

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

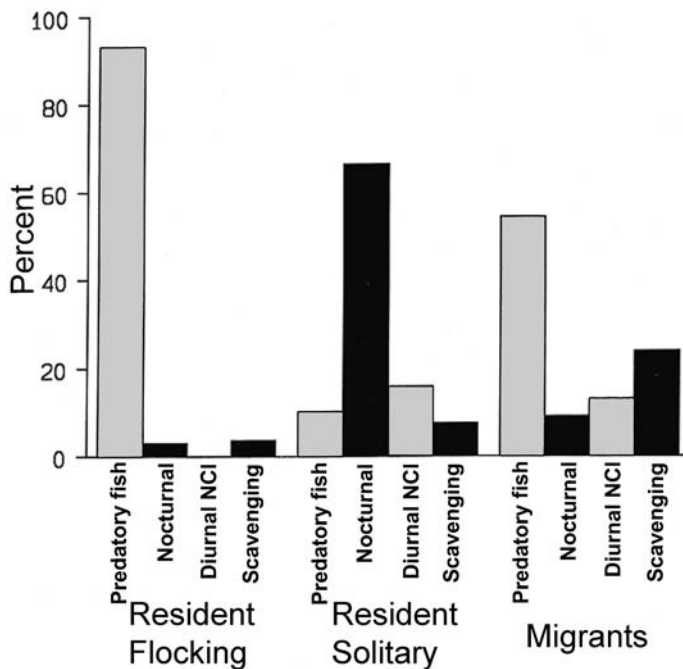


FIGURE 19. Proportion of prey mass obtained by each of three species groups when using four feeding strategies. Feeding over predatory fish is denoted by predatory fish; NCI = non-cephalopod invertebrates.

latitudes (Longhurst and Pauly 1987), it is noteworthy that the majority of seabirds occurring in the ETP breed in higher latitudes (Harrison 1983, Brooke 2004). Reduced prey availability and/or intense competition for resources during the nonbreeding period (Ainley et al. 1994) is indicated in that the majority of individuals, including three of the four most abundant species in the ETP (Leach's Storm-Petrel, Juan Fernandez Petrel, and Wedge-tailed Shearwater), fly considerable distances to the ETP in favor of remaining closer to their higher-latitude breeding areas. These species also have behavioral and morphological characteristics that make them well suited to feed in the ETP (Spear and Ainley 1998). Specifically, lower-latitude procellariids have larger wings, tails, and bills than their higher-latitude counterparts, enabling the former to make use of relatively light winds when foraging over wide ocean expanses to exploit sparse, highly mobile and/or volant prey.

A common finding among many multispecies studies has been that seabirds breeding at a given location have diets that share only a few major prey species, leading to extensive diet overlap (Ashmole and Ashmole 1967, Diamond 1983, Harrison et al. 1983, Furness and Barrett 1985, Schreiber and Hensley 1976, Ainley and

Boekelheide 1990). Our findings with respect to the diets among an avifauna of seabirds, primarily nonbreeders, feeding in the pelagic ETP are in some ways consistent with but in others contrary to these patterns. In the following, we summarize our findings on diet diversity and diet overlap among species representing each of five groups of seabird taxa.

#### SEABIRD DIETS

##### *Pelecaniformes*

The five species of this group exhibited the lowest diet diversity ( $H' = 0.5-1.8$ ) as well as considerable diet overlap; prey mass consumed was almost equally divided among fishes (2-5 families for each peleciform species including primarily hemirhamphids, exocoetids, carangids, coryphaenids, and scombrids) and cephalopods (1-4 families for each peleciform, but almost exclusively the ommastrephid squid [*Sthenoteuthis oualaniensis*]). These findings are very similar to those of Harrison et al. (1983) for the Hawaiian populations of these species, and also the findings for birds breeding on Christmas Island (Ashmole and Ashmole 1967, Schreiber and Hensley 1976). Also consistent with the findings of Harrison et al. (1983),

among the pelecyaniforms studied during their as well as our study, the Masked Booby consumed a much greater proportion of fish (97% by mass) than the other pelecyaniforms, for which fishes represented 20–53% of their diet mass.

