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Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species

Heidi M. Regehr, William A. Montevecchi*

Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1B 3X9

ABSTRACT: We investigated the roles of food shortage and predation in anticipated breeding failure of black-legged kittiwakes *Rissa tridactyla* at Great Island, Witless Bay, Newfoundland, Canada in 1992 and 1993, following widespread failure in 1991. Reduced and delayed availability of capelin *Mallotus villosus*, plus elimination of previously plentiful fish offal and discards following an eastern Canadian groundfish moratorium in 1992, induced food-stress on kittiwakes and on large predatory *Larus* gulls. Breeding was late, a low proportion of pairs laid eggs, and egg and clutch sizes were small, indicating that feeding conditions for kittiwakes were poor early in the season. Extreme food-stress resulted in low breeding success of *Larus* gulls that turned to kittiwake eggs as an alternate food source. Forced egg predation by great black-backed gulls *Larus marinus* was the primary cause of low hatching success (10 to 11%) in both years. Durations of incubation and chick-rearing shifts decreased following the inshore arrival of capelin, and chicks that hatched after capelin arrival survived longer than earlier hatched chicks. Unattended nests were uncommon, probably in response to predation. In 1992, earlier hatching, later capelin arrival, and apparent lack of alternate prey resulted in many chicks starving and poor fledging success (7%). In 1993, food appeared to be more available both before and after capelin arrival, parents were able to provision chicks, and fledging success was normal (68%). The interactive effects of food shortage and predation have important implications for the use of kittiwakes as indicator species and for the indirect effects of fishery activities on seabird interactions. Kittiwake productivity also reflects the resource base of their predators and caution is required when linking kittiwake breeding success to prey abundance. Moreover, fishery activities, such as the eastern Canadian groundfish moratorium that eliminated fish discards and offal for large scavenging gulls, can have profound second-order effects on other seabird species that are preyed on by scavengers.

KEY WORDS: Bio-indicators · Breeding success · Capelin · Fishery discards · Gulls · Kittiwakes · Offal · Predation

INTRODUCTION

Various components of the reproductive biology of seabirds have been used to indicate timing and availability of their marine prey (Cairns 1987, Montevecchi 1993, Ainley et al. 1995). Food shortage in the pre-breeding or laying periods can result in delayed breeding (Boersma & Ryder 1983, Safina et al. 1988), a low proportion of pairs attempting to breed (Hatch & Hatch 1988, Murphy et al. 1991), and reduced egg and clutch size (Nisbet 1973, Hatch & Hatch 1990, Hiom et al. 1991), all of which may reflect female body condition (Nisbet 1977, Drent & Daan 1980, Houston et al. 1983). Food shortage during incubation and chick rearing can cause low hatching success, high chick mortality (Harris & Wanless 1990, Hatch & Hatch 1990, Hamer et al. 1993), and, under severe conditions, abandonment of nests (Schreiber & Schreiber 1984, Montevecchi 1993). Food-stressed adults may search more or travel greater distances for food, and foraging trip durations have

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*E-mail: mont@morgan.ucs.mun.ca

been used as measures of foraging effort that reflect food availability (Cairns 1987, Verspoor et al. 1987, Burger & Piatt 1990). Nest attendance patterns of adults may therefore reflect feeding conditions (Barrett & Runde 1980, Wanless & Harris 1992, Hamer et al. 1993, but see Galbraith 1983, Roberts & Hatch 1993, Neuman 1994) Length of adult absence from the nest, foraging range and adult body mass have been linked to independent measures of varying food availability across years (Monaghan et al. 1996).

Black-legged kittiwakes *Rissa tridactyla* are small, surface-feeding, holarctic gulls that cope with energy constraints typical of small species (Pearson 1968, Furness & Monaghan 1987). Easily measured components of their breeding performance are sensitive to changes in food supply, and they have been recommended as seabird bio-indicators (Harris & Wanless 1990, Montevecchi 1993). However, their size makes them vulnerable to predation at the nest (e.g. Barrett & Runde 1980, Chapdelaine & Brousseau 1989, Hatch et al. 1993), and the effects of food shortage and predation can be confounded, especially when food shortages also affect predators. Food-stressed kittiwakes are less attentive to eggs and chicks, making them more vulnerable to predation (Hatch & Hatch 1990), and food-stressed predators at times rely more heavily on nest predation than they would when alternative food is adequate (Belopol'skii 1957, Beaman 1978). Interactive effects of food shortage and food-stress-induced predation may compromise the use of kittiwakes as indicators of prey conditions. Furthermore, such interactions hold important implications for human-induced reductions in fishery discards (Garthe et al. 1996).

Predation is difficult to observe directly and disappearance of eggs or chicks is the primary evidence for nest predation of kittiwakes (e.g. Barrett & Runde 1980, Baird 1990, Hatch & Hatch 1990). Thus, if observations to document predation are not conducted, measures of breeding success, including proportions of pairs initiating breeding, clutch size, and hatching and fledging success, may be biased and misinterpreted as indications of food shortage. Nest predation can be opportunistic (predators take advantage of unattended nests) or forced (adults are driven from nests by predators; Montevecchi 1978a, Hatch & Hatch 1990). Food shortage may facilitate both opportunistic and forced predation by causing birds to neglect their nests and by increasing the pressure by predators denied access to alternative food sources. Food shortage and predation will have their greatest interactive effects on breeding success when both predator and prey species exploit the same food sources.

