Feeding ecology of the Sooty Shearwater in the western subarctic North Pacific Ocean[1]

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1. Abstract

Stomach contents from 173 Sooty Shearwaters (*Puffinus griseus*) taken in deep, oceanic waters of the western subarctic North Pacific from spring to autumn, 1975–80 (except for 1976) were examined. By weight, fish was the most important food item (83.1%), particularly Pacific saury (*Cololabis saira*) which comprised 69.7% of stomach contents. Squid, the next most important prey, may have been underestimated due to a rapid rate of digestion. Squid increased and the saury decreased in importance with increasing latitude.

The prevalence of saury in the diet, by weight, shifted northwards in oceanographic areas with time: in June 78.1% in the Subtropic Region and 88.1% in the Transition Domain; in July 26.6% in the Transition Domain; in August 84.4% in the Transition Domain, 62.9% in the Subarctic Current, and 30.1% in the Alaskan Stream; in September and October 99.2% in the Subtropic Region, 89.0% in the Transition Domain, and 88.1% in the Subarctic Current. The prevalence of squid in the diet did not change with time. Sea surface temperatures (SST) ranging from 9 to 13°C at localities where numerous Sooty Shearwaters were often observed feeding were also favoured by shoals of saury; both the shearwater and saury moved northwards as SSTs warmed. The movements of Sooty Shearwaters in pelagic subarctic waters of the North Pacific may be related directly to change in the physical environment and to the availability of suitable prey.

2. Résumé

Nous avons examiné le contenu stomacal de 173 Puffins fuligineux (*Puffinus griseus*) recueillis dans les eaux pélagiques de l'ouest de l'océan Pacifique Nord subarctique, du printemps à l'automne, de 1975 à 1980 (sauf 1976). En poids, les poissons étaient l'aliment prédominant (83,1 %). Nous reconnaissions surtout le balaou japonais (*Cololabis saira*) qui constituait 69,7 % du contenu stomacal. Le calmar, la deuxième proie en importance, peut avoir été sous-estimé à cause de sa rapidité de digestion. Plus nous allions au nord, plus l'importance du calmar augmentait et plus celle du balaou diminuait.

Avec le temps, la prédominance, en poids, du balaou dans le régime changeait à mesure que nous montions vers le nord dans les zones océanographiques : en juin, 78,1 % dans la région subtropicale et 88,1 % dans le domaine de transition; en juillet, 26,6 % dans le domaine de transition; en août, 84,4 % dans le domaine de transition, 62,9 % dans le courant subarctique et 30,1 % dans le courant de l'Alaska; en septembre et octobre, 99,2 % dans la région subtropicale, 89,0 % dans le domaine de transition et 88,1 % dans le courant subarctique. La prédominance du calmar dans le régime ne changeait pas dans le temps. Les températures de la surface de la mer, se situant entre 9 et 13°C à des endroits où nous observions souvent de nombreux Puffins fuligineux en train de se nourrir, étaient aussi préférées par les bancs de balaous. Les puffins et les balaous se déplaçaient vers le nord à mesure que la surface de la mer se réchauffait. Les déplacements des Puffins fuligineux dans les eaux subarctiques pélagiques du Pacifique Nord peuvent être directement reliés aux changements dans le milieu physique et à la disponibilité des proies appropriées.

3. Introduction

The Sooty Shearwater (*Puffinus griseus*) migrates to the northern hemisphere after breeding in the southern hemisphere (Loomis 1921, Phillips 1963, Shuntov 1972), and in the subarctic regions of the North Pacific Ocean during summer it becomes one of the most important components of the marine avifauna. The species' feeding habits while in the northern hemisphere have been studied fragmentarily, and largely in neritic habitats (Wiens and Scott 1975; Baltz and Morejohn 1977; Morejohn *et al.* 1978; Sanger and Baird 1977*a*, 1977*b*; Sanger *et al.* 1978; Brown *et al.* 1981).

In the present study the prey of Sooty Shearwaters was determined for pelagic waters of the subarctic western North Pacific Ocean from June to October. The occurrence of this bird was then viewed in relation to oceanographic conditions and the distribution and migration of prey.

4. Materials and methods

Stomach contents from 173 Sooty Shearwaters that were incidentally entangled in gill nets set for salmon (*Onchorhynchus* spp.) tuna (Family Scombridae), and squid were used in this study. Stomach samples were collected in 1975, and 1977–80, from the following research vessels: TS *Oshoro Maru* (Os), TS *Hokusei Maru* (Ho), RV *Hakuman Maru No. 21* (Hb), RV *Shunyo Maru* (Sh), TS *Hokuho Maru* (Hk), RV *Hoyo Maru No. 67* (Hy), and RV *Hatsue Maru No. 62* (Ht).

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To determine the overall seasonal composition of the diet, sampling stations were grouped into four periods (Fig. 1, Table 1). The number of birds sampled in respective periods were as follows: 51 from 13 stations in June, 50 from 8 stations in July, 35 from 11 stations in August, and 37 from 14 stations in September and October. One bird was also caught in April.

