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Seasonal and annual variation in the diet of breeding and non-breeding Wilson's storm-petrels on King George Island, South Shetland Islands

Accepted: 30 September 2001 / Published online: 14 November 2001
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Abstract The diet of breeding and non-breeding Wilson's storm-petrels (*Oceanites oceanicus*) was analysed over four breeding seasons on King George Island, South Shetland Islands, in order to test if there are changes in diet composition within and between seasons. Krill was the most important food item, followed by myctophid fish and amphipods. Breeding birds showed a clear seasonal pattern of diet, with krill decreasing and alternative prey increasing from the incubation to the chick-rearing period. Non-breeders were not found to change their diet composition. The data suggest that Wilson's storm-petrels selectively choose alternative prey to krill in order to meet the nutrient demands of their chicks. In years of low food availability, Wilson's storm-petrels may have a limited option of prey choice.

Introduction

The diet of adult Wilson's storm-petrels (*Oceanites oceanicus*) has been analysed by various authors (Table 1). The species has been found to prey mainly on planktonic crustaceans, although a wide range of other food items has been found, as well as a large variability in the diet composition. None of these previous studies has examined seasonal changes in diet, and the possibility that such changes could partly account for the different results of the various studies. Because of the high temporal and spatial variability of the availability of the prey in the Antarctic (Sarhage 1988), the

previous studies, carried out in various places at various times, are only glimpses of the feeding ecology of this species. This paper attempts to give an insight into the variation in food composition of the birds of one colony within and between four breeding seasons.

Materials and methods

The study was carried out in the Tres Hermanos (Three Brothers Hill) colony on King George Island, South Shetland Islands (62°14'S, 58°40'W) in the maritime Antarctic from January to March 1996, 1998, 1999 and 2000. Wilson's storm-petrels are the smallest and one of the most abundant Antarctic seabird species. Their breeding biology was summarised by Beck and Brown (1972). They nest in colonies in scree slopes along ice-free Antarctic and sub-Antarctic coasts, where they lay a single egg in a natural cavity. Wilson's storm-petrels exhibit intensive biparental care. Incubation and chick feeding are shared between the sexes. The chicks remain in the nest for about 60 days and are fed during brief nightly visits.

Regurgitated food samples were obtained from mistnetted birds visiting the colony at night, and from breeding birds during standard controls (Quillfeldt and Peter 2000) on the nest. Each bird was sampled only once. Birds were mistnetted on 24 nights in 1996, 9 nights in 1998 and 10 nights in 1999, always in the same area of the colony on the southern slope of Three Brothers Hill. A 12-m mistnet was used in the same position each night. The mistnet samples mainly young prebreeders (e.g. 86% in January 1999; Quillfeldt et al. 2000). In order to obtain regurgitated samples of birds flying into the net, in 1996 a large sheet of plastic (10 by 4 m) was placed under the net. Samples were collected from the sheet with a piece of tissue and stored in plastic bags for later analysis. In 1998 and 1999, regurgitations were collected in a tin of 15 cm diameter, lined with a fresh plastic bag for each sample. Three birds were tested for stomach contents by stomach-flushing with water after they had regurgitated, but only traces of oil were found. For all other birds, only regurgitations were collected. Masses of food samples of Wilson's storm-petrels from the net ($n=41$) and the nest ($n=9$) were not different (Fig. 1, Mann-Whitney U -test, $P=0.94$), indicating that the samples were comparable. The analysis of the samples was carried out in the laboratory using a stereomicroscope. Otoliths were determined after Hecht (1987), and krill after Fisher and Hureau (1985). Data analysis was carried out in SPSS 10.0.

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Table 1 Former studies of the diet of Wilson's storm-petrels, methods for sample collection and results in frequency of occurrence in percent of samples (%F) or percent by mass (%M). The krill species recorded were: *E.sup.* (*Euphausia superba*), *E.crys.* (*Euphausia crystallorophias*), *E.vall.* (*Euphausia vallentini*), *E.tric.* (*Euphausia tricantha*), *E.frig.* (*Euphausia frigida*) and *Thys.sp.* (*Thysanoessa* sp.)