#### *Large Procellariiformes*

Diet diversity ( $H'$ ) among the 10 species of large procellariids (mass = 280–430 g) was moderate, ranging from 2.1 in Wedge-tailed and Christmas shearwaters to 2.9 and 3.1 in the Juan Fernandez and Tahiti petrels, respectively. Prey mass consumed was composed of 61% fishes (6–19 families among each large procellariid species), 39% cephalopods (2–12 families among each species), and 3% miscellaneous invertebrates. The predominance of fish in the diets of large ETP procellariids was consistent with the diets of large procellariids feeding in the Southern Ocean (Ainley et al. 1992). However, in the ETP, our results showing heavy use of fish among Murphy's, Phoenix, Herald, and Dark-rumped petrels differed appreciably from that observed at their primary breeding colonies on the Pitcairn and Galapagos islands, where they feed primarily on cephalopods (Imber et al. 1992, Imber 1995). Heavy use of cephalopods also was observed among the Sooty Shearwater and three large *Procellaria* breeding off New Zealand (Imber 1976, Cruz et al. 2001).

As noted by Imber (pers. comm.), studies, such as the above, of petrels' foods at colonies are adversely affected by the birds' behavior. Specifically, in nearly all colony studies of procellariids, biologists obtain food samples from chicks or adults arriving to feed them. Because adults come into the colonies only at night, and usually soon after dusk, any food in their stomachs has been subjected to digestion since the previous night, if eaten at night. This pattern matters less for cephalopods whose beaks are more resilient than fish otoliths, especially the smaller fish species such as myctophids. Thus, colony studies are undoubtedly biased against fish.

The PC analyses indicated high diet overlap among the large flocking procellariids and pelecyaniforms that typically fed over predatory fishes. Large procellariids that fed solitarily also had a high degree of diet overlap due to their reliance primarily on vertically migrating myctophids, melamphids, bregmacerotids, dirotmids, and cephalopods. The flocking and solitary procellariid groups also differed in their choice of cephalopods; flock feeders ate primarily ommastrephids and solitary feeders ate mostly onychoteuthids, histioteuthids, mastigoteuthids, chiroteuthids, and cranchiids (findings similar to

those of Imber and coworkers; references above). Little diet overlap occurred between large procellariids that feed over predatory fish vs. those that feed solitarily.

#### *Small Procellariiformes*

Diet diversity ( $H'$ ) was high among the 11 species of small procellariiform species, including storm-petrels, *Bulweria* and small *Pterodroma* (mass 25–160 g), averaging 2.9 and ranging from 2.5 in the Markham's and White-faced storm-petrels to 3.5 in Leach's Storm-Petrel and White-winged Petrel. The PC analyses also indicated that diet overlap among these 11 species (all solitary feeders) was high. Prey mass was composed of 91% fishes (2–20 families each), 7% cephalopods (0–11 families each), and 2% non-cephalopod invertebrates and exocoetid eggs (1–10 taxonomic groups each).

High diet diversity ( $H'$ ) and extensive diet overlap in these species reflected their predominant foraging strategy, nocturnal feeding, in which they ate primarily fishes of the highly speciose family Myctophidae. These results are consistent with those of Imber (1996) for Cook's Petrel. The small Procellariiformes were also highly opportunistic, feeding both nocturnally and diurnally on a diverse array of non-cephalopod invertebrates, occasionally in multispecies flocks over predatory fishes, and scavenging on dead cephalopods (primarily families listed above as cephalopod prey of large solitary procellariids).

#### *Laridae*

Diet diversity ( $H'$ ), for the four larids was low, averaging 1.8 and ranging from 1.4 in the Parasitic Jaeger and Gray-backed Tern to 2.1 and 2.2 in the White and Sooty terns, respectively. Prey mass consumed was composed of 70% fishes (3–9 families each), 20% cephalopods (1–4 families), and 8% noncephalopod invertebrates (1–3 taxonomic groups). PC analyses indicated high diet overlap between the Sooty Tern and other flock-feeding species, especially the pelecyaniforms and large procellariids. Little diet overlap was found between the Parasitic Jaeger and Gray-backed and White terns, with other ETP species; only the diets of the Gray-backed Tern and Parasitic Jaeger were similar, due to extensive feeding by both on non-cephalopod invertebrates. Heavy use of these prey by Gray-backed Terns on the Hawaiian Islands was also noted by Harrison et al. (1983). Low diet diversity and little diet overlap among the larid species resulted from the fact that each tended to specialize in one or two feeding strategies that differed among them,

resulting in the consumption of a distinct group of prey by each species.

