# BIOGEOGRAPHY OF PROCELLARIIFORM FORAGING STRATEGIES: DOES OCEAN PRODUCTIVITY INFLUENCE PROVISIONING?

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## SUMMARY

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Mounting evidence suggests that tubenose seabirds (Order Procellariiformes) balance the costs of parental care and the maintenance of adult body condition by regulating the duration of foraging trips during the chick-rearing period. In particular, several species exhibit a bimodal foraging strategy, alternating short (nearshore, 1-5 d) and long (offshore, 6-29 d) foraging trips. We conducted a literature review to assess the biogeographic correlates of provisioning strategies among Procellariiform seabirds, focusing our analysis on the taxonomic affiliation, geographic breeding location (i.e., latitude), and the extent of shallow shelves in the vicinity of breeding colonies. Although our statistical analysis indicated no significant differences in foraging strategies among tubenose families, the bimodal pattern has only been documented in the albatrosses (Diomedeidae) and the shearwaters and petrels (Procellariidae), being absent from the storm petrels (Hydrobatidae) and the diving petrels (Pelecanoididae). We also detected a higher incidence of the bimodal strategy in tropical-subtropical and temperate areas, compared to higher latitude polar-subpolar regions. Considering all the species surveyed, the delivery rates (% BM day$^{-1}$) were greatest for the shortest foraging trips and decreased with increasing trip length. Among bimodal species, delivery rates were significantly greater for short (mean = 9.8 % BM day$^{-1}$) than for long foraging trips (mean = 2.6 % BM day$^{-1}$). However, seabirds increased their effective delivery rates by alternating several short foraging trips for every long excursion. The resulting effective dual prey delivery rates, after combining short and long foraging trips, were undistinguishable from those for species with a unimodal foraging strategy. Additionally, we tested whether the use of a bimodal provisioning strategy was related to the spatial and temporal patterns of ocean productivity. We observed significantly greater chlorophyll a concentrations within the more distant foraging grounds (long trip destinations) targeted by bimodal species. Conversely, we did not detect a difference in the variability of chlorophyll a concentrations within the two types of foraging grounds, suggesting that ocean productivity is equally predictable within the areas targeted by long and short provisioning trips. Our results highlight the importance of ocean productivity patterns as determinants of marine bird foraging strategies and distributions during the breeding season.

Keywords: Provisioning, foraging ranges, bimodal foraging strategy, unimodal foraging strategy, delivery rate, Procellariiform, ocean productivity

## INTRODUCTION

Tubenose seabirds (Order Procellariiformes) exhibit exceptional life-history traits with high and extended parental care, while foraging on distant and unpredictable marine resources (Warham 1990, 1996). Procellariiformes may resolve these constraints in three ways. First, parents frequently overfeed their young to buffer them from an excessive body mass loss during periods of sparse prey resources and low provisioning (Lack 1968, Ashmole 1971). Second, tubenose seabirds have developed the ability to deliver energy-rich prey in a processed form, namely stomach oil, allowing them to feed chicks very energy-dense prey after prolonged foraging trips to sea (Place *et al*. 1989, Roby *et al*. 1989). Third, recent evidence suggests that many Procellariiformes, including albatrosses and shearwaters, employ a dual foraging strategy of interspersed long and short foraging trips designed to provide their young while maintaining adult body condition during the chick-rearing period (Weimerskirch *et al*. 1994a, Granadeiro 1998, Weimerskirch & Cherel 1998, Booth *et al*. 2000). Short foraging trips (1-5 days), typically targeting onshore areas in the vicinity of the colony, are energetically beneficial for chicks and costly for adults. Conversely, long foraging trips (6-29 days) to offshore waters help maintain parental body mass but result in lower food delivery rates (g day$^{-1}$) to the chick. Thus the decision to engage in a short (onshore) or a long (offshore) foraging trip represents a compromise between the energetic requirements of the parents and the chick (Weimerskirch *et al*. 1994a, Weimerskirch & Cherel 1998).

The bimodal foraging strategy was first reported for the blue petrel *Halobaena caerulea*; (Chaurand & Weimerskirch 1994) and subsequently for three other Procellariiform taxa nesting on subantarctic islands, the Thin-billed Prion *Pachyptila belcheri*, the Yellow-nosed Albatross *Diomedea chlororhynchos*, and the Wandering Albatross *Diomedea exulans* (Weimerskirch *et al*. 1994a). Since these initial observations, numerous publications have described similar foraging strategies in other tubenose species from temperate and subpolar regions. However, this strategy is by no means universal in the Procellariiformes. Dual foraging trips are not consistently observed from year to year within a given population, or across allopatric populations of the same species. In addition, the alternating sequence of short/long foraging trips varies greatly within a given species. While some populations switch between one long and one short trip, others alternate one long excursion for every three to six short trips. Moreover, some

bimodal species do not regularly alternate between short and long foraging trips, but switch between the two, depending on the body condition of the parent.

Our objective was to explore potential biogeographic correlates of provisioning strategies in Procellariiform seabirds. In particular, we wanted to assess the relationship between a foraging strategy and taxonomy (e.g., family affiliation), breeding location (e.g., colony latitude), habitat (e.g., extent of shelf area surrounding the colony), and ocean productivity (e.g., chlorophyll concentration). To determine if there was a difference in the profitability of the unimodal and the bimodal provisioning patterns across taxa, we compared the absolute (g day$^{-1}$) and standardized (% body mass day$^{-1}$) delivery rates for short and long foraging trips of the same species. The average delivery rates (% mass day$^{-1}$) were also compared, after weighting long and short trips by their relative frequency, for species that exhibit bimodal and unimodal foraging patterns. Lastly, we compared ocean productivity patterns (e.g. the mean and coefficient of variation in chlorophyll a concentration) at those areas visited during long and short foraging trips, to determine if foraging strategies were related to the abundance and the predictability of prey resources.

**METHODS**

We summarized a collection of 50 published articles, spanning the years 1985-2003, and some unpublished results made available by individual investigators (Table 1). Not all studies aimed to determine whether breeding birds employed a dual strategy of short and long foraging trips. However, if the papers provided detailed information regarding the variability in trip length, we assigned the study population to a bimodal or a unimodal foraging strategy. For a population to be assigned to the former pattern, the histogram of foraging trip durations had to show a distinct bimodal shape. If no distinct bimodality was observed, the population was assigned to a unimodal foraging pattern. Thus, this dichotomy was based solely on the shape of the frequency distribution of foraging trip durations. The absolute length of the foraging trips was not considered.

