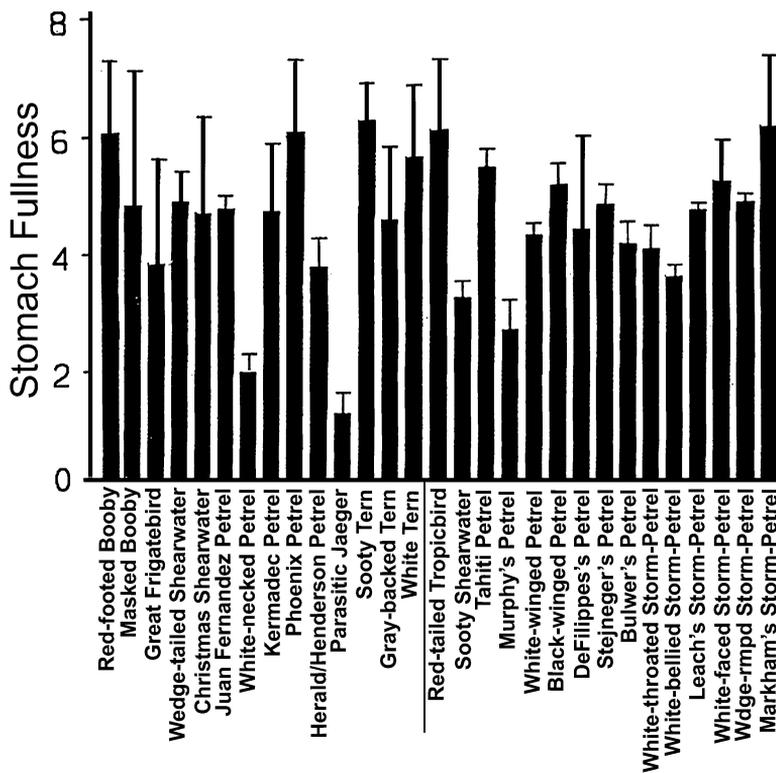


FIGURE 15. Stomach fullness (mean  $\pm$  SE) of 29 species of seabirds in the ETP (Nazca booby [*Sula granti*] excluded; see Methods). Stomach fullness is the mass of food in the stomach divided by the fresh mass of the predator (minus mass of the food) multiplied by 100. See Table 2 for approximate sample sizes. Vertical line projecting from x-axis separates flock-feeding species (left side) from solitary feeding species (right side)

TABLE 12. MEAN LOWER ROSTRAL LENGTHS (MILLIMETERS) OF CEPHALOPOD BEAKS<sup>a</sup> EATEN BY ETP PROCELLARIIFORMS.

	PTTA	PTJF	SHWT	PTPH	PTWW	PTBW	PTSJ	STLE	SHSO <sup>b</sup>
<b>Epipelagic cephalopods</b>									
<i>Sthenoteuthis oualaniensis</i>	1.1	1.3	1.2	1.1	1.1	1.0	0.4	0.7	1.2
<i>Onychoteuthis banksii</i>	2.0	2.1	2.1	-	-	-	-	1.4	2.0
<i>Pterygoteuthis giardi</i>	1.9	1.1	-	-	2.0	-	-	-	-
<i>Abraliopsis affinis</i>	1.7	-	-	-	-	-	-	1.3	1.5
<i>Cranchia scabra</i>	-	-	-	-	1.2	-	-	0.9	-
<i>Helicocranchia</i> sp.	-	0.7	-	-	0.9	-	-	0.8	-
<i>Liocranchia</i> sp.	1.2	-	-	-	-	-	-	-	-
<i>Liocranchia reinhardtii</i>	1.3	0.9	1.3	-	1.2	-	-	-	-
<i>Leachia dislocata</i>	-	1.7	-	-	-	-	-	1.2	-
<i>Ocythoe tuberculata</i>	-	2.4	-	-	-	-	-	-	-
<i>Japetella heathi</i>	-	-	-	-	0.9	-	-	-	-
<b>Mesopelagic-bathypelagic cephalopods</b>									
<i>Pholidoteuthis boschmai</i>	2.7	3.1	2.4	-	-	-	-	-	2.4
<i>Ancistrocheirus</i> sp.	4.7	5.2	-	-	5.3	-	-	-	-
<i>Octopoteuthis deletron</i>	6.4	-	-	-	2.7	-	-	-	-
<i>Octopoteuthis</i> sp.	-	2.0	-	-	-	-	-	-	-
<i>Histioteuthis hoylei</i>	4.0	3.1	1.7	-	2.7	-	-	-	2.6
<i>Histioteuthis</i> sp.	2.6	2.3	-	-	1.7	-	-	-	-
<i>Histioteuthis corona</i>	-	4.0	4.4	-	-	-	-	-	-
<i>Bathyteuthis bacidifera</i>	-	1.7	-	-	-	-	-	-	-
<i>Mastigoteuthis</i> sp.	-	1.5	-	-	-	-	-	-	-
<i>Chiroteuthis</i> sp.	2.9	-	-	-	-	1.4	-	-	-
<i>Ligurrella</i> sp.	1.9	2.3	-	-	2.7	-	-	-	-
<i>Megalocranchia</i> sp.	4.3	3.8	-	-	3.6	3.8	3.9	-	-
<i>Taonius pavo</i>	5.2	5.4	-	-	-	-	-	-	4.8
<i>Galiteuthis pacifica</i>	-	3.7	-	-	2.8	2.7	2.9	-	-
unidentified <i>Cranchiidae</i>	3.0	-	-	-	1.8	-	-	-	-
<i>Alloposus mollis</i>	3.4	-	-	-	3.6	-	-	-	-
Species scavenged	11	12	3	0	9	2	2	3	1
Prey scavenged	352	29	5	0	5	7	0	84	5
Prey eaten	500	487	281	57	136	33	19	0	34
Percent scavenged	70.4	6.0	1.8	0.0	3.7	21.2	10.5	0.0	14.7

<sup>a</sup>Beak lengths given in bold type represent those scavenged, those in standard type represent those taken alive.<sup>b</sup>See Fig. 3 for bird species' codes, species prey appendices for numbers of prey, Methods for estimation of number scavenged, and Appendix 1 for prey species' families.

1.30%, N = 12), Murphy's Petrel ( $2.65 \pm 1.59\%$ , N = 8), and Sooty Shearwater ( $3.21 \pm 2.10\%$ , N = 36). Thus, the mean SF ( $2.26\%$ ) for the latter four was about 50% of that of the other 25 species, whose SF ranged from 4–6%, except for the Great Frigatebird ( $3.83\%$ , N = 3), Herald Petrel ( $3.90\%$ , N = 13), and White-bellied Storm-Petrel ( $3.85\%$ , N = 19). Species with the highest SF means were the Sooty Tern ( $6.25\%$ , N = 68), Red-tailed Tropicbird ( $6.08\%$ , N = 10), and Phoenix Petrel ( $6.07\%$ , N = 21).