#### DIET PARTITIONING

Diet partitioning within tropical seabird communities has been demonstrated at their breeding colonies, mainly as a function of prey size (Ashmole and Ashmole 1967). In pelagic waters of the ETP, seabirds also partitioned diet but accomplished this in several ways. First, the foraging strategy used provided access to a distinct group of prey species. The resident flock feeders (composing 71.1% of the biomass of the ETP avifauna) used this one strategy almost exclusively and caught 93% of their prey (by mass) while feeding over large aquatic fish (mainly tuna). Solitary residents (16.5% of the avian biomass) and migratory opportunists (12.4% of the avian biomass) acquired 74% and 69%, respectively, of their prey mass while using both nocturnal feeding and feeding over predatory fish.

Second, the four feeding strategies indirectly provided both temporal (i.e., feeding at night vs. day) and spatial partitioning. Partitioning occurred even among species using a single feeding strategy. For example, among bird species that fed in association with large predatory fishes, spatial partitioning was achieved through differential use of air space, i.e., flying at different elevations above the aquatic predators (Ainley 1977, Ballance and Pitman 1999). Flying height also may have affected the depth to which different species could plunge for prey. Spatial partitioning also occurred among the Red-tailed Tropicbird and boobies that often fed solitary or in small monospecies groups, sometimes over large dolphinfish [*Coryphaena hippurus*], but usually where no predatory fish were observed (Spear and Ainley 2005; Spear and Ainley, pers. obs.). These Pelecaniformes ate many of the same prey (primarily exocoetids) as did the species that fed in multispecies groups over tuna.

Finally, partitioning by prey size occurred among species feeding over predatory fish and those feeding nocturnally, where larger predators ate larger prey (Ashmole and Ashmole 1967, Harrison et al. 1983). Prey-size partitioning also occurred between sexes of the same species (details below).

#### DIET VARIATION WITH RESPECT TO ENVIRONMENTAL FACTORS

Unlike the findings of Harrison et al. (1983), in which season was the primary factor affecting diet variation among species of seabirds

breeding in the Hawaiian Islands, we found no evidence for a seasonal effect (comparing spring vs. autumn) among the 10 most abundant species of seabirds feeding in the pelagic waters of the ETP. However, we found a temporal effect for Stejneger's and Bulwer's petrels, both of which consumed more non-cephalopod invertebrates during El Niño compared to La Niña. The Stejneger's Petrel also consumed a higher proportion of myctophids during El Niño. These results were unexpected because productivity in the ETP within these lower trophic levels is higher during La Niña than El Niño (Fiedler 2002).

Spatial effects on diet variation were detectable in the more abundant species—Stejneger's Petrel, Leach's Storm-Petrel, and Sooty Tern. Such variation must have reflected prey availability. The diets of all three species differed between the eastern and western ETP. The two small petrels had a higher intake of invertebrates and lower intake of myctophids in eastern than western waters; the Sooty Tern had a higher intake of the photichthyid *Vinciguerria lucetia* and lower intake of hemirhamphids, exocoetids, and ommastrephids in the East compared to the West. The Stejneger's Petrel also had a higher intake of invertebrates and lower intake of myctophids in the NECC compared to the SEC. Regarding the tern, higher intake of *Vinciguerria lucetia* in the East is likely due to what appeared to be considerably greater abundance of that prey species there, as it was a major prey in the diets of many seabird species collected east of 130° W (Pitman and Ballance 1990). We can not offer any explanations for the other patterns.

Unexpected were our findings for sex-related differences in prey-size for seven species of procellariiforms—Wedge-rumped and Leach's storm-petrels; White-winged, Black-winged, Tahiti, and Juan Fernandez petrels; and the Wedge-tailed Shearwater. We are aware of only two other procellariiform species in which sex-related dietary differences have been observed: the Northern and Southern giant petrels (*Macronectes halli* and *M. giganteus*, respectively). In these species, males scavenged more penguin and seal carcasses compared to females (Hunter 1983). This author suggested that the difference was probably due to male giant petrels being larger than females, resulting in male dominance when competing for fixed food sources.

In our study, females of the two storm-petrels, as well as Black-winged, White-winged, and Tahiti petrels, ate larger prey than males. In contrast, male Juan Fernandez Petrels and Wedge-tailed Shearwaters ate larger prey than

females. The sex-related differences among each of the seven species were not affected by differences in individual bird mass, and therefore, did not appear to be due to size-related competitive dominance, such as in the giant-petrels.