Previous studies of kittiwakes in Newfoundland, Canada documented high breeding success in 1969-70 (Maunder & Threlfall 1972), poor breeding success in 1990 and severe, widespread breeding failure in 1991 (Casey 1994, Neuman 1994). Recent poor kittiwake productivity coincided with other changes in this oceanographic region. Capelin *Mallotus villosus*, the main prey of breeding seabirds in the Northwest Atlantic (Brown & Nettleship 1984, Rodway & Montevecchi 1996, Montevecchi & Myers 1997), had delayed inshore spawning migrations following anomalous cold surface water temperatures in the early 1990s (Montevecchi & Myers 1992, 1996, Shackell et al. 1994, Nakashima 1996, see also Methven & Piatt 1991). Moreover, fishery discards, which are an important food source for many seabird species (Threlfall 1968, Pierotti & Annett 1987, Howes & Montevecchi 1992, Garthe et al. 1996, Oro 1996, Chapdelaine & Rail 1997), including kittiwakes, herring gulls *Larus argentatus* and great black-backed gulls *L. marinus*, were virtually eliminated in the Northwest Atlantic. Due to overfishing and drastic declines of northern cod *Gadus morhua* stocks (Harris 1990, Steele et al. 1992, Hutchings & Myers 1995, Montevecchi & Myers 1996), the ground-fishing industry in eastern Canada was closed in 1992. Great black-backed and herring gulls are nest predators of kittiwakes (Barrett & Runde 1980, Galbraith 1983, Neuman 1994), so we expected that kittiwake breeding success would be affected by both food shortage (e.g. Oro et al. 1995) and increased predation from food-stressed gulls.

Our study objectives were to document the temporal features and levels of kittiwake breeding success and to assess the interactive roles of food shortage and predation on breeding failures. We highlight (1) the indirect effects of decreased fishery offal and discards on seabird interactions, and (2) the difficulty of singling out a single species as a bio-indicator in a complex, dynamic ecosystem (Montevecchi 1993, 1996).

STUDY SITE AND METHODS

This study was conducted from 20 May to 28 August 1992, on 19 May 1993, and from 4 June to 30 August 1993, on Great Island (47° 11' N, 52° 46' W) in the Witless Bay Ecological Seabird Reserve, Newfoundland (Fig. 1). Nine seabird species breed on the island, including 23000 pairs of black-legged kittiwakes, 2700 pairs of herring gulls, 40 pairs of great black-backed gulls and 123000 pairs of Atlantic puffins *Fratercula arctica* (Cairns et al. 1989, Rodway et al. 1996). Great Island is located 10 km south of Gull Island, the site of previous kittiwake studies (Maunder & Threlfall 1972, Neuman 1994). Estimated populations on Gull, Green and Great Islands indicate an effective colony size of 43000 pairs of kittiwakes in the Witless Bay Ecological Seabird Reserve (Cairns et al. 1989).

Study plots and breeding success. Seven study plots with 469 active nests were monitored in 1992 (Fig 1). These plots were expanded in 1993 when Plot 8 was added; 755 active nests were monitored in 1993. At 'observation' Plots 1 to 4 and 8, nest contents were determined by observation from a distance with binoculars or telescope. In 'visited' Plots 5 to 7, nests were accessible. Plot 7, within a dense herring gull colony, was used to assess the effect of the proximity of larger predatory gulls on kittiwake success. Eggs were measured (maximum length and breadth) to the nearest 0.1 mm with vernier callipers. Observation plots served as controls for visited plots.

Plots were checked daily (Plot 1 in both years, Plot 2 in 1993), every 4 d (all other plots except 7) or every 10 d to minimize disturbance in the herring gull colony (Plot 7). During late incubation in 1993, we became concerned that herring gulls were starting to relate our disturbance with predation opportunities. Thus in 1993, Plot 7 was not visited after egg laying and Plots 5 and 6 were not visited during hatching and the early chick-rearing period when kittiwakes were most vulnerable to opportunistic predation. Hatching success (chicks hatched/eggs laid) and fledging success (chicks fledged/chicks hatched) were therefore not calculated for Plots 5 to 7, and breeding success (chicks fledged/eggs laid) was not calculated for Plot 7 in 1993.

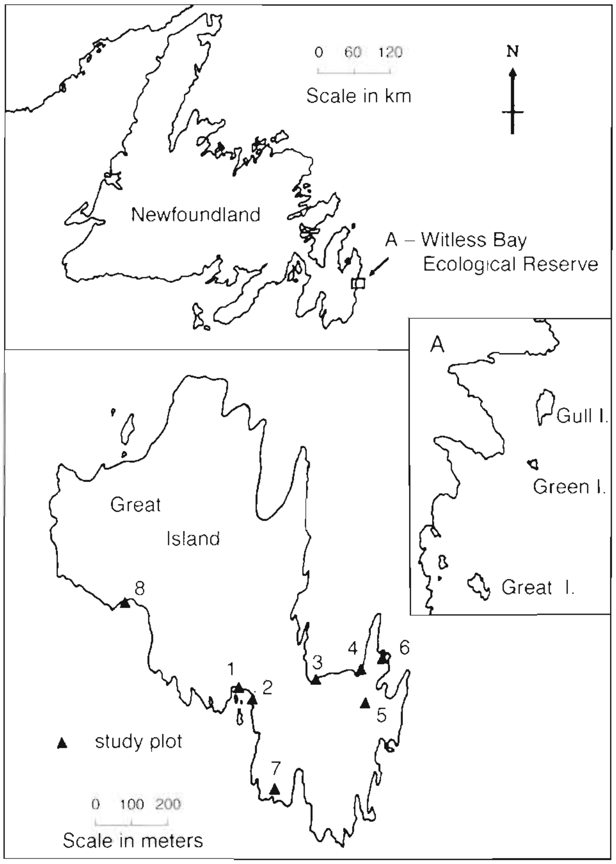

Fig. 1 Locations of the 8 study plots on Great Island, Witless Bay Ecological Seabird Reserve, Newfoundland, Canada

Egg laying. For nests checked daily, lay dates were the day eggs were first seen For other nests, lay dates were estimated as midpoints between visits or from known hatch dates by subtracting a mean incubation period of 27 d (Maunder & Threlfall 1972).

