DIET AND FORAGING BEHAVIOUR OF THE BRITISH STORM PETREL *HYDROBATES PELAGICUS* IN THE BAY OF BISCAY DURING SUMMER

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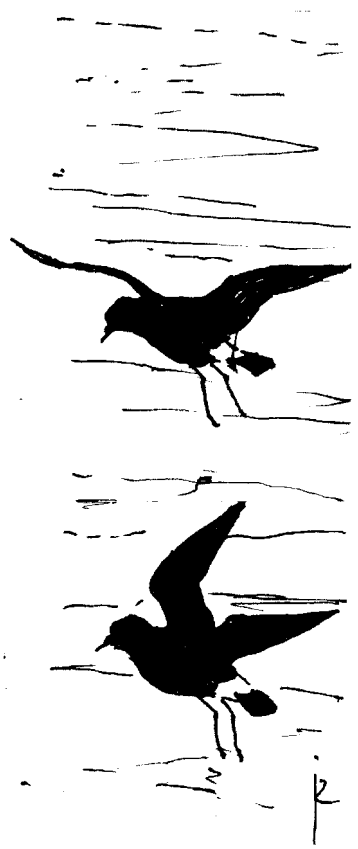

D'Elbée J. & G. Hémery 1998. Diet and foraging behaviour of the British Storm Petrel *Hydrobates pelagicus* in the Bay of Biscay during summer. Ardea 86: 1-10

The diet and the foraging behaviour of the British Storm Petrel *Hydrobates pelagicus* during the breeding period were studied from proventriculus contents obtained from adults belonging to two populations in the Bay of Biscay. The observed prey had various ecological affinities in two main groups. The first group were oceanic and neritic organisms, such as ichthyoplankton (Gadidae, Ammodytidae, Myctophidae) and microzooplankton (Copepoda, Euphausiacea, Chaetognatha, Anthomedusae, and meroplanktonic larvae), including bioluminescent species migrating vertically at night from deep water to the surface. The second group were littoral (Gobiidae) and suprabenthic intertidal organisms (mainly isopods Cirolanidae). 52% of total prey was zooplancton, and a further large percentage (37%) were littoral and intertidal benthic organisms. Our results show that British Storm Petrels regularly forage inshore during summer nights. This behaviour is not only linked to the necessity for breeders to feed their chick, but seems to be part of the foraging strategy of this species, enabling individuals to optimize their time-energy budgets. A relationship between the importance of inshore food resources and both colony location and colony size is suggested.

Key words: *Hydrobates pelagicus* - Bay of Biscay - breeding - diet - feeding - littoral foraging

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INTRODUCTION

Of the three breeding species of storm petrels (Hydrobatidae) of the north-eastern Atlantic, the British Storm Petrel *Hydrobates pelagicus* is the only one that breeds on the French coast. About 20 breeding sites have been censused on the Atlantic French coast, with a total of 460-500 breeding pairs in 1968-70 and approximatively 350 pairs in 1987-89 (Henry & Monnat 1981; Hémery 1994). In the northern part of the Bay of Biscay, the bulk of the population breeds in Finistère (Brittany), with Banneg archipelago harbouring important colonies. In the southern part of the Bay of Biscay, there are two colonies at Biarritz. In this locality, breeding numbers have declined from 78-80 pairs in 1976 to less than 20-30 pairs since 1987 (Hémery *et al.* 1986; Hémery 1991). These two colonies belong to the Cantabric (Atlantic coast of northern Spain) population which comprises at least 1300 breeding pairs in 29 colonies (Minguez *et al.* 1992; Minguez & Vigil 1995). This small species (30 g) comes ashore only during the breeding period (Apr-Oct). Storm petrels

