

# Capelin and seabirds in the northwest Atlantic

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## 1. Abstract

Capelin (*Mallotus villosus*) are central to the food webs of seabirds, marine mammals, and fish in Newfoundland waters. The area of Witless Bay, southeast Newfoundland (ca. 47°14'N 52°46'W) contains the largest breeding concentration of seabirds in Canada and includes ca. 1.25 million individuals whose principal diet is fish; these consume ca. 7300 t of capelin during the major part of the breeding season, 1 June – 15 August. The annual capelin consumption by all seabirds in Newfoundland waters is ca. 250 000 t, of the same order of magnitude as that by seals and whales, and one-tenth that of Atlantic cod (*Gadus morhua*). The proportion of the total Newfoundland capelin biomass consumed by these predators is not known. However the birds' requirement for prey at locally high densities for efficient foraging, and the limitations imposed by their inability to dive deeply and by their need to forage close to their colonies, suggest that only part of this total biomass is available to them.

Capelin were the principal prey brought to Atlantic Puffin (*Fratercula arctica*) chicks on Great Island, Witless Bay, in 1968–69, but the young birds were fed mainly on small gadids in 1981. In 1981, chicks received an average of only 13.47 g food/day (against 44.64 g in 1968–69), fledged at an average body weight of 217.0 g (against 261.6 g), and fledging success was only 45.0% (against 60.3%). It is concluded that capelin form an essential part of the diet of young puffins in eastern Newfoundland, and that there is no alternative prey, of comparable size, abundance, and nutritional value available to the birds within range of Witless Bay. The responses of puffins and other seabirds to scarcities of key food species elsewhere are reviewed. In most cases the more specialized seabird species have no acceptable alternative to their principal prey.

The fishery for capelin which has developed off Newfoundland since 1971 therefore places seabirds and people in potential competition for a common resource. It is not clear to what extent the scarcity of capelin off Witless Bay in 1981, and a failure in capelin stock recruitment on the Grand Banks in 1978, was an effect of the fishery and/or natural environmental factors. However, any serious decline in the Newfoundland capelin stocks would have adverse effects on the principal predators. A program to monitor the populations of these predators would provide an indication of the condition of the capelin stocks and give advance warning of population declines. The management of this fishery should proceed cautiously until the relationships between the capelin and its predators are better understood.

## 2. Résumé

Le capelan (*Mallotus villosus*) occupe une place clé dans la chaîne trophique des oiseaux aquatiques, des mammifères marins et des poissons des eaux de Terre-Neuve. La région de Witless Bay, au sud-est de Terre-Neuve (environ 47°14'N 52°46'O), abrite la plus grande concentration d'oiseaux aquatiques nidificateurs du Canada, dont près de 1,25 million de sujets qui se nourrissent principalement de poissons; ils consomment près de 7300 t de capelan durant la majeure partie de la période de nidification qui s'étend du 1<sup>er</sup> juin au 15 août. La consommation annuelle de capelan par tous les oiseaux aquatiques des eaux de Terre-Neuve se chiffre à environ 250 000 t, soit le même ordre de grandeur que celle des phoques et des baleines, et le dixième de celle de la morue (*Gadus morhua*). La proportion de la biomasse totale de capelan de Terre-Neuve absorbée par ces prédateurs n'est pas connue. Cependant, le fait que leurs proies doivent atteindre des densités localement élevées pour que les oiseaux pêchent efficacement, qu'ils soient limités par leur incapacité à plonger en profondeur ou par la nécessité de pêcher près de leurs colonies, laisse supposer que seule une partie de cette biomasse totale leur est accessible.

Le capelan a été la principale proie apportée à de jeunes Macareux arctiques (*Fratercula arctica*), à Great Island, Witless Bay, en 1968–1969, alors qu'en 1981, les jeunes oiseaux ont été nourris principalement de petits gadidés. En 1981, les oisillons n'ont reçu en moyenne que 13,47 g de nourriture par jour (comparativement à 44,64 g en 1968–1969); ils étaient en mesure de voler avec un poids corporel moyen de 217,0 g (contre 261,6 g), avec un succès d'envol de 45,0 % (contre 60,3 %). Ces observations ont amené à conclure que le capelan forme un élément essentiel du régime des jeunes macareux, à l'est de Terre-Neuve, et que ces oiseaux ne disposent d'aucune autre proie de taille, d'abondance et de qualité nutritive comparables, aux alentours de Witless Bay. Les auteurs reviennent les réactions des macareux et d'autres oiseaux aquatiques à la rareté d'espèces alimentaires clés ailleurs. Dans la plupart des cas, les espèces plus particulières d'oiseaux aquatiques ne disposent d'aucune autre nourriture acceptable pour remplacer leur proie principale.

La pêche au capelan qui s'est développée au large de Terre-Neuve depuis 1971 a créé une rivalité entre les oiseaux aquatiques et l'homme pour le partage de cette ressource. On n'a pu déterminer dans quelle mesure la rareté du capelan au large de Witless Bay en 1981 et le recrutement insuffisant des stocks à Grand Banks en 1978



résultent de la pêche et/ou de facteurs écologiques naturels. Toutefois, toute baisse importante des stocks de capelan de Terre-Neuve serait préjudiciable aux principaux prédateurs. Un programme de surveillance des populations de prédateurs donnerait une indication de l'état des stocks de capelan et signalerait à l'avance toute baisse de population. Cette pêche devrait être aménagée avec précaution jusqu'à ce que les relations entre le capelan et ses prédateurs soient mieux connues.

### 3. Introduction

There are several marine ecosystems in which certain animal species stand out as being central to the food webs of many higher predators. In the Canadian High Arctic, for example, the principal trophic pathways in ice-edge habitats pass from the phytoplankton on the underside of the ice via the epontic and free-swimming copepods and amphipods, to the arctic cod (*Boreogadus saida*), before branching out again to seabirds, whales, and seals (Dunbar 1981, Bradstreet and Cross 1982). In Newfoundland waters the capelin (*Mallotus villosus*), a small smelt, occupies a comparable, central position (Winters and Carscadden 1978; Carscadden *et al.* 1982; Carscadden, this volume; see below), as does the northern anchovy (*Engraulis mordax*) off Oregon (Wiens and Scott 1975). The chain may be even simpler than this, and run from the phytoplankton directly to the central prey species (anchovetas [*Engraulis ringens*] in Peru and euphausiid krill [*Euphausia superba*] in the Antarctic), and then to the predators (e.g. Murphy 1936, Mauchline and Fisher 1969, Schaefer 1970). Sometimes a small group of species has this central role: sprat (*Sprattus sprattus*), sandlance (*Ammodytes* spp.), and young Atlantic herring (*Clupea harengus*) for British seabirds (Pearson 1968, Harris and Hislop 1978), or pilchard (*Sardinops ocellata*) and anchovies (*Engraulis capensis*) for those in South Africa (Crawford and Shelton 1978).

In recent years most of these central prey species have become the actual or proposed targets for intensive fisheries. This raises a number of questions about the fate of the higher predators which depend on them. How much of the stock of the prey do the predators require, and how much is harvested in the fishery? Can the two coexist? If not, to what extent are the predators able to adjust their feeding habits to alternative prey? In fact, are there any acceptable alternative prey species available to them? The object of this paper is to examine these questions with reference to the interactions of capelin, seabirds and other predators, and the fishery, off Newfoundland.

