CANADIAN WILDLIFE SERVICE
P. O. BOX 1590
SACKVILLE, N. B.
E0A 3C0

REPORT
QL
685.L5
N475
1978

REPRODUCTIVE FAILURE AMONG ARCTIC SEABIRDS ASSOCIATED WITH UNUSUAL ICE CONDITIONS IN LANCASTER SOUND 1978

David N. Nettleship

Timothy R. Birkhead

Anthony J. Gaston

Canadian Wildlife Service

Bedford Institute of Oceanography

Dartmouth, Nova Scotia

Canada B2Y 4A2

REPORT

QL
685.L5
N475
1978

SNS MS no. 77

Summary. A comparison of breeding performance of populations of seabirds in Lancaster Sound and vicinity shows that 1978 was a disaster year. Breeding rates for surface-feeding species (Northern Fulmar, Black-legged Kittiwake, Glaucous Gull) were reduced to 10-20% while pursuit-diving species (Thick-billed Murre, Black Guillemot) which did manage to reproduce close to a normal level did so late and as a consequence suffered a very high pre- and post-fledging mortality. A detailed examination of Thick-billed Murres revealed a three-week delay in egg-laying, the production of smaller eggs and chicks, reduced chick-feeding rates and abnormal parental behaviours. These data represent the first detailed account of the effect of unusually severe ice conditions on reproduction of arctic seabirds.

Total reproductive failure among seabirds is an unusual event, particularly among species breeding in temperate or arctic regions (1). Here we present, for the first time, a detailed account of the effect of unusually severe ice conditions on the breeding biology of arctic seabirds. Such data are of interest not only for their own sake, but also because the birds' response to extreme conditions may help us to understand differences in their biology between more normal years and elucidate how they have successfully adapted to the severe environmental regime of high arctic regions.

The study was conducted at Prince Leopold Island (74°02'N, 90° 00'W), at the western end of Lancaster Sound, N.W.T., with some additional observations near Cape Hay (73°46'N, 80°23'W), Bylot Island at the eastern entrance to Lancaster Sound, and at Cambridge Point (75°48'N, 79°25'W) Coburg Island, some 200 km north of Cape Hay (Fig. 1). Detailed records of ice conditions in the region have been kept since about 1940, and in all previous years ice in Lancaster Sound (west to Prince Leopold) has remained open or broken up and moved out during the spring or summer, usually by late April. In 1978, however, Prince Leopold Island remained ice-locked, and Lancaster Sound was choked with large ice-pans throughout the summer (Fig. 1). Cape Hay was near the ice edge in 1978, and Coburg Island was ice-free throughout the 1978 breeding season (Fig. 1). The community of seabirds on Prince Leopold Island comprises approximately 86,000 pairs of Thick-billed Murres Uria lomvia, 62,000 pairs of Northern Fulmars Fulmarus glacialis, 29,000 pairs of Black-legged Kittiwakes Rissa tridactyla, 4,000 pairs of Black Guillemots Cepphus grylle, and 200 pairs of Glaucous Gulls Larus hyperboreus (2, 3). Cape Hay and Cambridge Point both hold large colonies of Thick-billed Murres and Black-legged Kittiwakes (4). Most observations at Prince Leopold Island were made on Thick-billed Murres and Northern Fulmars, but we also obtained some data for the other three species. We compared features of the breeding biology of these species at Prince Leopold Island in 1978 with data from three previous years (1975-1977), in which ice conditions were relatively normal (3, 5) and fell within the averages shown in Fig. 1. All results in the text refer to Prince Leopold Island unless otherwise stated. During 1975 and 1976 a number of study plots for each species were established at Prince Leopold Island and in each subsequent year the fate of the egg or clutch of each pair recorded, from laying through to fledging (3, 5). In this way we were able for each year, 1975-1978 inclusive, to monitor the timing of breeding, the proportion of pairs breeding and overall breeding success for 200-600 pairs of Thick-billed Murres, Northern Fulmars and Black-legged Kittiwakes, and about 40 pairs of Black Guillemots and Glaucous Gulls. In addition, we recorded egg volumes, and the growth (weight increase) of Thick-billed Murre and Northern Fulmar chicks, and adult body weight of Thick-billed Murres (3, 5).

Thick-billed Murre

The median egg laying date in 1978 (18 July, see (6)) was approximately 18 days later than in the years 1975-1977 (Fig. 2). Mean laying dates (7) differed significantly ($P < 0.001$) between years, and laying in 1978 was significantly later ($P < 0.05$) than in any previous year. Counts of the total number of eggs laid on four study plots showed that at least 97% of the 1975-77 population bred in 1978. The timing of breeding at Cape Hay in 1978 was similar to that at Prince Leopold Island; extrapolating from a small sample ($n = 63$) of hatching dates, the median laying date at Cape Hay was 20 July (see Fig. 2).

In addition to laying late in 1978, Thick-billed Murres produced relatively small eggs in comparison with previous years (Fig. 3A). Egg volumes differed significantly between years ($F_{3,446} = 15.6$, $P < 0.001$), but 1975 and 1976 volumes were not significantly different, nor were those in 1977 and 1978 (all other pair-wise comparisons were: Duncan's Multiple Range Test $P < 0.05$). In addition, there was no significant difference in egg volume between Prince Leopold Island, Cape Hay and Cambridge Point in 1978 (Fig. 3B). However, egg volumes were significantly more variable at Prince Leopold Island than at either Cape Hay or Coburg Island (Variance Ratio: $P < 0.05$). This indicates that ice conditions had very far reaching effects on food availability and these were not restricted to birds breeding at Prince Leopold Island. It is interesting that the smallest mean egg volumes in 1978 were those from ice-locked Prince Leopold Island, and the largest were from ice-free Coburg Island. This may reflect the different distances birds were having to fly to open-water feeding areas, or a slight gradient of food availability from west to east through Lancaster Sound associated with different degrees of ice cover.

The mean egg volume at Prince Leopold Island in 1978 was not significantly different from the mean volume of those laid in 1977. Interestingly, laying in 1977 was significantly later than in 1975 or 1976, although the difference in median laying dates was only four days (3). This suggests, first, that there might be a minimum viable egg volume (about 176-180 cm^3 for Thick-billed Murres in Lancaster Sound populations). Second, it suggests that there may be a trade-off between egg-volume and timing of breeding, so that the birds minimize the delay in laying by producing smaller eggs. In 1978 feeding conditions during the period of egg formation must have been considerably worse than in 1977 since it took 18 days longer than normal to accumulate sufficient food reserves to produce even minimum sized eggs. In fact it seems likely that food was so short early in the season, that all food was channelled into self-maintenance and only later did food availability increase sufficiently to allow egg formation to proceed, albeit, late.

Body weights of adult murres during the incubation period were not significantly lower in 1978 than in other years. Sample sizes for birds collected in 1975, 1976 and 1977 were small, so they have been combined in order to make comparisons with 1978 body weights. The mean $\pm$ S.E. for males over 1975-1977 was 919 g $\pm$ 11.7 ($n = 35$), and in 1978 was 881 $\pm$ 22.9 ($n = 7$), a difference of only 4.2 %, which was not significant ($t = 1.49$, 40df, NS). The mean weights of females for 1975-1977 was 898.3 g $\pm$ 22.1 ($n = 18$) and in 1978 was 845 $\pm$ 15.4 ($n = 16$), a difference of 5.9%, which verged on significance ($t = 1.96$, 32df, $P > 0.05 < 0.1$). Thus, the differences in body weights between the 'normal' ice years 1975-1977 and the bad ice year in 1978 were small, but those for females were slightly more pronounced than for males.