are generally known as 'pelagic' seabirds that mainly feed on zooplankton (Witherby *et al.* 1965; Cramp & Simmons 1977; Prince & Morgan 1987). Ichthyoplankton is a major food resource, amounting to 69% by eaten volume (Linton 1978). It includes different families of epipelagic (Gadidae) or mesopelagic fishes (Gonostomidae, Sternoptychidae, Stomiatidae, Myctophidae). Theses deep-water species are usually bioluminescent, migrate vertically at night to the surface and are seldom found inshore. Pelagic Coelenterata, small Cephalopoda, Amphipoda, Euphausiacea and Copepoda are also frequently eaten by these birds (Cramp & Simmons 1977; Imber 1981; Vermeer & Devito 1988). The occurrence of these items in diet varies for each species, and also between different feeding localities. The diet of the British Storm Petrel appears to be composed of pelagic fish such as Herring *Clupea harengus* and Sprat *Sprattus sprattus* (Scott 1970; Cramp & Simmons 1977), and Cephalopoda (Voous 1949; 1954; Bierman & Voous 1950). Storm petrels also feed on whale carcasses, and offal and kitchen scraps from fishing boats (Cramp & Simmons 1977). The presence of British Storm Petrels inshore at night, even far away of breeding colonies, is well known (Maguire 1980). Scattered reports suggest occasional inshore feeding by day (Allsopp & Hume 1983; Stegeman 1990; Koerts 1992) but there has been no conclusive proof. We test the assumption that British Storm Petrels are inshore as well as pelagic foragers by examining diets of birds caught at night without tape-luring on colonies in the bay of Biscay (France). This is a part of the long-term study of storm petrel population dynamics in relation to prey abundance (Hémery *et al.* 1986; Hémery 1987).

STUDY AREA AND METHODS

The study was conducted at two breeding localities on the Atlantic French coast, in Brittany (Banneg archipelago; 48°50'N, 4°30'W) and in Aquitaine (Biarritz; 43°30'N, 1°30'W). Field work was carried out during the chick-rearing period (July and August 1984-91; Table 1). Like many other petrels (Warham 1990), British Storm Petrels are strictly nocturnal when on land: adults (breeders and non-breeding prospectors) were mist-netted at night when returning to the colonies. We never used tape-recorded calls to lure them. Arrivals started at about 23.00h, with captures ending at about 04.00h (local time). Most birds regurgitated spontaneously on handling. We placed their head in a broad-mouthed flask to recover their proventriculus contents. In addition, a plastic cover was put under the nets at Banneg Isles. The proventriculus contents collected by this technique were pooled. Three 'collective' contents were recovered and analysed in this study.

The extent to which prey are digested depends on both their body size and the hardness of their skeleton (endoskeleton in fish, exoskeleton in crustaceans). Microplankton is rapidly processed, being converted to an oily liquid, the orange coloration of which is due to the presence of carotenoids. These derived from copepods and crustacean larvae feeding on phytoplankton. Digestion takes longer for large prey such as fish. This is because both mechanical (the largest prey items must be broken down before entering the gizzard) and chemical (lysis of chromatophores, skeletons and otoliths) processes occur, the latter making prey identification difficult.

Proventriculus contents were stored in 70% ethanol to preserve the chalky parts of prey skeletons. Examination of samples with a stereomicroscope showed that the organisms eaten were often damaged and fragmented, making prey identification difficult. Consequently fish species were determined and measurements taken only from entire specimens or otoliths (Härkönen 1986). In some instances, the number of eye lenses enabled us to estimate the number of items. Sample masses are expressed as wet mass.

RESULTS

Over the five summers, 73 individual samples (25 at Biarritz, 48 at Banneg Isles), plus the three

Table 1. Number of proventriculus contents recovered at the two study colonies of Biarritz and Banneg. Samples obtained at Banneg in 1991 (*) include 3 'collective' samples.

Year	Biarritz	Banneg	Total
1984	-	4	4
1985	9	4	13
1986	4	-	4
1987	12	3	15
1991	-	41 *	40
Total	25	51	76

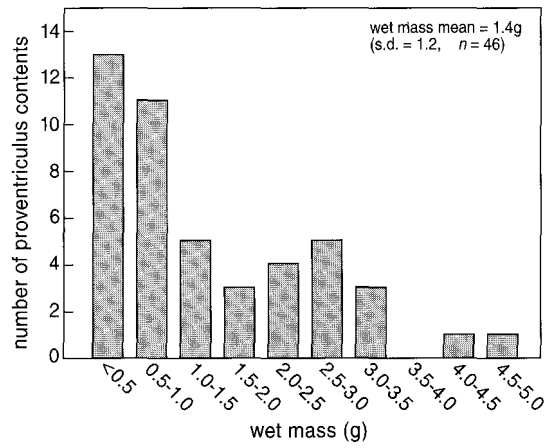

Fig. 1. Prey biomass (wet weight) distribution in proventriculus of British Storm Petrel.

