Foraging behaviour of thick-billed murres breeding in different sectors of the North Water polynya: an inter-colony comparison

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ABSTRACT: The North Water polynya is an area of open water that occurs year round between northwest Greenland and Canada. Oceanographic conditions differ between the western ('latent heat' polynya type) and extreme eastern ('sensible heat' polynya type) sectors of the polynya, and the effects of this variation on prey availability and foraging conditions for high trophic-level predators are unknown. Thick-billed murres *Uria lomvia* breed on both sides of the polynya, and we conducted inter-colony comparisons of their foraging ecology. We measured time allocation and foraging efforts of chick-rearing adults using electronic data-loggers which recorded dive profiles and flight activity. Murres on the western side of the North Water polynya foraged at relatively shallow depths and rarely (4.4 % of dives) explored depths beyond 70 m. In contrast, murres on the eastern side searched for prey at >70 m in 23 % of all dives, and spent a greater share of each trip actively diving. The Canadian birds made foraging trips of longer duration than the Greenland murres, but they also spent more time 'resting' at the sea surface. Rest time at sea was apparently the only time buffer available for increasing foraging effort. The Greenland birds had little room for increasing foraging effort, while the Canadian birds had spare capacity for additional work. Maximum potential foraging ranges were equal at the 2 colonies (75 % within 50 km), and the murres had access to approximately equally-sized areas of open sea. We estimate that the density of foraging birds at sea within the 50 km of colonies would be 6.5 times higher on the Canadian side due to the large breeding colony at Coburg Island. Intra-specific competition for food should increase with increasing colony size because the predators may reduce food resources within their foraging range. Nevertheless, the Canadian birds worked less than Greenland murres, indicating a relatively good food availability in the western part of the polynya. However, the higher foraging effort by Greenland murres paid off in a higher chick growth rate, so it remains unclear why the Canadian birds did not also make use of their spare capacity to increase foraging effort. Since high-level zooplankton/fish stock interactions are seldom part of oceanographic studies in the Arctic, seabird foraging behaviour and breeding ecology serve as two of the few indicators of possible local variation within the polynya ecosystem.

KEY WORDS: Polynya · *Uria lomvia* · High arctic · Diving · Foraging effort · Time allocation

INTRODUCTION

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Polynyas are open water areas in polar oceans that are otherwise covered in ice (Dunbar 1981). They are ecologically important because the ice-free areas allow

localised early primary production, which often supports abundant wildlife in the high arctic. For example, seabird colonies in the high arctic are often associated with polynyas that provide access to abundant food resources during the breeding season (Brown & Nettleship 1981, Massom 1988, Falk et al. 1997, Stirling 1997).

The North Water (NOW) polynya is located between northwest Greenland and Ellesmere Island in Canada, and typically has a surface area of 15 000 km^2 of open water in spring (Mysak & Huang 1992) when the seabirds arrive. This polynya is considered especially productive; possibly two thirds of the world's known breeding population of the dovekie *Alle alle* breed at the eastern margin of the NOW (Nettleship & Evans 1985, Boertmann & Mosbech 1998, Kampp et al. 2000), and over 350 000 pairs of thick-billed murres *Uria lomvia* breed in colonies on the margins of the polynya (Birkhead & Nettleship 1981, Falk & Kampp 1997). Furthermore, high numbers of sea mammals also utilise the North Water (Stirling et al. 1981, Richard et al. 1998).

Preliminary investigations suggest that oceanographic conditions differ between the eastern (Greenland) and western (Canadian) margins of the NOW polynya: Both 'latent heat' (wind-driven) and 'sensible heat' (upwelling of warmer water) contribute to maintain open water in the NOW. However, latent heat actions are dominant on the western side, whereas sensible heat effects appear only along the eastern margin of the NOW, close to the Greenland coast (Mysak & Huang 1992, Melling et al. 2001). The influence of these oceanographic differences on biological productivity and species distribution is largely unknown, but may affect the timing and magnitude of primary production and the availability of zooplankton for fishes within the polynya. Regional differences in fish population size and availability (spatially and temporally) could be expected to influence the foraging and reproductive ecology of seabirds breeding on the east and west margins of the polynya.

Thick-billed murres breed in colonies on both the east and west sides of the NOW, providing the opportunity to compare the ecology of a seabird foraging in 2 'sectors' of the polynya. The thick-billed murre is a pursuit-diving auk feeding on a variety of marine fishes and invertebrates (Gaston & Jones 1998). Both members of a pair provision their chick with a single fish per visit (typically 2 to 5 times per day; Gaston & Nettleship 1981, Gaston & Jones 1998). Provisioning of young requires substantial energetic costs (Gaston 1985, Benvenuti et al. in press), largely because of the commuting distances to foraging areas, and the number and depth of dives required (Benvenuti et al. 1998, Falk et al. 2000). Since murres have flexible time budgets, variation in the time allocated to flying, diving,

and rest probably reflects local variation in food availability near the colony within a breeding season, and potentially across years (Burger & Piatt 1990, Monaghan et al. 1994, Kitaysky et al. 2000). Hence, a comparison of dive depth and frequency, time allocation during foraging trips, and foraging range (time spent flying), may provide insights into the availability of forage fishes to seabirds nesting at different colonies. No data on the distribution and abundance of fishes and large zooplankton in the North Water polynya are available; thus, studies of seabird ecology currently provide the only indication of regional variation in the polynya food web.

