

FACTORS AFFECTING GROWTH OF A
BLACK GUILLEMOT COLONY IN NORTHERN ALASKA

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BLACK GUILLEMOT COLONY IN NORTHERN ALASKA

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DOCTOR OF PHILOSOPHY

By

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ABSTRACT

Annual variation in breeding populations at seabird colonies has been well documented, but there have been few long-term attempts to examine the environmental and demographic forces responsible. I studied breeding chronology and demography Black Guillemot in northern Alaska from 1975-1997 to identify the factors responsible for colony establishment and growth. The Black Guillemot is a cavity-nesting seabird whose populations are frequently limited by nest-site availability.

Snowmelt in spring and snow accumulation in autumn had major effects on annual nesting initiation and success, respectively. Annual arrival at the colony and median date of egg laying was well correlated with the date of snow disappearance, with annual clutch initiation advancing 4.5 days per decade in response to regional climate amelioration. Successful breeding requires a snowfree cavity for >80 days. Decreased breeding success and post-fledging survival occurred in a year with a snow-free period <80 days. Historic weather records indicate annual snowfree periods >80 days were uncommon until the 1960's, when the species was first recorded breeding in northern Alaska.

When additional nest sites were provided, growth of the colony was rapid, increasing from 18 pairs in 1975 to 225 pairs in 1989. Breeding numbers then decreased to 150 in 1996 as factors other than nest-site availability controlled population size. Annual population growth averaged 37% from 1976-1982 when nest site occupancy was

low, 3% from 1983-1989 when all or most nesting cavities were occupied, and -6% from 1990-1996 as breeding productivity decreased and mortality of adults increased. Without immigration and with the average annual vital rates the colony would have had an annual rate of growth of 4% during this study. Contrary to published models of seabird colony growth, I found immigration important (>60% of annual recruitment) in all phases of growth.

Philopatry showed previously unreported large variation among cohorts related to variation in nest-site vacancies at the natal colony and estimated recruitment opportunities at regional colonies. Philopatry was highest (>80%) for cohorts maturing when most regional recruitment opportunities were at the study colony but low (15%) when nest-site availability was likely similar at the natal colony and other colonies in the region.

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INTRODUCTION

The 8000 km of Alaskan coastline from southeast Alaska and the Aleutian Islands north to the central Chukchi Sea includes a diverse array of mainland cliffs, talus slopes, nearshore rocks and old-growth forest that provides breeding sites for members of the seabird family Alcidae. These coastal habitats offer isolation from predators near productive subarctic and arctic waters and make the region the global center of abundance and diversity for the Alcidae, the largest family of Northern Hemisphere seabirds. Fifteen species of alcids totaling more than 25 million individuals breed at approximately 1000 colonies in Alaska (Sowls et al. 1978). The high breeding densities that characterize this region come to an abrupt halt in the central Chukchi Sea where the northernmost extent of rocky shoreline on the Alaskan coast is found near Cape Lisburne. The remaining 1200 km of Alaskan coastline north and east of Cape Lisburne consists of sand and gravel beaches backed by low (< 5 m) earthen bluffs and provides little natural breeding habitat for alcids.

In 1972, during a census of the northern Alaska coast, I was surprised to find two small (≤ 10 pairs) colonies of Black Guillemots (*Cepphus grylle*) in the Point Barrow area on Seahorse and Cooper islands (Divoky et al. 1974). The Black Guillemot is a semi-colonial cavity nesting alcid known to be versatile in its choice of nest cavities (Storer 1952). The colony on Seahorse Island was in a natural driftwood pile and the one on Cooper Island in man-made debris (boxes and floorboards) left by the U.S. Navy in the

1950's. First breeding for the species in northern Alaska had been recorded at Point Barrow in 1966 (MacLean and Verbeek 1968), the first Alaskan breeding record for an alcid north of Cape Lisburne.

Nest sites I constructed on Cooper Island in 1972 were occupied by breeding birds that year, indicating that a "floating" population of nonbreeding birds was present in the region and unable to recruit to the breeding population due to a lack of nest sites. When I returned to the island in 1975, I monitored the breeding success of the colony and began a program of nest site construction to increase the number of breeding pairs. Occupation of the new nest boxes was rapid, with the colony expanding to 175 pairs by 1982. The population reached its maximum size of 225 in 1989 pairs when all nest boxes were occupied and the colony had become the largest Black Guillemot colony in Alaska.

From 1975 to the present I have conducted research annually on the breeding biology and demography of the Black Guillemot colony on Cooper Island. For several reasons the colony provided a unique research opportunity. First, unlike most guillemot colonies, where the depth and placement of many nest cavities make them inaccessible to investigators, I could reach the contents of all nests. This allowed accurate assessments of breeding variables for the entire colony, the banding of all chicks fledging from the colony, and the capture of most adults. Second, the paucity of alternative nest sites within a 500-km radius of the study colony, coupled with information on the location and approximate size of nesting colonies within 1000 km, allowed estimation of distances of

natal dispersal that would not be possible where population density was higher or distribution more uniform. Third, my study began shortly after climatic conditions in northern Alaska began to ameliorate and conditions continued to warm during the study.

The following three chapters address three aspects of my study. The first examines the effects of changes in northern Alaska meteorological conditions on Black Guillemot chronology and breeding success. Specifically it addresses the importance of changes in spring snowmelt and fall snow accumulation to timing and success of breeding during the study period and how changes in the past 50 years have affected the colonization of northern Alaska by Black Guillemots.

The second chapter is an examination of the timing and causes of growth of the Cooper Island colony from 10 pairs in 1975 to 225 pairs in 1989 and its decrease to 150 pairs by the mid-1990's. Because I banded all chicks fledging from the island since 1975, I knew the origin (immigrant vs. native) of all recruits from 1978 to 1995. Therefore, I could determine the relative contribution of immigrants to colony expansion and evaluate the accuracy of published hypothetical models of colony growth. Knowledge of the sizes and location of likely source colonies allowed determination of the minimum distance immigrants were dispersing from their natal colonies.

The third chapter examines the recruitment characteristics, such as age of return and first breeding, for individuals banded as chicks, and the importance of nest site availability and competition on age at first breeding, philopatry, recruitment success and

breeding dispersal.

Together these papers provide a unique documentation of the factors that facilitated the colonization of northern Alaska by Black Guillemots over the last 30 years. Although the regional and colony conditions of this study are unique, it is important to realize that the utility of the information I obtained is not diminished by those conditions. For example, the response of guillemots to climate change is not affected by the nature of the study colony. The findings on Black Guillemot colony formation, immigration and demography will assist in the understanding of these parameters in those alcid populations breeding in more typical but less accessible conditions.

**THE EFFECTS OF RECENT CLIMATIC CHANGE ON THE BREEDING OF
BLACK GUILLEMOTS IN ARCTIC ALASKA¹**

ABSTRACT

Black guillemots are high arctic seabirds closely associated with ice and snow habitats throughout the year. They nest in cavities and require a minimum of 80 days from first occupation of the cavity to chick fledging, an atypically long period for an arctic nesting species. Successful reproduction in the arctic is dependent on early occupation of a nest site shortly after cavities become snow-free.

I examined black guillemot breeding chronology in relation to snow melt in spring and initial accumulation of snow in autumn from 1975-1996 at colony in northern Alaska. Initiation of breeding was closely associated with snow disappearance. Annual arrival at the colony and median date of egg laying were well correlated with the date of snow disappearance. An advancement of snowmelt during the study resulted in the median date of clutch initiation advancing 4.5 days per decade. Late summer snow accumulation in a year with a snow-free period <80 days prevented the feeding and fledging of chicks and resulted in decreased breeding success and post-fledging survival.

Examination of historic weather records indicates that the snow-free period in

¹ Prepared for submission to ARCTIC as Divoky, G.J. THE EFFECTS OF RECENT CLIMATIC CHANGE ON THE BREEDING OF BLACK GUILLEMOTS IN ARCTIC ALASKA

arctic Alaska has only recently been sufficient to allow regular successful nesting of the Black Guillemot. The recent colonization and growth of colonies in northern Alaska may be the result of the century-long warming trend in the region.

INTRODUCTION

Arctic air temperatures have been increasing over the last 150 years and are now at their maximum for the last four centuries (Overpeck et al. 1997). Increases in surface air temperature associated with increasing levels of CO₂ are predicted to accelerate this rate of warming, with increases globally up to 1°C per decade over the next 50 years (Mitchell et al. 1990). In the Arctic, the influence of haze and increased snow melt because of soot deposition from industrialization likely will further accelerate the warming related to greenhouse gases (Foster et al. 1991). The anticipated changes in air temperature will have major effects on the distribution and biology of Arctic biota. Effects of elevated air temperature on snow and ice cover will be immediate and pronounced. Species either dependent on, or constrained by, the presence or amount of ice and snow would be expected to be among the first affected by warming. There is increasing evidence of climate warming in the Arctic in general (Overpeck et al. 1997, Cavalieri et al. 1997) and northern Alaska in particular (e.g., Foster 1989, Sharratt 1992). Although the consequences of the predicted warming on Arctic species have been the

subject of much speculation (Brown 1991, Peters and Lovejoy 1992) little has been done to monitor or document recent or ongoing effects (Jarvinen 1994).

The black guillemot (*Cephus grylle*) is a circumpolar arctic seabird typically associated with snow and sea ice habitats for the entire year. In the western Arctic this species breeds north of the Bering Strait in coastal locations (Sowls et al. 1988), which are typically snow-covered for approximately 9 months each year (Brower et al. 1977). The extended period of breeding for the species (approximately 80 days from initial nest occupation by breeding pairs to nest departure of fledging chicks) (Divoky unpubl.) means that successful reproduction in the Arctic is dependent on pairs occupying nesting cavities soon after cavities become free of snow and fledging chicks before snow again accumulates in late summer or early autumn.

I examined 2 decades of data on the breeding chronology and fledging success of the black guillemot to determine the potential effects of snowmelt in late spring and snow accumulation in late summer and autumn at a colony 25 km east of Point Barrow, Alaska. Using data from the U.S. National Weather Service (NWS), I analyzed annual trends in snow melt and accumulation and examined the correlation of annual variation in arrival at the colony and initiation of egg-laying for guillemots with snow and air temperature variables. I also documented the effect of early snow accumulation on fledging weight and pre- and post- fledging survival. My analysis is one of the first attempts to detect contemporary effects of climate change on breeding biology of an avian species.

My working hypotheses were that: 1) recent climate amelioration has occurred in northern Alaska and is reflected in snow conditions, 2) initiation of breeding in black guillemots is responsive to annual variation in the duration of the snow free period in summer, 3) guillemot reproductive success is negatively affected by snow-free periods shorter than the 80-day reproductive period of black guillemots.

STUDY SITE

I collected data on guillemot breeding chronology and success from 1975 to 1996 on Cooper Island (71°41' N, 155° 41'W), a low elevation (maximum elevation < 3 m above sea level) sand and gravel island in the western Beaufort Sea, 25 km ESE of Point Barrow, Alaska (Figure 1.1). In 1972, I discovered a population of 10 pairs of black guillemots breeding in man-made boxes and floorboards left on the island in the 1950's by the U.S. Navy (Divoky et al. 1974). Through the construction of additional sites, between 1975 and 1989 I increased the population to 225 pairs. The population began to decline in 1990, decreasing to 150 pairs in 1995-1996 and 110 pairs in 1997 (Chapter 2).

Air temperature and sea ice

Snow and sea ice severely restrict the period available for breeding by black guillemots in northern Alaska. Air temperature at Barrow remains below 0°C for most of the year, with daily average temperature exceeding 0°C an average of only 103 days

annually. Mean monthly temperatures are $< -15^{\circ}\text{C}$ in the winter (November-April) and $> 0^{\circ}\text{C}$ only in June-August (NWS).

Ice dominates the nearshore and pelagic waters of the Beaufort Sea at most times of year. Cooper Island is surrounded by sea ice from approximately mid-October to late June (Brower et al. 1977). Surrounding nearshore ice separates from the island in late June or early July, when the decreased albedo of the island forms a moat of meltwater. This moat isolates the island from arctic foxes (*Alopex lagopus*), which are nest predators of many Arctic birds (Larson 1960) and are common on the nearshore ice. Melting of nearshore ice occurs from June to mid-July. Extensive open water near the island typically occurs only from late July to late October. During this period, the amount of open water in the western Beaufort Sea is highly variable, with the southern edge of the pack ice on 15 September ranging 0-165 km north of Point Barrow (Brower et al. 1977).

From November to June, ice cover of the region is nearly complete, but limited open water is present near the study colony. A persistent lead between the shorefast ice and drifting pack ice occurs in the northern Chukchi Sea and extends north of Point Barrow into the extreme western Beaufort Sea (Brower et al. 1977). In spring, this lead is an important migratory pathway for birds and mammals (Woodby and Divoky 1983, Niebauer and Schell 1993) and a prebreeding staging area for black guillemots (J. C. George, pers. comm.). The lead allows some guillemots to winter at least as far north as

Point Barrow (Bailey 1948) and probably is also an important foraging area for guillemots during the initial stages of breeding.

Snow

Snow can fall any day of the year in northern Alaska but persistent accumulation typically occurs only when daily mean air temperature is $< 0^{\circ}\text{C}$ (mid-September to mid-June). In April and May, when guillemots are common in the lead off Point Barrow (J. C. George pers. comm.), snow cover of the island is usually complete. During the study, snow depths at Barrow on 15 May averaged 8.3 cm (s.d. = 8.0, range <0.1 - 32.5 cm, $n = 22$ years). Entrances of nesting cavities of black guillemots on Cooper Island have a median height of 13 cm (range 7-92 cm) and snow drifts, both next to and inside nest sites, prevent access until the later stages of snow melt in spring (Divoky unpubl.). In addition, during snow melt in spring, the daily melting and refreezing of snow in nest cavities can form ice lenses in nest depressions, further hindering initiation of egg-laying.

In early and mid summer (June to mid-August) snowfall sufficient to restrict access to nest sites is rare, and any snow accumulation usually melts within a day. As air temperature declines in late summer and early autumn, snow can persist and accumulate, however. Because nest sites have a higher vertical relief than the surrounding substrate, even small amounts of snowfall can accumulate as drifts around sites, blocking entrances and preventing the provisioning or fledging of chicks.

METHODS

Timing of breeding events

In 3 years (1981, 1983 and 1984) fieldwork began before guillemots returned to Cooper Island and allowed determination of date of first flights over the island, first landing on island, and first occupation of nest sites. These observations provided important prebreeding information relative to environmental conditions and the timing of clutch initiation.

Dates of clutch initiation (laying of the first egg in the clutch) were obtained for all years (1975-1996) except 1992, when an arctic fox preyed on eggs early in the breeding period. Daily examination of nest cavities began when I first detected birds sitting on nest depressions. In 1975-1978, I examined nests every other day and assigned clutch initiation dates to the day preceding the day I first found an egg. From 1979-1996 sites were examined daily. All potential nesting cavities were examined regularly until they contained a completed clutch, or until approximately 3 days after egg laying had ceased at all sites. Typically guillemots have a two-egg clutch, and the interval between eggs is usually 3 days (range 2-5 days, $n=958$) (Divoky, unpubl). In those instances when presence of one or both parents prevented timely discovery of the first egg, I assumed that the date of clutch initiation was 3 days before the laying of the second egg.

Occasionally (<5% of observations), when the clutch was already complete and the date of clutch initiation was uncertain, the approximate date of laying was determined by floating the egg to determine the stage of incubation or, if an egg hatched, assuming hatching occurred 31 days after clutch initiation for a two-egg clutch and 28 days after hatching for a one-egg clutch, mean incubation periods of this study. The number of nests used for determination of mean dates of clutch initiation for a particular year always exceeded 95% of the colony total.

Chick weight and fledging

I weighed chicks to the nearest 5 g and measured straightened wing chord to the nearest 1 mm daily or every other day in the week before fledging. Chicks fledge during the night, and I defined the day of fledging as the day after they were last present in the nest. Fledging measurements (weight and wing length at fledging) are the last measurements obtained for a chick (within 18-42 hours of fledging).

Environmental variables

I examined air temperatures and snow conditions for the period of my study (1975-1996) as well as the period from 1947-1974. I obtained data on snow depth and air temperature from the NWS monthly Local Climatological Data for Barrow, Alaska.

Barrow is 35 km WNW of Cooper Island. Daily depth of snow was recorded at 0800 h Alaska Daylight Time (ADT).

I used two dates of snowmelt: date when snow depth was first reduced to <1.3 cm, and date when snow depth was first reduced from a "trace" (<1.3 cm and >0 cm) to 0 cm. The latter measurement also is called "snow disappearance." Spring accumulation of snow after initial disappearance was uncommon and short-lived and I consider only initial disappearance. Two measures of persistent accumulation of snow in late summer and early autumn were examined: the first day that snow depth was at least a trace (>0 cm) with snow depth >0 cm for the next 3 days, and the first day snow depth was >1.3 cm with snow depth >0 cm for the next 3 days. I examined two measures of the annual snow-free period: the number of days from snow disappearance to a persistent (≥ 3 days) trace of snow cover and the number of days from snow disappearance to an accumulation of >1.3 cm of snow with snow >0 cm for the next 3 days.

RESULTS

Air temperature and snow conditions in 1975-1996

Regional change in climate occurred during the study (1975-1996), as evidenced by increases in spring and early summer air temperatures and advancement of spring snowmelt (Figures 1.2 and 3, Table 1.1). Mean monthly air temperatures showed significant annual increases for April-July, with April and May experiencing the greatest

increases, 2.3°C and 1.8°C per decade, respectively (Figure 1.2). From August-March, mean air temperatures showed no significant linear relationship to year (Figure 1.2).

Spring and fall accumulation of snow reflected the seasonal nature of annual variation in air temperature. Measures of spring snowmelt showed significant or marginal advancement, whereas dates of snow accumulation showed no annual trend during 1975-1996. The date snow was reduced to <1.3 cm ranged from 5 June in four years (1977, 1979, 1984 and 1988) to 13 May in two years (1990 and 1995) and showed a mean advancement of 5 days/decade during the study. Date of snow disappearance was only marginally correlated with year, however (Figure 1.3, Table 1.1). No annual trend was present in the two measures of snow accumulation in fall; first dates with (1) a persistent (≥ 3 days) trace (>0.1 cm) and (2) > 1.3 cm of snow accumulation averaged 9 September and 17 September, respectively. During the study (1975-1996) none of the measures of the snow-free period was significantly correlated with year (Table 1.1).

Return to the colony and clutch initiation

The annual return of guillemots to the colony was associated with the disappearance of snow from the island (Figure 1.4). In 1981, 1983 and 1984, when fieldwork began before the seasonal return of guillemots to the colony, I first observed birds near the island on 6 June, 30 May and 5 June; 4, 2, and 6 days, respectively, before snow depth at Barrow reached zero. On the date of the first sighting of guillemots, snow cover of the island was <50 % in 1981 and 1983, but was nearly complete in 1984. In all

3 years, first sightings occurred between 2300 h and 0200 h ADT, when compact flocks of 50-100 birds circled the island at >30 m above the ground, occasionally dropping down over snow-free patches of land. Circling lasted for 2-4 h, with similar behavior occurring on subsequent days until birds first visited nest sites. In all 3 years birds first landed on the island 2 days after first being observed near the island, and were then present at the island daily.

Annual return to nest sites was related to the status of snowmelt, and snow prevented access to some nest sites after other nest sites were occupied. In 1981 and 1983, when snow-free areas on the island were extensive, birds visited nest sites on the first day they alighted on the island, after roosting together for approximately 1 h in a snow-free patch. In 1984, when snow cover was more extensive, birds did not disperse to nest sites until the third day they roosted on the island, remaining in several communal roosts on the first 2 days. For 1981, 1983 and 1984, respectively, first visits to nest sites occurred 2 days before, 2 days after, and 5 days before snow depth at Barrow reached zero (Figure 1.4). New (temporary) accumulation of snow on the day of the birds' arrival in 1981 and 3 days after arrival in 1984, was sufficient to restrict access to some nest sites.

Black guillemots arrived at the colony unpaired and were not observed to pair until they visited nest sites. Adults that later mated were not associated in prebreeding roosting flocks, observed before birds returned to nest sites. In 1984 I censused roosting

flocks (typically <25 birds) on the initial day birds landed on the island and 2 days before they visited nest sites. Although annual mate fidelity was >90% during this study (Divoky unpubl.), within the roosting aggregation none of the birds was near their mate from the previous year or their future mate for that year.

Date of breeding initiation (as measured by the date of the first egg in the colony) was related to the date of arrival at the colony and annual snow melt. Although I was present on the day guillemots first arrived at the colony in only 3 years, the period between the date birds first visited nest sites and the laying of the first egg in the colony (the prelaying period) was nearly identical for all 3 years: 16 days in 1981 and 1983, and 17 days in 1984. For the entire (1975-1996) the date the first egg was laid in the colony was highly correlated ($r^2 = 0.55$) with the date of snow disappearance (Table 1.2). The lag between disappearance of snow and the first egg laid in the colony averaged 14.5 ± 1.2 days ($n = 19$, range 8-32 days), approximating the period of egg formation (Petersen 1981). The maximum lag between disappearance of snow and the first egg laid occurred in 1990, when snow depth at Barrow reached zero on 14 May, the earliest date on record.

Annual breeding chronology for the colony, as measured by the first egg in the colony and median date of clutch initiation, showed significant advancement during the study, in association with amelioration of spring and early summer meteorological conditions, discussed above (Figure 1.5). Median date of clutch initiation advanced a mean of 4.6 days per decade, from early July in the late 1970's to late June in the mid-

1990's. Median date of clutch initiation was positively correlated with mean air temperature in May and dates of snow melt and disappearance (Table 1.2).

Snow accumulation late summer and early autumn

Snow accumulation sufficient to block nest-site entrances and prevent the feeding or fledging of chicks was observed on four different occasions, all in the mid-1980's (Table 1.3). These are only the instances of snow accumulation that occurred between the initial through latter dates of fledging. Fieldwork typically ended when approximately 75-90% of all chicks had fledged, thus it is likely that I missed some instances of snow affecting the latest fledging chicks. On the basis of NWS records I believe those instances are few. All four documented instances of snow accumulation occurred between 26 August and 5 September. The two occasions when snow accumulation affected > 50 % of the active nest sites (30 August - 5 September 1983 and 26 August - 1 September 1988) were when snow depths were 5 and 10 cm at Barrow, respectively.

The amount of snowfall alone is not the only factor contributing to accumulation of snow in and around nest sites. Moderate to high winds accompanied by below-freezing temperatures that prevent melting can create substantial drifts from small amounts of snow. On 26 August 1986, snowfall totaling <1.3 cm resulted in > 15 cm of accumulation at some nest sites. On 26 August 1988 snowfall at Barrow totaled 1.8 cm

for the entire day, but by 1900 h winds gusting to 56 km/hr had formed drifts that blocked entrances and filled many nest sites. When winds were high, as they were in during the snow storms in 1986 and 1988, snow completely filled the majority of nest cavities, frequently surrounding the chicks. Several nests (<10) were not blocked by snow accumulation, either because they had high entrances or their entrances had a compass orientation that minimized drifting. Others (<10) had access sufficiently large to allow parents to pass fish to chicks but too small to permit fledging.

