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Ecology of ringed seals (*Phoca hispida*) in the North Water Polynya, northern Baffin Bay

by

Meike Holst ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master in Science

in

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ABSTRACT

A comparison of the biology, feeding ecology, and abundance of ringed seals (*Phoca hispida*) was made between populations on the east (Greenland) and west (Canada) sides of the North Water Polynya. Ringed seals on the east side of the polynya had faster growth rates and reached sexual maturity earlier, but attained shorter body lengths than seals from the west side. Arctic cod (*Boreogadus saida*) was a major prey item in the diet of ringed seals from both locations. Ringed seals on the west side also took a large proportion of polar cod (*Arctogadus glacialis*) and amphipods. Ringed seal densities were greater on the east side of the polynya. Biological differences between the two populations may result from higher biological productivity on the east side of the polynya. Overall, ringed seal distribution and abundance appear to be determined by a combination of productivity, prey abundance and availability, and ice conditions.

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1. INTRODUCTION

Polynyas are areas of open water surrounded by ice that remain open throughout the winter or re-open in early spring prior to widespread ice-breakup. Polynyas have various shapes and sizes and may be caused by a number of factors including wind, tidal fluctuations, currents, or upwelling (Smith *et al.* 1990). Polynyas are thought to be important spring feeding and breeding areas for several species of marine mammals and birds, because they are the only areas of open water during this season and because of the increased biological productivity usually associated with them (Stirling 1980, 1997; Stirling *et al.* 1981). Recurring polynyas occur at the same time and location each year, and because of their reliability, appear to be important for overwintering and migrant marine mammals and birds (Stirling 1980, 1997; Stirling *et al.* 1981). Marine mammals known to overwinter in polynyas or in the pack ice immediately adjacent to them include bearded seals (*Erignathus barbatus*), walruses (*Odobenus rosmarus*), belugas (*Delphinapterus leucas*) and, in the case of large polynyas like the North Water Polynya, bowhead whales (*Balaena mysticetus*) (Kiliaan and Stirling 1978; Finley and Renaud 1980; Stirling 1980, 1997; Dunbar 1981; Stirling *et al.* 1981; Richard *et al.* 1998; Holst and Stirling 1999). Ringed seals (*Phoca hispida*) also frequent polynyas and adjacent areas of landfast and pack ice, but are less dependent on them than other marine mammals, because they can maintain their own breathing holes through the ice, by using the heavy claws on their foreflippers (Vibe 1950, McLaren 1958).

Seabirds and marine mammals are often more abundant in and near polynyas than in non-polynya areas. For example, most colonies of cliff-nesting seabirds in the Canadian Arctic occur adjacent to polynyas (Brown and Nettleship 1981), and ringed seal densities downstream of two polynya areas in the Canadian High Arctic were found to be higher than they were upstream of the polynyas or in adjacent non-polynya areas (Kingsley *et al.* 1985). There are several reasons why the abundance of marine mammals and birds may be greater in open water adjacent to or surrounded by ice: calmer water may facilitate resting on the surface and diving for food; ice may provide platforms on which to rest or seek refuge from predators, as well as a navigational aid to migrating species or a temporary barrier to migration; and there may be increased productivity at the ice-water interface, resulting in greater biomass of invertebrate and fish prey for birds and mammals (Stirling 1997).

In the past, even though empirical data on biological productivity were not available, the presence of large numbers of seabirds and marine mammals in polynyas was hypothesized to reflect increased biological productivity in these areas (Stirling 1980, 1997; Stirling *et al.* 1981). Several studies now support the hypothesis that some polynyas are more biologically productive than the ice-covered waters surrounding them. For example, Bursa (1963) noted that primary production in the flaw lead at Point Barrow began two months earlier than in surrounding ice-covered water. This head start in primary production is thought to facilitate a higher level of secondary production of zooplankton that fuels the upper trophic levels. Hirche *et al.* (1991) found that the Northeast Water Polynya had a significantly higher primary productivity than the surrounding ice-covered areas. High productivity was also found in the Ross Sea Polynya in Antarctica (Arrigo and McClain 1994). Even so, there has been little quantitative research to evaluate the role that polynyas play in polar marine ecosystems, how variable the importance of polynyas of similar size might be in different locations or, in the case of large polynyas, how much geographic variability there might be in biological processes within the same polynya.

The North Water Polynya is one of the largest recurring polynyas in the Arctic and is thought to be one of the most biologically productive (Stirling 1980, 1997; Stirling *et al.* 1981). Historically, the North Water Polynya has been considered a latent heat polynya, maintained by the continuous removal of ice southward by off-shore winds and currents (Dunbar 1969, Muench 1971) and by the latent heat of fusion of ice that is continually forming (Massom 1988, Smith *et al.* 1990). Early in the winter, an ice bridge forms across Smith Sound (Fig. 1-1), preventing the southward flow of ice from the Arctic Ocean into northern Baffin Bay (Dunbar and Dunbar 1972, Dunbar 1981). Any new ice that is formed south of the bridge is continuously removed southward, away from the coast of Ellesmere Island, by strong northeasterly winds and by currents flowing southward from the polar basin along Ellesmere Island (Fig. 1-1) (Dunbar 1969, Muench

1971). The North Water Polynya thus remains at least partially open throughout the winter months, but expands south and westward by late March or early April (Fig. 1-1), until becoming indistinguishable from the open ocean, as the surrounding ice melts in late summer (Dunbar 1969).

Several studies have noted that there appear to be biological and physical differences between the east and west sides of the polynya. Vibe (1950) suggested that the east side of the polynya showed richer animal life than the west side, because of the nutrient-rich currents that enter the polynya on that side. For example, a greater number of dovekies (*Alle alle*) breed on the east side of the North Water Polynya compared to the west (Nettleship and Evans 1985, Boertmann and Mosbech 1998). As well, Steffen (1985) discovered the presence of "warm water cells" along the Greenland coast in the North Water Polynya during winter, which are indicative of upwelling.

These observations have led to a second hypothesis relating to the formation and maintenance of the North Water Polynya. This new hypothesis posits that a second source of heat is involved in maintaining the polynya. This hypothesis suggests that sensible heat is responsible for the formation of the polynya on the east side, whereas latent heat maintains the polynya on the west side (Steffen 1985, Steffen and Ohmura 1985, Mysak and Huang 1992, Darby *et al.* 1994, Lewis *et al.* 1996). Sensible heat originates from the upwelling of warmer subsurface water, which reduces or prevents ice formation (Massom 1988, Smith *et al.* 1990, Mysak and Huang 1992). If the hypothesis is correct, the most likely source of sensible heat on the east side of the North Water Polynya is a deep, warm current of nutrient-rich Atlantic water that flows north along the coast of west Greenland and upwells when it meets the denser, colder water flowing south from the Arctic Ocean (Brown 1927, Dunbar 1981, Lewis *et al.* 1996). The water then flows westward, south along Ellesmere Island, mixes with incoming water from polynya areas to the west through Lancaster and Jones Sound, before flowing south along the east coast of Baffin Island (Fig. 1-1) (Nutt 1969).

The mechanisms by which the wind and currents that shape the North Water Polynya influence biological productivity are still largely unknown. The two different heat sources have been hypothesized to stimulate differences in the timing and development of phytoplankton blooms and food webs on the east and west sides of the North Water Polynya and, ultimately, differences in total biomass between the two areas at all trophic levels. Open water areas maintained by sensible heat are generally thought to be more productive than latent heat areas, because of warmer temperatures and upwelling, which stimulate a greater amount of productivity than in areas where those processes do not occur. On the east side of the polynya, warmer surface temperatures cause areas to remain ice-free throughout the winter, by preventing ice formation or by melting the ice cover (Steffen 1985, Steffen and Ohmura 1985). The fresh water from melting ice and the warmer temperatures stratify the water column, keeping phytoplankton in the euphotic zone where sufficient light is available for growth. In addition, upwelling brings nutrients such as phosphates, silicates, and nitrates from the bottom to the depleted upper layer, thereby stimulating new phytoplankton growth, subsequent zooplankton growth, and increased abundance of fish, such as Arctic cod (*Boreogadus saida*). Thus, earlier and subsequent phytoplankton blooms, due to warmer water temperatures and upwelling, allow for a longer season of secondary productivity and, hypothetically, increased food availability for ringed seals.

The latent heat area on the west side of the polynya is thought to be less productive because of deep mixing, which causes delays in phytoplankton growth. As ice is continually forming, salt is rejected into the surface waters and the cold, salty, high-density water sinks, a process known as thermohaline circulation. Thermohaline circulation and wind cause vertical mixing of the water, preventing the warming of the surface layer and thus, stratification. Due to the vertical mixing, phytoplankton are kept out of the euphotic zone, in deep water, where growth is not possible. Thus, on the west side, a late summer bloom is expected, once warmer temperatures stratify the water column. On the basis of preliminary data, differences in productivity between the east and west sides of the polynya have already been demonstrated to exist by Legendre (unpublished data) and Lewis *et al.* (1996), who noted a phytoplankton biomass decrease from east to west of the North Water Polynya in May.

During August 1997, April - July 1998, and September 1999, a multi-disciplinary research cruise, the International North Water Polynya Study (NOW), was undertaken to study a wide array of physical and biological processes within the polynya. The NOW sought to test two central hypotheses: 1) that the polynya is maintained by two different sources of heat on the east and west sides, sensible and latent heat respectively, and 2) that because of these differences, the level of biological productivity may differ on the east and west sides of the polynya.

As part of the NOW project, I compared the distribution, abundance, food habits, and related aspects of the biology of ringed seals between the east and west sides of the polynya. The objectives of this thesis are to evaluate the biological importance of the North Water Polynya to the ringed seal and to determine whether the hypothesized differences in biological productivity on either side of the polynya are reflected in the biological parameters of the respective ringed seal populations. Chapter 2 of this thesis is a comparison of ringed seal biology on the two sides of the polynya, including age distribution, growth rates, sexual maturity, condition, and ovulation and pregnancy rates. Chapter 3 is a comparison of ringed seal feeding ecology on the east and west sides of the polynya. Finally, Chapter 4 examines the abundance of ringed seals within the North Water Polynya, to compare and explain differences in distribution.

Ringed seals were chosen for study because they are ubiquitous and abundant throughout the Canadian Arctic (King 1983), with an estimated population size of at least a few million (Reeves 1998) and perhaps as many as 6 - 7 million (Stirling and Calvert 1979). As well, ringed seal densities, reproduction, and growth rates have been shown to vary in relation to apparent differences in ecological circumstances, such as productivity (e.g., Stirling *et al.* 1977, Kingsley *et al.* 1985, Smith 1987, Stirling and Øritsland 1995, Kingsley and Byers 1998, Goodyear 1999). Furthermore, ringed seals may be important indicators of processes and changes occurring within the arctic marine ecosystem (e.g., Stirling and Lunn 1997), since they are near the top of the food chain and, because their breeding success can be significantly influenced by variation in marine productivity. Thus, I felt that the ringed seal would be the marine mammal most likely to reflect significant differences in biological factors within the North Water Polynya, if they indeed existed.

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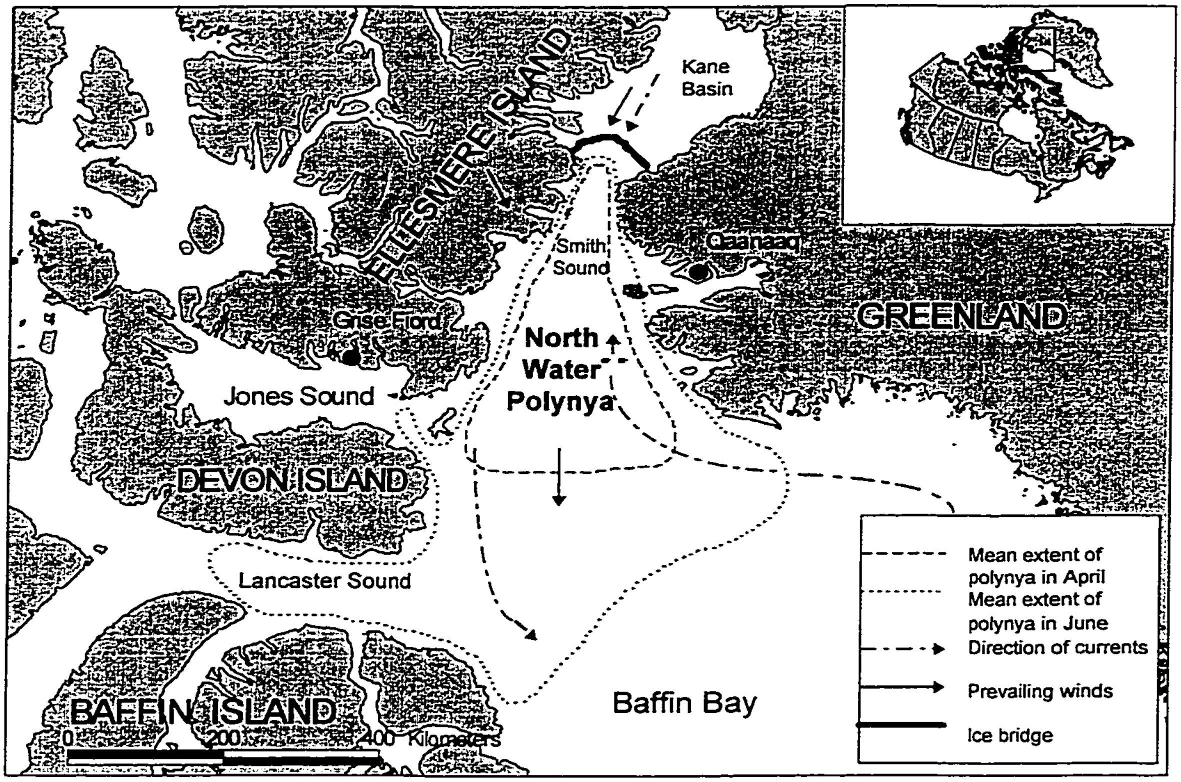

Figure 1-1: Location of the North Water Polynya, northern Baffin Bay, and the mechanisms responsible for its formation.

2. A COMPARISON OF RINGED SEAL BIOLOGY ON THE EAST AND WEST SIDES OF THE NORTH WATER POLYNYA

2.1. Introduction

The North Water Polynya is thought to be an important spring feeding and breeding area for several species of arctic marine mammals, including the ringed seal (*Phoca hispida*) (Stirling 1980, 1997; Stirling *et al.* 1981). Ringed seals are opportunistic feeders (McLaren 1958a), and their reproductive success and growth can be significantly influenced by changes in biological productivity and food abundance (Lowry *et al.* 1980). For example, studies in the Beaufort Sea and Amundsen Gulf have shown that reproductive rates sometimes vary markedly in response to differences in ecological circumstances that apparently affect productivity (e.g., Stirling *et al.* 1977, Smith 1987, Stirling and Øritsland 1995, Stirling and Lunn 1997, Kingsley and Byers 1998).

Two different heat sources have been hypothesized to maintain the east and west sides of the North Water Polynya, namely sensible and latent heat respectively. Thus, differences in the level of biological productivity may exist within the polynya and may in turn affect the biology of the ringed seal. In this chapter, I compare aspects of the biology of ringed seals from the east and west sides of the polynya, including age distribution, growth rate, sexual maturity, condition, ovulation rate, and pregnancy rate, in order to determine whether any significant differences exist that might relate to the hypothesized differences in productivity. If the biological productivity on the east side is significantly higher than on the west side, then I would predict that because of the increased amount and availability of food, ringed seals there should grow faster, attain sexual maturity at a younger age, be in better condition, and have higher ovulation and pregnancy rates than those on the west side.

2.2. Methods

Comparisons of ringed seal populations were based on samples collected by Inuit hunters on the west (Grise Fiord ⇒ 76°12 N, 83°06 W) and east sides (Qaanaaq ⇒ 77°40 N, 69°00 W) of the North Water Polynya (Fig. 2-1). From 27 May - 28 June, 1998, samples were collected from 99 ringed seals taken by Inuit hunters at Grise Fiord, Nunavut, of which 95% (94/99) were collected on landfast ice. Samples were also collected from 100 ringed seals near Qaanaaq, Greenland between 8 May - 11 July, 1998, of which 89% (88/99) were collected on landfast ice and 11% were collected in the water at the ice edge. Hunters were asked to collect seals non-selectively with respect to sex or age class so that the samples would be as representative as possible of the seals available at the time. Samples were frozen in the field and shipped by air to Edmonton for analysis.

The following data were recorded in the field for each seal collected: sex, date, and location of collection. Measurements for seals collected in Grise Fiord followed Scheffer (1967) and Bonner and Laws (1993) and included: standard length (straight line length from the tip of the nose to the tip of the tail), axillary girth, and fat thickness (on the ventral mid-line between the front flippers). Weights for seals collected in Grise Fiord were calculated using the formula described by McLaren (1958b):

$$\log(\text{weight}) = 3.005*\log(\text{length}) - 2.9882$$

For seals collected in Qaanaaq, axillary girth, fat thickness, and scale weight were recorded. Instead of standard length, length was measured from the nose to the base of the tail. Thus, length measurements had to be corrected by adding tail lengths. Measurements for tail length and length from nose to base of tail were obtained from 30 ringed seals near Holman, NWT, and the linear regression function in Sigma Plot Ver. 4.0 was used to fit a straight line to the data (Appendix A). The equation for calculating tail length from nose to base of tail measurements was:

$$\text{Tail length (cm)} = 0.0357x + 4.0832$$

where: x = length from nose to base of tail in cm

However, the r-squared value was low (0.07), since tail length seems to be quite variable among older animals (Appendix A). Nonetheless, the values obtained in the regression were similar to published tail length averages determined by McLaren (1958a). The equation was then used to add tail lengths to the measured lengths of ringed seals from

Qaanaaq to obtain standard lengths.

Mean lengths, girths, and weights were calculated for adults (≥ 6 years) only. Mean blubber thickness was used as an index of condition and was calculated only for animals collected in June, when animals were collected from both sides of the polynya. Other indices of condition (e.g., McLaren 1958a, Sergeant 1973, Ryg *et al.* 1990) were considered, but could not be used because some variables in these formulas were unknown. The condition of pups was assessed separately, since their mean condition at that time was probably still reflective of the condition of their mothers. Student's *t*-tests were used to test for differences in length, girth, weight, and condition of ringed seals from the east and west side of the polynya.

In order to compare growth rates of seals on either side of the polynya, von Bertalanffy growth curves, as parameterized by Hammill *et al.* (1995), were fitted to length versus age data using the nonlinear regression program of Sigma Plot Ver. 4.0. The von Bertalanffy model showed the best fit when compared to the Gompertz and logistic models. The von Bertalanffy equation used was:

$$l_a = L_\infty[1-(1-(l_o/L_\infty))*\exp(-k_o a/(L_\infty-l_o))]$$

where: l_a = length at age a

L_∞ = asymptotic length (cm)

l_o = estimated length at birth (cm)

k_o = absolute rate of growth at birth (cm/year)

For this comparison, l_o should be interpreted as the estimated length of a pup, since the samples included newborn seals as well as those that had already been weaned. Likelihood ratio tests were used to test for statistical differences between growth curves and curve parameters (Kimura 1980). Homogeneity of variances, an assumption under the Likelihood ratio method (Kimura 1980), was evaluated using an F-test (Sokal and Rohlf 1981).

Ages were determined using cementum growth layer groups in canine teeth from the lower jaw (Stewart *et al.* 1996). Seals less than one year of age are referred to as 0+ or young-of-the-year (YOY), seals 1 through 5 years of age as subadults, and those 6 years and older as adults because, on average, that is the age at which females in most populations reach sexual maturity (e.g., McLaren 1958a; Smith 1973, 1987). Since sample sizes were not large enough to compare sex-specific age structure for each individual age class, they were pooled as follows to facilitate statistical comparisons between age structure: 0+, 1-2, 3-5, 6-10, 11-15, 16-20, 21-25, 26-30, 31-35, 36-40, and 41+ years of age. YOY were treated as a single group because they have the highest mortality rate and have the potential to be the most variable. The subadults were divided into two groups (1-2 yr and 3-5 yr) because behavioural exclusion of subadults from feeding or breeding habitat by older animals (e.g., McLaren 1958a) most likely has a greater effect on the youngest animals. One- and 2 year-olds are the youngest subadults and ovulation has not yet occurred; thus, they may be more likely to be affected by competition with other seals. For 3-, 4-, and 5-year-olds, some proportion of females ovulate, so that their behaviour and distribution may be more similar to adults than younger subadults. These three maturing age classes may thus compete more successfully for resources and their distribution may be intermediate between younger subadults and adults. The adults were grouped into five-year age classes, since the distribution of individual age and sex classes would be similar, and the number in each class was too small to facilitate comparison. Likelihood chi-square tests were used to test for differences between the age distributions and Pearson chi-square tests were used for comparison of sex ratios. A Mann-Whitney *U* test was used to test for differences between mean ages of ringed seals from either side of the polynya, to determine whether they had similar age structures.

Ovaries were sectioned at 2 mm intervals and were then examined macroscopically for the presence of corpora lutea (indicative of ovulation in the current year) and corpora albicantia (indicative of pregnancy in the previous year) (McLaren 1958a). The proportion of females that had a corpus luteum or a corpus albicans was used to calculate age-specific ovulation rates and the age of sexual maturity for females (DeMaster 1978). Differences in ovulation and pregnancy rates between locations were tested for using Fisher's Exact test.

2.3. Results

2.3.1. Sex ratio

Although there were slightly more males than females in the sample of ringed seals from Qaanaaq and slightly more females than males in the sample from Grise Fiord, the difference was not statistically significant in either case (Table 2-1). Ringed seals from both sides of the polynya conformed to a 1:1 sex ratio (Grise Fiord, $x^2 = 1.71$, df = 1, $P = 0.19$; Qaanaaq, $x^2 = 1.00$, df = 1, $P = 0.32$).

2.3.2. Age distribution

The age distributions for males and females differed significantly between the two locations (males: $x^2 = 22.55$, df = 10, $P < 0.05$; females: $x^2 = 46.63$, df = 10, $P < 0.05$ (Fig. 2-2). In the Grise Fiord sample, 32% were YOY and 9% were subadults (ages 1 to 5), whereas the proportion of YOY in the Qaanaaq sample was only 7% and 56% were subadults. There was a greater proportion (18%) of older seals (31+ years) in the Grise Fiord sample than in the Qaanaaq sample (6%).

Adult females collected near Grise Fiord were significantly older than adult males (Mann-Whitney *U*-test, $P < 0.01$), whereas there was no significant difference between the mean ages of adult males and females collected near Qaanaaq ($P = 0.13$), although there was a trend towards older males (Table 2-1). The mean ages of adults of the same sex were not significantly different between the two locations ($P > 0.05$). The maximum ages for males and females collected near Grise Fiord were 34 and 43 respectively and for Qaanaaq, the maximum ages were 40 and 38 years respectively.

2.3.3. Morphometrics

Adult male ringed seals did not differ significantly in mean length or axillary girth from adult female seals from either Grise Fiord or Qaanaaq (Table 2-1), so the data were pooled for each location. Seals from Grise Fiord were significantly longer than those from Qaanaaq ($t = 2.76$, df = 88, $P < 0.01$). Although the axillary girths of seals collected in Grise Fiord were slightly greater, there were no significant differences between the mean girths of seals collected in Qaanaaq and those collected in Grise Fiord ($t = 0.93$, df

$= 86$, $P = 0.36$).

The sample variances for both von Bertalanffy growth curves were equal and thus Likelihood ratio tests were applied to compare them. The growth curves differed significantly between ringed seals from either side of the polynya (Fig. 2-3). Ringed seals from Qaanaaq grew significantly faster ($P < 0.01$) than those from Grise Fiord (Table 2-2). However, seals from Grise Fiord were significantly longer at birth ($P < 0.01$) and reached a significantly greater asymptotic length ($P < 0.01$) than those from Qaanaaq (Table 2-2).

2.3.4. Condition

There were no significant differences in the mean blubber thickness between males and females from the same location (Table 2-1). The mean blubber thickness of adult females from Grise Fiord was significantly lower than from Qaanaaq ($t = 2.45$, df = 41, $P < 0.05$) (Table 2-1). YOY from Grise Fiord had a greater blubber thickness than those from Qaanaaq. However, no tests were used to determine statistical significance, because sample sizes were small (Table 2-1). The mean weight of males did not differ significantly from the mean weight of females, thus the data were pooled (Table 2-1). The mean calculated weight of adult seals from Grise Fiord was significantly higher than the mean scale weight of adults from Qaanaaq (t-test = 3.64, df = 88, $P < 0.01$) (Table 2-1).

2.3.5. Reproduction

The age of sexual maturity for female ringed seals from Grise Fiord could not be determined, since no females aged 5 to 8 years were sampled. Ovulation had not taken place in the only 4-year-old female but had occurred in the one 9-year-old. All adult females (≥ 9 years) had ovulated (n = 25) (Table 2-1). A corpus albicans was found in the ovaries of 80% (20/25) of adult females, indicating pregnancies in the previous year. The age of sexual maturity for female ringed seals from Qaanaaq was 4.7 years. Ovulation had occurred in 2 of 7 4-year-old females, 3 of 3 5-year-olds, and 93% (13/14) adult females (≥ 6 years) (Table 2-1). A corpus albicans was found in the ovaries of 77% (10/13) of adult females.

2.4. Discussion

2.4.1. Sex ratio

The sex ratios of ringed seals from Grise Fiord and Qaanaaq did not differ from unity. Similarly, even sex ratios have been found to be characteristic of ringed seal populations throughout the Canadian Arctic, including Davis Strait (Smith 1973), the Beaufort Sea and Amundsen Gulf (Smith 1987), and Hudson Bay (Holst *et al.* 1999), as well as other locations in the Arctic, including Bothnian Bay (Helle 1974), the Sea of Okhotsk (Fedoseev 1965), and Svalbard (Lydersen and Gjertz 1987). In contrast, Teilmann and Kapel (1998) suggested that ringed seals in western Greenland may have a skewed sex ratio or, alternatively, that there may be differences in geographical distribution or behaviour between the sexes. However, skewed sex ratios have not been demonstrated in other studies, which makes it uncertain if the reported difference resulted from biological causes or possibly an unknown sampling bias.

2.4.2. Age distribution

In the sample from Grise Fiord, adult female ringed seals were significantly older than their male counterparts, as were adult females from Qaanaaq, although not significantly so. Similarly, in studies of ringed seals from other areas, the mean age of adult females in a population has generally been found to be greater than that of adult males (Helle 1974, 1979; Lydersen and Gjertz 1987). Male pinnipeds have shorter life spans than females, especially those species in which the degree of polygyny is most developed, because the adult age classes of males have higher mortality rates (e.g., Le Boeuf 1974, 1981; Le Boeuf and Reiter 1988). High mortality rates in males are most likely a consequence of increased intrasexual aggression resulting from competition for territories and access to breeding females (e.g., Le Boeuf 1971; Sandegren 1976; McCann 1980, 1981; Smith 1987; Le Boeuf and Reiter 1988). Male ringed seals, which maintain underwater territories around self-maintained breathing holes (Stirling 1973, 1977), are slightly polygynous (Stirling 1983) and thus males might be expected to have shorter longevity than females.

A low proportion of YOY in the samples of ringed seals from Qaanaaq and Grise Fiord was expected, since YOY are generally less available to sampling during late spring when older animals are molting on the landfast ice. Until about mid May, some pups may still be using subnivean lairs where they are less visible and thus less vulnerable to hunters. After that time, most pups are weaned and molted and spend less time on the ice than adults because they spend more time in the water feeding (Smith 1973). Thus, the low proportion of YOY in the spring sample from Qaanaaq is consistent with results obtained in other studies (e.g., Smith 1973, Lydersen and Gjertz 1987). However, the proportion of YOY in the Grise Fiord sample was higher than expected. This discrepancy may be at least partially explained by differences in the landfast ice habitat, where most of the sampling took place in each area. At Qaanaaq, seals were taken mainly in the breeding habitat in the landfast ice, although some were taken further out toward the floe edge where pupping occurs less frequently (Fig. 2-1). In comparison, hunters from Grise Fiord hunted further from the floe edge in Jones Sound and more in fiords on southern Ellesmere Island, where pupping was likely more prevalent, making pups more vulnerable to being sampled, even though they may have been spending a greater proportion of their time in the water at that time (Fig. 2-1).

The Grise Fiord sample had a significantly lower proportion (9%) of subadults (ages 1 to 5 years) than did the sample from Qaanaaq, which is also typical for spring samples taken on landfast ice (e.g., McLaren 1958a; Smith 1973, 1987; Smith and Stirling 1975). Several factors may have contributed to the under-sampling of subadults in Grise Fiord. The preferred habitat of mature ringed seals during spring is the stable landfast ice, where individual seals maintain territories around their breathing holes. There, adult females give birth to their pups in subnivean lairs and mating takes place in the water where adult males defend underwater territories (Stirling 1973, 1977), while subadults tend to be excluded to unstable moving ice areas further offshore where they are encountered less frequently by hunters focusing their efforts in the landfast ice (McLaren 1958a; Smith 1973, 1987; Smith and Stirling 1975).

As with the difference in proportions of pups in the samples from the two areas, the difference in the proportions of subadults is also likely related to relatively small, but important differences in the habitat in which the two samples were taken. There are likely to be fewer subadults present in habitat sampled farther from the floe edge, such as in Grise Fiord (Fig. 2-1), than in habitats that are sampled closer to the floe edge, like Qaanaaq (Figs 2-1). However, it is also possible that there may be an influx of subadults from other areas toward Qaanaaq, especially to the areas fringing on the landfast ice, where productivity is thought to be higher (Lewis *et al.* 1996). Subadult ringed seals have been reported to travel long distances in Baffin Bay and to cross the North Water Polynya (Heide-Jørgensen *et al.* 1992, Kapel *et al.* 1998, Teilmann *et al.* 1999).

It has also been suggested that high hunting pressure may depress the mean age of a ringed seal population (Fedoseev 1965, Lydersen and Gjertz 1987), leading to a greater proportion of subadults in the harvest. In the present study, 56% of seals collected at Qaanaaq were subadults, which is similar to the proportion of subadults sampled in the Sea of Okhotsk (Fedoseev 1965) and in western Greenland (Teilmann and Kapel 1998). However, it is unlikely that hunting pressures caused the differences in the proportion of subadults at Qaanaaq and Grise Fiord, since hunting pressure appears similar in both areas. Currently, for the municipality of Avanersuaq in north Greenland (including the town of Qaanaaq), an estimated 4000 ringed seals are harvested annually (Teilmann and Kapel 1998), whereas the estimated annual catch for Grise Fiord is less than 1000 (Finley and Miller 1980, Stewart *et. al* 1986), from a population in Baffin Bay that has been variously estimated at about half a million (Stirling and Øritsland 1995) to one million seals (McLaren 1958b, Finley *et al.* 1983, Kingsley 1990).