Stomach fullness averaged  $5.02 \pm 5.14\%$  (N = 1,597) among the 11 seabird species analyzed in the multiple regression examining SF in relation to various biological and environmental factors. The model explained 24% of the variance in SF (Table 13). Significant main effects were current system, ENSO period, and seabird species. For a given species, mean SF was greater in the SEC ( $5.10 \pm 5.02\%$ , N = 1,080) than in the NECC ( $4.95 \pm 4.20\%$ , N = 517), and was also greater during the neutral phase of ENSO ( $6.36 \pm 6.02\%$ , N = 510) than during El Niño ( $4.66 \pm 4.00\%$ , N = 633) or La Niña ( $4.33 \pm 4.12\%$ , N = 454).

The variable, seabird species, was involved in four interactions with other variables (ENSO phase, longitude, fat-load, and age-status; Table 13), indicating that the relationship between SF and each of these variables differed among bird species. For ENSO phase, this was due to (1) highest SF during the neutral phase and lowest SF during La Niña in Wedge-tailed Shearwaters and Juan Fernandez and Phoenix petrels, (2)

highest and lowest SF during La Niña and El Niño in Stejneger's Petrel, and (3) lack of a difference in SF with ENSO phase among the other seven species.

The interaction with longitude occurred because SF increased significantly with longitude (i.e., was highest in the western area) among Leach's and Wedge-rumped storm-petrels, but differed little with longitude among the other nine species. The effect of age-status on SF differed among species because (1) breeding adults had higher SF than fledglings among Juan Fernandez and Bulwer's petrels, (2) subadults had higher SF than fledglings in Black-winged Petrels, and (3) no significant age-related differences were found in SF for the other eight species.

#### TIMING OF FEEDING

Myctophid otoliths became significantly more eroded as the day progressed from dawn among storm-petrels ( $r = 0.224$ , N = 709 prey,  $P < 0.0001$ ), solitary-feeding procellariids ( $r = 0.120$ , N = 752,  $P < 0.001$ ), and flock-feeding procellariids ( $r = 0.241$ , N = 171,  $P < 0.01$ ; Fig. 16). Extrapolation of regression lines of best fit to the point where otolith condition = 1 (freshly eaten fish) indicates that storm-petrels ate myctophids on average at about 2200 H, whereas both groups of procellariids ate them on average at 2000 H, approximately 2 hr after sunset and 10 hr before daybreak the next

TABLE 13. RESULTS OF REGRESSION ANALYSES FOR THE RELATIONSHIP BETWEEN STOMACH FULLNESS AND CERTAIN INDEPENDENT VARIABLES<sup>a</sup>.

Term	Coefficient sign	F-value	P-value	df
<b>Main effects</b>				
Predator species	-	3.82	<0.0001	10
ENSO period	-	13.71	<0.0001	2
Current system	(-)	4.46	<0.05	1
<b>Interactions</b>				
Predator sp. X ENSO period	-	11.27	<0.0001	20
Predator sp. X longitude	-	4.92	<0.0001	10
Predator sp. X fat load	-	2.67	<0.01	10
Predator sp. X age status	-	2.19	<0.01	10
<b>Rejected terms</b>				
Mass	ns	0.00	0.9	1
Season	ns	0.18	0.7	1
Longitude	ns	0.11	0.7	1
Fat load	ns	2.91	0.09	1
Sex	ns	3.65	0.056	1
Predator sp. X current system	ns	0.81	0.6	10
Predator sp. X sex	ns	1.16	0.3	10
Predator sp. X mass	ns	1.31	0.2	10
Predator sp. X season	ns	1.75	0.066	10

Notes: Sample size was 1,315 birds. Predator species and ENSO period analyzed as categorical; all other independent variables analyzed as continuous. Analysis weighted by inverse of species N; see Methods. Model  $F_{[66, 1247]} = 5.90$ , 23.8% of variance explained.

<sup>a</sup>Independent variables include season, ENSO period, longitude, current system, predator species, mass, sex, age status and fat load among the 11 more abundant species of ETP seabirds.

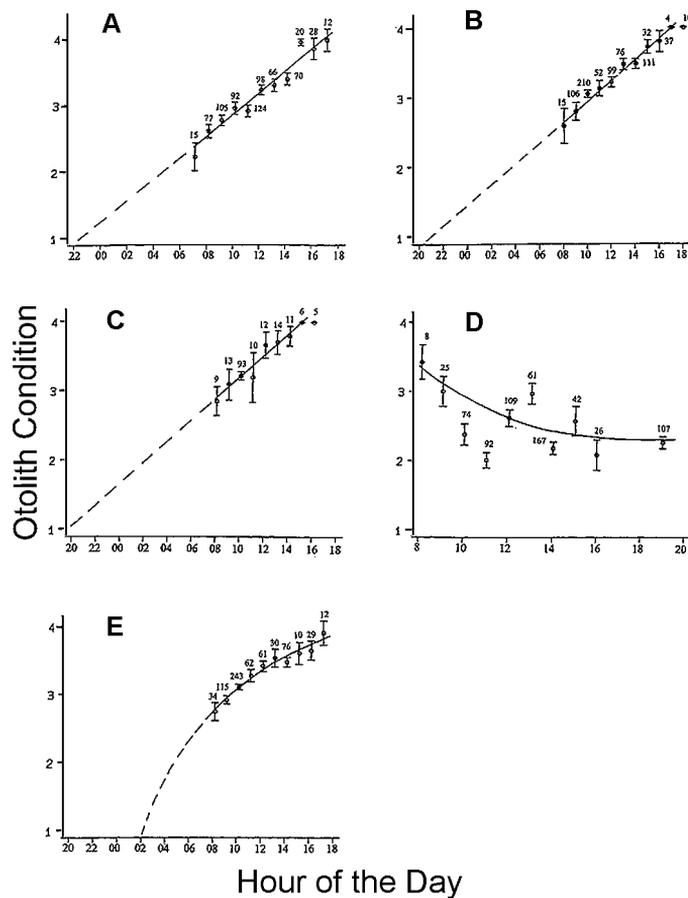


FIGURE 16. Otolith condition (mean  $\pm$  SE) in relation to hour-of-day among five groups of seabirds: (A), myctophids caught by storm-petrels, (B) myctophids caught by solitary procellariids, (C) myctophids caught by flocking procellariids, (D) exocoetid-hemiramphids caught by flock-feeders, and (E) diretms, melamphids, and bregmacerotids caught by all procellariiforms. Otolith condition 1 represents pristine otoliths of freshly caught fish and 4 represents highly-eroded otoliths of well-digested fish. Numbers adjacent to means are otolith sample sizes, where one otolith represents one individual fish (see Methods). For myctophids, diretms, melamphids, and bregmacerotids, the line of best fit (solid line) was extrapolated (dashed line) to the x-axis at otolith condition 1, and gives an estimate of the average hour when fish were caught by the seabirds.

day. That nearly (if not) all myctophids were eaten during the night is also indicated by the decline in the number of whole myctophids per bird collected as the day progressed (none after 1000 H; Fig. 17). In addition, the highly-eroded condition of myctophid otoliths in late afternoon, and the absence of heavily-eroded otoliths in the morning (Fig. 16), indicates that few of these otoliths were retained longer than 24 hr.