The snow accumulation from 26 August-1 September 1988 had a major effect on fledging success and postfledging survival. When snowfall and accumulation began on 26 August, only five chicks had fledged from the colony, with 241 young still remaining in nest sites (Figure 1.6). Snow partially or completely blocked most nest entrances for 3 days, resulting in weight loss or death of most chicks. Twenty-nine percent of 241 chicks either died in the nest or were presumed to have died shortly after leaving the nest. The latter chicks were still flightless (wing chord < 125 mm) that left the nest prematurely and walked away.

Timing of fledging and fledging weight were affected adversely by the snow accumulation. Chicks fledging either before initial snow accumulation on 26 August or in the following two days fledged at a mean of 329 g (s.e. = 6.4 g, range = 300 - 422 g, $n = 19$) (Figure 1.7). Fledging weights then declined as the period of no or limited provisioning increased. Chicks fledging from 31 August to 3 September, had

experienced intermittent provisioning for 4-7 days and averaged 260 g (s.e. = 3.1, range = 210 -345 g, n = 91). An increase in fledging weight occurred after snow depth decreased to <1.3 cm, when a few chicks fledged from sites where parents had provisioned them through the period of snow cover.

Chicks fledging during the 1988 snow event displayed atypical behavior likely related to their low weights and poor condition. Guillemot chicks typically fledge at night and are rarely seen at the colony immediately after fledging (Divoky unpubl.). In 1988 three chicks fledged during full daylight, the only such observations for the 22-year study, and eight fledglings remained in a pond on the island for one to three days after fledging; at least one of these birds was too weak to fly.

Although 70% of the chicks present at the time of snow accumulation fledged, low weight at fledging apparently decreased postfledging survival for the 1988 cohort. Only 3% of the 1988 cohort was subsequently captured as adults, the smallest recapture rate for any of the 16 cohorts from 1975-1990 (Chapter 3). Cohorts from the six years bracketing 1988, had an The average recapture percentage of the six cohorts bracketing 1988 was 18% of fledglings (s.d. = 5 %, range 13-28%).

Historic and long-term trends in snow conditions

The information presented above demonstrates that: 1) date of snow melt in northern Alaska has been advancing over the past two decades, 2) black guillemots delay

breeding in northern Alaska until nesting cavities are snow free and 3) a snow-free period of <80 days could greatly reduce breeding success. Based on these findings I examined historic (1947-1974) and long-term (1947-1996) trends in dates of snow melt and accumulation and duration of the snow free period (Table 1.1, Figure 1.8). I examined annual variation in the length of two measures of the snow-free period: disappearance of snow in spring to accumulation of a trace of snow in autumn and disappearance of snow in spring to accumulation of >1.3 cm of snow in autumn. For years with <80 days in the latter measure, I assumed guillemot breeding success would be reduced, as I observed in 1988.

Both measures of the snow-free period showed a significant increase during both the historic and long-term periods. Over the last five decades the annual snow free period has increased by >5 days per decade (Table 1.1, Figure 1.8). This increase has been due to an advancement of dates of spring snow melt, as dates of snow accumulation in autumn have shown no significant annual variation. The mean snow-free period (trace - >1.3 cm) was 88.2 days in the 28 years preceding the study and 101.9 days during the study. Conditions similar to those that caused the severe decrease in fledging success and post-fledging survival in 1988 (accumulation of > 1.3 cm <80 days after snow disappearance) would have occurred in 29% of the years preceding this study but in only 5% of the years during the study.

DISCUSSION

Regional climatic change in northern Alaska is evidenced by the changes in monthly spring air temperatures and an advancement of snow melt in the three decades before and the two decades of my study. During the latter period black guillemot breeding chronology, as measured by dates of colony occupation and clutch initiation, was correlated with snow melt at the colony and advanced in response to climate amelioration. I therefore accept the working hypotheses that recent regional climate change has occurred in northern Alaska, that black guillemots schedule their annual breeding activities to maximize use of the snow-free period and that a insufficient snow-free period (<80 days) can result in reduced breeding success. The importance of a snow-free period allowing access to nesting cavities for >80 days was demonstrated by the severe reductions in breeding success in 1988, indicating that black guillemots require access to a nest cavity for >80 days in order to reproduce successfully. Additionally, my analysis of historic data indicates that the snow-free period in northern Alaska in the recent past was frequently insufficient to allow successful reproduction. Below, I discuss the effects of snow on breeding chronology and the potential consequences of continuing regional climate amelioration.

Colony occupation

Black guillemots delayed attendance at nest sites at the Cooper Island colony until snow melt was complete or nearly so. This contrasts with many Arctic, subarctic and

montane birds that occupy breeding habitat before snow cover disappears. Least auklets (*Aethia pusilla*) and crested auklets (*A. cristatella*), both cavity-nesting alcids like the black guillemot, sit over and beside snow-filled nest sites until melt allows occupation of nesting cavities (Sealy 1975). Waterfowl frequently arrive on snow-covered tundra for nesting during the final stages of snow melt (Barry 1962), as do montane passerines (Morton 1978). Delaying colony occupation because of snow cover is atypical even for black guillemots. At other arctic colonies birds arrive as early as late March, >2 months before clutch initiation, although conditions are similar to those at Cooper Island (with many nesting cavities filled with snow and ice and the adjacent sea frozen) (Demme 1934, Uspenski 1958, de Korte 1972).

Black guillemots gather in the vicinity of Cooper Island >2 months before they return to the colony and their late occupation of the colony could not be the result of delayed migration or lack of suitable feeding habitat in the region. Behavior of the birds on first return to the colony suggests the risks of avian predation could be high. My first sightings of birds at the colony have been of dense flocks flying high over the island, typical of behavior seen later in the year only when the colony has flushed because of an avian predator (Divoky unpubl.). When first returning to the colony in late spring, guillemots appear wary of landing on the island, making many passes over an area before alighting and then flushing frequently. When an avian predator is present in the first days of colony occupation, birds will prematurely evacuate the colony, apparently returning to

offshore leads. Later in the season birds react to avian predators by sitting and diving in open water present on and next to the island (Divoky unpubl.). Typically this escape habitat is not available until the time of clutch initiation. Thus, guillemots breeding on Cooper Island may delay colony attendance until snow melt is almost complete because of high predation risks.

Avian predators also could be expected at other high Arctic colonies, and the ability of guillemots to occupy those sites early in the year may be related to the atypical physiographic nature of Cooper Island. Guillemots associated with nest sites on rocky headlands or cliffs with some vertical relief, characteristic of most colonies, may be less vulnerable and better able to avoid avian predators than those at Cooper Island. The flat (<3 m ASL) featureless terrain of Cooper Island and the adjacent nearshore ice makes guillemots highly visible and provides no haven for avoiding predators.

The atypically late occupation of the Cooper Island colony does not delay breeding past the time it occurs in other arctic colonies. Timing of egg laying at Cooper Island is similar to Prince Leopold Island and Novaya Zemlya, where first eggs are seen in the middle of June (Gaston and Nettleship 1981, Uspenski 1956). Late occupation of the Cooper Island colony does constrain pre-laying activities, however. The pre-laying period can last from 30-110 days at other Arctic and subarctic colonies (Asbirk 1979, Petersen 1981) but is compressed into approximately 16 days at Cooper Island. The extended period of pre-laying colony attendance at other arctic locations suggests that

important prebreeding social functions, such as pair-bonding, can occur before the nesting cavity is accessible. Both Uspenski (1956) and Portenko (1989) remarked on the social activities of black guillemots while nest sites were still full of snow or ice. The absence of guillemots from Cooper Island until shortly before females begin egg formation requires rapid nest occupation and pairing.

Clutch initiation

The initiation of clutches about two weeks following snowmelt is apparently the result of females not beginning egg formation until they have access to a nesting cavity. Some females apparently begin egg formation on the day cavities are initially occupied. For the three years initial nest site occupation was observed, the observed periods between first visit to nest sites and first egg in the colony (16-17 days) approximated the 15-17 days needed for egg formation in this species (Divoky unpubl., Petersen 1981). For the entire study period, excluding 1990 when snow melt was extremely early, the lag between snow disappearance and the first egg in the colony averaged 14.4 days, just slightly less than the average time required for egg development. The much higher value for 1990 of 32 days shows that factors other than snow melt can affect arrival at the colony or onset of egg formation, however, as it must in subarctic guillemot populations where snow is not a constraint on initiation of breeding.

Although some females apparently begin egg formation within one to two days of arrival at the colony, most take longer. The period between first visits to nest sites and

the median date of clutch initiation for those years when date of arrival was known (1981, 1983, 1984) averaged 22, 28, and 21 days, respectively. Assuming a 16-day period for egg formation, the median time between first visits to the nest site and the start of follicular development was 6, 12 and 5 days for those years, respectively. A stable pair bond and secure nesting cavity likely are required for follicle development, and the period a particular clutch lags after the first egg in the colony probably reflects the variation in time required to obtain a mate and a site as well as individual condition.

Why black guillemots, or other alcids, do not attempt to burrow into snow-filled nesting cavities to hasten the initiation of breeding, as the snow petrel (*Pagodroma nivea*) does in the Antarctic (Maher 1962) is uncertain. Because follicular development is apparently dependent on access to a nesting cavity (this study, Sealy 1975), ability to burrow into cavities could provide an important advantage, especially for high Arctic species. Several alcids, including the pigeon guillemot (*C. columba*), burrow into dirt banks to create nest sites (Thoreson and Booth 1958) and even black guillemots on Cooper Island will excavate sand and gravel to enlarge nest cavities (Divoky unpubl.). Similarly, adult guillemots never attempted to burrow through snow to provision nestlings, even though many of the drifts surrounding chicks only consisted of lightly drifted snow.

Guillemots also could advance breeding by anticipating the availability of nest sites and starting follicle development before cavities are snow free. Arctic waterfowl

begin follicle formation in the last stages of migration (Raveling 1978), shortening the period between arrival and egg laying, but this has not been documented in any alcid.

The black guillemot as an indicator of climate change in the Arctic

If future increases in air temperatures in the Arctic are as high as expected (1°C per decade over the next five decades; Mitchell et al. 1990) most birds in the region will undergo climate-related changes in distribution, abundance, and breeding performance. While most arctic birds have breeding strategies sensitive to the short arctic summer, the black guillemot has a suite of several life-history characteristics that should make it a particularly sensitive and early indicator of climate change in the Arctic. The black guillemot is one of the few truly circumpolar seabirds, in part because of its generalist strategies in both prey and nest-site selection (Storer 1952). Because guillemots can breed either as isolated pairs or colonially and at a relatively early age, unlike most seabirds, they can rapidly exploit nesting opportunities near suitable foraging areas. Additionally, most arctic nesting birds are highly migratory, but black guillemots have little or no migration, allowing them to respond more quickly to spring and summer conditions. Their residency in the Arctic throughout the year also makes them an ideal monitor for that region because their ecology will be affected only by arctic conditions, unlike those species that winter in temperate or tropical regions. Finally, black

guillemots are associated with snow and ice habitats throughout the year, which can be expected to show the immediate effects of changes in air temperature.

The recent establishment, growth and decline of the black guillemot population in northern Alaska (Chapter 2) demonstrates the sensitivity of guillemots to changes in snow and ice conditions. Although naturalists regularly recorded black guillemots at Barrow as early as the 1880's and suspected nesting (Bailey 1948), breeding was first observed only in 1966 (MacLean and Verbeek 1968). Although manmade sites have increased regional nesting potential, natural sites, such as the driftwood piles and burrows on Seahorse Island, where birds have bred since at least 1972 (Divoky et al. 1974), are not of recent origin. Although the increase in the Cooper Island colony between 1972 and 1989 was dramatic (increasing from 10 to 225 pairs) and could not have occurred without provisioning of nest sites, this increase also required the amelioration of climate for regular successful nesting.

My observations show that an insufficient snow-free period can result in decreased fledging success and post-fledging survival, probably to levels inconsistent with population persistence. Historic weather records indicate that breeding success would have been frequently depressed by snow accumulation in the middle part of this century. Snow-free periods <80 days at Barrow occurred in 44% of the years from 1947-1964. Although Arctic seabirds are able to sustain occasional breeding failures (Bertram et al. 1934, Murphy et al. 1991), birds experiencing chronic breeding failure likely would

not continue to breed in the region or would have such low success that a population could not persist. Decreases in fledging success and survival caused by snow accumulation need not be as extreme as I observed in 1988 for population-level effects to occur. If adult survival averages 85%, fledging success must average 1.0 chick per nest per year with 35% of fledglings surviving to recruitment in order to maintain a stationary population without immigration.

Other bird species may be responding to the increased snow-free summer period in arctic Alaska. Horned puffins (*Fratercula corniculata*), a subarctic species whose breeding range extends as far north as the central Chukchi Sea, have prospected potential breeding sites in the Barrow area since at least 1972 (Divoky 1982 and unpubl.), and the first breeding record occurred in 1986 when a pair bred successfully in a nest box on Cooper Island (Divoky unpubl.). Horned puffins have a longer nesting period than the black guillemot, requiring about 90 days from the onset of egg formation to chick fledging. Snow-free periods <90 days occurred regularly until the 1980's (Figure 1.8), and like that of the black guillemot, the first record of a Horned Puffin nesting in arctic Alaska may have been related to the increasing snow-free period.

Warming temperatures have allowed guillemots to breed in the Barrow area, but continued warming may be creating conditions unfavorable for the persistence of a regional population. The reliance on the pack ice as a foraging habitat through most of the year makes black guillemots sensitive to changes in the extent and nature of pack ice.

In northern Alaska annual variation in guillemot breeding success is inversely correlated with the distance of the pack ice from the shore in August due to the abundance of arctic cod (*Boreogadus saida*) at the ice edge and a lack of alternative prey in ice-free nearshore waters (Divoky unpubl.). In the eastern Canadian Arctic, changes in breeding distributions and abundance of black guillemots are associated with annual variation in distribution of sea ice (Prach and Smith 1992). If temperature increases in the arctic are as high as predicted, the Beaufort Sea pack ice may regularly retreat > 100 km from mainland Alaska (McGillivray et al. 1993), far greater than the foraging range of guillemots (typically <15 km).

While anticipated changes in the Beaufort Sea would affect the productivity of the Cooper Island colony, recent reductions in sea ice extent may already be contributing to the colony's decline. From 1989 to 1997 the colony decreased from 225 to 110 pairs, primarily due to decreases in immigration and annual survival of adults. Both decreases may be due to alterations in sea ice cover resulting in decreased prey abundance or availability. Winter sea ice has been decreasing throughout the arctic over the past 20 years (Johannessen et al. 1995), and summer sea ice extent decreased 9% in 1990-1995 compared with the previous ten years. Some of the greatest reductions in summer ice extent have been in the eastern Siberian Sea (Maslanik et al. in press). Guillemot colonies from that location may be in the same metapopulation as the Cooper Island colony (Chapter 3).

The observed advancement of clutch initiation and its close association with snow melt are of interest in light of recent concerns about the quality of the National Weather Service data on snow melt at Barrow. Foster (1989) reported a long term trend in advancement of spring snow melt at Barrow using National Weather Service data. His conclusions that this represented a regional climate change were challenged by Dutton and Endres (1991), who attributed the trend to urbanization at the location of observations. Many anthropogenic effects Dutton and Endres associate with the Barrow data set could not be expected to extend to Cooper Island, 25 km upwind of the prevailing wind direction from Barrow. The advancement of clutch initiation in black guillemots over the last two decades, and the demonstrated relationship between snow melt and clutch initiation, contradict the conclusions of Dutton and Endres (also see Foster et al. 1991) and show the utility of using an offsite biotic indicator to assist in the interpretation of local meteorological measurements (Smith 1994).

CONCLUSIONS

The years of my study (1975-1996) may have been the optimal period for black guillemot colonization and reproduction in northern Alaska. The observed warming in early summer temperatures at Barrow is part of a long term warming trend that began in the region early this century after approximately three centuries of cooler summer temperatures (Overpeck et al. 1997). The snow-free period in the region was probably

insufficient to allow successful breeding in the majority of nests for the preceding 350 years. Increased seasonal availability to nest cavities would both increase the number of potential nest sites for black guillemots but likely also increase their regional abundance and breeding productivity. However, it now appears that continued warming may be leading to decreases in prey abundance or availability in the pack ice resulting in increased black guillemot mortality. Continued monitoring of black guillemot breeding chronology and demographics at the Cooper Island colony should allow further insights into the biotic consequences of climate change in the arctic.

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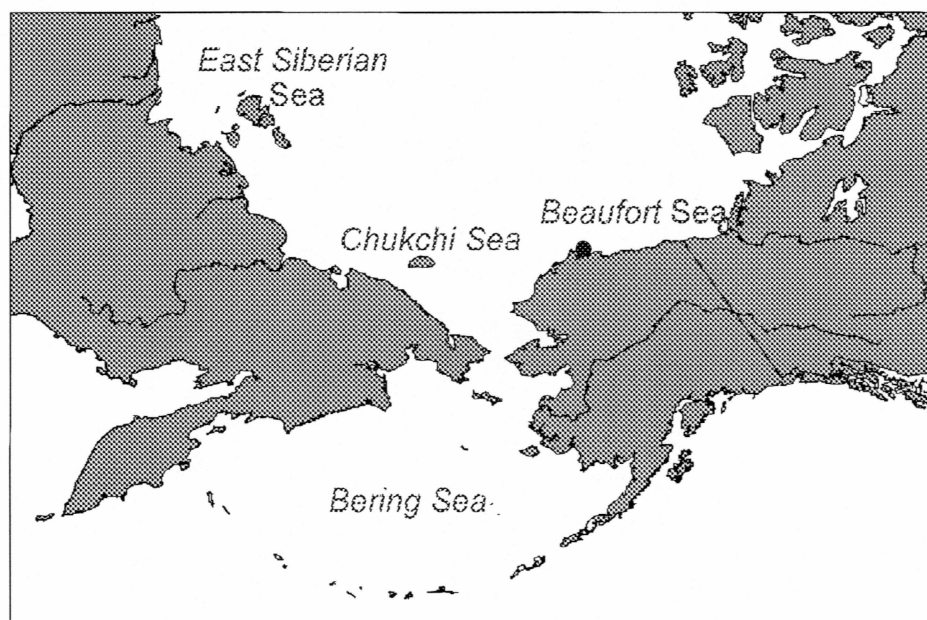


Figure 1.1. Western Arctic showing location of Cooper Island (circle on Alaskan Beaufort Sea coast)

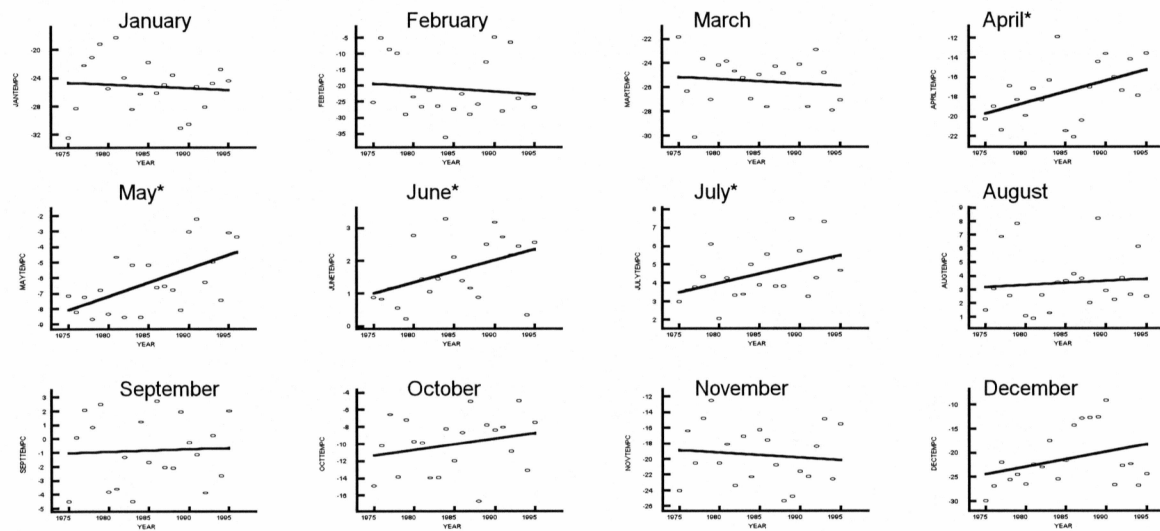


Figure 1.2. Mean monthly air temperatures at Barrow, Alaska, 1975-1996 (National Weather Service).

* Annual temperature trend significant at $P < 0.005$.

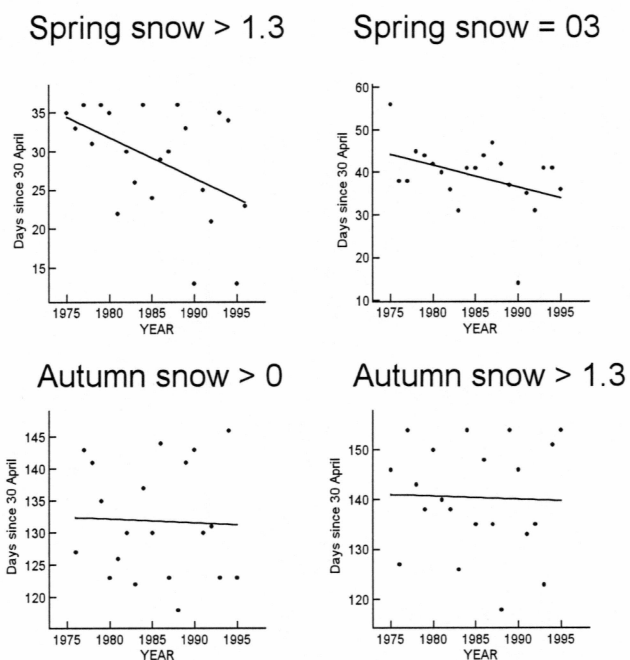


Figure 1.3. Dates of snow melt and persistent accumulation of snow at Barrow, Alaska, 1975-1996 (Source: National Weather Service)

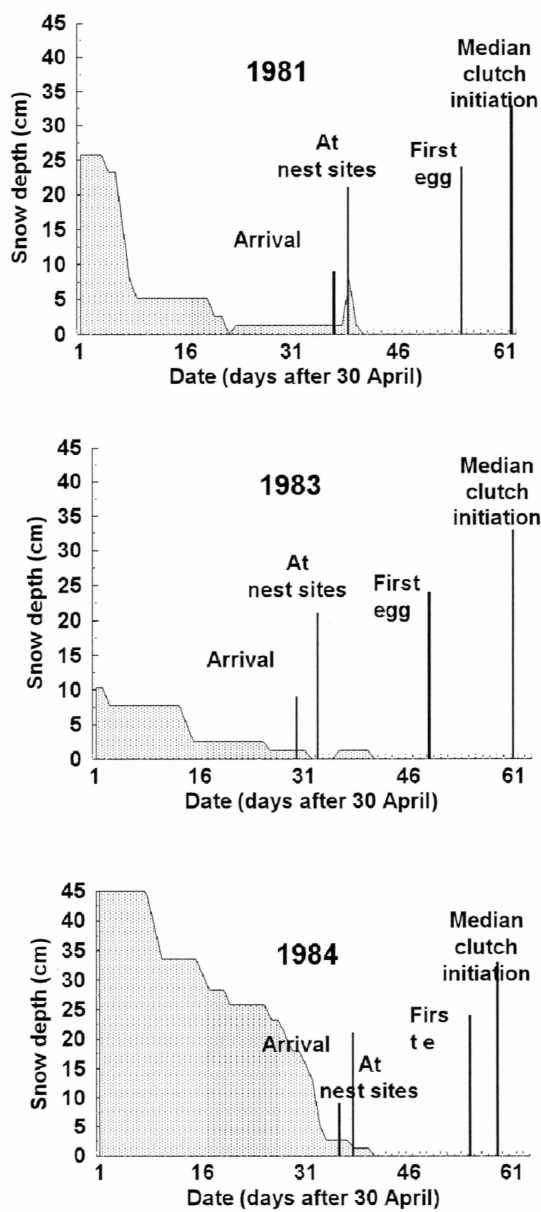


Figure 1.4. Dates of arrival at colony, first egg in the colony and median date of clutch initiation in Black Guillemots in relation to snowmelt (1981, 1983-1984) at Cooper Island, Alaska.