Here, we compare the time allocation and details of foraging behaviour of thick-billed murres breeding at Coburg Island (western side of the polynya—the latent heat sector) and Hakluyt Island (eastern side—sensible heat sector) as measured by means of computerised data-loggers recording dive frequency, dive profiles, and flight activity. We also examine annual variation in foraging behaviour on the eastern side of the polynya by comparing data from 2 years at Hakluyt Island (1997 and 1998).

MATERIALS AND METHODS

Study area. The study was carried out on 2 colonies about 220 km apart: Hakluyt Island (77° 26′ N, 72° 42′ W) in the Avanersuaq (Thule) district of northwest Greenland, and Coburg Island (75° 48′ N, 78° 25′ W) at the entrance to Jones Sound between Ellesmere and Devon Island in the southwestern side of the NOW polynya (Fig. 1). Hakluyt Island contains about 26 000 pairs of murres nesting from about 25 to 400 m above sea level (asl), and Coburg Island supports approximately 160 000 pairs of murres, breeding from 5 to 200 m asl (Birkhead & Nettleship 1981, Kampp 1990, Falk & Kampp 1997).

There was continuous daylight during the study period (sun above the horizon 24 h per day). Throughout this paper, time is given in local (solar) time at the colony (Coordinated Universal Time, UTC minus 4.85 h at Hakluyt Island, UTC minus 5.40 h at Coburg).

Sampling and potential bias. We obtained data from 9 thick-billed murres from each of Hakluyt and Coburg Islands, captured in different sub-colonies between 20 July and 18 August 1998. In addition, relevant data from 13 birds at Hakluyt Island in 1997 (Falk et al. 2000) are included and reanalysed for inter-year comparisons. All birds selected for these recorder experiments were adult breeders with 2 to 10 d-old chicks when first captured. Birds were captured from the nest by means of a noose-pole, and weighed by spring balance to the nearest 5 g.

The birds were captured within the following time spans: between 9:20 h in the morning and 0:46 h in the night at Hakluyt 1997; between 9:40 and 21:40 h at Hakluyt 1998, and 12:42 to 20:30 h at Coburg 1998. Although these intervals overlapped widely, the difference in capture times differed significantly between Coburg and Hakluyt in 1998 (U2 angular test, p < 0.05) but not between the 2 years at Hakluyt. In the thick-billed murre, the sexes are known to establish synchronised nest stints, so that in the high arctic males usually brood during night hours (Gaston & Nettleship 1981). Therefore, the non-random capture times in our study may have introduced a sex bias in our sample. At low latitudes, murres make very shallow dives or no dives during the dark hours (Croll et al. 1992, Falk et al. unpubl. data), so combined with different colony-attendance patterns, the 2 sexes may attain different average dive depths.

To assess whether a possibly biased sampling of birds could influence our comparative study we tested if dive patterns varied systematically during the 24 h continuous daylight. Our depth meters truncated readings deeper than 75 m (see subsection 'Data analyses' below), but since dive depth was closely correlated with dive duration within the 5 to 75 m interval (r^2 = 0.77, p < 0.0001, n = 775, based on 25 random dives for each bird), we used dive duration as an indicator of potential dive depth in this case to allow parametric statistics. From the total pool of dives we sampled 50 dives for each bird at random and data were used in a 1-way ANOVA of dive duration in relation to solar time.

Data logger devices and attachment. We used a data-logger designed by researchers in Pisa, Italy, to record dive profiles (operative range 0 to 75 m, resolution 30 cm) and periods of flight activity (Dall'Antonia et al. 1993, 1995). The times between successive recordings were 4 s for the depth meter and 10 s for the flight sensors. This schedule allowed continuous recording for about 4.1 d before logger memory was full.

The electronic units were fitted in carbon-fiber housing, and the total unit weighed approx. 29 g (but 0 g in sea water, i.e. with neutral buoyancy); the maximum dimensions of the streamlined container were (width × height × length) $31 \times 18 \times 80$ mm. The maximum cross-sectional area was 4.1 cm^2, corresponding to less than 5% of the estimated frontal area of a thick-billed murre. The front end was rounded to reduce drag. The device was attached to the feathers along the middle of the lower back of the bird by means of cyanoacrylate glue and 3 rings of thin brass wire (Benvenuti et al. 1998). The average total handling time from capture to release was 27 min (range 14 to 51 min), and upon release most birds were seen to return to their nest site within a few minutes (mean 10 min, SD = 15 min, n = 13 birds) and immediately resumed normal nest guard behaviour (see also Falk et al. 2000).

When the birds were recaptured 2.5 to 5.7 d after recorder attachment, they were re-weighed, the recorders removed, and data downloaded to a notebook PC.

