BREEDING PERFORMANCE OF BLACK-LEGGED KITTIWAKES ON GREAT ISLAND, NEWFOUNDLAND, DURING PERIODS OF REDUCED FOOD AVAILABILITY

HEIDI REGEHR

BREEDING PERFORMANCE OF BLACK-LEGGED KITTIWAKES ON GREAT ISLAND, NEWFOUNDLAND, DURING PERIODS OF REDUCED FOOD AVAILABILITY

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ABSTRACT

The breeding success of Black-legged Kittiwakes (Rissa tridactyla) was investigated on Great Island, Witless Bay, Newfoundland, in 1992 and 1993, following two years of breeding failure. Egg production was low in both years. High egg mortalities (90% and 89%) and high chick mortality in 1992 (93%), but not in 1993 (32%), resulted in a breeding success of 1% in 1992 and 7% in 1993. Timing of breeding was later than in previous years and clutches and eggs were smaller. Failure was extensive throughout the colony. The degree of failure varied consistently among regions between years which was probably related to cliff structure and therefore to nest predation. Comparison of egg shape indices among years suggested that a higher proportion of older individuals were breeding in years of poor productivity. This is consistent with the hypothesis that older breeders are more able and willing to expend effort and incur cost.

Egg predation, primarily by Great Black-backed Gulls (Larus marinus), accounted for most egg mortality. Results suggest that egg predation in both years and poor chick survival in 1992 were related to food shortage. Capelin (Mallotus villosus) arrived inshore for spawning up to 1 month later than normal, which, in conjunction with a lack of fish offal, was associated with food shortage in kittiwakes and in other gulls. Kittiwake incubation and chick-rearing shifts were shorter and survival time of chicks was longer after capelin arrival than before in 1992, indicating increased food availability. Observations and growth measurements indicated that chicks hatching before capelin arrival were starving. The effect of hatchdate on chick survival was less pronounced in 1993 than in 1992. Unattended eggs and chicks were uncommon and adults endured long nest shifts, probably in response to high predation risk. Incubation and chick-rearing shifts were shorter and feeding rates were greater in 1993 than in 1992, suggesting greater food availability in 1993. The seasonal migration of capelin into inshore waters in Witless Bay provides an important resource to kittiwakes, affecting their time budgets and survival of their chicks.

FOR MY FATHER

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CHAPTER 1 INTRODUCTION

The importance of seabirds as indicators of changes in the marine environment is becoming increasingly recognized (Furness and Barrett 1985, 1991, Chapdelaine and Brousseau 1989, Baird 1990, Harris and Wanless 1990, Furness and Nettleship 1991, Murphy et al. 1991, Montevecchi and Myers 1992, Monaghan et al. 1993, Montevecchi 1993). Seabirds are relatively easily studied and are often at the tops of food chains where they are vulnerable to changes throughout the tropic levels. Changes in marine food webs are therefore reflected in their breeding biology.

Some seabirds, such as the Black-legged Kittiwake (Rissa tridactyla), are particularly suitable indicators of change (Harris and Wanless 1990, Monaghan et al. 1993, Montevecchi 1993). Kittiwakes breed colonially on cliffs, with one distinctly formed nest per pair. They are therefore easily studied and surveyed, and the contents of their nests can be determined with little or no disturbance. Kittiwakes are usually among the first species in a seabird colony to reflect external changes in their breeding success (Hatch et al. 1993). They are small, pelagic surface feeders, faced by greater time and energy constraints than larger species (Pearson 1968, Furness and Monaghan 1987) and are unable to pursue their prey under water but depend on it to come to the surface. They are therefore thought to be more sensitive to food shortage (Cairns 1987, Burger and Piatt 1990, Furness and Barrett 1991, Montevecchi 1993). Clutches vary from one to three eggs and provide the potential for varying breeding effort and success. This permits greater opportunity for interpretation and comparison than in seabird species with single-egg clutches. In addition, Black-legged Kittiwakes have a holarctic distribution so that within and between ocean comparisons are possible.

In Witless Bay, Newfoundland, Black-legged Kittiwakes experienced low breeding success in 1990 and severe breeding failure in 1991 (Neuman 1994). Breeding failure of kittiwakes was widespread in Newfoundland in 1991 with food shortage speculated as the cause (Casey 1994, Neuman 1994). It is becoming clear that changes are taking place in this oceanographic region. Sea surface temperatures during the summers have been colder than normal, a situation which appears to be closely associated with prey shifts in some seabird species, and with the maturation, spawning and inshore movements of capelin (Mallotus villosus) (Methven and Piatt 1991, Montevecchi and Myers 1992). Capelin, the main prey species of breeding seabirds in much of the northwest Atlantic (Brown and Nettleship 1984, Burger and Piatt 1990, Montevecchi and Myers 1992), winter offshore and migrate to inshore Newfoundland waters to spawn on beaches during June and July (Templeman 1948, Carscadden 1984). The inshore arrival of spawning capelin has been delayed by two to four weeks in recent years (Montevecchi and Myers 1992, J. Carscadden, DFO, St. John's, pers. comm.). Seabird breeding is timed to benefit from the usual pattern of prey availability (Lack 1968, Pearson 1968, Ashmole 1971, Furness and Monaghan 1987), and therefore, changes in the timing of capelin inshore arrival could represent a severe food shortage to breeding seabirds.

There has also been much concern over the groundfish fishery in the northwest Atlantic in the 1990s. Northern Cod (Gadus morhua) stocks have drastically declined in recent years, and the fishing industry in eastern Newfoundland was virtually shut down in 1992. A fisheries moratorium could magnify food shortage because fish offal, which has been normally available to scavenging seabirds throughout the breeding season (Pierotti and Annett 1987), would be eliminated. Food shortage has been associated with an increase in predation in some studies (Belopol'skii 1957, Beaman 1978, Neuman 1994), and Herring Gulls (Larus argentatus) and Great Black-backed Gulls (Larus marinus), which are potential nest predators of kittiwakes, rely extensively on fish offal (Threlfall 1968, Furness 1984, Dunnet et al. 1990, Furness et al. 1992, Garthe and Huppop 1984). Thus, kittiwake breeding failure due to nest predation may be an indirect result of general food shortage.

The objectives of this study were to assess the breeding failure of kittiwakes in Witless Bay and to investigate its causes. Low productivity in 1990, followed by severe and widespread failure in 1991, suggested that breeding success would continue to be poor in subsequent breeding seasons. Food shortage was predicted to be responsible for breeding failure.

This thesis is divided into two main sections, both of which were written to stand on their own. Chapter 2 assesses kittiwake breeding success and the timing of egg and chick losses in 1992 and 1993 through comparison to previous studies in Witless Bay. Chapter 3 considers the causes of egg and chick mortalilty and examines changes in the behaviour of incubating adults and those feeding chicks relative to the timing of the inshore arrival of spawning capelin. General conclusions are presented in Chapter 4.

1.1. REFERENCES

Ashmole, N.P. 1971. Sea bird ecology and the marine environment. p. 223-286 in Farner, D.S., King, J.R., and Parkes, K.C. (eds.) Avian Biology Vol. 1. Academic Press, New York.

Baird, P.H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scand. 21:224-235.

Beaman, M.A.S. 1978. The feeding and population ecology of the Great Black-backed Gull in northern Scotland. Ibis 120:126-127.

Belopol'skii, L.O. 1957. Ecology of sea colony birds of the Barents Sea. Izv. Akad. Nauk SSSR, Moscow-Leningrad. (translated from Russian by Israel Program for Scientific Translations, Jerusalem, Israel, 1961).

Brown, R.G.B., and Nettleship, D.N. 1984. Capelin and seabirds in the northwest Atlantic. p. 184-194 in Nettleship, D.N., Sanger, G.A. and Springer, P.F. Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. Stud. Av. Biol. 14:71-83.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.

Carscadden, J.E. 1984. Capelin in the northwest Atlantic. p. 170-183 in Nettleship, D.N., Sanger, G.A., and Springer (eds.). Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Casey, J. 1994. Reproductive success of Black-legged Kittiwakes in the northwest Atlantic in 1991-1993. B.Sc. Honours Thesis (Biopsychology). Memorial University of Newfoundland, St. John's.

Chapdelaine, G., and Brousseau, P. 1989. Size and trends of Black-legged Kittiwake (Rissa tridactyla) populations in the Gulf of St. Lawrence (Quebec) 1974-1985. Am. Birds 43:21-24.

Dunnet, G.M., Furness, R.W., Tasker, M.L., and Becker, P.H. 1990. Seabird ecology in the North Sea. Netherlands J. Sea Res. 26:387-425.

Furness, R.W. 1984. Seabird-fisheries relationships in the northeast Atlantic and North Sea. p. 162-169 in Nettleship, D.N., Sanger, G.A., and Springer (eds.). Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Furness, R.W., and Monaghan, P. 1987. Seabird Ecology. Chapman and Hall, New York.

Furness, R.W., and Barrett, R.T. 1985. The food requirements and ecological relationships of a seabird community in north Norway. Ornis Scand. 16:305-313.

Furness, R.W., and Barrett, R.T. 1991. Seabirds and fish declines. Nat. Geogr. Res. Explor. 7:82-95.

Furness, R.W., Ensor, K., and Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80:105-113.

Garthe, S., and Huppop, O. 1994. Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Marine Ecol. Progr. Ser. 106:1-9.

Harris, M.P., and Wanless, S. 1990. Breeding success of British kittiwakes Rissa tridactyla in 1986-1988: evidence for changing conditions in the northern North Sea. J. Appl. Ecol. 27:172-187.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L., Jr. 1993. Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. p. 140-153 in Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D. (eds.). The Status, Ecology and Conservation of Marine Birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Methven, D.A., and Piatt, J.F. 1991. Seasonal abundance and vertical distribution of capelin (Mallotus villosus) in relation to water temperature at a coastal site off eastern Newfoundland. ICES J. Mar. Sci. 48:187-193.

Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., and Walton, P. 1993. The influence of changes in food abundance on diving and surface feeding seabirds. In Montevecchi, W.A (ed.). Studies of High Latitude Homeotherms: Multispecies comparisons of Feeding Ecology and Energetics. Can. Wildl. Serv. Occas. Pap.

Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. p. 217-266 in Furness, R.W., and Greenwood, J.J.D. (eds.). Birds as Monitors of Environmental Change. Chapman & Hall, London.

Montevecchi, W.A., and Myers, R.A. 1992. Monitoring fluctuations in pelagic fish availability with seabirds. CAFSAC Research Document 92/94.

Murphy, E.C., Springer, A.M., and Roseneau, D.G. 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla L.*) at a colony in western Alaska. J. Anim. Ecol. 60:515-534.

Neuman, J.A. 1994. Aspects of the behaviour and ecology of Black-legged Kittiwakes, *Rissa tridactyla*, breeding at two sites in Newfoundland, Canada, 1990-1991. M.Sc. Thesis. Memorial University of Newfoundland, St. John's.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Pierotti, R., and Annett, C. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. p. 417-442 in Kamil, A.C., Krebs, J.R, and Pulliam, H.R. (eds.). Foraging Behavior. Plenum Press, New York.

Templeman, W. 1948. The life history of the capelin (*Mallotus villosus* o.f. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory. No. 17 (Research). 151pp.

Threlfall, W. 1968. The food of three species of gulls in Newfoundland. Can. Field-Nat. 82:176-180.

CHAPTER 2 BREEDING SUCCESS OF BLACK-LEGGED KITTIWAKES ON GREAT ISLAND IN 1992 AND 1993

2.1. ABSTRACT

The breeding success of Black-legged Kittiwakes (Rissa tridactyla) was investigated on Great Island, Witless Bay, Newfoundland, in 1992 and 1993, following two years of breeding failure. Fewer pairs produced eggs in 1992 (64%) than in 1993 (77%), and these proportions were low relative to previous studies. High egg mortality in 1992 (90%) and in 1993 (89%) and high chick mortality in 1992 (93%), but not in 1993 (32%), resulted in a breeding success of 1% in 1992 and 7% in 1993. Timing of breeding was later than in previous years and clutches and eggs were smaller. Mean egg volume increased slightly throughout the laying period in 1992. Volume gradually decreased in 1993. An increase, as noted in 1992, may indicate that food availability improved with the season. Correlations among reproductive measures from 7 years were high: early breeding was associated with high egg production, large eggs and clutches, and high hatching, fledging and breeding success. The shape index of eggs increases with the age of the breeder. Comparison of shape index among years suggested that a higher proportion of older individuals was breeding in years of poor productivity. This is consistent with the hypothesis that older individuals are

more able and willing to expend effort and incur cost in a reproductive attempt.

Brood counts across Great Island in the late chick stage indicated that breeding failure was extensive throughout the colony. Breeding success varied among regions and differences were most extreme in 1992 when failure was greatest. The areas of greatest and least success were consistent between years and were probably related to differences in cliff structure and therefore to nest predation.

Breeding performance in study plots where adults were flushed was compared to study plots assessed by observation only. No statistical differences were found. Breeding success in each study plot was not different from the corresponding region of Great Island, but mean productivity of all plots was significantly lower than mean productivity for Great Island, emphasizing the importance of random or representative study plots.

2.2. INTRODUCTION

Breeding failure of Black-legged Kittiwakes (Rissa tridactyla) is typical of some colonies and geographical areas in some years. In Alaska, reproductive success of kittiwakes has been highly variable (Roberts 1988, Baird 1990, Murphy et al. 1991, Hatch et al. 1993), and more recently, productivity has been low in some colonies in the North Sea (Harris and Wanless 1990, Hamer et al. 1993). At a small, well studied colony in North Shields, England, breeding success was moderately high with little variation between years (Thomas and Coulson 1988). Variation in success has been attributed primarily to the reliability of a stable food supply (Barrett and Runde 1980, Coulson and Thomas 1985, Hatch 1987, Harris and Wanless 1990, Murphy et al. 1991, Monaghan et al. 1993). At the North Shields colony, abundant and available food was accessible to kittiwakes throughout the breeding season (Coulson and Thomas 1985), while Alaskan kittiwakes are subject to more variable marine conditions (Hatch 1987, Baird 1990, Murphy et al. 1991). Recent failures on the North Sea are attributed to food shortage because sandeel stocks (the main prey species of kittiwakes in Britain) have declined in the area in recent years (Dunnet et al. 1990, Harris and Wanless 1990, Monaghan et al. 1993). Breeding success of kittiwakes has been linked to independent measures of food abundance in both Alaska (Springer et al. 1986) and in the North Sea (Aebischer et al. 1990, Hamer et al. 1993).

Small, surface feeding seabirds such as kittiwakes are particularly vulnerable to changes in food availability due to time and energy constraints and to a specialized and limited feeding technique (Pearson 1968, Cairns 1987, Furness and Monaghan 1987, Burger and Piatt 1990, Harris and Wanless 1990, Furness and Barrett 1991). Kittiwakes are more marine in their feeding habits than are other gull species, which are opportunistic and scavenge fish offal and garbage at sea or on land (Threlfall 1968), and while many other gulls spend winters on land, kittiwakes spend non-breeding periods at sea (Cullen 1957). Although kittiwakes are known to take fish offal, they are often excluded by larger species (O'Connor 1974, Dunnet et al. 1990, Furness et al. 1992). Thus, changes in the breeding performance of kittiwakes is likely closely tied to changes in food availability in the marine ecosystem.

In Witless Bay, Newfoundland, previous studies indicated that Black-legged Kittiwake productivity was low in 1990, and severe failure was observed in 1991 (Neuman 1994). Capelin (Mallotus villosus), which is the main prey species of breeding seabirds in much of the northwestern Atlantic Ocean (Templeman 1948, Brown and Nettleship 1984, Burger and Piatt 1990, Montevecchi and Myers 1992), have been delayed in their inshore spawning migrations in recent years, an anomaly which seems to be closely tied to surface water temperature (Methven and Piatt 1991, Montevecchi and Myers 1992). Delayed capelin arrival or a reduction in their availability could represent a severe food shortage to breeding seabirds (Brown and Nettleship 1984). Neuman (1994) speculated that food shortage was involved in kittiwake breeding failure in 1991, and probably in 1990.

The timing of breeding failure, and comparisons of reproductive measures such as clutch size, egg size, timing of breeding, and proportions of pairs producing eggs, to years when productivity was high, can be indicative of the timing and severity of food shortage. The reproductive advantages of early breeding and of large eggs and clutches have been well established in birds, and many studies have linked these reproductive measures to food availability (Murphy et al. 1984, Springer et al. 1986, Cairns 1987, Safina et al. 1988).

Late breeders are known to lay smaller clutches (Coulson and White 1961, Lack 1968, Perrins 1970, Montevecchi 1978, Boersma and Ryder 1983, Nelson 1988), and generally experience poorer success than early breeders (Lack 1968, Nisbet and Drury 1972, Davis 1975, Ryder 1980, Toft et al. 1984, Martin 1987, Poole 1989, Harris et al. 1992). Timing of breeding seems to be linked to food supply, and the results of numerous studies comparing regions or years of high and low food availability have shown that the onset of laying can often be advanced through increased food supplies, either from natural variation, or by experimental supplementation (Drent and Daan 1980, Martin 1987, Arcese and Smith 1988). Some studies have shown that early laying is associated with superior physical condition (Drent and Daan 1980, Boersma and Ryder 1983).

Different studies have reported much variation in the response of clutch size to food supply (Winkler and Walters 1983, Murphy et al. 1984, Safina et al. 1988, Bolton et al. 1992), and studies of food supplementation have been inconsistent in their results (Arcese and Smith 1988). However, given optimal conditions, large clutch size allows maximization of reproductive potential, and larger eggs produce larger young (Pierotti and Annett 1987, Bolton et al. 1992) and increase their probability of survival (Parsons 1970, Pierotti 1982, Thomas 1983, Pierotti and Annett 1987). Part of the inconsistency found in studies of food supplementation may come from a lack of consideration of the food quality, as opposed to energetic content (Murphy et al. 1984, Bolton et al. 1993), from variation in the state of natural food availability (Bolton et al. 1993), and from differences between species (Safina et al. 1988). For example, Bolton et al. (1993) found that in a year of apparent food shortage, clutches and eggs of Lesser Black-backed Gulls (<u>Larus fuscus</u>) could be increased in size by the supplementation of protein but not fat, and that clutch size did not respond to food supplementation in years of no apparent food shortage. Similarly, some studies have found differences in egg size in relation to food availability (Nisbet 1973, 1977, Pierotti and Bellrose 1986) and some have not (Poole 1985, Safina et al. 1988). However, many studies have demonstrated that clutch size in seabirds reflects the body condition of the female (Nisbet 1973, 1977, Drent and Daan 1980, Boersma and Ryder 1983, Houston et al. 1983, Martin 1987).

Comparisons among years have often shown that in years of poor productivity, fewer birds attempt reproduction (Hatch and Hatch 1988, 1990, Roberts 1988, Murphy et al. 1991, Neuman 1994). This appears to be due to the physical body condition of breeders, since in years when food availability is very poor, birds may not attempt to breed at all (Drent and Daan 1980, Schreiber and Schreiber 1984, Cairns 1987, Montevecchi 1993), and for some species there is evidence that only females reaching a threshold body mass will breed (e.g., Weimerskirch 1992). Drent and Daan (1980) have shown that body condition (measured as mass or muscle tissue) is a good predictor of breeding success, and correlation between adult mass and breeding success or clutch size has been found in other studies (Nisbet 1973, Drent and Daan 1980, Martin 1987, Hamer et al. 1993). This is not surprising because body condition is likely associated with an ability to expend energy, which is required by processes such egg production, incubation, and chick feeding.

If in years of poor breeding conditions a low proportion of the population attempts reproduction, then this proportion is predicted to represent older, more experienced birds. Experienced birds may be more able to find and accumulate resources and attain the body condition necessary to attempt reproduction because foraging ability increases with age (Burger and Gochfeld 1979, Porter and Sealy 1982, Furness and Monaghan 1987, Burger 1988). Older birds may also be more willing to reproduce in poor years because more effort is required and a higher risk (in terms of mortality) is involved. Since seabirds are long-lived, and assuming that reproduction is energetically expensive and represents a cost in terms of mortality risks to the breeder (Wooller and Coulson 1977, Reznick 1985, Bryant and Tatner 1988, Nur 1988), adults are expected to protect their survival by reduced breeding or non-breeding if conditions are poor (Cairns 1987, Dunnet et al. 1990). Older individuals, with less remaining potential for reproduction, are expected to accept higher risks than young individuals, which have many more reproductive opportunities left (Pugesek 1984, 1990, Toft et al 1984, Hamer and Furness 1991).

In this study age of breeders was not known, but egg shape index (Coulson 1963) can provide information on the age composition of a breeding population, and can therefore be used to test the prediction that a higher proportion of older individuals will breed in poor conditions than in good ones. Egg shape index is a measure of the roundness of the egg, becoming greater when the egg is relatively short and broad, and is independent of the volume of the egg (Coulson 1963). Coulson (1963) has shown that shape index increases with the age of the female. Shape index is also associated with laying order: single eggs, second laid eggs in 2-egg clutches, and C-eggs (third laid) have lowest shape indices (long and narrow eggs). That single eggs have a low shape index reflects the fact that young birds tend to lay single egg clutches (Coulson and White 1958).

A comparison of shape index between years of varying productivity and food availability is predicted to reflect the association between age of breeding birds and breeding conditions. If older birds represent a higher proportion of the breeding population in poor years, then shape index would be higher in years of poor food availability than in years of abundant food supplies. Clutch size is related to the age and experience of breeders, with older, more experienced females laying larger clutches (Coulson and White 1961). Breeding conditions are also associated with changes in clutch size, and therefore single egg clutches in poor years may be laid by older individuals that would lay two or three egg clutches if conditions were better. Single eggs in poor years would then also be predicted to show higher shape indices than would be expected from single egg clutches in normal years.

The objective of this study was to investigate anticipated kittiwake breeding failures in Witless Bay, Newfoundland, by examining the reproductive measures egg size and shape, clutch size, timing of breeding, proportions of pairs producing eggs, and egg and chick mortalities, in 1992 and 1993, on Great Island. These reproductive measures were compared among years, including previous studies of kittiwakes from Witless Bay, and were predicted to reflect food shortage. The work of Maunder and Threlfall (1972) describes the breeding biology of kittiwakes on Gull Island, Witless Bay in 1969 and 1970. Productivity was high in 1969 and 1970, indicating adequate food availability. These two years may be more representative of kittiwake reproductive performance prior to recent years, and were used as a reference to the breeding performance documented in the two years of this study. Neuman (1994) studied kittiwake breeding biology on Gull Island in 1990 and 1991, and Chatman (1989) provided information for 1988.

Two questions of methodology were also addressed. In any study of breeding success the study itself may influence the results, and therefore investigator disturbance is a potential problem. Colonial nesters, such as many seabirds, seem to be particularly vulnerable to disturbance. While solitary nesters generally depend on cryptic nests and isolation for protection against predators, colonial species often rely on inaccessibility of nesting areas, such as cliffs or islands. Any disturbance in these "safe" areas may indicate a life-threatening situation to the adults and may therefore cause a severe reaction, and because nests are dense and conspicuous, nest predators can take advantage of abandoned eggs and young. In addition, because of the long lifespan of many seabirds, each breeding season is only a relatively small component of their lifetime reproductive success, and they may therefore be selected to respond to disturbance with caution (Gotmark 1992). When nests of kittiwakes are accessed to determine nest contents and egg size, breeding adults in the vicinity vacate their nests. The effect of this disturbance was examined through a comparison of the breeding success of plots which were disturbed in this manner to plots where reproductive measures were recorded by observation only.

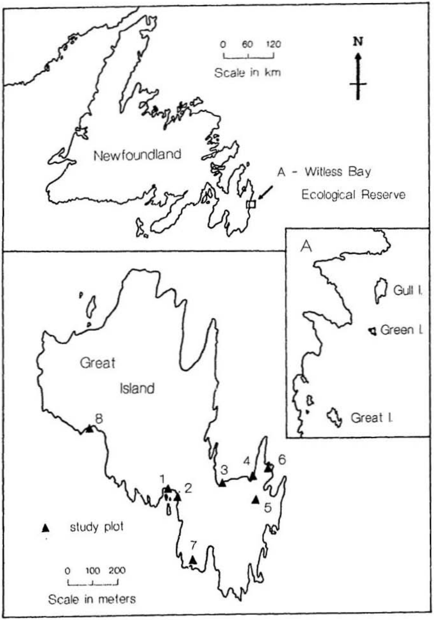
The use of study plots for the assessment of breeding success of a population may also create a bias. For practical reasons, estimates of breeding success are often derived from nests within study plots. When examined, however, variation between plots within a colony can be high (Hatch and Hatch 1988, Harris and Wanless 1990). In 1992 and 1993, I conducted island wide brood counts in the late-chick stage of reproduction. These brood counts allowed an assessment of variability in success across the island and determined how results derived from study plots compared to overall colony success.

2.3. METHODS

2.3.1. Study site and field schedule

This study was conducted on Great Island (47°11'N, 52°46'W), Witless Bay, Newfoundland, in 1992 and 1993. Great Island is the southern most of three islands in the Witless Bay Ecological Reserve, and is located about 2 km off the southeastern shore of the Avalon Peninsula (Figure 2.1). Dimensions of the island are about 1200 x 700 m. The interior of Great Island is partially forested (for a detailed description of Great Island, see Nettleship 1972) and cliffs surround most of the perimeter on which 23,229 pairs of Black-legged Kittiwakes breed (Cairns et al. 1989). Other seabirds breeding on the island include: Northern Fulmars (Fulmarus glacialis), Leach's Storm-Petrels (Oceanodroma leucorhoa), Herring Gulls (Larus argentatus), Great Black-backed Gulls (Larus marinus), Common Murres (Uria aalge), Razorbills (Alca torda), Black Guilemots (Cepphus grylle), and Atlantic Puffins (Fratercula arctica).

Figure 2.1 Location of Great Island in the Witless Bay Ecological Reserve and locations of the eight study plots on Great Island.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Scale in km
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Green I.
Great I.
Great
Island
8
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3
4
6
5
7
study plot
0 100 200
Scale in meters

Great Island is located about 10 km south of Gull Island (47°15.8'N, 52°46.3'W; Figure 2.1) where previous studies of kittiwake breeding biology took place (Maunder and Threlfall 1972, Chatman 1989, Neuman 1994). Descriptions of Gull Island can be found in Maunder and Threlfall (1972) and Neuman (1994). On Gull Island 10,140 pairs of kittiwakes breed. Both Great and Gull Islands are influenced by the Labrador Current, bringing cold water southward, past the east coast of the Avalon Peninsula.

Most of June, July and August were spent on Great Island in 1992 and 1993: from 20 May to 28 August in 1992, and from 4 June to 30 August in 1993. In 1992, 3 days in June were spent off island (22 June - 25 June). In 1993, arrival was delayed by poor weather, but the island was visited on 19 May.

2.3.2. Reproductive performance in the study plots

Seven study plots with a total of 469 nests, and 8 study plots with a total of 755 nests were monitored throughout the breeding season in 1992 and 1993, respectively (Figure 2.1). In 1993, the plots established in 1992 were reused and expanded and plot 8 was added. All nests considered here were regularly attended by adults, at least during the laying and incubation stage of the breeding season, even if no eggs were laid.

Date of laying of each egg, clutch size, hatchdate, date of disappearance of eggs or chicks, and approximate fledging date were recorded for all nests. Plot 1 in both years and plot 2 in 1993 were checked daily and other plots, except plot 7, were checked at least once in four days, weather permitting. Plot 7, which was located within a dense Herring Gull nesting area, was checked every 10 days. Eggs and chicks were accessible in three plots (plots 5, 6 and 7) and were marked for future identification. Eggs were marked with waterproof pens and were measured (maximum length and breadth) to the nearest 0.1 mm with Vernier callipers. Egg volume (the measure used for egg size) was calculated from the formula $V=(0.4866 \times \text{breadth}^2 \times \text{length})$, and shape index from $SI=(100 \times \text{breadth}/\text{length})$, as outlined in Coulson (1963). Chicks of 2-chick broods were marked under the chin with a small spot of colour from a waterproof pen; mass was measured with 50, 100, 300 and 500 g Pesola scales and winglength was recorded with a stopped (wing) ruler.

