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Components of productivity in black-legged kittiwakes *Rissa tridactyla*: response to supplemental feeding

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In contrast to the high productivity of black-legged kittiwakes in Britain, kittiwakes at many colonies in Alaska have failed chronically to reproduce since the mid 1970s. To determine if food is limiting productivity and, if so, at what stages of nesting food shortages are most severe, in 1996 and 1997 we supplementally fed kittiwakes nesting on an abandoned building. The effects of feeding were stronger in 1997 than in 1996, possibly because naturally occurring prey were of poorer quality in 1997. Consumption of supplemental herring declined as egg laying approached then increased slowly during incubation and more rapidly after hatching. All of the six components of productivity we studied were improved by supplemental feeding to some degree. Supplemental food did not significantly alter laying success in either year, although fed pairs bred at slightly higher rates than unfed pairs in 1997, the poorer food year. In 1996 and 1997, extra food noticeably increased clutch size and hatching success, but significantly so only in 1997. Fledging success and productivity were substantially augmented by feeding in both years. Fed pairs fledged twice as many chicks per nest as did unfed pairs in 1996 and three times as many in 1997. Fed and unfed pairs lost most of their potential productivity through the inability to hatch eggs, and secondarily because of their poor success at raising chicks. The benefits of supplemental feeding did not carry over from one stage of breeding to another. Pairs cut off from supplemental food after laying or hatching performed similarly to pairs that had not been previously fed. This study provides benchmark values of breeding performance attainable by kittiwakes in Alaska under optimal conditions. These values are comparable to highly productive colonies in Britain and suggest that differences in life-history characteristics between Pacific and Atlantic breeding populations are primarily controlled by food supply.

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The population ecology of black-legged kittiwakes *Rissa tridactyla* has been widely studied in both the Atlantic and Pacific portions of the species' range. In Alaska, kittiwakes have experienced chronic breeding failure at many colonies since the late 1970s (Murphy et al. 1991, Hatch et al. 1993a, Irons 1996). Mean productivity declined from 0.5 young per nest in the 1960s and 1970s to less than 0.2 young per nest in the 1980s (Hatch et al. 1993a). Annually between 1985 and 1989, about 50% of Alaskan colonies failed to produce any young (Hatch et al. 1993a). In contrast to the poor productivity of kittiwakes in the Pacific region, kittiwakes in Britain commonly rear more than one young per nest. Adult mortality also differs markedly between regions (Hatch et al. 1993b, Coulson and Strowger 1999; Table 1). Circumstantial evidence points to a deficient food supply as the cause of poor productivity in Pacific kittiwakes (Hatch 1987, Baird 1990, Hatch and Hatch 1990, Murphy et al. 1991, Hatch et al. 1993a, Roberts and Hatch 1993, Piatt and Anderson 1996). The question remains, however, whether differences in life-history characteristics between Pacific and Atlantic kittiwakes reflect proximate and transient environmental controls or genetically encoded adaptations to fundamentally different environments.

Breeding failure in Alaskan kittiwake colonies occurs at different stages of nesting, suggesting that prey availability fluctuates through the season. For instance, in 1993 most kittiwakes on Middleton Island (northern Gulf of Alaska) failed to produce eggs, whereas from 1994 to 1998 the majority of pairs hatched eggs but rapidly lost their chicks (S. A. Hatch and V. A. Gill unpubl. data). On the Semidi Islands (western Gulf of Alaska) in 1983 and on Eleanor Island (Prince William Sound) in 1989, kittiwakes failed to build nests or to lay and hatch eggs, but food appeared to be readily available during the chick-rearing stage (S. A. Hatch unpubl. data, Irons 1996). Studies of kittiwakes breeding in Britain have also detected differences in the timing of failure (Harris and Wanless 1990).

In evaluating food as a cause of breeding failure in kittiwakes, a confounding factor in many colonies is predation on eggs, chicks, and adults by corvids, raptors, and *Larus* gulls (Bonfield 1986, Klicka and Winker 1991, Irons 1996, Regehr et al. 1998). It is hard to argue conclusively that food supply is the ultimate determinant of productivity when populations also suffer intense pressure from predators. In all likelihood, an interaction between food supply and predation exists such that well-fed kittiwakes are better parents and more tenacious defenders of the nest site, whereas energetically taxed birds make easy targets for predators employing opportunistic and forcible tactics (Hatch and Hatch 1990).