Reaction of birds to devices. The average bird body mass of experimental birds at Hakluyt Island when first captured was 930 g (SD = 69, n = 13), and 961 g (SD = 71.8 g, n = 9) in 1997 and 1998, respectively. The mean body mass of birds at Coburg Island was 906 g (SD = 49.6, n = 9) in 1998. None of these differences were significant (between years at Hakluyt: Student's t = 1.00, df = 20, p = 0.32; between colonies in 1998: t = 1.89, df = 16, p = 0.077).
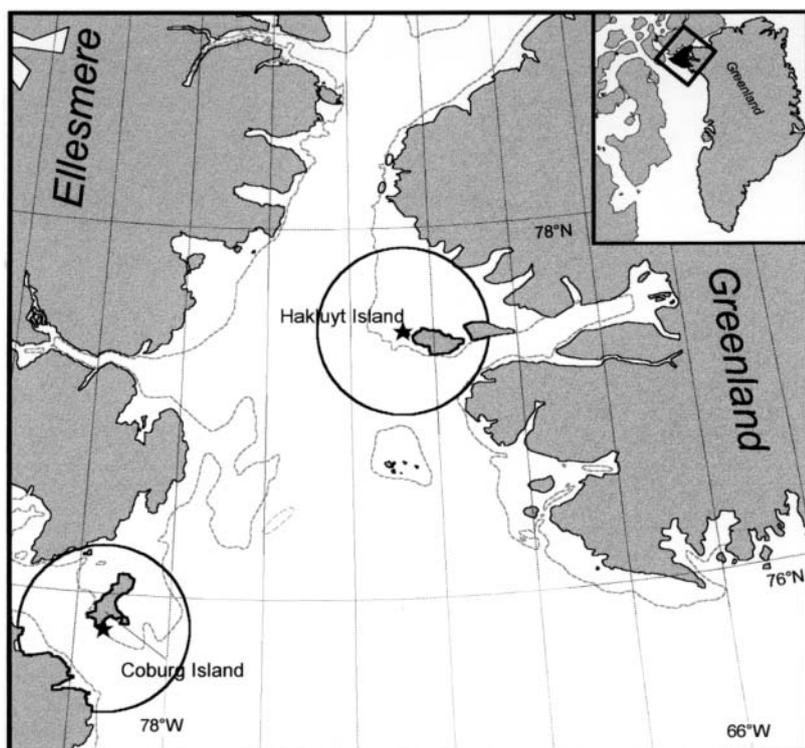

Fig. 1. Map of study area. Dashed lines are 200 m depth contour, and large circles indicate 50 km potential foraging range of murres in each studied colony (see 'Discussion'). In inset, black area indicates the approximate position during late spring of the North Water Polynya (adapted from Smith & Rigby 1981) between Ellesmere Island (Canada) and Northwest Greenland

All birds at Hakluyt Island lost mass during the time they carried the recorders (mean 12.7 g d^{-1}, SD = 7.0, n = 9), while 4 of 7 birds weighed at Coburg gained some mass during the experiment so that the average loss for all birds combined was smaller than at Hakluyt (mean 2.4 g d^{-1}, SD = 11.1, n = 7). Experiments were carried out during the chick-rearing period when adult murres often experience a natural mass loss, in some cases by as much as 3 to 4 g d^{-1} (Croll et al. 1991, Gaston & Perin 1993, Gabrielsen 1996). As in previous studies (see Falk et al. 2000 for further discussion on the effects of these devices on the murres), the birds appeared to behave normally, and no experimental pairs experienced breeding failure in relation to the experiments.

The main effect of the device may be hydrodynamic drag (Schmid et al. 1995), possibly affecting estimates of time allocation. However, since this is a comparative study where all birds are burdened equally, biases should be equal.

Data analyses. Flight and dive data were used to reconstruct the foraging trips as series of alternating flights and stops of known duration. Since the exact 'on' time of each instrument was known, an accurate timing of all events was possible. Flight and dive data were reviewed and analysed by a special software application, VISUA3 (designed by A. Ribolini, IEI, CNR, Pisa), while all computations and statistical analyses were performed using SAS version 6.11 (SAS Institute Inc. 1996).

We use the term 'trip' for the time between a nest departure and subsequent return. Each flight period was timed to the nearest 10 s, while all dives were timed to the nearest 4 s. In analyses of dive depths we applied a threshold of 2 m depth to exclude records of 'bathing splashes' and at the same time to account for slight shifts in the 0-level of the depth recorders. During the stops at sea, diving activity was computed as the number of dives for each 10 m depth interval. We defined 'bottom time' as the time spent within 10 m of the maximum depth reached at each specific dive. We considered the short time spent between individual dives as 'interdive breaks' while the longer breaks (between bouts) lasting more than 250 s were classified as 'rest' at the sea surface. Based on the total accumulated flight time for each trip, the 'maximum potential foraging range' (linear distance to colony) was estimated as half the total flight time multiplied by the average flight speed (65 km h^{-1}: Benvenuti et al. 1998). Of course this is not a measurement of foraging distance but a rough upper limit to how far the birds could have ventured. For further definitions and discussion on data accuracy refer to Falk et al. (2000).

All statistical tests are parametric and 2-tailed. However, since the depth gauges truncated depth readings beyond 75 m, we used non-parametric statistical tests in maximum dive depth comparisons. In addition, to overcome problems of non-independence in dive-depth data, we used the 50 random dives selected for each bird (see earlier subsection 'Sampling and potential bias') in inter-year and inter-colony comparisons of dive duration by randomisation tests (1000 resamplings in PROC MULTTEST: SAS Institute Inc. 1996). Data with a skewed distribution were log-transformed prior to statistical analyses. Since each experimental bird contributed several trips to the data set, trips are not independent, so where appropriate, data were analysed at the 'bird level' using the mean for all trips from each bird as the data values. Means are given ±1 SD; we use the word 'significant' in its statistical sense only.

