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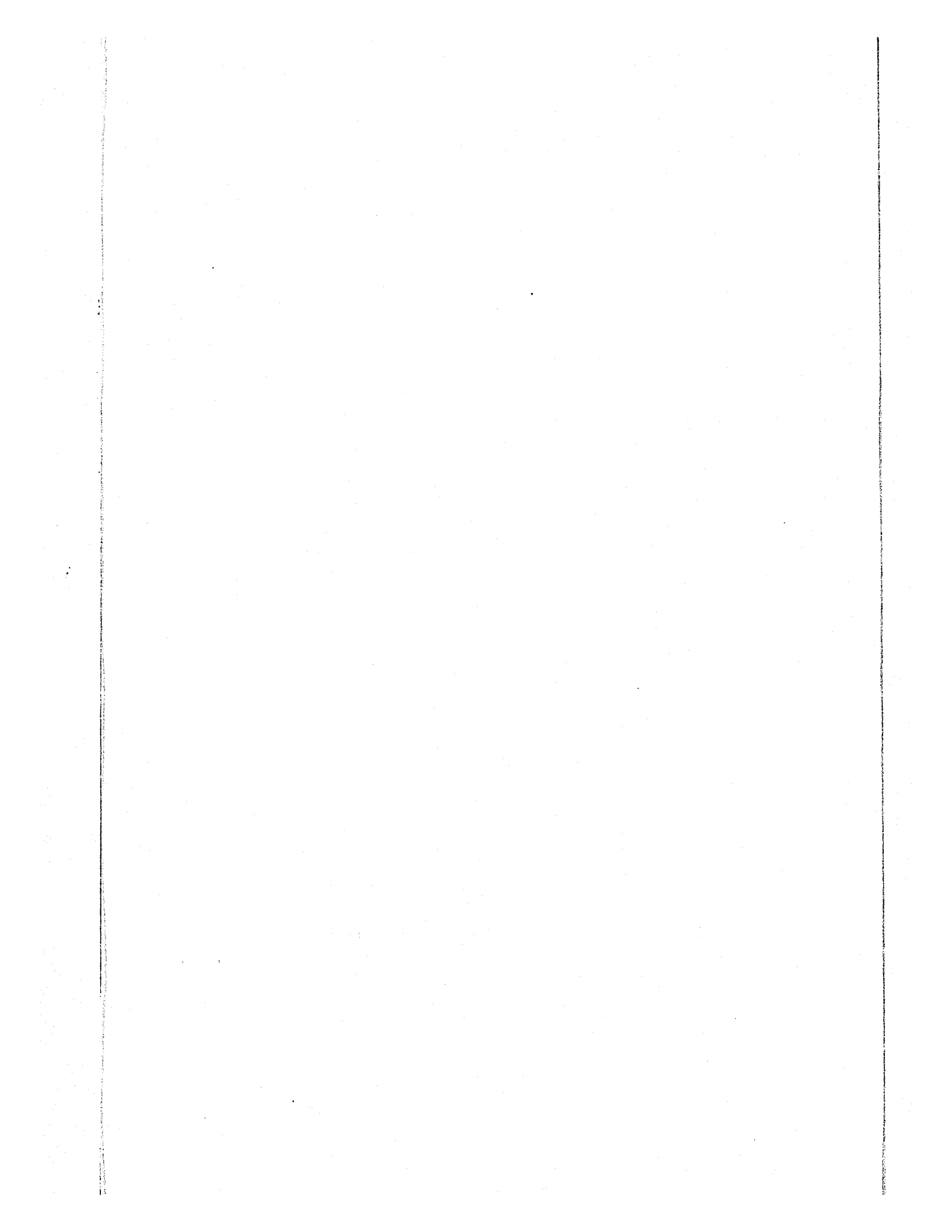
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THE EFFECTS OF AGE, TIMING OF BREEDING,
AND BREEDING SITE CHARACTERISTICS
ON THE REPRODUCTIVE SUCCESS
OF THE THICK-BILLED MURRE, Uria lomvia

by

Leah Naoko de Forest



Thesis submitted to the
School of Graduate Studies and Research
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L'Institut de biologie d'Ottawa-Carleton

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	i
TABLE OF CONTENTS.....	ii
LIST OF TABLES.....	iii
LIST OF FIGURES.....	v
ABSTRACT.....	vii
RÉSUMÉ.....	x
Chapter 1: GENERAL INTRODUCTION.....	1
Study Area.....	4
Study Animal.....	7
Weather Patterns.....	9
 Chapter 2: AGE-RELATED DIFFERENCES IN REPRODUCTIVE PARAMETERS AND THE SEASONAL DECLINE IN HATCHING AND REPRODUCTIVE SUCCESS	
Introduction.....	12
Materials and Methods.....	13
Results.....	27
Discussion.....	69
 Chapter 3: EXPERIMENTS TO DETERMINE THE EFFECT OF TIMING OF LAYING	
Introduction.....	78
Materials and Methods.....	81
Results.....	86
Discussion.....	102
 Chapter 4: DIFFERENCES IN BREEDING SITE CHARACTERISTICS AND THEIR EFFECT ON THE REPRODUCTIVE SUCCESS OF KNOWN AGE BREEDERS	
Introduction.....	109
Materials and Methods.....	111
Results.....	113
Discussion.....	124
 Chapter 5: GENERAL DISCUSSION.....	129
LITERATURE CITED.....	136
Appendix 1.....	147

LIST OF TABLES

Table 2.1: Total numbers of banded birds breeding on the study plots in 1990 and 1991, including both members of double banded pairs.....	16
Table 2.2: Mean laying dates of first eggs on 5 study plots.....	18
Table 2.3: Proportions of known age birds breeding in 1990 and 1991; triangular-type bands only.....	28
Table 2.4: Mean laying dates (\pm SD) of first eggs of known age birds.....	31
Table 2.5: Proportions of known age birds breeding in both years, and in 1991 only (triangular-type bands only).....	35
Table 2.6: Change in laying date of individual known age birds from 1990 to 1991.....	36
Table 2.7: Comparisons of 1990 laying dates of known age birds which bred only in 1990, and those which bred in both 1990 and 1991.....	38
Table 2.8: Differences in egg volume indices (cm^3) of known age breeders.....	39
Table 2.9: Egg loss by young and older birds and the proportion of birds laying a replacement egg.....	44
Table 2.10: Mean time to lay a replacement egg and coefficients of variation for young and older breeders....	45
Table 2.11: Mean durations of incubation and fledging periods of known age breeders.....	50
Table 2.12: Breeding success of first and replacement eggs for 5 study plots.....	52
Table 2.13: Comparison of the success of first and replacement eggs in 1990 and 1991 for all plots combined..	53
Table 2.14: Comparison of success of first and replacement eggs.....	54
Table 2.15: Locations and reproductive success of pairs containing young and older birds on 5 study plots.....	56
Table 2.16: Hatching, fledging and reproductive success of known age breeders.....	57
Table 2.17: Comparison of 1990 outcomes for known age breeders which did and did not return to breed in 1991....	59

Table 2.18: Hatching, fledging and reproductive success for total sample, young and older birds, and total sample without young and older birds.....	61
Table 3.1: Mean laying dates for first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991.....	87
Table 3.2: Difference in egg volume indices of first and replacement eggs of experimental breeders in 1990 and 1991.....	90
Table 3.3: Mean egg volume indices of first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991.....	91
Table 3.4: Incubation periods of first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991.....	92
Table 3.5: Hatching, fledging and reproductive success of control, experimental and young breeders in 1990 and 1991.	94
Table 3.6: Mean chick feeding rates for control and experimental breeders on plot D during 24-hour periods in 1991.....	96
Table 3.7: Comparison of chick weights and wing lengths at 14-days on control and experimental breeders on chick growth plots in 1991.....	100
Table 3.8: Comparison of chick weights and wing lengths at 14-days of young and older breeders in 1991.....	100
Table 3.9: Comparison of chick weights and wing lengths at 14-days of control, experimental and young breeders on study plots in 1991.....	101
Table 4.1: Site characteristics of all sites used at least once during 1990 and 1991.....	115
Table 4.2: The effect of individual site characteristics considered independently on the reproductive success of older breeders in 1990 and 1991.....	116
Table 4.3: The effect of individual site characteristics considered independently on the reproductive success of young breeders in 1990 and 1991.....	117
Table 4.4: Effect of site characteristics when considered together on reproductive success of older and young breeders in 1990 and 1991, using logistic regression.....	120
Table 4.5: Breeding site characteristics for the older and young birds in 1990.....	121

Table 4.6: Breeding site characteristics for older and young birds in 1991.....	122
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LIST OF FIGURES

Figure 1.1: Map of Coats Island and the eastern Northwest Territories.....	5
Figure 1.2: Map of main and east Thick-billed Murre colonies on the southeast tip of Coats Island.....	6
Figure 1.3: Daily wind speed recorded at 1700 h at Coats Island.....	10
Figure 1.4: Daily maximum and minimum air temperature recorded at 1700 h at Coats Island.....	11
Figure 2.1: Pattern of laying of first eggs at Coats Island.....	29
Figure 2.2: Pattern of laying of known age breeders.....	32
Figure 2.3: Time elapsed between laying and loss for eggs lost ≤ 33 days after laying.....	41
Figure 2.4: Proportion of pairs laying a replacement egg in relation to the date of loss of the first egg.....	42
Figure 2.5: Time elapsed between the loss of an egg and the laying of a replacement for young and older birds.....	46
Figure 2.6: Time elapsed between laying and loss for known age birds.....	47
Figure 2.7: Age at fledging in relation to date of hatching for chicks from first eggs.....	49
Figure 2.8: Seasonal decline in hatching success of the total sample.....	63
Figure 2.9: Seasonal decline in hatching success of young and older breeders combined and total sample excluding known age breeders.....	64
Figure 2.10: Fledging success for total sample by laying date.....	66
Figure 2.11: Seasonal decline in reproductive success of the total sample.....	67
Figure 2.12: 1990 seasonal decline in reproductive success of young and older breeders combined, compared to total sample excluding known age breeders.....	68

Figure 3.1: Laying dates of first eggs of young and control breeders, and replacement eggs of experimental breeders.....	88
Figure 3.2: Seasonal decline in hatching success.....	95
Figure 3.3: Growth curves of control and experimental a) chick weights and b) wing lengths on chick growth plots in 1991.....	99

ABSTRACT

Age-specific reproductive parameters, including reproductive success, of young (four and five-year old) and older (>7 years old) breeding Thick-billed Murres (Uria lomvia) were compared on a colony at Coats Island, N.W.T. in 1990 and 1991. Young birds laid smaller eggs later in the season than older birds. Older birds had higher hatching and reproductive success than young birds, but fledging success did not differ. The chicks of young birds at 14 days were lighter and smaller than those of older birds.

There was a seasonal decline in hatching and reproductive success in both years for the total sample, but no seasonal decline in fledging success. Most losses occurred during the incubation period, with a decreasing likelihood of laying a replacement egg as the season progressed.

Age-related improvement in breeding success may have been due in part to breeding experience. Second time breeders laid earlier than in their first year, and improved their reproductive success. Five-year olds breeding for the second time bred earlier and more successfully than five-year olds breeding for the first time. Differential survival in relation to reproductive success was not observed. Birds which performed poorly in their first year were not less likely to return to breed in the next year than birds which performed well in their first year.

Different proportions of young and older birds breeding throughout the season affected the seasonal decline in reproductive success of the overall colony. Young and older birds separately

showed no seasonal changes (except a slight decline in reproductive success in older birds in one year), but when combined they had a similar seasonal decline in hatching and reproductive success as the total sample.

In order to control for differences in timing of laying between young and older birds, a sample of early laying, presumably older breeders were experimentally delayed c. 14 days. Age, rather than timing of laying influenced the decline in reproductive success. Young birds had significantly lower hatching and reproductive success than experimental breeders. Although the chicks of younger birds were significantly smaller than experimental chicks, there was no decline in food availability detected at the end of the season, suggesting that young birds were not able to provision their chicks as well as more experienced breeders.

Breeding site characteristics had some effect on the reproductive success of young and older breeders. Older birds were more successful on sites which had neighbours. Site characteristics did not affect the success of young birds in 1990, but birds nesting on sites with neighbours and walls showed improved success in 1991. Young birds were less successful than older birds on all types of sites, and more likely to be found on suboptimal sites.

The lack of decline in reproductive success with date when age was controlled, and the high reproductive success of experimentally delayed birds suggest that it is the competence of young breeders,

rather than the date at which they lay, that determines their reproductive success. The high proportion of young Thick-billed Murres that lay later in the season may be the main cause of the seasonal decline in reproductive success for the colony as a whole.

LES EFFECTS DE L'ÂGE, DE LA DATE DE REPRODUCTION,
ET LES CARACTÉRISTIQUES DU SITE
SUR LE TAUX DE REPRODUCTION
DE LA MARMETTE DE BRÜNNICH, Uria lomvia

RÉSUMÉ

Les paramètres de la reproduction (incluant le taux de reproduction) liés à l'âge chez les marmettes de Brünnich (Uria lomvia) ont été comparé pour deux groupes d'âge: les jeunes (quatre et cinq ans) et les vieux (> sept ans). L'étude a été menée à une colonie de l'île Coats, Territoires du Nord-ouest en 1990 et 1991. Les jeunes oiseaux pondaient des oeufs plus petits et plus tard dans la saison que les vieux. Les vieux obtenaient un meilleur taux d'éclosion et de reproduction que les jeunes mais les taux d'envol des poussins étaient les mêmes. Les poussins des jeunes oiseaux étaient plus légers et plus petits à quatorze jours que ceux de vieux.

Il y avait une décroissance saisonnière des taux d'éclosion et de reproduction pour les deux années pour l'ensemble de l'échantillon, mais il n'y en avait pas pour le taux d'envol des poussins. La majorité des pertes étaient pendant la période d'incubation. Il y avait une baisse de la ponte d'oeuf de remplacement à mesure que la saison avançait.

L'amélioration du taux de reproduction liée à l'âge était due à l'expérience des parents. Les parents nichant pour la deuxième fois ont pondus plus tôt et ont eu un meilleur taux de reproduction

qu'à leur première année. Les parents de cinq ans nichant pour la deuxième fois avaient un taux de reproduction plus élevé que les parents de cinq ans nichant pour la première fois. Les oiseaux qui n'ont pas bien réussi la première année n'étaient pas moins tentés de retourner nicher l'année suivante que les autres.

L'âge avait un effet marqué sur la chute saisonnière du taux de reproduction à travers la colonie. Jeunes et vieux séparés ne montraient pas de variations saisonnières (excepté une légère baisse dans le taux de reproduction pour les vieux oiseaux une année), mais regroupés ils avaient une baisse saisonnière du taux d'éclosion et de reproduction semblable à l'échantillon total.

Pour contrôler la différence entre les périodes de ponte entre jeunes et vieux, des oeufs pondus tôt en saison (on assume qu'ils proviennent de vieux oiseaux) ont été retirés et les parents ont pondus de nouveau 14 jours plus tard. L'âge du parent plutôt que la période de ponte affecte la baisse du taux de reproduction. Les jeunes oiseaux avaient un taux d'éclosion et de reproduction significativement plus bas que les vieux parents ayant pondus en même temps. De plus, les poussins des jeunes étaient significativement plus petits que les poussins des vieux nés en même temps. Il n'y avait pas de changement dans la disponibilité de la nourriture décelée à la fin de la saison. Ceci suggère que les jeunes oiseaux n'arrivaient pas à trouver de la nourriture pour leurs poussins aussi bien que les adultes plus expérimentés.

Les caractéristiques du site de nidification affectaient le taux de reproduction des jeunes et vieux. Les vieux avaient un

meilleur succès dans les sites où il y avait des voisins. Les caractéristiques des sites n'ont pas affecté les jeunes en 1990, mais les sites avec voisins et parois ont augmenté le taux de reproduction des jeunes en 1991. Les jeunes réussissaient moins bien que les vieux dans tous les types de sites mais se retrouvaient plus fréquemment dans des sites moins bons.

L'absence de baisse dans le taux de reproduction en fonction de la date quant l'âge était contrôlé et le haut taux de reproduction des vieux oiseaux qui ont été retardés expérimentalement suggère que c'est la compétence des jeunes parents plutôt que la date de la ponte qui détermine leur succès. La grande proportion de jeunes marmettes de Brünnich pondant plus tard dans la saison peut être la principale cause de la baisse du taux de reproduction de toute la colonie.

Chapter 1: GENERAL INTRODUCTION

In many long-lived seabird species, younger, less experienced breeders differ from older, more experienced breeders in various reproductive parameters, including reproductive success (Coulson and White 1958, Davis 1975, Potts et al. 1980, Ryder 1980, Nisbet et al. 1984, Saether 1990). The effects of age alone on reproductive success are difficult to determine due to several confounding variables. Timing of breeding is closely related to reproductive success in many colonial seabirds, including alcids, with young birds usually laying later than older birds. Individuals laying early in the season are more successful than late breeders, with clutch size, egg volume, probability of relaying if eggs are lost, hatching success, fledging weights and fledging success declining with date of laying in various species, including murrelets (Coulson and White 1958, 1961, Parsons 1975, Lloyd 1979, Findlay and Cooke 1982b, Croxall et al. 1992; Common Murrelets, Uria lomvia: Birkhead 1977, Hedgren 1980, Birkhead and Nettleship 1987b, Wanless and Harris 1988, Hatchwell 1991; Thick-billed Murrelets, Uria lomvia: Birkhead and Nettleship 1981, Gaston and Nettleship 1981, Birkhead and Nettleship 1987b). Seasonal and annual changes in prey availability and weather may contribute to seasonal changes in reproductive parameters (Hedgren and Linnman 1979, Coulson and Thomas 1985, Sydeman et al. 1991). Quality of breeding site has also been shown to affect reproductive success in colonial seabirds (Coulson 1968, Gaston and Nettleship 1981, Birkhead et al. 1985). Differences in reproductive success between

young and older birds may be due to the age-related quality of their sites (Coulson and Horobin 1976, Potts et al. 1980). Quality of individual breeders and differing levels of experience further complicate the effects of age (Coulson 1968, Thomas and Coulson 1988, Mills 1989).

In murre (Uria spp.), several hypotheses have been suggested to explain the observed decline in reproductive success with laying date:

- 1) increased risk of predation for late birds not breeding synchronously (Birkhead 1977). High density and synchronous nesting reduced the effectiveness of avian predators, while later laying birds were isolated and more exposed, making them an easier target for predation.

- 2) seasonal declines in prey availability and/or quality causing later chicks to have reduced fledging success or lower fledging weights (Hedgren and Linnman 1979, Gaston and Nettleship 1981, Birkhead and Nettleship 1982).

- 3) poor performance by young, inexperienced and/or less productive birds breeding later in the season (Hedgren 1980). Part of the low reproductive success of young birds may be due to the quality of breeding sites that they select or are forced to use (Potts et al. 1980).

There have been many long-term population studies which have added to our knowledge of age-specific effects on reproductive success of seabirds (for reviews see Ryder 1980, Clutton-Brock 1988, Newton 1989, Saether 1990, Wooller et al. 1992). However,

there have been few studies of alcids involving large numbers of banded individuals of known age (see Hudson 1985, Emslie et al. 1992). During my study, Coats Island had a sample of known age banded Thick-billed Murres ranging from three to seven-years of age, as well as a sample of birds banded as breeding adults.

The objective of this thesis is to examine the effect of age on the reproductive success of the Thick-billed Murre, Uria lomvia. In Chapter 2, I examine differences in reproductive parameters between young and older birds and show when during the breeding cycle these birds fail. I describe seasonal changes in various reproductive parameters both for breeders of known age and for the total sample of breeders, most of which are of unknown age. These data are used to evaluate the effect of age-specific reproductive success on the seasonal trend in reproductive success for the population as a whole. In Chapter 3, I utilize an experimental approach to examine reproductive success corrected for timing of laying. By experimentally forcing early laying birds to lay a replacement egg later in the season, I was able to compare their success to that of young birds breeding at a similar date. In addition, I use measurements of feeding rates and chick growth to determine whether there was any seasonal change in prey availability. In Chapter 4, breeding sites of young and older birds are compared to examine whether reproductive success varies between different types of sites, and whether types of sites occupied by young and older birds differ. In the final chapter, I discuss how my findings relate to the hypothesis that age is the

main factor causing the seasonal decline in reproductive success in murres and other colonial seabirds.

STUDY AREA:

A colony of Thick-billed Murres on Coats Island, located in Hudson Strait, Northwest Territories, Canada (62°57'N, 82°00'W) was studied from early June to late August in 1990 and 1991 (Figure 1.1). There are two distinct colonies situated at the northeastern tip of the island, c. 1.5 km apart (Figure 1.2). All banding of adults and chicks has occurred on a portion of the western of the two colonies, which supports c. 18,000 breeding pairs of Thick-billed Murres. The eastern colony has c. 12,000 breeding pairs and is not as accessible as the study colony (Gaston pers. comm.). During periodic trips made each year to the eastern colony since 1985, only 1 banded bird has been seen. All results presented in this thesis were obtained at the western colony.

The colony is on a straight stretch of granite cliff c. 800 m long and 80 m high, with birds breeding densely from a few meters above sea level to grassy turf-covered sites c. 75 m up the cliff. The ledges are step-like, .1 to 1 m in width, interspersed with a few larger ledges up to 3 m wide.

Figure 1.1: Map of Coats Island and the eastern Northwest Territories (filled triangle is location of Thick-billed Murre colony).

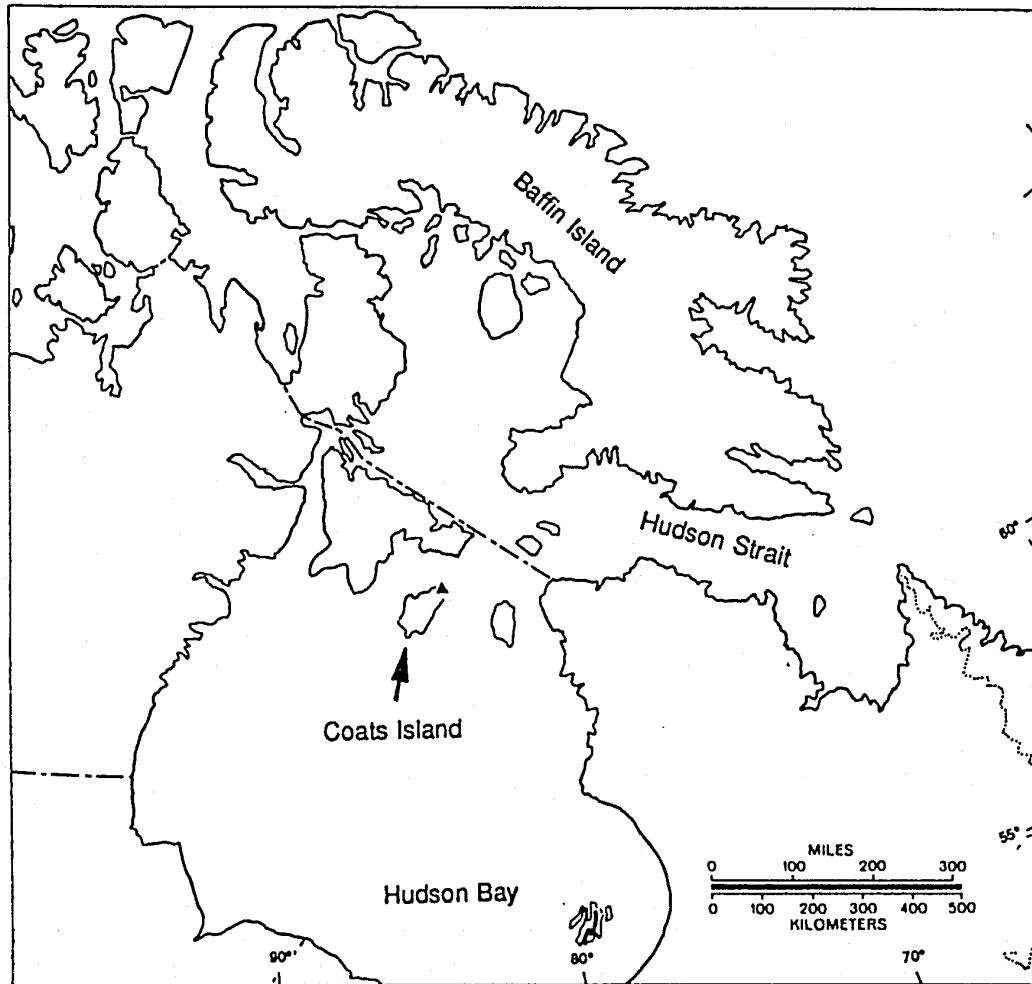
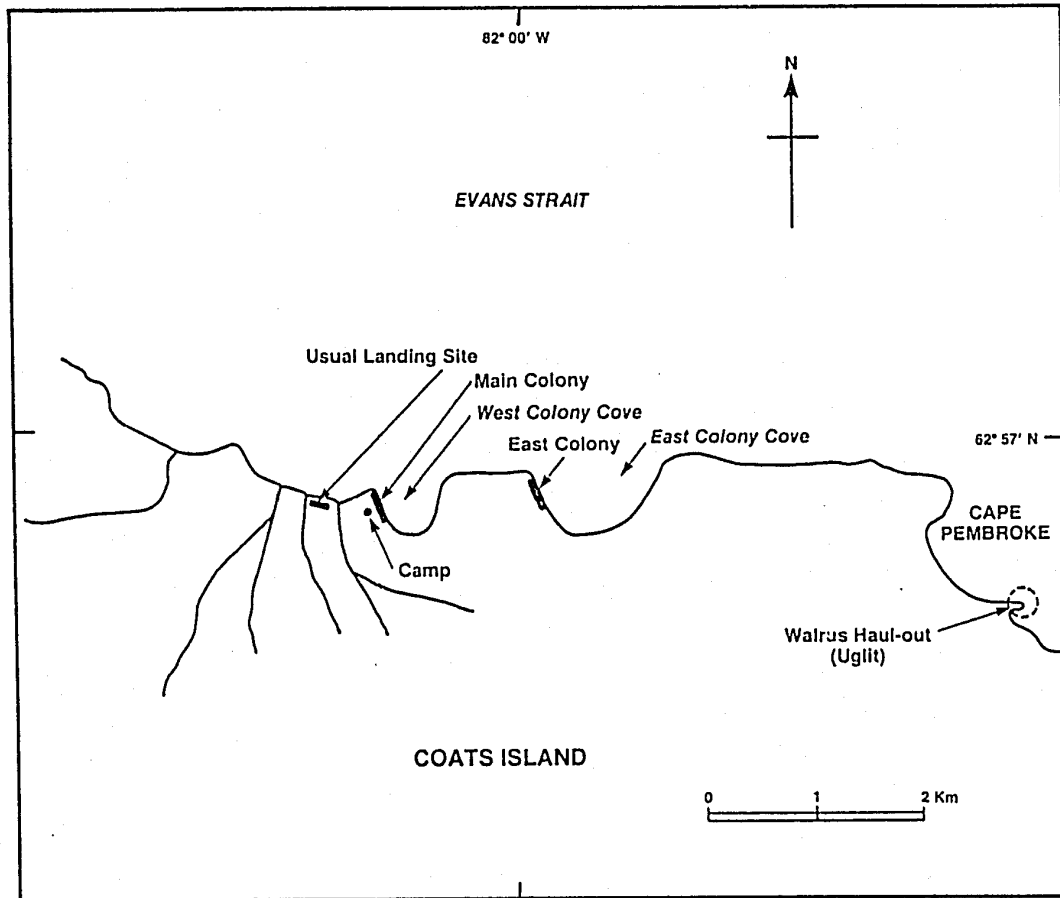


Figure 1.2: Map of main and east Thick-billed Murre colonies on the southeast tip of Coats Island.