We conducted a large-scale supplemental feeding experiment at a failing colony in the northern Gulf of Alaska to test whether food was limiting kittiwake productivity and, if so, at what stage or stages of breeding the effects of food limitation would be most evident. We measured six components of breeding productivity and compared the performance of fed and unfed pairs. Based on previous supplementation experiments involving seabirds and prior observations in our study colony (Roberts and Hatch 1993), we predicted the reproductive performance of supplemented pairs would dramatically exceed that of birds limited by natural foraging conditions. This experiment is unique among food supplementation studies of seabirds because we: (1) provided supplemental food throughout the breeding season to a cliff-nesting species, (2) provided food to both adults and young in a non-captive setting, (3) provided food at different stages in the season, enabling us to assess the timing of food limitation and the possibility of carryover effects between stages, and (4) removed confounding variables such as predation and nest-site quality.

Table 1. Comparison of demographic parameters in Pacific and Atlantic colonies of black-legged kittiwakes.

Parameter	Alaska	England
Adult survival (% per annum)	92.6 ± 0.01[a]	81.0 ± 1.5[b]
Adult life expectancy (years)	13.0[c]	4.8[c]
Productivity (chicks pair^{-1} year^{-1})	0.3 ± 0.03[d]	1.2 ± 0.03[e]

[a] Data from 1988 to 1991 (Hatch et al. 1993b).
[b] Average survival from 1955 to 1998 (estimated from Coulson and Strowger 1999).
[c] Based on the formula $(2 - m)/2m$ where m is annual mortality (Lack 1954).
[d] Data from 1960 to 1989 (Hatch et al. 1993a).
[e] Data from 1954 to 1982 (estimated from Coulson and Thomas 1985).

In addition to testing the response of breeding kittiwakes to an unlimited food supply, this study allowed us to measure the maximum potential breeding performance of kittiwakes, a useful standard for assessing annual breeding success in the northeastern Pacific. It capitalized on a unique opportunity to record accurately the food requirements and consumption patterns of free-living kittiwakes throughout their breeding cycle and to quantify the effect of food limitation on specific elements of productivity and failure.

Methods

Study area

This study was conducted at a kittiwake colony on Middleton Island (59° 26′ N, 146° 20′ W) in the north-central Gulf of Alaska from May through August in 1996 and 1997. The island (900 ha) is located about 120 km from the Alaska mainland and 16 km from the edge of the continental shelf (Fig. 1). Kittiwakes were first surveyed on Middleton in 1956 (Rausch 1958) and have been monitored there annually since 1981. Previously one of the largest aggregations of kittiwakes anywhere in the world, the Middleton population has declined by more than 80%, from 166 000 birds in 1981 to fewer than 25 000 in 1999 (Hatch et al. 1993b, S. A. Hatch and V. A. Gill unpubl. data). The colony has suffered total or near-total breeding failure in 15 of 17 years between 1983 and 1999, annual productivity averaging only 0.06 chicks per nest built. In contrast, the population of glaucous-winged gulls *Larus glaucescens*, the principal predator on kittiwake eggs and young, increased exponentially from fewer than 1000 birds in the 1970s to approximately 20 000 birds in the mid-1990s (S. A. Hatch and V. A. Gill unpubl. data).

Kittiwakes nest primarily on south and west facing cliffs on Middleton, though some pairs nest on man-made structures including an abandoned (1962) U.S. Air Force radar tower and a World War II shipwreck (circa 1944). The upper portion of the tower became accessible to nesting kittiwakes when exterior siding blew off during high winds, exposing horizontal wooden ledges. Kittiwakes using the tower have increased from 1 pair in 1986 to about 1200 pairs in 1997. In 1994 and 1995, plywood paneling and wooden ledges