In contrast, exocoetid/hemiramphid otolith condition improved as the day progressed among flock-feeding species ( $r = -0.188$ ,  $N = 710$ ,  $P < 0.0001$ ; Fig. 16). The relationship was curvilinear ( $P < 0.01$ ) due to a rapid improvement in otolith condition from 0800–1200 H,

followed by leveling of condition thereafter. The highly eroded condition in the first hours of day light compared to the lesser amounts of erosion observed later in the day indicates that some of these (very large) otoliths were retained overnight, and seabirds fed on those two fish families during the day and probably did not feed on them at night.

Otolith condition among flock-feeders (all otoliths considered; mean condition  $2.40 \pm 1.25$ ,  $N = 928$ ) was significantly better than that of solitary-feeders (all otoliths considered; mean  $2.77 \pm 1.13$ ,  $N = 2,664$ ;  $t$ -test = 8.47,  $df = 3,590$ ,  $P < 0.0001$ ). This pattern also is consistent with nocturnal feeding among the latter and diurnal feeding among the former.

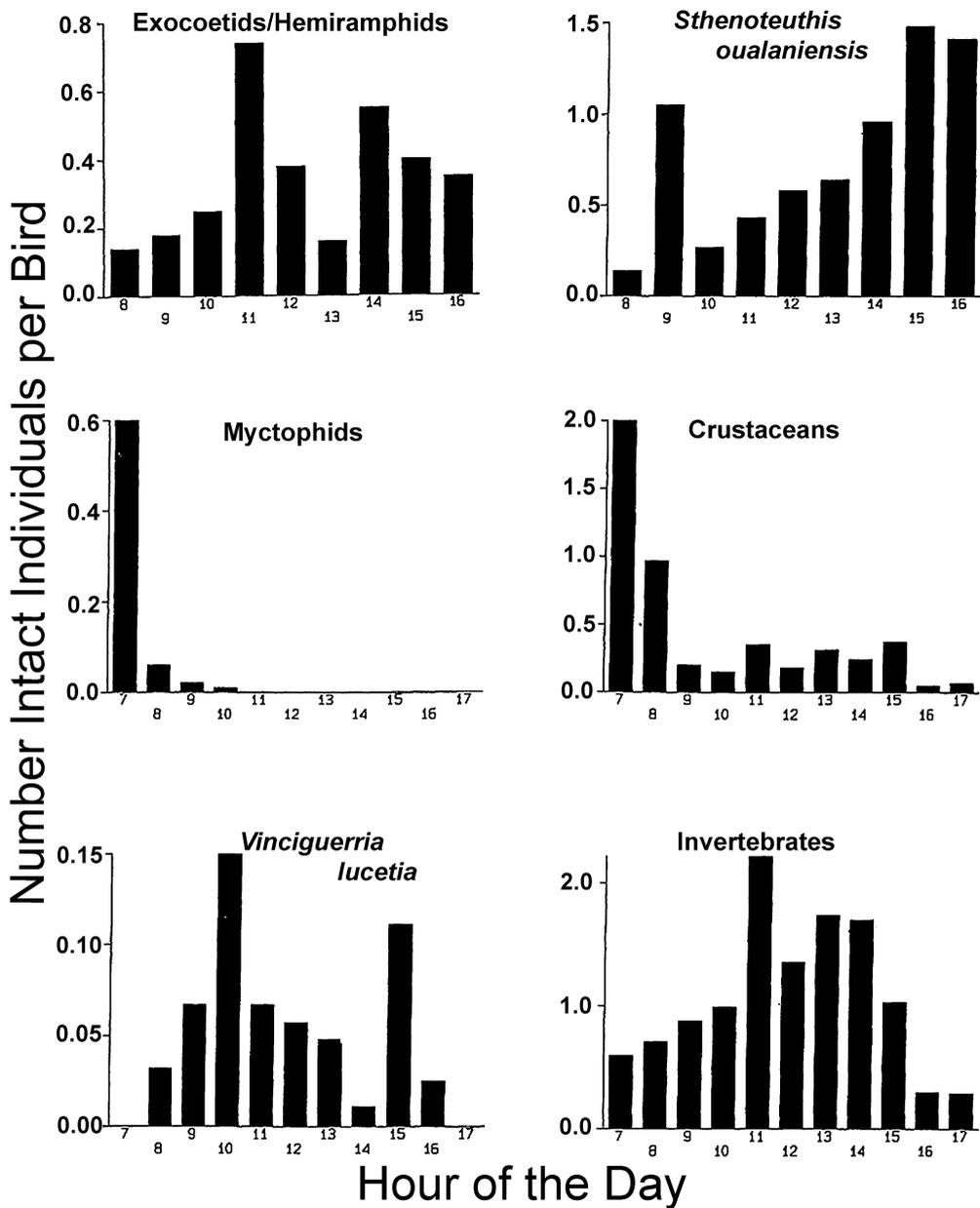


FIGURE 17. Number of intact prey representing six prey groups present in the stomachs of flock-feeding species (top two graphs) and storm-petrels (bottom four) in relation to time-of-day that the birds were collected.

Time-of-day when freshly caught (intact) food items were found in bird stomachs also provided information on feeding schedules (Fig. 17). The number of intact exocoetid/ hemirhamphid individuals per bird among flock-feeders increased between early and mid-morning and then stabilized or declined slightly in the afternoon. Compared to the occurrence pattern

of exocoetid/hemirhamphids, acquisition of intact squid (*Sthenoteuthis oualaniensis*) had a significantly different diurnal pattern among flock-feeders in that numbers of squid per bird increased with time of day to a peak in late afternoon ( $\chi^2 = 43.41$ ,  $df = 8$ ,  $P < 0.0001$ ; numbers of whole prey by hour, not percentages, compared between the two groups; Fig. 17).

Patterns in the time-of-day that different groups of prey were found intact in the stomachs of storm-petrels and small *Pterodroma* also differed significantly ( $\chi^2 = 134.22$ ,  $df = 30$ ,  $P < 0.0001$ ; numbers of whole items per hour compared between the four groups: myctophids, crustaceans, *Vinciguerria lucetia*, and scyphozoans; Fig. 17). This result reflects the following patterns. Intact myctophids were found only during early morning hours and none were found in birds collected after 1000 H. Similarly, crustaceans peaked in early morning although a few continued to be taken throughout the day. On the other hand, *Vinciguerria lucetia* and miscellaneous invertebrate numbers per bird stomach (scyphozoan, *Halobates*, snails, and other mollusks) peaked during mid-day and reached lowest levels during morning and late afternoon.