2.4.3. Sex-specific comparison of growth

Adult male ringed seals collected at Grise Fiord and Qaanaaq were similar in length to adult females, as was also reported for ringed seals in Svalbard (Lydersen and Gjertz 1987), and there were no significant differences in the mean weights of males and females collected at either location. In contrast, to the south in Davis Strait, Smith (1973) reported that males were significantly larger than females and Goodyear (1999) showed that males from Baffin Bay reached a greater asymptotic length than females. At Point Hope, Alaska, Johnson *et al.* (1966) found that males were heavier than females between November and May, but females were heavier than males in June. In Svalbard, females collected between March and July were significantly heavier than males (Lydersen and Gjertz 1987). Females may be heavier than males during the spring, because of different sexual behaviour associated with mating and pupping (Lydersen and Gjertz 1987). During the mating season, males are thought to become more aggressive while defending territories (Stirling 1973, 1977; Smith 1987) which may cause them to spend more energy than females suckling their young (Lydersen and Gjertz 1987). Marked sexual dimorphism is characteristic of highly polygynous pinnipeds, such as elephant seals (*Mirounga* spp.) and the otariid seals (see Riedman 1990 for review). However, ringed seals are only slightly polygynous (Stirling 1983) and hence show little or no dimorphism. Thus, large differences in length or weight between the sexes are not expected.

2.4.4. Regional differences in growth

The von Bertalanffy equation provided the best fit for the two ringed seal samples. However, as seen in Fig. 2-2 and above, the age distributions for the two samples were different, which could have affected the shape of the curves. Nonetheless, even though some of the age groups had small sample sizes, there were at least several animals represented in every age group. Thus, the shape of the curve should not have been affected significantly by the differences in age distribution. The l_o and k_o values for the von Bertalanffy equations should be considered relative rather than 'real' values, since not all YOY in the samples were newborns. In ringed seal populations, pupping occurs over the course of several weeks, with most births occurring within a 1 month period (Smith 1973, 1987). Thus, length measurements on YOY were made at variable, but unknown lengths of time after birth, and some could have been made up to several weeks after birth. During this study, YOY were collected between May and July, when pups were approximately between 3 to 16 weeks old. Ringed seals are approximately 65 cm in length at birth and reach a mean length of 88 cm at weaning, 36 - 41 days later (McLaren 1958a, Hammill *et al.* 1991). The absolute rate of growth at birth, k_o, will thus also vary accordingly. However, since YOY from either side of the polynya were collected during the same period, it is possible to use the growth curve parameters as relative values and to compare them between the two samples.

Ringed seals show considerable variation in adult length between populations throughout their circumpolar range (e.g., McLaren 1958a, 1993; Fedoseev 1965;

Fedoseev and Nazerenko 1970; Smith 1973, 1987; Helle 1979; Finley *et al.* 1983; Lydersen and Gjertz 1987; Goodyear 1999). Ringed seals from Grise Fiord were similar in size to other seal populations from the Canadian northeastern Arctic (McLaren 1958a, 1993; Finley *et al.* 1983; Goodyear 1999). However, adult ringed seals from Qaanaaq were shorter than those from Grise Fiord, but were comparable in size to those from Svalbard (Lydersen and Gjertz 1987), the Beaufort Sea and Amundsen Gulf (Smith 1987), southeastern Baffin Bay (McLaren 1958a, 1993; Smith 1973; Goodyear 1999), and the pack ice of Baffin Bay (Finley *et al.* 1983). Correspondingly, the growth curves showed that pups sampled at Qaanaaq were also smaller than those at Grise Fiord.

Several hypotheses may be invoked to explain differences in size between populations of ringed seals, including genetic variation, Bergmann's rule, stability of breeding habitat, density-dependent effects that might come into play as a result of differential levels of harvesting, and differences in food availability. Finley *et al.* (1983) speculated that differences in size between landfast ice and pack ice seals may be due to genetic differences, but demonstrated none. Similarly, from samples collected during this study, preliminary analyses indicate that ringed seals from Qaanaaq and Grise Fiord appear to be genetically similar (Davis *et al.* 1999), suggesting that at least some interbreeding occurs between ringed seals from either side of the polynya. Therefore any differences in size are likely the result of environmental factors.

Bergmann's rule (Bergmann 1847) states that body size within a species increases with latitude in association with a decrease in the environmental temperature. In this case, both populations exist at similar latitudes, so Bergmann's rule does not apply. McLaren (1958a) and Pastukhov (1969) suggested that differences in adult ringed seal sizes occur because of variation in the stability of ice conditions in the pupping habitat, i.e., pups born in more stable ice areas were likely to be nursed longer than those in less stable habitat and thus would be larger at weaning. For example, longer weaning periods in northern elephant seals (*Mirounga angustirostris*) were shown to result in larger pups (Reiter *et al.* 1978).

In general, coastal areas are more stable than drifting pack ice and thus are thought to be better habitat for pupping (McLaren 1958a). Finley *et al.* (1983) and Fedoseev

(1975) found seals from drift or pack ice to be smaller than seals from coastal landfast ice, and Smith (1973) concluded that differences in size between adult seals from southeastern Baffin Island were due to differences in ice stability. Ice conditions may partially explain size differences between my samples from ringed seal populations from the east and the west sides of the polynya. Although ringed seals collected in both Qaanaaq and Grise Fiord were harvested in generally similar landfast ice areas (see Fig. 2-1), Qaanaaq is situated more directly within the North Water Polynya, whereas Grise Fiord is situated in northern Jones Sound, just outside of the polynya. In 1998, the landfast ice break-up in the Qaanaaq collection area occurred on approximately May 26, 1998 (Fig. 2-4), whereas break-up in the Grise Fiord collection area appeared to have occurred around June 4, 1998 (Fig. 2-4). Therefore, most pups sampled in Grise Fiord should have been weaned at the time of the collection. Sampling around Qaanaaq started in early May and therefore, some of the pups may not have been weaned at this time, although only 1 pup was taken during May; thus, all other pups sampled should have been weaned at the time of the collection. If early break-up in the Qaanaaq area does indeed lead to a shorter suckling period, it remains uncertain whether ice condition would cause the significant difference in seal size observed, or whether other factors may also affect seal growth in the area.

Goodyear (1999) concluded that variation in stability of sea ice pupping habitat did not adequately explain differences in seal lengths for populations in the northeastern Canadian Arctic. He proposed that predation pressure from bears and hunters and availability of food resources have a greater effect on the growth of ringed seals than ice condition. An increase in hunting pressure would stimulate increased growth in order to attain sexual maturity earlier (e.g., Laws 1953, 1956a; Carrick *et al.* 1962; Capstick and Ronald 1982; Sjare *et al.* 1996). Since the predation pressures are similar between the Grise Fiord and Qaanaaq populations, other factors such as food availability and the quality of the prey are more likely to determine growth in these populations. Nutrition is thought to be the most important factor affecting the shape of growth curves, with improved nutrition leading to more rapid growth rates (Laws 1956b). By way of comparison, in Scottish red deer (*Cervus elaphus*), poor nutrition was shown to retard growth, leading to smaller sizes (Suttie and Hamilton 1983).

Preliminary data from the NOW study indicate that differences in food availability may exist between the areas around Grise Fiord and Qaanaaq. In May, chlorophyll *a* concentrations as well as primary productivity were higher on the east side than on the west side of the polynya, which corresponds to the earlier bloom on that side of the polynya (Appendix B) (L. Legendre, unpublished data). In June, high chlorophyll *a* levels were found throughout the polynya and in July, chlorophyll *a* levels were generally higher on the west side, most likely because nutrients had not been depleted there yet. Similar to the preliminary data from the NOW, Lewis *et al.* (1996) also demonstrated an increase in phytoplankton biomass on the east side of the North Water Polynya in May. Although productivity may not be higher on the east side of the polynya throughout the entire season, the early bloom on the east side in May could lead to increased food availability early in the season. Preliminary analyses of zooplankton abundance in the polynya show that densities were similar and relatively high around both collection areas near Qaanaaq and Grise Fiord (Appendix C) (L. Fortier, unpublished data). However, there were two areas in the southeast of the polynya, close to the Qaanaaq collection area, that had the highest concentrations of zooplankton (> 400 animals/m^3). Thus, ringed seals sampled near Qaanaaq may have access to an increased food supply and may thus have faster growth rates. Faster growth rates could also be due to increased consumption of prey with higher energy content, such as Arctic cod (*Boreogadus saida*). In Chapter 3, I show that the diet of ringed seals collected in Qaanaaq consisted mostly of cod, especially Arctic cod, whereas the diet of ringed seals collected in Grise Fiord consisted of Arctic cod, polar cod (*Arctogadus glacialis*), as well as other prey items, such as amphipods, with lower energy content.

Ringed seals from Svalbard, a highly productive area, have also been shown to have high growth rates (Lydersen and Gjertz 1987), as have seals from Arctic Bay, although data on productivity are not available for that area (Goodyear 1999). However, even though ringed seal populations from Svalbard, Arctic Bay, and Qaanaaq had higher growth rates than those from other areas, they did not attain higher asymptotic lengths when compared to slower growing populations (see review by McLaren 1993). It is not apparent why ringed seal populations with high growth rates do not reach greater asymptotic lengths.

2.4.5. Sexual maturity

Age of sexual maturity varies among species of pinnipeds, in both time and space. Factors that have been proposed to affect the onset of sexual maturity are density dependent factors and overall ecosystem productivity. Age of sexual maturity of seals has been linked to a density-dependent response, decreasing during periods of low population size in Atlantic harp seals, *Phoca groenlandica* (Capstick and Ronald 1982, Sjare *et al.* 1996) and southern elephant seals, *Mirounga leonina* (Laws 1953, 1956a; Carrick *et al.* 1962). When the population size is low, competition for food resources and space are reduced so that younger animals are more successful and, consequently, the age of sexual maturity tends to decrease. However, when population size is high, resources and breeding space may be limited, reproductive opportunities for younger animals may not exist, and the age of sexual maturity increases.

In female ringed seals of different geographic regions, the age of sexual maturity varies greatly (Table 2-3), ranging from 4.4 years in Svalbard (Lydersen and Gjertz 1987), to 5.9 years in Foxe Basin (McLaren 1958a), and as high as 7.0 years in Cumberland Sound, Baffin Bay (Smith 1973). The data on growth rates and size from Grise Fiord are similar to those from surrounding areas in the Canadian northeastern Arctic (McLaren 1958a, 1993), suggesting that age of sexual maturity is likely similar as well. The relatively higher growth rates for ringed seals from Qaanaaq is consistent with achieving sexual maturity at an earlier age than those from Grise Fiord, as noted by Laws (1956b). Ringed seals from Qaanaaq reached sexual maturity earlier than those from all other areas in the Arctic, except for Svalbard (Lydersen and Gjertz 1987). It is unlikely that density-dependent factors reduced the age of sexual maturity, since ringed seals are thought to be numerous in that area and hunting pressures are low.

Laws (1956b) suggested that nutrition was likely the most important factor that caused early sexual maturation, by increasing growth rates, whereas a decrease in food availability would lead to delayed sexual maturation (Eberhardt 1977). In the Antarctic, increased prey abundance was suspected to cause a decrease in age of sexual maturity in crabeater seals, *Lobodon carcinophagus* (Laws 1977, Bengtson and Siniff 1981, Bengtson and Laws 1985). Similarly, in Svalbard, Lydersen and Gjertz (1987) suggested that early sexual maturation of ringed seals could be explained by the abundance of food in that area. Thus, in Qaanaaq, the hypothesized increase in food availability on the east side of the polynya (see section above), may explain early sexual maturation in ringed seals.

It has been suggested that early maturing female pinnipeds may have shorter life spans than those that reach sexual maturity later (Laws 1959, Reiter 1984). Stewart (1983) found that young harp seal females invested more energy in raising their pup than did older females, although it is not known whether this resulted in a reduced life span. In this study, it appeared that females from Qaanaaq matured earlier than those from Grise Fiord and adult females were, on average, younger than those at Grise Fiord, even though the difference was not significant (Table 2-1). In addition, the oldest female from Grise Fiord was 43 years whereas at Qaanaaq, the oldest female was 38 years.

2.4.6. Regional differences in condition and reproduction

Ringed seals follow an annual cycle, in which they reach a maximum weight and blubber thickness during early winter, and a minimum in late spring and early summer after mating and molting (McLaren 1958a, Johnson *et al.* 1966, Frost and Lowry 1981, Smith 1987). In this study, ringed seals were taken in late spring, when body weights and condition are expected to decline. However, the samples from the two areas were taken at a similar time, so that differences resulting from seasonal variation should be minimal. The most likely reason the seals from Grise Fiord were heavier than those from Qaanaaq, is because overall, their lengths were greater. The seasonal mean weights for seals collected in Grise Fiord are similar to those of ringed seals collected at a similar time near Pond Inlet, northern Baffin Island (Finley *et al.* 1983) and those of Qaanaaq are comparable to mean weights of seals sampled at Svalbard (Lydersen and Gjertz 1987). The mean blubber thickness of ringed seals collected near both Grise Fiord and Qaanaaq was similar to the blubber thickness of seals collected in the same season in the Barents Sea (Wathne 1997) and southeastern Baffin Island (Goodyear 1999).

The reproductive status of female ringed seals has been shown to be affected by their condition, with a decrease in reproductive rates when body condition is low (e.g., Smith 1987, Kingsley and Byers 1998). Even though adult females from Grise Fiord had less blubber than those from Qaanaaq, females from both locations were likely in good condition, since both had high ovulation and pregnancy rates. However, it is unknown what percentage of pregnancies were successful. Thus, it is possible that even though females from Grise Fiord had high ovulation and pregnancy rates, they may have had lower reproductive rates because they stored less fat. Nonetheless, the mean condition of YOY from Grise Fiord was generally higher than that for YOY collected in Qaanaaq. Several studies have shown that larger female pinnipeds produce larger pups, as seen with southern elephant seals (e.g., McCann *et al.* 1989; Campagna *et al.* 1992; Arnbom *et. al.* 1993, 1994, 1997; Fedak *et al.* 1996), grey seals, *Halichoerus grypus* (e.g., Iverson *et al.* 1993) and other phocids, otariids, and walruses (e.g., Kovacs and Lavigne 1986, 1992). Thus, pups produced by larger females in Grise Fiord may be in better condition than those produced by smaller females in Qaanaaaq. Even though the mean condition of YOY from Qaanaaq was generally lower than that for YOY from Grise Fiord, this observation is consistent with the smaller size of the adult females. However, the sample sizes were too small to allow for meaningful statistical tests.

2.5. Conclusions

The major differences between ringed seals inhabiting the east and west sides of the North Water Polynya were in growth rates, age of sexual maturity, and total body lengths. Seals on the east side of the polynya had faster growth rates and appeared to attain sexual maturity earlier, but had shorter lengths than seals on the west side of the polynya. These differences may have been caused by a combination of factors. Whereas factors such as genetic variation and hunting pressure probably have little effect on ringed seal growth in the two areas, ice stability and food availability likely have an additive effect on growth rates. The timing of the break-up of the landfast ice may have caused differences between ringed seals from either side of the polynya, at least between the areas where the samples were taken, since seals may have been weaned earlier on the east side then on the west side, due to the earlier break-up. As well, food availability may have been greater on the east side of the polynya, if the hypothesized differences in biological productivity between the east and west sides of the polynya are correct.

Although differences in growth were observed, ringed seals on both sides of the polynya appeared to be in similar condition and had high but similar ovulation and pregnancy rates, despite the hypothesized differences in biological productivity and food availability between the two areas. Since polynyas are considered to be more productive than surrounding non-polynya areas, an increase in biological productivity within the polynya may have a limited effect on the biology of ringed seals on either the east or west sides, since an adequate food supply is most likely available throughout the entire polynya.

2.6. Literature cited

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Table 2-1: Comparison between ringed seal populations on the east and west sides of the North Water Polynya (means ± standard deviation; numbers in brackets are sample sizes; M = males, F = females; adults ≥ 6 years).

Comparison	**Grise Fiord**	**Qaanaaq**	**Significance**
Sex ratio	43M:56F	55M:45F	No
Age of adults (yrs.)			No
Males	19.4 ± 9.4 (27)	15.6 ± 10.3 (22)	
Females	27.1 ± 8.4 (31)	21.4 ± 11.4 (14)	
Length of adults (cm)			Yes
Males	136.3 ± 14.3 (25)	129.3 ± 15.7 (22)	
Females	136.0 ± 13.5 (29)	125.6 ± 11.4 (14)	
Girth of adults (cm)			No
Males	107.0 ± 13.9 (25)	102.5 ± 12.7 (21)	
Females	101.9 ± 17.2 (29)	99.2 ± 13.7 (13)	
Weight of adults (kg)			Yes
Males	75.8 ± 24.5 (25)	62.7 ± 11.3 (22)	
Females	75.2 ± 22.3 (29)	56.3 ± 12.7 (14)	
Blubber thickness (cm fat)			
YOY	4.4 ± 1.1 (30)	2.4 ± 1.5 (7)	
Males ≥ 1 year old	4.3 ± 1.2 (24)	4.2 ± 0.7 (17)	No
Females ≥ 1 year old	3.7 ± 1.2 (35)	4.4 ± 1.2 (16)	Yes
Age of sexual maturity (yrs.)	N/A	4.70	
Ovulation rate	100% (25)	93% (14)	No
Pregnancy rate	80% (25)	77% (13)	No

Table 2-2: Parameter estimates (±SE) and R^2 values for the von Bertalanffy growth curves for ringed seals collected around Qaanaaq and Grise Fiord. L_∞ = asymptotic length (cm), k_0 = absolute growth rate at birth (cm/year), and l_0 = length at birth (cm).

Sample	**Sample size**	**L_∞**	**k_0**	**l_0**	**R^2**
Grise Fiord	89	137.50 ±1.99	9.60 ± 2.43	94.53 ± 2.28	0.72
Qaanaaq	98	128.23 ± 1.97	26.94 ± 6.14	81.15 ± 4.16	0.58

Table 2-3: Age-specific ovulation rates of female ringed seals aged 3 - 10 years from selected areas of the Arctic and the age of sexual maturity.

Location	% Ovulating in age class								Age of sexual maturity	Data Source
	3	4	5	6	7	8	9	10		
Northwestern Hudson Bay	17	29	33	57	100	100	100	100	5.64	Holst *et al.* 1999
Foxe Basin, Hudson Strait	0	12	22	78	100	100	100	100	5.88	McLaren 1958
Cumberland Sound, Baffin Bay		13	20	12	58	92	100	100	7.05	Smith 1973
Hoare Bay, Davis Strait		40	33	80	100	75	100	100	5.72	Smith 1973
Ellesmere Island and Northwest Baffin Island		22	53	72	81	98			ca. 5.74	Miller and Finley 1982
Grise Fiord, Southern Ellesmere Island	0	0					100			This study
Qaanaaq, northwestern Greenland	0	29	100	100	100	100	100		4.71	This study
Point Hope, Alaska	0	8	60	55	93	100	100	100	5.84	Johnson *et al.* 1966
Amundsen Gulf and Southestern Beaufort Sea	0	25	53	61	100	100	100	100	5.61	Smith 1987
Svalbard	20	60	80	100	100	100	100	100	4.40	Lydersen and Gjertz 1987

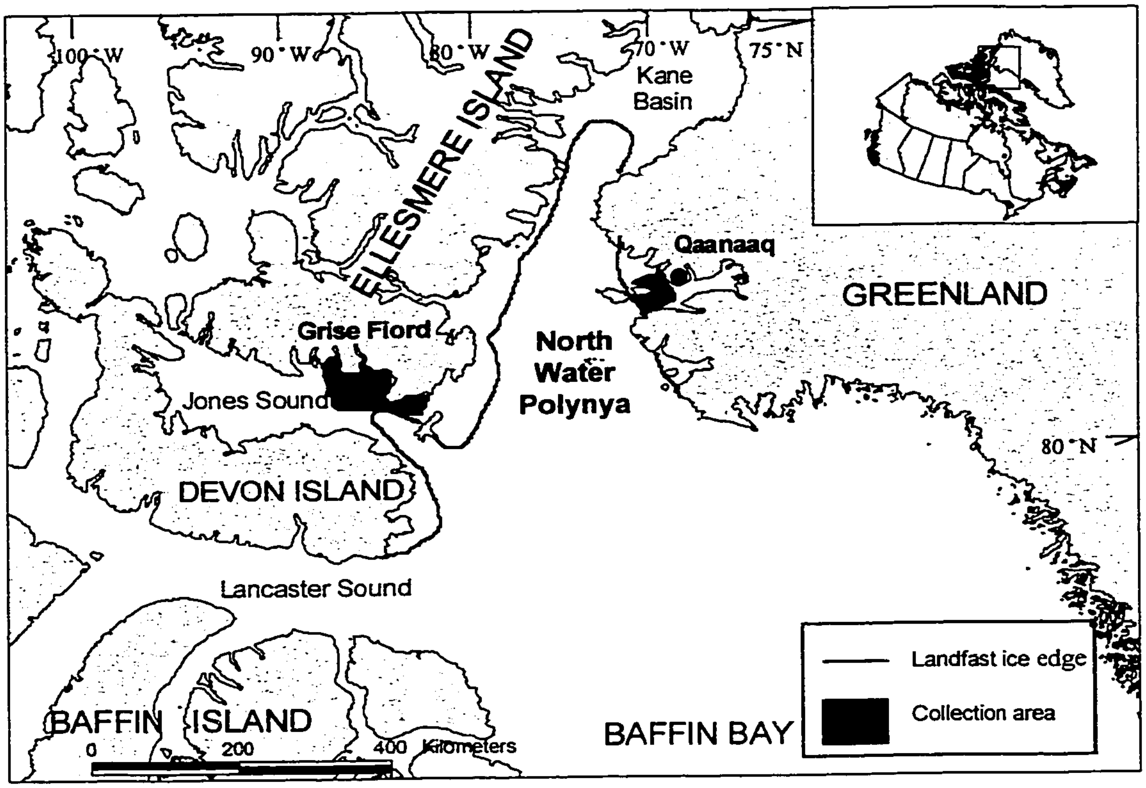
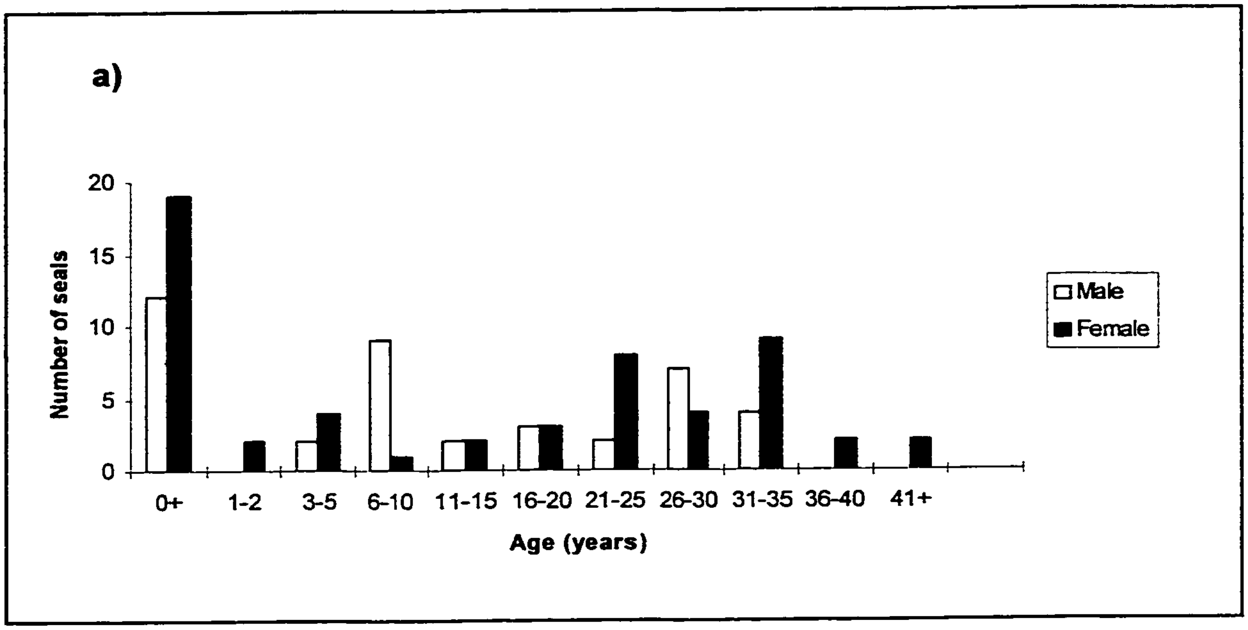


Figure 2-1: Ringed seal collection sites in the North Water Polynya in 1998.



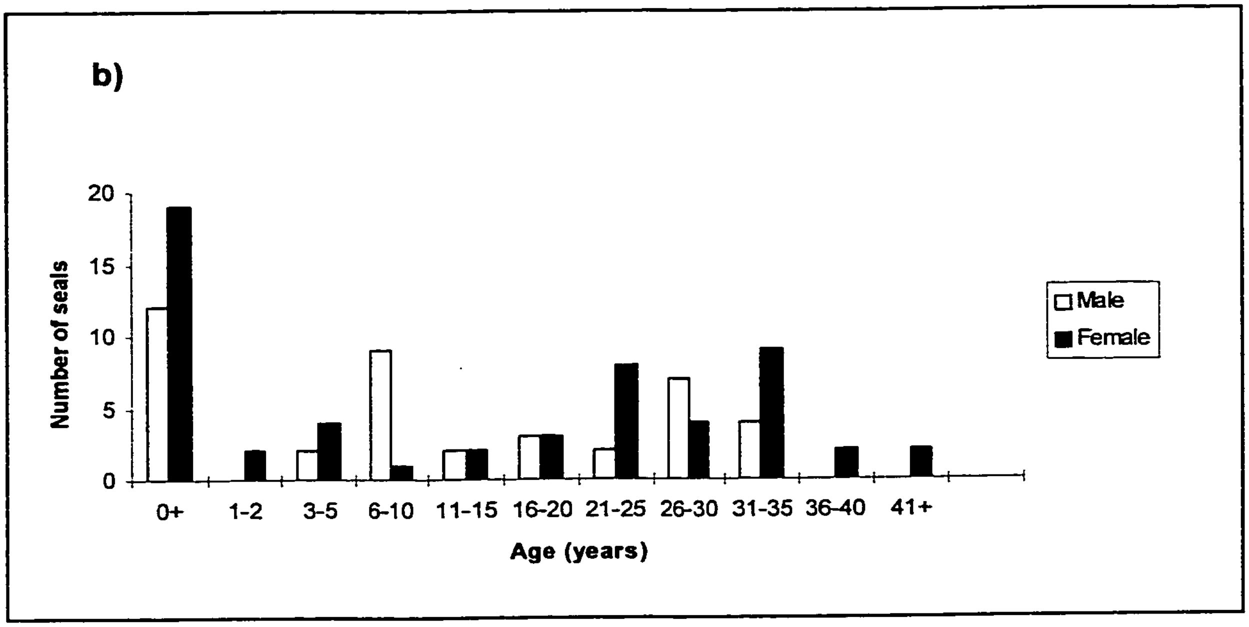


Figure 2-2: Age distributions of a) male (n = 41) and female (n = 56) ringed seals collected in Grise Fiord and b) male (n = 55) and female (n = 43) ringed seals collected in Qaanaaq between May - July, 1998.

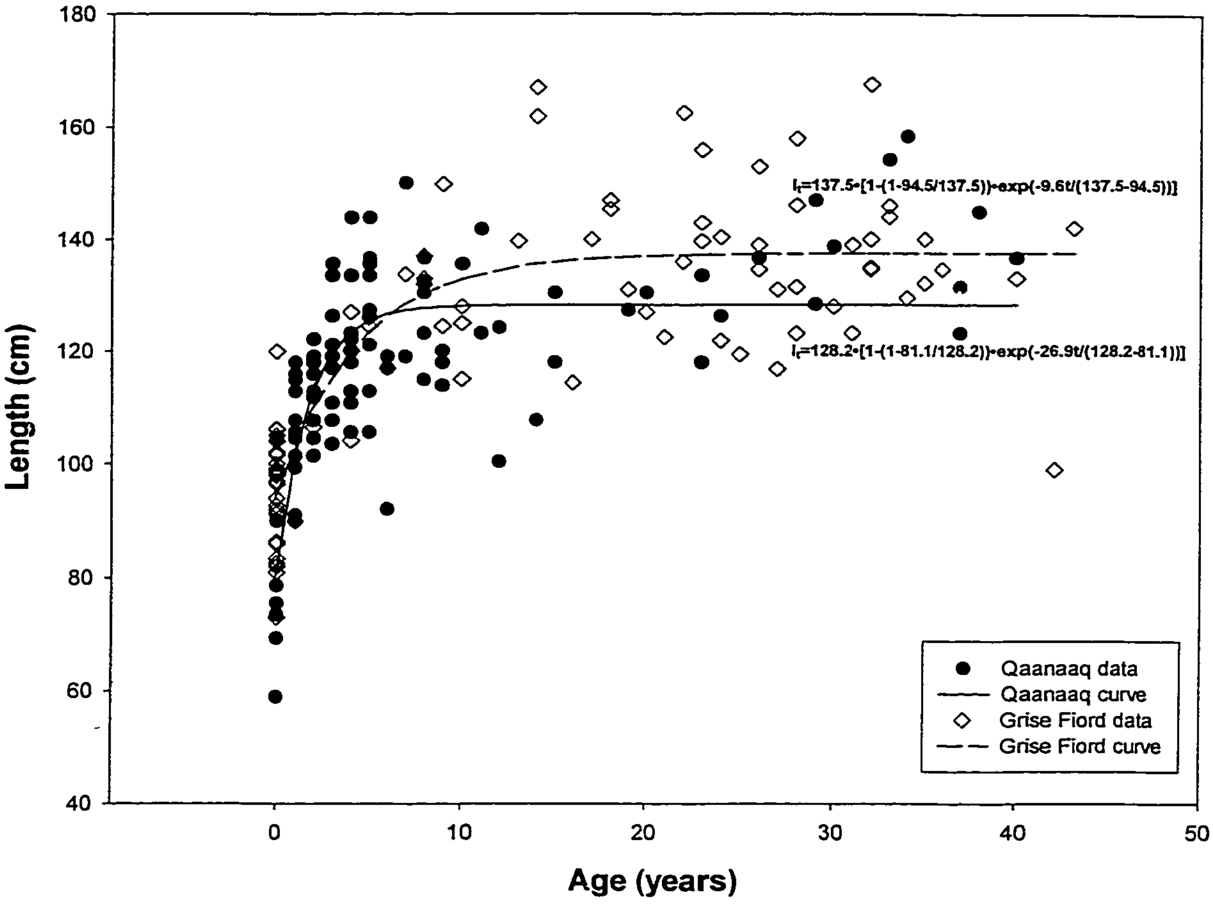


Figure 2-3: Von Bertalanffy growth curves for ringed seals collected around Grise Fiord, Canada and Qaanaaq, Greenland.