We compare effects of overall time allocation of birds in the 3 experiments (Hakluyt 1997, Hakluyt 1998, and Coburg 1998) using daily energy expenditure of each experimental bird estimated by allometric equations for each activity (resting at the nest, swimming at the sea surface, flying, and diving) as summarised by Diamond et al. (1993).

Table 1. *Uria lomvia.* Inter-year (Hakluyt 1997 vs 1998) and inter-colony (Hakluyt vs Coburg islands) comparisons of trip duration, trip flight time, duration of longest stopover in a foraging patch during each trip, and dive duration in the high arctic. Trip flight time was analysed on log-transformed data because of skewed data; dive duration was based on 50 dives (selected at random) for each bird. Rand. test = randomisation test (permutation test with SAS PROC MULTTEST), adjusted p-values

Colony, year	No. of birds	Trip duration (h) Mean (SD)	t-test	Trip flight time (h) Mean (SD)	t-test	Longest stopover (h) Mean (SD)	t-test	Dive duration (s) Mean (SD)	Rand. test
Hakluyt 1997	13	9.27 (3.15)		1.17 (0.48)		4.06 (1.35)		123.9 (41.3)	
			t = 1.11 p = 0.28		t = 0.43 p = 0.67		t = 0.48 p = 0.63		p = 0.0001
Hakluyt 1998	9	7.97 (1.77)		1.06 (0.35)		3.72 (2.01)		111.9 (49.9)	
			t = 5.41 p < 0.0001		t = 0.44 p = 0.66		t = 2.65 p = 0.018		p = 0.0001
Coburg 1998	9	12.78 (1.99)		1.22 (0.60)		6.15 (1.88)		85.6 (37.3)	

RESULTS

Foraging trip duration and behaviour

The data-loggers provided data from 51.1 bird-days (n = 13 murres) at Hakluyt Island in 1997, 29.5 d in 1998 (n = 9), and 27.3 d (n = 9) at Coburg Island in 1998.

The mean duration of foraging trips (excluding short bathing trips) per bird was similar in the 2 study years at Hakluyt Island (9.27 and 7.97 h, respectively), while trips lasted significantly longer (12.78 h) for Coburg murres (Table 1).

During a foraging trip, the birds normally made a number of relatively short flights interrupted by short diving bouts until they reached an area where they stayed and dived (and rested) for a long time (herein termed the 'main foraging patch'). The maximum stopover during each trip in these patches lasted significantly longer for Coburg birds (6.15 h: Table 1) than for Hakluyt birds (3.72 h), while there was no difference between years at Hakluyt (Table 1).

The time spent diving (submerged) was positively correlated with trip duration for all the experiments. Regression slopes were very similar between years at Hakluyt (Fig. 2), but Coburg birds spent significantly less time submerged than Hakluyt birds in 1998 (ANCOVA, $F = 26.2$, $p < 0.0001$). However, the variances were greater in the Coburg birds—reflected in the lower r^2 value—than was the case at Hakluyt during the same year (Fig. 2).
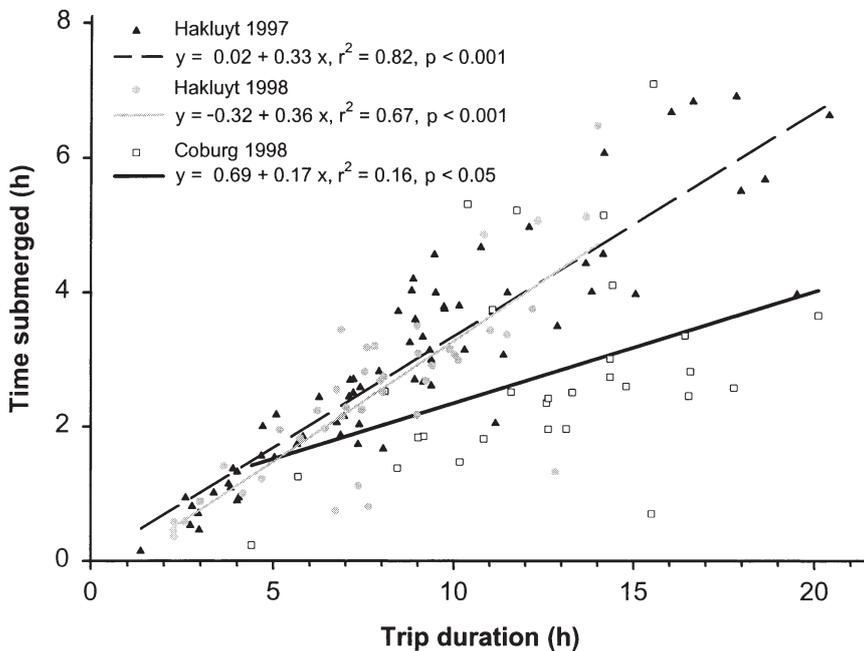
Table 2. *Uria lomvia*. Potential foraging range (km) at Hakluyt and Coburg Islands

	Hakluyt 1997	Hakluyt 1998	Coburg 1998
Mean	42.5	37	42
SD	26.5	15.3	29.9
Max.	119.9	62.3[a]	137.8
75% quantiles	56	49.7	49.8
50% quantiles	39	37.7	37.4
25% quantiles	25.8	26.5	22
n (trips)	67	41	29

[a]One extreme flight of 3 h 31 min excluded (see second subsection of 'Results')

