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Pelagic Feeding Ecology of Dovekies, *Alle alle*, in Lancaster Sound and Western Baffin Bay

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ABSTRACT. Adult (AD), subadult (SA), and hatching year (HY) dovekies were collected at sea in 1976, 1978, and 1979 ($n = 410$) for food habits studies. In May and June, AD and SA dovekies ate mostly copepods (99.8% of dry weight in AD, 100% in SA); in August, amphipods became more important (59% in AD, 90% in SA). Adult males accompanied chicks to sea where both groups fed largely on *Parathemisto* amphipods (99.7% in AD, 97% in chicks). Once abandoned by the adults, HY dovekies ate *Parathemisto* (59.8% of dry weight), *Apherusa glacialis* (13.6%), and *Onisimus glacialis* (5.6%) amphipods; arctic cod (*Boreogadus saida*) (14.5%); calanoid copepods (5.5%); and other items (1%). Seasonal changes in diet were, in part, related to a presumed seasonal increase of suitable amphipods in surface waters.

HY dovekie diets varied geographically and with year. Some food taxa were larger in dovekies collected in waters associated with an intrusive current flowing into and out of the mouth of Lancaster Sound than in those collected in offshore Baffin Bay. In 1978, *Parathemisto* and *Apherusa glacialis* were smaller than in 1979 or 1976; HY dovekies apparently compensated by taking more copepods. HY dovekies were smaller on a given date in 1978 but ate similar total amounts of food and grew at similar rates in all three years. The small size of amphipods in 1978 was probably due to unusually late breakup of ice and its probable inhibitory effects on primary and secondary production.

In 1978, many non-breeding (AD and SA) dovekies molted in pack ice that persisted until mid-August. In 1979, when pack ice dispersed early, no non-breeding dovekies were collected in August.

Key words: dovekie, *Alle alle*, trophic relationships, pelagic seabird ecology, arctic marine systems, molt

RÉSUMÉ. Les mergules nains adultes (AD), enfants (SA) et bébés (HY) ont été relevés en mer en 1976, 1978 et 1979 ($n = 410$) pour l'étude de leurs habitudes alimentaires. En mai et juin, les mergules nains adultes et bébés mangeaient principalement des copépodes (99.8% du poids sec pour AD, 100% pour HY), en août, les amphipodes deviennent plus importants (59% pour AD, 90% pour HY). Les males adultes accompagnent les poussins à la mer où l'ensemble du groupe s'alimente largement de *Parathemisto*, amphipodes (99.7% pour AD, 97% pour HY). Lorsqu' abandonnés par les adultes, les mergules nains HY mangeaient des *Parathemisto* (59.8% du poids sec): *Apherusa glacialis* (13.6%) et *Onisimus glacialis* (5.6%) amphipodes: morues arctiques *Boreogadus saida* (14.5%): calanoid copépodes (5.5%): et autres (1%). Les changements saisonniers dans la diète sont, en partie, rattachés aux augmentations saisonnières présumées des amphipodes disponibles à la surface de l'eau.

La diète des mergules nains HY différait géographiquement et selon l'année. Les mergules nains receuillis dans eaux associées aux courants intrusifs à l'intérieur et à l'extérieur de l'embouchure du détroit de Lancaster avait en général une classification de nourriture plus grande que celle relevée sur les oiseaux receuillis au large de la baie de Baffin. En 1978, *Parathemisto* et *Apherusa glacialis* étaient plus petits qu'en 1979 ou 1976: les mergules nains HY ont apparemment compensé cette difference en prenant plus de copépodes. Les mergules nains HY étaient plus petits à une date donnée, en 1978, mais mangeaient une quantité de nourriture totale similaire et croissaient au même rythme au cours des trois ans. La petite taille des amphipodes en 1978 était probablement due à l'inhabituelle retard du bris des glaces et ceci a probablement influé sur les productions primaires et secondaires.

En 1978, plusieurs mergules nains (AD et SA) non fécondés se sont assemblés sur les glaces en dérive qui ont persisté jusqu'à la fin d'août. En 1979, lorsque les glaces en dérive se sont dispersees tôt, aucun mergule nain non fécondés n'a été receuillis en août.

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INTRODUCTION

The dovekie (*Alle alle*) is the smallest alcid inhabiting the Atlantic Ocean and may be the world's most abundant alcid (Salomonsen, 1950; Norderhaug, 1970). Some of the largest colonies of these marine diving birds are located along the west coast of Greenland in northern Baffin Bay. Offshore from the coasts of Canada's eastern arctic islands, dovekies are common birds from May to October (Brown *et al.*, 1975; Renaud *et al.*, 1982), but they do not nest on the Canadian side of Baffin Bay.

Several recent studies of the food habits of dovekies have focused on the diet of chicks at the colonies (Norderhaug, 1970, 1980; Golovkin *et al.*, 1972; Zelickman and Golovkin, 1972; Evans, 1981; Roby *et al.*, 1981; Bradstreet *et al.*, 1981). There are few data about the diet of birds when at sea. This is not surprising in view of the logistic problems of collecting dovekies in the northern, ice-rich waters that they prefer.

In this paper, I describe the diets of various age classes of dovekies at sea and provide information on the size and condition of birds in various years of study. I concentrate on the diet of hatching year (birds of the year) dovekies and relate year-to-year variability in their diet to growth and various characteristics of the marine waters in which they occur. This study complements a study of the diet of dovekie chicks at Greenland colonies in 1978 and 1979 (Roby *et al.*, 1981; Bradstreet *et al.*, 1981). Together, these studies provide new information on the pelagic ecology of these birds during the breeding season.

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METHODS

Boat- and ice-based collections of dovekies at sea in the Lancaster Sound and western Baffin Bay area were made during 1976, 1978, and 1979. Collections (n = 410) spanned the period from the arrival of the birds in May until most had departed in mid-September.

Dovekies were shot in each of three years (Table 1, Fig. 1). Collection procedures followed Bradstreet (1980). Soon after death, birds were weighed, their gonads were removed, measured, and preserved, and any food items found in the esophagus, proventriculus, and gizzard were removed and stored in 10% neutral formalin. Carcasses were then frozen for later inspection.

During laboratory inspections, some (rarely all) of the following measurements, weights, and determinations were made on each bird. Measurements included length of flattened left and/or right wing, length of left and/or right tarsus, culmen length (from edge of feathers at dorsal base and/or from anterior edge of nostril to tip), bill depth (at ventral notch on lower mandible and/or at anterior edge of nostril), and bill width at the gape. Tarsi and bill measurements were ± 0.1 mm; wing measurements were ± 1.0 mm. The breast muscles (*pectoralis, supracoracoideus* and *coracobrachialis*) on one side of the sternum and the entire liver were weighed (both ± 0.1 g). The bursa, if present, was removed and preserved, and the amount of fat deposition was estimated visually and recorded on an ordinal scale of none (0), through light (2) and moderate (4), to heavy (6) and very heavy (8).

Birds were assigned to age classes using several criteria. Adults (AD) were classified as fully-grown birds with no bursae; subadults (SA) were smaller in size than adults and had bursae. The classification 'after hatching year' (AHY—birds more than one calendar year old) was used in 1976 when bursae were not looked for and adults could not be absolutely separated from subadults. Hatching year (HY) birds (birds collected in the calendar year of hatch) were much smaller than subadults, had poorly ossified skeletons, and had bursae. Chicks (CH) were defined as those birds of the year that were still accompanied by an adult.

Prey in the stomach was identified and sorted, usually to species, and lengths of whole food items were measured and assigned to appropriate size categories. The measurement taken, in the case of crustaceans, was from the front of the rostrum or eye to the tip of the urosome or uropod; and in the case of arctic cod (*Boreogadus saida*), from the tip of the snout to the fork in the tail. Copepods were assigned to 1 mm length categories, other crustaceans to 3 mm categories, and fish to 10 mm categories.

Partial food organisms were found in almost all stomachs examined. Total lengths of broken or partially digested food items were estimated on the basis of measured parts, following Bradstreet (1980). Empirically determined relationships between lengths and dry weights were then used to convert length-frequency distributions into estimates of the relative dry weight of each taxon in the diet (Bradstreet, 1980; Bradstreet *et al.*, 1981). Dry weight values better represent the energetic importance of various taxa in the

TABLE 1. Numbers of dovekies collected in Lancaster Sound and western Baffin Bay, 1976-1979

Year	Date	Collection Location			No. Collected (no. with empty stomachs)	Age/Sex Composition[b]
		code[a]	N Lat.	W Long.		
1976	3 July	GI	74°29′	95°22′	14 (2)	4 AHY-M, 10 AHY-F
	22 July	EM	74°06′	81°30′	1 (1)	1 AHY-M
	29 Aug.	MM	74°07′	82°37′	20 (5)	9 HY-M, 10 HY-F, 1 HY-U
	29 Aug.	EM	74°06′	81°30′	21 (8)	11 HY-M, 7 HY-F, 3 HY-U
	1 Sep.	WM	74°12′	87°57′	15 (5)	9 HY-M, 6 HY-F
	4 Sep.	EM	74°06′	81°30′	20 (0)	8 HY-M, 10 HY-F, 2 HY-U
	8 Sep.	CS	74°32′	80°20′	12 (6)	9 HY-M, 3 HY-F
	11 Sep.	WM	74°07′	82°37′	10 (2)	5 HY-M, 3 HY-F, 2 HY-U
1978	26 July	E4	74°11′	74°43′	10 (2)	1 AD-M, 5 SA-M, 4 SA-F
	11 Aug.	I4	72°45′	71°47′	1 (1)	1 AD-M
	24 Aug.	A4	74°56′	76°52′	30 (8)	10 AD-M, 1 AD-F, 3 SA-F, 9 HY-M, 5 HY-F, 1 HY-U, 1 U-F
	25 Aug.	A2	74°55′	78°40′	15 (4)	2 AD-M, 6 HY-M, 4 HY-F, 1 HY-U, 1 U-M, 1 U-F
	1 Sep.	A2	74°55′	78°40′	26 (5)	1 AD-M, 17 HY-M, 5 HY-F, 1 HY-U, 2 U-M
	5 Sep.	D4	74°30′	77°19′	25 (0)	1 SA-F, 14 HY-M, 7 HY-F, 2 HY-U, 1 U-F
1979	21 May	OP	73°35′	74°55′	33 (14)	15 AD-M, 18 AD-F
	22 May	OP	73°35′	74°20′	58 (7)	30 AD-M, 24 AD-F, 1 SA-M, 2 SA-F
	22 June	1E	72°45′	76°00′	3 (2)	1 AD-F, 1 SA-F, 1 SA-U
	21 Aug.	3E	74°58′	76°29′	3 (7)	11 AD-M, 4 HY-M, 4 HY-F, 8 CH-M, 3 CH-F, 1 CH-U
	25 Aug.	CH	73°46′	80°23′	2 (0)	1 HY-M, 1 HY-F
	25 Aug.	13A	73°21′	76°29′	20 (2)	1 AD-U, 10 HY-M, 6 HY-F, 1 CH-F, 2 HY-U
	6 Sep.	CY	73°53′	82°07′	43 (20)	16 HY-M, 22 HY-F, 5 HY-U
All years					410 (101)	

[a]Codes refer to oceanographic stations, as shown on Fig. 1. GI (Griffith Island) is not shown on the figure.