'collective' ones from Banneg Isles, were recovered (Table 1). In total 339 items were recorded in the 76 samples, 216 in those from Brittany. 279 organisms were identified (Tables 2 and 3). Most of the 60 unidentified prey were fish larvae. At least one organism was found in 64 proventriculus contents, the remaining twelve containing stomach oil only. Each individual sample contained on average 3.6 organisms, of which 2.8 were identified. The 'collective' samples contained 76 organisms (Table 3). 32 different taxa were identified from the proventriculus contents, including coelenterates, nematodes, chaethognaths, copepods, isopods, ostracods, *Cypris* larvae (Cirripedia), decapod larvae, euphausiids, insects, fish larvae and plant seeds. Wet biomass was measured for 46 samples, the mean ± SD being 1.4 ± 1.2 g (n = 46) and the highest value 5.0 g (Fig. 1). Ichthyoplankton made up the bulk of the biomass eaten.

Table 2. Number of identified and unidentified prey items and number of fish of which the size could be assessed at the two study colonies, with 'collective' samples obtained at Banneg listed separately from samples taken from individuals.

	Number of prey items				abundance		Frequency		
	Biarritz	Banneg			(n = 73)		Biarritz	Banneg	
	ind.	ind.	coll.	Total	mean	max	ind.	ind.	coll.
Identified taxa, other than fish	17	150	47	214	2.3	18	8	35	3
Identified fish	21	16	28	65	0.5	7	9	11	3
Unidentified fish	9	50	1	60	1.8	6	7	33	1
Total prey items	47	216	76	339	3.6	18	17	44	3
Measured fish	25	21	23	69			14	13	3

Table 3. Abundance (number of prey items found), occurrence and mean number per sample of 32 prey taxa at Biarritz and Banneg. All data, except 'mean number' include those from 'collective' samples.

Phylum or				Biarritz		Banneg		
class	Taxa	*n* =	%	*n* =	freq.	*n* =	freq.	mean number
Cnidaria	*Velella velella*	4	1.4	4	4			0.05
Nematoda	(unidentified)	108	38.7	5	1	103	27	1.1
Ostracoda	(unidentified)	1	0.4			1	1	0.01
	Candacia armata	2	0.7			2	2	0.03
	Chirundina streetsi	1	0.4			1	1	< 0.01
	Pareuchaeta norvegica	1	0.4			1	1	< 0.01
	Corycaeus spp.	1	0.4			1	1	0.01
Copepoda	*Euterpina acutifrons*	1	0.4			1	1	0.01
	Centropages typicus	1	0.4			1	1	0.01
	Metridia lucens	1	0.4			1	1	0.01
	Temora longicornis	1	0.4			1	1	< 0.01
	Anomalocera patersoni	1	0.4	1	1			0.01
Cirripedia	*Cypris* larvae	1	0.4			1	1	0.01
Isopoda	*Eurydice pulchra*	54	19.4	2	2	52	18	0.6
	Eurydice affinis	9	3.2			9	4	0.08
Euphausiacea	*Nyctiphanes couchi*	5	1.8	2	2	3	3	0.05
Decapoda	*Zoea* larvae of Porcellanidae	1	0.4			1	1	0.01
	Culicidae	7	2.5			7	6	0.08
Insecta	Muscidae	5	1.8			5	5	0.05
	Hymenoptera	1	0.4			1	1	0.01
Chaetognatha	*Sagitta* spp.	2	0.7	2	1			0.03
Pisces	*Trisopterus minutus*	31	11.1			31	12	0.2
	Pomatoschistus spp.	10	3.6	5	4	5	2	0.08
	Aphia minuta	8	2.9	7	1	1	1	0.1
	Pomatoschistus microps	4	1.4			4	1	< 0.01
	Myctophiidae	3	1.1	2	1	1	1	0.04
	Gadidae	3	1.1	3	1			0.04
	Merluccius merluccius	2	0.7	2	2			0.03
	Pomatoschistus minutus	2	0.7	2	1			0.03
	Belone belone	1	0.4			1	1	< 0.01
	Ammodytiidae	1	0.4			1	1	< 0.01
Planta	seeds	6	2.1	1	1	5	3	0.08
Total		279	100	38	22	241	98	2.8

