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Estimation of carbon flux to dovekies (*Alle alle*) in the North Water

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Abstract

We modeled the energy demand of seabirds in the North Water, focusing on the planktivorous dovekie (*Alle alle*), the dominant species in the polynya. For the dovekie we provided an estimate of carbon flux that included aspects of spatial and temporal variability. We estimated the density, diet, and carbon consumption of dovekies throughout the polynya, from the time of their arrival in mid-May until they began to migrate south in September. Our model showed that this species is responsible for 92–96% of the energy demand and therefore carbon flux to seabirds. Dovekies consumed $73.7–147 \times 10^3$ mt C yr^{-1} in the North Water. Average flux rates to dovekies in the polynya were 0.74 g C m^{-2} yr^{-1}, with a maximum estimated rate of 24 mg C m^{-2} d^{-1} in the eastern portion of the study area in May. However, when averaged over the entire polynya and period of occupancy, the proportion of pelagic primary production that went to dovekies was negligible (0.3–0.6%). Our observations of dovekie distribution, indicate that the major flux of carbon to seabirds occurred close inshore along the Greenland coast. There in May, carbon flux to dovekies was estimated to be 5–14% of the potential particulate export of phytoplankton. Our estimates of the spatial distribution of carbon flux to birds suggest the extraordinary importance of production along the west coast of Greenland.

1. Introduction

The North Water, between Ellesmere Island and northwest Greenland, supports some of the largest concentrations of seabirds anywhere in the High Arctic (Stirling, 1980). At maximum extent, the North Water comprises about 100,000 km^2 of open water. Every year, millions of seabirds migrate to the North Water to feed in the productive ice-free waters and to breed along its shores. The most abundant of these birds is the dovekie (*Alle alle*) with an estimated population of 15–30 million pairs (Salmonsen, 1981; Renaud et al., 1982; Nettleship and Evans, 1985; Boertman and Mosbech, 1998; Kampp et al., 2000). Dovekies are small subsurface planktivores that can dive to a depth of 35 m (Falk et al., 2000). They breed on the steep scree slopes of the Greenland coast adjacent to the North Water (Roby et al., 1981; Boertman and Mosbech, 1998) and spend their winters along the Labrador coast and as far south as the Gulf of Maine (Bradstreet and Brown, 1985; Brown, 1988; Stenhouse and Montevecchi, 1996).

In other marine ecosystems with large concentrations of seabirds, birds consume between 16%

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and 29% of secondary production (Furness, 1978; Logerwell and Hargreaves, 1997). Seabirds are also good indicators of the spatial heterogeneity of prey distributions (Hunt, 1990, 1991; Hunt et al., 1990) and pathways of carbon flux (Schneider et al., 1986). Earlier work in Lancaster Sound, adjacent to the North Water, documented the trophic ecology of seabird populations in the region (Bradstreet, 1982; Bradstreet and Cross, 1982; Welch et al., 1992). Welch et al. (1992) presented a model of energy flow and showed how Arctic cod (*Boreogadus saida*) and to a lesser extent the amphipod *Themisto libellula* were of central importance to black guillemots (*Cepphus grille*), northern fulmars (*Fulmaris glacialis*) and thick-billed murres (*Uria lomvia*) in this area. Using stable isotope analyses, Hobson (1993) demonstrated that copepod-eating dovekies occupy the lowest trophic level amongst the seven seabirds tested. This work provided a background for our studies in the North Water.

In the present study, we hypothesized that in areas of the North Water where high densities of foraging seabirds occurred, a significant amount of carbon would be removed from the marine ecosystem. The overall energy demand of seabirds was estimated on an annual basis in the North Water. In particular, we examined the spatial and temporal patterns of carbon flux to dovekies, which are major consumers among the seabird assemblage of the polynya.

2. Methods

2.1. Estimation of energetic demands of seabirds in the North Water

We estimated the energy requirements of seabird populations in the North Water using two methods. As a starting point we estimated annual energy demand of all seabirds based on published estimates of population, metabolic rates and number of days of occupancy in the polynya (Table 1). Based on the results of these preliminary calculations, we focused this paper on the dovekies. We modeled the patterns of carbon flux to dovekies using established methods of estimating energy and prey demand in free-ranging birds (Wiens and Scott, 1975; Furness, 1978; Furness

Table 1

Seabird population numbers, field metabolic rates (FMR), days of occupancy in the North Water and annual energy demand

Species	Population numbers	FMR (kJ/d)	Occupancy (d)	Energy demand (kJ/yr)
Northern Fulmar (*F. glacialis*)[a,b,c]	100,000	1223	168	2.1×10^{10}
Glaucous Gull (*L. hyperboreus*)[c,d]	50,000	2190	168	1.8×10^{10}
Black-legged kittiwake (*R. tridactyla*)[a,b,e]	60,000	1046	132	8.3×10^{9}
Ivory Gull (*P. eburnea*)[c,f]	2000	1726	132	4.6×10^{8}
Dovekie (*Alle alle*)[a,g]	$30–60 \times 10^{6}$	904	128	$3.5–6.9 \times 10^{12}$
Thick-billed murre (*U. lomvia*)[a,h,i]	1,000,000	2298	117	2.7×10^{11}
Black guillemot (*C. grylle*)[a,j] (migratory)	50,000	1116	183	1×10^{9}
Black guillemot (*C. grylle*)[a,j] (resident)	50,000	1116	365	2×10^{9}