### 4. The distribution and habits of capelin

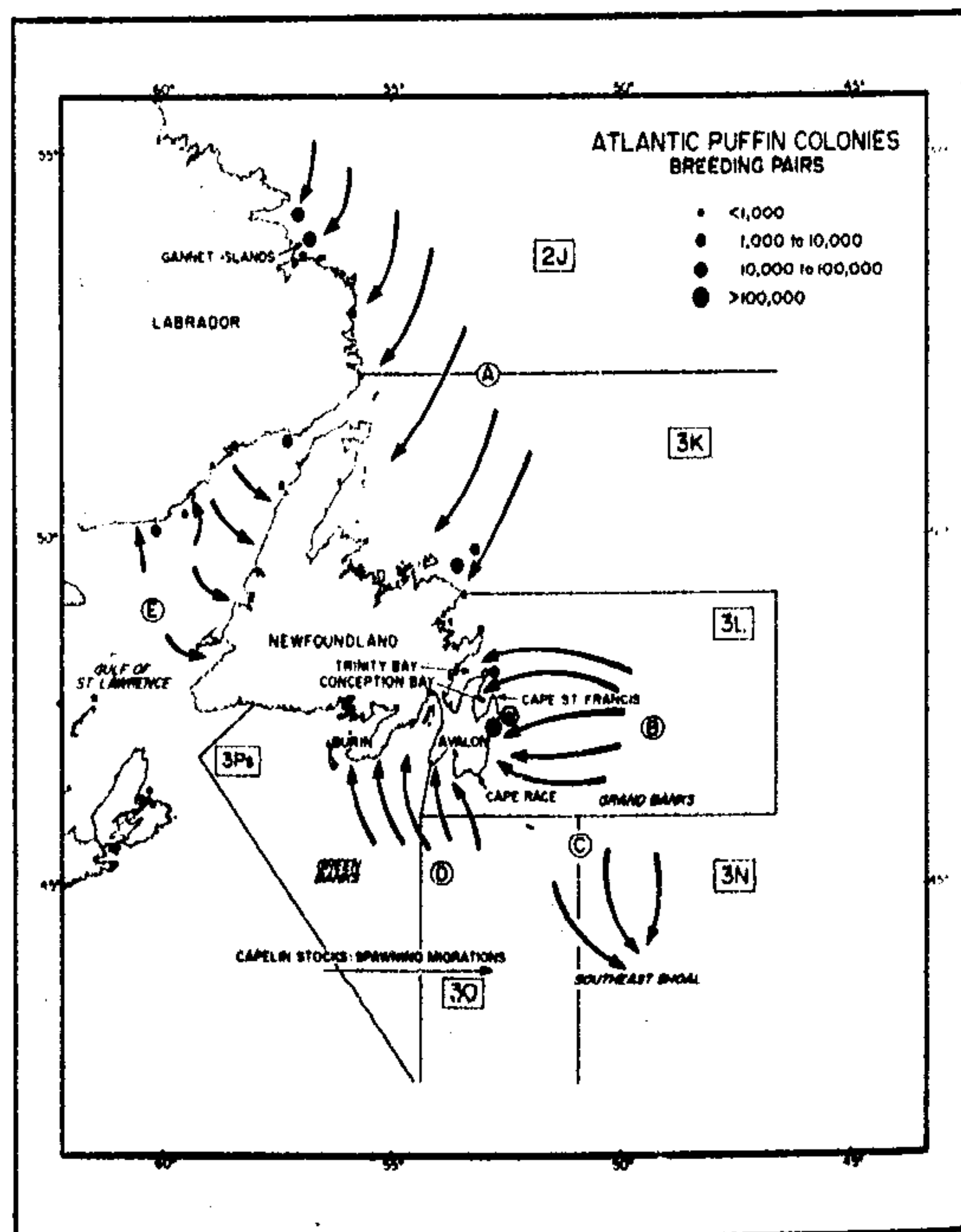
Capelin occur in the low arctic waters of both the North Atlantic and the North Pacific (Jangaard 1974). In the Atlantic the species is especially abundant off Newfoundland, southern Greenland, and Iceland, and in the Barents Sea (Leim and Scott 1966, Jangaard 1974). There are several discrete populations off eastern Canada (Carscadden, this volume; see also Fig. 1). Stock A occurs on the banks off southeast Labrador and northeast Newfoundland (International Commission for the Northwest Atlantic Fishery/Northwest Atlantic Fisheries Organization [ICNAF/NAFO] subareas 2J + 3K), and spawns on beaches along those coasts. Stock B, on the northern Grand Banks (3L), spawns on the beaches of eastern Newfoundland from Cape

Freels to Cape Race. Stock C winters on the northern Grand Banks and spawns on the shallow Southeast Shoal of the Bank (3N0). Stock D, from the western Grand Banks and Green Bank (3Ps), spawns on beaches from the southern Avalon Peninsula to the Burin Peninsula. Stock E is confined to the Gulf of St. Lawrence. We are concerned primarily with stocks A–C in this paper.

Spawning occurs in June and July, earlier in southern Newfoundland than in Labrador (Templeman 1948; Jangaard 1974; Carscadden, this volume). The spawning schools consist mainly of 3–5 year-old fish, though younger fish may also migrate inshore at this season. Most of the adults die after they have spawned. The remainder, along with the immature fish, withdraw offshore again from August onwards, though part of stock A apparently winters off northeast Newfoundland. A small population also winters in deep water in Trinity Bay, southeast Newfoundland (Winters 1970).

In Newfoundland waters capelin are important to many higher predators (Jangaard 1974, Winters and Carscadden 1978, Akenhead *et al.* 1982). They are taken in large numbers by Atlantic cod (*Gadus morhua*) (and thus are of indirect importance to the many predators which feed on

**Figure 1**  
Distributions of Atlantic puffins (*Fratrercula arctica*) and capelin in Newfoundland and Labrador (after Brown *et al.* 1975 and Carscadden, this volume, respectively). The letters (A, B, C, D, E) refer to capelin stocks. The codes (2J, 3K, 3L, 3N, 3O, 3Ps) refer to ICNAF/NAFO subareas (ICNAF/NAFO 1963–83). W identifies the major colonies of puffins and other seabirds in Witless Bay, Newfoundland (see Table 1 and the text)



cod), Greenland halibut (*Reinhardtius hippoglossoides*), American plaice (*Hippoglossoides platessoides*), and other demersal fish; by Atlantic salmon (*Salmo salar*), and bluefin tuna (*Thunnus thynnus*); by harp seals (*Pagophilus groenlandicus*), and fin, sei, and minke whales (*Balaenoptera physalus*), (*B. borealis*), and (*B. acutorostrata*); by short-finned squid (*Illex illecebrosus*); and by many seabirds.

## 5. The importance of capelin to seabirds in Newfoundland

Newfoundland and Labrador support a large population of breeding seabirds. The largest concentration, in Canada as well as Newfoundland, breeds on Gull, Green, and Great islands in Witless Bay on the Avalon Peninsula, ca. 47°14'N 52°46'W (Nettleship 1980, see Fig. 1). The

Table 1

Population sizes of the principal seabird species breeding in Witless Bay, Newfoundland, and estimates of their consumption of capelin over the 45-day period 1 July – 15 August. Estimates of sizes of the breeding populations are from Nettleship (1980); those for non-breeding subadults

were calculated by using productivity figures from Maunders and Threlfall (1972), Nettleship (1972), Pierotti (1979), and survival rates from Coulson and White (1959), Coulson (1968), Kadlec and Drury (1968), Burkhead and Hudson (1977), and Hudson (in press).