#### RELIANCE OF ETP SEABIRDS ON LARGE PREDATORY FISH

The importance of large predatory fish in making prey available to the ETP avifauna, as well as to cetaceans, is well known (Ashmole and Ashmole 1967, Au and Pitman 1986, Ballance and Pitman 1999), but has not previously been quantified. Indeed, the fact that an estimated 76% of the prey mass consumed by the ETP avifauna was made available by these apex predators (mainly tuna) underscores their importance to the trophodynamics of the ETP ecosystem (Cox et al. 2002, Olson and Watters 2003, Hinke et al. 2004). Moreover, Essington et al. (2002) have shown that the four primary methods of harvesting yellowfin tuna contrast greatly in age selectivity on tuna stocks and also, given current catch rates, in sustainability.

Although the prey of seabirds foraging over tunas was primarily hemirhamphids, exocoetids, carangids, coryphaenids, scombrids, gempylids, and epipelagic cephalopods, several of these families (hemirhamphids, exocoetids, and scombrids) have not been found in the diets of yellowfin tuna (Murphy and Shomura 1972, Bertrand et al. 2002). This was also noted by Ashmole and Ashmole (1967) who were surprised by the lack of correlation between the diets of tuna and that of flock-feeding seabirds. These authors suggested that exocoetids and some hemirhamphids, because of their abilities to leave the water, were more likely to escape fish predators than birds. They also suggested that the lower occurrence of scombrids in the diets of the tuna compared to the birds was not surprising because of the scombrids' ability to swim at high speed (Cairns et al., unpubl. data).

#### NOCTURNAL FEEDING

An estimated 19% of the prey mass consumed by the ETP avifauna was obtained when feeding at night, making this the second most important feeding strategy. All procellariiform species fed nocturnally at least occasionally. Similar conclusions had been reached by Harrison et al. (1983) regarding small procellariiforms (Bonin Petrel [*Pterodroma hypoleuca*], Bulwer's Petrel, and Sooty Storm-Petrel [*Oceanodroma tristrami*]) breeding on the Hawaiian Islands, for Northern Fulmars (*Fulmarus glacialis*) breeding in Scotland (Furness and Todd 1984), and for many other

species of procellariiforms (Imber 1976, 1981, 1995, 1996; Imber and Berruti 1981, Imber et al. 1992, Croxall and Prince 1980, Ainley et al. 1992, Catard and Weimerskirch 1999).

Indeed, in our study, nocturnal feeding was by far the most important feeding strategy of solitary feeders, especially the smaller procellariiform species; the following species are listed in order of increasing importance of nocturnal feeding: Bulwer's Petrel, DeFilippi's Petrel, Herald/Henderson Petrel, White-winged Petrel, White-bellied Storm-Petrel, Wedge-rumped Storm-Petrel, Stejneger's Petrel, White-faced Storm-Petrel, Black-winged Petrel, and Leach's Storm-Petrel. Among the larger species of procellariiforms, nocturnal feeding was used, in order of increasing importance, by Murphy's, Tahiti, Phoenix, White-necked and Kermadec petrels, and Sooty Shearwater (Imber 1981, 1995). Results of this study indicated that non-procellariiform species that occasionally fed nocturnally included the Sooty Tern, White Tern, Parasitic Jaeger, and Great Frigatebird. The inclusion of vertically migrating prey in the diet of the jaeger and frigatebird could represent kleptoparasitism on terns and small procellariids (Spear and Ainley 1993; pers. obs.), although nocturnal feeding has been described previously among Sooty Terns (Morzer Bruyns and Voous 1965, Gould 1967).

Nocturnal feeding by seabirds is not surprising; it is well known that many species of smaller mesopelagic fishes (e.g., myctophids, melamphids, bregmacerotids, and diretmids) and cephalopods ascend to shallow depths at night and descend again during the day (Marshall 1960, Maynard et al. 1975, Roper and Young 1975, Clarke 1978, Gjosaeter and Kawaguchi 1980, Watanabe et al. 1999). Because of this, nocturnal feeding has been inferred by the presence of myctophids and bioluminescent cephalopods in the diets of seabirds, but because of the lack of direct evidence as to when these prey were consumed, this idea has been questioned (Ballance and Pitman 1999). Thus, this is the first study to unequivocally validate nocturnal feeding as an important foraging method among members of a pelagic avifauna.