Time	Location	Method	Fish	Krill	Amphipods	Others	Reference
March 1985	Bird Island, South Georgia	Mistnet regurgitations (n = 51)	42% F, 28% M (all myctophids)	54.7% M (<i>E.sup.</i>), 51% F, <i>E.tric.</i> 4% F, <i>Thys.sp.</i> 2% F, <i>Thys.sp.</i> 22% F)	44.6% M (mainly <i>Thermisto gaudichaudii</i>)	Copepods, cirripeds, mysids	Croxall and North (1988); Croxall et al. (1988)
Jan/Feb 1983	Bonaparte Point, Anvers Island	Regurgitations		85% M, 95% F			Obst (1985)
Jan/Feb 1982	Pointe Géologie, Adélie Land	Nest captures regurgitations (n = 7)	57% F, 39% M (not determined)	86% F, 37% M (<i>E.crys.</i>)	5% M, Hyperiidae 43% F, Gammaridae 57% F		Ridoux and Offredo (1989)
Jan/Feb 1982	Crozet Islands	Mistnet regurgitations (n = 15)	20% F, 12% M (larval fish)	54.7% M (<i>E.vall.</i>), 53% F, <i>E.tric.</i> 7% F, <i>Thys.sp.</i> 20% F)	15% M	Copepods (26% F, 5% M); cirripeds (67% F, 12% M); mysids, gastropods, chaetognaths, hydrozoa	Ridoux (1994)
Dec 1979–Feb 1980	King George Island, South Shetlands	Mistnet regurgitations (n = 82)	1% F (larval fish)	96% F (<i>E.sup.</i>), 78% F, <i>E.crys.</i> 6% F)	4% F		Wasilewski (1986)
Feb/Mar 1980	King George Island, South Shetlands	Chicks regurgitations (n = 21)		100% F			Wasilewski (1986)
1977–1980	Ross Sea	Mistnet at sea, stomachs (n = 28)	7% F (mainly <i>Pleuragramma antarcticum</i>)	61% F (<i>E.sup.</i>)	21% F (Lysianassidae)	50% F cephalopods	Ainley et al. (1984)

Results

Food content

Because the mistnet samples mainly young prebreeders, mistnet samples were analysed separately from samples from breeding birds throughout this study.

A total of 1,106 food samples were collected from regurgitating birds, 427 (39%) of which contained stomach oil only. The remaining 679 samples contained food items, which were analysed. Of these samples, 291 (43%) were obtained from mistnetted birds and a further 388 (57%) samples were regurgitations from adults and chicks from nests.

Of the 291 food samples collected at the net, a total of 285 (97.9%) contained crustaceans and 35 (12.0%) contained fish. Of the identified crustaceans, 86.5% were krill and 13.5% were amphipods.

Of the 388 identified food samples from nests, 328 (84.5%) contained crustaceans and 122 (31.4%) contained fish. The fish content was significantly higher ($\chi^2 = 35.3$, $df = 1$, $P < 0.001$) and the crustacean content lower ($\chi^2 = 34.0$, $df = 1$, $P < 0.001$) in samples from nests as compared to mistnet samples. Of the identified crustaceans in samples from nests, 83.3% were krill and 16.7% were amphipods.

Most samples were partly digested, and thus determination of prey at species level was in most cases not possible. All determined krill were *Euphausia superba*.

Of all 157 fish samples, only 11 could be identified as Myctophidae by the presence of the characteristic luminous organs, and the only 2 otoliths recovered from the regurgitations were of the myctophid *Electrona antarctica*. All other fish remained undetermined, as fish were always regurgitated without heads and thus without otoliths.

Several species of amphipods were determined. The most common species was *Cylopus magellanicus* Dana,

1852 (Hyperiididae). A further hyperid amphipod found only once was *Vibilia* sp. In 15 of 94 amphipod samples, individuals of more than 50 mm length were found, which were always too much digested to allow secure determination, but their large size hints at the planktonic amphipod *Eurythenes gryllus* (Lysianassidae, O. Coleman, personal communication). One sample also contained Phoxocephalidae (two individuals in March 2000).

Seasonal change

In breeding birds, the proportion of samples containing crustaceans decreased during the breeding season (Table 2) from 96.6% of the samples in January (incubation) to 79.9% in March (chick feeding). The decrease was statistically significant (ANCOVA, controlled for year, month as factor, $F = 7.79$, $df = 3,385$; $P = 0.006$). Chick-rearing birds at the same time increased the amount of fish taken (Fig. 2, ANCOVA, controlled for year, month as factor, $F = 13.04$, $df = 3,385$; $P < 0.001$) from 6.9% in January to 39.9% in March. The composition of samples obtained from the mistnet, in contrast, did not change over the season (ANCOVA, controlled for year, month as factor, for fish: $F = 0.60$, $df = 2,289$; $P = 0.438$; for crustaceans: $F = 2.01$, $df = 2,289$; $P = 0.157$). In these samples, the content of fish remained below 15% and crustaceans were consistently found in more than 96% of the samples (Fig. 2).