[b]Codes are as follows: M = male, F = female, U = unknown, AD = adult, SA = subadult, AHY = after hatching year, HY = hatching year, CH = chick (at sea and accompanied by an adult male).

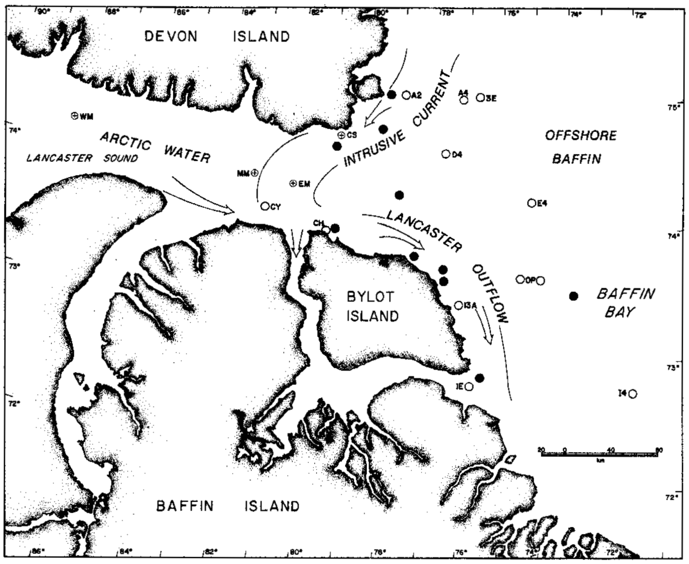

FIG. 1. Map of the study area. Open circles indicate areas where birds were collected (see Table 1); vertical zooplankton hauls were conducted at some collection locations and in other areas indicated by closed circles. Surface water circulation features, based on physical measurements (currents, conductivity, temperature), are *fide* D.B. Fissel, Arctic Sciences Ltd.

diet than do occurrence or frequency values; but occurrence and frequency values give other types of information. Herein, all three measures are used. Occurrence is the number of stomachs containing a taxon as a percentage of the total numbers of stomachs with food. Frequency is the number of items of a given taxon as a percentage of all food items.

Some food items could not be identified to species and were assigned to a broader taxon (genus, family, order). Such items were assigned average lengths and dry weight values determined from species in the appropriate taxonomic and size categories, and were incorporated into the descriptive analyses of diet. When statistical tests were performed, however, such items were excluded from the analyses.

An attempt was made to collect only birds that appeared to be feeding, but exigencies of weather and scheduling often meant collections had to be made under less than ideal conditions. In such situations, all dovekies were collected, without predetermining whether each individual was actively feeding. Fully 25% of the 410 dovekies collected had empty stomachs; these birds are ignored in all diet analyses but considered in comparisons involving specimen measurements, weights and condition.

Numbers of food items found per dovekie stomach varied significantly ($P<0.01$) among the various collections of birds (see below). Therefore statistical comparisons were necessarily based on standardized data. Standardization involved representing the number of a food taxon in a given stomach as a percentage of the total number of food items in that stomach. To be consistent, dry weight values were also standardized in a similar manner. After standardization, statistical comparisons were made between the relative numbers or dry weights of various food taxa in different groups of birds. Results from each bird (even if a particular bird contained no items of the prey taxon in question) constituted a unit of observation. When sizes of a food taxon taken by two or more groups of birds were compared, only birds containing measured items of the food taxon in question were considered, and the mean length of that taxon in each stomach constituted a unit of observation. Lengths of food items were not standardized.

Statistical analyses of specimen measurements and weights were based on parametric tests; analyses of diet and fat levels were based on non-parametric tests. Probability values <0.01 are considered significant.

In this study, food items found in the esophagi, proventriculi, and gizzards of collected birds were combined prior to item identification, enumeration, and measurement. Differential digestibility of various taxa could bias assessments of dietary importance (cf. Bradstreet, 1980). In dovekies, however, where the bulk of the diet is comprised of soft-bodied crustaceans, it is unlikely that one taxon is effectively digested before another; in no stomach, for example, were most or all of the copepods partially digested while other taxa remained whole. Also, unlike Zelickman and Golovkin (1972), I never observed layering of various taxa in the stomach tracts. Furthermore, my method of estimating lengths and weights at ingestion from measurements of broken and partially digested organisms compensates at least partially for effects of differential digestion. Thus, in this study of dovekie feeding, interpretations are probably negligibly influenced by any biases due to differential digestion.

At sea, dovekie abundance and distribution were determined during 10-minute watches from a moving ship using standard PIROP techniques (Brown *et al.*, 1975). Age classes of birds at sea could not be determined. Actual counts were used to compare results between 1978 and 1979.

RESULTS

Adults, Subadults, and Chicks

Diet. Dovekies arrive in eastern Lancaster Sound and northern Baffin Bay in May, probably en route to their large breeding colonies in northwest Greenland. In 1979, Renaud *et al.* (1982) estimated that in a 336 000 km^2 area north and east of Bylot Island (their northwest sector), 695 000 dovekies were present on 17-21 May and 1.9 million dovekies were present on 24-26 May. Five collections of dovekies were made in two parts of this sector on 21-22 May (Table 1, Fig. 1). Most (88) of the birds collected were adults; three subadults were also taken (Table 1). All birds were collected in small areas of open water within vast areas of pack ice.

Many (21 of 88) of the adult dovekies collected in May had empty stomachs (Table 1). Those stomachs with food contained well-digested copepods (Table 2) and most of the copepods that were identified to species were *Calanus glacialis*. As a group, copepods dominated the diet of adults in May (Table 2). There were no significant differences in the standardized numbers (Kruskal-Wallis $H = 2.82$, df $= 4$, $P > 0.1$), standardized dry weights ($H = 2.82$, $P > 0.1$), or mean lengths ($H = 12.17$, $P < 0.05$) of calanoid copepods among the five collections. Likewise, adult male and adult female dovekies took similar standardized numbers and dry weights, and similar lengths of calanoids (all Mann-Whitney $P > 0.05$).

Based on collections made during different years of study, there seemed to be a seasonal change in the diet of adult dovekies. Copepods dominated the dry weight diets of adult dovekies collected in May 1979 and AHY birds from July 1976 (99.8% and 74%, respectively), but were less important in adults collected in August 1978 (10%) and August 1979 (0.1%, Table 2). The August diet was dominated by fish and hyperiid amphipods in 1978 and by hyperiids alone in 1979. The differences between the two August collections suggest that year and (or) status may be at least as important as season in determining diet. The adults collected in August 1978 could have been failed, non-, or post-breeders (none were with chicks); whereas adults collected in August 1979 were all active breeders (i.e. still accompanying chicks at sea).

In May-June 1979, the diet of four subadult dovekies, like that of adults, was dominated by copepods (Table 3). Like adults, subadults fed less on copepods in summer (8% of dry weight) than in spring (100%). In summer, the diet of subadults was dominated by amphipods, particularly *Apherusa glacialis* (77%). Mysids were also taken in summer.

In August 1979, the 11 adults collected at sea were still accompanying chicks. All 11 adults were males (binomial $P = 0.001$). Percent composition of the diet of dovekie chicks (based on eight stomachs, 131 food items, and an estimated dry weight at ingestion of 420.6 mg) was as follows:

TAXON	OCCURRENCE	FREQUENCY	DRY WEIGHT
Parathemisto libellula	25.0	5.3	4.5
P. spp.	87.5	90.8	92.3
All Hyperiidae	87.5	96.2	96.8
All Calanoida (unid.)	12.5	2.3	0.1
Boreogadus saida	25.0	1.5	3.1

Diet of the chicks was very similar to that of the 11 adult males which accompanied them (Table 2). There were no adult *vs.* chick differences in the standardized numbers and dry weights, or mean lengths of all *Parathemisto* (all Mann-Whitney $P > 0.1$).

Measurements. Considering only adults, males and females collected in May had similar wing lengths (Table 4, *t*-test

TABLE 2. Percent composition of adult (AD) and after hatching year (AHY) dovekie diets, 1976-1979[a]

Taxon	AD — May 1979			AHY — Jul. 1967			AD — Aug. 1978			AD — Aug. 1979		
	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.
Parathemisto libellula	—	—	—	—	—	—	40.0	4.8	5.1	63.6	8.4	9.9
P. spp.	—	—	—	—	—	—	60.0	10.4	8.8	100.0	90.3	89.7
Hyperia galba	1.5	P[b]	0.2	—	—	—	—	—	—	—	—	—
All Hyperiidae	1.5	P	0.2	—	—	—	60.0	15.2	13.8	100.0	98.7	99.7
Onisimus glacialis	—	—	—	—	—	—	20.0	1.2	1.0	—	—	—
O. spp.	—	—	—	16.7	0.4	5.0	—	—	—	9.1	0.4	0.1
All Lysianassidae	—	—	—	16.7	0.4	5.0	20.0	1.2	1.0	9.1	0.4	0.1
All Calliopiidae (*Apherusa glacialis*)	—	—	—	25.0	2.5	21.0	—	—	—	—	—	—
ALL AMPHIPODA	1.5	P	0.2	50.0	3.0	26.1	60.0	16.4	14.9	100.0	99.2	99.7
Euchaeta spp.	—	—	—	—	—	—	—	—	—	9.1	0.4	0.1
Calanus glacialis	47.8	17.3	17.1	25.0	3.8	0.8	20.0	1.7	0.1	—	—	—
C. hyperboreus	1.5	0.1	0.6	50.0	85.3	71.2	30.0	74.0	9.7	—	—	—
C. spp.	97.0	82.6	82.0	58.3	7.9	2.0	30.0	7.1	0.3	—	—	—
ALL COPEPODA	99.0	100.0	99.8	66.7	97.0	73.9	40.0	82.7	10.0	9.1	0.4	0.1
ALL CRUSTACEA	100.0	100.0	100.0	100.0	100.0	100.0	60.0	99.2	24.9	100.0	99.6	99.8
ALL FISH (*Boreogadus saida*)	—	—	—	—	—	—	40.0	0.8	75.1	9.1	0.4	0.2
n	67 stomachs	3582 items	432.6 mg	12 stomachs	708 items	341.2 mg	10 stomachs	481 items	1459 mg	11 stomachs	237 items	1067.6 mg

[a]I did not look for bursae in the July 1976 collection. Based on comparative gonad size (with the May 1979 collection), all birds collected in July 1976 were probably adults.
[b]P = present in amounts <0.005%.