[a] Based on population estimates from Nettleship and Evans (1985).
[b] Based on population estimates from McLaren (1982).
[c] Based on multiple of resting metabolic rates from Gabrielsen and Mehlum (1988).
[d] Derived from population estimates from Evans (1984).
[e] Based on field metabolic rate from Gabrielsen et al. (1987).
[f] Based on population estimates of Thomas and MacDonald (1987).
[g] Based on population estimates of Boertmann and Mosbech (1998); Kampp et al. (2000); Renaud et al. (1982); and Salmonsen (1981).
[h] Based on field metabolic rate from Kitaysky et al. (2000).
[i] Based on population estimate from Kampp (1990).
[j] Based on field metabolic rate from Mehlum et al. (1993).

and Cooper, 1982). These methods require knowledge of the numbers of birds breeding in the region of concern, the length of time that they occupy the region, estimates of their energy requirements during different stages of the breeding season, and the amount of prey required to meet those energy needs. The amount of prey required is calculated based on the energy density of the prey. The amount of carbon flux to the birds depends on both the amount of prey consumed and the estimated carbon content of the prey. To obtain the amount of carbon flux to dovekies in the North Water region, we calculated the daily carbon flux for the published low and high (15 and 30 million pairs) population estimates for dovekies nesting in the Thule region of Greenland (Salmonsen, 1981; Renaud et al., 1982; Nettleship and Evans, 1985; Boertman and Mosbech, 1998; Kampp et al., 2000).

Most species of seabirds arrive in the North Water in April or May and depart in September. Estimation of the number of days that each seabird population occupies the polynya (Table 1) was based on our observations of seabirds at sea and reproductive status of birds collected at sea (N. Karnovsky, unpublished) combined with published data on incubation lengths and fledging ages (Lovenskiold, 1964; Roby, 1981; Falk et al., 1997). Some black guillemots are known to remain in the polynya throughout the winter (Renaud and Bradstreet, 1980). For this species we thus assumed that half of the population migrates out of the polynya during the winter months (Table 1). The numbers of dovekies utilizing the polynya in the fall were adjusted on the basis of the results of our at-sea surveys. In May–June our counts indicated about 3 million dovekies foraging in the survey area, or between 5% and 10% of the 30–60 million dovekies believed to be dependent on the North Water. In May, we assumed that the entire population of breeding birds was present. However, in late August and September, failed breeders would have left the study area and chicks and parents would have been migrating south. To obtain an estimate of the total population using the polynya, including waters not available for survey, we assumed that we had observed the same percentage of the overall population in August–

September (5–10%) as we had earlier in the summer. Therefore, using the ratio of 5–10% in the survey area to 95–90% outside of it, the total population using the polynya would be 2–4 million birds in the later part of August and 860,000–1,700,000 in September. These estimates were used to derive carbon flux to the total population of dovekies present in the polynya in August and September.

The estimates of daily energetic requirements of seabirds in the North Water were based on published values of adult field metabolic rates (FMR) (Table 1) that were made in the Arctic using the doubly labeled-water technique. These estimates were used rather than the allometric equations often employed by others (Lasiewski and Dawson, 1967; Kendeigh et al., 1977; Furness and Tasker, 1996), because the latter underestimate the energetic needs of birds that breed in the cold temperatures of high latitudes (Gabrielsen and Mehlum, 1988). When FMR were not available, we considered the active metabolic rate to be three times the resting metabolic rate (Gabrielsen et al., 1991). FMR for adults and chicks were adjusted for assimilation efficiency by dividing by an assimilation efficiency of 0.8 to provide an estimate of the amount of energy that a bird would have to consume to meet its daily energy requirements (Taylor and Konarzewski, 1992). The energy requirements calculated for seabirds other than the dovekie should be considered rough estimates, as we did not include the energetic impacts of reproduction.

The estimates of the energy demand of dovekies were made from a more detailed model that included adjustments of the FMR during incubation, the energetic costs of egg-laying and chick energetic demands. Dovekies, with their small size and northerly distribution, have the highest metabolic rate of any alcid of their size (Gabrielsen et al., 1991; Konarzewski et al., 1993). We used $696 \, kJ \, d^{-1}$ based on doubly labeled-water experiments (Gabrielsen et al., 1991) that, after taking into account assimilation efficiency, converts to a daily intake of $904 \, kJ \, d^{-1}$ (Konarzewski et al., 1993). The estimates of dovekie energy intake used in this study are 16% higher than those developed

by Diamond et al. (1993) using estimates of time-energy budgets.