Ichthyoplankton

In total 65 of the 125 fish recovered from our samples were identified. They belonged to 11 genera or species and 4 families: Gadidae, Gobiidae, Myctophidae and Ammodytidae (Tables 2 and 3). Gadidae were neritic species, the most common of which being the Poor Cod *Trisopterus minutus* (31 specimens identified). The other species were of lesser importance (e.g. Hake *Merluccius merluccius* and some unidentified Gadidae).

The Poor Cod was exclusively recorded from the Breton proventriculus contents, the other Gadidae species being found at Biarritz. Gobiidae, all coastal species, were identified in 24 samples, including 16 *Pomatoschistus* spp. and 8 Transparent Goby *Aphia minuta*. Although *Pomatoschistus* spp. were found both at Banneg Isles and Biarritz, species distribution varied between the two localities, with Common Goby *Pomatoschistus microps* occurring only at Banneg Isles, and Sand Goby *P. minutus* at Biarritz. Three oceanic Myctophidae, bioluminescent species that migrate at night to the surface were found, occurring at the two localities, and one Sandeel (Ammodytidae) was found in a sample from Banneg Isles. The number of fish per proventriculus content averaged 1.32 (range 0-7; Table 2). However, few samples contained more than two fish. Diet composition varied between localities and individuals. Poor Cod seemed to be regularly eaten only at Banneg Isles (13 out of 31 identified prey, including the 3 'collective' contents; Table 3). 69 fish measurements were taken, from entire specimens or otoliths, including 34 Poor Cod. Body length for all species pooled averaged 39.9 ± 15.8 mm (range 5-92 mm).

Microzooplankton and associated organisms

A sizeable number of zooplanktonic organisms less than 1 mm (microzooplankton) were observed in our samples. There were 4 anthomedusae (By-the-wind Sailors *Velella velella*), 2 chaethognaths, 1 ostracod, 1 *Zoea* larva (Porcellanidae), 10 copepods of 9 different species and 5 euphausiids (*Nyctiphanes couchi*, the most common species being highly bioluminescent and carrying out nyctemeral migration). Their density and biomass were generally low. Apart from By-the-wind Sailors and chaetognaths, all these organisms were found in the regurgitates from Brittany. Three other categories of organisms were recorded. The most important group was nematodes; 38% of the total identified, and the only group in which mean abundance per sample exceeded one (Table 3). The maximum number in a sample was 12. The species were not determined. Nematodes are endoparasites of fish, being generally found in their muscles. The fish from the Banneg Isles area probably suffer high parasitism, since nematodes occurred in 27 out of the 51 samples. In this locality, the second group was terrestrial insects (Culicidae, Muscidae and Hymenoptera, totalling 13 specimens). Angiosperm seeds were found at the two localities (total 6 seeds in 4 samples).

Suprabenthic organisms

Most suprabenthic organisms were isopods *Eurydice* spp. (Cirolanidae). These crustaceans live in the upper ten centimetres of sand in the intertidal zone. *Eurydice pulchra* was the most common benthic-littoral prey with a total of 54 specimens founded in 20 regurgitates, including the 'collective' ones. However, it seemed more scarce in Aquitaine than in Brittany, where this species was found in 18 individual stomach contents (Table 3). The maximum numbers per sample were 11 (one case) and 6 (one case). The petrels from Banneg Isles preyed on *E. affinis*, a closely related species, although on a lesser scale (six specimens for three samples).