Before we could assess potential environmental correlates of provisioning patterns in the Procellariiform seabirds, we had to ascertain whether the foraging patterns were related to taxonomic affinity (i.e., family). Once we had discounted potential taxonomic biases, we determined whether the latitude of the breeding locations influenced Procellariiform foraging strategies. We considered four domains on the basis of long-term average sea surface temperature (SST) data from the World Ocean Database 1998 (WOA 1998; http://las.pfeg.noaa.gov): tropical (> 23° C), subtropical (15-23° C), temperate (5-15° C), and polar-subpolar (0-5° C) (Ashmole 1971, Lalli & Parsons 1997). These long-term monthly averages have a spatial resolution of 1 degree latitude/longitude and covered the time period 1945-1996 (Boyer *et al*. 1998). We calculated the mean SST for each study colony by averaging the monthly temperature values for the time period overlapping the satellite telemetry studies (Table 1).

Because the presence of highly-productive continental shelves could also influence the availability of localized prey to breeding seabirds, we tested whether foraging strategies were correlated with the extent of shelf area surrounding breeding colonies. We obtained bathymetric data from NOAA's National Geophysical Data Center ETOPO 5-minute gridded elevation dataset (NGDC

1998) and determined the extent of the contiguous shelf area (depth ≤ 200 m) surrounding each study colony. Because these bathymetric data are relatively coarse (pixel size: 5-10 km), we considered three broad continental shelf categories: small (area < 500 km$^2$), intermediate (area between 500 and 5000 km$^2$), and large (area > 5000 km$^2$) (Table 1). Finally, we assessed if there were differences in the provisioning rates and the ocean productivity patterns (i.e., phytoplankton standing stocks) within the foraging grounds targeted during short and long provisioning trips by those species exhibiting a bimodal strategy.

We determined the foraging grounds for those study populations where published tracking studies had been conducted during the chick-rearing period, or where there was information on the foraging locations of chick-provisioning individuals. Foraging grounds were mapped using four types of data: telemetry information, dietary studies, estimates of the average trip duration and flight speed, and at-sea observations of foraging birds (Table 1). Three types of telemetry data were considered: satellite tracking locations, movement tracks, and kernel activity ranges. For studies that reported raw locations and tracks, we determined those areas where the birds seemed to engage in searching behavior, characterized by contorted paths and slower movement rates. For articles that provided kernel plot estimates, which depict where satellite-tracked individuals spent their time at sea, we selected "core" activity areas delineated by the 50% time contour. In some cases, the satellite tracking was conducted in conjunction with provisioning and dietary studies at breeding colonies. In other instances, the tracking data did not overlap temporally with provisioning and dietary studies at the colonies.

Second, some provisioning papers provided information regarding general foraging areas, based upon the types of prey (e.g., pelagic versus neritic) brought back to the nest after each type of foraging trip (e.g., long versus short). Other studies estimated the maximum roundtrip distance traveled by foraging birds, by dividing the amount of time spent away from the colony (trip duration) by the average flight speed. Finally, at-sea observations of foraging birds during the chick-rearing period also were used to identify the destinations of short and long foraging trips.

Once the foraging grounds targeted by short and long foraging trips were mapped, we quantified the patterns of ocean productivity within these areas using remotely-sensed ocean color imagery. Values of Chlorophyll a concentration (chl a) were derived from level 3 Sea-viewing Wide Field-of-view Sensor (SeaWiFS) monthly composites, with a spatial resolution of 9 km. The Goddard Space Flight Center filters, calibrates, and converts satellite-derived radiometric measurements into estimates of chlorophyll a, the main photosynthetic pigment produced by phytoplankton in the marine environment (Perry 1986, Hooker & McClain 2000), and makes these data available at the SeaWiFS project web-site (http://seawifs.gsfc.nasa.gov/SEAWIFS.html). Satellite estimates are within 35% of concurrent in-situ observations within the range of chlorophyll a concentration between 0.05-50 mg m$^{-3}$ (Hooker & McClain 2000). The biggest discrepancies between in-situ and satellite measurements occur in areas of high chlorophyll a concentrations, ranging between 1-10 mg m$^{-3}$ (Kahru & Mitchell 1999).

To ensure that the dietary and foraging range data were representative of the published foraging destinations and

**TABLE 1**

**Biogeography of provisioning patterns of (A) Northern and (B) Southern Hemisphere Procellariiform seabirds.**

| (A) Species | Breeding Location | Foraging Strategy | Short Trips (d) | Long Trips (d) | Shelf Habitat | Mean Monthly SST | Body Size (kg) | Study Dates | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **DIOMEDEIDAE** | | | | | | | | | |
| Laysan Albatross (*Phoebastria immutabilis*) | Tern Island, French Frigate Shoals, Hawaii | $B_{na}$ | 1-6 | 12-28 | SS | 24.32 | 3 | Jan-Jun 98-99 / Jan-Jun 98-99 | Fernández et al. 2001 / Hyrenbach et al. 2002 |
| Black-footed Albatross (*Phoebastria nigripes*) | Tern Island, French Frigate Shoals, Hawaii | $B_{na}$ | 1-4 | 12-29 | SS | 24.32 | 3.2 | Jan-Jun 98-99 / Jan-Jun 98 | Fernández et al. 2001 / Hyrenbach et al. 2002 |
| **PROCELLARIIDAE** | | | | | | | | | |
| Cory's Shearwater (*Calonectris diomedea*) | Svelagem Grande, NE Atlantic | B | 1-2 | 3-9* | SS | 22.34 | 0.89 | Aug-Sep 97 | Granadeiro et al. 1998 |
| Cory's Shearwater (*Calonectris diomedea*) | Berlenga, Portugal | U | 1-3 | | LS | 18.77 | 0.89 | Aug-Sep 96 | Granadeiro et al. 1998 |
| Wedge-tailed Shearwater (*Puffinus pacificus*) | Tern Island, French Frigate Shoals, Hawaii | U | 1-2 | | SS | 26.74 | 0.40 | Aug-Oct 96 / Sep-Nov 97 | Baduini 2002 |
| Manx Shearwater (*Puffinus puffinus*) | Skomer Island, Whales | U / B** | 1-4 | 5-7** | LS | 14.22 | 0.44 | May-Aug 99 / Jul-Sep 95-96 | Gray & Hamer 2001 / Hamer et al. 1999 |
| Little Shearwater (*Puffinus assimilis*) | Svelagem Grande, NE Atlantic | U | 1-2 | | SS | 18.55 | 0.17 | Mar-Apr 93 | Hamer 1994 |
| Northern Fulmar (*Fulmarus glacialis*) | Shetland, UK St. Kilda, Scotland | U / U | 1 / 1 | | LS | 12.24 | 0.79 | Jul-Sep 97 / Jul 94 | Phillips & Hamer 2000 / Hamer & Thompson 1997 |
| Northern Fulmar (*Fulmarus glacialis*) | Bjornoya, Barents Sea | U | 0.3-3.5 | | LS | 5.29 | 0.85 | Jun-Jul 99 | Weimerskirch et al. 2001 |
| **HYDROBATIDAE** | | | | | | | | | |
| Leach's Storm-petrel (*Oceanodroma leucorhoa*) | Kent Island, New Brunswick | U | 1-4 | | LS | 11.62 | 0.045 | Aug 83 / Aug 86 | Ricklefs et al. 1985 / Ricklefs 1992 |
| European Storm-petrel (*Hydrobates pelagicus*) | Shetland, UK | U | 1-2 | | LS | 10.64 | 0.029 | May-Oct 92 / Jul-Nov 93 | Bolton 1995a / Bolton 1995b |