$P>0.1$) but males were significantly larger than females in whole weight, tarsi lengths, culmen length, and breast weight (all t-test $P<0.001$). Fat levels in males (mean value 4.4) and females (5.1) were similar ($\chi^2 = 7.09$, df $= 2$, $P<0.05$).

Adult males collected in July-August 1978 and August 1979 were similar ($P>0.01$) in all measurements listed in Table 4 except breast weight ($P<0.01$). Adult males collected in May and August 1979 were also of similar size; only culmen length differed significantly ($P<0.01$) between these two months. Too few adult females were collected in August to permit statistical comparisons.

Subadult males collected in July-August 1978 were similar to subadult females in all measurements (Table 4) but breast weight ($P<0.01$). Subadult males were smaller than adult males collected at the same time (July-August 1978) in whole weight, wing length, and liver weight ($P<0.01$); other measurements were similar. Subadult females collected in July-August 1978 were significantly smaller ($P<0.01$) than adult females collected in May 1979 in all measurements but tarsi (Table 4).

TABLE 3. Percent composition of subadult dovekie diets in 1978 and 1979

	May-June 1979			July-August 1978		
Taxon	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.
Parathemisto libellula	—	—	—	20.0	0.7	1.8
P. spp.	—	—	—	30.0	3.8	10.9
All Hyperiidae	—	—	—	40.0	4.4	12.7
All Lysianassidae (*Onisimus* spp.)	—	—	—	10.0	0.1	0.7
All Calliopiidae (*Apherusa glacialis*)	—	—	—	60.0	71.3	76.9
ALL AMPHIPODA	—	—	—	80.0	75.8	90.3
ALL MYSIDACEA (*Mysis* spp.)	—	—	—	10.0	0.6	1.7
Metridia longa	—	—	—	40.0	10.0	0.3
Calanus glacialis	—	—	—	30.0	0.8	0.1
C. hyperboreus	—	—	—	40.0	11.5	7.4
unident. calanoida	75.0	100.0	100.0	50.0	1.4	0.2
ALL COPEPODA	75.0	100.0	100.0	90.0	23.6	8.0
ALL CRUSTACEA	75.0	100.0	100.0	100.0	100.0	100.0
n	4 stomachs	44 items	5.3 mg	10 stomachs	1330 items	1044.1 mg

Molt. In 1978 considerable pack ice remained in northern Baffin Bay during July-August (NOAA satellite imagery). Dovekies associated strongly with this pack ice. It seems that various age groups of dovekies were most abundant in the study area at different times:

PERIOD	ADULT	SUBADULT	HATCHING YEAR
26 July-11 August	2	9	0
24-25 August	13	3	26
1-5 September	1	1	46

The subadults collected in late July to mid-August had brown wings; those collected in late August had new, black primaries that were almost full grown; and the one collected in early September had fully grown, new primaries (Fig. 2). In contrast, adults collected from late July to mid-August had darker wings than subadults. By late August, many adults (9 of 13) still had old dark wings but four birds had previously dropped their old primaries and had new primaries less than one-quarter grown (Fig. 2). These birds were flightless. Hatching year dovekies formed increasing proportions of the total numbers collected at sea as the season progressed in 1978.

By late August 1978, most of the pack ice had retreated southwards from the study area; few adult and subadult dovekies were collected after 1 September. Pack ice was not prevalent in northern Baffin Bay during July-September 1979 (NOAA imagery) and no adults (except those accompanying chicks) or subadults were collected.

TABLE 4. Measurements (mean ± 1 SD [n]) of adult (AD) and subadult (SA) dovekies collected at sea in 1978-1979

	Males				Females		
Measurement	1978 SA Jul.-Aug.	1978 AD Jul.-Aug.	1979 AD Aug.	1979 AD May	1978 SA Jul.-Aug.	1978AD Aug.	1979 AD May
Whole weight, g	155.4±2.9 (5)	177.7±8.7 (13)	177.4±9.3 (11)	174.7±8.5 (45)	151.8±10.1 (8)	166 (1)	167.3±10.1 (43)
Left wing, mm[a]	113.8±1.5 (3)	119.0±3.5 (11)	121 ±2.0 (11)	120.3±2.7 (44)	109.2± 5.0 (6)	—	120.7± 2.9 (43)
Right wing, mm[a]	113.8±1.8 (5)	118.6±3.3 (11)	120.9±1.7 (11)	120.5±2.8 (45)	108.3± 5.9 (6)	—	120.7± 3.0 (42)
Left tarsus, mm	20.4±0.3 (5)	20.5±0.5 (13)	21.0±0.7 (11)	21.3±0.7 (44)	20.3± 0.4 (8)	20.5 (1)	20.8± 0.7 (43)
Right tarsus, mm	20.5±0.3 (5)	20.3±0.6 (13)	20.7±0.6 (10)	21.3±0.8 (43)	20.1± 0.4 (8)	20 (1)	20.7± 0.8 (42)
Culmen length (nostril-tip, mm)	11.6±0.5 (5)	11.4±0.6 (13)	11.2±0.4 (9)	12.0±0.5 (43)	10.5± 0.3 (8)	10.5 (1)	11.4± 0.5 (42)
Bill depth (at notch, mm)	6.3±0.4 (5)	6.6±0.5 (10)	—	—	5.8± 0.4 (6)	6.4 (1)	—
Breast weight, g	15.0±0.4 (5)	14.3±1.0 (13)	16.0±1.0 (11)	16.3±1.0 (39)	12.0± 1.4 (8)	13.5 (1)	15.4± 1.0 (36)
Liver weight, g	5.9±0.3 (5)	7.0±0.9 (12)	8.4±1.6 (10)	—	5.3± 0.6 (7)	7.1 (1)	—

[a]Values presented do not include data from birds in active primary molt during Jul.-Aug.

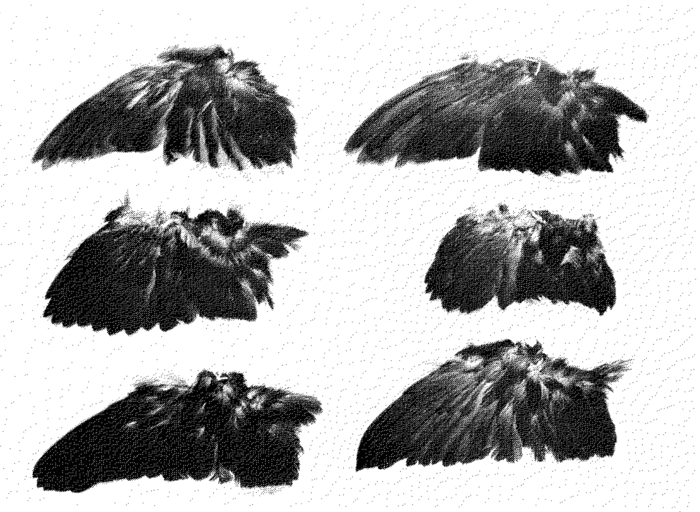

FIG. 2. Flattened wings of dovekies collected in 1978. From top to bottom the three left wings are from: a subadult collected on 26 July — note dull (brown) wings and heavily worn primary tips; a subadult collected on 24 August — primaries are dark, tips unworn, and almost full grown; and a subadult collected on 5 September — primaries fully grown. From top to bottom the three right wings are from: an adult collected on 26 July — note darker wing than subadult from same date and less-worn primary tips; an adult collected on 24 August — note that all old primaries are missing and that new primaries are only partially grown; and a HY bird collected on 6 September — primaries almost fully grown.

Counts of birds at sea during the 1-15 August period (i.e., before hatching year birds were present in the study area; Table 1) also suggest that greater numbers of adult and subadult birds summered in the study area (western side of Baffin Bay between Ellesmere Island and Clyde) in 1978 than in 1979. Numbers seen per 10-minute watch were significantly greater in 1978 (23 ± 1 SD 59 birds; $n = 89$ counts) than in 1979 (1 ± 2 birds; $n = 244$; Mann-Whitney $z = 3.76$, $P < 0.001$).

Hatching Year Dovekies

In all three years of study, I collected HY dovekies during their fall migration southwards through the study area in late August and early September (Table 1). There were no sex-related differences in the actual numbers or actual dry weights of all food items found in the stomachs examined (Table 5). There were, however, among-year differences in the actual numbers (but not dry weights) of food items ingested. Numbers ingested were higher in 1978 and 1979 than in 1976 (Table 5).

In each of the three years and by each method of analysis, amphipods (especially *Parathemisto*) dominated the diet of southbound hatching year dovekies (Table 6). In some years, copepods occurred in many stomachs, and formed nearly half of the total number of food items present but, because of their small size relative to amphipods, copepods generally comprised small percentages of dry weight diet. Fish (*Boreogadus saida*) were important in HY dovekie diets (by dry weight) in 1976 (28%) and to a lesser degree in 1978 (9%) but not in 1979 (<1%). Considering all years together, the five major taxa in terms of dry weight were all *Parathemisto* (59.8%), *Boreogadus saida* (14.5%), *Apherusa glacialis* (13.6%), *Onisimus glacialis* (5.6%), and all calanoid copepods (5.5%).