These results are not unexpected. First, considering differences in weight, we can predict that female body weights should be affected more than male body weights because it is the female which bears the strain of producing the egg. Second, among long-lived, iteroparous species, such as Thick-billed Murres, Northern Fulmars and Black-legged Kittiwakes (which fall at the K end of the avian r-K continuum), breeding should take place in any one year, only if females can accumulate sufficient resources over and above those needed for self-maintenance to ensure that their chances of subsequent survival are only slightly lower if they breed than if they forgo the opportunity for that season.

In contrast, there is evidence that some birds (e.g., Quelea) at the r end of the r-K continuum, which have a lower chance of surviving from one breeding season to the next, put relatively more effort into reproduction. This increased effort may even involve a significant depletion on the females' own body reserves, which in turn decreases their chances of survival (8).

Incubation proceeded normally in 1978, and the mean incubation period (32.1 days) was similar to that in previous years (9).

The mean weight of 2-day old chicks in 1978 was 66.0 g $\pm$ 1.72 S.E. (n = 21), a value which was lower than in any previous year (where it varied only slightly, between 70.8 and 72.2 g). The low weight of 2-day old chicks in 1978 was due in part to the relatively small eggs laid in that year. Comparing mean egg volumes with mean 2-day old chick weights for 1975-1978 (Fig. 4) suggests a positive relationship between these two variables. A significant positive correlation was found between these variables in another Alcid, the Razorbill Alca torda (10), and several studies have shown that egg volume can affect chick growth and survival (11).

Low weights of 2-day old chicks in 1978 may also have been the result of reduced food intake. Feeding rates in 1978 were similar to those in 1975-1977 (3), but we have no information on the size, weight or calorific value of food items in 1978, so it is difficult to make comparisons. In 1977 when Thick-billed Murres produced relatively small eggs (Fig. 3), the adults were able to compensate for this later in the season, and by fledging age, chicks were relatively heavy and breeding success above average (3).

In 1978 the reverse was true, the percentage difference in mean weights between 1978 and 1975-1977 increased through the nestling period from 8% lower for day-2 chicks to 17% by day 14 and 21% at fledging (Table 1, Fig. 5).

This difference could be due to a reduction in calorific intake or to increased energy consumption due to changes in brooding attentiveness of the adults or differences in air temperatures. Mean air temperatures during the nestling period were slightly lower in 1978 (12), and in marked contrast to previous years (3) and other studies (13) some adult murres left their chicks unattended for up to four hours at a time, especially towards the end of the season (14).

Despite these marked differences in growth patterns and behaviour, the mean duration of the nestling period did not differ between years (9, 15).

Thick-billed Murre breeding success over four years is presented in Table 2. The proportion of eggs which hatched was similar in each year, but the proportion of young which survived to fledge in 1978 was low compared with 1975-1977: combining data for 1975-1977 this difference is significant (x_1^2 = 21.2 $P < 0.001$). In addition several chicks were found dead on their sites, apparently having succumbed to starvation. No deaths from starvation were suspected in earlier years (3). Overall breeding success, although lower in 1978 than in any of the preceeding years, was not drastically different. Evidence from fledging weights, however, suggested that young murres in 1978 fledged at about 20% below normal weight. Although there are no data on the subsequent survival of murre chicks fledging at different body weights, it seems likely that very light chicks would have less chance of surviving than average or heavy chicks (11).

Murre chicks fledge at about three weeks of age, when only partly grown and before they can fly. At fledging the chick leaps from its cliff-ledge site and "parachutes" or glides down onto the sea below, where it is soon joined by its male parent (3). After fledging the male continues to care for the chick for several weeks. Fledging chicks and their accompanying adults from Prince Leopold Island swim east out of Lancaster Sound, and then south to southwest Greenland where they overwinter. In 1978 fledging did not proceed normally, and adults attempted to encourage chicks less than 15 days old (i.e., below the minimum fledging age) to fledge. During fledging most chicks managed to alight in open water between pans of ice which encompassed the island. Chicks appeared to have some degree of control over their descent and actively avoided the ice. Fledging chicks and adults were confronted with approximately 300 km of heavy ice concentration including enormous ice floes (5-10 km across), which separated them from open water near the entrance to Lnacaster Sound (16). Adults and chicks started to walk over the ice, but virtually all chicks perished as a result of exhaustion and/or exposure; a few, were taken by Glaucous Gulls. It seems likely that no chicks from Prince Leopold Island survived in 1978. At Cape Hay and Coburg Island, ice cover was much less (i.e., very open pack ice to bergy water and open water areas), so most chicks fledged successfully and initiated their southward migration. However, if they also fledged at very low body weights (and the available evidence suggests they did), it therefore seems likely that survival during their first winter would be low.

Northern Fulmar

In 1978 about 80% of fulmar pairs apparently failed to lay, as only 20% of the normal complement of eggs was present when observers arrived at the colony. Those which did attempt to reproduce, however, did so at the normal time (Table 3). There were no significant differences in the volume of eggs laid by fulmars in different years (17), although the sample sizes were small.

The growth rates of fulmar chicks in 1978 have been compared with data for 1976 and 1977 (we have not used 1975 values since hatching dates were not known accurately in that year). For both 1976 and 1977 a similar size sample to the 1978 sample was taken at random from the data. Because the differences between 1976 and 1977 were not significant, the values have been combined to make comparisons with 1978. The mean weight of chicks on days 1-2 (18) in 1978 were 6% lower than in 1976-1977, although this difference was not significant (Table 4). However, by days 5-6 there was a 14.4% difference in weight between chicks in 1978 and 1976-1977 ($t = 2.09$, 37df, $P < 0.05$). This difference is due to reduced feeding rates which resulted from exceptionally long incubation shifts ($\bar{x} = 5.42$ days $\pm$ 1.12 S.E.) over the hatching period in 1978 (cf.1976 and 1977 combined $\bar{x} = 2.36 \pm 0.17$ days: $z = 2.14$, $P = 0.016$). This suggests that in 1978 adult fulmars had difficulty finding food and that chicks had to wait three times longer than normal for their first meal after hatching, hence their low weight at day 5-6. Analysis of the weights of older chicks is not possible because the 1978 sample size decreased through the nestling period due to chick deaths. In 1978, 39% of chicks died on the ledges, whereas in 1976-1977 an average of only 16% died ($x^2_1 = 6.71$, $P < 0.01$). The consequence of this was very low breeding success, and of course, an even lower productivity (Table 5).

Black-legged Kittiwakes, Black Guillemots and Glaucous Gulls

Approximately 80% of the Black-legged Kittiwake population failed to breed in 1978: of 174 nests examined only 38 (22%) contained eggs. As far as we could tell, those pairs which did attempt to breed, did so at the normal time. However, of 38 breeding attempts recorded, 37 (97%) resulted in the production of just a single egg, and only 1 (3%) pair produced the more normal clutch of two eggs (19). A similar situation was recorded at Cape Hay and Coburg Island. We have no details of chick development or breeding success in 1978, but it was obvious that overall productivity was very low.

Most Black Guillemots attempted to breed in 1978, but like Thick-billed Murres, breeding was delayed by about three weeks (20). Clutch-size did not appear to be reduced in 1978. Unfortunately, we have no information on breeding success in this species for 1978.

Glaucous Gulls showed a very reduced breeding effort. Of 40 pairs known to have attempted to reproduce each year between 1975-77 (21), only 5 had chicks when first examined in early August 1978. Most nests were empty and contained little evidence of having been used (i.e., presence of egg shell fragments, chick down, etc.) and 4 of the 5 pairs with young had only a single chick instead of the more normal brood size of two or three chicks at this time of the breeding season (i.e., early August). Timing appeared to have been within the normal range (based on developmental stage of the 6 chicks observed), but too little information exists to be certain. It therefore seems likely that no more than 20% of the Glaucous Gull population produced eggs in 1978 and overall productivity was extremely low.