B = Bimodal provisioning strategy; $B_{na}$ = Bimodal trips but no regular alternation between the long and short trips
U = Unimodal provisioning strategy; *Bimodal trips conducted during food limited year only; **Females only conduct bimodal provisioning pattern; ***Parents coordinate bimodal forage patterns
Three shelf habitats are considered: SS = Small shelf (< 500 km$^2$); LS = Large Shelf (> 5000 km$^2$); IS = Intermediate Shelf (500-5000 km$^2$)

**TABLE 1**

**Biogeography of provisioning patterns of (A) Northern and (B) Southern Hemisphere Procellariiform seabirds.**

| (B) Species | Breeding Location | Foraging Strategy | Short Trips (d) | Long Trips (d) | Shelf Habitat | Mean Monthly SST | Body Size (kg) | Study Dates | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **Diomedeidae** | | | | | | | | | |
| Black-browed Albatross (*Diomedea melanophris*) | Kerguelen Island | U | 1-9 | | IS | 5.19 | 3.7 | Dec-Jan 91-92 / Feb 94-95 | Weimerskirch *et al.* 1994a / Weimerskirch *et al.* 1997a |
| Black-browed Albatross (*Diomedea melanophris*) | Bird Island, South Georgia | U | 1-12 | | IS | 2.79 | 3.7 | Jan-Jun 90 / Jan-Jun 92-94 | Huin *et al.* 2000 |
| Grey-headed Albatross (*Diomedea chrysostoma*) | Bird Island, South Georgia | U | 1-12 | | IS | 2.79 | 3.4 | Jan-Jun 93-96 | Huin *et al.* 2000 |
| Shy Albatross (*Thalassarche cauta*) | Albatross Island, Tasmania | U | 1-2 | | LS | 16.13 | 4.5 | Jan-Feb 96 / Jan-Feb 97 | Hedd *et al.* 2001 / Hedd *et al.* 2002 |
| Wandering Albatross (*Diomedea exulans*) | Possession Island, Crozet | B | 1-5 | 6-20 | SS | 5.68 | 9.3 | Dec-Jan 91-92 / Jun-Jul 92 | Weimerskirch *et al.* 1994b / Weimerskirch *et al.* 1997b |
| Wandering Albatross (*Diomedea exulans*) | Bird Island, South Georgia | B | 1.5-3 | 12-18 | IS | 1.74 | 10 | May-Aug 96-97 | Berrow *et al.* 2000 |
| Waved Albatross (*Phoebastria irrorata*) | Isla Española, Galapagos Islands | B | 1-5 | >7 | IS | 21.04 | 4.5 | Jun-Oct 96 | Fernández *et al.* 2000 |
| Yellow-nosed Albatross (*Diomedea chlororhynchos*) | Amsterdam Island | B | 1-5 | 6-12 | IS | 15.41 | 2.1 | May-Aug 90 / Dec-Mar 95-96 | Weimerskirch *et al.* 1994a / Weimerskirch *et al.* 2000a |
| **Procellariidae** | | | | | | | | | |
| Antarctic Petrel (*Thalassoica antarctica*) | Svarthamaren, Antarctica | U | 3-9 | | LS | 1.05 | 0.69 | Dec-Feb 91-92 / Dec 96-Feb 97 | Lorentsen *et al.* 1996 / Tveraa *et al.* 1998 |
| Blue Petrel (*Halobaena caerulea*) | Kerguelen Island | B | 1-3 | 5-10 | IS | 5.19 | 0.17 | Jan-Feb 90 | Chaurand & Weimerskirch 1994 |
| Little Shearwater (*Puffinus assimilis*) | Lady Alice Island, New Zealand | B | 1-2 | 7*** | LS | 15.88 | 0.22 | Aug-Dec 94 | Booth *et al.* 2000 |
| Sooty shearwater (*Puffinus griseus*) | Snares Island, New Zealand | B | 1-2 | 8-17 | LS | 12.25 | 0.85 | Feb-Mar 95 | Weimerskirch 1998 |
| Short-tailed Shearwater (*Puffinus tenuirostris*) | Bruny Island, Tasmania | B | 1-3 | 9-17 | LS | 15.05 | 0.70 | Jan 97 / Mar 97 | Weimerskirch & Cherel 1998 |
| Thin-billed Prion (*Pachyptila belcheri*) | Kerguelen Island | B | 1-3 | 5-9 | IS | 5.19 | 0.13 | Dec-Jan 91-92 | Weimerskirch *et al.* 1994a |
| Wedge-tailed Shearwater (*Puffinus pacificus*) | Heron Island, Great Barrier Reef Australia | B | 1-3 | 8 | LS | 26.28 | 0.38 | Feb-Mar 01-02 | B. Smithers (unpubl. data) |
| White-chinned Petrel (*Procellaria aequinoctialis*) | Possession Island, Crozet | B | 0.5-2 | 3-13 | SS | 5.98 | 1.5 | Jan-Feb 97 | Catard *et al.* 2000 |
| **Pelecanoididae** | | | | | | | | | |
| Common Diving Petrel (*Pelecanoides urinatrix*) | Kerguelen Island / Bird Island, South Georgia | U | 1-3 | | IS | 5.19 / 3.31 | 0.15 | Dec-Jan 91-92 / Jan-Feb 1982 | Weimerskirch *et al.* 1994a / Roby 1991 |

provisioning rates, we restricted our analyses to those months where there was concurrent information about foraging ranges and provisioning rates. SeaWiFS imagery was obtained for those chick-rearing months that overlapped the tracking/provisioning studies of each study population (Table 2), and these data were used to calculate the average and the variability in ocean productivity within different foraging areas. We discarded unreasonably high chlorophyll a concentrations ($\geq 50$ mg m$^{-3}$) resulting from high cloud cover reflectance (Hooker & McClain 2000), and calculated the median for the remaining pixels within each foraging area. We repeated this procedure for every month each population was studied, using the five years of SeaWiFS data currently available (January 1998-December 2002).