At plots 1 to 4 (in 1992 and 1993) and 8 (in 1993), reproductive status was determined by observation only and adults with eggs or young in the nest never left the nest due to the observer. Thus, these plots also served as suitable control plots for those at which eggs and chicks were marked and measured. These plots are referred to as "observation" plots in analysis or discussion of researcher effects, and contrasted with "disturbed" plots where adults flushed from nests whenever reproductive status was assessed.

Nests and plots were chosen primarily for visibility from nearby observation posts or for accessibility for egg and chick measurements. Random choice of nests or plots was therefore not feasible. A comparison of reproductive status between study plots and brood counts across the island addresses the question of whether the results obtained from the study plots were representative for the region of the island in which the plot was located, and whether the average breeding success of the study plots was representative of overall island productivity.

All observation plots (plots 1 to 4 and 8) were included in calculations of hatching success (chicks hatched per egg laid), fledging success (chicks fledged per chick hatched), and breeding success (chicks fledged per egg laid) in both years. In 1992, my disturbance seemed to have little effect on breeding performance in plots 5, 6 and 7 (see Results) and these plots were included in calculations of breeding performance. In 1993, Herring Gulls seemed to cue in to the opportunity for predation that my disturbance created (see Discussion) and visits had to be reduced to plots 5 and 6 later in the season, and to plot 7 (located within a dense Herring Gull colony) throughout the season. All data are reported in plot summaries, but in 1993, data from plot 7 were excluded in calculation of hatching, fledging and breeding success, and data from plots 5 and 6 were excluded from calculation of hatching and fledging success.

The proportion of pairs producing eggs was calculated for each breeding season. In 1993, this proportions was calculated only from plots 1 and 2 (which were checked daily) because the rate of egg disappearance throughout incubation was high. In 1992, egg predation was low until most eggs had been laid (see Chapter 3), and the proportion of pairs producing eggs was considered reliable for all plots.

Proportions of 1- and 2-egg clutches and average clutch sizes were calculated from clutches of known size. Clutch size was considered unknown when a single egg was found for the first time on one visit and the nest was empty in the next (in disturbed plots) or when a clear view of nest contents had not been obtained (in observation plots). Unknown clutches were assigned the average clutch of that year in the calculation of total eggs laid per plot.

2.3.2.1. Timing of breeding

Laying distributions (distributions of percentage of eggs laid by date) were based on the laydates of first laid eggs of each clutch. For nests checked daily, laydate was considered to be the day an egg was found. For nests not checked daily, laydate was taken to be the midpoint between visits, unless hatchdate was known, in which case laydates were calculated from hatchdate (by subtracting mean incubation time, 27 days). Back-dating from hatchdate could not be used to estimate laydate in most cases because few eggs hatched.

In 1993, my arrival on the island was delayed until 4 June and early laying had already begun. To estimate the laydates of these earliest eggs, laydates were calculated from hatchdates when eggs hatched, and when eggs did not hatch, the mean laydate of eggs already laid on the same date in 1992 was calculated and used for the laydate of such eggs. This approach seemed justified because judging by the number of eggs present relative to the number present at that time in 1992, and by the number of those nests which had only one egg and subsequently gained another, timing was very similar in the two years. The condition of nests and the behaviour of birds on a visit to the island on 19 May 1993 matched closely to what was observed on 21 May 1992. Although this method of estimating early laydates in 1993 biased the early part of the laying distribution in 1993, analysis revealed that there was no statistical difference between the laying distributions of 1992 and 1993 (see Results) and this procedure therefore provided a good estimate of laydate for eggs laid prior to 4 June in 1993.

Hatchdate was considered to be the day a chick was found for nests checked daily. For nests not checked daily, the midpoint between visits was used. In plots where chicks were measured, this was refined using chick size and the growth curves provided by Maunder and Threlfall (1972).

2.3.2.2. Analysis of disturbance effects

Proportions of 1- and 2-egg clutches, and hatching, fledging, and breeding success were compared between observation and disturbed plots in 1992. In 1993, because visits to disturbed plots were not frequent enough during the hatching period to record all small chicks (some of which would have died or disappeared soon after hatching), hatching and fledging success was not compared between plots. A comparison of breeding success between observed and disturbed plots was used to test the effect of my disturbance on breeding performance in 1993.

As an additional test of the effect of my disturbance, a section of accessible cliffs south of plot 5 was not disturbed in 1992 during regular nest checks. This area was surveyed in the late incubation, early hatching period, and total nests, nests with eggs, and nests with chicks were counted. Nest contents of this area were compared to the nest contents in plot 5 on the same day. This area was of the same habitat type as plot 5 (although in one section, cliffs were slightly steeper and more difficult to access), and was therefore considered to be a suitable comparison. In the results it is referred to as the control section south of plot 5.

2.3.2.3. Comparison of reproductive success among years

The proportion of pairs producing eggs, hatching success, fledging success, breeding success, proportions of different sized clutches, and laying distributions were compared between 1992 and 1993. Results from this study were compared to reproductive measures for 1969 and 1970 (Maunder and Threlfall 1972). Egg mortality (proportion of eggs laid that did not hatch), chick mortality (proportion of chicks that died), and egg to fledging mortality (proportions of eggs that did not produce fledglings) were reported by Maunder and Threlfall (1972) and were compared among years of this study to determine timing of failure. Data from 1992 and 1993 were combined if no statistical differences were found in these reproductive measures. Similarly, data from 1969 and 1970 were combined if no statistical differences were found, and the two sets of years were then compared. Hatching, fledging and breeding success, timing of breeding, clutch size and egg volume were also compared with values for Gull Island in 1988 (Chatman 1989) and in 1990 and 1991 (Neuman 1994), when possible. It was assumed that egg measurements taken by different researchers did not bias the comparison. This seemed justified because methods of obtaining egg measurements were the same and because eggs have clear boundaries and are not difficult to measure. Egg length, breadth, volume and shape index in 1992 and 1993 were compared to data from 1969. The mean shape indices of all eggs, of A-eggs (first laid eggs in 1- and 2-egg clutches), and of first laid eggs in 2-egg clutches in 1969 were compared to the shape indices of all eggs in 1992 and 1993.

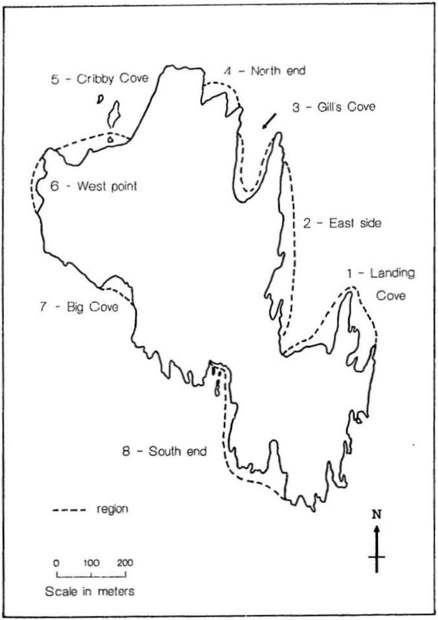
Changes in egg volume with laydate were compared to the relationship found in 1969 and 1970 (Maunder and Threlfall 1972). Volumes of eggs laid on and after the median laydate were considered separately to test if volume decreased in the second half of the laying period.

2.3.3. Brood counts on Great Island during the late chick stage

Brood counts were conducted on Great Island on August 9 and 10 in 1992, and on August 7 to 10 in 1993. Suitable dates were based on chick sizes in the study plots, so that all chicks could be seen but none had fledged. In a given area (Appendix 1), visible nests, nests attended by adults, and brood sizes were counted. Most areas easily visible from land were surveyed. Areas surveyed were grouped into 8 regions (Figure 2.2), and data were summarized for each.

Reproductive success, as determined from island brood counts, was compared among regions and years. Proportions of

Figure 2.2 Great Island, Newfoundland, showing the 8 regions for which nest and brood counts were summarized in the late chick stage of Black-legged Kittiwake reproduction in 1992 and 1993.


5 - Cribby Cove
4 - North end
3 - Gill's Cove
6 - West point
2 - East side
1 - Landing Cove
7 - Big Cove
8 - South end
---- region
N
0 100 200
Scale in meters

young counted per nest were compared among regions and overall proportions were compared between years. Proportions of young counted per nest were in reference to total nests and not to attended nests because attendance of non-breeders and failed breeders varied considerably on a daily basis (unpubl. data).

The results of island brood counts were also used to assess how representative the study plots were of the productivity of the colony. The variable compared among study plots and island surveys was proportion of total nests with at least one young. Data from the study plots correspond to the same dates as the island surveys. Study plots were first compared to the region of the island in which they were located to test for a difference in proportion of nests with chicks between plot and region. The overall proportion of nests with at least one young for all study plots was then compared to the proportion for the entire island, testing for differences between study plots and island productivity.

2.3.4. Statistics

SYSTAT (Wilkinson 1990) was used for statistical analysis. Chi-square analysis was used to compare proportions, the Kolmogorov-Smirnov method was used to compare laying distributions, Student's t-tests compared the relationships between two categories of a continuous variable, and regression analysis tested for seasonal trends in continuous variables. ANCOVA was used to examine the relationship between egg volume and laydate and year, with laydate as a covariate; the interaction term was tested for significance and if significant, separate regressions were performed to examine the relationship between egg volume and laydate for each year. Tolerance for type I error was set at 0.05 and residuals were examined for normality and independence. Means are reported ± standard error.

When multiple Chi-square comparisons were made (in the analysis of proportions of 1 and 2 egg clutches among years and in the comparison of proportions of young produced among regions of Great Island), Bonferroni adjustments were made to correct the familywise error rate (Hays 1988).

In the comparison of egg length, breadth, volume and shape index between the years of this study and 1969 (Maunder and Threlfall 1972), a critical value was calculated for each variable for 1969, which allowed statistical comparison. For the variables egg length, breadth and volume, a critical value was calculated for each from the formula $X = X_0 - 1.65(SE)$ (one-tailed comparison; Hays 1988), where X_0 is the mean of 1969, SE is the standard error of 1969, and X is the critical value. For each variable, the critical value for 1969 was compared to the means of that variable from 1992 and 1993. If X was greater than the means of that variable in 1992 and 1993, then the mean of 1969 was significantly greater than the means of 1992 and 1993 at $p \leq 0.05$ (Hays 1988). Standard errors were not reported for 1969 and were therefore calculated using the larger of the standard deviations of 1992 or 1993 (to be conservative) and the sample size of 1969. Using the standard deviation of 1992 or 1993 probably provided a conservative test because ranges in 1969 were smaller than in 1992 and 1993 for all variables considered, and since egg measurements are normally distributed, range and standard deviation are related. For the variable shape index, 1.65(SE) was added instead of subtracted (see above equation) because values in 1992 and 1993 were predicted to be larger and not smaller than in 1969, and mean shape index of 1992 and 1993 had to exceed that critical value to be statistically different from the mean shape index of 1969 at $p \leq 0.05$.

2.4. RESULTS

2.4.1. Effect of researcher disturbance on reproductive success in the study plots

No differences were observed between observation and disturbed plots in proportions of 1- and 2-egg clutches, and in hatching, fledging, and breeding success in 1992 (X^2 tests, $p<0.05$; Table 2.1). Only three chicks fledged from all study plots in 1992 and all were from a disturbed plot. In 1993 there were no significant differences between proportions of

Table 2.1 Comparison of the breeding performance of Black-legged Kittiwakes in observation and disturbed plots on Great Island, Newfoundland, in 1992 and 1993.

	1992		1993	
Breeding performance	observation plots [%(N)]	disturbed plots [%(N)]	observation plots [%(N)]	disturbed plots [%(N)]
1-egg clutches	58 (100)	57 (126)	70 (256)	59 (59)
2-egg clutches	42 (100)	43 (126)	30 (256)	41 (59)
Hatching success	10 (218)	9 (231)	11 (506)	-[1]
Fledging success	0 (22)	14 (21)	68 (57)	-[1]
Breeding success	0 (218)	1 (231)	8 (506)	5 (118)

[1] hatching and fledging success could not be assessed for disturbed plots in 1993.

1- and 2-egg clutches or breeding success in observation and disturbed plots (X^2 tests, $p<0.05$; Table 2.1).

Nests in the control section south of plot 5 were counted on 4 July 1992, in the late incubation period. This was the first day on which no eggs or chicks were found in plot 5. Of 133 nests in the area, only one nest contained one egg and one nest contained one small young. Both these nests were on a section where a steep cliff face made accessibility difficult

2.4.2. Kittiwake breeding performance in the study plots in 1992 and 1993, and in comparison to previous years

2.4.2.1. Breeding performance

In seven study plots and 469 nests in 1992, 64% of pairs produced eggs, 11% of pairs with eggs produced chicks, 9% of pairs with chicks fledged young, and 1% of pairs with eggs fledged young (Table 2.2). In 1993, with 8 study plots and 755 nests, 77% of pairs produced eggs, 12% of pairs with eggs laid produced chicks, 76% of pairs with chicks fledged young, and 9% pairs with eggs fledged young (Table 2.3).

There was no significant difference between 1992 and 1993 in the proportion of pairs producing eggs ($X^2_1=0.42$, $p=0.84$) and the proportion of pairs with eggs producing chicks ($X^2_1=0.25$, $p=0.62$). More nests with chicks fledged young

Table 2.2 Summary of reproductive success of Black-legged Kittiwakes on Great Island, Newfoundland, for 7 study plots, in 1992.

Plot no.	Total nests	Nests with 0 eggs	Nests with eggs	1 egg clutch	2 egg clutch	Unknown clutch size	Relay[1] eggs	Total[2] eggs	Nests with chicks	Total chicks	Fledged 1 young	Fledged 2 young	Total fledged	%Nests with eggs	Chicks hatched per egg	Fledged per chick	Fledged per egg
1	60	25	35	18	10	7	11	59.0	0	0	0	0	0	58.3	0	0	0
2	57	26	31	7	8	16	1	46.9	1	1	0	0	0	54.4	.021	0	0
3	92	34	58	20	20	18	1	86.7	11	17	0	0	0	63.0	.196	0	0
4	30	12	19	13	4	2	1	24.9	3	4	0	0	0	63.3	.161	0	0
5	122	28	94	48	30	16	2	132.9	4	6	0	0	0	77.0	.045	0	0
6	31	10	21	11	6	4	2	30.7	3	3	0	0	0	67.7	.098	0	0
7	77	33	44	13	18	13	0	67.6	10	12	3	0	3	57.1	.178	.250	.044
Tot.	469	168	302	130	96	76	18	448.7	32	43	3	0	3				
Mean														64.3	.096	.070	.007

[1] eggs laid after first clutch was lost.

[2] total number of eggs calculated using an average clutch size of 1.43 to estimate unknown clutches.

Table 2.3 Summary of reproductive success of Black-legged Kittiwakes on Great Island, Newfoundland, for 8 study plots, in 1993.

Plot no.	Total nests	Nests with 0 eggs	Nests with eggs	1 egg clutch	2 egg clutch	Unknown clutch size	Relay[1] eggs	Total[2] eggs	Nests with chicks	Total chicks	Fledged 1 young	Fledged 2 young	Total fledged	%Nests[3] with eggs	Chicks[4] hatched per egg	Fledged per chick	Fledged[4] per egg
1	94	30	64	33	25	6	3	94.0	0	0	0	0	0	68.1	0	0	0
2	116	19	97	35	18	44	3	132.5	6	9	3	2	7	83.6	.068	.778	.053
3	129	68	61	29	5	27	0	74.9	3	4	0	1	2	47.3	.053	.500	.027
4	158	76	82	44	14	24	0	103.9	17	20	11	1	13	51.9	.192	.650	.125
5	107	37	70	33	21	16	7	103.3	4	6	2	2	6	65.4	.058	1.00	.058
6	13	3	10	2	3	5	0	14.7	0	0	0	0	0	76.9	0	0	0
7	31	11	20	10	7	3	0	28.0	4	5	3	1	5	64.5	.179	1.00	.179
8	107	30	77	37	16	24	0	100.9	19	24	15	1	17	72.0	.238	.708	.221
Tot.	755	274	481	223	109	149	13	652.2	53	68	34	8	50				
Mean														63.7[3]	.104	.735	.077

[1] eggs laid after first clutch was lost.

[2] total number of eggs calculated using an average clutch size of 1.33 to estimate unknown clutches.

[3] estimates of % nests with eggs from plots 3 to 8 are probably underestimates because eggs disappeared throughout incubation; a mean of 76.7% from plots 1 and 2 only (which were checked daily) is considered more reliable.

[4] because some eggs were likely missed in plots 3 to 8, chicks hatched per egg and chicks fledged per egg are probably slight overestimates.

(X^2_1=32.81, p<0.0001) and more nests with eggs fledged young (X^2_1=15.530, p=0.0001) in 1993 than in 1992.

Eggs were produced in 92% and 91% of nests in 1969 and 1970, respectively (Maunder and Threlfall 1972). Egg, chick, and egg to fledging mortality were not different in 1969 and 1970 (Table 2.4) and these two years were combined (hereafter 1969/70). Egg mortality was not different in 1992 and 1993 (Table 2.4), and in 1992 and 1993 combined (1992/93) egg mortality was significantly higher than in 1969/70 (X^2_1=436.09, p<0.0001). Chick mortality was significantly higher in 1992 than in 1993 (Table 2.4), and was significantly higher in 1992 than in 1969/70 (X^2_1=72.54, p<0.0001). Chick mortality in 1993 was not significantly different from chick mortality in 1969/70 (X^2_1=0.29, p=0.26). Egg to fledging mortality was also significantly higher in 1992 than in 1993 (Table 2.4), and in both years it was significantly higher than in 1969/70 (p<0.0001). In 1992, both high egg and chick mortality (90% and 93%) contributed to breeding failure. In 1993, only high egg mortality (89%) reduced reproductive output, while chicks that did hatch fledged normally (Figure 2.3).

2.4.2.2. Clutch size

When clutch sizes recorded over 7 years in Witless Bay were compared, mean clutch size was greatest in 1970 and lowest in 1991 (Table 2.5). There were no statistical

Table 2.4 Comparison of egg, chick, and egg to fledging mortality of Black-legged Kittiwakes in Witless Bay, Newfoundland, in 1992 and 1993 (Great Island, this study), and in 1969 and 1970 (Gull Island, Maunder and Threlfall 1972). X^2 compare proportions of mortality between years (df=1).

	1992 vs 1993				1969 vs 1970			
	1992	1993	X^2	p	1969	1970	X^2	p
Egg mortality [%(N)]	90 (449)	89 (506)	0.72	0.40	28 (81)	27 (181)	0.05	0.82
Chick mortality [%(N)]	93 (43)	32 (57)	37.99	<0.0001	19 (58)	26 (141)	1.18	0.28
Egg to fledging mortality [%(N)]	99 (449)	93 (624)	26.16	<0.0001	42 (81)	46 (181)	0.34	0.56

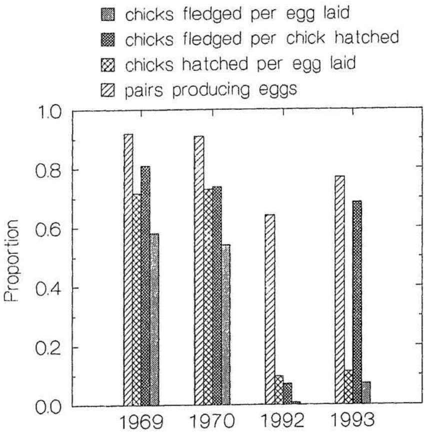


Figure 2.3 Comparison of the breeding performance of Black-legged Kittiwakes in Witless Bay, Newfoundland, in 1992, 1993, 1969, and 1970. Data for 1969 and 1970 taken from Maunder and Threlfall (1972).

Table 2.5 Comparison of proportions of 1, 2, and 3 egg clutches and mean clutch sizes of Black-legged Kittiwakes in 1969, 1970, 1988, and 1990 to 1993, in Witless Bay, Newfoundland.

	Percent (N)				
Year	1-egg	2-egg clutches	3-egg	Significant differences[5]	Mean clutch size
1969[1]	22 (23)	78 (80)	0 (0)	A,B	1.78
1970[1]	12 (14)	85 (104)	3 (4)	A	1.95
1988[2]	38 (43)	60 (67)	2 (2)	B,F	1.63
1990[3]	49 (44)	49 (44)	2 (1)	C,E,F	1.49
1991[3]	72 (105)	28 (41)	0 (0)	D	1.28
1992[4]	58 (130)	43 (96)	0 (0)	C,D,E	1.43
1993[4]	67 (222)	33 (110)	0 (0)	C,D,E	1.37

[1] data from Maunder and Threlfall (1972).

[2] data from E. Chatman and J.M. Porter cited in Neuman (1994).

[3] data from Neuman (1994).

[4] data from this study.

[5] different letters indicate significant differences between proportions of 1- and 2-egg clutches between years using X^2 tests with Bonferroni adjustments. For years with the same letter, no significant difference in the proportion of 1- and 2-egg clutches was found.

differences between proportions of 1- and 2-egg clutches in 1992 and 1993 and proportions from these two years were not different from 1990 or 1991. More 1-egg clutches and fewer 2-egg clutches were recorded in 1992 and 1993 than in 1969, 1970, and 1988. No 3-egg clutches were recorded in 1991 through 1993.

2.4.2.3. Egg size and shape

I measured 210 eggs in 1992 and 127 eggs in 1993. Egg length was greater in 1993 than in 1992 ($t=2.36$, $df=335$, $p=0.019$), but egg breadth and volume were not significantly different between years (breadth: $t=0.0.06$, $df=335$, $p=0.96$; volume: $t=0.86$, $df=335$, $p=0.39$). The mean values of egg length and volume in 1992 and 1993 were smaller than the critical values calculated for 1969 (Table 2.6). This indicates that egg length and volume were smaller in 1992 and 1993 than in 1969 ($p \leq 0.05$). Mean egg breadth was smaller in 1992 and 1993 than in 1969, but not smaller than the critical value for egg breadth.

Mean shape index (SI) was greater in 1992 than in 1993 ($t=1.99$, $df=335$, $p=0.047$). Mean SI in 1992 and 1993 was larger than the critical value for all eggs in 1969 and for A-eggs in 1969 (Table 2.7). Mean SI was significantly larger ($p \leq 0.05$) in 1992 than mean SI of first laid eggs in 2-egg clutches in 1969. Mean SI in 1993 was also larger than mean

Table 2.6 Mean values and ranges of egg length, breadth, and volume, for Black-legged Kittiwakes breeding in Witless Bay, Newfoundland, in 1992, 1993 (this study) and 1969 (Maunder and Threlfall 1972). Standard errors are given for 1992 and 1993 and estimated for 1969; critical values were calculated using estimated standard errors and determine statistically different means at $p=0.05$.

Year		N	Length (mm)	Breadth (mm)	Volume (cc)[1]
1992		210			
	Mean		54.1	40.1	42.4
	Range		43.7-60.7	36.8-51.6	33.3-70.6
	SD		2.2	1.6	4.4
	SE		0.16	0.11	0.30
1993		127			
	Mean		54.7	40.1	42.8
	Range		48.9-60.6	36.6-48.7	34.4-62.7
	SD		2.29	1.41	3.69
	SE		0.20	0.13	0.33
1969		176			
	Mean		55.8	40.3	44.2
	Range		52.0-61.5	34.5-44.5	34.6-54.2
	est. SD[2]		2.2	1.6	4.4
	est. SE[3]		0.17	0.12	0.33
	X[4]		55.5	40.1	43.7

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[1] calculations of volume from Coulson (1963).

[2] est. SD = estimated standard deviation; the larger standard deviation (1992) was used as a conservative estimate.

[3] est. SE = estimated standard error; est. SE = est. SD/$(175)^{0.5}$.

[4] X represents the critical value (see methods). Means of length, breadth and volume of 1992 and 1993 must be less than this value to be significantly different from 1969 with $p=0.05$.

Table 2.7 Comparison of the egg shape index of all eggs in 1992 and 1993 (this study) to all eggs, A-eggs (first laid eggs), and A-eggs of 2-egg clutches from 1969 (Maunder and Threlfall 1972) for Black-legged Kittiwakes breeding in Witless Bay, Newfoundland. Mean values, ranges, standard deviations and standard errors are given for 1992 and 1993; standard deviation and standard error for 1969 are estimated; a critical value (X) determines statistically different means at p=0.05.

		Egg shape index[1]					
Year	Eggs	N	Mean	Range	SD[2]	SE[3]	X[4]
1992	All	210	74.2	65.2-94.6	3.4	0.24	
1993	All	127	73.4	62.1-89.7	3.8	0.34	
1969	All	176	72.4	57.0-81.7	3.8	0.29	72.9
1969	A-eggs[5]	99	72.6	57.0-79.7	3.8	0.39	73.2
1969	A-eggs in 2-egg clutches	77	72.8	65.3-77.6	3.8	0.44	73.5

[1] calculation for shape index from Coulson (1963).

[2] SD = standard deviation; for 1969 the larger standard deviation (1992) was used as a conservative estimate.

[3] SE = standard error; SE is estimated for 1969 with SE = est. SD/(n-1)$^{0.5}$.

[4] X is the critical value which must be exceeded by the means of 1992 and 1993 to be significantly different from 1969 with p=0.05.

[5] A-eggs includes all first laid eggs in 1 and 2-egg clutches.

SI of first laid eggs in 2-egg clutches in 1969, but the difference was not significant. Calculation of the critical value (X) was probably overly conservative in this case, because the range of SI of A-eggs in 2-egg clutches in 1969 was very small (Table 2.7), indicating that the standard deviation was probably much smaller than that of 1993. If the real standard deviation could be used in the calculation of X, the difference would probably be significant. Thus, eggs from 1992 were shorter and broader than eggs from 1993, and eggs laid in 1992 and 1993 were shorter and broader than all eggs, A-eggs, and first laid eggs of 2-egg clutches laid in 1969.

2.4.2.4. Changes in egg volume with laydate

When mean egg volume was calculated in 7 day intervals across the laying period, a decrease in egg volume was observed in the first half of the laying period in 1992, followed by an increase (Figure 2.4). In 1993, egg volume gradually decreased throughout the laying period. Results of the ANCOVA with laydate as a covariate showed that the interaction between laydate and year was significant ($F_{1,305}$=7.08, p=0.008), thus the relationship between volume and laydate was different between years and separate regressions were performed. When volume was regressed on laydate, there was a small increase in volume in 1992, but variance in volume explained by date was only 3% ($F_{1,140}$=4.10, p=0.045, R^2=0.028;

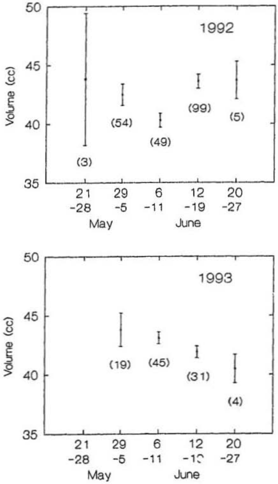

Figure 2.4 Mean egg volume (± standard error) according to the date of laying for Black-legged Kittiwakes breeding on Great Island in 1992 and 1993. Sample sizes are shown in brackets.

$\hat{y}$=37.0+0.13X). In 1993, there was a significant decrease in volume ($F_{1,89}$=5.40, p=0.02, R^2=0.057; $\hat{y}$=49.7-0.17X). When laydates before the median where excluded (to test for changes in volume in the second half of the laying period), neither year had any significant change of volume with laydate, although 1992 again showed a trend towards an increase of volume with date, and 1993 a trend towards a decrease. In 1969 and 1970, there was a decrease in volume with laydate (Maunder and Threlfall 1972).