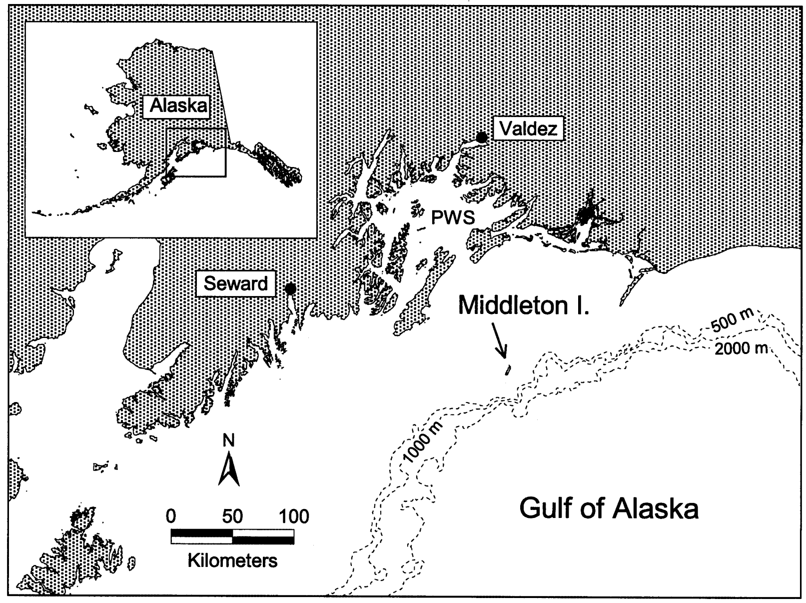


Fig. 1. Location map showing position of Middleton Island near the edge of the continental shelf in the northern Gulf of Alaska. Dashed lines indicate depth contours; PWS = Prince William Sound.

were added to the walls of the tower about 13–15 m above ground level (Fig. 2A).

Experimental design

To identify the stages of nesting at which kittiwakes may be food-limited, we supplementally fed site-holding pairs on the radar tower from our arrival in early May until egg laying (fed-to-laying group), chick hatching (fed-to-hatching group), or the normal age of chick departure (fed-all-season group). Birds in the fed-to-laying group received supplemental food until the appearance of the second egg in the clutch, or until 4 days after the first egg – a mean period of 29.8 ± 1.4 days in 1996 ($n = 26$ pairs) and 28.3 ± 1.0 days in 1997 ($n = 27$ pairs). Individuals in the fed-to-hatching group were fed until the last egg in the clutch hatched or until all eggs were lost, averaging 57.5 ± 1.5 days in 1996 ($n = 26$ pairs) and 52.7 ± 1.0 days in 1997 ($n = 26$ pairs). The fed-all-season group was supplementally fed until the youngest chick was 40 days old or until all nest contents were lost – 90.1 ± 2.1 days in 1996 ($n = 27$ pairs) and 85.4 ± 3.4 days in 1997 ($n = 25$ pairs). Finally, pairs were assigned to a control group that received no supplemental food (63 pairs in 1996, 65 pairs in 1997). Differences in sample sizes within treatments between years occurred because pelagic cormorants *Phalacrocorax pelagicus* invaded some kittiwake nest sites.

This study design allowed an assessment of "carry-over" effects of feeding from one stage to another and ensured that adequate numbers of breeding pairs progressed to the later breeding stages. Prior breeding success by kittiwakes on Middleton suggested that most pairs would have failed by early chick rearing had they not been fed during egg laying and incubation.

Breeding pairs within each of the four treatment groups were clustered on one to one and a half walls of the 12-walled polygonal-shaped tower. Thus, the entire experiment used six adjoining walls of the building. The dimensions of each panel were 3.7 m wide by 2.4 m high. Nests were considered independent sample units, even though treatment groups were assigned to the same panels during both years of the study. Although assigning treatments randomly among panels would have increased statistical independence of the nest sites, that approach likely would have resulted in unfed birds stealing food from supplemented neighbors, effectively eliminating our treatment groups. Indeed, the few stealing attempts we witnessed were between neighboring pairs of the same treatment group. The design we used is similar to that employed by Arcese and Smith (1988) and Hiom et al. (1991), in which song sparrows *Melospiza melodia* and lesser black-backed gulls *Larus fuscus* were grouped in blocks rather than randomly dispersed, to eliminate food stealing. The six tower walls used in the experiment were located on the same (west) side of the tower and thus all treatment groups were exposed to similar environmental conditions. The two extreme treatment groups (control and fed-all-season) were on adjacent walls. The entire set-up occupied only about 22 m of linear wall space, a small area relative to that of most cliff colonies of kittiwakes. The artificial nature of the nest sites ensured that habitat quality was uniform across all treatments, and the vertical sides of the tower prevented avian predators, including glaucous-winged gulls, from landing at any of the sites. No landing or approach of gulls near the ledge nest sites was ever observed during the study.

We used 144 artificial nest sites installed on the tower in 1994 and 1995 (Fig. 2B). Each wooden ledge was 35 cm wide by 24 cm deep. The center of one site to the center of the neighboring site was approximately 0.5 m. Sliding panes of one-way mirror glass (30 cm high by 26 cm wide) and feeding tubes (20 cm long by 5 cm wide) were installed at nest sites (Fig. 2C). The feeding tubes, made from plastic pipe cut lengthways to form a tray, slid back and forth through the wall, allowing food to be presented unobtrusively from inside the tower (Fig. 2D). The one-way glass facilitated monitoring of birds and nests from inside the building and the capture of individuals at their nest sites for banding, measurements, and food sampling.