To assess the climatology of ocean productivity patterns within the foraging grounds exploited by chick-provisioning seabirds, we averaged the monthly medians across years (1998-2002). In addition to calculating this long-term average, the annual values were used to determine the temporal variability in ocean productivity, using the coefficient of variation [CV = (standard deviation/mean) * 100%] across all months and years. The coefficient of variation provides a standardized measure of variability, scaled by the magnitude of the mean (Zar 1984).

We quantified the spatial and temporal variability in ocean productivity patterns in two ways. First, to determine if there were significant differences in ocean productivity within the foraging grounds targeted by short and long provisioning trips, we compared the mean chlorophyll a concentrations for species with a bimodal foraging strategy. Then, we contrasted the variability (CV) of these pigment values to determine if ocean productivity was more predictable within the foraging grounds far/close to breeding colonies. More specifically, we used paired t-tests to contrast the chlorophyll a concentrations for the long and the short foraging destinations on a species-specific basis. Thus, the sample size of each test was eight paired species-specific measurements (Table 2).

Finally, to explore whether a unimodal foraging strategy (e.g., exploiting nearby resources) could be as profitable as a bimodal mode (e.g., alternating between near and distant prey), we compared species-specific delivery rates (g day$^{-1}$) for both types of foraging trips. Although delivery rates were not recorded in every study, they could be estimated using the ratio of the average meal size and the average trip duration for short and long foraging excursions separately. To compare among taxa of varying body size, delivery rates were normalized as the percentage of the adult body mass delivered to the chick per day (% BM day$^{-1}$). Adult body mass information, was usually provided within the provisioning results. However, when unavailable, other published sources were used to obtain information on average adult body mass for the specific population and colony where the provisioning study was conducted. Paired t-tests were used to determine if delivery rates were significantly different for short and long trips by a given population. Additionally, the delivery rates for species that conduct several short trips for every long foraging excursion were weighted using the ratio of short to long trips conducted. The effective bimodal delivery rates resulting from combining short and long trips were then compared to those for unimodal species. Since delivery rates were expressed as a percentage of adult body mass and percentage data are typically non-normally distributed, all delivery rate values were arc sine transformed before performing the statistical analyses (Zar 1984).

## RESULTS

We observed a great variety of foraging strategies in Procellariiform seabirds, ranging from unimodal foraging trips, to the alternation of 1-6 short foraging trips for every long excursion We summarized 12 unimodal and 14 bimodal Procellariiform species (Table 1). The species that exhibited a bimodal foraging strategy alternated between short trips to nearshore feeding grounds along continental shelves adjacent to breeding colonies, and long trips to pelagic waters associated with polar and sub-polar frontal zones (Fig. 1, Table 2). Short trips ranged from 1-3 d duration in the medium-sized shearwaters to 1-9 d in the larger albatrosses (Table 1). Long trips ranged from 5-17 days across all albatross and shearwater populations studied. However, not all species regularly alternated between short and long forays, with substantial interspecific variability in the ratio of short/long foraging trips. In shearwaters, two short feeding excursions were conducted for every long foraging trip (Granadeiro *et al*. 1998, Weimerskirch & Cherel 1998, Weimerskirch 1998), except for the Little Shearwater (*Puffinus assimilis*) which exhibited a 6/1 ratio (Booth *et al*. 2000). In the Wandering Albatross, five short trips were undertaken for every long excursion (Berrow *et al*. 2000).

Our study revealed a significant association between Procellariiform foraging strategies and ocean productivity patterns, once we had accounted for taxonomic and geographic biases. There was no significant association between taxonomic affiliation (i.e., family) and foraging pattern (i.e., unimodal or bimodal) (Table 1; Chi-Square Log likelihood ratio = 5.84, $P = 0.120$, df = 3, n = 28). This result suggests that the taxonomic affiliation of a species does not determine the adoption of a unimodal or bimodal foraging strategy in Procellariiform seabirds. However, it is worth noting that bimodal species are disproportionately represented in the albatrosses (Diomedeidae) and the shearwaters and petrels
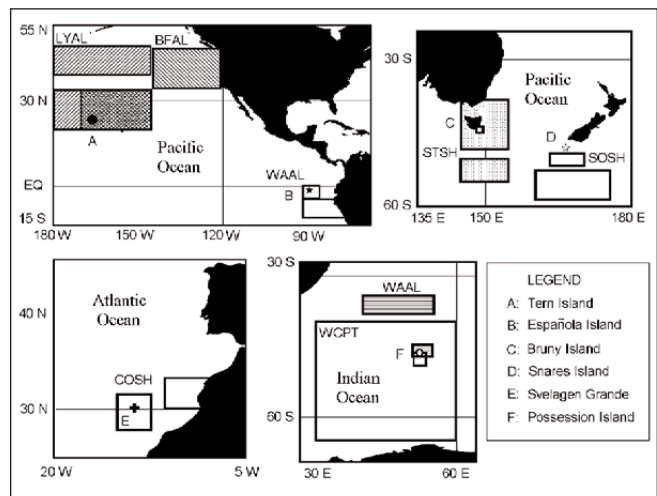


**Fig. 1.** Breeding locations and foraging ranges of the eight bimodal species listed in Table 2. The Black-footed Albatross (BFAL) and Laysan Albatross (LYAL) at Tern Island, Hawaii (black circle, A), the Waved Albatross (WAAL) at Española Island, Galapagos (black star, B), the Short-tailed Shearwater (STSH) at Bruny Island, Tasmania (white square, C), the Sooty Shearwater (SOSH) at Snares Island, New Zealand (white star, D), the Cory's Shearwater (COSH) at Svelagem Grande, (black cross, E), and the White-chinned Petrel (WCPT) and the Wandering Albatross (WAAL) at Possession Island, Crozet (white circle, F).

