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FEEDING ECOLOGY AND BODY SIZE DEPENDENCE ON DIET OF THE SOOTY SHEARWATER, *PUFFINUS GRISEUS*, IN THE NORTH PACIFIC

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Abstract: The diet of the Sooty Shearwater (*Puffinus griseus*) was examined by using a total of 1139 stomachs of the bird sampled during April-October, 1982, 1985-1989. Of all stomachs, 586 were empty. Predominant prey species was the Japanese sardine (*Sardinops melanosticta*), the wet weight percentage of which was 57.9% in the Confluence Zone, April-May, and 55.8% in the Subarctic Current, June-September. Other identified prey species were the Pacific saury (*Cololabis saira*), squid (*Berryteuthis anonychus*), pelagic barnacle (*Lepas fascicularis*), and jellyfish (*Vellela lata*). In the Subtropical Zone, June-July and the Transition Domain, June-October, the relative importance of squid and pelagic barnacle as prey items for the bird increased in both frequency of occurrence and weight.

The importance of fish in the diet increased with body weight increment of the bird, while that of squid and barnacle decreased. This trend was remarkably observed in the Subtropical Zone and the Transition Domain. It is, therefore, suggested that the diet of the bird changes with their growth.

1. Introduction

Over the North Pacific Ocean, the Sooty Shearwater occurs from April to November, and plays an important role in the pelagic marine ecosystem as a top predator (OGI *et al.*, 1981; GUZMAN and MYRES, 1983; BRIGGS and CHU, 1986, 1987). Total population of the Sooty Shearwater is poorly known, but probably between 20 and 40 millions. If this is true, the total biomass attains to 16000-32000 tons. Thus the Sooty Shearwater is one of the most dominant species in the North Pacific avifauna in summer, which accounts for 20-30% of the total seabirds density, showing 30-40% of their biomass in western and central subarctic regions (SANGER and AINLEY, 1988).

Though several studies of feeding habits of the Sooty Shearwater have been done mainly in neritic habitats (SANGER and BAIRD, 1977a, 1977b; SANGER *et al.*, 1978; SANGER, 1983; BALTS and MOREJOHN, 1977; BROWN *et al.*, 1981; CHU, 1984; JACKSON, 1988), their feeding habits in pelagic waters are poorly known except for OGI's (1984) study in the western subarctic North Pacific Ocean. During their stay in the subarctic North Pacific, their body weight ranges widely from 500 to 1300 g (CHU, 1984; OGI *et al.*, 1981). Assuming that their body weight exhibits the growth stages of the bird, the birds were grouped into three size classes, and the diet was analyzed for each class.

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2. Materials and Methods

A total of 1139 stomachs of the birds, which were incidentally entangled in gill net sets for salmon and squid, were sampled in offshore waters of the North Pacific Ocean from 24 April to 24 October 1982, 1985–1989 (Fig. 1).

The sampling stations were grouped into the following four oceanographic areas based on smapling months and oceanographic structures (FAVORITE *et al.*, 1976; Hokkaido Univ , 1983, 1986–1990; OGI, 1984; WAHL *et al.*, 1989): CNFL, Confluence Zone (April–May); STRP, Subtropical Zone (June–July); TRND, Transition Domain (June–October); SARC, Subarctic Current (June–September).

We examined 1139 stomachs, 586 of which were empty. Then we used 553 stomachs with contents to clarify the food habits of the bird. Each of all stomach contents was sorted and weighed according to the following eleven items: Japanese sardine (*Sardinops melanosticta*), Pacific saury (*Cololabis saira*), lantern-fish (Myctophidae), unidentified fish, squid. barnacle, jellyfish, euphausiid, amphipod, mysid, and digested matter. Percentage frequency of occurrence and wet weight percentages in each area were calculated for all items, except for digested matter. Furthermore, all birds in each oceanographic area were classified into three body weight classes: small-sized (under 800 g), medium-sized (800–1000 g), larger-sized birds (more than 1000 g), and the diet was analyzed for each class.