DISCUSSION

Zooplankton represented 52% of the number of prey eaten (Fig. 2), a low percentage compared with previous studies (Witherby *et al.* 1965; Cramp & Simmons 1977). 6.4% of the zooplankton were made up by continental slope species with strong oceanic affinities, such as the copepods *Chirundina streetsi* and *Pareuchaeta norvegica* (Rose 1933; D'Elbée & Castel 1991). 16.4% were represented by the two Gobiidae genera (*Pomatoschistus sp.* and *Aphia sp.*; 37% of identified fish), the copepod *Euterpina acutifrons*, and meroplankton, all of which are more coastal (Whitehead *et al.* 1986; D'Elbée 1995; D'Elbée & Castel 1995). Despite the small numbers found (2.9% of zooplanktonic prey), the occurence of neuston items shows that the sea-air interface is also exploited by storm petrels. In particular the

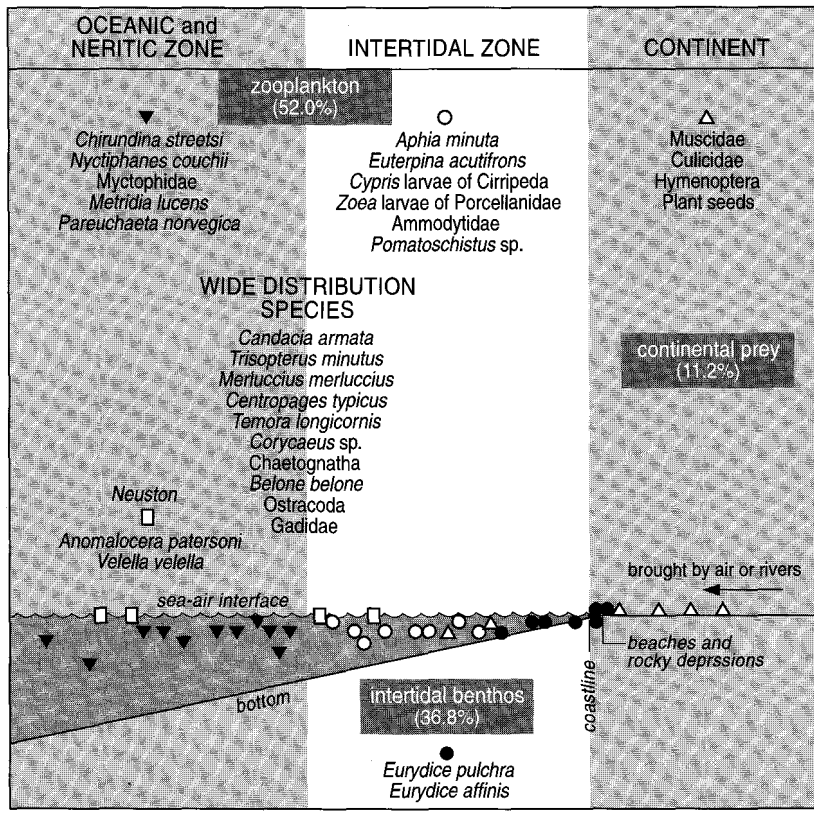

Fig. 2. Ecological affinities of the prey species eaten by the British Storm Petrel on the Atlantic coast of France. Percentages refer to prey abundance.

By-the-wind Sailor *Velella velella*, an open sea species (Hubbs 1948), is frequently eaten (Vermeer & Rankin 1984; Vermeer & Devito 1988).

Intertidal organisms were the second most important food resource by number (36.8% of prey eaten; Fig. 2) and belonged to two species, *Eurydice pulchra* and *E. affinis*. Both live in the intertidal zone only (Jones & Naylor 1967; Jones 1970; Macquart-Moulin 1992). They occurred in 24 samples, suggesting their frequent consumption by storm petrels. Both migrate vertically during the night when the tide is high. This 'pelagic' life lasts about two hours, being slightly longer in *E. pulchra* (Salvat 1966), which dominated in our samples. Such a behaviour might make their localization and their capture easier for petrels. The frequency of occurrence of these species in regurgitates, more especially at Banneg Isles, shows that birds routinely forage over intertidal sandy beaches during summer nights. Thus, British Storm Petrels exploit a large area over the continental shelf, including the continental slope, but also the intertidal zone. They may even forage in the estuaries situated near their breeding sites, as suggested by the occurrence of Transparent Goby in the stomach contents from Aquitaine, the two Biarritz colonies being less than 5 km far from the mouth of the Adour river. This species inhabits neritic polyhaline zones and also occurs in estuaries (Whitehead *et al.* 1986; Quéro *et al.* 1989). This phenomenon could explain the sightings of some Storm Petrels on land or near the shoreline (Witherby *et al.* 1965). Littoral feeding is also indicated by the occasional presence of terrestrial

Table 4. Occurrence of prey by foraging zone and ecological categories in the samples of the two localities (χ^2_1 = 0.09, n.s.).