2.4.2.5. Timing of breeding

Mean laydates were 10 June (median 10 June) in 1992, and 10 June (median 9 June) in 1993. The Kolmogorov-Smirnov method detected no differences between laying distributions (p>0.05). Egg laying began earlier in 1992 than in 1993 but peaked more quickly in 1993 (Figure 2.5). Eggs were laid over a 40 day period in 1992 (from 21 May to 29 June), and in 1993 the last egg was laid on 27 June and the first egg presumed laid around 21 May, a range of 38 days. Only one egg was laid as early as 21 May in 1992, and it preceded all other eggs in the study plots by 5 days. In 1993, no eggs were found on 19 May during a visit to the colony, but the nest which held its first egg so much earlier than all the rest in 1992 looked ready for laying while no other nests were being built. On arrival on 4 June 1993, this nest contained an egg.

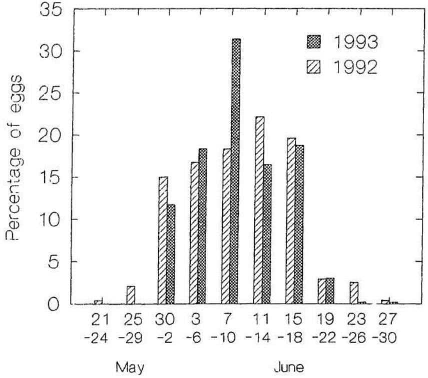

Figure 2.5 Percentage of first laid eggs by date of Black-legged Kittiwakes breeding on Great Island, Newfoundland, in 1992 and 1993. Laydates before 4 June 1993 were estimated from dates in 1992 (Kolmogorov-Smirnov test found no difference between distributions; see text).

Because egg laying had already begun by my arrival on the island in 1993, the number of eggs present was compared to what was present at the same time in 1992, considering only nests used in both years. All plots had been visited by 5 June 1993, and at that time 48 eggs were present with one 2-egg clutch. At that time in 1992, 62 eggs were present with nine 2-egg clutches. This also suggests that a higher percent of total eggs was laid early in the season in 1992.

In 1969, on Gull Island, Witless Bay, eggs were laid over a 32 day period (21 May to 22 June) with a mean of 3 June. In 1970, eggs were laid over a 47 day period (15 May to 1 July) with a mean of 29 May (Maunder and Threlfall 1972). On average, mean laydates were 10 days earlier in 1969 and 1970 than in 1992 and 1993.

Overall late breeding by Black-legged Kittiwakes was also observed on Gull Island in 1990 and 1991, with significantly later laying dates compared to 1970 (Neuman 1994). Mean laydates of first eggs in 1990 were 4 days earlier than in 1992 and 1993, but in 1991, there was no difference in date from 1992 and 1993. Additional records for Witless Bay from 1966, 1973, 1974, 1975, 1976, 1986 (W.A. Montevecchi, unpubl. data) and from 1988 (Chatman 1989) indicate that timing of breeding by kittiwakes has been late in the past four breeding seasons (1990 - 1993), in comparison to these other years (Appendix 2).

2.4.2.6. Association between reproductive measures among years

When reproductive measures of Black-legged Kittiwakes breeding in Witless Bay (Great and Gull Islands) were compared across 7 years, there was considerable association among timing of breeding, mean clutch size, egg size, percent of pairs producing eggs, and hatching, fledging and breeding success (Table 2.8). In general, in years where breeding was early, a higher proportion of nests contained eggs, clutch and egg sizes were greater, and hatching, fledging, and egg to fledging success was high. Correlations between variables were high. All measures of reproductive success correlated negatively with mean laydate and positively with all other variables (Table 2.9). As an exception, fledging success was not highly correlated with timing, clutch size, and egg size, and was only moderately correlated with hatching success. Overall breeding success (chicks fledged from eggs laid) was highly correlated with all other variables.

2.4.3. Island productivity in 1992 and 1993

On 9 and 10 August 1992, 2.3% of 11,643 nests, and 2.7% of 9,712 attended nests contained chicks (Appendices 1, 3 and 4). A total of 272 young were counted. Only six nests (0.05% of total nests) contained two chicks. Big Cove and Gill's Cove (Figure 2.2) had the highest proportions of nests with

Table 2.8 Comparison of timing, mean clutch and egg size, percent of nests with eggs, and hatching, fledging and breeding success of Black-legged Kittiwakes breeding on Great and Gull Islands, Witless Bay, Newfoundland, in 1969, 1970, 1988, and 1990 through 1993.

Year	Mean lay date[1]	Mean clutch size	Egg volume (cc)[2]	%Nests with eggs	Hatching[3]	Fledging[4]	Breeding[5]
					success (%)		
1969[6]	3 June	1.78	44.2	92	71.6	81.0	58.0
1970[6]	29 May	1.95		91	72.9	73.7	54.0
1988[7]	-[10]	1.63	44[11]	80			
1990[8]	6 June	1.49	43.2	83	45.9	50.8	23.3
1991[8]	10 June	1.28	41.1	60	13.4	52.0	7.0
1992[9]	10 June	1.43	42.4	64	9.6	7.0	0.7
1993[9]	10 June	1.37	42.8	77	11.3	68.4	7.2

[1] mean date of all first laid eggs.

[2] egg volume is the mean of all eggs measured.

[3] chicks hatched per egg laid.

[4] chicks fledged per chick hatched.

[5] chicks fledged per egg laid.

[6] data from Maunder and Threlfall (1972).

[7] data from Chatman (1989) and E. Chatman and J.M. Porter, cited in Neuman (1994).

[8] data from Neuman (1994).

[9] data from this study.

[10] in 1988, egg laying began mid to late May (Chatman 1989), therefore mean lay date was earlier than in 1992 and 1993, and later than in 1969 and 1970.

[11] mean volume for 1988 estimated from Fig. 2-5 in Neuman (1994).

Table 2.9 Pearson's correlation coefficients between reproductive measures of Black-legged Kittiwakes from Witless Bay, Newfoundland, in the years 1969, 1970 (Maunder and Threlfall 1972), 1988 (Chatman 1989, E. Chatman and J.M. Porter cited in Neuman 1994), 1990, 1991 (Neuman 1994), 1992, and 1993 (this study).

	Lay	Clutch	Volume	%Egg	%Hatch	%Fledge
Lay[1]	1.00					
Clutch[2]	-0.97	1.00				
Volume[3]	-0.83	0.92	1.00			
%Egg[4]	-0.86	0.87	0.89	1.00		
%Hatch[5]	-0.94	0.91	0.80	0.92	1.00	
%Fledge[6]	-0.57	0.50	0.44	0.72	0.64	1.00
%Breed[7]	-0.91	0.89	0.77	0.93	0.98	0.78

[1] mean lay date of all first laid eggs.

[2] mean clutch size.

[3] mean egg volume of all eggs.

[4] proportion of nests with eggs; arcsin transformed.

[5] hatching success: proportion chicks hatched per egg laid; arcsin transformed.

[6] fledging success: proportion chicks fledged per chick hatched; arcsin transformed.

[7] breeding success: proportion chicks fledged per egg laid; arcsin transformed.

young and with two young (Table 2.10). In no other region were nests with two young counted. The percent of nests with young in Big Cove was 3.5 times greater than the mean. The lowest production was on the south end of the island where the percentage of nests with young was seven times lower than the mean.

From 7 to 10 August 1993, 13,541 nests were counted, 13.0% of all nests and 14.1% of attended nests had young, and 1.6% of total nests had more than one young (Appendices 1, 5 and 6). Big Cove and Gill's Cove again had the highest percentages of nests with young, but Gill's Cove had a higher proportion than Big Cove (Table 2.11). The proportion of nests with young in Gill's Cove was 1.4 times greater than the mean. The south end produced fewest young per nest.

There was great variance in breeding success across regions of Great Island in 1992, with two areas in particular producing the bulk of the young (Figure 2.6). In 1993, there was less variance, but in both years the same regions had most young per nest and the same regions had fewest.

In 1992, Big Cove produced 25% of all young with only 7% of nests. Big Cove and Gill's Cove together produced 78% of chicks with 42% of nests (Figure 2.6). In Big Cove, the proportion of nests with young was significantly greater than all other regions (Bonferroni adjusted; $p<0.0003$ for all comparisons). In 1993, substantially more young were raised

Table 2.10 Summary of percentage of young and percentage of different brood sizes relative to total number of nests, for the 8 regions of Great Island, in 1992.

	Region[1]	Total nests	% of total nests attended	Percentage of total nests			
				With young	With 1 young	With 2 young	With 3 young
1	Landing Cove	1565	82	0.51	0.51	0.00	0.00
2	East side	1084	77	1.48	1.48	0.00	0.00
3	Gill's Cove	4086	84	3.45	3.35	0.01	0.00
4	North end	365	81	1.37	1.37	0.00	0.00
5	Cribby Cove	1726	92	1.04	1.04	0.00	0.00
6	West point	466	90	1.50	1.50	0.00	0.00
7	Big Cove	815	91	8.10	7.85	0.25	0.00
8	South end	1536	74	0.33	0.33	0.00	0.00

[1] regions of Great Island shown in Figure 2.2.

Table 2.11 Summary of percentage of young and percentage of different brood sizes relative to total number of nests, for the 8 regions of Great Island, in 1993.

			% Of total	Percentage of total nests			
	Region[1]	Total nests	nests attended	With young	With 1 young[2]	With 2 young	With 3 young
1	Landing Cove	1657	88	7.60	6.70	0.91	0.00
2	East side	1645	88	10.76	9.79	0.91	0.06
3	Gill's Cove	4487	94	18.72	16.58	2.14	0.00
4	North end	745	90	10.07	6.44	3.62	0.00
5	Cribby Cove	1717	96	15.08	12.80	2.27	0.00
6	West point	504	98	13.49	11.71	1.79	0.00
7	Big Cove	971	97	17.10	15.86	1.13	0.10
8	South end	1815	85	2.37	1.93	0.44	0.00

[1] regions of Great Island shown in Figure 2.2.

[2] nests with at least 1 young included.

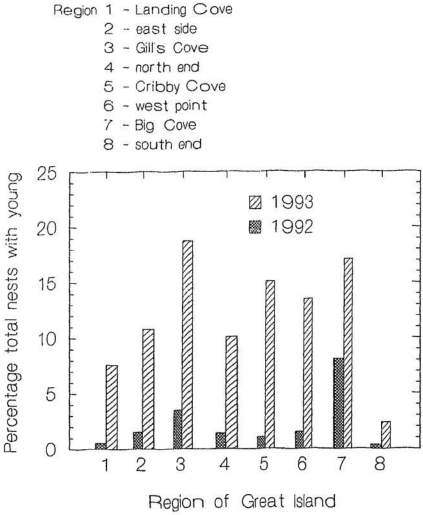

Figure 2.6 Percentage of kittiwake nests with young in the 8 regions of Great Island, as surveyed in the late chick stage of reproduction in 1992 and 1993.

in all areas of Great Island with less variability between regions (Figure 2.6). Big Cove and Gill's Cove, with 40% of nests, produced 56% of all young. Gill's Cove had the highest proportion of nests with young but this was not statistically different from Big Cove or West point, and Big Cove, with the second highest proportion, was not statistically different from Cribby Cove or West point. Nests with two young were found in all areas in 1993, with proportions ranging from 0.4% (south end) to 3.6% (north end). The south end of the island had the poorest success in both years. With 13% of nests, only 1.8% and 2.6% of all chicks were found here in 1992 and 1993, respectively. Region 1 (Landing Cove), also on the south end of the island, had the second poorest reproductive success in both years.

Kittiwakes produced more young per nest in 1993 than in 1992. Percentage of nests with young, with one young, and with two young were higher in 1993 than in 1992 (Table 2.12). No 3-chick broods were counted in 1992 and only two were counted in 1993. In 1993, nests scored as 1+ young and nests with one young were combined for comparison to 1-chick broods of 1992. Thus, the number of 1-chick broods was slightly overestimated, and 2-chick broods slightly underestimated for 1993 in this comparison.

Table 2.12 Percentage of nests with young and percentage of different brood sizes relative to total number of nests, summarized for Black-legged Kittiwakes breeding on Great Island, in 1992 and 1993.

			Percentage of total nests			
	Total nests	% of total nests attended	With young	With 1 young[1]	With 2 young	With 3 young
1992	11,643	83	2.28	2.23	0.05	0.00
1993	13,541	92	12.95	8.79	1.62	0.01
X^2_1			965.81	495.74	174.21	
p			<0.0001	<0.0001	<0.0001	

[1] nests with at least 1 young included.

2.4.4. Overall island productivity of 1992 and 1993 in comparison to estimated productivity in 1969 and 1970

The island survey results can be compared to expected productivity in a year with the success of 1969 and 1970 (average productivity of 1969 and 1970). Given that 91% of nests produced eggs, that clutch sizes were in a ratio of 16% 1-egg clutches : 82% 2-egg clutches : 2% 3-egg clutches, and that egg to fledge mortality was 45% (Maunder and Threlfall 1972), then 22,845 eggs in total and 10,212 fledglings would have been produced from the 13,541 nests counted in 1993. This figure of 10,212 fledglings expected in 1969/70 compares to 1,978 large chicks observed in 1993, some of which probably did not fledge. The 1992 comparison is 8,781 fledglings produced in 1969/70 from 11,643 nests, and 272 large chicks observed in 1992. Thus, relative to the success of two years similar to 1969 and 1970, Great Island produced about 3% and 19% the expected number of fledglings in 1992 and 1993, respectively.

2.4.5. Island productivity in comparison to productivity in the study plots

In both years, the proportions of total nests with chicks in the study plots were not different from that proportion in the same regions as the study plots, as calculated from the island brood count (Table 2.13). When compared to overall

Table 2.13 Percent of total nests with young in the study plots and proportions of total nests with young on Great Island as recorded in island brood counts. Study plots are compared to corresponding regions of the island and to the overall average of Great Island. Dates for study plots correspond to dates of island survey.

	Study plots		Island brood counts	
Year	Plot #	Percent nests with young	Corresponding region[1]	Percent nests with young
1992	1	0	8 south end	0.3
	2	0	8 south end	0.3
	3	0	1 Landing Cove	0.5
	4	0	1 Landing Cove	0.5
	5	0	1 Landing Cove	0.5
	6	0	1 Landing Cove	0.5
	7	5.2	8 south end	0.3
	All	0.9	1 and 8 $X^2_1=1.62$, $p=0.20$	0.4
	Total	0.9	Great Island $X^2_1=4.24$, $p=0.04$	2.3
1993	1	0	8 south end	2.4
	2	4.3	8 south end	2.4
	3	0.8	1 Landing Cove	7.6
	4	7.6	1 Landing Cove	7.6
	5	3.7	1 Landing Cove	7.6
	6	0	1 Landing Cove	7.6
	7	12.9	8 south end	2.4
	8	15.0	7 Big Cove	17.1
	All	5.6	1,7 and 8 $X^2_1=3.75$, $p=0.05$	7.5
	Total	0.056	Great Island $X^2_1=35.56$, $p<0.0001$	12.9

[1] regions of Great Island shown in Figure 2.3.

island productivity, however, the study plots produced significantly fewer nests with chicks. Only two of the island's regions were represented with study plots in 1992, and three regions were represented in 1993. In both years 3 study plots were in the south end (41% and 32% of nests in 1992 and 1993 respectively), the region of the island which in both years had the lowest proportions of nests with chicks. Four study plots in both years were in region 1, the region which had the second lowest reproductive success in both years (Figure 2.6, Table 2.10, Table 2.11).

2.5. DISCUSSION

2.5.1. Effect of researcher disturbance

I found no differences in Black-legged Kittiwake breeding success between observation and disturbed plots at all stages of reproduction. A survey of the control section south of plot 5 also supported the conclusion of no disturbance effect on breeding performance. Unlike seabirds such as puffins (Harris 1984, Pierce and Simons 1986, Rodway 1994), Least and Crested Auklets (Piatt et al. 1990), and Ancient Murrelets (Gaston et al. 1988), which often desert their eggs or young when disturbed, nest desertion due to investigator disturbance was not a problem with kittiwakes. Adults often stayed on their nests until I was within a few metres of them, and they returned to their nests immediately after I moved away from the area. The relative immobility of kittiwake chicks with behaviour suited to cliff nesting means that chicks are limited in their ability to run away when approached. This is a cause of chick mortality due to investigator disturbance for ground-nesting gull species (Gotmark 1992).

The main risk to kittiwakes due to my disturbance was indirect: Herring Gulls attempted to rob nests when adults were flushed. Nest predation that is facilitated by investigator disturbance has been documented for many seabird species (Ellison and Cleary 1978, Gotmark 1992). In a survey of studies on avian investigator disturbance, Gotmark (1992) found this was the cause of reduced productivity in study plots in the majority of cases, particularly for gull species, where nest desertion did not occur. Larids and corvids were frequently recorded as opportunistic nest predators, taking eggs or young when adults are flushed, or even learning to follow humans to their study plots.

Risks of gull predation seemed to increase as the season progressed, probably due to the increasing numbers of Herring Gulls which had failed in their breeding attempts. Herring Gulls still incubating or with chicks were preoccupied with defence of their own nests. Herring Gulls seemed to cue in to the opportunity my disturbance presented more quickly in 1993 than in 1992. Reducing visits to plots in 1993 when risks of predation were high probably minimized the effect of disturbance.

Neuman (1994) found lower hatching success in study than in control plots, but differences were due to cliff structure rather than to disturbance. Topography, and therefore accessibility to predators at the two types of plots differed. This may often occur in such comparisons, because nests accessible to humans are also more likely to be accessible to predators. Few studies of kittiwakes have addressed this question quantitatively.

2.5.2. Breeding failure of kittiwakes in Witless Bay

Breeding success on Great Island, Witless Bay, was poor in both 1992 and 1993, but failure was extreme in 1992, with lower success at all stages of reproduction. Proportions of pairs producing eggs was low in both years in comparison to 1969 and 1970 (Maunder and Threlfall 1972), and clutches and eggs were small. Egg loss was high in both years, and chick mortality was higher than egg mortality in 1992, resulting in near complete breeding failure. In 1993, chicks that hatched fledged at a rate comparable to 1969 and 1970, but because egg mortality was so high, overall egg to fledging success was only 7.2%. Similar egg mortality occurred on Gull Island in 1991 (Neuman 1994). In 1990, when failure was less severe, hatching success was relatively high, and productivity was lowered by a steady loss of chicks to predation throughout the nestling period (Neuman 1994).

Reduced laying and small eggs and clutches in Witless Bay in 1991 through 1993 (Neuman 1994, this study) suggest that breeding condition of adult kittiwakes may have been poor in recent years, and food supply may have been limited during the laying and pre-breeding periods. In Alaska, where kittiwake breeding failure is frequent, productivity is primarily limited by an inability of many pairs to achieve breeding condition (Hatch et al. 1993) and there is high variation among years in proportions of pairs attempting to breed (Hatch and Hatch 1988). Clutch sizes are also reduced in poor years.

At kittiwake colonies in the North Sea, where recent breeding failures are associated with a decline in sandeel populations, most failures occurred in the chick stage (Harris and Wanless 1990, Hamer et al. 1993). Food shortage was speculated to be at least partially responsible because there were widespread reports of chick deaths, chick growth rates were low, a low proportion of sandeels were found in the diet of chicks, and an unusually high proportion of unattended young were observed (Harris and Wanless 1990). In a recent year of complete breeding failure in Shetland, clutch and egg sizes, hatching success and timing of laying were not affected, but chick survivorship was drastically reduced (Hamer et al. 1993, Monaghan et al. 1993), suggesting that food shortage may not have been severe in the early stages of reproduction, but was inadequate for raising young.

Witless Bay kittiwakes, similar to Alaskan kittiwakes, seemed to be experiencing food shortage early in the season, prior to the normal timing of the inshore arrival of spawning capelin. Small eggs and clutches, late laying, and poor hatching success suggest that food supplies were limiting throughout the pre-breeding and laying periods. Breeding failure was primarily associated with the egg stage in both years, through reduced laying and severe egg predation (Chapter 3). In 1992, food appeared to be unavailable during the early chick period as well because capelin arrival was late (see Chapter 3), while relatively high chick survival in 1993 suggests that food supplies were adequate at that time. In colonies in the North Sea, where reproductive measures early in the season were unaffected, shortage of the main prey species on which chicks are fed may have been the primary factor influencing failure.

Food shortage was indirectly responsible for high egg mortality in both years by affecting egg predation. Several studies have documented that food stressed adults are less attentive to eggs and young, and abandon them more frequently (Barrett and Runde 1980, Harris and Wanless 1990, Monaghan et al. 1993, Roberts and Hatch 1993). Some predation of abandoned eggs was observed in this study (opportunistic predation), but egg loss was caused primarily by forced predation (incubating adults are forced from nests by a predator), and food-stressed predators, such as Great Black-backed Gulls (<u>Larus marinus</u>), were very persistent (Chapter 3).

2.5.2.1. Weather, climate and oceanographic conditions

Weather and climate may be important factors affecting kittiwake productivity. Coulson and Porter (1985) have suggested that in northern parts of the species' range, late springs can have severe effects on food availability, resulting in much variation in body condition of breeders. A significant latitudinal effect on breeding success has been documented in some years of highly variable productivity in the North Sea, with the most severe failures occurring farthest north (Harris and Wanless 1990). This may be primarily due to the association between oceanographic conditions and latitude. In Alaska, where breeding success of kittiwakes is typically variable and failures are frequent, annual food variability or poor feeding conditions near the colony are believed to primarily limit kittiwake productivity (Springer et al. 1986, Roberts 1988, Baird 1990, Murphy et al. 1991, Hatch et al. 1993, Roberts and Hatch 1993), and in some cases this has been linked to climate or oceanographic conditions (Aebischer et al. 1990, Dunnet et al. 1990, Harris and Wanless 1990, Murphy et al. 1991, Hatch et al. 1993). May temperature, which is associated with spring ice break up, has been found to be closely associated with productivity over a 15 year period in western Alaska (Murphy et al. 1991). Fewer and smaller capelin fed to chicks in a year of poor productivity was associated with water temperatures, rainfall, and timing of storms (Baird 1990). Roberts (1988) associated a year of poor success on Middleton Island, Alaska, with abnormally cold water temperatures resulting in sandlance and capelin moving to warmer water and deeper depths.

In Newfoundland, cold water temperature may have played a role in recent breeding failures (Casey 1994, Neuman 1994), as the maturation, spawning, and inshore movements of capelin are affected by water temperature (Methven and Piatt 1991, Montevecchi and Myers 1992). Relative to previous years, capelin inshore arrival was at least two weeks to a month late in 1991 through 1993 (Neuman 1994, Chapter 3, J. Carscadden, DFO, St. John's, pers. comm.), three years of severe kittiwake breeding failure. Cold water temperature and the associated changes in the physiology and behaviour of capelin may be related to the extent and movements of ice in the northwest Atlantic Ocean in the spring (Casey 1994).

Both summers of this study were colder and wetter than normal (Atmospheric Environmental Service, St. John's). Neuman (1994) attributed delayed breeding of kittiwakes on

Gull Island in 1991 to colder air as well as water temperatures. In 1992, July air temperatures were 3.0°C colder than normal (30-year average), and June, July and August temperatures were 1.7, 3.0, and 1.2 °C below normal in 1993. However, in both years temperatures were normal in May, which is presumably the most influential month for egg laying.

Severe rain and wind storms causing exposure and starvation of chicks can reduce kittiwake productivity (Roberts 1988). Almost twice the normal amount of rainfall was recorded in June and July in 1992 and 1993 (Atmospheric Environmental Service, St. John's). Atlantic Puffin (Fratercula arctica) nests flooded causing mortality of eggs and small young (Rodway 1994), but wet chicks or flooded kittiwake nests were not seen, and rainfall probably had little impact on kittiwake success during this study.

Low kittiwake reproductive success was widespread in Newfoundland between 1991 and 1993. Kittiwakes produced few young on Baccalieu Island (48°07'N, 52°48'W), Funk Island (49°45'N, 53°11'W), Witless Bay, and Cape St. Mary's (46°50'N, 54°12'W). Highest success occurred at Cape St. Mary's in all years (Casey 1994, Neuman 1994). Cape St. Mary's is furthest south of the four locations, is less affected by the inshore polar waters of the Labrador Current moving past Great and Gull Islands in Witless Bay, and has warmer water in spring and summer (Steele et al. 1979). In addition, alternative food sources may be available to seabirds at Cape St. Mary's and capelin migration is earlier further south (Carscadden 1984). The greater breeding success of kittiwakes at Cape St. Mary's in all years supports the association of breeding success with latitude, water temperature, and food availability.

Kittiwakes tend to be more variable in their breeding success than many other seabird species and are therefore considered good indicators of oceanographic conditions (Hatch and Hatch 1990, Baird 1990, Furness and Barrett 1991, Hatch et al. 1993, Montevecchi 1993). On Great Island, although kittiwakes failed in 1992 and 1993, the productivity of murres (unpubl. data) and puffins (Rodway 1994) was much higher. Murres and puffins are pursuit divers and fish may therefore be more accessible to them than to birds such as kittiwakes, which can only take prey from the ocean's surface. Thus, kittiwakes are probably more vulnerable to reduced food supplies than murres and puffins, and are therefore more susceptible to breeding failure.

In Alaska, kittiwake failure is frequent and productivity is highly variable, but unlike Alaska, previous records of kittiwake breeding performance in Witless Bay show no indication of severe failures prior to 1990, although data are sparse. Existing records indicate that breeding success was at least moderately high in 1969, 1970 (Maunder and Threlfall

1972), 1973, 1974, 1986 (W.A. Montevecchi unpubl. data) and 1988 (Chatman 1989), and that hatching success was high in 1966, 1975, and 1976, with no data on fledging in those years (W.A. Montevecchi unpubl. data). There is some evidence that 1981 was a poor year for seabirds in Witless Bay, due to lack of capelin (Brown and Nettleship 1984), and success of kittiwakes may have been poor in 1985, a year of late ice break-up and breeding failure at the Gannet Islands, Labrador (Birkhead and Nettleship 1988). In general, however, the seasonal flush of capelin, although not without variation (Burger and Piatt 1990, Piatt 1990, Methven and Piatt 1991), appears to have provided breeding seabirds with a fairly abundant and predictable food supply (Threlfall 1968).

Recent changes in this oceanographic region are becoming apparent. Newfoundland has recently been faced with a drastic decline in Northern Cod (Gadus morhua) populations. Capelin spawning has been abnormally delayed, and capelin are smaller than normal (J. Carscadden, DFO, St. John's, pers. comm.), which appears to be related to cold summer sea surface temperatures (Methven and Piatt 1991, Montevecchi and Myers 1993). Kittiwakes are constrained by their small size (Furness and Monaghan 1987, Harris and Wanless 1990) and by their surface feeding habits (Burger and Piatt 1990, Montevecchi 1993). Although some species, such as Common Murres, may be able to compensate for reduced prey abundance

(Burger and Piatt 1990, Furness and Barret 1991), availability of prey appears to have been insufficient to support kittiwake reproduction.

2.5.2.2. Associations between reproductive measures among years

Correlations between measures of kittiwake breeding success among seven years in Witless Bay were high. High overall success was associated with early laying, a high proportion of nests with eggs, and relatively large clutch and egg size. Clutch and egg size and proportion of nests with eggs was lowest in 1991, and hatching, fledging, and breeding success were lowest in 1992. This may indicate that food availability early in the season in 1992 was somewhat superior to 1991, and that other factors reduced productivity during incubation and the early chick period. Although low egg and chick survivorship are often associated with food shortage, these measures can be affected and compounded by forces such as predation. Timing of breeding, egg size, clutch size, and proportion of nests with eggs may be more predictably linked to food shortage early in the season.