Predation presented problems for determining proportions of pairs laying (proportion of nests ever containing eggs/total nests) and clutch size. Egg predation was negligible until most eggs had been laid in 1992 (see 'Results'), and the proportion of pairs producing eggs was considered reliable for all plots. In 1993, egg disappearance throughout incubation was high, and the proportion of pairs producing eggs was calculated only for Plots 1 and 2 that were checked daily. Clutches were excluded from calculations of clutch size when a single egg was seen on only 1 visit or when a clear view was not obtained. Unknown clutches were assigned the average clutch of that year in the estimation of total eggs laid that was needed to estimate hatching and breeding success. Egg volume (V) was calculated from Coulson's (1963) equation: V (cm^3) = 0.0004866 × length × breadth^2 J Maunder (Newfoundland Museum, St. John's) provided raw data of egg measurements taken from kittiwakes on Gull Island in 1969-70.

Predation. To observe predation on kittiwake nests, 0.5 to 7 h observation sessions spread throughout daylight were conducted for a total of 104 h in Plot 1 from 12 June to 3 July 1993. Opportunistic observations of predation were made whenever possible.

Capelin arrival inshore. The onset of inshore availability of mature capelin to kittiwakes was assumed to be the date on which Atlantic puffins were first recorded carrying mature capelin to chicks during continuous and systematic observations (Rodway & Montevecchi 1996) These dates coincided with the first observations of inshore capelin in Bauline South, a fishing community 2 km from Great Island (M. Reddick pers. comm.).

Incubation shifts. Individual kittiwakes were identified by wing-tip patterns (J W. Chardine pers. comm.), and sex was determined from mating behaviour when possible. Nests of incubating pairs were checked every 4 h during daylight and the identity of the incubator recorded at 14 nests from 18 to 21 June and at 17 nests from 28 June to 9 July 1992, and at 40 nests from 12 June to 2 July 1993. Midpoints of intervals between checks were used as the times of shift changes when calculating durations of incubation shifts (DIS). In some cases (particularly in 1992), incomplete incubation shifts were included to avoid excluding very long shifts, i.e. when a bird was incubating at the start of observation (start time of shift unknown), the partial shift was included when it was as long or longer than the longest observed complete shift at that nest. Thus, our estimates of mean incubation shifts are conservative.

Chick survival. Chicks were categorized as hatching either before or after capelin arrival, the division between the 2 groups being set at 2 d before capelin arrival because chicks were observed to survive for about 2 d with little or no food. Chicks were classified as dying in the nest, disappeared or fledging.

Chick-rearing shifts. Durations of chick-rearing shifts (DCS) before capelin arrival were measured in 1992 concurrently with the incubation shift observations described above. To compare shifts after capelin arrival, three 24 h observation sessions, from noon to dark one day and from dawn to noon the next, were conducted on 8/9 July, 17/18 July and on 25/26 July 1992. A second measure, changeovers per h (CPH), the number of times mates replaced each other at the nest per h of observation, was used to compare chick-rearing shifts between years. Twelve 3 to 9 h (71 h total) chick-rearing observation sessions were conducted on 2 to 6 chicks ranging in age from 0 to 28 d at 6 nests from 8 to 30 July 1992. Eighteen 3 h observation sessions were conducted on 7 to 9 chicks ranging in age from 0 to 29 d at 7 nests between 8 and 30 July 1993.

Statistical analysis. Means are reported ±SD. Parametric statistical tests were employed for most comparisons and tolerance for type I error was set at 0.05. Kolmogorov-Smirnov 1-way analysis of variance (ANOVA) was used to test differences in temporal laying distributions between years. Residuals were examined for normality and independence and, when not acceptable, randomization tests (Edgington 1980, Sokal & Rohlf 1981), in which p is based on the data distribution, were used. The dependent variable was sampled 500 times, the statistical test was performed each time with the randomized data, and results were compared to those of the non-randomized statistical test. The new p-value was calculated as the proportion of randomized *F*-ratios exceeding the observed ratio, i.e. the probability that the observed relationship occurred by chance. When both p-values agreed, the original parametric statistic was reported. When p-values were different (1 case), the p-value from the randomization test was reported.

Table 1. *Rissa tridactyla*. Comparison of the breeding performance of black-legged kittiwakes in observation and visited plots on Great Island, Newfoundland, in 1992 and 1993. Number of observations given in parentheses. –: hatching and fledging success were not measured in visited plots in 1993 (see 'Study site and methods')

Breeding performance	1992		1993	
	Observation (%)	Visited (%)	Observation (%)	Visited (%)
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)	–
Fledging success	0 (22)	14 (21)	68 (57)	–
Breeding success	0 (218)	1 (231)	8 (506)	5 (118)

RESULTS

Researcher disturbance

There were no differences between observation and visited plots in proportions of 1- and 2-egg clutches nor in hatching, fledging or breeding success in 1992 or 1993 (χ^2 tests, $p_s > 0.05$; Table 1) Plots were combined for calculations of breeding performance.