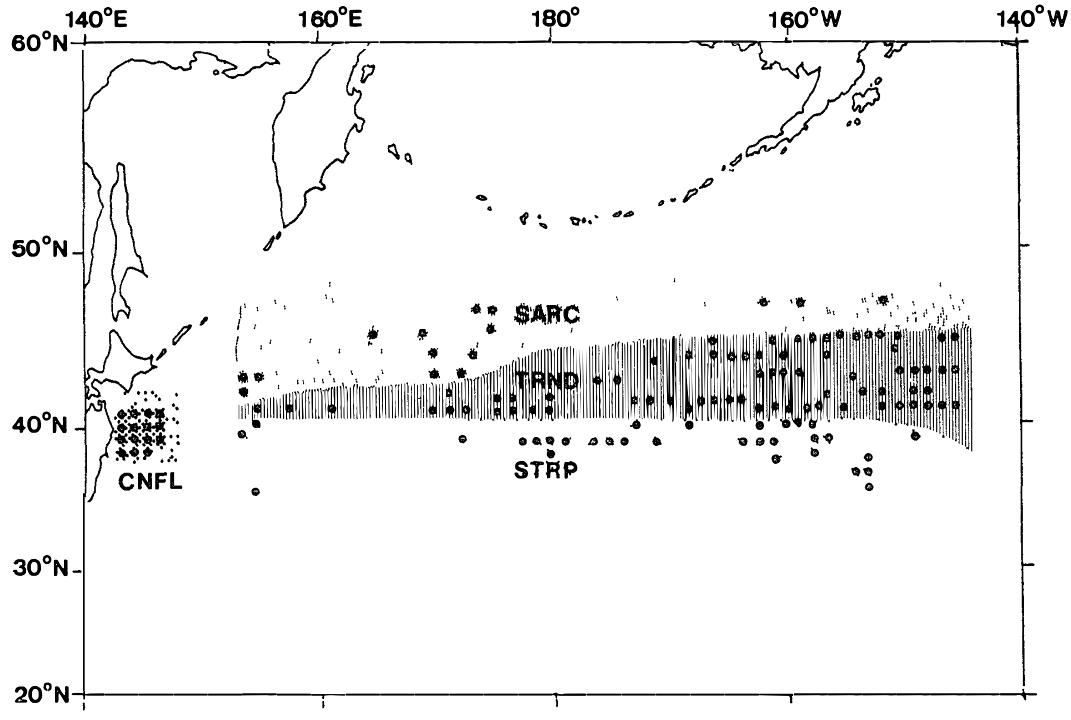

Fig 1 Sampling locations for Sooty Shearwaters in the North Pacific in 1982, and 1985–89. CNFL, Confluence Zone during April–May, STRP, Subtropical Zone during June–July, TRND, Transition Domain during June–October, SARC, Subarctic Current during June–September

Table 1. Percentage frequency of occurrence and wet weight percentages of prey items except for digested matter in the stomachs of the Sooty Shearwater by sea area and month.

Prey item		Confluence Zone, April–May (N=193)				Subtropical Zone, June–July (N=123)			
		n	% Frequency of occurrence	w (g)	% Wet weight	n	% Frequency of occurrence	w (g)	% Wet weight
Fish	Japanese sardine *Sardinops melanosticta*	44	22 80	1590.47	57 87	1	0 81	24 49	2 76
	Pacific saury *Cololabis saira*	1	0 52	40 40	1.47	8	6 50	111 97	12 61
	Lantern-fish	1	0 52	7 10	0 26	1	0 81	19 11	2 16
	Unidentified fish	142	73 58	1077.08	39 19	39	31 71	304 09	33 83
	(Total fish)	174	90 16	2715 05	98 79	43	34 96	459 66	51 37
Squid		3	1 55	32.20	1 17	28	22 76	474 44	30 90
Barnacles									
Lepas fascicularis		—	—	—	—	32	26 0	134 99	15 20
Jellyfish									
Vellela lata		3	1 55	0 20	0 01	9	7 32	20 22	2 27
Euphausiids		1	0 52	0 60	0 02	1	0 81	0 37	0 04
Amphipods		—	—	—	—	—	—	—	—
Mysids		1	0 52	0.05	—	2	1 63	1 89	0 21
Digested matter		22		15.18		27		55 95	