#### FLOCK COMPOSITION AND PREY AMONG BIRDS FEEDING OVER TUNA

The 131 seabirds collected while feeding over yellowfin and skipjack tuna contained 702 prey items. All prey species consisted of fishes except for two cephalopod species (*Sthenoteuthis oualaniensis* and *Leocranchia reinhardtii*). Seabirds collected from yellowfin- vs. skipjack-induced flocks shared three of the five most abundant prey species found intact in their stomachs (*Sthenoteuthis oualaniensis*, *Exocoetus* spp., and *Gempylus serpens*; Table 14). However, the other two most abundant prey species differed among the two flock types: *Oxyporhamphus micropterus* and *Vinciguerria lucetia* taken in yellowfin-induced flocks, and *Euthynnus* spp.

and *Hemirhamphus* spp. taken in skipjack-induced flocks. Comparison of the proportions that the seven prey species represented among diets of the two flock types showed a significant difference in prey made available to birds feeding over yellowfin vs. skipjack tuna ( $\chi^2 = 304.82$ ,  $df = 6$ ,  $P < 0.0001$ ; numbers of whole items, not percentages, compared between the two groups; Fig. 18).

Flock composition of seabird species feeding over the two tuna species also differed considerably. In fact, only two seabird species were observed in both flock types: Sooty Tern and Great Frigatebird (Table 15). Flocks feeding over skipjack were composed of 97.8% larids and those over yellowfin were composed of 83.4% procellariiforms. Mean flock size did not differ significantly (t-test = 1.53,  $df = 32$ ,  $P = 0.14$ ) between yellowfin-induced (29.4  $\pm$  19.3 birds,  $N = 23$  flocks) and skipjack-induced flocks (42.4  $\pm$  29.5 birds,  $N = 11$  flocks).

#### SUMMARY OF DIET COMPOSITION

The majority of prey taken among species of pelecaniforms was composed of cephalopods, although prey composition, by mass, was nearly equally divided among both fishes and cephalopods (Table 16). Numbers of prey taken by large procellariids were nearly equally divided between fishes and cephalopods, although prey mass was dominated by fishes. Small procellariids, hydrobatids, and larids also consumed primarily fishes, both in number and mass, although both the hydrobatids and larids also consumed large numbers of miscellaneous invertebrates and eggs.

TABLE 14. COMPOSITION OF WHOLE PREY FOUND IN THE STOMACHS OF SEABIRDS<sup>a</sup> COLLECTED WHILE FEEDING IN FLOCKS INDUCED BY YELLOWFIN AND SKIPJACK TUNA<sup>b</sup>.

Prey species	Number (%)		Prey species	Number (%)	
Yellowfin tuna ( <i>Thunnus albacares</i> ) flocks			Skipjack tuna ( <i>Euthynnus pelamis</i> ) flocks		
<i>Sthenoteuthis oualaniensis</i>	343	71.0	<i>Euthynnus</i> sp.	90	41.1
<i>Exocoetus</i> spp.	47	9.7	<i>Sthenoteuthis oualaniensis</i>	56	25.6
<i>Oxyporhamphus micropterus</i>	40	8.2	<i>Exocoetus</i> spp.	32	14.6
<i>Vinciguerria lucetia</i>	24	4.9	<i>Gempylus serpens</i>	15	6.9
<i>Gempylus serpens</i>	13	2.7	<i>Hemirhamphus</i> sp.	12	5.5
<i>Coryphaena</i> spp.	3	0.6	<i>Promethichthys prometheus</i>	7	3.2
<i>Liocranchia reinhardtii</i>	3	0.6	<i>Cubiceps carnatus</i>	4	1.8
<i>Hemirhamphus</i> sp.	2	0.4	<i>Oxyporhamphus micropterus</i>	1	0.5
<i>Euthynnus</i> sp.	2	0.4	<i>Cypselurus spilopterus</i>	1	0.5
<i>Naucrates ductor</i>	1	0.2	<i>Naucrates ductor</i>	1	0.5
<i>Auxis</i> sp.	1	0.2			
<i>Cypselurus</i> sp.	1	0.2			
<i>Cubiceps carnatus</i>	1	0.2			
<i>Sternoptyx obscura</i>	1	0.2			
<i>Symbolophorus evermanni</i>	1	0.2			

<sup>a</sup> See Table 16 for flock composition.

<sup>b</sup> Yellowfin ( $N = 11$  flocks) and skipjack ( $N = 5$  flocks); prey species are given in order of decreasing occurrence.

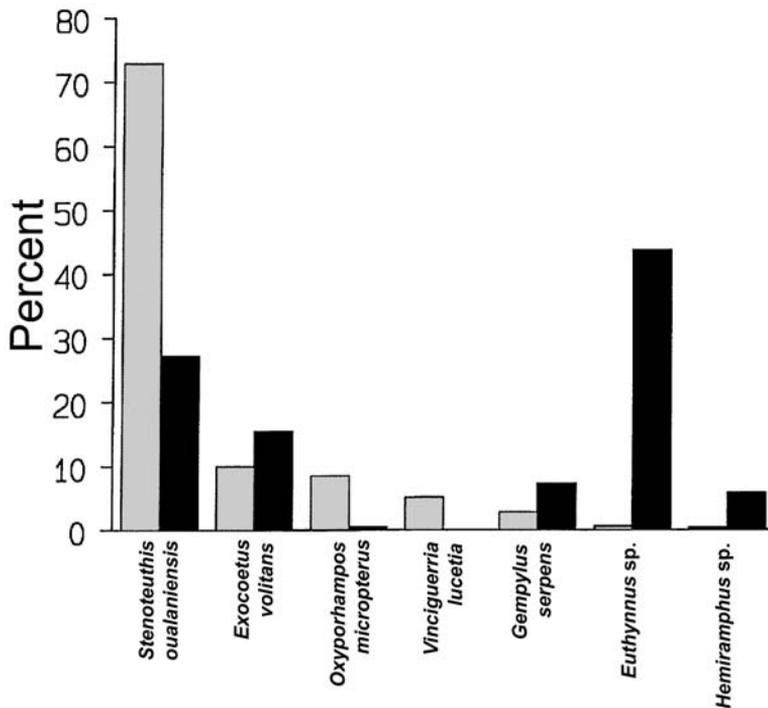


FIGURE 18. Percent composition of the seven most frequently consumed prey species within the diets of sea-birds feeding in flocks over yellowfin (*Thunnus albacares*) (light bar, N = 11 flocks) and skipjack tuna (*Euthynnus pelamis*) (dark bar, N = 7 flocks). For a given flock type, percentages are the number of prey of a given prey species divided by the total number of prey representing all seven prey species multiplied by 100. Number of prey for the seven prey species was 471 individuals from birds collected over yellowfin, and 206 prey from birds collected over skipjack tuna.