Timing of breeding

The first egg was found on 21 May 1992. No eggs were laid in study plots by 19 May 1993 and 10% (n = 624) had been laid by 4 to 6 June 1993. No difference was detected in the cumulative frequency distributions of laying dates in 1992 and 1993 (n = 667; Kolmogorov-Smirnov *H*, p > 0.05). Mean lay date of first laid eggs per clutch was 10 June 1992 (SD = 6.5 d), and mean hatch date was earlier in 1992 (2 July ± 5.9 d) than in 1993 (7 July ± 5.0 d; $t_{109} = 5.51$, $p < 0.001$).

Egg production and survival

Proportionately fewer pairs laid eggs in 1992 (64%, n = 469) than in 1993 (77%, n = 210; $\chi^2_1 = 10.1$, p = 0.002). Mean clutch size was 1.4 ± 0.5 and 1.3 ± 0.57 eggs in 1992 and 1993, respectively. A lower proportion of 1-egg clutches was recorded in 1992 (58%, n = 226) than in 1993 (67%, n = 332; $\chi^2_1 = 5.0$, p = 0.025); no 3-egg clutches were found in either year. Egg volume was not different in 1992 (42.2 ± 3.6 cm^3) and 1993 (42.8 ± 3.3 cm^3; $t_{335} = 1.55$, p = 0.12), but increased slightly through the laying period in 1992 ($F_{1,208} = 5.54$, p = 0.020, $R^2 = 0.026$; $y = 38.4 + 0.09x$) though not in 1993 (p > 0.2). Hatching success did not differ in 1992 (10%, n = 449) and 1993 (11%, n = 506; $\chi^2_1 = 0.7$, p = 0.40). In 1992, mean lay dates of eggs that hatched (4 June ± 5.1 d) were earlier than those of eggs that did not hatch (11 June ± 6.1 d; $t_{332} = 6.4$, p < 0.001).

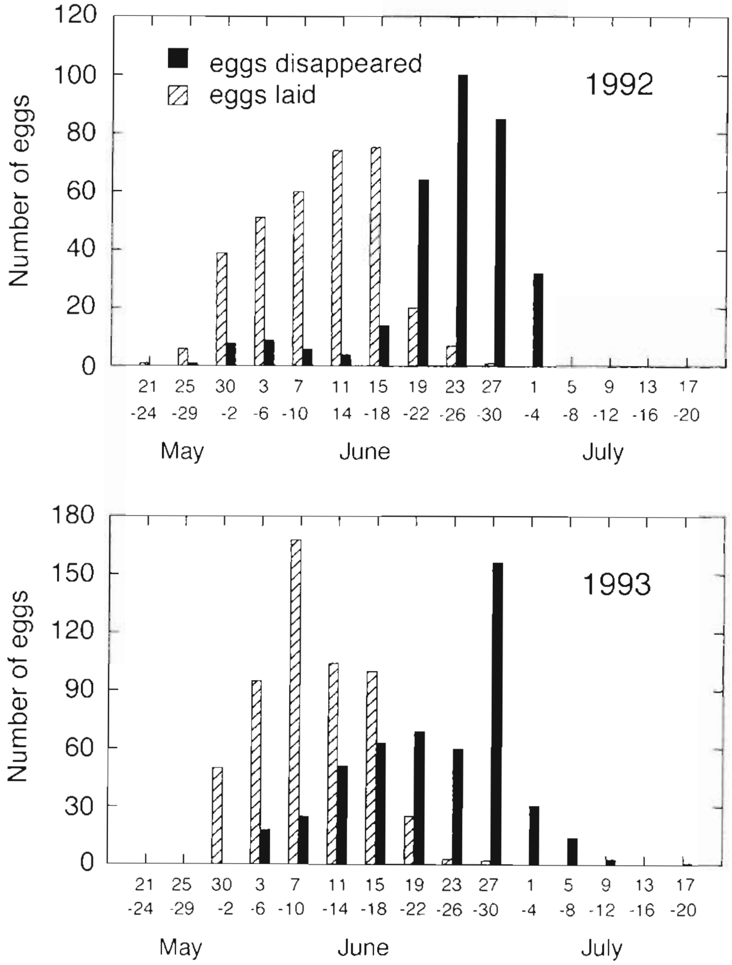

Fig. 2. *Rissa tridactyla*. Timing of black-legged kittiwake egg laying and disappearance in 1992 and 1993 on Great Island. Intervals on the *x*-axis are days of the month

Egg predation

Most eggs that did not hatch disappeared in both years (only 0.5 and 2.7% of eggs were addled in 1992 and 1993, respectively). Eggs disappeared earlier in 1993 (mean date 22 June ± 8.1 d) than in 1992 (24 June ± 7.0 d; $t_{812} = 2.17$, $p = 0.03$). Few eggs disappeared in the first month of laying in 1992, but in 1993, eggs disappeared more gradually as they were laid (Fig. 2).

Virtually all eggs that disappeared were taken by predators. We observed predators take 73% (n = 93) of all eggs laid in the predation observation plot. Other eggs classified as disappeared were most likely taken by predators. Great black-backed gulls took 85% (n = 68) of eggs, herring gulls took 12%, and an American crow *Corvus brachyrhynchos* took 1 egg (1%). Forced predation (an incubating adult was driven from the nest) occurred in 88% of cases, whereas 12% of the eggs were taken opportunistically when parents were temporarily absent. Great black-backed gulls accounted for 88% of forced and 63% of opportunistic predation events, whereas herring gulls accounted for 12% of forced and 25% of opportunistic predation events. Observations indicated that these levels of predation were representative of the entire island.