Prey item		Transition Domain, June–October (N=205)				Subarctic Current, June–September (N=32)			
		n	% Frequency of occurrence	w (g)	% Wet weight	n	% Frequency of occurrence	w (g)	% Wet weight
Fish	Japanese sardine *Sardinops melanosticta*	3	1.46	81.66	7 06	5	15 63	203 57	55 76
	Pacific saury *Cololabis saira*	3	1 46	64.58	5.59	1	3 13	3 41	0 93
	Lantern-fish	1	0 49	12 21	1 05	—	—	—	—
	Unidentified fish	63	30 73	437.54	37.83	15	46 88	154 27	42 27
	(Total fish)	70	34.15	595.99	51.53	19	59.38	361 28	98 96
Squid		59	28.78	385.56	33.33	2	6 25	3 51	0 94
Barnacles									
Lepas fascicularis		17	8.29	135.71	11.74	1	3.13	0 04	0 01
Jellyfish									
Vellela lata		10	4 88	19 82	1.72	—	—	—	—
Euphausiids		5	2.44	9.95	0.86	—	—	—	—
Amphipods		2	0 98	0 92	0.08	1	3 13	0 29	0 08
Mysids		7	3 41	8 62	0 75	1	3 13	0 02	0 01
Digested matter		60		100.46		12		8 78	

n, the number of stomachs in which each item occurred; w (g), the weight of each item.

3. Results

3.1. Geographical variation in diet

Fish was the dominant prey for the Sooty Shearwater in all oceanographic areas in the North Pacific (Table 1). Interestingly, the Japanese sardine (*Sardinops melanosticta*) and the Pacific saury (*Cololabis saira*), both of which are the seasonal migratory fish between the subtropical and the subarctic areas, constituted the most important prey for the bird. Particularly, in CNFL and SARC, sardines dominated the diet. Squid (*Berryteuthis anonychus*) was a secondly important food item in STRP and TRND, decreasing with latitudinal increment. The importance of pelagic barnacle (*Lepas fascicularis*) and jellyfish (*Vellela lata*) which are typical organisms in the subtropical and tropical areas, increased with decreasing latitude.

Indices of the percentage similarities for diet composition between the four oceanographic areas using MORISITA's (1959) formula are shown in Table 2. Categories used for the calculation were total fish, squid, barnacle, jellyfish, euphausiid, amphipod, and mysid. Highest indices of percentage similarities were observed in the following two pairs: CNFL vs SARC, and STRP vs TRND The main prey contributing to similarities was fish in the above two pairs However, in the second pair (STRP vs TRND), squid and barnacle except for fish were contributing to the high similarity

3 2. Prey size of the Sooty Shearwater

Identified fresh preys taken by the Sooty Shearwaters are shown in Table 3. Body length of sardines ranged 115–180 mm with an average of 138 mm (n=22), which cor-

Table 2. MORISITA's *indices of percentage similarities for diet composition of the Sooty Shearwater by wet weight percentages among four areas*

Areas			Cλ
Confluence Zone	vs	Subtropical Zone	0 754
Confluence Zone	vs	Transition Domain	0 751
Confluence Zone	vs	Subarctic Current	1 000
Subtropical Zone	vs	Transition Domain	0 997
Subtropical Zone	vs	Subarctic Current	0 753
Transion Domain	vs	Subarctic Current	0 749

Table 3 Length (mm) of individual prey of major prey species taken by the Sooty Shearwaters

Prey Species	Body length				Dorsal Mantle length			
	N	Mean	SD	Range	*N*	Mean	SD	Range
Sardinops melanosticta	22	138 45	19 77	115 18–179 73	—	—	—	—
Cololabis saira	5	119 63	27 89	79 00–158 48	—	—	—	—
Berryteuthis anonychus	—	—	—	—	6	78 32	6 68	68 94–87 26
Lantern-fish A	1	77 57	—	—	—	—	—	—
B	1	71 46	—	—	—	—	—	—

Table 4. Diet composition by wet weight percentages for each body size class of the Sooty Shearwater by sea area and month.