STUDY ANIMAL

Thick-billed Murres, Uria lomvia, are colonial cliff nesting alcids found in the arctic and subarctic. They are pursuit divers, feeding on a variety of fish and invertebrates, which tend to be patchy and ephemeral in distribution (Gaston and Noble 1985). Breeders fly up to 150 km from the colony (Nettleship and Gaston 1978, Gaston et al. 1985) and dive as deep as 100 m to capture prey (Croll et al. 1992). Breeding murres lay a single egg on a bare rock ledge, which is incubated for approximately 33 days. If a breeder loses its first egg, it can lay a replacement egg after c. 14 days, although the tendency to relay decreases as the season progresses. Once the chick hatches, it is fed and brooded on the cliff for 14 to 30 days (Gaston and Nettleship 1981). At this time, although the chick cannot yet manage sustained flight, it "fledges" by jumping off the cliff and gliding down to the sea, accompanied by its male parent (Bradstreet 1979, in Harris and Birkhead 1985). The pair begin their journey to the wintering grounds off the coast of Newfoundland, while the female remains on the breeding site for several days, after which time it also departs (Gaston and Nettleship 1981).

The Canadian Wildlife Service has been conducting a long term demographic study on Coats Island since 1984. Between 1,361 and 2,686 chicks have been banded annually. All chicks were banded on the right leg with a metal band and a year coded color darvic band. Only one three-year old bred during the two year study, and only 3 have been observed to breed at this age in previous years (Noble

1990). Consequently most birds breeding at 4 and 5 years of age were probably making their first or second reproductive attempt. For most analyses I combined these two age classes as "young" breeders.

Since 1981, 1,256 breeding adults captured while incubating eggs or brooding chicks have been banded. Adults were banded with the year coded color band on the left leg, and a metal and light green darvic band on the right leg. I assumed that these birds were at least four-years old at date of capture. As I considered birds of at least 7 years of age as older birds, I included in this category any bird banded as a breeder in 1987 or earlier (in 1990) and 1988 or earlier (in 1991). The majority of these birds were almost certainly older than 7 years of age.

Most known age pairs included only one banded bird, which determined the age class given to the pair. Murres are not sexually dimorphic, so birds were sexed by observing copulations in the early part of the season. Not all birds were sexed, hence it was not always known whether the known age bird was the male or the female. Although females determine both the size and the laying date of the egg, most losses occurred during the incubation period (see Chapter 2), when males and females do not differ in the length of incubation shifts (Gaston and Nettleship 1981, Verspoor et al. 1987). Thus both sexes probably had an equal chance of causing the loss. My analyses could be considered to be conservative, as an older female in a pair might reduce the differences between young and older groups.

Two types of metal bands were used to individually mark birds during the course of the study. U.S. Fish and Wildlife Service (USFWS) bands were used for all birds banded in 1984, and for 50% of chicks banded in 1985. The number on these circular bands is inscribed once around the band, making it difficult to read the number completely without capturing the bird. The remaining chicks in 1985 and all birds in the following years were banded with special alcid bands (manufactured by Lambourn, U.K.). These triangular bands have the number inscribed on two sides of the band, making the complete number much easier to read from a distance with a scope or binoculars.

WEATHER PATTERNS

Wind speed, precipitation and temperature were measured daily at 1700 h. Conditions in 1990 were generally colder, wetter and windier than in 1991. During the incubation period, there were winds ≥ 30 km/h on 42% of days in 1990 (N=36), compared to 29% in 1991 (N=34) (Figure 1.3). In 1990, there was some precipitation on 61% of days during this period, but on only 34% of days in 1991. Daily low temperatures were below zero until 21 June in 1990, while temperatures remained above zero beginning on 10 June in 1991 (Figure 1.4). During the incubation period, maximum temperatures were $\geq 10^{\circ}\text{C}$ on 47% of days in 1990, and 74% of days in 1991.

Figure 1.3: Daily wind speed recorded at 1700 h at Coats Island (vertical dashed lines show mean laying and mean hatching dates for the total sample).

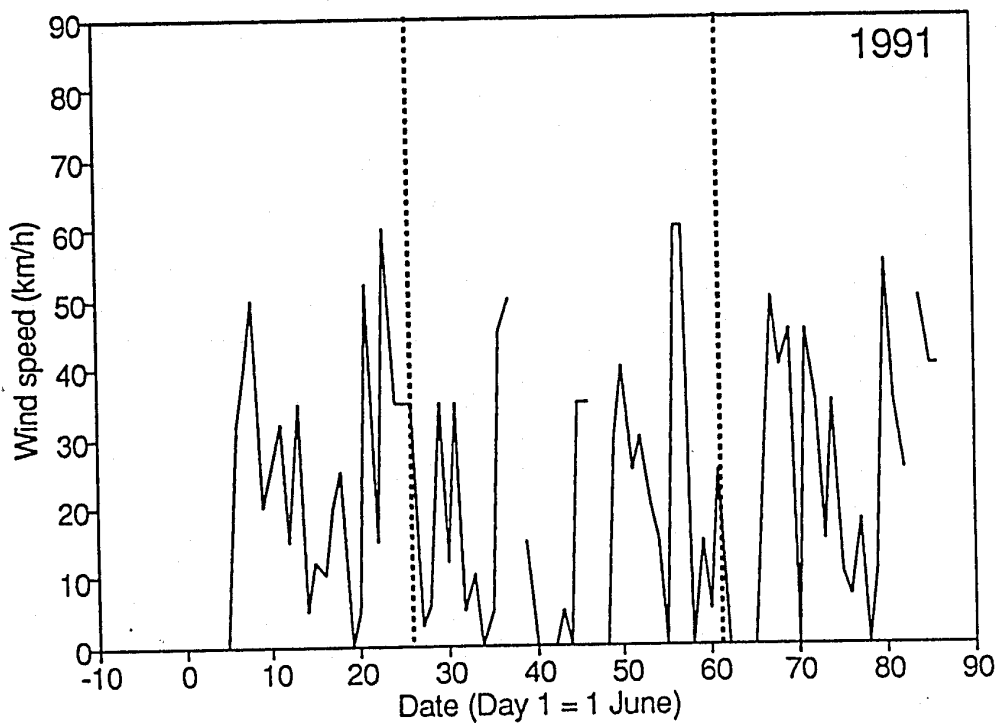
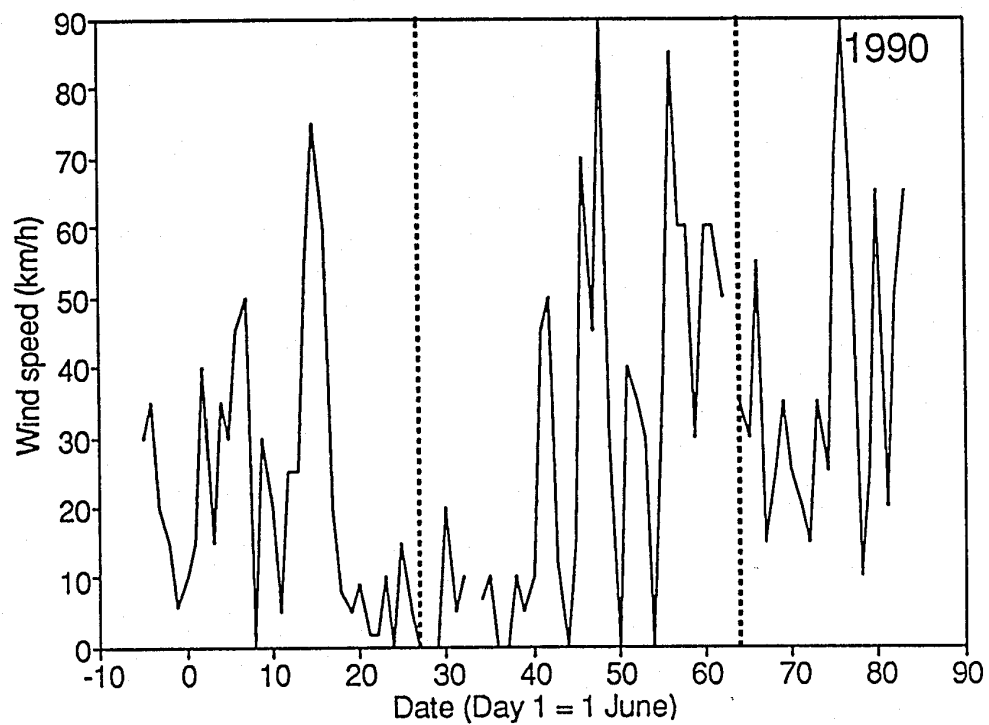
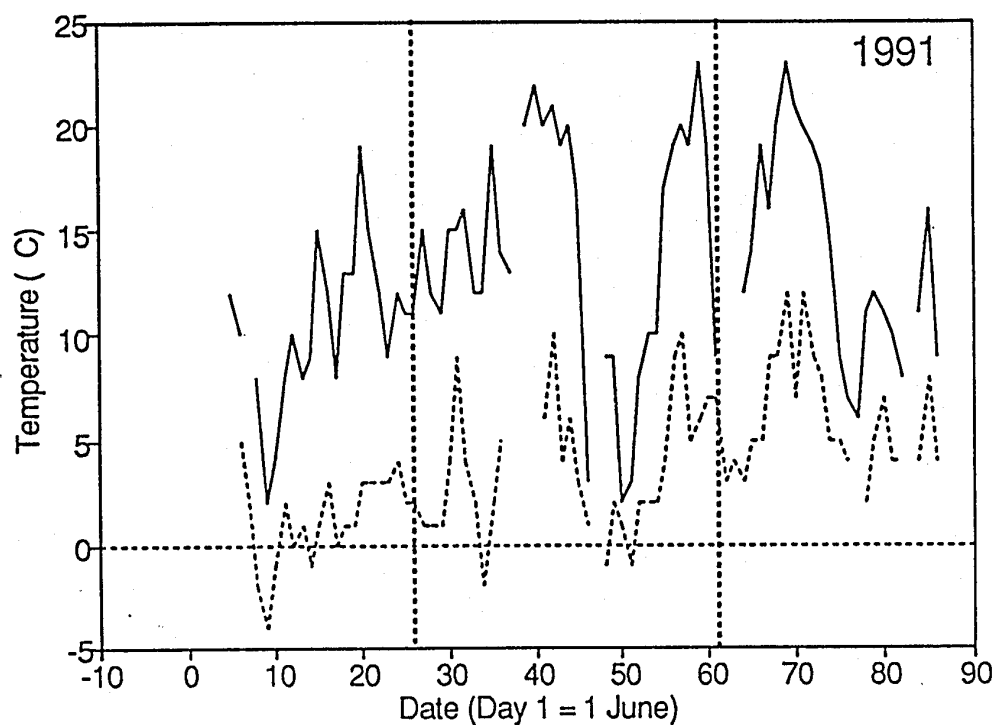
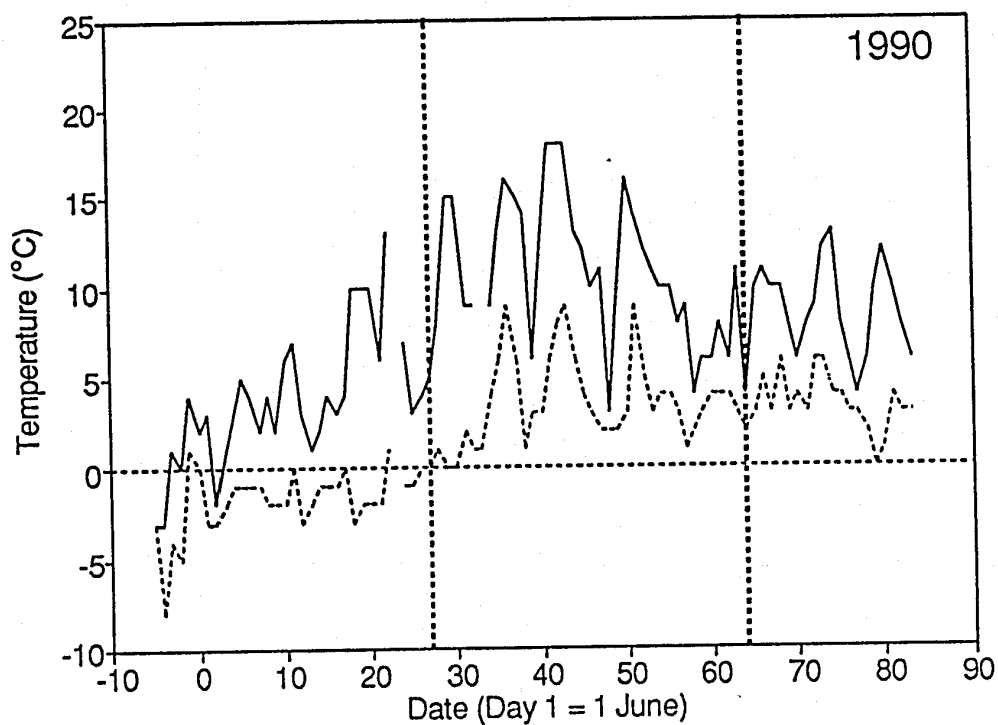


Figure 1.4: Daily maximum (solid line) and minimum (dashed line) air temperature recorded at 1700 h at Coats Island (vertical dashed lines show mean laying and mean hatching dates for the total sample).



**Chapter 2: AGE-RELATED DIFFERENCES IN REPRODUCTIVE PARAMETERS
AND THE SEASONAL DECLINE IN HATCHING AND REPRODUCTIVE SUCCESS**

INTRODUCTION

In many colonially nesting seabirds, older breeders are more successful than younger birds in most reproductive parameters. Almost all studies show that older birds lay earlier than younger birds, and lay both larger clutches and eggs (Coulson and White 1958, Fisher 1975, Weimerskirch 1990; but see Coulson and Horobin 1976). Older birds of species which lay only a single egg also tend to lay larger eggs than younger birds (Gannet, Sula bassana: Nelson 1966, Razorbill, Alca torda: Lloyd 1976, Manx Shearwater, Puffinus puffinus: Brooke 1978, Great Skua, Catharacta skua: Furness 1983). Younger birds often show both reduced hatching (Coulson and White 1958, Lloyd 1976, Croxall et al. 1992) and fledging success (Ainley and Schlatter 1972, Sydeman et al. 1991).

In northern latitudes, the breeding season is limited, with conditions becoming unpredictable as winter approaches. Laying date is often highly synchronized in colonial birds, but not all birds lay during the peak (Gochfeld 1980). A seasonal change in reproductive success is found in many species, with birds laying their egg(s) early and/or during the peak of laying usually being more successful than late layers. Seasonal declines have been found in egg volume (Parsons 1972, Birkhead and Nettleship 1982), clutch size (Parsons 1975), hatching success (Gaston and Nettleship 1981), fledging success (Ainley and Schlatter 1972, Thomas 1983,

Hamer et al. 1991), and age of chicks at fledging (Hedgren and Linnman 1979, Gaston and Nettleship 1981).

In this chapter, I examine differences in reproductive parameters between young and older Thick-billed Murres. I also determine the extent to which seasonal effects on reproductive success are influenced by age.

MATERIALS AND METHODS

GENERAL OBSERVATIONS

1. TOTAL SAMPLE

The total sample was made up of 415 and 361 pairs of Thick-billed Murres, mainly of unknown age, breeding on 5 study plots (Plots D, N, P, Q, and S) in 1990 and 1991 respectively. Plots were selected on the basis of their visibility along the top 50 m of the cliffs within the section of the colony where banding was carried out from 1984 to 1991. Most birds banded as chicks returned to this area (Noble et al. 1991). To determine the reproductive success of all breeding birds, observers viewed each study plot daily for >2 hours from blinds (located 1-20 m from the plots) using binoculars and scopes. We tried to establish laying, hatching and fledging dates, dates of egg and chick loss, and final outcome for each site. These observations did not involve any disturbance of breeding birds.

Minor disturbance caused by experimental removal of some eggs (see Chapter 3) and banding of chicks after most eggs had hatched did not seriously affect the reproductive outcomes on the plots.

Those sites where eggs or very young chicks were lost because of such disturbance (N=7 in each year) were omitted from the analyses. There were 12 chicks in 1990 and 2 chicks in 1991 which were lost but classified as having successfully fledged, as they had reached fledging age. Eggs removed for experimental purposes were included in data on the laying dates of first eggs, length of time taken to relay, and incubation periods (of replacement eggs), but were excluded from analyses of reproductive outcome.

2. KNOWN AGE BREEDERS

Fifty-seven (in 1990) and 72 (in 1991) birds banded as chicks bred on the study plots, ranging in age from three to seven years. There were also 112 and 91 older birds (> 7 years of age) breeding on the study plots in 1990 and 1991, respectively (Table 2.1). Two year olds began arriving in early July after 93% of the breeding plot sample had laid, and were never recorded attempting to breed. I assumed that four-year old birds seen breeding in 1990 were doing so for the first time. It is possible that more three-year olds attempted to breed in both years but lost their eggs before being observed.

Not all banded birds were equally useful for examining the success of individuals in successive years. The USFWS bands could only be read with difficulty making the chances of identifying an individual rather low if it had changed sites in successive years. Moreover, because the birds carrying the special triangular bands could be identified rapidly, more were recorded on loafing areas, increasing the total number identified on a given area and reducing

the apparent proportion breeding. When considering the proportions of a given cohort breeding in a particular year I used only data from birds banded with triangular bands; half of the chicks and all the adults banded in 1985 and all birds banded thereafter.

When calculating proportions of known age birds breeding on the study plots, bands of any known age birds seen on plots had to be read at least twice to be included. This was to minimize the possibility of including incorrectly read band numbers due to observer error.

Numbers were read from any visible bands during daily nest checks and scheduled periods of intensive band reading. Special efforts were made to read the band numbers of birds breeding on the study plots and a few birds whose bands could not be read from a distance were captured near the end of the season to verify their band number. Banded birds were considered to have attempted breeding if they were seen incubating an egg or brooding or feeding a chick. A few that attempted to breed but lost an egg soon after laying may not have been recorded as breeders.

Most banded birds were mated to unbanded birds, but there were 17 sites over the 2 years where both members of the pair were banded, and at least one bird was of known age. When assigning these pairs to an age class the age of the younger member was used.

Exact laying, hatching and fledging dates and reproductive outcomes were not known for all sites, thus sample sizes often differ for various analyses of the same groups of birds.

Table 2.1: Total numbers of banded birds breeding on the study plots in 1990 and 1991, including both members of double banded pairs.

Age*	1990	1991
3	0	1
4	13	11
5	27	25
6	17	21
7	0	15
Known age	57	72
Older	112	91
Total	169	163

* Birds age 3 to 7 were banded as chicks, "older" birds were banded as adults and were least 7 years of age.

LAYING DATES

1. TOTAL SAMPLE

Most laying dates were recorded to within 24 h. Observations of a freshly laid egg or newly hatched chick are often difficult, so all dates known to within 72 h were included in the analyses. The event was assumed to have occurred on the first day of that period. Differences in laying dates were analyzed using ANOVA and SNK (Student-Newman-Keuls) test for multiple comparisons. Mean laying dates of first eggs on the 5 plots differed in 1990 (ANOVA: $F_{4,337}=3.46$, $P<0.01$), but not in 1991 (ANOVA: $F_{4,321}=1.79$, NS) (Table 2.2). In 1990, only Plots Q and S were significantly different from one another by c. 3 days (SNK test: $P<0.05$). As mean laying dates were fairly similar and the timing of different plots was not consistent between years, all plots were combined by year for further analyses.

Table 2.2: Mean laying dates of first eggs on 5 study plots (Day 1 = 1 June).

Year	Plot	N	Mean	SD	Median	Range
1990	Q	48	25.4	5.9	24.5	15-44
	D	89	26.1	6.0	25	17-59
	N	42	26.7	3.2	26	22-34
	P	91	27.5	5.9	26	19-53
	S	72	28.7	5.7	27	19-43
	Total	342	27.0	5.7	26	15-59
1991	Q	57	25.9	6.0	25	15-47
	D	121	24.9	3.9	24	18-38
	N	63	26.1	4.8	25	18-44
	P	29	27.3	5.6	27	19-45
	S	56	25.9	5.2	25	17-52
	Total	213	25.7	4.9	25	15-52

2. KNOWN AGE BREEDERS

Laying dates of four and five-year old birds did not differ in either year (SNK: $P > 0.05$, NS), so were grouped together as "young" breeders. "Older" breeders were those birds which were banded as adults (see Chapter 1). In 1991, the laying dates of 3 six-year olds and 3 older birds were excluded, as they were considered to be relays of first eggs that were lost before they had been recorded. In all 6 cases, the eggs were laid from 14 to 17 days later than the mean for that age class, and from 7 to 10 days after the last egg laid for that age class.

3. LAYING DATES OF KNOWN AGE BREEDERS BETWEEN YEARS

Murres are highly philopatric, with banded birds returning to the general area from which they fledged (Noble et al. 1991), as well as breeding on the same site from year to year. The vantage point from the blinds made most areas of the study plots visible to the observer, so a bird would have to move several meters to be out of view. Hence, if they were not seen near their previous site they probably did not breed in that year. I considered a bird to be absent in a given year if the band number was not read and present if the band number was recorded at least twice during the breeding season. Returning breeders may have been underestimated, as those seen near their old site but not considered to have laid in 1991 may have bred but lost their egg before it was observed.

The laying dates of breeders compared within a given year were not transformed. When comparing individual pairs between years,

laying dates were standardized to correct for annual differences of means and standard deviations, with day 1 = 1 June.

laying date - mean laying date

SD_{LAY}

A difference of one day was ± 0.18 in 1990 and ± 0.20 in 1991. A standardized laying date of zero indicates an egg laid on the mean laying date, with a positive date for later eggs and a negative date for earlier eggs. When comparing laying dates between years ($LD_{1990} - LD_{1991}$), the closer the mean difference is to zero, the more consistent the laying dates are between years. A positive difference indicates an earlier laying date in 1991. Differences between years were analyzed using paired t-tests.

EGG SIZE

Egg volume index (length x breadth²) of eggs of several known age breeders was measured in both 1990 and 1991. Gaston and Nettleship (1981) used this index to compare egg size within a population of Thick-billed Murres. There is no evidence that egg shape varies with age (pers. obs.). Comparisons of egg size were made using t-tests. Paired t-tests were used when comparing eggs laid by the same pair in successive years.

EGG LOSS AND REPLACEMENT EGGS

Incubation periods were c. 33 days in both years (see below), therefore egg losses were separated into those lost on or before 33 days, and those lost after 33 days. There were 23 sites in 1990

and 5 sites in 1991 where I could not determine whether the egg had hatched before loss. I recorded these as lost as eggs although in some cases a chick may have hatched and died shortly after. Consequently, hatching success may have been underestimated, and fledging success overestimated correspondingly. The proportion of chicks fledging of eggs laid was not affected.

The length of time elapsing between the loss of an egg and its replacement was calculated by subtracting the laying date of the replacement egg (known to within 48 h) from the date of loss of the first egg. The probability of laying a replacement egg was calculated using only those eggs which were lost prior to 33 days of incubation.

INCUBATION AND FLEDGING PERIODS

Incubation periods were calculated by subtracting the date of hatching from the date of laying, and fledging periods by subtracting the hatching date from the fledging date. A chick was considered to have fledged successfully if it was at least 14 days of age on the day of disappearance. Most chicks fledged in the evening (Harris & Birkhead 1985), hence, if a chick was not present at its site in the morning, the fledging date was taken as the previous day. Successful fledgings may have been slightly overestimated as some disappearances at ages of more than 15 days were probably caused by predation.

Incubation and fledging periods were calculated only for sites where both laying and hatching dates were known to within 72 h.

Sample sizes for incubation and fledging periods were larger in 1991, as more effort was put into establishing hatching dates in that year.

In 1990 there were 41 chicks and in 1991 there were 18 chicks which had not yet fledged at the time of our departure (not including experimental chicks - see Chapter 3). Of these, 33 and 12 were ≥ 14 days of age in 1990 and 1991, respectively, and would have been classified as 'fledged' in any case. The remaining 8 and 6 chicks which were > 5 days old were considered to have fledged successfully because survival from hatching was generally high and did not show a seasonal decline (see below). One chick which hatched on the day of our departure in 1991 was omitted from the analyses.

FORAGING SHIFTS DURING INCUBATION

Both young and older birds on several plots were observed hourly from 2-5 July 1991 to determine the duration of foraging trips during incubation. Banded birds and their mates were marked the day before to facilitate identification. A non-toxic felt marker mounted on a pole was used to individually mark the birds without capturing them. Only the first foraging trip made by each known age bird during the observation period was considered because some birds did not complete more than one trip.

REPRODUCTIVE OUTCOME

One of 5 possible reproductive outcomes was recorded for each site:

- 1) an egg was laid but lost before hatching and not replaced;
- 2) both the first and replacement eggs were lost;
- 3) the first egg hatched, but the chick was lost before fledging;
- 4) a replacement egg hatched, but the chick was lost before fledging;
- 5) a chick was reared successfully to fledging.

Hatching success was defined as the proportion of pairs which succeeded in hatching an egg, fledging success as the proportion of chicks hatched that successfully fledged (left the cliffs), and reproductive success as the proportion of pairs which laid an egg that successfully fledged a chick. χ^2 was used to analyze differences in reproductive outcome.

SEASONAL DECLINE

Logistic regression was used to determine if there was a seasonal trend in hatching, fledging and reproductive success. Logistic regression helps explain variation in a binary response variable (i.e. a chick hatches or does not hatch, fledges or does not fledge) to a discrete or continuous explanatory variable (i.e. date of laying) (Chatfield and Collins 1980). As there are only two possible outcomes, data points can only be entered as a success or a failure.

The logistic transformation of p , the probability of success:

$$\ln(p/(1-p))$$

is known as the logit for a given p value. The logits of probabilities which range from 0 to 1 now range in value from negative to positive infinity, forming a linear model, analogous to regular regression models (Chatfield and Collins 1980).

CATMOD (CATegorical data MODelling) fits linear models to functions of response frequencies using maximum likelihood estimation of parameters (SAS Institute Inc. 1985). This procedure gives more weight to those proportions with larger sample sizes, and by computer iteration, fits the best model to the logits of the observed points. A maximum likelihood ANOVA table uses χ^2 to test whether the line produced is significantly different from a line with slope and intercept of zero.

A log-likelihood ratio is used as a statistic to measure agreement between observed and expected frequencies (Sokal and Rohlf 1981).

$$L = p_{\text{exp}}/p_{\text{obs}}$$

If the proportions are the same, the probabilities, or likelihoods, will be equal and the ratio will equal 1. The log-likelihood ratio test for goodness of fit is approximated by the χ^2 distribution and determines how likely it is that the model fits the observed data.

To calculate the effect of date on breeding success, all sites where both laying dates of first eggs and reproductive outcome were known were included in the analyses. Separate analyses were performed for the total sample (all birds on the 5 study plots),

for young and older birds (separately and together), and for the total sample excluding young and older birds. In the cases (8 of 30) where the data did not fit the model generated by the computer, the data were reanalyzed by 3-day intervals and rerun. In 6 of the 8 cases, the model fit the reanalyzed data (see Appendix 1).