Some great black-backed gulls appeared to specialize and made extensive use of kittiwake eggs to feed chicks: kittiwake eggshells and eggs were found regularly in 3 and 5 of 14 great black-backed gull territories in 1992 and 1993, respectively (H. M. Regehr & M. S. Rodway unpubl. data). Two of these pairs collected large numbers of kittiwake eggs in both years. As many as 61 intact and broken eggs were found in one territory at one time in 1992. Egg yolk around the bills of the chicks indicated that they were fed these eggs. In both years, egg disappearance peaked after great black-backed gull chicks hatched (Regehr 1994), which may reflect the increasing food requirements of growing chicks.

Incubation shifts

Atlantic puffins were first seen carrying mature capelin on 8 July 1992 and on 6 July 1993. Duration of incubation shifts (DIS) was greater before capelin arrival than after in 1992 (Table 2). In 1993, all eggs were lost from observation nests by 2 July, so DIS before and after capelin arrival could not be compared. Mean DIS before capelin arrival was significantly greater in 1992 than in 1993 (Table 2). Incomplete incubation shifts were included in 17 cases in 1992 and in 3 cases in 1993, so mean and maximum DIS were probably underestimated in 1992, as was the difference between years. Of 2 nests where incubation

Table 2. *Rissa tridactyla*. Mean duration (h) of incubation shifts (DIS) before and after capelin arrival in 1992, and a comparison of DIS in 1992 and 1993. *Result from randomization test (see 'Study site and methods')

Year	Hatch date	N	Mean DIS	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		0.002*

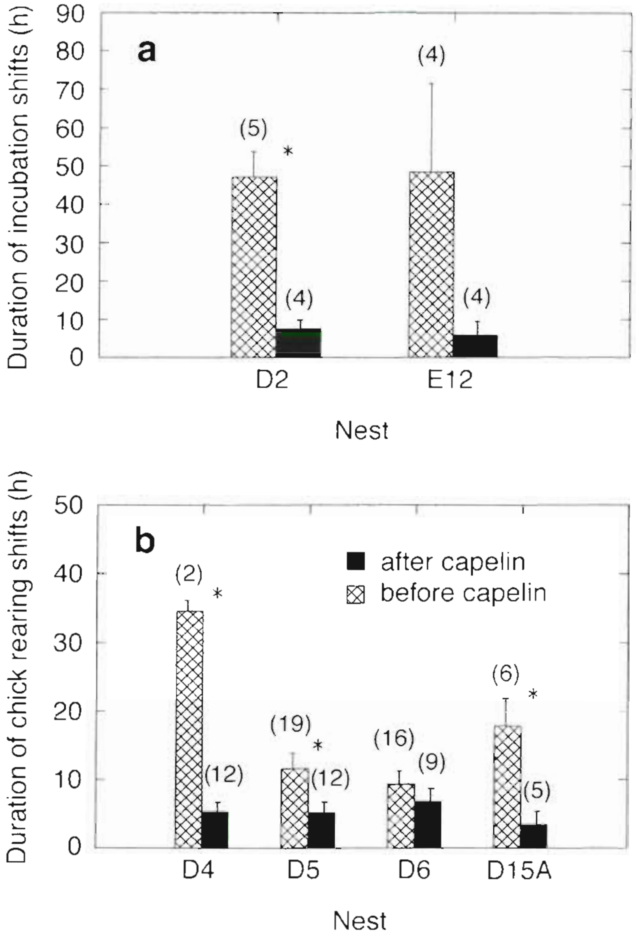

Fig. 3. *Rissa tridactyla*. Mean (±SE) duration of incubation and chick-rearing shifts of black-legged kittiwakes before and after capelin arrival in 1992 for (a) 2 nests where incubation spanned capelin arrival, and (b) 4 nests where chick-rearing spanned capelin arrival. Sample sizes are given above bars and significant differences before and after capelin arrival are indicated with an asterisk

spanned capelin arrival (pairs were incubating both before and after capelin arrival) in 1992, mean DIS was significantly greater before capelin arrival than after at 1 nest ($t_7 = 5.0$, p = 0.002; Fig. 3a). No difference in DIS was observed between sexes in either year (*t*-tests, p > 0.5).

Chick survival

Fledging success was lower in 1992 (7 %, n = 43) than in 1993 (68 %, n = 57; $\chi^2_1 = 38.0$, $p < 0.0001$), as was breeding success (0.7 %, n = 449 in 1992; 7 %, n = 624 in 1993; $\chi^2_1 = 26.2$, $p < 0.0001$). In 1992, 70 % of chicks died within 1 wk of hatching, whereas 18 % died in 1993 (Fig. 4). The proportion of chicks that died in the nest did not differ between 1992 and 1993 (28 %, n = 43 in 1992 vs 13 %, n = 68 in 1993; $\chi^2_1 = 3.7$, p = 0.05).