Procedures

Fed pairs were provided adult herring *Clupea pallasi*, a natural prey species of kittiwakes in the northern Gulf of Alaska and Prince William Sound (Irons 1992, Suryan et al. 2000, this study). Frozen fish were thawed and cut into ingestible pieces before presenting them to

Fig. 2. (A) An abandoned radar tower on Middleton Island provides high quality nest sites for black-legged kittiwakes. (B) The interior of the building offers a laboratory-like setting in which to study wild, cliff-nesting birds. (C) Artificial nest sites backed by one-way mirror glass enable close observation and manipulation (glass removed from site at right). (D) A small tray slides through the wall at each site to facilitate supplemental feeding.

Table 2. Definitions of components of productivity in black-legged kittiwakes.

Component	Units of measure
Laying success	Pairs laying eggs/sites with pairs
Clutch size	Eggs laid/nests with eggs
Hatching success	Eggs hatched/eggs laid
Fledging success	Chicks fledged/eggs hatched
Breeding productivity	Chicks fledged/nests with eggs
Overall productivity	Chicks fledged/sites with pairs

the birds. Food was supplied daily from 9 May to 16 August at 09:00 and 17:00 in both 1996 and 1997. In 1997, we also presented food at 13:00 once chicks began to eat from the tubes, about 2 weeks post-hatching. A supplement of thiamine (vitamin B_1) was added to each meal to offset deficiencies of this nutrient associated with freezing (Altman et al. 1997, Crissey 1998). Feeding tubes were cleaned and sanitized at each feeding with a chlorine solution. Filled tubes contained about 163 g of herring (SD = 13.1 g). The gross amounts (i.e., all tubes combined) of herring supplied and remaining after each feeding were recorded, and the amount of herring consumed and left uneaten per nest site per day was calculated based on the number of pairs fed. In 1996, data were not collected on food consumption prior to 13 May or after 26 July.

To quantify breeding performance, nest sites were checked each morning and evening for new eggs and hatchlings and for losses of eggs and chicks. We measured six variables related to reproductive success (Table 2). For purposes of calculating fledging success, we considered chicks to be fledged at 40 days of age.

Adults were captured and identified by unique combinations of plastic color rings and a U.S. Fish and Wildlife Service (USFWS) stainless steel ring. Chicks were also marked with a metal ring and a single color ring to identify their year class. Regurgitated food samples from adults and chicks were collected throughout the season to determine composition and seasonal changes in the natural food supply at Middleton. Samples from experimental birds that clearly contained only supplemental food (identified by size of herring) were not collected. Diet composition was quantified as percent frequency of prey occurrence in 1996 and both percent frequency of occurrence and percent mass in 1997. To reduce disturbance, diet sampling focused only on adults and chicks handled for banding and measurements.

Predictions

We expected fed Pacific kittiwakes with access to unlimited food to increase their productivity to the same levels as, or greater levels than, those observed in Atlantic colonies where natural foraging conditions appear to be excellent (Coulson and Thomas 1985). Because previous studies have indicated that supplemental feeding makes little difference when marine resources are abundant (Hiom et al. 1991, Van Klinken 1992, Bukaciński et al. 1998), we expected to find smaller differences between fed and unfed birds in years with good natural food conditions than in poor years. We further hypothesized that carryover effects of feeding would result in differences in breeding performance between previously fed pairs and controls during later stages of breeding in which both groups were unfed. Finally, we expected that egg laying and incubation would be the stages most enhanced by supplemental feeding, because previous investigations suggested the pre-hatching period contributes strongly to the variability of kittiwake breeding success in Alaska (Hatch et al. 1993a).

Data analysis

To determine when food limitation was strongest, we classified pairs as either fed or unfed at each breeding stage and calculated mean effects on overall productivity associated with failure to lay eggs, failure to hatch eggs, and failure to fledge chicks. This required expressing the components of productivity as percentages of maximum potential productivity. Maximum potential productivity represents an idealized outcome in which the number of kittiwake pairs breeding and clutch sizes are maximal (see below), every egg hatches, and every chick fledges (Hatch et al. 1993a). Because a small percentage of kittiwakes may forego breeding even in optimal conditions (Wooller and Coulson 1977), we used the highest proportion of pairs observed to lay eggs in any treatment group in either year (97.4%) as the standard for maximum laying potential. Similarly, maximum potential clutch size was taken to be 1.94 eggs, the largest mean clutch size recorded in any treatment group in either year.