EXPERIMENTAL BREEDERS

Eggs were removed from a sample of pairs in 1990 and 1991 including some older birds (see Chapter 3). It was possible that the 1990 manipulations may have affected the success of those experimental birds breeding in 1991. Of 21 experimental older birds in 1990, 14 returned and bred and 7 did not breed in 1991 (although 3 of these were seen in 1991). This rate of return was comparable to 51 non-experimental older birds on the same plots (D, Q and S), with 33 returning to breed, and 18 not breeding in 1991 (4 of these 18 birds were seen in 1991) ($\chi^2=0.03$, $P>.50$). The laying dates in 1991 of experimental birds which returned ($N=12$) were not significantly different from those of older birds which were not experimentally manipulated in 1990 and returned to breed ($N=36$) ($t=0.65$, $P>.50$). The 1990 experimental birds which bred in both years showed little difference between years in mean laying dates (Paired t-test: $t=-1.35$, $P>.05$, NS) and were therefore included in laying date analyses in 1991. Experimental birds were left out of any calculations of reproductive outcome for the year which they had their eggs removed, but 1990 experimental birds were included in the calculations of outcomes for 1991. All

experimental breeders in a given year were excluded from seasonal decline data for that year.

In all analyses in this and following chapters (except for the logistic regression in Chapter 4), I selected a significance level of 0.05.

RESULTS

PROPORTIONS OF KNOWN AGE BIRDS BREEDING

Age of first breeding in Thick-billed Murres appears to be quite variable, with large proportions of younger cohorts not breeding (Table 2.3). The proportion of birds breeding, among those recorded on the study plots, tended to increase with age.

SEXES OF KNOWN AGE PAIRS

Of 17 pairs with both members banded and at least one bird which was banded as a chick, the female was younger in 8 pairs, the male was younger in 4 pairs, the mates were the same age in 4 pairs, and sexes were unknown in the remaining pair.

LAYING DATES OF FIRST EGGS

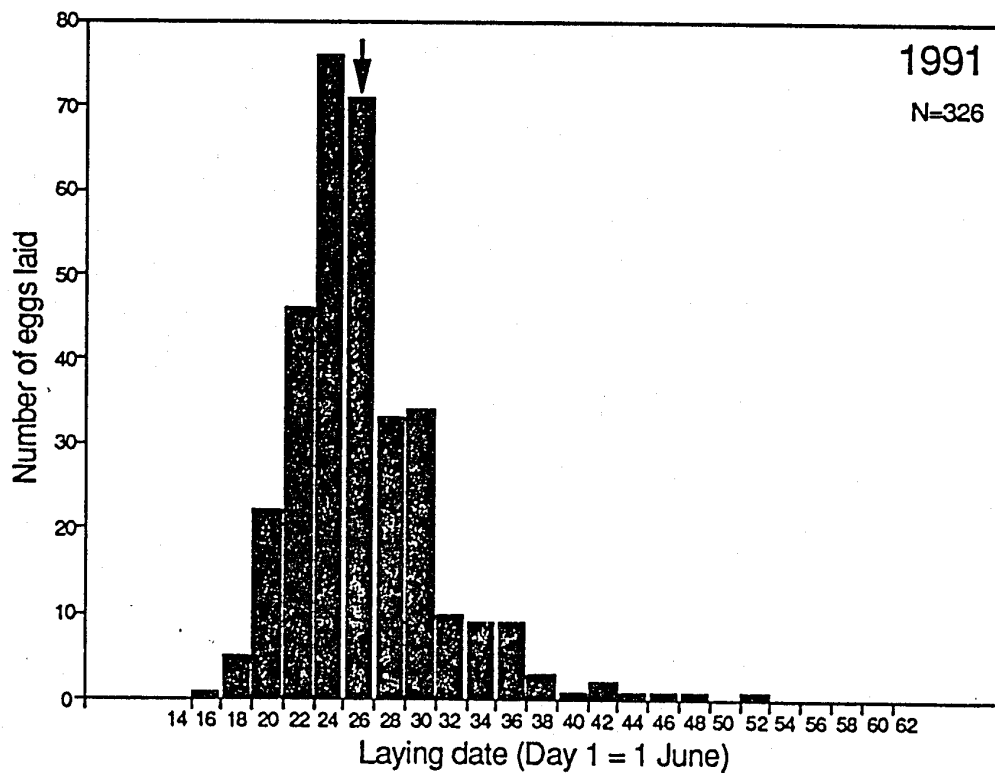
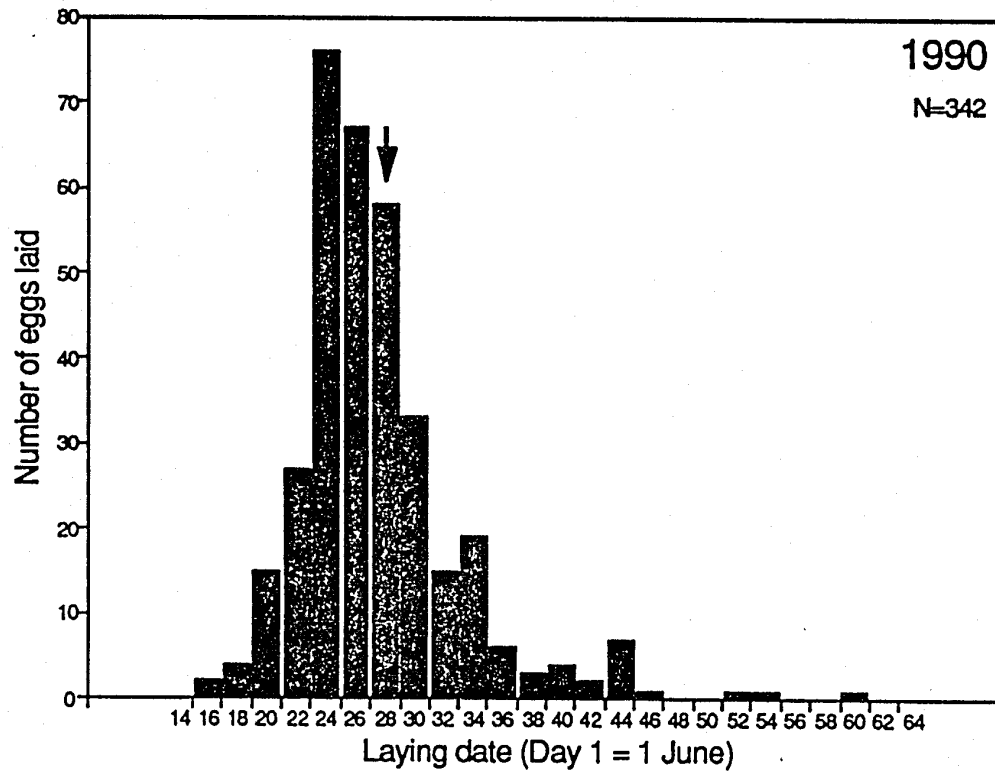
1. TOTAL SAMPLE

Mean laying dates for the colony differed significantly between years: 27 June \pm 5.7 in 1990 (N=342) and 26 June \pm 4.9 in 1991 (N=326) ($t=3.17$, $P<.005$). Laying dates of first eggs were right skewed in both years, with a few early eggs, the middle 80% of eggs laid over c. 13 days, and a tail of less synchronized late eggs (Figure 2.1).

Table 2.3: Proportions of known age birds breeding in 1990 and 1991; triangular bands only (N=numbers of individuals seen at least twice on breeding plots).

Age	1990		1991	
	# breeding on plots	% breeding on plots (N)	# breeding on plots	% breeding on plots (N)
2	0	0 (97)	0	0 (57)
3	0	0 (60)	1	0.9 (116)
4	13	22.8 (57)	11	11.7 (94)
5	7	21.2 (33)	25	24.0 (104)
6	17	NA	10	21.7 (46)
7			15	NA

Figure 2.1: Pattern of laying of first eggs at Coats Island (total sample, arrow indicates mean laying date).



2. KNOWN AGE BREEDERS

In both years, older birds laid 5 to 7 days earlier than young birds (Table 2.4), with each successive age class having an earlier mean laying date. In 1990, six-year olds and older birds laid significantly earlier than young birds (ANOVA: $F_{2,116}=23.74$, $P=.0001$; SNK: $P<0.05$). In 1991, older birds laid significantly earlier than all younger birds (ANOVA: $F_{3,114}=17.42$, $P=0.0001$; SNK: $P<0.05$). Laying dates of six-year olds did not differ significantly from those of young birds or seven-year olds in 1991 (SNK: $P>0.05$, NS, Figure 2.2). The one three-year old female which bred with a five-year old male laid on 22 July. They were the fifth last pair recorded laying a first egg.

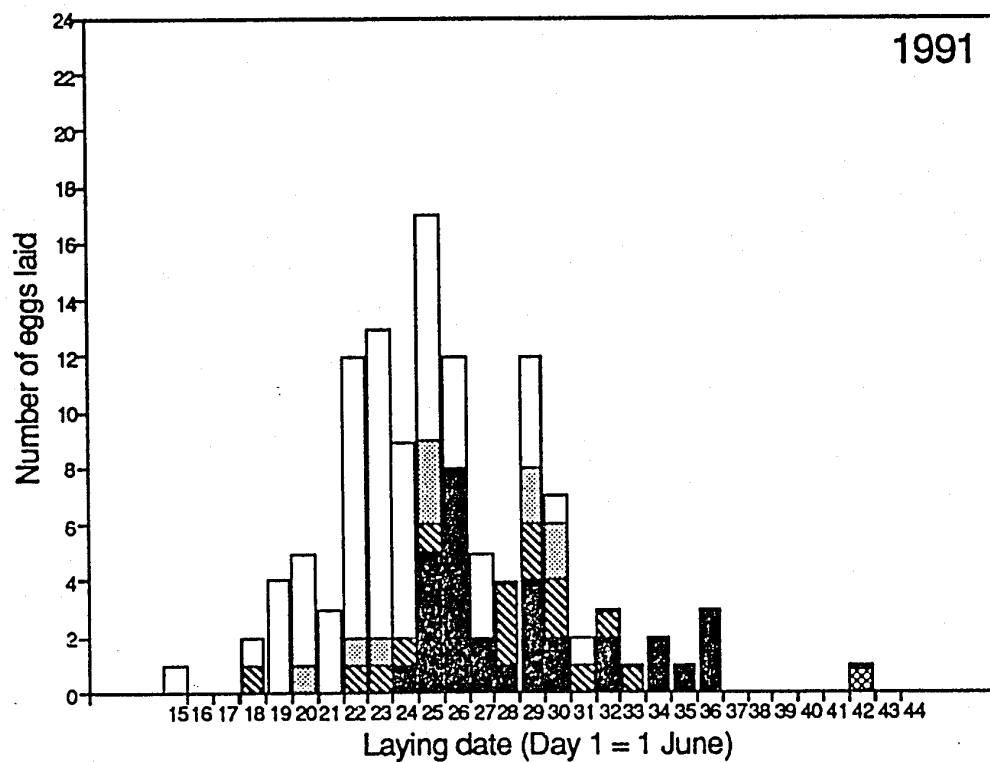
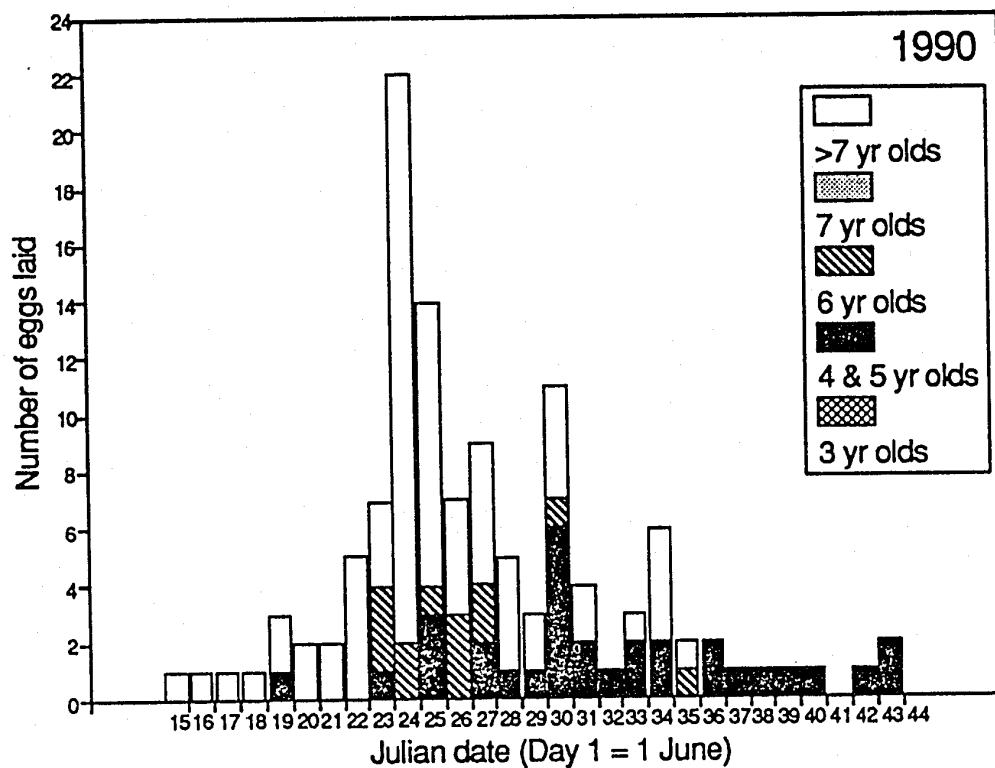
During the first 10 days of the laying period (day 15 to 24), older birds laid c. 84% of all known age eggs, while young birds laid < 5% for that period. Conversely, during the last 10 days of the laying period (day 35 to 44), older birds laid <10% of eggs, while young birds laid >80% (Figure 2.2).

Table 2.4: Mean laying dates (\pm SD) of first eggs of known age birds (Day 1 = 1 June).

Age	1990		1991	
	Laying date	N	Laying date	N
3			42.0	1
4	33.0 (5.80)	11	29.4 (3.72)	11
5	31.4 (6.07)	20	28.4 (3.91)	20
Young*	31.9 (5.93)	31	28.7 (3.81)	31
6	26.1 (3.35)	13	27.3 (4.13)	15
7			25.8 (3.55)	10
Older	25.2 (4.15)	75	23.5 (3.08)	62

* Young = four and five-year old breeders

Figure 2.2: Pattern of laying of known age breeders (Age conventions same for both years).



3. COMPARISON OF LAYING DATES FOR INDIVIDUAL KNOWN AGE BREEDERS BETWEEN YEARS.

In 1991, 17 of 25 (68%) five-year old birds were not known to have bred previously, and the remaining 8 (32%) had at least one year of breeding experience (Table 2.5). The mean laying date of second time breeders (25.7 June \pm 1.0 (N=6)) was significantly earlier than that of first time breeders (29.0 June \pm 3.9 (N=12)) (t=2.70, NS). Likewise in 1991, 60% (6 of 10) of six-year olds that bred had not been observed to do so in the previous year. However, some of the six-year olds could have bred in 1989 as four-year olds and then skipped breeding in the following year.

Comparing the laying dates in 1990 and 1991 of pairs with birds of known age that bred in both years, I found that those of the 1986 cohort (four-year olds in 1990) advanced their mean date of laying by c. 6 days, with all pairs laying earlier in 1991, relative to the mean date, than in 1990 (Table 2.6). The difference for all older age classes was less than one day and not significant.

In 1990, 18 pairs in which both birds were banded consisted of two older birds. Of these, seven pairs bred together again in 1991 and 11 birds had unbanded mates. No cases were observed where both members of a 1990 pair were mated to different birds in 1991. Pairs which bred together in both years showed a great similarity in laying dates (mean difference 0.01 \pm 0.55 SDs), whereas laying dates for birds that changed mates differed by 0.38 \pm 0.83 SDs. Although the difference is not significant (t=1.04, NS), the result

suggests that laying date is likely to be more constant from year to year for pairs which stay together. There was no evidence that it made any difference whether it was the male (mean difference: -0.29 ± 0.91 , $N=6$) or the female (mean difference: -0.40 ± 0.76 , $N=6$) of the pair that returned to breed.

Table 2.5: Proportions of known age birds breeding in both years, and in 1991 only (birds with triangular bands only).

Age in 1991	Birds breeding in 1991	Bred in 1990 and 1991	Bred in 1991 only	% breeding in 1991 only
3	0	0	1	100
4	11	0	11	100
5	25	8	17	68.0
6	10	4	6	60.0

Table 2.6: Change in laying date of individual known age birds from 1990 to 1991 (for standardized mean laying dates (\pm SE) see text).

Cohort	N	Age 1990	Laying date 1990	Age 1991	Laying date 1991	Difference	Paired t-test	P
1986	5	4	1.16 (0.52)	5	-0.08 (0.10)	1.24 (0.47)	2.65	0.057 NS
1985	9	5	0.66 (0.38)	6	0.63 (0.23)	0.02 (0.47)	-0.63	>0.50 NS
1984	6	6	0.00 (0.36)	7	0.03 (0.23)	-0.03 (0.30)	-0.11	>0.50 NS
Older	38	>7	-0.45 (0.11)	>7	-0.34 (0.14)	-0.11 (0.16)	-0.71	>0.25 NS

4. KNOWN AGE BIRDS NOT RETURNING TO BREED IN 1991

Of known age birds breeding in 1990, c. 50% did not return to breed in 1991. There were no differences in 1990 laying dates for four, five, and six-year olds which returned and those which did not return to breed in 1991 (all $t < 0.83$, NS, Table 2.7).

EGG SIZE

1. KNOWN AGE BREEDERS

Egg volume indices of older birds averaged c. 13.6% and 11.7% larger in 1990 and 1991 than the eggs of young birds (Table 2.8). In 1990, 3 of the 5 smallest eggs measured were laid by young breeders (4 out of 5 in 1991).

Table 2.7: Comparisons of 1990 laying dates of known age birds which bred only in 1990, and those which bred in both 1990 and 1991 (mean (\pm SD)).

Cohort	Bred in 1990 and 1991	Bred in 1990 only	t	P
1986 N	33.2 (6.0) 6	32.8 (6.2) 5	-0.10	>0.05 NS
1985 N	31.9 (6.9) 11	30.8 (5.6) 8	-0.39	>0.05 NS
1984 N	27.0 (4.7) 6	28.2 (8.9) 5	0.29	>0.05 NS
Older N	25.2 (4.5) 35	26.2 (4.4) 22	0.83	>0.05 NS

Table 2.8: Differences in egg volume indices (cm³) of known age breeders (mean (\pm SD)).

Year	Egg volume		T-test	P
	Young	Older		
1990	189.3 (12.8)	219.1 (17.5)	-2.67	<.05
N	3	9		*
1991	182.7 (19.0)	207.0 (15.8)	-3.94	<.0005
N	9	34		**

EGG LOSS AND REPLACEMENT EGGS

1. TOTAL SAMPLE

First eggs were lost at 36% (151 of 415) and 32% (115 of 361) of all sites laying eggs in 1990 and 1991, respectively. Approximately 7% of all first eggs laid were incubated past 33 days and did not hatch in each year. Of birds which lost their egg before 34 days of incubation, 50% were lost in the first 6 days of incubation in 1990 and first 8 days in 1991 (Figure 2.3). The number of eggs lost on the day of laying (days to loss = 0) was probably underestimated as some eggs could have been lost before they were observed. Several cases of eggs being lost within the first few hours after laying were observed in both years and in 1990, 2 birds were observed stealing a freshly laid egg from their neighbour (Gaston et al. in press, Chapter 3).

Pairs that lost their first eggs laid a replacement in 25% (N=151) of cases in 1990 and 24% (N=115) of cases in 1991. The mean time between loss and replacement of an egg was slightly but not significantly shorter in 1990 than in 1991 ($X_{1990}=12.9\pm 2.8$ days (N=28); $X_{1991}=14.0\pm 2.4$ (N=20); $t=-1.39$, NS).

The proportion of pairs laying replacement eggs declined sharply as the season progressed (Figure 2.4). Eggs lost at the mean laying date had approximately a 50% chance of being relaid in both years, dropping to zero after 10 July (day 40).

Figure 2.3: Time elapsed between laying and loss for eggs lost ≤ 33 days after laying.

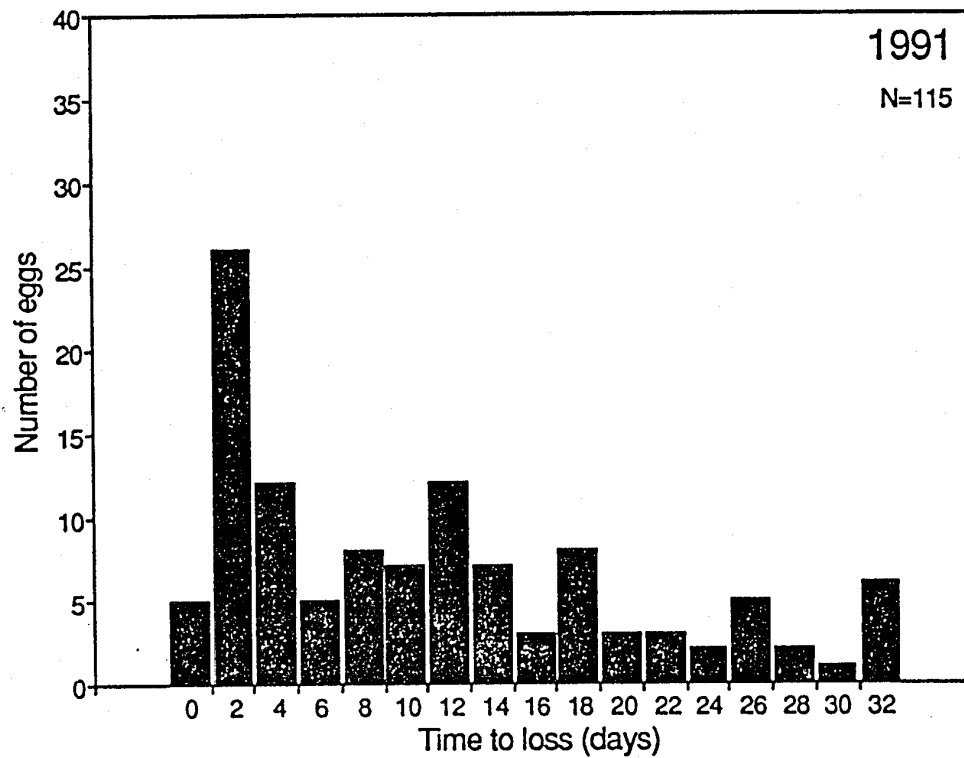
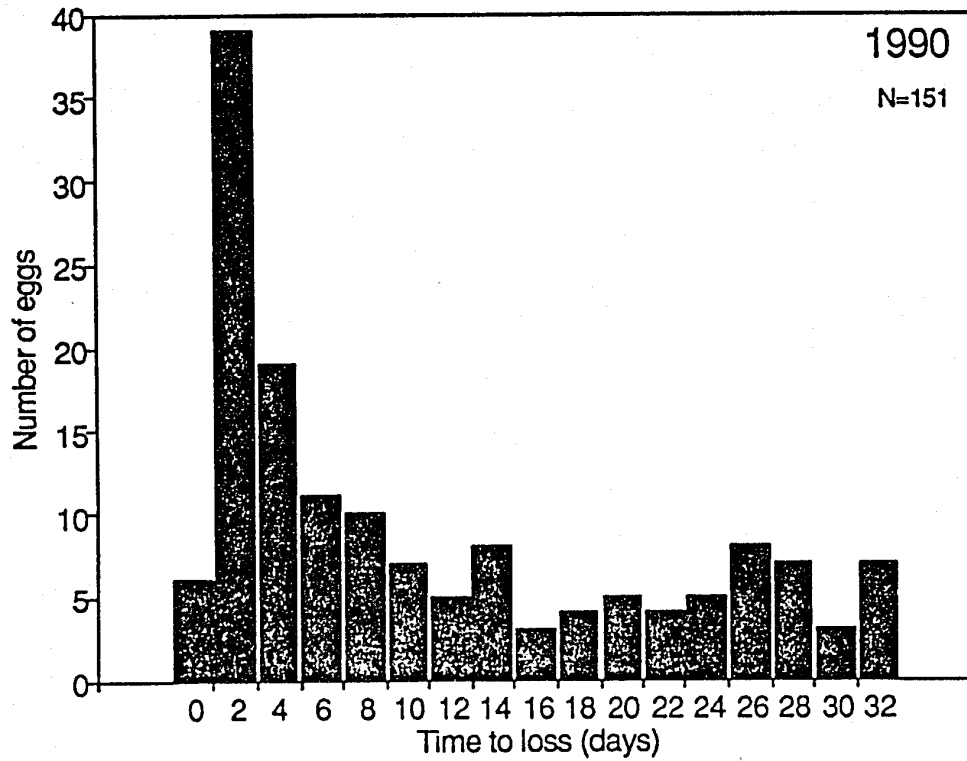
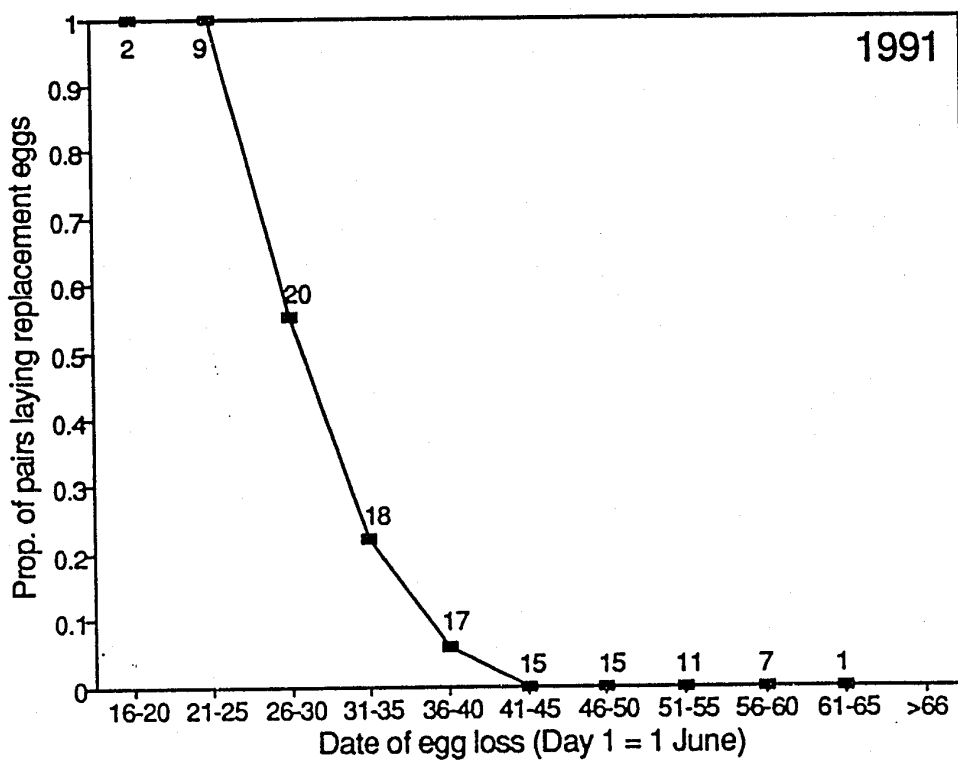
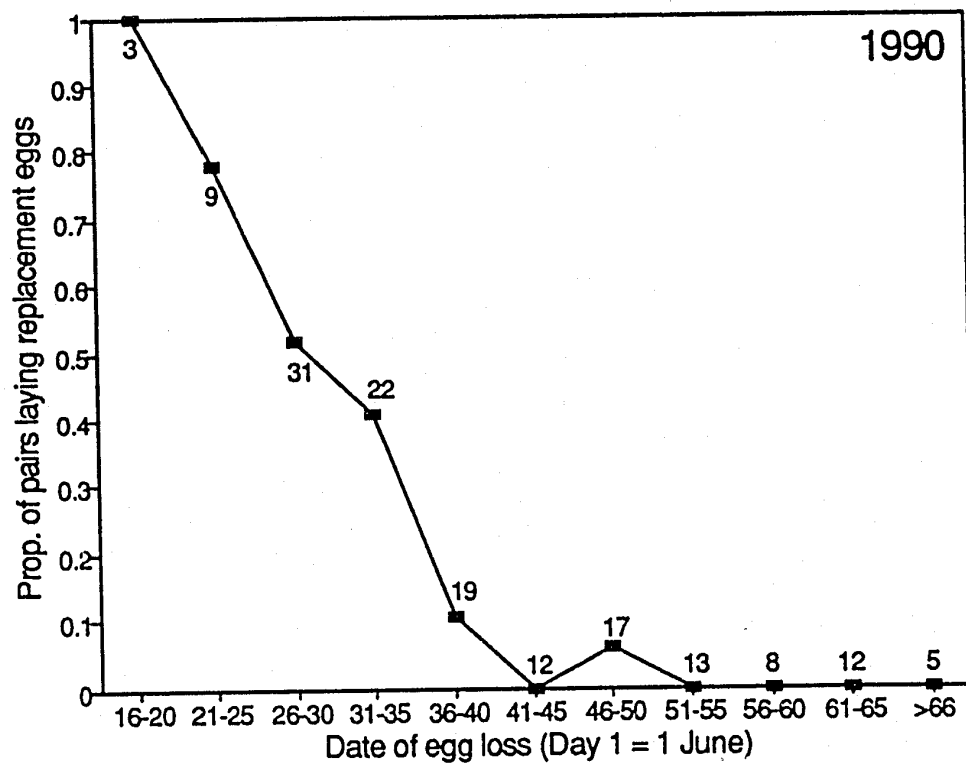


Figure 2.4: Proportion of pairs laying a replacement egg in relation to the date of loss of the first egg (numbers indicate sample sizes).