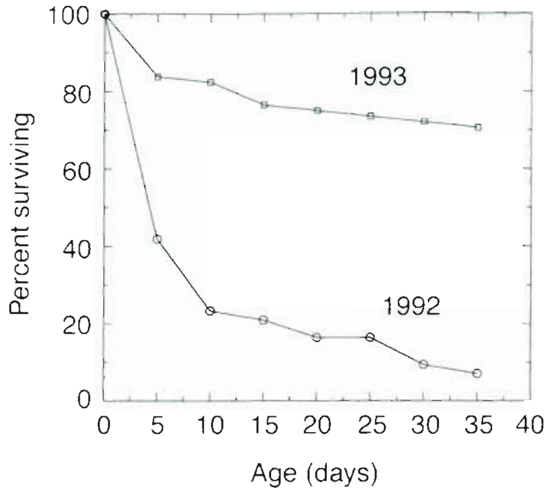

Fig. 4. *Rissa tridactyla*. Percent survival of black-legged kittiwake chicks with age in 1992 and 1993

In 1992, chicks that fledged hatched later than those that died in the nest (Tukey, p = 0.004) and those that disappeared (Tukey, p = 0.045; Table 3). In 1993, chicks that fledged did not hatch significantly later than chicks that did not (Table 3). Survival time increased with hatch date in 1992 ($F_{1,41} = 18.3$, $p < 0.001$, $R^2 = 0.31$, $y = 60.1 + 0.27x$) but not in 1993 (*F*, p > 0.3).

In 1992, most chicks hatched before capelin arrival, whereas in 1993, most chicks hatched after capelin arrival ($\chi^2_1 = 28.49$, $p < 0.0001$; Table 4) Results of a 2-way ANOVA showed that survival time was greater for chicks hatching after capelin than before ($F_{1,107} = 11.9$, p = 0.001) and greater in 1993 than in 1992 ($F_{1,107} = 30.2$, $p < 0.001$). Although the interaction between year and capelin effects failed to attain significance ($F_{1,107} = 3.5$, p = 0.06), there were marked differences between years in the proportions of chicks hatching before and after capelin that fledged. All of the 3

Table 3. *Rissa tridactyla*. Comparison of mean hatch dates of black-legged kittiwake chicks that died in the nest, disappeared, and fledged in 1992 and 1993

Year	Chick fate	N	Mean hatch	SD	*F*	p
1992	Dead in nest	12	29 June	4.98		
	Disappeared	28	2 July	5.35	6.17	0.005
	Fledged	3	10 July	4.58		
1993	Dead in nest	9	5 July	3.18		
	Disappeared	9	6 July	5.52	1.33	0.270
	Fledged	50	8 July	5.09		

Table 4. *Rissa tridactyla*. Survival time (d) of black-legged kittiwake chicks hatching before and after the inshore arrival of capelin in 1992 and 1993

Year	Hatch date	N	Mean survival time	SD
1992	Before capelin	33	5.5	7.94
	After capelin	10	22.3	13.97
1993	Before capelin	17	28.8	19.22
	After capelin	51	33.8	14.75

chicks fledged from the study plots in 1992 hatched after capelin arrival. In 1993, 65% of chicks that hatched before and 76% of chicks that hatched after capelin arrival fledged.

Chick-rearing shifts

In 1992, mean duration of chick-rearing shifts (DCS) before inshore arrival of capelin (13.6 ± 11.5 h, n = 54) was longer than that after capelin arrival (5.6 ± 5.1 h, n = 58; $t_{110} = 4.85$, $p < 0.001$). Of 4 nests where chick rearing spanned capelin arrival in 1992, DCS was significantly greater before capelin arrival than after at 3 nests ($t_{12} = 7.95$, $t_{29} = 2.02$, and $t_9 = 3.01$, $p_s \leq 0.05$; Fig 3b). No difference in DCS was detected between males and females (t_{69}, $p > 0.4$). Mean number of changeovers per h (CPH) was less in 1992 (0.23 ± 0.16, n = 57) than in 1993 (0.53 ± 0.38, n = 90; $t_{145} = 5.63$, $p < 0.001$) Chicks were seldom left unattended, and only 1 adult absence longer than 1 min was observed in each of 71 and 54 h of chick-rearing observations in 1992 and 1993, respectively.

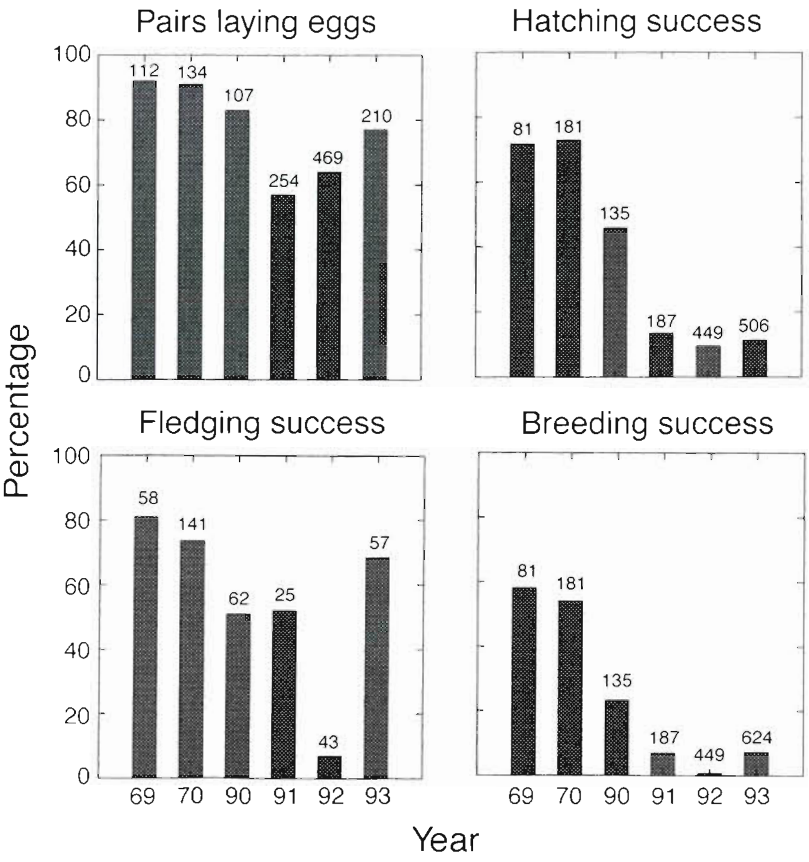

Fig. 5. *Rissa tridactyla*. Percentage of pairs of black-legged kittiwakes laying eggs, and the percentages of hatching, fledging, and breeding success in 1969, 1970 (Maunder & Threlfall 1972), 1990, 1991 (Neuman 1994), 1992 and 1993 (this study). Sample sizes are given above bars