Discussion

A summary of the effect of the late ice break-up is presented in Table 6. Northern Fulmars, Black-legged Kittiwakes and Glaucous Gulls responded similarly with just a small proportion of the population breeding, but at the normal time. In contrast, Thick-billed Murres and Black Guillemots delayed breeding by nearly 3 weeks, but virtually all pairs attempted to breed. Fulmars, kittiwakes and Glaucous Gulls use similar feeding techniques: 'surface seizing', 'dipping' and 'surface filtering' (22), but very different ones from Thick-billed Murres and Black Guillemots, which are both 'wing-propelled pursuit divers' (22). However, despite their different feeding methods, in normal ice years in Lancaster Sound, there is considerable overlap in adult and chick diet (3, 5 and 23). All species rely heavily on Arctic Cod _Boreogadus saida_, but fulmars and kittiwakes also feed their chicks on invertebrates (i.e., amphipods, copepods and pteropods). The different responses of fulmars, kittiwakes and large gulls, and Thick-billed Murres and Black Guillemots to the 1978 ice conditions could have arisen in a number of ways. One possibility is that the surface feeding fulmar, kittiwake and Glaucous Gull were short of food simply because the extensive ice cover (80%) in Lancaster Sound drastically reduced their available feeding area. In contrast, Thick-billed Murres and Black Guillemots were able to forage under the ice, so their feeding area was not so markedly reduced. However, ice cover _per se_ does not completely account for the difference between the two groups of species. Murres and kittiwakes breeding at Cape Hay and Coburg Island, which had access to open water adjacent to their colonies, were affected in a similar way to those breeding at Prince Leopold Island (Table 6, Fig. 3). This means that conditions prevailing in 1978 were not restricted to the vicinity of Prince Leopold Island, but instead, had far reaching effects on the distribution and abundance of prey species. The data indicate that all five seabird species had difficulty obtaining sufficient food to permit breeding in 1978, but that the surface feeders were worst affected (Table 6). The fact that some surface-feeders were able to lay at the normal time perhaps indicates that for these species conditions either remained poor for a considerable period or deteriorated as the season progressed, whereas it apparently improved for the pursuit divers which were eventually able to lay in more-or-less normal numbers. Differences in the flexibility of mechanisms controlling the timing of breeding in different species may also be involved. And finally it is worth pointing out, that changes in the distribution and/or abundance of prey organisms in the water column may be expected to be reflected more strongly in birds restricted to feeding on the upper 0.5 m of water than those foraging over a much wider range of water depths. Unfortunately techniques used by oceanographers to examine plankton in Lancaster Sound in 1977 and 1978 were not sufficiently sensitive to detect such changes (24).

The long-term effect of one year's reproductive failure on subsequent population size of these species must be considered in relation to their population dynamics. We have no data for adult mortality rates or for the age of first breeding for any seabird population in Lancaster Sound. However, population studies of these species have been made elsewhere, and we know that all species share a number of life-history features. These are: low adult mortality with a breeding life of between 5.6 and 34 years, and delayed onset of breeding (commencing between the 4th and 9th year of life)(25). In addition we know that at Prince Leopold Island, and elsewhere, annual productivity is low. This particular combination of features means that for all species a decrease in productivity or juvenile survival in one year, will have only a minor affect on subsequent population size (26), particularly if juvenile mortality is density dependent. Thus, low productivity one year may be offset by increased juvenile survival in the next. On the other hand, even a small increase in adult mortality is likely to have a substantial and long-lasting effect on population size. For example, a species with a 95% annual adult survival rate, need only suffer a 5% decrease in survival to double its mortality rate. What this means is that seabird populations can readily withstand a 'natural' disaster (such as the 1978 ice conditions), which affects only productivity because their life-history pattern is evolved to cope with such events. They are, however, much less likely to recover from any factor (such as oil pollution, gill-netting and hunting) which increases adult mortality. Of all seabirds breeding in Lancaster Sound, Thick-billed Murres are especially vulnerable to increased adult mortality, through man's activities in arctic regions. Already, salmon gill-net fishing off southwest Greenland (the wintering area for the Lancaster Sound and vicinity Thick-billed Murre population) has caused massive mortality, and, now, in addition, there is the threat of oil pollution as a result of off-shore drilling (27).

David N. Nettleship

Timothy R. Birkhead*

Anthony J. Gaston

Canadian Wildlife Service

Bedford Institute of Oceanography

Dartmouth, Nova Scotia

Canada B2Y 4A2

References and Notes

1. L.O. Belopol'skii, Ecology of sea colony birds of the Barents Sea (Israel Program for Scientific Translations, Jerusalem, 1961); P. Freuchen and F. Salomonsen, The Arctic Year (G.P. Putman's Sons, New York, 1958); F. Salomonsen, Proceedings of XV International Ornithological Congress, pp. 25-77 (1972).
2. D.N. Nettleship, Canadian Wildlife Service Progress Notes No. 73, 1-11 (1977); D.N. Nettleship and A.J. Gaston, Canadian Wildlife Service Occasional Paper No. 39, 1-40 (1978).
3. A.J. Gaston and D.N. Nettleship, Thick-billed Murres on Prince Leopold Island - a study of the breeding ecology of a colonial high arctic seabird (Monograph Series, Canadian Wildlife Service, Ottawa, in preparation).
4. R.G.B. Brown, D.N. Nettleship, P. Germain, C.E. Tull and T. Davis, Atlas of Eastern Canadian Seabirds (Canadian Wildlife Service, Ottawa, 1975).
5. A. Linton and D.N. Nettleship, Breeding ecology of Northern Fulmars at Prince Leopold Island, in preparation; D.N. Nettleship, in preparation.
6. Egg laying dates for 1978 were extrapolated from hatching dates using the mean incubation period derived from the 1975-77 data (see also (9)).
7. Data for some years are not normally distributed; to correct this a number of transformations were made, but none were satisfactory. We therefore 'trimmed' the data, using only the mid 80%, thereby cutting off the tails of the distribution. ANOVA showed significant heterogeneity between years ($F_{3,1456}$ = >700, $P < 0.001$). Duncan's Multiple Range test was used to determine which differences were significant (at the $P = 0.05$ level); all pair wise comparisons except 1975-1976 were significantly different.

8. P. Jones and P. Ward, J. Zool. Lond. (in press). See also: S.C. Stearns, Q. Rev. Biol. 51: 3-27 (1976); D. Goodman, Am. Nat. 108: 247-268 (1974).

9. Incubation periods mean duration: 1975: 32.7 days ± 0.15 S.E. (n = 112), 1976: 32.1 ± 0.13 (n = 207), 1977: 32.1 ± 0.10 (n = 179) and 1978: 32.1 ± 0.45 (n = 25). Although there is a significant difference ($F_{3,519} = 3.8$, $P < 0.01$) between years, the maximum mean difference is only 0.6 days, and may have come about because sites were inspected only once every 24 hours. Similarly for nestling periods: 1975: 20.8 days ± 0.14 S.E. (n = 318), 1976: 21.4 ± 0.15 (n = 400), 1977: 20.3 ± 0.10 (n = 447) and 1978: 20.71 ± 0.15 (n = 219) ($F_{3,1380} = 13.28$, $P < 0.001$). The mean maximum here is 1 day, which again falls within the observational error.

10. C.S. Lloyd, Ibis 121, 165-176 (1979).

11. R.K. Murton, N.J. Westwood and A.J. Isaacson, Ibis 116: 52-73 (1974); J. Parsons, Nature 228: 1221-1222 (1970); J.W.F. Davis, Ibis 117: 460-473 (1975); A.J. Mills, Ibis 121: 53-67 (1979).

