REPRODUCTIVE BIOLOGY OF THICK-BILLED MURRES (URIA LOMVIA): AN INTER-COLONY COMPARISON

T. R. BIRKHEAD¹ AND D. N. NETTLESHIP

Canadian Wildlife Service, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2

ABSTRACT.—Observations of the reproductive biology of Thick-billed Murres were made at Cape Hay, Bylot Island and at Coburg Island, Northwest Territories, Canada simultaneously by two teams between June and September 1979. The median laying date at Coburg (2 July) was 4 days earlier than at Cape Hay (6 July), and this resulted in the following differences in breeding biology. At Coburg egg volumes were larger, chick growth rates higher, and the proportion of chicks fledged per pair higher than at Cape Hay. An additional factor that reduced breeding success at Cape Hay, independent of laying date, was ice- and rockfalls onto incubating birds. At both colonies chicks were fed mainly on arctic cod (*Boreogadus saida*). At Cape Hay 48% of the pairs raised a chick to fledging, with a mean fledging weight of 190.6 g, whereas the corresponding values for Coburg were 71% and 206.1 g. *Received 2 May 1980, accepted 12 September 1980.*

THE Thick-billed Murre (Uria lomvia) is one of the most numerous seabird species in the Northern Hemisphere, breeding in a relatively small number of very large colonies (see Brown et al. 1975). Various aspects of the breeding biology of this species have been studied (Uspenski 1956, Belopol'skii 1957, Tuck 1961, Swartz 1966), and an outline of its life cycle and reproduction can be found in Tuck (1961) and Gaston and Nettleship (in press). This study is part of a broader program of work conducted by the Canadian Wildlife Service on the biology of seabirds, including Thick-billed Murres, and aims to provide baseline information in order to assess the impact of man's industrial activities on seabird breeding biology in the eastern Canadian Arctic (Nettleship 1977, Gaston and Nettleship in press). Most of our previous work on Thick-billed Murres was conducted at Prince Leopold Island, Lancaster Sound from 1975 to 1978 (Gaston and Nettleship in press, Nettleship et al. MS). Earlier studies (Belopol'skii 1957) have shown that the timing of breeding of Thick-billed Murres can vary between colonies and between years. In the present study, we have compared timing of breeding and reproductive success at two high arctic colonies in a single season to obtain a measure of inter-colony variability in these features.

STUDY AREA AND METHODS

Location of the study.—Observations were made at the Thick-billed Murre colony just west of Cape Hay $(73^{\circ}46'N, 80^{\circ}23'W)$, Bylot Island and at Cambridge Point $(75^{\circ}48'N, 79^{\circ}25'W)$, Coburg Island. The Cape Hay colony is situated at the entrance of Lancaster Sound, and Coburg Island lies 200 km due north at the entrance to Jones Sound (Fig. 1). We made preliminary observations at both colonies in July and August 1978 during which we located suitable study areas, collected samples of adults for body measurements, and assessed colony size. Both colonies hold about 100,000–200,000 pairs of Thick-billed Murres, 20,000–30,000 pairs of Black-legged Kittiwakes (*Rissa tridactyla*), 50–100 pairs of Glaucous Gulls (*Larus hyperboreus*), and about 100 pairs of Black Guillemots (*Cepphus grylle*).

In 1979, observations at both colonies were started just before egg laying in late June and continued until most chicks had fledged in early September. The two field parties were in daily radio contact, which facilitated co-ordination of the studies at each colony.

¹ Present address: Department of Zoology, University of Sheffield, Sheffield S10 2TN, England.

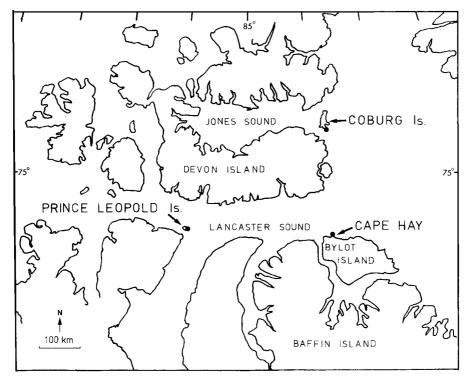


Fig. 1. Lancaster Sound and Jones Sound, N.W.T., Canada showing the location of Thick-billed Murre colonies (\bullet) mentioned in the text.