High correlations between reproductive measures have been found in other studies, particularly in Alaska (Roberts 1988, Hatch and Hatch 1990, Murphy et al. 1991). In a comparison including 15 years of breeding performance of kittiwakes in

Alaska, Murphy et al. (1991) found that in years of high productivity, more nests were built, more pairs produced eggs, the onset of laying was earlier, and clutches were larger. Years of extreme failure were often associated with reduced overall effort as early as the nest-building stage. Hatch and Hatch (1990) also found a significant correlation between the proportion of pairs laying eggs, clutch size and overall productivity, and Roberts (1988) found a similar pattern in two years of differing food availability. In the North Sea, the extent and severity of breeding failures were associated with the timing of failure, so that most serious failures were those that occurred earliest (Harris and Wanless 1990).

The relationships between clutch size, egg size and laydate have been well established for kittiwakes. Coulson and White (1961) have shown that clutch size is directly influenced by laydate, with clutch size decreasing over the season, regardless of the age or experience of the female. Egg size also declines predictably with season (see section 2.5.2.4.). The association between clutch size and laydate has been documented for many birds (Perrins 1970, Parsons 1976, Drent and Daan 1980, Toft et al. 1984, Forslund and Larsson 1992), but the strength of the relationship may vary among species. In some species (e.g., kestrels), timing of laying determines clutch size and it is not possible to dissociate the two (Meijer et al. 1988). In other species, such as Lesser Black-backed Gulls, clutch size and laydate can vary independently and clutch size but not laydate have been increased by supplemental feeding (Bolton et al. 1992). This difference may reflect life history strategies and the dependability of food availability in the laying period as a predictor of food availability during chick rearing (Bolton et al. 1992). It is not clear whether the association between clutch size, egg size, and laydate is obligatory for kittiwakes, as it is for kestrels, or whether this trend is predictably the best response to breeding conditions.

Early breeding and large clutches can also be associated with complete breeding failure (Monaghan et al. 1992, Hamer et al. 1993, Monaghan et al. 1993). For kittiwakes breeding in Shetland in two years of very different sandeel availability and abundance, early breeding, large clutch size, and high hatching success were followed by complete failure at the chick stage (Hamer et al. 1993, Monaghan et al. 1993). The authors suggested that food supply before hatching was not severely reduced, and that high hatching success reflected the capacity of kittiwakes to increase foraging range and effort. Apparently kittiwakes were able to buffer a decrease in food availability through changes in their time budgets during the relatively undemanding egg laying and incubation periods, but during chick feeding, chicks starved and increasing foraging reproductive seasons left, may be to expend energy reserves to maintain clutch size and thereby increase mortality risks, while the optimal strategy of a young bird, with many potential breeding attempts remaining, may be to maintain body reserves at the expense of clutch size, egg size and laying date.

Thus, early laying and large eggs and clutches are not necessarily indicative of good food supplies or of good adult body condition. However, a reduction in these measures is probably indicative of food shortage. Low food availability early in the season may physiologically restrict the reproductive output of birds, because body condition may limit laydate, egg size and clutch size (Lack 1968, Drent and Daan 1980). Alternatively, food availability (and/or body condition) may act as a cue to breeding adults, and birds may choose tactics which are likely to maximize their life-time reproductive success (Perrins 1970, Winkler and Walters 1983, Toft et al. 1984, Martin 1987, Monaghan et al. 1992).

Food supply early in the season is also highly influential in determining overall productivity because losses throughout the breeding season are cumulative. Losses or low productivity early in the season cannot be compensated for later in the season, and food shortage early in the season, either during egg laying (e.g., Perrins 1970), or during the pre-laying period (e.g., Drent and Daan 1980, Coulson and effort meant that chicks were left unattended and therefore vulnerable to predation (Hamer et al. 1993).

Breeding failure associated with large eggs and clutches and early laying can also reflect alternative reproductive strategies. Monaghan et al. (1992) suggested that when faced with poor feeding conditions early in the season, Arctic Terns (Sterna paradisaea) may "choose" not to delay laying, nor to decrease clutch size, but to expend reserves with the hope of replenishing them later and with the possibility of deserting if conditions do not improve. Choices made by adults can depend on a number of factors such as length of season and migration requirements (Monaghan et al. 1992), food availability and predictability (Perrins 1970, Bolton et al. 1992), foraging skills (Safina et al. 1988), body condition (Drent and Daan 1980, Monaghan et al. 1989) and age of the breeder (Pugesek 1984, 1990). Birds laying late may lay small clutches, not because late breeders are incapable of producing a larger clutch, but because late small clutches do better than late large clutches when food supplies decrease with the season (Perrins 1970), and when limited by body reserves or feeding conditions, there may be a trade-off between laydate and clutch size, so that to produce a larger clutch an individual must delay the onset of laying (Drent and Daan 1980). Age of the breeder may be important, because the optimal behaviour for old birds, with few potential

Thomas 1985), can be expected to lower breeding success even if food supply during chick rearing is good. Poor productivity in 1993, for example, was associated with high chick survivorship, but decreased egg production and poor egg survival strongly limited the role that chick survival could play in overall performance. Thus, early failure, associated with food shortage early in the season, can have severe effects on productivity.

2.5.2.3. Egg shape

Egg shape index was greater indicating that eggs were shorter and broader in 1992 and 1993 than in 1969. Coulson (1963) found that shape index shows an almost continuous increase as breeding experience of the female increases. Shape index is also associated with laying order, and last laid eggs tend to be long and narrow. First and second laid eggs of 3-egg clutches and first laid eggs of 2-egg clutches typically have a high shape index (short and broad), while C-eggs, the second egg of 2-egg clutches, and single eggs have a low shape index (long and narrow). In 1992 and 1993, a higher proportion of total clutches were single egg clutches, relative to 1969. In years of good food supplies, single egg clutches would be laid by young birds, and these eggs would have low shape indices. However, in 1992 and 1993, mean shape index was higher than mean shape index in 1969, in spite of a high proportion of 1-egg clutches. This suggests that older, more experienced birds, which would normally be laying 2 and 3-egg clutches, were laying single egg clutches, and that young birds, which normally lay single egg clutches, were not breeding. Since no 3-egg clutches were laid in 1969, the first laid eggs of 2-egg clutches had highest shape indices. When mean shape indices of 1992 and 1993 were compared to the mean shape index of only first laid eggs in 2-egg clutches of 1969, the means of 1992 and 1993 were still greater. This suggests that eggs from all clutches in 1992 and 1993 were produced by older, more experienced birds relative to eggs produced in 1969.

Mean shape index of all eggs laid in 1992 compares to the highest values of shape index recorded by Coulson (1963): that of first and second laid eggs of 3-egg clutches. This suggests that the age composition of breeders in 1992 and 1993 corresponded to the age composition of breeders laying 3-egg clutches in Coulson's study. Shape index in 1993 was slightly lower than in 1992, suggesting that the proportion of older birds was slightly less.

It has been hypothesized that breeders respond to selective pressures causing them to increase breeding effort with age, because with increasing age, there is a decrease in potential breeding attempts remaining (Pugesek 1984, 1990, Toft et al 1984, Hamer and Furness 1991). In poor years, such as 1992 and 1993, experienced birds may be more able to find and accumulate the resources necessary to attempt reproduction (Burger and Gochfield 1979, Porter and Sealy 1982, Furness and Monaghan 1987, Burger 1988) and older birds may be more willing to reproduce in years when more effort is required and a higher risk may be involved (Pugesek 1984, 1990).

The indication that a higher proportion of older individuals attempted reproduction in the years of this study relative to years when conditions were good (1969 and 1970) concurs with predictions based on this hypothesis and is consistent with the relationships between shape index, proportions of nests with eggs, and overall productivity among years. Shape index was inversely related to the quality of the breeding season, as measured by overall reproductive success. In 1993, breeding success was higher than in 1992 at all stages of reproduction, and an intermediate mean shape index was recorded, lower than in 1992 but higher than in 1969. In 1992, productivity was lowest and mean shape index was highest of the three years. Shape index was also inversely related to proportion of nests with eggs: 64% in 1992, 77% in 1993, and 92% in 1969. Thus, birds of all ages may attempt reproduction in good years, and predominantly older, more experienced birds will breed in poor years.

2.5.2.4. Relationship between egg volume and laydate

A relationship between egg volume and date has been shown in other studies (Coulson 1963, Maunder and Threlfall 1972, Runde and Barrett 1981). Coulson (1963) found that egg volume increased in the first half of the laying period and then decreased rapidly, probably because older females laid early. Runde and Barrett (1981) found a similar pattern: an increase during the first 10 days followed by a gradual decrease. This trend was not observed on Great Island. In 1992, a small seasonal increase occurred, but there was no seasonal decrease. Egg volumes in 1993 showed a small decrease with date throughout the season. On Gull Island, Neuman (1994) found that egg volumes did increase then decrease, as described by Coulson (1963), but only in 1990. In 1991, no significant relationship was found.

Patterns of food availability may account for the lack of decrease in volume over the breeding season in 1991 and 1992. Overall breeding success was lowest in these two years and it seems unlikely that relationships between age and laying date would change in poor years. A lack of decrease or an increase in volume may indicate that food availability was poor early in the laying period and either subsequently improved enough to counter the normal decrease in volume with date, or else by delaying breeding, females were able to lay larger eggs. In addition, if a biased sample of older birds were breeding in poor years, then variance in egg volume may be low, and trends may be less pronounced.

2.5.3. Productivity across Great Island

Brood counts across Great Island at the late chick stage indicated that breeding failure was extensive throughout the colony in both years. Variability on the island was high, however, and significant differences in productivity among regions were found. The areas of Great Island with the highest success were consistent between years (Big Cove and Gill's Cove), and in both years, the south end of the island (including Landing Cove) produced fewest large chicks per nest. Variability between regions was greater in 1992, when failure was most severe.

Differences in cliff structure may partly explain significant and consistent differences in productivity between areas. The cliffs at Big Cove were very steep. In some places the cliff face was vertical or overhung, and the surface was relatively smooth. In contrast, cliff faces on the south end of the island were more irregular and less steep. Nest predators such as Great Black-backed Gulls were observed to make frequent use of rocky perches near kittiwake nests, thereby gaining access to them. Barrett and Runde (1980) also found that colonies in Norway with more horizontal cliff structure suffered more from nest predation than colonies with steep cliffs. Neuman (1994) accounted for a 13 fold difference in hatching success between control and study plots with increased predation at the study plots where topography was relatively horizontal and nests were accessible. Similar links between predation and cliff structure have been found in other studies (Galbraith 1983, Roberts 1988, Chapdelaine and Brousseau 1989).

Large concentrations of nests may swamp the needs of local predators (Lack 1968, Wittenberger and Hunt 1985), thereby allowing a relatively high proportion of chicks to fledge. Gill's Cove supported the largest concentration of kittiwake nests on Great Island and had relatively high success in both years. Fewer kittiwakes nested at Big Cove, and cliff structure was probably more important than predator swamping. At the south end of the island, cliff structure may have facilitated nest predation and concentration of nests may not have been sufficient to swamp predators. In addition to the variability of predation pressure experienced by different areas due to cliff structure, nest predators may habitually frequent certain areas or even defend feeding territories (Montevecchi 1979, Roberts 1988, Neuman 1994, Chapter 3).

Some parts of a colony, such as central locations, may predictably have higher success. Age, differential mortality rates (Coulson and Dixon 1979, Aebischer and Coulson 1990), and competition for high quality nest sites (Coulson 1968), result in higher quality individuals in these areas. Spatial clumping of birds of variable quality may therefore also result in differential productivity within a colony. However, such effects would be more localized than was observed in this study.

The variability found across the island has implications for the establishment of study plots. In the majority of cases, inferences about a population are drawn from a small sample of study plots. Unless study plots are randomly distributed throughout the colony (which is highly impractical if not impossible in many cases), estimates of breeding success may be biased. High spatial variability in breeding success between plots within a colony has also been identified as a potential problem in other studies (Hatch and Hatch 1988, Harris and Wanless 1990).

In this study, productivity from the study plots was significantly lower than the overall productivity of Great Island in both years. The south end of Great Island (including Landing Cove) produced fewest chicks in both years and contained all of the study plots in 1992 and all but one in 1993. Although researcher disturbance is a plausible explanation, study plots were representative of the regions they were in. Differences in regions were likely due to variable predation pressure, probably related to cliff structure and concentration of nests.

2.6. REFERENCES

Aebischer, N.J., and Coulson, J.C. 1990. Survival of the kittiwake in relation to sex, year, breeding experience and position in the colony. J. Anim. Ecol. 59:1063-1071.

Aebischer, N.J., Coulson, J.C., and Colebrook, J.M. 1990. Parallel long-term trends across four marine trophic levels and weather. Nature 347:753-755.

Arcese, P., and Smith, J.N.M. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. J. Anim. Ecol. 57:119-136.

Baird, P.H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scand. 21:224-235.

Barrett, R.T., and Runde, O.J. 1980. Growth and survival of nestling Kittiwakes Rissa tridactyla in Norway. Ornis Scand. 11:228-235.

Birkhead, T.R., and Nettleship, D.N. 1988. Breeding performance of Black-legged Kittiwakes, Rissa tridactyla, at a small, expanding colony in Labrador. Can. Field-Nat. 102:20-24.

Boersma, D., and Ryder, J.P. 1983. Reproductive performance and body condition of earlier and later nesting Ring-billed Gulls. J. Field Ornithol. 54:374-380.

Bolton, M., Houston, D., and Monaghan, P. 1992. Nutritional constraints on egg formation in the Lesser Black-backed Gull: an experimental study. J. Anim. Ecol. 61:521-532.

Bolton, M., Monaghan, P., and Houston, D.C. 1993. Proximate determination of clutch size in Lesser Black-backed Gulls: the roles of food supply and body condition. Can. J. Zool. 71:273-279.

Brown, R.G.B., and Nettleship, D.N. 1984. Capelin and seabirds in the northwest Atlantic. p. 184-194 in Nettleship, D.N., Sanger, G.A. and Springer, P.F. Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Bryant, D.M., and Tatner, P. 1988. The costs of brood provisioning: effects of brood size and food supply. Proc. Int. Ornithol. Congr. 19:364-379.

Burger, J. 1988. Effects of age on foraging in birds. Proc. Int. Ornithol. Congr. 19:1127-1140.

Burger, J., and Gochfeld, M. 1979. Age differences in Ring-billed Gull kleptoparasitism on starlings. Auk 96:806-808.

Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. Stud. Av. Biol. 14:71-83.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.

Cairns, D.K., Montevecchi, W.A., and Threlfall, W. 1989. Researcher's guide to Newfoundland seabird colonies. Memorial University of Newfoundland Occasional Papers in Biology No. 14.

Carscadden, J.E. 1984. Capelin in the northwest Atlantic. p. 170-183 in Nettleship, D.N., Sanger, G.A., and Springer (eds.). Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Casey, J. 1994. Reproductive success of Black-legged Kittiwakes in the northwest Atlantic in 1991-1993. B.Sc. Honours Thesis (Biopsychology). Memorial University of Newfoundland, St. John's.

Chapdelaine, G., and Brousseau, P. 1989. Size and trends of Black-legged Kittiwake (Rissa tridactyla) populations in the Gulf of St. Lawrence (Quebec) 1974-1985. Am. Birds 43:21-24.

Chatman, E. 1989. The influence of nesting density on the reproductive success of the Atlantic Puffin Fratercula arctica (L.) and the Black-legged Kittiwake Rissa tridactyla (L.) on Gull Island, Witless Bay, Newfoundland in 1988. B.Sc. Honours Thesis. Memorial University of Newfoundland, St. John's.

Coulson, J.C. 1963. Egg size and shape in the kittiwake (Rissa tridactyla) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140:211-227.

Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature 217:478-479.

Coulson, J.C., and Dixon, F. 1979. Colonial breeding in seabirds. p. 445-458 in Larwood, G., and Rosen, B.R. (eds.). Biology and Systematics of Colonial Organisms. Academic Press, London.

Coulson, J.C., and Porter, J.M. 1985. Reproductive success of the kittiwake Rissa tridactyla: the roles of clutch size, chick growth rates and parental quality. Ibis 127:450-466.

Coulson, J.C., and Thomas, C.S. 1985. Changes in the biology of the kittiwake Rissa tridactyla: a 31-year study of a breeding colony. J. Anim. Ecol. 54:9-26.

Coulson, J.C., and White, E. 1958. The effect of age on the breeding biology of the kittiwake Rissa tridactyla. Ibis 100:40-51.

Coulson, J.C., and White, E. 1961. An analysis of the factors influencing the clutch size of the kittiwake. Proc. Zool. Soc. Lond. 136:207-217.

Cullen, E. 1957. Adaptations in the kittiwake to cliff nesting. Ibis 99:275-302.

Davis, J.W.F. 1975. Age, egg-size and breeding success in the Herring Gull Larus argentatus. Ibis 117:460-473.

Drent, R.H., and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225-252.

Dunnet, G.M., Furness, R.W., Tasker, M.L., and Becker, P.H. 1990. Seabird ecology in the North Sea. Netherlands J. Sea Res. 26:387-425.

Ellison, L.N., and Cleary, L. 1978. Effects of human disturbance on breeding of Double-crested Cormorants. Auk 95:510-517.

Forslund, P., and Larsson, K. 1992. Age-related reproductive success in the Barnacle Goose. J. Anim. Ecol. 61:195-204.

Furness, R.W., and Monaghan, P. 1987. Seabird Ecology. Chapman and Hall, New York.

Furness, R.W., and Barrett, R.T. 1991. Seabirds and fish declines. Nat. Geogr. Res. Explor. 7:82-95.

Furness, R.W., Ensor, K., and Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80:105-113.

Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes Rissa tridactyla. Bird Study 30:109-120.

Gaston, A.J., Jones, I.L., and Noble, D.G. 1988. Monitoring Ancient Murrelet breeding populations. Col. Waterbirds 11:58-66.

Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. Curr. Ornithol. 9:63-104.

Hamer, K.C., and Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas Catharacta Skua. J. Anim. Ecol. 60:693-704.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P., and Burns, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes Rissa tridactyla in Shetland. Ibis 135:255-263.

Harris, M.P. 1984. The Puffin. T & A D Poyser, Calton.

Harris, M.P., and Wanless, S. 1990. Breeding success of British kittiwakes Rissa tridactyla in 1986-1988: evidence for changing conditions in the northern North Sea. J. Appl. Ecol. 27:172-187.

Harris, M.P., Halley, D.J., and Wanless, S. 1992. The post-fledging survival of young guillemots Uria aalge in relation to hatching date and growth. Ibis 134:335-339.

Hatch, S.A. 1987. Did the 1982-1983 El Nino-Southern oscillation affect seabirds in Alaska. Wilson Bull. 99:468-474.

Hatch, S.A., and Hatch, M.A. 1988. Colony attendance and population monitoring of Black-legged Kittiwakes on the Semidi Islands, Alaska. Condor 90:613-620.

Hatch, S.A., and Hatch, M.A. 1990. Components of breeding productivity in a marine bird community: key factors and concordance. Can. J. Zool. 68:1680-1690.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L., Jr. 1993. Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. p. 140-153 in Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D. (eds.). The Status, Ecology and Conservation of Marine Birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Hays, W.L. 1988. Statistics. Holt, Rinehart and Winston, Fort Worth.

Haymes, G.T., and Blokpoel, H. 1980. The influence of age on the breeding biology of Ring-billed Gulls. Wilson Bull. 92:221-228.

Houston, D.C., Jones, P.J., and Sibley, R.M. 1983. The effect of female body condition on egg-laying in Lesser Black-backed Gulls _Larus fuscus_. J. Zool. Lond. 200:509-520.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Ann. Rev. Ecol. Syst. 18:453-487.

Maunder, J.E., and Threlfall, W. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk 89:789-816.

Meijer, T., Daan, S., and Dijkstra, C. 1988. Female condition and reproduction: effects of food manipulation in free-living and captive kestrels. Ardea 762: 141-154.

Methven, D.A., and Piatt, J.F. 1991. Seasonal abundance and vertical distribution of capelin (_Mallotus villosus_) in relation to water temperature at a coastal site off eastern Newfoundland. ICES J. Mar. Sci. 48:187-193.

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C., and Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in Arctic Terns _Sterna paradisaea_. J. Anim. Ecol. 58:261-274.

Monaghan, P., Uttley, J.D., and Burns, M.D. 1992. Effect of changes in food availability on reproductive effort in Arctic Terns _Sterna paradisaea_. Ardea 80:71-81.

Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., and Walton, P. 1993. The influence of changes in food abundance on diving and surface feeding seabirds. in Montevecchi, W.A. (ed.). Studies of High Latitude Homeotherms: Multispecies Comparisons of Feeding Ecology and Energetics. Can. Wildl. Serv. Occas. Pap. in press.

Montevecchi, W.A. 1978. Nest site selection and its survival value among Laughing Gulls. Behav. Ecol. Sociobiol. 4:143-161.

Montevecchi, W.A. 1979. Predator-prey interactions between ravens and kittiwakes. Z. Tierpsychol. 49:136-141.

Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. p. 217-266 in Furness, R.W., and Greenwood, J.J.D. (eds.). Birds as Monitors of Environmental Change. Chapman & Hall, London.

Montevecchi, W.A., and Myers, R.A. 1992. Monitoring fluctuations in pelagic fish availability with seabirds. CAFSAC Research Document 92/94.

Murphy, E.C., Day, R.H., Oakley, K.L., and Hoover, A.A. 1984. Dietary changes and poor reproductive performance in Glaucous-winged Gulls. Auk 101:532-541.

Murphy, E.C., Springer, A.M., and Roseneau, D.G. 1991. High annual variability in reproductive success of kittiwakes (Rissa tridactyla L.) at a colony in western Alaska. J. Anim. Ecol. 60:515-534.

Nelson, J.B. 1988. Age and breeding in seabirds. Proc. Int. Orn. Congr. 19:1081-1097.

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

Neuman, J.A. 1994. Aspects of the behaviour and ecology of Black-legged Kittiwakes, Rissa tridactyla, breeding at two sites in Newfoundland, Canada, 1990-1991. M.Sc. Thesis. Memorial University of Newfoundland, St. John's.

Nisbet, I.C.T. 1973. Courtship-feeding, egg size and breeding success in Common Terns. Nature 241:141-142.

Nisbet, I.C.T. 1977. Courtship-feeding and clutch size in Common Terns, Sterna hirundo. p. 101-109 in Stonehouse, B., and Perrins, C. (eds.). Evolutionary Ecology. University Park Press, Baltimore.

Nisbet, I.C.T., and Drury, W.H. 1972. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. Bird-Band. 43:161-172.

Nur, N. 1988. The cost of reproduction in birds: an examination of the evidence. Ardea 76:155-168.

O'Connor, R.J. 1974. Feeding behaviour of the kittiwake. Bird Study 21:185-192.

Parsons, J. 1970. Relationship between egg-size and post-hatching chick mortality in the Herring Gull. Nature, London 228:1221-1222.

Parsons, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. Condor 78:481-492.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

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

Piatt, J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. p.36-51 in Sealy, S.G. (ed.). Auks at Sea. Studies in Avian Biology No. 14., Cooper Ornithological Society.

Piatt, J.F., Roberts, B.D., Lidster, W.W., Wells, J.L., and Hatch, S.A. 1990. Effects of human disturbance on breeding Least and Crested auklets at St. Lawrence Island, Alaska. Auk 107:342-350.

Pierce, D.J., and Simons, T.R. 1986. The influence of human disturbance on Tufted Puffin breeding success. Auk 103:214-216.

Pierotti, R. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63:854-868.

Pierotti, R., and Annett, C. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. p. 417-442 in: Kamil, A.C., Krebs, J.R., and Pulliam, H.R., (eds.). Foraging Behavior. Plenum Press, New York.

Pierotti, R., and Bellrose, C.A. 1986. Proximate and ultimate causation of egg size and the "Third-chick Disadvantage" in the Western Gull. Auk 103:1401-407.

Poole, A.F. 1989. Ospreys, a natural and unnatural history. Cambridge U. Press, Cambridge, UK.

Porter, J.M., and Sealy, S.G. 1982. Dynamics of multispecies feeding flocks: age-related feeding behavior. Behaviour 81:91-109.

Pugesek, B.H. 1984. Age-specific reproductive tactics in the California Gull. Oikos 43:409-410.

Pugesek, B.H. 1990. Parental effort in the California Gull: tests of parent-offspring conflict theory. Behav. Ecol. Sociobiol. 27:211-215.

Reznick, D. 1985. Cost of reproduction: an evaluation of the empirical evidence. Oikos 44:257-267.

Roberts, B.D. 1988. The behavioral ecology of breeding Black-legged Kittiwakes (Rissa tridactyla) on Middleton Island, Alaska. M.A. Thesis. University of California, Santa Barbara.

Roberts, B.D., and Hatch, S.A. 1993. Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor 95:330-342.

Rodway, M.S. 1994. Intra-colony variation in breeding success of Atlantic Puffins: an application of habitat selection theory. M.Sc. Thesis. Memorial University of Newfoundland, St. John's.

Runde, O.J., and Barrett, R.T. 1981. Variations in egg size and incubation period of the kittiwake Rissa tridactyla in Norway. Ornis Scand. 12:80-86.

Ryder, J.P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. p. 153-168 in Burger, J., Olla, B.L., and Winn, H.E. (eds.). Behavior of Marine Animals Vol. 4. Plenum Press, New York.

Safina, C., Burger, J., Gochfeld, M., and Wagner, R.H. 1988. Evidence for prey limitation of Common and Roseate tern reproduction. Condor 90:852-859.

Schreiber, R.W., and Schreiber, E.A. 1984. Central pacific seabirds and the El Nino southern oscillation: 1982-1983 perspectives. Science 225:713-716.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Company, New York.

Springer, A.M., Roseneau, D.G, Lloyd, D.S., McRoy, C.P., and Murphy, E.C. 1986. Seabird responses to fluctuating prey availability in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 32:1-12.

Steele, D.H., Green, J.M., and Carter, J. 1979. A biological and oceanographic study of the Atlantic southwest coast marine region. Report submitted to Parks Canada, Dept. of Indian and Northern Affairs.

Templeman, W. 1948. The life history of the capelin (Mallotus villosus o.f. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory. No. 17 (Research). 151pp.

Thomas, C.S. 1983. The relationships between breeding experience, egg volume and reproductive success of the kittiwake Rissa tridactyla. Ibis 125:567-574.

Thomas, C.S., and Coulson, J.C. 1988. Reproductive success of kittiwake gulls, Rissa tridactyla. p. 251-262 in Clutton-Brock, T.H. (ed.). Reproductive success. University of Chicago Pree, Chicago.

Threlfall, W. 1968. The food of three species of gulls in Newfoundland. Can. Field-Nat. 82:176-180.

Toft, C.A., Trauger, D.L., and Murdy, H.W. 1984. Seasonal decline in brood sizes of sympatric waterfowl (Anas and Aythya, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53:75-92.

Weimerskirch, H. 1992. Reproductive effort in long-lived birds; age-specific patterns of condition, reproduction and survival in the Wandering Albatross. Oikos 64:464-473.

Wilkinson, L. 1990. SYSTAT: The System for Statistics. Evanston, IL: SYSTAT, Inc.

Winkler, D.W., and Walters, J.R. 1983. The determination of clutch size in precocial birds. Curr. Ornithol. 1:33-68.

Wittenberger, J.F., and Hunt, G.L., Jr. 1985. The adaptive significance of coloniality in birds. Avian Biology 8:1-78.

Wooller, R.D., and Coulson, J.C. 1977. Factors affecting the age of first breeding of the kittiwake Rissa tridactyla. Ibis 119:339-349.