DISCUSSION

Reproductive parameters

Of the 6 yr on record in Witless Bay, breeding success of black-legged kittiwakes was the lowest in 1992 (Maunder & Threlfall 1972, Neuman 1994; Fig. 5). Late breeding, a low proportion of pairs laying, and small eggs and clutches implicated food shortage during the pre-breeding and laying periods in 1991 (Neuman 1994), 1992 and 1993. Mean laying dates were 7 to 10 d later, fewer pairs laid eggs (Fig. 5), and clutch sizes were smaller in 1992-93 (mean = 1.4) than in 1969-70 (mean = 1.9; Maunder & Threlfall 1972). Egg volume also was smaller in 1992-93 (42.4 ± 3.5 cm^3) than in 1969-70 (44.1 ± 3.6 cm^3; $t_{623} = 5.82$, $p < 0.001$). Contrary to most studies (Coulson 1963, Maunder & Threlfall 1972, Runde & Barrett 1981), egg volume did not decrease with laying date in 1991 (Neuman 1994) to 1993. Seasonal decreases in egg volume have been attributed to older females laying earlier, larger eggs (Coulson 1963, Montevecchi 1978b), and the absence of such a decrease in this study may reflect food constraints in the pre-laying period.

Breeding success and food availability

Food availability appeared to be greater throughout the season in 1993 than in 1992. Chick survival was substantially higher in 1993, when fledging success was not different from previous years of good success (Maunder & Threlfall 1972; Fig. 5). Food shortage due to lack of capelin was experienced by fewer chicks in 1993, when a smaller proportion of chicks hatched before capelin arrival (25%) than in 1992 (77%). The timing of these events cannot entirely account for the difference in chick survival between years, because measures of success and behaviour indicate that food was more available in 1993 than in 1992 both before and after capelin arrival. In 1993 compared to 1992, incubation shifts before capelin arrival were shorter, adults replaced each other more frequently during chick feeding, the relationship between chick survival time and hatch date was less pronounced, and survival time of chicks was greater regardless of hatch date relative to capelin arrival. Little is known about the diet of adult kittiwakes before the arrival of capelin in inshore Newfoundland. Research on the feeding ecology of kittiwakes is needed to better understand variations in their breeding performance.

Parental nest attendance, food availability and predation pressure

Excessively long incubation and chick-rearing shifts prior to capelin arrival inshore implicated long foraging trips and food stress in both years (Cairns 1987, Cairns et al. 1990, Wanless & Harris 1992, Hamer et al. 1993). Before capelin arrival, average incubation shifts in 1992 and 1993 exceeded averages reported in years of good (4.5 to 12 h; Coulson & Wooller 1984, Roberts 1988, Hamer et al. 1993) and poor (15 h; Hamer et al. 1993) feeding conditions. Some incubation shifts were so long that a chick hatched and starved in the nest before the on duty parent was relieved by its mate. Average chick-rearing shifts before capelin arrival were also long compared to averages reported in good (1.3 to 4.9 h) and in poor (6.3 to 9.6 h) years (Pearson 1968, Coulson & Wooller 1984, Furness & Barrett 1985, Wanless & Harris 1992, Hamer et al. 1993, Roberts & Hatch 1993).

Food shortage was alleviated by the inshore arrival of capelin, which was delayed by over a month in 1992 and 1993 (Nakashima 1996). Survival times of chicks increased significantly after capelin arrival, and mean nest shift durations compared more closely to those observed in other studies, indicating that food was adequate at that time. Delayed capelin arrival in 1992 resulted in a reversal of the relationship normally observed between early breeding and success, which has been attributed to age and experience (Coulson & White 1958, Montevecchi 1978b, Ryder 1980, Nelson 1988, Sydeman et al. 1991). Although early breeders hatched more eggs than late breeders in 1992, late breeders raised more chicks (see also Hatch 1990).

Low nest attendance during chick-rearing was expected to be a good indicator of foraging conditions, as adults attempt to compensate for food shortage by increasing foraging time (Barrett & Runde 1980, Hatch & Hatch 1990, Wanless & Harris 1992, Hamer et al. 1993). However, some studies, including this one, did not support the expected relationship. This lack of relationship may reflect predation pressure, which compelled parents to stay at the nest. We rarely observed unattended nests with eggs or chicks, and single adults maintained long nest shifts, even though productivity was poor, food supplies appeared to be low, and chicks were starving. Neuman (1994) never saw unattended chicks in 1991 on Gull Island, where herring gull predation was occurring, and attendance was lower in 1990 when productivity was higher. Roberts & Hatch (1993) also noted a surprisingly low correlation between parental attendance and chick success on Middleton Island, Alaska, USA, where predation risk was high. On the Isle of May, Scotland, chicks were continuously attended when predation risk was high (Galbraith 1983), but when nest predation was not occurring, a significant difference in nest attendance was observed in 2 years of differing food availability (Wanless & Harris 1992). Coulson & Johnson (1993) caution the use of unattended chicks as a measure of food shortage because short-term abandonment of older chicks is normal. We suggest caution for a different reason: adult nest attendance may only reflect feeding conditions at colonies with low predation pressure, and high nest attendance may not be a good indicator of feeding conditions (cf Cairns 1987, Roberts & Hatch 1993).