Within the identified crustaceans, there was a tendency for amphipods to increase in frequency during the season in proportion to krill. This was significant in nest samples, where 7.1% of identified crustacean samples were amphipods in January and 25.8% in March (multi-factor analysis, controlled for year, $F = 13.77$, $df = 1$, $P < 0.001$), and the respective residuals to 100% were krill samples. The occurrence of amphipods in nest samples in February was intermediate at 11.4%.

Annual change

Mistnet samples were taken in January and February 1996 ($n = 103$), February 1998 ($n = 39$) and January to March 1999 ($n = 149$). In all years and months, the occurrence of crustaceans was close to 100% in the mistnet samples, while fish occurred only occasionally (0–10%), except in 1996, when fish were present in 20% of the samples in January ($n = 76$) and 28% in February ($n = 25$).

Samples from breeding birds on their nests were collected in 1996 ($n = 84$), 1998 ($n = 19$), 1999 ($n = 89$) and 2000 ($n = 196$). The samples from 1998 were not included in the statistical analyses because of the small sample size. Crustaceans occurred in all years in more than 80% of the samples, and no statistical differences were detected in total crustacean content ($\chi^2 = 4.0$, $df = 2$, $P = 0.138$). The proportion of samples containing krill,

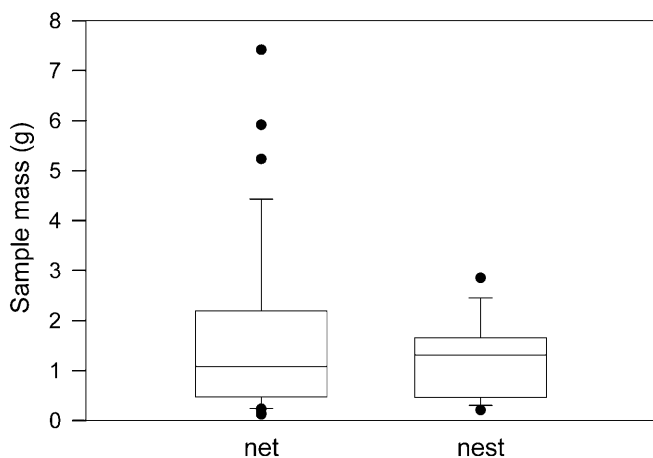


Fig. 1 Masses of food samples of Wilson's storm-petrels from the net ($n = 41$) and nest ($n = 9$) with median, 10th, 25th, 75th and 90th percentiles and outliers

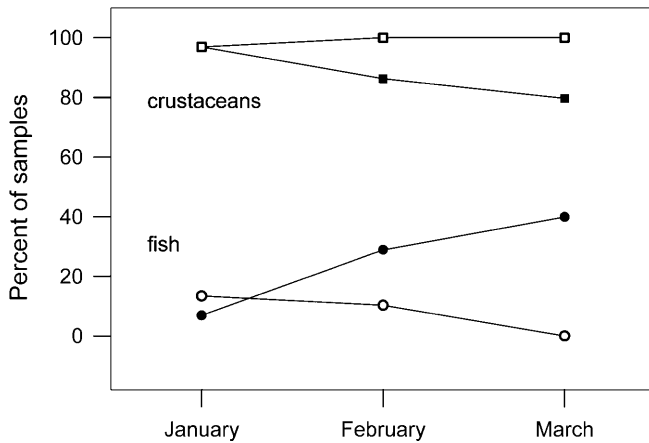


Fig. 2 Seasonal change in the food content of Wilson's storm-petrels on King George Island, South Shetland Islands for pooled samples from four breeding seasons. Unfilled circles and squares show the content of fish and crustaceans, respectively, in samples from the mistnet. Filled circles and squares were used for the content of fish and crustaceans, respectively, in samples from nests

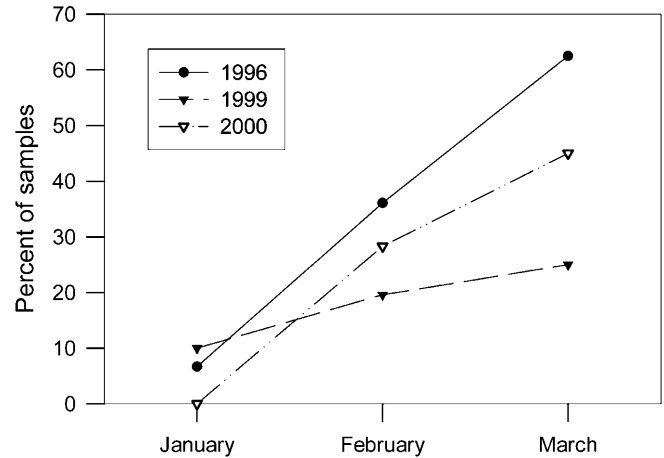


Fig. 3 Seasonal change in the proportion of samples containing fish in the diet of Wilson's storm-petrels on King George Island, South Shetland Islands, in three breeding seasons. All samples in the analysis were collected from breeding birds on their nests