#### PROPORTION OF PREY OBTAINED USING THE FOUR FEEDING STRATEGIES

Flocking procellariids, larids, and pelecani-forms obtained an average of 77%, 94%, and 100%, respectively, of the daily prey mass they consumed by flock feeding (Table 17), whereas hydrobatids and solitary and flocking procellariids obtained 78%, 57%, and 20%, respectively, of their daily prey mass by feeding nocturnally. The three groups of procellariiforms also obtained about 17%, 5%, and 1%, respectively, of their daily prey mass by foraging diurnally on non-cephalopod surface-dwelling invertebrates and fish eggs. The three groups obtained 3%, 13%, and 2% of their daily prey mass, respectively, by scavenging. Larids obtained 3% of their daily prey mass by diurnal solitary feeding, and another 3% nocturnally. Hydrobatids obtained 2% of their daily intake by flock feeding, and there was little incidence of scavenging by larids or pelecaniiforms. Thus, all procellariids fed nocturnally at least occasionally, 18 of the 21 species (86%) used flock feeding and

15 species scavenged. Solitary, diurnal feeding on surface-dwelling invertebrates and fish eggs was confined to larids, solitary procellariids, and hydrobatids, particularly the latter; the only non-cephalopod invertebrates eaten by pelecaniiforms were exocoetid ectoparasitic isopods taken incidentally with those fish.

#### SIZE OF THE SEABIRD AVIFAUNA AND TOTAL PREY MASS OBTAINED ACCORDING TO FEEDING STRATEGY

The average daily mass of prey obtained per bird representing the 30 ETP avian species when using each of the four feeding strategies (Table 17) is the basis for the following estimates of total daily prey mass obtained by each species.

The GAM used to estimate abundance of the ETP avifauna was very successful in modeling the ETP at-sea survey data as indicated by the very low coefficient of variation (CV = 5.9; details in Clarke et al. 2003). Our estimate for the total number of birds representing the 30 species in the study area was 31,860,300 (95% confidence interval = 28,418,800–35,089,900).

TABLE 15. SPECIES COMPOSITION OF SEABIRD FLOCKS OBSERVED WHILE FEEDING IN FLOCKS INDUCED BY YELLOWFIN AND SKIPJACK TUNA<sup>a</sup>.

Species	Number (%)	Species	Number (%)
Yellowfin tuna ( <i>Thunnus albacares</i> ) flocks		Skipjack tuna ( <i>Euthynnus pelamis</i> ) flocks	
Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	310 45.9	Sooty Tern ( <i>Onychoprion fuscatus</i> )	365 78.3
Juan Fernandez Petrel ( <i>Pterodroma externa</i> )	218 32.2	White Tern ( <i>Gygis alba</i> )	27 5.8
Sooty Tern ( <i>Onychoprion fuscatus</i> )	103 15.2	Gray-backed Tern ( <i>Onychoprion lunatus</i> )	22 4.7
Phoenix Petrel ( <i>Pterodroma alba</i> )	12 1.8	Black Noddy ( <i>Anous minutus</i> )	14 3.0
Kermadec Petrel ( <i>Pterodroma neglecta</i> )	6 0.9	Brown Noddy ( <i>Anous stolidus</i> )	13 2.8
Christmas Shearwater ( <i>Puffinus nativitatus</i> )	5 0.7	Blue-gray Noddy ( <i>Procelsterna cerulea</i> )	10 2.2
Newell's Shearwater ( <i>Puffinus newelli</i> )	5 0.7	Great Frigatebird ( <i>Fregata minor</i> )	9 2.1
Great Frigatebird ( <i>Fregata minor</i> )	3 0.4	White-tailed Tropicbird ( <i>Phaethon lepturus</i> )	3 0.6
Parasitic Jaeger ( <i>Stercorarius parasiticus</i> )	3 0.4	Red-footed Booby ( <i>Sula sula</i> )	2 0.4
White-winged Petrel ( <i>Pterodroma leucoptera</i> )	2 0.3	White-throated Storm-Petrel ( <i>Nesofregatta fuliginosa</i> )	2 0.4
Stejneger's Petrel ( <i>Pterodroma longirostris</i> )	2 0.3	Black-winged Petrel ( <i>Pterodroma nigripennis</i> )	1 0.2
Pomarine Jaeger ( <i>Stercorarius pomarinus</i> )	2 0.3		
Leach's Storm-Petrel ( <i>Oceanodroma leucorhoa</i> )	2 0.3		
South Polar Skua ( <i>Catharacta maccormicki</i> )	1 0.2		
Herald Petrel ( <i>Pterodroma heraldica/atrata</i> )	1 0.2		
Dark-rumped Petrel ( <i>Pterodroma phaeopygia</i> )	1 0.2		

<sup>a</sup>Species are given in order of decreasing abundance; 676 birds were associated with yellowfin (N = 23 flocks) and 467 were associated with skipjack (N = 11 flocks).

Using the mean mass for each species (Table 4), we estimated the mass of the avifauna to be 6,763 mt (Table 18). The six most abundant species, in decreasing order of abundance, were Leach's Storm-Petrel, Sooty Tern, Wedge-tailed Shearwater, Juan Fernandez Petrel, Wedge-rumped Storm-Petrel, White-winged Petrel, and Black-winged Petrel. These species composed an estimated 85% and 75% of the entire avifauna in terms of numbers and biomass, respectively.

The estimate of the daily prey mass obtained by the ETP avifauna within the study area was 1,588.1 mt (Table 18), 76.3% of which was taken by seabirds feeding over predatory fish, 18.6% by birds feeding nocturnally, 3.3% by scavenging, and 1.8% by feeding on non-cephalopod invertebrates and fish eggs.

In this analysis, we reclassified five of the 17 species previously considered as solitary feeders (Sooty Shearwater, White-necked Petrel, Murphy's Petrel, Stejneger's Petrel,

and Parasitic Jaeger) as migrant opportunists, based on low stomach fullness which in turn indicated a propensity to move directly through the study area. We estimated that for each 24-hr period, resident flock feeders consumed 1,198 mt, resident solitary feeders consumed 280 mt, and migrant opportunists consumed 100 mt. However, proportions of the total daily prey mass consumed while using each of the four feeding strategies differed significantly among the three groups ( $\chi^2 = 902.75$ ,  $df = 6$ ,  $P < 0.0001$ ; mass of prey, not percentages, compared between groups; Fig. 19).

These results were due to: (1) the very high proportion of prey mass obtained by resident flock feeders feeding over large predatory fish (Fig. 19), (2) the high proportion of prey mass obtained nocturnally by the resident solitary group, and (3) the use of all four strategies by the migrant opportunists, although prey consumed by the latter were taken predominantly over large predatory fish.

TABLE 16. PERCENT OF FISHES, CEPHALOPODS, AND NON-CEPHALOPOD INVERTEBRATES IN THE DIETS OF THE 30 MOST-ABUNDANT ETP SEABIRDS<sup>a</sup>.