Description of the colonies.—At both colonies Thick-billed Murres bred on cliff ledges, from 5 m above sea level to the top of the cliffs (300 m at Cape Hay, 200 m at Coburg). The rock structure and accessibility of breeding areas were quite different at the two colonies. The Coburg cliffs consisted of an irregular series of peaks and gullies, with some areas sloping at 45° to the sea. At Cape Hay the limestone cliffs were almost vertical, and there were few irregularities (Fig. 2). The Coburg camp site was situated at sea level on a beach 2 km north of the colony, and, because of the cliff structure, access to the colony was by Zodiac rubber inflatable boat, from the foot of the cliffs only. At Cape Hay the camp was situated on the cliff tops at about 300 m near the western end of the colony. There were differences in climatic conditions at the two colonies in 1979. Cape Hay experienced almost perpetual fog throughout the summer, whereas Coburg had relatively few foggy days. Over the entire season (24 June-1 September) mean temperatures were lower at Cape Hay (+1.5°C) than at Coburg (+2.57°C) (t = 4.65, 134 df, P <0.001), allowing for altitudinal differences of weather stations at each camp. On a day-to-day basis, mean temperatures were correlated (r = 0.476, 64 df, P < 0.001). Wind speeds were also correlated (r =0.327, 68 df, P < 0.01) but were not significantly different between colonies (Cape Hay, $\bar{x} = 17.7$ km/ h; Coburg, $\bar{x} = 15.5$ km/h).

Study plots.—At each colony several study plots were located, photographed, and delineated. These were observed each day (sea-surface conditions permitting at Coburg) from 25 June until early September from blinds located 5–50 m away. The laying date of each egg was recorded using methods outlined in Birkhead and Nettleship (1980) and Gaston and Nettleship (in press). The fate of each egg, and subsequently each chick, was recorded, and in this way we obtained data on timing of breeding, number of pairs, and breeding success (proportion of pairs rearing a chick to fledging) for each study plot.

Egg size.—An index of egg volume was provided by the length multiplied by the square of the maximum breadth. This index has a close linear relationship with the internal volume and also with the weight of the egg at pipping (recorded one or two days before hatching) (Fig. 3). Thick-billed Murre eggs lose an average of 0.56 g/day during the 32-day incubation period (Uspenski 1956, Gaston and Nettleship in press), so at pipping, eggs weigh about 18 g less than at laying. Eggs were measured in areas other than those used as study plots.

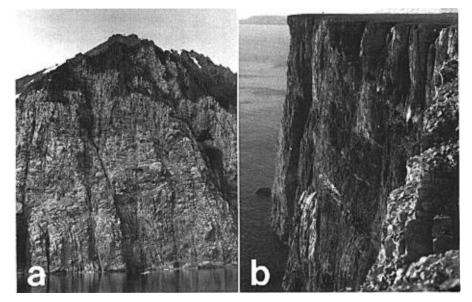


Fig. 2. View of a portion of the Thick-billed Murre colonies at (a) Coburg Island, and (b) west of Cape Hay, Bylot Island.

Adult body measurements.—In 1978 measurements were obtained for 40 adult Thick-billed Murres, which were collected, dissected, and sexed, at both Coburg and Cape Hay; together with live unsexed birds measured in 1978 and 1979, this gave totals of 69 and 91 birds for Coburg and Cape Hay, respectively. We measured culmen length and depth (Gaston and Nettleship in press) and body weight for all birds. Bill dimensions were used as a measure of body size, and, because these measurements are unlikely to vary between years for any particular population, we combined data for 1978 and 1979. Adult body weight, on the other hand, is much more likely to vary between years, so we have used body weight measurements from 1979 only. The 1979 samples, all live, incubating birds, were taken during early incubation between 1000 and 1450 local time (C.D.T.) at areas away from study plots. Most of the birds were probably female, because females usually incubate at this time (Roelke and Hunt 1978, Gaston and Nettleship in press). The samples for bill measurements, however, probably contained a similar proportion of each sex (see Table 1).

Chick growth.—Most of the chicks that we used in growth studies hatched from eggs of which the volume index was known. Towards the start of hatching we visited ledges every second day and, where possible, recorded the pipping weight of each egg. Incubating and brooding adults usually left the ledge

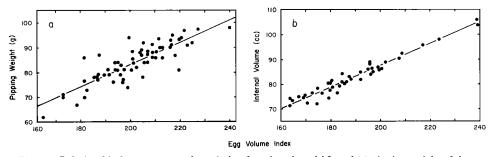


Fig. 3. Relationship between egg volume index (length \times breadth²) and (a) pipping weight of the egg (r = 0.848, 64 df, P < 0.001, regression equation: y = 0.448x + 2.59), and (b) internal volume (r = 0.969, 46 df, P < 0.001, regression equation: y = 0.437x + 0.657). Internal volume was measured by filling blown eggs with water from a pipette. Only 43 points are shown because five points overlapped.