**TABLE 2**

**Mean and variability (CV) in chlorophyll a concentration (mg m⁻³) of cell grids (9 X 9 km) within Procellariiform foraging ranges targeted by short (ST) and long (LT) foraging trips. Four methods were used to delineate the foraging grounds: foraging range (trip duration divided by average flight speed, FR) estimates; locations (TL, tracks (TT) and kernel plots of satellite tracking data (KP); at-sea observations (OB); and diet during foraging trips (DI).**

| Species | Location | ST Range | LT Range | Mean chl a ST | CV chl a ST | Mean chl a LT | CV chl a LT | Method of determination (Reference) |
|---|---|---|---|---|---|---|---|---|
| **UNIMODAL** | | | | | | | | |
| Cory's Shearwater (*Calonectris diomedea*) | Berlenga, Portugal | 38-41 N 8-11 W | - | 0.283 | 27.01 | - | - | FR, OB (Granadeiro *et al.* 1998) |
| Black-browed Albatross (*Diomedea melanophris*) | Kerguelen Islands | 47-50 S 69-71 E | - | 0.826 | 26.70 | - | - | TL (Weimerskirch *et al.* 1997a) |
| Shy Albatross (*Thalassarche cauta*) | Albatross Island, Tasmania | 40-42 S 143.5 -145.5 E | - | 0.496 | 19.60 | - | - | KP (Hedd *et al.* 2001) |
| **BIMODAL** | | | | | | | | |
| Laysan Albatross (*Phoebastria immutabilis*) | Tern Island, Hawaii | 20-34 N 145-180 W | 38-50 N 145-180 W | 0.086 | 21.43 | 0.357 | 12.71 | KP (Hyrenbach *et al.* 2002) |
| Black-footed Albatross (*Phoebastria nigripes*) | Tern Island, Hawaii | 20-34 N 145-170 W | 34-48 N 121-145 W | 0.087 | 21.29 | 0.298 | 19.96 | KP (Hyrenbach *et al.* 2002) |
| Cory's Shearwater (*Calonectris diomedea*) | Svelagem Grande, NE Atlantic | 28-31 N 14-17 W | 30-33 N 9-12 W | 0.107 | 13.84 | 0.184 | 20.62 | FR (Granadeiro *et al.* 1998) |
| Waved Albatross (*Phoebastria irrorata*) | Isla Española, Galapagos Islands | 0-4 S 86-93 W | 4-10 S 78-86 W | 0.418 | 34.78 | 0.556 | 21.81 | TL (Fernández *et al.* 2001) |
| Wandering Albatross (*Diomedea exulans*) | Possession Island, Crozet | 46-47 S 51-53 E | 34-38 S 40-55 E | 0.162 | 12.64 | 0.253 | 17.28 | KP (Weimerskirch *et al.* 1997b) |
| Short-tailed Shearwater (*Puffinus tenuirostris*) | Bruny Island, Tasmania | 38-48 S 145-155 E | 50-55 S 145-155 E | 0.263 | 16.60 | 0.219 | 10.16 | TL, DI, OB (Weimerskirch & Cherel 1998) |
| Sooty shearwater (*Puffinus griseus*) | Snares Island, New Zealand | 48-51 S 163-170 E | 52-58 S 160-176 E | 0.238 | 17.76 | 0.337 | 16.32 | (Weimerskirch 1998) |
| White-Chinned Petrel (*Procellaria aequinoctialis*) | Possession Island, Crozet | 46.5-47 S 51-52 E | 40-65 S 30-60 E | 0.288 | 33.51 | 0.227 | 16.40 | TT (Catard *et al.* 2000) |

(Procellariidae), while no storm-petrels (Hydrobatidae) and diving petrels (Pelecanoididae) have been documented to employ a dual foraging mode.

Moreover, bimodal species appear to be concentrated south of the equator. In the northern hemisphere, two species of albatross and three shearwaters employed a bimodal foraging pattern. However, although Laysan *Phoebastria immutabilis* and Black-footed Albatrosses *P. nigripes* undertake long and short foraging trips during the chick-rearing period, there is no evidence of a progressive alternation between long and short trips. Interestingly, no Northern Fulmar *Fulmarus glacialis* population has been documented to employ a dual foraging strategy, in spite of the broad range of this species. In the southern hemisphere, the dual foraging pattern is pervasive, and has been observed in three of six albatross species previously studied, the Yellow-nosed *Diomedia chlororhynchos*, the Wandering *D. exulans*, and the Waved *P. irrorata* Albatross. Additionally, six petrel species, including four shearwaters, the Blue Petrel, and the Thin-billed Prion conduct bimodal foraging trips, and there is evidence that in at least another species, the Little Shearwater, there is alternation and coordination of short and long foraging trips among parents (Booth *et al.* 2000, Smithers unpubl. data).

The analysis of Procellariiform provisioning strategies with respect to the geographic location of breeding colonies revealed no significant difference in the distribution of populations exhibiting a bimodal foraging strategy across tropical-subtropical (0-35º N and S), temperate (35-50º N and S), and polar subpolar (> 50º N and S) regions (Chi-Square Log likelihood ratio = 5.37, $P$ = 0.068, df = 2, n = 28). Only one of the five (20%) polar-subpolar populations considered in this analysis exhibited a bimodal foraging pattern, while 71% and 67% of the populations breeding in tropical-subtropical and temperate latitudes employed this strategy respectively.

There were no significant relationships between the size of shelf area surrounding colonies and foraging strategy (Chi-Square Log likelihood ratio = 2.11, $P$ = 0.348, df = 2, n = 28). A greater percentage (71% and 67% respectively) of the species breeding in colonies surrounded by small and intermediate shelf areas used a bimodal foraging strategy, relative to the species breeding in areas characterized by large (area > 5000 km$^2$) continental shelves (42% bimodal species).

We detected significantly greater mean chlorophyll a concentrations within the foraging areas targeted by Procellariiform seabirds during long (mean = 0.30 +/- 0.04 SE mg m$^{-3}$) than in areas of short foraging trips (mean = 0.21 ± 0.04 SE mg m$^{-3}$) (Table 2; Paired t-test among individual species $t_{two-tailed}$ = -2.45, $P$ = 0.045, df = 7, n = 8). This result suggests that the foraging grounds where petrels go to feed on long forays are relatively more productive than those areas where they fed during short foraging trips. However, there was no significant difference in the variability in chlorophyll a (CV) within the areas where Procellariiform seabirds feed during long (mean = 16.91 ± 1.41 SE) and short (mean = 21.48 ± 2.97 SE) foraging trips (Paired $t_{two-tailed}$ = 1.56, $P$ = 0.163, df = 7, n = 8).