To assess the energetic cost of the single large egg that dovekie females produce each season, the allometric equation from Wiens and Innis (1974) was used: cost of egg production = EW(CS)(1.05)(1.37) kcal, where 'EW' is egg weight (20 g), 'CS' is clutch size (1), 1.05 is the caloric value of a gram of egg, and 1.37 is an adjustment for the efficiency of egg production (73%). The estimated cost of 120.3 kJ to produce a dovekie egg was ascribed to half the population (females). Daily energetic demands were assumed to be equal between the sexes, since both males and females gather food for chicks throughout the chick-rearing period. We assumed that energy expenditures during incubation were somewhat lower than during chick-rearing and that both parents shared incubation costs equally. Metabolic costs during the incubation period were set at two times the resting metabolic rate (87% of the FMR) versus a field metabolic rate during chick-rearing that is closer to three times the resting metabolic rate (Table 2).

Estimates of the energetic requirements of growing dovekie chicks were based on the results of doubly labeled-water experiments done on chicks in the Svalbard area (Table 2; Konarzewski et al., 1993). Changes in daily energetic demands

Table 3
Chronological events in breeding season used in the calculation of daily energetic demands of the dovekie population

Event	Date	Reference
Arrival	7 May	This study
Lay date	22–24 June	Roby et al. (1981)
Hatch date	20 July	Roby et al. (1981)
Fledge date	12–14 August	Roby et al. (1981)

throughout the entire period of occupancy were calculated from published phenological events (Table 3). In this study, it was assumed that all birds were breeding.

2.2. Seabird diets

Estimations of daily energy demands of the dovekie population were converted to grams of dry weight of prey and then to grams of carbon. Approximations of the amount of different prey needed to meet the energy demands of dovekies in the North Water were developed based on examinations of stomach contents of birds collected in the North Water during May, June, and July 1998 and August and September 1999 (Fig. 1). Birds were collected by shotgun under Canadian Wildlife Service permits. The stomach and the proventriculus of each bird were removed in the field and preserved in 80% ethanol. In the laboratory, gut contents were analyzed under a dissecting microscope. All identifiable prey were classified into broad categories: copepods, pelagic amphipods, epontic amphipods, and fish. Because most of the stomach samples included only one type of prey, we presented the frequency of occurrence of each prey category within the birds collected during each month of the study. Detailed analyses of the diet samples, including species, stages, and sizes of prey, will be presented elsewhere (N. Karnovsky et al., in preparation).

Chick diets were estimated from data collected on Haklyut Island, Thule district, northwest Greenland, by Pedersen and Falk (2001) in 1998, the same year in which we collected most of the adult stomach samples at sea and the dovekie distributional data. On the basis of their results (Pedersen and Falk, 2001), we estimated that
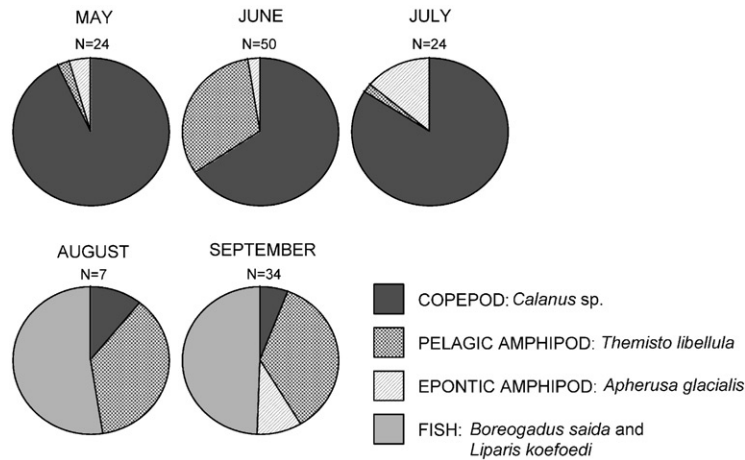
Table 2
Energetic requirements (intake) for dovekies at different life stages

Stage	Energetic requirements (kJ/d)[a]	Stage	Reference
Adult	801	Incubation	
Adult	904	Chick-rearing	Gabrielsen et al. (1991)
Chick	262	7–9 days old	Konarzewski et al. (1993)
Chick	348	13–15 days old	Konarzewski et al. (1993)
Chick	332	20–22 days old	Konarzewski et al. (1993)
Chick	86	25–26 days old	Konarzewski et al. (1993)

[a] Rates represent daily intake, not energy expended.

Fig. 1. Seasonal variation in the percent frequency of occurrence of different prey taxa in dovekie diet samples. N = number of stomachs containing food which were included in the analysis.

Table 4
Energy density values of prey types used by dovekies in this study[a]

Prey type	Energy density values (kJ g^{-1} dry wt)
Calanus sp.	26.0
Themisto libellula	16.7
Apherusa glacialis	19.7
Larval fish	24.2

[a] From Weslawski et al. (1994).

dovekie chick diets consisted of 75% copepods and 25% the large amphipod *Themisto libellula* in July and that the ratio was 50/50 in August. The dry weight (in grams) of the different prey was calculated from published energy density values (Table 4; Weslawski et al., 1995) and converted to carbon using a conversion factor of 0.4 g C g^{-1} dry weight (Curl, 1962). In this study, we assumed that all prey ingested were utilized, including the chitin of crustaceans. When inspecting the guts of collected birds, no evidence that chitinous prey were expelled undigested was found.