April 1981]

Biology of Thick-billed Murres

when we approached closer than 2 m, although some birds continued to brood and allowed us to remove the chicks from beneath them. Most birds returned to their chicks a few minutes after we had weighed and measured them. Eggs recorded as pipping on one visit and hatched on the next were assumed to have hatched the previous day. If the chick was still wet, however, we counted the chick as having hatched that day. Chicks were marked by toe-nail clipping or color bands. Chicks were weighed and their wing length measured every second day, except at Coburg where bad weather sometimes increased the interval to 3 or 4 days. Weights for those days on which chicks were not measured were estimated by linear interpolation (see Hussel 1972). Measures of chick growth used for inter- and intra-colony comparisons are: (1) weight on day 1 or 2 (hereafter referred to as hatching weight for convenience), (2) weight at day 14, and (3) weight at fledging (i.e. the last recorded weight before the chick fledged).

Feeding rate of chicks.—A series of continuous 4-h watches, between 1300 and 1700, was made on two groups of about 30 chicks of known age at each colony. A total of 15 4-h watches was made at Coburg and 20 at Cape Hay. We recorded time of arrival of each adult, whether it had a food item, whether the item was fed to the chick, identity and size of food item (where possible), and time of departure of each adult. The size of food items was estimated against the length of the adult's bill and was later converted into centimeters. Chick-feeding rate (meals/chick/4 h) and the duration of adults' periods of absence between successive meals were recorded. The period of absence is comparable between colonies, even though it is not a precise measure of feeding trip duration (it is biased towards trips of less than 4 h duration and because adult murres spent part of their time away from the colony engaged in activities other than foraging for their chick; see also Gaston and Nettleship in press).

RESULTS

Timing of breeding.—Although the first eggs were seen on 25 and 26 June, at Coburg and Cape Hay, respectively, laying proceeded more rapidly and synchronously at Coburg, where 52% of the eggs were laid in the first 8 days of the laying period. Over the same time period at Cape Hay, only 25% of the eggs were laid. The median laying date at Coburg was 2 July and at Cape Hay 6 July (Fig. 4). The onset of egg laying at Coburg and Cape Hay was about 3–7 days later than the average for Prince Leopold Island between 1975 and 1977 (Gaston and Nettleship in press). Further evidence for 1979 being a late season comes from Tuck's (1961) observations made at Cape Hay in 1957: he recorded the first eggs on 20 June and a median laying date of 28 June.

Egg size.—Mean egg volume indices for the two colonies were compared in two ways in order to distinguish between within-colony effects and an overall seasonal effect. We first compared the volume index of eggs laid at the same stage of the breeding season relative to the median laying date for each colony and found that eggs at Coburg were significantly larger than those at Cape Hay. Second, we compared the volume indices of eggs laid on approximately the same calendar dates. The volume indices of eggs laid between 30 June and 5 July at each colony were not significantly different (Table 1). This suggests that the difference in egg volume indices for the two colonies was due to a seasonal effect, that is, to differences in timing of breeding. Overall, eggs at Cape Hay were smaller than those laid at Coburg, even though the size of birds did not differ between colonies (Table 2).

Development of the young.—Weights of chicks from the two colonies were similar initially but started to diverge at day 7 (Fig. 5), after which Coburg chicks were consistently heavier than Cape Hay chicks of the same age. Mean weights at day 14 and at fledging were significantly higher at Coburg than at Cape Hay (Table 3). Although the mean volume of eggs laid at Coburg was higher than at Cape Hay, the volumes of eggs that produced chicks used in the growth study were not significantly different (Table 3). Consequently, the weight of 1- and 2-day-old chicks did not differ significantly (Table 3), which means that subsequent differences in chick

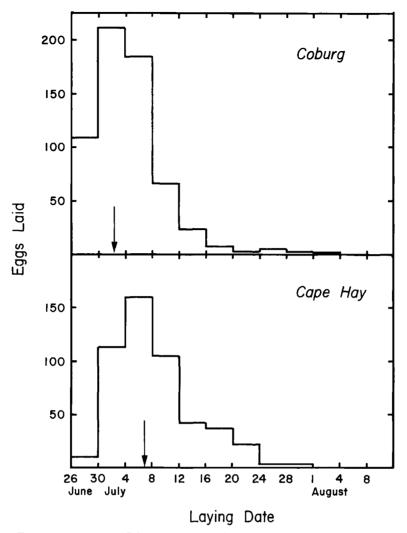


Fig. 4. Timing of breeding at Coburg (upper) and Cape Hay in 1979. Data are grouped into 4-day time periods from 26 June through 4 August. Arrows indicate median laying dates. Laying was significantly earlier at Coburg (median test, $\chi^2 = 69.67$, P < 0.001) and more synchronous: a significantly higher proportion of eggs was laid during the first 8 days of the laying period of Coburg than at Cape Hay ($\chi^2 = 84.27$, P < 0.001).

growth between the two populations are unlikely to have been due to egg size or hatching weight.