Area*	Month	Size Class (g)	No of Stomachs	Wet weight percentages**										
				SAR	SAU	LAN	uif	F	Sq	Ba	Je	E	A	My
CNFL	Apr -May	BW<800	43	54 84	—	1 12	42 48	98 43	1 54	—	0 02	—	—	0.01
		800≦BW<1000	148	58 80	1 92	—	38 19	98 91	1 06	—	—	0 03	—	—
		1000≦BW	2	—	—	—	100 00	100 00	—	—	—	—	—	—
STRP	Jun.–Jul.	BW<800	46	—	—	8 54	31 25	39 78	42 30	16 58	1 13	0 16	—	0 04
		800≦BW<1000	72	3 84	16 94	—	33 63	54 40	27 47	15 35	2 78	—	—	—
		1000≦BW	5	—	13 07	—	65 64	78.71	15 39	—	—	—	—	5.90
TRND	Jun -Oct.	BW<800	113	4 88	7 25	2 11	36 41	50 65	36 48	7 32	2 45	1 73	0 15	1 23
		800≦BW<1000	83	4 85	4 20	—	41 98	51 03	31 27	17 09	0 32	—	0 01	0.28
		1000≦BW	9	72.17	—	—	—	72 17	14 82	2 60	10.41	—	—	—
SARC	Jun -Sep.	BW<800	8	61 87	2 47	—	35 45	99 79	—	—	—	—	0 21	—
		800≦BW<1000	22	43.35	—	—	54 63	97 98	1 99	0 02	—	—	—	0.01
		1000≦BW	2	82.55	—	—	17 45	100.00	—	—	—	—	—	—

* CNFL, Confluence; STRP, Subtropical Zone; TRND, Transition Domain; SARC, Subarctic Current.

** SAR, Japanese sardin; SAU, Pacific sauriy, LAN, Lantern-fish; uif, unidentified fish; Sq, squid; E, euphausiids; A, amphipods; Ba, barnacles; Je, jellyfish, My, mysids; F, fish total.

respond to late immature stage (HIRAMOTO, 1981) Sauries ranged 79–158 mm in body length with an average of 120 mm (n=5), which also correspond to young stage (ODATE and HAYASHI, 1977). Dorsal mantle length of *Berryteuthis anonychus* ranged 69–87 mm with an average of 78 mm (n=6), belonging to adolescent or more progressed stages (KUBODERA and JEFFERTS, 1984)

3.3. Diet-body weight relation

There was a clear dietary change along with the body size increment in STRP and TRND, where squid and barnacle were more important food items (Table 4). The contribution of sardine and saury in diet increased with body weight increment, while squid and barnacle decreased Otherwise, there was a slight change in the CNFL and SARC, where fish dominated overwhelmingly the diet, constituting 98.8% and 99 0%, respectively Highest indices of percentage similarities between three body size classes were observed in these two areas (indices of the following all pairs, 0 999; small vs medium-sized birds, small vs large-sized birds, and medium vs large-sized birds). Therefore, the diet-body weight relation was not detected

4. Discussion

4 1 Feeding ecology of the Sooty Shearwater

The Sooty Shearwater feeds mainly on abundant planktivorous fish in the neritic habitats: capelin (*Mollotus villosus*) ranging 80–137 mm in the Gulf of Alaska (SANGER and BAIRD, 1977a, 1977b; SANGER *et al.*, 1978; SANGER, 1983), and juvenile rockfish (*Sebastes* spp.) and northern anchovy (*Engraulis monrdax*) in the sea areas off California (CHU, 1984)

In this study, the most important prey of the Sooty Shearwater was also planktivorous fish: immature sardines and sauries ranging 115–180 mm and 79–158 mm, respectively. These fishes are highly abundant commercial fishes in CNFL, and the subtropical and subarctic waters in the North Pacific (ODATE, 1977; KENYA, 1982; HIRAMOTO, 1981; KOUNO, 1984). Though OGI (1984) reported that sauries were the most important prey in the northwestern Pacific during the period from 1975 to 1980, our results showed that sardines were more important prey than sauries during the period from 1982 to 1989. It is suggested that the high abundance of sauries should have been replaced by that of sardines in the North Pacific In fact, catch of sauries by Japanese fisheries decreased during OGI's (1984) study period, while that of sardines increased during the period in this study (Nourin suisan sho (Min Agr Forest Fish Japan), 1984, 1990).