	Herring Gull	Black-legged Kittiwake	Common Murre	Atlantic Puffin	Totals
No. breeding adults (A)	13 700	84 000	156 000	450 000	
No. eggs laid (X clutch size)	17 125 (2.5)	77 700 (1.85)	78 000 (1)	225 000 (1)	
No. chicks hatched (hatching, %)	12 673 (74%)	55 944 (72%)	66 300 (85%)	157 500 (70%)	
No. chicks fledged (fledging, %)	9 885 (78%)	42 517 (76%)	56 670 (90%)	102 375 (65%)	
Average no. chicks present (B)	11 000	49 000	63 000	125 000	
No. non-breeding subadults					
1-year-olds	3 022	33 588	20 835	51 000	
2-year-olds	3 425	28 550	22 376	38 250	
3-year-olds			19 020	30 600	
4-year-olds			16 167	26 010	
Total subadults (C)	6 447	62 138	87 398	145 860	
Total no. birds	ca. 31 000	ca. 195 000	ca. 306 000	ca. 721 000	
Food consumption					
a. adults	(ca. 400 g × 75 d × A)	(ca. 50 g × 75 d × A)	(ca. 200 g × 75 d × A)	(ca. 100 g × 75 d × A)	
(% capelin)	411 t (30%)	315 t (40%)	2340 t (90%)	3375 t (90%)	
b. chicks	(ca. 200 g × 15 d × B)	(ca. 50 g × 45 d × B)	(ca. 27 g × 20 d × B)	(ca. 52 g × 45 d × B)	
(% capelin)	165 t (30%)	110 t (90%)	119 t (90%)	292 t (90%)	
c. subadults	(ca. 400 g × 45 d × C)	(ca. 50 g × 45 d × C)	(ca. 200 g × 45 d × C)	(ca. 100 g × 45 d × C)	
(% capelin)	116 t (30%)	110 t (40%)	787 t (90%)	656 t (90%)	
Total food consumption	692 t	565 t	3246 t	4323 t	8826 t
Total capelin consumption	208 t	281 t	2921 t	3891 t	7301 t

\*The adults of all four species are present on the Witless Bay colonies all through June as well as from 1 July – 15 August. These would require an additional 2576 t of food (Herring Gull: 164 t; kittiwake 126 t; murre: 936 t; puffin 1350 t) for this additional 30-day period, or 2152 t of capelin if the suggested ratios for percent capelin also apply to the beginning of the season.

Five other seabird species breed in the Witless Bay colonies (Nettleship 1980), ca. 780 000 pairs of the planktivorous Leach's Storm Petrel, and well under 1000 pairs each of the wholly or partly fish-eating Great Black-backed Gull, Thick-billed Murre, Razorbill, and Black Guillemot. These will not be taken into consideration in the present paper.

Table 2

The occurrence of various classes of food items (%) in the diets of Herring Gulls (HG), Black-legged Kittiwakes (BLK), Common and Thick-billed murre (CM, TBM), and Greater Shearwaters (GSH) in eastern Newfoundland. n = the number of samples on which the percentages are based. Samples from Witless Bay (WB) refer to breeding birds; those from eastern Newfoundland (ENFLD), eastern Grand Bank (EGB), Placentia Bay (PB), and Notre Dame Bay (NDB) to non-breeders. The percentages

for Herring Gulls, Kittiwakes, and murre refer to the number of meals (WB) or stomachs (ENFLD) in which the item in question was the *sole* or *principal* constituent. Greater Shearwater percentages refer to every stomach in which the item occurred, and so the sum of the percentages exceeds 100%. Data from Rees (1961), Luck (1961), Maunders (1971), Brown *et al.* (1979), Mahoney (1979), Pierotti (1979).

Area:	WB						ENFLD		EGB	PB	NDB
Species:	HG*			BLK*	CM		CM	TBM		GSH	
Season:	June–July			June–August	June–July		Winter		June	June	September
Year:	1976	1977	1978	1970	1977	1978	—	—	1961	1978	1975
Item											
Capelin	34.4	26.4	30.8	40.8	92.9	94.1	91.7	93.1	21.0	60.0	100.0
Other fish	5.7	6.2	3.8	20.9	2.2	2.9	7.0	5.9	0	0	0
Squid	0.8	14.5	10.1	0.3	4.9	0	0	0	23.7	50.0	7.7
Crustaceans	0	0	0	1.4	0	0	0	0	15.8	10.0	7.7
Birds	46.5	18.5	20.0	0	0	0	0	0	0	0	0
Other	12.5	27.9	28.5	6.0	0	2.9	1.3	1.0	0	0	0
Offal–garbage	12.5	6.4	7.3	30.6	0	0	0	0	42.1	0	0
No.	494	1200	891	265	372	183	44	611	38	20	13

\*"Birds" refers to young Atlantic Puffins or adult Leach's Storm Petrels; "Other" consists mainly of littoral molluscs and barnacles. See Table 3 for the foods brought to young Atlantic Puffins.

+18.9% of the "other fish" in 1970 were sandlance; however capelin was the principal food brought to the chicks in 1970 and also 1969 (Maunders 1971, Maunders and Threlfall 1972).



**Table 3**  
Comparison of breeding performance in Atlantic Puffins in Witless Bay, Newfoundland, in 1968–69 and 1981<sup>a</sup>

Measure	1968–69 <sup>b</sup>	1981 <sup>b</sup>	$\chi^2$ or $t$	$P$	
<b>Fledging success</b>	60.3% (126/209)	45.0% (45/100)	$\chi^2 = 29.37$	<0.001	
<b>Chick mortality</b>					
(a) found dead in burrow (i.e. starvation)	15.7% (13/83)	44.4% (24/54) <sup>d</sup>	$\chi^2 = 13.75$	<0.001	
(b) disappeared prematurely (i.e. gull predation/ early departure)	84.3% (70/83)	55.6% (30/54) <sup>d</sup>	$\chi^2 = 13.75$	<0.001	
<b>Chick condition at fledging</b>	( $n = 126$ )	( $n = 45$ )			
(a) body weight, g	261.6 ± 34.07 (159–323)	217.0 ± 38.22 (145–276)	$t = 6.91$	<0.001	
(b) wing length, mm	142.1 ± 14.19 (127–154)	140.0 ± 6.36 (126–152)	$t = 1.42$	NS <sup>f</sup>	
<b>Chick diet</b>	$n$	$n$			
(a) meal size, g	155	101	5.86 ± 4.95	$t = 10.02$	<0.001
(b) composition:	208 (1969)	101			
capelin	175	13	12.9%	$\chi^2 = 144.92$	<0.001
immature <i>Gadus</i>	7	65	64.3%	$\chi^2 = 141.51$	<0.001
sandlance	26	14	13.9%	$\chi^2 = 0.11$	NS
total fish	208	92	91.1%	$\chi^2 = 19.09$	<0.001
invertebrate	0	9	8.9%	$\chi^2 = 19.09$	<0.001
(c) $\bar{x}$ feeding rate (meals/chick/d) <sup>e</sup>	17 (1969)	20	2.3 ± 2.65	$t = 2.01$	≈0.05
(d) estimated $\bar{x}$ chick food c.d. g [(a) · (c)]	17	20	13.47		

<sup>a</sup>Same study plots and habitats (slope) used in 1981 as base years 1968–69.

<sup>b</sup>1968–69 was prior to international capelin fishery; 1981 was 9 years after beginning of fishery. 1981 was 3rd consecutive year of apparent capelin spawning failures in SE Newfoundland waters.

<sup>c</sup>Statistical tests used (from Sokal and Rohlf 1969) are either chi-square ( $\chi^2$ ) from 2 × 2 contingency tables testing the significance of the difference between the proportions indicated, or Student's  $t$ -distribution.

<sup>d</sup>Fate of one chick uncertain though known *not* to have fledged.

<sup>e</sup>Chicks watched for 3 days and therefore 1969 = 51 chick-days, and 1981 = 60 chick-days.

<sup>f</sup>NS,  $P > 0.05$ .

ca. 2.2 million individuals there include, in descending order of abundance, Leach's Storm-petrels (*Oceanodroma leucorhoa*), Atlantic Puffins (*Fratercula arctica*), Common Murres (*Uria aalge*), Black-legged Kittiwakes (*Rissa tridactyla*) and Herring Gulls (*Larus argentatus*), along with smaller numbers of Thick-billed Murres (*Uria lomvia*), Razorbills (*Alca torda*), Black Guillemots (*Cepphus grylle*), Great Black-backed Gulls (*Larus marinus*), and Northern Fulmars (*Fulmarus glacialis*) (Table 1).

Of these species, Leach's Storm-petrel is planktivorous (e.g. Palmer 1962). The remainder are all, to some extent, fish-eaters. Tables 2 and 3 show that murres and puffins, the dominant alcids, feed almost entirely on fish and the two gulls, kittiwake and Herring Gull, also take fish to a lesser degree. Overall, the tables show that capelin are the dominant fish in the diets of Witless Bay seabirds.