Because there was a seasonal decline in the growth rates of chicks at both colonies (Birkhead and Nettleship MS), it is possible that the observed difference between the two populations could have been due to Cape Hay birds breeding later than those at Coburg. We tested this by comparing the slopes and intercepts of the regression lines for the relationship between hatching date and fledging weight (Birkhead and Nettleship MS). There was no difference between the slopes (t = 0.734, 70 df, NS) or the intercepts (t = 0.52, 70 df, NS), which suggests that the difference

TABLE 1.	Volume ir	ndices of egg	s laid at Co	burg and	Cape Hay	in relation	to median	laying date and
calende	er date. Val	ues are mear	is ± standa	rd error, a	nd sample	sizes are given	ven in pare	entheses.

Laying dates	Coburg	Cape Hay
In relation to median ^a	$188.92 \pm 1.79 (65)$	$180.52 \pm 3.11 (30)$
In relation to calender date ^b	184.00 ± 3.22 (23)	$180.52 \pm 3.11 (30)$

^a From the start of laying up to 2 or 3 days before median (t = 2.34, 93 df, P < 0.02).

^b During the period 30 June-5 July (t = 0.78, 51 df, NS).

in the growth of chicks between the two colonies (Fig. 5 and Table 3) was due to the difference in timing of breeding.

Chick food intake.—The proximate cause of the difference in chick growth rates between Coburg and Cape Hay could have been due to a difference in food intake of chicks. The mean feeding rate over the entire chick-rearing period was higher and feeding trips shorter at Cape Hay than at Coburg (Table 4). This was unexpected, although a difference in prey size or quality could account for it. At both colonies the main prey was arctic cod (Boreogadus saida) (see Appendix). Unfortunately, because adults delivered food items to chicks very rapidly and because prey items ranged from about 1 g to 30 g, it was impossible to obtain a reliable estimate of average meal sizes at the two colonies.

Breeding success.—Breeding success was significantly higher at Coburg than at Cape Hay, due mainly to differential egg loss at the two colonies. At Cape Hay 46% of eggs were lost before hatching, while at Coburg only 20% were lost. In contrast, the proportion of chicks hatched that survived to fledge did not differ between colonies (Table 5). The difference in egg loss is probably related in part to climatic conditions. Persistent freezing fog at Cape Hay produced heavy hoar frost on the cliffs above breeding areas, including the study plots. During warmer periods this ice, together with rocks, fell onto breeding birds and broke many eggs. In addition, birds left their eggs unattended when ice or rockfalls occurred, and many of these exposed eggs were taken by Glaucous Gulls. Rockfalls (but not ice-falls) occurred at Coburg, but eggs were rarely left unattended. Because eggs were left unattended at Cape Hay, gull predation was nonselective [i.e. there was no difference in the mean volume indices of eggs measured on the ledges compared with those taken by gulls (Table 6)]. In contrast, at Coburg eggs lost to gulls were significantly smaller

Colony Measure ^a	Males ^b	Females	Both sexes		
Coburg					
Culmen length (mm)	$34.90 \pm 0.45 (23)^*$	$33.43 \pm 0.51 (15)$	$34.04 \pm 0.23 (69)^{c}$		
Culmen depth (mm)	$13.94 \pm 0.13 (25) **$	$13.24 \pm 0.19(15)$	$13.90 \pm 0.09(71)$		
Body weight (g)			$849.81 \pm 8.15 (31)$		
Cape Hay					
Culmen length (mm)	$34.94 \pm 0.38 (27)$	$34.11 \pm 0.47 (13)$	$34.66 \pm 0.19 (91)^{\circ}$		
Culmen depth (mm)	$14.02 \pm 0.09 (27) **$	$13.52 \pm 0.16(13)$	$14.04 \pm 0.06 (91)$		
Body weight (g)			874.23 ± 11.73 (26)		

TABLE 2. Adult body measurements of Thick-billed Murres from Coburg and Cape Hay. Values are means \pm standard error, and sample sizes are given in parentheses.

^a Bill measurements are from birds measured in 1978 and 1979, body weight values are from 9–11 July 1979, only (see text). ^b Significant differences between the sexes are indicated thus: * P < 0.05, ** P < 0.01.