Stomach contents in the proventriculus and gizzard of each shearwater were identified and grouped into the following categories: fish, squid, euphausiids, amphipods, shrimp, pelagic barnacles, jellyfish, unidentified digested matter, and other materials. The latter were further classified into fish otoliths, cephalopod beaks, pebbles, vegetable matter (including seaweed, grass seed, and small pieces of wood), and plastic particles.

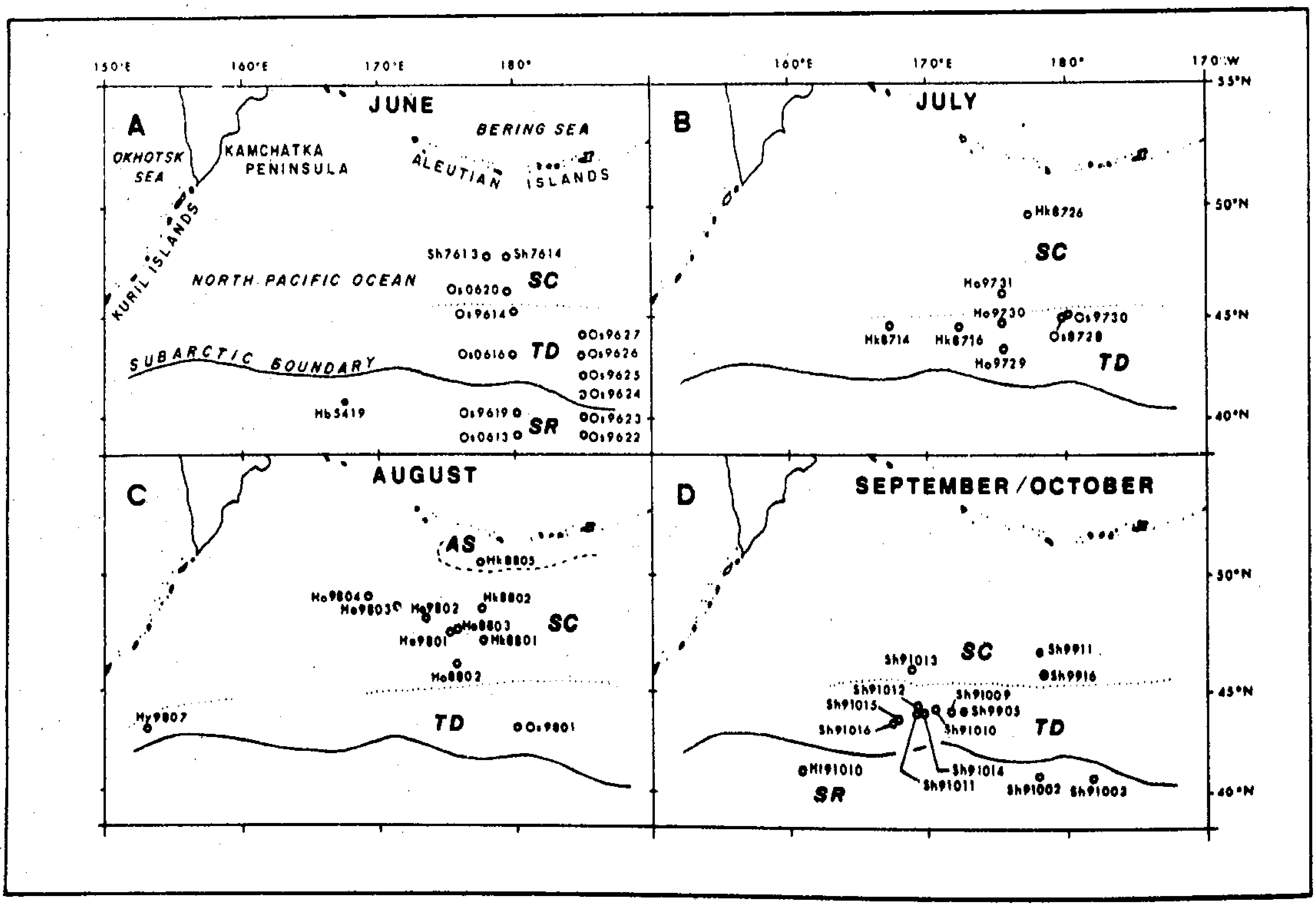
All whole items were weighed wet to the nearest 0.001 g. When possible, items were identified to species. Stomach contents were preserved in neutral formaldehyde solution for up to 6 months, so some otoliths disappeared and others became corroded beyond identification. Eight intact otoliths from three stomachs were identified to family level.