2. KNOWN AGE BREEDERS

Young birds were significantly more likely to lose their first eggs and tended to lay a replacement egg less often than older birds in both years (Table 2.9). In 1991, when weather conditions during the incubation period were markedly better than in the previous year (see Chapter 1), both young and older birds lost fewer eggs than in 1990 ($\chi^2_{\text{young}}=5.43$, $P<0.02$; $\chi^2_{\text{older}}=4.48$, $P<0.05$), while proportions relaying did not differ between years (both $\chi^2<0.50$, $P>0.50$). When replacement eggs for both years were combined, older birds laid significantly more replacements than young birds ($\chi^2=3.87$, $P<0.05$).

Young birds tended to take longer to relay in both years (1990: $t=2.24$, $P=0.05$; 1991: $t=1.45$, NS) (Table 2.10, Figure 2.5). Time to relay a replacement egg tended to be more variable in young birds, but this was not significant in either year (Levene's test: both years $F<3.33$, NS).

Both young and older breeders lost a high proportion of eggs within the first 10 days after laying, although both groups continued to lose their eggs throughout the season (Figure 2.6). Young birds were no more likely than older birds to lose their eggs soon after laying, but older birds, because they laid earlier, had a greater chance of laying a replacement egg (Figure 2.4).

Table 2.9: Egg loss by young and older birds and the proportion of birds laying a replacement egg (sample sizes given in parentheses).

	Year	Young	Older	Chi-sq	P
Egg lost	1990	86.1% (31/36)	31.3% (21/67)	28.1	<.0001 **
Egg relaid	1990	19.4% (6/31)	33.3% (7/21)	1.31	>.05 NS
Egg lost	1991	61.8% (21/34)	15.3% (9/59)	21.4	<.0001 **
Egg relaid	1991	14.3% (3/21)	44.4% (4/9)	Fisher Exact	>.05 NS

Table 2.10: Mean time to lay a replacement egg (\pm SD) and coefficients of variation (CV) for young and older breeders.

Year	Days to relay				T-test	P
	Young	CV	Older	CV		
1990 N	14.8 (3.0) 6	20	11.8 (1.3) 6	11	2.24	=0.05 NS
1991 N	18.0 (5.0) 3	28	13.8 (1.0) 4	7	1.45	>0.05 NS

Figure 2.5: Time elapsed between the loss of an egg and the laying of a replacement for young and older birds.

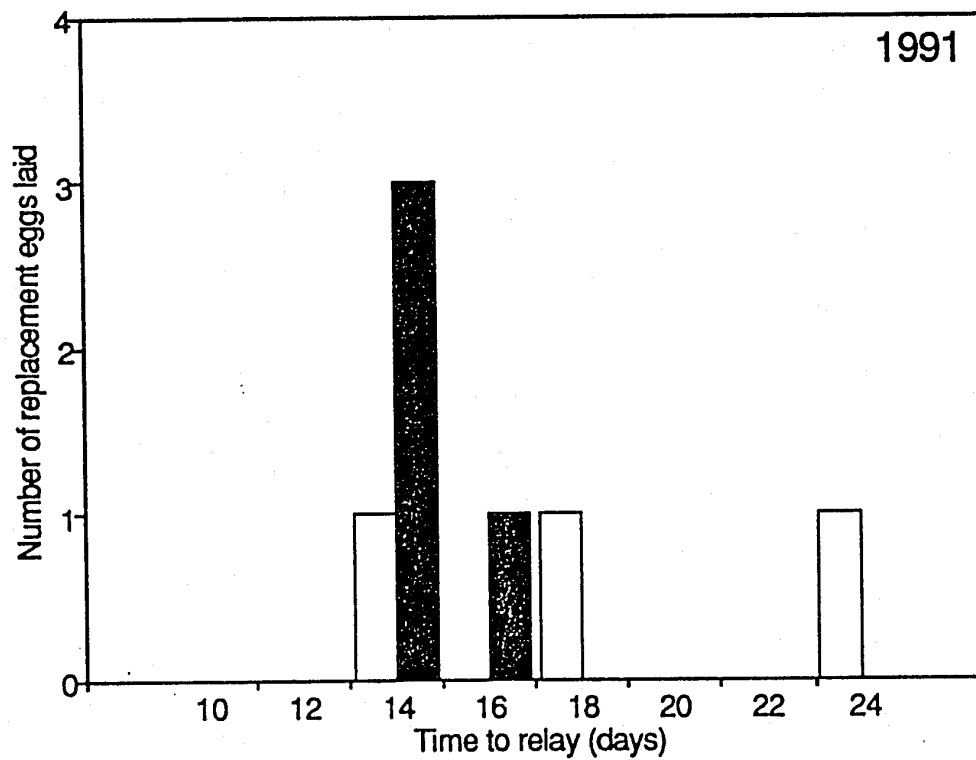
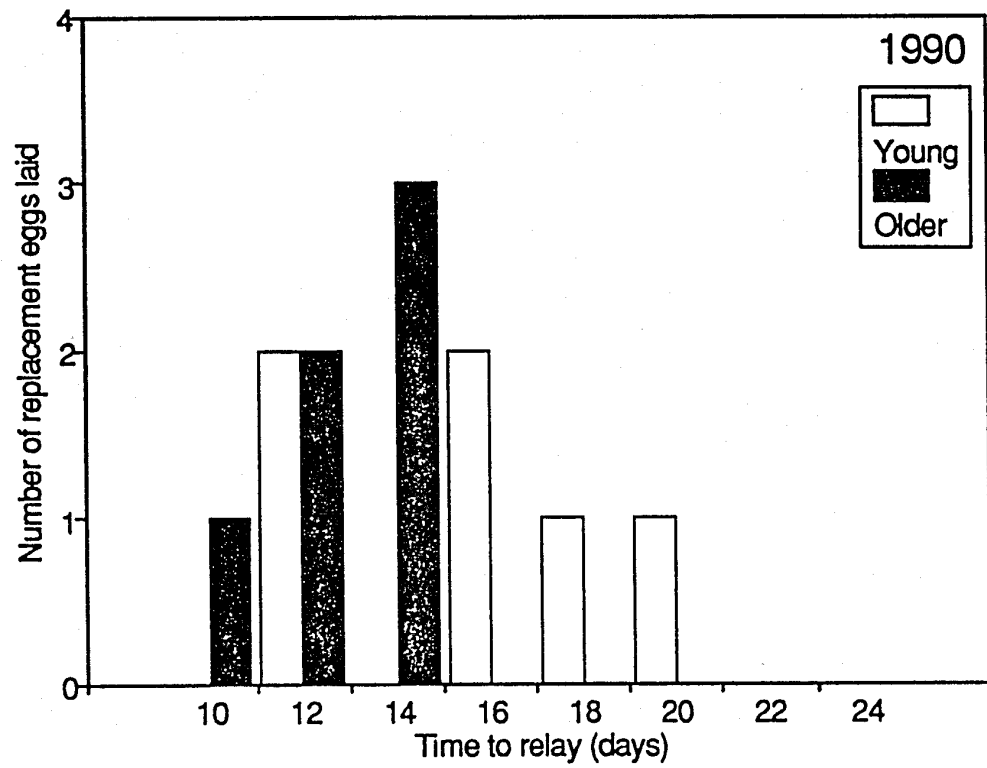
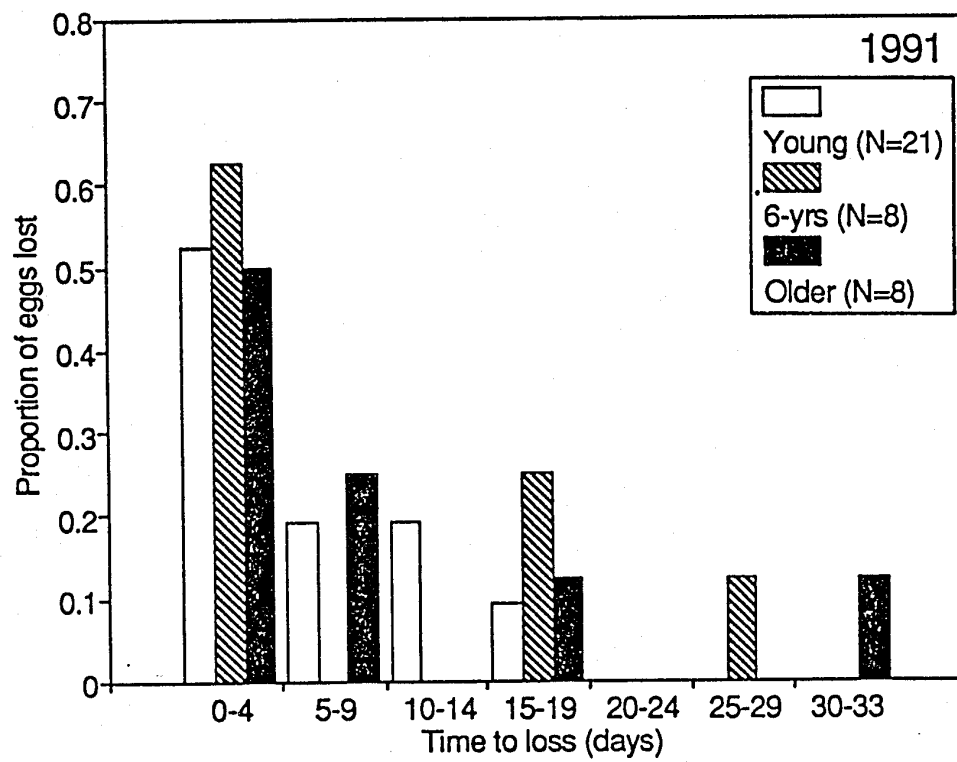
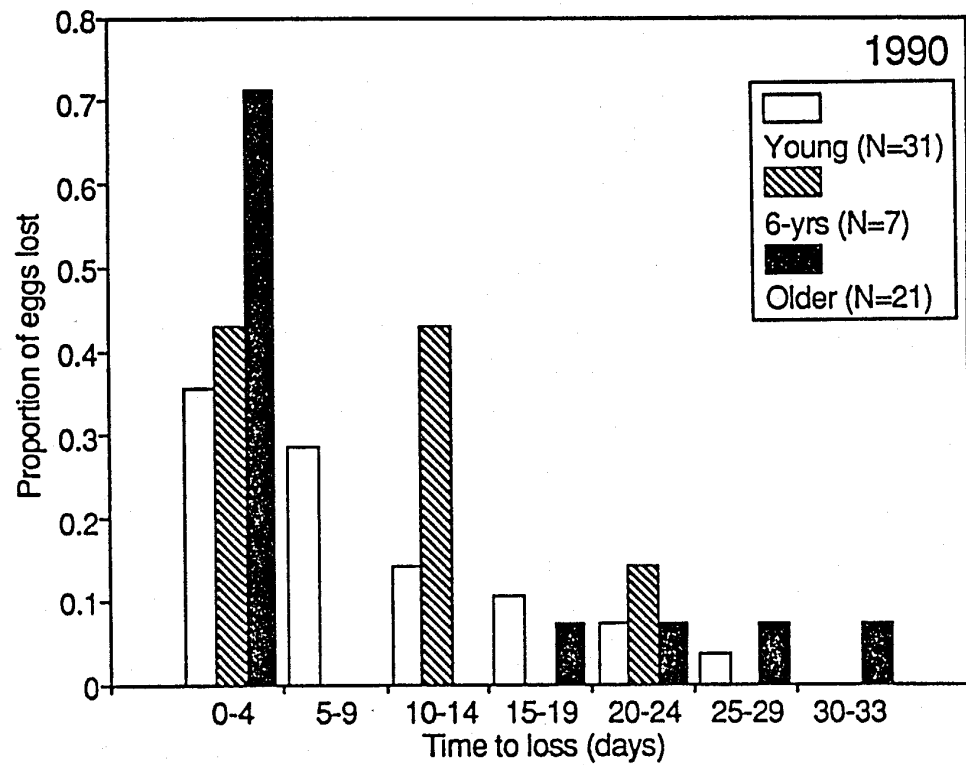


Figure 2.6: Time elapsed between laying and loss for known age birds.



INCUBATION AND FLEDGING PERIODS

1. TOTAL SAMPLE

The mean incubation period for first eggs was 33.0 ± 1.4 days in 1990 (N=29) and 33.3 ± 1.8 days in 1991 (N=71) ($t = -0.67$, NS). There was no effect of date on incubation period of first eggs in either year (1990: $r^2_{1,27} = 0.03$, $F = 0.71$, NS; 1991: $r^2_{1,69} = .002$, $F = 0.16$, NS). The mean incubation periods of replacement eggs were shorter than those of first eggs in both years, although the difference was significant in 1991 only (1990: $X_{\text{relays}} = 31.5 \pm 3.5$ days: N=15, $t = 1.58$, NS; 1991: $X_{\text{relays}} = 32.3 \pm 1.1$ days: N=18, $t = 2.79$, $P < 0.01$).

Fledging periods of chicks hatched from first eggs ranged from 20 to 30 days in 1990 ($X = 23.9 \pm 3.1$, N=21) and from 17 to 28 days in 1991 ($X = 21.9 \pm 2.3$, N=75). Fledging periods of chicks hatched from first eggs declined as the season progressed in both years, although the decline was significant in 1990 only (1990: $r^2 = 0.40$, $F_{1,19} = 12.45$, $P < 0.005$; 1991: $r^2 = 0.02$, $F_{1,73} = 1.69$, NS) (Figure 2.7).

2. KNOWN AGE BREEDERS

There was no difference in either incubation or fledging periods between young and older birds (Table 2.11).

FORAGING SHIFTS DURING INCUBATION

Foraging shift lengths of young and older birds did not differ significantly ($X_{\text{young}} = 15.8 \pm 8.6$ h, N=8; $X_{\text{old}} = 12.8 \pm 7.9$ h, N=19; $t = -0.85$, NS), although older birds were gone for slightly shorter trips (Median_{young} = 15 h, Median_{old} = 9 h).

Figure 2.7: Age at fledging in relation to date of hatching for chicks from first eggs.

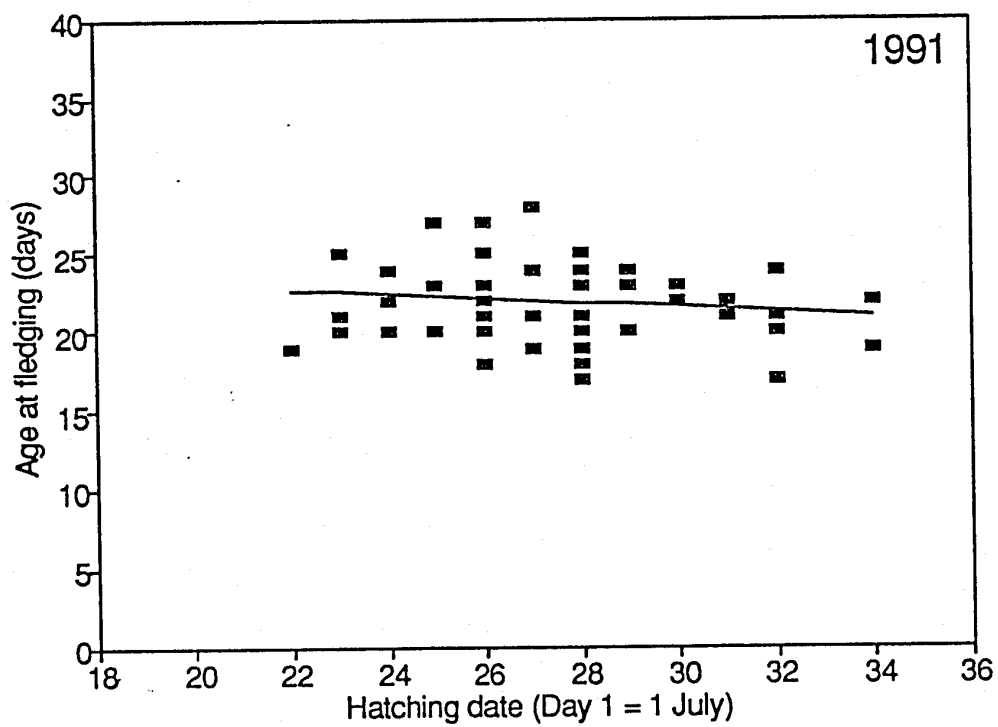
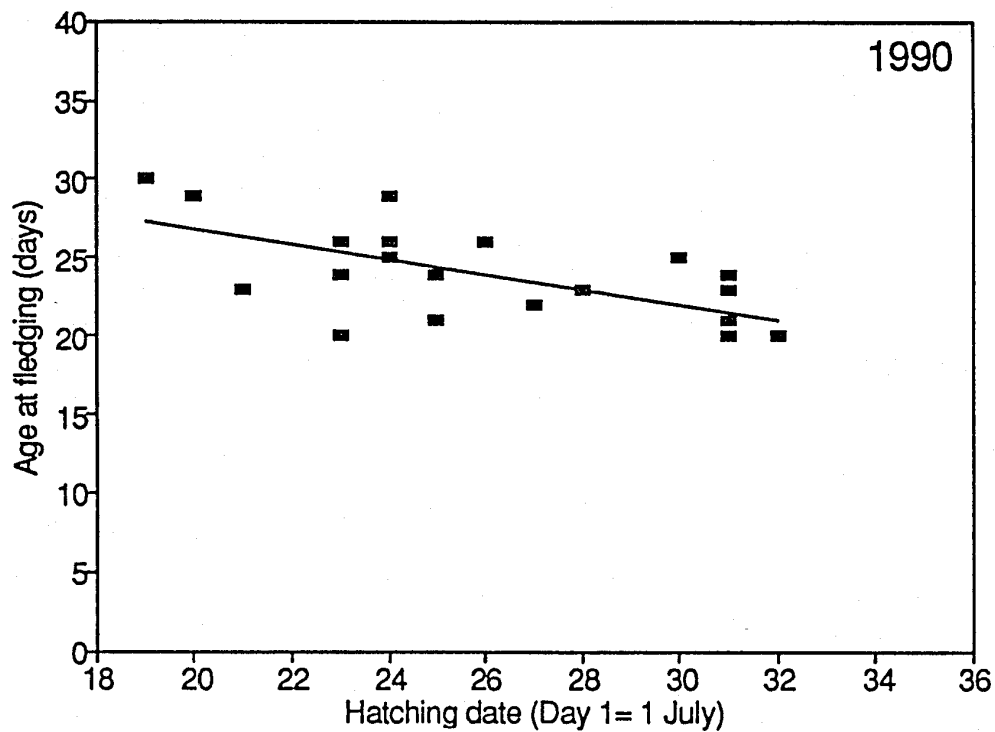


Table 2.11: Mean durations (days (\pm SD)) of incubation and fledging periods of known age breeders.

1990	Young	Older	T-test	P
Incubation period N	33.6 (1.14) 5	33.7 (1.57) 10	0.13	>.05 NS
Fledging period N	19.0 (4.55) 4	23.1 (3.73) 10	1.76	>.05 NS
1991				
Incubation period N	33.0 (0.93) 9	33.0 (1.04) 23	0.28	>.05 NS
Fledging period N	22.1 (1.95) 7	22.0 (1.96) 21	-0.11	>.05 NS

REPRODUCTIVE OUTCOME

1. TOTAL SAMPLE

The hatching success of first eggs laid differed significantly among the 5 study plots in 1990 ($\chi^2_4=10.67$, $P<0.05$), but not in 1991 ($\chi^2_4=8.58$, NS) (Table 2.12). Fledging success did not differ among plots in either year. Overall reproductive success differed significantly among plots in both years ($\chi^2_{1990}=10.04$, $P<0.05$; $\chi^2_{1991}=13.35$, $P=0.01$), with low success at plot S in 1990 and at plot D in both years. In 1990 Plot S had a higher proportion of young birds than any other plot (see Table 2.15). Plot D has many narrow ledges and is situated at 90 degrees relative to the other plots making it more vulnerable to gull predation due to updrafts (G. Gilchrist pers. comm.).

When considering all plots together, the hatching and fledging success of first eggs did not differ significantly between years. Overall reproductive success was significantly higher in 1991 (59%) than 1990 (51%) (Table 2.13).

Replacement eggs were much less successful than first eggs in hatching success in both years, and in reproductive success in 1990, although the difference was not significant in 1991 (Table 2.14). The fledging success of first and replacement eggs did not differ in either year (both $\chi^2<0.40$, NS).

Table 2.12: Breeding success of first and replacement eggs for 5 study plots.

Plot	FIRST EGGS			REPLACEMENT EGGS			Overall reproductive success
	Hatching success	Fledging success	Hatching success	Hatching success	Fledging success	Fledging success	
<u>1990</u>							
D	53/99 (53.5%)	43/53 (81.1%)	1/14 (7.1%)	1/1 (100.0%)	44/99 (44.4%)		
N	77/127 (60.5%)	68/77 (88.3%)	2/6 (33.3%)	2/2 (100.0%)	70/127 (55.1%)		
P	49/75 (65.3%)	46/49 (93.9%)	1/3 (33.3%)	1/1 (100.0%)	47/75 (62.7%)		
Q	21/36 (58.3%)	18/21 (85.7%)	2/5 (40.0%)	2/2 (100.0%)	20/36 (55.6%)		
S	33/78 (42.3%)	30/33 (90.9%)	4/10 (40.0%)	2/4 (50.0%)	32/78 (41.0%)		
TOTAL	233/415 (56.1%)	205/233 (88.0%)	10/38 (26.3%)	8/10 (80.0%)	213/415 (51.3%)		
<u>1991</u>							
D	54/98 (55.1%)	45/54 (83.3%)	4/8 (50.0%)	3/4 (75.0%)	48/98 (49.0%)		
N	52/91 (57.1%)	49/52 (94.2%)	0/8 (0%)	0	49/91 (53.8%)		
P	30/49 (61.2%)	27/30 (90.0%)	3/4 (75.0%)	3/3 (100.0%)	30/49 (61.2%)		
Q	29/47 (61.7%)	26/29 (89.7%)	3/4 (75.0%)	3/3 (100.0%)	29/47 (61.7%)		
S	58/76 (76.3%)	56/58 (96.6%)	1/3 (33.3%)	1/1 (100.0%)	57/46 (75.0%)		
TOTAL	223/361 (61.8%)	203/223 (91.0%)	11/27 (40.7%)	10/11 (90.9%)	213/361 (59.0%)		

Table 2.13: Comparison of the success of first and replacement eggs in 1990 and 1991 for all plots combined.

Year	FIRST EGGS		REPLACEMENT EGGS		Overall reproductive success
	Hatching success	Fledging success	Hatching success	Fledging success	
1990	56.1% 233/415	88.0% 205/233	26.3% 10/38	80.0% 8/10	51.3% 213/415
1991	61.8% 223/361	91.0% 203/223	40.7% 11/27	90.9% 10/11	59.0% 213/361
Chi square	2.52	1.12	1.5	Fisher Exact	4.6
P	0.11 NS	0.29 NS	0.22 NS	0.59 NS	0.03 **

Table 2.14: Comparison of success of first and replacement eggs.

1990	First egg	Replacement egg	Chi square	P
Hatching success	56.1% (233/415)	26.3% (10/38)	12.46	0.0004 **
Fledging success	88.0% (205/233)	80.0% (8/10)	0.56	0.45 NS
Reproductive success	49.4% (205/415)	21.1% (8/38)	11.23	0.0008 **
1991	First egg	Replacement egg	Chi square	P
Hatching success	61.8% 223/361	40.7% (11/27)	4.64	0.03 **
Fledging success	91.0% (203/223)	90.9% (10/11)	0	1 NS
Reproductive success	56.2% (203/361)	37.0% (10/27)	3.74	0.05 NS

2. KNOWN AGE BREEDERS

The proportions of known age birds differed significantly among plots in 1990 ($\chi^2=32.89$, $P=.0001$; Table 2.15), but not in 1991 ($\chi^2=8.78$, NS). In 1990, 61% (22 of 36) of all young birds bred on plot S, with most failing to fledge a chick. In 1991, Plot S had only 38% (12 of 32) of young birds, and these were more successful.

In both years, older birds had higher hatching and reproductive success than young birds (Table 2.16) but fledging success did not differ significantly between young and older breeders in either year. The success of six and seven-year olds was intermediate between young and older birds. In 1990, six-year olds hatched more eggs than young birds ($\chi^2=9.58$, $P<0.005$) but had only slightly higher reproductive success ($\chi^2=3.20$, NS). In 1991, six-year old birds were less successful than young birds in both hatching and reproductive success, although not significantly so. Six-year olds did not differ from older birds in 1990, but performed quite poorly in 1991. The performance of seven-year olds in 1991 was comparable to that of older birds, and slightly better than six-year olds.

Table 2.15: Locations and reproductive success of pairs containing young and older birds on 5 study plots.

		Plot	4-year olds	5-year olds	Young* birds	# failed	# fledged	Older birds	# failed	# fledged
1990	D	0	2	2	2	2	0	16	5	11
	N	2	8	10	9	1	14	21	7	14
	P	0	2	2	2	0	0	2	2	0
	Q	0	0	0	0	0	0	19	7	12
	S	10	12	22	17	5	5	9	4	5
Total		12	24	36	30	6	67	25	42	
1991	D	1	2	3	2	1	7	9	2	7
	N	3	5	8	7	1	9	12	3	9
	P	3	2	5	4	1	3	3	0	3
	Q	2	2	4	3	1	18	21	3	18
	S	1	11	12	5	7	13	14	1	13
Total		10	22	32	21	11	59	9	50	

Table 2.16: Hatching, fledging, and reproductive success of known age breeders.