^c The only significant difference between Coburg and Cape Hay birds was culmen length for birds of both sexes (t = 2.08, 158 df, P < 0.05)

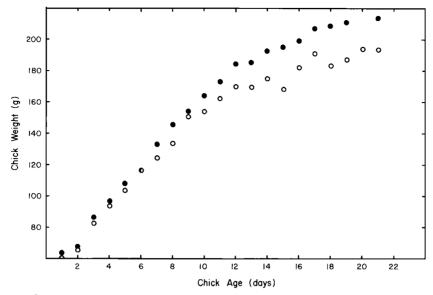


Fig. 5. Changes in body weight of Thick-billed Murre chicks at Coburg (\bullet) and Cape Hay (\bigcirc). Sample sizes for each point are between 20 and 40.

than those on the ledges. This suggests that Glaucous Gulls on Coburg took a disproportionate number of eggs from sites occupied by young or poor quality birds.

At both colonies birds breeding early in the season were more productive than those breeding later (Fig. 6). Neither the slopes nor the intercepts of the regression lines in Fig. 6 are different, suggesting that the difference in overall breeding success between Coburg and Cape Hay was due to differences in timing of breeding. Falling ice at Cape Hay, however, probably increased egg losses still further. The mean number of chicks produced per pair and their mean weight at fledging at Cape Hay were lower than at Coburg. If subsequent survival is related to fledging weight, then the difference in productivity between the two populations will be even more pronounced than the breeding-success figures in Table 5 suggest.

Fledging.—Murre chicks usually fledge at night, when the light intensity is lowest in the Arctic (Cullen 1954, Gaston and Nettleship in press), or at dusk in boreal regions (Birkhead 1976, Hedgren 1979). The flightless chick parachutes from the cliff down onto the sea accompanied by its male parent (Roelke and Hunt 1978,

Colony	Egg volume index	Pipping weight of egg (g)	Day 1–2 chick weight (g)	Day 14 chick weight (g)	Fledging weight (g)
Coburg	181.69 ± 2.30 (47)	83.15 ± 1.09 (42)	68.0 ± 1.24 (48)	199.81 (37)	206.11 ± 4.59 (36)
Cape Hay	178.63 ± 1.99 (58)	80.44 ± 0.96 (58)	66.52 ± 1.17 (58)	175.29 (22)	190.62 ± 3.79 (24)
t and P values	1.00 NS	0.1 > P < 0.05	0.95 NS	3.73, 55 df, P < 0.001	2.60, 58 df, P < 0.02

TABLE 3. Egg and chick growth characteristics of Thick-billed Murres chicks from Coburg and Cape Hay in 1979. Values are means \pm standard error, and sample sizes are given in parentheses.

TABLE 4. Mean feeding rates and feeding trip duration of Thick-billed Murres at Coburg and Cape Hay.	
Values are means \pm standard error, and sample sizes are given in parentheses.	

	Coburg	Cape Hay
Meals/chick/4 h ^a Trip duration (min) ^b	$\begin{array}{rrrr} 0.75 \ \pm \ 0.03 \ (15) \\ 99.5 \ \ \pm \ 10.4 \ (26) \end{array}$	$\begin{array}{c} 0.81 \pm 0.04 \ (20) \\ 70.7 \pm 5.6 \ \ (69) \end{array}$

^a t = 1.28, 33 df, NS.

^b t = 2.43, 93 df, P < 0.02.

Gaston and Nettleship in press), which continues to care for it for several weeks (M. S. W. Bradstreet pers. obs.). The first chicks were recorded fledging on 14 and 20 August at Coburg and Cape Hay, respectively. The spread of fledging was considerably less than the spread of laying, for two reasons. First, chicks hatched early in the season fledge at an older age than those hatched later (Gaston and Nettleship in press), so that most chicks fledge at about the same time. For example, at Cape Hay the mid 80% of eggs was laid over an 18-day period, while the mid 80% of chicks fledged over just 9 days. Second, fledging is generally confined to (a few) calm evenings. At Coburg fledging occurred from 14 August until all chicks had left the colony in early September, but the majority of chicks fledged on just two nights (20 and 28 August). Between 17 and 19 August there were heavy seas at Coburg, and very few chicks fledged; on 20 August during calm conditions, however, tens of thousands of chicks fledged. On this date fledging started early, at 1700. On subsequent nights, relatively few chicks fledged because of heavy seas, until 28 August, when calm conditions prevailed and again huge numbers of chicks fledged. On this occasion fledging was in progress by 1300, suggesting that heavy seas had delayed fledging of chicks that were ready to depart earlier.