To quantify losses of potential productivity, we followed the procedures outlined in Hatch et al. (1993a). At the egg stage, loss was based on the formula $100 \times [1 - (B_oC_o/B_mC_m)]$, where B_o = observed proportion of pairs laying eggs in the group being analyzed, C_o = observed clutch size in the group analyzed, B_m = maximum proportion of pairs laying eggs observed in any group during the study, and C_m = maximum observed clutch size. Thus, the quantity B_oC_o/B_mC_m represents the number of eggs laid as a fraction of maximum potential egg production. Pairs achieved maximum potential egg production when $B_oC_o = B_mC_m$, i.e., eggs not laid were $100 \times (1 - 1) = 0\%$. If egg production in the group considered was less than the maximum observed across all groups, then $B_oC_o < B_mC_m$ and $B_oC_o/B_mC_m < 1$ – a reduction in the actual production of eggs compared to the potential. Loss of productivity at the laying stage was further partitioned into the proportion of loss due to pairs not breeding, using the formula $[(B_m - B_o)C_o]/[(C_m - C_o)B_o + (B_m - B_o)C_o] \times$ [eggs not laid], and losses due to pairs laying smaller than maximum clutch sizes, using the formula $[(C_m - C_o)B_o]/[(C_m - C_o)B_o + (B_m - B_o)C_o] \times$ [eggs not laid]. For any given treatment group, we then expressed the number of eggs and chicks lost as percentages of a cohort of 100 potential offspring that included eggs not laid. By expressing the components of breeding failure in this manner, the losses associated with failure to lay, failure to hatch, and failure to fledge become additive, and the contributions of lost production at each stage of nesting (including nonbreeding and reduced clutches) to total losses for the season are evident.

Having quantified the components of breeding failure as above, we took the difference in unrealized potential for productivity between fed and unfed groups as our summary measure of the effect of feeding. We subtracted unfed from fed values, resulting in a negative value if fed pairs did worse than unfed pairs. Finally, we calculated the relative enhancement of breeding performance achieved by food supplementation at any stage of breeding as the difference between fed and unfed treatment groups at that stage divided by the sum of differences for all stages. In effect, this analysis gauged the responsiveness of each component of productivity to food supplementation.

Means are reported ± 1 SE throughout the paper. We used nonparametric tests when a variable did not meet the assumptions of normality or homogeneity of variances. Among-treatment comparisons involving clutch size or productivity were tested using Kruskal-Wallis ANOVA. If differences among groups were significant, pairwise comparisons of treatment groups were tested using the Mann-Whitney U test. Proportional measures such as laying success, hatching success, fledging success, and carryover effects of supplemental feeding were tested using the Pearson chi-square (χ^2) statistic for all comparisons. All expected cell frequencies were ≥ 5 in contingency tables for which a significant outcome is reported using chi-square.

Results

Daily consumption of supplemental food

The quantity of herring left uneaten per nest site per day varied through the season. Fed kittiwakes decreased their consumption of supplemented herring before (1997) or during early egg laying (1996 and 1997), increased it gradually during early incubation, and increased their intake more rapidly after hatching in 1997 (Fig. 3). Prior to laying, supplemented kittiwakes consumed 292 ± 4 g of herring nest^{-1} day^{-1} in 1996 (n = 79) and 324 ± 7 g nest^{-1} day^{-1} in 1997 (n = 78). During laying and incubation, pairs consumed 258 ± 5 g of herring nest^{-1} day^{-1} in 1996 (n = 53) and 282 ± 5 g nest^{-1} day^{-1} in 1997 (n = 51). In the nestling period, adults and chicks combined consumed 300 ± 2 g of herring nest^{-1} day^{-1} in 1996 (n = 27) and 414 ± 14 g nest^{-1} day^{-1} in 1997 (n = 25). The abrupt increase in average consumption during the middle of the chick-rearing period in 1997 reflected the addition of a third, midday feeding on 21 July (Fig. 3).

Natural foods

Prior to chick rearing in 1996, lanternfish (Myctophidae) were the most common prey item of adults, followed by capelin *Mallotus villosus*, unidentified smelt (Osmeridae), and Pacific sand lance *Ammodytes hexapterus* (Appendix). Neither lanternfish nor capelin were present in any samples collected during the same period in 1997, when Pacific sand lance and copepods dominated the diet. Sablefish *Anoplopoma fimbria*, amphipods, and Pacific herring *Clupea pallasi* were also frequent in the diet in 1997. Based on biomass, Pacific sand lance and herring were the dominant food items of the diet in 1997.