For species in which both unimodal and bimodal strategists have been observed, the delivery rate of food (% BM day$^{-1}$) was greatest for the foraging trips of the shortest duration, and decreased with increasing trip length (Grandeiro *et al.* 1998, Baduini 2002). Overall, among those species that conducted a bimodal foraging strategy, the delivery rates were significantly greater (Paired $t_{two-tailed}$ = 9.82, $P$ < 0.001, n = 10) for short (mean = 9.83 ± 1.35 SE% BM day$^{-1}$) than for long (mean = 2.50 ± 0.39% BM day$^{-1}$) foraging trips (Table 3). Furthermore, bimodal species increased their effective provisioning rates by conducting several short foraging trips for every long excursion.

Once we adjusted the delivery rates of bimodal species to account for the unequal sequence of short and long foraging trips, we detected no significant difference (t = -1.93, $P_{two-tailed}$ = 0.069, n = 20) in the delivery rates (% BM day$^{-1}$) of unimodal species (mean = 9.39 +/- 0.97 SE) compared with the effective provisioning rates of bimodal species with a mixed foraging strategy (mean = 6.97 ± 0.79 SE). In fact, there was no significant difference (t = 0.17, $P_{two-tailed}$ = 0.870, n = 20) between the delivery rates of unimodal species and those for bimodal taxa engaged exclusively in short trips (Table 3).

## DISCUSSION

This review addresses the taxonomic and geographic determinants of foraging strategies in Procellariiform seabirds at a broad, multi-species level. Since the discovery of a novel dual provisioning strategy in Southern Ocean Procellariiform seabirds (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994), the use of bimodal foraging trips has been increasingly reported for other tubenose species around the world. Nevertheless, this dual strategy is not ubiquitous across all Procellariiform taxa. In those species with bimodal trip distributions, there appears to be some plasticity in this foraging behavior with gender-based differences, disparities across colonies, and substantial year-to-year variability (Granadeiro *et al.* 1998, Hamer *et al.* 1999, Gray & Hamer 2001). Substantial within-population variability has been documented across genders, as well as from year to year. For example, there is evidence of significant differences among genders, as in the Manx Shearwater *Puffinus puffinus*, where only females engaged in a bimodal foraging pattern. Males, on the other hand, conducted 1-4 day-long unimodal foraging trips and delivered food at a greater rate, thus making a greater overall contribution to chick provisioning than females (Hamer *et al.* 1999, Gray & Hamer 2001). Additionally, researchers have documented interannual variability. Cory's Shearwaters (*Calonectris diomedea*), for instance, employed a flexible foraging strategy with relatively uniform feeding intervals during years of "average" food availability, and a dual foraging strategy (long and short trips) in "low" food years (Granadeiro *et al.* 1998).

Despite this great deal of variability, several results emerged across the studies we reviewed. One pervasive pattern we observed was the negative relationship between provisioning rate and foraging trip duration. Although the meals delivered to the young tended to be larger after longer foraging trips, the average amount of food provisioned per day decreased with increasing trip length. It is interesting that the effective prey delivery rates of the dual strategy (% BM day$^{-1}$ for short and long trips combined) were just as profitable as those for the species with a unimodal foraging trip distribution. Moreover, the delivery rates for short trips in bimodal species were indistinguishable from those of taxa with a unimodal foraging strategy. Thus, the question remains, what is the function of the long foraging trips if chick-provisioning rates for bimodal/unimodal foraging strategies are the same?

**TABLE 3**
**Prey delivery rates (g day⁻¹ and % BM day⁻¹) for species that exhibit unimodal and bimodal provisioning patterns.**
**ST = Short foraging trips. LT = Long foraging trips.**

| Species | Body Mass (kg) | Delivery rate (g/day) | | Delivery rate (% BM/day) | | Ratio ST/LT | Average delivery rate (ST / LT) combined |
|---|---|---|---|---|---|---|---|
| | | ST | LT | ST | LT | | |
| **Unimodal** | | | | | | | |
| Black-browed Albatross | 3.7 | 266 | - | 7.1 | - | - | 7.1 |
| Grey-headed Albatross | 3.4 | 253 | - | 7.5 | - | - | 7.5 |
| Shy Albatross | 4.5 | 400 | - | 8.9 | - | - | 8.9 |
| Antarctic Petrel | 0.69 | 38 | - | 5.5 | - | - | 5.5 |
| Cory's Shearwater | 0.89 | 48 | - | 5.4 | - | - | 5.4 |
| Little Shearwater | 0.17 | 22 | - | 13.0 | - | - | 13.0 |
| Northern Fulmar | 0.80 | 75 | - | 9.3 | - | - | 9.3 |
| Wedge-tailed Shearwater | 0.40 | 45 | - | 11.4 | - | - | 11.4 |
| European Storm-petrel | 0.029 | 3 | - | 11.4 | - | - | 11.4 |
| Leach's Storm-petrel | 0.045 | 4 | - | 8.0 | - | - | 8.0 |
| Common Diving Petrel | 0.15 | 23 | - | 15.8 | - | - | 15.8 |
| **Bimodal** | | | | | | | |
| Wandering Albatross | 9.3 | 341 | 98 | 3.7 | 1.1 | 5/1 | 3.3 |
| Yellow-nosed Albatross | 2.1 | 142 | 53 | 6.7 | 2.5 | ND | 4.6** |
| Blue Petrel | 0.17 | 30 | 9 | 17.5 | 5.3 | 1/1 | 11.4 |
| Cory's Shearwater | 0.89 | 45 | 20 | 5.1 | 2.4 | 2/1 | 4.2 |
| Little Shearwater | 0.22 | 21 | 3 | 9.6 | 1.6 | 6/1 | 8.5*** |
| Manx Shearwater | 0.44 | 53 | 10* | 12.1 | 2.3 | ND | 7.2** |
| Short-tailed Shearwater | 0.70 | 60 | 14 | 8.6 | 2.1 | 2/1 | 6.4 |
| Sooty Shearwater | 0.85 | 96 | 18 | 11.2 | 2.1 | 2/1 | 8.2 |
| Thin-billed Prion | 0.13 | 20 | 5 | 14.9 | 3.9 | ND | 9.4** |
| White-chinned Petrel | 1.5 | 133 | 26 | 8.9 | 1.7 | 2/1 | 6.5 |

\* Females only conduct bimodal foraging trips
\*\* Assuming a ST/LT ratio of 1:1
\*\*\* Parents coordinate bimodal foraging trips

ND = no data available

A likely function of long foraging trips may be to restore the body condition of breeding adults, by increasing their own rate of resource provisioning at the expense of a lower feeding rate for the offspring. According to this scenario, the trade-off between self-maintenance and the delivery of resources to the chick influences the ratio of long and short foraging trips. Empirical evidence suggests that the body condition of the adults determines whether they engage in a short or a long foraging trip. Sooty and Short-tailed Shearwaters, for instance, conduct several consecutive short foraging trips (usually two) until the parent body condition reaches a threshold level, and subsequently make a long foraging trip (Chaurand & Weimerskirch 1994, Weimerskirch & Cherel 1998, Weimerskirch 1998). Decisions about whether to forage near or far from the breeding colonies are thus influenced by parent body condition just prior to leaving the colony, rather than by the condition of the chick. Good parental body condition has been associated with high prolactin blood levels and offshore foraging, while poor parental condition has been linked with the onset of long foraging excursions (Weimerskirch & Cherel 1998). Incidentally, adults return to the nest in better body condition after long excursions (e.g., large mass gain), than after short foraging trips (e.g., mass loss) (Weimerskirch *et al*. 1997b).