Species	Fishes	Cephalopods	Misc. invertebrates
<b>Pelecaniformes</b>			
Masked Booby (RF) ( <i>Sula dactylatra</i> )	93.1 (97.4)	4.9 (2.6)	2.1 (0.0)
Nazca Booby (RF) ( <i>Sula granti</i> )	35.5 (53.1)	63.0 (46.9)	1.4 (0.0)
Red-footed Booby (RF) ( <i>Sula sula</i> )	10.9 (19.7)	89.1 (80.3)	0.0 (0.0)
Great Frigatebird (RF) ( <i>Fregata minor</i> )	42.3 (50.4)	53.8 (49.6)	3.8 (0.0)
Red-tailed Tropicbird (RS) ( <i>Phaethon rubricauda</i> )	23.8 (40.4)	76.2 (59.6)	0.0 (0.0)
Mean	41.1 (52.2)	57.4 (47.8)	1.5 (0.0)
<b>Large Procellariiformes</b>			
Sooty Shearwater (MS) ( <i>Puffinus griseus</i> )	52.3 (78.8)	57.4 (20.9)	10.3 (0.3)
Christmas Shearwater (RF) ( <i>Puffinus nativitatus</i> )	52.6 (63.3)	47.4 (36.7)	0.0 (0.0)
Wedge-tailed Shearwater (RF) ( <i>Puffinus pacificus</i> )	39.1 (67.3)	60.5 (32.6)	0.4 (0.0)
Juan Fernandez Petrel (RF) ( <i>Pterodroma externa</i> )	47.2 (54.3)	52.0 (45.7)	0.8 (0.0)
White-necked Petrel (MF) ( <i>Pterodroma cervicalis</i> )	66.7 (83.9)	30.3 (16.0)	3.0 (0.1)
Tahiti Petrel (RS) ( <i>Pterodroma rostrata</i> )	39.1 (44.7)	57.6 (55.2)	3.3 (0.0)
Murphy's Petrel (MS) ( <i>Pterodroma ultima</i> )	56.8 (57.7)	43.2 (42.3)	0.0 (0.0)
Kermadec Petrel (RF) ( <i>Pterodroma neglecta</i> )	41.9 (47.7)	58.1 (52.3)	0.0 (0.0)
Phoenix Petrel (RF) ( <i>Pterodroma alba</i> )	44.2 (33.3)	50.4 (66.6)	5.3 (0.0)
Herald/Henderson Petrel (RF) ( <i>Pterodroma heraldica/atrata</i> )	72.7 (74.3)	21.2 (25.6)	6.1 (0.0)
Mean	51.3 (60.5)	47.8 (39.4)	2.9 (0.0)
<b>Small procellariids</b>			
White-winged Petrel (RS) ( <i>Pterodroma leucoptera</i> )	72.6 (89.6)	19.6 (10.2)	7.8 (0.1)
Black-winged Petrel (RS) ( <i>Pterodroma nigripennis</i> )	85.7 (92.9)	13.6 (7.1)	0.7 (0.0)
DeFillippe's Petrel (RS) ( <i>Pterodroma defilippiana</i> )	74.8 (94.2)	4.9 (5.4)	20.3 (0.4)
Stejneger's Petrel (MS) ( <i>Pterodroma longirostris</i> )	62.2 (95.4)	6.8 (3.6)	31.0 (0.1)
Bulwer's Petrel (RS) ( <i>Bulweria bulwerii</i> )	47.6 (75.2)	25.8 (18.4)	26.6 (6.4)
Mean	68.6 (89.5)	14.1 (8.9)	17.3 (1.4)
<b>Hydrobatids</b>			
White-throated Storm-Petrel (RS) ( <i>Nesofregatta fuliginosa</i> )	47.1 (87.8)	8.0 (9.9)	44.8 (2.3)
White-bellied Storm-Petrel (RS) ( <i>Fregatta grallaria</i> )	53.6 (90.9)	26.8 (9.8)	19.6 (0.2)
White-faced Storm-Petrel (RS) ( <i>Pelagodroma marina</i> )	22.9 (93.6)	0.0 (0.0)	77.1 (6.4)
Markham's Storm-Petrel (RS) ( <i>Oceanodroma markhami</i> )	53.8 (86.4)	15.4 (7.5)	30.8 (6.1)
Wedge-rumped Storm-Petrel (RS) ( <i>Oceanodroma tethys</i> )	83.4 (99.1)	3.4 (0.7)	13.2 (0.2)
Mean	52.8 (92.6)	9.9 (4.9)	37.2 (2.3)
<b>Stercorariidae and Laridae</b>			
Parasitic Jaeger (MF) ( <i>Stercorarius parasiticus</i> )	12.2 (36.6)	16.3 (22.1)	71.4 (41.3)

TABLE 16. CONTINUED.

Species	Fishes	Cephalopods	Misc. invertebrates
Sooty Tern (RF) ( <i>Onychoprion fuscata</i> )	58.1 (59.5)	41.4 (40.5)	0.5 (0.0)
Gray-backed Tern (RF) ( <i>Onychoprion lunatus</i> )	42.0 (97.5)	2.0 (2.2)	56.0 (0.3)
White Tern (RF) ( <i>Gygis alba</i> )	62.7 (86.6)	8.5 (13.2)	28.8 (0.2)
Mean	43.7 (70.1)	17.1 (19.5)	39.2 (8.4)

<sup>a</sup> Percentages are given for numbers of prey and prey mass (in parentheses); letters in parentheses are defined as: R = resident, M = migrant, F = flock feeder, S = solitary feeder. See Methods for classification of resident versus migrant seabird.

TABLE 17. AVERAGE PREY MASS IN GRAMS (MEAN  $\pm$  SE) OBTAINED BY ETP SEABIRDS WHEN USING EACH OF FOUR FEEDING STRATEGIES DURING A GIVEN 24-HR PERIOD<sup>a</sup>.