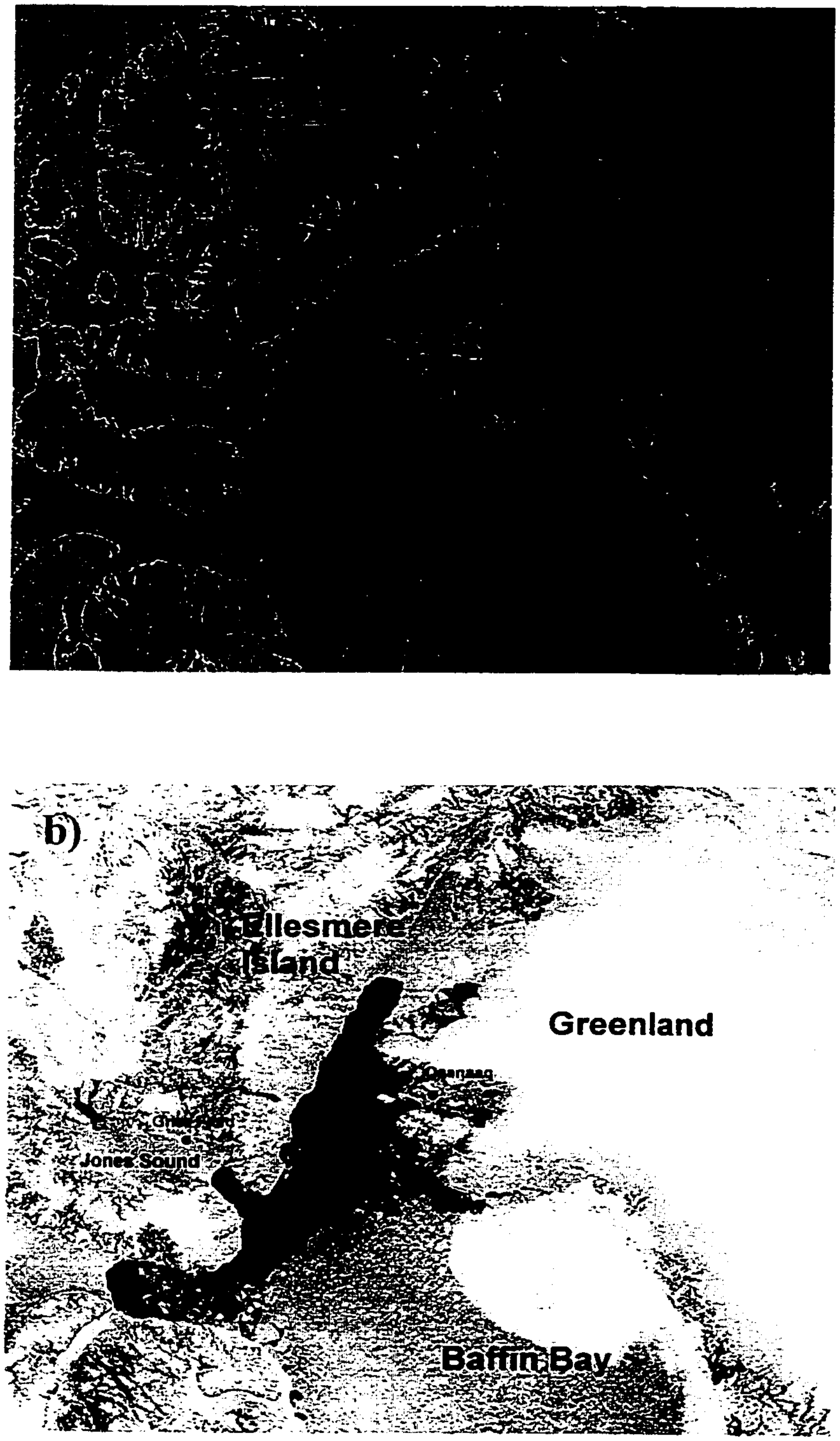


Figure 2-4: Satellite images of the North Water Polynya on a) May 26, 1998 and b) June 4, 1998.

3. RINGED SEAL FEEDING ECOLOGY ON THE EAST AND WEST SIDES OF THE NORTH WATER POLYNYA

3.1. Introduction

The North Water Polynya is an important feeding area for several species of arctic marine mammals and birds, including the ringed seal *(Phoca hispida)* (Stirling 1980, 1997; Stirling *et al.* 1981). Ringed seals are generally considered to be opportunistic feeders (McLaren 1958, Fedoseev 1965, Johnson *et al.* 1966, Lowry *et al.* 1978, Weslawski *et al.* 1994), consuming a wide variety of amphipods, euphausiids, mysids, shrimp and other benthic invertebrates, as well as cephalopods, and fish. The ringed seal diet in a given area usually consists of no more than 10 - 15 prey species (Weslawski *et al.* 1994), although up to 40 were reported by McLaren (1958) for Ungava Bay. Two to four species typically predominate most of the ringed seal diet (Fedoseev 1965, Lowry *et al.* 1980, Bradstreet and Cross 1982, Smith 1987). The most common prey taxa in the diet of ringed seals are Arctic cod (*Boreogadus saida*) and pelagic amphipods, such as the hyperiid amphipod *Themisto libellula*, and shrimp are the most important benthic taxon (Weslawski *et al.* 1994).

The feeding habits of ringed seals in the North Water Polynya may be influenced by differences in heat sources within the polynya that are hypothesized to contribute to variation in timing and development of phytoplankton blooms and food webs on the east and west sides of the polynya (see Chapter 1). The east side of the polynya is thought to be more productive, since an earlier phytoplankton bloom may fuel an increase in secondary production of zooplankton, followed by an increase in fish production. Consequently, plankton and fish biomass are likely higher on the east side, especially early in the season.

The food webs are also thought to differ between the east and west sides of the North Water Polynya due to the hypothesized differences in heat sources. The number of trophic levels varies between different kinds of marine communities, and those with the shortest food chains are expected to produce the greatest fish biomass (Ryther 1969). Ryther (1969) suggested that communities in which nutrients are recycled through the microbial web rather than upwelled, as on the west side of the polynya, have food chains with 3 to 5 trophic levels. In these communities, only small phytoplankton can grow; these are eaten by small zooplankton, followed by large zooplankton, planktivores, and piscivores. Thus, the conversion of organic matter from small plant cells to higher consumers takes more trophic levels (Ryther 1969). In comparison, a community where nutrient upwelling occurs, as proposed on the east side of the polynya, is thought to have fewer than 3 trophic levels (Ryther 1969). Larger phytoplankton, such as diatoms, are able to grow because of increased nutrient availability, and these may be eaten directly by planktivores (e.g., fish) or larger zooplankton followed by planktivores.

To determine whether any variation in overall productivity and food webs on either side of the polynya are reflected in the higher trophic levels, I compared the feeding ecology of ringed seals on the east and west sides of the polynya. Because I expected increased productivity, leading to increased food availability and fish biomass on the east side of the polynya, I predicted that ringed seals from Qaanaaq, on the east side of the North Water Polynya, would feed trophically lower (i.e., food chains would be shorter on that side) and on a greater proportion of fish than seals on the west side of the polynya.

3.2. Methods

Comparisons of ringed seal feeding ecology were based on samples collected by Inuit hunters on the west (Grise Fiord ⇒ 76°12 N, 83°06 W) and east sides (Qaanaaq ⇒ 77°40 N, 69°00 W) of the North Water Polynya (see Fig. 2-1). From 27 May through 28 June, 1998, samples were collected from 99 ringed seals taken at Grise Fiord, Nunavut, and from 9 May through 11 July, 1998, 100 ringed seals were collected near Qaanaaq, Greenland. The majority of the seals were taken on landfast ice in near shore areas. The date of collection and sex of each seal were recorded. Stomachs, jaws, and muscle tissue were frozen in the field and shipped by air to Edmonton for analysis.

Seal ages were determined using cementum growth layer groups in canine teeth from the lower jaw (Stewart *et al.* 1996). Muscle tissue from 97 seals collected in Qaanaaq and 94 seals collected in Grise Fiord were analyzed for stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) (Hobson *et al.*, in prep.). Stable carbon isotope ratios can reflect input of dietary resources from different areas, such as pelagic *vs.* benthic or inshore *vs.* offshore (e.g., McConnaughey and McRoy 1979, Rau *et al.* 1983, Dunton *et al.* 1989, Hobson 1993), whereas stable nitrogen isotope ratios allow for the determination of trophic relationships (Hobson *et al.* 1994). The trophic levels for ringed seals from each location were determined relative to a primary herbivore, the copepod *Calanus hyperboreus*, using the following formula (Hobson *et al.*, in prep.):

$$\text{Trophic level} = 2 + (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{copepod}})/3.8$$

where: 2 is the trophic level occupied by *Calanus hyperboreus*

$\delta^{15}N_{\text{consumer}}$ is the stable nitrogen isotope value for the seal (in $^{o}/_{oo}$)

$\delta^{15}N_{\text{copepod}}$ is the stable carbon isotope value for *Calanus hyperboreus* (in $^{o}/_{oo}$)

3.8 is the isotopic enrichment between trophic levels (in $^{o}/_{oo}$)

Stomachs were thawed in the laboratory. The stomach contents were weighed, washed onto a series of 1 mm and 0.5 mm sieves and weighed again. The contents were preserved in 70% isopropyl alcohol before further analysis. Stomach contents were sorted into fish and invertebrate remains. Fish otoliths were used to identify fish prey remains using several keys (Frost 1981, Finley and Gibb 1982, Härkönen 1986). The number of fish eaten was estimated by dividing the total number of otoliths in half, since there are two sagittal otoliths per fish skull. Otolith lengths were measured along the longest axis using vernier callipers, and regression equations were used to estimate the length and weight of the ingested fish (Finley and Gibb 1982, Härkönen 1986). Since no regression equations were available for Arctic staghorn sculpin, *Gymnocanthus tricuspis*, the equation for four-horn sculpin, *Myoxocephalus quadricornis*, was used since the otolith to fish length ratios are similar for the two fish (Härkönen 1986). Regression equations for the gelatinous snailfish, *Liparis koefoedi*, were determined from specimens obtained in the area. The relationship between otolith length in mm (OL) and total fish length in mm (FL) is $FL = 5.62*OL - 0.29$ and the relationship between otolith length in mm (OL) and fish weight in grams (FW) is $FW = 0.70*OL^{4.394}$ (L. Fortier, pers. comm.).

The mean otolith lengths, fish lengths, and weights, as well as size ranges were calculated for fish taken by ringed seals in Grise Fiord and Qaaanaaq.

Crustaceans were identified using several reference keys (Sars 1895, Dunbar 1954, Kathman *et al.* 1986, Keast and Lawrence 1990, Klekowksi and Weslawski 1990, Squires 1990). Counts of identifiable heads or telsons were made and added to whole individual counts to estimate the total number of specimens ingested. The weight of crustaceans was determined by measuring or calculating total length from telson length (Finley and Gibb 1982, Bradstreet and Finley 1983) and then calculating the weight from known length-weight relationships (Finley and Gibb 1982, Bradstreet and Finley 1983, Berestovskij *et al.* 1989). Where large numbers of crustaceans occurred in a sample (i.e., > 50), a subsample of 25 were measured. No equations were available for the amphipod *Atylus carinatus*, so individuals were weighed, and regression equations for calculating total length from telson length and weight from total length were determined (Appendix D). Although only intact *Atylus* specimens were used for determining the regression equations, the weights were post-ingestion weights and are most likely lower than pre-ingestion weights.

Cephalopod beaks were identified using reference keys (Clark 1962, 1986; Akimushkin 1965). The number of cephalopods eaten was estimated by the number of dorsal mandibles in the sample. Most mandibles were paired, although there was one unpaired dorsal mandible. Beak lengths were measured and used to derive prey weight (Clark 1962).

As well as determining the numbers of prey items, several feeding indices were calculated to obtain the most accurate picture of the ringed seal diet. Stomachs that contained only unidentifiable contents were not included in these analyses.

1) The frequency of occurrence (FO_i) of each food category i:

   $FO_i = (f_i/f_t) * 100$ where f_i is the number of stomachs containing prey species i and f_t is the total number of stomachs containing food.

2) The relative frequency of occurrence by number (N_i) of each food category i in all of

the stomachs containing food:

$N_i = (n_i/n_t)*100$ where n_i is the number of individuals of species *i* and n_t is the total number of all prey species.

3) The relative frequency of occurrence by biomass (B_i) of each food category *i* in all of the stomachs containing food:

   $B_i = (b_i/b_t)*100$ where b_i is the total estimated fresh mass of prey category *i* in all seals and b_t is the total estimated mass of all prey categories.

4) The index of relative importance (IRI_i) of each food category *i*:

   $IRI_i = (N_i + B_i) * FO_i$.

5) The percent index of relative importance ($\%IRI_i$) of each food category *i* as proposed by Cortés (1997):

   $\%IRI_i = 100 * IRI_i / IRI_t$ where IRI_t it the sum of all food categories.

The index of relative importance was calculated in order to facilitate dietary comparisons between sexes, ages classes, and locations.

The presence or absence of stones in the stomachs, and the presence or absence of parasitic nematodes in the stomach wall, were noted and the frequency of occurrence calculated. Differences between the occurrence of parasites or empty stomachs were tested using Fisher's Exact test. To test for differences in prey size selection between the two areas, Mann Whitney *U* tests were used to compare lengths of prey items taken at each location.

To determine sex- and age-related variations in diet and dietary differences between ringed seals from Grise Fiord and Qaanaaq, dietary overlap was calculated using Horn's index of overlap (Horn 1966; R_o). Horn's index of overlap was calculated using the index of relative importance (IRI_i) for each prey type. Overlap values greater than 0.60 were considered to indicate significant overlap in the diets (e.g., Zaret and Rand 1971, Wallace 1981, Brodeur and Pearcy 1990). Every prey taxon similar between the two groups being compared was included as a separate unit; thus, there was no grouping of prey taxa in this analysis. To test for sex-related dietary differences, only adult seals were used in the analysis. To test for age-related dietary variations, the diet of immature seals (< 6 years of age) was compared to that of adult seals (≥ 6 years). Young-of-the-year (YOY, 0+ years) were included in the immature seal category. To compare the diets of ringed seals in Grise Fiord and Qaanaaq, immature seals and adult seals were compared separately.

In addition to Horn's index of overlap, the graphical method of Cortés (1997) was used to facilitate dietary comparisons between Grise Fiord and Qaanaaq. This three-dimensional graphical representation of diet uses the frequency of occurrence (FO_i), the relative frequency of occurrence by number (N_i), and the relative frequency of occurrence by biomass (B_i) to depict prey importance, predator feeding strategy, and the degree of homogeneity of feeding in the population (Cortés 1997). The following points describe how to interpret such a three-dimensional graphical representation of stomach content data (Fig. 3-1):

Vertex *a*: a prey point near vertex *a* is the dominant food type
Vertex *b*: a prey point near vertex *b* is a rare food type
Vertex *c*: a prey point near vertex *c* indicates that most predators take several different food types in low abundance
Vertex *d*: a prey point near vertex *d* indicates a specialized diet by a few predators that take large numbers of heavy items
Vertex *e*: a prey point near vertex *e* indicates a generalized diet of light food items that are consumed by most predators
Vertex *f*: a prey point near vertex *f* indicates a specialized diet by a few predators that take a few heavy items
Vertex *g*: a prey point near vertex *g* indicates that most predators take a few heavy items
Vertex *h*: a prey point near vertex *h* indicates a specialized diet by a few predators that take large numbers of light items

T. libellula was graphed separately from other amphipods in this analysis and there was a separate category for non-amphipod invertebrates taken. Cod were graphed separately from other fish species.

In addition to the stomach content analysis, stable isotope ratios of $\delta^{13}C$ and $\delta^{15}N$ were used to make sex-, age-, and region-related dietary comparisons. To determine age-related differences, seals were classified into three different age classes: YOY (0+ years), subadults (< 6 years), and adults (≥ 6 years). Statistical differences were tested using General Linear Model (GLM) in Systat Ver. 7.0 (SPSS Inc. 1996).

Sex-, age-, and region-related differences in prey size selection were examined by comparing the mean size of Arctic cod taken by male and female adults and different age classes (YOY, subadults, and adults) for each location, as well as between locations. Differences in prey size selection were also determined for *T. libellula* and polar cod (*Arctogadus glacialis*) for seals collected in Grise Fiord only and between regions. Prey sample sizes for seals collected in Qaanaaq were too small to warrant statistical analyses. Mann Whitney *U* tests were used to compare prey size between sexes and locations, and Kruskal -Wallis tests were used to compare prey size between the three age classes.

3.3. Results

3.3.1. Diet composition

Of 97 stomachs from Grise Fiord, 53% had some dietary contents, other than parasites or stones, and of 99 stomachs collected near Qaanaaq, 40% had dietary contents. There was no significant difference between the number of empty stomachs for the two locations ($P = 0.11$). For the Grise Fiord sample, 3 of 51 stomachs with food remains contained only unidentifiable prey. Two of those stomachs contained only fish bones or tissue, and the third stomach contained unidentifiable invertebrate remains. For Qaanaaq, 12 of 40 stomachs with food remains contained only unidentifiable fish bones and tissue.

Stones were found in 11% of the stomachs from Grise Fiord, with 4 of 11 stomachs containing stones without any other prey remains. In the Qaanaaq sample, 4% of stomachs contained stones and no stomachs contained only stones. The occurrence of parasites in the stomach was significantly greater for ringed seals collected in Qaanaaq

(69%) than those collected in Grise Fiord (41%) ($P < 0.01$).

Seals collected in Grise Fiord fed on sixteen different prey items, including 4 species of fish (Arctic cod, polar cod, four-horn sculpin, Arctic staghorn sculpin), 8 species of amphipod, 1 shrimp species, 1 mysid species, 1 gastropod, and 1 bivalve (Table 3-1). One seal had ingested seaweed. Seals fed predominantly on fish, mainly Arctic cod and polar cod, but crustaceans, especially *T. libbelula*, as well as *Onisimus litoralis*, occurred frequently in the diet (Table 3-1).

Fourteen different food items were found in seal stomachs from Qaanaaq, including 5 species of fish (Arctic cod, polar cod, four-horn sculpin, Arctic staghorn sculpin, gelatinous snailfish), 3 amphipod species, 2 shrimp species, 2 species of cephalopod, and 2 gastropods (Table 3-2). Food intake consisted predominantly of fish, mainly Arctic cod and some polar cod. Although crustaceans were not frequent in the diet, *T. libellula* was the predominant crustacean taken (Table 3-2). The mean sizes of the fish species taken by seals in the two sample areas are shown in Appendix E.

3.3.2. Sex, age, and regional dietary variation by stomach content analysis

The diets of adult male and female ringed seals showed a high degree of overlap in both Grise Fiord and Qaanaaq, with R_o values of 0.89 and 0.95 respectively, although there were a number of minor differences between males and females. Some males in Grise Fiord took shrimp and mysids, whereas no females were recorded with these prey items in their stomachs. For seals collected in Grise Fiord, there were no sex-related differences in prey size selection of *T. libellula* ($\chi^2 = 0.13$, $P = 0.72$), although female seals took larger Arctic cod ($\chi^2 = 44.61$, $P < 0.001$) and polar cod ($\chi^2 = 6.20$, $P = 0.01$) than males (Table 3-3). There were no sex-related differences in prey size selection of Arctic cod for seals in Qaanaaq ($\chi^2 = 0.01$, $P = 0.94$).

The diet of immature and adult seals collected in Grise Fiord did not overlap significantly ($R_o = 0.59$) and thus differed. Adult seals fed predominantly on fish (mostly Arctic and polar cod), whereas immature seals fed mainly on pelagic amphipods, especially *T. libellula*, with a smaller proportion of fish in their diet (Fig. 3-2). Even though polar cod was a major component of the adult diet, it did not make up a large proportion of the fish intake of the diet of immature seals. There was no difference in the prey size selection of *T. libellula* between YOY, subadults, or adults (Kruskal-Wallis, $P = 0.98$), although adult seals took larger Arctic cod than subadults and YOY (Kruskal - Wallis, $P < 0.001$) and larger polar cod than YOY ($P = 0.002$) (Table 3-3).

There was a significant degree of overlap in the diets of immature and adult seals collected in Qaanaaq ($R_o = 0.94$). Both adults and immature seals took predominantly fish, especially Arctic cod (Fig. 3-3). Conversely, immature seals took relatively more amphipods, especially *T. libellula*, than adults. Subadults took significantly larger Arctic cod than adults, which took significantly larger cod than YOY (Kruskal-Wallis, $P < 0.001$) (Table 3-3).

The diet of immature seals collected in Grise Fiord and Qaanaaq showed significant overlap ($R_o = 0.66$), since both diets consisted of a large proportion of cod. However, immature seals in Grise Fiord generally took a greater proportion and a wider variety of amphipods than did immature seals at Qaanaaq. The dominant prey in the diet of immature seals collected near Grise Fiord was *T. libellula* (Fig. 3-2). Other amphipods were eaten occasionally, but Arctic cod was eaten by most seals in small quantities, and other items were eaten rarely. In contrast, the dominant prey of immature seals in Qaanaaq was Arctic cod, whereas only a few seals took *T. libellula*, and other prey items were rarely eaten (Fig. 3-3). Subadult ringed seals from Grise Fiord took significantly larger *T. libellula* than subadults from Qaanaaq ($\chi^2 = 86.23$, $P > 0.001$), but significantly smaller Arctic cod ($\chi^2 = 133.16$, $P < 0.001$) (Table 3-3). However, YOY from Grise Fiord took significantly larger Arctic cod than YOY from Qaanaaq ($\chi^2 = 13.85$, $P < 0.001$) (Table 3-3).

The diets of adult seals from Grise fiord and Qaanaaq did not overlap significantly ($R_o = 0.59$). Ringed seals from both locations took mostly fish; however, ringed seals from Grise Fiord took more polar cod, whereas ringed seals in Qaanaaq took almost all Arctic cod. The diet of ringed seals collected in Grise Fiord consisted mainly of Arctic cod as well as polar cod (Fig. 3-2). Invertebrates were eaten only rarely (Fig. 3-2). For ringed seals collected in Qaanaaq, the dominant prey type was Arctic cod, while other fish as well as invertebrates were only rarely eaten (Fig. 3-3). Ringed seals from Qaanaaq also took significantly larger Arctic cod than ringed seals from Grise Fiord ($\chi^2 = 120.57$,

$P < 0.001$) (Table 3-3).

3.3.3. Sex-, age-, and regional-related dietary variation determined by stable isotope analysis

For seals collected in Grise Fiord, there were no sex-related differences in $\delta^{15}N$ or $\delta^{13}C$ within adult seals (ANOVA, $P = 0.86$ and $P = 0.97$ respectively), subadults ($P = 0.87$ and $P = 0.45$ Respectively), or YOY ($P = 0.94$ and $P = 0.73$ respectively) (Table 3-4). However, for seals collected in Qaanaaq, adult males were enriched in $\delta^{15}N$ over adult females ($P = 0.04$) and subadult males had higher $\delta^{13}C$ levels than subadult females ($P = 0.05$). For seals collected in Qaanaaq, there were no sex-related differences in $\delta^{15}N$ within YOY or subadult seals ($P = 0.41$ and $P = 0.79$ respectively), and there was no separation in $\delta^{13}C$ between adults ($P = 0.85$) or YOY ($P = 0.23$) (Table 3-4).

YOY collected in Grise Fiord were nitrogen enriched over adults and subadults ($P < 0.01$), but no age-related differences in nitrogen isotope ratio were apparent for seals collected in Qaanaaq (Table 3-4). Subadult seals had significantly lower carbon isotope ratios than adults for seals collected in both Grise Fiord and Qaanaaq ($P < 0.05$) (Table 3 - 4).

When the two regions were compared, seals collected in Grise Fiord had significantly higher carbon isotope ratios than those collected in Qaanaaq ($P < 0.001$), but there was no separation in $\delta^{15}N$ between the two samples ($P = 0.06$). Thus, the overall trophic levels for ringed seals collected in Grise Fiord (4.5) and Qaanaaq (4.4) also did not differ significantly (Hobson *et al.*, in prep.).

3.4. Discussion

3.4.1. Diet composition

The methods associated with traditional stomach content analysis have several limitations associated with them (Hyslop 1980, Wallace 1981, Pierce and Boyle 1991, Amundsen *et al.* 1996). Primarily, there is the problem of differential digestion of prey items, where softbodied prey are digested quickly, and hardparts of other prey items remain in the gastrointestinal tract for longer periods of time. As well, stomach content analysis focuses on prey items that were ingested recently, since the digestive clearance rate in ringed seals ranges from 6 to 8 hours (Parsons 1977). Stomach content analysis provides only a "snapshot" of the diet over the period of one day and may not be representative of the diet over a longer time frame. However, aspects of the long-term diet can be acquired through stable isotope analysis since this information is based on prey items that have been assimilated into the tissues. The measurement of concentrations of naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) can provide information on what prey types are being used by the consumer and at what trophic level over a longer period of time (reviewed by Fry and Sherr 1988, Owens 1988). This analysis is based on the observation that these isotopes either undergo a step-wise enrichment between the prey and the consumer tissue (e.g., ^{15}N) or remain little changed and indicate isotopic ratios of primary productivity sources (e.g., ^{13}C) (reviewed by Peterson and Fry 1987). Muscle tissue of marine mammals likely provides an estimate of the diet over a 4 to 6 week period (Tieszen *et al.* 1983). Since both the stomach content analysis and the stable isotope analysis contribute unique and important information to a dietary study, using a combination of both of these techniques is desirable (Hobson and Sealy 1991, Hobson *et al.* 1994). Thus, both techniques were used to determine the food habits of ringed seals in the North Water Polynya.

The volume of food consumed by ringed seals varies seasonally, with an increase from late summer to early spring and a decrease in late spring to early summer (Ryg *et al.* 1990, Ryg and Øritsland 1991). Thus, the large proportions of empty stomachs in this study for both samples is not unusual and is consistent with other studies conducted during spring, when the majority of animals haul out on the ice for extended periods while undertaking their seasonal molt and feed less often than at other times (McLaren 1958, Fedoseev 1965, Johnson *et al.* 1966, Lowry *et al.* 1980).

The occurrence of stones in the stomachs of ringed seals has also been noted in previous studies (e.g., McLaren 1958, Johnson *et al.* 1966), although it remains unknown why they are ingested. Johnson *et al.* (1966) suggested that stones may be ingested accidentally during foraging or may be in the stomachs of gadid fish that are ingested, while Smith (1987) suggested that stones may be eaten to fill the stomach during periods of extreme hunger.

Parasites also occur frequently in the gastrointestinal tracts of ringed seals (e.g., Dunbar 1941, McLaren 1958, Finley *et al.* 1983, Measures and Gosselin 1994). The slightly higher occurrence of parasites in the seals from Qaanaaq may be related to the predominance of fish in their diet. Bertram (1938) found that plankton-eating crabeater seals (*Lobodon carcinophagus*) had fewer parasites compared to fish-eating Weddell seals (*Leptonychotes weddelli*). Thus, parasite load may be directly related to the amount of fish consumed. Finley *et al.* (1983) found that parasite loads in ringed seals from the landfast ice were higher than those for seals from the pack ice, and Delyamure (1955) noted that the parasitic fauna of ringed seals in coastal areas was much richer. These observation are likely related to the generalization that seals in coastal areas eat more fish than seals off shore (McLaren 1958, Fedoseev 1975, Finley *et al.* 1983).

The prey species that had the highest frequencies of occurrence in ringed seal stomachs from both locations were Arctic cod, polar cod, and the amphipod *T. libellula*. *T. libellula* has been reported to be one of the most important prey species for ringed seals in several studies (Dunbar 1941, McLaren 1958, Lowry *et al.* 1980, Finley *et al.* 1983, Weslawski *et al.* 1994). *T. libellula* is common and numerous throughout the Arctic (Klekowski and Weslawski 1990) and was the most common invertebrate in zooplankton net tows in the North Water Polynya (L. Fortier, unpublished data).

Arctic cod is one of the most prevalent prey types in several collections and appears to be the dominant fish prey species for ringed seals throughout the Arctic (McLaren 1958, Johnson *et al.* 1966, Bradstreet and Finley 1983, Smith 1987, Weslawski *et al.* 1994, Wathne 1997). Nonetheless, polar cod was also found to be a major component of the ringed seal diet in this study, as well as in the eastern Canadian High Arctic (Bradstreet and Finley 1983) and in east and northwest Greenland (Siegstad *et al.* 1998). Since polar cod are found primarily in deep water (Boulva 1972), ringed seals in the Grise Fiord area likely forage in deeper waters than seals around Qaanaaq. Overall, Bradstreet and Finley (1983) showed that Arctic cod, followed by polar cod, were the most important food items in terms of energy intake of ringed seals in northwestern

Baffin Bay. However, it is not possible to relate the ringed seal diet to the distribution and abundance of Arctic and polar cod, as this information is unavailable for the polynya.

Other prey items encountered in the diet of ringed seals collected in Grise Fiord and Qaanaaq were less common and included mysids, shrimp, amphipods, cephalopods, gastropods, a bivalve, and non-gadid fish species. For the Grise Fiord sample, the amphipods *O. litoralis*, *Gammarus setosus*, and *Atylus carinatus* were taken by about 20% of seals, whereas other prey species were taken less frequently. Oddly, these three amphipods were not obtained in any of the net tows examined during preliminary analyses (L. Fortier, unpublished data). Similarly, the amphipod *Hyperia galba* and the shrimp *Lebbeus polari* were also taken by seals, although rarely, but were not found in net tows (L. Fortier, unpublished data). Although mysids were obtained relatively frequently in net tows (33% of the time; L. Fortier, unpublished data), only 4% of the seal samples from Grise Fiord included this prey type. Similarly, other studies have shown that although mysids are taken by ringed seals, they usually are not a major prey item (Dunbar 1941; Johnson *et al.* 1966; Lowry *et al.* 1978, 1980; Bradstreet and Finley 1983; Weslawski *et al.* 1994; Siegstad *et al.* 1998), although McLaren (1958) found mysids to be important prey for ringed seals in coastal areas. The amphipods *Gammaracanthus loricatus* and *Anonyx nugax* were taken rarely by either seals or net tows (L. Fortier, unpublished data). Sculpins were taken only rarely by ringed seals. Overall, the diet of ringed seals collected in Grise Fiord in this study was similar to that previously reported for seals in that area (Bradstreet and Finley 1983).