12. Mean air temperature during the nestling period in four years. Ambient temperatures were recorded each day at 0700 and 1900 hours local time, and the mean values determined. The nestling period was here defined as from the start of hatching through to the median fledging date. Average daily temperatures: 1975: + 2.5°C, 1976: +0.7°C, 1977: +2.5°C, and 1978: -1.0°C.

13. T.R. Birkhead, <u>Breeding biology and survival of Guillemots Uria aalge</u> (D. Phil. thesis, Oxford University, Oxford, England, 1976).

14. During 4 hour observation periods (from 1400-1800 hours) in 1978 unattended chicks were not recorded until 31 August when 2 out of 116 were noted. The

proportion increased up to 11 September, after which there were no further observations: 4 September = 6/81 (7.4%), 7 September = 4/62 (6.4%), 9 September = 4/57 (7.0%), and 11 September = 8/24 (33.3%). The mean minimum period of absence per chick per four hours also increased: 31 August = 2.1 minutes, 4 September = 1.1 minutes, 7 September = 4.2 minutes, 9 September = 5.0 minutes, and 11 September = 44.7 minutes.

15. Fledging age is slightly biased upwards in 1978, since only chicks of 15 days or older were considered to have fledged. In 1978 chicks less than 15 days old were recorded fledging - although they were unlikely to survive.

16. Ice conditions in Lancaster Sound were variable through the fledging period. Concentrations in the vicinity of Prince Leopold Island remained high throughout this time with large numbers of ice floes encircling the Island and therefore forming a physical barrier to murres which were undergoing a swimming migration. Ice concentrations ranged from open pack ice (4/10 to 6/10 ice cover) with many leads and polynyas (floes generally not in contact with one another) to areas with compact pack ice (10/10 ice cover where no water is visible but floes are not frozen together). Even at lower concentrations, however, large floes (500 m to over 10 km across) pose a serious threat to migrating murres as the birds attempted to walk across them rather than circumnavigate the floes by swimming. The usual outcome of attempts by chick-adult pairs to walk across large ice pans was the death of the chick through exhaustion, exposure and/or gull predation.

17. Northern Fulmar egg volumes ($\bar{x}$ cm^3 ± S.E.), 1975: 176.4 ± 2.7 (n = 18), 1976: 166.0 ± 4.8 (n = 14), 1977: 175.1 ± 2.5 (n = 10), 1978: 170.0 ± 5.8 (n = 10). $F_{3,48}$ = 1.57 NS.

18. Northern Fulmar chick sample sizes, data from day 1 and 2 and day 5 and 6 were combined, because for any particular day, sample sizes were small. Equal numbers of chicks on days 1 and 2 and day 5 and 6 were used.

19. D.N. Nettleship, Breeding biology of Black-legged Kittiwakes at Prince Leopold Island, in preparation.

20. D.N. Nettleship, Breeding biology of Black Guillemots at Prince Leopold Island, in preparation.

21. D.N. Nettleship, Breeding observations of the Glaucous Gull at Prince Leopold Island, in preparation.

22. N.P. Ashmole, Avian Biology, D.S. Farner and J.R. King, Eds. (Academic Press, New York, 1971), vol. 1,pp. 223-286.

23. M.S.W. Bradstreet, Summer feeding ecology of seabirds in eastern Lancaster Sound, 1976 (LGL Ltd. Report to Norlands Petroleums Ltd., Calgary, Alberta 1976).

24. A. Serkerak, in preparation and personal communication.

25. T.R. Birkhead and P.J. Hudson, Ornis. Scand. 8: 145-154 (1977); J.C. Coulson and R.D. Wooler, J. Anim. Ecol. 45: 205-213 (1976); R.D. Wooler and J.C. Coulson, Ibis 119: 339-349 (1977); G.M. Dunnet and J.C. Ollason, J. Anim. Ecol 47: 507-520 (1978); J.C. Ollason and G.M. Dunnet, J. Anim. Ecol. 47: 961-976 (1978).

26. R.D. Wooler and J.C. Coulson, Ibis 119: 339-349 (1977).

27. D.N. Nettleship, in Symposium Proceedings: Canada's Threatened Species and Habitats, Ottawa, 20-24 May 1976, T. Mosquin and C. Suchal, Eds. (Canadian Nature Federation, Ottawa, 1977), pp. 96-108; A.R. Milne and B.D. Smiley, Offshore drilling in Lancaster Sound - possible environmental hazards (Institute of Ocean Sciences, Sidney, British Columbia, 1978).

28. Research funded by the Canadian Wildlife Service and Petro-Canada Ltd., with logistic support from Polar Continental Shelf Project and travel expenses for T.R. Birkhead from the Royal Society and Sheffield University Research Fund. We thank S. Currie, B. Dodge, E. Greene, S.R. Johnson, A. Linton and L. Patterson for technical field assistance in 1978 and R.A. Davis (LGL Ltd.) and G.T. Glazier (Petro-Canada Ltd.) for their interest and encouragement.

* Permanent address: Department of Zoology, University of Sheffield, Sheffield England S10 2TN

Table 1. Mean body weight of Thick-billed Murre chicks at day 2, day 14, maximum weight and fledging at Prince Leopold Island.

Year	Day 2 (g)	Day 14 (g)	Maximum weight (g)	Fledging weight (g)
1975	71.6	187.7	204.5	200.5
1976	72.2	174.1	211.6	209.2
1977	70.8	199.7	221.5	215.8
1978	66.0	155.7	171.5	165.3

Sample sizes: 1975 n = 19; 1976 n = 28; 1977 n = 25; 1978 n = 21 (day 2), n = 22 (day 14, max. wt.), n = 20 (fledging weight).

Table 2. Breeding success of Thick-billed Murres at Prince Leopold Island.

Year	Number of eggs	Eggs hatched	Chicks fledged	Breeding success (%)
1975	358	309 (86.3)*	284 (91.9)	79.3
1976	359	296 (82.5)	269 (90.9)	74.9
1977	351	294 (83.8)	270 (91.8)	76.9
1978	344	280 (81.4)	229 (81.8)	66.6

* Values in parentheses are percentages of total numbers.

Notes: Breeding success figures derived from 4 study plots (G1, G4, S1 and U; see (3)) followed in all years. All data include relays and breeding success is therefore the fraction of pairs which fledged a chick. $Chi^2 = 21.2$, $P < 0.001$ (comparing fledging success 1975-77 to 1978).

Table 3. Timing of breeding (median dates) of Northern Fulmars at Prince Leopold Island.

Year	Laying	Hatching	Fledging	n
1975	10 June*	28 July	17 August	(75,75,88)
1976	11 June	28 July	19 August	(107,76,94)
1977	7 June	25 July	14 August	(98,92,97)
1978	10 June*	28 July	18 August	(19,19,19)

* Derived from median hatching dates.

Table 4. Mean body weight of Northern Fulmar chicks at 1-2 days and 5-6 days of age at Prince Leopold Island.

Age	1976 + 1977*			1978			t	P
	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	N		
1-2 days	76.9	2.89	30	72.1	2.29	15	1.30	NS
5-6 days	157.9	7.06	26	135.2	8.24	13	2.09	<0.05

* Differences between 1976 and 1977 were not statistically significant and therefore were combined to increase the sample size.

Table 5. Breeding success and productivity of Northern Fulmars at Prince Leopold Island.