	Flock feeding	Nocturnal feeding	Solitary-diurnal feeding	Scavenging
<b>Hydrobatids</b>				
White-throated Storm-Petrel ( <i>Nesofregatta fuliginosa</i> )	0.8 $\pm$ 0.2 (5)	11.1 $\pm$ 1.7 (69)	3.6 $\pm$ 1.0 (23)	0.5 $\pm$ 0.3 (3)
White-bellied Storm-Petrel ( <i>Fregatta grallaria</i> )	0.1 $\pm$ 0.2 (2)	9.6 $\pm$ 1.2 (83)	1.0 $\pm$ 0.2 (9)	0.6 $\pm$ 0.3 (5)
White-faced Storm-Petrel ( <i>Pelagodroma marina</i> )	0.1 $\pm$ 0.3 (1)	8.8 $\pm$ 1.4 (88)	1.1 $\pm$ 0.4 (11)	0.0 (0)
Leach's Storm-Petrel ( <i>Oceanodroma leucorhoa</i> )	0.0 $\pm$ 0.0 (0)	9.4 $\pm$ 0.4 (92)	0.7 $\pm$ 0.1 (7)	0.1 $\pm$ 0.0 (1)
Wedge-rumped Storm-Petrel ( <i>Oceanodroma tethys</i> )	0.1 $\pm$ 0.0 (0)	5.3 $\pm$ 0.3 (84)	1.0 $\pm$ 0.2 (16)	0.0 (0)
Markham's Storm-Petrel ( <i>Oceanodroma markhami</i> )	0.0 (0)	8.0 $\pm$ 1.3 (63)	4.1 $\pm$ 1.8 (32)	0.7 $\pm$ 0.3 (5)
Mean	0.2 (1.8%)	8.7 (78.4%)	1.9 (17.1%)	0.3 (2.7%)
<b>Solitary procellariids</b>				
Sooty Shearwater ( <i>Puffinus griseus</i> )	76.8 $\pm$ 21.3 (80)	11.8 $\pm$ 0.9 (12)	2.2 $\pm$ 0.2 (2)	5.5 $\pm$ 1.6 (6)
Tahiti Petrel ( <i>Pterodroma rostrata</i> )	10.3 $\pm$ 1.2 (10)	55.3 $\pm$ 7.2 (54)	0.1 $\pm$ 0.0 (0)	36.4 $\pm$ 1.3 (36)
Murphy's Petrel ( <i>Pterodroma ultima</i> )	9.4 $\pm$ 4.2 (20)	32.4 $\pm$ 8.4 (70)	0.0 (0)	4.2 $\pm$ 1.0 (9)
White-winged Petrel ( <i>Pterodroma leucoptera</i> )	5.6 $\pm$ 0.9 (14)	31.8 $\pm$ 3.3 (78)	2.0 $\pm$ 0.5 (5)	1.2 $\pm$ 0.3 (3)
Black-winged Petrel ( <i>Pterodroma nigripennis</i> )	1.2 $\pm$ 0.7 (3)	34.7 $\pm$ 1.9 (89)	1.4 $\pm$ 0.4 (3)	1.6 $\pm$ 0.3 (4)
DeFilippi's Petrel ( <i>Pterodroma defilippiana</i> )	0.0 (0)	28.5 $\pm$ 4.9 (73)	8.6 $\pm$ 4.3 (22)	2.0 $\pm$ 1.7 (5)
Stejneger's Petrel ( <i>Pterodroma longirostris</i> )	1.8 $\pm$ 0.9 (5)	30.6 $\pm$ 2.0 (85)	2.9 $\pm$ 0.8 (8)	0.7 $\pm$ 0.4 (2)
Bulwer's Petrel ( <i>Bulweria bulwerii</i> )	2.6 $\pm$ 0.1 (11)	17.3 $\pm$ 1.7 (72)	2.2 $\pm$ 1.9 (9)	1.9 $\pm$ 0.5 (8)
Mean	13.5 (25.4%)	30.5 (57.3%)	2.5 (4.7%)	6.7 (12.6%)
<b>Flocking procellariids</b>				
Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	92.1 $\pm$ 12.6 (97)	1.9 $\pm$ 0.3 (2)	0.1 (0)	1.0 $\pm$ 0.9 (1)
Christmas Shearwater ( <i>Puffinus nativitatus</i> )	75.0 $\pm$ 12.7 (95)	3.9 $\pm$ 2.5 (5)	0.0 (0)	0.0 (0)
Juan Fernandez Petrel ( <i>Pterodroma externa</i> )	92.0 $\pm$ 12.5 (86)	9.6 $\pm$ 2.5 (9)	0.0 (0)	5.4 $\pm$ 0.9 (5)
White-necked Petrel ( <i>Pterodroma cervicalis</i> )	40.0 $\pm$ 14.4 (76)	12.0 $\pm$ 2.1 (23)	0.5 (1)	0.0 (0)
Kermadec Petrel ( <i>Pterodroma neglecta</i> )	75.4 $\pm$ 15.7 (82)	15.6 $\pm$ 4.6 (17)	0.9 (1)	0.0 (0)
Phoenix Petrel ( <i>Pterodroma alba</i> )	51.5 $\pm$ 11.3 (71)	20.2 $\pm$ 1.2 (28)	0.7 $\pm$ 0.2 (1)	0.0 (0)

TABLE 17. CONTINUED.

	Flock feeding	Nocturnal feeding	Solitary-diurnal feeding	Scavenging
Herald/Henderson Petrel ( <i>Pterodroma heraldica/atrata</i> )	10.5 ± 0.7 (15)	52.5 ± 16.3 (76)	2.1 ± 0.5 (3)	4.2 ± 1.5 (6)
Mean	62.4 (77.0%)	16.5 (20.4%)	0.6 (0.7%)	1.5 (1.9%)
<i>Laridae</i>				
Parasitic Jaeger ( <i>Stercorarius parasiticus</i> )	8.3 ± 0.5 (18)	11.5 ± 3.5 (25)	17.9 ± 7.9 (39)	4.1 ± 0.8 (18)
Sooty Tern ( <i>Onychoprion fuscata</i> )	44.7 ± 7.8 (97)	0.9 ± 0.3 (2)	0.5 ± 0.3 (1)	0.0 (0)
Gray-backed Tern ( <i>Onychoprion lunatus</i> )	31.0 ± 9.8 (100)	0.0 (0)	0.2 ± 0.3 (0)	0.0 (0)
White Tern ( <i>Gygis alba</i> )	22.6 ± 7.0 (94)	1.0 ± 0.6 (4)	0.4 ± 0.2 (2)	0.0 (0)
Mean	27.7 (93.6%)	1.0 (3.4%)	0.8 (2.72%)	0.1 (0.3%)
<i>Pelecaniformes</i>				
Red-tailed Tropicbird ( <i>Phaethon rubricauda</i> )	186.0 ± 18.2 (100)	0.0 (0)	0.0 (0)	0.0 (0)
Red-footed Booby ( <i>Sula sula</i> )	292.0 ± 30.5 (100)	0.0 (0)	0.0 (0)	0.0 (0)
Masked Booby ( <i>Sula dactylatra</i> )	407.0 ± 41.0 (100)	0.0 (0)	1.0 (0)	0.0 (0)
Nazca Booby ( <i>Sula granti</i> )	372.0 ± 27.8 (100)	0.0 (0)	0.5 (0)	0.0 (0)
Great Frigatebird ( <i>Fregata minor</i> )	335.6 ± 36.2 (99)	3.1 ± 1.2 (1)	0.3 (0)	0.0 (0)
Mean	318.5 (99.7%)	0.6 (0.2%)	0.4 (0.1%)	0.0

<sup>a</sup> See Table 2 for sample sizes, i.e., total number of birds collected for a given species. Numbers in parentheses are percentages.

TABLE 18. ESTIMATE OF THE TOTAL PREY MASS CONSUMED BY ETP SEABIRDS USING EACH OF FOUR FEEDING STRATEGIES<sup>a</sup>.