2.3. Surveys

To assess the spatial distribution of dovekies, surveys were conducted from the bridge of the Canadian Coast Guard icebreakers whenever the icebreakers were underway (Fig. 2): the CCGS *Louis St. Laurent* in August of 1997 and the CCGS *Pierre Radisson* in April–July 1998 and August–October 1999. Data from different years were combined to give a composite picture of seasonal changes in bird distributions and abundance. Surveys were conducted close to the Canadian coast except where landfast ice was prohibitive. Surveys along the Greenland coast were not possible because of international restrictions that kept us well offshore of the ice edge.

During surveys, all birds were counted within a 300-m wide arc from the bow on the side of the ship with the best visibility. Data were entered directly into a notebook computer by the observer. The boundary of the area in which birds were counted was determined using the method of Heinemann (1981). Periodically during cruises, bird observers would work together on the bridge to provide inter-calibration of their observations. We noted bird behavior (flying, sitting on water, etc.) as well as ship speed and course. Only birds sitting on the water were considered for this analysis, because we assumed these birds were likely to be, or had recently been, engaged in feeding activity, whereas flying birds were commuting to and from other foraging areas.

The study area was divided into blocks 1°latitude × 1°longitude (Fig. 3). Transects conducted
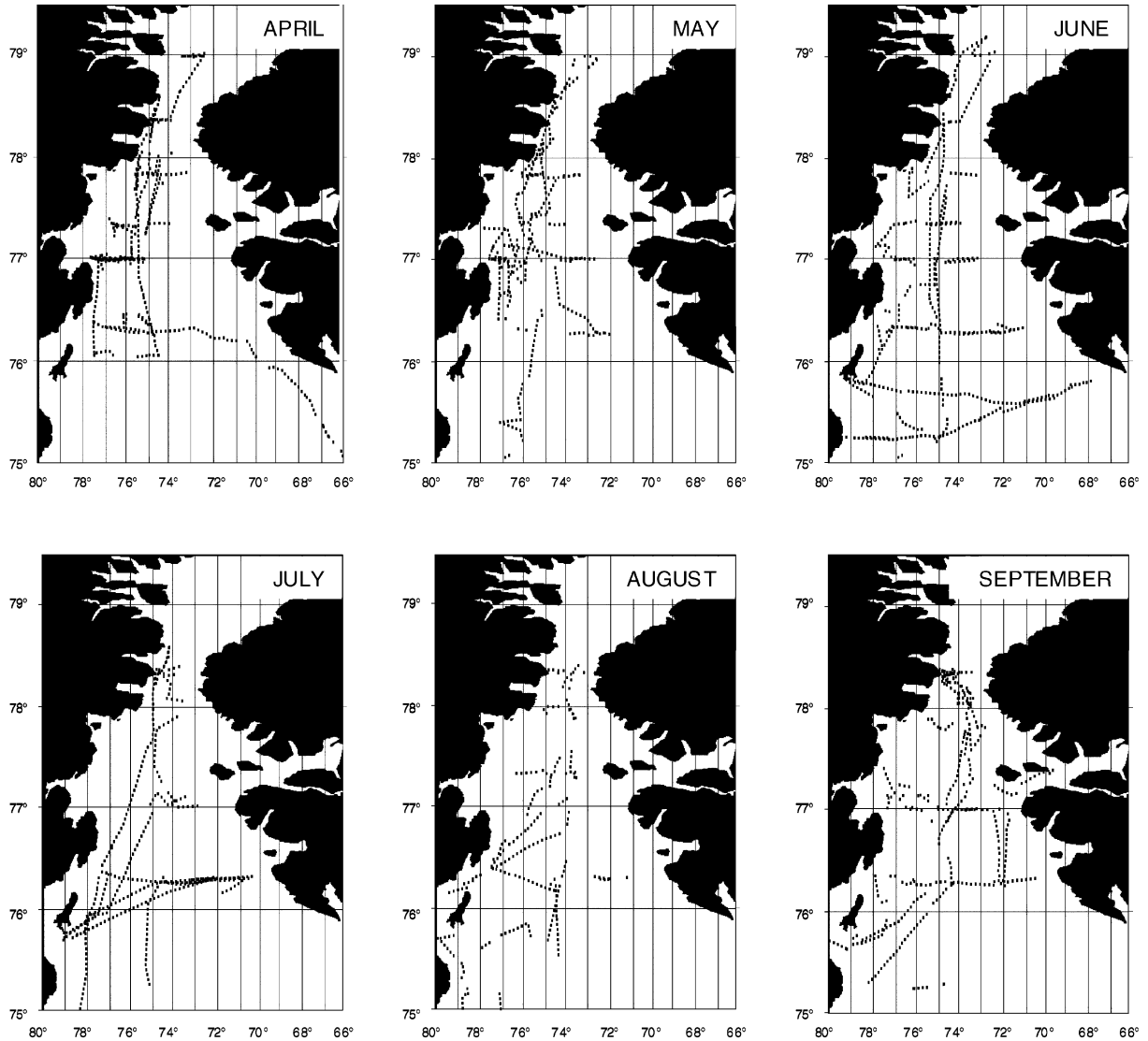
Fig. 2. Distribution of seabird surveys. Each dot represents one 3-nm transect (bin). August surveys included 1997 and 1999 transects.

within each block were divided into bins 3 nautical miles in length and having an area of $1.67\,km^2$. The average density of birds per bin within each degree block was multiplied by the area of open water in a block to estimate the number of birds foraging in each block.