Specifically, our analyses of otolith condition, number of whole prey, and the hour of day when birds were collected clearly demonstrated that hydrobatids and procellariids (but rarely pelecaniforms, larids, and stercorarids), including both solitary- and flock-feeding species, ate large numbers of myctophids, melamphids, bregmacerotids, diretmids, and crustaceans, generally caught between 2000 and 2400 H. Otoliths of these fishes were retained no longer than 24 hr, a retention period similar to that

found among other species of seabirds when consuming (smaller) shoaling fishes (Uspenski 1956, Duffy and Laurenson 1983, Jackson and Ryan 1986). Furthermore, the occurrence of only a single individual representing these fishes within a sample of 131 seabirds (containing 702 prey) collected while feeding in direct association with surface-feeding yellowfin and skipjack tunas is additional evidence that few of these vertically migrating fishes were caught diurnally (i.e., tunas also are diurnal feeders; Buckley and Miller 1994, Roper 1994). Thus, although vertically migrating fishes are known to occur near the surface during the day on rare occasions (Alverson 1961), the rare occurrence of these fishes in the diets of avian species feeding diurnally is not surprising. This applies also to bird species that feed over large predatory fish, especially yellowfin tuna that feed mostly in the upper 100 m (Bertrand et al. 2002), well above waters where vertical migrating prey aggregate during the day (Kawaguchi et al. 1972).

An exception, however, are the myctophid-sized photichthyids (*Vinciguerria* spp.), which aggregate diurnally at depths from 200 m to the ocean surface (Pitman and Ballance 1990, Marchal and Lebourges 1996). The frequent occurrence of freshly caught *Vinciguerria lucetia* in ETP seabirds collected during the day in our study (Pitman and Ballance 1990) indicates regular diel movements of these fish to the ocean surface, although this could, in part, be related to foraging activities of tuna. This was indicated in another study of *Vinciguerria nimbaria* in the tropical Atlantic, where these fish were frequently eaten by tuna during the day (Marchal and Lebourges 1996).

The evidence from our study also indicates that most of the fish caught at night were caught alive. One indication of this was the pattern in their time of capture. If these fish were occurring at the surface as injured or dead individuals, we would not have expected the tight pattern in timing of capture, i.e., some of these prey would have been consumed during the day. Yet, we found only a single whole myctophid in one seabird collected after 0900 H.

The second line of evidence indicating that these prey were caught alive was their size-related selection by procellariiforms feeding nocturnally. If prey were occurring at the surface mostly as singles, after they had died or become incapacitated, we would not have expected the birds to have consistently had an opportunity to be discriminatory. We believe that prey-based size selection by birds feeding nocturnally indicates that the prey were arriving at the surface in schools, allowing the birds to be selective among groups of individuals. This idea is consistent with

the findings of Auster et al. (1992) who observed very densely aggregated monospecific shoals of myctophids representing a very large biomass. Selection among seabirds foraging nocturnally is similar to that of diurnal flock feeders that also select prey by size when schools of the latter are chased to the surface by piscine predators.

The data indicating that many species of fishes including myctophids (particularly *Diaphus* and *Lampanyctus*), melamphids, bregmacerotids, and diretmids are caught alive at or very near the ocean surface at night presents an enigma in that, with exception of diving-petrels (*Pelecanoides* spp.), procellariiform seabirds seldom pursuit-dive to a depth >10 m (Huin 1994, Prince et al. 1994, Chastel and Bried 1996, Bried 2005) although many of the prey fish and cephalopod species recorded in this study have not been caught at night <90 m from the surface during thousands of kilometers or hours of net tows (Appendix 1 and 3; Hartmann and Clarke 1975, Roper and Young 1975).

Occurrence of the mesopelagic and bathypelagic cephalopods at the ocean surface at night is explainable in that juveniles and subadults (i.e., of the size generally caught alive during this study) of some of these species are known to occur at or near the surface (Roper and Young 1975). However, we can imagine only two possible explanations for the infrequent surface records of the fishes summarized above. First, an idea that also applies to cephalopods, the net-tow methods may be flawed, e.g., due to net avoidance facilitated by factors such as pressure waves preceding towed nets; warning from vibrating lines attached to (and preceding) nets; vibrations/noises from the ship's engines preceding the nets; and/or the ship's lights that usually also precede net tows (Clarke 1966, Wormuth and Roper 1983). A second possibility is that prey that normally do not occur at the ocean surface occasionally stray there after becoming mixed with schools of species that migrate to the surface at night. This idea is consistent with the findings of Auster et al. (1992) who noted that when myctophids occurred in loose aggregations they formed multispecies groups without any affinity for a particular taxon. Upon arriving at the surface, some species possibly not well adapted for surface feeding, may be more vulnerable to predation than others. If this is true, the stragglers should be represented in the diets of seabirds in higher proportions than expected given the proportion represented by these species among fishes occurring at the surface at night.