For the Qaanaaq sample, another common prey type in the diet was *Liparis koefoedi*. Similarly, *Liparis* species have been found to be important in the diet of ringed seals in other areas of Greenland (Siegstad *et al.* 1998). Sculpins, squid, octopus, the amphipods *O. litoralis* and *G. setosus*, and the shrimp, *L. polari* and *Hymenodora glacialis* were taken infrequently. The occurrence of *H. glacialis* in net tows in the North Water Polynya was also quite rare, occurring in 5% of the tows (L. Fortier, unpublished data). Overall, the diet of ringed seals collected in Qaanaaq was similar to that reported for seals in that area in late summer by Siegstad *et al.* (1998). Two prey items known to be taken by ringed seals, *Thysanoessa* spp. and *Parathemisto abyssorum* (e.g., Dunbar

1941; McLaren 1958; Lowry *et al.* 1980, 1978; Weslawski *et al.* 1994; Siegstad *et al.* 1998) were present in net tows, although only infrequently (L. Fortier, unpublished data), but not in any of the ringed seal stomachs.

Several studies have documented seasonal differences in feeding habits of ringed seals (e.g., McLaren 1958, Johnson *et al.* 1966, Smith 1987, Weslawski *et al.* 1994, Siegstad *et al.* 1998), which likely reflect changes in prey availability (Johnson *et al.* 1966). During the present study, ringed seals were collected between May and early July, corresponding to late spring/early summer. Arctic cod was the dominant prey item in the diet of adult and immature seals from Qaanaaq, and it was also a major prey item in the diet of seals from Grise Fiord, whereas amphipods and other invertebrates were rarely taken. Several studies have shown that Arctic cod appears to be the major source of food in late autumn to early spring, whereas in the summer, mysids and benthic crustaceans are thought to become important in nearshore areas (Johnson *et al.* 1966, Lowry *et al.* 1980), and pelagic amphipods are thought to become important in offshore areas (Lowry *et al.* 1980, Weslawski *et al.* 1994). In high Arctic regions, hyperiid amphipods are the most common pelagic crustacean in seal diets, whereas euphausiids are more commonly eaten in areas such as Barrow, Alaska (e.g., Lowry *et al.* 1980) and Ungava Bay (e.g., McLaren 1958), which are influenced by subarctic water (Dunbar 1954, 1957).

Bradstreet and Finley (1983) noted that the seasonal patterns in diet reported from other areas did not seem to hold true for ringed seals in the Canadian High Arctic, since cod seemed to dominate the diet of ringed seals throughout the summer. Similarly, in the present study, Arctic cod was also the dominant prey type in the late spring/early summer. Even though mysids and hyperiid amphipods were taken by ringed seals collected in Grise Fiord, they were mostly taken by immature seals, and Arctic cod remained an important component of their diet as well.

3.4.2. Age-related dietary variation

Stomach content analysis revealed age-related dietary differences for ringed seals in the North Water Polynya. Although McLaren (1958) and Gjertz and Lydersen (1986) did not find any obvious age-related differences in the diet of ringed seals, other studies have shown that diet does vary with the age of the seal (Bradsteet and Finley 1983, Lowry *et al.* 1980, Bradstreet and Cross 1982, Smith 1987, Siegstad *et al.* 1998). Bradstreet and Finley (1983) as well as Bradstreet and Cross (1982) showed that the predominance of crustaceans in the diet decreased with age and, conversely, consumption of fish, particularly Arctic cod, increased with age.

Dietary differences between young and older seals may be due to differences in foraging experience, diving capabilities, and/or spatial segregation. Younger animals may be focusing on foods that are easier to capture (e.g., Garshelis 1983, VanBlaricom 1988), such as plankton or other invertebrates, since they lack the foraging experience that older animals have. However, Lowry *et al.* (1980) noted that Arctic cod appear to be caught as easily by pups as by older seals. Kooyman (1967) found that Weddell seal pups (*Leptonychotes weddelli*) were unable to dive as deep as adults, and that diving ability may affect foraging strategy and prey consumed (Kooyman *et al.* 1983). Ferren (1980) predicted that older ringed seals would be able to dive longer than young ringed seals, and Kelly and Wartzok (1996) showed that dive duration was positively correlated to body mass. Thus, dive duration as well as depth may affect ringed seal foraging; lighter, younger seals may be less successful at foraging for Arctic cod, which are typically associated with the undersurface of the ice (Andriyashev 1954, McAllister 1975), but may also be found near the bottom as well as in open water (Bradstreet *et al.* 1986). In this study, adult seals took larger cod than younger seals, which has also been shown in a previous study (Bradstreet and Finley 1983). Dietary differences among ages could also be influenced by the spatial distribution of young seals. Immature seals tend to be excluded from the landfast ice breeding areas and are thus likely to be found feeding on plankton offshore (McLaren 1958). However, the diets of immature and adult seals collected in Qaanaaq did not show this variation, and all seals fed mainly on Arctic cod.

The stable isotope analysis also showed age-related dietary differences. YOY tend to be nitrogen enriched over adults, as shown in Grise Fiord, since the first six weeks of their diet consists mostly of milk produced by their mothers (Hobson *et al.* 1997). Adults are predicted to have higher nitrogen ratios than subadults, since adults tend to forage at higher trophic levels. The carbon ratios for adults in Grise Fiord and Qaanaaq were higher than those for subadults. Since $\delta^{13}C$ values are typically higher in benthic food webs than in pelagic food webs (McConnaughey and McRoy 1979, Rau *et al.* 1983, Dunton *et al.* 1989, Hobson 1993), adults appear to be taking more benthic prey than younger seals, which is reflected in the lower proportion of pelagic crustaceans and greater proportion of fish in the diet of adult seals.

3.3.3. Sex-related dietary variation

Horn's index showed that there was significant overlap in the diet of male and female ringed seals from both Grise Fiord and Qaanaaq, although females in Grise Fiord took larger fish than males. No sex-related differences were found in the diet of ringed seals from the Canadian High Arctic (Bradsteet and Finley 1983), Svalbard (Gjertz and Lydersen 1986), or Alaska (Johnson *et al.* 1966, Lowry *et al.* 1980). Stable isotope analysis showed that males in Qaanaaq had higher nitrogen isotope ratios than females, indicating that males fed trophically higher than females. This was also shown to be true for Steller sea lions (*Eumetopias jubatus*) in Alaska, although other dietary studies have not shown sex-related differences (Hobson *et al.* 1997). Males in Qaanaaq fed on cephalopods as well as a greater variety and a slightly greater proportion of fish than females, which may influence their trophic levels. However, nitrogen isotope ratios for different sizes of Arctic cod and polar cod are not known. Higher carbon isotope ratios in subadult males may indicate that males are taking more benthic prey than females. For example, subadult males from Qaanaaq tended to take more shrimp and fewer *T. libellula* than subadult females.

3.3.4. Regional dietary variation

Ringed seals were collected in similar coastal, landfast ice habitats around Grise Fiord and Qaanaaq; thus, it was possible to compare the feeding habits of these two ringed seal samples. Arctic cod was the most important component of the adult ringed seal diet around Qaanaaq and Grise Fiord. Arctic cod was also the dominant prey species of immature ringed seals collected around Qaanaaq. But for immature seals collected in Grise Fiord, *T. libellula* was the dominant prey item, followed by Arctic cod. Preliminary analyses of zooplankton distribution and densities within the polynya showed that *T. libellula* densities did not vary significantly between the east and west sides of the polynya (L. Fortier, unpublished data; Appendix F).

Adult and immature seals collected in Qaanaaq took few amphipods, even though amphipods were just as abundant on the east side of the polynya compared to the west side, as determined by comparing mean overall amphipod densities for east and west sampling sites (L. Fortier, unpublished data; Appendix G). Arctic cod biomass and abundance may have been greater in this area than in Grise Fiord, due to the hypothesized differences in productivity between the two sides of the North Water Polynya. An earlier phytoplankton bloom (L. Legendre, unpublished data; Appendix B) and warmer temperatures (Steffen 1985) have already been demonstrated to exist on the east side of the polynya, and these factors are thought to support increased Arctic cod reproduction. Michaud *et al.* (1996) have demonstrated that foraging activity, feeding success, and growth of Arctic cod larvae were limited by low temperatures and only larvae hatched at above-zero temperatures survived. An increase in Arctic cod abundance could lead to increased encounter rates and capture success of cod by immature seals. Thus, ringed seals collected in Qaanaaq might be expected to have a greater proportion of fish in their diet, which was shown at least for immature seals in this study.

Arctic cod is most likely the preferred prey type of ringed seals, because it has one of the highest energy content per unit mass ratios of any prey item (Bradstreet and Finley 1983, Weslawski *et al.* 1994). However, the energy content per unit mass of polar cod is not known. As well, since Arctic cod are much larger than amphipods, the required daily energy intake can be achieved by taking several cod compared to hundreds of *T. libellula* (Lowry *et al.* 1980). Thus, immature ringed seals feeding predominantly on invertebrates in Grise Fiord may have to work harder to fulfill their daily energy requirements. This may lead to differences in growth rate between ringed seals from the east and west sides of the polynya (See Chapter 2). Although fish, especially cod, were also a major component of the diet of ringed seals collected around Grise Fiord, amphipods, especially *T. libellula* and *O. litoralis,* were also taken regularly, which may indicate that fish biomass is lower on the west side of the polynya compared to the east side.

Ringed seals collected at Grise Fiord had higher carbon isotope ratios, which suggests that they were taking more benthic prey than seals at Qaanaaq. Although pelagic amphipods were more common in the stomachs of seals from Grise Fiord than in those from Qaanaaq, the greater proportion of polar cod in their diet may also have led to increased $\delta^{13}C$ levels. Polar cod are found mostly near the bottom in deep water (Boulva 1972), whereas Arctic cod is mainly associated with the undersurface of ice (Andriyashev 1954, McAllister 1975). In contrast to the traditional stomach content analysis which suggested dietary differences between ringed seals from the east and west sides of the polynya, the stable isotope analysis did not show any significant differences between the trophic levels of ringed seals from either side of the polynya. Nonetheless, the trophic levels of both ringed seal samples agree with those given for ringed seals in the eastern Canadian High Arctic (Hobson and Welch 1992). A ringed seal diet consisting exclusively of *T. libellula* or Arctic cod should show $\delta^{15}N$ values close to 13.5 and 17.8°/₀ respectively (Hobson *et al.*, in prep.). Considering only these trophic options, the mean $\delta^{15}N$ values obtained in this study for Grise Fiord and Qaanaaq seals (17.5°/₀₀ and 17.0°/₀₀) suggest that the diet of ringed seals in these two locations consists almost exclusively of fish, which is supported by the stomach content analysis.

Ringed seals collected in Qaanaaq had a trophic level of 4.4 and not less than 3, as would be expected for a top predator foraging in an area with upwelling (Ryther 1969). This suggests that any dietary differences between ringed seals from the east and west sides of the polynya may not result from upwelling on the east side of the polynya as hypothesized. Regional differences in diet probably reflect water depth, prey preference, and prey availability (Reeves 1998). Ringed seals from Grise Fiord may have been foraging in deeper water since they tended to take more polar cod, a deep water fish, than ringed seals in Qaaanaaq, although deep water areas are prominent in both locations. Alternatively, prey availability influenced by the hypothesized differences in productivity between the east and west sides of the polynya, may be the main cause of regional differences in diet. Secondary productivity, in terms of zooplankton density, was similar on both sides of the polynya, with the exception of one station in the southeast of the polynya that had the greatest density (L. Fortier, unpublished data; Appendix C). As well, densities of *T. libellula* were similar on both sides of the polynya (L. Fortier, unpublished data; Appendix F). However, details of the distribution and abundance of Arctic and polar cod are unknown for either area.

Geographic variation in stable isotope ratios, especially $\delta^{13}C$, have been documented in some areas (reviewed by Dunton *et al.* 1989) and may affect the interpretation of stable isotope analyses. For example, when comparing the stable isotope ratios between two samples, differences may be due to geographic variation in ratios instead of actual differences in prey selection. However, in this study, the stomach content analysis, as well as the stable carbon isotope ratios, showed that the diet of ringed seals from Grise Fiord and Qaanaaq were different. Thus, I conclude that differences in stable isotope ratios between ringed seals from the east and west sides of the polynya are most likely due to dietary differences and not geographic variation.

3.5. Conclusions

It appears that dietary differences exist between ringed seals inhabiting the east and west sides of the polynya. Immature ringed seals collected in Grise Fiord fed predominantly on amphipods, whereas immature seals collected in Qaanaaq fed mainly on fish. As well, adult ringed seals in Grise Fiord fed on a greater proportion of polar cod than did ringed seals from Qaanaaq. These differences in the diets of ringed seals may reflect differences in prey availability within the polynya, although it is uncertain at this point whether and how prey availability and abundance are affected by the hypothesized differences in heat sources and productivity. Ringed seals on the east side of the polynya fed at a higher trophic level than might be theoretically predicted in a sensible heat system with upwelling. However, it has been shown that the phytoplankton bloom occurs earlier on the east side than on the west side (L. Legendre, unpublished data; Appendix B), whether due to a sensible heat source or not. Thus, food webs may still be different between the two sides of the polynya and differences may be reflected in ringed seal feeding habits.

Without further data on the distribution and abundance of prey in the area, especially Arctic and polar cod, and detailed information on ringed seal foraging behaviour and prey preferences, it remains uncertain to what degree the diet of ringed seals is affected by prey preference compared to prey abundance and distribution. Arctic cod appears to be one of the most common prey items in the diet of ringed seals in the

North Water Polynya, although it seems likely that seals take alternative prey when fish availability is low.

3.6. Literature cited

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Table 3-1: Prey taxa found in ringed seal stomachs collected in Grise Fiord (n = 48). FO_i - frequency of occurrence; Number - total number of animals per prey taxon; N_i - relative frequency of occurrence by number; Weight - total weight of all animals per prey taxon; B_i - relative frequency of occurrence by biomass; IRI_i - index of relative importance; $\%IRI_i$ - percent index of relative importance.

Prey Items	FO_i	Number	N_i	Weight (g)	B_i	IRI_i	$\%IRI_i$
Amphipoda							
Themisto libellula	54.2	2572	46.1	1245.6	8.8	2973.9	42.1
Gammarus setosus	20.8	22	0.4	11.9	0.1	10.3	0.1
Onisimus litoralis	20.8	2248	40.3	71.2	0.5	847.9	12.0
Atylus carinatus	18.8	69	1.2	21.6	0.2	27.0	0.4
Gammaracanthus loricatus	6.3	9	0.2	3.9	0.0	1.0	0.0
Anonyx nugax	2.1	1	0.0	0.5	0.0	0.0	0.0
Hyperia galba	2.1	7	0.1	1.1	0.0	0.3	0.0
Onisimus edwarsi	2.1	1	0.0	0.0	0.0	0.0	0.0
Mysidacea							
Mysis oculata	4.2	81	1.5	11.9	0.1	6.5	0.1
Decapoda							
Lebbeus polari	4.2	3	0.1	4.4	0.0	0.2	0.0
Pisces							
Boreogadus saida	77.1	451	8.1	2409.6	17.0	1933.5	27.3
Arctogadus glacialis	22.9	111	2.0	10257.8	72.5	1705.8	24.1
Gymnocanthus tricuspis	6.3	5	0.1	84.5	0.6	4.3	0.1
Myoxocephalus quadricornis	2.1	1	0.0	23.1	0.2	0.5	0.0
Mollusca							
Bivalve	2.1	1	0.0	-	-	-	-
Colus spp.	2.1	1	0.0	-	-	-	-

Table 3-2: Prey taxa found in ringed seal stomachs collected in Qaanaaq (n = 28). FO_i - frequency of occurrence; Number - total number of animals per prey taxon; N_i - relative frequency of occurrence by number; Weight - total weight of all animals per prey taxon; B_i - relative frequency of occurrence by biomass; IRI_i - index of relative importance; $\%IRI_i$ - percent index of relative importance.

Prey taxon	**FO_i**	**Number**	**N_i**	**Weight (g)**	**B_i**	**IRI_i**	**$\%IRI_i$**
Amphipoda							
Themisto libellula	21.4	268	30.7	68.2	0.8	674.8	5.0
Gammarus setosus	3.6	1	0.1	0.3	0.0	0.4	0.0
Onisimus litoralis	3.6	2	0.2	0.1	0.0	0.8	0.0
Decapoda							
Lebbeus polari	7.1	4	0.5	6.5	0.1	4.0	0.0
Hymenodora glacialis	3.6	1	0.1	0.2	0.0	0.4	0.0
Cephalopoda							
Bathypolypus arcticus	3.6	3	0.3	388.4	4.8	18.5	0.1
Rossia moelleri	7.1	3	0.3	39.8	0.5	6.0	0.0
Pisces							
Boreogadus saida	85.7	555	63.6	6851.3	85.5	12781.9	94.1
Arctogadus glacialis	14.3	10	1.1	551.1	6.9	115.1	0.8
Gymnocanthus tricuspis	7.1	2	0.2	35.8	0.4	4.5	0.0
Myoxocephalus quadricornis	3.6	1	0.1	16.6	0.2	1.1	0.0
Liparis koefoedi	21.4	20	2.3	126.0	1.6	83.3	0.6
Mollusca							
Margarites spp.	3.6	1	0.1	-	-	-	-
Unidentified gastropod	3.6	1	0.1	-	-	-	-

Table 3-3: Sizes of prey items (mean lengths ± SD) taken by ringed seals collected in Grise Fiord and Qaanaaq. Sample sizes in brackets.

Group	***Themisto libellula***	**Arctic cod**	**Polar cod**
Grise Fiord			
Adults	30.87 ± 3.97 (272)	89.69 ± 36.47 (287)	201.97 ± 30.98 (108)
Females	30.83 ± 3.91 (142)	94.34 ± 35.85 (224)	197.09 ± 29.98 (75)
Males	30.89 ± 4.03 (130)	65.60 ± 27.18 (63)	204.06 ± 31.27 (33)
Subadults	30.97 ± 4.33 (326)	66.65 ± 29.25 (55)	-
YOY	31.00 ± 4.22 (1974)	67.58 ± 21.53 (105)	170.02 ± 16.81 (3)
All	30.97 ± 4.18 (2572)	80.78 ± 33.94 (447)	201.08 + 31.10 (111)
Qaanaaq			
Adults	33.10 ± 2.86 (7)	114.98 ± 32.17 (278)	161.91 ± 44.99 (8)
Females	33.10 ± 2.86 (7)	112.84 ± 17.49 (153)	-
Males	-	115.75 ± 39.94 (125)	161.91 ± 44.99 (8)
Subadults	23.69 ± 5.30 (261)	120.39 ± 41.06 (228)	167.40 ± 99.23 (2)
YOY	-	58.28 ± 6.27 (49)	-
All	23.80 ± 5.37 (268)	111.39 + 38.8 (555)	162.82 + 53.19 (10)

Table 3-4: Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope abundance (mean ± SD, in $^{o}/_{oo}$) in muscle tissue of ringed seals collected in Grise Fiord and Qaanaaq.

Group		Sample size	$\delta^{15}N$	$\delta^{13}C$
Grise Fiord				
Adults				
	Females	32	17.3 ± 1.0	-18.2 ± 0.4
	Males	26	17.4 ± 0.4	-18.2 ± 0.3
Subadults				
	Females	4	17.0 ± 1.7	-18.7 ± 0.4
	Males	3	16.9 ± 0.6	-19.1 ± 1.4
YOY				
	Females	18	17.9 ± 0.9	-18.3 ± 0.5
	Males	11	18.0 ± 0.6	-18.2 ± 0.4
All		94	17.5 ± 0.9	-18.3 + 0.5
Qaanaaq				
Adults				
	Females	13	16.8 ± 0.8	-19.2 ± 1.0
	Males	22	17.4 ± 0.6	-19.3 ± 0.8
Subadults				
	Females	25	16.9 ± 0.6	-19.8 ± 0.8
	Males	30	16.9 ± 0.8	-19.4 ± 0.7
YOY				
	Females	5	17.6 ± 0.7	-19.3 ± 0.6
	Males	2	17.1 ± 0.5	-20.0 ± 0.5
All		97	17.0 ± 0.7	-19.5 + 0.8

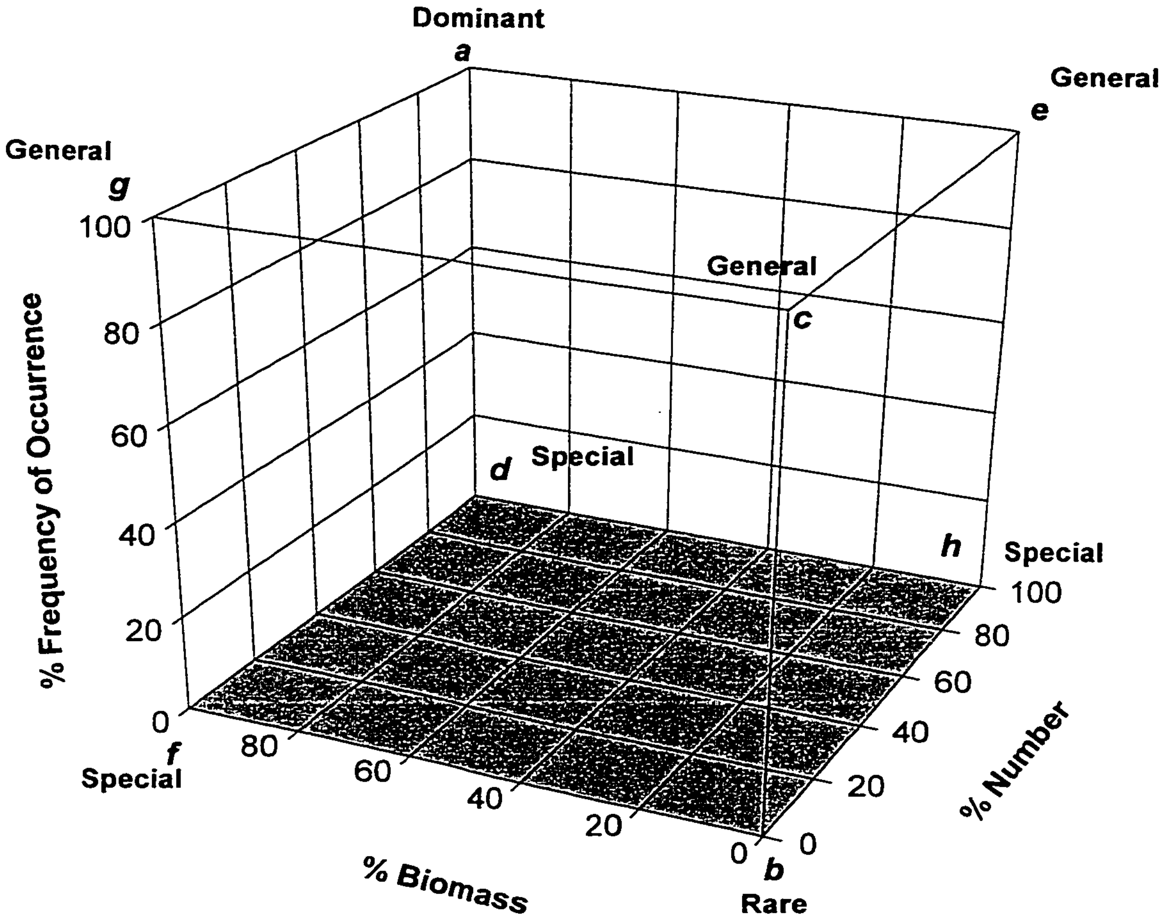

Figure 3-1: A three-dimensional graphical representation of stomach content data. Special, specialized diet; General, generalized diet; Dominant, dominant food category; Rare, rare food category (Cortés 1997).

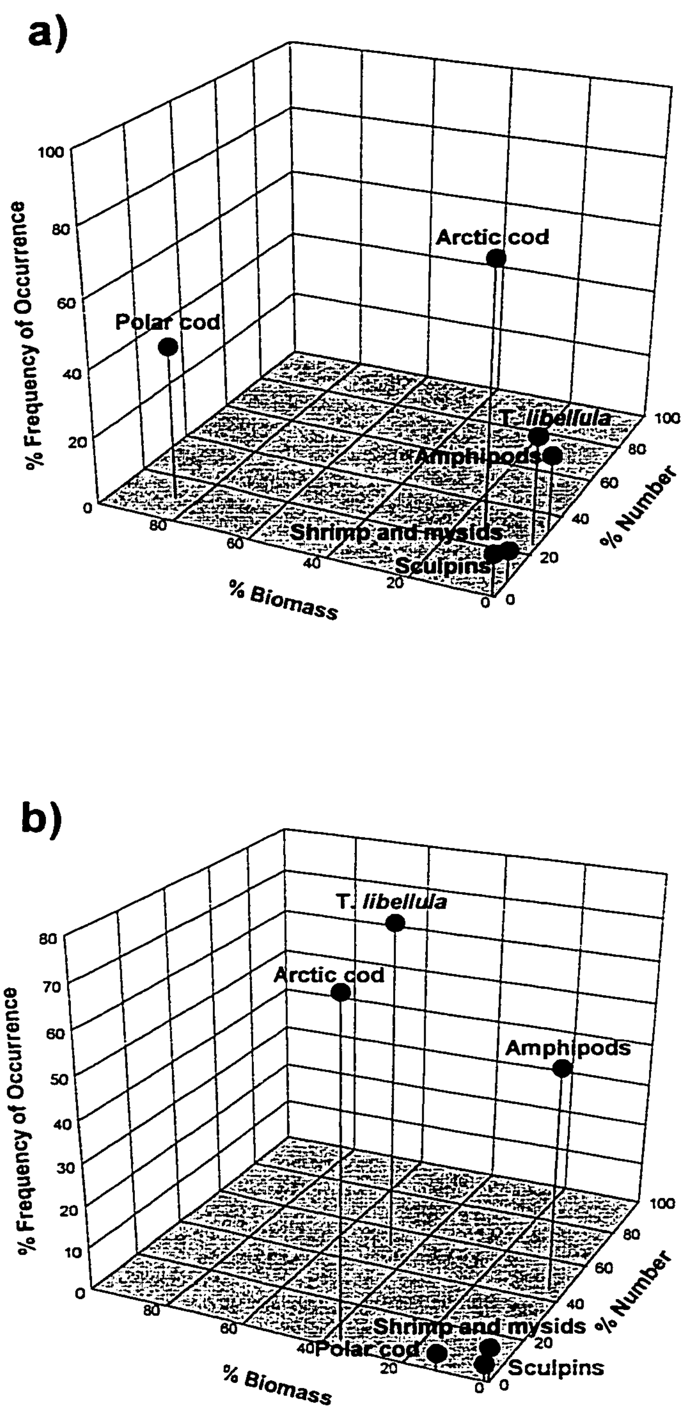

Figure 3-2: 3-D graphical representations of the diet of a) adult ringed seals (≥ 6 years, n = 22) and b) immature ringed seals (< 6 years, n = 25) collected around Grise Fiord.

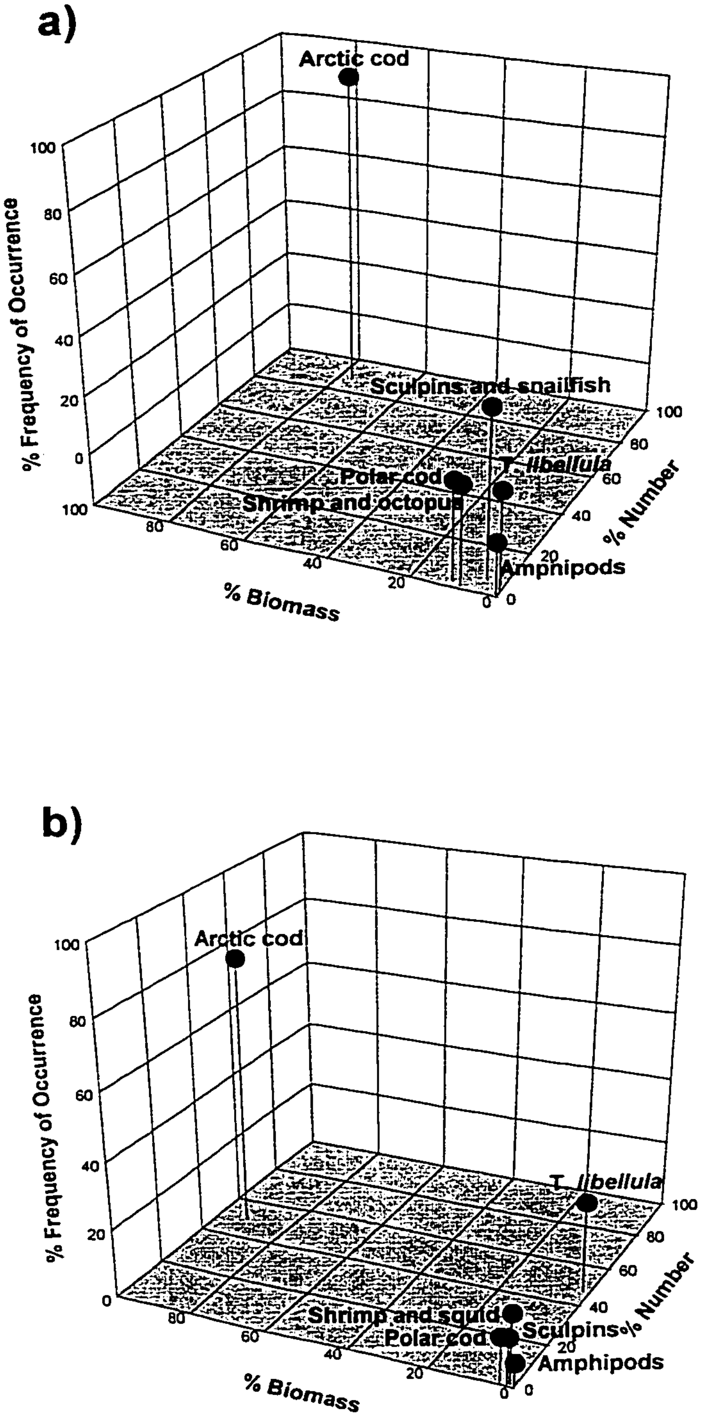

Figure 3-3: 3-D graphical representations of the diet of a) adult ringed seals (≥ 6 years, n = 13) and b) immature ringed seals (< 6 years, n = 15) collected around Qaanaaq.