The estimated numbers of dovekies foraging within a block was multiplied by the daily energetic demands of dovekies during that month. To assess seasonal variation in the spatial dis-

tribution of carbon flux to dovekies, monthly estimates were made of the distribution of carbon flux throughout the polynya from April–September.

3. Results

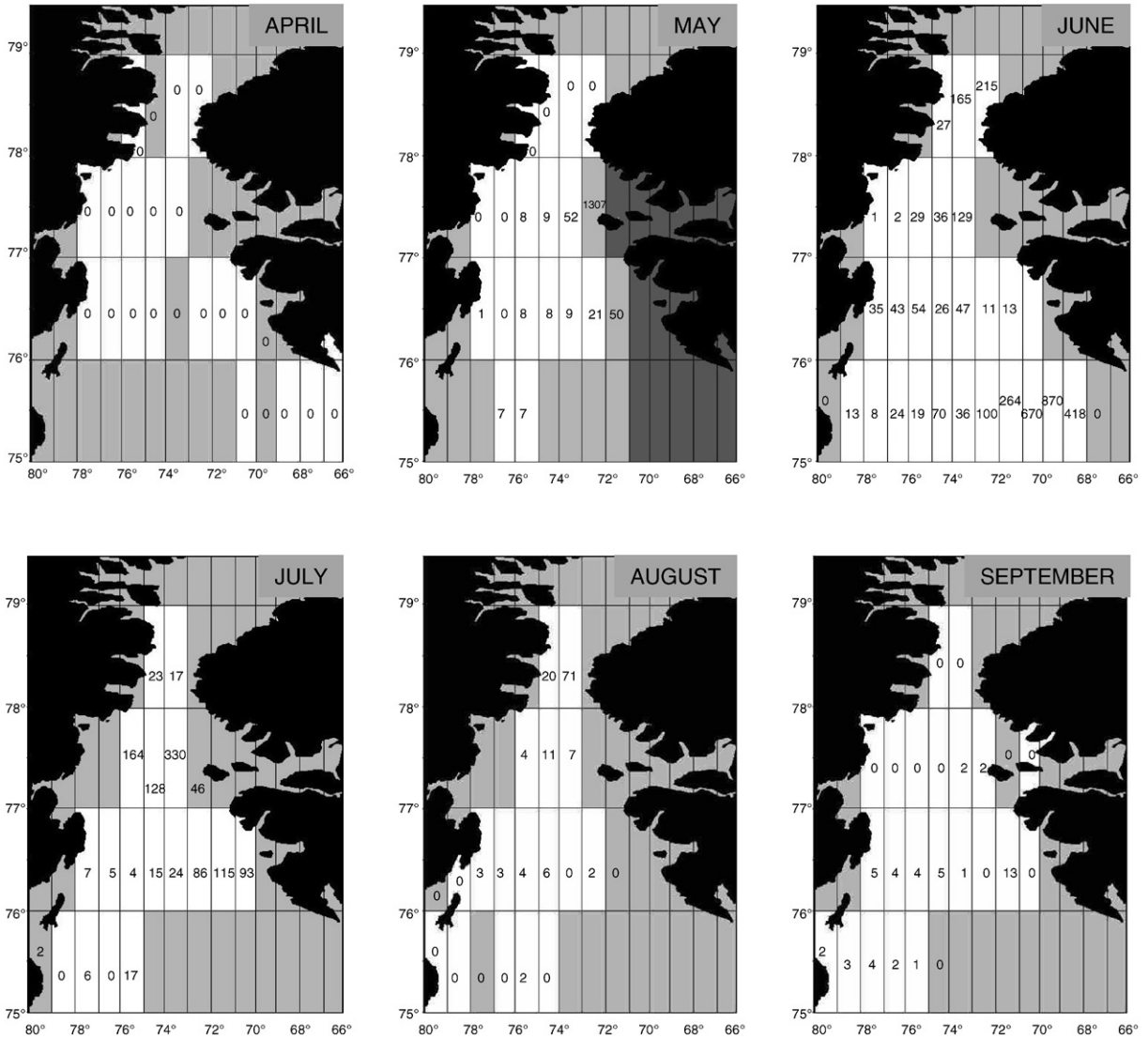Based on the published estimates of populations breeding in the vicinity of the polynya, the total

Fig. 3. Spatial and temporal variation in carbon flux to dovekies in the North Water. Numbers in each block represent number of metric tons of carbon taken by dovekies from that degree block. Gray blocks without numbers are where no surveys were conducted. Gray blocks with numbers are where there were fewer than 5 bins per block. The darker gray area along the west coast of Greenland on the May map represents the area where most of the dovekie population were likely to have been foraging.