Flight duration and potential foraging range

From the 'main foraging patch', a murre normally returned to the colony in a single flight. More rarely, a bird sometimes interrupted this flight with a few short breaks on the way (Fig. 4 in Falk et al. 2000). Therefore the longest continuous flight periods always occurred when the birds were returning to the colony (i.e. one of the last flights), and the mean duration of the longest flights on each trip did not differ between colonies (log-transformed data; Hakluyt 1998: 36.6 ± 31.1 min, Coburg: 28.4 ± 21.2 min; $t = 1.33$, df = 70, $p = 0.19$) or between years (Hakluyt 1997: 37.6 ± 31.1 min; $t = 0.12$, df = 72.8, $p = 0.91$). One murre (Hakluyt 1998) made a very long flight, remaining airborne for a continuous period of 3 h and 31 min. However, since the corresponding 'outbound flights' in this case were short (5 flights adding up to 48 min) the last prolonged flight period could be considered a real 'home flight', and we excluded this odd trip from inter-year and inter-colony comparisons.

During each foraging trip, the average time spent flying per bird was very similar in the 3 experiments (Table 1) and, hence, the maximum 'potential foraging range' was consistent between years as well as between colonies (Table 2). Average foraging distance was 42.5 and 37.0 km for Hakluyt birds in 1997 and 1998, respectively, and for Coburg it was 42.0 km. At Coburg, only 2 trips (7%) could have exceeded 100 km, while the corresponding value for Hakluyt was 4 trips (6%) in 1997 and none in 1998 (1 odd trip excluded, see above).

Fig. 2. *Uria lomvia*. Total time spent submerged in relation to duration of individual foraging trips in 3 experiments
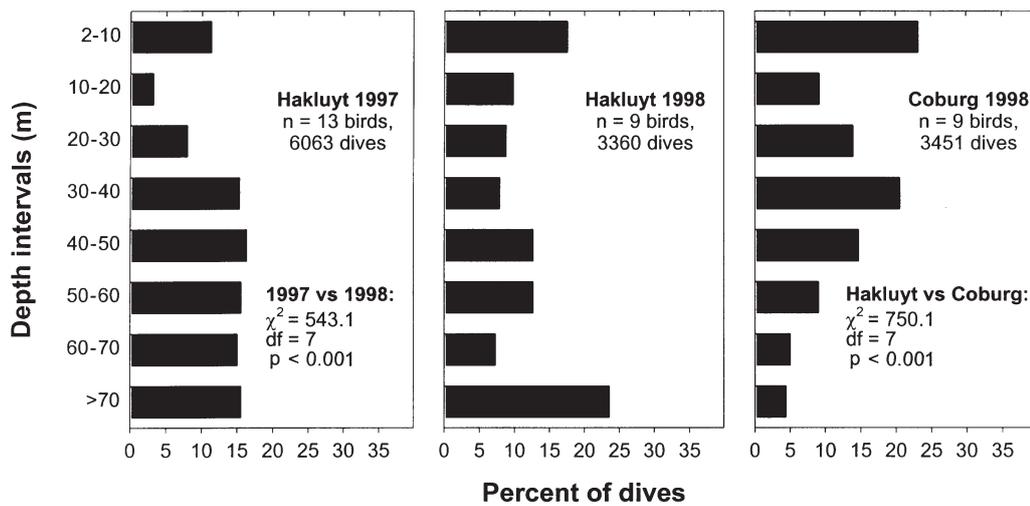
Fig. 3. *Uria lomvia*. Proportions of dives reaching each 10 m interval for all birds combined in each of the 3 experiments. Statistics for inter-year and inter-colony comparisons are given in the graphs

Diving behaviour

Birds at Hakluyt Island dove significantly deeper in 1997 than in 1998 (Kolmogorov-Smirnov test, $D = 0.279$, $p = 0.0001$), and Hakluyt birds in 1998 dove significantly deeper than Coburg Island murres ($D = 0.125$, $p = 0.0001$). This is clearly reflected in the depth categories reached during individual dives (Fig. 3), which differed significantly between years as well as between colonies (see χ^2 test results in Fig. 3). While all depth categories deeper than 30 m were used to the same extent in 1997, Hakluyt birds in 1998 went beyond 70 m in 23% of all dives, and also made many shallow dives (17.5% in the 2 to 10 m category). In contrast, the Coburg birds generally made shallow dives (23.2% in the 2 to 10 m category), and rarely went deeper than 70 m (4.4%). These descriptions are based on all dives, which cannot be considered independent. However, the differences were confirmed by testing dive duration (i.e. an indicator of potential dive depth) of 50 random dives from each bird by randomisation tests (Table 1): dive duration was significantly longer at Hakluyt than at Coburg, and significantly longer in 1997 than in 1998 at Hakluyt.

The birds did not distribute their dives randomly over the 24 h of daylight in any of the 3 experiments (χ^2 test of homogeneity, $\chi^2 = 568.8$, df = 23, $p = 0.001$). In all 3 cases, the diving activity was low at noon (Fig. 4). At Hakluyt in 1997 the pattern was clearly bimodal, with peaks in the morning and evening and with marked lows at noon and midnight. In 1998, the second activity peak was much reduced, and most dives were performed between 05:00 and 10:00 h in the morning. At Coburg the main peak occurred about midnight, 4 h earlier (local solar time) than at Hakluyt.