Table 1 attempts to quantify these diets during the central part of the breeding season. During 1 July – 15 August, adult birds, their growing chicks at the nest sites, and subadult birds are all present at the colony. The adults are also there earlier, during the incubation period (roughly 1–30 June), but subadult seabirds tend to arrive later in the season (e.g. Salomonsen 1967) and for present purposes we assume that they are absent before 1 July. The estimates of food consumption in the table are necessarily speculative but we believe that they are reasonably accurate — more so for the specialist murres and puffins than for the gulls, generalist feeders — and consistent with estimates for murre colonies elsewhere (Table 4). We conclude that the Witless Bay seabird population consumes ca. 8830 t of food during this 75-day period, of which ca. 7300 t are capelin. Birds are at the colonies for at least 2 months before, and

1 month after this central period. However we hesitate to extrapolate our estimates further, partly for lack of information about the birds' diets at these times, and partly because the capelin are farther offshore then, and may be less accessible (Jangaard 1974).

Because the distributions of the principal colonies of puffins and other seabirds coincide with those of spawning capelin (Fig. 1; see also Nettleship 1973, 1977, 1980; Brown *et al.* 1975), it is reasonable to extrapolate our estimates for Witless Bay to cover the whole Newfoundland seabird population for the period 1 June – 15 August. There is not enough information to do this for Herring Gulls, but we estimate (Table 4) that the murres, puffins, and kittiwakes combined take a total of ca. 25 600 t of capelin, of which ca. 17 300 t comes from stock A (subareas 2J and 3K) and ca. 7900 t from stock B (subarea 3L, including Witless Bay). These estimates take partial account of consumption by the subadults of these species. However, they do not include consumption by the large numbers of non-breeding Greater and Sooty shearwaters (*Puffinus gravis* and *P. griseus*), migrants from the southern hemisphere, which are widely distributed in subareas 2J + 3KLNOPs during this period (Brown *et al.* 1975). Too little is known about the diets or population sizes of either species to estimate their consumption of capelin with any accuracy, but we conclude from the calculations in Table 4 that, as a first approximation, it may be of the order of 25 000 t. Finally, large numbers of seabirds feed on capelin while they are wintering off Newfoundland; most notably ca. 4 million Thick-billed Murres from Greenland and the Canadian Arctic, and many of the ca. 1 million Common Murres which breed in Newfoundland and Labrador, both capelin-feeders in win-

Table 4

A preliminary estimate of food consumption, by breeding Black-legged Kittiwakes, Common Murres, and Atlantic Puffins in southeast Labrador and eastern Newfoundland in the season 1 June – 15 August. NAFO subareas 2J and 3K = capelin stock A, 3L = stock B, and 3Ps = stock D (Carscadden, this volume). Numbers of breeding adults from Nettleship

(1980), supplemented by Brown *et al.* (1975); subadults and chicks calculated from the adult-subadult-chick ratios for the Witless Bay colonies (Table 1). Feeding rates and periods, and capelin consumption, also from Table 1

Capelin stock: Subarea:		A 2J		A 3K		B 3L		D 3Ps		Totals
		No. birds	Food, t	No. birds	Food, t	No. birds	Food, t	No. birds	Food, t	
<b>Kittiwake</b> (1 ad./0.74 subadults/0.58 chicks)										
Adults	(75 d @ 50 g/d)	100	0.4	6 000	22.5	105 060	394.0	22 944	86.0	
Subadults	(45 d @ 50 g/d)	74	0.2	4 440	10.0	77 744	174.0	16 978	48.2	
Chicks	(45 d @ 50 g/d)	58	0.1	3 480	7.8	60 935	137.1	13 307	29.0	
Total		232	0.7	13 920	40.3	243 739	706.0	53 229	154.1	
<b>Common Murre</b> (1 ad./0.56 subadults/0.40 chicks)										
Adults	(75 d @ 200 g/d)	68 200	1023.0	799 200	11 988.0	157 600	2369.4	20 440	302.4	
Subadults	(45 d @ 200 g/d)	38 192	343.7	447 552	4 028.0	88 458	796.1	11 278	101.5	
Chicks	(20 d @ 27 g/d) (25 d @ 54 g/d)	27 280	{ 14.7 36.8	319 680	{ 172.6 431.6	63 184	{ 34.1 85.3	8 056	14.3 10.9	
Total		133 672	1418.2	1 566 432	16 620.3	309 602	3824.0	39 774	418.8	
<b>Atlantic Puffin</b> (1 ad./0.32 subadults/0.28 chicks)										
Adults	(75 d @ 100 g/d)	91 730	688.0	25 000	187.5	471 840	3538.8	0	0	
Subadults	(45 d @ 100 g/d)	29 354	132.1	8 000	36.0	150 980	679.4	0	0	
Chicks	(45 d @ 52 g/d)	25 684	60.1	7 000	16.4	132 115	309.1	0	0	
Total		146 768	880.2	40 000	239.9	754 941	4527.3	0	0	
Total food, t			2291		16 900		9058		553	28 822
Total capelin consumption			2069		15 195		7887		458	25 600

NOTE: — Additional species:

**Herring Gull:** the size of the Newfoundland population is not known, but Table 1 estimates the capelin consumption for this period in Witless Bay as ca. 208 t.

**Shearwaters:** 5–10 million Greater Shearwaters breed in the South Atlantic and winter in the North Atlantic in June–October, along with large numbers of Sooty Shearwaters – initially off eastern North America (Rowan 1952; Phillips 1963; Voous and Wattel 1963; Brown *et al.* 1975, 1981; Bourne 1980). For present purposes we will assume that 3 million shearwaters are present 1 June – 15 August in 2J + 3KL NOPs and that each bird, weighing 800 g, consumes 175 g/d (based on the 200–250 g/d of 900 g Common Murres, Sanford and Harris [1967], Swennen and Duiven [1977]), half squid and half capelin by weight (Table 2). Total food = 39 400 t; total capelin = 19 700 t. Alternatively, we follow Morejohn *et al.* (1978) in assuming that the calorific content of the squid is 5.1 kJ/g (wet), and that a shearwater can assimilate 80% of the calorific content of its food and requires, resting, 271 kcal/d (1135 kJ/d). With capelin @ 4.2–4.5 kJ/g (Jenkins [1974]; Montecocchi and Porter [1980]; samples from summer, eastern Newfoundland) the birds consume 70–76 000 t of food (35–38 000 t of capelin) in a 75-d period. With capelin @ 17.8 kJ/g (M.S.W. Bradstreet, in prep; summer, southeast Labrador), total

consumption would be ca. 48 000 t if 100% of the diet was capelin, and progressively less with increasing proportions of squid. However the lack of definite information on shearwater numbers, diets, and metabolic rates makes these figures first approximations only.

**Comparative data:** Wiens and Scott (1975), using an energy flow model, estimate that 3–4 million Sooty Shearwaters consume 30 717 t of food (80% of it northern anchovies @ 4.3 kJ/g) in a 2.5–3 month period off Oregon. On the same model they estimate that 2 49 800 breeding Common Murres consume 6 400 t (mainly anchovies) during a 4-month breeding season, and 21 142 t over the whole year. Other estimates for Common and/or Thick-billed murres, based on daily consumption rates over a 4-month breeding season, are 1300 t (Wiens and Scott 1975), 25 000 t (Uspenski 1956; 2 million birds in Novaya Zemlya) and 49 000 t (Swartz 1966; 157 000 birds in the Bering Sea).

More generally, Wiens and Scott (1975) estimate that seabirds take ca. 20% of the production of pelagic fish in the neritic zone (up to 37 km offshore) off Oregon. Furness (1978) estimates ca. 29% within a 15-km radius of Shetland, and Furness and Cooper (1982) give a figure of ca. 30% within 50 km of Saldanha Bay, South Africa. Schaefer (1970) estimates ca. 20% for the seabirds of Peru.

ter (Tuck 1961, Gaston 1980). We suggest (Table 5), again as a first approximation, that the breeding and non-breeding seabirds take a total of ca. 250 000 t of capelin from Newfoundland waters in the course of the year.