in contrast, varied between years (Table 2, $\chi^2=6.1$, $df=2$, $P=0.048$). The presence of amphipods ranged from 6.0% in 1996 to 30.3% in 1999, and there were statistically significant differences between years (Table 2, $\chi^2=22.8$, $df=2$, $P<0.001$). In 1999, 81.5% of the amphipod samples were identified as *Cylopus magellanicus* (Hyperiididae), while this species did not occur in the samples of other years.

The fish content increased throughout the breeding season in all years (Fig. 3), but there were differences in the proportion of samples containing fish between years (Table 2, $\chi^2=7.4$, $df=2$, $P=0.025$).

Discussion

As in all previous studies (Table 1), krill represented the most important food source for Wilson's storm-petrels in the present analysis. Myctophids were also present in a large proportion of the samples, and amphipods were the third most important food item. There was large annual, as well as seasonal, variation in the diet composition.

Seasonal variation

The spatial and temporal distribution of krill, the main prey species, are characterised by large variability within and between seasons (Sarhage 1988; Siegel 1988; Siegel

et al. 1998). Krill abundance in the area west of the Antarctic Peninsula is typically low until early December and it decreases from early March (Siegel 1988). Peak abundance of krill was found in January and February, and the autumn decrease was dramatic. Croxall et al. (1984) analysed the seasonal change in food consumption of the seabird community of South Georgia and found that the consumption of krill showed a general increase from spring to late summer with some reduction thereafter, which corresponded to the krill abundance pattern. The breeding season of *O. oceanicus* extends far into the period of the decrease in krill described by Siegel (1988) in March and April. Therefore, there are two possible explanations for the seasonal variation in the diet composition observed in Wilson's storm-petrels in this study. Firstly, the birds may respond to a change in availability of prey types by taking the easiest available prey at any time throughout the season. This hypothesis predicts that the behaviour of breeding and non-breeding birds should be identical. Secondly, the prey choice of breeding birds may differ from that of non-breeders, according to the nutrient requirements for chick growth (selective prey choice hypothesis). This hypothesis predicts that breeders have a preference for certain types of food, and thus the behaviour of breeders (samples from nests) and non-breeders (samples from the net) should be different.

To test the above hypotheses, the contents of the nest and mistnet samples (the latter samples more than 80% non-breeders) were compared. In all years and months, the occurrence of crustaceans was close to

Table 2 Prevalence of food items (frequency of occurrence) in the diet of Wilson's storm-petrels in three breeding seasons

Year	Crustaceans	Krill	Amphipods	Fish	<i>n</i>
1996	81.0%	64.3%	6.0%	33.3%	84
1999	91.0%	78.7%	30.3%	20.2%	89
2000	83.2%	77.0%	12.2%	36.2%	196

100% in mistnet samples. The fish content was higher and the crustacean content lower in samples from breeding birds as compared to mistnet samples. Furthermore, there was a seasonal increase in fish and amphipods in the diet of breeders, while non-breeders were not found to change their diet composition during the same period. These results support the hypothesis of selective prey choice, indicating that the seasonal change in food items taken by Wilson's storm-petrels is not simply a response to the decreased availability of krill at the end of the Antarctic summer, but that the increase in the fish component of the diet is caused by selective prey choice of breeding birds. Similarly, incubating and non-breeding Cape petrels (*Daption capense*) took more crustaceans than chick-feeding birds at the same time (Creet et al. 1994). Adult guillemots (*Uria aalge*) took euphausiids, but at the same time fed their chicks exclusively with fish (Ainley et al. 1996b).