CHAPTER 3 CAUSES OF BREEDING FAILURE OF BLACK-LEGGED KITTIWAKES ON GREAT ISLAND, NEWFOUNDLAND, IN 1992 AND 1993

3.1. ABSTRACT

Egg and chick mortalities of Black-legged Kittiwakes (Rissa tridactyla) breeding on Great Island, Witless Bay, Newfoundland, were directly and indirectly associated with food shortage in 1992 and 1993. Capelin (Mallotus villosus) arrived inshore for spawning up to 1 month later than normal in both years, which, in conjunction with a lack of fish offal due to a fisheries moratorium, was associated with food shortage in kittiwakes and in other gull species. Severe egg predation accounted for most kittiwake egg mortality, with 89% (1992) and 87% (1993) of eggs disappearing from nests. Great Black-backed Gulls (Larus marinus) robbed 87% of nests depredated during observations, some specializing on kittiwake eggs and feeding them to their chicks. Herring Gulls (Larus argentatus) robbed 11% of nests depredated. Kittiwake nest defense was rarely successful against Great Black-backed Gulls but was frequently successful against Herring Gulls. Few eggs were taken in the first month of incubation in 1992, but predation peaked sharply in late incubation. In 1993, egg loss was more gradual throughout incubation but with a similar peak. Food shortage and the demands of provisioning gull

chicks were suspected to play a large role in the timing and degree of nest predation.

High chick mortality in 1992 was related to food shortage prior to the inshore migration of spawning capelin. Chicks survived longer and adult incubation and chick-rearing shifts were shorter after capelin arrival than before in 1992, indicating that capelin arrival resulted in increased food availability. Observations and growth measurements indicated that chicks hatching before capelin arrival were starving. The effect of hatchdate on chick survival was less pronounced in 1993 than in 1992. More chicks hatched before capelin arrival in 1992 (77%) than in 1993 (25%). Unattended eggs and chicks were uncommon and adults endured long incubation and chick-rearing shifts, probably in response to high predation risk. Nest shifts were shorter and feeding rates were greater in 1993 than in 1992, suggesting greater food availability in 1993. Feeding rate did not increase with age in either year, but the quantity fed to chicks did. The seasonal migration of capelin into inshore waters in Witless Bay provides an important resource to kittiwakes affecting their time budgets and survival of their chicks.

3.2. INTRODUCTION

Seabirds are known to breed at times and in locations where food is abundant (Lack 1968, Pearson 1968, Ashmole 1971, Furness and Monaghan 1987). In Witless Bay, Newfoundland, most species of breeding seabirds depend primarily on capelin (Mallotus villosus) for raising their young (Templeman 1948, Brown and Nettleship 1984, Burger and Piatt 1990, Montevecchi and Myers 1992). Capelin is a small, cold-water, pelagic, schooling fish inhabiting high and low arctic oceanographic regions in the Atlantic and Pacific (Carscadden 1984). Large populations winter offshore and migrate to inshore Newfoundland waters to spawn on beaches during June and July (Templeman 1948, Carscadden 1984). The inshore migration of spawning capelin provides an important food source to most seabirds breeding in this area. In recent years, however, capelin spawning has been delayed and capelin are smaller than normal (Montevecchi and Myers 1992, J. Carscadden, DFO, St. John's, pers. comm.). This change may reflect environmental conditions because capelin maturation and spawning is closely tied to water temperature (Templeman 1948, Methven and Piatt 1991) which has been colder than normal in recent years (Montevecchi and Myers 1992). Seabirds respond physiologically and behaviourally to changes in the abundance and distribution of prey species (Cairns 1987, Martin 1987, Hamer et al. 1993, Montevecchi 1993). When otherwise predictable patterns of resource availability fluctuate, timing of breeding may not correspond as closely to timing of food availability, and if no alternative resources exist, changes in the breeding performance and in the behaviour of seabirds can be expected.

Black-legged Kittiwakes (Rissa tridactyla) have experienced poor reproductive success in Witless Bay and in other parts of Newfoundland from 1990 to 1993 (Casey 1994, Neuman 1994, Chapter 2). Like other seabirds in this area, Black-legged Kittiwakes rely extensively on capelin for feeding their chicks (Maunder and Threlfall 1972, Brown and Nettleship 1984). Kittiwakes are a small, surface feeding gull, and therefore face the time and energy constraints typical of small species (Pearson 1968, Cairns 1987, Furness and Monaghan 1987, Burger and Piatt 1990, Furness and Barrett 1991) and depend on prey to come to the water surface. They are therefore expected to be particularly vulnerable to changes in the timing and abundance of capelin.

The availability of alternative food sources could complicate interpretation of breeding performance and behaviour during apparent food shortage. For example, Barrett and Furness (1990) found unexpectedly high breeding performance of seabirds in Norway despite an enormous reduction in the Barents Sea capelin stock, and hypothesized the existence of a separate and distinct stock of capelin. In Witless Bay, alternative natural food sources do not appear to be available, particularly to specialized feeders (Brown and Nettleship 1984). Although fish offal has normally been accessible to seabirds throughout the breeding season (Pierrotti and Annett 1987), in 1992, the fishing industry in Newfoundland was virtually shut down, and normally plentiful fish offal has not been available to scavenging species. A lack of alternative food sources suggests that the breeding performance and behaviour of kittiwakes breeding in this area will respond to capelin availability and to the timing of capelin inshore arrival.

Feeding conditions during the egg laying or the pre-breeding period appear to have been poor in Witless Bay in 1991, 1992, and 1993, judging from a low proportion of pairs producing eggs and by small egg and clutch sizes relative to previous years (Neuman 1994, Chapter 2). Very low productivity in these years was primarily due to high egg mortality, exacerbated by substantial chick mortality in 1991 and 1992 (Neuman 1994, Chapter 2). During years of food shortage, poor incubation behaviour can directly and indirectly result in hatching failure. Food stressed adults may abandon eggs which can reduce their viability (Murphy et al. 1991) and permit opportunistic nest predation, (Hatch et al. 1993). Similarly, chicks may be abandoned and death can occur through predation or exposure. Attendance of eggs and chicks by adults may therefore reflect feeding conditions (Barrett and Runde 1980, Galbraith 1983, Roberts 1988, Wanless and Harris 1989, Harris and Wanless 1992, Hamer et al. 1993, Roberts and Hatch 1993).

Food stressed adults spend more time away from the nest because they need to travel greater distances to find food. Thus, time spent on foraging trips, either during incubation or during the chick-rearing period, may be indicative of foraging effort, which in turn reflects food availability (Cairns 1987, Verspoor et al. 1987, Burger and Piatt 1990, Wanless and Harris 1992, Hamer et al. 1993, Monaghan et al. 1993, Uttley et al. 1993). This has been demonstrated for kittiwakes through an association between foraging range, length of adult absence, adult body mass, and an independent measure of varying food availability between years (Hamer et al. 1993, Monaghan et al. 1993). The association between different foraging distances and length of incubation and chick feeding shifts also holds among seabird species, with long-range foragers having longest nest shifts (Lack 1968, Pearson 1968, Verspoor et al. 1987). Variation in incubation and chick-feeding shifts of kittiwakes between years and within a breeding season can be expected to reflect differences in feeding conditions.

Predation pressure can also be affected by food shortage, with food-stressed predators relying more heavily on nest predation than in years of adequate food supplies. Neuman (1994) suspected that increased predation by Herring Gulls (Larus argentatus) was caused by food shortage, and suggested that their expanding population may be contributing to the kittiwakes' breeding failure in Witless Bay. Witless Bay Herring Gulls utilize capelin almost exclusively for raising young (Pierotti 1982, Pierotti and Annett 1987), and Herring Gulls and Great Black-backed Gulls (Larus marinus) rely on fish offal (Threlfall 1968, Furness 1984, Dunnet et al. 1990, Furness et al. 1992, Garthe and Huppop 1994). Delayed capelin arrival and reduced capelin availability, in conjunction with a lack of fish offal, could create food stress in potential nest predators. Nest predation has played a significant role in kittiwake breeding failure at some colonies (Barrett and Runde 1980, Roberts 1988, Chapdelaine and Brousseau 1989), and an increase in nest predation, or in predation of fledgling kittiwakes, due to food shortage, has been noted in other studies (Belopol'skii 1957, Beaman 1978).

The objectives of this study were to investigate the causes of high egg and chick mortalities of recent kittiwake breeding failures in Witless Bay. Timing of breeding was predicted to be associated with breeding success, as early breeders generally experience higher success than late breeders (Coulson and White 1958a, Lack 1968, Toft et al. 1984, Martin 1987). Relationships between timing of breeding and success were also expected to be tied to the timing of food availability. Changes in breeding performance and behaviour were expected after spawning capelin arrived in Witless Bay. In 1992 and 1993, when laying and pre-breeding conditions appeared to be poor (Chapter 2), and when no alternative food sources seemed to be available, duration of incubation and chick-rearing shifts were expected to decrease in response to capelin arrival. The difference in the degree of failure between the two years and the effects of food shortage on nest predators were examined.

3.3. METHODS

3.3.1. Study site

This study took place on Great Island (47°11'N, 52°46'W), Witless Bay, Newfoundland (Chapter 2, Figure 2.1).

3.3.2. Breeding performance

Seven study plots in 1992 and eight study plots in 1993 were monitored throughout the breeding season, and date of laying of each egg, hatchdate, date of disappearance of egg or chick, and approximate fledge date was recorded (see Chapter

2 for detailed methods on the collection and calculation of reproductive measures). Plots 5, 6 and 7 were accessible and reproductive data were collected by reaching into nests. All other plots were not accessible and data were collected by observation. Plot 7 was located in a dense Herring Gull colony and some kittiwake nests were within 1 m of a Herring Gull nest.

3.3.3. Egg fates

Eggs were categorized according to their fate. In both years, eggs either disappeared, were observed depredated, rotted in the nest, or hatched. In 1993, eggs that disappeared or were depredated because they were abandoned by adults were coded separately. Included were eggs that were observed taken from unattended nests, and eggs that disappeared from a nest that was unattended on the previous check.

3.3.3.1 Egg predation

The timing and distribution of egg predation was compared between years and to the timing of eggs laid. All eggs that disappeared were included.

Kittiwake nests were observed for 104 hr from 12 June to 3 July, 1993, in Southern Cove, on a large section of cliffs containing study plots 1 and 2 (Figure 2.1). Observations were conducted from inside a research cabin (which served as a blind) from a distance of 40 to 70 m throughout the daylight hr, but with most observations conducted in the mornings. Observation sessions were 0.5 to 7 hr in duration. Potential predators that landed or moved onto the cliffs near kittiwake nests were identified and unsuccessful attempts at the predation of eggs (hereafter "attempts") and nests robbed were recorded. The number of eggs taken was recorded when possible. "Landings" of aerial predators included movements onto the cliffs and from one area of the cliff to another, even when flight was not involved. When more than one predator was in the area at once, both were observed unless their distance apart made simultaneous observation impossible, in which case the first predator seen was observed. Proportions of landings, attempts, and nests robbed were compared among predators.

3.3.3.2. Role of kittiwake eggs in Great Black-back Gull chick diet

Signs of chick diet are obvious around gull nests when food brought by parents includes inedible parts. When kittiwake eggs were brought to the nest, eggshells were discarded and could be found around the nest. Throughout the breeding season in 1992 and 1993, 14 Great Black-backed Gull nests were monitored and eggshells found in the territories were counted. These Great Black-backed Gull nests were located in the southern part of Great Island near the research cabin and were surveyed every 10 days or more frequently. Hatchdates of gull chicks at 16 nests in 1992 and nine nests in 1993 were known, or could be estimated from pipping eggs and in a few cases, from the masses of larger chicks. The distribution of hatchdates was compared to the timing of kittiwake egg predation.

3.3.4. Fate of chicks

Fates of chicks were grouped into three main categories for analysis. "Dead in the nest" chicks were found or seen dead or dying in the nest, "fledged" chicks were judged large enough to fledge by wing measurements or by age and observation, and "disappeared" chicks vanished without known cause. In 1993, in four cases the disappearance of the younger chick in a two chick brood was coded as "dead in the nest". In these cases death in the nest was strongly suspected because the sibling and chicks in surrounding nests were unharmed (suggesting that predation was unlikely), because death of the younger sibling was common in two-chick broods, and because when small second-hatched chicks died in the nest, they were often trampled into the nest cup until they were difficult to see.

Chicks that died in the nest and disappeared were combined for comparison to chicks that fledged. Chicks were also classified as either surviving for at least 14 days, or dying before that time. Two weeks represents about one-third of the nestling period and provides an intermediate measure of success which can be used to differentiate moderately successful parents (which can raise their chicks to a large size) from parents which cannot feed small chicks. This measure of success was particularly useful when few or no chicks fledged.

3.3.5. Relationship between timing of breeding and reproductive success

The relationship between laydate and chicks hatched, and between hatchdate and the fate of chicks was examined to test the null hypothesis of no effect of timing of breeding on success. The laydates of eggs that produced chicks were compared to those that did not, and hatchdates of chicks that fledged and chicks that lived to 14 days were compared to those that did not. I compared hatchdate among chicks that disappeared, died in the nest, or fledged. The length of time (in days) a chick remained in the nest ("survival time") was considered as a measure of success of parent or chick and was calculated from the difference between the date of disappearance, death or fledging of the chick, and its hatchdate. The relationship between survival time and hatchdate was examined.

3.3.6. Food availability: timing of inshore capelin arrival, incubation shifts, chick feeding, diet, and growth

3.3.6.1 Timing of capelin in relation to reproductive success

The start of accessibility of capelin to kittiwakes was judged from the dates on which Atlantic Puffins (Fratercula arctica) were first observed carrying mature capelin to their chicks. Puffins began carrying other prey items (such as larval fish and crustaceans) by 1 July in both years, but a sudden switch to mature capelin by most puffins was an indication that capelin had arrived inshore for spawning and were accessible to seabirds. Atlantic Puffins were observed on a daily basis.

Kittiwake chicks were divided into two groups in accordance with their hatching date: those that hatched before mature capelin was accessible and those that hatched at or after capelin arrival. The division in hatchdate between the two groups of chicks was set at two days before capelin arrival because it was believed that those which hatched just before capelin arrival could benefit from it as well. Kittiwake chicks were observed to survive for about 2 days with little or no food. The survival times of the two groups were compared in both years.

3.3.6.2. Incubation shifts

The duration of an incubation shift (DIS) was defined as the length of time from the initiation of incubation by one member of a pair until it was replaced by the other member of the pair (i.e., length of time from one changeover to the next). DIS was assessed by checking the nests of incubating pairs every 4 hr (usually) or less, recording the identity of the incubator, and then calculating total number of hr of each shift. It was assumed that when the same individual was seen on two successive observations no changeovers had occurred. This was a reasonable assumption because: two changeovers would have to occur within 4 hr for the event to be missed, numerous hourly checks indicated that this was unlikely, and mean incubation shifts of kittiwakes reported in other studies ranged from 4 to 15 hr (see Discussion). Individual kittiwakes were identified by the patterns of their wing-tips (J. Chardine in prep.) and sex was determined from courtship and mating behaviour when possible. If exact shift time was unknown, the midpoint of the period between checks (including only daylight hr) was used as the time of changeover.

In some cases, particularly in 1992, very long incubation shifts made the inclusion of incomplete shifts necessary because excluding them would bias the data by removing some of the longest shifts. When one bird was incubating at the start of the observations (i.e., start time of the shift was unknown), and the partial shift recorded was as long or longer than the longest shifts at that nest, then this period was included in the analysis as an incubation shift even though it was incomplete. In 1992, where the starting times of several long shifts were unknown, mean and maximum DIS were probably underestimated.

In 1992, incubation shifts were recorded at up to 14 nests between 18 and 21 June in plot 1, and at up to 17 nests between 28 June and 9 July in plot 3. Eggs were lost throughout observations, and at some nests in plot 3, chicks hatched and chick feeding shifts were then recorded (see below). In 1993, up to 40 nests in plot 1 were monitored from 12 June to 2 July, after which time all eggs had disappeared.

The hypothesis that food availability increased with inshore capelin arrival was examined by comparing DIS before and after capelin in 1992, for all samples, and separately for two individual nests where pairs were incubating both before and after capelin arrival (incubation spanned capelin arrival). Observations in 1993 ended before capelin arrival, thus no such comparison for 1993 was possible. Incubation shifts before capelin arrival in 1992 were compared to shifts in 1993 to test the null hypothesis of no difference in DIS in the two years.

3.3.6.3. Chick feeding

In 1992, twelve 3- to 9-hr chick feeding observation sessions were conducted at plot 3, from 8 July to 31 July (71 hr). Six nests and 2 to 6 chicks were observed, ranging in age from 0 (hatched same day) to 28 days. In 1993, 18 3-hr observation sessions were conducted at plot 4, between 8 July and 4 August on 7 nests and 7 to 9 chicks ranging in age from 0 to 34 days. Observation sessions in both years were spaced throughout the daylight hr.

The number of feeds was recorded for each chick, and each feed was coded as one of five size categories. Feed size categories were estimated using the bills and heads of adults and chicks for reference, and each feed size category was assigned a mass in grams using the mass of similar sized prey items collected from Atlantic Puffins (M. Rodway, unpubl. data). The smallest feed size (a peck at a larger food item held in the mouth of the adult) was considered equivalent to the mass of a larval capelin (0.02 g), and the largest feed size equivalent to the mass of a large capelin (15 g). Categories two to four were assigned intermediate masses (0.3 g, 1.5 g, 4.5 g). Because other studies record "boluses" fed, with no reference to size, analyses were performed on feeds of all sizes and also on only the three largest size categories, which were believed to qualify for the "bolus" definition used by others.

Feeding rates are often reported as feeds per pair (or per nest) per hr in other studies, and my data were therefore analyzed in this way. Feeding rate was calculated as total number of feeds per pair per hr (FPH) and quantity fed per pair per hr (QPH). QPH was generated by multiplying the feed frequency of each size class by the mass index of that class. QPH therefore approximately represents grams fed per pair per hr, but because masses were visually estimated as well as categorized, comparison to measured masses in other studies is not possible. Boluses where size could not be estimated were excluded from analyses of QPH, and therefore QPH represents an underestimate of mass fed to chicks per hr, but is assumed to be comparable among chicks and between years (boluses where size could not be estimated were infrequent and it was assumed that there was no bias between pairs in the number of unknown size boluses). I compared feeding rates between years and across chick ages.

3.3.6.4. Chick-rearing shifts

Mate changeovers at the nest were recorded in both years during chick feeding observation sessions. In 1992, a 9-hr and a 7-hr observation session, conducted from noon to dark one day and from dawn to noon the following day, produced a sample of feeding shifts during a 24 hr period. Three such paired observation sessions were conducted: on 8 and 9 July, on 17 and 18 July, and on 25 and 26 July. Duration of chick-rearing shifts (DCS) was calculated from these observation periods and was compared to DCS before capelin arrival, which was provided by chicks hatching during the regular incubation checks. DCS before and after capelin was also compared for four individual nests where pairs were feeding chicks before and after capelin arrival (chick feeding spanned capelin arrival). In 1993, no feeding observations of long enough duration to calculate DCS (without bias) were conducted. In both 1992 and 1993, two variables were calculated to permit comparison of chick-rearing shifts between years: changeovers per hr (CPH) and mean shift interval (MSI). CPH represents the number of times an adult replaced its mate at the nest per hr of observation, and is therefore inversely related to DCS. This variable was calculated for each nest for each observation session. MSI represents the mean chick-rearing shift duration for all nests during an observation session and was calculated from:

$$\text{MSI (hr)} = \frac{\text{length of observation session (hr)}}{\text{(total \# changeovers / number of nests observed)}}$$

Data from dates past 30 July (4 sessions) were excluded from 1993 in the analysis of CPH and MSI because this was the date of the last feeding observation in 1992.

3.3.6.5. Diet

In 1993, food samples were collected on 21 July and 5 August from the regurgitations of two adults and nine chicks in plots 5 and 7 and in an accessible area south of plot 5. Two adults were captured by noose pole, one of which regurgitated. One regurgitate was opportunistically collected when an adult regurgitated into a nest cup. Nine chicks regurgitated when handled. In 1992, too few adults with accessible nests had chicks for diet samples to be collected, but one regurgitate was collected from a nest cup. In both years food items seen during chick feeding observations were recorded.

3.3.6.6. Chick growth

Chick growth measurements were taken from all accessible chicks (plots 5, 6, and 7) in 1992. Mass was measured with 50, 100, 300 and 500 g Pesola scales and wing measurements were taken with a stopped (wing) ruler. For 11 of 19 chicks, only one set of measurements was recorded and chicks subsequently died. Of the remaining eight with more than one set of measurements, four died, three fledged, and one almost fledged, being taken by a predator at 34 days of age. This chick was considered fledged for analysis of growth. The growth curves of these eight chicks are compared. Growth rate was calculated as the rate of mass gain during the period of linear growth (age 6 to 20 days). In 1993, no regular chick measurements were taken because the effect of my disturbance was too great.

3.3.7. Statistics

SYSTAT (Wilkinson 1990) was used for statistical analysis. Chi-square analysis was used to test differences between proportions, ANOVA compared continuous variables grouped into two or more categories, and regression analysis was used to test for relationships between two continuous variables. ANCOVA was used to examine the relationship between feeding rate and chick age and year, with chick age as a covariate; the interaction term was tested for significance and dropped from the model if not significant. Tolerance for type I error was set at 0.05 and residuals were examined for normality and independence. Means are reported ± standard error.

3.4. RESULTS

3.4.1. Egg mortality

3.4.1.1. Fate of eggs

The majority of eggs that did not hatch disappeared in both years. In 1993, when predation observations were conducted, 16% of all eggs were observed depredated (Table 3.1). In 1992, no predation observations were conducted and therefore fewer predatory events were observed. Few eggs (0.5-2%) rotted in the nest, presumably due to neglect or infertility. Few replacement clutches were recorded in both years (Chapter 2, Table 2.2 and 2.3).

The proportion of eggs that produced chicks were not different in 1992 and 1993 (X^2_1=0.24, p=0.62). An average of 88% of eggs disappeared from the nests in the two years, and an average of 11% of eggs produced chicks.

3.4.1.2. Egg predation

In 104 hr of observations of kittiwake nests in Southern Cove between 12 June and 3 July, Great Black-backed Gulls accounted for the majority of all landings by potential nest predators (71%), for most predatory attempts (72%), and for the great majority of nests robbed (87%, Figure 3.1). Herring Gulls accounted for almost all of the remaining landings,

Table 3.1 Fates of Black-legged Kittiwake eggs in 1992 and 1993 on Great Island, Newfoundland.

	1992		1993	
Fate	Number of eggs	%	Number of eggs	%
Disappeared	365	87.7	389	63.6
Known depredated[1]	6	1.4	95	15.5
Abandoned then depredated[2]	-	-	46	7.5
Rotten	2	0.5	14	2.3
Hatched	43	10.3	68	11.1
Totals	416	100	612	100

[1] predator observations were only conducted in 1993.

[2] only coded in 1993; includes eggs that disappeared and were unattended at last observation.

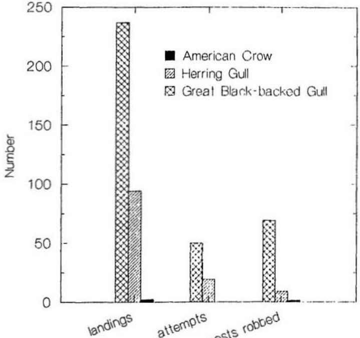

Figure 3.1 Number of landings, unsuccessful predatory attempts, and nests robbed by nest predators of Black-legged Kittiwakes, in 104 hours of observation in Southern Cove, Great Island, 1993.

predatory attempts, and nests robbed, but although Herring Gulls accounted for 28% of all landings and attempts at eggs, only 11% of nests were robbed (Figure 3.1). American Crows (Corvus brachyrhynchos) played only a small role in egg predation, landing only twice, robbing one nest and carrying away one well developed egg. This egg had been temporarily abandoned and the parent was not at the nest at the time of predation. Common Ravens (Corvus corax) were never recorded as a potential egg predator during observations in the observation area. They were, however, seen at other times and in other areas carrying eggs and flushing kittiwakes. Landing Cove and Big Cove seemed to be more preferred areas for raven activity and they were observed flushing kittiwakes from nests in these areas on several occasions.

Close approach of Great Black-backed Gulls almost always caused incubating kittiwakes to flush from the nest and several nests at once could then be robbed. Kittiwake mobbing behaviour was occasionally successful in deterring Great Black-backed Gulls, but was usually ineffective. Kittiwakes primarily circled and called, and physical contact was rarely observed. Kittiwake mobbing was most successful when Great Black-backed Gulls were not securely perched but were slipping on rocks or were otherwise unsure of their footing.

In contrast, Herring Gulls were rarely able to flush kittiwakes from the nest unless they managed to surprise a snoozing incubator. Kittiwakes were often observed to successfully defend their nest against Herring Gulls, but Herring Gulls were able to pull kittiwakes from the nest if a physical struggle resulted. The most successful kittiwakes were those that did not respond to a Herring Gull's presence. A kittiwake which jabbed at a Herring Gull could be pulled from the nest by its bill. Herring Gulls were mobbed much more vigorously than Great Black-backed Gulls, although usually by only the few kittiwakes whose nests were specifically at risk.

Because kittiwakes abandoned their eggs at the presence of Great Black-backed Gulls but not Herring Gulls, Herring Gulls were sometimes observed to take advantage of the hunting behaviour of Great Black-backed Gulls. Herring Gulls followed Great Black-backed Gulls on at least 13 occasions during the 104 hr of observation. They cleaned up spilt egg remains on two occasions and robbed two nests when kittiwakes were flushed by Great Black-backed Gulls. On seven occasions a Great Black-backed Gull attacked a Herring Gull which was hunting in the same area.

Great Black-backed Gulls were often observed taking advantage of wind for nest predation. A strong wind blowing into a cliff allowed gulls to soar alongside and remain suspended above kittiwake nests, from where they could reach down and pick up eggs. This was a successful tactic because kittiwakes usually left their nests when a Great Black-backed Gull soared above them. Hunting this way appeared to be fairly effortless, and allowed the gulls to access nests on sheer parts of the cliff which would normally be difficult to reach. Fifteen percent of eggs taken by Great Black-backed Gulls during predation observations were taken in this way. Herring Gulls also used the wind for hunting, but because kittiwakes did not leave their nests they were less successful (no eggs observed taken in this way). Soaring Herring Gulls seemed mainly to cue in to the location of Great Black-backed Gulls, taking advantage of the disturbance created by them.

Predation observations ended after 3 July as almost all eggs were gone from the nests. Two Great Black-backed Gulls harassed the observation area almost continuously on 3 July from morning to well past dusk. Almost no Great Black-backed Gulls were seen looking for eggs in this area after this day. Of seven nests in plot 2 that still contained eggs at that time, none were depredated and five fledged chicks.

Eggs were taken earlier in 1993 than in 1992. In 1992, mean date of egg predation was 24 June while in 1993, it was 22 June (t=2.17, df=812, p=0.031). Few eggs were taken in the first month of the egg laying period in 1992, but predation peaked sharply between 19 June and 30 June, at which point most eggs disappeared (Figure 3.2). In 1993, egg predation was more gradual than in 1992, with more eggs taken as they

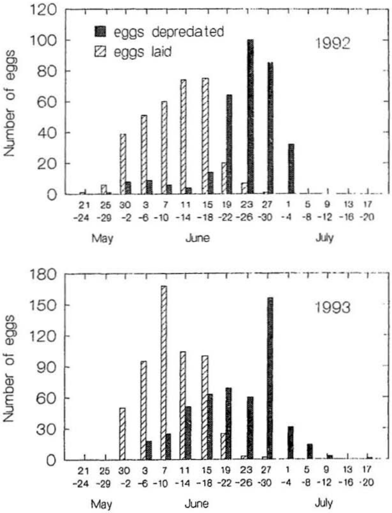

Figure 3.2 Timing of Black-legged Kittiwake eggs laid and depredated in the study plots on Great Island, Newfoundland, in 1992 and 1993.

were laid. Predation peaked once between 19 and 22 June,though less steeply than in 1992, and a second time, between 27 and 30 June (Figure 3.2).