Sampling stations were grouped according to four oceanographic areas (Fig. 1) based on the literature (Dodimead *et al.* 1963; Favorite 1967; Hokkaido Univ. 1976, 1978–82; Kikuchi and Tsujita 1977; Favorite *et al.* 1976; and Ogi 1980) and longitudinal sections of temperature profiles, as follows: along longitude (long.) 167°30′E from latitude (lat.) 39°50′N to 52°30′N during 18–30 April 1975 by RV *Habomai Maru No. 21* (Hokkaido Univ. 1976); along long. 180° from lat. 39°N to 46°N during 12–20 June 1979 and along long. 175°W from lat. 39°N to 45°N during 21–28 June 1979 by TS *Oshoro Maru* (Hokkaido Univ. 1980); along long. 175°30′E from lat. 39°54′N to 47°32′N during 26–31 July 1979 (Hokkaido Univ. 1980) and *ca.* long. 170°E from lat. 35°N to 47°41′N during 28 July – 5 August 1977 by TS *Hokusei Maru* (Hokkaido Univ. 1978). Gill nets were set for fish along all these lines, and all Sooty Shearwaters caught incidentally in these nets were used.

The distribution of Sooty Shearwaters was determined from two sources: the data on gill-netted seabirds by various research vessels from 1969 to 1981 (Ogi, unpubl. data) and seabird sighting data during six cruises from April to November 1979–81 (Ogi, unpubl. data).

Data on the distribution of the Pacific saury (*Cololabis saira*) came from gill nets set by the TS *Oshoro Maru* and TS *Hokusei Maru* (Hokkaido Univ. 1980, 1981 and 1982) and TS *Hatsue Maru No. 62* (Mishima *et al.* 1981). Each of the above vessels used a non-selective net composed of mesh sizes ranging from 25 or 37, to 204 or 233 mm (stretched

Figure 1
Sampling stations for Sooty Shearwaters in the North Pacific in 1975, and 1977–80. (A) Black dot denotes April sampling station. (D) Black dots denote September sampling stations. AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region



measurement). In addition to these mesh sizes, additional nets were added that were particularly effective for Pacific saury, albacore (*Thunnus alalunga*), and Pacific salmon. Nets with mesh ranging from 25 to 48 mm were most effective for catching saury. I also used the unpublished sighting records of saury shoals at sea compiled from the logs of various research vessels. The occurrence of saury in bird stomachs was also used to confirm the fish distribution.

Only one bird was caught in April (at station Hb5419 in 1975: Fig. 1A) and squid ranked first in its stomach (64.0% by weight). Also, the sample in September was so small (one bird at each of three stations: Sh9905, Sh9911, and Sh9916: Fig. 1D) those stomach contents data were combined with those from October in the following analysis.

5. Results

5.1. Diet composition by weight percentage

Overall, fish was the most important food item in stomachs by weight (83.1%), followed by squid (7.3%), unidentified digested matter (5.4%), and pelagic barnacles (2.9%) (Table 1). Other items were of minor importance.

Through the months studied, fish was the dominant food item in almost all areas (Table 1). In the Subarctic Current in June and Alaskan Stream in August, however, squid was the top ranking item, respectively comprising 88.9 and 39.8% of the diet, followed by unidentified digested matter (8.2%) in the former and fish (30.1%) in the latter. Squid were not found in bird stomachs in the Subtropic Region. Euphausiids and amphipods occurred only in the Subarctic Current during June and August, whereas pelagic barnacles and jellyfish were found in the Transition Domain and/or Subtropic Region from June to September–October.

5.2. Stomach content weight per bird

Stomach content weights of Sooty Shearwaters (Table 2) were slightly higher than for other species of seabirds, taken in the same areas, such as Short-tailed Shearwaters (*Puffinus tenuirostris*: Ogi *et al.* 1980) and Thick-billed Murres (*Uria lomvia*: Ogi 1980). The maximum stomach content weight was 106.5 g or about 12.3% of the body weight.

5.3. Prey species of the Sooty Shearwater

The prey species and their weights are summarized in Table 3. In all, Pacific sauries were found at 16 out of 47 stations, and in 41 of 173 bird stomachs. During July, this fish was eaten only by shearwaters caught in the Transition Domain, but this may have been an artifact of sampling because six of eight (75%) stations during this month occurred there. The maximum number of fish per bird was two in most cases. Fresh sauries occurred in two stomachs in the Transition Domain during June and one in the Subtropic Region during September–October. The fork lengths of these fish were 160, 175, 190, 209, and 262 mm; the first four of these individuals were immature ("small-sized type" of Odate [1977]) and the last one was an adult ("medium-sized type"). Sauries penetrate into the subarctic North Pacific beyond the Subarctic Boundary during early summer (Odate 1977, Fukushima 1979), and stay in the Subarctic for about 3 or 4 months. Its northward migration into the Subarctic lasts about 3 months. By late August the fish ranges across the entire northwestern North Pacific. Some Pacific sauries reach lat. 55°N in the Okhotsk Sea (Ogi, unpubl. data) and lat. 60°N along the southeastern