4. THE DISTRIBUTION AND ABUNDANCE OF RINGED SEALS IN THE NORTH WATER POLYNYA DURING SPRING AND SUMMER

4.1. Introduction

The North Water Polynya, in northern Baffin Bay, is thought to be an important spring feeding and breeding area for several species of marine mammals and birds, and it appears to be important for overwintering and migrant marine mammals during times when the sea is mostly ice-covered (Stirling 1980, 1997; Stirling *et al.* 1981). The ringed seal (*Phoca hispida*) is a year-round inhabitant of the polynya and adjacent landfast ice areas and is considered to be abundant there (Vibe 1950). The total population of ringed seals in Baffin Bay has been estimated at anywhere from half a million (Stirling and Øritsland 1995) to one million animals (Finley *et al.* 1983, McLaren 1958a, Kingsley 1990), supporting Vibe's (1950) observation that ringed seal numbers are high in northern Baffin Bay.

Ringed seals are considered opportunistic feeders (McLaren 1958b, Fedoseev 1965, Johnson *et al.* 1966, Lowry *et al.* 1978, Weslawski *et al.* 1994), so their distribution and relative abundance may be indicative of variations in biological productivity in different areas. Densities of ringed seals have been shown to vary with ecological circumstances elsewhere (e.g., Stirling *et al.* 1977, Kingsley *et al.* 1985, Stirling and Øritsland 1995). For example, Kingsley *et al.* (1985) found that ringed seal densities in Wellington Channel and Barrow Strait, downstream of polynyas in Queens Channel and Penny Strait, were double what they were in non-polynya areas that were otherwise geographically similar and at the same latitude. They suggested that ringed seal densities in and downstream of polynya areas were higher because of increased biological productivity. In northern Baffin Bay, it has been hypothesized that two different heat sources play a role in the maintenance of the North Water Polynya and that the levels of biological productivity resulting for each might be different (see Chapter 1). Studies have shown that greater numbers of seabirds, especially dovekies (*Alle alle*), breed on the east side of the North Water Polynya compared to the west (Nettleship and Evans 1985, Boertmann and Mosbech 1998), and this is thought to be related to higher levels of biological productivity there. Thus, I hypothesized that if there were oceanographic and biological differences between the east and west sides of the North Water Polynya, and these had a significant influence on the relative levels of biological productivity, the differences would be reflected in various aspects of the distribution, abundance, and biology of ringed seals.

The objective of this chapter is to examine the distribution and abundance of ringed seals within the North Water Polynya, relative to variation in productivity expected from the two different heat sources that are hypothesized to maintain the polynya. If the occurrence of sensible heat on the east side of the polynya stimulates increased biological productivity, I would predict that the abundance of ringed seals would be higher there than on the west side.

4.2. Methods

Between 1997 and 1999, a multi-disciplinary research cruise, the International North Water Polynya Study (NOW), was undertaken to study a wide array of physical and biological processes within the North Water Polynya, northern Baffin Bay (see Chapter 1 for details and Fig. 1-2 for location). Observations of ringed seals were made from the bridge of a Canadian Coast Guard icebreaker. There were three cruises to the polynya:

1) A preliminary cruise on the *Louis S. St -Laurent* (August 15 to August 29, 1997).
2) The main NOW cruise on the *Pierre Radisson* (April 7 to July 24, 1998).
   The 1998 cruise consisted of 4 legs: 1) April 7 to May 4, 2) May 7 to May 31, 3) June 4 to June 28, and 4) June 29 to July 24.
3) A cruise on the *Pierre Radisson* to gather additional data (August 24 to October 3, 1999).

For the purposes of data analyses and presentation, I will refer to the legs by the months in which they mainly occurred: Leg 1 - April, Leg 2 - May, Leg 3 - June, Leg 4 - July. One leg of the cruise corresponded to at least one complete cycle through all of the sampling stations in the study area. I will refer to the 1997 cruise as August and the 1999 cruise as September.

Each month, depending on ice conditions, the ship traversed as much as possible of a series of predetermined survey lines (Appendix H), laid out to facilitate the oceanographic sampling required to test the central hypotheses of the NOW. Surveying for ringed seals took place whenever the ship traveled along the survey lines, or between them. The original survey design called for an equal number of sites and distances of cruising on the east (Greenland) and west (Canada) sides of the polynya, especially closer to the coast, since productivity is generally greater over the continental shelf (Subba Rao and Platt 1984, Smith and Sakshaug 1990, Legendre *et al.* 1992), and higher densities of marine mammals have been observed in this zone (Ainley and DeMaster 1990). However, in the end, the ship was not permitted by the Greenland government to approach the Greenland coast closer than 22 km, and the ship was restricted to entering and leaving Greenland waters along the same pre-approved transect lines which further restricted the ability to collect comparative data. In addition to the predetermined survey lines that took place in pack ice of the polynya, several surveys were also conducted along the floe edge of the west side of the polynya between May and July, 1998. These transects followed the landfast ice edge and were conducted specifically to search for ringed seals and other marine mammals.

All ringed seals seen from the bridge of the ship, 16 m above the surface of the water, were counted. Surveys were undertaken by one observer at all times of the day, whenever the ship was steaming in ice-covered or open water, and in all sea states. The observer surveyed the water from his/her side of the ship from the bow to a line perpendicular to the ship's track (through 90°). The survey area was scanned with the naked eye and with 7 X 50 Fujinon binoculars, to sight and identify all ringed seals in the area. Ringed seals seen on the same side of the ship as the observer were recorded as *on* transect, whereas all other seals were recorded as *off* transect. Unless stated otherwise, all analyses, figures, and tables in this chapter include only those seals seen *on* transect.

When a seal was sighted, the species, group size, time (EST), location, sighting angle, and sighting distance were recorded. In addition, sea state, ice cover, and habitat (whether the animal was seen on ice or in water) were recorded in order to relate these to seal distribution and abundance. The sea state was determined subjectively on a scale of 1 to 5 as follows:

1 ⇒ very flat, calm water
2 ⇒ calm water with some ripples
3 ⇒ some swell but no whitecaps
4 ⇒ large swell with a few whitecaps
5 ⇒ very large swell with many whitecaps

Ice cover was estimated in tenths, 0/10 being open water with no ice cover and 10/10 being continuous pack ice.

The sighting angle, which is the angle of the seal relative to the ship's track, was determined with the help of a protractor. The sighting distance was determined in two ways depending on the distance of the seal from the observer. If the distance of the seal to the observer was less than 200 m, the sighting distance was calculated using trigonometry, using the height of the bridge above the waterline and the angle of inclination from the seal to the observer (Fig. 4-1). A clinometer was used to measure the angle of inclination, but its use was limited to measuring angles of nearby seals, since its accuracy decreases with increasing distance of the animal from the ship. When the distance of the seal to the observer was estimated to be greater than 200 m, the sighting distance was determined using binoculars with reticles, which are scaled vertical marks incorporated into the lens. By recording the number of units on the scale between the horizon and the animal, the sighting distance can be calculated (Buckland *et al.* 1993). The sighting distance and sighting angle are then used to calculate the perpendicular distance of the seal to the ship using trigonometry (Fig. 4-2).

For each transect line, the latitude and longitude were recorded at the beginning and end of the transect, as well as when the ship changed direction, using the ship's Global Positioning System (GPS), to determine the distance traveled. The formula used for calculating distance was:

$$\text{Distance (km)} = ((\text{acos}(\sin(\text{lat}_1)*\sin(\text{lat}_2)+(\cos(\text{lat}_1)*\cos(\text{lat}_2)*\cos(\text{long}_2-\text{long}_1))))*60)*1.852$$

where: lat_1 is the latitude at the start of the transect
lat_2 is the latitude at the end of the transect
$long_1$ is the longitude at the start of the transect
$long_2$ is the longitude at the end of the transect
1.852 is the factor to convert nautical miles to kilometres

To determine the relative amount of surveying conducted in open water and ice-covered water for each month, open water was defined as ≤ 4/10 ice cover and ice-covered water was defined as ≥ 5/10 ice cover. The amount of surveying conducted in open water in calm sea states (1 and 2) and rough sea states (3 to 5) was also determined. The distinction between calm and rough sea states was made on the observation that seal sightings were lower in sea states of 3 to 5 (see results section 4.2.2.). In ice-covered waters, the presence of ice usually dampens the effect of wave action; thus, ice-covered waters are typically calm and were not included in this analysis.

Due to the constraints of working in conjunction with a multi-disciplinary study, data collection was conducted on an opportunistic basis, within an overall planned study design. Thus, survey transects were not necessarily straight lines and sometimes even crossed. Although parallel line transects across the North Water Polynya would have been the most effective way to survey the area and to ensure randomness with respect to the distribution of seals (Buckland *et al.* 1973), this was not possible due to constraints imposed by the ship's predetermined schedule of visiting the various sampling stations and, to a lesser degree, variable ice conditions. However, it is unlikely that the same seal was spotted more than once, since they usually depart the vicinity of the ship by swimming away underwater.

The number of ringed seals seen in each habitat relative to ice cover was examined using utilization tests based on the Bonferroni inequality (e.g., Neu *et al.* 1974, Byers *et al.* 1984, Haney and Solow 1992). This method tests for differences in the use of individual resource preferences by comparisons between observed and expected proportions (Haney and Solow 1992). This method was deemed to be the most appropriate, since it is simple to apply, addresses data derived from counts, and results in inherently low rates of Type I error (Haney and Solow 1992). For this analysis, the numbers of ringed seals seen *on* transect on ice (observed values) were compared to the distance surveyed in each of the eleven different ice coverages (expected values). A separate utilization test was done to compare the number of seals seen in the water *on* transect to the distance surveyed in each ice cover. A utilization test was also used to determine the sightability of seals in different sea states. The number of seals seen *on* transect in the water (observed values) were compared to the distance surveyed in each sea state in open water with ≤ 4/10 ice cover (expected values). For these analyses, data for all months were grouped, and significance was set at $\alpha \leq 0.05$.

To determine the effect of water depth on the distribution of ringed seals, seal locations for June, the only month for which the sample size was adequate, were plotted on a bathymetric map of the area using the Geographic Information Systems software package ArcView. The numbers of seals seen in June on ice over six different depth intervals were determined and compared to the total distance of ice surveyed in June over each depth interval. The depth intervals were as follows: < 200 m, 200 - 300 m, 300 - 400 m, 400 - 500 m, 500 - 600 m, and 600 - 700 m. The number of kilometres surveyed in ice was calculated by multiplying the total distance surveyed by the amount of ice during the transect. For example, if 5 km were surveyed in 9/10 ice cover, the total number of kilometres surveyed in ice was calculated as 5x0.9. Therefore, for this example, 4.5 km were surveyed in ice and 0.5 km were surveyed in open water.

Since the ship moved around the clock to meet the predetermined schedule of visiting oceanographic sampling sites, travel often conflicted with surveying at optimal times for ringed seals. Several studies have demonstrated that ringed seals show a diurnal haul-out pattern, with the maximum number of animals hauled out on the ice around mid-day to mid-afternoon (Burns and Harbo 1972; Smith 1973a,b; Finley 1979; Smith and Hammill 1981); haul-out was generally higher between 9 am and 6 pm compared to the period between 6 pm and 9 am. Thus, the numbers of seals seen on the ice in June were corrected by taking into account time of day of the survey. The number of seals seen during surveys conducted between 6 pm and 9 am were adjusted by multiplying the total number of seals seen by a factor of 2, whereas all other sightings were kept the same. The correction factor was chosen conservatively in relation to estimates that 48 to 70% of the total number of seals in an area are seen on the ice during the peak haul-out period

(Smith 1973b, Finley 1979, Smith and Hammill 1981, Stirling and Øritsland 1995).

To test for east-west and north-south differences in ringed seal distribution and abundance within the polynya, the North Water Polynya was divided into six strata: NW (northwest), NE (northeast), CW (central west), CE (central east), SW (southwest), and SE (southeast) (Fig. 4-3). The north to south strata were selected subjectively after assessing the main ecological and physical characteristics of the area that might affect the biological productivity of the North Water Polynya and thus the distribution and abundance of ringed seals. I considered the northern parts of the polynya as separate strata, since these areas receive inflow of water from the polar basin, which is cold and relatively unproductive, and has not mixed with currents flowing north along the west Greenland coast (see Fig. 1-1). The eastern and western sides of the central regions were considered as separate strata, since a warm, Atlantic current is thought to upwell along the west coast of Greenland, after which the water circulates toward the centre of the polynya and mixes with water flowing south along the east coast of Ellesmere Island (see Fig. 1-1). These regions are thought to be more productive than the strata to the north, although the western part of the central region receives more cold water from the polar basin than the eastern side. The east and west sides of the southern strata receive mixed waters from the centre of the polynya, and the west side also receives water through Jones Sound; thus these areas may be nutrient-rich (see Fig. 1-1). The Greenland/Canada boundary was chosen as the arbitrary division between east and west sides of the polynya. The number of kilometres surveyed and the number of seals seen were determined separately for each stratum using ArcView, in order to make comparisons between strata.

The surveying effort for each stratum varied greatly and tended to be more extensive in the central and southwestern portions of the polynya. There were several reasons for this: 1) Greenland and Canada are further apart in the south than the north, so that there were more sampling stations and longer transect lines in the central and southern parts of the polynya than the northern region; 2) the Greenland government would not allow the ship to approach the Greenland coast closer than 22 km and other planned transects were not permitted, so that surveying could not be done in some of the areas where seal densities were expected to be highest; and 3) it was often not possible to approach as close as desired to the Canadian coastline because of heavy ice conditions and shallow or uncharted water.

Densities of ringed seals were calculated to make comparisons between months, strata, and other studies. To calculate densities, the number of seals seen *on* transect within 600 m of the ship was divided by the total area surveyed (length of transect in kilometres x 600 m). A strip width of 600 m was chosen, since the probability of detecting a seal farther than 600 m is notably reduced (e.g., Gelatt and Siniff 1999), especially when surveying for seals in open water. Sightings of seals in open water were analyzed separately from those seen on ice because the sightability of seals differs in these two circumstances. Densities were calculated as follows:

$$\text{Density}_{\text{ice}} = \text{number of seals seen on ice corrected for time of day/km}^2 \text{ of ice}$$

$$\text{Density}_{\text{water}} = \text{number of seals seen in calm open water/km}^2 \text{ of calm open water}$$

The total number of kilometres surveyed in ice and in water were determined as explained previously for the bathymetric data. The distance surveyed in water was corrected for sea state, since sea state is thought to affect the detection of seals in open water (McLaren 1961). Therefore, only the number of kilometres surveyed in open water ($\leq 4/10$ ice) and the number of seals seen in calm sea states (1 and 2) were used for estimating density. Density calculations for seals seen on the ice were corrected for time of day as described for the utilization test for depth.

Utilization tests were used to determine differential use of strata in the polynya by ringed seals. The total number of ringed seal sightings *on* transect at any distance from the ship (observed values) were compared to the total number of kilometres surveyed (expected values) for each stratum. The utilization test was performed separately on ringed seals seen both on ice and in calm open water. The corresponding numbers of kilometres surveyed on ice and in calm water were used, as for the density calculations. Since seasonal changes in haul-out duration and frequency have been noted in previous studies (e.g., Smith 1973b, Finley 1979, Smith and Hammill 1981, Kelly and Quakenbush 1990, Heide-Jørgensen *et al.* 1992, Teilmann *et al.* 1999, E.W. Born pers. comm.), only ringed seal sightings for June were used to test for differences in habitat utilization for seals seen on ice because that is when maximum haul-out occurs (McLaren 1958b; Smith 1973a,b), and the sample sizes for all other months were small (Table 4-4). The number of seals seen on ice in each stratum were corrected for time of day. For seals seen in open water, all seals seen over all months were pooled, and significance was set at $\alpha \leq 0.05$ for all utilization tests. The "floe edge" surveys were not included in the utilization tests, as marine mammals are known to be more abundant along ice edges (Bradstreet 1982, Stirling 1997), and floe edge surveys were not distributed equitably across strata.

4.3. Ice conditions in the North Water Polynya in spring and summer, 1998

In winter and early spring, the west, east, and north margins of the North Water Polynya are defined by landfast ice edges along eastern Ellesmere Island, northwestern Greenland, and across Smith Sound, whereas the southern limit is delineated by Baffin Bay pack ice (Fig. 4-4). In late spring, the polynya expands, as the pack ice in Baffin Bay drifts southward. During April 1998, most of the polynya was still ice-covered, although open water with drifting pack ice was prevalent in the northern parts of the polynya (Fig. 4-4). During May 1998, the polynya expanded southward and most of the polynya, except for the most southerly areas, were ice-free by the end of the month, with some drifting pack ice (Fig. 4-4). During June 1998, break-up of the landfast ice edges occurred and by June 12, the ice bridge across northern Smith Sound had collapsed, releasing drifting pack ice into the polynya area (Fig. 4-5). By the end of June, the pack ice at the southern margin of the polynya had receded dramatically (Fig. 4-5). In July, the polynya was continuous with the rest of Baffin Bay, with varying amounts of drifting pack ice (Fig. 4-5). The ice conditions within the polynya area for August 1997 and September 1999 were similar to those in July 1998.

4.4. Results

4.4.1. Transect lines

The greatest distance was surveyed in June, followed by April, May, and September respectively, whereas the fewest number of kilometres were surveyed in July and August (Table 4-1). The greatest distance was surveyed along the floe edge in June and July, and the fewest kilometres were surveyed in May (Table 4-1). The number of hours required to conduct the monthly surveys depended on ice conditions and the ship's speed. During April, most surveying took place in ice-covered waters, whereas most surveying took place in open or only partially ice-covered water during May, June, July, August, and September (Table 4-2). During April, June, and July, more surveying in open water was conducted when the seas were calm (1 - 2), whereas more surveying was conducted in rough seas (3 - 5) during May, August, and September (Table 4-3).

4.4.2. Ringed seal distribution and abundance

The fewest numbers of ringed seals were seen during April and May (Table 4-4, Fig. 4-6). The greatest numbers of seals were observed in June (Table 4-4, Fig. 4-7), while an intermediate number of seal sightings were made from July to September (Table 4-4, Figs. 4-7, 4-8). More ringed seals were seen during floe edge surveys in June than in May or July (Table 4-4, Fig. 4-9). For April through June, more seals were seen on ice than in water, whereas between July and September, more seals were seen in the water between July and September (Table 4-4).

Significantly fewer seals were seen than expected on ice in areas where ice cover was ≤ 2/10, and significantly more seals were seen than expected in areas where ice cover was ≥ 3/10 (Table 4-5). Significantly fewer seals were seen than expected in the water in areas where ice cover was ≥ 8/10, and more seals were seen than expected in areas with 3/10 ice cover (Table 4-6). For ringed seals seen in the water in open water areas with ≤ 4/10 ice cover, significantly fewer seals than expected were seen in rougher sea states, whereas more seals than expected were seen in the calmest sea state (Table 4-7). Ringed seals were seen in all depth intervals in June, but fewer seals than expected were seen in water depth < 200 m and 500 - 600 m, whereas more seals than expected due to chance were seen in the depth intervals 200 - 300 m and 600 - 700 m (Table 4-8). The number of seals seen in water depths between 300 - 500 m did not differ from the expected numbers (Table 4-8).

Ringed seals hauled out on ice in June used strata CE and SW more than expected by chance (Table 4-9). Stratum CW was used less than expected by chance, stratum SE was used as expected, and seals were not recorded using the northern strata (Table 4-9). The highest density of seals seen on ice in June occurred in stratum CE followed by strata SW and SE (Table 4-10). Generally, ringed seal densities on ice were lowest in April and May (up to 0.01 seals/km^2) compared to June, August, and September (up to 6.11 seals/km^2) (Table 4-10). Intermediate densities were seen in July (up to 0.28 seals/km^2). Although unexpected, the highest density of ringed seals/km^2 ice was observed in stratum NE in September (Table 4-10). During the months with low ringed seal densities, densities were highest in stratum CW.

The utilization test showed that ringed seals seen in the water were observed in all strata of the polynya as expected, except for stratum SW, in which they were sighted significantly less than expected (Table 4-11). The highest density of ringed seals in the water was observed in stratum NE (Table 4-11). Densities were lowest between April and June (up to 0.02 seals/km^2) and highest between July and September (up to 0.24 seals/km^2) (Table 4-12). The highest densities of ringed seals seen in the water were observed in strata NE and CW in August. Relatively high densities were also seen in strata CE and CW in September and in stratum NE in July (Table 4-12). From April to June, the highest densities were seen in strata NW, SW, and SE.

4.5. Discussion

4.5.1. Effect of ice cover, sea state, and water depth on ringed seal observations

Ringed seals are known to prefer to haul out in areas of high ice cover (Stirling *et al.* 1982, Kingsley *et al.* 1985, Lunn *et al.* 1997). Similarly, in the polynya, ringed seals were more frequently seen hauled out on ice in areas where the ice cover was 3/10 or greater. In contrast, seals were more likely to be seen in the water if the ice cover was less than 8/10 which, to some degree, may simply have been a reflection of more open water in which to search for seals. More seals were likely seen on the ice than in the water between April and June, since there were still large amounts of drifting pack ice within the polynya during this period. By July, most of the polynya was ice-free and thus most seals were seen in the water.

A rough sea state may affect the ability of the observer to detect seals in open water because of high swells and whitecaps. Therefore, McLaren (1961) suggested that all shipboard surveying be conducted in flat, calm water when possible. Because of the opportunistic nature of this study, and because I wanted to evaluate the merit of surveying for seals in different conditions, I decided to survey during all opportunities regardless of sea state. Only 6% of seals observed were seen in rough waters (Table 4-7); thus, detection appeared to be best in sea states of 1, as suggested by McLaren (1961).

Analysis of data collected from aerial surveys of ringed seals hauled out on the ice in June in the Canadian High Arctic (Kingsley *et al.* 1985) and in the Beaufort Sea (Stirling *et al.* 1982) indicated that ringed seals tended to avoid water deeper than 175 m, although no explanation for this pattern of distribution was speculated upon. Most other aerial surveys simply noted a preference for landfast ice, as opposed to pack ice which, coincidentally, mainly lies over relatively shallow water over the continental shelf, and made no further attempts to quantify other habitat preferences (e.g., Burns and Harbo 1972; Smith 1973a,b). Although ringed seals are capable of diving to depths of more than 250 m (Teilmann *et al.* 1999), benthic prey does not typically constitute a large proportion of their diet (Weslawski *et al.* 1994). Thus, it is not apparent why water depth should have a direct effect on the distribution of ringed seals. In the North Water Polynya, ringed seals were frequently seen in water deeper than 200 m and ranging up to 700 m. This apparent contradiction might indicate that, if ringed seals do show preferences for water depth in some areas, the phenomenon is site specific or, more likely, that water depth is not a critical determinant of habitat preferences.

Since polar bears are mainly dependent on ringed seals for food (Stirling and Archibald 1977, Stirling and Ørtisland 1995), and there is a close relationship between the size of polar bear and seal populations resident in the same area (Stirling and Øritsland 1995), it is reasonable to expect that the seasonal distribution of polar bears would be indicative of areas where the greatest number of seals are located (DeMaster and Stirling 1981). For example, in the southern Beaufort Sea, polar bear movements are predominantly within 250 - 300 km of the coast (Amstrup and Gardner 1994), where ringed seal densities are greatest and water is relatively shallow (Stirling *et al.* 1982). In contrast, polar bears are abundant throughout central Baffin Bay (M.K. Taylor pers. comm., Ferguson *et al.* 1998), where ice is present and depths range between 500 to 2400 m, which suggests that seals are abundant there as well. In surveys reported by Finley *et al.* (1983) and this study, ringed seals were found to be abundant in the pack ice of Baffin Bay, which explains why the polar bears are there and also suggests that depth by itself is not a significant factor determining the distribution of ringed seals.

In the Arctic, photosynthesis and primary production are dependent on ice cover and thickness. Biological productivity is typically higher in areas where the ice cover melts early in the season or where ice thickness is reduced, because more sunlight penetrates the ice (Cross 1982, Subba Rao and Platt 1984, Legendre *et al.* 1992). In the southern Beaufort Sea, where depth preferences appeared to be indicated, seals were most abundant in annual ice over the continental shelf (Stirling *et al.* 1982), where productivity is likely highest. Further offshore than about 250 - 300 km, where both seals and polar bears were not abundant (Stirling *et al.* 1982, Amstrup and Gardner 1994), thick multiyear ice predominates over the deep polar basin where biological productivity is greatly reduced (Pomeroy 1997, Gosselin *et al.* 1997). In contrast, the deep waters in central Baffin Bay are covered in annual ice and receive water from the North Water Polynya and polynyas of Jones and Lancaster Sound, where upwelling and mixing have occurred and biological productivity in the water column is higher than in the deep polar basin (Subba Rao and Platt 1984). The algae that is able to grow under annual sea ice (epontic algae) can sustain large populations of sub-ice amphipods and Arctic cod (*Boreogadus saida*), which are primary food sources for ringed seals (Bradstreet 1982, Bradstreet and Cross 1982, Welch *et al.* 1992). Epontic and general biological productivity in the water column are likely higher under the annual ice of Baffin Bay compared to the thick multiyear ice in offshore areas of the Beaufort Sea. Thus, biological productivity under the ice is a more likely determinant of ringed seal distribution than water depth and probably explains the abundance of ringed seals in the deep areas of Baffin Bay.

4.5.2. Temporal differences in observations of ringed seals in the North Water Polynya

Ringed seal distribution is not restricted by ice cover, since ringed seals are able to maintain breathing holes in the ice using the claws on their front flippers, and are known to be resident in and adjacent to the North Water Polynya throughout the year (Vibe 1950, McLaren 1958b). However, the numbers of seals seen on the ice in April and May were low. Similarly, during aerial surveys in the North Water Polynya along the floe edge in March and April, Finley and Renaud (1980) only saw 11 ringed seals, most of which were swimming in leads, areas of open water, along the landfast ice.

Although there was still extensive ice coverage throughout the polynya in April and May, the small number of sightings indicates that, as in other areas, ringed seals haul out on the ice infrequently at that time of year (Kelly and Quakenbush 1990, E.W. Born pers. comm.). This was likely related to low ambient temperatures in April, as ringed seals generally prefer to haul out onto ice when conditions are calm, sunny, and warm (Smith 1973a, Finley 1979, Smith and Hammill 1981, Stirling *et al.* 1982, Kingsley *et al.* 1985). In addition, during April and May, adult ringed seals are likely to stay in bays and fiords where landfast ice is available for breeding and pupping (McLaren 1958a). Heide-Jørgensen *et al.* (1990) found that ringed seals remained within their landfast ice habitat in western Greenland until late June to early July and then dispersed widely. Although subadult seals are usually excluded from the preferred breeding habitat in the landfast ice (McLaren 1958b; Smith 1973b, 1987; Smith and Stirling 1975), they are likely to stay near the floe edge and adjacent offshore pack ice areas (Burns and Harbo 1972). As well, the landfast ice edge is thought to have higher levels of primary production than surrounding areas (e.g., McRoy and Goering 1976, Cross 1982). Under-ice fauna may concentrate along these ice edges and provide a rich food source for ringed seals (Bradstreet and Cross 1982), so that ringed seal densities may be higher in these areas (e.g., Gulliksen 1984). Thus, seals were likely less available to be surveyed within the polynya, since most of the surveying there was done in offshore areas and not close to the landfast ice. However, several studies have suggested that breeding populations of ringed seals are present in the Baffin Bay pack as well as on the landfast ice (Koski and Davis 1979, Finley *et al.* 1983). This does not seem to be the case for the mostly open water areas of the polynya.

In June, a general movement of seals from the landfast ice to offshore areas occurs (Heide-Jorgensen *et al.* 1990). As expected, the greatest numbers of seals on ice were seen at this time, as the maximum number of seals haul out on the ice to molt then (McLaren 1958b; Smith 1973a,b). During the molt, ringed seals haul out more frequently (e.g., Smith 1973b, 1987). Ringed seals typically spend about 50% of the day on the ice (Kelly and Quakenbush 1990, Heide-Jørgensen *et al.* 1992, E.W. Born pers. comm.), although some individuals may remain hauled out for as long as 48 hrs. (Finley 1979). Most seals counted in June were seen in the southern part of the polynya, where considerable amounts of ice to haul out on were still available. During aerial surveys in June of the southwestern portion of the North Water Polynya east of Devon Island, Koski and Davis (1979) observed densities of up to 20 seals/km^2. In contrast, Koski (1980) observed fewer seals in June than in May, with most areas being devoid of seals and some areas with densities only ranging up to 0.5 seals/km^2, which is similar to the density calculated for that area in this study.

Sightings in open water were low in all months, partially because it is more difficult to spot seals in water than on the ice. During July, August, and September, the months with the greatest numbers and densities of seals in the water, most of the polynya was ice-free, as indicated by the high survey effort in open water during these months (Table 4-2). In addition, seals do not tend to haul out onto the ice as much between July and September (Heide-Jørgensen *et al.* 1990, Lydersen 1991) because of the intense feeding that occurs at this time to prepare for winter and to replace energy used for reproduction and molting (Lowry *et al.* 1980). Ringed seals may also have emigrated out of the polynya (e.g., Heide-Jørgensen *et al.* 1992, Kapel *et al.* 1998) to follow the ice southward or to find new feeding areas closer to shore, where survey effort in this study was limited. However, aerial surveys conducted over Baffin Bay in August and September of 1978 and 1979 suggested that ringed seals leave offshore areas for coastal waters when the ice disappears in late summer (Koski and Davis 1979, 1980; Koski 1980). During aerial surveys in the southwestern portion of the North Water Polynya in July 1979, Koski (1980) only observed ringed seals close to the shore of Devon Island and the highest densities (up to 5 seals/km^2) were seen in eastern Lancaster Sound south of Devon Island. In contrast, during surveys of the same area in July 1978, ringed seal densities up to 5 seals/km^2 were seen east of Devon Island (Koski and Davis 1979).