3.4.1.3. Role of kittiwake eggs in the diet of Great Black-backed Gull chicks

Of 14 Great Black-backed Gull territories visited regularly in 1992, 13 hatched at least one young, and at three of these, kittiwake eggs were found. At one territory (pair #1), five kittiwake eggs were found on 21 June; the chicks disappeared shortly after hatch and no further eggs were brought to the nest. At the second territory (pair #4), the shells of 57 eggs and four intact eggs were found on 27 June. The intact eggs contained embryos of all stages of incubation. On 30 June, four more intact eggs and seven eggshells were found. Also found at this nest were four kittiwake skulls, a pellet containing kittiwake feathers and feet, and one broken Herring Gull egg. At the third territory (pair #7), fish bones were regurgitated by a chick on 21 June and the eggshells of 18 kittiwake eggs were found on 27 June. Egg yolk around the bills of the two chicks indicated that they were feeding on these eggs. At the remaining 10 territories with young, no evidence of kittiwake egg predation was found. Other signs of diet at these nests include: Leach's

Storm-Petrel pellets, puffin carcasses, large fish bones, kittiwake skulls and wings, and garbage.

In 1993, the territories of the two main egg specialists of 1992 (pairs #4 and #7) again contained kittiwake eggs, although smaller numbers were found. Eggshells amounting to about 32 eggs were found at territory #4 between 10 June and 2 July, with a maximum of 11 eggs found at one time. At territory #7, the shells of 30 eggs were found between 25 June and 2 July. Eggshells were found at three other territories but no more than a total of three eggs were found at each. Other signs of diet in 1993 were similar to what was found in 1992. At no Herring Gull nests were eggshells of kittiwake eggs found in either year.

Hatching of Great Black-back Gull chicks ranged from 3 to 24 June, in 1992, with a mean of 14 June and a median of 13 June (n=34). In 1993, hatching ranged from 4 to 22 June with a mean of 11 June and a median of 8 June (n=15). In both years the peak of kittiwake egg predation occurred about 10 days after the median gull chick hatch (Figure 3.3).

3.4.2. Chick survival

In 1992, 43 chicks hatched in 11 2-chick broods and 21 1-chick broods in the study plots. In 1993, 68 chicks hatched in 15 2-chick broods and 38 1-chick broods. Ratios of 2-chick to 1-chick broods were not different in the two years

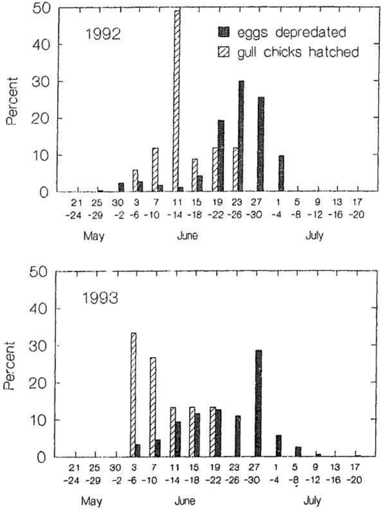

Figure 3.3 Timing of the depredation of Black-legged Kittiwake eggs from the study plots in relation to the timing of Great Black-backed Gull chick hatch in 1992 and 1993 on Great Island, Newfoundland.

(X^2_1=0.35, p=0.56). Of the 2-chick broods in 1992, none fledged two chicks, one fledged one chick and 10 fledged none. In 1993, eight of 15 2-chick broods fledged both chicks, five fledged one chick and two fledged none. The proportion of 2-chick broods fledging any chicks was higher in 1993 than in 1992 (X^2_1=15.36, p=0.0001). The proportion of total chicks fledging, and the proportion of total chicks living to 14 days was greater in 1993 than in 1992 (X^2_1=46.77, $p<0.0001$; X^2_1=36.71, $p<0.0001$, respectively; Table 3.2).

Chick survival was markedly higher in 1993 than in 1992 (Figure 3.4). In both years, chick mortality was greatest soon after hatching and was low after an age of 10 days. In 1992, 58% of chicks died in the first five days after hatching, and 70% died within one week. In 1993, 16% died within five days and 18% died within a week. 23% of chicks were surviving at 10 days of age in 1992, while 82% of chicks survived to that age in 1993.

3.4.3. Relationship between timing of breeding and reproductive success

3.4.3.1. Influence of laydate on hatching

In both years early layers were more likely to hatch chicks than late layers (Table 3.3). The relationship was

Table 3.2 The fates (a) and survival times (b) of Black-legged Kittiwake chicks hatched on Great Island, Newfoundland, in 1992 and 1993.

	1992		1993	
Fate	Number of chicks	%	Number of chicks	%
(a) <u>Fate</u>				
Fledged	3	7	50	74
Disappeared	28	65	5	7
Dead in nest	12	28	9	13
Suspect dead in nest[1]	-	-	4	6
Totals	43	100	68	100
(b) <u>Survival time</u>				
Lived $\geq$ 14 days	9	21	54	79
Lived < 14 days	34	79	14	21

[1] disappearance of youngest of 2 siblings.

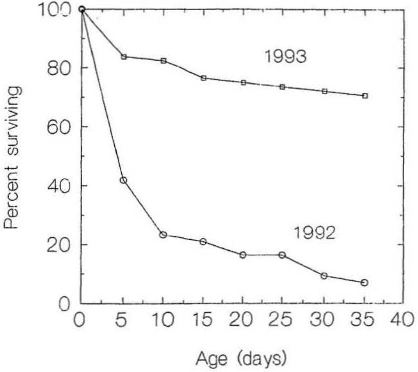

Figure 3.4 Chick survivorship curves for Black-legged Kittiwakes from the study plots on Great Island, Newfoundland, in 1992 and 1993.

Table 3.3 Mean laydates of Black-legged Kittiwakes that did hatch chicks compared to laydates of kittiwakes that did not hatch chicks in 1992 and 1993.

Year	Egg Fate	N	Mean lay-date	SD (days)	t	P
1992	Hatched	27	4 June	5.12		
	Not hatched	307	11 June	6.13	6.39	<0.001
1993	Hatched	57	9 June	4.42		
	Not hatched	490	10 June	5.49	2.15	0.032

stronger in 1992, with seven days difference in mean laydate between kittiwakes that hatched chicks and those that did not. In 1993, mean laydate of birds hatching chicks was one day earlier than of those not hatching chicks.

3.4.3.2. Influence of hatchdate on the fate of chicks

Mean hatchdate was 2 July in 1992 (median=30 June, n=43), and 7 July in 1993 (median=7 July, n=68). Chicks that hatched later were more likely to fledge and more likely to survive to 14 days in 1992 (Table 3.4). The mean hatchdate for chicks that fledged was nine days later than for those that did not fledge, and the mean hatchdate of those that survived to 14 days was eight days later than for those that did not. In 1993, mean hatchdates of fledging chicks and those surviving for 14 days were two days later than those not fledging or surviving for 14 days, but this difference was not significant (Table 3.4).

In 1992, the mean hatchdates of chicks that disappeared, died in the nest, and fledged were different (Table 3.5). Chicks that fledged hatched later than those that died in the nest (Tukey's pairwise comparisons, p=0.003) and disappeared 'p=0.030). In 1993, although chicks that fledged had the latest mean hatchdates and chicks that died in the nest had the earliest, no significant differences between the hatchdates of chicks with different fates were found.

Table 3.4 Comparison of hatchdates between Black-legged Kittiwake chicks that fledged and did not fledge, and between those that lived to 14 days or more and those that died before 14 days, in 1992 and 1993.

Year	Chick fate	N	Mean hatch date	SD (days)	t	P
1992	Fledged	3	10 July	4.58		
	Not fledged	40	1 July	5.44	2.77	0.008
	Lived ≥ 14 days	9	8 July	6.50		
	Lived < 14 days	34	30 June	4.57	3.96	<0.001
1993	Fledged	50	8 July	5.09		
	Not fledged	18	6 July	4.44	1.50	0.139
	Lived ≥ 14 days	54	8 July	5.02		
	Lived < 14 days	14	6 July	4.69	1.29	0.201

Table 3.5 Comparison of mean hatchdates of Black-legged Kittiwake chicks that died in the nest, disappeared, or fledged in the study plots on Great Island, in 1992 and 1993.

Year	Chick fate	N	Mean hatch date	SD	F	P
1992	Dead in nest	12	29 June	5.22		
	Disappeared	28	2 July	5.36	6.66	0.003
	Fledged	3	11 July	5.03		
1993	Dead in nest	9	5 July	3.18		
	Disappeared	9	6 July	5.52	1.34	0.270
	Fledged	50	8 July	5.09		

Regression analysis showed a strong trend for survival time to increase with hatchdate in 1992 ($F_{1,41}$=18.25, p<0.001, R^2=0.31, $\hat{y}$=60.1+0.27X). Later hatched chicks survived longer than early hatched chicks. There was no relationship between survival time and hatchdate in 1993 ($F_{1,66}$=0.88, p=0.352, R^2=0.01).

3.4.4. Food availability

3.4.4.1. Timing of inshore capelin arrival in relation to kittiwake chick survival

The first Atlantic Puffin was seen carrying mature capelin on 8 July 1992 and on 6 July 1993. These dates coincided with the first observations of capelin by residents of Bauline, a community 2 km from Great Island (M. Reddick, pers. comm.). These dates were taken as the inshore arrival of mature capelin, and the start of their potential accessibility to kittiwakes.

Chicks hatching before capelin arrival in 1992 survived for shorter periods of time than did chicks hatching after capelin arrival, with a difference in mean survival time of 17 days (Table 3.6). In 1993, the mean survival time for chicks hatching before capelin arrival was also less than for those hatching after capelin arrival, but the difference of five days was not significant. A greater proportion of chicks that

Table 3.6 Comparison of survival time of Black-legged Kittiwake chicks hatching before and after inshore capelin arrival in 1992 and 1993.

Year	Hatch date[1]	N	Mean survival time (days)	SD	t	P
1992	Before capelin	33	5.5	7.94		
	After capelin	10	22.3	13.97	4.86	<0.001
1993	Before capelin	17	28.8	19.22		
	After capelin	51	33.8	14.75	1.12	0.268

[1] chicks hatching two days before capelin arrival are included in the after group.

fledged hatched after capelin arrival in both years. Only three chicks fledged in 1992 and all hatched after capelin arrival. In 1993, 78% of fledged chicks hatched after capelin arrival.

In 1992, most chicks hatched before capelin arrival (33 of 43), while in 1993, most chicks hatched after capelin arrival (51 of 68; $X^2_1=28.49$, $p<0.0001$). Capelin arrived two days later in 1992 and overall mean hatchdate was five days earlier in 1992 than in 1993.

3.4.4.2. Incubation shifts

The duration of incubation shifts (DIS) was greater before capelin arrival than after capelin arrival in 1992, with a difference in mean DIS of 24 hr (Table 3.7). Before capelin arrival, DIS ranged from 1.3 to 124.8 hr, and after capelin the range was from 1.6 hr to a maximum of 16.9 hr. Mean DIS before capelin arrival in 1992 was 7 hr greater than mean DIS in 1993 (Table 3.7). In 1992, incomplete incubation shifts were included in 17 cases, while in 1993, only three incomplete incubation shifts were included. Thus mean and maximum DIS in 1992 were probably underestimated, as was the difference between the two years.

Incubation shifts spanned capelin arrival at two nests observed in 1992. At both, mean DIS was greater before capelin arrival than after (Figure 3.5a), although the

Table 3.7 Mean DIS (duration of incubation shifts) before and after capelin arrival in 1992, and a comparison of DIS in 1992 and 1993.

Year	Hatch date[1]	N	Mean DIS (hr)	SD	t	P
1992	Before capelin	79	30.7	24.6		
	After capelin	8	6.7	5.8	2.73	0.008
1992	Before capelin	79	30.7	24.6		
1993	Before capelin	376	23.6	21.4	2.59	0.010

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[1] chicks hatching two days before capelin arrival are included in the after group.

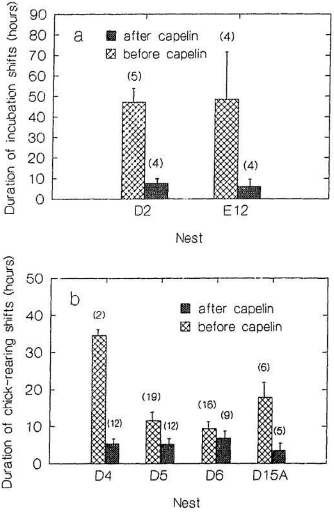


Figure 3.5 Mean duration of incubation and chick-rearing shifts (± standard error) of Black-legged Kittiwakes before and after capelin arrival in 1992 for (a) two nests where incubation spanned capelin arrival, and (b) four nests where chick feeding spanned capelin arrival. Sample sizes are shown in brackets.

difference was only significant at nest D2 (t=5.0, df=7, p=0.0.002). At nest D2, DIS before capelin arrival ranged from 27.0 to 69.3 hr, while after capelin arrival the range was from 2.4 to 12.4 hr. At nest E12, DIS before capelin arrival ranged from 7.1 to 110.3 hr, and after capelin arrival the range was from 1.6 to 16.9 hr.

No difference in DIS was observed between sexes in either year (t=0.71, p=0.48; t=0.31, p=0.76, for 1992 and 1993 respectively). In 1992, mean DIS was 24.4 hr for females (n=30), and 21.1 hr for males (n=30), including shifts from before and after capelin arrival. In 1993, mean DIS was 23.8 hr for females (n=178), and 23.1 hr for males (n=186).

Abandoned eggs were seen primarily at nests where adults had endured long incubation shifts. In 1992, adult absence was recorded at one nest during a 56 hr incubation shift. In 1993, abandonments were observed during eight incubation shifts. These shifts ranged in duration from 50 to 115.4 hr with a mean of 78.9 hr. One shift of 87 hr was incomplete. During five of these incubation shifts, one adult absence was recorded, during two shifts, 87 hr (incomplete) and 109.5 hr in duration, two separate adult absences were recorded, and during one shift of 52.6 hr, three separate absences were recorded. The length of time eggs were abandoned ranged from just under 2 hr to 11.5 hr. Shorter absences may have been missed. Four cases involved overnight absences.

3.4.4.3. Chick-rearing shifts

Chick-rearing shifts before inshore arrival of capelin in 1992 were longer than shifts after capelin arrival, with a difference in means of 8 hr (Table 3.8). At three nests observed in 1992, a chick hatched during an incubation shift and then starved in the nest, the incubator never having been relieved by its mate. These three chicks died on 29 June, 30 June and 1 July, all before the arrival of capelin.

Chick rearing spanned the period of capelin arrival at four nests in 1992. In all cases mean DCS decreased after capelin arrival, although this decrease was more pronounced at some nests than others (Figure 3.5b), and was statistically significant at nests D4, D5 and D15A (t-tests, $p \leq 0.05$). DCS before capelin arrival ranged from minimum values of 33.1, 2.5, 2.2, and 4.2 hr to maximum values of 36.1, 42.3, 30.4, and 28.6 hr, for nests D4, D5, D6 and D15A, respectively. DCS after capelin arrival ranged from minimum values of 0.6, 0.4, 1.0, and 0.8 hr to maximum values of 13.4, 15.0, 16.7, and 10.9 hr for nests D4, D5, D6, and D15A, respectively. There was no difference in DCS between males and females in 1992 ($t=0.77$, $p=0.45$). Mean DCS was 7.4 hr for females ($n=36$) and 8.8 hr for males ($n=35$).

The mean number of changeovers per hr (CPH) was 0.23 ± 0.02 in 1992 ($n=57$) and 0.53 ± 0.04 in 1993 ($n=90$). This difference was significant ($t=5.63$, $df=145$, $p<0.001$). Because

Table 3.8 Comparison of mean DCS (duration of chick-rearing shifts) of Black-legged Kittiwakes before and after the arrival of capelin in 1992.

Year	Hatch date[1]	N	Mean DCS (hr)	SD	t	P
1992	Before capelin	54	13.6	11.5		
	After capelin	58	5.6	5.1	4.85	<0.001

[1] chicks hatching two days before capelin arrival are included in the after group.

adults replaced their mates more frequently in 1993 than in 1992 (higher CPH in 1993), this suggests that feeding shifts were of longer duration in 1992 than in 1993. The mean shift interval (MSI), calculated as an average for each observation session, was greater in 1992 (mean MSI=5.25 ± 0.7 hr, n=12) than in 1993 (mean MSI=3.76 ± 1.5 hr, n=13), but the difference was not significant (t=0.88, df=23, p=0.390).

Chicks were seldom left alone in the nest in either year. One 27 day old chick was left alone for 3 min in 1992. In 1993, only one abandonment greater than 1 min was observed: two siblings, aged 23 and 24 days, were alone in the nest at the start of an observation session and were joined by an adult 20 min later. A total of six abandonments of 1 min or less were observed in 1993, four of which occurred at a nest where chicks died. These chicks were 18 and 19 days old when left alone briefly. Such short flights from the nest were observed at two other nests: one with siblings aged 25 and 26 days, and one with a 33 day old chick. Because chick age is an important consideration, and short term abandonment of older chicks is normal (Coulson and Johnson 1993), the time spent observing older chicks was calculated. With only chicks 20 days or older considered, 79 and 171 nest-hr were spent observing chicks in 1992 and 1993, respectively. In this time, only one abandonment longer than 1 min was observed in each year. Because of the nature of the observation sessions, overnight adult absences may have been missed, particularly in 1993.

3.4.4.4. Chick feeding rates

Mean feeding rates were 1.4 ± 0.2 and 3.1 ± 0.3 feeds per pair per hr in 1992 and 1993 respectably. When only the three largest feed size categories were included, mean feeding rates were 0.7 ± 0.1 and 1.4 ± 0.1 boluses per pair per hr in 1992 and 1993, respectively. ANCOVA results indicated that feeds/pair/hr (FPH) did not increase significantly with chick age ($F_{1,176}=2.28$, $p=0.13$), but differed between years ($F_{1,176}=17.58$, $p<0.000$), with higher feeding rates in 1993. Quantity fed/pair/hr (QPH) increased with chick age ($F_{1,176}=5.84$, $p=0.017$; $\hat{Y}=1.58+0.075X$) and the quantity of food fed to chicks per pair was higher in 1993 than in 1992 ($F_{1,176}=10.78$, $p=0.001$; Figure 3.6). These relationships also held when only the three largest feed size categories were included.

3.4.4.5. Chick diet

Eleven food samples were collected on 21 July and 5 August, 1993, from the regurgitations of two adults and 10 chicks. All except two boluses were identified as capelin (Appendix 5). In two cases the fish species could not be identified because of digestion. In 1992, a crustacean

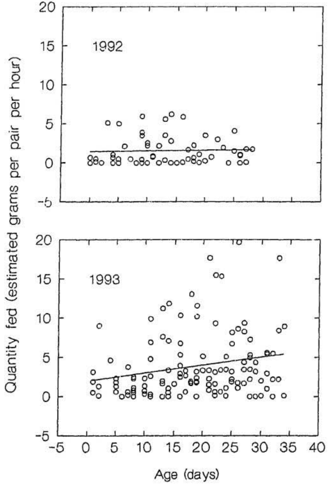


Figure 3.6 The relationship between estimated quantity of food fed to Black-legged Kittiwake chicks per pair per hour and chick age for 1992 and 1993. Least squares lines are fitted through the data points. Feed sizes were estimated by observation.

regurgitate found in one nest was identified as <u>Parathemisto gaudichaudi</u>.

Feeding observations indicate that chicks were fed primarily fish in both years, although prey items other than fish were more frequently observed in 1992 than in 1993, particularly early in the season. Crustaceans were fed to two chicks at different nests on 8 July 1992, although fish was also fed to one of these chicks. At the other nest, a bolus of crustaceans was regurgitated into the nest cup where most of it remained uneaten. At all other nests, all observed feedings were of fish on this day. On 25 and 26 July, crustaceans and fish were fed at one nest. At this nest and at one other, the pink faeces of the chicks suggested that crustaceans constituted part of the diet. In 1993, only feedings of fish were observed from 8 July to 4 August in 6 of 7 nests. At one nest crustaceans were fed to a chick on 29 July, but fish was fed as well. This chick was growing very poorly, being only one-third the size of equal aged chicks, and had disappeared by the next day.

3.4.4.6. Chick growth

In 1992, the mass of four surviving chicks peaked at a mean age of 29 days with a mean mass of 430g (Figure 3.7a). Growth rates during the linear period of growth (6 to 20 days) were 21.7, 24.0, 22.7 and 19.0 g/day for chicks A through D,

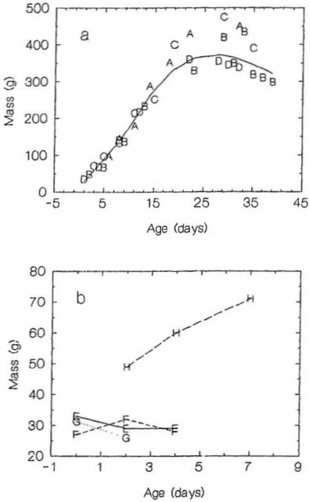


Figure 3.7 Growth of Black-legged Kittiwake chicks on Great Island in 1992 that (a) survived to fledging or near fledging, and (b) died. Each letter represents a different chick.

respectively, and 22.1 g/day overall (Figure 3.7a). Chicks A, B and C fledged, and chick D was taken by predators at age 34 days. Growth curves of 3 of 4 chicks that died in 1992, show that mass did not increase with age (Figure 3.7b; chicks E, F and G). Chick E was found dead in the nest. The weakness of chick G at age 2 days and the lack of mass gain of chick F suggests that these two chicks starved as well. In one of four chicks that died (chick H), mass increased with age up until disappearance of the chick. It seems likely that chick H was taken by a predator.

3.5. DISCUSSION

3.5.1. Egg mortality

Egg mortality was very high in both years of this study (see also Chapter 2). The percentage of eggs that disappeared from nests was close to 90% in both years. From predation observations in 1993, and incidental observations in both years, I suspect that egg disappearance was overwhelmingly caused by predators. High egg loss was also observed by Neuman (1994) in 1991, another year of poor productivity of Witless Bay kittiwakes.

3.5.1.1. Egg predators

Great Black-backed Gulls were the most persistent and successful nest predators in both years, robbing 87% of all nest depredated during observations in 1993. Their size, relative to the size of kittiwakes, made them powerful predators. Great Black-backed Gulls were occasionally seen killing adult kittiwakes or eating freshly killed birds. Kittiwakes abandoned their nests readily at the approach of these large gulls. Great Black-backed Gulls were often seen walking across rows of kittiwake nests, swallowing numerous eggs whole. They were observed making use of the wind for hunting, and were able to remove eggs from steep or otherwise difficult cliffs. Gaston and Nettleship (1981) also observed Glaucous Gulls (Larus hyperboreus) taking advantage of updraughts to hover beside ledges of breeding Common Murres (Uria aalge), taking eggs from places which would probably not have been accessible otherwise.

Although Herring Gulls took most of the remainder of the eggs depredated during observations, kittiwakes often defended their nests successfully. Herring Gulls robbed fewer nests per landing and per attempt than Great Black-backed Gulls. Herring Gulls also landed less often and tried for fewer eggs, presumably because their chances of success were lower. They were often seen standing near incubating kittiwakes and watching them, sometimes moving closer, but usually moving away again without incident. Neuman (1994) found Herring Gulls to be the main nest predator of kittiwakes on Gull Island in 1990 and 1991, but forced egg predation (incubating adults are forced from nests by a predator) was seen only twice.

As indicated by predator observations, American Crows took some kittiwake eggs, but the extent of crow predation was probably limited to the removal of some abandoned eggs.

Common Ravens were never seen during predation observations but they were seen carrying kittiwake eggs and flushing adults throughout the breeding season, primarily in other areas. The effect of raven predation on the loss of kittiwake eggs and young is difficult to estimate, but it seems unlikely that the impact of raven predation was as severe as that of Great Black-backed Gull predation. In another colony (on the southeastern coast of the Avalon Peninsula, Newfoundland), however, ravens have been observed to carry away numerous kittiwake eggs in rapid succession (pers. obs.). The cashing of eggs, presumably for future use, resulted in the disappearance of a large number of eggs in a short period of time.

Similar to Great Black-backed Gulls, Common Ravens seemed to have little difficulty robbing nests. The agility and relatively small size of ravens allowed them to access well protected nests, and kittiwakes were observed to readily vacate their nests in most cases when a raven was close by. This behaviour of kittiwakes contrasts with that observed in other studies. Montevecchi (1979) found that kittiwakes sometimes physically attacked ravens, and Maccarone (1992) noted that kittiwakes vigorously defended their nest and young on 40% of attacks, and often chased and dove at the ravens. Kittiwake reaction to predation by Great Black-backed Gulls may also vary, and in some cases they defend their nests more successfully (P. Monaghan pers. comm.). Degree of nest defense of kittiwakes may be related to intensity of predation. Montevecchi (1979) found nest defense to increase in association with increased hunting intensity and predation success by ravens. On Great Island the reverse seemed to be true. Increased harassment by Great Black-backed Gulls seemed to increase the caution exhibited by kittiwakes. As gulls became more persistent, kittiwakes became more flighty, and appeared to leave the nest with less and less provocation.

3.5.1.2. Herring Gulls as a factor in kittiwake breeding performance

The suggestion that expanding Herring Gull populations may be contributing to kittiwake breeding failures (Neuman 1994) was not supported by this study. Observations suggest that although Herring Gulls took some eggs, they were often not successful, and kittiwakes were not defenceless against them. In addition, only three kittiwake chicks fledged from study plots in 1992 and all were from plot 7 (Chapter 2, Table 2.2), situated within a dense Herring Gull colony. If Herring Gulls represented a serious threat to kittiwakes, pairs nesting within such a dense colony would be expected to show the poorest performance. Instead, the only chicks fledging from all nests in the study plots fledged from the centre of such a gull colony, in a year when predation pressure was severe. In 1993, plot 7 again fledged more chicks per egg than the other study plots used in both years, with only Big Cove (added in 1993) having greater productivity (Table 2.3).

Pierrotti (1983) suggested that breeding puffins may prefer areas of high Herring Gull density, despite occasional loss of eggs or chicks, because through them, they receive protection from more serious predators, such as Great Black-backed Gulls. Such protection gained by nesting in the centre of a gull colony has been demonstrated for some species of ducks and terns (Hilden 1965, Dwernychuk and Boag 1972). Hostility of Herring Gulls directed at Great Black-backed Gulls in a dense nesting area can be substantial. My results suggest that Great Black-backed Gulls represent a much more serious threat to breeding kittiwakes than Herring Gulls, and that protection gained from Great Black-backed Gulls by nesting in close proximity to Herring Gulls may compensate for the loss of some eggs and young.

3.5.1.3. Factors involved in the intensity of predation

Kittiwakes are often assumed to be relatively free from predation because of their cliff-nesting habits (Cullen 1957, Coulson and Wooller 1984). Some studies have reported heavy nest predation on low or stepped cliffs which were accessible to predators, and less on steeper, less accessible cliffs (Barrett and Runde 1980, Galbraith 1983, Roberts 1988, Chapdelaine and Brousseau 1989). Almost no nest predation was observed in 1969 and 1970 in Witless Bay (Maunder and Threlfall 1972), which may lead to the assumption that cliff structure in this area prohibits predation (e.g., Roberts 1988). My observations suggest that effects of food availability may be more important than cliff structure in determining the severity of predation. Food was apparently plentiful in 1969 and 1970 when Maunder and Threlfall (1972) observed little nest predation. Accessible cliff structure facilitated predation and influenced the degree of predation in different parts of Great Island (see Chapter 2), but the persistence of Great Black-backed Gulls suggests that kittiwake eggs may only be safe when alternate and preferred food supplies exist.