Very few chicks were killed by Glaucous Gulls during fledging (cf. Williams 1975), but some were apparently killed as a result of striking rocks during their descent. Most chick mortality was due to adults and chicks failing to link up once on the water. Unattended chicks swam around at the base of the cliffs and were eventually dashed against ice or rocks and drowned. During fledging at Coburg Island on 28 August, a total of about 500 dead chicks was recorded at the base of the cliffs, but we estimated that these constituted only about 2% of the chicks fledging that day.

DISCUSSION

Lack (1968) suggested that birds should time their breeding so that young are reared during the peak of food availability. The difficulty of finding sufficient food for egg formation early in the season, however, may prevent some birds from breeding at the best time (Perrins 1970). Species breeding in the Arctic experience abrupt seasonal changes with unpredictable environmental conditions that may affect the

TABLE 5. Breeding success of Thick-billed Murres at Coburg and Cape Hay in 1979.

Colony	Number of pairs	Number of eggs hatched (%)	Number of chicks fledged (%)	Percentage success
Coburg	632	503 (79.6)	449 (89.3)	71.0
Cape Hay	513	275 (53.6)	247 (89.8)	48.1
χ^2 and <i>P</i> values		71.24, $P < 0.001$	0.06, NS	44.65, $P < 0.001$

	Ledge ^a			Gull predation				
Colony	x	SE	n	x	SE	n	d	Р
Coburg Cape Hay	187.27 180.52	1.78 3.11	80 30	172.99 179.71	1.64 1.79	42 143	4.96 0.23	< 0.001 NS

TABLE 6. Egg volume indices (length \times breadth²) of eggs suffering Glaucous Gull predation and of eggs on ledges at Coburg and Cape Hay in 1979.

^a Coburg ledge samples were laid between 25 June and 10 July; 90% of birds had laid by 10 July. Cape Hay ledge samples were all laid before the median laying date, so data are biased toward giving a significant result when compared with the gull predated sample.

time of egg laying. In the present study, median laying dates at the two colonies differed by 4 days. This was probably due to differences in the timing and pattern of ice break-up (affecting the availability of food) in the vicinity of each colony. Aerial surveys have shown that the maximum foraging range of Thick-billed Murres from Prince Leopold Island is just over 100 km (Nettleship and Gaston 1978), so it seems likely that birds from Cape Hay and Coburg had almost exclusive foraging ranges. Unfortunately, we do not have sufficient information on ice conditions early in the season or the birds' foraging areas to show that these resulted in the difference in timing at the two colonies. The data comparing different years, however, provides good evidence that the time of ice break-up affects the onset of breeding.

The break-up of sea ice in the Lancaster Sound and Jones Sound region in 1979 occurred later than average (Fig. 7), corresponding with late breeding at both Cape

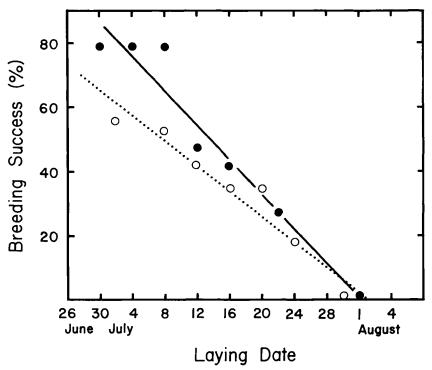


Fig. 6. Seasonal decline in breeding success (proportion of pairs rearing a chick to fledging), at Coburg (\bullet) (r = -0.971, 5 df, P < 0.001, regression equation: y = -10.80x + 97.49) and Cape Hay (\bigcirc) (r = -0.963, 5 df, P < 0.001, regression equation: y = -7.86x + 73.37). Neither the slopes (t = 0.655, NS) nor the intercepts (t = 1.01, NS) differed significantly (see text).

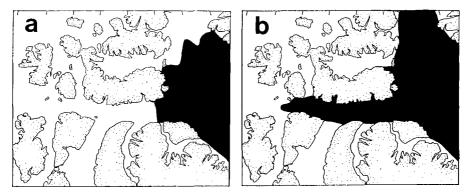


Fig. 7. (a) Ice edges and areas of open water (black) on 16 June 1979, drawn from LANDSAT photographs. (b) Average position of ice edges and areas of open water for the period 1–15 June. Ice break-up in the region was late in 1979.

Hay and Coburg. At Prince Leopold Island between 1975 and 1977 the timing of ice break-up and egg laying varied by only a few days, but in 1978 exceptionally late break-up delayed breeding by 18 days (Nettleship et al. MS). Uspenski (1956) and Belopol'skii (1957) also recorded Thick-billed Murres breeding late in bad ice years.