energy demand of all seabird species in the North Water ranged from approximately 3.8 (minimum population estimate) to $7.3 \times 10^{12} \, \mathrm{kJ \, yr^{-1}}$ (maximum population estimate, Table 1). Dovekies alone were responsible for 92–96% of total energy demand. The estimated amount of carbon taken by dovekies over the entire breeding season was

73,700 mt for the minimum population estimate of 30 million birds and 147,400 mt for an estimate of 60 million birds. When averaged over the polynya as a whole, the annual carbon flux to dovekies was 0.74 or 1.48 g $\mathrm{C \, m^{-2} \, yr^{-1}}$, depending on the population estimate used. During the period of occupancy of the polynya, the daily carbon flux

was estimated at 5.1 (10.2) mg $C\,m^{-2}\,d^{-1}$ (60 million birds). Peak carbon flux occurred during the month of May in one block of the eastern sector of the polynya, where it reached 24 mg $C\,m^{-2}\,d^{-1}$ (Fig. 3).

Carbon flux to dovekies varied temporally due to changes in the numbers of birds occupying the polynya and changes in energy demand per bird. In April, no foraging dovekies were observed in the North Water. The species arrived *en masse* in May. Peak densities of feeding birds in that month occurred on the eastern side of the polynya, exceeding 1700 birds km^{-2}. The energy demand of the dovekie population varied seasonally (Fig. 3) and reached a maximum of 8.22×10^{11} or 1.63×10^{12} kJ month^{-1} (depending on population estimate) during the chick-rearing period in July. By August and September, the numbers of feeding dovekies declined. Chicks fledged in August; parents and chicks were seen vacating the study area shortly thereafter. Carbon flux was low during the fall, because numbers of birds were low and energetic demands had declined dramatically. By the end of September, despite the presence of open water, most of the birds had migrated south (N. Karnovsky, unpublished data).

The pathways of carbon flux to dovekies differed as the season of occupancy progressed (Fig. 1). The diet of dovekies in May and June was composed predominately of copepods, in particular female *Calanus hyperboreus* and female *Calanus glacialis*. In one area, we found dovekies eating juvenile *T. libellula*. In July, dovekies fed on the smaller stages of *Calanus* copepods as well as the under-ice amphipod *Apherusa glacialis*. In August and September the dovekies fed primarily on the pelagic predatory amphipod *T. libellula* and juvenile Arctic cod *Boreogadus saida* (Fig. 1).

The spatial distribution of carbon flux to dovekies (Fig. 3) varied seasonally due to changes in foraging distributions, energy demands (Fig. 4) and seasonal differences in diets (Fig. 1). In May, carbon consumption by dovekies was concentrated along the eastern side of the polynya. In June, energy demands had increased and birds had spread throughout the polynya. However, carbon flux to dovekies was still highest along the southeastern side. In July, energy demands were at their
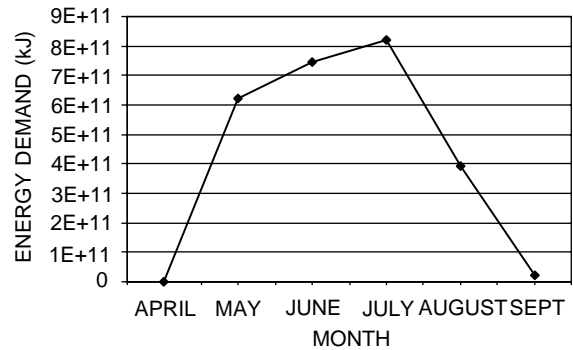

Fig. 4. Seasonal variation in energy demand of the dovekies. Plotted values represent the number of kilojoules (kJ) needed to support 30 million dovekies during each month.

peak and the birds appeared to have shifted their feeding distribution to include more of the northern part of the study area. In fall, most energy flux to dovekies occurred in the south.

4. Discussion

With their high abundance and elevated metabolic rate, dovekies represented 92–96% of the energy demand of the seabird community in the North Water (Table 1) and were responsible for the bulk of the particulate carbon taken from the North Water by seabirds. The dominance of dovekies in the polynya most likely reflects that this species is the only copepod specialist in the seabird community of the High Arctic. The two other sub-surface feeders in the North Water are the thick-billed murre, which prey mainly on *T. libellula* and *B. saida*, and the black guillemot, which, in addition to *T. libellula* and *B. saida*, also consume subtidal and epibenthic fish and ice-associated fish and crustaceans. The black-legged kittiwake (*Rissa tridactyla*) and northern fulmar are mainly surface feeders, though fulmars consume copepods on occasion (Bradstreet and Cross, 1982; Hobson and Welch, 1992; N. Karnovsky, unpublished data).

The patterns of carbon flux to dovekies showed strong temporal and spatial variation that appeared to reflect underlying patterns of primary and secondary production. Within the portion of

the polynya surveyed, dovekies initially restricted their foraging to the southeastern side of the polynya where the earliest blooms were found (Klein et al., 2002; Mei et al., 2002) and where zooplankton were found in high numbers in the upper water column (Ringuette et al., 2002). Later, dovekies expanded their foraging range into the west and north to take advantage of later developing production. At-sea estimates of numbers of birds are subject to error, which become larger when sample sizes are small. However, errors in our at-sea estimations of numbers of birds will affect only the spatial carbon flux and not the total carbon flux, which was estimated from colony counts.