	Proportion	Bird number (1,000s)	Bird mass (mt)	Prey mass obtained			
				Over aquatic predators	At night	Diurnal NCI <sup>b</sup>	By scavenging
<b>Resident flock feeders</b>							
Red-footed Booby ( <i>Sula sula</i> )	0.0017	54.2	63.4	10.1	0.0	0.0	0.0
Masked Booby ( <i>Sula dactylatra</i> )	0.0030	95.6	156.1	38.9	0.0	0.1	0.0
Nazca Booby ( <i>Sula granti</i> )	0.0004	12.7	18.1	4.7	0.0	0.0	0.0
Great Frigatebird ( <i>Fregata minor</i> )	0.0011	35.0	47.4	11.7	0.1	0.0	0.0
Juan Fernandez Petrel ( <i>Pterodroma externa</i> )	0.1178	3,753.1	1,602.6	345.3	36.0	0.0	20.3
Wedge-tailed Shearwater ( <i>Puffinus pacificus</i> )	0.1195	3,807.3	1,450.6	350.7	7.2	0.4	3.8
Kermadec Petrel ( <i>Pterodroma neglecta</i> )	0.0030	95.6	35.3	7.2	1.5	0.0	0.0
Christmas Shearwater ( <i>Puffinus pacificus</i> )	0.0029	92.4	29.2	6.9	0.4	0.0	0.0
Phoenix Petrel ( <i>Pterodroma alba</i> )	0.0028	89.2	25.6	4.6	1.8	0.1	0.0
Herald/Henderson Petrel ( <i>Pterodroma heraldica/atrata</i> )	0.0018	57.3	16.0	0.6	3.0	0.1	0.2
Sooty Tern ( <i>Onychoprion fuscata</i> )	0.2270	7,232.3	1,330.7	323.3	6.5	3.6	0.0
Gray-backed Tern ( <i>Onychoprion lunatus</i> )	0.0002	6.4	0.8	0.2	0.0	0.0	0.0
White Tern ( <i>Gygis alba</i> )	0.0110	350.5	34.0	0.9	0.4	0.1	0.0
Total	0.4922	15,681.6	4,810.6	1,112.1	56.9	4.4	24.3

TABLE 18. CONTINUED.

	Proportion	Bird number (1,000s)	Bird mass (mt)	Prey mass obtained			
				Over aquatic predators	At night	Diurnal NCI <sup>b</sup>	By scavenging
Resident solitary feeders							
Red-tailed Tropicbird ( <i>Phaethon rubricauda</i> )	0.0024	76.5	56.8	14.2	0.0	0.0	0.0
Tahiti Petrel ( <i>Pterodroma rostrata</i> )	0.0146	465.2	192.1	4.8	25.7	0.0	16.9
White-winged Petrel ( <i>Pterodroma leucoptera</i> )	0.0321	1,022.7	163.6	5.7	32.5	2.0	1.2
Black-winged Petrel ( <i>Pterodroma nigripennis</i> )	0.0415	1,322.2	203.6	1.6	45.9	1.9	2.1
DeFilippi's Petrel ( <i>Pterodroma defilippiana</i> )	0.0077	245.3	37.8	0.0	7.0	2.1	0.5
Bulwer's Petrel ( <i>Bulweria bulwerii</i> )	0.0100	318.6	29.9	0.8	5.5	0.7	0.6
Leach's Storm-Petrel ( <i>Oceanodroma leucorhoa</i> )	0.2474	7,882.2	323.2	0.0	74.1	5.5	0.8
Wedge-rumped Storm-Petrel ( <i>Oceanodroma tethys</i> )	0.0653	2,080.5	52.0	0.1	11.0	2.1	0.0
Markham's Storm-Petrel ( <i>Oceanodroma markhami</i> )	0.0227	723.2	36.9	0.0	5.8	3.0	0.5
White-throated Storm-Petrel ( <i>Nesofregatta fuliginosa</i> )	0.0011	35.0	2.2	0.0	0.4	0.1	0.1
White-bellied Storm-Petrel ( <i>Fregatta grallaria</i> )	0.0041	130.6	6.0	0.0	1.3	0.1	0.1
White-faced Storm-Petrel ( <i>Pelagodroma marina</i> )	0.0094	299.5	12.0	0.0	2.6	0.3	0.0
Migratory opportunists							
Sooty Shearwater ( <i>Puffins griseus</i> )	0.0265	844.3	651.0	64.8	10.0	1.9	4.6
White-necked Petrel ( <i>Pterodroma cervicalis</i> )	0.0037	117.9	48.8	4.7	1.4	0.0	0.0
Murphy's Petrel ( <i>Pterodroma ultima</i> )	0.0012	38.2	14.3	0.4	1.2	0.0	0.2
Stejneger's Petrel ( <i>Pterodroma longirostris</i> )	0.0123	391.9	56.8	0.7	12.0	1.1	0.3
Parasitic Jaeger ( <i>Stercorarius parasiticus</i> )	0.0056	178.4	65.5	1.5	2.1	3.2	0.7
Total	0.0493	1570.7	836.4	72.1	26.7	6.2	5.8
Total (all 3 groups)	0.9999	31,860.3	6,763.1	1,211.5	295.4	28.4	52.8

<sup>a</sup> Shown are the proportion of the ETP avifauna contributed by each seabird species, estimates of bird numbers, bird mass, and prey mass eaten (in metric tons [mt]).

<sup>b</sup> NCI = non-cephalopod invertebrates.

Notes: See Methods for details on calculation of prey mass consumed and Table 3 for species' mass.

The seabird species estimated to have taken the most prey mass while feeding nocturnally was the Leach's Storm-Petrel (74.1 mt/d; Table 18). Other species that took large amounts of prey while feeding nocturnally were, in decreasing amounts of prey taken, Black-winged Petrel (45.9 mt/d), White-winged Petrel (32.5 mt/d), Juan Fernandez Petrel (36.0 mt/d), Tahiti Petrel (25.7 mt/d), Stejneger's Petrel (12.0 mt/d), Wedge-rumped Storm-Petrel (11.0 mt/d), Sooty Shearwater (10.0 mt/d) and Sooty Tern (6.5 mt/d).

Species consuming the largest mass of prey while scavenging cephalopods were the Juan Fernandez (20.3 mt/d) and Tahiti petrels (16.9

mt/d; Table 18), as well as the Black-winged and White-winged petrels and Sooty Shearwater (1.2–4.6 mt/d). The species estimated to have taken by far the most prey mass while feeding diurnally on non-cephalopod invertebrates was the Leach's Storm-Petrel (5.5 mt/d), although the Sooty Tern (3.6 mt/d), Parasitic Jaeger (3.2 mt/d), Stejneger's Petrel (3.2 mt/d), and Markham's Storm-Petrel (3.0 mt/d) also took relatively large amounts of these prey.

## DISCUSSION

Considering the reduced food availability in tropical oceans compared to those of higher