Heide-Jørgensen *et al.* (1990) tracked ringed seals via satellite and found that they dispersed widely after the landfast ice broke up around the end of June, although most showed fidelity to the polynya (Teilmann *et al.* 1999). Little is known about the seasonal movements of ringed seals, but several studies have shown that ringed seals are capable of moving long distances of 1000 km or more during the summer months (Kapel *et al.* 1998, Heide-Jørgensen *et al.* 1990, Teilmann *et al.* 1999). However, further investigation by satellite tracking or telemetry is necessary to determine the movement patterns of both subadult and adult ringed seals.

4.5.3. Ringed seal distribution and abundance in the North Water Polynya

The northern strata of the North Water Polynya typically showed lower ringed seal densities than the central or southern strata. Similarly, Kingsley *et al.* (1985) noted that ringed seal densities were lower in northern areas of the Canadian High Arctic, and suggested that this was because these areas receive cold nutrient-poor water from the polar basin and are covered by thick ice. The northern strata of the polynya are likely less productive than the more southerly strata because of the influence of cold and biologically unproductive water that comes from the polar basin and enters the polynya through Smith Sound.

Vibe (1950) suggested that the overall abundance of animals was greater on the east side of the polynya than the west side, because of the nutrient-rich currents that enter the polynya there. In this study, the density of ringed seals seen on the ice in June was twice as high in stratum CE compared to SW and SE, and about three times as high as in stratum CW (Table 4-10). Correspondingly, the utilization test showed that ringed seals on ice were seen in strata CE and SW more than expected due to chance (Table 4-9), and that ringed seals were seen in stratum SE as expected. However, it seems anomalous that ringed seals in the water were seen less than expected in the southwestern stratum, though this may simply be a result of low sample sizes.

It is uncertain why ringed seals used stratum CE more than other areas in the polynya and that densities of seals were highest here, though it may be, as predicted by the underlying hypothesis of this study, that productivity was significantly greater on the east side of the polynya than the west side. If so, increased productivity in this area may have caused an increase in food availability and a consequent increase in abundance of ringed seals in this area. Studies have already shown that far greater numbers of dovekies (*Alle alle*) and other seabirds breed on the east side of the North Water Polynya compared to the west, likely because of increased food abundance on that side (Nettleship and Evans 1985, Boertmann and Mosbech 1998). In their study of satellite-tagged ringed seals, Teilmann *et al.* (1999) noted a tendency for the seals to stay in the eastern part of the polynya where they had been tagged. They speculated that this may be due to the increased productivity on the east side. Indeed, increased biological productivity has already been demonstrated to exist on the east side of the polynya, at least for the month of May, when the spring bloom occurs (Lewis *et al.* 1996). On the west side of the polynya, the bloom does not occur until June (L. Legendre, unpublished data). Productivity may have also been higher in the southwestern stratum than in other strata, with the exception of stratum CE, because this area receives nutrient-rich water from the centre of the polynya, as well as from Jones Sound.

Ringed seals are believed to be generalist feeders (McLaren 1958b, Fedoseev 1965, Johnson *et al.* 1966, Lowry *et al.* 1978, Weslawski *et al.* 1994); thus, McLaren (1958b) suggested that they are likely not food limited. In contrast, Lowry *et al.* (1980) suggested that prey species that occur in concentrations, such as Arctic cod and *Themisto libellula*, are of particular importance in the ringed seal diet, and when these kinds of prey are unavailable, seals may be food-limited at certain times or in certain areas. Lowry *et al.* (1980) suggested that in the summer, ringed seals are concentrated in areas where hyperiid amphipods, such as *T. libellula*, are abundant and Chapskii (1940) found a direct relationship between the relative abundance of ringed seals and Arctic cod in the Siberian Arctic.

Preliminary analyses of zooplankton tows conducted in the North Water Polynya, do not show any significant differences between the east and west sides of the polynya in the densities of all zooplankton, amphipods, or *T. libellula*, an important prey species of ringed seals (L. Fortier, unpublished data, Appendices C, G, and F respectively). The abundance and distribution of fish prey species within the North Water Polynya, mainly Arctic cod and polar cod (*Arctogadus glacialis*) are unknown, but likely play important roles in ringed seal distribution and abundance. Smith (1987) and Harwood and Stirling (1992) demonstrated that ringed seals aggregated in summer into groups of up to 30 animals to feed in areas with apparently high concentrations of food. No such aggregations were seen during this survey. Although a difference in biological productivity between the two sides of the polynya could cause increased food abundance on one side over the other, it could also cause differences in the types of prey species available to ringed seals in these areas, as described in Chapter 3. McLaren (1958b, 1962) suggested that ringed seal distribution and abundance were less driven by food resources than by ice condition, with the rationale that ringed seals were sometimes scarce in areas where food was abundant and common in areas of low productivity. It seems likely that areas where ringed seals hauled out on ice are abundant have greater productivity below the ice and thus greater ice-associated prey abundance than areas where ringed seals occur at low densities or are absent.

4.5.4. Limitations of shipboard and aerial surveys for ringed seals

Few shipboard surveys have been conducted to assess ringed seal populations with some notable exceptions (e.g., McLaren and Mansfield 1960; McLaren 1958a, 1961; Zyryanov and Kondakov 1994). In general, shipboard surveys have been shown to be mostly ineffective to determine ringed seal densities (e.g., McLaren 1958a), as ringed seals spend most of their time underwater (McLaren 1961, Heide-Jørgensen *et al.* 1990, Lydersen 1991). In addition, it is difficult to see seals unless sea conditions are ideal; that is, when the sea is relatively smooth and there is no glare (e.g., McLaren 1958a). Thus, I expected that open-water surveys would lead to lower density estimates than surveys conducted in ice-covered waters, as indicated in Tables 4-12 and 4-10 respectively. Although corrections could be made to account for the availability bias of submerged ringed seals during open water surveys (e.g., McLaren 1958a, 1961; Marsh and Sinclair 1989), they are believed to underestimate densities. Because sample sizes in this study were small, an attempt to correct densities seemed unwarranted. Since this study was a comparison of the relative densities of ringed seals within the polynya, I assumed that the effect of submerged animals on survey numbers were similar for each area; thus, I did not deal with this factor in the analyses.

In contrast, aerial surveys for ringed seals hauled out on ice to molt in June are widely used and considered to be the most effective way to evaluate the distribution and abundance of seals (e.g., Burns and Harbo 1972, Stirling *et al.* 1977, Finley *et al.* 1983, Kingsley *et al.* 1985, Lunn *et al.* 1997). Aerial surveys are generally conducted in June, when the maximum number of seals are hauled out on the ice to molt (McLaren 1958b; Smith 1973a,b). Densities of ringed seals are typically higher in landfast ice than in pack ice (Kingsley *et al.* 1985, Finley *et al.* 1983, Lunn *et al.* 1997). Only one study has used aerial surveys to assess the distribution and abundance of ringed seals over open water (Harwood and Stirling 1992).

Ringed seal densities on the pack ice of stratum CE in the North Water Polynya in June (Table 4-10) were similar to those determined by aerial surveys for the pack ice of other polynya areas in the Canadian High Arctic (Kingsley *et al.* 1985) and Baffin Bay (Finley *et al.* 1983). Ringed seal densities in the pack ice of strata CW, SW, and SE in the North Water Polynya in June were at the lower end of the range of densities calculated for polynya areas in the eastern Canadian High Arctic, but were generally higher than reported for non-polynya areas (Kingsley *et al.* 1985). Thus, the seal densities I calculated from shipboard surveys of seals hauled out on the ice in June in the North Water Polynya are comparable to those from aerial surveys in adjacent areas. Therefore, shipboard surveys appear to be an effective method of surveying for seals hauled out on ice and can be used for making comparisons between seal densities within the polynya.

4.5.5. The effect of ship noise on ringed seal behaviour

The icebreaker may have affected ringed seal behaviour, thereby influencing the number of seals seen from the vessel, especially in open water. Richardson *et al.* (1995) reviewed the subject of the effect of noise on marine mammals, but cautioned that most observations are anecdotal. For example, Brueggeman *et al.* (1992) noticed that ringed seals hauled out on ice often show escape reactions when an icebreaker breaking ice approached within about 1 km, but that seals were less sensitive when the ship was moving in open water. Similarly, Kanik *et al.* (1980) found that most ringed seals 1 km or more from the icebreaker remained hauled out, whereas seals closer to the icebreaker dove into the water. In the present study, I observed that ringed seals, hauled out on ice up to 1 km or more ahead of the ship, sometimes dove into the water in response to the approaching vessel whether it was breaking ice or not. Fortunately, since most ringed seals are easily spotted on the ice up to several kilometres away, the ship probably did not have a significant effect on counts of seals on ice. How the ship may have affected the sightability of ringed seals in water is uncertain, although several seals were observed as close as 50 m. Similarly, Brewer *et al.* (1993) observed ringed seals feeding in the ship's track, close behind icebreakers. However, Smultea *et al.* (1999) observed that ringed seals tended to keep their distance from playbacks of icebreaker noise and that seals tended to linger longer in an area with no playbacks. Thus, the behaviour of ringed seals in response to icebreakers is variable and it is uncertain what effect it may have had on distribution or density estimates reported here. However, since the same survey platform was used for all observations, I considered whatever effect the ship had on ringed seal behaviour to be constant throughout the study area and survey period.

4.6. Conclusions

Ringed seal distribution and abundance in the North Water Polynya are likely governed by a combination of factors, including productivity, prey abundance, and ice condition. It is evident that the effectiveness of shipboard surveys for counting seals in open water is limited. However, if it is not possible to conduct aerial surveys, shipboard surveys for ringed seals on ice may be an effective method for determining distribution and relative abundance during June, when the greatest number of animals haul out on the ice to molt (McLaren 1958a; Smith 1973a,b). With regards to the east/west comparison, aerial surveys of ringed seals in both landfast ice and pack ice would probably have been a more effective way of quantifying differences in densities, since densities are usually higher in landfast ice (Kingsley *et al.* 1985, Finley *et al.* 1983, Lunn *et al.* 1997), and the number of variables affecting seal distribution would have been reduced (e.g., water depth and ice cover). However, due to the opportunistic survey design of this study and the limitations imposed by the Greenland government, it was not possible to survey the landfast ice.

Generally, greater numbers and densities of ringed seals were seen in the central-eastern stratum of the polynya compared to other areas, which may reflect increased productivity and thus food availability in the eastern portion of the polynya. Similarly, high densities of ringed seals in the southwestern stratum may be due to higher levels of productivity in that area. However, increased food availability on the east side of the North Water Polynya, although apparently likely, has not yet been demonstrated.
This study shows that the habitat preferences of ringed seals are complex and variable. More studies involving satellite tagging and tracking of these animals may provide a better understanding of their habitat preferences and movements.

4.7. Literature cited

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Table 4-1: The total number of hours and kilometres surveyed during regular surveys and "floe edge" surveys for each month.

	Month	Hours surveyed	Distance surveyed (km)
Regular surveys			
	April	131.6	2438.9
	May	118.2	2178.2
	June	120.7	2756.3
	July	87.8	1918.2
	August	138.1	1836.0
	September	117.0	2084.1
Floe edge surveys			
	May	0.6	54.7
	June	19.5	369.2
	July	7.1	127.8

Table 4-2: The number of kilometres surveyed in water and in ice during each month.

Strata	Distance surveyed (km)	% of Distance surveyed in water (≤ 4/10 ice)	% of Distance surveyed in ice (≥ 5/10 ice)
April	2438.9	4	96
May	2178.2	66	34
June	2756.3	72	28
July	1918.2	91	9
August	1836.0	89	11
September	2084.1	88	12

Table 4-3: The number of kilometres surveyed in open water (≤ 4/10 ice) during rough (≥ 3) and calm (≤ 2) sea states for each month.

Month	Distance surveyed (km)	% of distance surveyed in poor seastate	% of distance surveyed in good seastate
April	85.7	35	65
May	1435.2	60	40
June	1974.7	32	68
July	1752.7	16	84
August	1629.1	58	42
September	1843.4	61	39

Table 4-4: Total numbers of ringed seals seen *on* and *off* transect on ice or in water during each month and the number of ringed seals seen during floe edge surveys between May and July, 1998.

Month	On transect	On ice	In water
April	9	6	3
May	11	6	5
June	517	508	9
July	54	19	35
August	69	11	58
September	75	14	61
	Off transect		
April	8	2	6
May	2	1	1
June	82	80	2
July	13	11	2
August	1	0	1
September	13	0	13
	Floe edge		
May	0		
June	15		
July	4		

Table 4-5: Differential use of areas with different ice coverages by ringed seals seen *on*-transect on ice (n = 539) during 13211.7 km of surveying. Observations are pooled over months. Tests are based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Ice Cover	**Survey effort in km; effort ratio (p_{io})**	**Number; proportion of ringed seals observed (p_i)**	**Confidence interval on observed proportion of occurrence (p_i)**	**Significance**
0/10	5339.4 (0.404)	0 (0.000)	$0.000 \leq p_1 \leq 0.000$	N/A
1/10	2009.7 (0.152)	2 (0.004)	$-0.004 \leq p_2 \leq 0.011$	Lower
2/10	450.3 (0.034)	6 (0.011)	$-0.002 \leq p_3 \leq 0.024$	Lower
3/10	409.0 (0.031)	92 (0.171)	$0.125 \leq p_4 \leq 0.217$	Higher
4/10	342.4 (0.026)	36 (0.067)	$0.036 \leq p_5 \leq 0.097$	Higher
5/10	427.9 (0.032)	38 (0.071)	$0.039 \leq p_6 \leq 0.102$	Higher
6/10	91.2 (0.014)	27 (0.050)	$0.023 \leq p_7 \leq 0.077$	Higher
7/10	326.6 (0.025)	12 (0.022)	$0.004 \leq p_8 \leq 0.040$	NS
8/10	890.7 (0.067)	149 (0.276)	$0.222 \leq p_9 \leq 0.331$	Higher
9/10	2404.2 (0.182)	174 (0.323)	$0.266 \leq p_{10} \leq 0.380$	Higher
10/10	420.3 (0.032)	14 (0.026)	$0.006 \leq p_{11} \leq 0.045$	NS
Total	13211.7 (1.000)	539 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
Higher - the observed use is significantly higher than expected use.
NS - the observed use did not differ from expected use.
N/A - not applicable since no seals were seen.

Table 4-6: Differential use of areas with different ice coverages by ringed seals seen *on* transect in the water (n = 171) during 13211.7 km of surveying. Observations are pooled over months. Test is based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Ice Cover	**Survey effort in km; effort ratio (p_{io})**	**Number; proportion of ringed seals observed (p_i)**	**Confidence interval on observed proportion of occurrence (p_i)**	**Significance**
0/10	5339.4 (0.404)	64 (0.374)	$0.269 \leq p_1 \leq 0.479$	NS
1/10	2009.7 (0.152)	37 (0.216)	$0.127 \leq p_2 \leq 0.306$	NS
2/10	450.3 (0.034)	16 (0.094)	$0.030 \leq p_3 \leq 0.157$	NS
3/10	409.0 (0.031)	18 (0.105)	$0.039 \leq p_4 \leq 0.172$	Higher
4/10	342.4 (0.026)	5 (0.029)	$-0.007 \leq p_5 \leq 0.066$	NS
5/10	427.9 (0.032)	12 (0.070)	$0.015 \leq p_6 \leq 0.126$	NS
6/10	191.2 (0.014)	3 (0.018)	$-0.011 \leq p_7 \leq 0.046$	NS
7/10	326.6 (0.025)	2 (0.012)	$-0.012 \leq p_8 \leq 0.035$	NS
8/10	890.7 (0.067)	5 (0.029)	$-0.007 \leq p_9 \leq 0.066$	Lower
9/10	2404.2 (0.182)	9 (0.053)	$0.004 \leq p_{10} \leq 0.101$	Lower
10/10	420.3 (0.032)	0 (0.000)	$0.000 \leq p_{11} \leq 0.000$	N/A
Total	13211.7 (1.000)	171 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
Higher - the observed use is significantly higher than expected use.
NS - the observed use did not differ from expected use.
N/A - not applicable since no seals were seen.

Table 4-7: Sightability of ringed seals seen *on* transect (n = 149) in different sea states during a total of 8720.8 km of surveying in open water ($\leq$ 4/10 ice cover). Sea states 1 and 2 are considered good and sea states 3 to 5 are considered poor (see text for further explanation). Test is based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Sea State	Survey effort in km; effort ratio (p_{io})	Number; proportion of ringed seals observed (p_i)	Confidence interval on observed proportion of occurrence (p_i)	Significance
1	2449.5 (0.281)	106 (0.711)	$0.616 \leq p_1 \leq 0.807$	Higher
2	2336.2 (0.268)	34 (0.228)	$0.140 \leq p_2 \leq 0.317$	NS
3	1510.5 (0.173)	5 (0.034)	$-0.004 \leq p_3 \leq 0.072$	Lower
4	1339.0 (0.154)	1 (0.007)	$-0.011 \leq p_4 \leq 0.024$	Lower
5	1085.6 (0.124)	3 (0.020)	$-0.009 \leq p_5 \leq 0.050$	Lower
Total	8720.8 (1.000)	149 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
Higher - the observed use is significantly greater than expected use.
NS - the observed use did not differ from expected use.

Table 4-8: Differential use of depths in the polynya by ringed seals seen *on* transect hauled out on ice (n = 508) during a total of 744.5 km of surveying in ice in June. Ringed seal numbers were corrected for diurnal haul-out. Tests are based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Depth (m)	Survey effort in km; effort ratio (p_{io})	Number; proportion of ringed seals observed (p_i)	Confidence interval on observed proportion of occurrence (p_i)	Significance
< 200	20.5 (0.028)	3 (0.004)	$-0.002 \leq p_1 \leq 0.009$	Lower
200 - 300	34.4 (0.046)	106 (0.128)	$0.098 \leq p_2 \leq 0.159$	Higher
300 - 400	131.0 (0.176)	137 (0.166)	$0.132 \leq p_3 \leq 0.200$	NS
400 - 500	146.0 (0.196)	173 (0.209)	$0.172 \leq p_4 \leq 0.246$	NS
500 - 600	359.5 (0.483)	334 (0.404)	$0.359 \leq p_5 \leq 0.449$	Lower
600 - 700	53.1 (0.071)	74 (0.089)	$0.063 \leq p_6 \leq 0.116$	NS
Total	744.5 (1.000)	827 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
Higher - the observed use is significantly greater than expected use.
NS - the observed use did not differ from expected use.

Table 4-9: Differential use of polynya strata by ringed seals seen *on* transect hauled out on ice (n = 827) during a total of 744.5 km of surveying in ice in June. Ringed seal numbers are adjusted for time of day. Tests are based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Strata	**Survey effort in km; effort ratio (p_{io})**	**Number; proportion of ringed seals observed (p_i)**	**Confidence interval on observed proportion of occurrence (p_i)**	**Significance**
NW	12.8 (0.017)	0 (0.000)	N/A	N/A
NE	0.2 (0.000)	0 (0.000)	N/A	N/A
CW	105.6 (0.142)	43 (0.052)	$0.032 \leq p_3 \leq 0.072$	Lower
CE	32.3 (0.043)	89 (0.108)	$0.079 \leq p_4 \leq 0.136$	Higher
SW	113.1 (0.152)	192 (0.232)	$0.193 \leq p_5 \leq 0.271$	Higher
SE	480.5 (0.646)	503 (0.608)	$0.563 \leq p_6 \leq 0.653$	NS
Total	744.5 (1.000)	827 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
Higher - the observed use is significantly greater than expected use.
NS - the observed use did not differ from expected use.
N/A - not applicable since no seals were seen.

Table 4-10: Density of ringed seals (*Ph*) per km^2 of ice sampled for each strata of each month, adjusted by diurnal haul-out. Numbers in brackets under columns 'Adusted # of *Ph* seen on ice' and '# of *Ph* seen per km of ice' are the actual number of ringed seals seen.

Month	Stratum	Adjusted # of *Ph* seen on ice	Distance surveyed (km)	Distance surveyed in ice (km)	# of *Ph* seen per km of ice	# of *Ph* seen within 600m	Density of *Ph*/km^2 ice
April	NW	0 (0)	403.0	342.2	0.000	0 (0)	0.000
	NE	0 (0)	14.6	11.6	0.000	0 (0)	0.000
	CW	8 (6)	1200.5	995.0	0.008	4 (3)	0.007
	CE	0 (0)	425.3	355.6	0.000	0 (0)	0.000
	SW	0 (0)	168.1	155.4	0.000	0 (0)	0.000
	SE	0 (0)	227.4	198.6	0.000	0 (0)	0.000
May	NW	1 (1)	429.4	206.3	0.005	1 (1)	0.008
	NE	0 (0)	0.0	0.0	0.000	0 (0)	-
	CW	7 (5)	1113.0	399.9	0.018	3 (2)	0.013
	CE	0 (0)	354.8	2.5	0.000	0 (0)	0.000
	SW	0 (0)	184.6	44.6	0.000	0 (0)	0.000
	SE	0 (0)	96.4	5.6	0.000	0 (0)	0.000
June	NW	0 (0)	261.2	12.8	0.000	0 (0)	0.000
	NE	0 (0)	9.4	0.2	0.000	0 (0)	0.000
	CW	43 (28)	764.0	105.6	0.407	22 (14)	0.347
	CE	89 (45)	251.4	32.3	2.755	21 (11)	1.084
	SW	192 (127)	676.6	113.1	1.698	37 (19)	0.545
	SE	503 (308)	793.7	480.5	1.047	159 (96)	0.552
July	NW	0 (0)	127.4	25.4	0.000	0 (0)	0.000
	NE	0 (0)	12.3	1.2	0.000	0 (0)	0.000
	CW	11 (6)	395.9	48.0	0.229	8 (4)	0.278
	CE	4 (2)	131.1	12.9	0.310	0 (0)	0.000
	SW	16 (8)	757.2	42.4	0.377	4 (2)	0.157
	SE	6 (3)	494.3	143.8	0.042	2 (1)	0.023
August	NW	6 (3)	167.2	27.7	0.217	6 (3)	0.361
	NE	2 (1)	106.4	44.1	0.045	2 (1)	0.076
	CW	8 (4)	609.7	74.4	0.108	2 (1)	0.045
	CE	0 (0)	473.6	43.9	0.000	0 (0)	0.000
	SW	6 (3)	369.3	15.5	0.387	4 (2)	0.430
	SE	0 (0)	109.8	0.0	0.000	0 (0)	-
September	NW	0 (0)	244.6	63.5	0.000	0 (0)	0.000
	NE	22 (11)	120.2	6.0	3.667	22 (11)	6.111
	CW	1 (1)	385.2	141.8	0.007	1 (1)	0.012
	CE	0 (0)	650.2	47.7	0.000	0 (0)	0.000
	SW	2 (2)	359.9	17.7	0.113	2 (2)	0.188
	SE	0 (0)	324	12.2	0.000	0 (0)	0.000

Table 4-11: Differential use of polynya strata by ringed seals seen *on* transect in water (n = 161) during 5258.6 km of surveying in calm water with sea states of 1 & 2. Observations are pooled over months. Tests are based on individual comparisons of observed proportions (p_i) to expected proportions (p_{io}).

Strata	**Survey effort in km; effort ratio (p_{io})**	**Number; proportion of ringed seals observed (p_i)**	**Confidence interval on observed proportion of occurrence (p_i)**	**Significance**
NW	668.5 (0.127)	18 (0.112)	$0.046 \leq p_1 \leq 0.177$	NS
NE	66.6 (0.013)	5 (0.031)	$-0.005 \leq p_2 \leq 0.067$	NS
CW	1439.2 (0.274)	50 (0.311)	$0.214 \leq p_3 \leq 0.407$	NS
CE	980.9 (0.186)	28 (0.174)	$0.095 \leq p_4 \leq 0.253$	NS
SW	1319.4 (0.251)	26 (0.161)	$0.085 \leq p_5 \leq 0.238$	Lower
SE	784.0 (0.149)	34 (0.211)	$0.126 \leq p_6 \leq 0.296$	NS
Total	5258.6 (1.000)	161 (1.000)		

Note: Lower - the observed use is significantly lower than expected use.
NS - the observed use did not differ from expected use.

Table 4-12: Density of ringed seals (*Ph*) per km^2 of calm water (sea states 1 & 2) sampled for each strata of each month.

Month	Stratum	# of *Ph* in water	Distance surveyed (km)	Distance surveyed in calm water (km)	# of *Ph* seen per km of water	# of *Ph* seen within 600m	Density of *Ph*/km^2 calm water
April	NW	2	403.0	60.8	0.033	1	0.027
	NE	0	14.6	3.0	0.000	0	0.000
	CW	1	1200.5	176.5	0.006	1	0.010
	CE	0	425.3	69.7	0.000	0	0.000
	SW	0	168.1	12.7	0.000	0	0.000
	SE	0	227.4	27.6	0.000	0	0.000
May	NW	4	429.4	188.1	0.021	2	0.018
	NE	0	0.0	0.0	0.000	0	-
	CW	0	1113.0	215.9	0.000	0	0.000
	CE	0	354.8	207.1	0.000	0	0.000
	SW	0	184.6	94.8	0.000	0	0.000
	SE	0	96.4	54.5	0.000	0	0.000
June	NW	0	261.2	152.8	0.000	0	0.000
	NE	0	9.4	9.2	0.000	0	0.000
	CW	1	764.0	341.5	0.003	1	0.005
	CE	0	251.4	139.0	0.000	0	0.000
	SW	5	676.6	463.3	0.011	5	0.018
	SE	3	793.7	241.7	0.012	3	0.021
July	NW	2	127.4	73.9	0.027	2	0.045
	NE	1	12.3	11.1	0.090	1	0.150
	CW	3	395.9	344.2	0.009	3	0.015
	CE	3	131.1	113.5	0.026	3	0.044
	SW	12	757.2	560.4	0.021	11	0.033
	SE	14	494.3	300.1	0.040	12	0.067
August	NW	8	167.2	92.9	0.086	8	0.144
	NE	3	106.4	20.5	0.146	3	0.244
	CW	28	609.7	186.0	0.151	26	0.233
	CE	9	473.6	236.4	0.038	8	0.056
	SW	8	369.3	138.2	0.058	6	0.072
	SE	0	109.8	0.0	0.000	0	-
September	NW	2	244.6	100.0	0.020	2	0.033
	NE	1	120.2	22.8	0.044	1	0.073
	CW	17	385.2	175.1	0.097	17	0.162
	CE	16	650.2	215.2	0.074	16	0.124
	SW	2	359.9	50.0	0.040	2	0.067
	SE	17	324.0	160.1	0.106	17	0.177

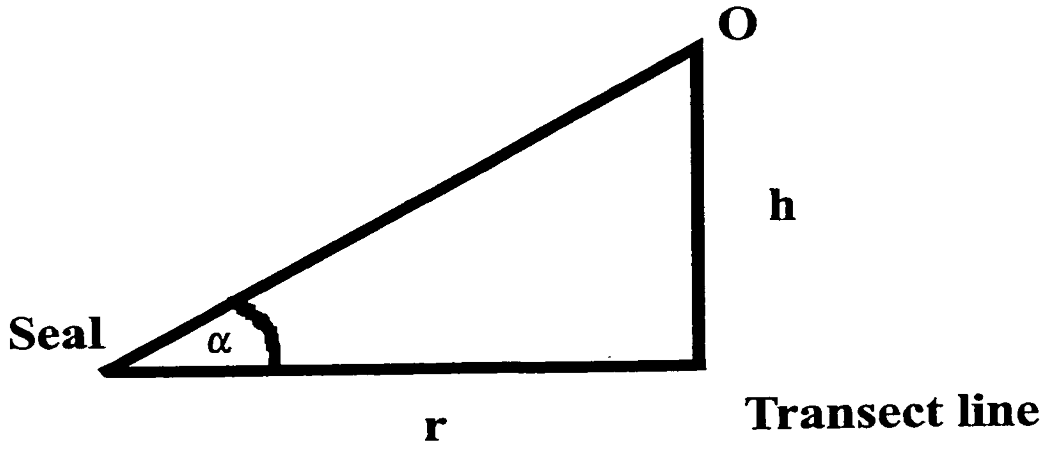


Figure 4-1: Diagram of the method used to determine the sighting distance of a seal to the ship. **O** is the point at which the observer firsts detects the seal. The height of the bridge above the waterline is denoted by **h** and the angle of inclination is denoted by α. The sighting distance (**r**) is calculated as $r = h[\cot(\alpha)]$.

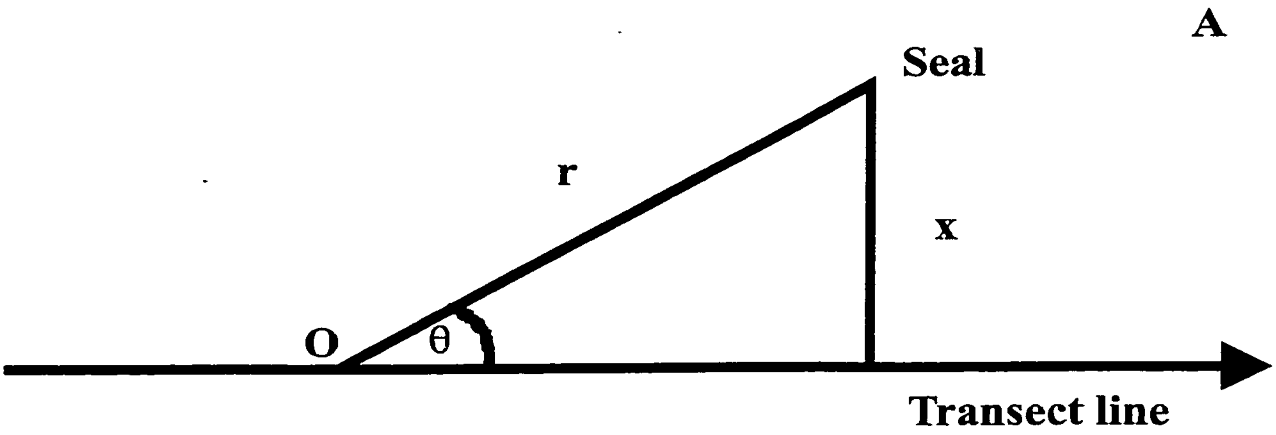


Figure 4-2: Diagram of the trigonometric method used to determine the perpendicular distance of a seal to the ship. **A** is the area being surveyed. **O** is the point at which the observer first detects the seal. The sighting distance is denoted by r and the sighting angle is denoted by θ. The perpendicular distance of the seal to the ship's track, **x**, is calculated as $x = r[\sin(\theta)]$.