Year-to-year variation in diet. The standardized numbers and dry weights and the mean lengths of some of the five major food taxa found in HY dovekie stomachs varied significantly among years (Table 7, Fig. 3). There were no significant year-to-year differences in standardized numbers or dry weights of *Onisimus glacialis* and *Boreogadus saida* taken by dovekies ($P > 0.1$ in all comparisons) but year-to-year differences were significant ($P < 0.01$) for other taxa.

Amphipods made greater relative contributions to diet in 1976 and 1979 than in 1978; the reverse was true for copepods (Table 7). Amphipods were mostly of two taxa, all *Parathemisto* and *Apherusa glacialis*. In both cases item size decreased significantly from 1976 to 1979 to 1978. Calanoid size did not vary significantly among the three years (Fig. 3).

In addition to inter-year variation in diet, there was considerable intra-year variation (Table 8). Given the gen-

TABLE 5. Numbers and dry weights (mean ± 1 SD [n]) of all food items of hatching year (HY) dovekies, August-September 1976-1979

All food items	Year	HY males	HY females	Mann-Whitney z[a]	All HY birds[b]
Number	1976	37.5 ± 85.1 (31)	17.3 ± 27.2 (23)	0.062	27.1 ± 65.0 (58)
	1978	65.1 ± 61.5 (39)	62.3 ± 51.2 (18)	0.103	62.7 ± 57.0 (61)
	1979	52.5 ± 79.9 (19)	60.0 ± 94.1 (24)	0.270	55.0 ± 84.9 (47)
Kruskal-Wallis H (df = 2)		12.36 ($P<0.01$)	9.39 ($P<0.01$)		25.35 ($P<0.001$)
Dry weight (mg)	1976	174.1 ± 244.5 (31)	117.6 ± 167.2 (23)	0.709	142.2 ± 209.6 (58)
	1978	124.5 ± 137.2 (39)	92.1 ± 79.8 (18)	0.301	111.3 ± 119.9 (61)
	1979	112.1 ± 120.9 (19)	121.7 ± 120.2 (24)	0.379	114.8 ± 116.4 (47)
Kruskal-Wallis H[a] (df = 2)		0.05[a]	1.13[a]		0.59[a]

[a]$P>0.1$ in each case.
[b]Includes HY birds that could not be sexed.

TABLE 6. Percent composition of HY dovekie diets, August-September 1976-1979

	1976			1978			1979			All years		
Taxon	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.	Occur.	Freq.	Dry wt.
Parathemisto libellula	—	—	—	57.8	9.3	19.1	52.1	8.1	22.1	33.7	7.1	12.2
P. spp.	56.9	17.5	30.2	76.6	39.7	55.6	93.8	31.2	64.3	73.4	32.6	47.6
Hyperia galba	—	—	—	—	—	—	2.1	P	0.1	0.5	P[a]	P
H. spp.	—	—	—	—	—	—	2.1	P	0.1	0.5	P	P
All Hyperiidae	56.9	17.5	30.2	76.6	49.0	74.7	95.8	39.4	86.5	73.9	39.7	59.8
Onisimus glacialis	18.1	7.1	11.5	23.4	0.6	2.3	8.3	0.2	0.7	17.4	1.8	5.6
O. spp.	—	—	—	1.6	P	0.1	4.2	0.1	0.8	1.6	P	0.1
All Lysianassidae	18.1	7.1	11.5	23.4	0.6	2.4	12.5	0.3	0.8	18.5	1.8	5.7
All Calliopiidae (*Apherusa glacialis*)	25.0	73.3	28.6	10.9	0.4	0.2	8.3	15.0	7.6	15.8	19.5	13.6
Gammarus wilkitzkii	11.1	0.6	1.1	1.6	P	0.1	4.2	0.2	0.4	6.0	0.2	0.6
G. spp.	—	—	—	1.6	P	0.1	2.1	0.2	0.4	1.1	0.1	0.1
Gammaracanthus loricatus	1.4	0.1	0.1	1.6	P	P	—	—	—	1.1	P	P
All Gammaridae	12.5	0.7	1.2	3.1	0.1	0.3	4.2	0.3	0.8	7.1	0.3	0.8
ALL AMPHIPODA	91.7	98.7	71.5	78.1	50.1	77.6	95.8	55.0	95.7	88.0	61.2	79.9
ALL MYSIDACEA (*Mysis oculata*)	1.4	0.1	P	—	—	—	—	—	—	0.5	P	P
Metridia longa	—	—	—	1.6	0.1	P	—	—	—	0.5	P	P
Calanus glacialis	—	—	—	29.7	0.8	0.1	18.8	5.1	0.3	15.2	2.1	0.1
C. hyperboreus	—	—	—	53.1	47.0	13.1	22.9	8.2	2.0	24.5	25.2	4.9
C. spp.	12.5	0.9	0.1	—	—	—	—	—	—	4.9	0.2	P
unident. calanoida	—	—	—	34.4	1.8	0.1	29.2	31.3	1.8	19.6	11.0	0.5
ALL COPEPODA	12.5	0.9	0.1	60.9	49.7	13.3	31.3	44.6	4.0	34.2	38.5	5.5
ALL CRUSTACEA	98.6	99.6	71.6	95.3	99.8	91.0	97.9	99.7	99.8	97.3	99.7	85.5
ALL OSTEICHTHYES (*Boreogadus saida*)	8.3	0.4	28.4	7.8	0.1	9.0	10.4	0.2	0.2	8.7	0.3	14.5
n	72 stomachs	1569 items	8250 mg	64 stomachs	3828 items	6790 mg	48 stomachs	2587 items	5397 mg	184 stomachs	7984 items	20437 mg

[a]P = present in amounts <0.005%.

TABLE 7. Statistical comparisons of the standardized numbers and dry weights of selected prey in the diets of hatching year dovekies, August-September 1976-1979

	Mean ± 1 SD			Kruskal-Wallis		
Standardized (%) composition[a]	1976 58 stomachs	1978 61 stomachs	1979 47 stomachs	*H* (df = 2)	*P*	Dunn's interpretations (χ = 0.01)
All *Parathemisto*						
Number	52.3 ± 45.7	48.3 ± 42.1	76.7 ± 36.8	18.27	<0.001	79>76>78
Dry weight	52.9 ± 46.9	55.8 ± 38.9	88.3 ± 24.5	24.83	<0.001	79>78>76
All *Onisimus*						
Number	11.3 ± 27.1	1.0 ± 2.6	0.2 ± 0.6	3.48	>0.1	—
Dry weight	13.2 ± 31.1	3.3 ± 10.6	0.9 ± 3.4	3.03	>0.1	—
Apherusa glacialis						
Number	23.5 ± 38.0	1.3 ± 8.6	2.7 ± 14.5	14.20	<0.001	76>79>78
Dry weight	18.5 ± 34.2	1.1 ± 7.3	2.8 ± 13.5	13.76	<0.01	76>79>78
All amphipoda						
Number	91.2 ± 22.4	50.8 ± 43.2	79.7 ± 34.5	30.51	<0.001	76>79>78
Dry weight	88.7 ± 29.6	60.3 ± 39.8	92.4 ± 18.5	29.22	<0.001	76=79>78
All Calanoida						
Number	4.9 ± 17.0	49.1 ± 43.3	19.9 ± 34.7	37.76	<0.001	78>79>76
Dry weight	2.9 ± 15.5	36.2 ± 40.5	7.5 ± 18.5	38.81	<0.001	78>79>76
Boreogadus saida						
Number	0.1 ± 0.3	0.1 ± 0.3	0.1 ± 0.3	0.22	>0.1	—
Dry weight	40.4 ± 147.3	10.1 ± 41.3	0.2 ± 0.6	0.22	>0.1	—

[a]For standardization procedure, see Methods.

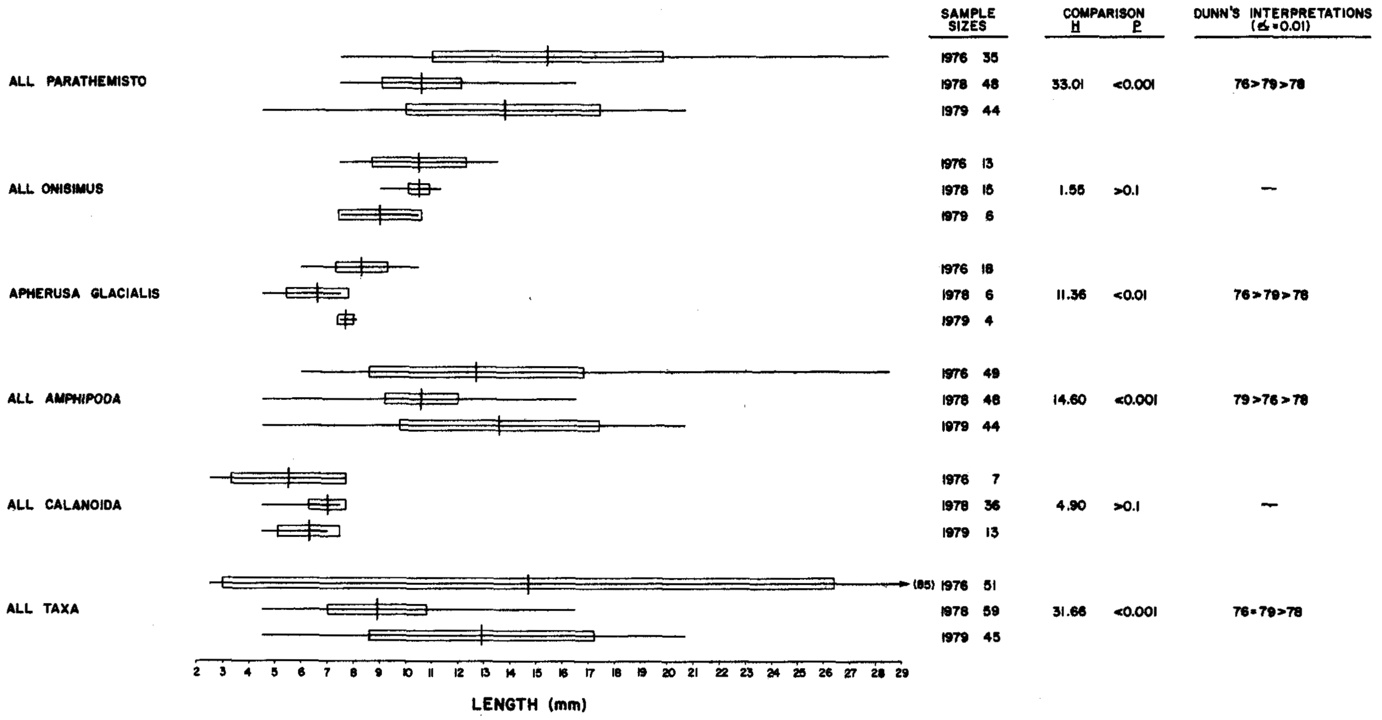

FIG. 3. Lengths of various food taxa found in the stomachs of HY dovekies collected in 1976, 1978, and 1979 showing mean (vertical line), standard deviation (open bar) and range (horizontal line). Sample sizes are number of stomachs containing various taxa.