Although dive duration differed significantly within the 24 h high arctic day (1-way ANOVA, $p < 0.0001$, $r^2 = 0.04$), there was no clear pattern of long or short dive times made at any particular time of the day (Fig. 5), and the r^2 value was very low. In addition, the deepest dives recordable by the depth gauges (75 m, corresponding to approx. 185 s) were reached at all times of day.

Time allocation

Overall time allocation was similar in the 2 years at Hakluyt Island, whereas birds at Coburg apparently differed from Hakluyt birds by spending significantly more time engaged in surface swimming at sea and less time on nest duty (Fig. 6). Fig. 6 (right panel) splits the time budget into 6 categories: (1) nest attendance, (2) flying, (3) time spent commuting through the water column (ascent and descent) to reach the working depth, (4) time at depth available for chasing prey (bottom time), (5) interdive breaks on the surface following dives before initiating the next dive, and (6) long breaks between diving bouts which we considered to be true resting periods (rest at the surface); in the left panel the categories (3) and (4) are combined as 'Surface swimming', and (5) and (6) as 'diving'. A multivariate ANOVA on proportion of time spent on each of the categories (arcsine-transformed data) showed no overall difference between years at Hakluyt ($F = 0.84$, df = 6, $p = 0.84$). The total model which compared colonies verged on significance ($F = 3.07$, df = 6, $p = 0.051$) in this conservative test, and the Coburg birds devoted significantly more time to rest at surface than the murres from Hakluyt ($F = 10.83$, df = 1, $p = 0.0046$).

Converting the time allocation data into the birds'
total energy expenditure (cf. Diamond et al. 1993), the
Hakluyt murres in 1997 and 1998 spent on average
1618 (± 138) and 1559 (± 210) kJ d^{-1}, respectively
($t = 0.80$, df = 20, p = 0.43), whereas Coburg birds used
1428 (± 179) kJ d^{-1}—not significantly different from
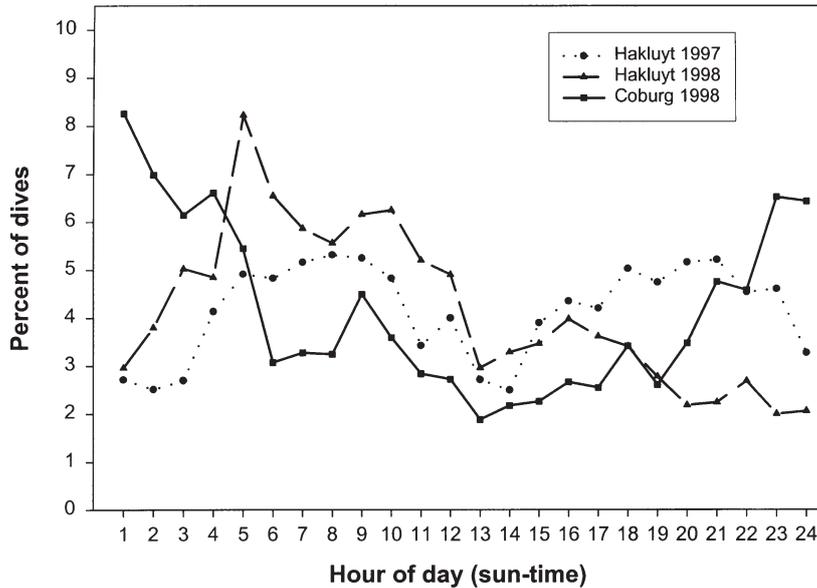Hakluyt birds the same year ($t = 1.42$, df = 16, p = 0.077).

Fig. 4. *Uria lomvia*. Daily diving activity patterns at Haklut Island in 1997
and 1998, and at Coburg Island 1998 (data for Hakluyt 1997 from Falk
et al. 2000)
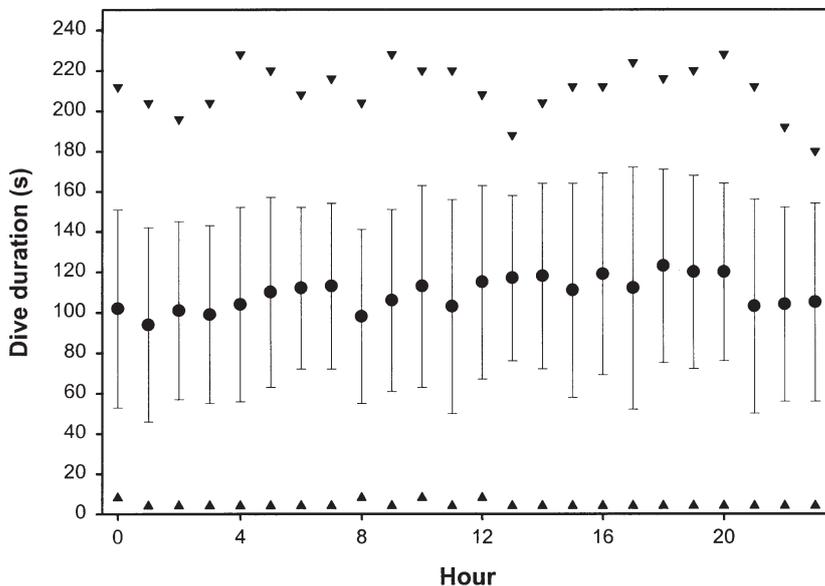
Fig. 5. *Uria lomvia*. Average dive duration (± SD) within each hour of the
24 h day; (▼) symbols indicate minimum and maximum values. Data based
on 50 dives (selected at random) for each bird (n = 31)

DISCUSSION

Inter-year and inter-colony comparison

This comparative study revealed few differences be-
tween 2 yr at Hakluyt Island at the eastern (Greenland)
side of the NOW polynya. The depth categories used by
foraging murres shifted, so that in 1998 the
most shallow (2 to 10 m) and the deepest
(>70 m) categories were used more than in
the previous year, and the 24 h foraging ac-
tivity pattern changed from clearly bimodal
in 1997 to a main foraging peak in early
morning in 1998, and a less marked elevated
activity in the afternoon. All other inter-year
comparisons showed small and insignificant
differences.