The seabirds' annual consumption of capelin in subareas 2J + 3KL NOPs is therefore of the same order of magnitude as consumption in those areas in the 1970s by the fishery at its peak, by harp seals, and by fin and minke whales; it is about a tenth the consumption calculated for Atlantic cod in the same period and subareas (Winters and Carscadden 1978, see also Table 5 and Fig. 2). It is difficult to view these figures in the wider perspective of the absolute biomass of capelin in these subareas, since the estimates of consumption given by Winters and Carscadden (1978) and Table 5 are minima which take no account of the biomass of

fish left unconsumed. Population estimates based on acoustic surveys suggest that the peak biomass of capelin in subareas 2J + 3KL NOPs in 1976 was ca. 10.3 million metric tons (using the higher estimate in Table 5); the fishery took only ca. 3.5% of this, against ca. 37% by all natural predators combined, including only ca. 2.4% by the seabirds. On the other hand the seabirds alone would have required ca. 23% and the natural predators ca. 350% of the ca. 1.1 million metric tons estimated for 1979. The results of acoustic surveys vary with the method used, and they are more reliable as *relative* indices of annual changes in capelin numbers than as *absolute* estimates of capelin biomass (Carscadden, this volume). Even so, the figures suggest that the present low level of capelin biomass may be imposing limits on the populations of the higher predators.



However, it is important to emphasize that the significant index for the predators is probably not so much the overall size of the capelin stock in a given subarea, as the local density of the fish within relatively small areas. It is this which determines the foraging efficiency of the predators. Brodie *et al.* (1978) have calculated that a fin whale feeding on euphausiids on the Scotian Shelf cannot meet its daily energetic requirements at a prey density of only  $0.1 \text{ g/m}^3$ , the average density of euphausiids in that area; it must instead search for "patches" of euphausiids as dense as  $17.5 \text{ g/m}^3$  or higher. The use which seabirds make of "fronts," tidals upwellings and similar oceanographic systems which concentrate their prey suggests that their foraging is also determined by local concentrations rather than overall abundance (Nettleship 1977, Brown 1980). Off Novaya Zemlya the Dovekie (*Alle alle*), a small, diving, planktivorous alcid, can in theory reduce the time it spends foraging underwater by two-thirds, if it hunts in areas of maximum rather than average prey density, and the feeding birds do indeed concentrate in such areas (Zelickman and Golovkin 1972, Brown 1981). It is not possible to say precisely what such a reduction in foraging time means in energetic terms, but there can be little doubt that it represents a significant saving. The energetic costs of swimming transport in a Mallard (*Anas platyrhynchos*) are about six times greater than those of flying (Prange and Schmidt-Nielsen 1970). It is likely that fish-eating alcids like

murres and puffins can also reduce their energetic costs by foraging on locally dense concentrations of capelin.

Whether the index of capelin biomass is local or general, seabirds are further limited in their access to the resource by restrictions that do not apply to the other natural predators. Seabirds breed only on land, and so the

**Table 5**

Consumption, in metric tons, of capelin by seabirds, other predators and people off eastern Newfoundland

Annual consumption by seabirds in subareas 2J + 3KLNOs	
4 million Thick-billed Murres, November–March @ 200 g/d (Gaston 1980)	108 000
1.6 million Common Murres, January–December @ 200 g/d (from Brown <i>et al.</i> 1975 and Tables 1,4)	105 000*
0.8 million Atlantic Puffins, April–October @ 100 g/d (from Brown <i>et al.</i> 1975 and Tables 1,4)	15 000
3 million Greater and Sooty shearwaters, June–August (Table 4)	25 000
Total	ca. 250 000

Annual consumption in subareas 2J + 3KLNOs (based on Winters and Carscadden 1978; Carscadden, this volume)

Predator	ca. 1955–57	early 1970s	Exploitable surplus†
Seabirds	250 000	250 000	—
Harp seals ( <i>Pagophilus groenlandicus</i> )	432 000	300 000	132 000
Fin whales	360 000	250 000	110 000
Minke whales	35 000	20 000	15 000
Atlantic cod	3 970 000	3 000 000	970 000
Totals	5 047 000	3 820 000	1 227 000

Peak capelin catch, 1975, areas 2,3	365 971‡
Capelin catch, 1981, areas 2,3	36 678‡

Estimated absolute biomass 1976§	10 344 000
Estimated absolute biomass 1979§	1 104 000

**The requirement for capelin by seabirds breeding in Witless Bay (1 June – 15 August) in relation to the biomass of mature, 3–5 year-old fish potentially available to them at increasing distances from the colony**

Foraging radius from Witless Bay, km	Local capelin biomass**	Birds' requirement (= ca. 7300 t: as % of local biomass)
5	4 450	164
20	17 800	41
50	44 500	16
100	89 000	8

\*It is assumed that the whole population winters off Newfoundland. However Common Murres also occur in winter as far south as Georges Bank, outside the range of capelin (e.g. Powers and Ramage 1978); if these are Newfoundland birds, the actual capelin consumption from November–March will, to an unknown degree, be less than that estimated here.

†Based on the estimated biomass of capelin left unconsumed by the decline in predator populations between the late 1950s and early 1970s; no estimates of changes in seabird populations available.

‡Probably too low; see caption to Figure 2.

§1976 and 1979 are, respectively, the peak and minimum biomasses for 2J + 3KL, extrapolated to cover 3NOPs as well following the calculations of Winters and Carscadden (1978) for cod (Akenhead *et al.* 1982). Another method of estimating biomass gives 1 890 000 t (1975, peak) and 495 000 t (1979). Both methods are more reliable as relative indices of year-to-year changes than absolute values of population size (Carscadden, this volume).

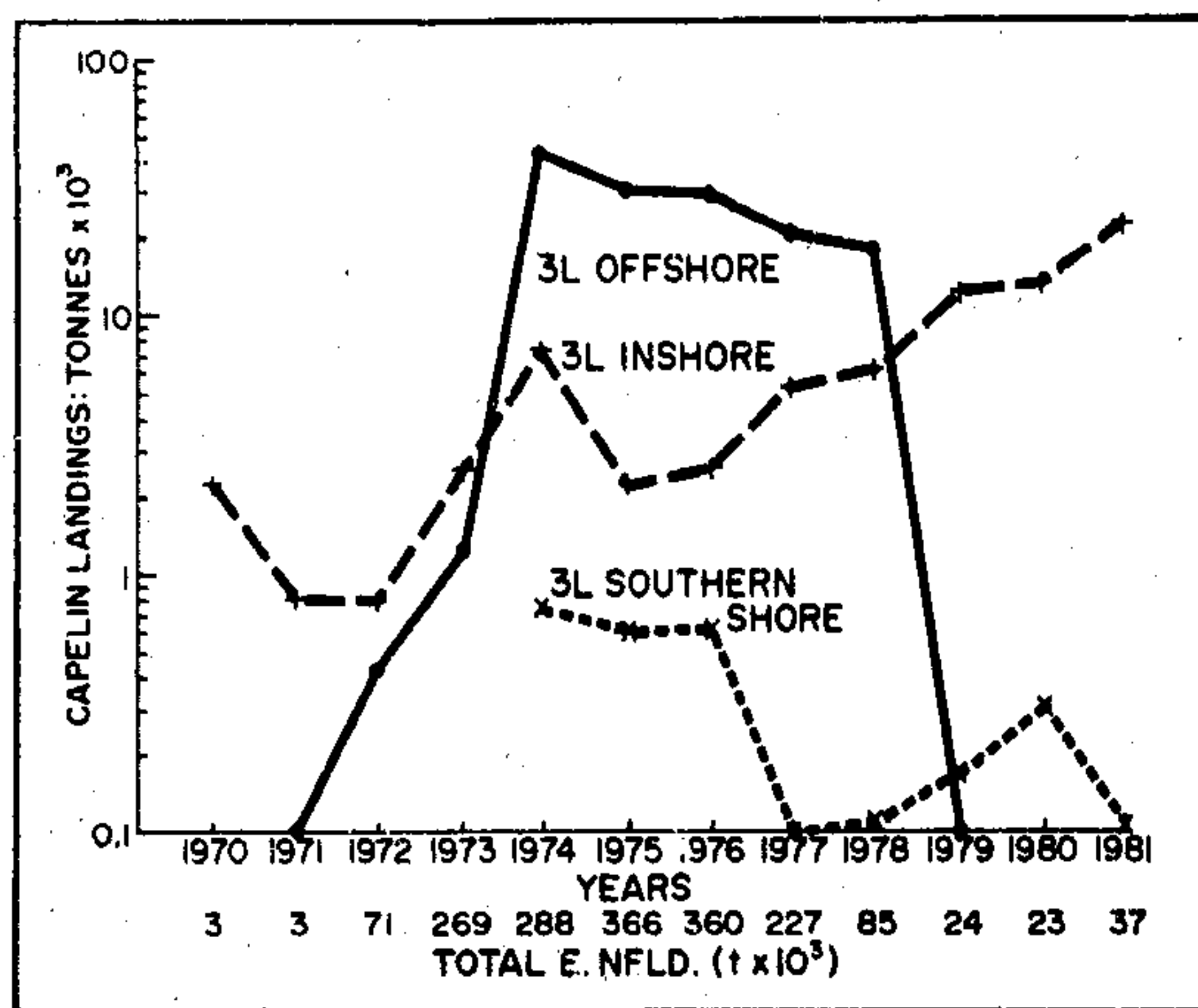
\*\*The total biomass of capelin projected for 3L in 1981 was ca. 300 000 t (NAFO 1981). In the absence of a finer-scale analysis of distribution, we here assume that this biomass was evenly distributed along the ca. 800 km of shoreline in the subarea @ 445 t/km. However the catch statistics (Anon. 1982) suggest that this was not so and that capelin densities were lower than average in the Witless Bay area. In Trinity and Conception bays in 1981, 19 682 t of fish were caught (44 t/km or 46 t per licensed fisherperson), against only 66 t on the southern shore (0.4 t/km or 2.5 t/fisherperson).