Food-stressed predatory gulls

Great black-backed and herring gulls also were food-stressed and experienced poor breeding success on Great Island and elsewhere in Newfoundland in 1992 and 1993. On Great Island, herring gull breeding success was only 7 and 16% in 1992 and 1993, respectively (H. M. Regehr & M. S. Rodway unpubl. data), compared to 56–64% in 1976–1978 (Pierotti 1982), and that of great black-backed gulls was 17 and 23% in 1992 and 1993, respectively (H. M. Regehr & M. S. Rodway unpubl. data) compared to 42% on Gull Island in 1984 (Roy 1986). The relatively greater success of great black-backed gulls may be related to their dietary flexibility and larger size, making them better foraging competitors (Furness et al. 1992) and more effective predators of other seabirds (Mylne 1960, Threlfall 1968, Harris 1980, Buckley 1990, Russell &

Montevecchi 1996), which would help to buffer them when other prey is scarce.

Previous studies in Witless Bay reported no predation by great black-backed gulls on kittiwake eggs (Maunder & Threlfall 1972, Neuman 1994), and no bird eggs were found in their diets (Threlfall 1968). In contrast, based on our predation observations, great black-backed gulls took an estimated 73 to 76% of all kittiwake eggs laid in 1992-93, most resulting from flushing incubating kittiwakes off nests. Great black-backed gulls were also occasionally seen killing adult kittiwakes, and kittiwakes left their nests readily at their approach. Herring gulls took some eggs, but kittiwakes often defended their nests successfully against them. Pairs nesting within the herring gull colony (Plot 7) were the only ones to fledge chicks in 1992, possibly gaining protection from great black-backed gulls by herring gulls (see also Hilden 1965, Dwernychuk & Boag 1972, Pierotti 1983).

The eastern Canadian groundfish moratorium began in 1992 and eliminated previously consistently plentiful fish discards (Pierotti & Annett 1987) which great black-backed gulls use extensively (Threlfall 1968, Beaman 1978, Buckley 1990, Dunnet et al. 1990, Garthe & Hüppop 1994, see also Howes & Montevecchi 1992, Chapdelaine & Rail 1997). This event, in conjunction with delayed capelin arrival, presumably intensified the predatory behaviour of great black-backed gulls (see Russell & Montevecchi 1996, Rodway & Regehr unpubl. data). The groundfish moratorium may account for the greater predation in 1992 and 1993 compared to 1990 and 1991 (Neuman 1994) because the arrival of capelin was delayed in both studies (Montevecchi & Myers 1992, Nakashima 1996). Large-scale exploitation of kittiwake eggs by great black-backed gulls for chick feeding has not, to our knowledge, been previously reported. The timing of egg predation was earlier in 1993 than 1992, even though hatching phenology of great black-backed gulls did not differ between years (H. M. Regehr & M. S. Rodway unpubl. data), possibly because 1992 was the first year that great black-backed gulls relied heavily on kittiwake eggs. Due to behavioural specialization, the gulls may have been quicker to exploit this alternative food in a subsequent year

Food supply, fisheries and seabird interactions

The interactive effects of food shortage and predation observed in this study have important implications for understanding the indirect effects of fishery activities, such as discarding and offal production, on seabirds, as well as for the use of kittiwakes as bioindicators. Reduced kittiwake productivity in the 1990s paralleled a decadally anomalous cold water event in the Northwest Atlantic (Montevecchi & Myers 1992, Drinkwater 1996, Nakashima 1996), suggesting that breeding success was a robust indicator of oceanographic conditions. Lowest productivity corresponded with cold sea surface temperatures and late inshore migration of capelin in 1991 to 1993 (Nakashima 1996). However, low hatching success due to severe egg predation by food-stressed *Larus* gulls played the largest role in breeding failure in both 1992 and 1993. In 1992, productivity may have still been low in the absence of predation because most parents were unable to provision chicks. In 1993, however, kittiwakes were able to feed chicks and fledging success was normal, following severe egg predation. It is important to emphasize that the intense predatory pressures imposed by gulls were also indirect effects of food shortages resulting from late capelin arrivals *and* from fishery closures and the resultant elimination of fish offal production and discarding. Under these conditions, kittiwake productivity was not a good indicator of food supplies in both years, contrary to recommendations of Harris & Wanless (1990), Monaghan et al. (1991) and Montevecchi (1993). Thus, the breeding success of kittiwakes may reflect not only their resource base but also those of their predators. Predation effects may exacerbate effects of food shortage and may also produce contrary and misleading results when using kittiwakes as bioindicators of prey conditions. Degree of potential biases depends on the timing and intensity of predation relative to the frequency of nest checks.

Egg size and foraging trip duration were probably the most robust estimators of feeding conditions for kittiwakes. The former may provide a useful assessment of conditions in the pre-laying period, and foraging trip duration appears to respond consistently to poor feeding conditions during incubation and chick rearing, regardless of predation intensity (Roberts 1988, Wanless & Harris 1992, Hamer et al. 1993, this study). Adult nest attendance may not be a useful indicator when predation risk is high.

Finally, the intense predatory pressures imposed by *Larus* gulls show the robust second-order or indirect effects that fishing activities can have on seabird production and interspecies interactions. These are often overlooked in single-species investigations of environmental and prey interactions (see Montevecchi 1996).

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