Inter-colony differences were more pro-
nounced. Compared to murres at Haklyt
Island, birds at Coburg island: (1) took
longer foraging trips, (2) foraged at shal-
lower depths, and (3) concentrated diving
activity around midnight — about 4 h ear-
lier than the Greenland birds. Murres from
the Coburg Island colony also spent larger
parts of each trip sitting on the sea surface,
and less time actively diving.

Because of their capture times, our sam-
ple of birds may have been sex-biased be-
cause the males tend to attend the chick
during 'night' hours (Gaston & Nettleship
1981). However, the large spread in cap-
ture times over the day should make a
strong sex bias unlikely. In addition, the ar-
rival and departure times recorded for the
tagged birds showed that 35% of the birds
could be away on foraging trips at any time
of the day, i.e. at no time were individual
birds guaranteed to be at their nest site.
Consequently, it was difficult to define in-
dividual birds as either 'night' or 'day'
birds. Furthermore, there was no clear di-
urnal pattern in dive duration during the
24 h of daylight (birds dived beyond 75 m
at all times of the 24 h day: Fig. 5).
Thus, any sex bias would not affect our
inter-colony comparisons of dive patterns.
Therefore, based on Fig. 5 and the very
low r^2 value of the analysis of dive duration
in relation to hour of the day, we consider
that the statistical significance of the test is
without biological importance, and the
variation cannot account for the marked
differences in dive depths observed in the
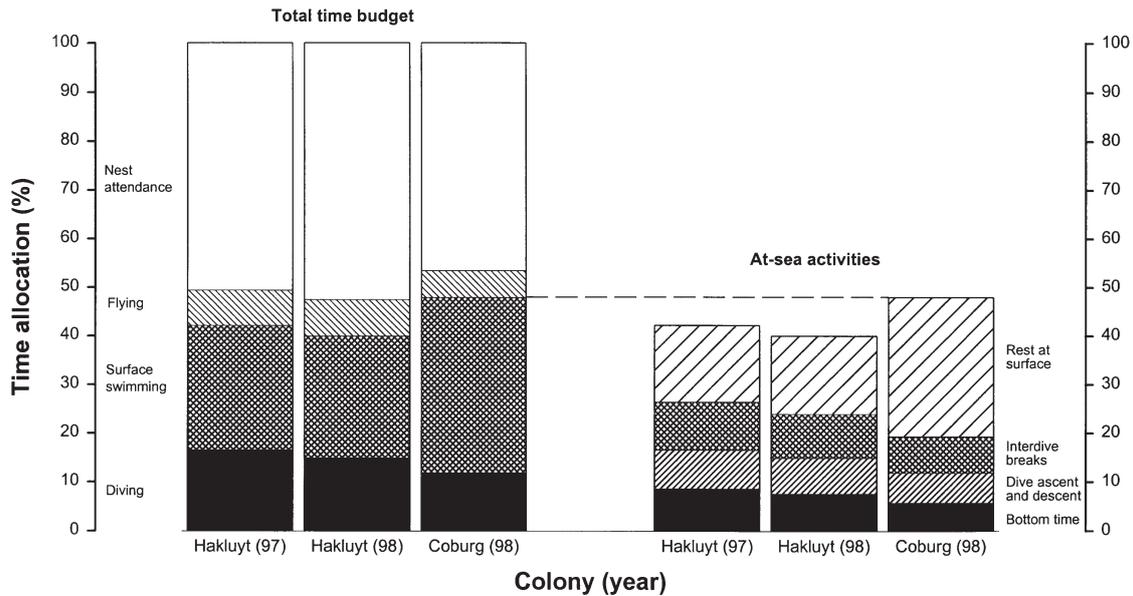inter-colony and inter-year comparisons.

Fig. 6. *Uria lomvia*. Time allocation at Hakluyt Island in 1997 and 1998, and at Coburg Island in 1998; 'At-sea activities' are breakdown of at-sea time only

Seabirds as indicators of the polynya environment

The marked behavioural differences between birds breeding on the 2 sides of the polynya suggest that foraging conditions differ in the 2 sectors of the NOW polynya.

Although the time allocation differed somewhat between the 2 colonies in 1998, and less so between years at Hakluyt Island, it caused only near-significant (p = 0.077) differences in the birds' total energy expenditure. However, considering the tendency of Coburg murres to spend much time resting at the sea, the lower level at Coburg may be real, albeit not detectable at these small sample sizes (9 birds from each island). The equation (cf. Diamond et al. 1993) applied to estimate energetic costs of underwater swimming is likely to overestimate the expenditure of this activity (Gabrielsen et al. 1988, Gabrielsen pers. comm.), and the total energetic cost for all 3 groups of experimental birds should probably be adjusted somewhat downwards.