Year	Number of eggs	Eggs hatched	Chicks fledged	Breeding success (%)	Productivity*
1975	257	180 (70.0)**	121 (67.2)	47.1	46.9
1976	228	109 (47.8)	96 (88.1)	42.1	37.2
1977	259	143 (55.2)	111 (77.6)	42.9	43.0
1978	51	23 (45.1)	14 (60.9)	27.5	5.4

* Productivity is the proportion of pairs which produced a fledgling relative to the mean breeding population size for 1975-77 (n = 258 pairs); in 1976 30 pairs known to have bred previously failed to produce eggs in this year (see (5)).

** Values in parentheses are percentages of total numbers.

Table 6. A summary of the breeding performance of five seabird species breeding at Prince Leopold Island in 1978 relative to the 1975-77 seasons.

Species	Timing of breeding	Proportion breeding (%)	Chick growth	Breeding success	Productivity
Pursuit divers:					
Thick-billed Murre	c̲ 3 weeks late	97%	low weight	normal to low	low to zero
Black Guillemot	c̲ 3 weeks late	c̲ 95%	?	?	?
Surface feeders:					
Northern Fulmar	Normal	c̲ 20%	low weight	low	low
Black-legged Kittiwake	Normal	c̲ 20%	?	?	low
Glaucous Gull	?	c̲ 20%	?	?	low

FIGURE LEGENDS

FIGURE 1. Distribution and concentration of ice in Lancaster Sound and vicinity in normal years and in 1978: hatched lines show boundaries between ice and water areas (double hatched: normal years; single hatched: 1978). Early - shows locations of fast ice edges (1.0 or 10/10 ice cover). Middle - shows areas of close pack ice (0.8 or 8/10 ice cover) to compact or consolidated pack ice (1.0 or 10/10 ice cover). Late - shows areas of open pack ice to close pack ice in normal years and open pack ice to compact pack ice in 1978 (see (16)).

FIGURE 2. Egg-laying dates of Thick-billed Murres at Prince Leopold Island in four seasons. The heavy arrow indicates the median laying date.

FIGURE 3. (A) Mean volume indices (length x breadth^2) of eggs laid by Thick-billed Murres at Prince Leopold Island, 1975-1978. (B) Mean volumes of eggs laid by Thick-billed Murres in 1978 at Prince Leopold Island (PLI), Cape Hay, Bylot Island, and Cambridge Point, Coburg Island (see text p. 00).

FIGURE 4. The relationship between mean egg volume and mean chick weight at day 2 for four years. The data suggest a positive relationship.

FIGURE 5. Development of Thick-billed Murre chicks in 1978 compared with 1975-77. The y axis is the mean percentage difference in weight between 1978 and 1975-77. The first point (-7.7), which lies on the dotted line, shows that in 1978 2-day old chicks were 7.7% below average weight. Egg volume was low in 1978, so the difference could have been due to egg volume. If this was the case, then all other things being equal, chicks might have remained at a 7.7% disadvantage (the dotted line). In fact, the percentage weight difference increased. Max = maximum weight reached, F = weight on the day on or before fledging.