The pathways of carbon flux changed from copepods in the spring and summer to fish and predatory amphipods in the fall. The seasonal changes in the amounts and spatial distribution of carbon flux to dovekies are the result of dovekies shifting their diets and distributions, as well as changes in the levels of energetic requirements during the breeding season.

4.1. Physical and biological factors influencing spatial and temporal patterns of carbon flux

Shifts in the distribution and diets of the dovekies appear to reflect physical processes responsible for the temporally and spatially staggered opening of the polynya and subsequent food-web dynamics. In 1998, the timing and location of carbon flux to dovekies appeared to be determined more by primary production and the ontogenetic upward migration of copepods that were cropping the production than by the availability of open water. The polynya 'opened' in late March 1998. Although during April there was, on average, 23% open water (Mundy and Barber, 2001), no dovekies were present. The arrival of the dovekies coincided with the availability of *Calanus* spp copepods (Ringuette et al., 2002), their primary prey in May, June, and July. In August and September the dovekies fed at a higher trophic level on the pelagic predatory amphipod *Themisto libellula* and juvenile Arctic cod, *Boreogadus saida*. During August and September the calanoid copepods migrate downward, out of the upper

mixed layer, in preparation for winter diapause at depth (Conover, 1967). Bradstreet (1982) described a similar shift in diets of dovekies feeding in Lancaster Sound. This shift to foraging at a higher trophic level is significant because it reflects an additional step away from primary production, which is important when determining the amount of carbon from phytoplankton required to support dovekies.

4.2. Extrapolation to un-surveyed areas

In May, dovekies had recently completed migration and should have been accumulating energy prior to breeding by foraging intensely in the polynya. However, only 5 million feeding birds were accounted for in the area surveyed in May. Assuming a population of 30–60 million birds (Salmonsen, 1981; Renaud et al., 1982; Nettleship and Evans, 1985; Boertman and Mosbech, 1998; Kampp et al., 2000), the remaining unaccounted 25–55 million birds must have been in areas that were not surveyed. Several lines of evidence suggest that these birds were packed along the Greenland coast in an area of ca. 22,250 km^2 (represented in dark gray, Fig. 3). First, the numbers of birds per degree block increased rapidly approaching Greenland. Second, high densities of birds could be detected from the ship towards the Greenland coast. Third, one brief helicopter survey during a trip to Qaanaaq, Greenland, revealed large flocks of dovekies adjacent to the coast.

If all of the unaccounted dovekies were congregated within the coastal area of Greenland, densities there would exceed 1000 birds km^{-2} (28 million in 22,250 km^{-2}). Such densities are plausible, since the number of birds in the surveyed block closest to Greenland reached this level. The carbon flux to these birds, east of longitude 71°W to the Greenland coast would have been 8000–17,600 mt C month^{-1} in May or approximately 16–34 mg C m^{-2} d^{-1} over the 23-d period in May when dovekies were present. To support that many feeding birds within such a small area, the biomass of copepods in the upper water column must have been extraordinary.

4.3. The impact of dovekies on carbon cycling in the North Water

In the estimates of the proportion of primary production taken by dovekies, only the pelagic phytoplankton production was taken into account, excluding primary production by ice microalgae on the underside of the ice. Some of the zooplankton consumed by dovekies, in particular *Apherusa glacialis* and *Onisimus littoralis*, were likely dependent on ice-algal production. Partitioning of avian carbon demand between pelagic phytoplankton and ice-algal primary production would have a negligible effect on estimates of avian requirements.

In the North Water, levels of primary production were high ($251 \, \mathrm{g \, C \, m^{-2} \, yr^{-1}}$) and showed strong spatial and temporal trends (Klein et al., 2002). Phytoplankton biomass was highest in the east in May and June, reaching $210 \, \mathrm{mg \, chl} \, a \, \mathrm{m^{-2}}$. Phytoplankton production in the east in May was up to $5200 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$, most of which was attributable to large diatoms ($> 5 \, \mu\mathrm{m}$). Klein et al. (2002) calculated the potential particulate export (PPE) from primary production and f-ratio data (where PPE refers to the potential export via sinking, grazing or transfer to higher trophic levels). PPE was highest in the east during May, reaching values between 2400 and $3150 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$ (Klein et al., 2002). Copepods eaten by dovekies were herbivores (Hobson et al., 2002). Assuming a 10% transfer efficiency across the two trophic levels, dovekies required between 95,960 and 191,920 mt of phytoplankton carbon in May to support their consumption levels.

In the area along the Greenland coast not surveyed in May, dovekies would require between 170 and $340 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$ of primary production to support the secondary production on which they feed. Assuming a PPE of $3150 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$ and a population of 25 million birds in May, dovekies would be responsible for using 5% of the potential particulate export. If 55 million dovekies were in that area and the PPE was $2400 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$, then dovekies may have taken as much as 14% of the PPE. In the rest of the eastern sector, where we were able to account for 5 million dovekies during our surveys in May, dovekies required $1.4 \, \mathrm{mg \, C \, m^{-2} \, d^{-1}}$ of primary production or only 0.04–0.06% of the PPE.