TABLE 8. Significance (Kruskal-Wallis test) of among-collection within-year differences in the standardized numbers and dry weights of selected prey in the diets of HY dovekies collected in August-September of 1976-1979

Standardized (%) composition[a]	1976 6 collections		1978 4 collections		1979 collections[b]	
	H	*P*	*H*	*P*	*H*	*P*
All Parathemisto						
Number	22.41	<0.001	37.07	<0.01	23.21	<0.001
Dry weight	22.92	<0.001	33.10	<0.01	22.07	<0.001
All *Onisimus*						
Number	14.06	<0.02	8.72	<0.05	9.02	<0.02
Dry weight	12.83	<0.05	7.79	<0.1	9.02	<0.02
Apherusa glacialis						
Number	11.56	<0.05	3.27	>0.1	(35)[c]	>0.1
Dry weight	11.15	<0.05	2.99	>0.1	(35)[c]	>0.1
All Amphipoda						
Number	12.72	<0.05	36.01	<0.001	21.91	<0.001
Dry weight	14.00	<0.02	19.17	<0.001	20.58	<0.001
All Calanoida						
Number	13.03	<0.05	36.96	<0.001	28.34	<0.001
Dry weight	13.35	<0.05	36.66	<0.001	28.34	<0.001
Boreogadus saida						
Number	7.67	>0.1	0.98	>0.1	0.23	>0.1
Dry weight	7.93	>0.1	0.86	>0.1	0.37	>0.1

[a]For standardization procedure, see Methods.
[b]HY dovekies were collected at 4 areas in 1979 (Table 1). However, only two birds were collected at the Cape Hay (CH) station; this area is excluded from the analysis.
[c]No *A. glacialis* were found in dovekies collected in one of three areas. Probabilities are based on Mann-Whitney *U* statistics.

erally great variability among collections made at different sites within a given year, it is not possible to ascribe among-year differences solely to year effect.

Diet in various surface water zones. Fissel *et al*. (1980) used current meters (depth 35 m), satellite-tracked drogues (4-11 m), and CTD (conductivity-temperature-depth) data to define broad-scale, near-surface circulation of the study area in 1978-79. From their work, I have broadly outlined four surface water zones (Fig. 1). Each collection location for HY dovekies and/or vertical zooplankton tow (50 m-surface) was assigned to one of these four zones based on information provided by D.B. Fissel (Arctic Sciences Ltd., pers. comm.).

Diets of HY dovekies were substantially different in the four zones of surface water (Table 9). Generally, all *Parathemisto* and all amphipods were relatively more important in the diets of birds from the Intrusive Current and Arctic Water zones than in the diets of birds from the Lancaster Outflow and, especially, Offshore Baffin zones; the reverse was true for all calanoid copepods. The mean lengths of all *Parathemisto* taken by HY dovekies were similar in the Arctic Water and Intrusive Current zones and smaller in the Lancaster Outflow and, especially, Offshore Baffin zones. Mean lengths of calanoid copepods did not vary significantly among zones.

There were no among-zone differences in analogous comparisons involving all *Onisimus*, *Apherusa glacialis*, and *Boreogadus saida*. *B. saida* was so rarely encountered in the food samples (24 fish in 16 of 184 samples; Table 6) that the

TABLE 9. Statistical comparisons of selected prey in the diets of hatching year dovekies collected in different surface water zones, August-September 1976-1979[a]

	Mean ± 1 SD (n): Intrusive Current (IC)	Arctic Water (AW)	Lancaster Outflow (LO)	Offshore Baffin (OB)	Kruskal-Wallis: H	P	Dunn's interpretations (χ = 0.01)
All *Parathemisto*							
% Number	76.8 ± 38.1 (80)	51.9 ± 48.4 (26)	43.4 ± 38.6 (19)	31.0 ± 34.9 (41)	26.01	<0.001	IC>AW=LO>OB
% Dry weight	76.8 ± 37.5 (80)	50.5 ± 50.4 (26)	71.2 ± 32.0 (19)	44.1 ± 37.0 (41)	21.24	<0.001	IC>AW=LO>OB
Mean length, mm	14.3 ± 4.1 (64)	14.3 ± 3.7 (15)	12.1 ± 2.7 (18)	10.2 ± 1.8 (30)	29.85	<0.001	IC=AW>LO>OB
All Amphipoda							
% Number	95.6 ± 17.1 (80)	85.0 ± 30.3 (26)	50.8 ± 39.5 (19)	32.0 ± 35.4 (41)	75.04	<0.001	IC>AW>LO>OB
% Dry weight	94.5 ± 20.2 (80)	80.2 ± 37.9 (26)	81.5 ± 25.8 (19)	48.1 ± 37.9 (41)	64.76	<0.001	IC>LO>AW>OB
Mean length, mm	13.2 ± 3.8 (71)	12.6 ± 4.2 (22)	11.8 ± 2.8 (18)	10.3 ± 1.7 (30)	13.95	<0.01	IC=AW=LO>OB
All Calanoida							
% Number	3.4 ± 16.3 (80)	8.7 ± 23.8 (26)	49.1 ± 39.5 (19)	67.9 ± 35.5 (41)	84.41	<0.001	OB=LO>AW=IC
% Dry weight	2.5 ± 15.7 (80)	6.4 ± 22.9 (26)	18.4 ± 25.8 (19)	48.9 ± 38.8 (41)	84.44	<0.001	OB>LO>AW=IC
Mean length, mm	4.8 ± 1.9 (7)	6.7 ± 1.2 (4)	6.3 ± 1.2 (13)	7.2 ± 0.3 (32)	12.22	<0.02	—

[a]For standardization procedure (% number, % dry weight) see Methods. Kruskal-Wallis probabilities were >0.01 for comparisons involving all *Onisimus, Apherusa glacialis* and *Boreogadus saida.*

tests are not meaningful. All *Onisimus* (probably all *O. glacialis*) and *A. glacialis* were closely associated with the undersurface of ice pans that drifted through all zones during all years (pers. obs.), and were of similar importance (and sizes) in the diets of dovekies collected in the four water masses. Elsewhere, *A. glacialis* and *O. glacialis* are also known to associate with the undersurface of ice (e.g. MacGinitie, 1955; Barnard, 1959; George and Paul, 1970; Golikov and Scarlato, 1973; Golikov and Averincev, 1977; Cross, 1982).

Dovekies were collected in the Intrusive Current zone in all three years and in the Offshore Baffin zone in both 1978 and 1979 (collections in the other two zones were made in only one year — 1976 [Arctic Water] and 1979 [Lancaster Outflow]). In the Intrusive Current zone, there were no among-year differences in the relative importances of all amphipods or all copepods (Table 10). In the Offshore Baffin zone, however, the importance of all amphipods was less in 1978 than in the few birds (n = 6) collected in 1979; the reverse was true for all calanoids.

TABLE 10. Among- and between-year differences in the importance of amphipods and calanoids in the diets of HY dovekies collected in two surface water zones

	Intrusive Current: All Amphipoda	Intrusive Current: All Calanoida	Offshore Baffin: All Amphipoda[b]	Offshore Baffin: All Calanoida[c]
% Number				
1976	96.2 ± 11.2 (32)[a]	1.9 ± 7.2 (32)	—	—
1978	91.7 ± 27.1 (26)	8.0 ± 27.1 (26)	20.4 ± 22.9 (35)	79.5 ± 23.0 (35)
1979	92.2 ± 2.8 (22)	0.0 ± 0.0 (22)	99.6 ± 1.1 (6)	0.0 ± 0.0 (6)
Test statistic	H = 2.43 (df = 2)	H = 4.87 (df = 2)	z = 3.77	z = 3.79
P	>0.1	0.1>P>0.05	<0.001	<0.001
% Dry weight				
1976	95.6 ± 18.5 (32)	0.1 ± 0.4 (32)	—	—
1978	88.6 ± 28.2 (26)	7.7 ± 27.2 (26)	39.2 ± 33.8 (35)	57.3 ± 35.7 (35)
1979	99.8 ± 0.6 (22)	0.0 ± 0.0 (22)	99.7 ± 0.8 (6)	0.0 ± 0.0 (6)
Test statistic	H = 3.09	H = 4.98	z = 3.76	z = 3.75
P	>0.1	0.1>P>0.05	<0.001	<0.001

[a]Values are mean ± 1 SD (n)
[b]Interpretations: 1979>1978 (for both % numbers and % dry weights).
[c]Interpretations (1978>1979 for both % numbers and % dry weights) are risky due to small number of samples in 1979 (no calanoids in 6 samples).

Measurements. In all three years, both male and female HY dovekies were collected at sea in August and September (Table 11). For each sex and year, whole weight and flattened wing length increased significantly ($P < 0.01$) from August to September. Breast muscles were not weighed in 1976, but weights increased significantly in three of the other four sex-year combinations. For other measurements, August and September values generally were not significantly different (P>0.01).

Mean fat class values (n — sexes combined) were as follows:

YEAR	AUGUST	SEPTEMBER	χ^2	df	P
1976	2.43 (37)	2.64 (55)	1.23	1	>0.1
1978	5.84 (25)	4.19 (43)	10.26	1	<0.01
1979	4.68 (28)	3.74 (42)	7.46	1	<0.01

Fat levels declined significantly from August to September in two of three years; in 1976, fat levels were similar in the two months. Among-year variation in fat levels was significant for both August (χ^2 = 78.68, df = 4, $P < 0.001$) and September (χ^2 = 32.05, df = 4, $P < 0.001$).