**Figure 2**

Annual landings of capelin in eastern Newfoundland (metric ton  $\times 10^3$ , round, wet). The combined catches from areas 2 and 3 (mainly 2L + 3KLNOs) are listed under "E.N.F.L.D." "3L Offshore" and "Inshore" indicate, respectively, the catches by foreign and by Newfoundland vessels in subarea 3L, and "3L Southern Shore" those taken inshore between Cape St. Francis and Trepassey (and including Witless Bay). 3L catches refer primarily to capelin stock B, though part of the offshore catch may include fish from stock C (Carscadden, this volume). Data from ICNAF/NAFO (1963–83) and Anon. (1982); the data for 1981 are provisional.

Note that part of the "inshore" catch in 3L in 1974 may have been taken by large Newfoundland vessels operating offshore; the offshore catch in 3L (and in E.N.F.L.D.) in 1975 may have been underestimated by ca. 25 000 t (Carscadden, this volume).

Since 1979 the inshore fishery in 3L has concentrated on the harvesting of mature female capelin for their roes (Anon. 1982). As a consequence, males and unripe or substandard females are rejected and do not appear in the landings statistics (Rowe and Collins 1982). The actual catch inshore in 1979–81 may therefore have been double that shown here





breeding birds have access only to that proportion of the biomass that is within economical foraging range of their colonies. These ranges vary widely between species and colonies and may change rapidly, depending on the availability of prey (e.g. Tuck and Squires 1955, Nettleship and Gaston 1978, Gaston and Nettleship 1981). Their outer limits become crucial during the chick-rearing period, when the chick must receive a quantitatively and qualitatively sufficient daily intake of food to sustain its rapid growth. The foraging parents are further limited to a maximum 16 h day-length (Civil Twilight) at the latitude of Witless Bay because Common Murres, at least, are unable to pursue fish at night (Sanford and Harris 1967).

The actual foraging ranges of Witless Bay seabirds are not known with any certainty, but puffins and murres are regularly taken in gill nets set along the coast of the Avalon Peninsula at least 20 km from the colony (Piatt *et al.*, this volume). This suggests that the birds may travel quite far, though there is no indication of the foraging ranges of parents actually foraging for their young. Observations elsewhere suggest that most seabirds forage within a 35–50 km radius of their colonies (e.g. Wiens and Scott 1975, Furness 1978, Furness and Cooper 1982, see also Table 4). A Witless Bay puffin, with a flight speed of *ca.* 50 km/h (Pennycuik 1969: Fig. 8), could thus, in theory, have access to capelin of stock B along the entire length of the eastern Avalon Peninsula, from Cape St. Francis to Cape Race, in an hour's flight. If the fish were present at the depths and local concentrations suitable for efficient foraging, it could meet its food requirements from the biomass of capelin within 20–50 km of the colony (Table 5c). On the other hand, the fish of stock C on the Southeast Shoal offshore, *ca.* 370 km away from Witless Bay, would almost certainly be inaccessible to it. The only seabirds commonly seen out there during the capelin spawning season are the non-breeding shearwaters (Brown *et al.* 1975; R.G.B. Brown, in prep.).

The seabirds' access to their prey is also limited by their diving abilities; unlike competing predators, they cannot stay under water for long periods. Kittiwakes and Herring Gulls cannot submerge deeper than their own body length. Shearwaters may stay under for *ca.* 12–30 s and reach a depth of *ca.* 20 m (Brown *et al.* 1978, 1981; Skira 1979). The specialized alcids are more efficient divers, however. Common and Thick-billed murres have been recorded as diving for up to 140 and 192 s, respectively (Scott 1973, Bradstreet 1983), and the former will feed on the bottom at 60 m (Scott 1973). In the Witless Bay area, Common Murres are regularly taken in gill nets set at depths of 30–100 m but not in those at 6–10 m (Piatt *et al.*, this volume), which suggests that the species is a deep diver; however, the reverse is true of puffins. In general, most Newfoundland seabirds are limited to foraging in the top 30 m of the water column, and only the murres regularly go deeper. This would not limit foraging in the vicinity of the spawning beaches, where the capelin schools are at depths of 5–10 m or less (Templeman 1948). Shearwaters may be unable to reach fish spawning on the bottom offshore on the Southeast Shoal (minimum depth *ca.* 50 m), but they can probably take them there at shallower depths in mid water. On the other hand, the seabirds' access to capelin in deeper waters off Newfoundland is almost certainly limited by the depth of the schools. Acoustic surveys have shown that young, 1-year capelin stay close to the surface off Newfoundland during the summer, but that the larger, 2–3 year-old fish remain close to the bottom (*ca.* 100 m) during

the daytime; they rise at night, but reach the surface only if the surface waters are cool (Devold 1970, Devold *et al.* 1972, Kovalyov and Kudrin 1973). Much of the capelin population is therefore too deep for any birds but murres to reach it during the daytime, and it is accessible to the other, diurnal and shallow, diving seabirds for only a limited period of daylight at dawn and dusk.

We therefore conclude that capelin are an extremely important prey for the more specialized seabird species breeding in Newfoundland, such as murres and puffins, and to a lesser extent generalist feeders such as kittiwakes and other gulls as well. They are also important to non-breeding shearwaters off Newfoundland in summer, and to migrant murres from the Arctic which winter on the Grand Banks. The seabirds' annual consumption, estimated very approximately at 250 000 t, is of the same order as that of the seals and whales, and also of the Newfoundland capelin fishery at its peak. However, it is difficult to relate this consumption to the overall size of the capelin biomass in Newfoundland waters, partly for lack of adequate information about the latter, but partly also because seabirds, like other higher marine predators, depend on *local* densities rather than overall biomass for foraging efficiency. The seabirds are further constrained by their limited diving abilities, and by the restrictions on their foraging ranges imposed by their need to breed on land. Taken together, these constraints mean that seabirds, and to some extent the other higher predators as well, have access to a smaller capelin population than is, in theory, available to them.