Sardines dominated the diet in CNFL, April–May and the contribution of sardine in the diet increased with latitudinal increment (Table 1) Immature sardines migrate northward in spring posterior to adults and southward in autumn (HIRAMOTO, 1981; KOUNO, 1984). The northern distribution limit of the sardines was assumed to coincide with the 8°C isotherm of surface water temperatures and their accumulations were usually observed only at 10–20°C of surface water temperatures in the northwestern Pacific (KENYA, 1982) On the other hand, the Sooty Shearwater also migrates northward in spring and southward in autumn. High density areas of the birds were observed from 9 to 13°C of the surface water temperatures in the North Pacific (OGI, 1984). It is, therefore, suggested that the latitudinal migration of the Sooty Shearwater should coincide with that of sardines and sauries judging from the high contribution of them in the diet as reported by OGI (1984) and this study.

4.2. Occurrence of barnacles

Pelagic barnacles (*Lepas fascicularis*) are important food organisms in STRP and TRND (Table 1). Foraging behavior of the Sooty Shearwater has been proposed as "pursuit diving" and "pursuit plunging" (ASHMOLE, 1971), but we propose another foraging behavior "grazing" in this study as OGI (1984) observed that the Sooty Shearwater grazed sessile organisms, such as pelagic barnacles on floating matter.

4.3. Body size dependence on diet

The Sooty Shearwater has not any morphological characteristics for age determination. Body weight of the bird has a very wide range compared with other external measurements (body length, wing length, tarsus length, etc.), the variation of which is small and gives no information on the growth stages (OGI *et al.*, 1981; CHU, 1984). Assuming that their body weight has to exhibit the growth stages, the birds were grouped into the three body weight classes based on the following hypotheses

If the Sooty Shearwaters feed little during the long migration from the southern hemisphere to the northern hemisphere, the immature birds which are poorly experienced in migration must consume more energy than adults. In this case, though the body weight of immature birds is similar to that of adults when they leave the breeding area (WARHAM *et al.*, 1982), they should have decreased in body weight as compared with the adults when the both reached the subarctic North Pacific waters. This phenomenon was also reported in some birds such as Short-tailed Shearwaters (OKA, pers. commun. 1991) and Pacific Golden-Plovers (JHONSON *et al.*, 1989). Therefore, most of small-sized and large-sized birds in the North Pacific should be immature birds and adults, respectively. In autumn body weight of breeding adults increases for pre-migratory fattening for migratory success (CHU, 1984), and so they are heavier than immature birds. Therefore, most of large-sized birds should be adults in pre-migratory period to the southern hemisphere. We have given proof of this, based on the relation between development of reproductive organs and body weight (SHIOMI, unpubl. data). The difference in diet between the small-sized birds (under 800 g) and large-sized birds (more than 1000 g) shows the age-related difference in diet depending on growth stages.

Generally the immature bird has less ability to dive or take food than the adult bird. In fact, GREIG *et al.* (1983) and WEATHERS and SULLIVAN (1991) reported different foraging skills and efficiency in adults and immature Herring Gulls (*Larus argentatus*), and Yellow-eyed Juncos (*Junco phaeonotus*), respectively. If this phenomenon could be applied to the Sooty Shearwater, the immature bird has to be a less effecient predator of sardines and sauries than the adult birds in the feeding spot where prey organisms are less abundant. As a result, in this case there may be no dietary overlap between immature birds and adults. Therefore, the immature bird (small-sized birds) would feed mainly on small squid and less mobile floating organisms such as pelagic barnacles or jellyfish in STRP and TRND. On the contrary, when the prey organisms are quite abundant in the foragoing areas, the dietary overlap between immature birds and adults of Sooty Shearwaters becomes the same as shown in CNFL and SARC (Table 3)

On the other hand, the breeding adult has a tendency to take higher caloric preys, such as sardines and sauries, for pre-migratory fattening in southward pre-migratory and migratory periods as reported by CHU (1984). Therefore, the breeding adult would select the higher-caloric prey to store fat for long migration to the southern hemisphere.

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