Why should breeding birds change their foraging behaviour? In order to survive and grow, chicks need energy and nutrients. The quality of a type of prey is thus determined by its digestibility, and energy and nutrient content. The availability of calcium, for example, may act as a constraint for the development of plankton-feeding seabirds such as little auks (*Alle alle*) chicks (Taylor and Konarzewski 1989). Having satisfied the energetic demands of parents and chicks, chick-provisioning birds should selectively choose more nutrient-rich food over nutrient-poor food (e.g. Harper et al. 1990; Roby 1991). In the present study, such a selectiveness was suggested. The chemical composition of the two main food sources of Wilson's storm-petrels, krill and fish, differs significantly (Clarke and Prince 1980). While krill and myctophid fish both had about the same calorific value, myctophids contained a nearly fivefold greater amount of calcium (0.70% of fresh matter) than krill (0.16%), as well as 1.5 times the amount of protein. By choosing high-lipid pelagic fish the storm-petrels can thus satisfy energy and nutrient demands better than with a pure crustacean diet.

Short-tailed shearwaters (*Puffinus tenuirostris*) are the only tube-nosed seabird on which there is year-round dietary information (Warham 1996). In this species, too, chick-feeding birds increased the fish content of the diet, but this has been interpreted as a response to changing food availability (Montague et al. 1986). This interpretation may need re-evaluation, because diet selection may also occur. Furthermore, pelagic fish tend to occur in the same swarms as planktonic crustaceans (Williams 1985) on which they feed, and thus the availability of the two prey types is usually correlated.

Annual variation

The overall food availability to Wilson's storm-petrels differed between the years (Quillfeldt 2001). Mean krill biomass density indices (g/1000 m³ wet weight) from scientific net sampling surveys in the Elephant Island

area during summer were the highest of the years of the diet analyses at 28.72 in 1996, lowest at 5.61 in 1999, and intermediate at 15.61 in 2000 (Siegel et al., in press). This is in line with results obtained from feeding rates of Wilson's storm-petrels (Quillfeldt 2001). The very poor food supply in 1999 resulted in chick mortality of 49% by starvation (compared with 15% in 1996 and 6% in 2000).

In the year of poor food supply, amphipods were taken in a much larger proportion of samples than in the good years (Table 2), suggesting that amphipods may be a less preferred alternative prey. In the mistnet samples in the later part of the poor food year, amphipods were present in similar proportions (38% in March 1999) to nest samples at the same time, suggesting that the shortage in krill and fish left both breeding and non-breeding birds without possibilities for prey choice.

However, the much higher proportion of fish in breeding birds as compared to non-breeders and in good food years as compared to poor food years suggest that pelagic fish were taken preferentially by birds provisioning chicks. Fish contributed to the chick diet as much or more than krill in the later part of chick feeding in years of good food supply (Fig. 3). Non-breeders regurgitated fish only occasionally (0–10%), except in 1996. It should be noted, however, that even in this year of apparently high availability of pelagic fish, the proportion of fish recorded in net samples was still much lower than in breeding birds. The differences between the breeding seasons thus support the selective prey choice hypothesis in these storm-petrels.

Several authors have pointed out the value of easily accessible marine predators for studies of the dynamics of marine food webs (Croxall et al. 1985; Cairns 1987; Ainley et al. 1995; Ainley et al. 1996a). However, most studies comprise only data from single breeding seasons, and parts of the season only. Studies of intra- and interannual variation in diet composition of plankton-feeding seabirds include some species of auks and penguins, and generally show that in times of better overall food availability, chick-feeding birds prefer energy- and nutrient-rich prey such as pelagic fish, while in periods of low food availability, birds switch to inferior prey such as demersal fish or amphipods. For example, Cassin's auklets fed on *Euphausia pacifica* during the breeding season, but switched to juvenile fish when they became available after a period of nutrient upwelling (Ainley et al. 1996a). At South Georgia, gentoo penguins (*Pygoscelis papua*) switched to low-lipid demersal fish during a krill shortage in 1994, while macaroni penguins (*Eudyptes chrysolophus*) took mainly amphipods (Croxall et al. 1999).

The results of the present analysis are in line with these findings, and suggest that diet studies of Wilson's storm-petrels may be useful in assessing the variability of the marine food web within the foraging zone of the species.

Acknowledgements I would like to thank Steffen Hahn, Tim Schmoll and Hans-Ulrich Peter for their help in the field. Oliver Coleman kindly determined the amphipod samples. I am grateful to Volker Siegel for unpublished krill biomass data. I received logistical support from the Alfred-Wegener Institute for Marine and Polar Research (Bremerhaven, Germany), the National Antarctic Institute of Argentina and Hapag Lloyd Seetouristik GmbH. This study was partly funded by grants provided by the German Science Foundation DFG (Pe 454/1 ff), Studienstiftung des Deutschen Volkes and the State of Thuringia, Germany (Landesgraduierstipendium). The study was carried out with permission of the Environmental Agency (Umwelt-Bundesamt) of Germany.

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