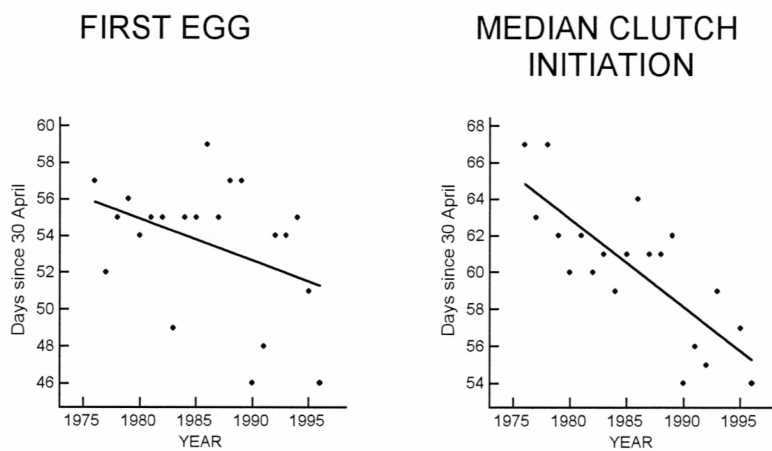


Figure 1.5. First egg in colony and median date of clutch initiation for Black Guillemots on Cooper Island, Alaska (1975-1991, 1993-1996).

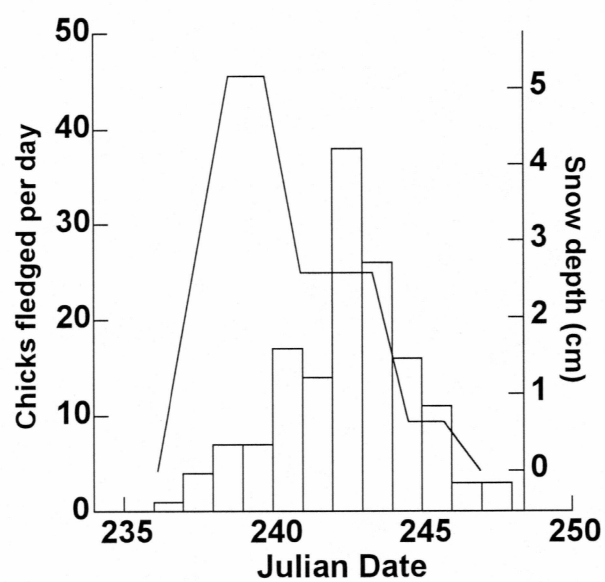


Figure 1.6. Dates of Black Guillemot fledging at Cooper Island, Alaska in 1988 (bars) and Barrow snow depth (line).

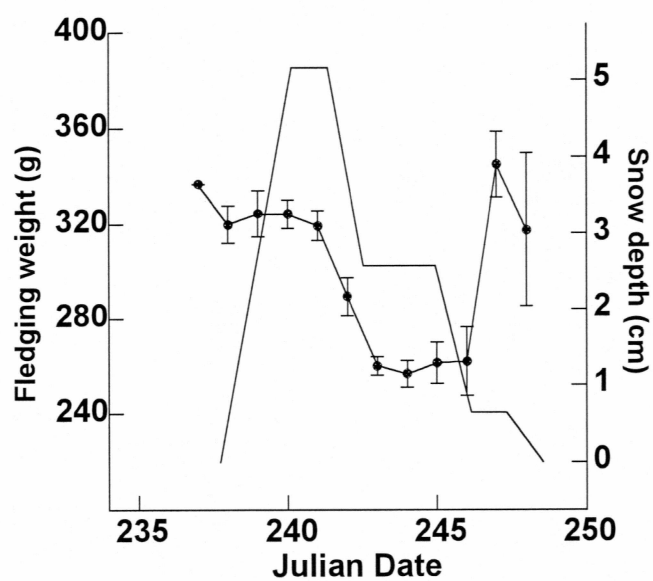


Figure 1.7. Average daily weight at fledging (\pm s.e.) of Black Guillemots at Cooper Island, Alaska and daily Barrow snow depth (line).

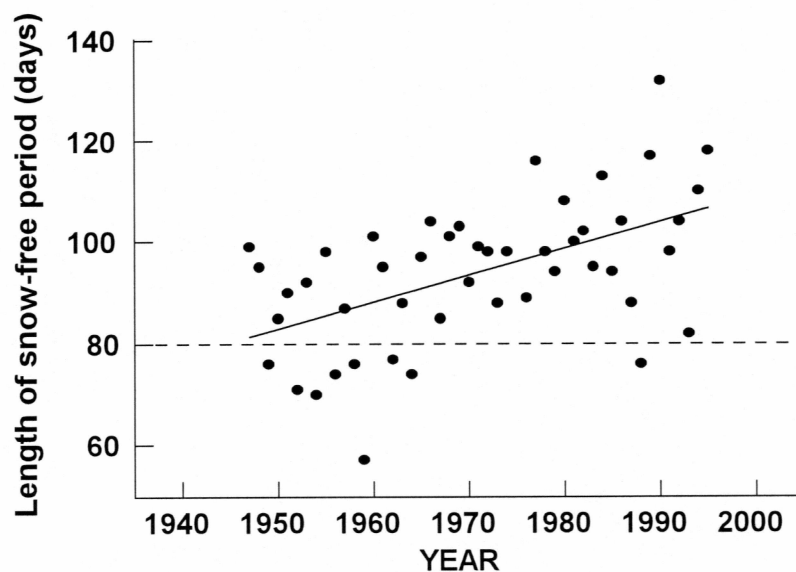


Figure 1.8. Length of snow-free period (disappearance in spring to >1.3 in autumn) at Barrow, Alaska, 1947-1996. See Table 1.1 for analysis. Black Guillemots require a snow-free cavity for at least 80 days (broken line) for successful nesting.

Table 1.1. Trends in annual dates of snow melt and accumulation and duration of snow-free period for 1975-1996, 1947-1974 and 1947-1996 at Barrow, Alaska.

	Study Period 1975-1996			Historic Period 1947-1974			Long-term 1947-1996		
	r^a	r^2	P	r	r^2	P	r	r^2	P
DATE OF SNOW MELT									
Snow depth <1.3 cm	-0.53	0.16	0.02	-0.27	0.23	<0.01	-0.48	0.65	<0.01
Snow depth = 0	-0.52	0.23	0.07	-0.41	0.27	<0.01	-0.57	0.62	<0.01
DATE OF SNOW ACCUMULATION									
Snow depth > 0	-0.07	<0.01	0.85	0.13	0.01	0.56	-0.03	<0.01	0.80
Snow depth >1.3	0.08	<0.01	0.74	0.14	<0.01	0.98	-0.06	<0.01	0.61
LENGTH OF SNOW-FREE PERIOD									
Trace-trace	0.27	0.17	0.58	0.55	0.15	0.04	0.56	0.34	<0.01
Trace - > 1.3 cm	0.35	0.23	0.52	0.49	0.34	0.08	0.52	0.28	<0.01

^a Correlation coefficient for variable x year trend.

Table 1.2. Date of first egg in colony and median date of clutch initiation in relation to year and Barrow weather conditions (1975-1991, 1993-1996).

	First egg in colony		Median date of clutch initiation	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Year	0.39	0.08	0.77	<0.001
Mean May temperature	0.73	<0.001	0.71	0.001
Date snow < 1.3 cm	0.59	0.005	0.55	0.02
Date snow = 0 cm	0.74	<0.001	0.59	0.01

Table 1.3. Snowfall, snow depth and average air temperature at Barrow, Alaska during periods when snow accumulation blocked entrances to Black Guillemot nest cavities on Cooper Island, Alaska.

Dates	Cumulative Snow fall (cm)	Maximum Snow Depth (cm)	Mean Air Temperature (°C)	Sites blocked (%)
30 Aug - 5 Sept 1983	6.0	10.0	-2.1	50
26-27 Aug 1986	0.3	>1.3	-0.3	25
30 Aug - 3 Sept 1986	3.8	>1.3	0.7	24
26 Aug - 1 Sept 1988	6.0	2.5	-2.1	90

**POPULATION GROWTH AND IMMIGRATION AT A COLONY OF BLACK
GUILLEMOTS IN NORTHERN ALASKA²**

ABSTRACT

Models of colony growth in seabirds have assumed immigration is important during periods of rapid growth but that native birds constitute the vast majority of recruits in periods of population stasis or decline. I examined population growth and immigration at a colony of Black Guillemots breeding in manmade nest cavities in arctic Alaska. The colony increased from 15 to more than 200 pairs through the provision of cavities and later declined to 150 pairs as factors other than nest-site availability limited population size. Banding of all native chicks from 1975-1994 and banding of most breeding adults since 1980 allowed determination of the relative contribution of immigrant and native birds to recruitment and colony composition. Annual population growth averaged 37% from 1976-1982 when nest site occupancy was low, 3% from 1983-1989 when all or most nesting cavities were occupied, and -6% from 1990-1996 as breeding productivity decreased and mortality of adults increased. Without immigration and with the average annual vital rates the colony would have had an annual rate of growth of 4% during this study. Immigrants comprised the majority (92%) of recruits not only during colony

² Prepared for submission to AUK as Divoky, G.J. POPULATION GROWTH AND IMMIGRATION AT A COLONY OF BLACK GUILLEMOTS IN NORTHERN ALASKA

growth but also during periods of stasis (87%) and decline (60%). These results refute previous models of seabird population growth that assume immigration is high only immediately after colony formation and during rapid colony growth and that native birds have a recruitment advantage at their natal colony. Between 200 and 1200 breeding pairs were needed to produce the 70 and 63 immigrants recruiting annually during rapid growth and stasis, respectively, and dispersal > 700 km apparently has been common in the region.

INTRODUCTION

Most (98%) species of seabirds are colonial breeders (Lack 1968), and ornithologists frequently assume that most birds surviving to breeding age recruit or attempt to recruit at the natal colony (Gill 1994). The assumption of high philopatry has been incorporated into demographic models of seabird colonies that have assumed inter-colony movements are negligible (Birkhead and Hudson 1977, Hatchwell and Birkhead 1991) and dispersal to nonnatal locations occurs primarily through indirect, density-dependent emigration from the natal colony (Cairns 1992). Recently, however, the banding of large numbers of nestlings has shown that many individuals will recruit to a nonnatal colony in at least some species of seabirds (Coulson and Neve de Mevergnies 1992, Harris and Wanless 1991, Danchin and Monnant 1992). Additionally, prospecting at nonnatal colonies during the several-year period of delayed sexual maturity also has

been observed in some species (Halley and Harris 1993), demonstrating the potential for emigration without first returning to the natal colony. Although recognition of the frequency and extent of intercolony movements has assisted development of some models (Petersen 1981, Cairns 1992), such models still incorporate the untested assumption that most emigration is caused by density-dependent constraints at the natal colony and that immigration is primarily to locations with limited density-dependent constraints on recruitment.

Two models that examine the relative contribution of native and immigrants during colony growth and stability have been developed for seabirds. First, Petersen (1981) used his observations of growth of a Black Guillemot colony in Iceland with mean values of breeding success and adult survival to provide estimates of the number of native birds and immigrants recruiting during rapid growth and subsequent stasis (Figure 2.1). As part of an examination of growth of seabird colonies, Cairns (1992) developed a theoretical model for a hypothetical nest-site limited seabird (Figure 2.2). Both models assumed (1) all birds surviving to breeding age return to the natal colony and recruit the 1st year they are able to breed, except when the potential number of native recruits exceeds the number of recruitment opportunities and (2) immigrants constitute the majority of recruits when nest sites are not limiting and colony growth is rapid, but no longer recruit when there is competition for nest sites with native birds.

I was able to test the applicability of these models, and the validity of their underlying assumptions, to a colony of Black Guillemots (*Cepphus grylle*) breeding in manmade nest sites in northern Alaska. Guillemots (*Cepphus* spp.) are cavity-nesting alcids; their populations frequently are limited by availability of nest sites (Storer 1952, Preston 1968). Members of this genus utilize a wide range of nesting cavities and, unlike most other alcids, are not strictly colonial. Pairs nest solitarily, in loose aggregations, or colonially (Sowls et al. 1978). The ability of guillemots to occupy newly available cavities rapidly (Preston 1968) allowed me to increase the size of the breeding population, while the nature of the nest structures I constructed permitted unique investigator access to all nesting cavities, permitting the banding of all fledging chicks and most breeding birds. This provided a unique opportunity to distinguish the origin of recruits (natives vs. immigrants).

During the study the colony experienced: 1) a rapid increase in numbers related to provisioning of artificial nest cavities, 2) a period of slower growth and relative stability in numbers when few additional cavities were provided, most of the cavities were occupied, and many nonbreeders were present, and 3) a period of decline associated with increased adult mortality and decreased productivity when nest sites were no longer limiting. Below, I refer to these periods as rapid growth, stasis and decline, respectively. Based on the two demographic models previously published, I hypothesized that immigration would: 1) constitute the majority of recruitment during colony expansion, 2)

decrease as production of native birds increased, and 3) be negligible during periods of stability and decline.

STUDY AREA

I conducted research from 1975 to 1995 on Cooper Island, a low sand and gravel island in the extreme western Beaufort Sea, 25 km ESE of Point Barrow, Alaska (Figure 2.3). A population of 10 pairs of Black Guillemots breeding in manmade boxes and floorboards left in the mid-1950's was discovered on the island in 1972 (Divoky et al. 1974). I created five additional sites in 1972, and by early 1975 the population had increased to 15 pairs. From 1975 to 1985, I created 185 additional nest sites on the island and the population increased to more than 225 breeding pairs by 1990 (Figure 2.4).

The northern Alaska coastline provides limited breeding opportunities for Black Guillemots. Although able to breed in a wide range of cavities offering overhead cover (Storer 1952), members of the genus *Cepphus* typically nest in crevices in rock cliffs and talus (Harris and Birkhead 1985, Sowls et al. 1980). Throughout the region the shoreline consists primarily of low, slowly eroding earthen and permafrost bluffs (typically < 5 m ASL (above sea level)) with low depositional sand and gravel islands in the nearshore. No rocky headlands or offshore rocks are present within 600 km (by sea) of Cooper Island, the nearest being Cape Lisburne, Alaska 600 km to the west, and Cape Parry, Northwest Territories, 1,000 km to the east.

Before I enlarged the colony on Cooper Island, the largest colony of Black Guillemots in Alaska was at Cape Lisburne with small colonies of <20 pairs elsewhere in the state (Figure 2.3, Table 2.1). When I began my study in 1975, the number of breeding pairs in the state was approximately 200-225 with an additional 50 pairs in Canada (Kuyt et al. 1976, Sowls 1980, Johnson and Ward 1985). Except at Seahorse Island, where guillemots breed in cavities in a natural driftwood pile (Divoky et al. 1974), all pairs breeding east of Cape Lisburne and west of Cape Parry are in cavities associated with manmade structures.

The Alaskan Black Guillemot population is part of an east-west gradient in abundance in the western Arctic, apparently reflecting nest-site availability and the distribution of rocky shorelines. West of Alaska, the largest guillemot concentrations occur on the rocky headlands of the DeLong Islands, some 2,500 km west of Point Barrow, where an estimated 25,000 pairs breed (Uspenskii 1959). The Siberian coast along the Chukchi Sea and associated islands support numbers similar to the Alaskan coast (<500 pairs; Golovkin 1984). East of Alaska, the Canadian population is limited to approximately 50 pairs, more than half at a manmade colony at Herschel Island (Kuyt et al. 1976). East of Cape Parry there is a gap of approximately 1,000 km to the farthest west breeding location in the eastern Arctic at Somerset Island (Nettleship and Evans 1985) with apparently little if any exchange of birds between regions (Storer 1952). In Alaska, Black Guillemots do not breed south of the Bering Strait (Sowls et al. 1978)

where they are replaced by the subarctic and temperate breeding Pigeon Guillemot (*C. columba*).

METHODS

Banding

Beginning in 1976, I banded breeding and nonbreeding adult guillemots with a unique combination of three PVC color bands, allowing individual identification. The PVC bands used for both chicks and adults were overlapping bands sealed with a cyanoacrylate glue at banding. Adult birds were captured both by using noose mats and by netting birds exiting nest sites. Noose mats fashioned after Williamson (1945) were placed at the most frequently occupied roosting site of the target individual or on the top of or entrance to the nest site. Breeding birds that eluded capture in this way were typically captured after clutch completion by netting them as they left the nest site. To reduce potential disruption during egg laying, breeding females were not captured between the time the first egg was present in the colony and the completion of the clutch at the target site. Because the presence of other birds facilitated the return of a released bird to its nest site or subcolony, adults were usually captured during daily periods of high colony attendance (2400-1000 h Alaska Daylight Time [ADT]). No attempt was made to capture previously individually marked birds. Those captured accidentally were checked for color band deterioration and rebanded if necessary.

Nonbreeding birds prospecting or competing for nest cavities were noosed both incidentally during attempts to capture breeders and, because many nonbreeders show nest-site or roost-site fidelity (Divoky unpubl.), by placing noose mats in locations frequented by specific nonbreeders. Additionally, noose mats were placed on and next to temporary nest sites placed specifically to capture prospecting nonbreeders.

The netting of birds exiting nest sites and noosing of birds directly outside nest sites resulted in the capture of individuals either breeding or actively prospecting for nest sites. The placement of noose mats typically involved flushing birds from the subcolony (an aggregation of nest-sites). Displaced birds landed on an adjacent area of the island until I departed the subcolony. Within a few minutes (typically < 2) a few birds returned to the subcolony, followed shortly by the remaining birds. Often the occupants of a nest site were wary of a noose mat and remained a few meters away from the site. This provided nonbreeders an opportunity for greater access to the site than when it was actively defended by its occupants and increased the chances of capturing nonbreeders associated with a nest site. Additionally, when a breeding bird, particularly the male, was captured at its nest site, the period between capture and return to the site (typically < 15 minutes) allowed nonbreeders a temporary opportunity to occupy the top of the site. In subcolonies where competition for sites was high, several nonbreeders could be noosed during the absence of the breeding bird.

Censusing

I censused the breeding and nonbreeding population annually during the pre-egg and early incubation periods. Censuses were conducted at the daily period of maximum colony attendance (2400-1000 h ADT). For purposes of censusing, the colony was subdivided into 23 subcolonies of 2 to 12 nests. Breeding and nonbreeding birds in each subcolony were counted. I identified individually banded adults and tallied the number of individuals in each subcolony. All breeders and many nonbreeders show subcolony fidelity in a particular year (Divoky unpubl.), and the possibility of counting individuals more than once on the same census was minimal.

The identity of all individuals occupying nest sites was determined by observing the pair defending and performing courtship activity (Preston 1968) at the nest site. At nest sites where (1) individuals occupying the site changed during the pre-egg period, (2) eggs were displaced shortly after laying or (3) excessive aggressive behavior was observed, observations to confirm the site occupants were continued into the incubation period. A pair was not considered to breed in a given year unless it occupied a nest cavity where eggs were laid.

Annual mortality of breeding birds is the percentage of birds that bred the previous year that did not return to the colony the following year. No previously breeding birds that were unrecorded in one year were resighted in subsequent years. I believe there is little possibility that non-returning, breeding birds dispersed to other colonies. Nest-

site fidelity is high (>95%), and breeding dispersal typically averages < 10 m, with only three instances of breeders moving >100 m (Divoky unpubl.). When previously breeding birds entered the floating population they showed fidelity to the subcolony where they previously bred and were repeatedly detected during censusing.

I estimated growth of the colony in the absence of immigration by using vital rates obtained during this study. Adult survival was averaged from 1980-95 observations and breeding productivity from 1975-95, excluding those years when terrestrial predators significantly reduced productivity (1990, 1992 and 1994). The percentage of a cohort surviving to breeding and recruiting locally was obtained from the 1975-1978 cohorts that experienced no nest-site limitation at maturity.

The following terms are used to categorize individuals: nonbreeding birds that do not inhabit a structure with a nesting cavity are called "floaters" and collectively "the floating population." The term "floater" is somewhat inappropriate, as noted by Smith (1978), because, as in many species, nonbreeding guillemots display site and mate fidelity. This term, however, is in wide use in the literature (Smith and Arcese 1989, Eckert and Weatherhead 1987). Birds banded as nestlings on Cooper Island are termed "locals" or "natives." Birds that fledged elsewhere are called "nonnative," when present as nonbreeders, or "immigrants," if they have recruited into the breeding population at the study colony.

The number of native birds recruiting (initially entering the breeding population) annually was known from direct observation of recruitment. The number of immigrants recruiting annually was determined from: 1) observation of banded floaters entering the breeding population, 2) observation of unbanded birds occupying a vacant nest site or replacing a banded occupant at an occupied site and 3) estimating the number of immigrants recruiting to locations where unbanded birds bred the previous year. The latter was obtained by multiplying the observed annual mortality of banded breeding birds times the number of unbanded breeding birds in the previous year.

RESULTS

Rates of colony growth and recruitment

The study population increased rapidly when additional nest sites were provided, increasing from 18 breeding pairs in 1975 to 225 breeding pairs in 1989 (Figure 2.4). From 1976 to 1982, the average annual increase in the breeding population was 37% (range 17-59 %; Figure 2.5), decreasing to an average of 3% (range 0 - 9%) in 1983-1989, when I created few nest sites and occupancy exceeded 90% (Figure 2.4). The number of breeding pairs exceeded the number of nesting cavities in 1989-1991 because pairs recruited to sites already occupied by breeding pairs and laid eggs in separate nest depressions in the same cavity. From 1990-1994 the population declined at an annual rate of 6% (range = -14-0%), with 150 pairs breeding in both 1994 and 1995.

The observed annual increases in the population from 1976-1982 were far higher than could be explained by native recruitment. The estimated average annual growth for a population having the average demographic parameters at Cooper Island (breeding success of 1 chick per nest, 15% annual mortality of breeders, recruitment of 37% of a fledging cohort at 4 years) with no limitation of nest sites, emigration, or immigration, would be 4% per year.

Annual growth of the breeding population was highest when unoccupied sites were available and when mortality of breeding adults was low. Occupancy rate the previous year explained 57% of the variation in annual change in the number of breeding adults ($n = 20$, $P < 0.001$) for 1976-95 (Figure 2.5). For the period when mortality of breeders was known (1980-1995), annual variability in the percent of nest-sites occupied the previous breeding season and mortality of breeders during the preceding year together explained 72% of the variation in annual growth in number of breeding adults ($n = 17$, $P < 0.001$).

Annual recruitment rate (the percentage of the breeding population consisting of new breeders) was related to the number of vacancies available in the colony. It averaged 37% (range 26-43%) in 1975-1982 during rapid colony growth but declined to an average of 18% (range %) during stasis and fell to 14% (range %) during decline (Figure 2.6). Annual rate of recruitment was related to nest-site availability and, when nest-site occupancy was high, to overwinter mortality of breeders. For the entire study period the

percentage of nest sites occupied the previous year accounted for 73% of the variation in annual recruitment rate ($n=20$, $P < 0.001$). When occupancy exceeded 70% (1983-95) annual mortality of breeders explained 52% of the variation in recruitment rate ($n = 13$, $P < 0.05$).