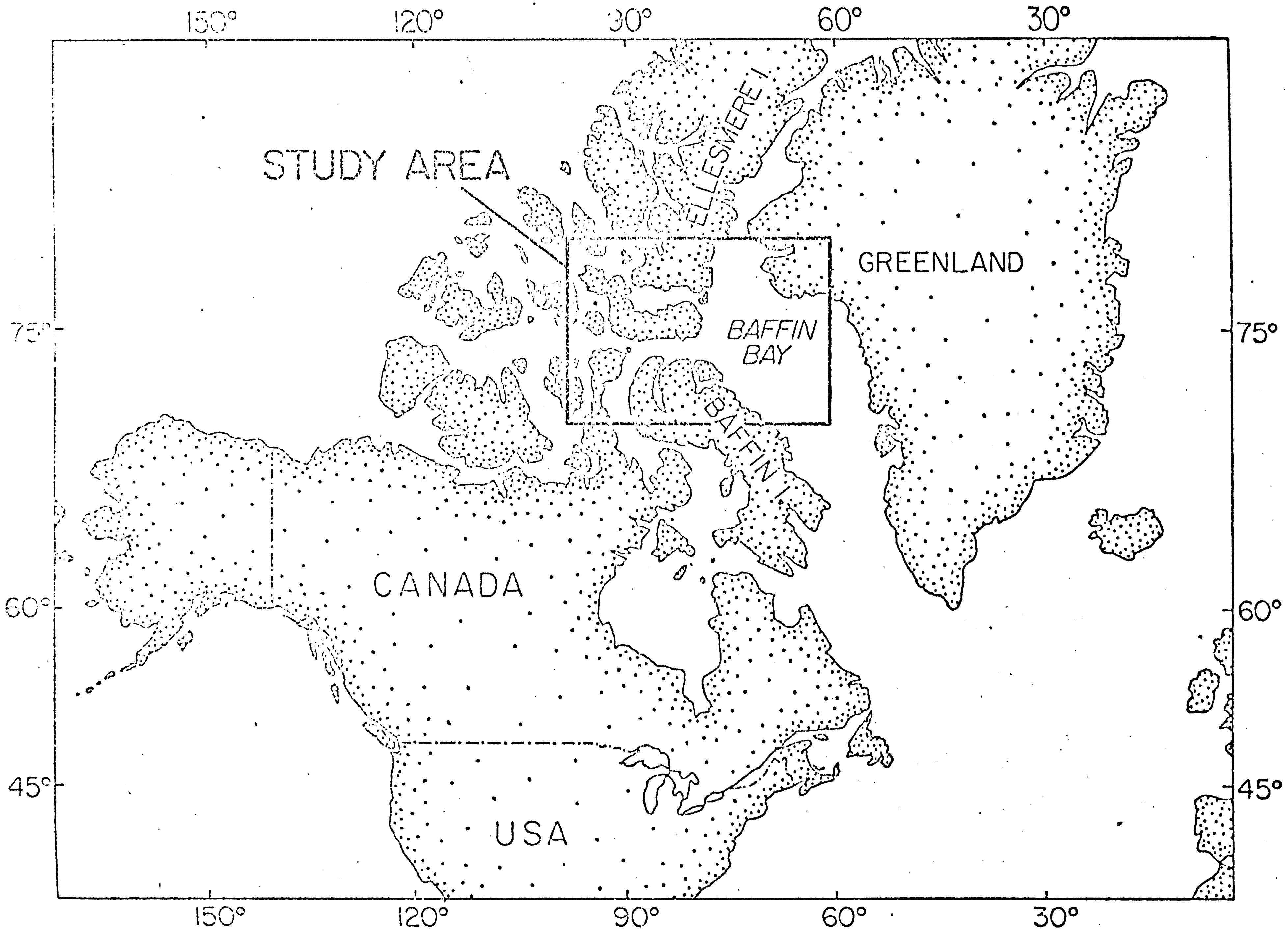
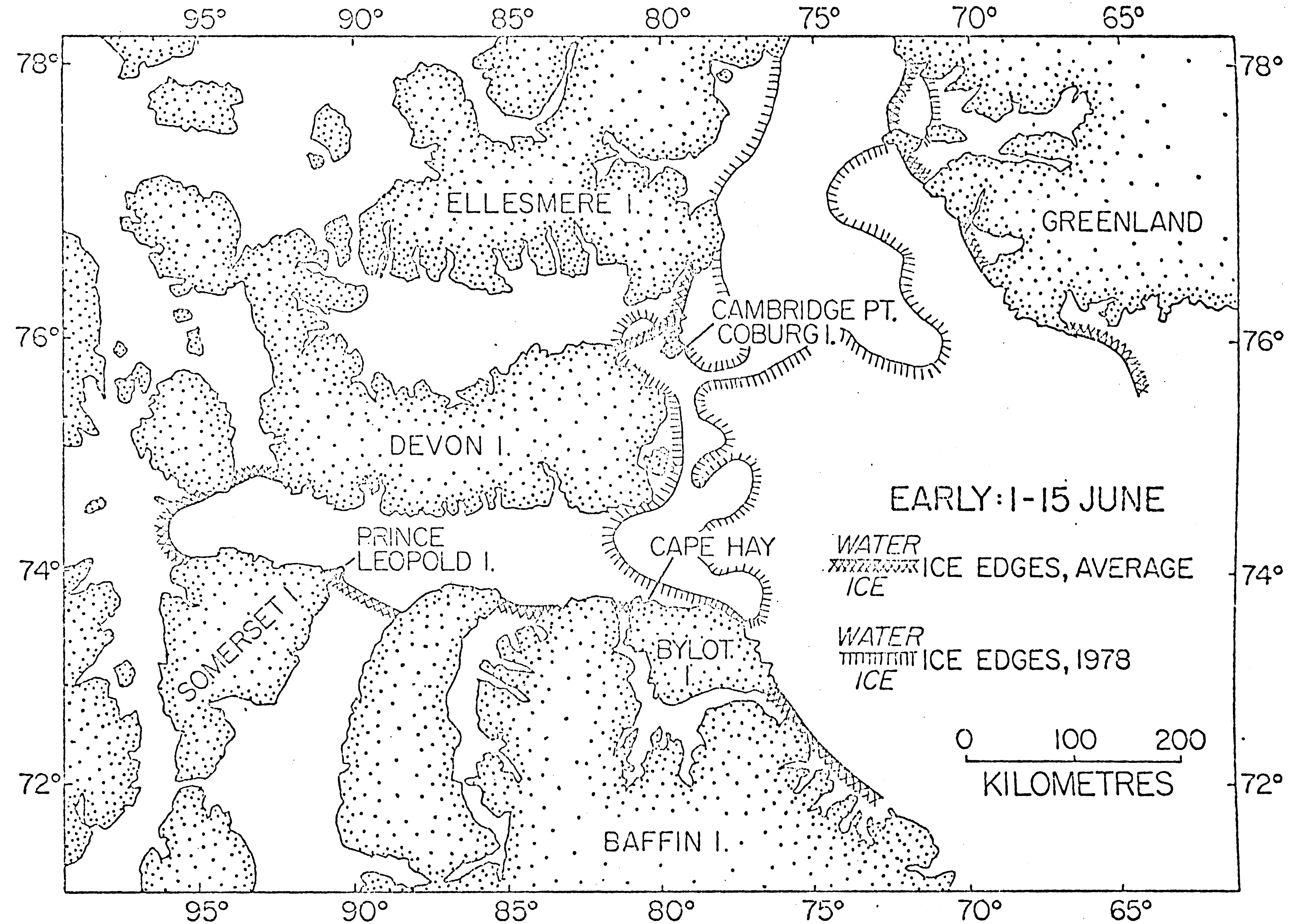
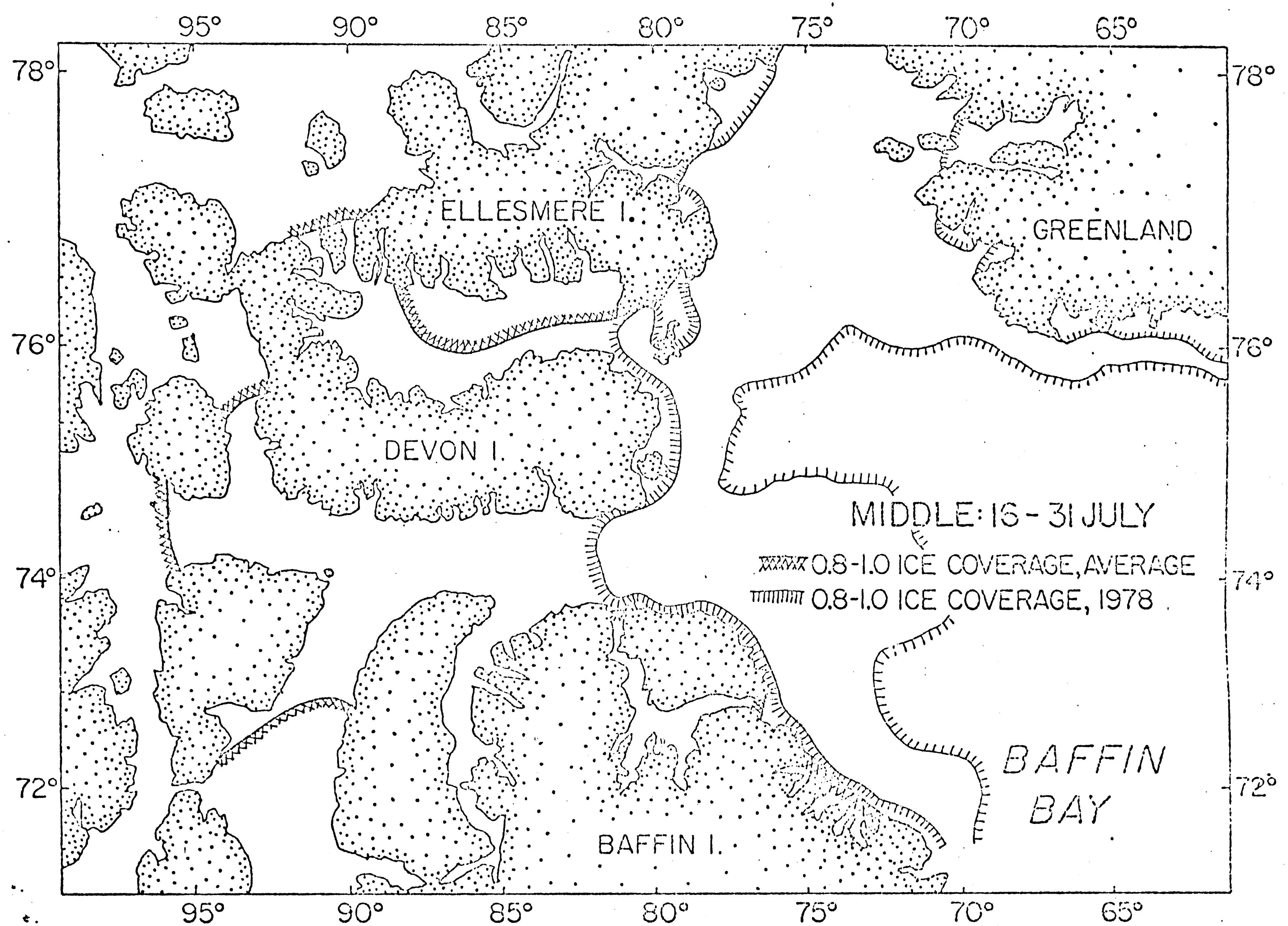
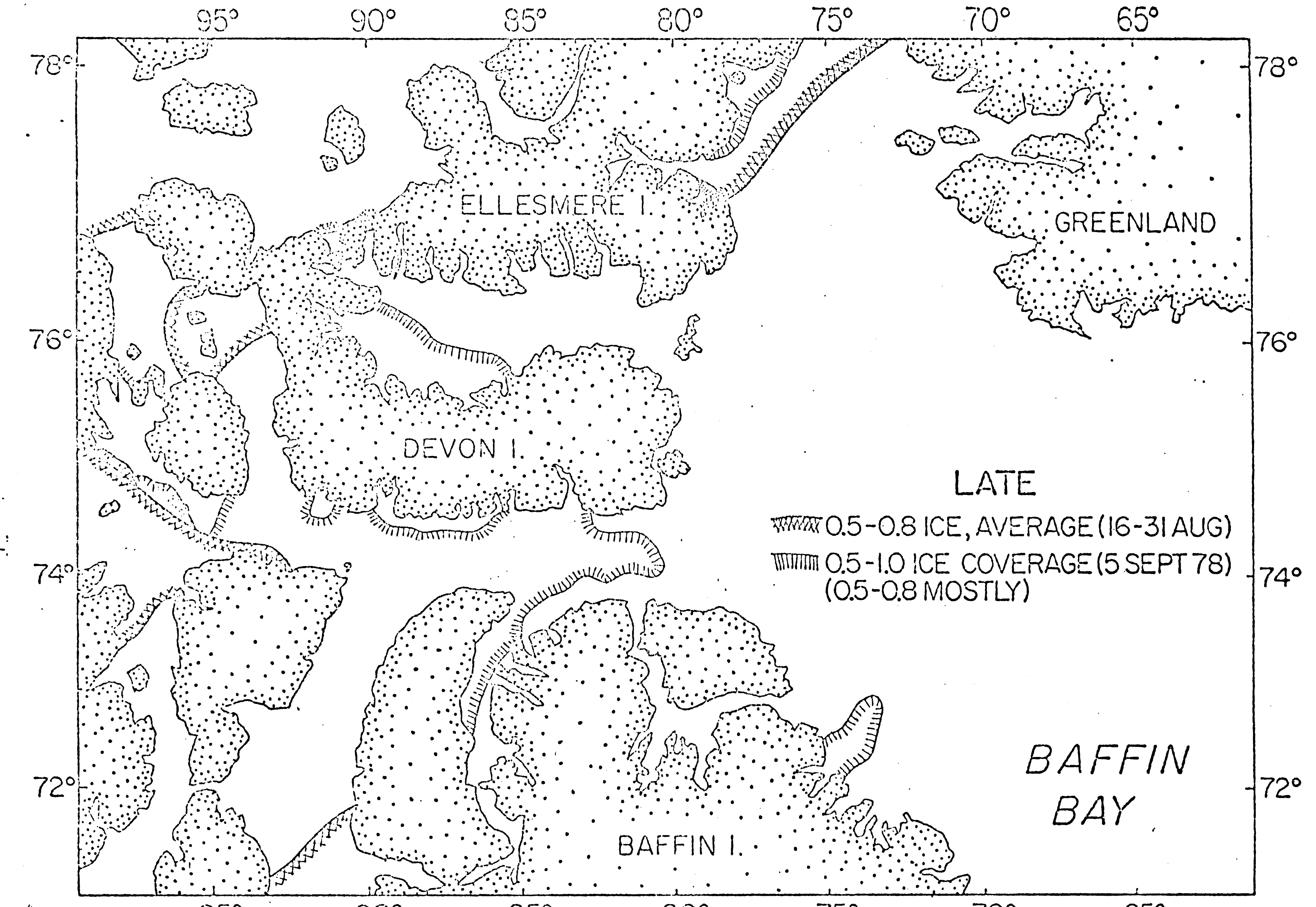