The intensity of the nest predation by Great Black-backed Gulls observed in this study is unusual, judging from previous studies in Witless Bay. Threlfall (1968) found mainly fish and no bird eggs in the diet of Great Black-backed Gulls.

Maunder and Threlfall (1972) recorded low kittiwake egg mortality (28% and 27%) in 1969 and 1970 on Gull Island, of which 10 to 41% was attributed to predation. Ravens were cited as the main egg predators and Herring Gulls were once seen taking an egg, but no mention of Great Black-backed Gulls was made. Neuman (1994) reported no Great Black-backed Gull predation on kittiwake eggs on Gull Island in 1990 and 1991. In contrast, in 1992 and 1993, Great Black-backed Gulls were observed to take virtually all eggs in some areas on Great Island. A difference in numbers of pairs nesting on the two Islands can not be held responsible for the difference in observations because more pairs nest on Gull than on Great Island (Cairns et al. 1989).

Lack of normally available resources appears to be involved in the severity of predation in 1992 and 1993. Capelin were delayed in their inshore arrival by two to four weeks in Witless Bay in both years of this study. In contrast to the capelin arrival dates of this study (8 July 1992 and 6 July 1993), spawning capelin first appeared on or near the beaches in Witless Bay on 1 June 1969, and capelin already constituted about 90% of the diet of adult kittiwakes by mid-May in 1970 (Maunder 1971). Herring Gulls were eating capelin by mid-June in 1977 (Pierotti and Annett 1978), and in 1982-84, capelin first appeared in Witless Bay in late May and peaked in abundance in the last 10 days of June and the first two weeks of July (Burger and Piatt 1990).

In northern Scotland, Great Black-backed Gulls feed primarily on surface-schooling sandeel (the main prey species of seabirds there), and an early failure of sandeel schools in inshore waters increased predation on newly fledged kittiwakes (Beaman 1978). Herring Gulls in Witless Bay depend almost solely on capelin (which normally arrive before the hatching of gull chicks) for raising their chicks, even when specializing on other food items before chick hatch (Pierotti 1982, Pierotti and Annett 1987). In previous years, Great Black-backed Gulls in Witless Bay presumably also made use of the abundant capelin shoals for raising their young.

Normally available alternative food sources were also absent or much reduced in 1992 and 1993. A cod fishery moratorium began in eastern Newfoundland in 1992 resulting in a great reduction of the normally plentiful fish offal. Before 1992, fish offal was available to gulls from early May to early November (Pierotti and Annett 1987). Great Black-backed Gulls are known to make use of fishery wastes (Threlfall 1968, Beaman 1978, Furness 1984, Buckley 1990, Dunnet et al. 1990, Furness et al. 1992, Garthe and Huppop 1994). In Shetland and the British Isles, Great Black-backed Gulls fed extensively on fish discards from trawlers, and due to their large size, they successfully competed with other scavenging species (Furness et al. 1992). Great Black-backed Gulls breeding on Cape Clear Island, Ireland, depended heavily on food provided by commercial fishing activities, to the extent that a change in fishing practices, reducing the supply of waste fish, was predicted to result in population decline (Buckley 1990). In addition, a lack of fishing activity in 1992 and 1993 in Newfoundland meant that few seabirds were drowned in nets, a resource that Great Black-backed Gulls have utilized when available (Threlfall 1968, Buckley 1990).

A lack of capelin at chick hatch in conjunction with an absence of fish offal probably meant a significant food shortage for Great Black-backed Gulls attempting to raise young. Being opportunists, some gulls apparently turned to the plentiful and fairly accessible resource of kittiwake eggs. Compensation for reduced fish availability by nest predation has been documented for Herring Gulls (Belopol'skii 1957). As the fishing moratorium began in 1992, this may explain the discrepancy in predation observations between this study and Neuman's (1994) and may also reflect the dependence of Great Black-backed Gulls on fish offal, as capelin was delayed in both studies.

In addition to changes in the behaviour of Great Black-backed Gulls in response to food shortage, low egg production by kittiwakes (Chapter 2) could mean that predator swamping was not effective. One benefit of colonial and synchronous nesting is believed to be a localized swamping of the needs of predators during a short, vulnerable period in reproduction, so that the chances of raising young are increased for any individual (Lack 1968, Wittenberger and Hunt 1985). If not enough eggs are produced to satiate the needs of the predators, then this strategy is ineffective. A combination of low egg production and severe need of predators could result in the observed decimation of kittiwake eggs.

3.5.1.4. Specialists

Egg remains found at Great Black-backed Gull nests indicate that at least some parents were bringing kittiwake eggs to their chicks. The proportion of adults feeding themselves on kittiwake eggs is unknown. Substantial numbers of egg remains found at only 2 of 13 territories with chicks suggested foraging specialization. On some days, one or two Great Black-backed Gulls spent hours combing the observation area taking eggs. One easily identified individual made continuous appearances. I suspected a few gulls regularly hunted in a particular area. Near complete depletion of eggs in the observation area on 3 July by two gulls, followed by a near complete end of all hunting behaviour, suggested that those two individuals were the primary specialists in the area. Territoriality of kittiwake nest predators has been observed in other studies (Belopol'skii 1957, Montevecchi 1979, Neuman 1994, Roberts and Hatch 1993).

3.5.1.5. Timing of egg predation

The timing of egg predation was different between years. In 1992, numbers of eggs increased in the study plots with little predation observed until mid-way through the laying period when suddenly eggs began to disappear quickly. A peak was also observed in 1993, but some predation occurred throughout laying, and the increase was more gradual. A lack of predation followed by a peak could indicate that a sudden need forced gulls to search for new sources of food. The hatching of gull chicks could produce such a requirement. Alternatively, this pattern could represent discovery of a resource in mid-season, and then a thorough exploitation of that resource.

Timing of peak hatch of Great Black-backed Gull chicks did not coincide with peak kittiwake egg predation, with gull chick hatch occurring approximately 10 days earlier in both years. Possibly the lag time in predation reflects increasing food requirements of growing chicks. Eggs were brought to newly hatched chicks at one of three Great Black-backed Gull territories with kittiwake eggs in 1992, but at the other two, eggs were not found at the nest until chicks were about eight days and two weeks old.

It seems unlikely that kittiwake eggs were not discovered by gulls until midway through the season in 1992 because some eggs did disappear early on, and because kittiwakes and Great Black-backed Gulls nest in close proximity. However, the fact that more predation occurred throughout laying in 1993 than 1992, lends some support to this idea. It is possible that 1992 was the first year that Great Black-backed Gulls relied heavily on the eggs of kittiwakes, as it was the first year of the fishery moratorium, and therefore the first year where there may have been no alternative food sources. In the following year (1993), gulls may have been quicker to tune in to this normally unexploited resource. Thus, the distribution of predation found in 1993 may primarily represent need, while in 1992, the peak of predation may represent a combination of need and the start of behavioural specialization. The fact that Neuman (1994) recorded no egg predation by Great Black-backed Gulls in 1991, further supports the idea that 1992 may have been the first year of their substantial utilization of kittiwake eggs.

In both years, most egg predation occurred in the mid to late incubation period. This may explain why few replacement clutches were laid. Most replacement clutches were recorded in plot 1 (Chapter 2, Table 2.2). In this plot there was a small peak in predation early in the season, but after most early laid eggs were removed, eggs began to accumulate again and remained on the plot until the late incubation predation peak (Figure 3.2). This early peak in predation was primarily observed in plot 1 and is probably associated with the relatively high number of relayed clutches recorded for this plot.

3.5.2. Chick survival

In 1993, chick survival was comparable to previous years of high productivity (Maunder and Threlfall 1972, Chapter 2), but in 1992, death of small chicks was extreme, with 70% of all chicks dying within one week. Most mortality occurred soon after hatch in both years. This pattern of mortality is typical for gulls (Paynter 1949, Kadlec et al. 1969, Hunt 1972, Haycock and Threlfall 1975, Barrett and Runde 1980). Small chicks, which are not yet homeothermic (Belopol'skii 1961, Maunder and Threlfall 1972), are at greatest risk to adverse weather (Baird 1990) and to parental neglect (Barrett and Runde 1980), and are most vulnerable to sibling aggression (Cullen 1957). The brooding period may be energetically the most demanding stage in reproduction (Ricklefs 1983), and adult behavioural transition from incubation to caring for young may be inadequate (Kadlec et al. 1969, Barrett and Runde 1980). Deviation from this normal pattern of mortality, such as gradual mortality throughout the nestling period, may indicate that other factors, such as predation, are acting on chicks regardless of age (Barrett and Runde 1980, Neuman 1994, Roberts and Hatch 1993).

Timing and amount of chick loss suggests that typical mortality factors caused the loss of small chicks in 1993. In 1992, early chick loss was extreme. Adults were apparently faced with unusually stressful conditions and were unable to care for their young at that time. A substantial proportion of chicks starved in 1992. This was also observed by Neuman (1994) on Gull Island, during the 1991 breeding failure. Although predation of some chicks probably occurred, predation observations suggested that after the majority of eggs were depleted, the intensity of predation strongly subsided. The persistent hunting effort observed on 3 July resulted in the removal of all but seven eggs from plot 2, but no further eggs were depredated and very little hunting was observed after this date. The predators apparently turned to alternative food sources, presumably because hunting effort was no longer profitable.

3.5.3. Timing of breeding in relation to breeding success

The importance of timing of breeding in the success of individuals has been well established for kittiwakes (Coulson and White 1958a, Roberts 1988) and for birds in general (Lack 1968, Toft et al. 1984, Martin 1987), and is closely associated with age and experience of the breeder. Early breeders tend to be older and more experienced individuals, which generally have higher breeding success (Coulson and White 1958a, Ryder 1980, Nelson 1988). That early breeders hatched more chicks than late breeders in both years of this study was, therefore, not surprising.

Contrary to expectation, however, chicks that hatched earlier survived less well. The fate of chicks in relation to hatchdate gave consistent results in both years: early hatching was associated with death and starvation, while late hatching was associated with survival and fledging. This relationship was strong in 1992, while in 1993, differences were not significant.

Hatchdate relative to capelin arrival appeared to be of critical importance in the fate of chicks. Kittiwake chicks that hatched early in the season hatched before capelin arrival and many starved, while chicks of late breeders hatched after capelin arrival and more survived. This trend was more pronounced in 1992, probably partially because a higher proportion of chicks hatched before capelin arrival in 1992 (77%), than in 1993 (25%). Hatch was earlier and capelin arrival was later in 1992, thus food shortage associated with lack of capelin was experienced by more chicks. However, not all chicks in 1993 hatching before capelin arrival died, suggesting that other factors were involved.

The reason for the difference between proportions of chicks hatching before and after capelin between years is not clear, but timing of egg predation may have played a role. In 1992, few eggs were taken until most eggs had already been laid. Thus, eggs were taken from early and late breeders equally. In 1993, more eggs were taken throughout laying and therefore early layers had a lower probability of keeping their eggs, relative to late layers. This may partially explain why mean hatchdate was five days later in 1993 even though timing of laying was very similar in the two years (Chapter 2).

Capelin arrived only two days earlier in 1993 than in 1992, but because this occurred within the period of peak chick hatch, the difference in chick survival could have been substantial. In addition, feeding conditions prior to capelin arrival seem to have been better in 1993, judging by the proportion of pairs producing eggs (Chapter 2), and by the length of incubations shifts (see below). Greater food availability before capelin, in combination with later hatching and earlier capelin arrival, may explain why fewer chicks died in 1993 than in 1992.

Even though early breeders were more successful at hatching chicks in both years, late breeders were more successful at fledging chicks. Assuming that early breeders represent older, more experienced birds (Coulson and White

1958a), parental age and quality apparently was influential in hatching success. Older, more experienced birds were perhaps more able to incubate successfully and to fend off predators, or were more willing to do so. In years of poor food supplies, the difference in success resulting from age and experience may be more pronounced because long incubation shifts and predation pressure requires good foraging skills, good body condition, and a willingness to risk mortality or other costs. Older birds are superior foragers (Burger and Gochfeld 1979, Porter and Sealy 1982, Furness and Monaghan 1987, Burger 1988), and are more willing to expend effort and incur cost (Pugesek 1984, 1990, Toft et al. 1984, Hamer and Furness 1991). However, parental age or quality may have had little effect on fledging success, and the most important factor influencing chick survival appeared to be the timing of hatch in relation to the timing of capelin arrival, particularly in 1992.

Late breeders had higher success than early breeders, which is unusual (Burger 1981) but has been observed in relation to timing of food availability in other studies. Hatch (1990) found that late breeding Northern Fulmars (Fulmarus glacialis) were more successful than early breeders, and suggested that foraging conditions were not adequate to support the stress of incubation early in the season, but improved with date. In Witless Bay, late capelin inshore arrival in recent years (Montevecchi and Myers 1992, Neuman 1994, J. Carscadden, DFO, St. John's, pers. comm., this study) resulted in unusual feeding conditions. Kittiwake breeding would presumably be timed to benefit from the normal pattern of seasonal food availability. In 1969 and 1970, two years of high productivity and normal capelin timing and abundance, the food of breeding kittiwakes was almost exclusively capelin (Maunder and Threlfall 1972). This also was the case after capelin arrival in this study. A change in the behaviour of capelin in recent years, resulting in severe food shortage at the time of chick hatch in 1992, apparently outweighed the effect of individual differences associated with early and late breeding pairs, and age and experience were unable to overcome the lack of resources.

3.5.4. Incubation and chick-rearing shifts

A marked decrease in DIS and in DCS was associated with capelin arrival in 1992. Range and duration of foraging trips has been linked to independent measures of food availability, breeding success, and adult body condition in kittiwakes (Hamer et al. 1993, Monaghan et al. 1993), providing evidence that duration of shifts at the nest can be an indicator of feeding conditions. Shift durations can therefore be assumed to be an index of the time spent on foraging trips. The significant difference in shift duration before and after capelin arrival observed in this study indicates that capelin inshore arrival is an important event for kittiwakes, particularly when overall feeding conditions are poor.

Other studies have found differences in shift duration in association with differences in food availability, primarily between years. In Alaska, Roberts (1988) found that in a year of good productivity the number of changeovers of kittiwakes during incubation were significantly greater than during a year of poor productivity. Wanless and Harris (1992) recorded feeding trips two to three times longer in a poor year relative to a good one, and Hamer et al. (1993) linked feeding conditions in two years to trip duration and foraging range, showing that in the year of food shortage kittiwakes foraged eight times as far from the colony and that foraging trips lasted three times as long. Verspoor et al. (1987) noted a significant difference between chick-rearing shifts in Common Murres, within and between years, and speculated that changes in food availability was the cause.

Prior to capelin arrival, average incubation shifts observed in this study were very long. DIS averaged 31 and 24 hr in 1992 and 1993, respectively, and the maximum duration recorded was 125 hr. These values exceed those of other studies. In a year of poor food supplies, Hamer et al. (1993) recorded a mean incubation shift of 15 hr and maximum shifts over 44 hr. The longest continuous incubation shifts recorded by Coulson and Wooller (1984) averaged 67 ± 5 hr ($n = 4$), occurring in extreme cases when mates failed to return. The authors suggested that this may represent the maximum time that an adult kittiwake will go without drinking. Because continuous records were not kept in this study, brief trips could have been made for drinking.

The mean duration of incubation shifts of 6.7 hr after capelin arrival compares more closely to that observed in other studies. In a year of high food availability in Shetland, Hamer et al. (1993) recorded mean incubation shifts of 4.5 hr. Roberts (1988) recorded mean incubation shift durations of 5.3 hr in a relatively good year in Alaska. In North Shields, England, Coulson and Wooller (1984) recorded average shifts of about 12 hr, or two changeovers per day. In comparison to these observations, incubation shifts before capelin arrival in this study were exceptionally long, and indicate food stress, but shifts after capelin arrival suggest that food was adequate at that time.

Average shifts at the nest during chick-rearing also responded to capelin arrival. Mean DCS after capelin arrival (5.6 hr) was significantly less than the mean DCS before capelin arrival (13.6 hr). Average shift at the nest after capelin arrival was comparable to the mean of 4.1 hr found by Roberts and Hatch (1993) in Alaska, and the overall mean of 4.9 hr during a good year on the Isle of May (Wanless and

Harris 1992). It was, however, more than twice as long as the mean of 2.6 hr per foraging trip recorded by Pearson (1968) in a year of a "superabundance" of food, and the means of 2.5 hr, 1.3 hr, and 2.2 hr per trip found by Coulson and Wooller (1984), Furness and Barrett (1985) and Hamer et al. (1993), respectively, which were presumably also during years of good feeding conditions. In years of poor food availability and productivity, Wanless and Harris (1992) and Hamer et al. (1993) recorded mean durations of feeding trips of 9.6 hr and 6.3 hr, respectively. In this study, mean DCS before and after capelin arrival were long in comparison to other studies, suggesting food shortage, but the difference was markedly greater before capelin arrival, indicating that food was very scarce or distant at that time and then became considerably more plentiful or nearer to the colony.

Comparison of durations of incubation shifts before capelin arrival, and of the number of changeovers per hour during chick feeding between years, suggests that food was more available in 1993 than in 1992. This is consistent with other results of this study. A greater proportion of pairs produced eggs in 1993, which is presumably indicative of better feeding conditions in the laying and pre-laying period (Chapter 2), chicks of all hatchdates had a markedly higher survival 1993, and feeding rates of chicks were higher in 1993 than in 1992 (see below).

Mean DIS and DCS and variation of shift duration differed among pairs. All pairs responded to the arrival of capelin with shorter shifts at the nest, but the degree of this response was also variable. High variability in the behaviour of pairs was also observed in other studies (Coulson and Wooller 1984, Coulson and Johnson 1993) and Coulson and Wooller (1984) found that variation in incubation patterns was not associated with environmental parameters, but primarily with breeding experience.

There was no significant difference between the sexes in incubation or chick-rearing shifts, although females took on slightly longer incubation shifts than males, and males had slightly longer shifts at the nest during chick-rearing. Other studies have also found that the sexes share incubation fairly equally, but that females incubate slightly more (Coulson and Wooller 1984, Roberts 1988). Coulson and Johnson (1993) found that male foraging trips are longer, which is in contrast to the results of this study, and to studies in Alaska (Roberts 1988, Roberts and Hatch 1993), where no differences between sexes were found. The overall pattern appears to be that, with some variation, incubation shifts and chick feeding are shared equally between sexes in kittiwakes.

3.5.5. Adult nest attendance

Poor breeding success has been associated with egg and chick abandonment due to food shortage in many studies (Barrett and Runde 1980, Galbraith 1983, Hatch and Hatch 1990, Baird 1990, Harris and Wanless 1990, Wanless and Harris 1992, Monaghan et al. 1993). Failure during the incubation stage in Alaska appears to be primarily due to inattentiveness or improper incubation behaviour of adults, either directly reducing hatchability of chicks, or else indirectly facilitating opportunistic predation (Baird 1990, Hatch and Hatch 1990, Hatch et al. 1993). In a 15-year study of kittiwake productivity in western Alaska, Murphy et al. (1991) found that low hatching success was often associated with long or short term abandonment of eggs.

Opportunistic predation is considered to be an indirect result of food shortage, and Hatch et al. (1993) stress the importance of distinguishing such predation from forced predation, which may be independent of food availability and condition of adults. In Alaska, Hatch and Hatch (1990) found that virtually all predation was opportunist resulting from an inadequate food supply causing adults to abandoned their eggs. Severe egg predation in this study was also believed to be an indirect result of food shortage, but predation was primarily forced, and food shortage appeared to affect the behaviour of

Great Black-backed Gulls, causing them to search out alternative food.

Although eggs are normally attended by one adult throughout incubation (Coulson and Wooller 1984), some abandonment of older chicks seems to be normal, even when food is plentiful (Cullen 1957, Coulson and Johnson 1993). However, substantial proportions of unattended broods have been associated with food shortage (Barrett and Runde 1980, Galbraith 1983, Roberts 1988, Harris and Wanless 1990, Wanless and Harris 1992, Hamer et al. 1993, Roberts and Hatch 1993). Parents presumably attempt to compensate for food shortage by leaving the nest to increase foraging time. Hamer et al. (1993) found that more chicks were left unattended in a year of food shortage in Shetland, and that this was associated with increased foraging time and range, and decreased adult mass. Roberts and Hatch (1993) suggested that continuously attended chicks are typical of thriving kittiwake colonies. In this study chick abandonment was rare even though productivity was poor, food supplies appeared to be low, and chicks were starving. During chick feeding observations in both years, chicks of all ages were almost never left unattended and adults maintained long shifts at the nest. Neuman (1994) also found nest abandonment rare in 1990 and 1991. In 1991 unattended chicks were never seen, and attendance was lower in 1990 when overall productivity was higher.

Predation risk may affect the optimum behaviour of adults, in the trade-off between nest attendance and foraging (Galbraith 1983, Barrett and Runde 1980, Hamer et al. 1993, Neuman 1994). Predation pressure may force parents to stay and protect the nest and thereby risk starving the chick, because leaving the nest to forage would almost surely result in chick loss through predation. Most starvation appeared to affect small chicks in this study. Since small chicks are vulnerable to numerous size and temperature related dangers, incentive to stay at the nest would be high, even if predation were not a factor. However, in both years of this study, and in 1991 (Neuman 1994), chicks of all ages were almost never abandoned, suggesting that a number of factors were influencing adult behaviour. Roberts and Hatch (1993) also noted a surprisingly low correlation between parental attendance and chick-rearing success on Middleton Island, Alaska, and predation risk at this colony was also high. On the Isle of May, Galbraith (1983) found that temporary desertion only occurred at night, presumably because the danger of chick predation was lowest at this time, and the lack of daytime absence was associated with high predation risk in the study area. In contrast, Wanless and Harris (1992) found a significant difference in unattended young in two years of differing food availability and productivity, also on the Isle of May, but noted that despite the proximity of breeding gulls, there was little evidence of predation of unattended chicks. Thus, colonies, or areas within colonies, with low predation pressure may be more likely to reflect feeding conditions by adult attendance of chicks.

Coulson and Johnson (1993) suggest caution in using unattended chicks as a measure of food shortage because short term abandonment of older chicks is normal. The results of this study, and the relationship between food availability (or productivity) and attendance of chicks across studies with varying predation pressure, suggests that nest predation may be an important factor affecting adult attendance. The intensity of egg predation observed on Great Island in 1992 and 1993, in conjunction with the length of incubation shifts and chick feeding shifts endured by kittiwakes, supports the idea that although thriving colonies probably have little abandonment of eggs and young, predation pressure may force adult attendance in a food stressed colony, and a lack of unattended eggs or chicks may not be a good indicator of breeding conditions. The study of Coulson and Johnson (1993) may not represent normal conditions of abundant food supplies because there was no nest predation at the colony in North Shields (Coulson and White 1958, Coulson and Wooller 1984, Coulson and Porter 1985), possibly because the colony was on a warehouse instead of in a more typical environment. Risk of predation is likely to encourage adult attendance, and if food supplies are abundant, 100% attendance, as described by Barrett and Runde (1980), might well be expected.

3.5.6. Chick feeding and growth

Much variation in the feeding rate of kittiwake chicks has been reported, ranging from mean rates as low as 0.20 feeds/hr (Galbraith 1983) to 3.1 feeds/hr (this study). Part of the differences may reflect different food availability between studies, but chick feeds are often not clearly defined, and the potential discrepancy of what constitutes a feeding event makes comparison difficult. A further complication in the comparison is that different foods have different quality (energy content). It is possible that in some cases higher feeding rates do not mean greater food availability but that higher rates may be required to nourish chicks with a lower quality food. This complication is difficult to address and requires knowledge of the energy content of feeds corresponding to different feeding rates.

In this study, when all feeding events were included, mean feeds/pair/hr were higher in both years than those found in other studies. In some studies feeds are defined as "boluses" swallowed, (Neuman 1994, Roberts and Hatch 1993), and therefore feeding rates in this study were also calculated from starvation but no difference was found in the feeding rates of successful and unsuccessful pairs. Burger and Piatt (1990) also found that feed frequency did not increase with age of Common Murre chicks, but that fish size increased with age. Thus, a measure of feed size may be a more valuable indicator of food received. In both years of this study there was an increase in quantity fed with chick age.

Growth curves of dying young in 1992 suggest that food was lacking, as three of four chicks that died did not increase mass over the first two to four days of life. This was consistent with the many incidences of starvation and the length of chick feeding shifts observed before capelin arrival. Neuman (1994) also found a lack of mass gain in chicks that died in 1991. Comparison of the growth of four fledging chicks in 1992 to the growth curve in Witless Bay in 1970 (Maunder and Threlfall 1972), however, indicates that some chicks grew well after the arrival of capelin. In both 1970 and 1992, mass peaked at a mean age of 29 days, with a mean mass of 420g (Maunder and Threlfall 1972) and 430g (this study).

Several studies have shown a relationship between productivity and growth rate (Barrett and Runde 1980, Bertram et al. 1991, Murphy et al. 1991). Considering the poor productivity of kittiwakes of 1992, growth rates of fledging chicks were surprisingly high in comparison to most other excluding the smallest two size categories. When only the three largest feed sizes were considered, the mean feeding rate in 1992 (0.7 boluses/pair/hr) was similar to that found by Neuman (1994) on Gull Island, Newfoundland, in 1990 and 1991 (0.5 boluses/pair/hr), and by Roberts and Hatch (1993) in a poor year in Alaska (0.43 boluses/pair/hr). Feeding rate in 1993 (1.4 boluses/pair/hr) was similar to that found by Roberts and Hatch (1993) in 1984 (1.1 boluses/pair/hr), a relatively productive year in Alaska. Because 1993 was a more productive year than 1992 in Newfoundland, these rates are roughly comparable to those found elsewhere when productivity is taken into account, and (assuming a similar diet) suggest that 1993 had greater food availability than 1992.

There was no increase in feeding rate of chicks with age in either 1992 or 1993, which is consistent with some studies (Neuman 1994, Roberts and Hatch 1993), although Galbraith (1983) found a slight but significant increase of feeding rate with chick age. A difference in feeding rate was found between years of this study, and between two years of varying productivity in Alaska (Roberts and Hatch 1993). Thus, differences in food availability appear to affect feeding rate, however, this measure does not seem to be a good indicator of energy intake by the chick because it is not consistently linked to chick growth or size. Roberts (1988) found that some chicks on Middleton Island, Alaska, suffered studies (Pearson 1968, Barrett and Runde 1980, Galbraith 1983, Coulson and Porter 1985, Chapdelaine and Brousseau 1989, Murphy et al. 1991). The mean growth rate in 1992 of 22.1 g/day compared most closely to the growth of chicks in productive years of western Alaska (19.7 g/day; Murphy et al. 1991), to growth rates in north Norway when breeding success was high (21.7 g/day; Barrett and Runde 1980), and to single chick broods on the Isle of May (19.8 g/day; Galbraith 1983). Breeding latitude is a complicating factor because kittiwakes are larger in northern areas (Pearson 1968). Within Witless Bay, chick growth was comparable to the productive year of 1970 (19.2 g/day; Maunder and Threlfall 1972), but the mean growth rate in 1992 exceeded that of all chicks measured in 1990 (Neuman 1994), a year in which productivity was low, but substantially superior to that of 1992 (Chapter 2).

Differences in brood sizes offer a possible explanation for the discrepancy of high growth rate in association with poor breeding success. All chicks in 1992 were first hatched chicks and were single chicks through most of their growth period, while in 1970 and in 1990, there was a high proportion of 2- and 3-chick broods (Maunder and Threlfall 1972, Neuman 1994). Slower growth has been documented for larger broods (Galbraith 1983), although some studies have shown that growth rate is not affected by brood size (Pearson 1968, Coulson and White 1958b).