## 6. Alternatives to capelin in the diets of Newfoundland seabirds

The importance of capelin in the diets of Newfoundland seabirds is also demonstrated by the reduced breeding success of the birds in seasons when the fish are scarce or absent during the chick-rearing period.

In 1981 the Atlantic Puffins nesting on Gannet Islands, southeast Labrador (Fig. 1) bred successfully, feeding their young almost entirely on capelin (Birkhead and Nettleship 1982). This was not true of the birds on Great Island in Witless Bay. The principal fish in the chicks' diets at this colony in 1981 were young gadids (64.3%), supplemented by small numbers of sandlance (13.9%), capelin (12.9%), and invertebrates (8.9%) (Table 3). Only 45.0% of the chicks fledged, and 44.4% of those which failed to do so died of starvation in their burrows. This is in sharp contrast to the 1968 and 1969 breeding seasons at this colony, when the food brought to the chicks consisted entirely of fish: mainly capelin (84.1%), with smaller numbers of sandlance (12.5%) and a few gadids (3.4%). Sixty percent of the young birds fledged in these two seasons, and only 15.7% of those which failed to do so were found dead of starvation in their burrows; the remainder were probably taken by gulls (Nettleship 1972).

The weights of the young puffins which did fledge at Great Island in 1981 averaged only *ca.* 83% of those which fledged in 1968–69. The subsequent survival of seabird chicks is apparently correlated with their fledging weight (e.g. Perrins *et al.* 1973), so the true chick mortality was probably higher than the fledging percentage suggests. These lower weights were partly the result of a lower feeding rate: weight of the chicks' daily ration in 1981 was only 30% of that in 1968–69. It is likely that qualitative, nutritional differences were also important. Harris and



Hislop (1978) found that the clupeids and sandlance which were the preferred foods of puffins at Scottish colonies had a higher calorific value and a higher fat content than the gadids which were only fed to the chicks when these preferred species were scarce. Capelin, like clupeids and sandlance, have a variable but relatively high fat and oil content (Jangaard 1974; see also Table 4), and so they may have been nutritionally superior to the Newfoundland gadids. However, we cannot comment further on this point until the nutritional analyses of the fish brought to the Witless Bay puffin chicks in 1981 have been completed.

Capelin are thus extremely important in the diets of young puffins at colonies in Newfoundland. At first sight it is surprising that their parents could find no substitute prey in 1981, given the variety of foods which puffins are known to bring back to their chicks. Apart from capelin, sandlance, and gadids of several genera, the list at colonies on one or both sides of the Atlantic includes Atlantic herring, Atlantic mackerel (*Scomber scombrus*), sticklebacks (*Gasterosteidae*), gurnards (*Triglidae*), flatfishes (*Pleuronectidae*), gobies (*Gobiidae*), squid, polychaetes, and crustaceans, all of which occur in the northwest Atlantic, as well as such fish as sprat and weevers (*Trachinus vipera*) which do not (Belopol'skii 1957, Myrberger 1962, Corkhill 1973, Ashcroft 1976, Harris and Hislop 1978, Hudson 1979, Lid 1981; see also Table 3, and Leim and Scott 1966). However this gives the misleading impression that the puffin is a versatile bird with a wide choice of potential preys. In actual practice, the birds are limited to prey with an average body depth of 15 mm (maximum 26 mm; Swennen and Duiven 1977); to species with a relatively high calorific value and fat content (Harris and Hislop 1978); and, for maximum foraging efficiency (see above), to species which school. This means that there are only four prime species in the Witless Bay area: capelin, sandlance, and young Atlantic herring and Atlantic mackerel (Leim and Scott 1966). It is not clear why the puffins did not, or could not, increase their consumption of sandlance to compensate for the scarcity of capelin in 1981. It is possible that the bulk of the sandlance population is in the relatively shallow waters of the Grand Banks (e.g. Winters 1983), ca. 85 km from the colony at their nearest point, and thus probably outside the birds' foraging range (see above). Eastern Newfoundland is at the northern edge of the range of mackerel in Canadian waters and the species' main spawning grounds are in the Gulf of St. Lawrence (Leim and Scott 1966); the puffins almost certainly could not have had access to the young fish, small enough for them to take. There is an important spawning ground for herring off the south coast of Newfoundland (Leim and Scott 1966). However, the prevailing currents would tend to carry the larvae westwards towards the Gulf of St. Lawrence where, like the mackerel, the young fish would be beyond the birds' foraging range. In short, there seems to be no acceptable substitute for capelin available to the puffins which breed in southeast Newfoundland.

The situation in Witless Bay in 1981 has close parallels with recent events at Røst in the Lofoten Islands, northern Norway, where the puffin colony of ca. 700 000 pairs is the largest in Norway (Brun 1979). The preferred prey at this colony was formerly young Atlantic herring, but these have been virtually absent since 1969 (Anon. 1972-79) and, as at Great Island, the adult birds have been bringing young gadids to their chicks instead (Lid 1981, see also Mills 1981). With the exception of 1974, when sandlance and young Atlantic mackerel were available, virtually

no young puffins have fledged from this colony since 1969; most die of starvation within the first 10 days after hatching (Lid 1981). Common Murres, Razorbills, and Kittiwakes breeding in the Røst area have also had a very low breeding success (Barrett 1981). The Norwegian fisheries statistics (Anon. 1972-79) suggest that Røst is too far away for the birds to turn to alternative prey, such as capelin farther east off Finnmark, or sprat farther south, off southwest Norway. By contrast the seabird colonies in Finnmark and southwest Norway are apparently breeding successfully (Barret 1981).

Seabirds elsewhere have had varying success in adjusting to the scarcity of a preferred prey species. Harris and Hislop (1978) show that puffins at Scottish colonies have access to several alternative preys — sprat, sandlance, and young herring as well as young gadids — and these act as "buffers" which allow the birds to respond to temporary shortages with reduced breeding success at worst, rather than outright failure. In British Columbia the Rhinoceros Auklet (*Cerorhinca monocerata*), a small Pacific auk, was able to adjust to a scarcity of sandlance by taking sauries (*Cololabis saira*) instead, although the size and nutritional qualities of this alternative were not completely satisfactory and many young auklets starved (Vermeer 1978, 1980; Vermeer *et al.* 1979). However, the Common Murres and Tufted Puffins (*Lunda cirrhata*) breeding in the same area could not make this adjustment apparently because they, unlike the auklets, were unable to feed at night when the sauries were available close to the surface. The principal food of the three guano birds of the Peruvian upwelling system, the Piquero Booby (*Sula variegata*), pelican (*Pelecanus thagus*), and Guanay Cormorant (*Phalacrocorax bouganvillei*), is normally the superabundant anchoveta (Murphy 1936, Jordán 1967). From time to time an intrusion of warm tropical water (the "El Niño" phenomenon) suppresses the upwelling; the fish become very scarce and the guano-bird populations decline drastically (Murphy 1936, Továr and Galarzo 1977, Valdivia 1978). The other preys available to the birds, such as sardines (*Sardinops sagax*) and pejerreyes (*Odontesthes regia*) (Továr and Fuentes 1980), are evidently quantitatively or qualitatively inadequate to support them. In the analogous Benguela upwelling the South African anchovy has recently increased relative to the formerly dominant pilchard and other species. The populations of the South African guano birds, the Cape Gannet (*Sula capensis*), Cape Cormorant (*Phalacrocorax capensis*), and Jack-ass Penguin (*Spheniscus demersus*) have all declined as a consequence of this. The penguin is the species most affected because its limited foraging range apparently restricts its ability to adjust to the different and less predictable migrations of the anchovies, in contrast to those of the pilchards, its preferred prey (Crawford and Shelton 1978, Crawford 1981). These examples suggest that the more specialized seabird species have fewer choices of prey than might at first appear, and that the scarcity or absence of a preferred species is usually detrimental to them.