1990	Young	6-years	7-years	Older
Hatching success	16.7% (6/36)	60.0% (9/15)		73.1% (49/67)
Fledging success	100%	66.7%		85.7%
Reproductive success	16.7% (6/36)	40.0% (6/15)		62.7% (42/67)
1991				
Hatching success	43.8% (14/32)	38.5% (5/13)	76.9% (10/13)	88.1% (52/59)
Fledging success	78.6%	80.0%	80.0%	96.2%
Reproductive success	34.4% (11/32)	30.8% (4/13)	61.5% (8/13)	84.7% (50/59)
Hatching success	Chi-square	P		
1990 Young vs. older	30.01	<0.0001		
1991 Young vs. older	16.71	<0.0001		
1990 Young vs. 6-yrs	9.58	<0.005		
1991 6-yrs vs. old	15.94	<0.0005		
Reproductive success				
1990 Young vs. older	19.93	<0.0001		
1991 Young vs. older	23.82	<0.0001		
1991 6-yrs vs. older	16.55	<0.0001		

* All other chi-square and Fisher Exact tests NS (P>0.05).

3. COMPARISON OF OUTCOMES FOR INDIVIDUAL KNOWN AGE BREEDERS BETWEEN YEARS

In 1991, five-year olds breeding for the second time fledged a chick in 4 of 7 cases, while five-year olds breeding for the first time only succeeded in 3 of 16 cases (Fisher Exact test: $P=0.13$).

Five-year olds that had bred in the previous year (1986 cohort) improved their success in 1991 (1990: 2/8 chicks fledged; 1991: 4/8 chicks fledged). However, neither the 1984 nor the 1985 cohort showed much improvement (Chicks fledged_{1984 cohort}: 1990: 3/7, 1991: 3/7; Chicks fledged_{1985 cohort}: 1990: 3/11, 1991: 4/11).

4. KNOWN AGE BIRDS NOT RETURNING TO BREED IN 1991

Known age birds which failed in 1990 were as likely to return in the following year as birds which succeeded (Table 2.7). Both young and older birds which bred only in 1990 were as successful as birds which bred in both years (Table 2.17).

Table 2.17: Comparison of 1990 outcomes for known age breeders which did and did not return to breed in 1991.

Cohort	Year	Fledged a chick		Fisher Exact
		Yes	No	
1986	1990 only	1	4	>0.50 NS
	Both years	2	5	
1985	1990 only	0	9	>0.20 NS
	Both years	3	10	
1984	1990 only	2	4	>0.50 NS
	Both years	3	3	
Older	1990 only	23	14	>0.50+ NS
	Both years	24	13	

+ Chi-square test, =0.06

SEASONAL DECLINE IN REPRODUCTIVE SUCCESS

Seasonal changes in reproductive success were analyzed for the total sample, young and older birds (separately and pooled), and the total sample without known age birds in each year. The actual values obtained with logistic regression are given in Appendix 1. There were no differences between the two years in hatching, fledging or reproductive success of both first and replacement eggs for any group (Table 2.18; all χ^2 NS). All groups were more successful in 1991. Numbers in Table 2.18 differ from those in Table 2.13, because laying date was not known to within 72 h for all pairs included in Table 2.13.

In all cases of hatching and reproductive success, older birds were more successful and young birds were less successful than the total sample without known age birds. In 1991, older birds were significantly more successful ($\chi^2_{\text{Hatch}}=8.21$, $p=0.005$; $\chi^2_{\text{Reprod}}=10.35$, $P=.001$).

Table 2.18: Hatching, fledging, and reproductive success for total sample, young and older birds and total sample without young and older birds (for sites where all laying dates were known to 72 hours).

	1990				1991						
	Sites	Hatched	Fledged	Hatching success	Sites	Hatched	Fledged	Hatching success	Reprod success	Fledging success	Reprod success
Total sample	292	159	135	54.5%	277	164	145	59.2%	46.2%	88.4%	52.3%
Older birds	54	37	32	68.5%	48	38	36	79.2%	59.3%	94.7%	75.0%
Young birds	31	6	6	19.4%	28	12	10	42.9%	19.4%	83.3%	35.7%
Older & Young	85	43	38	50.6%	76	50	46	65.8%	44.7%	92.0%	60.5%
Not known age	207	116	97	56.0%	201	114	99	56.7%	46.9%	86.8%	49.3%

1. SEASONAL DECLINE - HATCHING SUCCESS

There was a significant decline in hatching success for the total sample as the season progressed in both years (Figure 2.8). Birds laying >4 days after the mean date of laying had less than 50% chance of successfully hatching their egg. The exclusion of known age breeders from the total sample did not alter the trend.

Both young and older birds analyzed separately showed no seasonal trend in hatching success. Young birds tended to fail before hatch consistently throughout the season.

When combined, young and older birds showed a significant decline in hatching success with laying date in both years (Figure 2.9), very similar to the decline of the total sample without known age breeders, which was especially evident in 1990. In 1991, the hatching success of known age birds laying after the peak was higher than in 1990, causing the hatching success of the known age sample to diverge from the rest of the breeding sample later in the season.

Figure 2.8: Seasonal decline in hatching success of the total sample (curves generated by logistic regression, asterisks give 5 day averages of hatching success).

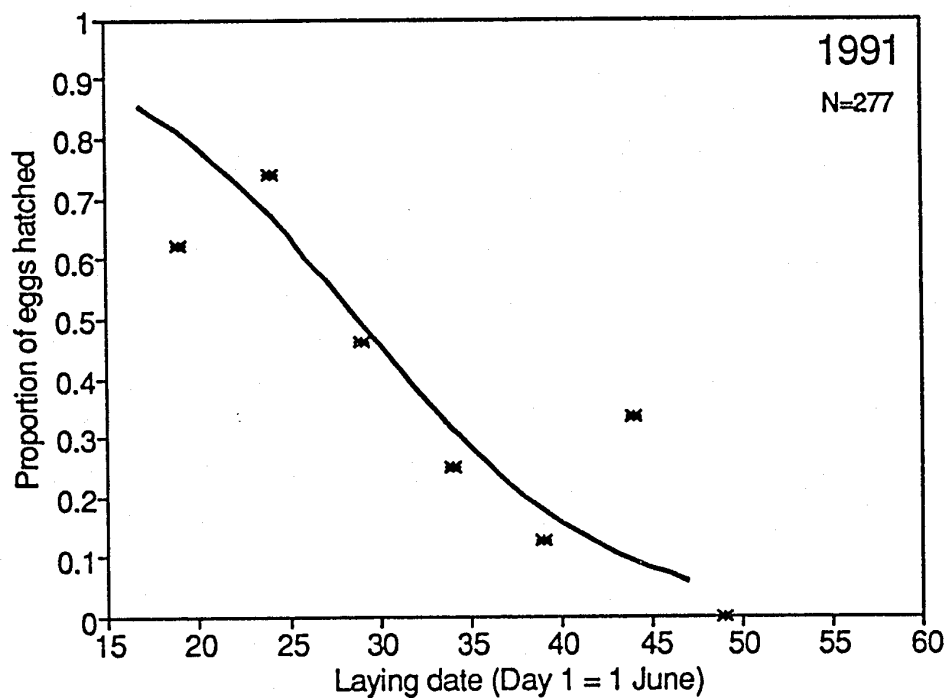
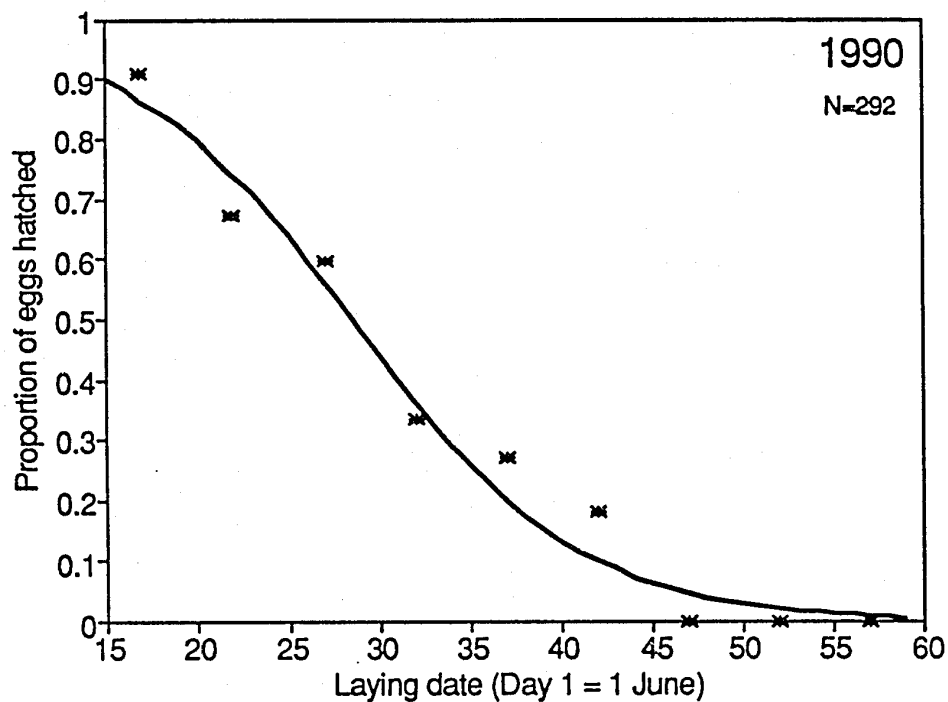
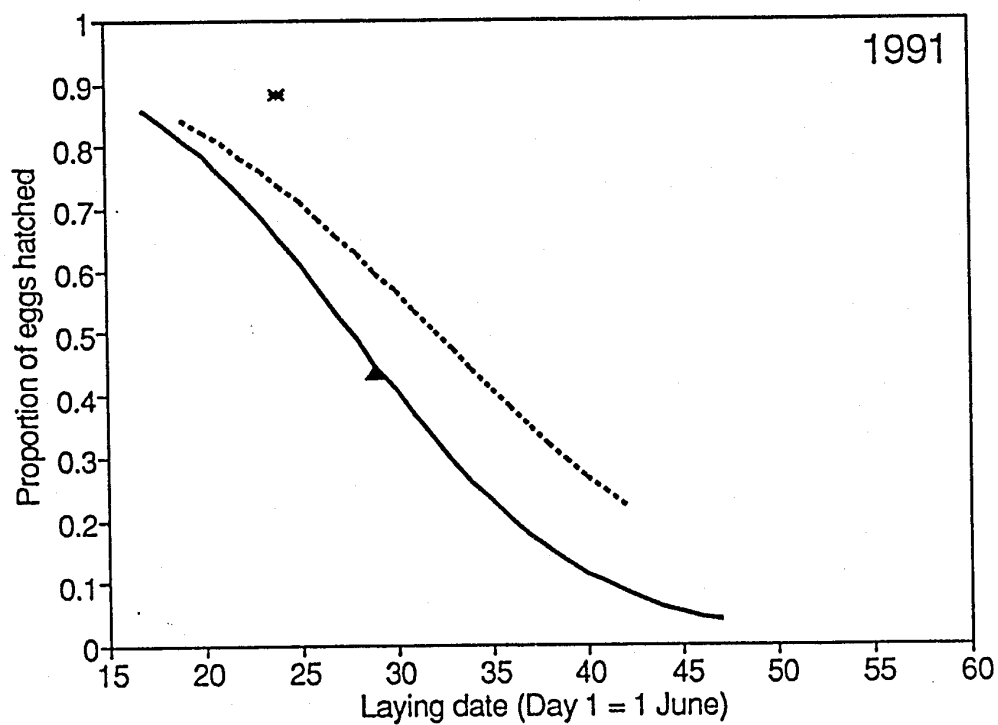
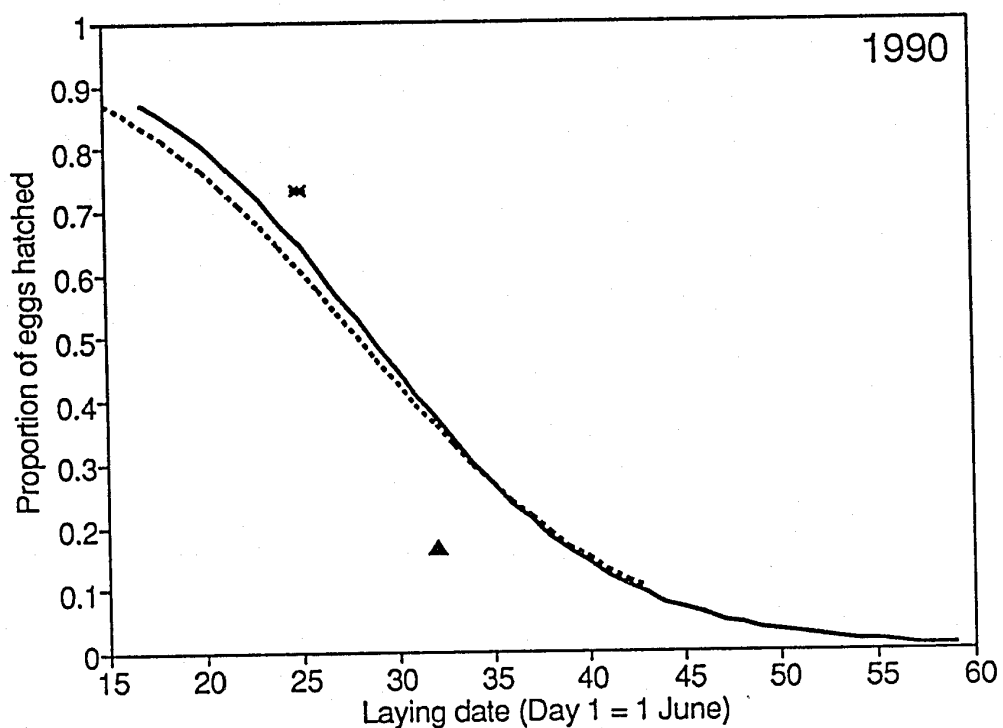


Figure 2.9: Seasonal decline in hatching success of young and older breeders combined (dotted line) and total sample excluding known age breeders (solid line) (curves generated by logistic regression, * = mean hatching success of older birds, \blacktriangle = mean hatching success of young birds).



2. SEASONAL DECLINE - FLEDGING SUCCESS

If an egg survived to hatch, there was no seasonal trend in the ability of a pair to raise and fledge the chick. Fledging success was not affected by date of laying for the total sample (Figure 2.10) or young and older birds separately. When combined, fledging success of young and older birds in both years did not decline significantly.

3. REPRODUCTIVE SUCCESS

The seasonal pattern for reproductive success was similar to that of hatching success, with a few exceptions. In 1990 there was a seasonal decline in reproductive success for the total sample, but the 1991 data did not fit the logistic model, although there was still a significant decline (Figure 2.11). In 1990, the decline in reproductive success in older birds with date was just significantly different from a slope of zero ($P=0.0455$). In all other cases, young and older birds, when looked at separately, showed no change as the season progressed. When pooled, young and older birds showed a significant seasonal decline in reproductive success in both years, although the data did not fit the logistic model in 1991 (Figure 2.12). However, there was still a negative trend with date of laying for 1991.

Figure 2.10: Fledging success for total sample by laying date (*=5 day averages of fledging success).

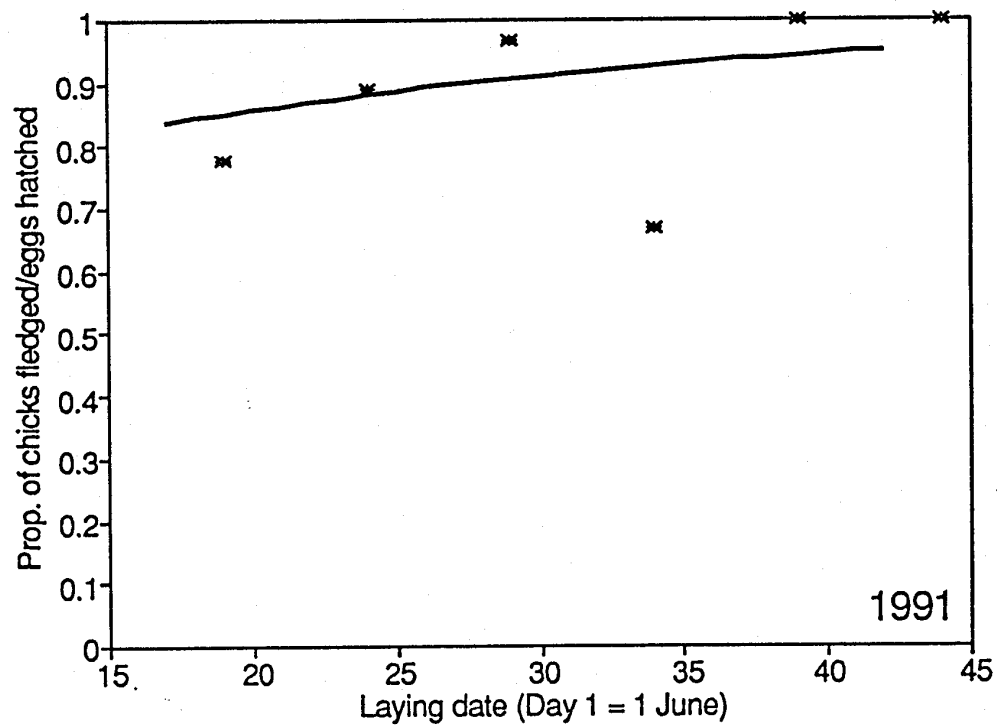
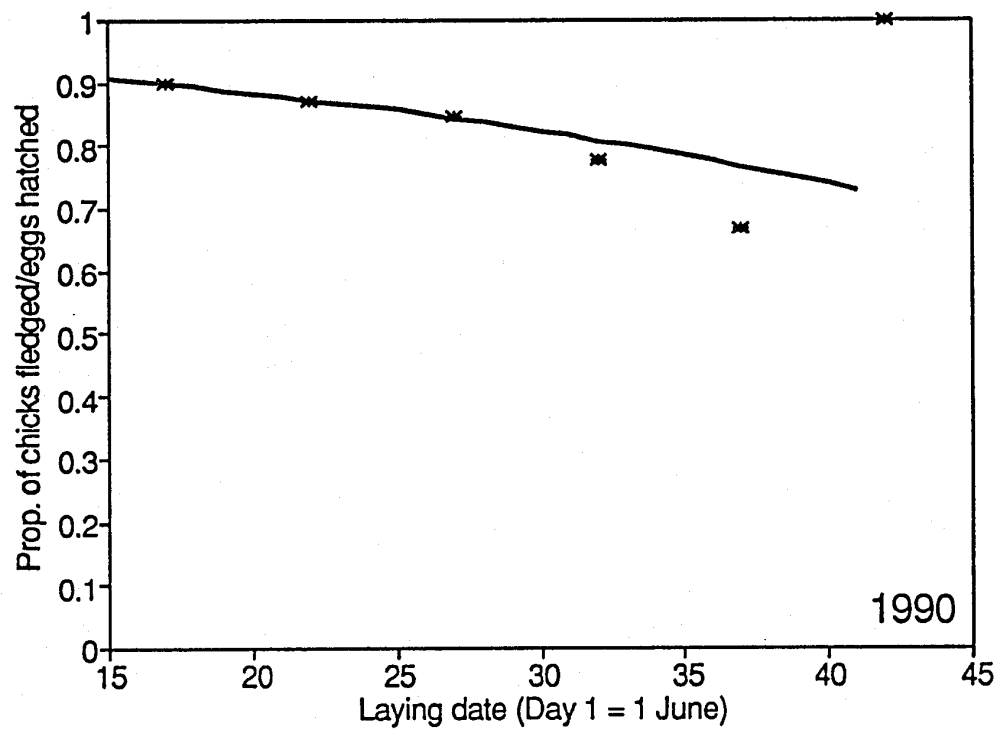


Figure 2.11: Seasonal decline in reproductive success of the total sample (* = 5 day averages of reproductive success). Data from 1991 do not fit the logistic regression model.

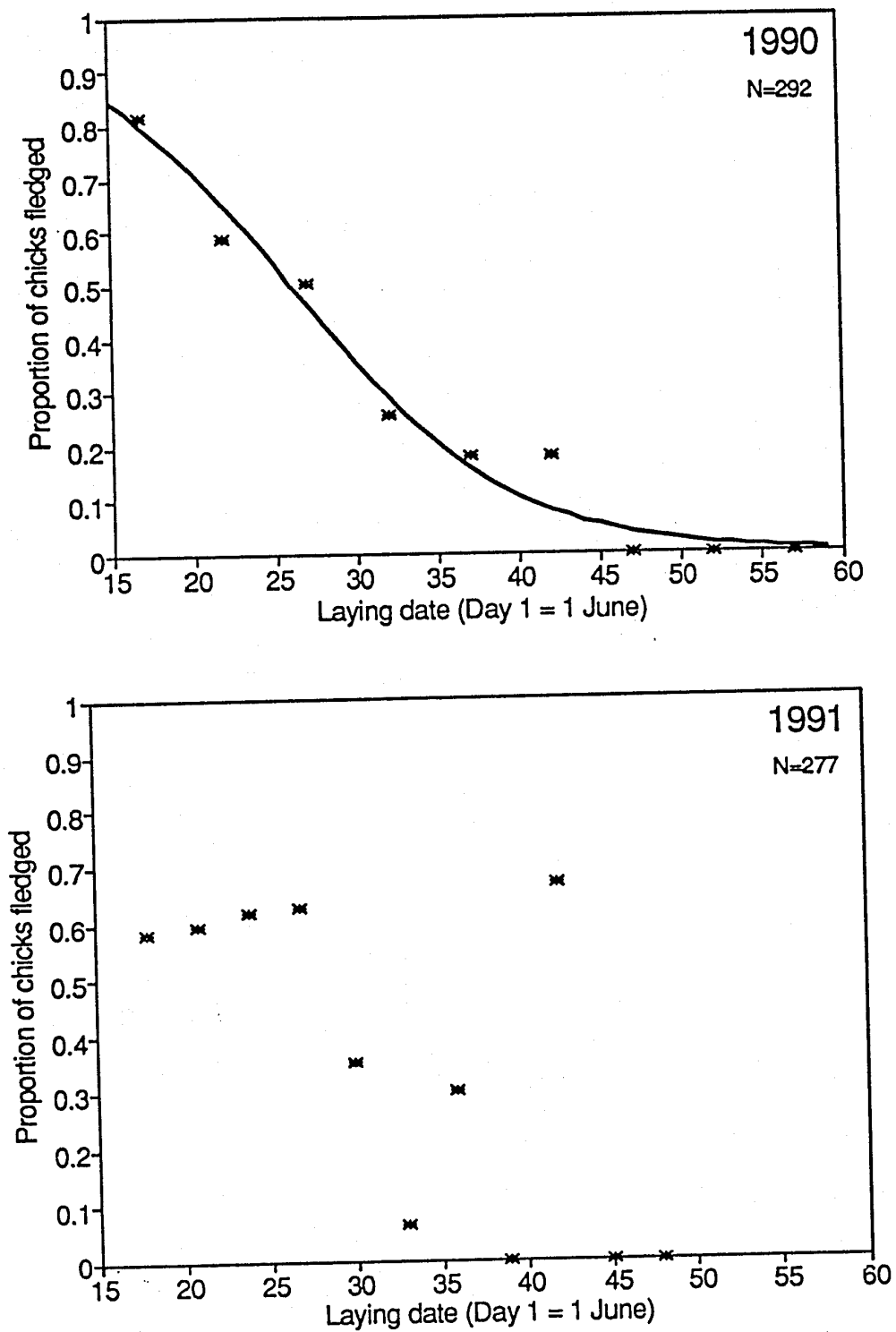
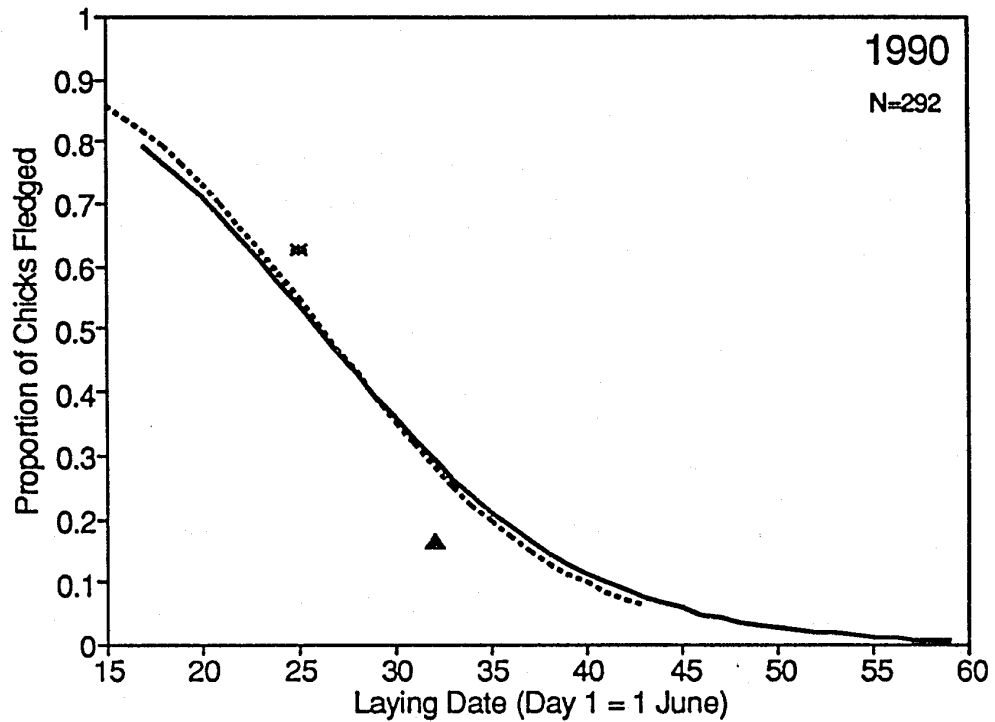


Figure 2.12: 1990 seasonal decline in reproductive success of young and older breeders combined (dotted line), compared to total sample excluding known age breeders (solid line) (* = mean hatching success of older birds, \blacktriangle = mean hatching success of young birds). Data from 1991 do not fit the logistic regression model.



DISCUSSION

Thick-billed Murres show age-related differences in reproductive parameters similar to those shown in other seabird species (for reviews see Ryder 1980, Wooller et al. 1992). Not all birds of a particular cohort begin breeding at the same age, but instead do so in increasing proportions as the birds get older, as demonstrated in many studies of breeding in long-lived seabirds (Perrins et al. 1973, Ollason and Dunnett 1978, Mills 1989, Noble 1990). Young birds laid an average of 5 to 7 days later in the season than older birds, and made up the majority of known age birds laying at the end of the egg laying period. Lack (1954) suggested that egg laying is timed to coincide with a peak in food availability during the chick rearing period. In my study, laying date was highly synchronized with an initial rapid peak which trailed off later in the season (Figure 2.1). Gaston and Nettleship (1981) suggested that some Thick-billed Murres which are capable of breeding early delay their egg laying to the peak period, to take advantage of the peak in food availability during the chick rearing period, while those laying later in the season may have been unable to form eggs at the optimum time.

The availability of food supplies early in the season and the ability of the female to find and exploit these resources probably also affects date of laying (Perrins 1970). In northern latitudes, time available to lay a clutch and successfully raise a brood to the point where they can survive the trip to the wintering grounds is limited. For birds breeding at Coats Island, the earliest

possible time to lay would depend on the pattern of ice melt and movement for that particular year, providing open areas for birds to find their prey. Late breeding was found at high Arctic Thick-billed Murre colonies in years of late ice breakup (Birkhead and Nettleship 1981, 1987a). It may take several years for young birds to recognize the cues of good feeding areas (Ryder 1980, Nelson 1988) and they may not forage as efficiently as older breeders (Orians 1969, Morrison et al. 1978, Burger 1987). Common Murres took 14-15 days to form an egg, during which time the females were probably mostly feeding (Birkhead and del Nevo 1987). If young birds were taking longer to build up the nutrient levels to lay an egg, this could explain the later appearance of younger birds at the colony, and the increased amount of time spent on the cliffs by older birds (Coulson and White 1958, Noble 1990).