High growth rates in 1992 apparently contradict the significantly lower feeding rates of that year relative to 1993. Differences in feeding rates between years may have been exaggerated, and growth rates may have been unrepresentative for the island. I suspect sampling methods introduced a bias into the comparison of feeding rates and into the assessment of chick growth. Feeding observations were not taken at the same plots in the two years, and in 1992, no chicks used for feeding observations fledged, while in 1993, seven of nine fledged. Furthermore, surviving chicks were almost exclusively from late breeders in 1992, while in 1993, chicks of early breeders also survived. Thus, pairs observed in 1993 may have been more experienced birds (Coulson and White 1958a). Small sample size may have resulted in a bias in the growth of chicks in 1992. The four chicks measured were the only chicks in all study plots which fledged and were all located in the same area on the island (Chapter 2). These factors may have contributed to the apparently paradoxical result of low feeding rate in 1992 (relative to 1993) in combination with apparently normal growth rates.

3.6. REFERENCES

Ashmole, N.P. 1971. Sea bird ecology and the marine environment. p. 223-286 in Farner, D.S., King, J.R., and Parkes K.C. (eds.). Avian Biology Vol. 1. Academic Press, New York.

Baird, P.H. 1990. Influence of abiotic factors and prey distribution on diet and reproductive success of three seabird species in Alaska. Ornis Scand. 21:224-235.

Barrett, R.T., and Runde, O.J. 1980. Growth and survival of nestling Kittiwakes <u>Rissa</u> <u>tridactyla</u> in Norway. Ornis Scand. 11:228-235.

Barrett, R.T., and Furness, R.W. 1990. The prey and diving depths of seabirds on Hornoy, North Norway after a decrease in the Barents Sea Capelin stocks. Ornis Scand. 21:179-186.

Beaman, M.A.S. 1978. The feeding and population ecology of the Great Black-backed Gull in northern Scotland. Ibis 120:126-127.

Belopol'skii, L.O. 1957. Ecology of sea colony birds of the Barents Sea. Izv. Akad. Nauk SSSR, Moscow-Leningrad. (translated from Russian by Israel Program for Scientific Translations, Jerusalem, Israel, 1961).

Bertram, D.F., Kaiser, G.W., and Ydenberg, R.C. 1991. Patterns in the provisioning and growth of nestling Rhinoceros Auklets. Auk 108:842-852.

Brown, R.G.B., and Nettleship, D.N. 1984. Capelin and seabirds in the northwest Atlantic. p. 184-194 in Nettleship, D.N., Sanger, G.A., and Springer, P.F. Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Buckley, N.J. 1990. Diet and feeding ecology of Great Black-backed Gulls (Larus marinus) at a southern Irish breeding colony. J. Zool., Lond. 222:363-373.

Burger, J. 1981. A model for the evolution of mixed species colonies of Ciconiformes. Quart. Rev. Biol. 56:143-167.

Burger, J. 1988. Effects of age on foraging in birds. Proc. Int. Ornithol. Congr. 19:1127-1140.

Burger, J., and Gochfeld, M. 1979. Age differences in Ring-billed Gull kleptoparasitism on starlings. Auk 96:806-808.

Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. Stud. Av. Biol. 14:71-83.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.

Cairns, D.K., Montevecchi, W.A., and Threlfall, W. 1989. Researcher's guide to Newfoundland seabird colonies. Memorial University of Newfoundland Occasional Papers in Biology No. 14.

Carscadden, J.E. 1984. Capelin in the northwest Atlantic. p. 170-183 in Nettleship, D.N., Sanger, G.A., and Springer (eds.). Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Casey, J. 1994. Reproductive success of Black-legged Kittiwakes in the northwest Atlantic in 1991-1993. B.Sc. Honours Thesis (Biopsychology). Memorial University of Newfoundland, St. John's.

Chapdelaine, G., and Brousseau, P. 1989. Size and trends of Black-legged Kittiwake (Rissa tridactyla) populations in the Gulf of St. Lawrence (Quebec) 1974-1985. Am. Birds 43:21-24.

Coulson, J.C., and Johnson, M.P. 1993. The attendance and absence of adult kittiwakes Rissa tridactyla from the nest site during the chick stage. Ibis 135:372-378.

Coulson, J.C., and Porter, J.M. 1985. Reproductive success of the kittiwake Rissa tridactyla: the roles of clutch size, chick growth rates and parental quality. Ibis 127:450-466.

Coulson, J.C., and White, E. 1958a. The effect of age on the breeding biology of the kittiwake Rissa tridactyla. Ibis 100:40-51.

Coulson, J.C., and White, E. 1958b. Observations on the breeding of the kittiwake. Bird Study 5:74-83.

Coulson, J.C., and Wooller, R.D. 1984. Incubation under natural conditions in the Kittiwake Gull, Rissa tridactyla. Anim. Behav. 32:1204-1215.

Cullen, E. 1957. Adaptations in the kittiwake to cliff nesting. Ibis 99:275-302.

Dunnet, G.M., Furness, R.W., Tasker, M.L., and Becker, P.H. 1990. Seabird ecology in the North Sea. Netherlands J. Sea Res. 26:387-425.

Dwernychuk, L.W., and Boag, D.A. 1972. Ducks nesting in association with gulls - an ecological trap? Can. J. Zool. 50:559-563.

Furness, R.W. 1984. Seabird-fisheries relationships in the northeast Atlantic and North Sea. p. 162-169 in Nettleship, D.N., Sanger, G.A., and Springer (eds.). Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.

Furness, R.W., and Monaghan, P. 1987. Seabird Ecology. Chapman and Hall, New York.

Furness, R.W., and Barrett, R.T. 1985. The food requirements and ecological relationships of a seabird community in north Norway. Ornis Scand. 16:305-313.

Furness, R.W., and Barrett, R.T. 1991. Seabirds and fish declines. Nat. Geogr. Res. Explor. 7:82-95.

Furness, R.W., Ensor, K., and Hudson, A.V. 1992. The use of fishery waste by gull populations around the British Isles. Ardea 80:105-113.

Galbraith, H. 1983. The diet and feeding ecology of breeding kittiwakes Rissa tridactyla. Bird Study 30:109-120.

Garthe, S., and Huppop, O. 1994. Distribution of ship-following seabirds and their utilization of discards in the North Sea in summer. Marine Ecol. Progr. Ser. 106:1-9.

Gaston, A.J., and Nettleship, D.N. 1981. The Thick-billed Murres of Prince Leopold Island. Can. Wildl. Serv. Monogr. Ser. No. 6.

Hamer, K.C., and Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas Catharacta Skua. J. Anim. Ecol. 60:693-704.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P., and Burns, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes Rissa tridactyla in Shetland. Ibis 135:255-263.

Harris, M.P., and Wanless, S. 1990. Breeding success of British kittiwakes Rissa tridactyla in 1986-1988: evidence for changing conditions in the northern North Sea. J. Appl. Ecol. 27:172-187.

Hatch, S.A. 1990. Individual variation in behavior and breeding success of Northern Fulmars. Auk: 750-755.

Hatch, S.A., and Hatch, M.A. 1990. Components of breeding productivity in a marine bird community: key factors and concordance. Can. J. Zool. 68:1680-1690.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L., Jr. 1993. Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. p. 140-153 in Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D. (eds.). The status, ecology and conservation of marine birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Haycock, K.A., and Threlfall, W. 1975. The breeding biology of the Herring Gull in Newfoundland. Auk 92:678-697.

Hilden, O. 1965. Habitat selection in birds. Ann. Zool. Fenn 2:53-75.

Hunt, G.L., Jr. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. Ecology 53:1051-1061.

Kadlec, J.A., Drury, W.H., and Onion, D.K. 1969. Growth and mortality of Herring Gull chicks. Bird-Band. 40:222-233..

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Maccarone, A.D. 1992. Predation by Common Ravens on cliff-nesting Black-legged Kittiwakes on Baccalieu Island, Newfoundland. Col. Waterbirds 15:253-256.

Martin, T.E. 1987. Food as a limit on breeding birds: a life-history perspective. Ann. Rev. Ecol. Syst. 18:453-487.

Maunder, J.E. 1971. The breeding biology of the Black-legged Kittiwake (Rissa tridactyla L.) on Gull Island, Newfoundland. B.Sc. Thesis. Memorial University of Newfoundland, St. John's.

Maunder, J.E., and Threlfall, W. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk 89:789-816.

Methven, D.A., and Piatt, J.F. 1991. Seasonal abundance and vertical distribution of capelin (Mallotus villosus) in relation to water temperature at a coastal site off eastern Newfoundland. ICES J. Mar. Sci. 48:187-193.

Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., and Walton, P. 1993. The influence of changes in food abundance on diving and surface feeding seabirds. In Montevecchi, W.A. (ed.). Studies of High Latitude Homeotherms: Multispecies comparisons of Feeding Ecology and Energetics. Can. Wildl. Serv. Occas. Pap. in press.

Montevecchi, W.A. 1979. Predator-prey interactions between ravens and kittiwakes. Z. Tierpsychol. 49:136-141.

Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. p. 217-266 in Furness, R.W., and Greenwood, J.J.D. (eds.). Birds as Monitors of Environmental Change. Chapman & Hall, London.

Montevecchi, W.A., and Myers, R.A. 1992. Monitoring fluctuations in pelagic fish availability with seabirds. CAFSAC Research Document 92/94.

Murphy, E.C., Springer, A.M., and Roseneau, D.G. 1991. High annual variability in reproductive success of kittiwakes (Rissa tridactyla L.) at a colony in western Alaska. J. Anim. Ecol. 60:515-534.

Nelson, J.B. 1988. Age and breeding in seabirds. Proc. Int. Orn. Congr. 19:1081-1097.

Neuman, J.A. 1994. Aspects of the behaviour and ecology of Black-legged Kittiwakes, Rissa tridactyla, breeding at two sites in Newfoundland, Canada, 1990-1991. M.Sc. Thesis. Memorial University of Newfoundland, St. John's.

Paynter, R.A., Jr. 1949. Clutch-size and the egg and chick mortality of Kent Island Herring Gulls. Ecology 30:146-166.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Pierotti, R. 1982. Habitat selection and its effect on reproductive output in the Herring Gull in Newfoundland. Ecology 63:854-868.

Pierotti, R. 1983. Gull-puffin interactions on Great Island, Newfoundland. Biol. Conservation 26:1-14.

Pierotti, R., and Annett, C. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. p. 417-442 in: Kamil, A.C., Krebs, J.R., and Pulliam, H.R. (eds.). Foraging Behavior. Plenum Press, New York.

Porter, J.M., and Sealy, S.G. 1982. Dynamics of multispecies feeding flocks: age-related feeding behavior. Behaviour 81:91-109.

Pugesek, B.H. 1984. Age-specific reproductive tactics in the California Gull. Oikos 43:409-410.

Pugesek, B.H. 1990. Parental effort in the California Gull: tests of parent-offspring conflict theory. Behav. Ecol. Sociobiol. 27:211-215.

Ricklefs, R.E. 1983. Some considerations on the reproductive energetics of pelagic seabirds. Studies in Avian Biology No. 8:84-94.

Roberts, B.D. 1988. The behavioral ecology of breeding Black-legged Kittiwakes (Rissa tridactyla) on Middleton Island, Alaska. M.A. Thesis. University of California, Santa Barbara.

Roberts, B.D., and Hatch, S.A. 1993. Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor 95:330-342.

Ryder, J.P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. p. 153-168 in Burger, J., Olla, B.L., and Winn, H.E. (eds.). Behavior of Marine Animals Vol. 4. Plenum Press, New York.

Templeman, W. 1948. The life history of the capelin (Mallotus villosus o.f. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory. No. 17 (Research). 151pp.

Threlfall, W. 1968. The food of three species of gulls in Newfoundland. Can. Field-Nat. 82:176-180.

Toft, C.A., Trauger, D.L., and Murdy, H.W. 1984. Seasonal decline in brood sizes of sympatric waterfowl (Anas and Aythya, Anatidae) and a proposed evolutionary explanation. J. Anim. Ecol. 53:75-92.

Uttley J., Walton, P., and Monaghan, P. 1993. The effects of food availability on breeding performance of adult time budgets of Common Guilemots. Ibis in press.

Verspoor, E., Birkhead, T.R., and Nettleship, D.N. 1987. Incubation and brooding shift in the Common Murre, Uria aalge. Can. J. Zool. 65:247-252.

Wanless, S., and Harris, M.P. 1992. Activity budgets, diet and breeding success of kittiwakes Rissa tridactyla on the Isle of May. Bird Study 39:145-154.

Wilkinson, L. 1990. SYSTAT: The System for Statistics. Evanston, IL: SYSTAT, Inc.

Wittenberger, J.F., and Hunt, G.L., Jr. 1985. The adaptive significance of coloniality in birds. Avian Biology 8:1-78.

CHAPTER 4 CONCLUSIONS

Several lines of evidence suggested that the breeding failures of Black-legged Kittiwakes (Rissa tridactyla) on Great Island in 1992 and 1993 were directly and indirectly caused by low food availability. Small eggs and clutches, overall late breeding, and a low proportion of pairs producing eggs provided evidence of the direct effects of food shortage during the laying or pre-breeding periods. Long incubation shifts and death of early hatching chicks suggested that food availability was poor until spawning capelin became accessible to kittiwakes, particularly in 1992. After capelin became available, durations of incubation and chick-rearing shifts decreased, and chick survival increased. High egg mortality played the largest role in breeding failure in both years and was believed to be an indirect result of food shortage. A great reduction in the production of fish offal in Witless Bay in combination with delayed capelin arrival appeared to cause food stress in nest predators, particularly in Great Black-backed Gulls (Larus marinus) which were persistent and successful in their predatory attempts.

Food availability seemed to be greater in 1993 than in 1992 because a higher proportion of pairs produced eggs in 1993, incubation and chick-rearing shifts were shorter, and chick survival was substantially greater. Although egg mortality was primarily responsible for breeding failure in both years, chick survival was also very poor in 1992 (7%) while in 1993, chick survival was not significantly depressed from that of productive years (68%). Thus food shortage would have caused breeding failure regardless of egg predation in 1992, but in 1993 nest predation was the main cause of failure. In some colonies nest predation occurs opportunistically because food-stressed kittiwakes abandon eggs or young more frequently (Barrett and Runde 1980, Harris and Wanless 1990, Monaghan et al. 1993, Roberts and Hatch 1993, Hatch et al. 1993). This was occasionally observed in this study, but in most cases adults were forced from their nests by predators. Thus, although food availability seemed to be low in the laying and pre-breeding periods in 1993, in the absence of egg predation, many pairs would have succeeded in raising young.

The fact that kittiwakes were able to feed and raise chicks to fledging in 1993, but that substantial breeding failure was observed, has important implications for the use of kittiwakes as indicator species. Kittiwakes are considered good indicators of changes in marine conditions because they appear to be very sensitive to food shortage and have little buffering capacity in their time and energy budgets (Pearson 1968, Cairns 1987, Furness and Monaghan 1987, Furness and Barrett 1991, Montevecchi 1993). There can be little doubt that food was insufficient to support kittiwake reproduction in 1992, but in 1993 failure was not primarily associated with an inability of kittiwakes to deal with food shortage, but with their inability to deal with nest predators. The small size of kittiwakes entails energetic constraints, making them sensitive to food shortage, but it also makes them vulnerable to nest predation by larger gulls. Although food shortage was directly involved to some extent, kittiwake breeding failure in 1993 seemed to result primarily from food stress of other species. It seems likely that Herring Gulls (Larus Argentatus) and Great Black-backed Gulls make greater use of fish offal than do kittiwakes and are therefore more sensitive to a reduction of this resource. Breeding failure in 1993 may have been largely a consequence of the indirect effects of a reduction in human wastes on the larger, scavenging, gull species. Thus, the causes of breeding failure in kittiwakes may be complicated by other factors and cannot be directly related to changes in their resource base.

When considering the breeding performance of kittiwakes as indicators of food availability, some measures of reproductive success may be more easily interpreted than others. Egg and clutch sizes, and the proportion of pairs producing eggs may be more dependably related to the quality or amount of food available to kittiwakes than overall breeding success because breeding success can reflect many factors other than the ability to produce eggs and feed young.

However, large eggs and clutches may not necessarily indicate good food supplies but may represent strategies of resource allocation which may vary in different environmental conditions (Monaghan et al. 1992, Hamer et al. 1993). The ability of breeders to buffer unfavourable conditions with reserves acquired in the pre-breeding period must also be considered, or conversely, poor production may reflect previous stresses (e.g., Coulson and Thomas 1985). In addition, egg and clutch sizes only reflect energy budgets early in the season, and food availability may change substantially as migratory prey species become available. In this study. comparison of reproductive measures among years showed that high production early in the season (early breeding and egg production) was associated with high overall breeding success. However, the fact that fledging success was not highly correlated with timing, clutch size, and egg size suggests that food supply early in the season may be independent from food supply late in the season, and that different resources may be used at these different times. A measure of chick survival is, therefore, useful as an index of food availability later in the season.

Results from 1993 emphasize that overall breeding success can be influenced by many factors other than food availability and is particularly vulnerable to factors acting early in the season. Thus, the assumption of a direct relationship between kittiwake breeding success and food availability in the upper layer of the ocean can lead to misleading conclusions. It is important to supplement data on breeding success with other assessments of performance, such as chick growth or adult behaviour, when drawing conclusions about the availability of food or the health of the marine ecosystem.

4.1. REFERENCES

Barrett, R.T., and Runde, O.J. 1980. Growth and survival of nestling Kittiwakes Rissa tridactyla in Norway. Ornis Scand. 11:228-235.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5:261-271.

Coulson, J.C., and Thomas, C.S. 1985. Changes in the biology of the kittiwake Rissa tridactyla: a 31-year study of a breeding colony. J. Anim. Ecol. 54:9-26.

Furness, R.W., and Monaghan, P. 1987. Seabird Ecology. Chapman and Hall, New York.

Furness, R.W., and Barrett, R.T. 1991. Seabirds and fish declines. Nat. Geogr. Res. Explor. 7:82-95.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P., and Burns, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes Rissa tridactyla in Shetland. Ibis 135:255-263.

Harris, M.P., and Wanless, S. 1990. Breeding success of British kittiwakes Rissa tridactyla in 1986-1988: evidence for changing conditions in the northern North Sea. J. Appl. Ecol. 27:172-187.

Hatch, S.A., Byrd, G.V., Irons, D.B., and Hunt, G.L., Jr. 1993. Status and ecology of kittiwakes (Rissa tridactyla and R. brevirostris) in the North Pacific. p. 140-153 in Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D. (eds.). The status, ecology and conservation of marine birds of the North Pacific. Can. Wildl. Serv. Spec. Publ., Ottawa.

Monaghan, P., Uttley, J.D., and Burns, M.D. 1992. Effect of changes in food availability on reproductive effort in Arctic Terns Sterna paradisaea. Ardea 80:71-81.

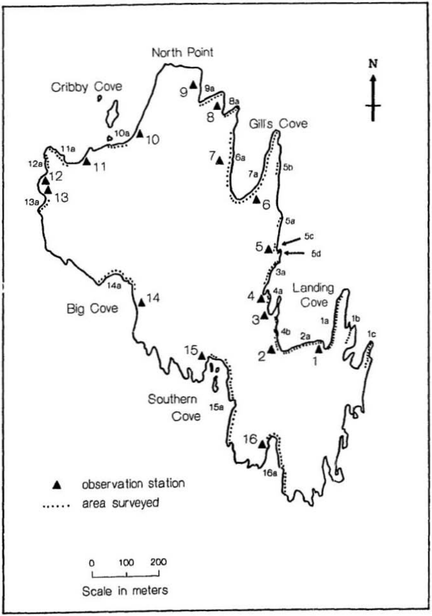
Monaghan, P., Wright, P.J., Bailey, M.C., Uttley, J.D., and Walton, P. 1993. The influence of changes in food abundance on diving and surface feeding seabirds. In W.A Montevecchi (ed.). Studies of High Latitude Homeotherms: Multispecies comparisons of Feeding Ecology and Energetics. Can. Wildl. Serv. Occas. Pap. in press.

Montevecchi, W.A. 1993. Birds as indicators of change in marine prey stocks. p. 217-266 in Furness, R.W., and Greenwood, J.J.D. (eds.). Birds as Monitors of Environmental Change. Chapman & Hall, London.

Pearson, T.H. 1968. The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Roberts, B.D., and Hatch, S.A. 1993. Behavioral ecology of Black-legged Kittiwakes during chick rearing in a failing colony. Condor 95:330-342.

Appendix 1 Great Island, Witless Bay, Newfoundland, showing station number and area surveyed during brood counts in the late chick stage of Black-legged Kittiwake reproduction in 1992 and 1993.


North Point
Cribby Cove
Gill's Cove
Landing Cove
Big Cove
Southern Cove
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1
1a
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▲ observation station
...... area surveyed
0 100 200
Scale in meters

Appendix 2 Comparison of the timing of breeding of Black-legged Kittiwakes among 13 years in Witless Bay, Newfoundland. Records from other studies are listed as "observations". Timing of the earliest young in the nests was estimated from these records, and are listed for comparison.

Year	Date of observation	Observations	Estimate of date of earliest young in nests
1966[1]	20 June	few chicks hatched	20 June
1969[2]	3 June	mean laydate	mid June
1970[2]	29 May	mean laydate	mid June
1973[1]	17 May	eggs in 5% of nests	mid June
1974[1]	23 July	nearly all chicks fledged	end of May
1975[1]	18 May	first eggs	mid June
1976[1]	27 June	most young have hatched	mid June
1986[1]	22 June	first young	22 June
1988[3]	mid May	egg laying began	mid June
1990[4]	6 June	mean laydate	late June
1991[4]	10 June	mean laydate	end of June
1992[5]	10 June	mean laydate	end of June
1993[5]	10 June	mean laydate	beginning of July

[1] data from W.A. Montevecchi, unpubl.
[2] data from Maunder and Threlfall (1972).
[3] data from Chatman (1989).
[4] data from Neuman (1994).
[5] data from this study.

Appendix 3 Summary of counts of attended and unattended kittiwake nests with different brood sizes for 16 observation stations, on Great Island, in the late chick stage of reproduction, on 9 and 10 August, 1992.

Station[1] number and area	Attended nests	Unattended nests	Total nests	Nests With 1 young	With 2 young	With young	Without young	Total number of young
1 a	303	90	393	4	0	4	389	4
1 b	60	10	70	0	0	0	70	0
1 c	169	29	198	0	0	0	198	0
2 a	753	151	904	4	0	4	900	4
3 a	61	68	129	1	0	1	128	1
4 a	68	36	104	1	0	1	103	1
4 b	646	117	763	14	0	14	749	14
5 a	5	17	22	0	0	0	22	0
5 b	41	10	51	0	0	0	51	0
5 c	13	2	15	0	0	0	15	0
6 a	161	69	230	2	0	2	228	2
7 a	3253	603	3856	135	4	139	3717	143
9 a	296	69	365	5	0	5	360	5
10 a	424	58	482	1	0	1	481	1
11 a	1160	84	1244	17	0	17	1227	17
12 a	277	31	308	7	0	7	301	7
13 a	143	15	158	0	0	0	158	0
14 a	742	73	815	64	2	66	749	68
15 a	467	154	621	0	0	0	621	0
16 a	670	245	915	5	0	5	910	5
Total	9,712	1,931	11,643	260	6	266	11,377	272

[1] station locations are shown in Appendix 1.

Appendix 4 Summary of counts of attended and unattended kittiwake nests with different brood sizes for the 8 regions of Great Island, in the late chick stage of reproduction, on 9 and 10 August, 1992.

				Nests				
	Region[1]	Attended nests	Unattended nests	With 1 young	With 2 young	With young	Total nests	Total number of young
1	Landing Cove	1285	280	8	0	8	1565	8
2	East side	834	250	16	0	16	1084	16
3	Gill's Cove	3414	672	137	4	141	4086	145
4	North end	296	69	5	0	5	365	5
5	Cribby Cove	1584	142	18	0	18	1726	18
6	West point	420	46	7	0	7	466	7
7	Big Cove	742	73	64	2	66	815	68
8	South end	1137	399	5	0	5	1536	5
	Total	9,712	1,931	260	6	266	11,643	272

[1] regions of Great Island shown in Figure 2.2.

Appendix 5 Summary of counts of attended and unattended kittiwake nests with different brood sizes for 16 observation stations, on Great Island, in the late chick stage of reproduction, on 7 to 10 August, 1993.

				Nests						
Station[1] number and area	Attended nests	Unattended nests	Total nests	With 1 young	With at least 1 young	With 2 young	With 3 young	With young	Without young	Total number of young
1 a	432	73	505	25	4	4	0	33	472	37
1 b	61	7	68	2	0	2	0	4	64	6
1 c	182	8	190	11	8	3	0	22	168	25
2 a	788	106	894	49	12	6	0	67	827	73
* 3 a	460	49	509	23	5	2	1	31	478	35
4 a	76	13	89	16	1	0	0	17	72	17
4 b	748	110	858	66	33	12	0	111	747	123
5 a	31	0	31	0	1	0	0	1	30	1
5 b	57	3	60	4	2	0	0	6	54	6
5 c	16	3	19	3	0	1	0	4	15	5
** 5 d	58	21	79	4	3	0	0	7	72	7
6 a	293	38	331	13	2	1	0	16	315	17
7 a	3913	243	4156	577	152	95	0	824	3332	919
** 8 a	248	22	270	25	2	5	0	32	238	37
9 a	423	52	475	10	11	22	0	43	432	65
10 a	526	16	542	47	23	16	0	86	456	102
11 a	1125	50	1175	114	36	23	0	173	1002	196
12 a	298	6	304	39	6	6	0	51	253	57
13 a	195	5	200	12	2	3	0	17	183	20
14 a	942	29	971	122	32	11	1	166	805	179
15 a	677	42	719	13	2	6	0	21	698	27
16 a	874	222	1096	15	5	2	0	22	1074	24
Total	12,423	1,118	13,541	1,190	342	220	2	1,754	13,541	1,978

[1] station locations are shown in Appendix 1.

* count expanded in 1993.
** stations which were added in 1993.

Appendix 6 Summary of counts of attended and unattended kittiwake nests with different brood sizes for the 8 regions of Great Island, in the late chick stage of reproduction, on 7 to 10 August, 1993.

Region[1]	Attended nests	Unattended nests	Nests with					Total nests	Total number of young
			1 young	At least 1 young[2]	2 young	3 young	young		
1 Landing Cove	1463	194	87	24	15	0	126	1657	141
2 East side	1446	199	116	45	15	1	177	1645	194
3 Gill's Cove	4206	281	590	154	96	0	840	4487	936
4 North end	671	74	35	13	27	0	75	745	102
5 Cribby Cove	1651	66	161	59	39	0	259	1717	298
6 West point	493	11	51	8	9	0	68	504	77
7 Big Cove	942	29	122	32	11	1	166	971	179
8 South end	1551	264	28	7	8	0	43	1815	51
Total	12,423	1,118	1,190	342	220	2	1,754	13,541	1,978

[1] regions of Great Island shown in Figure 2.2.

[2] only 1 young confirmed.

Appendix 7 Food regurgitated by Black-legged Kittiwake chicks and adults on Great Island, on 21 July and 5 August, 1993.

			Contents of bolus	
Date (1993)	Age class	Bolus mass (g)	Species	Estimated size and sex where possible
21 July	adult	17.0	capelin	15 cm, ripe female
			capelin	11 cm
			capelin	
21 July	adult		capelin	male
21 July	chick	27.7	capelin	16-17 cm male
			capelin	15 cm male
21 July	chick	17.3	capelin	12-13 cm
			capelin	12-13 cm
21 July	chick	13.3	capelin	13 cm
21 July	chick	4.9	capelin	13 cm
5 August	chick	18.0	unidentified	
5 August	chick	12.5	unidentified	
5 August	chick	35.0	capelin	15 cm
			capelin	15 cm
5 August	chick	7.3	unidentified[1]	
5 August	chick	16.7	capelin	10 cm
			capelin	8 cm

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[1] suspect capelin.