On the other hand, the idea that myctophids, melamphids, bregmacerotids, and diretmids

being consumed at night by petrels may be represented by a predominance of stragglers is not well supported because it would be expected that scientific sampling methods would have succeeded in netting them occasionally near the surface. Nevertheless, the avian consumption of an estimated 252 mt of these fish per night (i.e., after subtraction for the mass of crustaceans also caught at night) represents a consumption rate of 10.0 g (about two individual fish) of these fishes per square kilometer per night, or about 5,000,000 fish caught at or near the surface per night by birds over a surface area of ocean of about 25,000,000 km<sup>2</sup>.

#### SCAVENGING

Although a large proportion of the diets of procellariids in most parts of the world includes offal scavenged from commercial fisheries (Jackson 1988, Catard et al. 2000), we found little evidence for this in the ETP. Yet, scavenging of dead cephalopods accounted for an estimated 2% of the prey mass consumed by ETP seabirds. Consistent with the findings of Imber and Berruti (1981) and Lipinski and Jackson (1989), this feeding strategy was most prevalent among the 17 procellariiform species, 81% of which scavenged at least occasionally. This behavior is likely to depend largely on these species' well-developed olfactory sense (Wenzel 1980).

Within the ETP avifauna, scavenging was most frequently used by the Tahiti Petrel, a resident that scavenged an estimated average of 36 g of cephalopods/individual petrel/day. Other species that were major scavengers were the Juan Fernandez Petrel and Herald/Henderson's petrels (4.4 g/bird/d), and migrating Sooty Shearwaters and Murphy's Petrels (each scavenging 4.2–5.5 g/bird/d); species of small *Pterodroma* also consistently scavenged cephalopods.

The morphological adaptations of the Tahiti Petrel for scavenging have been noted previously (Spear and Ainley 1997a, 1998). These birds possess wings having the highest aspect ratio among ETP seabirds, an adaptation similar to that of albatrosses (with the highest aspect ratios of all seabirds). The latter forage over wide ocean areas while using minimum amounts of energy, and feed often by scavenging large dead squid (Imber and Russ 1975, Clarke et al. 1981, Croxall and Prince 1994). Tahiti Petrels also have adaptations, unique among ETP seabirds, for consuming dead cephalopods too large to swallow whole—a very large, strongly hooked beak for pulling and ripping, and long legs with heavily clawed feet that are used to brace against the dead floating animal when the beak is pulling

flesh in the opposite direction (L. Spear, pers. obs.). In fact, we believe that this species is the ecological counterpart of the larger albatrosses that are essentially absent from tropical waters because of the lack of winds strong enough to provide the mobility needed to forage over wide expanses (Spear and Ainley 1997a).

The only non-procellariiform species that frequently fed as a scavenger was the Parasitic Jaeger, although there was evidence that the Sooty Tern may have done so rarely.

#### DIURNAL FEEDING ON NON-CEPHALOPOD INVERTEBRATES

Diurnal feeding on non-cephalopod invertebrates accounted for an estimated 3.3% of the prey mass consumed by ETP seabirds, making this the third most important feeding strategy. Resident species for which this strategy was especially important were the Markham's, Leach's and Wedge-rumped storm-petrels. Non-cephalopod invertebrates consumed by these seabirds were primarily scyphozoans (predominantly *Porpida* spp. and *Physalia* spp.), insects (*Halobates* spp.), and mollusks (primarily *Janthina* spp.).

The Sooty Shearwater, a migrant opportunist, consumed twice as much mass of non-cephalopod invertebrates compared to any of the other ETP avian species, although its diet consisted of only 12% by mass of these prey. The Parasitic Jaeger was an exception among the entire avifauna in that 39% of the mass of all prey it consumed was obtained through diurnal feeding on these invertebrates, primarily gooseneck barnacles (*Lepas* spp.).

#### SUMMARY OF USE OF THE FOUR FEEDING STRATEGIES

The resident flock feeders were the most consistent in their use of a single feeding strategy—association with feeding groups of large predatory fish. Large procellariids using this strategy supplemented their diets by scavenging dead cephalopods and feeding at night on fishes that migrate to the ocean surface. Although nocturnal feeding was by far the most important foraging strategy of the solitary residents, these species supplemented their diets by feeding during the day, using about equal proportions of each of the other three strategies—scavenging, feeding over large aquatic predators, and diurnal feeding on non-cephalopod invertebrates. Migrants were the most opportunistic of the three groups. Although they predominantly associated with large piscine predators, they also obtained appreciable amounts of prey by scavenging,

diurnal feeding on non-cephalopods, and by feeding nocturnally (given in increasing order of importance).