Origin of Recruits

The origin (natives vs. immigrants) of all individuals entering the breeding population since 1978 was known because all native fledglings were banded starting in 1975. Most unbanded native birds fledging earlier than 1975 likely would have recruited before 1978 because the 1975 and 1976 cohorts recruited at a median age of 3 years (Chapter 3).

The contribution of immigrants to annual recruitment was large in all phases of colony growth, exceeding that of natives in periods of colony growth, stasis and decline (Figure 2.7). Immigrants comprised 92% of recruits during colony growth. During stasis, the percentage of immigrants was only slightly less (87%). During colony decline immigrants comprised 60% of recruits.

The percentage of annual recruitment consisting of natives reflected both local production and the competition with immigrants for nest sites. Natives composed 30% of annual recruitment in 1978 but <15% of annual recruitment in 1980-1985 (Figure 2.7). After 1985, the large cohorts that fledged after 1982 were reaching breeding age, but

relative levels of native recruitment increased only slightly (to 20%) in 1988-1989. Only after 1989, when the number of breeding pairs and competition for nest sites began to decline (Figure 2.4), did the percentage of native birds begin to increase, averaging 54% of annual recruitment (range 41-71%) from 1990-1993. Decreased native recruitment in 1994-1995 was the result of (1) a small 1990 cohort, due to polar bear (*Ursus maritimus*) predation on chicks and (2) a complete nesting failure in 1992, due to arctic fox (*Alopex lagopus*) predation on eggs. Overall, native birds comprised 18% of the 1163 birds recruited to the colony in 1978-1995.

Annual censusing allowed accurate determination of the composition of the breeding population (natives vs. immigrants) for 1978-1995. Except for the estimated 26 experienced birds breeding in 1978, the origin (native vs. immigrant) of all breeding birds from 1979 to the present was known. The birds recruited before 1978 composed a decreasing percentage of the breeding population as the study progressed, and, by 1981, the source of more than 90% of all breeders was known (Figure 2.8). Native birds composed <15% of all breeding birds from 1981-1989. As the population began to decline after 1989, native birds composed a larger percentage of the population, averaging 37% for 1993-1995.

Recruitment of immigrants

There was no indication that native birds had a recruitment advantage over non-natives based on the recruitment characteristics of birds captured as nonbreeders. Of 462 non-native birds captured as floaters between 1980 and 1990, 45% successfully recruited into the breeding population. Similarly, 45% of the 166 native floaters captured over the same time period.

Sources of immigrants

The colony recruited 954 nonnative birds from 1978-1995, averaging 55 immigrants annually (range 25-155). Annually, the mean number of nonnative recruits during colony growth, stasis and decline was 70, 63, 27 respectively. The natal colonies of these birds were not known. Banding at other guillemot colonies in northern Alaskan has been incidental, and only three immigrants to the Cooper Island population had been banded elsewhere (two from Point Barrow and one from Seahorse Island) (Divoky unpubl.).

To determine the size of the source population needed to produce these immigrants, I created a model to estimate emigration from a source population. I obtained two estimates for each of the time periods (growth, stasis and decline); one was the number of breeding pairs needed to produce the observed immigrants if all source birds surviving to four years of age dispersed to Cooper Island. The other assumed that

15% (the average adult mortality and the recruitment rate needed to maintain a stable population) of the source birds surviving to breeding recruited at their natal colonies and the remainder immigrated to Cooper Island. I assumed that 1st-year mortality was 50%, subsequent mortality 15%, and all birds recruit at four years of age.

The size of the source population needed to produce the 55 immigrants recruited per year was 150 pairs if all source chicks emigrated to Cooper Island and 915 pairs if only “surplus” birds emigrated. Estimated numbers of pairs needed to produce appropriate numbers of chicks during growth, stasis and decline were 200 and 1200, 100 and 1000, and 75 and 500, respectively. Colonies in Alaska and Canada account for only approximately 250 pairs, suggesting that during colony growth and stasis immigrants from the western Chukchi Sea were recruiting to Cooper Island, a distance of >600 km. The 27 immigrants per year recruited in the period of colony decline could have come from colonies in Alaska, but natal dispersal would still exceed 300 km for at least some of these recruits.

DISCUSSION

My observations showed that the previous models of population growth underestimated the importance of immigration, and consequently overestimated the importance of natal recruits, during rapid population growth and stasis of the Black

Guillemot population on Cooper Island. This underestimation was related to a number of incorrect assumptions about the mechanisms of dispersal and immigration in seabirds.

First, the models developed by Cairns (1992) and Petersen (1981) assumed birds first attempt to recruit at the natal colony and emigrate only in response to density-dependent constraints at the colony. My findings on philopatry in Black Guillemots (Chapter 3) indicate that a natal bias may operate at the regional, rather than the colony scale, and that emigration to nonnatal colonies can occur independent of constraints at the natal colony. Second, both models assume that immigration decreases as production of natives increases and that immigration ceases when native production can account for recruitment.

Processes that would result in the decrease and cessation of immigration are not stated for either model. Unless the source colonies that allowed colony formation and initial rapid growth decline in size or productivity, the potential immigrants to the target colony should remain the same through time. Two possible explanations for the models' decline in immigration are (1) the exclusion of potential immigrants through recruitment advantages of natives and (2) a density-dependent decrease in the attractiveness of recruitment opportunities to potential immigrants.

A recruitment advantage to native birds has not been demonstrated for seabirds, and there is little reason to think that one exists for Black Guillemots. Guillemot chicks remain in the nest site until fledging, fledge at night and do not remain near the colony

after fledging (Divoky unpubl.). Unlike surface nesters, with chicks that see the colony from hatching until fledging, or species with chicks that forage near the colony after fledging, guillemot chicks and fledglings do not obtain extensive information about the location or characteristics of their natal colony. Native birds would not be expected to obtain any advantage over nonnatives during the period before recruitment because guillemots disperse widely during their first and second summers (Petersen 1981) and one-year-olds are more likely to prospect at nonnatal colonies than at their natal colony (Chapter 3). Preferential recruitment of native birds through mate choice could also result a decrease in immigration and has been proposed, but not demonstrated, to be a mechanism allowing the evolution of kin groups in Thick-billed Murres (*Uria lomvia*) (Friesen et al. 1996).

The second explanation for a decrease in immigration would be source-specific variation in recruitment strategies. This explanation requires that: 1) potential immigrants have a preference for vacant sites and cease to immigrate when recruitment opportunities are limited to replacement at occupied sites, typically requiring joining a queue (Chapter 3) and 2) native birds attempt to recruit to a colony regardless of the type of recruitment opportunities or competition. There is no reason to think that either of these occurs in guillemots or any other seabird. On Cooper Island nonnative birds regularly join queues and compete for nesting opportunities at occupied sites, and native birds decrease natal

recruitment in response to changes in recruitment opportunities and competition (Chapter 3).

Recruitment in Black Guillemots can occur through discovery of an unoccupied nesting cavity or replacement of a previous occupant at an occupied cavity. Because the creation of nest cavities is relatively uncommon, most recruitment for guillemots likely occurs through replacement of a member of an established pair.

Sources and avenues of immigration

Immigrants likely come from a metapopulation extending from at least as far west as the East Siberian Sea and as far east as the eastern Beaufort Sea. Cooper Island is at an optimum location to attract birds from this metapopulation. The large summering population of nonbreeders in the Chukchi Sea reaches its eastern extent only 25 km from Cooper Island (Divoky 1987). Arctic cod (*Boreogadus saida*), the principal food returned to chicks on Cooper Island (Divoky unpubl.), are most common and available at the ice edge (Divoky 1976, Bradstreet and Cross 1982). Breeding birds foraging at the ice edge could be expected to attract nonbreeders when they return to the island. East of Cooper Island, Black Guillemots are rare to uncommon in pelagic and nearshore waters (Divoky 1982); thus colonies to the east in the Beaufort Sea could be expected to have fewer potential recruits.

CONCLUSIONS

Levels of immigration remained high during colony growth, stasis and decline. Therefore I reject the hypotheses that immigration is important only during colony growth and inconsequential in periods of stability or decline. The size of the source populations needed to account for observed immigration indicates that natal dispersal regularly exceeds 300 km in this region, and my results indicate that both the rate and distance of immigration are higher than previously thought.

Immigration-emigration processes similar to those observed for Black Guillemots on Cooper Island may be common in seabirds. Seabird populations monitored over longer than a decade have rarely been stable, and rapid colony growth or decreases are common (Hudson 1985), frequently exceeding what could be explained by local production. While immigration has always been recognized in the latter case, my findings indicate that immigration, frequently from distant source colonies, needs to be considered even when levels of native production are sufficient to account for observed recruitment.

Past models have underestimated the importance of immigration between colonies due to invalid assumptions of: 1) high colony philopatry, 2) density-dependent emigration and 2) preferential recruitment of natives. The first two assumptions are based in the view that a seabird colony functions as an ecological patch with a resulting overestimation of the benefits of philopatry and the costs of emigration. My findings here and elsewhere (Chapter 3) indicate that a seabird colony may be only part of a larger

geographic area comprising an ecological patch, within which the benefits of philopatry and costs of emigration are low. Future models of seabird populations will need to be done at the ecological scale upon which dispersal constraints operate. In many, if not most cases, this scale will be larger than the colony.

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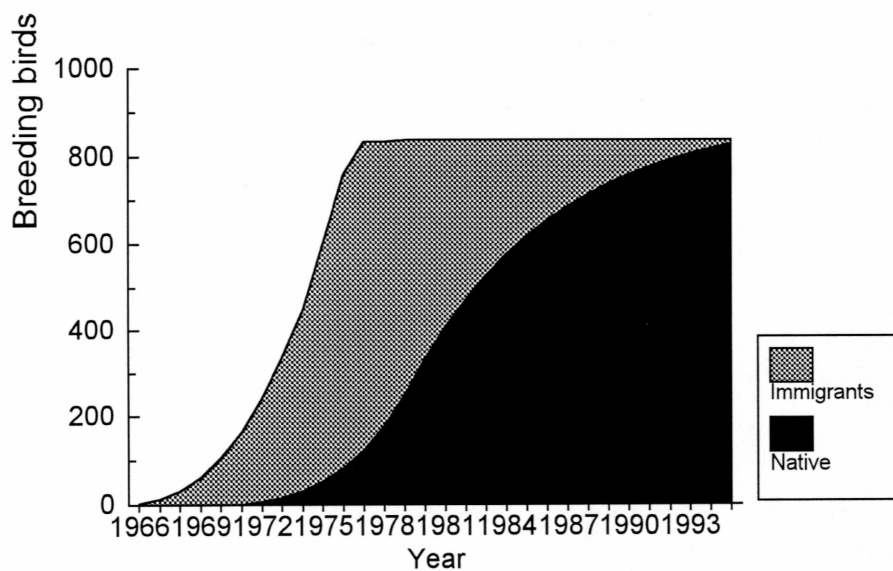


Figure 2.1. Observed growth of Flatey Island Black Guillemot population with assumed numbers of native and immigrant birds in breeding population. Based on Petersen (1981).

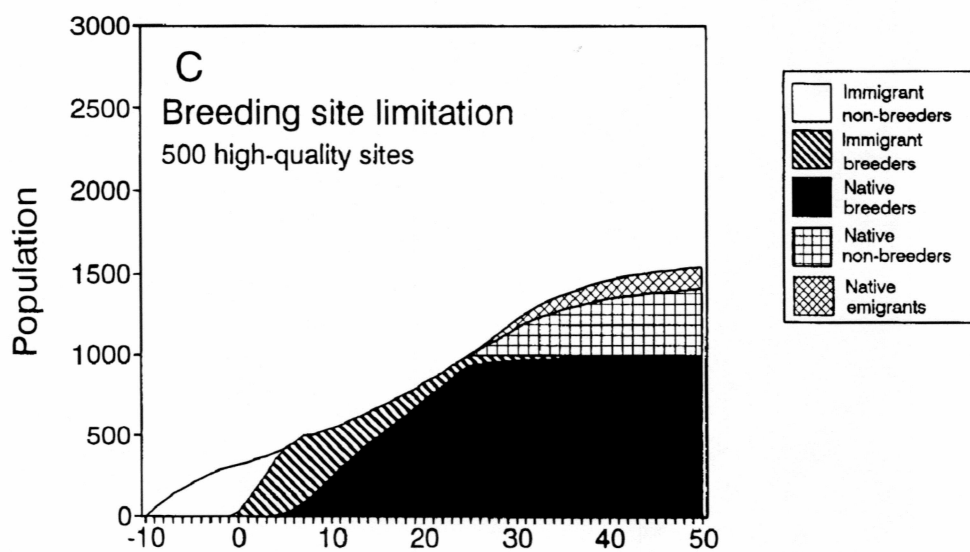


Figure 2.2. Simulated growth of seabird colony with 500 breeding sites. From Cairns (1992).

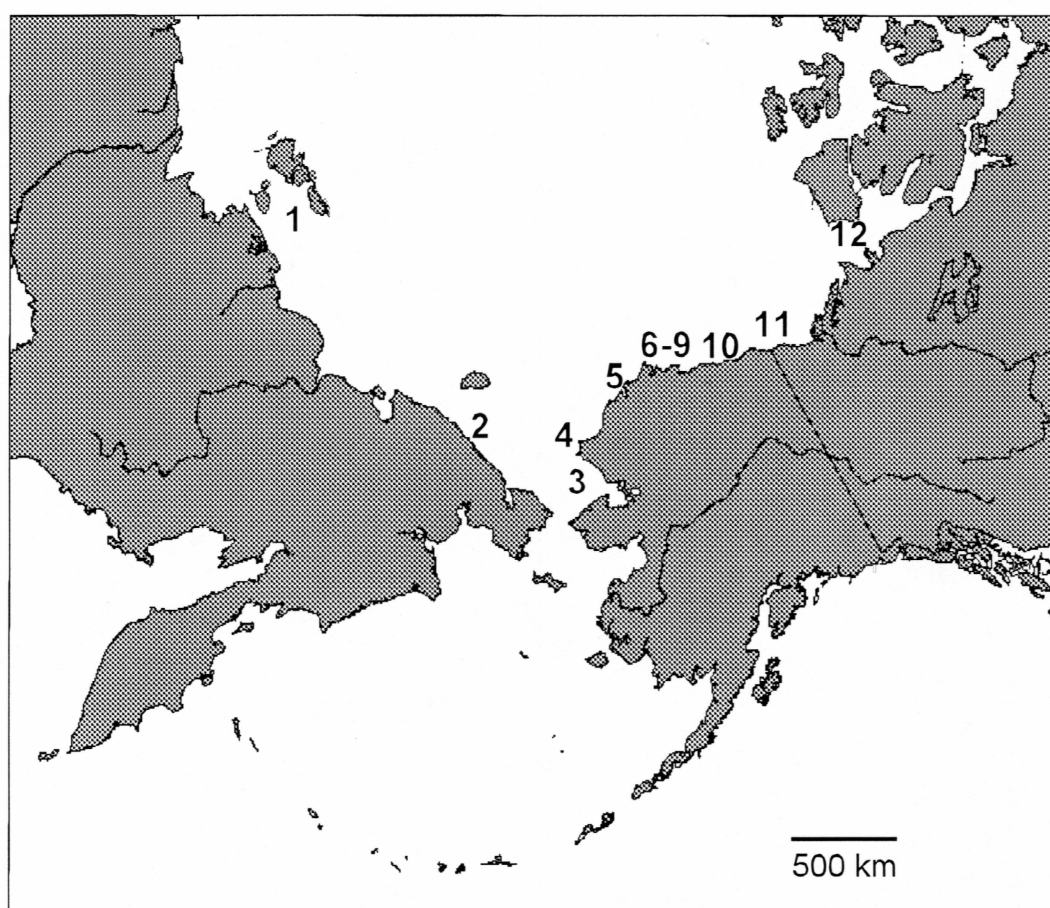


Figure 2.3. Location of Black Guillemot colonies in the western Arctic. Descriptions of numbered colonies are provided in Table 2.1.

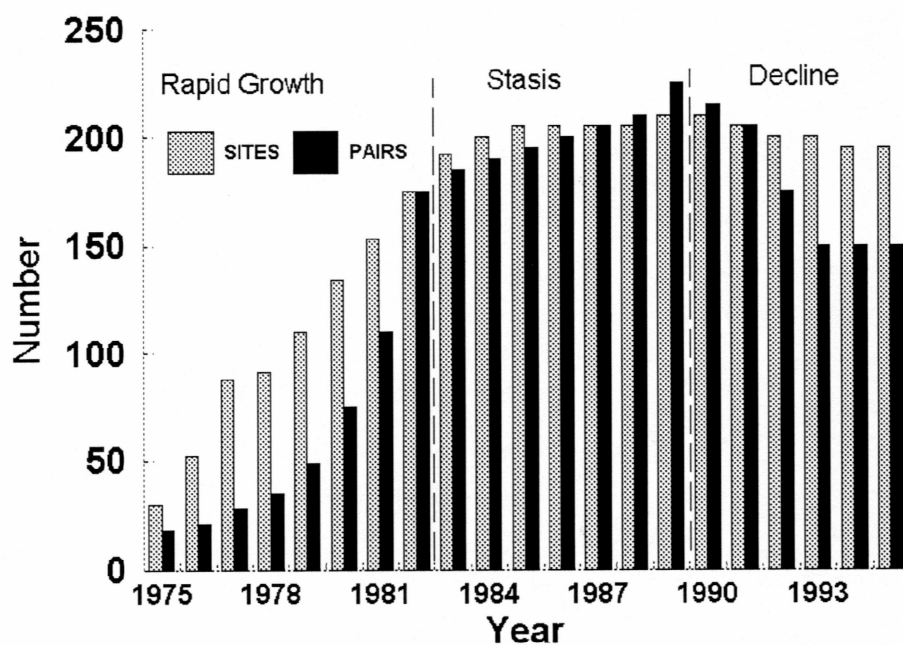


Figure 2.4. Number of Black Guillemot nest sites and breeding pairs, Cooper Island, Alaska

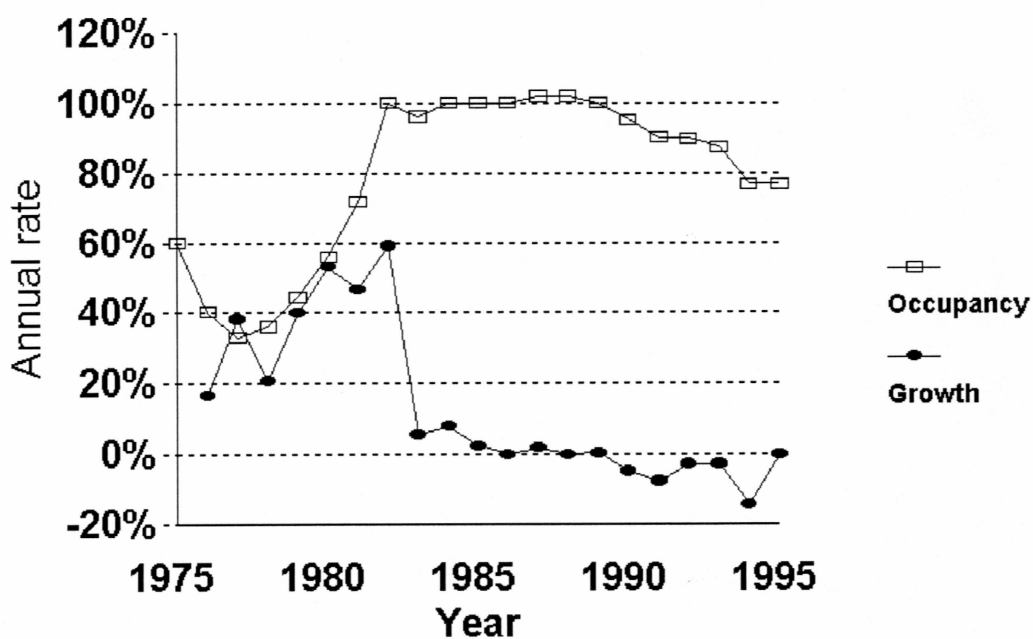


Figure 2.5. Rates of population growth and percentage of nest sites occupied the previous breeding season at the Cooper Island, Alaska Black Guillemot colony.

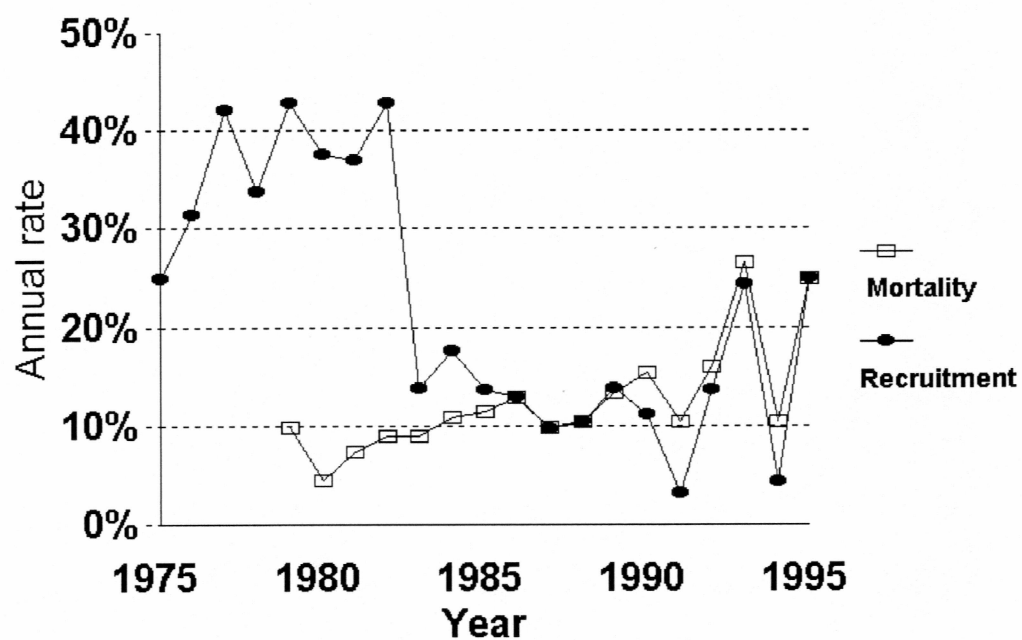


Figure 2.6. Rates of recruitment and adult mortality at the Cooper Island, Alaska Black Guillemot colony, 1975-1995.