Not only did young Thick-billed Murres lay later, but they also produced smaller eggs than older birds. Younger birds may not be as physiologically mature as older birds, and thus take longer to initiate reproductive behaviors and convert food into yolk reserves to lay an egg. Mills (1973) found that the maturation of the testes and ovaries in Red-billed Gulls (Larus novaehollandiae) began earlier with increasing age. Both the probability of breeding at a young age and reproductive success are related to physiological maturity in Adélie Penguins (Pygoscelis adeliae: Ainley 1975). Coulson et al. (1969) suggested that young birds may come into breeding condition later, and therefore have only a limited time to develop their eggs.

I found that individual young birds advanced their laying dates after one year of experience, which has been demonstrated in several species (Coulson and White 1958, Lloyd 1979, Forslund and Larsson 1992, Perdeck and Cavé 1992). Timing of laying is affected by the pair bond, with young birds breeding with the same mate laying earlier than the previous year (Coulson 1966, Mills 1973, Brooke 1978). Young Thick-billed Murres on Coats Island may have advanced their laying dates in 1991 because they were familiar with their mate from the previous year, and did not have to spend time early in the season searching for a new one (Mills 1973). A second time breeder might also have to spend less time defending its site. Birds which remain together for several years often lay at the same relative time each year (Brooke 1978, Findlay and Cooke 1982a, Gauthier 1989). On Coats Island, pairs of older breeders which stayed together laid at approximately the same relative date from 1990 to 1991, while a change of mate made the laying date more variable from the year before. Pairs which remain together have higher breeding success than birds which change mates (Davis 1976, Ollason and Dunnet 1978, Perrins and McCleery 1985), probably due to compatibility throughout the breeding cycle, which would help to reduce breeding failure (Nelson 1988).

HATCHING SUCCESS AND EGG LOSS

Young birds on Coats Island were not as successful as older birds, due mainly to high hatching failures in both years. Pairs breeding together for the first time have to synchronize their

activities in order to incubate their egg fully to hatch. Poor coordination of incubation shifts (Davis 1988), temporary neglect or desertion (Coulson and White 1958, Weimerskirch 1990) and improper incubation techniques (Coulson and White 1958, Nelson 1966) could cause egg loss or a reduction in eggs hatched in young or inexperienced breeders. An exposed egg might be more visible to a predator. Thick-billed Murre eggs are bright blue or green in color, and a freshly laid egg is highly visible if not covered completely (pers. obs.).

Although I expected young birds to lose their eggs soon after hatch due to ineptitude, time to egg loss was not related to age (Figure 2.6). It is possible that more young birds laid eggs and lost them before they were observed, which would further lower their hatching success.

There was no difference in incubation periods of young and older Thick-billed Murres on Coats Island, suggesting that the young birds which were able to hatch their egg were incubating efficiently. Young birds were found to have longer incubation periods than older birds in Yellow-eyed Penguins (Megadyptes antipodes: Richdale 1957, in Ryder 1980) and Manx Shearwaters (Brooke 1978), which could have been due to periodic egg neglect.

Young birds on Coats Island had a reduced chance of laying a replacement egg compared to older birds. The seasonal decline in the proportion of eggs replaced was very steep (Figure 2.4; Gaston and Nettleship 1981, Birkhead and Nettleship 1987b, Hatchwell 1991). Wanless and Harris (1988) found that the probability of

relaying an egg depended on the date that it was lost, rather than the length of time that it was incubated, thus even if a young bird lost its egg right after laying, it might not be replaced if its laying date was late initially. Young birds also tended to take longer to lay a replacement egg than older birds. This further supports the idea that young birds are not capable of developing an egg at the same rate as an older, more experienced bird feeding at the same time.

Both young and older birds had higher hatching success in 1991, which could be related to better weather conditions in that year. During the incubation period in 1990, there were higher winds and more days with rain (see Chapter 1). Birkhead (1976) found that chick feeding rates of Common Murres decreased with rough sea conditions, possibly due to fish moving to deeper water, or dispersing (Dunn 1973). If young birds were having difficulties feeding themselves, it could have led to a delayed return to the colony. There was some indication at Coats Island that young birds had longer foraging trips during the incubation period. Shift length in both Thick-billed Murres (Gaston and Noble 1986) and Common Murres (Verspoor et al. 1987) has been related to availability of food.

FLEDGING AND REPRODUCTIVE SUCCESS

Once the egg hatches, both parents take turns foraging for themselves and the growing chick, and must return to the colony more often to feed the chick. Consequently the chick rearing stage

might be more stressful than the incubation period for breeders, especially during a first breeding attempt. Most young birds which hatched their egg in this study were able to successfully raise a chick to fledging age. There was no difference in fledging success between chicks of young and older birds, although 14-day weights for the chicks of young birds were lighter than for the chicks of older birds (see Chapter 3). This accords with several other studies that found that younger, inexperienced birds had lower hatching success than older birds, but for those which hatched their egg, showed little age-related differences in the ability to fledge a chick (Nelson 1964, Coulson and Horobin 1976, Thomas 1983, Boekelheide and Ainley 1989, Weimerskirch 1990). Young birds which are capable of hatching their eggs may therefore be of high quality and fully capable of foraging for themselves and their chick.

Fledging periods did not differ with age in 1990, but chicks of young birds tended to fledge at a younger age than older chicks in 1991. There is a tendency for later chicks to fledge at a younger age, and hence closer to the peak in fledging (Gaston and Nettleship 1981). This could have a swamping effect on predators, and reduce the time spent isolated on the cliffs once the majority of chicks have fledged (Williams 1975, Birkhead 1977).

AGE-RELATED IMPROVEMENTS IN REPRODUCTIVE SUCCESS

Breeding experience as well as age improved the reproductive outcome for young breeders. Not only did five-year old Thick-billed Murres that bred for the second time lay their egg earlier,

they were also more successful than five-year olds breeding for the first time in 1991. This increased success with experience rather than age alone has been shown in several studies (Davis 1976, for review see Saether 1990). Another possible interpretation could be that better quality individuals begin to breed at a younger age. Longer term breeding data on individual birds would be needed to confirm this.

Although it appears that the advancement of laying date and improvement of reproductive success in Thick-billed Murres with age are due to age and experience, it is also possible that there is some difference in the quality of breeders, and that age-related increases might also be due to differential survival of differing quality birds (Curio 1983, Nol and Smith 1987). Of known age Thick-billed Murres which bred in 1990, there were no significant difference in laying dates or reproductive success for birds which did and did not return to breed in 1991. Hence, birds laying late were as likely to return to breed as birds laying early, regardless of success. Forslund and Larsson (1992) found that barnacle geese which bred poorly during their first breeding season survived as well as those which bred successfully.

The residual reproductive value hypothesis implies that improvements with age may be due to older birds putting more effort into breeding attempts. If mortality increases with age, older birds will have fewer breeding attempts left, thus their residual reproductive value will decline. To compensate for the reduction of years they have left to breed, older birds should increase their

reproductive effort to maximize their lifetime reproductive success (Pianka and Parker 1975, Pugsek 1981, 1983, Curio 1983). This is a difficult hypothesis to test (Nur 1984, Pugsek 1984, Reid 1988), and my data were not designed to address this question. Most losses occurred during the incubation period, rather than during the chick rearing period. Since neither young nor older birds left their eggs unattended, it was not necessarily less effort on the part of young breeders that caused them to lose their eggs, but more likely ineptitude, or poor quality sites (see Chapter 4).

SEASONAL DECLINE

There was a seasonal decline in hatching and reproductive success in both years for the total sample, which was made up mainly of birds of unknown age. I did not detect a decline in fledging success as the season progressed.

Most studies of murrelets have shown marked seasonal declines in hatching and reproductive success (Gaston and Nettleship 1981, Birkhead and Nettleship 1981, Birkhead and Nettleship 1987b, Wanless and Harris 1988, Hatchwell 1991).

Young and older birds, when examined separately, did not show any seasonal decline in hatching, fledging or reproductive success in either year. However, when the poor hatching success of the young birds later in the season was combined with the high hatching success of early breeding older birds, the seasonal decline was similar to that of the total sample over the breeding season. The combined reproductive success also declined seasonally, while

combined fledging success remained unchanged with date of laying. This suggests that age is a major factor in determining the seasonal trend in reproductive outcomes, and that it is largely determined during the incubation period. Hedgren (1980) found that although there was a marked seasonal decline in reproductive success, there was no difference in reproductive success for experienced pairs of Common Murres breeding during the early, middle, or late period. The seasonal decline was suggested to be due to young, inexperienced birds breeding at a later date (Hedgren 1980).

In summary, there are differences between young and older Thick-billed Murres in many reproductive parameters, which may be due to foraging ability, physiological development, status of the pair bond, or behavior during incubation. Age-related differences are influenced by prior breeding experience. Age appears to have a strong effect on the seasonal decline in reproductive success, due to losses during the incubation period. However, the relative contribution of age is difficult to determine, as timing of laying differs significantly between the two groups, and conditions may vary during the breeding season. In Chapter 3, I experimentally alter the timing of laying of early breeders to control for age.

Chapter 3: EXPERIMENTS TO DETERMINE THE EFFECT OF TIMING OF LAYING

INTRODUCTION

The effect of age on reproductive success is difficult to isolate due to additional confounding variables such as date of laying, and seasonal changes in prey or conditions. Young Thick-billed Murres laid later and had lower hatching and reproductive success than older birds (see Chapter 2). For my study plots as a whole, both hatching and reproductive success declined seasonally. This poses the question: are differences in reproductive parameters due to age and experience, or are they due to the timing of laying? Is it the quality of the young breeders which causes them to perform poorly, or is there some change in the environment, i.e. prey availability, which would cause later breeders, however skilled, to be unsuccessful?

There are several studies which have experimentally removed eggs to prolong the breeding season in order to examine the effects of timing of laying (Herring Gull, Larus argentatus: Parsons 1975, Common Murre: Hedgren and Linnman 1979, Hatchwell 1991). Parsons (1975) and Hatchwell (1991) removed eggs as they were being laid, and found that the delayed breeders were as successful as the control breeders, and much more successful than unmanipulated late layers. In both control and experimental groups, birds laying during the peak were more successful than early or later laying birds. They concluded that group synchrony was more important than

calendar laying date.

A seasonal decline in chick fledging weights has been demonstrated in several species, including murre (Atlantic Puffin, Fratercula arctica: Nettleship 1972, Great Skua: Furness 1983, Common Murre: Hedgren 1979, Thick-billed Murre: Gaston and Nettleship 1981, Birkhead and Nettleship 1981, 1987a). Early hatched chicks have been shown to have lower mortality rates, and late chicks were less likely to return to breed (Manx Shearwater: Perrins 1966, Perrins et al. 1973; Herring Gull: Nisbet and Drury 1972). Thus chicks fledging at a lighter weight late in the season may be less likely to survive to breed in the future.

To investigate the decline in chick fledging weight late in the season, Hedgren and Linnman (1979) experimentally induced Common Murres to relay later in the season and compared these birds to control birds breeding earlier in the season. Reproductive success of the control and experimental birds was very similar, however, the experimentally late chicks fledged at a much lighter weight than the control chicks. Feeding rates for the 2 groups were found to be the same, suggesting a reduction in the size and nutritional value of prey fed to chicks as the season progressed.

Hedgren and Linnman (1979) looked only at early, presumably older birds, which were considered equally experienced. Birds laying later in the season were assumed to be young and/or inexperienced. One would assume that late, inexperienced breeders would find it even more difficult to successfully fledge a chick under reduced prey conditions.

Several studies have found chick growth rate to be associated with food supply (Boersma 1978, Brown and Nettleship 1984, Ricklefs et al. 1984, Barrett et al. 1987, Van Heezik 1990). If food is abundant, growth is probably not constrained, but if the food supply is poor, growth may vary more closely with food supply (Cairns 1987).

In order to distinguish between effects due to age of the breeders and timing of laying, I conducted an experiment by removing eggs of early breeders to induce laying of a replacement egg c. 10 days later than young breeders. By forcing these early laying birds to breed late in the season, I could compare their performance to earlier control breeders to look at seasonal differences in the environment, as these two groups should be equally skilled. I compared the reproductive outcomes of the experimental birds to young breeders to establish the effect of age and experience corrected for date. To detect changes in prey availability as the season progressed, I measured early control chicks and chicks from experimental replacement eggs to detect changes in growth rates early and later in the season. Any differences in growth could be due to seasonal differences in prey availability or quality, rather than ability of the breeder.

MATERIALS AND METHODS

LAYING DATES

Control and experimental breeders were observed at different locations: 1) STUDY PLOTS - the study plots already referred to in this study; and 2) CHICK GROWTH PLOTS - plots away from the study plots that were visited only for measuring chick growth.

To create experimental sites on the study plots, 48 eggs in 1990 and 40 eggs in 1991 were selected randomly from 3 study plots and removed (under permit from the Canadian Wildlife Service) when approximately 50% of the eggs on a given plot had been laid. These dates were 1-2 days before the mean dates of laying for all plots in each year. In 1990 eggs laid before 26 June were removed on 26 and 29 June, and in 1991 eggs laid on or before 24 June were removed on 24 and 25 June. Older birds made up at least one member of 42% and 35% of experimental pairs in 1990 and 1991, respectively.

Almost all experimental birds laid a replacement egg. In 1990 three sites acquired an egg within 3 days after egg removal. In 1991, 8 sites acquired eggs within 5 days and one site was rejected due to confusion in dates. The possibility that eggs had been removed from the wrong sites was ruled out for most of these cases. Either the breeding pair shifted sites, an egg fell from a ledge above and was adopted, or a bird took a neighbour's egg. An egg was observed being stolen from a neighbour at 3 of these sites (Gaston et al. in press). These sites were left out of reproductive outcome analyses.

Five pairs which became experimentals (cases where an egg was seen or implied to have been removed by a neighbour as a result of the experimental removals) were included in the experimental sample.

All other birds laying on or before the cut-off dates for the experimental sample on all 5 study plots were considered to be controls (174 in 1990, 132 in 1991). In both years, c. 22% of control pairs had at least one older bird. There were also 10 pairs containing a six-year old in 1990, and 4 pairs in 1991.

Mean laying dates of first eggs for control and experimental pairs did not differ in either year ($t=-0.8$, NS), and were lumped when discussing laying dates and the size of first eggs.

Most young birds (four and five-year olds) laid their first eggs later than the early group of control and experimental first eggs, but there were 6 young birds in 1990 (1 four-year old, 5 five-year olds) and 5 young birds in 1991 (1 four-year old, 4 five-year olds) that laid before the cut-off dates. These birds were excluded from the control and experimental groups but were included in the sample of young breeders.

When calculating relaying and incubation periods, only those known to within 72 hours were included (see Chapter 2).

EGG SIZE

Egg volume indices (length x breadth²) were measured on both the study plots and chick growth plots. In both years, early eggs measured were experimental eggs which had been removed from the

study plots and eggs measured on the control chick growth plots. In the 1991 sample, first eggs removed from the experimental chick weighing plot were also included. The egg volume indices of eggs which were removed did not differ from those of control eggs in either year (1990: $t=0.89$, NS; 1991: ANOVA: $F=0.20$, NS). The egg volume indices of several eggs of known age breeders were also measured (see Chapter 2), although in some cases, these eggs were not laid on the study plots, and the dates of laying were unknown.

REPRODUCTIVE OUTCOMES

I observed the outcomes of all control, experimental and young breeders on the study plots. In both 1990 and 1991, we departed before many of the experimental chicks had fledged (1990: $N=19$, 1991: $N=18$). In 1990, 8 and in 1991, 12 of the experimental chicks had reached the minimum fledging age of 14 days. The remaining 11 of the 1990 and 6 of the 1991 experimental chicks were younger than 14 days. As fledging success was high and did not decline seasonally (see Chapter 2), these chicks were still considered to be successful if they had reached at least 5 days of age. One experimental bird in 1991 lost its replacement egg, and relaid a third egg, which hatched. The chick was 5 days old when we departed, and considered to be successful and therefore included in the analyses.

CHICK FEEDING RATES

Twenty-four hour feeding watches were conducted each year

during the chick rearing period to determine rates of feeding (3 in 1990, 4 in 1991). All observations of chicks being fed were made on Plot D, and sample sizes of sites followed depended on the number of birds with chicks within a comfortably observable area. In 1990, two of the feeding watches included pairs with one bird fitted with electronic activity timers (<10 g total weight). During both watches, these birds fed their chicks slightly more often than birds without timers (Gaston 1991). As this difference was not significant, these sites were included in the analysis of feeding rates.

CHICK GROWTH

Weights and wing lengths of chicks were measured on 3 growth plots (Q north, T, and Z) in 1990 and two growth plots (T and Z) in 1991. A 300 g Pesola spring balance was used for weights (± 1 g), and calipers were used to measure wing length from the carpus to the tip of the longest covert (± 1 mm). In both years, most of these chicks hatched about 28 July, which coincided with the peak hatching of the total sample.

In 1991, an experimental chick growth plot was created by removing first eggs from 30 sites on Plot X on 25 June. I returned later in the season to weigh and measure chicks from replacement eggs. Only 13 of the original 30 eggs on the experimental chick growth plot were present when checked before hatch. These losses were probably due to predation, as a marked gull (from another study) was seen systematically attacking this ledge over several

days. Consequently 10 extra eggs were added to the experimental sample at Plot X. Most of these eggs were from adjacent ledges where eggs had been lost during the initial removal of eggs. As their hatch dates coincided with those of the experimental eggs, they were probably replacements. These eggs were not included in the egg volume measurements for replacement eggs.

Measurements were taken every three days although this was dependent on good weather. Chicks were assumed to have fledged successfully if they reached 14 days of age before disappearance. Six control chicks were growing normally but disappeared before 14 days of age, while one experimental chick was not gaining weight and was gone at 8 days of age. All 7 chicks were excluded from the analyses.

In 1991, I weighed accessible chicks of control, experimental, young and older breeders on the study plots, and chicks on the control and experimental growth plots at c. 14 days of age. Most were 14 days of age, but a few were 15 to 17 days of age. When comparing chick weights and wing lengths, all measurements were corrected to 14 days. Control and experimental chicks were corrected using the regression coefficients derived from the control and experimental chick samples respectively, while the regression coefficient for the experimental chicks was used to correct the measurements of the chicks of young birds.

RESULTS

LAYING DATES OF FIRST EGGS

The mean laying dates for all early breeders were c. 4 days earlier than the total sample means in both years, while young birds laid 5 days later than the total sample mean in 1990 and 3 days later in 1991. Young birds laid their first eggs 9 and 6 days later than early layers in 1990 and 1991, respectively (1990: $t=-7.90$, $P<0.0001$; 1991: $t=-8.90$, $P<0.0001$; Table 3.1, Figure 3.1).

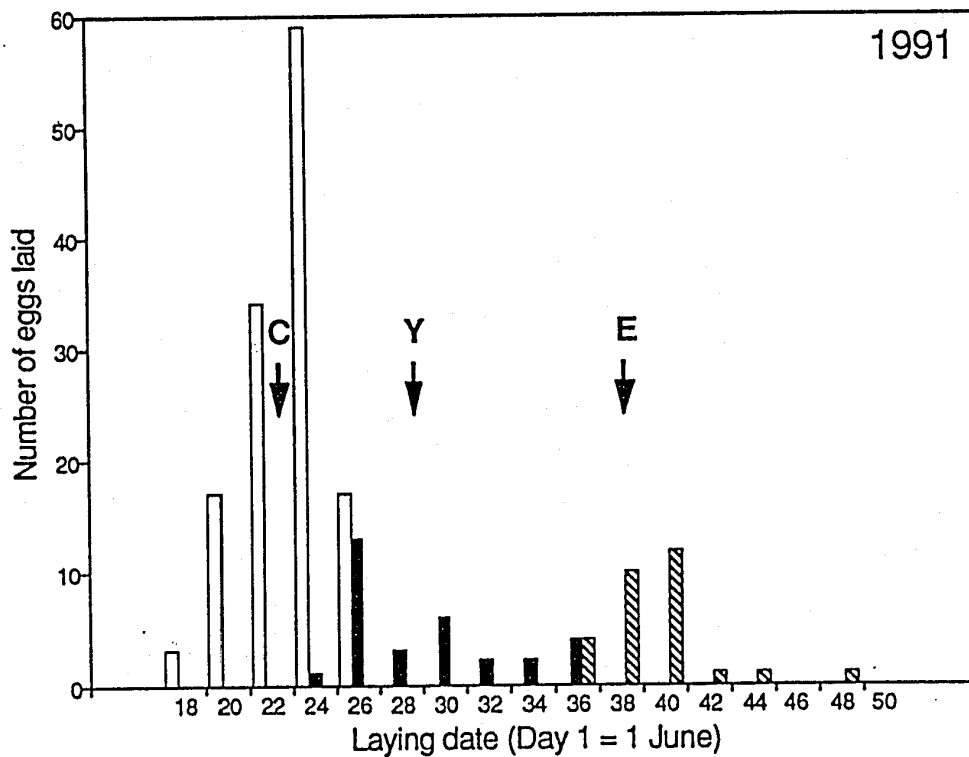
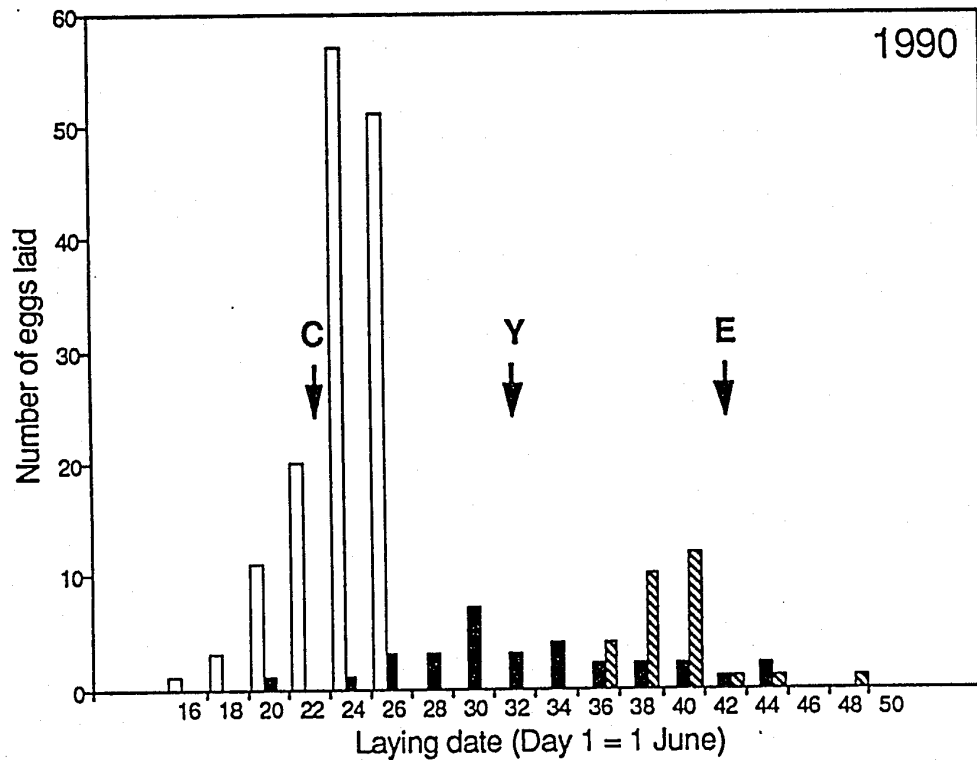
LAYING DATES OF REPLACEMENT EGGS

All experimental females ($N=45$) laid a replacement egg in 1990. In 1991, a replacement egg was laid at 94% (32 of 34) of experimental sites. The replacement eggs of experimental breeders were laid c. 10 days later than the first eggs of young birds (1990: $t=8.03$, $P<0.0001$; 1991: $t=12.33$, $P<0.0001$; Figure 3.1). The mean time to relay replacement eggs was 14.6 ± 1.9 days in 1990 and 14.1 ± 2.2 days in 1991 ($t=0.88$, NS).

Table 3.1: Mean laying dates (\pm SD) for first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991 (Day 1 = 1 June).

Year	EARLY first eggs	YOUNG first eggs	EXPERIMENTAL replacement eggs
1990	23.4 (2.21)	31.9 (5.93)	42.0 (2.30)
N	183	31	25
1991	22.5 (1.95)	28.7 (3.81)	38.8 2.25
N	172	26	29

Figure 3.1: Laying dates of first eggs of young and control breeders, and replacement eggs of experimental breeders (arrows indicates mean laying dates).



EGG SIZE

Replacement eggs of experimental breeders were 5.0% and 6.6% smaller than their first eggs in 1990 and 1991, respectively (paired t-tests, both years $t > 3.2$, $P < .01$; Table 3.2). In both years, the replacement eggs of experimental breeders were significantly smaller than early eggs (Table 3.3).

The eggs of young birds tended to be smaller than early eggs. Sample sizes were small in 1990, but the trend was significant in 1991 (Table 3.3). The eggs of young breeders did not differ in size from experimental replacement eggs in either year (all $t < 1.72$, NS), but tended to be slightly smaller, even though they were laid c. 10 days earlier. There was a decline in egg volume with date of laying in both years (Gaston 1991, pers. comm.).

Early eggs were larger in 1991 than in 1990 ($t = 2.68$, $P < 0.01$), but neither the first eggs of young breeders nor the replacement eggs of experimental breeders varied between the two years (both $t < 0.02$, NS; Table 3.3).

INCUBATION PERIODS

Experimental incubation periods were slightly shorter than control periods, although this was significant in 1991 only ($t = 2.25$, $P < 0.05$; Table 3.4). Incubation periods of young breeders were not significantly different from either control or experimental incubation periods in either year (all $t < 1.8$, NS; Table 3.4).

Table 3.2: Difference in egg volume indices, cm^3 ($\pm\text{SD}$), of first and replacement eggs of experimental breeders in 1990 and 1991.

Year	N	First eggs	Replacement eggs	Mean difference	Paired t-test	P
1990	27	202.0 (15.34)	191.9 (16.05)	10.1 (16.11)	3.24	<0.005 **
1991	10	204.3 (18.41)	190.5 (12.52)	13.8 (12.08)	3.61	<0.01 **

Table 3.3: Mean egg volume indices ($\text{cm}^3(\pm\text{SD})$) of first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991.

Year	EARLY first eggs#	YOUNG first eggs	EXPERIMENTAL replacement eggs
1990	200.9 (18.06)	189.3 (12.77)	192.2 (16.99)
N	109	3	32
1991	207.2 (16.75)	182.7 (19.04)	192.1 (12.95)
N	109	9	11
		T-test	P
1990	EARLY vs. YOUNG	1.10	>0.05 NS
1990	EARLY vs. EXPTAL	2.43	<0.05 *
1991	EARLY vs. YOUNG	4.17	<0.005 **
1991	EARLY vs. EXPTAL	2.90	<0.005 **

All other comparisons were not significant.

Includes eggs from experimentals on study plots and control chick weight plots in both years, plus experimental eggs from chick weight plots in 1991.

Table 3.4: Incubation periods in days (\pm SD) of first eggs of early and young breeders and replacement eggs of experimental breeders in 1990 and 1991.