Conversely, the association between body condition and trip duration does not hold for populations exhibiting a unimodal foraging strategy. For instance, the parental body mass and condition of Wedge-tailed Shearwaters *Puffinus pacificus* nesting in French Frigate Shoals, Hawaii, do not change significantly over the chick-rearing period, and are insensitive to foraging trip duration (Baduini 2002). These results reinforce the notion that long foraging excursions serve to restore adult body mass, and are not required in populations where the condition of breeding birds is not compromised during the chick-rearing period. Moreover, these observations suggest that in those populations and species that employ a bimodal foraging strategy, parental body condition is likely compromised during chick-rearing.

Energetic foraging costs for long and short foraging trips must be considered when a dual foraging strategy is adopted. Energy expended may be 1.5-2.2 times greater for short trips compared to long excursions, as demonstrated in the Blue Petrel (Weimerskirch *et al*. 2003). Thus, the function of longer trips may be to maximize the energetic efficiency of foraging while adults restore their body condition, resulting in lower energetic foraging costs compared to shorter trips. Also, the use of wind for dynamic soaring on long

trips has been shown to maximize efficiency by lowering the cost of flight. For instance, in the Wandering Albatross, energetic foraging costs are not correlated to the distance traveled or to flight speed, but are closely related to the number of landings at sea (Weimerskirch *et al*. 2000b, Shaffer *et al*. 2001). Thus, foraging on distant, yet abundant prey resources is likely energetically more efficient than exploiting small unpredictable patches closer to the breeding colony.

Previous provisioning studies have suggested that tubenose species with a bimodal provisioning strategy switch between short trips to less productive waters around colonies, and long foraging excursions to more productive distant areas, frequently associated with subpolar frontal zones (Weimerskirch & Cherel 1998, Weimerskirch 1998). One of the objectives of this study was to test the hypothesis that the purpose of long foraging trips is to target more productive foraging grounds. Additionally, it could be argued that to maintain high chick-provisioning rates during short trips, the foraging grounds close to breeding colonies may represent more predictable foraging grounds, capable of ensuring persistent food resources despite their lower relative ocean productivity. We addressed these hypotheses by comparing the mean and the CV of the chlorophyll a concentration, a metric of ocean productivity, for the destinations of short and long foraging trips undertaken by bimodal species. This paired analysis, involving eight different species addressed by published provisioning papers, revealed that ocean productivity was greater in areas targeted by long foraging trips. On the other hand, the mean chlorophyll a concentrations were equally variable within the foraging grounds close and far from the breeding colonies, suggesting that ocean productivity within the foraging areas targeted by short and long foraging trips are equally predictable.

Because a bimodal foraging strategy could arise in response to several distinct productivity patterns, we propose three possible models for consideration by future provisioning studies: (1) spatially/temporally unpredictable ocean productivity, (2) spatially predictable/temporally shifting ocean productivity, and (3) reliance on diverse resources found exclusively within foraging grounds close and far from breeding colonies. These simplified models are based on the underlying assumption that spatially/temporally predictable and persistent ocean productivity patterns would favor a unimodal foraging pattern, whereby birds commute to the same foraging grounds throughout the provisioning period. Moreover, these models focus exclusively on the spatial and temporal distribution of ocean productivity, and do not incorporate important ecological factors such as interspecific competition, the potential depletion of prey resources in the vicinity of the colony during the breeding season, and the significance of wind patterns for the large-scale movements of foraging birds (e.g., Weimerskirch *et al*. 1985, 1988, 2000b). These factors have been previously invoked to explain the segregation of breeding seabirds, but are beyond the scope of this review.

The spatially/temporally unpredictable ocean productivity hypothesis envisions a scenario whereby, seabirds exploit foraging areas close to and far from breeding colonies to account for temporally and spatially unpredictable ocean productivity. Foragers search for prey as they transit away from the colony towards distant foraging grounds. If the birds encounter sufficient prey within the closer feeding areas, such that prey delivery rates and body condition are maintained, they engage in a short foraging trip.

Otherwise, they continue their excursion and venture to distant foraging grounds. This scenario predicts significant differences in ocean productivity across foraging areas (space) or months (time), with the alternation between exploratory searches to foraging grounds in the vicinity of breeding colonies and long foraging trips to distant foraging locations. This model seems particularly appealing for the Wandering Albatross, a species which forages on widely dispersed prey patches not associated with bathymetric habitats and engages in large-scale Levy flight searching patterns suggestive of scale-invariant distribution of prey resources (Weimerskirch *et al*. 1994b, Viswanathan *et al*. 1996).

According to the shifting productivity model, we would expect a significant interaction between chlorophyll a concentrations across months and foraging areas, such that birds engage in short and long foraging trips sequentially to exploit prey resources driven by out-of-phase ocean productivity patterns close and far from their colony. Under this scenario, birds that initially exploit resources in one area, shift to use other foraging grounds as the provisioning season proceeds. These spatio-temporal shifts could be associated with the delayed onset of seasonal (i.e., spring-time) peak in ocean productivity within distant high latitude foraging grounds, and could be influenced by the seasonal migration of frontal zones characterized by high chlorophyll concentrations (e.g., Vinogradov *et al*. 1997, Polovina *et al*. 2001). It is unlikely that this model can be applied to many of the groups reviewed in this paper, because most species regularly alternate between short and long foraging trips throughout the chick-rearing period. However, some Procellariiformes have been observed to increase their foraging ranges and trip lengths as the chick-rearing period progresses (Fernández *et al*. 2001).