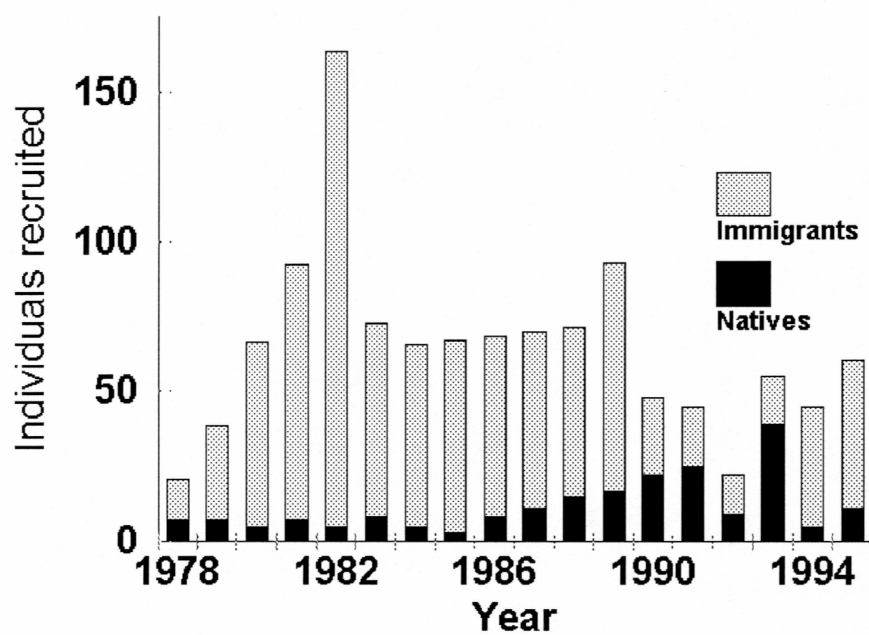


Figure 2.7. Number of native and immigrant Black Guillemots recruited annually at the colony on Cooper Island, Alaska.

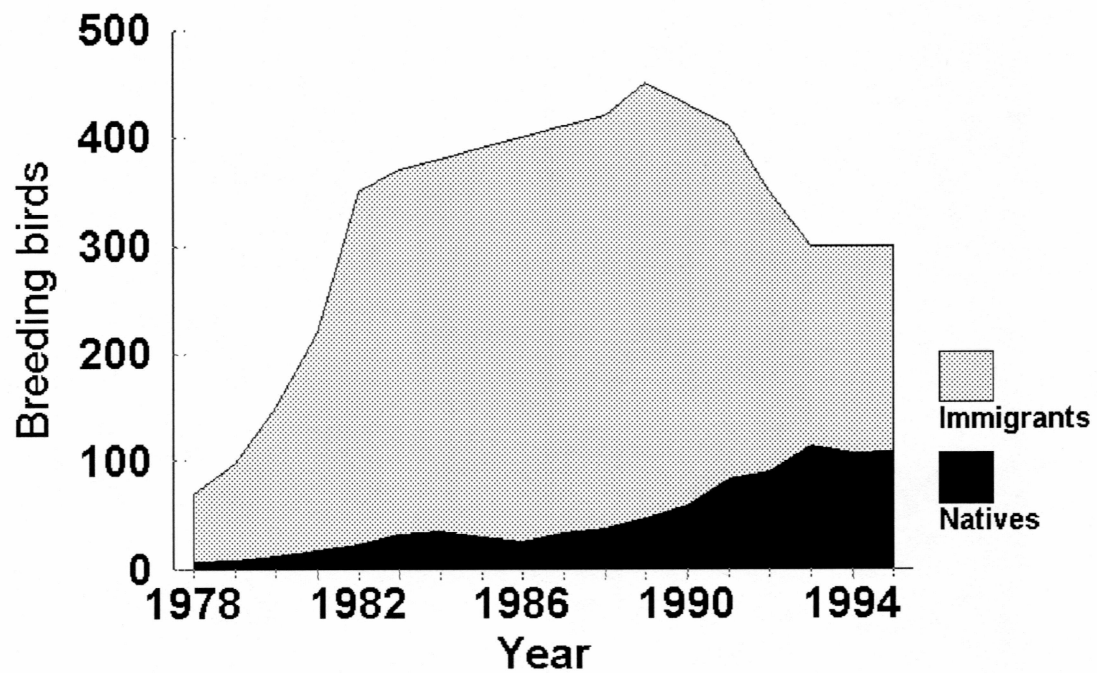


Figure 2.8. Number of native and immigrant Black Guillemots recruited annually at the Cooper Island, Alaska, Black Guillemot colony.

Table 2.1. Locations, habitats, estimated breeding pairs, and distance from Cooper Island for Black Guillemot colonies in the East Siberian, Chukchi and Beaufort seas.

Location ^a	Breeding habitat	Pairs	km from Cooper I.	Sources
East Siberian Sea				
Delong Islands, East Siberian Sea (1) ^b	rock cliffs and talus	25,000	2300	Uspenskii 1959
Chukchi Sea				
Russian Chukchi Sea (2)	rock cliffs and talus	150	900	Golovkin 1984
Cape Thompson (3)	rock cliffs and talus	6	650	Swartz 1960
Cape Lisburne area (4)	rock cliffs and talus	250	500	D. Roseneau, USFWS, pers. com.
Seahorse Island (5)	driftwood	10		Divoky <i>et al.</i> 1974 R. Suydam, North Slope Borough, pers. com.
Point Barrow (6)	debris	5	25	Maclean and Verbeek 1968 Divoky unpubl.
Beaufort Sea				
Deadman Island (7)	beached barge	15	20	Divoky unpubl.
Cooper Island (8)	debris, nest boxes	225	-	Divoky unpubl.
Igalik Island (9)	beached barge	15	10	Divoky unpubl.
Prudhoe Bay (10) (beginning in 1976)	docks, drilling pads	15	350	L. Quakenbush, USFWS, pers. com.
Herschel Island, N.W.T.(11)	abandoned building	30	650	Kuyt et al. 1976
Cape Parry, N.W.T.(12)	rock cliffs and talus	20	1100	Johnson and Ward 1985
TOTAL PAIRS		25,726		

^a See Figure 2.3.

^b Numbers are map keys in Figure 2.3.

CONSTRAINTS ON PHILOPATRY AND AGE AT RECRUITMENT IN BLACK GUILLEMOTS³

SUMMARY

1. The Black Guillemot is a cavity-nesting seabird whose populations are frequently limited by nest site availability. We examined the return and recruitment of 16 Black Guillemot cohorts in relation to annual variation in recruitment opportunities, particularly the availability of vacant nest sites, at their natal colony.
2. Variation among cohorts in the percentage returning was pronounced and related to vacancies at the natal colony and estimated recruitment opportunities at regional colonies. Philopatry was highest (>80%) for cohorts reaching two years of age when most regional recruitment opportunities were at the study colony. Philopatry declined to 15% for cohorts reaching two when adults greatly outnumbered recruitment opportunities at the study colony and when nest-site availability was likely similar at the natal colony and other colonies in the region.
3. Success and age at recruitment at the natal colony showed large variation by cohort in response to the number and type of recruitment opportunities. For cohorts reaching two years of age when vacant nest sites were abundant, 85% of returnees recruited at a mean

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age of 3.9 years. For cohorts reaching two years when occupancy was high and recruitment occurred primarily through joining a queue, only 35% of returnees recruited and at a mean age of 5.8 years. Once individuals returned and associated with the natal colony emigration was uncommon.

4. The high among-cohort variation in philopatry in response to regional and local recruitment opportunities demonstrates that philopatry is not a static life history characteristic. Studies attempting to accurately assess a natal bias in recruitment need to better design and document the circumstances associated with observed levels of philopatry.

INTRODUCTION

The location of recruitment relative to that of natality has major implications for the fitness of an individual, the demography of populations, and the metapopulation structure of species (Greenwood and Harvey 1982, Davis and Howe 1992). This is especially true for long-lived species that display high levels of fidelity to their initial breeding location. Philopatry, as a life-history trait of a species, is the tendency to recruit preferentially at the natal location. The extent to which prospecting and recruitment is biased to the natal location should reflect the relative benefits of philopatry compared with those of emigration.

Although philopatry is assumed to be common in birds, including seabirds (Greenwood and Harvey 1982, Gill 1990), direct evidence for its benefits is scarce or lacking for most species (Plissner and Gowaty, 1996). The potential benefits of philopatry and costs of dispersal are evident not only for nonmigratory species (Weise and Meyer 1979), especially those that are cooperative breeders (Stacey and Koenig 1990) but also for young of migratory species that obtain important familiarity with the natal location after hatching (C. Babcock. pers. com.). These conditions do not occur, however, in seabirds. Most seabirds have extensive annual migrations and a multi-year subadult period that provide the potential for sampling nonnatal locations without the increased risks of mortality presumed or demonstrated for nonmigratory species (Greenwood et al. 1979). In addition, familiarity with the natal area that would enhance subsequent recruitment or breeding success would not be expected for most seabirds, because fledging typically is followed immediately by movement to offshore or distant feeding areas (Ydenberg 1989).

Despite the lack of an obvious benefit of philopatry in seabirds, uniformly high levels of colony philopatry have been assumed (Wynne-Edwards 1962, Hatchwell and Birkhead 1991), generally on the basis of resightings of banded adults at their natal colony. Although philopatry is high for some species, for example, >95% in the Jackass Penguin, *Spheniscus demersus* (Randall et al. 1987), it is low in other species, e.g., <3% in the Northern Fulmar, *Fulmarus glacialis* (Dunnet et al. 1979). The costs and benefits

of philopatry compared to those of dispersal will vary depending on the temporal and spatial distribution of resources needed for successful recruitment, breeding and survival. Philopatry and dispersal rarely have been recognized as labile life history characteristics that would be expected to vary among species, populations or individuals within populations (but see Coulson and Neve Mevergnies 1992). The assumption of uniformly high levels of philopatry in seabirds has led to the belief that seabirds emigrate primarily in response to density-dependent constraints on recruitment at the natal colony (Cairns 1992), a concept that has hindered the broader consideration of natal dispersal and immigration in seabirds.

We investigated variation in philopatry and age at recruitment by cohort at a Black Guillemot (*Cepphus grylle*) colony in northern Alaska from 1975-1996. The Black Guillemot is a semi-colonial, nearshore alcid with populations that typically are limited by availability of nest sites (Storer 1952). We created nest sites at a colony composed entirely of manmade nest cavities, resulting in (1) a period of rapid growth of the colony during an abundance of recruitment opportunities (1975 to 1982), (2) a period of relative stasis during which nest occupancy and competition for nest sites were high (1983 to 1989), and (3) a period of decline in the number of breeding pairs and competition for nest sites because of increasing adult mortality and decreased immigration (1990 to 1996). We banded all fledglings from 1975 to 1996 and monitored their return and recruitment in relation to known recruitment opportunities at the natal colony and

assumed opportunities at other colonies in the region. This allowed an examination of the regional and natal colony characteristics affecting the location and timing of recruitment.

Potential sources of variation in the percentage of a cohort returning (prospecting for breeding opportunities) and recruiting (actually breeding) at the natal colony were identified using a schematic model of seabird philopatry and emigration (Figure 3.1) based on current assumptions of colony philopatry (Cairns 1992). Briefly these sources include: 1) juvenile (first year) and subadult mortality, 2) direct emigration (before returning to the colony), 3) indirect emigration to nonnatal colonies in response to recruitment constraints at the natal colony 4) mortality of adult nonbreeding floaters associated with the natal colony. We examined the effect of these sources of variation on three demographic variables: 1) the percentage of a cohort returning to the natal colony, 2) the percentage of returning birds recruiting at the natal colony and 3) the age of recruitment.

Based on previous studies of seabirds, we hypothesized that Black Guillemots would display high levels of colony and subcolony philopatry, preferentially returning and recruiting to the natal colony and subcolony, and that emigration would increase with constraints on recruitment at the natal colony.

MATERIALS AND METHODS

Study area

We conducted research from 1975 to 1996 on Cooper Island, a low-elevation sand and gravel island in the extreme western Beaufort Sea, 25 km ESE of Point Barrow, Alaska (Figures 3.2 and 3.3). In 1972 we observed a breeding population of 10 pairs of Black Guillemots on the island. All nests were in manmade boxes and floorboards left in the mid-1950's (Divoky et al. 1974). From 1975 to 1982 we created additional sites, facilitating an increase in the population to 225 breeding pairs by 1989 (Figure 3.4). The population then declined to 150 pairs because of decreased survival of adults and decreased immigration (Chapter 2). Most of the colony is within a 1-km long section of the island. For purposes of censusing and examining subcolony affinities, we divided the colony into 23 subcolonies ranging in size from 2 to 14 nest sites (Figure 3.3).

The northern Alaska coastline provides few cavities suitable for successful breeding by Black Guillemots. Although able to breed in a wide range of cavities offering overhead cover (Storer 1952), the species typically breeds along rocky shorelines and headlands or on offshore rocks (Harris and Birkhead 1985, Sowls et al. 1980). The 1500-km shoreline between Cape Lisburne, Alaska and Cape Parry, Northwest Territories, Canada consists primarily of low, slowly eroding earthen and permafrost bluffs (typically <5 m above sea level), with low depositional sand and gravel islands in the nearshore waters. In this region, potential cavities for nesting are rare, and guillemot

breeding is limited almost entirely to cavities in manmade structures on barrier islands (Table 3.1). Predation by arctic fox (*Alopex lagopus*) (Larson 1960) on the mainland tundra is apparently the reason manmade sites there are used rarely.

Methods

Terminology

The following terms are used to categorize individuals: a bird is considered breeding in a given year when it is part of a pair that occupies a nest cavity where eggs are laid. Nonbreeding birds include both behaviorally paired and unpaired birds that do not occupy a nest site or occupy a site where no eggs are laid. Nonbreeders are also called “floaters” and collectively “the floating population.” Although “floaters” include nonbreeders that display inter- and intra-annual site and mate fidelity (Smith 1978, Divoky unpubl.), this term is widely used (Smith and Arcese 1989, Eckert and Weatherhead 1987), and we use it to refer to nonbreeders. A “float class” refers to the collection of nonbreeders initially caught as adults in a particular year. Float classes could contain both individuals captured in their 1st year at the colony and birds that had avoided capture for ≥ 1 yr.

“Cohort” refers to the fledglings from Cooper Island for a particular year. “Returnees” are those members of a cohort that return to Cooper Island as adults and include both individuals that are philopatric (recruit at the natal colony) and birds

captured as nonbreeders that do not recruit at the natal colony. Capture percentage is the percentage of a fledged cohort, regardless of breeding status, subsequently captured as adults at the study colony. This value is an estimate of the minimum number of individuals returning because it does not include birds that returned to the colony at least briefly and avoided capture through lack of either association with a nest site or subcolony or vigilance on our part. The study colony is referred to as the natal colony and all other regional colonies (<650 km from the study colony) as nonnatal colonies.

Banding

From 1975 to 1995, 2,162 fledglings were banded at the study colony with metal U.S. Fish and Wildlife Service (USFWS) bands, for individual identification in the hand, and were “cohort-marked” with single polyvinyl chloride (PVC) color bands to denote the year of fledging. Because of the several-year lag between fledging and breeding only the 1975-1990 cohorts are used for the analysis of returnees.

Beginning in 1976, we banded breeding and nonbreeding adult guillemots with a unique combination of three PVC color bands, allowing individual identification at a distance. The PVC bands used for both chicks and adults were overlapping bands sealed with a cyanoacrylate glue at banding; these bands showed excellent color retention and little loss (<1%) during this study.

When banding adults, highest priority was given to breeding birds and natal nonbreeders. All birds natal to the colony that fledged after 1974 were captured in their first year of breeding, if not earlier as floaters. We captured birds both by using noose mats (Williamson 1945) near nest sites and netting birds exiting nests. Noose mats were placed at the most frequently occupied roosting site of the target individual or next to the nest site. Breeding birds that eluded capture in this way were typically captured immediately after clutch completion by netting them as they exited the nests. To reduce potential disruption during egg laying, we did not attempt to capture breeding females between the time the first egg was present in the colony and the completion of the clutch (second egg or six days after the first egg) at the target site. Because the presence of other birds accelerated the return of a released bird to its nest site or subcolony, adults were usually captured during daily periods of high colony attendance between 2400-1000 h ADT (Alaska Daylight Time). No attempt was made to capture birds that previously had been individually marked. Those captured accidentally were checked for the status of PVC bands and rebanded if necessary.

Nonbreeding birds prospecting or competing for nest cavities were noosed both incidentally during attempts to capture breeders and, because many nonbreeders showed nest-site or roost-site fidelity, by placing noose mats in locations frequented by specific nonbreeders. Additionally, noose mats were placed on and next to temporary nest sites constructed specifically to capture prospecting nonbreeders. We banded 167 native birds

(returnees) as nonbreeders and used them to examine recruitment success and indirect emigration.

The method of capture for adults (e.g., netting birds exiting nest sites and noosing birds directly outside nest sites) selected for individuals breeding, actively prospecting for nest sites, or displaying an attachment to a nest or area (subcolony). The placement of noose mats typically involved flushing birds from the subcolony. Displaced birds would usually sit on an adjacent area of the island until we departed the subcolony. Within a few minutes (typically <2 min), a few birds returned to the subcolony, followed shortly by the remaining animals. Often occupants of nest sites were wary of a noose mat and remained 1-2 m away from the site. This provided nonbreeders an opportunity for greater access to the site than when it was actively defended by the breeding pair and increased the chances of capturing nonbreeders. Additionally, when a breeding bird, particularly the male, was captured at its nest site, the period between capture and return to the site (typically < 15 min) allowed nonbreeders an opportunity to inspect that site. In instances when competition for nest cavities sites was high, several nonbreeders could be noosed during the temporary absence of the occupant. Nonbreeders only casually visiting a subcolony at the time we flushed birds to place noose mats likely departed the area, rather than returning to the subcolony after a bout of trapping.

Censuses

We conducted censuses of the breeding and nonbreeding population annually from before clutch initiation through the period of egg laying. Incidental observations during the nestling period indicated that the number of birds associated with the colony decreased during the breeding season, consistent with the seasonal pattern of attendance at other colonies of Black Guillemots (Preston 1968, Peterson, 1981). Censuses were conducted at the daily period of maximum colony attendance (2400-1000 h ADT). We counted of the total number of birds in each subcolony and obtained individual identifications on as many breeders and nonbreeders as possible from vantage points sufficiently far away to preclude flushing. All breeders and many nonbreeders show subcolony fidelity in a particular year (Divoky unpubl.), reducing the possibility of counting individuals more than once on the same census. The number of nonbreeders in the colony was computed by subtracting the number of breeding birds from the high count for the colony. The identity of all site-occupants was determined by observing the pair defending the site and performing courtship activity (Preston 1968). At nest sites where we observed high levels of competition, displacement of eggs, and the presence of supernormal clutch sizes (>2 eggs), we continued observations into the incubation period to confirm the identity of breeders.

For birds fledging from the study colony and captured as adults, age was determined from the year of fledging. Other than classifying probable first-year birds, we could not age birds that had fledged from other colonies. Birds retaining some basic

plumage during the breeding season were assumed to have fledged the previous summer (Petersen 1981, Asbirk 1979). Individuals were sexed primarily by observing positions during copulations, with multiple observations obtained for most birds. Reverse copulations (female superior) in birds occur rarely (Neuchterlein and Storer 1989), and the three instances we observed were limited to the same female. That bird was most frequently mounted by its mates and determined to be a female based on patterns of colony attendance. Sex designation of most individuals was further confirmed by observing the attendance patterns of pairs immediately preceding and during egg laying. During the period before incubation, males return to the colony earlier and remain later each day than their mates (Nelson 1987, Divoky unpubl.). In the interval between the laying of the first and second egg, the daily period of nest attendance by the female typically is further reduced.

Data analysis

We examined variation among cohorts in 1) the percentage of fledglings returning, 2) the percentage of returnees recruiting to the natal colony, and 3) the mean age at recruitment. In analyses of variance (ANOVA's) we used independent variables that either measure or can be assumed to be proxies for the sources of reduction of a cohort before return to the colony or recruitment constraints at the natal colony.

Juvenile survival could not be measured, and we used two proxies for potential interannual variation: mean weight at fledging and annual survival of breeding birds (as

measured at the study colony) in a cohort's 1st year. Weight at fledging has been correlated with subsequent survival of chicks in some seabirds (Perrins et al. 1973) but not alcids (Harris 1982), although Gaston (1986) suggested that it should be important in the Black Guillemot because of the lack of parental care after fledging. Annual mortality of adults in a cohort's first year is the percentage of banded breeding birds in the year a cohort fledged that did not return to the colony the following breeding season. We believe that few if any breeding birds dispersed to other colonies from the study colony. Nest-site fidelity of birds returning to the colony was high (>95%) and breeding dispersal within the study colony was rare. When it did occur it typically averaged <10 m; in only three instances breeders moved >100 m (Divoky unpubl.). When previously breeding birds entered the nonbreeding population (<5% per year), these individuals generally showed fidelity to the nest site or subcolony where they had bred, and we observed them repeatedly during censuses. No previously banded breeding birds that were not recorded in one year were resighted in any subsequent year. No birds previously banded and breeding at the study colony have been observed on the few censuses of nearby colonies (Divoky unpubl.).

Direct emigration (occurring without first returning to the natal colony) could be expected to be related to the number and type of nonnatal recruitment opportunities available at 2 and 3 years of age (see results for information on age of prospecting for nest sites). We used the estimated total number of recruitment opportunities at 2 and 3 years of age as an indicator of annual recruitment opportunities at nonnatal colonies. We also

used the percentage of estimated regional opportunities at the study colony at 2 and 3 years-of-age to determine if association with the natal colony was related to its regional importance. Regional recruitment opportunities are defined as those <650 km from Cooper Island. With the exception of one colony we assumed that nonnatal colonies had no net change among years in nest cavities and that all nest cavities were occupied by breeders. At Prudhoe Bay we estimated 15 sites were created in docks and offshore drilling pads in the late 1970's. Annual opportunities for recruitment at nonnatal colonies were computed by multiplying the estimated number of breeding birds (Table 3.1) by the observed mortality of breeding adults at Cooper Island for the previous year. Estimates of recruitment opportunities in 1975-79 assume an annual adult mortality equivalent to that initially observed at Cooper Island for 1980. Until 1990, nest sites were assumed to be limiting at nonnatal colonies, with all mortality-caused vacancies filled the year they occurred. After 1990, the vacancy rate of nonnatal sites was assumed to be equal to that observed on Cooper Island.

The recruitment characteristics (percentage recruiting and age at recruitment) of a cohort at its natal colony could be expected to be related to the number and type of recruitment opportunities, the level of competition for those opportunities, and the productivity of the colony, i.e., its suitability relative to other colonies where the birds could prospect. Recruitment opportunities were present in vacant sites (sites that were not occupied the previous breeding season) and in mortality-caused vacancies at sites that had supported breeding the preceding year. Mortality-caused vacancies were those that

occurred when a breeding bird from the previous year did not return to the colony and was assumed dead. Mortality of breeding adults typically resulted in a recruitment opportunity with the surviving partner that was sex-specific. Less commonly, a surviving partner might move to an adjacent site where there was a vacancy, and the previously used site would present two recruitment opportunities at one vacant site. The number of mortality-caused vacancies on Cooper Island equaled the number of breeding birds the previous year ($n-1$) that were not resighted in year n . For each cohort we used both the total number of recruitment opportunities and total number of each type (in vacant sites or established pairs) at both 2 and 3 years-of-age.

Annual competition for recruitment opportunities was measured with a Competition Index (CI), which is a measure of the number of potential recruits per recruitment opportunity. Thus,

$$CI = PR/ARO,$$

where:

PR (potential recruits at beginning of season) is the number of nonbreeding birds plus the number of recruits for that year;

and

ARO (annual recruitment opportunities) is the number of vacancies from mortality of breeders plus twice the number of vacant sites in the previous year.