The analyses of dive depth categories (and dive duration) indicated that in the western (Canadian) side of the NOW, chick-rearing birds could collect much of their daily food at relatively shallow depths (i.e. they rarely dived beyond 70 m). In contrast, the murres at the Greenland side searched for prey at >70 m in 23% of all dives, and spent a greater proportion of each trip actively diving (Figs. 2 & 6).

The average potential foraging ranges were remarkably similar in all 3 experiments (Table 2), with 75% of all trips within 50 km, although a few birds could have ventured much further. Icelandic thick-billed murres tended to seek foraging areas situated either 'close' (10 to 37 km) or 'far' (128 to 168 km) from their colony (Benvenuti et al. 1998), and aerial surveys of high arctic birds in Canada suggested normal foraging distances of about 56 km during the chick-rearing period (Gaston & Nettleship 1981, Gaston 1985).

Within their potential foraging ranges, murres from both colonies had access to relatively shallow shelf areas as well as deep 'pelagic' zones of the NOW polynya (Fig. 1). Both colonies occurred on islands away from the mainland. Thus, within a 50 km radius of each colony, 95 and 88% of the areas were open ocean at Hakluyt and Coburg, respectively. Roughly 3000 km^2 (38%) of the area would be within the 200 m isobath in both cases; Falk et al. (2001) showed that chick-rearing Hakluyt murres mainly foraged over the shallow shelf area. Since the estimated potential maximum foraging range for both sites was equal, but the population at Coburg much larger than at Hakluyt, the density of foraging birds was higher in the vicinity of Coburg. With about 160 000 murre pairs at Coburg, and assuming that 19% of birds on the cliff at any given time would be non-breeding prospectors (Gaston & Nettleship 1981), a total of about 406 000 murres would belong to the colony and feed in adjacent waters. This translates to approximately 59 birds km^{-2} of water within a 50 km radius. In the same manner, Hakluyt supports about 65 000 murres, and about 9 murres km^2 of sea within the same radius. Intra-

Table 3. *Uria lomvia* and *U. aalge*. Trip duration and time allocation during foraging trips at various locations

Species, Location	Trip duration (h)	Percent of trip spent			Comments	Source
		diving	flying	swimming		
U. lomvia						
Hakluyt 1997	9.27	33.6	14.7	51.7		Falk et al. (2000)
Hakluyt 1998	7.97	31.5	15.8	52.7		Present study
Coburg 1998	12.78	22.3	10.4	67.3		Present study
U. aalge						
Scotland	6.78	34.2	6.9	58.9	Poor year	Monaghan et al. (1994)
Scotland	1.12	15.4	2.7	81.9	Good year	Monaghan et al. (1994)
Newfoundland 1985		16.6	13.4	70.0		Cairns et al. (1990)
Newfoundland 1986		12.5	8.5	79.0		Cairns et al. (1990)

specific competition for food may increase with increasing colony size because seabirds may substantially reduce food resources within their foraging range of the colony (Cairns 1992, Furness & Birkhead 1984, Hunt et al. 1986, but see Ainley et al. 1995). But even though the density of foraging birds would be 6.5 times higher on the Canadian side, the birds there worked less than on the Greenland side.

The birds at Coburg apparently did not use their longer trip duration (time away from the nest) to reach more distant foraging grounds, and clearly spent more time resting at the sea surface. The time allocation during foraging trips summarised in Table 3 shows the small inter-year difference at Hakluyt, and the relatively light 'workload' of the Coburg birds, although compared to similar data for common murres, *Uria aalge*, thick-billed murres foraging in the NOW put greater effort into foraging during the chick-rearing period (Table 3). Since the rest time at sea would be the only real buffer the birds could use to increase foraging effort in case of low food availability, the Hakluyt birds had little room for increasing foraging effort, while those at Coburg had some spare capacity. From these observations it seemed that food was more available to murres at Coburg than to the birds on the Greenland side.

However, other observations contradict this deduction. The extended trip duration of Coburg birds meant that their chicks experienced a lower feeding rate than Hakluyt chicks. Preliminary analyses of chick growth rates (linear regression slope of age/mass observations of individual chicks) recorded at sample plots in each of the 2 colonies revealed that Hakluyt chicks had a significantly higher growth rate than Coburg chicks (mean 10.4 ± 4.1 g d^{-1} at Hakluyt, versus 7.1 ± 4.4 g d^{-1} at Coburg; $t = -2.80$, df = 53, p = 0.007: Falk & Gilchrist unpubl. data). Since the higher foraging effort of the Hakluyt birds seemed to pay off in terms of chick growth rate, it appears strange that the Coburg birds did not make use of their spare capacity to increase their foraging effort. Further analyses of breeding ecology data from the colonies are needed to shed light on these apparent contradictions.

Overall, our data suggested that living conditions for this diving fish and zooplankton predator differed between the 2 sides of the NOW polynya. As the conditions in the eastern 'sensible heat side' of the polynya should favour earlier production, it is surprising that food availability to the murres here should be poorer than in the western 'latent heat side', as this study has indicated. The foraging ecology of murres feeding on large zooplankton (part of adult diet) and fishes (adult and chick diet) suggests that variation in the marine food webs exists geographically within the polynya, even late in the summer when murres are provisioning chicks. These findings are important, given that high-level zooplankton and fish stock interactions are seldom part of oceanographic studies in the arctic.

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