Foraging zone	Ecological category	Biarritz		Banneg		Total	
		n =	%	*n* =	%	*n* =	%
Oceanic/ neritic	Ichthyoplankton (Gadiidae, Myctophiidae)	4		15		19	
	Microzoplankton	8		14		22	
	Total	12	60	29	53	41	55
Intertidal	Ichthyoplankton (Gobiidae)	6		4		10	
	Suprabenthic	2		22		24	
	Total	8	40	26	47	34	45
Total		20		55		75	

Table 5. Occurrence of each ecological category of prey in the samples of the two localities (χ^2_2 = 6.09, $P < 0.05$).

Ecological category	Biarritz		Banneg		Total	
	n =	%	*n* =	%	*n* =	%
Ichthyoplankton	10	50	19	35	29	39
Microzoplankton	8	40	14	25	22	29
Suprabenthic	2	10	22	40	24	32
Total	20		55		75	

items such as insects and angiosperm seeds (11% of items; Fig. 2).

In this study, fish were the bulk of the biomass eaten by the British Storm Petrel, despite the very large numbers of microzooplanktonic prey. Fish size showed a high intraspecific variability. The longest fish was a 92 mm specimen of Common Goby, whose exceptionally large size greatly skewed average body size. This is likely to be about the largest prey possibly eaten by the British Storm Petrel. Zooplankton represented 52% of items by numbers and fish only 36.8%, but fish are the most important energetic resource. The importance of microzooplankton compared with that of ichthyoplankton may be underestimated, the former being digested and converted into stomach oil more rapidly than the latter (Ashmole & Ashmole 1967; Vermeer & Devito 1988).

Exploitation of the intertidal zone by Storm Petrels was suggested at both colonies. Its relative importance compared with neritic and oceanic preys, did not differ significantly between the north and the south of the Bay of Biscay (Table 4; χ^2_1 = 0.088, n.s.). It appears, however, that the components of the diet in summer differed between the two localities: ichthyoplankton and microzooplankton are consumed significantly more at Biarritz than at Banneg Isles (Table 5; χ^2_2 =

6.09, $P < 0.05$). Suprabenthic and littoral crustaceans were preyed more frequently at Banneg. In more detail, at a specific level of Gadidae fish, Poor Cod is the sole species appearing in the samples in Banneg, other Gadidae being present only at Biarritz (Fisher's exact test, $P = 0.004$, two tailed). The differences found between Biarritz and Banneg Isles, and those between the French colonies and that of Skokholm (Scott 1970) may be due to different food availability around each colony, or to particuliar feeding habits of the birds. Temporal variability may also play a role when comparing samples collected different years.

CONCLUSION

Many previous studies using observation from boats or proventriculus content analyses have shown that the British Storm Petrel fed offshore exclusively (Prince & Morgan 1987; Vermeer & Devito 1988; Steele & Montevecchi 1994). The individuals which breed in the Bay of Biscay do forage far from land, but also over the intertidal zone in summer. These latter areas are close to breeding sites and exploited at night only, i. e. when nest reliefs and chick feeding occur. In this way, breeding adults may simultaneously decrease the distance (and perhaps the duration) of their foraging trips and increase the time devoted to food acquisition, so that their time-energy budget is optimized. Nocturnal inshore feeding may have two advantages. Prey density in offshore areas is very low, intertidal organisms are concentrated within a narrow coastal band. Beaches and rocky depressions also make the environment patchier. Here, since potential prey densities are important, olfaction enables birds to reach the best places more rapidly (Waldvogel 1989; Verheyden & Jouventin 1994). Secondly, storm petrels are less at risk from predators (mainly gulls *Larus* spp.; MacNeil *et al.* 1993; Hémery *et al.* 1995) when foraging near the coast at night. Coastal foraging would account for the high numbers of birds captured on shores, even distant from breeding sites, using playback of calls at night (Fowler *et al.* 1986).