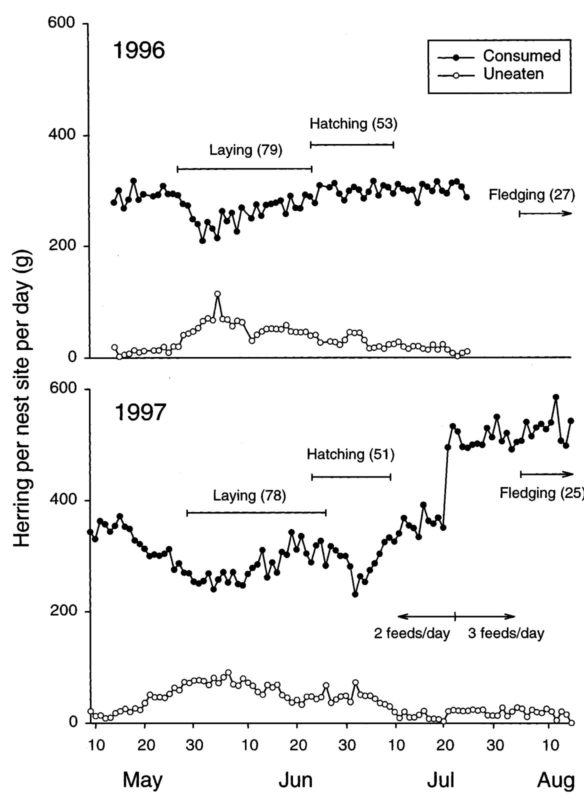


Fig. 3. Mean quantities of supplemental food consumed or left uneaten nest^{-1} day^{-1} by adult and nestling black-legged kittiwakes on Middleton Island, 1996–1997. Sample sizes (fed pairs) at each breeding stage in parentheses.

Table 3. Components of productivity in black-legged kittiwakes in relation to supplemental feeding treatments on Middleton Island, 1996–1997.

Component	Year	Treatment group[a]				
		Fed to laying	Fed to hatching	Fed all season	Control	P[b]
Laying success	1996	0.92 ± 0.05 (26)	0.92 ± 0.05 (26)	0.93 ± 0.05 (27)	0.94 ± 0.03 (63)	0.994
	1997	0.96 ± 0.04 (27)	0.96 ± 0.04 (26)	1.00 ± 0.00 (25)	0.91 ± 0.04 (65)	0.328
Clutch size	1996	1.92 ± 0.06 (24)	2.00 ± 0.06 (24)	1.88 ± 0.07 (25)	1.85 ± 0.05 (59)	0.308
	1997	1.81 ± 0.08 (26)	1.88 ± 0.07 (25)	1.80 ± 0.08 (25)	1.63 ± 0.06 (59)	0.058
Hatching success	1996	0.57 ± 0.07 (24)	0.67 ± 0.07 (24)	0.85 ± 0.05 (25)	0.69 ± 0.04 (59)	0.027
	1997	0.51 ± 0.07 (79)	0.77 ± 0.06 (25)	0.71 ± 0.07 (25)	0.50 ± 0.04 (59)	0.004
Fledging success	1996	0.54 ± 0.10 (15)	0.56 ± 0.09 (17)	0.85 ± 0.06 (22)	0.52 ± 0.06 (43)	0.005
	1997	0.50 ± 0.10 (13)	0.58 ± 0.08 (21)	0.81 ± 0.07 (21)	0.46 ± 0.07 (32)	0.014
Breeding productivity	1996	0.58 ± 0.13 (24)	0.75 ± 0.14 (24)	1.32 ± 0.15 (25)	0.66 ± 0.08 (59)	0.001
	1997	0.46 ± 0.11 (26)	0.84 ± 0.13 (25)	1.04 ± 0.17 (25)	0.37 ± 0.06 (59)	<0.001
Overall productivity	1996	0.54 ± 0.13 (26)	0.69 ± 0.13 (26)	1.26 ± 0.15 (27)	0.62 ± 0.08 (63)	0.001
	1997	0.44 ± 0.11 (27)	0.81 ± 0.12 (26)	1.04 ± 0.17 (25)	0.34 ± 0.06 (65)	<0.001

[a] Values in table are mean ± SE (n).
[b] Within-year variation among treatment groups tested using Pearson chi-square statistic for laying, hatching, and fledging success, and Kruskal-Wallis ANOVA for clutch size, breeding productivity, and overall productivity.