The results presented here indicate that the timing of breeding in late years such as 1978 and 1979 is controlled mainly by the ability of females to form eggs, as late ice break-up reduces the availability of prey. In contrast, the seasonal cycle of prey abundance is controlled mainly by photoperiod (Sverdrup et al. 1942) and is less affected by a delay in ice break-up. Our observations can be explained by the following mechanism. In "normal" years, the break-up of sea ice occurs at a time that allows birds to time their breeding so that young are being reared during (or close to) the peak of food availability. In late ice-years the birds' breeding cycle is delayed more than the cycle of prey abundance so that the two cycles are out of phase.

At Cape Hay, egg laying was later and less synchronous than at Coburg Island, and both these factors may have contributed to the reduced breeding success at Cape Hay. At Prince Leopold Island, we also found that delayed breeding was associated with reduced synchrony (Nettleship et al. MS). In some species synchrony affects breeding success [e.g. Common Murre (U. aalge), Birkhead 1977; see also Emlen and Demong 1975], although such an effect has not been demonstrated in Thick-billed Murres. It is clear, however, that a delay in the onset of egg laying results in reduced breeding success, both in terms of the quality and the quantity of young produced. Most of the differences in reproductive biology between the two colonies are probably attributable to the 4-day difference in time of breeding. Breeding success also showed a seasonal decline (Fig. 6), and the overall difference between the two colonies (Table 5) was due to the difference in timing and also to iceand rockfalls at Cape Hay. Late-hatched chicks grew more slowly than those hatched early; this was true within each colony (Birkhead and Nettleship MS) and is apparent within the 1979 season, if one compares mean values for each colony (Table 3). Similar seasonal declines in chick growth have been reported for Common Murre (Hedgren and Linnman 1979), Razorbill (Alca torda) (Lloyd 1979), and Atlantic Puffin (Fratercula arctica) (Nettleship 1972).

268

ACKNOWLEDGMENTS

This research was funded by the Canadian Wildlife Service and Petro-Canada Ltd., with additional financial and logistic support from the Polar Continental Shelf Project. E. Greene, B. Lyon, and G. Calderwood provided outstanding assistance in the field and cheerfully tolerated unpleasant weather conditions and polar bears at Cape Hay. D. Reid, K. Clarkson, and W. Carson also provided indefatigable field support and resolutely coped with some difficult boating conditions at Coburg Island. We are also grateful to F. Alt, G. Benoit, and F. Hunt for assistance at Resolute and to pilots R. Bromberry, P. Doyle, and D. Grant for their invaluable twin-otter flying in supplying the camps. D. Pittis provided helpful helicopter support at Coburg Island, and H. Hume gave assistance at Pond Inlet on several occasions. K. Clarkson, A. J. Erskine, M. P. Harris, and D. Reid read and commented on the manuscript. The help of all these individuals is greatly appreciated. This investigation is associated with the program "Studies of northern seabirds," Seabird Research Unit, Canadian Wildlife Service, Environment Canada (Report No. 86).

LITERATURE CITED

BELOPOL'SKII, L. O. 1957. Ecology of sea colony birds of the Barents Sea (English translation from Russian 1961). Jerusalem, Israel Program for Sci. Transl.

BIRKHEAD, T. R. 1976. Breeding biology and survival of Guillemots (Uria aalge). Unpublished Ph.D. dissertation. Oxford, Oxford Univ.

- ——.: 1977. The effect of habitat and density on breeding success in the Common Guillemot (Uria aalge). J. Anim. Ecol. 46: 751-764.
- ——, & D. N. NETTLESHIP. 1980. Census methods for murres, Uria species: a unified approach. Can. Wildl. Serv. Occ. Pap. No. 43.

BROWN, R. G. B., D. N. NETTLESHIP, P. GERMAIN, C. E. TULL, & T. DAVIS. 1975. Atlas of eastern Canadian seabirds. Ottawa, Can. Wildl. Serv.

CULLEN, J. M. 1954. The diurnal rhythm of birds in the arctic summer. Ibis 96: 31-46.

EMLEN, S. T., & N. J. DEMONG. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. Science 188: 1029–1031.

GASTON, A. J., & D. N. NETTLESHIP. In press. The Thick-billed Murres on Prince Leopold Island a study of the breeding ecology of a colonial, high arctic seabird. Ottawa, Can. Wildl. Serv., Monogr. Ser., No. 6.

HEDGREN, S. 1979. Seasonal variation in the fledging weight of Guillemots Uria aalge. Ibis 121: 356–361.