Year	EARLY first eggs	YOUNG first eggs	EXPERIMENTAL replacement eggs
1990 N	33.2 (1.65) 18	33.6 (1.14) 5	32.1 (1.85) 10
1991 N	33.6 (1.72) 42	32.9 (0.93) 9	32.4 (1.24) 12

REPRODUCTIVE OUTCOMES

Although experimental breeders were delayed by about 14 days, neither their hatching nor their reproductive success differed significantly from those of control eggs (All $\chi^2 < 0.95$, NS, Table 3.5). Birds laying their first egg at this time were much less successful than experimental birds breeding at the same date (Figure 3.2).

Although experimental birds laid replacement eggs c. 10 days later than the first eggs of young birds in both years, they had significantly higher hatching success than young breeders in 1990, and significantly higher reproductive success in both years (Table 3.5). Almost all (30 of 36) young birds failed to hatch their egg in 1990, but performed as would be expected for their mean date of laying in 1991 (Figure 3.2).

CHICK FEEDING RATES

Chick feeding rates were quite variable in 1991 (Table 3.6). The rate at which experimental chicks were fed on 17 August did not differ from the rates observed for control chicks either on that day or on earlier feeding watches (all t-tests, NS). The feeding rate for experimental chicks on 21 August was significantly higher than those observed for control and experimental chicks on any earlier watch. Only one control bird remained on Plot D during the final feeding watch.

Table 3.5: Hatching, fledging and reproductive success of control, experimental and young breeders in 1990 and 1991.

1990	Control	Experimental	Young	Young vs. Exptal	
				Chi-sq	P
Hatching success	72.0% (116/161)	69.7% (23/33)	16.7% (6/36)	19.87	<.0001 **
Fledging success	86.2%	87.0%	100%	Fisher Exact	>.50 NS
Reproductive success	62.1% (100/161)	60.6% (20/33)	16.7% (6/36)	14.16	<.0002 **
<hr/>					
1991					
Hatching success	69.0% (89/129)	67.6% (23/34)	43.8% (14/32)	3.82	.0506 NS
Fledging success	84.3%	95.7%	78.6%	1.18	>.25 NS
Reproductive success	58.1% (75/129)	64.7% (22/34)	34.4% (11/32)	6.07	<.05 **

All comparisons of Control and Experimental success: all chi-square < 0.95, NS.

Figure 3.2: Seasonal decline in hatching success, with curved lines generated by logistic regression (solid line = total sample without young and old birds, dotted line = young and old birds combined; \square = mean hatching success of control breeders, \blacksquare = mean success of experimental breeders, \blacktriangle = young breeders).

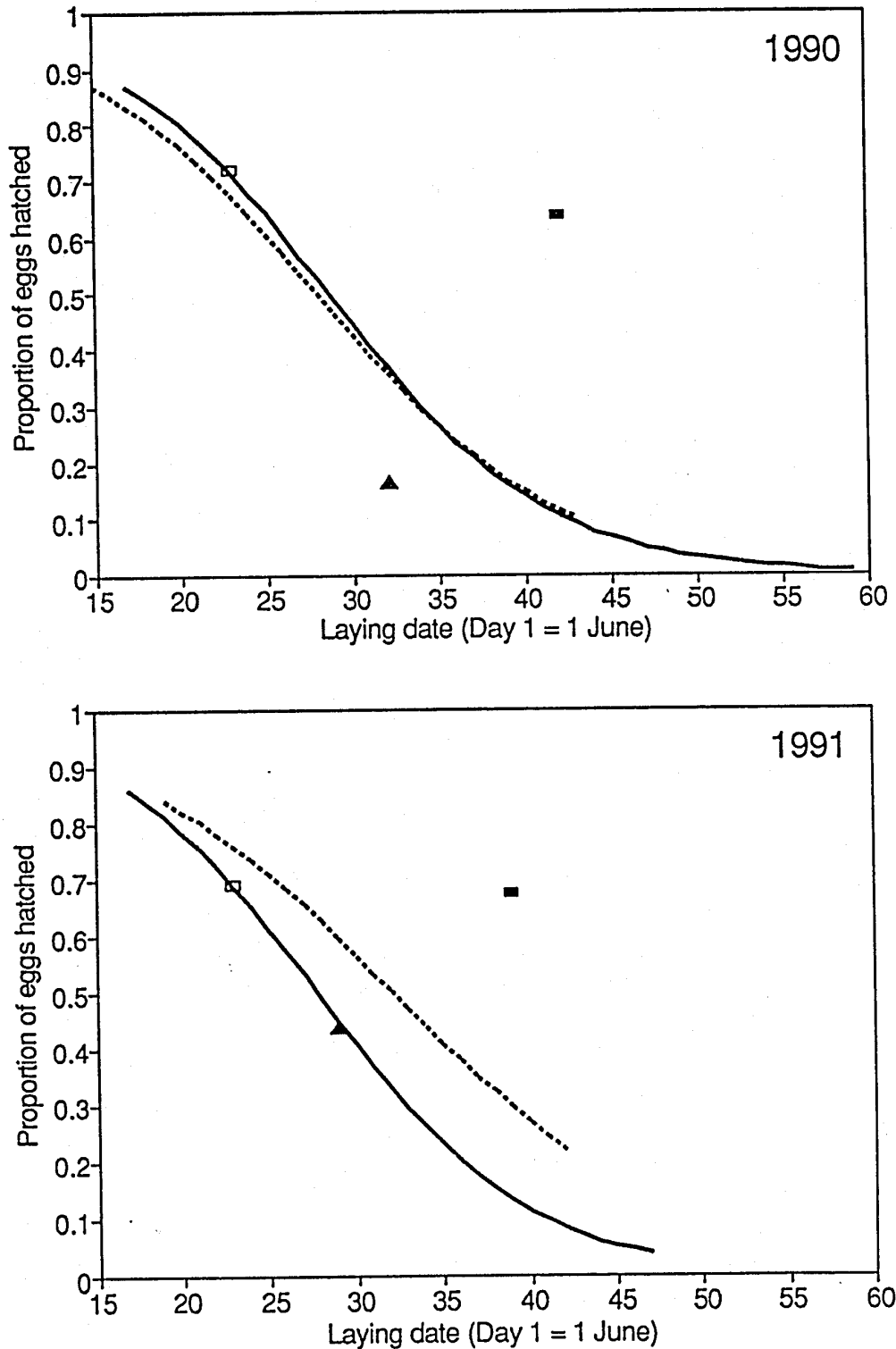


Table 3.6: Mean chick feeding rates (\pm SD) for control and experimental breeders on Plot D during 24-hour periods in 1991.

	Feeds / Chick			
	31 July	7 August	17 August	21 August
Control	3.45 (1.70) 20	5.30 (1.78) 20	3.92 (1.98) 13	8 1
Experimental	-	-	4.33 (1.73) 9	10.86 (2.34) 7
		t-test	P	
E(21 Aug) : C(31 Jul)		-9.00	<0.0001	
E(21 Aug) : C(7 Aug)		-6.56	<0.0001	
E(21 Aug) : C(17 Aug)		-7.03	<0.0001	
E(17 Aug) : E(21 Aug)		6.42	<0.0001	

* All other comparisons of Control and Experimental feeding rates were not significant.

CHICK GROWTH

Chick growth of control and experimental chicks was examined separately on the growth and study plots. Several studies have shown that chicks which are subjected to repeated handling have slower growth rates (see Gaston 1985). Hence, the chick growth plot data gives an idea of the pattern of growth between similarly treated/handled control and experimental chicks, while the 14 day weights of control and experimental chicks on the study plots give a more accurate comparison to chicks of young and older breeders, both groups being only weighed once.

Growth of control and experimental chicks on the chick growth plots did not differ in 1991. Although experimental eggs were c. 6% smaller than control eggs, by day 3 the experimental chicks were slightly heavier than control chicks. Although experimental chicks were being raised c. 15 days later in the season, the rates of both weight gain and wing growth did not differ from control chicks (Figure 3.3 a) and b); WEIGHT: $Y_{\text{cont}}=63.4\pm 7.1\text{g}$, $Y_{\text{expt}}=64.0\pm 13.7\text{g}$; WING: $Y_{\text{cont}}=7.7\pm 1.2\text{ mm}$, $Y_{\text{expt}}=6.4\pm 2.4\text{ mm}$). Control chick weights and wing lengths were slightly, but not significantly lower than those of experimental chicks at 14 days of age (Table 3.7).

The chicks of young birds were c. 19% lighter and their wings were slightly shorter than those of older birds at 14 days of age, but neither difference was significant (Table 3.8). Experimental chicks on the study plots were significantly heavier and had longer wings at 14 days than the chicks of young breeders, but were not different from control chicks (Table 3.9). Chicks of young

breeders were significantly lighter than control chicks at 14 days, but wing length was not significantly different (Table 3.9).

Figure 3.3: Growth curves of control (\square) and experimental (\blacksquare) a) chick weights and b) wing lengths on chick growth plots, 1991 (dotted line=growth of control chicks, solid line=growth of experimental chicks).

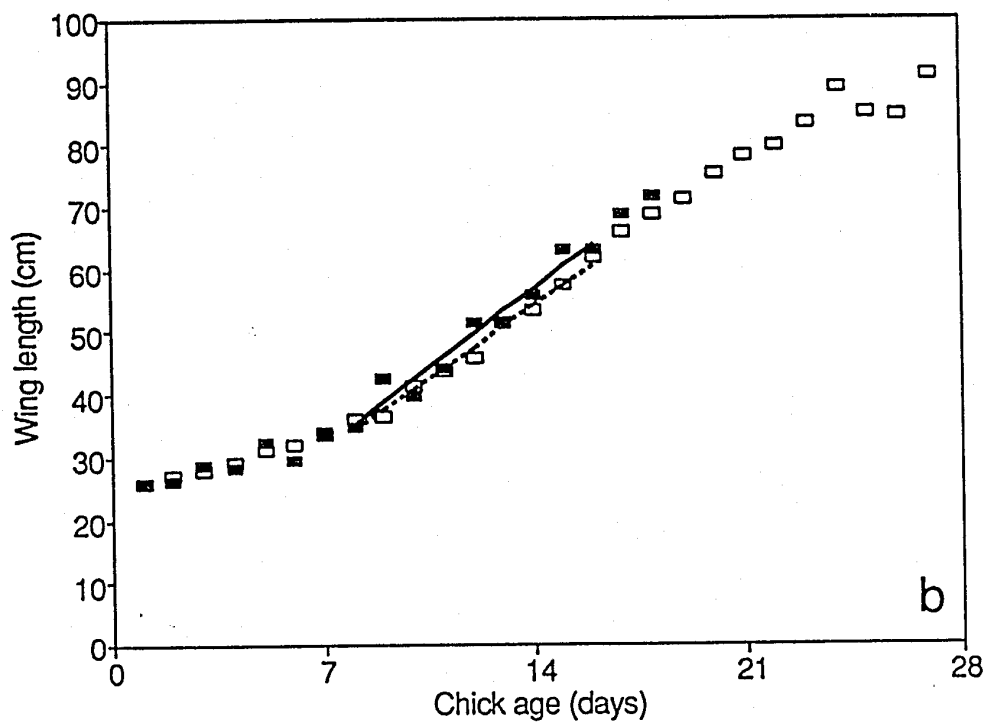
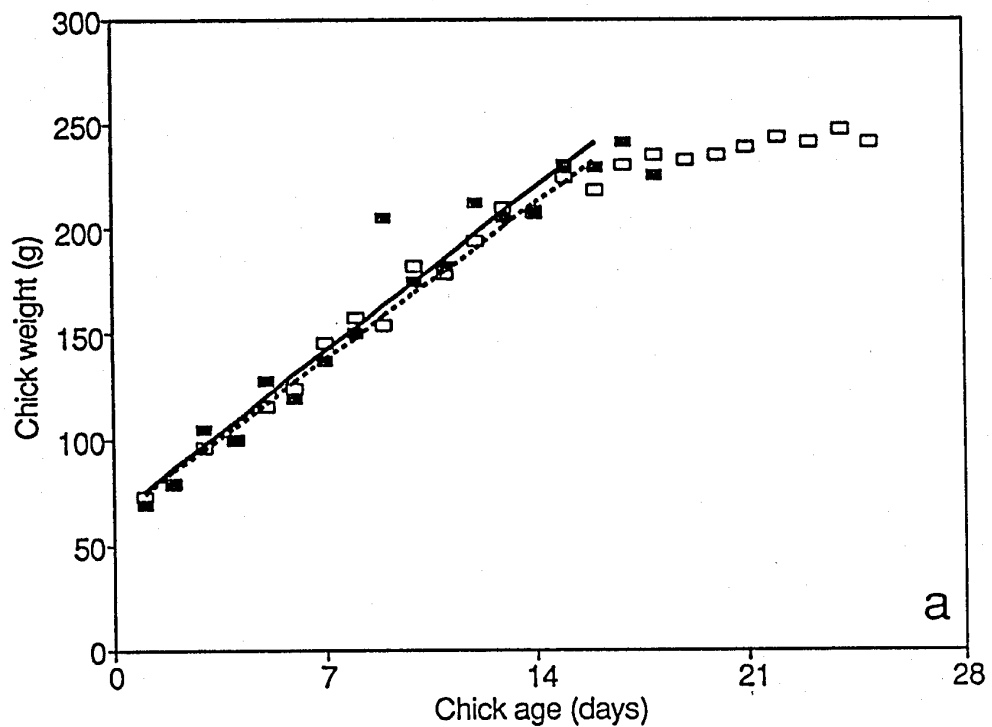


Table 3.7: Comparison of chick weights and wing lengths at 14 days on control and experimental chick growth plots in 1991 (mean (\pm SD)).

	Experimental chicks*	Control chicks	T-test	P
Weights	213.6 (22.4)	207.5 (26.9)	-0.06	>0.05
N	9	19		NS
Wing lengths	55.3 (2.9)	53.5 (3.7)	-1.28	>0.05
N	9	19		NS

*Experimental chicks include 6 chicks weighed at 13 days of age, corrected to 14 days.

Table 3.8: Comparison of chick weights and wing lengths at 14-days of young and older breeders in 1991 (mean (\pm SD)).

	Young chicks	Older chicks	T-test	P
Weights	171.2 (23.8)	210.5 (41.0)	-2.05	0.07
N	7	4		NS
Wing lengths	49.8 (6.8)	55.9 (5.2)	-1.55	0.16
N	7	4		NS

Table 3.9: Comparison of chick weights and wing lengths at 14-days of control, experimental, and young breeders, 1991 (mean (\pm SD)).

	Experimental chicks	Control chicks	Young chicks
Weights	234.2 (17.2)	201.6 (39.3)	171.2 (23.8)
N	11	6	7
Wing lengths	57.3 (4.1)	53.4 (6.1)	49.8 (6.8)
N	11	6	7
WEIGHTS			
EXPTAL vs. CONTROL		1.93	>0.05 NS
CONTROL vs. YOUNG		-1.72	>0.05 NS
EXPTAL vs. YOUNG		6.54	<0.001 **
WINGS			
EXPTAL vs. CONTROL		1.57	>0.05 NS
CONTROL vs. YOUNG		-0.99	>0.05 NS
EXPTAL vs. YOUNG		2.93	<0.01 **

DISCUSSION

The results of the experimental delay of laying date suggest that there is some difference in the ability of young and older birds, rather than an effect due to the timing of laying. Experimental birds on Coats Island were breeding c. 16 to 19 days later than early control birds, at a time when birds laying their first eggs performed very poorly (Figure 3.2). However, they showed very similar hatching and reproductive success to the early control breeders, which suggests that their high performance was due to their abilities as breeders. Lloyd (1979) found that early laying Razorbills which lost their first egg and laid a replacement egg were more successful than first eggs laid at the same time, suggesting that naturally late laying birds were not as proficient.

Hatchwell (1991) concluded that group synchrony in Common Murres was important in determining reproductive success rather than calendar date of laying. Birds that lay later than the mean for their breeding group are not as successful, regardless of the actual date the egg is laid relative to the population mean (Birkhead 1977, Wanless and Harris 1988, Hatchwell 1991). In the Common Murre, the spread in median laying dates between groups can be as large as 18 days (Harris and Wanless 1988). Birkhead and Harris (1985) suggested that calendar date may have a greater effect on Arctic-breeding alcids than group synchrony. The results from Coats Island, where there was a maximum difference of only 3 days among groups in mean date of laying (see Chapter 2, Table 2.2), support this suggestion.

In this study, experimental eggs were removed randomly over several breeding plots, while Hatchwell (1991) removed all experimental eggs from a single ledge. At the end of the season when most unmanipulated chicks had departed, the experimental breeders on Coats Island were relatively isolated from each other. Thus, group synchrony could not have been acting on these birds. Nevertheless, they performed as well as the earlier breeding control birds.

Experimental birds had much higher hatching and reproductive success than young birds, even though they were breeding c. 10 days later. Young birds were more likely to lose their eggs, probably due to ineptitude during incubation (see Chapter 2), or sites which were of lower quality than early breeders (see Chapter 4).

Replacement eggs of experimental birds on Coats Island were smaller than their first eggs, but did not differ in size from eggs of young birds. Both were significantly smaller than eggs of control birds. There was a seasonal decline in egg size on Coats Island in both years (Gaston 1991, pers. comm.), and replacement eggs usually follow this decline (Lloyd 1979, Birkhead and Nettleship 1984, Birkhead and Harris 1985). This suggests that in addition to differences due to age (i.e. ability to form a large egg, foraging differences), the decline in egg size could also be in response to the lateness in the season. It is could be advantageous for a bird breeding later than the optimum date of laying to produce a smaller egg as soon as possible, if conditions affecting reproductive success or the subsequent survival of the

chick deteriorate with date (Birkhead and Nettleship 1982). See Chapter 2 for further discussion on egg size.

Egg size has been shown to affect survival during the first few days of the chick rearing period (Coulson et al. 1969, Lloyd 1979, Furness 1983), while parental quality is often more important for chick growth up to the point of fledging (Davis 1975, Barrett and Runde 1980, Amundson and Stokland 1990, Bolton 1991). In this study, egg size did not differ between young and experimental breeders, suggesting that it was the ability of the parents to forage that determined the observed difference in chick growth.

CHICK FEEDING RATES

In 1991, feeding rates of control and experimental breeders did not differ until late in the chick rearing season (21 August). Feeding rates for experimental birds were very high that day, and prey may have been especially abundant. These results suggest that there was no difference in prey availability during the chick rearing period, and that at least on 21 August, 1991, there may have been an increase in the amount of prey available. In the Thick-billed Murre, different prey species appear to change in abundance and quality during the season and among years (Gaston and Noble 1985, Birkhead and Nettleship 1987c).

CHICK GROWTH

The growth and weight (at 14 days) of control and experimental chicks did not differ significantly, although they were being fed more than 2 weeks apart. This suggests that food was abundantly available to older, more experienced breeders throughout the season. Although the experimental eggs were smaller than control eggs, the chicks did not differ in weight at 3 days of age. Hedgren and Linnman (1979) also found no initial difference in weight. However, the late chicks in their study did not grow as quickly as the control chicks, with significant differences apparent by 10 days of age. They attributed these differences to a change in quality of prey, as control and experimental chicks were being fed at the same rate.

On Coats Island, the chicks of older birds breeding earlier in the season tended to be larger and heavier than the chicks of young birds at 14 days of age. When corrected for date of laying, chicks of experimental birds were also larger and heavier than the chicks of young birds. This suggests that although there was no seasonal decline in prey availability for older, more experienced breeders on Coats Island, young breeders either were not familiar with good foraging areas, or were not as proficient at capturing fish of suitable quality as older birds. However, it is worth noting that even the young breeders had chicks substantially heavier than those normal over 3 years at Digges Island, the nearest Thick-billed Murre colony to Coats Island (Gaston et al. 1983). This suggests that weights observed at Coats Island for the chicks of young

breeders were probably heavy enough to survive successfully after fledging.

Although Hedgren and Linnman (1979) identified late laying birds as possibly young, less experienced breeders in their experiment, they chose to remove the eggs 4 days after the mean laying date for the group, after 84% of the birds had laid, at a time when both probability of relaying was reduced, and many young birds may have laid (see Chapter 2, Figure 2.4). I removed eggs after c. 50% of birds had laid on a given plot, so that the mean laying date for those removed was several days before the mean laying date. Hence, Hedgren and Linnman (1979) may have removed eggs from young, later laying birds, and the poor chick growth rate could have been due to age-related differences in foraging ability. Furness (1983) found lower growth rates in later hatching Great Skua chicks, and suggested that this could be due to a reduction in food, or a lack of drive from its parent.

A young breeder can raise a chick to fledging age and be considered successful, but the chick may be lighter than one of a more experienced breeder, and may not survive as well after fledging. In alcids, there is often a seasonal decline in chick fledging weight (see Gaston 1985). There has been no evidence that post-fledging survival is related to fledging weight of alcids (Razorbill: Lloyd 1979; Common Murre: Hedgren 1981, Harris et al. 1992; Atlantic Puffin: Harris and Rothery 1985), and only recently has hatching date been shown to affect survival of late chicks in some years (Harris et al. 1992, see below). Razorbill and murre

chicks fledge at c. 25% of adult weight, and go to sea with their male parent. In the Common Murre, the parent continued to feed its chick for 2 to 3 months (Varoujean et al. 1979 in Harris et al. 1991), hence weight at independence may be more important than fledging weight in determining post-fledging survival (Harris et al. 1991).

The survival of late Thick-billed Murre chicks from high Arctic colonies and in Hudson Strait may also be affected by the rapid onset of winter. Late breeding birds from Coats Island probably leave Hudson Strait by late September/early October (Gaston 1980, Orr and Ward 1982). The weather at the end of the breeding season becomes quite rough and unpredictable, which could accentuate any decline in prey availability, making it more difficult for the adult to find food for its chick. As well, the adult molts at this time and both it and the chick are unable to fly for several weeks (Birkhead and Taylor 1977). The adult is therefore restricted in its foraging range due to the inability to fly and the need to stay close to its chick.

Harris et al. (1992) showed that in 2 highly productive years at a Common Murre colony, chicks of late breeders did not survive as well as those of early breeders. In 4 other years, there was no significant effect of hatching date on subsequent survival. Harris et al. (1992) suggested that chicks of earlier laying breeders had some advantage over later chicks in good years. An alternative hypothesis could be that in good years, a higher proportion of young breeders might hatch their egg, and raise a chick at the end

of the season to fledging age (such as in 1991 in this study). If their post-fledging survival was lower due to the inability of the parent to raise the chick up to independence, this could have caused the decline in survival in productive years.

There was no evidence from my egg removal experiments that birds laying later in the season encountered any adverse conditions with respect to reproductive success or prey availability. I conclude that little of the difference between older and younger birds in reproductive parameters is caused by timing of laying. In the next chapter I examine the possibility that the differences are related to differences in breeding sites.

**Chapter 4: DIFFERENCES IN BREEDING SITE CHARACTERISTICS AND THEIR
EFFECT ON THE REPRODUCTIVE SUCCESS OF KNOWN AGE BREEDERS**

INTRODUCTION

The characteristics of breeding sites have been shown to affect reproductive success in many colonial birds (Kittiwake, Rissa tridactyla: Coulson 1968; Atlantic Puffin: Nettleship 1972; Shag, Phalacrocorax aristotelis: Potts et al. 1980; and Razorbill: Hudson 1982).

Among colonial birds, older birds often occupy the best quality sites, preventing younger, less experienced birds from using these sites. Young birds often arrive after older birds have established their sites (Coulson and Horobin 1976, Potts et al. 1980), but in some species, breeders of all ages arrive at the same time, with older birds excluding the younger birds from better quality areas (Harrington 1974, Ryder 1975, Chabryzk and Coulson 1976). Coulson (1966, 1968) found a difference in success between birds breeding in the center and periphery of the colony, and suggested that age and pairbond along with individual quality could contribute to these differences. In the Shag, age and nest-site quality were the main factors affecting reproductive success (Potts et al. 1980). When a large number of older shags died off making high quality sites available, young birds were able to occupy these sites and breed much more successfully than on their previous poor quality sites.

Thick-billed Murres breed colonially on narrow cliff ledges (Tuck 1961, Williams 1974). As they do not build a nest, breeding sites are structurally quite simple and can be characterized by a few basic traits (Gaston and Nettleship 1981, Squibb and Hunt 1983). Various site characteristics have been shown to have an effect on the reproductive success of Thick-billed Murres depending on the structure of the colony itself and the causes of egg and chick mortality (Gaston and Nettleship 1981, Birkhead et al. 1985, Birkhead and Nettleship 1987b). Birkhead et al. (1985) found that much of the variation in reproductive success could be explained by differences in site characteristics, with differences in the quality of individual birds and overall physical differences in breeding areas also contributing.

Differences in reproductive success between young and older Thick-billed Murres demonstrated in Chapter 2 may be due, in part, to differences in breeding site quality. In this chapter, I will examine the effect of site characteristics on reproductive success in birds of known age and compare the sites of young and older birds to see if there is a difference in types of sites occupied.

MATERIALS AND METHODS

All breeding sites for which reproductive outcome was known in at least one year, whether the site produced a fledged chick or not; (N=527) were classified for the following traits:

- 1) number of neighbours in contact with the bird on its site (0, 1, 2, >2);
- 2) number of rock walls bordering on the site (0, 1, 2, 3);
- 3) width of the ledge (narrow (<.25 m - the breeder's tail protrudes over the edge), wide (>.25 m));
- 4) if on a wide ledge, whether the site was near the edge or away from the edge; and
- 5) slope of the site (level, sloped).

In a few cases, the bird was not against a wall, but was leaning up against a rock. These sites were considered to have one wall. Only 3 sites in each of the two years were sloped towards the cliff, and were included with sites which sloped away from the cliff.

The breeding sites classified as above included those occupied by young (four and five-year olds; $N_{1990}=35$; $N_{1991}=33$) and older (> 7-year olds; $N_{1990}=67$; $N_{1991}=65$) breeders.

INDEPENDENT EFFECT OF SITE CHARACTERISTICS

Age-related differences in site characteristics were compared using χ^2 tests between young and older birds in 1990 and 1991. χ^2 (with Yates correction if ≥ 1 expected frequency was <5) and Fisher Exact tests (if total sample sizes were <35) were used to establish

the effect of individual site characteristics on reproductive success of these two groups of birds when considered independently.

COMBINED EFFECT OF SITE CHARACTERISTICS

Stepwise logistic regression was used to see how breeding site characteristics affected reproductive success (see Birkhead et al. 1985 for statistical details). Each classified site was either successful or unsuccessful and the data were modelled using SAS (SAS Institute Inc. 1990). Parameters were added one at a time into the model and those which helped explain some of the variation (i.e. improved the fit) remained in the model. Site characteristic #4 above was excluded for this analysis as not all sites were on wide ledges. The p-level for entry and removal of breeding site variables was set at 0.10, as a p-level of 0.05 is considered to be too conservative for logistic regression (Hosmer and Lemeshow 1989).

SITE CHANGE

A bird changed its site if it moved >20cm from its previous site. Proportions of birds moving sites were underestimated, as only site changes of known age birds whose band numbers were read in both years were considered.

RESULTS

Most sites on the study plots had one or more neighbours (86%) and one or more walls (86%, Table 4.1). Narrow and wide ledges were used in equal proportions although the majority of birds on wide ledges (82%) nested away from the edge. Level sites were more common (62%) than sloped sites. Over 47% of sites had one or more neighbours, one or more walls, and was not sloped.