During chick rearing in 1996, herring were the most frequent item in the diet (46.2%), sablefish ranked second (19.2%), while Pacific sand lance and lanternfish ranked third (9.6% each) (Appendix). Large shifts in diet composition occurred at the same stage in 1997. Herring were a smaller portion of the diet in 1997 – only 2.7% in frequency of occurrence, and 1.7% by weight. Sablefish largely replaced herring in the diet that year. All herring in regurgitations from unfed birds were juvenile fish; no adult (i.e., supplementally fed) herring were present.

Components of reproduction

The breeding performance of kittiwakes was better in 1996 than in 1997 for all but the fed-to-hatching group (Table 3). Clutch sizes were larger, hatching and fledging rates were higher, and more chicks were produced per nest and breeding pair in 1996 than in 1997. Laying success was an exception, as the proportion of pairs laying eggs in every fed group was lower (though not significantly so) in 1996 than in 1997 (Table 3).

No differences were detected in laying success or clutch size among the four groups in either 1996 or 1997, but hatching success differed significantly among groups in both years (Table 3). Hatching success was highest (85%) in the fed-all-season group in 1996 and the fed-to-hatching group (77%) in 1997. In contrast, hatching success was lowest (57%) in the fed-to-laying group in 1996 and the control group (50%) in 1997. Pairwise comparisons of groups in 1997 indicated that pairs fed at least to hatching had significantly higher hatching success than control pairs or those whose supplemental feeding was terminated after laying. In 1996, however, pairs fed all season hatched significantly more eggs than any other treatment group, including the pairs fed to hatching ($\chi^2_1 = 4.40$, $P = 0.036$). Hatching success of the fed-to-hatching group was similar to that of the control and fed-to-laying groups in 1996.

Fledging success also differed significantly among the four groups in both years. Pairs fed all season had greater fledging success (85% in 1996 and 81% in 1997) than any other group. Rates of fledging success in control, fed-to-laying, and fed-to-hatching groups did not differ from one another. Fledging success was lowest in the control group (52% in 1996 and 46% in 1997) in both years.

Productivity was highest in the fed-all-season group – greater than one chick per breeding pair and per nest built – in both 1996 and 1997. It was lowest in the fed-to-laying group in 1996 (0.54 and 0.58 chicks per nest and breeding pair, respectively) and the control group in 1997 (0.34 and 0.37 chicks per nest and breeding pair, respectively) (Table 3). In 1996, the fed-to-laying, fed-to-hatching, and control groups did not differ from one another, but all three groups produced substantially fewer chicks than pairs fed all season. In 1997, the fed-to-hatching and fed-all-season treatments resulted in similar numbers of chicks, and both groups produced more chicks per pair than did the fed-to-laying or control groups.

Carryover effects

To test for possible carryover effects of supplemental feeding, we compared hatching and fledging success among the control, fed-to-laying, and fed-to-hatching groups. Laying success and clutch size were not included, because all groups except controls were fed through egg laying or longer. In all cases, pairs denied food after a particular breeding stage had similar rates of hatching or fledging success to the appropriate comparative group(s), whether control pairs or those cut off at a previous stage (Table 4). This outcome allowed us to combine the control and fed-to-laying pairs as one "unfed" group for analyzing hatching success and to add the fed-to-hatching group to the "unfed" sample when analyzing fledging success. Any treatment group was pooled with the "fed" group if supplemental food was provided during the breeding stage being analyzed. Thus, fed-to-laying pairs are included as "fed" for laying success and clutch size analyses but are regarded as "unfed" for comparisons of hatching success.

We then compared all components of productivity for pooled samples of fed and unfed pairs, as above (Table 5). Other than laying success in 1996, supplemental food increased, to varying degrees, breeding performance in the fed group over the unfed group. Fed pairs laid significantly larger clutches and achieved substantially higher hatching success than unfed pairs in 1997. However, laying success did not differ statistically between fed and unfed kittiwakes in 1996 or 1997, nor did clutch size or hatching success in 1996. Fed pairs fledged twice as many chicks per nest built as did unfed pairs in 1996 and three times as many in 1997. Results were similar for the number of chicks fledged per egg-laying pair.

Components of failure and limiting factors

In both years, fed pairs attained a higher percentage of their maximum potential productivity (i.e., young fledged) than did unfed pairs (Fig. 4). Failure to hatch eggs was the factor contributing most to the reduction in overall productivity in both groups and years. However, the extent to which hatching success and other components of breeding performance were enhanced by supplemental feeding differed between years. Prior to chick rearing, food provisioning enhanced breeding performance by 40% in 1996 and 82% in 1997 (summing enhancement of laying, clutch size, and hatching performance; Table 6). After hatching, supplemental feeding resulted in a 60% enhancement of breeding performance in 1996 and 18% enhancement in 1997 (Table 6). Thus, the differential between fed and unfed pairs was greatest during chick rearing in 1996 and prior to hatching in 1997.