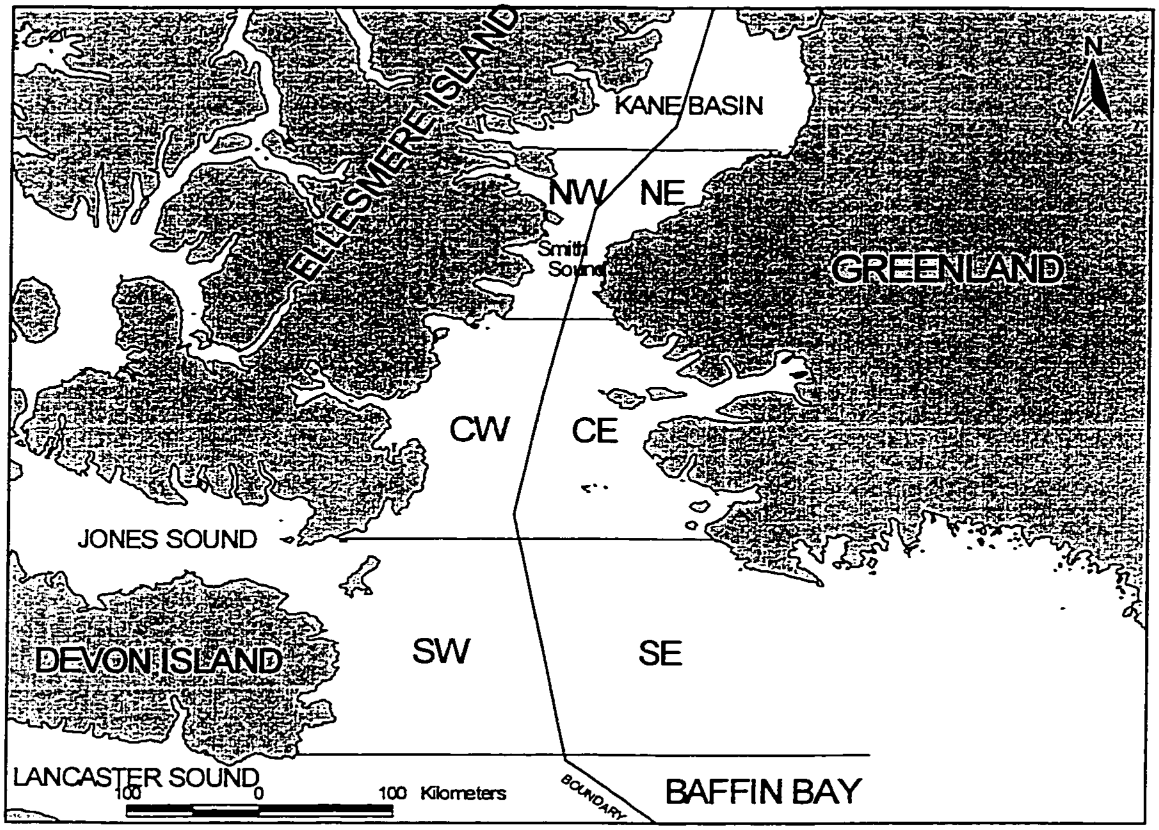


Figure 4-3: Division of the North Water Polynya into six different strata based on ecological and physical characteristics.

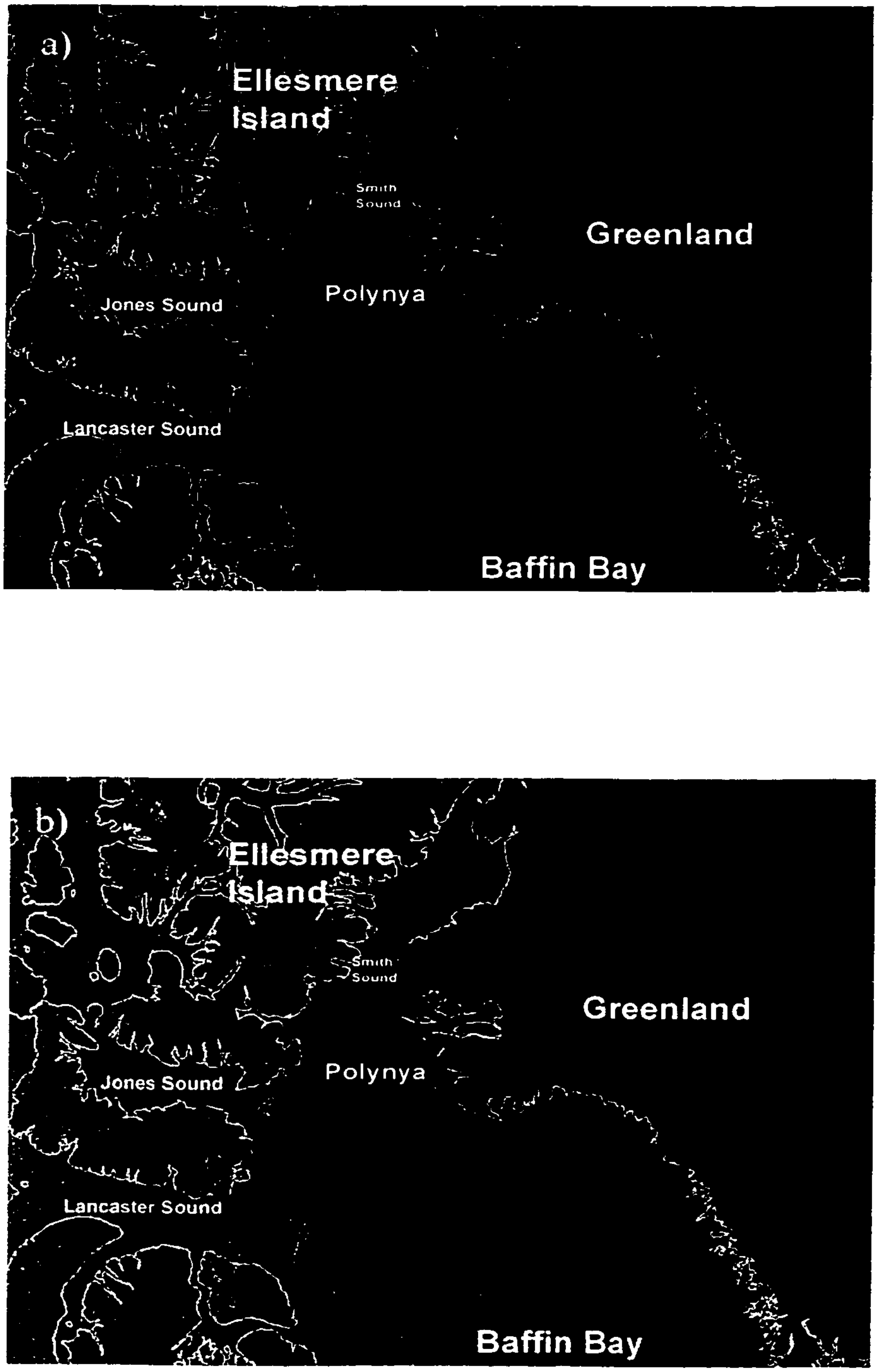
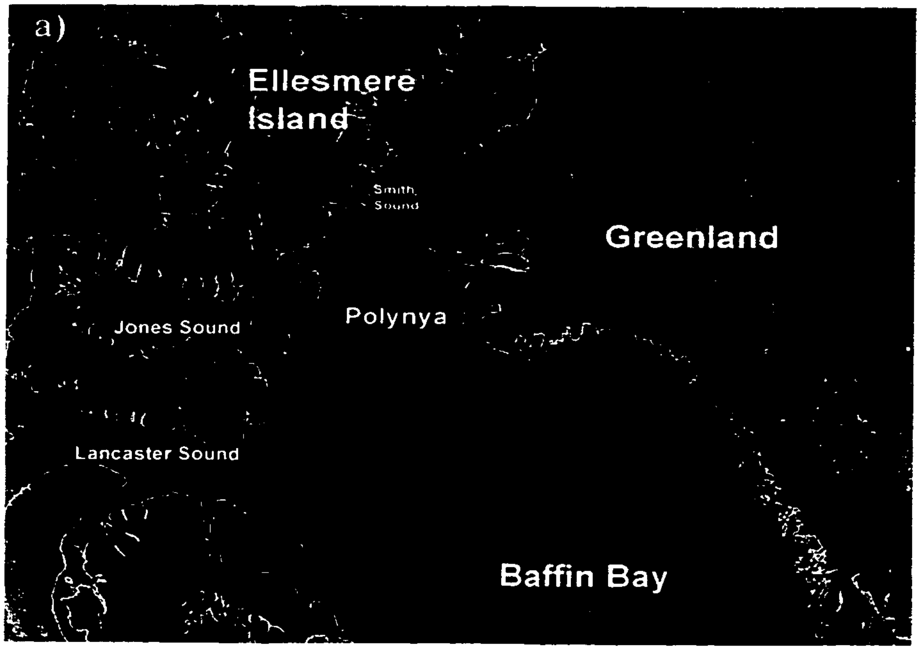


Figure 4-4: Satellite images of the North Water Polynya for a) April 17, 1998 and b) May 21, 1998.



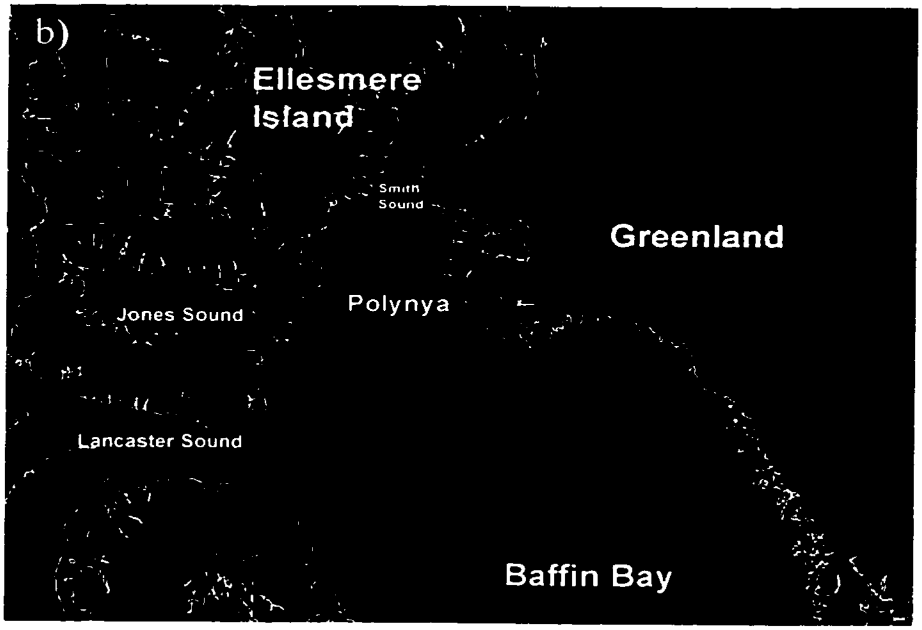


Figure 4-5: Satellite images of the North Water Polynya for a) June 28, 1998 and b) July 26, 1998.

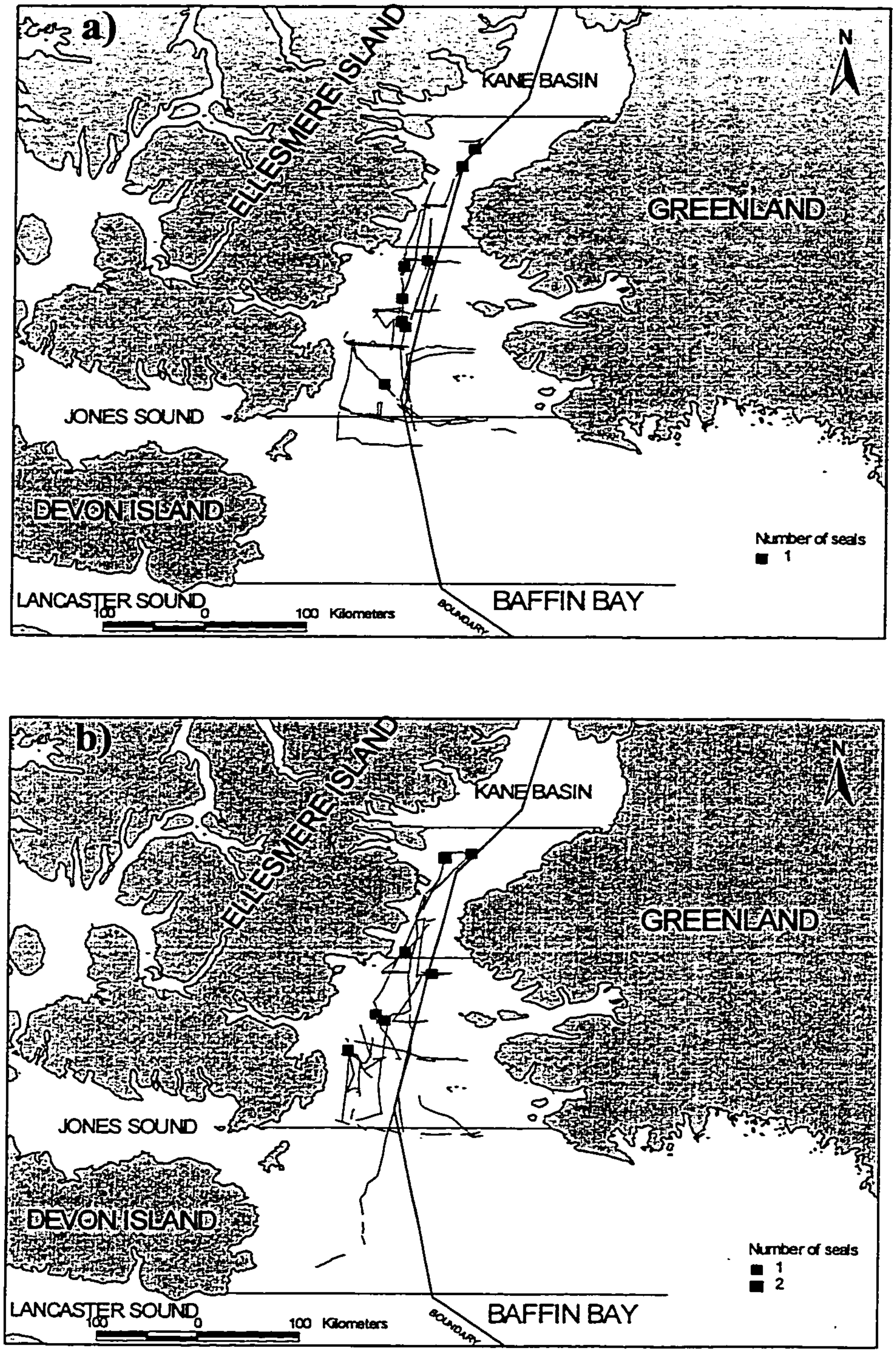


Figure 4-6: Locations of ringed seal observations in the North Water Polynya and ship transect lines for a) April 1998 and b) May 1998.

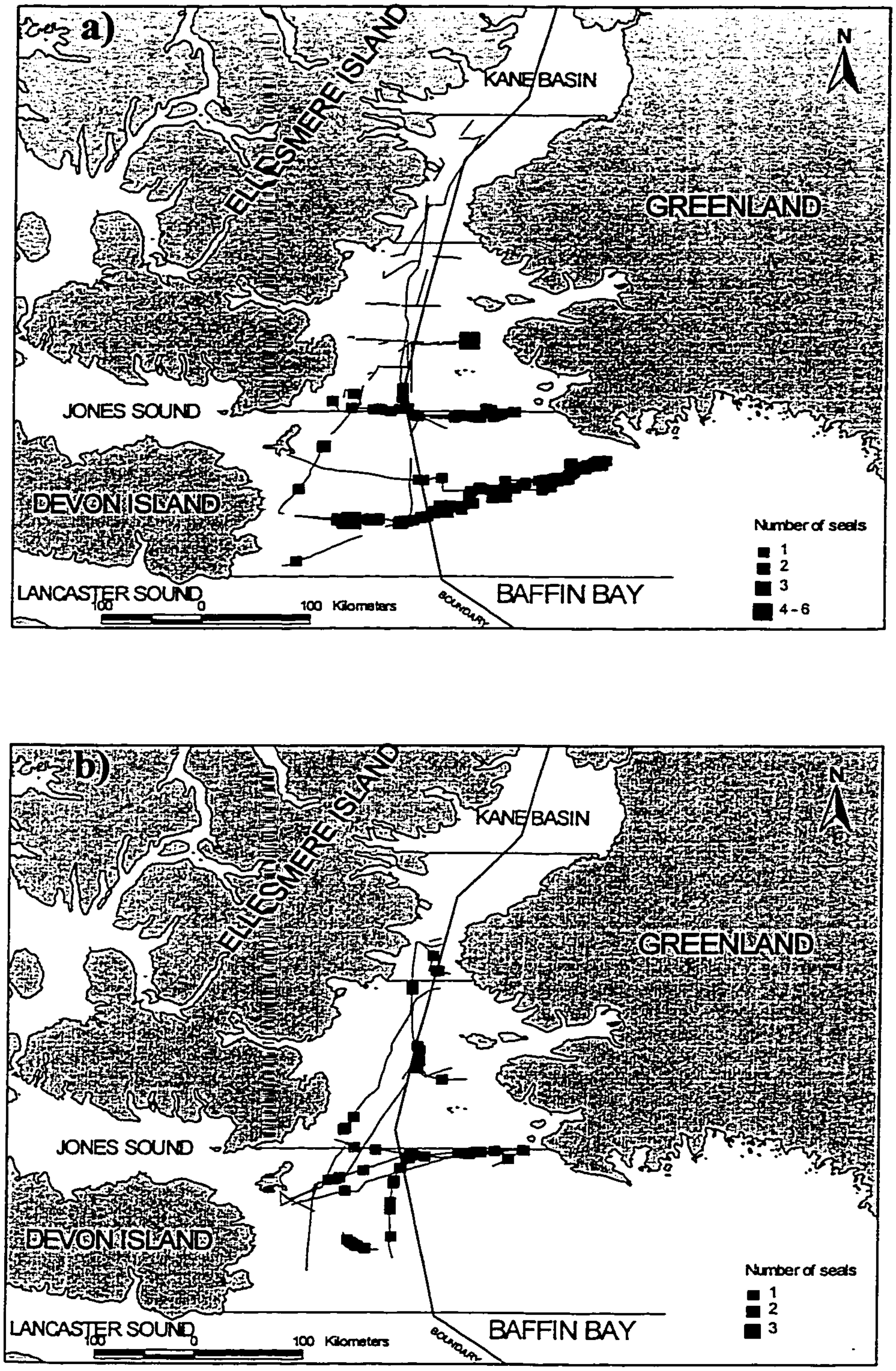


Figure 4-7: Locations of ringed seal observations in the North Water Polynya and ship transect lines for a) June 1998 and b) July 1998.

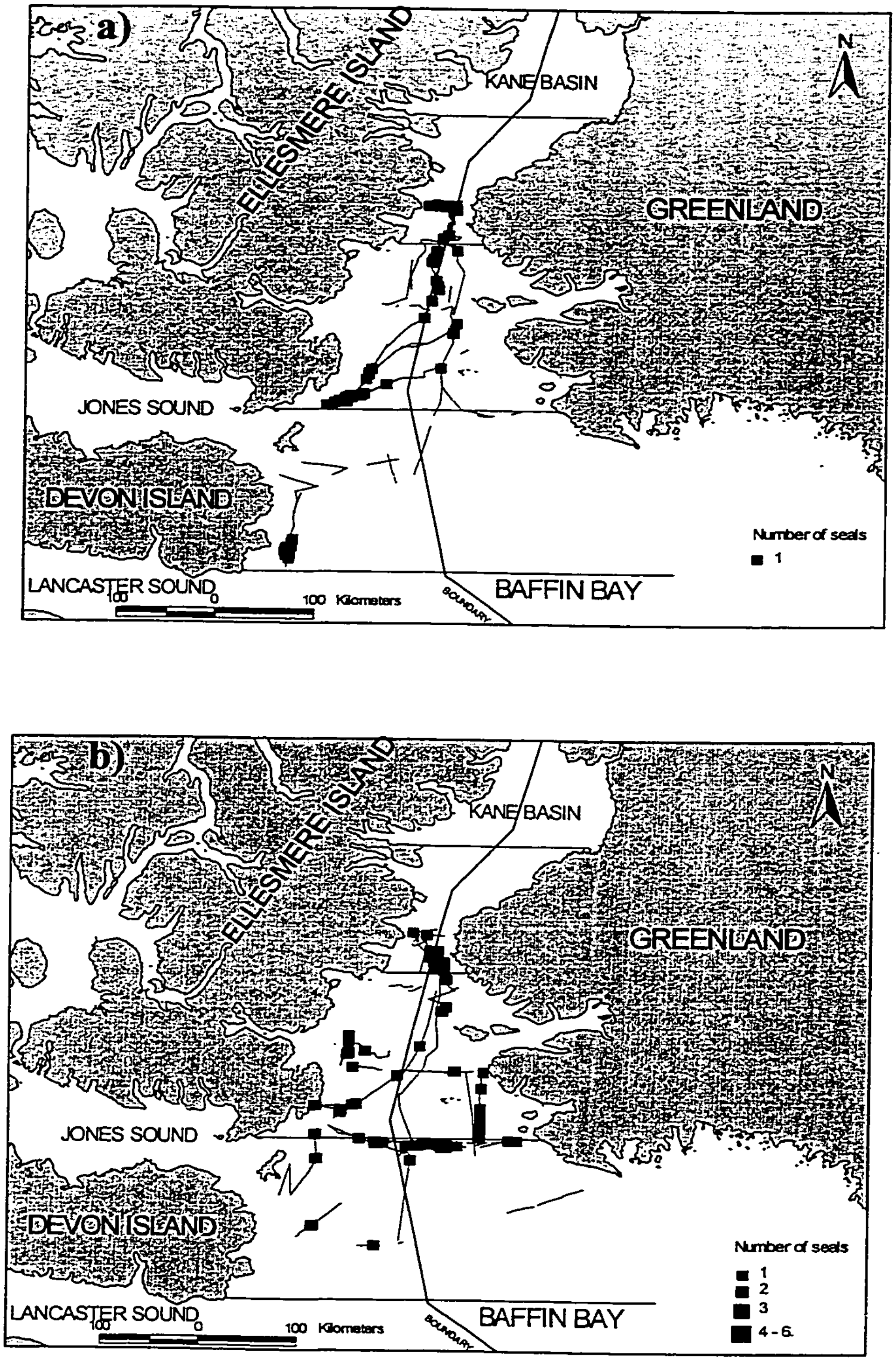


Figure 4-8: Locations of ringed seal observations in the North Water Polynya and ship transect lines for a) August 1997 and b) September 1999.

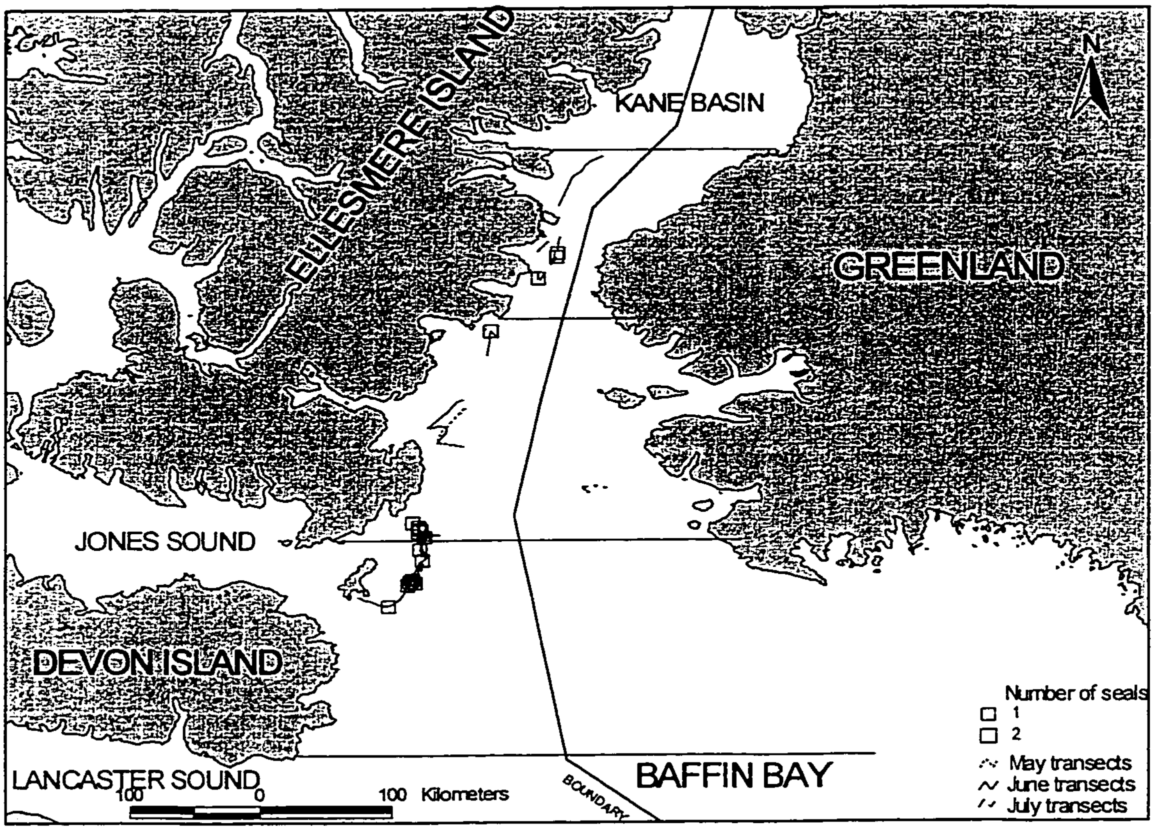


Figure 4-9: Locations of ringed seal observations in the North Water Polynya and ship transect lines for floe edge surveys between May and July 1998.

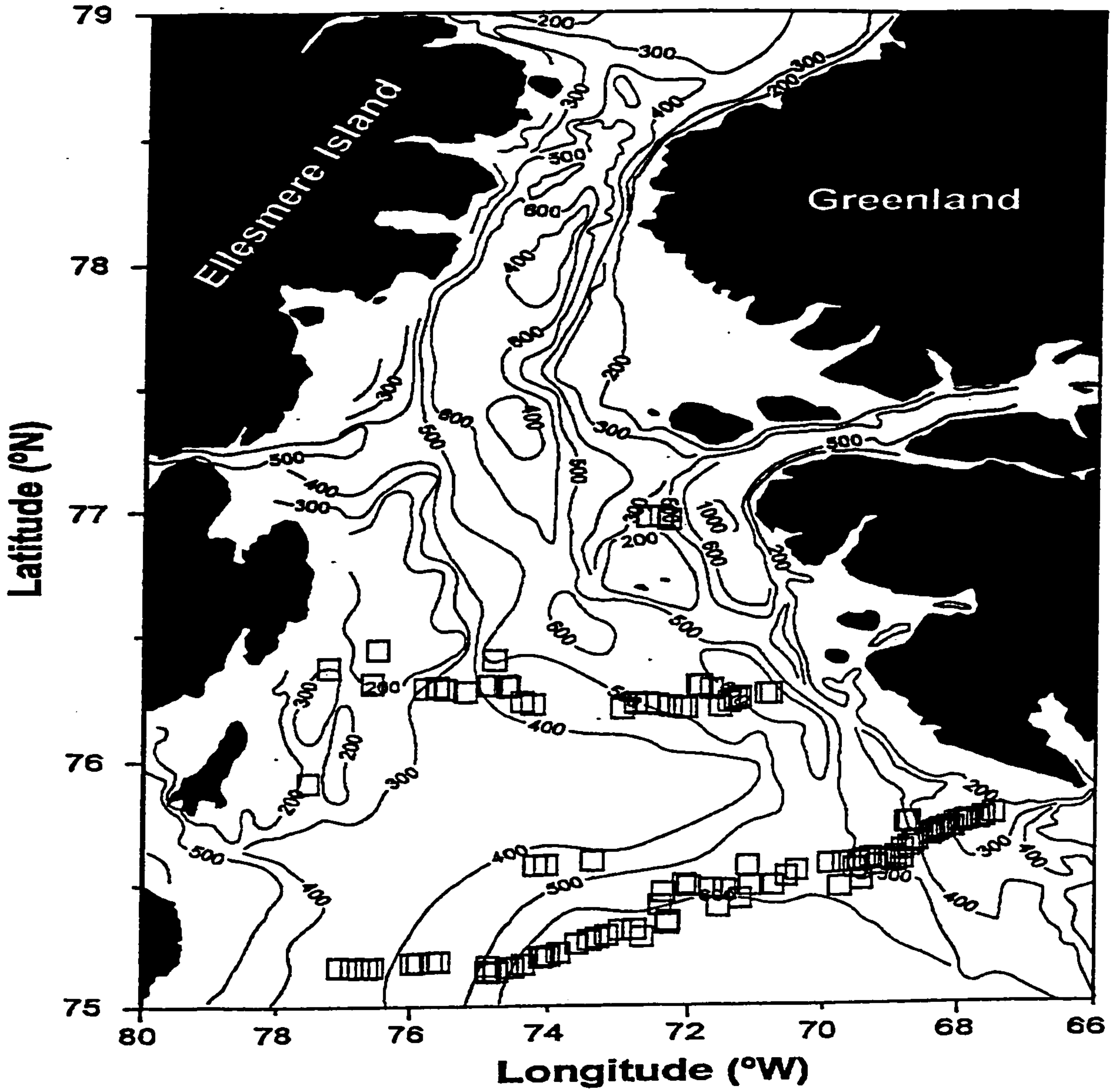


Figure 4-10: Bathymetric map of the North Water Polynya and the locations of ringed seal observations on ice (n = 508) for June 1998. Depth contours are shown in metres.

5. SUMMARY

The North Water Polynya, in northern Baffin Bay, is an important spring feeding and breeding area for several species of arctic marine mammals, including the ringed seal (*Phoca hispida*) (Stirling 1980, 1997; Stirling *et al.* 1981). The North Water Polynya is one of the largest recurring polynyas in the Arctic and is thought to be one of the most biologically productive (Stirling 1980, 1997; Stirling *et al.* 1981). Because of the relatively higher abundance of animal life on the east (Greenland) side of the polynya, it has generally been considered to be more productive than the west (Canada) side (e.g., Vibe 1950, Nettleship and Evans 1985, Boertmann and Mosbech 1998).