Fig. 1. Note: figure is subdivided into 4 sections (this p. + next 3 pp.) but will be in a single format after photo reduction. i.e.



95°
90°
85°
80°
75°
70°
65°
78°
76°
74°
72°
ELLESMERE I.
GREENLAND
CAMBRIDGE PT.
COBURG I.
DEVON I.
EARLY: 1-15 JUNE
PRINCE
LEOPOLD I.
CAPE HAY
WATER
ICE EDGES, AVERAGE
ICE
BYLOT
I.
WATER
ICE EDGES, 1978
ICE
SOMERSET I.
0 100 200
KILOMETRES
BAFFIN I.


95°
90°
85°
80°
75°
70°
65°
78°
76°
74°
72°
ELLESMERE I.
GREENLAND
DEVON I.
MIDDLE: 16 - 31 JULY
0.8-1.0 ICE COVERAGE, AVERAGE
0.8-1.0 ICE COVERAGE, 1978
BAFFIN BAY
BAFFIN I.


95°
90°
85°
80°
75°
70°
65°
78°
76°
74°
72°
ELLESMERE I.
GREENLAND
DEVON I.
LATE
0.5-0.8 ICE, AVERAGE (16-31 AUG)
0.5-1.0 ICE COVERAGE (5 SEPT 78)
(0.5-0.8 MOSTLY)
BAFFIN BAY
BAFFIN I.

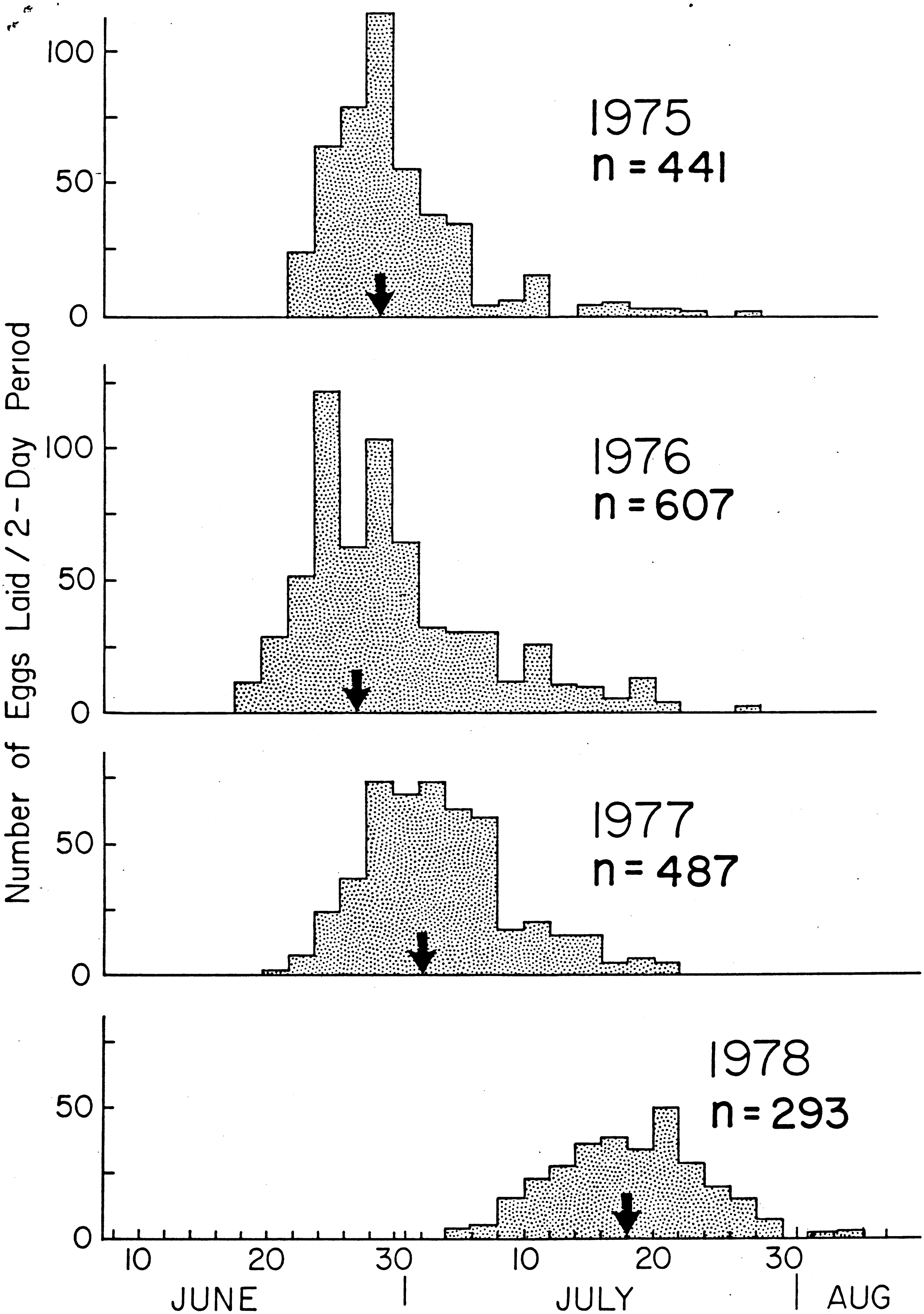

Number of Eggs Laid / 2-Day Period
1975
n = 441
1976
n = 607
1977
n = 487
1978
n = 293
0
50
100
10
20
30
JUNE
JULY
AUG

Figure 2.