Table 2
Weights of Sooty Shearwater stomach contents and their maximum proportion of body weight, by month

Month	N	Range, g	Mean, g	*BW*, g*	Percent†
Jun.	51	0.10–85.91	12.55	814	10.4
Jul.	50	0.06–106.45	5.27	863	12.3
Aug.	35	0.02–35.07	3.57	844	4.2
Sep.–Oct.	37	0.67–73.09	11.80	975	7.7

*Body weight of the bird that has the maximum stomach content weight (*BW* does not include the stomach content weight)
†(Maximum stomach content weight/*BW*) × 100 (%)

Table 1
Overall composition of Sooty Shearwater diet by month and sea area

Month	Sea area*	Number of Station	Number of Stomachs	Weight percentages† F	Sq	E	A	Sh	Ba	Je	dm
Jun.	SC	3	8	0.06	88.9	1.7	1.1				8.2
	TD	6	30	88.3	1.6		—		6.4	0.7	3.1
	SR	4	13	78.1	—	—			10.9	8.8	2.1
	Total	13	51	79.9	8.1	0.4	0.09	0	6.6	1.9	3.3
Jul.	SC	2	8	82.5	17.4	—	—				0.09
	TD	6	42	74.9	0.04			0.6		0.7	23.8
	Total	8	50	79.4	10.3	0	0	0.2	0	0.3	0.7
Aug.	AS	1	1	30.1	39.8	—		—			30.0
	SC	8	28	73.4	1.5	7.1	0.2	—	—		17.4
	TD	2	6	85.6	—					13.6	0.8
	Total	11	35	64.6	11.9	3.3	0.09	0	0	3.7	16.5
Sep.–Oct.	SC	3	4	96.7	—	—		—			3.3
	TD	8	24	89.5	6.1	—		—	0.4	—	4.0
	SR	3	9	99.6	—	—	—	—	—	—	0.4
	Total	14	37	95.1	2.4	0	0	0	0.2	0	2.3
Grand total		46	173	83.1	7.3	0.3	0.04	0.01	2.9	1.0	5.4

*AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region
†F: fish; Sq: squid; E: euphausiids; A: amphipods; Sh: shrimp; Ba: barnacles; Je: jellyfish; dm: digested matter

Kamchatka Peninsula in the western Bering Sea (Parin 1968). In early autumn the fish turns southward for its contranatant migration; it spawns and winters in the Subtropic Region (Odate 1977, Fukushima 1979).

A chub mackerel was found in one bird stomach in July in the Transition Domain. Like the saury, this fish also penetrates into the subarctic North Pacific and reaches about lat. 49°N in the Subarctic Current during July (Murakami 1969). In this study this fish species was of minor importance to shearwaters.

Table 3
Prey species of the Sooty Shearwater

Month	Sea area*	Station	N†	n‡	(No. of prey) prey weight (g) of individual bird (FL or DML)§
a. Pacific saury					
Jun.	TD	Os9626	7	1	(2)45.0(FL: 209 mm) and 39.0(FL: 190 mm)
		Os9625	9	2	10.6, (1)30.7
		Os9624	9	7	46.6, 9.6, 32.2, (2)41.4, (2)45.8 (FL: 175 mm) and 35.2(FL: 160 mm), 36.8, 59.9
	SR	Os0613	3	1	0.6
		Os9619	5	2	(2)40.2, (1)33.4
		Os9623	4	2	2.1, 0.9
Jul.	TD	Ho9729	4	2	(1)26.5, 2.0
Aug.	AS	Hk8805	1	1	10.6
	SC	Ho9803	3	2	8.9, 2.4
		Ho9802	12	2	18.6, 5.3
	TD	Os9801	2	2	6.0, 2.2
		Hs9807	4	2	5.9, 14.4
Sep.–Oct.	SC	Sh9916	1	1	68.2
	TD	Sh91011	2	1	0.6
		Sh91010	11	7	5.0, (2)47.1, 11.1, (2)31.0, 33.8, 12.2, 13.6
	SR	Sh91003	7	6	9.9, 15.0, 13.1, (1)75.1(FL: 262 mm), 36.5, (2)38.6
b. Chub mackerel (*Scomber japonicus*)					
Jul.	TD	Os9730	4	1	(1)43.8(FL: 190 mm)
c. Threespine stickleback (*Gasterosteus aculeatus*)					
Jul.	SC	Hk8726	4	1	(9)15.1
d. Rockfish (*Sebastes* sp.)					
Jul.	SC	Hk8726	4	1	91.3
e. Unidentified fish larva					
Jun.	SC	Sh7614	4	1	(1)0.03
f. *Berryteuthis anonychus*					
Jun.	SC	Os0620	2	1	(4)44.2(DML: 66, 64, 80, 84 mm)
g. Barnacles (Cirripedia sp.)					
Jun.	TD	Os9626	7	1	7.0
		Os9625	9	5	1.1, 2.0, 1.2, 13.3, 4.4
		Os9624	9	1	2.1
	SR	Os9623	4	4	0.8, 0.2, 4.9, 4.6
		Os9622	1	1	0.4
Sep.–Oct.	TD	Sh91016	3	1	0.7
H. *Vellela lata*					
Jun.	TD	Os9627	3	2	0.4, 0.1
		Os9626	7	1	2.0
		Os9624	9	2	0.2, 0.7
	SR	Os9619	5	2	4.4, 4.3
Jul.	TD	Os9730	4	1	0.7
Aug.	TD	Os9801	2	1	4.6