ACKNOWLEDGEMENTS

We are greatly indebted to J.P. Cuillandre and the members of the Société pour l'Etude et la Protection de la Nature en Bretagne who collected the stomach contents at Banneg Isles; to E. D'Elbée, Director of the C.R.B.P.O. of Biarritz at the Musée de la Mer, who has been dealing with logistics for access to the colonies and petrel ringing for many years. We are very grateful to J. Bried who made helpful comments and translated manuscript into English. Thanks are also due to J.C. Vignes for field assistance at Biarritz. Two referees, K. Reid (British Antarctic Survey) and B. Zonfrillo (Glasgow University), have improved the text.

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SAMENVATTING

Het Stormvogeltje komt in Frankrijk aan de Atlantische kust op tenminste 20 plaatsen als broedvogel voor (460-500 paren in 1968-70, 350 paren in 1987-89). De kolonies worden net als elders alleen 's nachts door de broedvogels en bezoekende, niet-broedende exemplaren bezocht. Broedende vogels houden zich overdag schuil in de nestholtes. De pelagische levenswijze van het Stormvogeltje heeft tot de algemeen geaccepteerde veronderstelling geleid dat het meeste voedsel van deze zeevogels op open zee, ver uit de kust, wordt verzameld. Toch werden op verschillende plaatsen in Europa, en lang niet alleen rond de bekende broedkolonies, opvallend vaak Stormvogeltjes in mistnetten gevangen, al dan niet aangetrokken door het afspelen van op band opgenomen geluid. Deze vangsten en enkele verspreide waarnemingen van overdag langs de kust fouragerende exemplaren suggereren dat Stormvogeltjes misschien meer tijd in de kustwateren doorbrengen dan tot dusverre werd aangenomen en het is mogelijk dat het foerageergebied van Stormvogeltjes zich bijvoorbeeld 's nachts zelfs tot de kustwateren uitstrekt. De veronderstelling dat Stormvogeltjes niet alleen ver op zee fourageren werd onderzocht aan de hand van opgebraakte voedselresten van 's nachts in mistnetten gevangen Stormvogeltjes (zonder gebruik te maken van afgespeeld geluid) op twee locaties aan de Franse kust (Banneg Eilanden in Bretagne (48°50'N, 4°30'W) en Biarritz, Aquitaine (43°30'N, 1°30'W) aan de kust van de Golf van Biskaje).

Van in totaal 339 verzamelde prooiresten konden er 279 worden geïdentificeerd (Tabel 2-3). In totaal konden 32 taxa worden onderscheiden, waaronder Bazaantjes *Velella velella* (Coelenterata), rondwormen (Nematoda), pijlwormen (Chaethognatha), roeipootkreeftjes (Copepoda), zeepissebedden (Isopoda), mosselkreeftjes (Ostracoda), rankpotigen (Cirripedia), krill (Euphausiacea), larven van tienpotigen (Decapoda), vis (Ichthyoplankton) en plantenzaden. Ichtyoplankton vormde de belangrijkste voedselsoort in massapercentages. Zooplankton werd aanmerkelijk minder vaak aangetroffen dan bij eerdere dieetstudies van deze soort. Zowel in Bretagne als Biarritz was net iets meer dan de helft van de geïdentificeerde prooien van Oceanische/Neritische herkomst. Een zeer aanzienlijke fractie bleek echter afkomstig uit de intergetijdegebieden (Tabel 4). Het fourageren in de kustwateren kan een aantal belangrijke voordelen hebben voor Stormvogeltjes. De van open zee terugkerende Stormvogeltjes kunnen in de kustzone aanvullend voedsel verzamelen, waardoor ze tegelijk de duur en lengte van de voedselvlucht naar open zee kunnen beperken en meer tijd kunnen spenderen aan het zoeken van voedsel. De prooidieren in de kustwateren komen plaatselijk in veel hogere concentraties voor dan op open zee en deze 'patches' kunnen wellicht vrij eenvoudig op de geur worden opgespoord. De duisternis maakt dat de vogels weinig risico's lopen voor toch meestal dagactieve predatoren zoals meeuwen. (CJC)

Received 15 September 1997, accepted 12 February 1998
Corresponding editor: Kees (C.J.) Camphuysen