The variation in overall levels of productivity between the two sides of the polynya has been hypothesized to result from different sources of water, and consequently heat, that enter the ecosystem. Upwelling of a deep Atlantic current, flowing north along the coast of west Greenland, brings warmer water and nutrients to the east side of the polynya (e.g., Steffen 1985). On the west side, water from the polar basin flows south into the polynya, and latent heat escapes to the atmosphere from the surface, precluding any warming of the marine system (See Chapter 1). These differences in heat are thought to cause variation in the timing and development of phytoplankton blooms and food webs on either side of the polynya. This study was undertaken in order to determine whether differences in biological productivity within the polynya, if they exist, are reflected in various aspects of the biology, distribution, and abundance of ringed seals.

Biological productivity and food availability, as well as ice conditions, appeared to differentially affect ringed seal populations inhabiting the east and west side of the North Water Polynya. Ringed seals on the east side of the polynya had faster growth rates and appeared to attain sexual maturity earlier, but had shorter lengths than seals on the west side of the polynya. The timing of the break-up of the landfast ice in the areas where the seals were collected may partially explain the difference in lengths between the ringed seal populations. Seals may have been weaned earlier on the east side than on the west side, due to the earlier ice break-up, resulting in shorter animals (e.g., McLaren 1958a, Pastukov 1969). However, it is more likely that the dietary differences that were found between the two populations caused the differences in ringed seal growth, since improved nutrition is known to lead to accelerated growth and early sexual maturation in marine mammals (Laws 1956).

Immature ringed seals collected on the east side of the polynya fed predominantly on Arctic cod (*Boreogadus saida*), whereas immature seals collected on the west side fed mainly on amphipods. Adult seals collected on the east side fed predominantly on Arctic cod, whereas the diet of adult seals from the west side consisted of large proportions of Arctic cod as well as polar cod. Fish, especially Arctic cod, appears to be the preferred prey of ringed seals, because it has one of the highest energy content per unit mass ratios of any prey item (Bradstreet and Finley 1983, Weslawski *et al.* 1994). Since immature seals from the west side of the polynya took more amphipods, which are not as rich in calories as Arctic cod, they may have had less energy available, after meeting maintenance requirements, to allocate to growth. Thus, ringed seals that feed mainly on fish, as did those from the east side of the polynya, may have relatively faster growth rates and thus reach sexual maturity earlier.

The increased proportion of Arctic cod in the diet of immature seals from the east side of the polynya, and greater numbers and densities of ringed seals in the central-eastern stratum of the polynya, suggest that food abundance and thus productivity levels are higher on the east side of the polynya. An earlier phytoplankton bloom (Appendix B) and warmer water temperatures (Steffen 1985) have already been demonstrated to exist on the east side of the polynya, and these factors are thought to cause increased Arctic cod reproduction (Michaud *et al.* 1996). However, the distribution and abundance of Arctic cod in the polynya are unknown, and greater levels of productivity on the east side of the polynya have not yet been demonstrated to exist.

In addition to biological productivity, ringed seal distribution in the polynya is likely also affected by ice conditions. Most ringed seals seen hauled out on ice were seen in June, when the greatest number haul out on the ice to molt (McLaren 1958, Smith 1973a,b). Several studies have shown that ringed seals prefer to haul out in areas with high ice cover (Stirling *et al.* 1982, Kingsley *et al.* 1985, Lunn *et al.* 1997). Thus, in June, most ringed seals were seen in the southern areas of the polynya, where ice coverage was still relatively high.

Even though the results were somewhat inconsistent with respect to the hypothesis that biological productivity differs between the east and west sides of the North Water Polynya, some differences between the two ringed seal populations were demonstrated and appeared to indicate that productivity was higher on the east side of the polynya than the west. However, in the final analysis, the factors that determine the distribution and abundance of ringed seals are more complex and include other factors as well, such as prey abundance, ice conditions, and likely interannual fluctuation.

As more results from different biological and physical studies undertaken in the North Water Polynya between 1997 and 1999 become available in the future, it will facilitate further assessment of whether and how productivity within the North Water Polynya is related to ringed seal distribution and biology. Future studies should focus on determining the distribution and abundance of fish species, especially Arctic and polar cod, within the North Water Polynya, so that these can be related to the distribution and feeding ecology of ringed seals. In addition, more studies involving satellite-tagged ringed seals would increase our understanding of their habitat preferences and movements.

5.1. Literature cited

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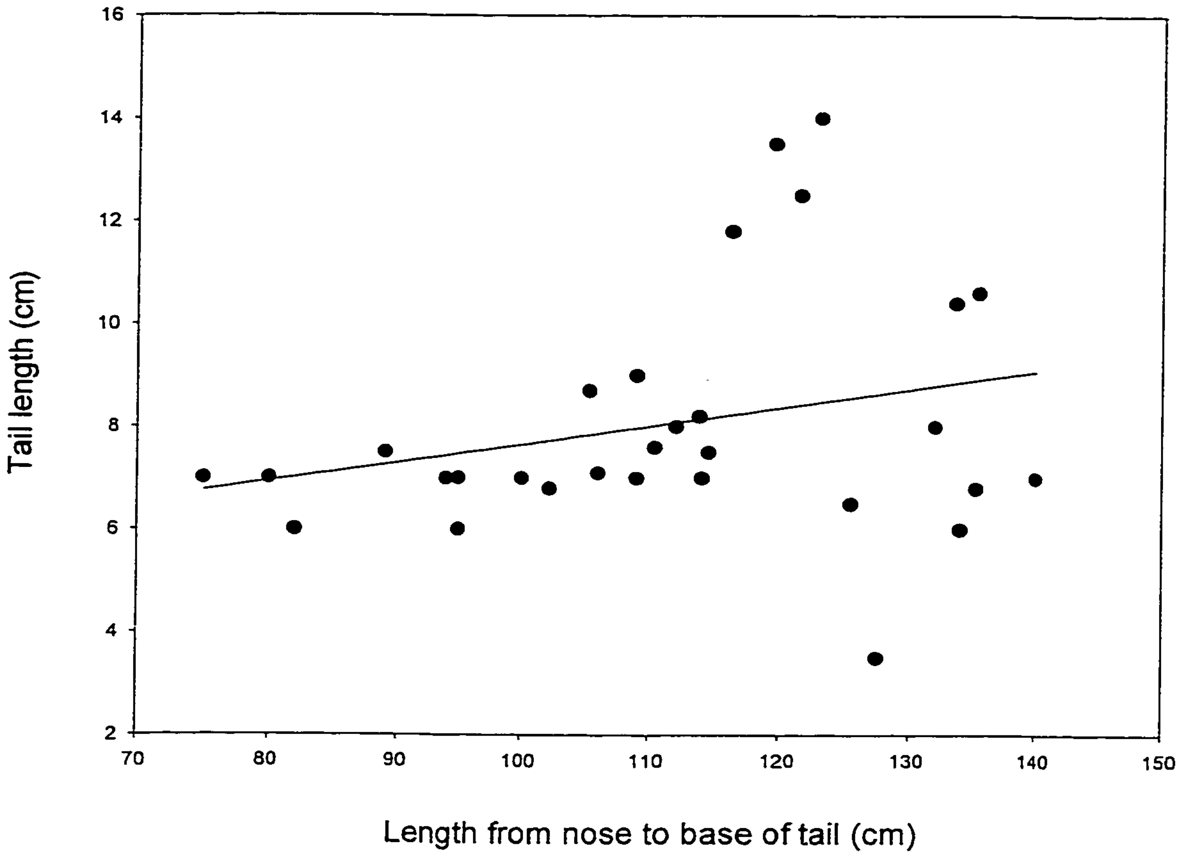
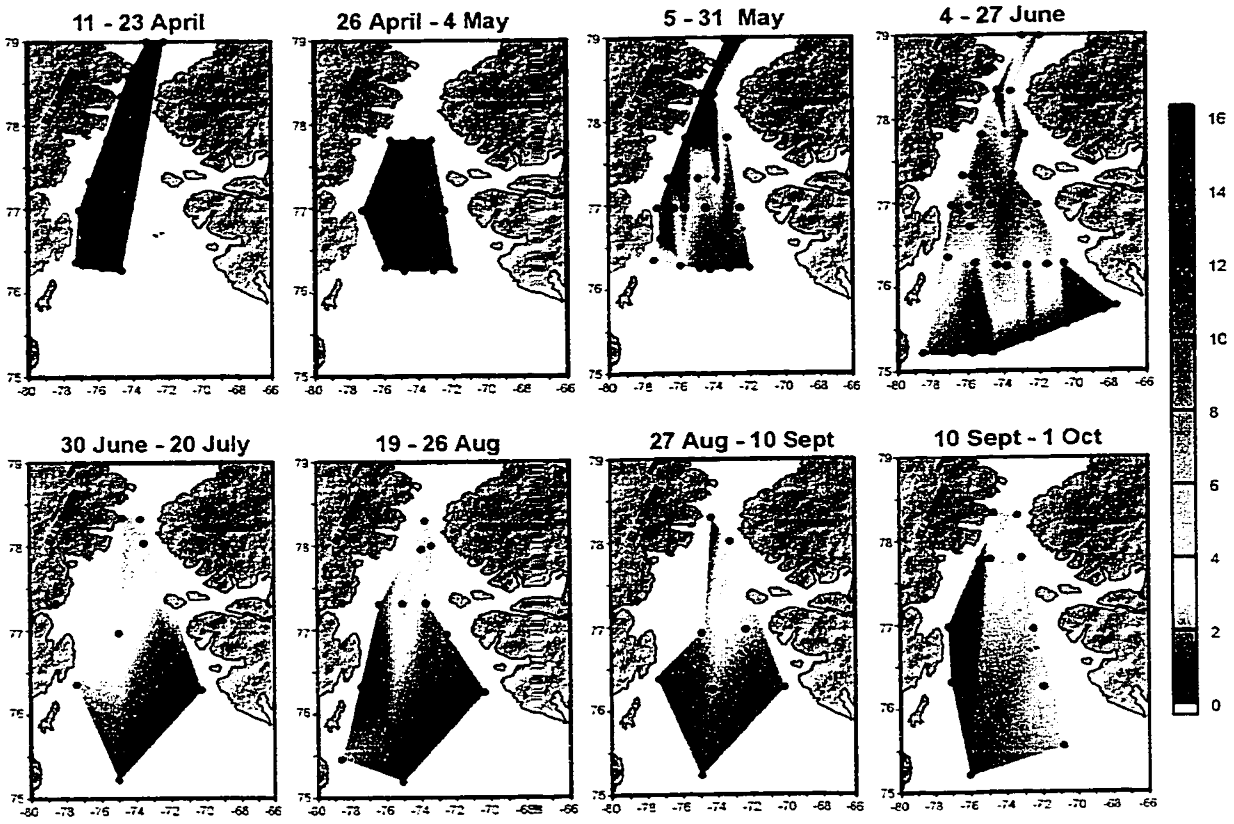
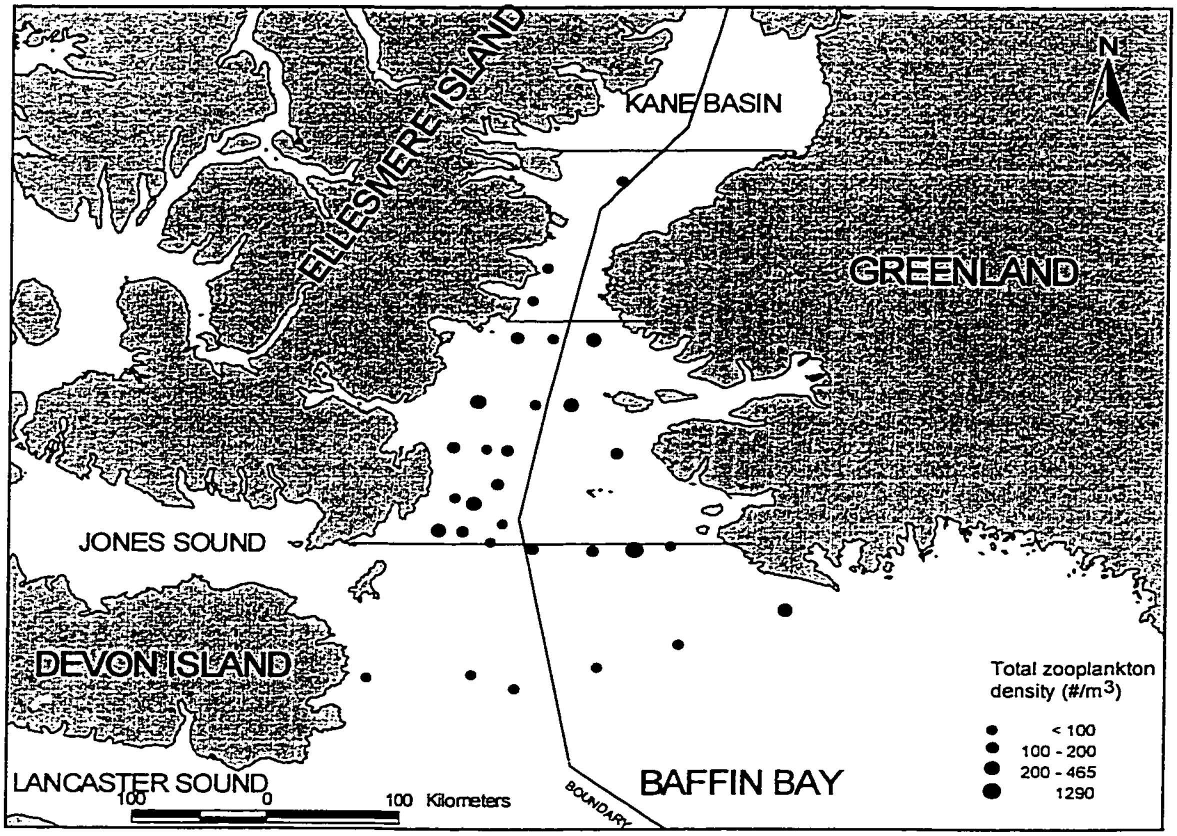


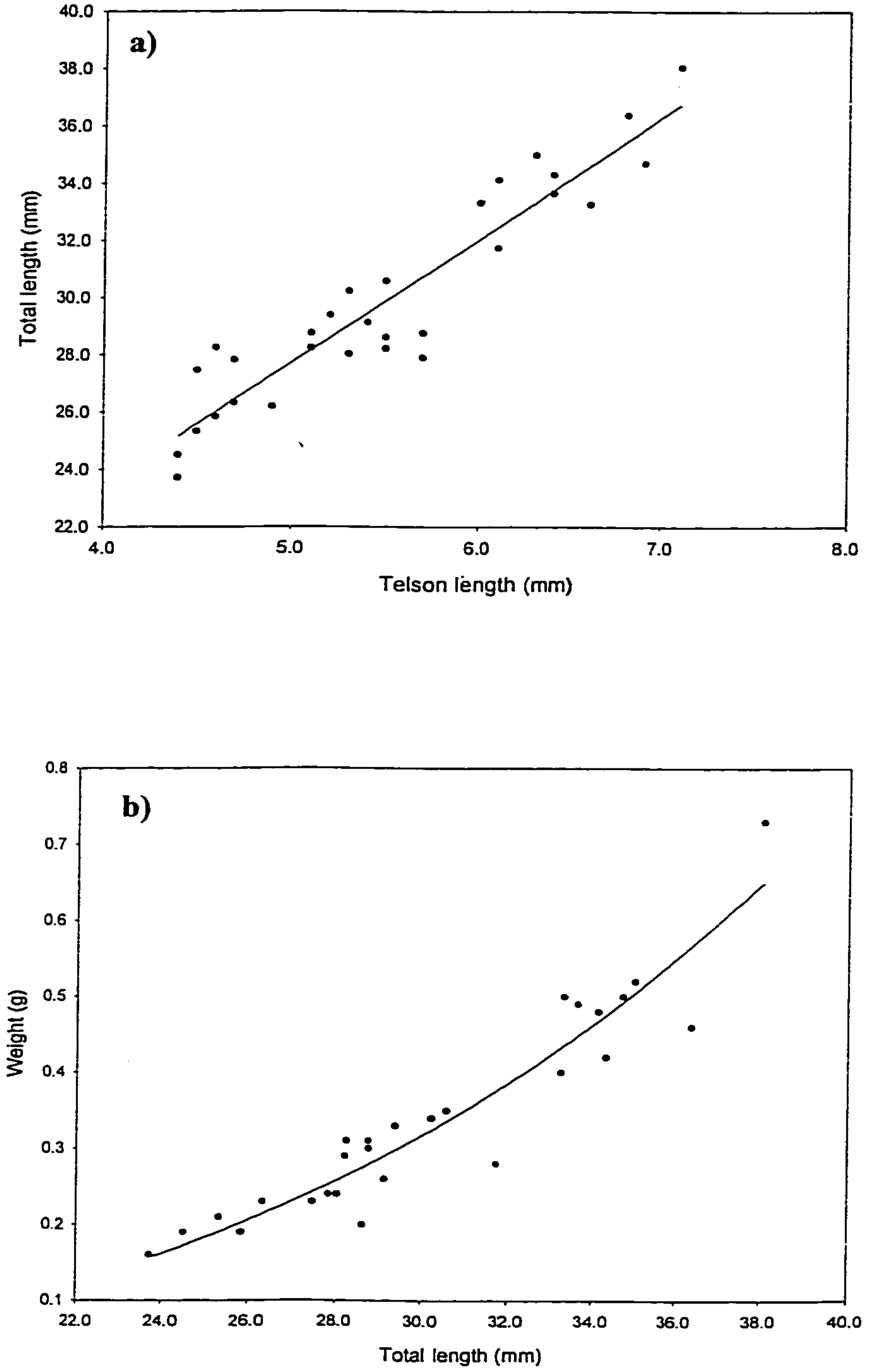
Appendix A: Regression line for calculating ringed seal tail lengths from measurements of length from nose to base of tail.



Appendix B: Average phytoplankton biomass expressed as chlorophyll *a* concentrations (µg/L) in the euphotic zone of the North Water Polynya.



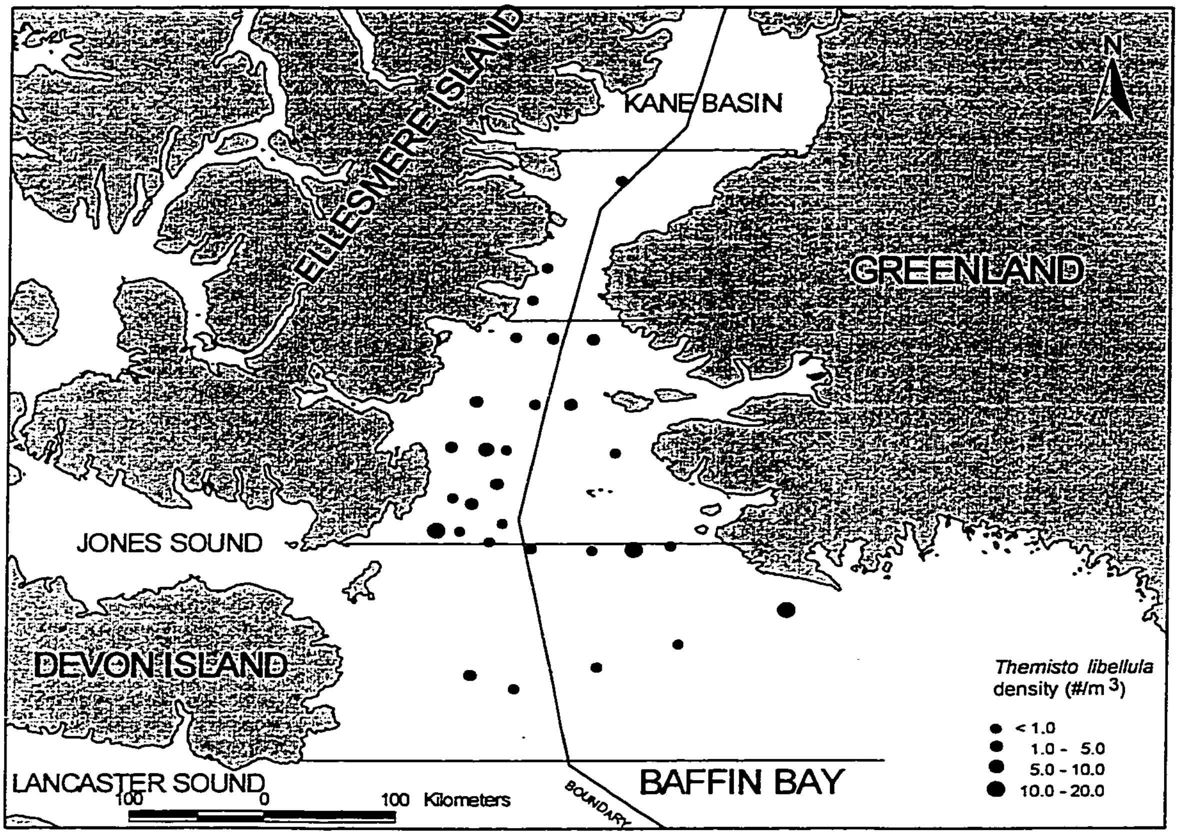
Appendix C: Total zooplankton densities in the North Water Polynya. Densities do not differ between the east and west sides of the polynya (Mann Whitney *U* test, $\chi^2 = 3.29$, $P = 0.07$)



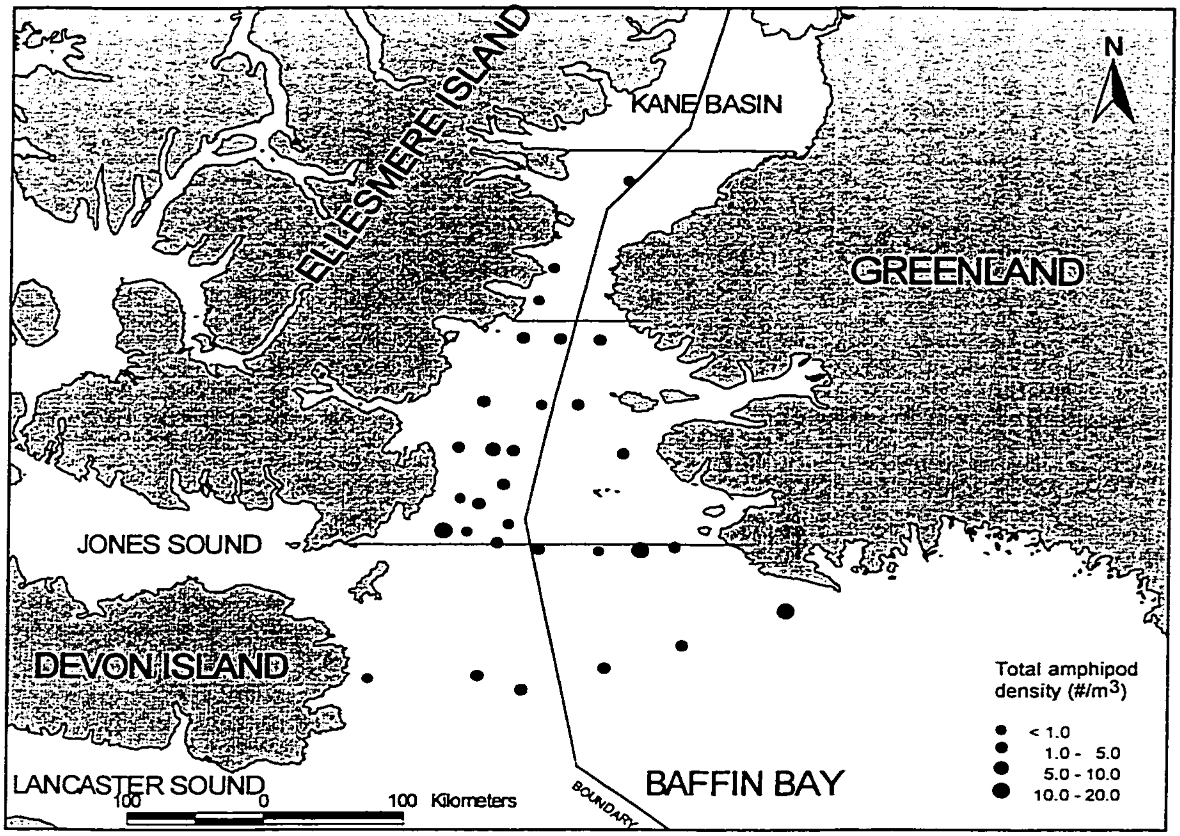
Appendix D: Regression lines and equations to calculate a) total length from telson length (n = 30) and b) weight from total length (n = 27) for the amphipod *Atylus carinatus*.

Fish species	Sample Size	Mean otolith size (mm)	Mean fish length (mm)	Mean fish weight (g)
Boreogadus saida				
Grise Fiord	447	3.06 ± 1.63	80.78 ± 33.94	5.42 ± 7.95
		(1.00 - 9.99)	(37.71 - 223.36)	(0.30 - 76.78)
Qaanaaq		4.53 ± 1.86	111.39 ± 38.80	12.38 ± 12.32
	555	(1.06 - 10.42)	(38.96 - 234.21)	(0.33 - 89.02)
Arctogadus glacialis				
Grise Fiord	111	7.17 ± 1.34	201.08 ± 31.10	94.98 ± 49.54
		(3.50 - 12.56)	(116.13 - 325.68)	(14.48 + 422.10)
Qaanaaq		5.52 ± 2.30	162.82 ± 53.19	61.24 ± 64.08
	10	(2.28 - 10.67)	(87.91 - 281.97)	(5.83 - 263.47)
Gymmnocanthus tricuspis				
Grise Fiord	5	2.70 ± 0.76	100.05 ± 15.78	16.90 ± 4.92
		(1.96 - 3.98)	(84.57 - 126.60)	(12.56 - 25.63)
Qaanaaq		2.90 ± 0.88	104.03 ± 18.39	17.90 ± 5.50
	2	(2.27 - 3.52)	(91.02 - 117.03)	(14.01 - 21.79)
Myoxocephalus quadricornis				
Grise Fiord	1	3.69	120.47	23.1
Qaanaaq	1	2.78	101.11	16.63
Liparis spp.				
Qaanaaq	20	1.65 ± 0.24	8.97 ± 1.37	7.30 ± 5.26
		(1.21 - 2.18)	(6.51 - 11.97)	(1.60 - 21.25)

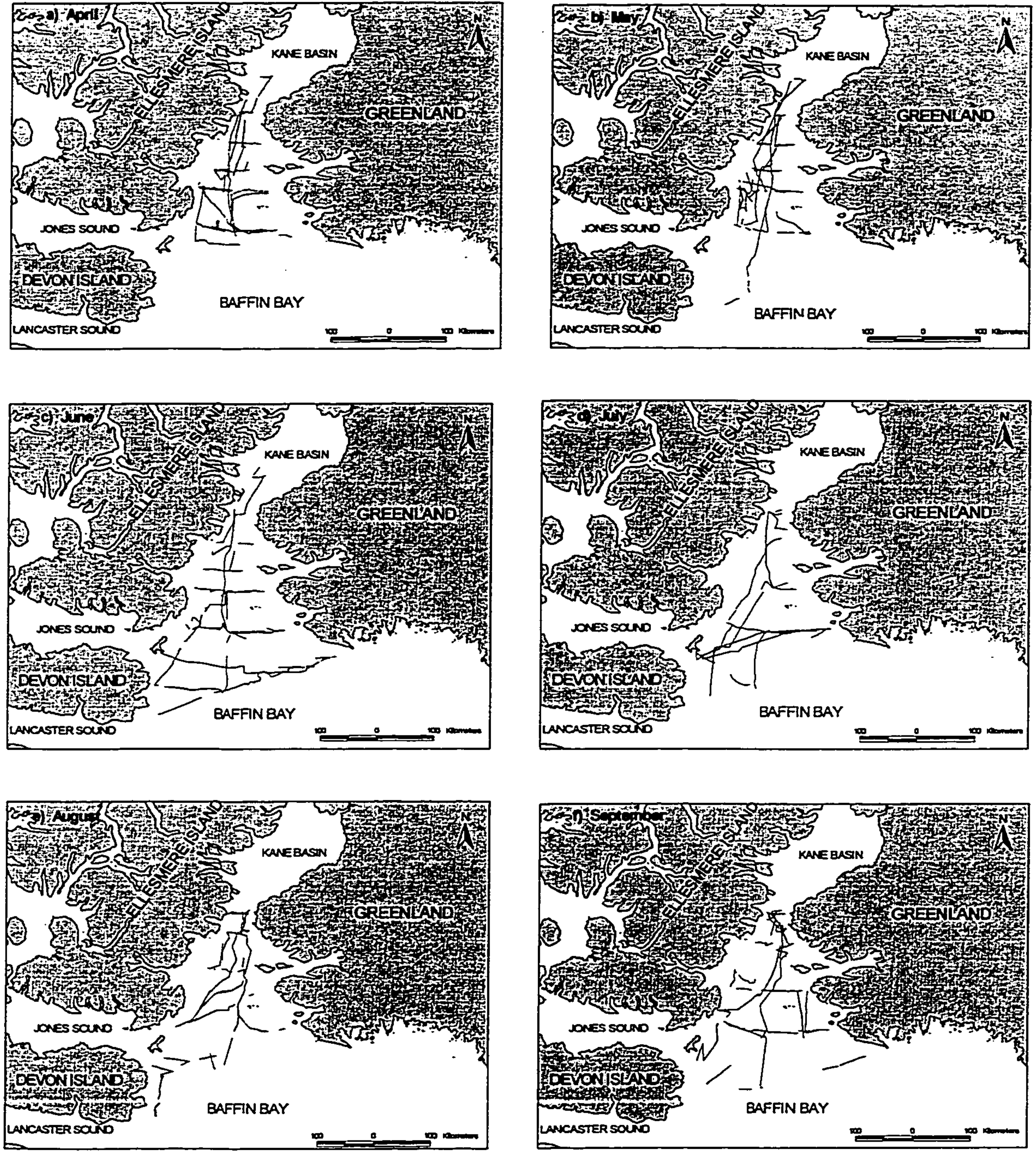
Appendix E: Otolith length, fish length, fish weight (mean ± SD), and size ranges (in brackets) of fish species taken by ringed seals in Grise Fiord and Qaanaaq.



Appendix F: *Themisto libellula* densities in the North Water Polynya. Densities do not differ between the eas t and west sides of the polynya (Mann Whitney *U* test, $\chi^2 = 0.78$, $P = 0.38$)



Appendix G: Total amphipod densities in the North Water Polynya. Densities do not differ between the east and west sides of the polynya (Mann Whitney *U* test, $\chi^2 = 1.80$, $P = 0.18$)



Appendix H: Survey transect lines in the North Water Polynya for a) April 1998, b) May 1998, c) June 1998, d) July 1998, e) August 1997, and f) September 1999.