Our estimate of the prey mass consumed per day by the ETP avifauna feeding within the study area is about 1,589 mt. Estimates for the mass of prey taken per day by each of the three species' groups was 1,198 mt for resident flock feeders, 280 mt for resident solitary feeders, and 111 mt for migrant opportunists. We are aware of only one other study that has estimated the prey mass consumption rate of an avifauna within an ocean system having well-defined boundaries (Briggs and Chu 1987). These authors estimated that the avifauna residing in the California Current off California (between 32.5° N and 42.0° N, and from the coast to 370 km offshore) consumed 500–600 mt/day within those waters (covering ca. 330,000 km<sup>2</sup>). Assuming a value of 550 mt/day, this amounts to a consumption rate of 0.165 mt/100 km<sup>2</sup> per day, compared to 0.0064 mt/100 km<sup>2</sup> per day consumed by the ETP avifauna (1,590 mt/25,000,000 km<sup>2</sup> × 100), or a consumption rate about 25 times lower in the latter. This result is consistent with that expected when comparing an eastern boundary current, such as the California Current, with a tropical ocean, due to lower productivity in the latter. Bird densities in the California Current were also much higher, particularly in the upwelling zone over the shelf (11,000 birds/100 km<sup>2</sup>; Briggs and Chu 1987) compared to the ETP study area (127.4 birds/100 km<sup>2</sup>).

#### FLOCK VERSUS SOLITARY FORAGING

The 30 avian species separated into two feeding guilds, one that preyed primarily on exocoetids and hemirhamphids and epipelagic cephalopods during the day by feeding in flocks and the other that was solitary and fed nocturnally, primarily on myctophids. Only two exceptions to this were noted: the Phoenix and Herald petrels, two sibling species (Brooke and Rowe 1996) whose diets were composed of a large proportion of myctophids caught at night. Yet, these species often occurred in feeding flocks (flock indices of 16.7 and 21.6, putting them well into the flock-feeding category) where myctophids were seldom caught.

#### SPECIES ABUNDANCE IN RELATION TO DIET

The most abundant species in the ETP study area were, in increasing order: Wedge-rumped Storm-Petrel, Juan Fernandez Petrel, Wedge-tailed Shearwater, Sooty Tern, and Leach's Storm-Petrel. The predominant prey by mass

for each of these species was fishes, contributing an average of 76% of the prey they consumed. Cephalopods composed an average of 35% of the prey mass consumed by the shearwater, petrel, and tern. These findings are similar to those of Harrison et al. (1983), in their study of the diets of breeding Hawaiian seabirds, although these authors concluded that the most abundant Hawaiian seabird species were those that ate cephalopods. Among the above species, the shearwater, petrel, and tern also consumed most of their prey biomass using the flock-feeding strategy, although each of them except the tern supplemented their diet considerably by nocturnal feeding (the strategy used most extensively by the two storm-petrels). With the exception of the two storm-petrels, the more abundant bird species rarely consumed non-cephalopod invertebrates and exocoetid eggs.

#### COMPARISON WITH A POLAR MARINE AVIFAUNA

An extensive and analogous study to this one was conducted on the foraging dynamics of the open-ocean avifauna of the Scotia and Weddell seas during spring, autumn and winter 1983–1988 (Ainley et al. 1991, 1992, 1993, 1994; Rau et al. 1992, Hopkins et al. 1993). The Scotia-Weddell Confluence is considered to be a highly productive region. As in our ETP study, both breeding and non-breeding portions of the avifauna were sampled. Procellariids (12 species), spheniscids (three species), and larids and stercorarids (four species) made up the polar avifauna. Unlike the tropics, there was no apparent relationship between seabirds and foraging piscine predators, and all foraged solitarily although the avifauna was composed of two distinct assemblages demarcated by habitat: one associated with sea ice and the other with the adjacent open water. Most of the open-water component departed the region during winter, migrating to warmer latitudes (Ainley et al. 1994), and one replaced the other to feed in the same waters on the same prey depending on the daily to seasonal vagaries of ice movement (Ainley et al. 1993). There was some species overlap in the occurrence between the two habitats, but stomach fullness indicated better foraging success for each species when in its preferred habitat.