Other species of seabirds have adapted more successfully to changes in their food supply, but these are generalist feeders and the changes have usually taken the form of the exploitation of human wastes: for example, the Northern Fulmar in the boreal North Atlantic (Fisher 1952), the Black-legged Kittiwake in Norway and elsewhere (e.g. Norderhaug *et al.* 1977), and the Herring and Great Black-backed gulls in eastern North America (Drury 1973-4). However, the breeding success and, ultimately, the sizes of the populations of specialist fish-feeders like the



alcids and the guano birds almost always decline when preferred items in their diet become unavailable and there is no acceptable alternative. In general, the decline is sharpest in the species or the colonies which rely on the fewest species of prey.

## 7. Seabirds and the Newfoundland capelin fishery

In the examples quoted above, the fluctuations in the availability of prey at the Scottish and British Columbian alcid colonies were apparently the result of natural phenomena (Harris and Hislop 1978; Vermeer 1978, 1980; Vermeer *et al.* 1979). On the other hand, the scarcity or absence of the birds' preferred prey in other cases was the direct or indirect result of fisheries. This is true of the decline of pilchards off South Africa (Crawford and Shelton 1978, Crawford 1981) and of Atlantic herring off Norway (Anon. 1972-79). The collapse of the anchoveta population off Peru was initiated by an "El Niño" event, but compounded by overfishing of the surviving stock (Valdivia 1978).

The fishery for capelin off Newfoundland has expanded dramatically in the last 10 years. To what extent could this have contributed to the scarcity of these fish off Witless Bay in 1981?

Capelin are or have been harvested for food, fish-meal, fertilizer, and bait (Jangaard 1974). The traditional fishery in Newfoundland took capelin close to the spawning beaches and accounted for *ca.* 23 000 t/year around 1900, declining to *ca.* 5000 t by the late 1970s (ICNAF/NAFO 1963-82; Templeman 1948; see also Fig. 2). Meanwhile a large offshore fishery developed in the Barents Sea in the early 1960s, and was extended to Icelandic waters soon afterwards (ICES 1963-82, Jangaard 1974). It extended farther west to the Grand Banks in the early 1970s, and the catch reached a peak of *ca.* 350 000 t/year by mid-decade (ICNAF/NAFO 1963-82; see also Fig. 2). In the spring of 1978 the rate of recruitment of young capelin into the stocks was found to be very low, and the offshore fishery was suspended and remains so, apart from a limited harvest in subarea 2J (Carscadden *et al.* 1982; Carscadden, this volume). At just that time, however, the inshore fishery expanded rapidly to supply the Japanese market with the roes of mature female capelin (Anon. 1982, Rowe and Collins 1982). Most of this harvest is taken in subarea 3L (stock B), especially in Trinity and Conception bays (Figs. 1 and 2). Landings of 24 529 t were reported from this subarea in 1981 though the actual catch was probably at least twice this figure, because of the inevitable wastage of males and unripe and substandard females which accompany a specialized fishery of this kind.

There is a parallel between the expansion of the capelin fishery off eastern Newfoundland and the decline of the breeding success of the puffins at Witless Bay. Capelin were abundant in the Witless Bay area in the late 1960s, just before the start of the offshore fishery in subarea 3L, but scarce in 1981 after a decade of inshore and offshore fishery there for stock B (Table 3). Is there a causal connection? Capelin mature and spawn at 3-5 years of age (Carscadden, this volume). This interval is too long for the scarcity of 1981 to have been caused by overfishing the spawning stock inshore, because the inshore fishery did not start to expand until 1979. It could, however, have been the result of overfishing offshore, in 1976 and 1977, just before that fishery was suspended. There is evidence that offshore

capelin were overfished in the 1970s (Carscadden, this volume), but the population affected was stock C, which spawns on the Southeast Shoal out of range of the Witless Bay seabird colonies, and not stock B in subarea 3L. Carscadden points out that the fishery at its peak was taking only *ca.* 10% of the exploitable biomass (e.g. Table 5), seemingly too small a proportion to affect the population as a whole. He suggests that the decline in the recruitment rate which was detected on the Grand Banks in spring 1978 reflects the dying-out of the unusually large year-class of capelin that was spawned in 1973. He notes that the size of a year-class depends on many factors among which the unpredictable effects of the weather on egg and larval survival are particularly important (e.g. Frank and Leggett 1981a, 1981b), and that it is not necessarily related to the size of the spawning population. Moreover, there is not necessarily a correlation between the biomasses of the capelin and its predators, as Akenhead *et al.* (1982) note for Atlantic cod. It is also possible that capelin were present and abundant off Witless Bay in 1981 but, because of high surface temperatures, were spawning in deep water instead of on the beaches (e.g. Templeman 1948). This might have placed them below the puffins' diving limits (see above). The failure of the Witless Bay puffins to find capelin in 1981 may therefore have been the result of a scarcity of fish brought about either by naturally occurring factors, by the fishery, or by a change in the behaviour of the spawning fish, or by a combination of all of these. It is therefore not possible to go further on the present evidence.

## 8. Discussion

Capelin are extremely important to many predators in eastern Newfoundland waters; this is especially true of the seabirds. It is clear that the more specialized species, such as murre and puffins, have few acceptable alternative prey available to them when capelin are scarce off Newfoundland. The reproductive strategy of such birds is to maintain a stable population by balancing a low natural adult mortality rate against a low annual reproductive rate combined with a long period of pre-breeding adolescence (e.g. Ashmole 1971, see also Table 1). Up to a point, the populations can remain stable in the face of irregular, natural environmental perturbations which temporarily increase adult mortality or reduce reproductive success; the response of Scottish puffins to natural fluctuations in the abundance of their various prey species (Harris and Hislop 1978) is a case in point. However, such a strategy makes them especially vulnerable to additional, repeated mortalities directly or indirectly imposed on them, in Newfoundland and elsewhere, by such human activities as excessive hunting, drownings in gill nets, oil pollution, and competition from the fisheries. The almost complete breeding failure of the puffins on Rost since 1969 (Lid 1981), apparently due to the overfishing of their preferred prey, will inevitably result in a massive decline in the population as the older birds die off, and the species' low reproductive rate will make the population slow to recover if and when the herring stock recovers. It is important to keep a close watch on the comparable recent events in the puffin population at Witless Bay to determine the extent to which these puffins are also being affected by fluctuations in their principal prey, capelin. Such monitoring will provide us with advance warning of the state of the puffin population and, by extension, of the capelin stocks as well.



For this, we need more information about the feeding ecology of seabirds in general, at Witless Bay and elsewhere. We also need to know much more about the population biology of capelin. It is unfortunate that the capelin fishery has expanded faster than its scientific base, and that most current research on the species is devoted to stock assessment techniques and other aspects of management, rather than basic biology (Carscadden, this volume). Even here, there is still no reliable method of assessing the *absolute* as opposed to the relative biomasses of capelin stocks. This makes it almost impossible to judge how realistic are the quotas set for the capelin fishery, not just in relation to the capelin population as a whole, but also to the requirements of the populations of the various animals which prey on these fish. To allow for these unknown factors the catch limits are purposely set at conservative levels: 10% of the projected capelin "surplus," or 30 000 t, in subarea 3L in 1981 (NAFO 1981). But are they conservative enough? Even if we ignore the importance of *local* as opposed to overall capelin abundance, and the inaccessibility of the deep schools to most seabirds, the evidence suggests that they are not. The overall biomass estimates, for all their limitations, seem to show a decline of the order of 75–90% in capelin biomass off eastern Newfoundland during the 1970s, perhaps to a level below that needed to support the predators' populations at the levels they held only 20 years ago (see above, and Table 5). If this is true, the predators of the capelin can respond only by switching to an alternative prey — an unlikely option for seabirds, at least — or by reducing their own biomass by emigration or starvation. In the latter case we have too few data to predict whether the decline in the populations of the higher predators will be total or only partial, and there is a danger that the answers will not become apparent until it is too late for remedial measures. This is an unsatisfactory situation from every point of view.

In conclusion, we are struck by the extreme vulnerability of ecosystems which depend on a single central prey species, however abundant that species may appear to be. We find it very disturbing that human exploitation should already have reached a high level without any proper means of understanding, or even measuring, its effects on the populations of such species, let alone on those of the predators which depend on such prey.

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