INDEPENDENT EFFECT OF SITE CHARACTERISTICS

In 1990, 76% (28 of 37) of breeding sites of older birds with two or more neighbours were successful, while only 43% (13 of 30) of all other sites fledged a chick ($\chi^2=8.25$, $P<.005$). Birds breeding on wide ledges were not as successful if breeding on the edge (1 of 16) than those breeding away from the edge (18 of 25; Fisher Exact test, $P=.02$, Table 4.2a). In 1991, breeding sites with one or more neighbour fledged a chick in 49 of 57 cases (86%). Those without neighbours had a significantly lower reproductive success of 38% ($N=8$, $\chi^2=14.54$, $P=0.0001$, Table 4.2b). No other site characteristics affected reproductive success significantly in either year, although there was a trend for success to increase with the number of walls.

In 1990, only 17.1% (6 of 35) young pairs successfully fledged a chick. Site characteristics did not have a significant effect on reproductive success in young birds, although only 1 of 12 sites at the edge of wide ledges were successful, compared to 5 of 15 on the inside (Fisher Exact test, $P=0.18$) (Table 4.3a). In 1991, when

success was higher (36.7%, N=33), sites with 2 or more neighbours were significantly more successful than sites with 0 or 1 neighbours (Table 4.3b). Only 1 of 10 sites which did not have a wall were successful, while 11 of 22 sites with at least one wall fledged a chick (Fisher Exact test, $P=.05$). As in 1990, birds on sites away from the edge of wide ledges were more successful than those close to the edge in 1991 (Table 4.3a and b).

When comparing young and older birds on the same type of site, older birds were always more successful than young birds (Table 4.2 and 4.3).

Table 4.1: Site characteristics of all sites used at least once during 1990 and 1991 (N=527).

Site characteristics	N	%
Neighbours		
0	73	13.9
1	171	32.4
2	199	37.8
>2	84	15.9
Walls		
0	75	14.2
1	393	74.6
2	48	9.1
>2	11	2.1
Width		
Narrow	265	50.3
Wide	262	49.7
Wide sites (N=262)		
At edge	48	18.3
Away from edge	214	81.7
Slope		
Level	328	62.2
Sloped	199	37.8

Table 4.2: The effect of individual site characteristics considered independently on the reproductive success of older breeders in a) 1990 and b) 1991.

a)

Site characteristic	Reproductive success % (N)		χ^2 or FE	P
Neighbors	0 + 1 43.3 (30)	< ≥ 2 75.7 (37)	7.30	0.007 **
Walls	0 33.0 (6)	= ≥ 1 63.9 (61)	1.06	0.30 NS
Width	Narrow 61.1 (36)	= Wide 61.3 (31)	0.0002	0.99 NS
Wide sites	Edge 16.7 (6)	< Inside 72.0 (25)	FE	0.02 **
Slope	Level 66.7 (45)	= Sloped 50.0 (22)	1.73	0.19 NS

b)

Site characteristic	Reproductive success % (N)		χ^2 or FE	P
Neighbors	0 37.5 (8)	< ≥ 1 86.0 (57)	7.49	0.006 **
Walls	0 50.0 (4)	= ≥ 1 82.0 (61)	0.82	0.37 NS
Width	Narrow 85.0 (40)	= Wide 72.0 (25)	1.63	0.20 NS
Wide sites	Edge 100 (3)	= Inside 68.2 (22)	FE	0.53 NS
Slope	Level 79.1 (43)	= Sloped 81.8 (22)	0.00	1.00 NS

Table 4.3: The effect of individual site characteristics considered independently on the reproductive success of young breeders in a) 1990 and b) 1991.

a)

Site characteristic	Reproductive success % (N)		χ^2 or FE	P
Neighbors	0	= ≥ 1	0.14	0.71 NS
	9.1 (11)	20.8 (24)		
Walls	0	= ≥ 1	0.14	0.71 NS
	9.1 (11)	20.8 (24)		
Width	Narrow	= Wide	0.87	0.35 NS
	0.0 (8)	22.2 (27)		
Wide sites	Edge	= Inside	FE	0.18 NS
	8.3 (12)	33.3 (15)		
Slope	Level	= Sloped	0	1.00 NS
	18.8 (16)	15.8 (19)		

b)

Site characteristic	Reproductive success % (N)		χ^2 or FE	P
Neighbors	0	< ≥ 1	4.24	0.04 **
	0.0 (12)	57.1 (21)		
Walls	0	(<) ≥ 1	FE	0.0496 NS
	10.0 (10)	47.8 (23)		
Width	Narrow	= Wide	FE	0.72 NS
	31.3 (16)	41.2 (17)		
Wide sites	Edge	= Inside	FE	0.10 NS
	0.0 (4)	53.8 (13)		
Slope	Level	= Sloped	FE	0.48 NS
	43.8 (16)	29.4 (17)		

COMBINED EFFECTS OF SITE CHARACTERISTICS

When all site characteristics were considered together, only the number of neighbours had a significant effect on the reproductive success of older birds in 1990 (Table 4.4a). Those with more than one neighbour were successful at 65% (37 of 57) of these sites, while only 4 of the remaining 10 without neighbours fledged a chick.

In 1991, both the number of neighbours (positively) and width of ledge (negatively) contributed significantly to reproductive success (Table 4.4a). In 1991, breeding sites with one or more neighbours and on the edge of a ledge fledged a chick in 35 of 37 cases (95%). All other sites had a significantly lower reproductive success of 61% (N=28) ($\chi^2=11.43$, $P<0.001$).

As with site characteristics analyzed separately, no site characteristics when considered together had a significant effect on reproductive success for young breeders in 1990 (Table 4.4b). This result is most likely due to the high failure rate in that year, with almost all young breeders failing regardless of site quality. In 1991, number of neighbours and number of walls significantly improved the reproductive success of young breeders (Table 4.4b). The success of sites of young birds with one or more neighbour and one or more walls was 69% (N=16), while the rest of the sites had an overall success of only 6% (1 of 18) ($\chi^2=15.54$, $P<0.0001$).

AGE-RELATED SITE DIFFERENCES

In 1990, there were significant differences between sites of young and older birds in all characteristics considered (Table 4.5). In 1991, trends were similar but differences were significant only for numbers of neighbours and numbers of walls (Table 4.6). Older birds were more likely to have two or more neighbours and at least one wall at their site than young birds. Young breeders bred on wide ledges more often than older birds. When looking at wide ledge sites separately, both young and older birds tended to breed on sites away from the edge, although a higher proportion of young birds were found near the edge in both years. More older birds than young birds bred on level ledges than young birds.

Table 4.4: Effect of site characteristics when considered together on reproductive success of a) older and b) young breeders in 1990 and 1991, using logistic regression.

a) Older

Year	Site characteristic	P†	
1990	Neighbors:>2 > 2 > 1 > 0	0.05	**
	Wall	0.25	NS
	Slope	0.31	NS
	Width	0.46	NS
1991	Neighbors: >2 > 2 > 1 > 0	0.02	**
	Width: Narrow > Wide	0.04	**
	Wall	0.24	NS
	Slope	0.96	NS

b) Young

Year	Site characteristic	P†	
1990	Wall	0.11	NS
	Width	0.14	NS
	Neighbors	0.29	NS
	Slope	0.82	NS
1991	Neighbors:>2 > 2 > 1 > 0	0.0004	**
	Wall: 2 > 1 > 0	0.02	**
	Slope	0.61	NS
	Width	0.74	NS

† P-values are for χ^2 statistic of site characteristics.

Table 4.5: Breeding site characteristics for the older and young birds in 1990.

1990	OLDER (N=67)	1990 %	YOUNG (N=35)	1990 %	χ^2	P
Neighbors					0+1/≥2	
0	10	14.9	11	31.4	5.23	0.02
1	20	29.8	13	37.1		**
2	32	47.8	7	20.0		
>2	5	7.5	4	11.5		
Walls					0/≥1	
0	6	9.0	11	31.4	8.36	0.004
1	51	76.1	20	57.1		**
≥2	10	14.9	4	11.4		
Width						
Narrow	36	53.7	8	22.9	8.93	0.003
Wide	31	46.3	27	77.1		**
Wide sites						
Edge	6	19.4	12	44.4	4.24	0.04
Inside	25	80.6	15	55.6		**
Slope						
Level	45	67.1	16	45.7	4.40	0.04
Sloped	22	32.9	19	54.3		**
<u>Reproductive success</u>						
Failed	26	38.8	29	82.9	17.96	<0.0001
Succeeded	41	61.2	6	17.1		**

Table 4.6: Breeding site characteristics for older and young birds in 1991.

1991	OLDER (N=65)	1991 %	YOUNG (N=33)	1991 %	χ^2	P
Neighbors					0+1/≥2	
0	8	12.3	12	36.4	9.49	0.01
1	20	30.8	11	33.3		**
2	30	46.2	8	24.2		
>2	7	10.7	2	6.1		
Walls					0/≥1	
0	4	6.2	10	30.3	8.55	0.004
1	54	83.0	22	66.7		**
≥2	7	10.8	1	3.0		
Width						
Narrow	40	61.5	16	48.5	1.52	0.22
Wide	25	38.5	17	51.5		NS
Wide sites						
Edge	3	12.0	4	23.5	0.97	0.33
Inside	22	88.0	13	76.5		NS
Slope						
Level	43	66.2	16	48.5	2.85	0.09
Sloped	22	33.8	17	51.5		NS
<u>Reproductive success</u>						
Failed	13	20.0	21	63.6	18.39	<.0001
Succeeded	52	80.0	12	36.4		**

SITE CHANGE

Young birds were more likely to change breeding sites (4 of 20) than older birds (1 of 54) ($\chi^2=5.02$, $P<0.03$). Three of the 4 young birds improved their outcome at their new site, although only two birds "improved" its site by moving against a wall and gaining a neighbour.

Sites occupied in 1990 that were vacant in 1991 failed more often (27.6%, $N=58$) than sites which were occupied in both years in 1991 (1990 success: 56.8%, $N=259$; $\chi^2=16.1$, $P=0.001$).

DISCUSSION

Both the quality of an individual breeding on a site and the particular quality of the site can affect the chances of fledging a chick (Gaston and Nettleship 1981). When site characteristics were considered independently, older birds were more successful if they had ≥ 1 neighbour, and if their site was away from the edge if on a wide ledge. Most older birds were found on these types of sites. In 1991, young birds were more successful if their site had ≥ 1 neighbours, and ≥ 1 walls. Almost all young birds failed in 1990, and it appears that site characteristics had no effect on reproductive success, although the trends were similar to 1991. Since all characteristics of a given site must interact, logistic regression was used to establish their relative importance to reproductive success. The results of the analysis of the combined effects of site characteristics was similar to independent effects.

Neighbours might affect reproductive success in several ways. Breeding beside other birds could reduce the chances of a successful predation attempt, as a group of birds is more vigilant and less likely to flush than a single bird incubating (Hoogland and Sherman 1976, Birkhead 1977, Harris 1980). The only avian predator on Coats Island is the Glaucous Gull, Larus hyperboreus. Gulls tend to attack murre sites in two ways: either they grab eggs/chicks or pull murre off their sites during surprise aerial attacks, or they land on broad ledges and walk up to a site, attempting to grab an egg or chick from under its parent (Elliot et al. in prep). If a bird is not on its breeding site, an egg might

be less likely to be taken by a predator when there are neighbours remaining nearby, as murrelets in groups often turn their heads towards an intruder, presenting them with a solid wall of sharp bills (Birkhead 1977). Chicks actively seek shelter under neighbouring adults when their parent is not present (Tuck 1961). If neighbouring birds are synchronized in their timing of breeding, the chances of being predated will be reduced (Hamilton 1971, Birkhead 1977, Hatchwell 1991). Alternatively, an egg might be more likely to be dislodged because of increased fighting with increasing numbers of neighbours (Gaston and Nettleship 1981, Hatchwell 1991). Increasing numbers of neighbours improved reproductive success in murrelets in all similar studies (Gaston and Nettleship 1981, Birkhead and Nettleship 1987b, Hatchwell 1991).

Walls act as a support for incubating birds, as well as provide protection to the egg and chick from predation to some extent (Gaston and Nettleship 1981). Birds breeding away from a wall would be more likely to be jostled or attacked by birds passing to get to their sites.

Many studies have found that birds breeding in the central, denser areas of colonies are often older, and begin to breed earlier, lay larger clutches, and are more successful than birds breeding in peripheral areas (Coulson 1966, Tenaza 1971, Harrington 1974, Ryder 1975, Charbryzk and Coulson 1976, Coulson and Horobin 1976, Finney and Cooke 1978). Murrelets breed on discrete ledges, with sites on each ledge located either centrally or peripherally in relation to other breeders. Young birds were more likely to be

found on sites upon which older birds performed poorly (i.e. no neighbours, no walls; Tables 4.5 and 4.6). This suggests that young birds occupy sites at the edge of or away from groups of birds, and more often near the edge of a ledge, while older birds are more likely to be against a wall in a group of birds. Poor performance by birds on the edges of groups could be due to an inability to compete successfully for a better quality site because of late arrival (Potts et al. 1980). Chabryzk and Coulson (1976) found that in the Herring Gull, denser areas were more attractive to new recruits, but they had less success in establishing sites than those which chose to breed in the less dense areas.

Older Thick-billed Murres arrive at the colony earlier than young birds (Noble 1990), hence they might have an advantage in securing the best sites (Coulson and Horobin 1976). As prior occupation is an important determinant in territorial contests (Davies and Houston 1981), older birds would have a consequent advantage in defending their sites against later arrivals.

For each particular site characteristic, older birds were more successful than young birds (Tables 4.2 and 4.3), thus the ability of the breeder also affected their outcome. Birds may improve their outcome on different quality sites as they get older. For example, a young bird on a sloping narrow ledge might lose its egg quickly, while an older bird on the same type of site may have learned how to incubate its egg to hatching without losing it. Finney and Cooke (1978) found that older Snow Geese (Anser caerulescens caerulescens) performed better than young breeders in

areas where young birds bred predominantly.

Murres are highly site philopatric, with banded birds returning to the general area from which they fledged (Noble 1990), as well as breeding on the same site from year to year (Birkhead 1977). Hedgren (1980) found that birds that failed were more likely to change sites than birds that succeeded. Sites that are less successful are occupied less frequently than successful sites, and if they are more likely to be occupied by young inexperienced birds, their poor quality would be emphasized (Gaston and Nettleship 1981). I found that young birds did not obtain good quality sites, and were more likely to move, although only 2 of the 4 young birds in this study which changed sites moved towards a wall or a group of birds. The one older bird which moved went from a site at the end of a narrow ledge to its neighbour's site, gaining a second neighbour from the move.

The quality of a particular site may change over a number of years. A bird may breed on the edge of a group one year, but gain neighbours as the ledge becomes more densely occupied in future years. A peripheral could become a central site as new pairs join the breeding population. Murres appear to colonize ledges once a critical number of birds decides to breed (Gaston pers. comm.), and new pairs often breed at the edge of a group of breeders.

A higher proportion of sites occupied by young birds are of the type that older birds perform poorly on, which suggests that quality of breeding site may determine some of the difference in reproductive success between breeders of different ages. However,

younger birds consistently had lower reproductive success than older birds when type of site was controlled, although sites which are classified the same are not necessarily identical.

Chapter 5: GENERAL DISCUSSION

The results of this thesis provide novel information on breeding of known age individuals in an alcid species, the Thick-billed Murre. Thick-billed Murres show similar age-related and seasonal trends in reproductive parameters to many other seabirds studied. The marked seasonal decline in both hatching and overall reproductive success appears to be related to differences in age and experience in birds breeding at different times during the season, although other factors probably also contribute to the overall decline.

Several hypotheses have been suggested to explain the seasonal decline in reproductive success in murres (Uria spp.):

- 1) increased risk of predation for late birds not breeding synchronously. In the Common Murre, density and synchrony of nesting appear to be important on colonies with high levels of avian predation (Birkhead 1977, Hatchwell 1991). Late nesting birds on low density ledges were more likely to be predated. Thick-billed Murres do not breed as densely as Common Murres, which are often found in large groups several birds deep on broad ledges (Williams 1974, Birkhead and Nettleship 1987b). Few Thick-billed Murres on Coats Island had more than 2 neighbours. Although density may not play as important a role in determining reproductive success for Thick-billed Murres (Gaston and Nettleship 1981), having neighbours does improve their outcome, even if they are breeding on narrow ledges. Young birds, which are found away from groups and often on broader ledges, would not benefit from the

added defense or vigilance gained from having neighbours.

In my study, the cause of egg loss was rarely established, although a few eggs were seen rolling into cracks or falling off ledges due to fights or ineptitude. Predation events are more likely to be noticed by an observer, due to the disturbance created by the predator. On Coats Island, roughly 8% of egg and chick loss was caused by the 14 breeding pairs of Glaucous Gulls breeding on the western colony each year (Gilchrist, pers. comm.). The gulls constantly patrol the cliffs, grabbing eggs and chicks, or landing on ledges and harrassing breeding murres on the ledges (Elliot et al. in prep). Later in the season on Coats Island, just after peak fledging of the murre chicks, the Glaucous Gulls reduced the amount of time they patrolled the colony, and switched to scavenging dead or abandoned chicks on the water. The gull chicks were beginning their initial flights at this time, and the family groups dispersed soon after (Gilchrist, pers.comm.). This reduction of the intensity of predation on late laying Thick-billed Murres could help explain the lack of a decline in fledging success late in the season (Chapter 2).

Much of the loss from late sites occurred during incubation, when most birds were still present on the cliffs with chicks. Fledging success did not decline seasonally, and experimental chicks breeding very late in the season were as successful as earlier chicks, even though they were scattered across several plots and therefore vulnerable to predation.

2) Prey quality and/or availability. The decline in success

on Coats Island was due to an increase in egg loss for late breeders. It seems unlikely that prey quality could be the cause of these losses, as the later laying birds are failing when food is still abundant, and earlier layers are successfully raising their offspring (Newton and Marquiss 1984, Wanless and Harris 1988, Weimerskirch 1990). Fledging success in murres is usually quite high (c. 90%), but most studies do not discuss seasonal trends in fledging (e.g. Hatchwell 1991). A seasonal decline in fledging success was found in Thick-billed Murres on Prince Leopold Island by Gaston and Nettleship (1981). They found that chicks from replacement eggs had very low fledging success, suggesting that the decline was due to deteriorating conditions, rather than young or inexperienced birds breeding later in the season. On Coats Island, naturally occurring replacement eggs had low hatching success, but fledging success of chicks which hatched remained high (Table 2.14).

Several studies also discuss the reduction in fledging weight as a decline in reproductive success (Hedgren and Linnman 1979, Gaston and Nettleship 1981). Weight at fledging has not yet been shown to affect future survival in alcids (see Chapter 3 discussion). Late Common Murre chicks have been shown to have lower post-fledging survival than earlier chicks in some years, but there was no difference in growth between chicks which did and did not survive (Harris et al. 1992). Seasonal declines in Thick-billed Murre chick weights do not always occur, and may be due to local changes in food near particular colonies in some years

(Gaston et al. 1983, Gaston 1985). On Coats Island, growth of chicks of control and experimental breeders did not differ although they were being fed over 2 weeks apart. Since these two groups presumably had similar experience and hence similar foraging abilities, there was no evidence of a change in prey availability. Cairns et al. (1990) found that Common Murres spent <30% of their foraging trips actively flying and diving, and therefore may be able to increase the amount of time spent foraging when food resources are low without altering the time spent away from the colony (Burger and Piatt 1990). Thick-billed Murres spend less time on the cliffs (Gaston unpubl.) and hence probably more time foraging. A decline in food availability may not have affected feeding rates of the more experienced experimental birds in this study, but might have caused young birds to provision their chicks at a slower rate, or with prey of lesser quality. Unfortunately, I was not able to measure growth rates of chicks of naturally late laying breeders and was not able to observe feeding rates of known age birds. These data would have allowed me to determine whether there was a seasonal decline in fledging weights, and whether the chicks of young birds followed this decline.

3) My data support the hypothesis that the seasonal decline in reproductive success is caused by a higher proportion of young or inexperienced birds breeding late in the season. Thick-billed Murres return to their natal colony at c. two years of age, but only begin to breed when four or five-years old (Noble 1990). First-time (and often second-time) breeders are performing new

reproductive activities such as laying an egg, changing over during incubation and chick rearing periods, synchronizing shifts, foraging for chicks, and raising the chick after fledging.

The combination of earlier, more successful older birds and the later, less successful young birds approximated the seasonal decline in hatching success for the total sample (Figure 2.12). Although young birds may only make up a small proportion of the total population at a colony of long-lived birds (Birkhead and Harris 1985), the actual numbers breeding late in the season are usually quite small, especially in murres, where the pattern of laying tends to be skewed right. Hence young birds may constitute a disproportionate part of the population towards the end of the laying period. Although we do not know how representative our known age sample of breeding birds is to the overall Coats Island population, it suggests that the difference in timing of breeding between older, more successful birds breeding earlier and younger, less successful birds could explain a large part of the seasonal decline in reproductive success.

The performance of the experimentally late breeding birds (Chapter 3) lends further support to the hypothesis that age affects the decline in reproductive success. The experimental breeders, assumed to be older and more experienced, were as successful late in the season as the earlier breeding control birds, and much more successful than the young breeders.

The effects of age and breeding experience are difficult to separate, and probably both contribute to some extent to

improvements of reproductive success (Saether 1990). Pyle et al. (1991) suggested that in the Western Gull (Larus occidentalis), experience contributed to improved hatching success, while age affected timing of breeding and fledging success. This could be the case with Thick-billed Murres, where most loss occurs during the incubation period, and young birds lose eggs more often than older birds, probably due to ineptitude during changeovers, poor coordination of nest reliefs, failure to incubate properly (Nelson 1966), and possibly site quality (see Chapter 4).

Davis (1976) hypothesizes that there are advantages and disadvantages to breeding at a young age. If a young bird fails, it will not contribute any offspring to its lifetime total, and may incur a higher rate of mortality due to the effort. If age alone is important, then the number of offspring produced is the only benefit of early breeding. If experience is also important, the actual experience gained could outweigh an unsuccessful breeding attempt, especially in a long-lived bird (Davis 1976, Weimerskirch 1990). Young Thick-billed Murres appear to benefit from breeding experience, even if they do not successfully hatch their egg during their first breeding attempt.

The fledging period has often been considered to be the most stressful part of the breeding cycle, but in many seabirds, the coordination of the incubation period may also be difficult, and experience gained during this time is probably important for future breeding attempts (Weimerskirch 1990). In the case of the Thick-billed Murre, efficiency in incubation is a more important

component of reproductive success than the ability to provision a chick, especially when breeding at a young age.

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Appendix 1: Logistic regression results for seasonal decline in 1990 and 1991.

SUCCESS	AGE	N	RANGE	SLOPE DIFF?		PROB	FITS	MODEL?		INT	SE	SLOPE	SE		
				CHI-SQ	CHI-SQ			CHI-SQ	PROB D.F.						
1990															
HATCH	TOTAL SAMPLE	292	15-59	Y	31.1	0	Y	33.86	0.33	31	4.625	0.7983	-0.1624	0.0291	
FLEDGE	TOTAL SAMPLE	159	15-41	N	0.88	0.35	Y	17.1	0.76	22	2.9927	1.382	-0.0489	0.0521	
REPROD	TOTAL SAMPLE	292	15-59	Y	26.74	0	Y	31.02	0.47	31	3.9688	0.7929	-0.152	0.0294	
HATCH*	NO YG&OLD	207	17-59	Y	19.31	0	Y	9.68	0.56	11	4.6136	0.9934	-0.1607	0.0366	
FLEDGE	NO YG&OLD	116	19-41	N	0.03	0.86	Y	17.7	0.34	16	1.9318	1.7565	-0.0118	0.0678	
REPROD	NO YG&OLD	207	17-59	Y	15.68	0.0001	Y	35.22	0.13	27	3.8298	0.9918	-0.147	0.0371	
HATCH	YOUNG	31	19-43	N	1.08	0.3	Y	18.89	0.27	16	1.3039	2.6026	-0.088	0.0847	
FLEDGE	YOUNG	6	19-40	N	ALL HATCHED FLEDGED										
REPROD*	YOUNG	31	19-43	N	1.18	0.28	Y	7.36	0.39	7	1.5457	2.6941	-0.0961	0.0884	
HATCH*	OLDER	54	15-35	N	1.25	0.26	Y	5.27	0.38	5	2.6821	1.747	-0.0728	0.0651	
FLEDGE	OLDER	37	15-34	N	3.36	0.07	Y	8.35	0.87	14	8.7291	3.9623	-0.2565	0.1399	
REPROD	OLDER	54	15-35	Y	4	0.0455	Y	18.36	0.37	17	3.8434	1.7703	-0.1339	0.067	
HATCH	YG&OLD	85	15-43	Y	10.11	0.002	Y	27.65	0.32	25	4.0868	1.2917	-0.1458	0.0459	
FLEDGE	YG&OLD	43	15-40	N	1.91	0.17	Y	12.18	0.73	16	5.7307	2.8334	-0.1369	0.099	
REPROD	YG&OLD	85	15-43	Y	11.01	0.0009	Y	26.68	0.37	25	4.2204	1.3388	-0.1608	0.0485	
1991															
HATCH	TOTAL SAMPLE	277	17-47	Y	24.74	0	Y	32.6	0.17	26	4.3095	0.7994	-0.1496	0.0301	
FLEDGE	TOTAL SAMPLE	164	17-42	N	0.53	0.47	Y	26.88	0.08	18	0.7287	1.7939	0.0529	0.0729	
REPROD	TOTAL SAMPLE	277	17-47	Y	17.61	0	N	43.14	0.02	26	3.2489	0.7568	-0.1207	0.0288	
HATCH*	TOTAL SAMPLE	277	17-47	Y	16.76	0	N	20.29	0.02	9	3.0255	0.7222	-0.1119	0.0273	
FLEDGE*	NO YG&OLD	201	17-47	Y	19.55	0	Y	28.25	0.25	24	4.6197	0.989	-0.1667	0.0377	
REPROD*	NO YG&OLD	114	17-47	N	0.28	0.6	Y	5.52	0.36	5	0.8442	1.9746	0.0426	0.0806	
HATCH	YOUNG	201	17-47	Y	13.18	0.0003	Y	12.73	0.18	9	3.1724	0.8854	-0.1234	0.034	
FLEDGE	YOUNG	28	24-42	N	1.12	0.29	Y	17.94	0.06	10	2.6546	2.7866	-0.1023	0.0968	
REPROD*	YOUNG	12	24-42	N	0.12	0.73	Y	6.2	0.29	5	3.0021	4.1578	-0.0492	0.1424	
HATCH	YOUNG	28	24-42	N	0.74	0.39	Y	8.51	0.07	4	1.742	2.7072	-0.0819	0.0952	
FLEDGE	OLDER	48	19-41	N	1.5	0.22	Y	17.99	0.16	13	3.4336	1.7837	-0.0817	0.0668	
REPROD*	OLDER	38	19-41	N	1.17	0.28	Y	6.86	0.81	11	-5.1047	7.0925	0.3448	0.3186	
HATCH	OLDER	48	19-41	N	1.21	0.27	Y	9.5	0.09	5	2.9212	1.7082	-0.0708	0.0643	
FLEDGE	YG&OLD	76	19-42	Y	5.95	0.01	Y	27.05	0.1	19	4.0563	1.4254	-0.1265	0.0519	
REPROD*	YG&OLD	50	19-42	N	0	0.99	Y	13.33	0.5	14	2.471	3.0596	-0.00112	0.1182	
HATCH	YG&OLD	76	19-42	Y	4.89	0.03	N	33.12	0.02	19	3.4174	1.3757	-0.1119	0.0506	
FLEDGE	YG&OLD	76	19-42	Y	5.73	0.02	N	18.34	0.005	6	3.8237	1.44	-0.1264	0.0528	

* Original samples did not fit the model, data were regrouped into 3-day intervals and rerun.