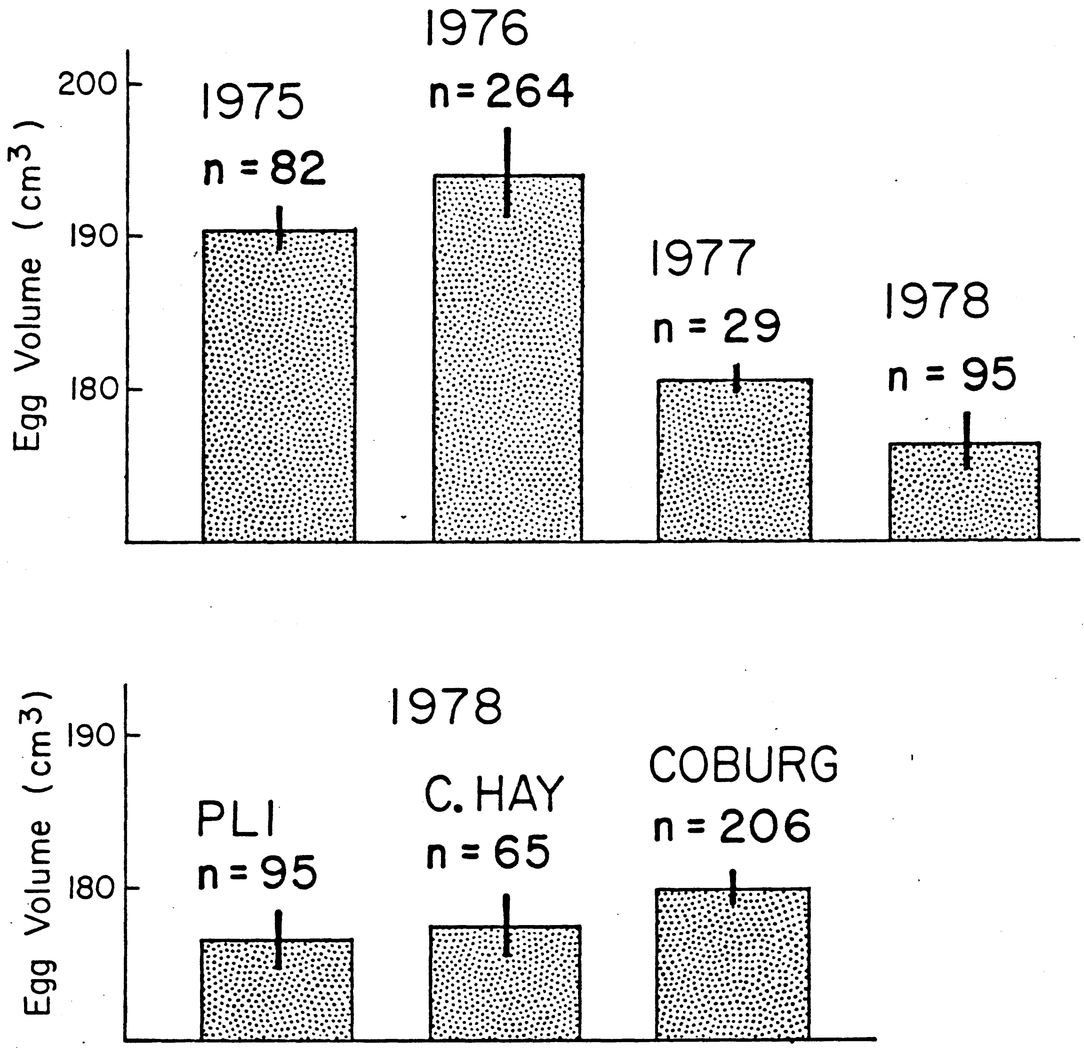

1975
n = 82
1976
n = 264
1977
n = 29
1978
n = 95
200
190
180
Egg Volume (cm3)
1978
PLI
n = 95
C. HAY
n = 65
COBURG
n = 206
190
180
Egg Volume (cm3)

Figure 3.

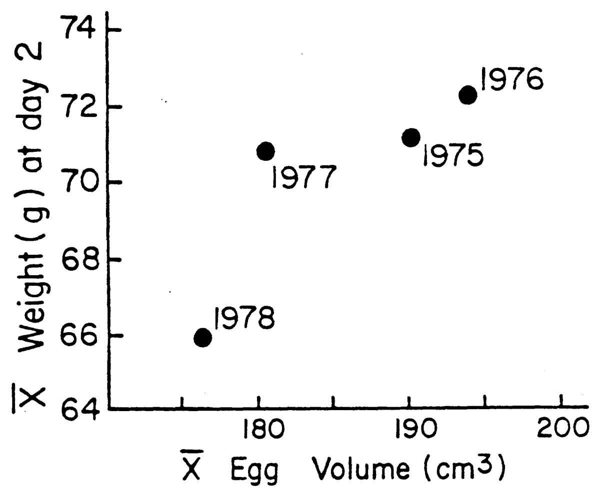
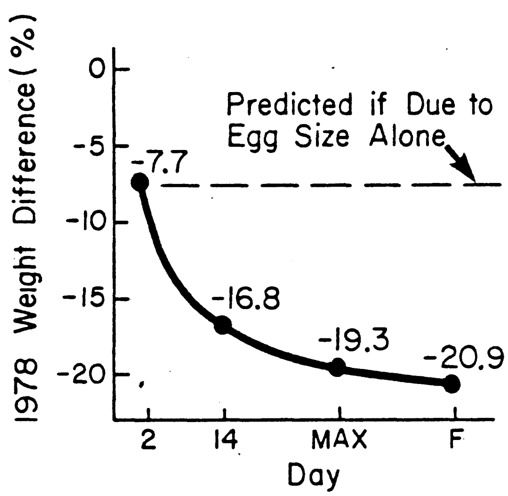

X̄ Weight (g) at day 2
74
72
70
68
66
64
1976
1975
1977
1978
180
190
200
X̄ Egg Volume (cm3)

Figure 4.



1978 Weight Difference (%)
0
-5
-10
-15
-20
Predicted if Due to Egg Size Alone
-7.7
-16.8
-19.3
-20.9
2
14
MAX
F
Day

Figure 5.

Table 6. A summary of the breeding performance of five seabird species breeding at Prince Leopold Island in 1978 relative to the 1975-77 seasons.

Species	Timing of breeding	Proportion breeding (%)	Chick growth	Breeding success	Productivity
<u>Pursuit divers</u>:					
Thick-billed Murre	<u>c</u> 3 weeks late	97%	low weight	normal to low	low to zero
Black Guillemot	<u>c</u> 3 weeks late	<u>c</u> 95%	?	?	?
<u>Surface feeders</u>:					
Northern Fulmar	Normal	<u>c</u> 20%	low weight	low	low
Black-legged Kittiwake	Normal	<u>c</u> 20%	?	?	low
Glaucous Gull	?	<u>c</u> 13%	?	?	low