Among-year differences in whole weight and wing and culmen lengths were analyzed with analysis of covariance (SAS, 1979). Each measurement was treated as the dependent variable in a separate analysis, with sex and year as crossed factors and date (days after 31 July) as a covariate. For all three measurements, interactions between year

TABLE 11. Measurements (mean ± 1 SD [*n*]) of hatching year (HY) dovekies collected at sea in August and September 1976-1979

Measurement	Year	HY males August	HY males September	*t*-test *P*	HY females August	HY females September	*t*-test *P*
Whole weight, g	1976	149.9 ± 12.7 (20)	160.5 ± 9.3 (31)	0.001	144.6 ± 12.9 (17)	157.7 ± 12.2 (22)	0.003
	1978	133.7 ± 17.0 (15)	145.6 ± 9.0 (30)	0.004	129.9 ± 14.0 (9)	146.8 ± 8.4 (11)	0.003
	1979	144.6 ± 11.6 (15)	159.1 ± 7.1 (16)	<0.001	133.5 ± 11.0 (11)	155.5 ± 9.2 (22)	<0.001
Left wing, mm	1976	111.3 ± 3.0 (20)	114.1 ± 3.5 (30)	0.004	110.9 ± 3.6 (17)	112.7 ± 2.9 (22)	0.91
	1978	107.3 ± 4.8 (14)	110.9 ± 3.2 (31)	0.005	104.3 ± 5.7 (9)	111.6 ± 2.8 (12)	0.001
	1979	111.1 ± 3.6 (15)	114.4 ± 1.9 (16)	0.003	109.6 ± 4.0 (11)	115.5 ± 2.8 (22)	<0.001
Right tarsus, mm	1976	20.5 ± 0.7 (20)	20.5 ± 0.9 (30)	0.911	20.2 ± 0.9 (17)	22.0 ± 1.0 (22)	0.959
	1978	20.8 ± 0.7 (15)	20.3 ± 0.8 (30)	0.029	20.2 ± 0.8 (8)	20.5 ± 0.5 (12)	0.408
	1979	20.9 ± 0.7 (15)	20.6 ± 0.7 (16)	0.322	20.6 ± 0.6 (11)	20.6 ± 0.6 (22)	0.984
Culmen length (nostril-tip, mm)	1976	9.6 ± 0.4 (20)	9.9 ± 0.5 (27)	0.020	9.3 ± 0.4 (17)	9.6 ± 0.6 (20)	0.058
	1978	8.5 ± 1.6 (15)	9.1 ± 0.5 (31)	0.054	8.6 ± 0.5 (9)	8.9 ± 0.4 (11)	0.115
	1979	9.2 ± 0.5 (15)	9.6 ± 0.5 (15)	0.045	9.0 ± 0.5 (7)	9.6 ± 0.6 (21)	0.029
Bill depth (at nostril, mm)	1976	6.7 ± 0.5 (19)	7.1 ± 0.4 (29)	0.008	6.8 ± 0.6 (17)	6.8 ± 0.4 (22)	0.972
	1978	6.8 ± 1.5 (14)	6.5 ± 0.4 (29)	0.273	6.4 ± 0.5 (8)	6.4 ± 0.3 (11)	0.914
	1979	—	—	—	—	—	—
Breast weight, g	1976	—	—	—	—	—	—
	1978	9.8 ± 1.2 (15)	11.0 ± 0.9 (30)	0.001	9.8 ± 1.5 (9)	11.2 ± 0.8 (12)	0.009
	1979	12.8 ± 1.0 (8)	12.8 ± 1.3 (9)	0.958	10.9 ± 1.3 (7)	12.6 ± 0.8 (10)	0.005
Liver weight, g	1976	—	—	—	—	—	—
	1978	5.7 ± 1.5 (15)	6.4 ± 1.1 (31)	0.056	5.3 ± 1.0 (9)	6.7 ± 0.7 (12)	0.001
	1979	6.5 ± 1.1 (15)	7.4 ± 1.7 (16)	0.065	6.3 ± 1.4 (11)	7.2 ± 1.4 (19)	0.101

and sex were not significant (P>0.02) and slopes of relationships to date were homogeneous for year and sex categories (P>0.4 in all cases).

All three measurements were similar for male and female HY dovekies, but differed significantly among years and with date (Table 12). HY dovekies grew at similar rates in all three years, even though birds were much smaller in 1978 than at the same date in 1976 or 1979 (Fig. 4).

Size selection of common food items. In 1978, zooplankton in the upper 50 m of the water were sampled on three occasions when HY dovekies were collected in the same area on the same date (stations A4 on 24 August, A2 on 25 August, and D4 on 5 September). Half-metre zooplankton nets with 239 μm mesh and equipped with flow meters were towed vertically from 50 m depth to the surface. Dovekies collected at A2 contained too few copepods for meaningful analysis, but samples of *Parathemisto* were adequate on all three occasions.

Dovekies took the largest copepods available in the upper 50 m of the water; they tended to take both the largest species (*Calanus hyperboreus*) and the largest life stage of each species (Fig. 5). Adult female *C. hyperboreus* were especially important; they comprised much larger proportions of the numbers in stomachs than of the numbers in the water column. The situation with all *Parathemisto* was less clear (Fig. 6). At two stations (A4, A2), the modal size of *Parathemisto* taken by HY dovekies was greater than the modal size of *Parathemisto* in the upper 50 m, but at station D4 the dovekie mode was similar to or perhaps slightly smaller than the zooplankton mode.

In summary, the diets of various age classes of dovekies consist mainly of amphipods, copepods, and fish. The adult and subadult dovekies arriving in May feed primarily on *Calanus*, but by August amphipods become very important in the diets of these two age classes. At the breeding colonies in Greenland, dovekie chicks are fed, in decreasing order of importance by dry weight, amphipods (53%), copepods (39%), *Spirontocaris* decapods (7%), and other zooplankton (Bradstreet *et al.*, 1981). Once the young leave the colonies (but while still accompanied by an adult) their diet is largely (97% by dry weight) *Parathemisto* amphipods. Once abandoned by the adults, hatching year dovekie diets are dominated in dry weight by amphipods (80%), arctic cod (15%), and copepods (5%).

For HY dovekies, the greatest caloric intake per item would come from *Parathemisto,* followed by *Apherusa,*

TABLE 12. Analyses of covariance for HY dovekie measurements in relation to year, sex, and date

Measurement	Term	*F* (df)	*P*
Whole weight	Year	13.42 (2,209)	0.0001
	Sex	5.66 (1,209)	0.02
	Date	91.61 (1,209)	0.0001
Left wing	Year	17.38 (2,212)	0.0001
	Sex	1.43 (1,212)	0.23
	Date	62.83 (1,212)	0.0001
Culmen length	Year	19.73 (2,201)	0.0001
	Sex	3.16 (1,201)	0.08
	Date	26.30 (1,201)	0.0001

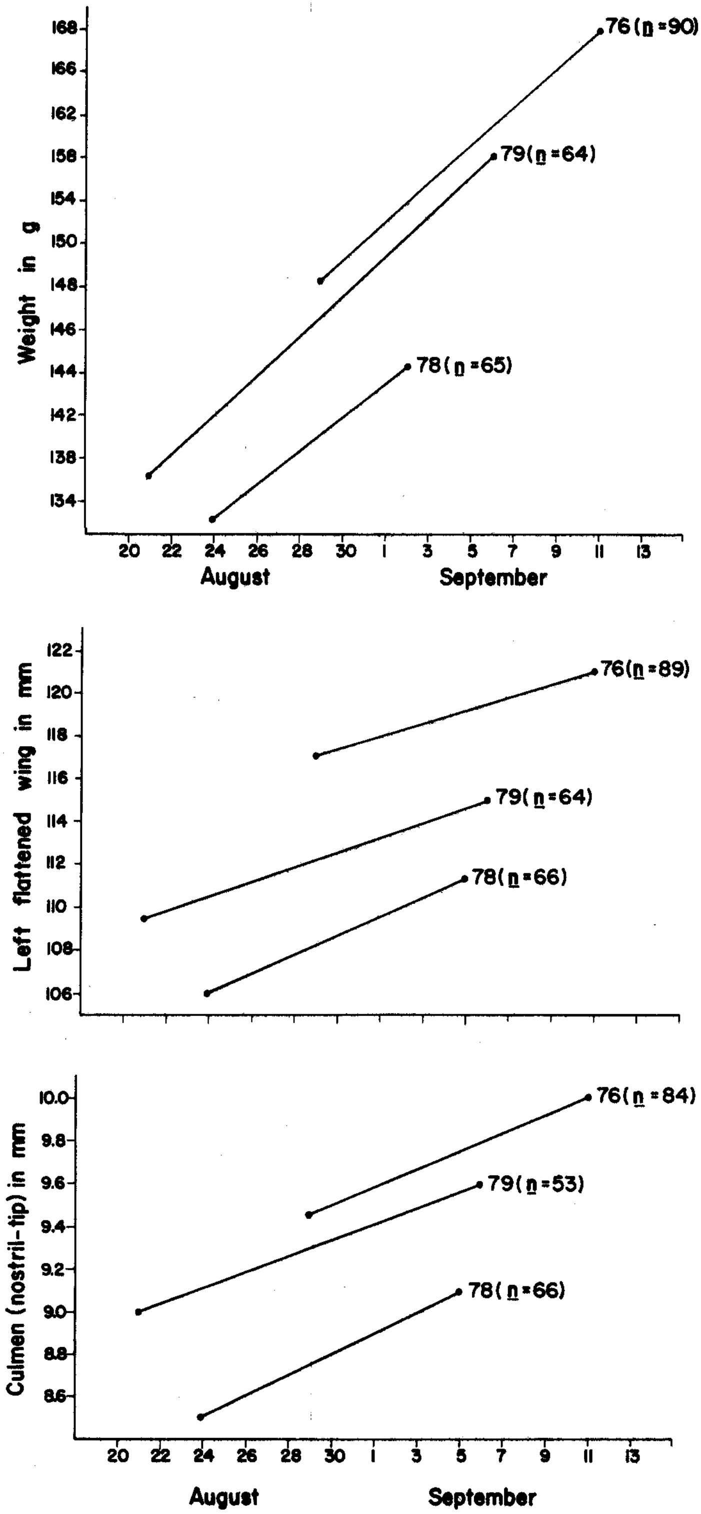

FIG. 4. Growth rates of HY dovekies in three years. For each measurement, t-tests of adjusted group means indicated that birds at date were of similar size in 1976 and 1979 (all $P>0.03$) and larger in each of these two years than in 1978 (all $P<0.001$).

young-of-the-year *Boreogadus*, and finally calanoid copepods (Table 13). Similar results for AD and SA dovekies further support the idea that amphipods are preferred food items.