The reliance on diverse resources model entails seabirds that are forced to forage within both close and distant localities because they require resources (e.g., specific types of prey, high provisioning rates versus large amounts of food) from each of these foraging grounds. This scenario is difficult to evaluate because the spatial and temporal use of the close/distant foraging grounds would be independent from the underlying ocean productivity patterns. Instead, we predict that the specific requirements of the chick/adult would determine the destination/duration of foraging trips. Thus, studies that address foraging strategies in the context of the diet and the body condition of adults and chicks are required to test this model (Weimerskirch *et al*. 1997b, Weimerskirch 1998, Weimerskirch & Cherel 1998).

Our analysis of ocean productivity patterns within the foraging grounds of Procellariiform seabirds must be interpreted with caution, because it relies on satellite-derived ocean color measurements constrained by two main limitations. Chlorophyll a concentrations (mg m$^{-3}$) provide a relative measure of the phytoplankton standing stock within an upper layer of the ocean, whose variable depth is determined by the attenuation of light in the water column. Thus, empirical correlations between near-surface and integrated water-column chlorophyll concentrations are required to estimate overall chlorophyll concentrations. Additionally, because the ratio of photo-pigments to carbon in phytoplankton cells is influenced by many factors including species-specific differences, light conditions, and nutrient availability, it is difficult to extrapolate phytoplankton biomass (grams of Carbon) from chlorophyll a concentrations (Gordon & Morel 1983, Perry 1986).

Despite these constraints, remotely-sensed ocean color provides information on relative phytoplankton concentrations, which are useful to characterize spatial and temporal patterns of ocean productivity. In particular, while chlorophyll a concentrations cannot always be directly linked with the rates of carbon fixation by primary producers, this metric does provide a relative index of the amount of phytoplankton available for carrying out primary production and for grazing by zooplankton (Perry 1986, Joint & Groom 2002). In this study, we used the remote sensing ocean color data to obtain a relative index of the spatial and temporal variability in ocean productivity patterns (e.g., Vinogradov et al. 1997, Chavez et al. 1999). The underlying assumption of our analysis is that ocean productivity influences prey availability to foraging seabirds.

Procellariiform seabirds do not eat phytoplankton, but consume higher trophic-level prey such as zooplankton, fish, and squid (Harper et al. 1985). Nevertheless, chlorophyll a concentrations provide valuable information about the physical processes underlying the dispersion of seabird prey over coarse - mega (10s-1000s km) spatial scales (Hunt & Schneider 1987, Hunt et al. 1999). In particular, the shallow continental shelves and hydrographic fronts where seabird prey aggregates are characterized by elevated chlorophyll concentrations (Springer et al. 1996, Vinogradov et al. 1997, Polovina et al. 2001). Thus, it is our contention that ocean color imagery can be used to assess the relative productivity of seabird foraging grounds across time (e.g., months and years), and space (e.g., short versus long trip destinations).

In addition to overall ocean productivity, other factors such as the availability (e.g., vertical distribution), the patchiness (i.e., predictability), and the quality (i.e., energy content) of the different prey types available, likely influence whether seabirds engage in a unimodal or a bimodal foraging strategy. Although no studies have quantitatively assessed prey quality for short and long foraging trips, mounting evidence suggests that tubenoses feed their offspring neritic species taken from shelf areas (e.g., euphausiids, fish, squid) after short foraging trips. Conversely, after long foraging trips parents deliver processed prey stored as stomach oil, and offshore fish and squid taken from pelagic waters (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994a, Weimerskirch & Cherel 1998, Catard et al. 2000, Cherel et al. 2002).

It is essential that researchers undertake studies of the diet and provisioning patterns of satellite-tracked seabirds, within the context of ocean productivity patterns and prey dispersion at sea. Because Procellariiform seabirds engage in extremely long foraging trips, reliance on remote sensing imagery is a necessity to obtain data at the appropriate temporal and spatial scales. Yet, while satellite-derived products provide a fine-scale temporal/spatial resolution of the dynamic ocean processes influencing ocean productivity patterns and prey distributions (Joint & Groom 2000, Nel et al. 2001, Hyrenbach et al. 2002), an understanding of seabird diet is essential to evaluate different foraging strategies. In particular, by matching the food items delivered to the colony with the oceanographic habitats sampled by foraging seabirds during individual trips, investigators can assess the importance of specific foraging grounds and oceanographic features to provisioning seabirds.

One of the main objectives of this review was to understand the biogeographic determinants of Procellariiform provisioning patterns, to predict whether a specific petrel population should undergo a unimodal or bimodal foraging strategy. It is mostly the larger petrel species (e.g., albatrosses and shearwaters) that employ a dual foraging strategy. Despite some exceptions, the bimodal foraging strategy is prevalent in subantarctic species that breed on offshore islands and alternate foraging trips to the surrounding broad shelf areas with long excursions to subpolar (e.g., Sooty and Short-tailed Shearwater) or subtropical (e.g., Wandering and Yellow-nosed Albatross) frontal zones. While it is conceivable that some of the smaller petrels (e.g., Blue Petrel and Thin-billed Prion) exhibit this same strategy but on smaller temporal scales, no bimodality has been observed in Storm-petrels and Diving petrels.

It is important to note, however, that provisioning studies may have failed to document the dual foraging strategy in species that engage in bimodal foraging trips exclusively during years of "poor" prey availability. Because many provisioning studies are short-lived, spanning one to three breeding seasons, the dual strategy may not have been observed if the research was conducted during years when adults did not have to work very hard to provision their chicks. As has been shown for Cory's Shearwaters *Calonectris diomedea* nesting on islands in the North Atlantic, Procellariiform foraging strategies are flexible, with populations switching from a unimodal to a bimodal strategy when adult body condition is compromised (Granadeiro et al. 1998).

The flexibility of the Procellariiform provisioning strategy underscores the ability of this taxon to adjust to current feeding conditions and to make decisions about where to feed when relying on distant and dispersed food resources. Our results suggest that this flexible foraging strategy is influenced by ocean productivity patterns. However, because Procellariiform seabirds may have developed a bimodal foraging strategy in response to different constraints, comparative studies are required to determine which factors influence the foraging strategy of specific populations and species. In particular, provisioning studies of sympatrically-breeding taxa and allopatric populations of the same species may be especially insightful. In addition to manipulation experiments (Weimerskirch et al. 1995, Bolton 1995b), interannual (e.g., El Niño) and longer-term (e.g., global warming) oceanographic variability provide opportunities to conduct natural experiments of the influence of ocean productivity and prey dispersion patterns on Procellariiform foraging strategies. In particular, if the productivity of the world's oceans is decreasing due to enhanced warming of near-surface waters (Levitus et al. 2000, Gregg & Conkright 2002), we may witness a greater number of Procellariiform seabirds employing a flexible bimodal foraging strategy in the future.

## ACKNOWLEDGEMENTS

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