------, & A. LINNMAN. 1979. Growth of Guillemot Uria aalge chicks in relation to time of hatching. Ornis Scandinavica 10: 29–36.

HUSSEL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317–364. LACK, D. 1968. Ecological adaptations for breeding in birds. London, Methuen.

LLOYD, C. S. 1979. Factors affecting breeding of Razorbills *Alca torda* on Skokholm. Ibis 121: 165–176.

NETTLESHIP, D. N. 1972. Breeding success of the Common Puffin (*Fratercula arctica*) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42: 239–268.

—. 1977. Seabird resources of Eastern Canada: status, problems and prospects. Pp. 96–108 in Canada's threatened species and habitats (T. Mosquin and C. Suchal, Eds.). Ottawa, Can. Nature Fed.

—, & A. J. GASTON. 1978. Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories in August and September 1976. Can. Wildl. Serv. Occ. Pap. No. 39.

PERRINS, C. M. 1970. The timing of birds' breeding seasons. Ibis 112: 242-255.

ROELKE, M., & G. HUNT. 1978. Cliff attendance, foraging patterns and post-fledging behaviour of known-sex adult Thick-billed Murres (*Uria lomvia*). Pacific Seabird Group 5: 81.

SWARTZ, L. G. 1966. Sea-cliff birds. Pp. 611-678 in Environment of the Cape Thompson region, Alaska (N. J. Willimovsky and J.N. Wolfe, Eds.). Springfield, Virginia, Clearing House for Fed. Sci. and Tech. Information, Natl. Bur. Standards, U.S. Dept. Commerce.

SVERDRUP, H. U., M. W. JOHNSON, & R. H. FLEMING. 1942. The oceans. Englewood Cliffs, New Jersey, Prentice-Hall.

TUCK, L. M. 1961. The murres. Ottawa, Can. Wildl. Serv., Monogr. Ser., No. 1.

USPENSKI, S. M. 1956. The bird bazaars of Novaya Zemlya. (English translation from Russian, 1958). Ottawa, Can. Wildl. Serv.

WILLIAMS, A. J. 1975. Guillemot fledging and predation on Bear Island. Ornis Scandinavica 6: 117-124.

APPENDIX. Prey species delivered to Thick-billed Murre chicks at Coburg Island and Cape Hay.

Prey species	Coburg	Cape Hay
Fish		
Arctic cod, Boreogadus saida (Lepechin) 1774	+	+
Arctic staghorn sculpin, Gymnocanthus tricuspis (Reinhardt) 1841	+	
Twohorn sculpin, Icelus biconnis (Reinhardt) 1841	+	
Arctic sculpin, Myoxocephalus scorpioides (Fabricius)	+	
Nybelin's sculpin, Triglops nybelini Jensen 1944		+
Sand lance, Ammodytes spp. [*]		+
Polar eelpout, Lycodes truneri Bean 1978	+	
Invertebrates		
Parathemisto libellula (Lichtenstein)	+	+
Parapasiphae sulcatifrons Smith		+
Gammarus wilkitzi Birula	+	
Harmothoe spp. ^a	+	

* All specimens were picked up from murre breeding ledges, except Ammodytes spp. and Harmothoe spp., which were visual identifications only of prey fed to chicks. All others or very similar species were seen fed to chicks by adults.

The fifth annual meeting of the Colonial Waterbird Group will be held 22-25 October 1981. A symposium on the factors affecting reproductive success in colonial birds is planned. Those interested in contributing to the symposium should submit an abstract by 1 August 1981; abstracts for contributed papers must be received by 1 September 1981. For information on either, contact J. Burger, Department of Biology, Livingston College, Rutgers University, New Brunswick, New Jersey 08903. For information on registration, contact Brian Chapman, Department of Biology, Corpus Christi State University, Corpus Christi, Texas 78412.

A Conference-Workshop on Southeastern Coastal and Estuarine Birds will be held at the field laboratory of the Belle W. Baruch Institute for Marine Biology and Coastal Research of the University of South Carolina, near Georgetown, South Carolina, 11–13 September 1981. Those working on coastal or estuarine species in the southeast are invited to present the results of their research; presentations by graduate students are especially welcome. A limited number of graduate student awards, covering room and registration fees, are available. Contact Keith L. Bildstein, Program Chairman, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733 for information on the program or student awards; contact Bobbie Christy, Local Chairman, Baruch Field Laboratory, P.O. Box 1630, Georgetown, South Carolina 29440 for information on registration and housing (this information will be mailed to AOU, COS, and WOS members in the southeast automatically).