When the $CI=1$ the number of potential recruits is equal to the number of recruitment opportunities. When this value is equals 2 there would theoretically be two competitors

for every recruitment opportunity. The CI does not take into account potential variation in competition related to the type and quality of recruitment opportunity. Competition could be expected to be higher for vacancies in established pairs, given the benefits of breeding with an experienced mate (Wooler and Coulson 1977), and for higher quality nest cavities (Nettleship 1972). The CI also does not address variation in competition caused by the subcolony fidelity of many nonbreeders that limits the spatial extent of their prospecting and thus recruitment opportunities (Divoky unpubl.) or sexual differences in recruitment opportunities.

We frequently have observed nonbreeding birds following adults returning to the nest with prey. When they are prospecting, nonbreeders may make recruitment decisions on the basis of breeding productivity of established pairs (Bouliner et al. 1996). Thus, we examined the relationship of the percentage of a cohort captured to breeding productivity (the number of chicks fledging per nest) two and three years after that cohort fledged.

Indirect emigration (emigration after associating with the natal colony) was estimated through capture of floating native birds and monitoring their subsequent recruitment. The percentage of a float class that emigrated was calculated as the number initially sighted minus the number observed recruiting and the number estimated to die before recruiting. Presumed mortality was calculated using annual survival of breeding birds until the year after last observed recruitment for a float class. Native float classes captured in 1982-1989 were used for this analysis.

Partitioning direct emigration and philopatry for a cohort requires an estimate of the percentage of a cohort surviving to breeding age. We obtained an estimate by calculating the number of young needed to survive to breeding to maintain a population with no growth ($\lambda=1.0$) when fledgling success is 1 chick per nest and annual adult mortality 15%, mean values for this study and other Black Guillemot populations (Petersen 1981, Chapter 2).

RESULTS

Local and nonnatal recruitment opportunities

Maximum recorded distance of natal dispersal for the region was 135 km by sea for a chick that had been banded on Seahorse Island that recruited at Cooper Island. Nonetheless, the large number of immigrants (>950 recruited between 1979-1995) and unbanded nonbreeders at the study colony indicated that guillemots in this region regularly recruited > 200 km from their natal colony (Chapter 2). Additionally, a nonnatal floater banded at Cooper Island in 1984 recruited 650 km away at Herschel Island 2 years later (Divoky unpubl.), indicating at least some birds prospect a minimum of 650 km from the location of recruitment. We therefore consider nonnatal recruitment opportunities for birds from Cooper Island to include all colonies <650 km distant (all Alaskan colonies and Canadian colonies and the Russian Chukchi Sea colonies, see Figure 3.2). “Region” and “regional” refer to the geographic area containing these colonies.

The number of natal and nonnatal recruitment opportunities varied greatly during the study (Figures 3.5 and 3.6). In 1975, there were an estimated 75 recruitment opportunities within 650 km of Cooper Island. Most (>66%) were at rocky headlands in the Chukchi Sea (Table 3.1), more than 500 km from the study colony. The estimated number of annual recruitment opportunities at Cooper Island in 1975 was 10. Creation of nest sites on Cooper Island increased the mean annual recruitment opportunities to 157 in 1977-1982 and the regional recruitment opportunities to >200 for that period. High levels of recruitment in the early 1980's decreased annual recruitment opportunities at the study colony to a mean of 57 in 1983-1990. Increased adult mortality (Chapter 2) in the 1990's resulted in increasing annual recruitment opportunities at the study colony, with 165 present in 1995. Assuming the annual trends in mortality and vacant sites observed at Cooper Island typified the region during the 1990's, the number of regional recruitment opportunities in 1995 was 338.

The changes in nest-site availability on Cooper Island affected its relative importance to regional opportunities for recruitment. In 1975, Cooper Island had approximately 20% of the recruitment opportunities within 200 km and <5% of those within 650 km. Creation of nest sites greatly increased the recruitment potential of Cooper Island, and from 1976 to 1995 the study colony averaged 89% of the recruitment opportunities within 200 km and 54% of the recruitment opportunities within 650 km. Cooper Island's regional importance was highest from 1977-1982 when it averaged 72% of the recruitment opportunities within 650 km.

The absolute and relative number of recruitment opportunities by type (vacant sites and mortality-caused vacancies) varied annually at the study colony (Figure 3.6) with less variation assumed for nonnatal colonies, where cavities were not being created artificially. Construction of nest sites at the study colony beginning in 1975 provided >100 annual recruitment opportunities in vacant sites from 1977-1982, when mortality-caused vacancies averaged <10 annually. The number of annual recruitment opportunities in vacant sites decreased to 34 in 1983. From 1986-1990, all recruitment at the study colony was through mortality-caused vacancies. Recruitment opportunities in vacant sites appeared again in 1991: reduced survival of both breeders and nonbreeders after 1989 increased the number of recruitment opportunities in vacancies to 90 in both 1994 and 1995. Vacant sites at nonnatal locations would be expected to occur after 1990, when nest sites were no longer limiting on Cooper Island (1991-1995).

Regional opportunities for recruitment in vacant sites were probably limited to the study colony for the first 15 years of this study. Assuming regional adult mortality was comparable to that on Cooper Island, the proportions of vacant sites at all regional colonies likely paralleled those at the study colony after the mid-1980's, first appearing in 1990 and increasing in 1991-1995.

Recruitment opportunities at the study colony attracted large numbers of Black Guillemots (Figure 3.7), primarily from other colonies (Chapter 2). The number of adults associated with the colony went from <50 in 1975 to >500 from 1982-1990. The percentage floating was <10% in the 1970's, increased to approximately 33% from 1982-

1990 and then decreased to $<10\%$ in 1994. Resulting recruitment constraints at the study colony, as measured by the Competition Index (CI), increased in the late 1970's, peaked in the mid 1980's and then declined (Figure 3.8). An initial period of low competition (<1 in 1976-1981), when we created most nest sites (Figure 3.4) and potential recruits were few, was followed by a middle period (1982-1991) when few or no nest sites were created and the influx of nonnatal birds was high, and a final period of low competition (1992-1995), when apparent region-wide increases in adult mortality increased the number of vacancies and decreased immigration and recruitment of natives (Chapter 2). The levels of competition at nonnatal colonies are unknown but we assume these colonies were nest-site limited and the $CI > 1$ until 1990.

Association with the natal colony

1st-year birds

The number of known (based on previous banding as chicks) or assumed (based on plumage) 1st-year birds visiting the study colony was small; most were from nonnatal colonies and their prospecting for nest sites was extremely limited. From 1976 to 1995, we observed seven cohort-marked individuals the summer after fledging. This is 0.3% of the chicks fledging from Cooper Island from 1975 to 1994. For that same period, we saw 21 nonnatal birds with partial retention of basic (winter) plumage. Based on these results, few 1st-year birds visited breeding colonies, and, of those that did, most visited nonnatal colonies.

The pattern of attendance and behavior of known or assumed 1st-year birds differed from other birds at the colony. Although most banded nonbreeders attended the colony during the entire breeding season, 75% of 28 first-year birds visited the colony on only 1 day and none was resident for more than five days. Unlike many older nonbreeders, known and assumed 1st-year birds showed no attachment to a location or subcolony. First year birds flew off in response to agonistic displays by adults and typically remained on the edge of subcolonies or other social aggregations. Our inability to capture any 1st-yr birds, although we placed noose mats in locations where we observed them, is evidence of their apprehensive nature and tentative nest-prospecting behavior. First-year birds also arrived later than the major influx of breeders and nonbreeders. In those years (1981, 1983, 1984) when we conducted observations from the 1st day guillemots returned to the colony in late spring, initial sightings of 1st-year birds were 7-10 days after the initial arrival of breeders and nonbreeders in adult plumage. First-year birds were absent for most of the chick period (approximately 20 July to 10 September). All observations were between 15 June and 1 August. Most 1st-year birds probably complete the pre-alternate molt during their first summer and are unrecognizable after the middle of the breeding season, but we did not see any known (cohort-banded) 1st-year birds after 1 August in any year.

Age and percentage captured as adults

Age at first capture ($\bar{x} \pm \text{se}$) as an adult for returning native birds was 3.7 ± 1.5 yr (range 2 - 10 yr, $n = 330$) with no significant variation by cohort (??Test statistic) $\text{df} = 15$, $P > 0.1$; Figure 3.9). An association with the natal colony that allowed capture often began in the 3rd summer after fledging with 16% of the 333 returnees first captured at 2 years, 42% at 3 years and 23% at 4 years of age. We observed no sexual bias in age at capture (males: $\bar{x} = 3.9 \pm 1.6$ yr, range 2 - 10 yr, $n = 105$; females: $\bar{x} = 3.8 \pm 1.6$ yr, range 2 - 10 yr, $n = 105$; t -test, $P = 0.75$) or number captured ($X^2 = 0.028$, $P = 0.89$).

The percentage of a cohort captured declined during the study ($r^2 = 0.63$, $P < .001$; Figure 3.10). The capture percentage for the 1975-1980 cohorts was $35 \pm 5\%$ (range 27 - 40%). Cohorts after 1980 had an average capture rate of $16 \pm 6\%$ (range 3 - 27%).

The percentage of a cohort captured was positively correlated with the recruitment opportunities at vacant sites and the regional importance of the study colony (percentage of regional sites at the study colony) in a cohort's 2nd year (3rd summer) (Table 3.2). Both variables explained approximately 60% of the variation by cohort. The percentage of a cohort captured was negatively correlated with the Competition Index at age 2 years but this explained far less of the variation (26%) in capture percentage than the number of vacant sites or the regional importance of the colony. Capture percentage was not correlated with breeding success at the study colony in a cohort's second summer but was correlated with colony productivity at 3 years-old, suggesting that if birds are making

recruitment decisions based on evidence of successful breeding, they may be doing so in the latter stages of prospecting.

Mean weight at fledging by cohort averaged 310 ± 5.4 g (range 258-345 g) and had a significant influence on the percentage captured (Table 3.2) because of the extremely low mean fledging weight (271 g) and low capture percentage (3%) of the 1988 cohort (Chapter 1). When the 1988 cohort was removed from analysis percentage recaptured was not correlated with mean fledging weight of the cohort.

Recruitment at the natal colony

Age at recruitment and percentage recruited

Black Guillemots typically do not breed until 3 years of age. Only 10% of the 60 birds captured at 2 years-old recruited that year. Just one of these recruits was from a cohort with a Competition Index > 2 in its second year. Five of the six birds recruited at sites that had been unoccupied the previous breeding season. That more birds did not recruit at 2 years-of-age, even when competition was low, suggests that behavioral and physiological immaturity restrict recruitment for most birds < 3 years old.

Age at recruitment averaged 4.8 ± 1.6 yr (range 2 - 9 yr, $n = 191$) and showed significant variation by cohort ($r^2 = 0.26$, $df = 15$, $P < 0.001$; Figure 3.11), increasing with increased competition for nest sites. Age at recruitment was significantly and positively correlated with the CI at age 3 years and negatively correlated with the total number of recruitment opportunities in the natal colony for that age. Both explained $> 60\%$ of the

variation in age at recruitment (Table 3.2). The 1975-1980 cohorts reached two years-of-age when vacant sites were abundant (Figures 3.3 and 3.6) and had an average recruitment age of 3.9 ± 1.3 yr (range = 2 - 8 yr, $n = 50$). The four subsequent cohorts (1981-1984) reached 2 years-of-age when few if any recruitment opportunities were in vacant nest sites and recruited at an average of 5.8 ± 1.9 yr (range 3 - 10 yr, $n = 51$). Age at recruitment decreased in cohorts fledging after 1984 as competition decreased in the late 1980's because of decreased immigration and survival of breeders (Chapter 2).

Returnees displayed a sex bias in recruitment success, with 89% of the captured native males but only 75% of the captured native females recruiting in their natal colony ($X^2 = 7.27$, $df = 1$, $P = 0.007$). There was no sexual bias in age at recruitment, however (males: $\bar{x} = 4.7 \pm 1.7$ yr, range = 2 - 10, $n = 93$; females: $\bar{x} = 4.9 \pm 1.5$ yr, range = 2 - 10, $n = 77$; $df = 168$, $P = 0.57$).

Percentage of captured individuals that recruited

The percentage of a returning cohort that recruited varied in response to recruitment constraints. This percentage was high for the 1975-1979 cohorts (Figure 3.12), averaging $85\% \pm 10\%$ (range 73-100%), but decreased dramatically to a mean of $35\% \pm 2\%$ (33-37%) for the 1980-1982 cohorts. The percentage recruited then increased successively for the 1983-1990 cohorts to values nearly equal to those of the late 1970's cohorts. Competition for nest sites at 3 years of age explained 69% of the variation among cohorts

(Table 3.2). Overall, of the 319 returnees that we captured, 61% recruited at the natal colony.

Philopatry

Colony philopatry, as defined as the percentage of individuals expected to survive to breeding age that recruits at the natal colony, showed significant among-cohort variation during the study. Colony philopatry averaged 82% for the 1975-1977 cohorts but declined for the 1978-1980 cohorts and averaged only 28% for the 1981-1991 cohorts (Figure 3.13). The low value for the 1988 cohort was apparently because of higher than average post-fledging mortality due to the low fledging weights associated with an early snowfall (Chapter 1).

*Floater*s

Once native nonbreeders developed an association with the colony, allowing capture, emigration was apparently uncommon. The percentage of native floaters assumed to have emigrated was low (<5%) for most float classes except the 1983 and 1984 float classes, in which >35% emigrated.

Subcolony philopatry and inter-colony dispersal

Returnees showed no tendency to recruit or attempt to recruit at the natal subcolony in preference to other subcolonies. Only 7% recruited to the natal subcolony and an additional 21% to a subcolony directly adjacent to the natal subcolony.

DISCUSSION

Colony philopatry and emigration

Black Guillemots demonstrated high variation in colony philopatry in response to recruitment constraints in the region and at the natal colony. There was no indication that birds either preferentially prospected or recruited to their natal colony, and we therefore reject the hypothesis that Black Guillemots possess high colony philopatry, as a life history characteristic. However, under certain conditions the percentage of a cohort recruiting to the natal colony can be high, indicating that the species does not have a pattern of dispersal that results in avoidance of the natal colony. Our findings are the first to document high levels of intraspecific variation in colony philopatry in a seabird. In our 16-cohort study philopatry averaged 43% and ranged 5-85%. This high level of variation is not simply because of the duration of the present study. The percentage of a natal cohort recruiting at a Black-legged Kittiwake colony over a 32-year period remained at 11%, although significant annual variation in recruitment opportunities occurred (Porter and Coulson 1987).

The level of philopatry (>80%) observed when vacant nest sites were abundant and regional alternatives few is among the highest for seabirds; only Jackass Penguins and Skuas have higher colony philopatry (Furness 1992, Randall et al. 1987). When the study colony had few vacant sites, or regional alternatives were common, the level of philopatry was among the lowest recorded for seabirds, but similar to that found in the only previous study of colony philopatry in Black Guillemots: 13% of the birds presumed to survive to breeding recruited at their natal colony in Iceland even though nest site availability was high for some cohorts (Frederiksen 1998). Northern Fulmars have lower observed philopatry (3%; Dunnet et al. 1979), but the two other alcids that have been studied have considerably higher philopatry (Common Murre: 57% and Atlantic Puffin: 50%; Harris et al. 1996, Harris and Wanless 1991, respectively).

The observations presented here allow a description of recruitment in the Black Guillemot and the spatial and temporal effects of nest site availability. Most prospecting for nest sites apparently occurs in the first and second year. While both one and two-year-olds occur farther from the natal colony than older birds (Petersen 1981), visits by one-year-olds to any colony are apparently uncommon. Assessment of an area's foraging opportunities could be expected at this age, however.

Most prospecting for nest sites apparently occurs at two years-of-age, and locating vacant nest cavities may be the primary objective of prospecting guillemots. The small percentage of two-year-olds breeding, even when recruitment opportunities are abundant, is an indication of reproductive immaturity that prevents them from immediately breeding

in vacant cavities. However, discovery of a vacant site when a bird is two-years-old allows an association with the site during the bird's second summer and development of local familiarity and dominance. This likely increases the chances of recruitment and successful breeding the following breeding season, the age at which successful reproduction is first possible for most individuals. Unlike mortality-caused vacancies, which are only evident when birds return to nests in spring, and are typically filled within a few days by members of the previous year's floating population, vacant nest cavities can be discovered for the entire snowfree period in northern Alaska, and longer in more temperate regions.

Discovery of a vacant nest site provides large recruitment advantages compared to recruiting through joining a queue for a mortality-caused vacancy at an occupied site. Thus vacant sites are probably the principal objective of prospecting two-year-olds. Individuals finding a vacant cavity are able to initiate breeding as soon as they are physiologically ready (the following year for most two-year-olds) and able to attract a mate. The average age at recruitment for native birds recruiting at vacant sites was 3.4 yr. Individuals joining a queue to recruit at a mortality-caused vacancy must: 1) assess the recruitment potential of occupied sites, 2) join a queue of nonbreeders and develop familiarity that will increase the chances of recruitment, 3) advance in the queue through competition or mortality of more dominant same-sex members of the queue, and 4) wait for the mortality of the same-sex occupant at the site or sites with which they are associated. This process resulted in native birds recruiting at mortality-caused vacancies

at an average of 5.8 yr, over 2 years more than the age of recruitment at vacant sites. Perhaps more important, annual mortality while in the queue reduces the chances of recruiting by approximately 15% annually (the average breeding adult mortality). Only 53% of the native birds captured as floaters when vacant sites were rare or absent recruited to the natal colony, with estimated annual mortality explaining the majority of the reduction. Individuals that do not find a vacant cavity in their second year, or any recruitment opportunity their third year, apparently can best increase their chances of recruitment by joining a queue at an occupied nest cavity. This is demonstrated by the large number of floaters captured at three years of age and showing fidelity to a nest site or subcolony (Divoky unpubl.).

The benefits of discovering a vacant cavity at age two are likely so great that selection for philopatry to the natal colony would be expected only if the probability of finding a vacant site is highest at that location. Because most guillemot colonies are nest-site limited with a large floating population of potential recruits (Hilden 1994), it is doubtful that prospecting individuals would display a natal colony preference. Preferential prospecting of the natal colony would be demonstrated by large numbers of native two-year-olds, which we did not observe. The low return rates of cohorts from the late 1980's, those that reached two years of age when vacant sites were common at the study colony, and apparently also regionally, is further evidence of a lack of natal colony preference.

The variable expression of colony philopatry is not surprising given the life history differences between guillemots (*Cepphus* spp.) and most other seabirds. Guillemots are able to breed as single pairs and in small colonies. In such instances a high degree of philopatry would increase the possibility of inbreeding. The ability to breed as single pairs would also select for a high level of prospecting in areas not occupied by conspecifics. The spatial distribution of colonies through much of the range of Black Guillemots (small, closely spaced colonies) (Nettleship and Evans 1985) could be expected to result in low colony philopatry, as the percentage of birds emigrating is negatively correlated with the distance between colonies in Shags (*Phalacrocorax aristotelis*) (Aebischer 1995).

While indirect emigration is thought to be the principal method of dispersal in seabirds (Cairns 1992) we found little evidence of it in Black Guillemots. For most float classes <5% emigrated. Indirect emigration was highest when the number of vacant sites was decreasing, apparently indicating birds can overestimate recruitment potential when the number of vacant sites is rapidly decreasing. The 1980 cohort had one of the highest capture percentages (40% of fledglings) but the lowest recruitment success (30% of captures) of any cohort. This cohort reached two years of age and began prospecting the colony when there were 65 vacant nest sites (130 recruitment opportunities). By the following breeding season, when most of the cohort could first breed, only 15 vacant sites remained (30 recruitment opportunities). Similar evidence of direct dispersal from the same time period comes from the 1983 and 1984 natal float classes. In both >35%

apparently dispersed after capture while no more than 5% of any other float class apparently dispersed.

Subcolony philopatry

We found no indication of subcolony philopatry and reject the hypothesis that guillemots display subcolony philopatry, at the scale of subcolonies examined in this study. The apparent lack of subcolony philopatry in this study contrasts with most other seabirds studied, including a previous study of Black Guillemots. The majority of birds recruiting to the natal colony recruit to the natal subcolony or area in Common Murres (57%; Halley et al. 1995), Herring Gulls (65%; Chabryk and Coulson 1976), Manx Shearwaters (86%, Perrins et al. 1973), Shags (50%; Aebischer 1995), and Atlantic Puffins (87%; Harris 1983). Frederiksen (1998) found a significant preference for the subcolony for Black Guillemots in Iceland. However, the percentage of birds recruiting to their natal subcolony was small, with only 34% of returnees recruiting to the natal subcolony. Coupled with the low return rate to the colony, the number of birds surviving to breeding that recruited to the natal subcolony was <5%.

Estimation of subcolony philopatry is complicated by the arbitrary nature of defining subcolonies, both in terms of spatial scale and breeding density. My subcolonies were typically <50 m wide, while those of Frederiksen (1998) encompassed as much as 500 m of shoreline, approximating the size of my entire study colony.

Interspecific comparisons of subcolony philopatry are complicated by interspecific variation in nesting density. Unlike most seabirds, guillemots do not typically nest in large colonies; single pairs or small colonies (< 50 pairs) are common (Nettleship and Evans 1985). In contrast, the Common Murre subcolonies studied by Harris et al. (1995) contained between 50 and 200 breeding pairs, and they did not observe ledge or area philopatry within the subcolony. On a population scale (the number of breeding pairs between the natal location and that of recruitment) guillemots returning to Cooper Island may have been breeding in the same relative proximity to their natal site as the Common Murres displaying subcolony philopatry. Most studies have not provided information on areal or spatial extent of the natal subcolony, except Aebischer (1995) and Harris (1983) who considered any bird recruiting within 100 meters of the natal nest to be philopatric. Given that definition, 22% of the guillemots on Cooper Island displayed subcolony philopatry.

The measurement and scale of philopatry

Our findings indicate that philopatry should not be considered a static species-specific life history attribute but one that is sensitive to the relative recruitment opportunities at the natal colony and colonies elsewhere. This sensitivity indicates that both regional and natal recruitment opportunities need to be documented and considered when assessing colony philopatry in seabirds. It also indicates that the traditional method of measuring philopatry in seabirds could be providing biased results. Seabird research is

typically conducted at the largest colony in a region, both to maximize sample size and to obtain demographic information from a numerically important location. While this strategy may be appropriate when assessing vital rates, it has the potential of providing overestimates of colony philopatry.

In this study, rates of colony philopatry were related to the regional importance of the study colony. Without providing an assessment of a colony's regional importance, observed rates of philopatry supply no information that can be used in an assessment of species-specific breeding dispersal. If observed colony philopatry is consistent with random settlement over a much larger region, then there is no greater tendency to recruit preferentially to the natal colony than randomly in a larger region. Additionally, larger colonies may be more attractive to prospecting birds, so that large study colonies could attract a disproportionate number of recruits independently of a natal preference. Given these problems with interpreting observations of colony philopatry from large colonies, assessments of colony philopatry, as a species-specific life history trait, may best be done at regionally less important colonies.

The emphasis on the colony as the spatial frame of reference in examination of seabird philopatry has hindered the examination and discussion of dispersal in seabirds. Assuming that philopatry as a life history characteristic operates at the scale of the colony presupposes benefits to recruitment to the colony as opposed to a larger area. While the colony may be the appropriate scale for species breeding in large widely-spaced colonies, individuals of species that breed in small closely spaced colonies may gain the benefits of

regional philopatry without displaying colony fidelity. In many cases it will be difficult to determine the region within which philopatry occurs, but providing an estimate of the regional importance of a colony when reporting observed philopatry will allow an estimation of regional vs. colony affinities.