Similar to the results for the solitary foragers in the ETP study, myctophids, squid, and non-cephalopod invertebrates were by far the predominant prey of the polar avifauna, with a huge degree of overlap in prey species and prey size. This was true regardless of a 1,000-fold difference in predator size, much larger than in the ETP avifauna with only a 65-fold



predator size difference. Diet diversity of the polar group was much lower than for ETP species, with the highest Shannon index value being 1.4 among the former, which is about the lowest for ETP species. Only two procellariid species fed predominantly during the day, and in their case by scavenging: Southern Giant Petrel and White-chinned Petrel (*Procellaria aequinoctialis*). The diving species, penguins (*Pygoscelis*, *Eudyptes*, and *Aptenodytes* spp.) and diving petrels (*Pelecanoides* spp.), fed during the day also, but were capable of deep diving. Otherwise, the majority of species fed at night, or in crepuscular periods in the case of larids and stercorarids, when myctophids and squid rose from meso-depths.

Even though crustaceans were abundant (i.e., krill [*Euphausia* spp.]), the polar birds preyed on the larger fish and squid, which were feeding on the crustaceans (Hopkins et al. 1993). The seabirds, thus, were maximizing their energy intake and minimizing their effort. Any prey selection was in proportion to availability which, in fact, was so high that avian predators were incredibly fat and stomachs were full (Spear and Ainley 1998).

The two studies demonstrate the great importance of the fish family Myctophidae to open-ocean seabirds, a fact that seems to be rarely appreciated. More importantly from an ecological perspective is the high degree of trophic partitioning evident within the tropical avifauna compared to that of the polar region. Unlike the tropics, in the polar avifauna no prey selection occurred by species or size among different predator species or between sexes. Like the tropics, however, a niche divergence was observed in the polar avifauna based on foraging behavior—scavenging, surface feeding, and diving. Unlike the tropics, differences in foraging behavior did not lead to the taking of different species of prey among polar seabirds.

#### THE IMPORTANCE OF TUNA TO TROPICAL SEABIRDS

The two studies also highlight the great importance of the tunas in tropical oceans (Ashmole and Ashmole 1967, Harrison et al. 1983, Longhurst and Pauly 1987). No such analogous fishes exist in polar regions (Eastman 1993). In fact, as one result of this importance, the niche of the pursuit diver among tropical seabirds is largely absent, at least in part owing to the high wing loading and high cost of flight needed by these birds (Ainley 1977); to keep pace with fast-moving fish, flight efficiency in the tropics is at a premium (Spear and Ainley 1998, Weimirskirch et al. 2004). Several other

factors have been proposed to explain this as well (Cairns et al., unpubl. data): (1) the temperature-induced swimming performance of ectothermic animals (fishes) vs. that of endothermic animals—burst speed of thermally adapted fishes increases dramatically as temperature increases above 15 C—results in reduced prey capture success by pursuit diving seabirds in tropical waters; (2) swimming performance of ectothermic sharks also is optimum in tropical waters (Cairns et al., unpubl. data), posing a serious threat to endothermic pursuit divers; and (3) subsurface prey can be taken during the day owing to foraging tuna which force them to within reach of surface feeding birds (Ainley 1977). Thus, only the non-pursuit diving species of seabirds are successful when feeding in tropical oceans (Ainley 1977).

However, regarding the importance of tuna to the ETP avifauna, it is important to note that the tuna catch volume has seen a large increase by commercial fisheries in recent decades (Cox et al. 2002, Myers and Worm 2003, Hinke et al. 2004, Hampton et al. 2005, Maury and Lehodey 2005). Unfortunately, the predation by tuna and other top fish predators has been found to have profound cascading effects on food-web structure of tropical seas (Essington et al. 2002, Schindler et al. 2002). Clearly, risks to seabirds that exploit prey over tunas, should the populations of tuna be greatly reduced by commercial fishing or the density of available schools be reduced, indicates the need for monitoring of tuna stocks, school frequency, size, and density over various spatial scales. Not just catch volumes or catch per unit effort (CPUE) should be monitored, if not by fishery agencies then by wildlife agencies charged with managing seabird populations.

Although not included in the present analysis owing to low population size, but definitely occurring in the study area (Spear et al. 1995), two endangered seabird species, the Hawaiian Petrel (*Pterodroma sandwichensis*) and Newell's Shearwater (*Puffinus auricularis newelli*), are both members of the flocking-feeding group of the ETP. The recovery plans for these species dwell only on colony-related impacts to populations (USDI Fish and Wildlife Service 1983), but given the state of the depleted tuna fisheries and the importance of tuna to these seabirds, further investigation about the relationship between bird population trends and tuna availability is warranted. At the least, a changed food-web structure may require re-definition of how much future growth is possible in these seabird populations. Further monitoring of all ETP seabird populations is important in this regard.