*AS is Alaskan Stream, SC is Subarctic Current, TD is Transition Domain, SR is Subtropic Region.
†Number of stomach samples.
‡Number of stomachs in which each prey species occurred.
§FL: fork length (mm) in fish; DML: dorsal mantle length (mm) in squid.

A threespine stickleback occurred in one bird stomach in the Subarctic Current in July. In the Subarctic Current and Transition Domain, this species occurred in stomach contents of Short-tailed Shearwaters (*Puffinus tenuirostris*) (Ogi *et al.* 1980), Thick-billed Murres (*Uria lomvia*) (Ogi 1980), Tufted Puffins (*Fratercula cirrhata*), and Horned Puffins (*Fratercula corniculata*) (Ogi, unpubl. data). Several times at night I saw thousands of threespine sticklebacks around the drifting ship in the Transition Domain and Subarctic Current. It would thus seem that Sooty Shearwaters would have the opportunity to feed on this fish during the daytime hours.

In the Subtropic Region, myctophid (lanternfish) otoliths were found from two birds in June and from one bird in October.

In the Subarctic Current in June, a shearwater had eaten four squid whose dorsal mantle lengths ranged from 64 to 84 mm. This was the only squid identified to species in this study.

Barnacles occurred in a total of 13 birds taken at six stations in the Transition Domain and Subtropic Region. On several occasions, I saw a number of shearwaters crowded around a floating log, the surface of which was densely covered with pelagic barnacles. When the ship approached closer, several grazed patches were evident on each log. In this way Sooty Shearwaters were able to feed on these sessile organisms.

5.4. Seasonal and oceanographic changes in diet

To study the incidence of saury in shearwater stomachs in more detail, I determined the frequency of occurrence (Table 4) and percentage by weight (Table 5) of the Pacific saury in the shearwater diet for each area and month. They appeared in stomachs from the Transition Domain (33.3%) and Subtropic Region (38.5%) during June; only in the Transition Domain (4.8%) during July; and in the Alaskan Stream (one bird), Subarctic Current (14.3%) and Transition Domain (66.7%) during August. Thus by early August saury had occurred in shearwater stomachs across the latitudinal extent of stations sampled in the subarctic North Pacific. From August onward, the occurrence of sauries in bird stomachs continued to be high: in the Subarctic Current, 25%; Transition Domain, 33.3%; and Subtropic Region, 66.7%. In all, the species was found in a minimum of 41 (23.7%) of 173 stomachs.

Based on weight, the importance of saury to shearwaters is even more obvious (Table 5). During June the saury comprised 88.1% of stomach contents weight in the Transition Domain and 78.2% in the Subtropic Region; 26.6% in the Transition Domain during July; 30.1% in the Alaskan Stream (one bird), 62.9% in the Subarctic Current, and 84.4% in the Transition Domain during August; and 88.1% in the Subarctic Current, 89.0% in the Transition Domain, and 99.2% in the Subtropic Region in September–October. Overall, the saury comprised 69.7% of the total weight of stomach contents.

The prevalence of Pacific sauries among total stomach content weights from June to September–October increased with decreasing latitude: 30.1% in the Alaskan Stream (one bird), 30.6% in the Subarctic Current, 79.9% in the Transition Domain, and 92.0% in the Subtropic Region. Since Sooty Shearwaters also increased in abundance with

decreasing latitude (see below), the above results indicate that the occurrence of Sooty Shearwaters and Pacific sauries coincided in the areas studied.

5.5. The importance of cephalopods

Precisely how long cephalopod beaks stay in a bird's gizzard is not known, but their presence indicates that the birds fed on cephalopods in the recent past. Both fresh and worn beaks were found in this study (Table 6). The maximum number of beaks in a single bird was 290 at station Ho9730 in the Transition Domain during July. Based on the frequency of occurrence of beaks in each oceanographic area regardless of month, squid decreased in importance as prey with decreasing latitude: 100% in the Alaskan Stream ($n = 1$ stomach) and Subarctic Current ($n = 48$), 66.7% in the Transition Domain ($n = 102$), and 43.5% in the Subtropic Region ($n = 22$) (Table 6). The same decreasing order was also observed in the average number of beaks per bird: 67.2 in the Subarctic Current, 40.3 in the Transition Domain, and 16.0 in the Subtropic Region. However, the number of beaks per bird between months did not show a trend. When all areas and seasons are combined, the frequency of squid beaks and the average number of beaks per bird are 72.8 and 48.6, respectively (Table 6). When compared with other seabirds in the same area such as Common Murres, Thick-billed Murres, and Short-tailed Shearwaters, Sooty Shearwater gizzards contained more cephalopod beaks (Ogi, unpubl. data).