Varying colony philopatry in relation to changing recruitment opportunities at the natal colony indicates that prospecting subadults weigh relative costs and benefits to fitness of returning to the natal colony vs. settling elsewhere. Our results indicate that individuals make different choices as relative opportunities at the natal colony change and that these choices occur hierarchically: prospect widely to find a nest-site vacancy and if not successful then restrict efforts to one or several sites where breeding will be delayed or precluded.

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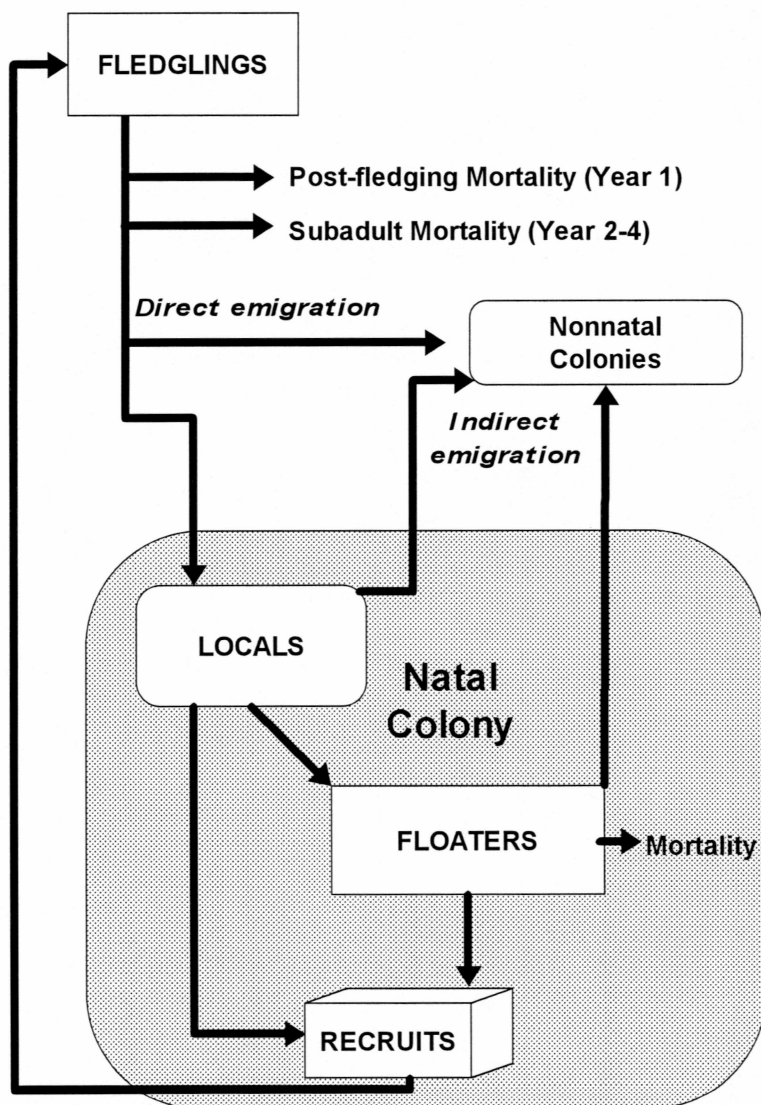


Figure 3.1. Schematic model of sources of reduction of guillemot cohorts from fledging to recruitment.

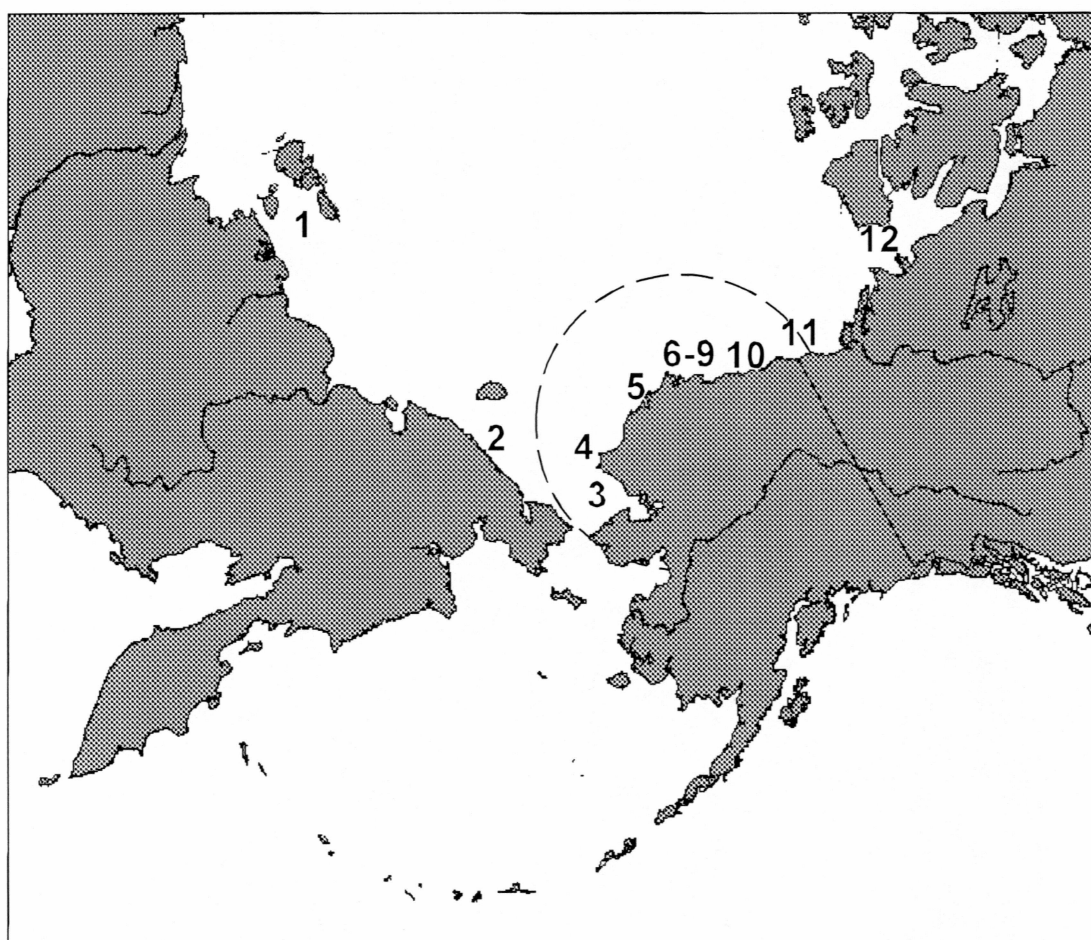


Figure 3.2. Location of Black Guillemot colonies in the western Arctic. Descriptions of numbered colonies are provided in Table 3.1. Circle shows 650 km radius from Cooper Island.

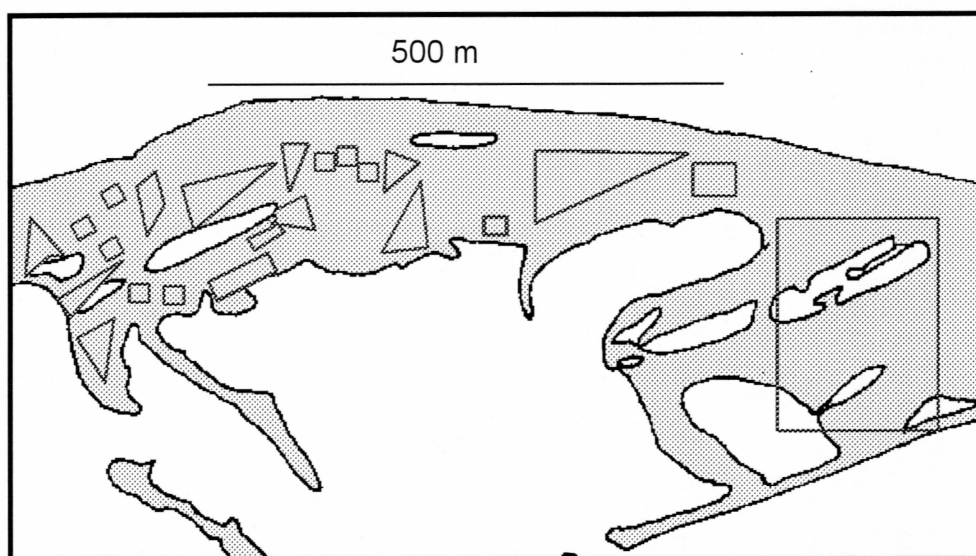


Figure 3.3. Cooper Island, Alaska showing approximate location of 23 Black Guillemot subcolonies.

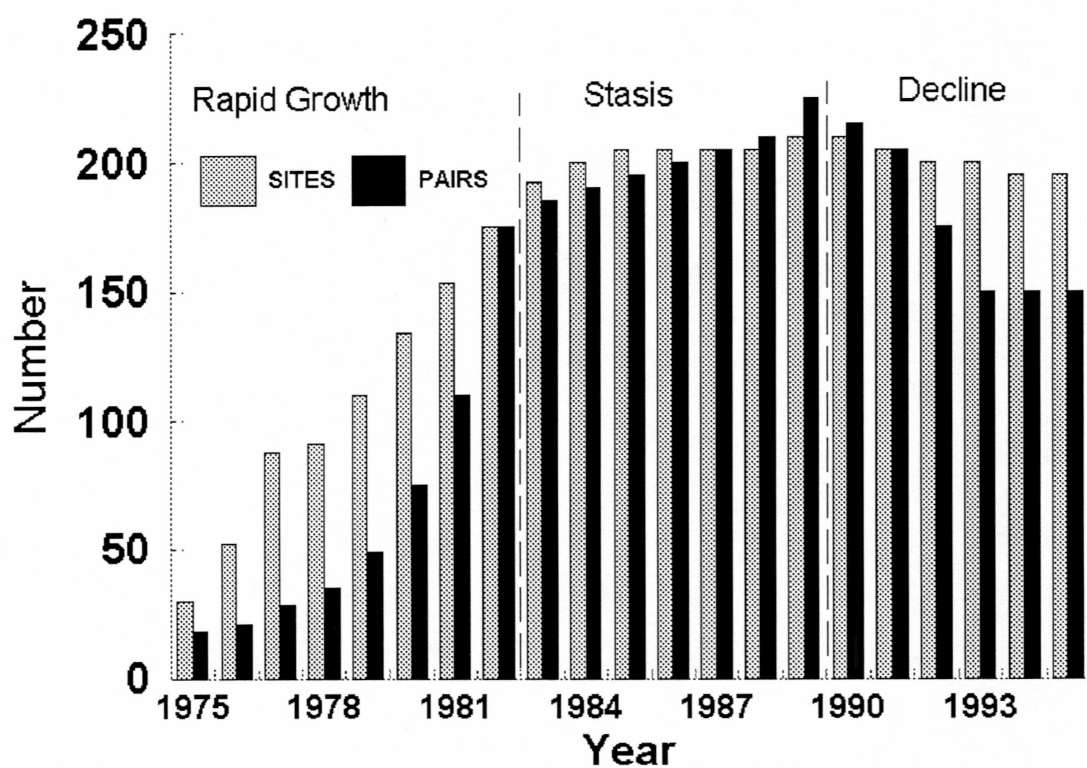


Figure 3.4. Number of Black Guillemot nest sites and breeding pairs, Cooper Island, Alaska, 1975-1995.

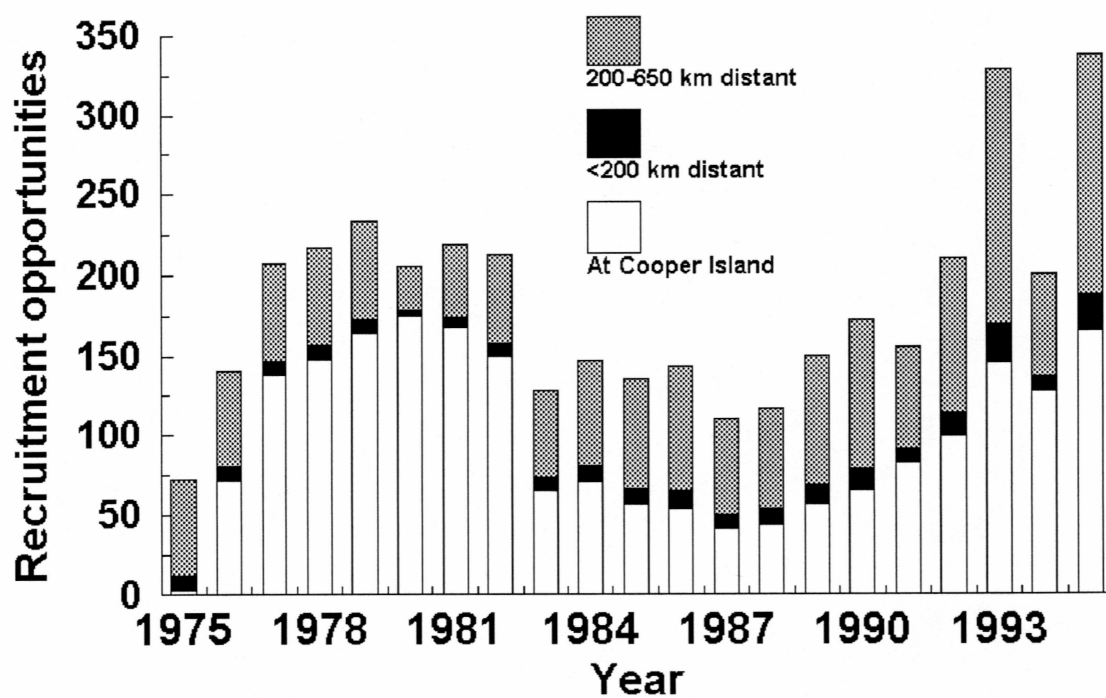


Figure 3.5. Numbers of regional breeding vacancies for Black Guillemots within 650 km of Cooper Island, Alaska, 1975-1995.

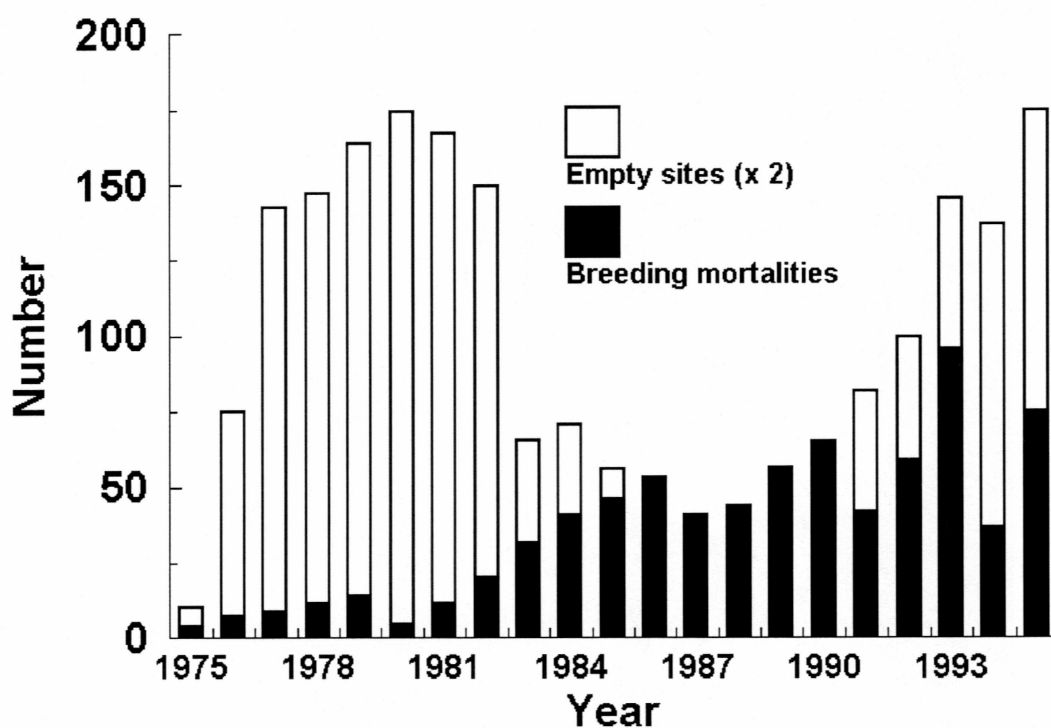


Figure 3.6. Numbers and types of breeding vacancies for Black Guillemots on Cooper Island, Alaska, 1975-1995. Number of opportunities at empty sites is the number of vacant sites the previous year $\times 2$. Number of opportunities due to mortality determined from annual overwinter survival of breeding adults.

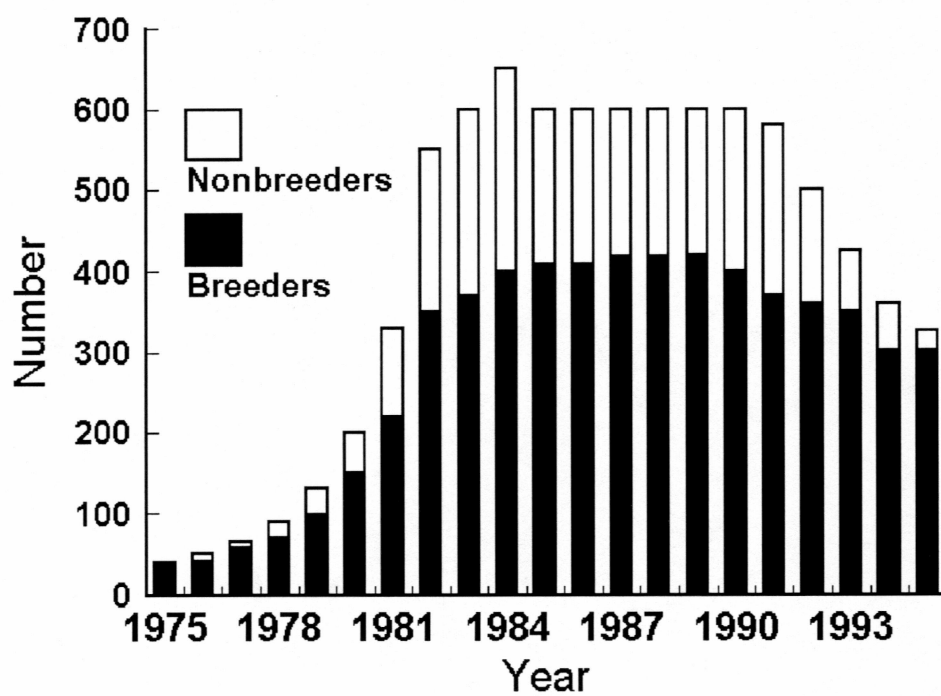


Figure 3.7. Numbers of breeding and nonbreeding Black Guillemots at Cooper Island, Alaska, 1975-1995. Nonbreeders are minimums.

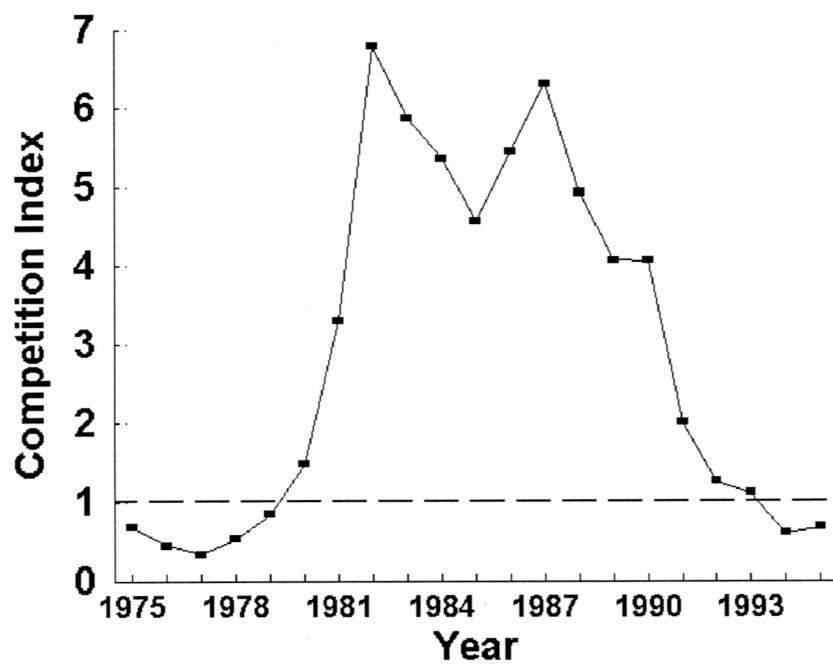


Figure 3.8. Competition Index (CI) for breeding vacancies at the Black Guillemot colony on Cooper Island, Alaska, 1975-1995. CI = number of potential recruits per recruitment opportunity. When $CI < 1$ there is no competition.

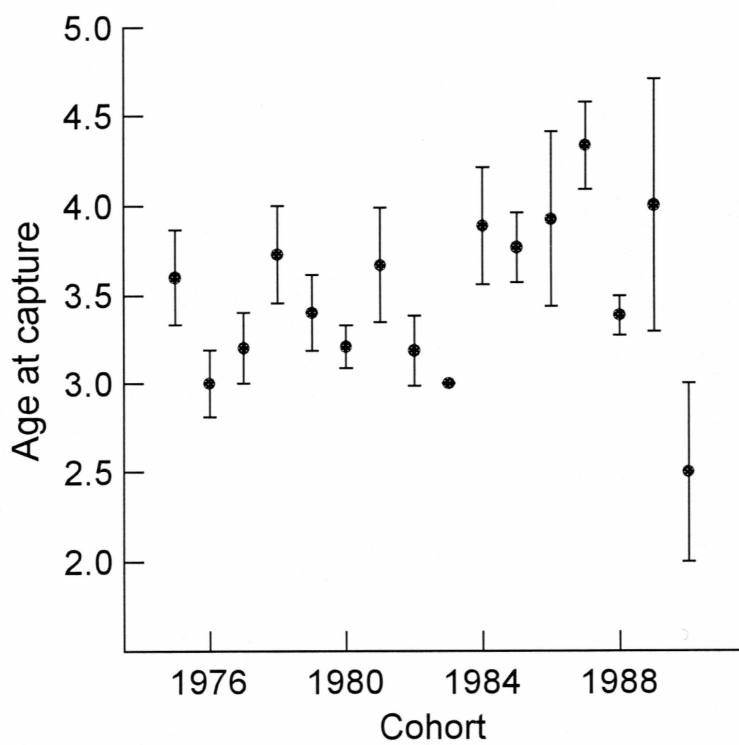


Figure 3.9. Age at capture as an adult at the natal colony (mean \pm s.e.) for Black Guillemot cohorts fledging in 1975-1990 from Cooper Island, Alaska.