TABLE 13. Energy content of selected prey items in the diets of dovekies

Taxa	Energy content[a] x kcal·g (dry weight) ± 1 SD (n)	No. items containing 100 kcal[b]: No. items	$\bar{x}$ length (mm)	Source
All *Parathemisto*	5.392 ± 0.077 (4)	4214	13.0	HY dovekies, 1976-1979
		4214	13.0	AD dovekies, Aug. 1979
Apherusa glacialis	5.829 ± 1.316 (3)	10 722	7.9	HY dovekies, 1976-1979
		7271	9.0	SA dovekies, Aug. 1978
		3615	11.5	AD dovekies, Aug. 1978
Calanoid copepods[c]	6.537 ± 0.834 (7)	38 244	6.6	HY dovekies, 1976-1979
		123 799	4.5	AD dovekies, May 1979
		37 544	6.8	AD dovekies, Aug. 1978
Boreogadus saida (young-of-the-year)	4.373 ± 1.012 (3)	11 434	15.0	HY dovekies, 1978-1979

[a]Energy values determined from microbomb calorimetry of frozen items collected in Lancaster Sound in July-September, 1976 and 1978. n = number of separate energy determinations.
[b]100 kcal equivalent = 100·[dry weight value of an item of mean length (following Bradstreet, 1980: Table 2)·energy content]$^{-1}$.
[c]Calanoid copepods show a seasonal pattern of fat levels (Lee, 1974), with relatively low values in spring and high levels in late summer; fat depots contain much energy. The energy content given is based on late summer determinations, so the 100 kcal equivalent for adult dovekies in May is probably an underestimate.

DISCUSSION

Prey Selectivity and Availability

Hatching year dovekies selected certain prey, particularly amphipods. At least in 1976 and 1978, copepods dominated zooplankton biomass in the upper 180 m of the ocean; other groups, including amphipods, were of secondary importance (Table 14; Buchanan and Sekerak, 1982). The relative biomass contribution of amphipods to HY dovekie diets was 15-20 times greater than that to zooplankton in the water column. HY dovekies also selected certain sizes of prey. Generally speaking, the birds took the larger sizes of appropriate taxa, and in four of five cases took large items in proportions greater than those in which they occurred in the water column (Figs. 5, 6). Zelickman and Golovkin (1972) combined with Golovkin *et al.* (1972) also demonstrated prey selectivity in dovekies collected off Novaya Zemlya.

The apparent switch in adult and subadult diets from mainly calanoid copepods in May to mainly amphipods (*Parathemisto* in adults, *Apherusa glacialis* in subadults) in late summer, and also the importance of *Parathemisto* and *Apherusa* in the late summer diets of HY birds, may reflect patterns in the development of the zooplankton community. Zooplankton availability at the May collection sites was not determined, but in general copepods dominate the zooplankton community of high arctic waters during spring (Tidmarsh, 1973; see also Bradstreet, 1980). *Parathemisto* and *Apherusa* may be unavailable to dovekies at this time of year. *Parathemisto* amphipods are positively phototropic and are well known to swarm in near-surface waters during the summer open-water period (Dunbar, 1946). May

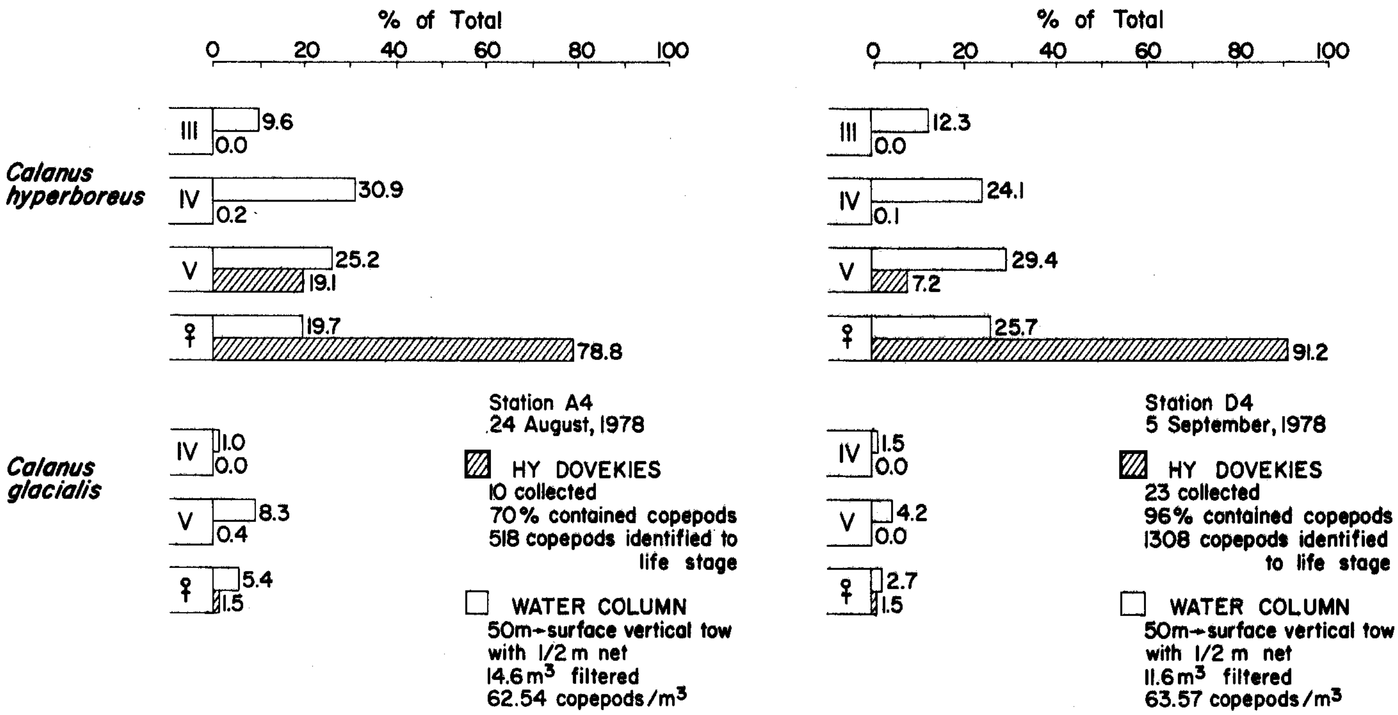

FIG. 5. Proportions of various life stages of copepods in two collections of HY dovekies and in the near-surface waters where they were collected.

collections were in vast areas of pack ice where light penetration into the water column would be less than in ice-free, open water later in the season. Under pack ice, surface swarming by *Parathemisto* probably does not occur, and this would reduce their availability to dovekies.

Availability of *Apherusa* may also vary seasonally. *A. glacialis* is well known to associate with the undersurface of ice (MacGinitie, 1955; Golikov and Scarlato, 1973). In 1979 in Pond Inlet, Cross (1982) found two cohorts of *A. glacialis* under fast ice in May. The smaller cohort (mean length 3 mm) formed 89% of the sample (n = 1144); the larger cohort (mean length 9 mm) formed 11%. By early July the smaller cohort (99% of 5212) had grown to a mean length of 6 mm, and the larger cohort (n = 44) to 11 mm. If the same size categories and growth patterns occurred under pack ice offshore, most *A. glacialis* present in May may have been too small for feeding dovekies. In May, the mean length of all taxa taken by adult dovekies was 4.5 mm (range 2.5-7.5); whereas in August and September, the mean length (7.8 mm) of *A. glacialis* taken by HY dovekies would be consistent with the size of Cross's small cohort after allowing for growth ($\sim$2.5 mm/month). Furthermore, in late summer *A. glacialis* are frequently seen darting about under pieces of ice (pers. obs.); in May divers did not observe this behavior in the abundant smaller-sized cohort (W.E. Cross, pers. comm.). I conclude that in May, the small size of most *A. glacialis* and their very close association with the under-ice surface probably account for their low importance in the diet. In late summer, when larger and more active *A. glacialis* are common, they form important percentages of the diets of subadult (Table 3) and HY (Table 6) dovekies.

Thus, for two amphipod taxa (*Parathemisto, Apherusa*), a seasonal increase in use by dovekies is consistent with information on seasonal availability in surface waters. Dovekies may prefer to ingest amphipods when they are at or above some threshold of availability in surface waters. This would be consistent with the relative energetic return from eating various items (Table 13).

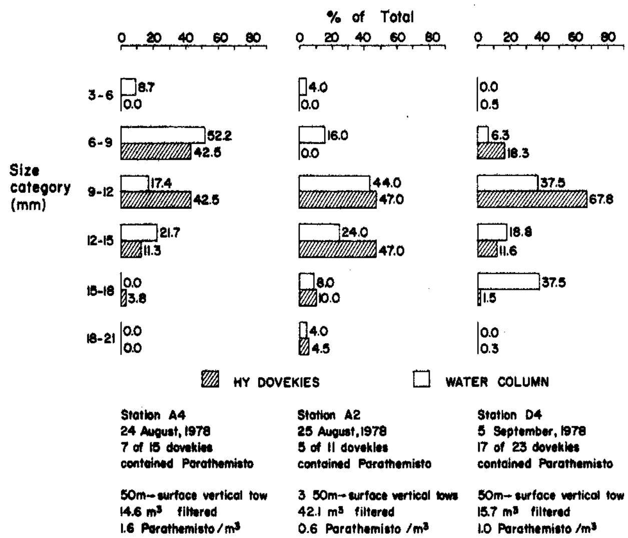

FIG. 6. Length-frequency distributions of *Parathemisto* in three collections of HY dovekies and in the near-surface waters where they were collected.