The large number of squid beaks in gizzards suggests a greater use of these prey than indicated by stomach contents analysis. Squid comprised only 7.3% of the total food by weight, although they accounted 72.8% by frequency of occurrence (Tables 1 and 6). It appears that cephalopods are digested much faster than other large prey, which causes problems in the quantitative analysis of seabird food. Furthermore, some tiny hard beaks may have come from cephalopods inhabiting waters farther south; though most beaks came from squid, the few *Japetella* and *Argonauta* beaks were probably from prey eaten south of the Subarctic Boundary (Kubodera 1982). Nevertheless, the large number of beaks found in the gizzard indicate that the Sooty Shearwater depends considerably on small cephalopods in some localities during some periods. Judging from beak

Table 4
Frequency of occurrence, by month and area, of Pacific saury in the stomachs of the Sooty Shearwater; N = the number of stomachs, n = the number of stomachs in which the Pacific saury occurred, %[(n/N) × 100] = the percentage occurrence

	Alaskan Stream			Subarctic Current			Transition Domain			Subtropic Region			Total		
Month	N	n	(%)	N	n	(%)	N	n	(%)	N	n	(%)	N	n	(%)
Jun.	—	—	—	8	0	(0)	30	10	(33.3)	13	5	(38.5)	51	15	(29.4)
Jul.	—	—	—	8	0	(0)	42	2	(4.8)				50	2	(4.0)
Aug.	1	1	(100)	28	4	(14.3)	6	4	(66.7)				35	9	(25.7)
Sep.–Oct.	—	—		4	1	(25)	24	8	(33.3)	9	6	(66.7)	37	15	(40.5)
Total	1	1	(100)	48	5	(10.4)	102	24	(23.5)	22	11	(50.0)	173	41	(23.7)

Table 5
Percentage by weight of Pacific saury in the stomach contents of the Sooty Shearwater by month and area; W = the total stomach content weight, w = the weight of the Pacific saury, %[(w/W) × 100] = the percentage by weight

	Alaskan Stream			Subarctic Current			Transition Domain			Subtropic Region			Total		
Month	W	w	(%)	W	w	(%)	W	w	(%)	W	w	(%)	W	w	(%)
Jun.	—	—	—	49.731	0	(0)	491.490	433.011	(88.1)	98.853	77.255	(78.2)	640.074	510.266	(79.7)
Jul.	—	—	—	156.020	0	(0)	107.241	28.493	(26.6)				263.261	28.493	(10.8)
Aug.	35.070	10.571	(30.1)	56.155	35.299	(62.9)	33.718	28.456	(84.4)				124.943	74.326	(59.5)
Sep.–Oct.	—	—	—	76.797	68.229	(88.1)	173.544	154.368	(89.0)	189.686	188.097	(99.2)	440.027	410.694	(93.3)
Total	35.070	10.571	(30.1)	338.703	103.528	(30.6)	805.993	644.318	(79.9)	288.539	265.352	(92.0)	1468.305	1023.796	(69.7)

Table 6
The number of cephalopod beaks in Sooty Shearwater stomachs, by month and area; N = the number of stomachs, n = the number of stomachs in which cephalopod beaks occurred, %[(n/N) × 100] = the percentage occurrence of cephalopod beaks