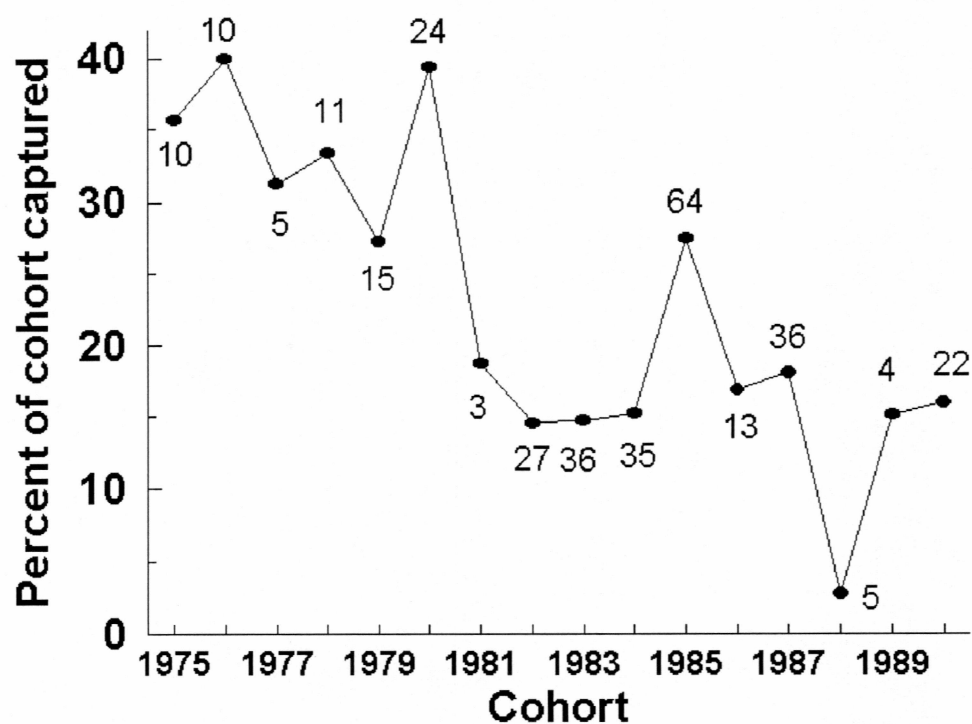


Figure 3.10. Percentage of cohorts captured as adults for Black Guillemot cohorts fledging in 1975-1990 from Cooper Island, Alaska. Numeric values are actual number captured.

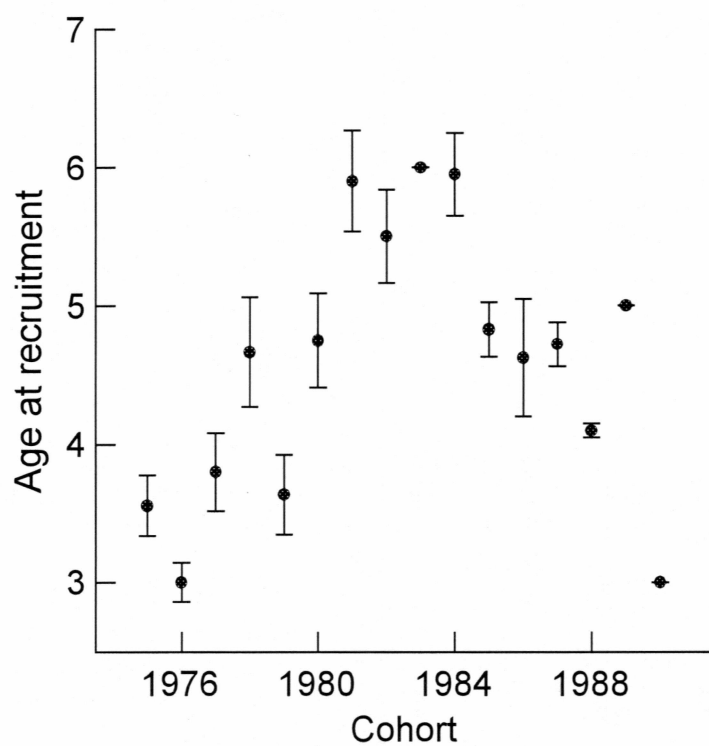


Figure 3.11. Age at recruitment at the natal colony (mean \pm s.e.) for Black Guillemot cohorts fledging in 1975-1990 from Cooper Island, Alaska.

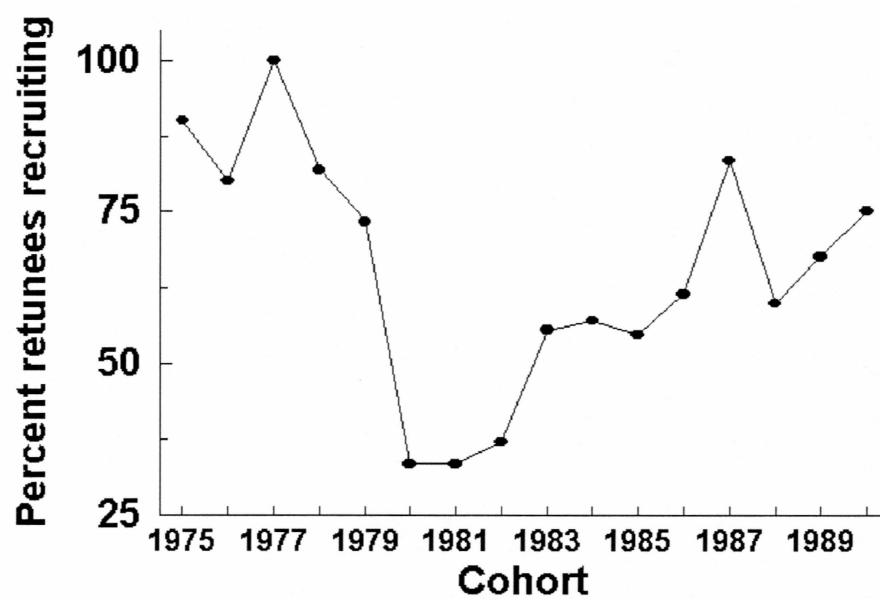


Figure 3.12. Percentage of individuals captured as adults (returnees) subsequently recruiting at the natal colony for Black Guillemot cohorts fledging in 1975-1990 from Cooper Island, Alaska.

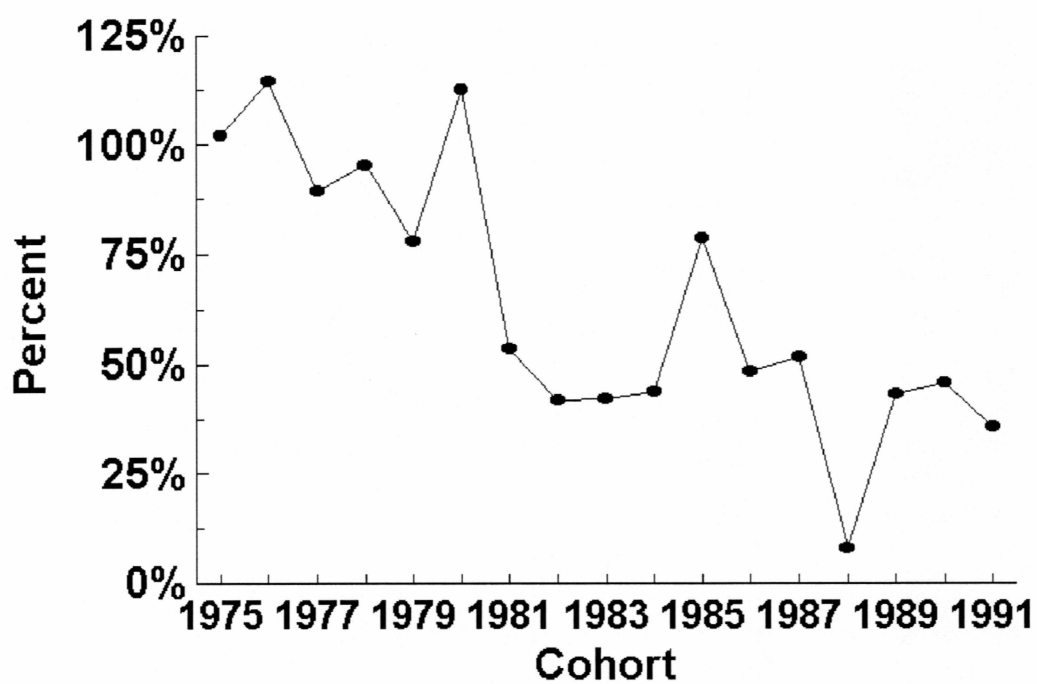


Figure 3.13. Percentage of assumed number of Black Guillemots surviving to breeding age that recruited at the natal colony for cohorts fledging in 1975-1990 from Cooper Island, Alaska.

Table 3.1. Locations, habitats, estimated breeding pairs, and distance from Cooper Island for Black Guillemot colonies in the East Siberian, Chukchi and Beaufort seas.

Location ^a	Breeding habitat	Pairs	km from Cooper I.	Sources
East Siberian Sea				
Delong Islands, East Siberian Sea (1) ^b	rock cliffs and talus	25,000	2300	Uspenskii 1959
Chukchi Sea				
Russian Chukchi Sea (2)	rock cliffs and talus	150	900	Golovkin 1984
Cape Thompson (3)	rock cliffs and talus	6	650	Swartz 1960
Cape Lisburne area (4)	rock cliffs and talus	250	500	D. Roseneau, USFWS, pers. com.
Seahorse Island (5)	driftwood	10		Divoky <i>et al.</i> 1974 R. Suydam, North Slope Borough, pers. com.
Point Barrow (6)	debris	5	25	Maclean and Verbeek 1968 Divoky unpubl.
Beaufort Sea				
Deadman Island (7)	beached barge	15	20	Divoky unpubl.
Cooper Island (8)	debris, nest boxes	225	-	Divoky unpubl.
Igalik Island (9)	beached barge	15	10	Divoky unpubl.
Prudhoe Bay (10) (beginning in 1976)	docks, drilling pads	15	350	L. Quakenbush, USFWS, pers. com.
Herschel Island, N.W.T.(11)	abandoned building	30	650	Kuyt <i>et al.</i> 1976
Cape Parry, N.W.T.(12)	rock cliffs and talus	20	1100	Johnson and Ward 1985
TOTAL PAIRS		25,726		

^a See Figure 3.3.

^b Numbers are map keys in Figure 3.3.

Table 3.2. Sources of variation in percentage of a fledging cohort recaptured percentage of a returning cohort recruited and age at recruitment.

Independent variables	Percentage of cohort captured			Age at recruitment			Percentage of returning cohort recruited		
	<i>Corr.</i>	<i>r</i> ²	<i>P</i>	<i>Corr.</i>	<i>r</i> ²	<i>P</i>	<i>Corr.</i>	<i>r</i> ²	<i>P</i>
Subadult survival									
Adult mortality - first winter	-	0.22	0.103	-	-	-	-	-	-
Fledging weight	+	0.38	0.015	-	-	-	-	-	-
Percentage regional recruitment opportunities at Cooper Island									
Total at age 2	+	0.60	0.001	-	-	-	-	-	-
Nonnatal recruitment opportunities ^a									
Total at age 2	-	0.18	0.094	-	-	-	-	-	-
Total at age 3	-	0.31	0.019	-	-	-	-	-	-
Natal colony characteristics									
Recruitment opportunities									
Total at age 2	+	0.43	0.004	-	0.37	0.013	+	0.23	0.065
Total at age 3	+	0.22	0.050	-	0.63	<0.001	+	0.56	0.001
In vacant sites at age 2	+	0.64	0.001	-	0.32	0.023	+	0.20	0.085
In vacant sites at age 3	+	0.36	0.011	-	0.43	0.006	+	0.46	0.004
In established pairs at age 2	-	0.67	<0.001	+	0.15	0.135	-	0.02	0.223
In established pairs at age 3	-	0.41	0.006	+	0.02	0.617	-	0.09	0.272
Other									
Competition Index at age 2	-	0.26	0.035	+	0.61	<0.001	+	0.57	0.001
Competition Index at age 3	-	0.04	0.440	+	0.50	0.002	+	0.74	<0.001
Productivity at age 2	+	0.06	0.330	-	-	-	-	-	-
Productivity at age 3	+	0.38	0.015	-	-	-	-	-	-

^a <650 km from Cooper Island.

CONCLUSIONS

The preceding three chapters detail the environmental change and demographic processes contributing to the establishment, growth and decline of a colony of Black Guillemots in northern Alaska in the late twentieth century. My findings show that recent climate change in the region allowed the colonization of northern Alaska approximately 3 decades ago and permitted population growth and an advancement of breeding initiation over the past 2 decades. These are among the first documented biological effects of the recently reported climate change in the region. Equally important are my findings on the patterns of philopatry and immigration observed during the growth, stasis and decline of the largest colony of Black Guillemots in this region. The observed patterns have been substantially different from those proposed in theoretical models (e.g., Cairns 1992) and indicate that the established views of the process of immigration and emigration in seabirds contain illogical and inappropriate assumptions and suffer from an overemphasis on the colony as a demographic unit.

ENVIRONMENTAL CHANGE

Black Guillemots have occupied the waters off northern Alaska and eastern Siberia for approximately 25,000 years (Kidd 1996). The area was part of a refugium during the last glaciation, allowing a population to persist when much of the adjacent Arctic was uninhabitable. Paleoclimate records of the last 400 years (Overpeck 1997),

weather records for the last 50 years, and knowledge of recent changes in nest-site availability in the region allow testing of hypotheses about the factors contributing to the colonization of northern Alaska.

In the recent past (1600-1950 A.D.) the Black Guillemot population in the Chukchi and Beaufort seas was probably smaller than when I began my study and limited by the number of nest sites and seasonal constraints (snow cover) on access to sites. From the middle of the 17th century to the beginning of the 20th century, during the period of global cooling known as the Little Ice Age, the region had much lower summer temperatures than the 1901-1960 average (Overpeck et al. 1997). Because the annual snow-free period has only recently begun to regularly exceed 80 days at Barrow, for much of the 300 years preceding my study restricted access to cavities probably limited the numbers, distribution and success of breeding pairs. Only cavities well above the ground, with an entrance or orientation that minimized snow accumulation, would have allowed successful breeding. These would have been at a premium and associated with rocky headlands, similar to portions of Cape Lisburne and Wrangel Island. Nest sites on flate terrain, such as those in northern Alaska, or prone to cover by drifting snow would not have supported successful nesting.

Extent and seasonal persistence of sea ice probably also were greater during the Little Ice Age than at present, although the potential effects on Black Guillemots are uncertain. Extent of arctic sea ice has been decreasing since at least 1978 (Cavalleri et al. 1997) and likely began when regional temperatures increased in the last century

(Overpeck et al. 1991). If the location of the pack ice edge in summer was closer to breeding colonies in the past, the proximity of ice-edge foraging areas would have resulted in high breeding success, similar to what I observed on Cooper Island in 1975 when pack ice retreat from the coast was minimal. If the annual period between the melting and freezing of seawater was also reduced, breeding may have been impaired by a lack of open water near breeding sites in spring and formation of ice during chick provisioning or shortly after fledging in late summer and autumn.

A rapid rise in regional temperatures and the provision of manmade cavities from post WWII activities and oil development allowed an expansion of the regional population in the mid 20th century. Increasing temperatures would allow successful breeding at more nest sites. Assuming the snow record for Barrow is representative of the region, most cavities at ground level would have regularly had an annual snow-free period of >80 days only after the mid-1960's. Prior to the middle of this century potential nesting cavities in northern Alaska were almost exclusively limited to natural sites, such as the driftwood pile on Seahorse Island. Numbers of cavities in manmade structures increased with accumulation of debris associated with increasing governmental activities in the late 1940's and 1950's and oil industry activities in the 1960' and 1970's. Although colonization of the region would likely have occurred had only natural nest sites been present, it would probably would have taken longer and the total number of pairs certainly would have been lower (<15). Even with manmade sites the number of nesting

pairs present six years after the discovery of the first nest was not large, <30 pairs, with all but 10 in manmade structures.

My creation of nest sites at Cooper Island may have begun at time when conditions for colony expansion were the best they had been in the preceding 400 years. Seasonal accessibility to nest sites was no longer as constraining as it had been in the recent past. In addition, the close proximity of the pack ice would allow high breeding success. High regional productivity would have resulted in large numbers of nonbreeders at the summer sea ice edge, which typically was in close proximity to the northern Alaska coast in summer. Prospecting of coastal locations in northern Alaska could be expected to be high. Observed colony growth on Cooper Island was similar to that seen in colonies within the established range of Black Guillemots (Petersen 1981).

The amelioration of climate that was necessary to increase nest-site accessibility may now be causing the recently observed decreases in the regional population of guillemots. From 1990 to 1997 the colony on Cooper Island experienced decreases in immigration, the pool of nonbreeders, number of breeding birds, and adult survival. The reasons for these decreases are unclear but could include a combination of low breeding success throughout the region and decreased overwinter survival of adult and subadult birds, both of which could be sensitive to decreases in ice extent. If the observed decreases are the result of low breeding success or increased adult mortality on the breeding grounds from climate-related changes in habitat quality, then the continuation

of the regional warming that allowed guillemots to flourish in northern Alaska from the late 1960's to the late 1980's could be causing the population decrease in the 1990's.

DISPERSAL

The observed growth of the colony at Cooper Island and its subsequent period of stasis and decline could have resulted from the traditional view of immigration and emigration processes of seabirds. This view holds that colony philopatry is typically high, with dispersal caused by density-dependent constraints at the natal colony. Immigration is thought to occur only in situations where recruitment constraints are minimal or the benefits of immigration are substantially higher than those of philopatry. Native birds are thought to have a recruitment advantage over potential immigrants. Within this framework, the colonization of northern Alaska by Black Guillemots would have occurred as individuals prevented from breeding at their natal colony by density-dependent constraints prospecting alternative breeding locations. Once a colony was established, recruitment would consist of native birds, with immigrants comprising only the recruits that could not be accounted for by natives.

Only through the banding of all fledglings since 1975 and monitoring of all recruitment since 1978 was I able to demonstrate that this traditional view is in error. The traditional view suffers from inappropriate spatial considerations, misuse of terminology, and illogical assumptions that have hindered study and analysis of seabird dispersal. Contrary to the accepted view I discovered that guillemot recruitment showed no clear bias to the natal colony, with birds choosing locations based on recruitment

opportunities. Immigration occurred both when recruitment constraints were minimal and when they were high. Moreover, native birds did not have a recruitment advantage at the natal colony and were frequently prevented from recruiting at the natal colony due to competition with nonnative birds.

Although these findings are contrary to the traditional view, they are not surprising considering the life history of seabirds. Delayed maturity allows seabirds to prospect for recruitment opportunities for several years before becoming sexually mature. If one of the main benefits of philopatry is that it allows birds to recruit at a location where conspecifics have been successful in the recent past, philopatry should be of greatest importance to species that can recruit during their 1st year and have little time to assess nonnatal recruitment opportunities. The prebreeding period in seabirds allows individuals to sample recruitment opportunities over a large area. Extensive prospecting during the pre-adult period would not be expected in instances where philopatry has evolved because of kin selection, which has yet to be proven in seabirds. In all other cases, prospecting of a larger region, as opposed to just the natal colony, allows birds to search for the location with the highest recruitment potential or chance of breeding success. Large-scale philopatry allows individuals to respond to changes in local resource availability, maximize their chances of recruitment, and locate conditions for which they are best adapted.

In conjunction with this change in spatial emphasis, there is a need to modify the terminology of dispersal. Immigration is frequently viewed as: 1) involving birds

unsuccessful at recruiting at the natal location, 2) having a cost (typically assumed to be increased mortality) to the individual, and 3) occurring only when recruitment constraints are minimal at nonnatal colonies. If birds are prospecting and assessing a region including the natal colony with no bias to the colony, the use of the term “immigration” needs to be reconsidered when referring to intercolony movement. Currently, no one considers natal dispersal from one subcolony to another to be migration and at least for some species the same considerations for movement between colonies should apply.

Unfortunately, the recent realization that philopatry in seabirds may not be as high as presumed and that immigration can play a major role in colony growth has been replaced with the view that seabird colonies function as patches in a metapopulations. In this context some colonies are thought to function as “sources” where production exceeds mortality and the resulting surplus of birds are forced to disperse. These birds are most likely to be recruited at “sink” populations where mortality exceeds production. Although this view does provide a perspective that is larger than that of the single colony, it suffers from a number of assumptions inappropriate for seabird populations. Standard metapopulation theory assumes that dispersal is environmental in nature and that dispersal occurs between patches in a matrix of habitat unsuitable to the species. Following the colony-centered view of seabird dispersal, early attempts at applying metapopulation theory to seabirds have resulted in discussion of “source’ and “sink” colonies, although there is no indication that the colony would be the appropriate patch size or that the demographic definition of the patch size would be the same for all species.

In addition, in a particular region, seabird colonies may not be separated by an uninhabitable matrix but within the habitat that is occupied by prospecting nonbreeders. Thus, a metapopulation theory could advance studies of seabird populations, but its utility will be limited until it addresses misplaced spatial and functional assumptions.

THE FUTURE

Further warming of the arctic is predicted in the next 50 years and could have major effects on the population of Black Guillemots in northern Alaska. Continued warming would result in increased distance of the ice from breeding colonies, decreasing productivity and perhaps post-fledging survival while also decreasing adult survival by increasing the costs of reproduction or decreasing winter habitat. Although the regional guillemot population would initially decline, the decline could be followed by an increase in numbers. If warming results in a northward movement and increase of subarctic marine species, such as sandlance (*Ammodytes hexapterus*), the losses resulting from the ice retreat could be offset by increases in nearshore prey. Although most Mandt's Black Guillemot (*C. g. mandti*) colonies are near the ice edge, the presence of colonies at Cape Lisburne and Cape Thompson, where water flowing through the Bering Strait increases prey abundance, shows that proximity to the ice edge during the entire breeding season is not a prerequisite for the subspecies. Moreover if warming results in decreased ice thickness, ice scour in the nearshore would be reduced, allowing for the development of a more robust nearshore benthic community. Benthic fish and invertebrates constitute most of the diet for guillemots (*Cephus* spp.) in many areas.

Warming, however, also could result in a northward expansion of Bering Sea alcids that could increase competition for nest sites. Already the longer summer has allowed Horned Puffins to prospect and breed on Cooper Island. Prospecting puffins displace guillemot eggs and kill guillemot chicks (Divoky unpubl). If the numbers of puffins in northern Alaska increases with increasing climate warming, competition for the limited nest sites could result in fewer guillemots.

In addition to climate change affecting the northern Alaska Black Guillemot population, the nature of the nest sites that allowed establishment and expansion in the region may now be contributing to its decline. While the nest sites provide conditions allowing for breeding success comparable to natural colonies, they may be unable to sustain populations over time. This is due to the access provided to terrestrial predators and the relative instability of the sites. In 5 of the last 8 years, terrestrial predation has resulted in decreased breeding success. Arctic fox predation on eggs resulted in complete breeding failures in three years and polar bear predation on chicks decreased breeding success in two years. While such predation could occur at typical rock cliff or talus colonies, there would typically be some sites spared due to their location or inaccessibility. In northern Alaska, the vulnerability of essentially all sites in northern Alaska, could make the population's existence vulnerable to increased predation.

The size of the northern Alaska population in the future will depend on whether the population is limited by nest sites or prey availability. If breeding productivity and survival in the regional population return to the levels observed between 1970 and 1990,

nest sites will be limiting and the northern Alaska colonies would be assured of a source of potential recruits searching for suitable nest sites. If low breeding success and high adult mortality continue to limit the regional population, the existence and size of the northern Alaska colonies will depend on their relative attractiveness to potential recruits, with size of a colony being dependent on the quality of its nest sites and adjacent foraging areas relative to other colonies. Even if ice edge retreat greatly decreases the abundance of prey and no alternative prey source is immediately available, complete extirpation of the Cooper Island colony seems unlikely given the generalist strategy of Black Guillemots and their ability to breed as single pairs. Except with an extreme decrease in nearshore prey some pairs would likely be able to breed successfully in the region. Smaller numbers of breeding guillemots would decrease the colony's attractiveness to predators with an resulting increase in breeding success. Although, the predicted Cooper Island colony would be limited by prey abundance rather than nest-site availability, it might closely resemble the colony of 10 pairs I discovered in 1972.