How the high fluxes to dovekies along the Greenland coast are maintained is an open question. Levels of primary and secondary production may be higher in the immediate vicinity of the ice edge. Alternatively, frontal processes near the fiords and islands may concentrate zooplankton in surface waters where planktivorous birds could exploit them efficiently. In the Bering Sea, least auklets (*Aethia pusilla*) exploit near-surface aggregations of copepods at a variety of frontal features (Hunt and Harrison, 1990). Observations in the immediate vicinity of the Greenland ice edge are required to resolve these questions.

4.4. The impact of dovekies on secondary production

We estimate that, on an annual basis, dovekies take 75,000–150,000 mt dry weight of copepods, 27,000–54,000 mt of *T. libellula* and 8500–17,000 mt of juvenile Arctic cod. Estimates of total secondary production in the polynya are not currently available. However, in the southeastern sector of the study area in May 0.6–2.6 dw of female *C. hyperboreus* (standing stock) were present in the upper water column (P. Saunders, unpublished). Given the extraordinary local concentrations of dovekies in this region (up to 4000 birds/km²), these birds were capable of consuming up to 24% of the standing stocks of these copepods in a day. This instantaneous estimate of local consumption by seabirds would be unsustainable on an annual basis. Estimates of annual consumption of prey in seabirds in other regions of the world range between 16 and 29% of secondary production. For example, murres and shearwaters took 16% of the juvenile herring around Vancouver Island (Logerwell and Hargreaves, 1997); seabirds off the Oregon coast took 20% of the secondary production (Wiens and Scott, 1975); and seabirds around the Shetland islands took 29% of fish production (Furness, 1978). Likewise, in the Benguela current, seabirds consumed 23% of the secondary production (Furness and Cooper, 1982). Our estimate of annual carbon consumption by seabirds in the

North Water is only exceeded by the consumption rates of birds in the upwelling systems of Peru (Schaeffer, 1970) and Oregon (Wiens and Scott, 1975) and is *en par* with values found by Croxall et al. (1985) for the Scotia Sea (Table 5).

4.5. Carbon flux to upper trophic predators in polar regions

Within the Arctic, the North Water represents a 'hot spot' for the transfer of energy to upper trophic levels. Seabirds consume almost 3000 times more carbon in the North Water than in the Northeast Water (Greenland Sea) (Falk et al., 1997). The Northeast Water supports small populations of Northern Fulmars and Black-legged kittiwakes (Falk and Moller, 1995) and virtually no subsurface feeders. This absence of subsurface feeders in the Northeast Water may reflect the low levels of production in terms of both copepod biomass and Arctic cod production (Fortier et al., 1994; Hirche et al., 1994; Ashjian et al., 1995; Falk et al., 1997).

Table 5
Food requirements of seabirds in different regions

Location	Food requirements (g wet wt m^{-2} yr^{-1})	Reference
Peru	11–45	Schaeffer (1970)
Oregon	8	Wiens and Scott (1975)
Georges Bank	1.6	Powers and Backus (1987)
Eastern Bering Sea	0.5–2.5	Schneider and Hunt (1982)
Shetland Islands waters	1.9	Furness (1978)
Scotia Sea (Antarctic)	6.5	Croxall et al. (1985)
Southern Davis Strait	1.0	Diamond et al. (1993)
Baffin Bay–Lancaster Sound	2.4	Diamond et al. (1993)
Eastern Canada (mean)	1.1	Diamond et al. (1993)
North Water (all seabirds)	5.1–9.7	This study
North Water (dovekies)	4.6–9.2	This study

Polar seas are often characterized by large numbers of upper trophic predators and relatively short and simple food webs whereby large amounts of fixed carbon are transferred to these predators. Huntley et al. (1991) estimated that Antarctic upper trophic predators respire 12% of the primary production back to the atmosphere. Reevaluating the model of Huntley et al. (1991), Moloney (1992) estimated the percentage at 5%, while Banse (1995) predicted that the value was only 2%. From direct measurements, van Franeker et al. (1997) estimated that Antarctic top predators respire between 0.3% and 0.6% of primary production depending on the estimate of primary production used. In this study, we found that the population of dovekies required 0.3–0.6% of annual primary production for their support and transferred to the atmosphere 0.23–0.46% of the annual primary production in the North Water. Inclusion of marine mammals and other seabirds would elevate the proportion of primary production respired by North Water upper trophic predators above that of Antarctic predators. Schneider et al. (1987) suggested that comparable amounts of carbon flux to seabirds would occur in similar areas with similar oceanographic conditions. The remarkably similar values among the studies reviewed suggest that there may be some maximum limit on the proportion of carbon that can be transferred to upper trophic levels. The comparatively high levels of carbon flux to seabirds in the North Water confirms that it is one of the most important Arctic polynyas for seabirds and one of the most vital areas for seabirds anywhere in the world.

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