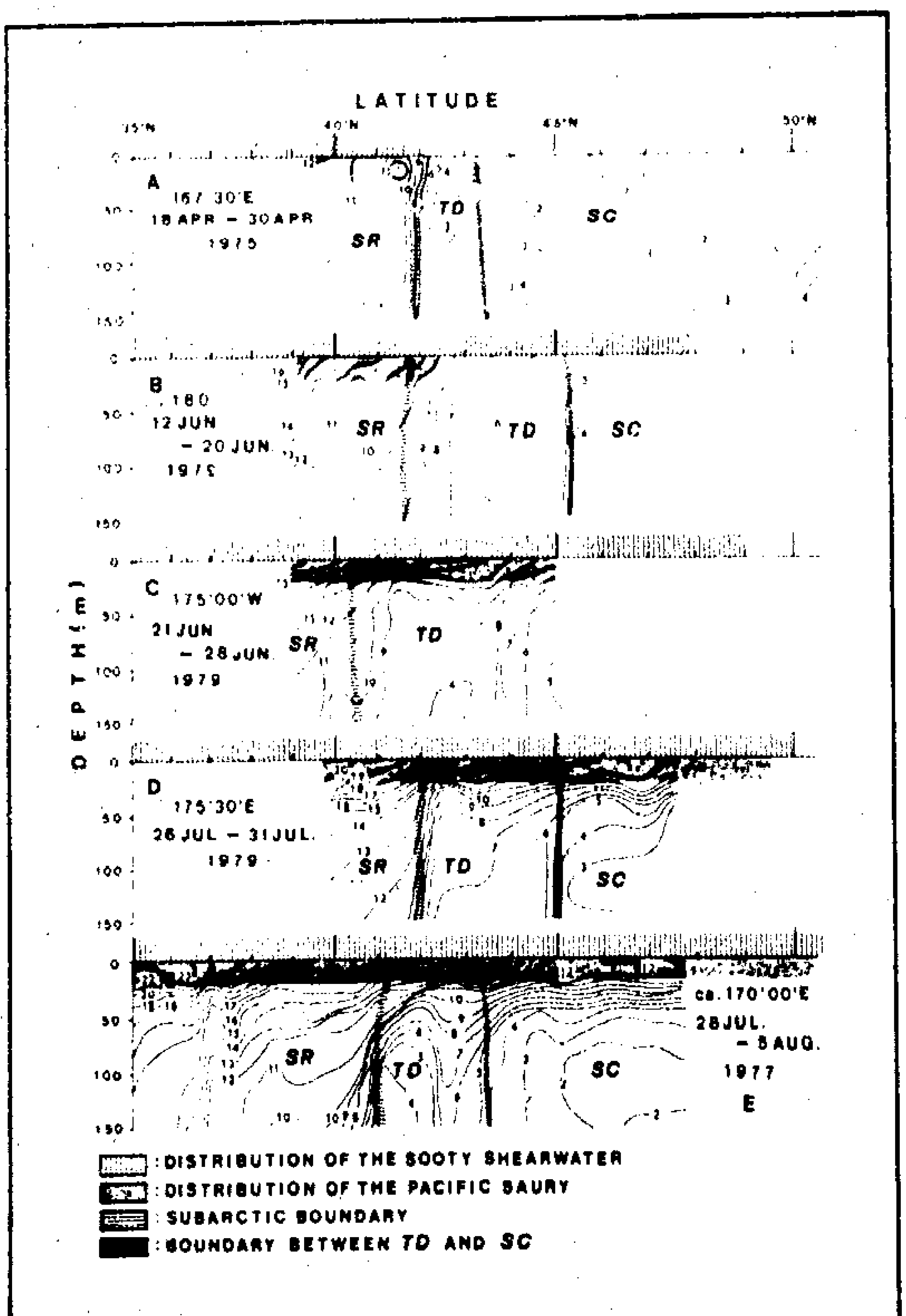
	Alaskan Stream				Subarctic Current					Transition Domain					Subtropic Region					Total				
Month	N	n	%	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean	N	n	%	Range	Mean
Jun.	—	—	—	—	8	8	100	37–171	76.8	30	7	23.3	1–68	12.7	13	3	23.1	7–24	14.0	51	18	35.3	1–171	41.4
Jul.	—	—	—	—	8	8	100	10–197	54.8	42	36	85.7	1–290	55.8	—	—	—		—	50	44	88.0	1–290	55.6
Aug.	1	1	100	8	28	28	100	2–273	75.0	6	3	50.0	1–2	1.3	—	—	—		—	35	32	88.6	1–273	66.0
Sep.–Oct.	—	—	—	—	4	4	100	9–32	19.0	24	22	91.7	2–116	29.1	9	6	66.7	8–32	17.0	37	32	86.5	2–116	25.6
Total	1	[illegible]	100	8	48	48	100	2–273	67.2	102	68	66.7	1–290	40.3	22	9	40.9	7–32	16.0	173	126	72.8	1–290	48.6

sizes, the original dorsal mantle lengths of most cephalopods probably ranged from 30 to 40 mm but some were as large as 250 mm (Kubodera, pers. comm.).

5.6. The occurrence of Sooty Shearwaters in relation to Pacific sauries and the oceanographic environment

Several seasons of systematically gathered transect counts of Sooty Shearwaters (Ogi, unpubl. data), along with concurrent data on Pacific sauries and shearwaters at gill-net fishing stations (Ogi, unpubl. data), and independently gathered information on Pacific sauries in various data records (Hokkaido Univ. 1979, 1980, 1981, and 1982) and the literature (Hotta and Fukushima 1970, Odate 1977, Fukushima 1979, Mishima *et al.* 1981), indicate that latitudinal movements of these two organisms in the North Pacific may be strongly affected by seasonal changes in the oceanographic climate. This was evident when the distribution of these two vertebrates were compared (Fig. 2) with the seasonal changes in the sea surface temperatures (SST).