TABLE 14. Percent contribution of major zooplankton groups to total biomass in the ocean and in hatching year dovekie diets[a]

	1976		1978	
	Ocean[a]	HY dovekies	Ocean[a]	HY dovekies
Amphipoda	4.8	71.5	3.9	77.6
Chaetognatha	4.0	—	5.1	—
Copepoda	78.7	0.1	83.8	13.3
Hydrozoa	2.9	—	1.9	—
Ctenophora	—	—	1.0	—
Cephalaspidea	7.3	—	3.8	—
Osteichthyes	0.6	28.4	0.4	9.0
Totals[b]	98.3%	100.0%	99.9%	99.9%
n	25 tows	72 stomachs	39 tows	64 stomachs

[a]Biomass in the water is based on half-metre nets (239 μm mesh) towed through the upper 150 m of water. Zooplankton data for 1976 are from Sekerak *et al.* (1976); data for 1978 are from Buchanan and Sekerak (1981).
[b]Totals do not equal 100% because minor groups are not included.

Geographic Variation in HY Dovekie Diet

Diets of HY dovekies differed considerably in four zones that showed different surface water characteristics. Unfortunately such results were not corroborated by marine sampling in three of these zones in 1978. A series of 29 vertical zooplankton tows (239 μm mesh, 0.5- m nets with flowmeters) was made at various locations in the study area in late July-September (Fig. 1; Buchanan and Sekerak, 1982). Nets were towed through the upper 50 m of water at approximately 2 $m \cdot s^{-1}$. The mean biomasses$\cdot m^{-3} \pm 1$ SD of two prey taxa that were important in HY dovekie diets were as follows:

ZONE (no. of tows)	*Parathemisto libellula*	*Calanus glacialis and C. hyperboreus*
Intrusive Current (n = 9)	14.8 ± 8.2	235.7 ± 242.6
Lancaster Outflow (n = 10)	15.4 ± 22.5	390.6 ± 269.3
Offshore Baffin (n = 10)	15.7 ± 12.4	321.8 ± 177.1

Differences among zones were not significant for either *P. libellula* (Kruskal-Wallis H = 1.10, df = 2, P>0.1) or *C. glacialis* and *C. hyperboreus* together (H = 2.22, df = 2, P>0.1).

These zooplankton tows are probably of limited value in interpreting diet. First, the nets sampled to depth 50 m whereas all feeding presumably was above this depth. Second, zooplankton exhibit marked temporal and small-scale geographic patchiness in the water column as well as large-scale geographic variation (Mackas and Boyd, 1979; Schulenberger, 1980; Steele, 1980). Third, nets may be as selective as birds in their capture of certain types or sizes of items (e.g. Brinton, 1967; see also Bradstreet, 1980 for *Parathemisto*). In this study, however, it seems that nets did sample items of the sizes eaten by dovekies (Figs. 5, 6). Such net samples may provide a broad perspective on the composition of the zooplankton community available to feeding dovekies. When nets capture items of similar sizes to those taken by birds (the case here), net samples can also provide, when controlled for location and time, information on the proportions of various-sized prey in the water column.

When investigating large-scale geographic or temporal variations in diet, the best sampling devices for determining food availability may be the birds themselves (Ashmole and Ashmole, 1968). The interpretation of such data is confounded by the fact that dovekies apparently prefer certain kinds and sizes of food items. However, when collection dates are comparable and birds of similar status (age, time of breeding, etc.) are considered, analyses of diet in different surface water zones as defined by physical parameters can clarify relationships between the birds and their marine environment.

In this study amphipods were more important and of larger size in the diets of HY dovekies collected in the Intrusive Current, Arctic Water and (to a lesser degree) Lancaster Outflow zones than in offshore Baffin Bay; the reverse was true for calanoid copepods (except that length differences were not significant — Table 9). The first three of these zones are in an area where arctic waters from Smith, Jones, and Lancaster sounds combine and begin to flow southeastwards along the Baffin Island coast as the Baffin Current. Upwelling along fronts between the Intrusive Current and other zones is of sufficient magnitude to support enhanced productivity in eastern Lancaster Sound (D.D. Lemon, pers. comm.). This may explain why the *Parathemisto* taken by dovekies in these three surface water zones are larger, and perhaps more abundant, than those taken in offshore Baffin Bay.

Apherusa glacialis and all *Onisimus*, two other important amphipod prey taxa, are closely associated with the undersurface of ice and are presumably regulated by epontic, and not pelagic, productivity. Sizes of these two gammarid amphipods would seem less likely to be related to upwelling, and indeed there were no among-zone differences in the importances or sizes of these prey in HY dovekie diets.

Calanoid copepods taken by HY dovekies in the Offshore Baffin zone were larger (albeit not significantly so) than those taken elsewhere. Given a preference for amphipods when available, and the apparent reduced availability of suitable amphipods in offshore waters (compare importance values in Table 9), HY dovekies may have selected the largest copepods offshore in order to make up for a scarcity of amphipods.

Year-to-year Variability in HY Dovekie Diet

While geographic location can explain much of the observed variability in diet, year of collection also affected diet. In 1978, all *Parathemisto, Apherusa glacialis*, and all amphipods in the diet were significantly smaller than in 1976 or 1979 (Fig. 3). While some of these differences may have been due to collecting in different surface water zones in different years, this cannot be the whole explanation. When controlled for surface water zone, relative importances of amphipods in 1978 HY dovekie diets were less than in 1976 (Intrusive Current zone) or 1979 (Intrusive Current and Offshore Baffin zones — Table 10). Conversely, relative importances of calanoid copepods in diets of HY dovekies collected in the Intrusive Current zone were greater in 1978 than in 1976 or 1979. Not all of these differences were statistically significant, but in each case the results support the idea that 1978 was a poor year for amphipods, and that dovekies compensated by taking more copepods. Similar trends were noted at the Greenland colonies in mid-August of 1978 and 1979 (Bradstreet *et al.*, 1981). In chick meals, amphipods were significantly ($P<0.01$ in all comparisons) more important in 1979 (21% of standardized numbers, 51% of standardized dry weights) than in 1978 (8% of numbers, 33% of dry weights); the reverse was true for all calanoids (73% of standardized numbers in 1979, 90% in 1978; 38% of standardized dry weights in 1979, 59% in 1978) (Bradstreet *et al.*, 1981).

Roby *et al.* (1981) indicate that fledging of dovekie chicks from the Siorapaluk colony, northwest Greenland, in 1978 was somewhat delayed. In the present study HY dovekies collected at sea were, at any given date, significantly smaller in 1978 than in 1976 or 1979 (Table 11, Fig. 4). Furthermore, weights of adult males collected at the Siorapaluk colony on 13-16 August 1978 (157.9 ± 1 SD 8.2 g, $n = 54$; Bradstreet *et al.*, 1981) were less than those of adult males collected near the Cape Atholl colony in Bylot Sound on 17-18 August 1979 (161.2 ± 7.6 g, $n = 58$; Bradstreet, unpubl. data) albeit only marginally so ($t = 1.99$, $P<0.05$). These data indicate that dovekies were in poorer condition in 1978 than in 1976 or 1979. Bédard (1969) noted relatively low adult weights of two Pacific alcids, *Aethia pusilla* and *A. cristatella* during one of three years and related this to changes in the nutritive quality of prey.

Assuming that body weight reflects body condition, it is tempting to correlate the small size and therefore poor condition of dovekies in 1978 with poor food resources. At the Greenland colonies food requirements for maintenance, foraging, and egg-formation by adults and for chick growth could place heavy demands on available food resources, especially if these resources were less abundant than normal. Unfortunately, food resources *per se* could not be compared between 1978 and any other year, either near the Greenland colonies or in my study area at those times in the breeding cycle when food demand was greatest.

Despite the apparent difficulties faced by dovekies in 1978, HY dovekies collected at sea during their southbound migration contained similar total amounts (dry weights) of food in each of the three years ($P>0.1$; Table 5); growth rates of HY dovekies were also similar among years (Fig. 4). Although preferred food items (amphipods) were smaller and perhaps less numerous or available in late August and early September of 1978 than in the other two years, it seems that sufficient food resources were available in all three years to allow HY dovekies, at sea, to grow at normal rates.

The zooplankton that comprised the bulk of dovekie diets (small *Parathemisto, Onisimus glacialis, Apherusa glacialis*, calanoid copepods) are all species that grow quickly in response to the spring bloom of epontic or planktonic algae (Dunbar, 1946; Lee, 1974; Cross, 1982). Late spring breakup retards the phytoplankton bloom and development of the zooplankton community (Pavshtiks, 1968), and may similarly retard development of epontic algae and their dependent predators.

Year-to-year variation in ice breakup probably influenced the composition and development of the epontic and zooplankton communities with concomitant effects on the diets of HY dovekies. In Lancaster Sound and western Baffin Bay, spring temperatures were lower and snowfall greater in 1978 than in 1977 (a 'normal' year) (P. Scholefield, Canadian Climatic Centre, unpubl. data); ice breakup was also later in 1978 than in 1979 or, especially, 1976 (McLaren, 1982; Renaud *et al.*, 1982).

Adult and Subadult Dovekies

Non-breeding adult and subadult dovekies leave the Greenland colonies sooner than do active breeders (Roby *et al.*, 1981) and then begin to molt (this study). Non-breeding birds apparently associate closely with pack ice at this time. Collections and counts of birds at sea showed that greater numbers of molting, non-breeding dovekies occurred in the study area in August 1978, when much pack ice occurred in northern Baffin Bay, than in August 1979, when open-water conditions prevailed. In 'normal' years, non-breeders probably fly south from the Greenland colonies until they encounter pack ice near southeast Baffin Island, where they may join other non-breeding birds that summer in this area. Brown (1980) found presumably non-breeding dovekies closely associated with pack ice off southwest Baffin Island as early as late July.

Molting dovekies probably associate with pack ice for several reasons, including both increased shelter and increased food resources relative to open sea conditions (Divoky, 1979). *Apherusa glacialis* and *Boreogadus saida*, two taxa that are important in the diets of molting birds, are closely associated with the ice undersurface and are of high food value (Table 14). Food availability would be especially important when dovekies are flightless, because their underwater agility is presumably diminished, and feather growth requires energy in addition to that needed for basic maintenance.

Adults, after abandoning their chicks at sea in northern Baffin Bay, apparently also leave the study area quickly. No adults were collected after 1 September. They probably fly some distance south before commencing molt. This means that the abundant food resources available in the surface waters of the study area during late summer are available to HY birds without competition from other, more experienced, age classes of dovekies.

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