Figure 2
Seasonal water temperatures by depth (isotherms in degrees Celsius), and occurrence of the Sooty Shearwater and Pacific saury. The position of the Subarctic Boundary coincided with the subsurface occurrence of 34 ‰ isohaline (Dodimead *et al.* 1963), and the boundary between the Transition Domain and the Subarctic Current coincided with the 4°C isotherm below 100 m (Favorite *et al.* 1976). SR: Subtropic Region; TD: Transition Domain; SC: Subarctic Current



Though temperatures optimal for the Pacific saury change seasonally with various stages of growth and migration, the fish was observed at SSTs ranging from 7 to 25°C; the most favourable fishing occurs at 14–18°C (Hotta and Fukushima 1970, Odate 1977). Thus, the northern distributional limit of the fish is assumed here to coincide with the 7°C isotherm, though the bulk of the population occurs farther south. Also to be considered in delineating the distribution of the Pacific saury, however, are the facts that larger fish (over 29 cm standard length) migrate farther north than smaller ones (Odate 1977) and that the frequency of occurrence of dense schools changes seasonally with SST as follows: 8.5–13.5°C (mode: 10.5°C) in June; 8.5–14.5°C (mode 12.5°C) in July; 10.5–16.5°C (mode: 11.5°C) in August; and 9.5–18.5°C (modes: 11.5, 14.5, and 17.5°C) in September (Odate 1977). These facts were taken into account for the preparation of Fig. 2.

Concurrent seabird censuses and gill-net fishing along long. 167°30'E from lat. 38°N to lat. 50°N during April indicated that both Pacific sauries and Sooty Shearwaters occurred just south of the Subarctic Boundary (Fig. 2A). At that time SSTs in adjacent sub-tropical and subarctic waters were 10.9–12.1°C and 2.2–4.2°C, respectively (Hokkaido Univ. 1976). By May the 7°C isotherm had reached the middle of the Transition Domain, and during this month both sauries and shearwaters crossed the Subarctic Boundary into the Transition Domain. By mid June at long. 180°, Sooty Shearwaters reached lat. 48°N in the Subarctic Current (Fig. 2B), but the 7°C isotherm reached only lat. 44°30'N near the northern edge of the Transition Domain (Hokkaido Univ. 1980). In fact, sauries were not then found in stomachs of sooties taken in the northern Transition Domain ($N = 30$) and Subarctic Current ($N = 3$). By July along long. 175°W, sauries entered the southern Subarctic Current (Hokkaido Univ. 1980: Fig. 2C). Sooty Shearwaters continued to occur yet farther north, some reaching the Alaskan Stream. From late July to early August, shearwaters and sauries occurred longitudinally across the Transition Domain, Subarctic Current, and Alaskan Stream (Hokkaido Univ. 1978, 1980: Fig. 2D and E). Along long. 175°30'E (Fig. 2D), Sooty Shearwaters reached north to lat. 50°N and sauries reached lat. 49°N, with schools occurring most frequently farther south in the northern Transition Domain (Hokkaido Univ. 1980).

6. Discussion

Dense feeding flocks of Sooty Shearwaters often occur where surface water temperatures range from 9 to 13°C in the North Pacific during summer, and compared with the similar Short-tailed Shearwater the sooty appears to prefer warmer waters (Ogi, unpubl. data). Its initial crossing of the Subarctic Boundary corresponds with the warming of surface waters beginning early in May. After this initial northward movement, lasting over a period of 1.5 months, its occurrence in the northern North Pacific is likely to be affected strongly by the occurrence and availability of suitable prey.

Sooty Shearwaters did not show changes in diet composition between oceanographic areas (as did *P. tenuirostris*, Ogi *et al.* 1980), but did show changes in diet by latitude: sauries decreased and squid increased with increasing latitude. In the overall diet, fish ranked highest by weight (83.1%), and the Pacific saury occupied 84% of this total fish weight. Weight of squid, however, was probably under-

estimated due to much more rapid digestion. The opposite trends with latitude shown by the prevalence of sauries and squid as Sooty Shearwater prey indicate that in the absence of this fish, squid was the dominant food. In the absence of both, the shearwater ate barnacles and jellyfish. It did not eat euphausiids which are important prey in upwelling areas closer to shore (Baltz and Morejohn 1977, Morejohn *et al.* 1978, Brown *et al.* 1981).

The periods during which the shearwater and the saury occur in the subarctic North Pacific coincided, and both species seemed to prefer 9–13°C temperatures (Odate 1977, this study). This may indicate that the distribution of this bird in the region may be related to water temperature, the occurrence of saury shoals, or both. The fact that shearwaters moved northward slightly ahead of the fish indicates that both organisms may be responding to temperature rather than the shearwater to the fish. Flying is a much more rapid means of dispersal than swimming. The additional fact that the importance of sauries as prey changed seasonally, but squid did not, suggests that the large-scale occurrrence of the shearwater was a response to temperature whereas its smaller-scale occurrence related to prey availability.

In the present study, averaging observations from different sets of data and years served to indicate that an interesting interrelationship does exist between bird, prey, and sea surface temperature, but for this relationship to be properly understood, additional data will have to be gathered simultaneously.

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