Discussion

Five of the six components of productivity we studied were significantly improved by supplemental feeding, indicating clearly that food was limiting the productivity of kittiwakes on Middleton Island. However, the degree to which productivity components were affected varied between years. Extra food noticeably increased clutch size and hatching success, although only significantly so in 1997, the poorer food year. Laying success did not seem greatly influenced by food supplementa-

Table 4. Contrasts and probability levels to test for carryover effects of supplemental food provided earlier on performance at later stages of breeding in black-legged kittiwakes on Middleton Island, 1996–1997.

Performance	Groups compared[a]	1996		1997	
		χ^2_1	P-value	χ^2_1	P-value
Hatching success	Fed to laying vs control	2.15	0.142	0.01	0.905
Fledging success	Fed to hatching vs fed to laying+control	0.14	0.709	1.19	0.276
Fledging success	Fed to hatching vs fed to laying	0.03	0.855	0.40	0.525
Fledging success	Fed to hatching vs control	0.16	0.687	1.29	0.257

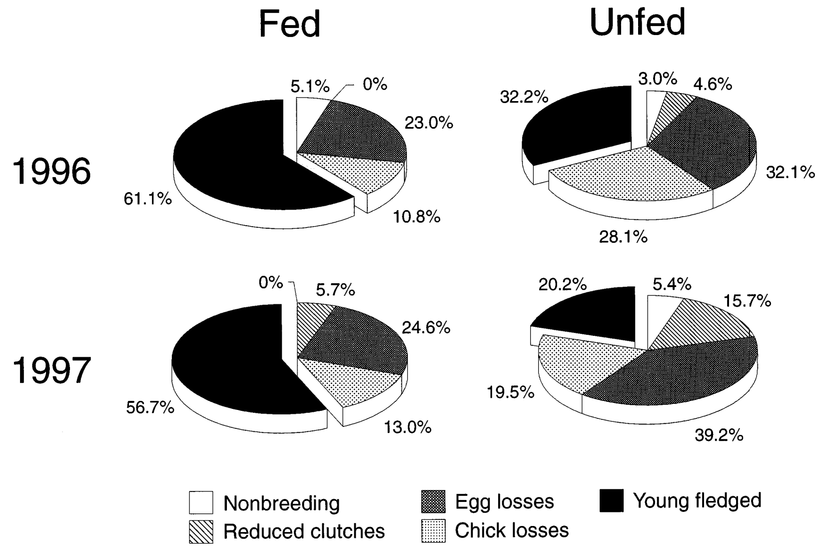
[a] 2 × 2 contingency tables comparing means or combinations of means from Table 2.

Table 5. Components of productivity in fed and unfed pairs of black-legged kittiwakes (pooled groups) on Middleton Island, 1996–1997.[a]

Component	1996			1997		
	Fed	Unfed	P[b]	Fed	Unfed	P[b]
Laying success	0.92 ± 0.03 (79)	0.94 ± 0.03 (63)	0.773	0.97 ± 0.02 (78)	0.91 ± 0.04 (65)	0.084
Clutch size	1.93 ± 0.04 (73)	1.85 ± 0.05 (59)	0.153	1.83 ± 0.04 (76)	1.63 ± 0.06 (59)	0.008
Hatching success	0.76 ± 0.04 (49)	0.65 ± 0.04 (83)	0.077	0.74 ± 0.05 (50)	0.50 ± 0.04 (85)	<0.001
Fledging success	0.85 ± 0.06 (22)	0.53 ± 0.04 (75)	<0.001	0.81 ± 0.07 (21)	0.51 ± 0.05 (66)	0.002
Breeding productivity	1.32 ± 0.15 (25)	0.66 ± 0.08 (59)	<0.001	1.04 ± 0.17 (25)	0.37 ± 0.06 (59)	<0.001
Overall productivity	1.26 ± 0.15 (27)	0.62 ± 0.08 (63)	<0.001	1.04 ± 0.17 (25)	0.34 ± 0.06 (65)	<0.001

[a] Values in table are mean ± SE (n of pairs).
[b] Within-year variation between treatment groups tested using Pearson chi-square statistic for laying, hatching, and fledging success, and Mann-Whitney U test for clutch size, breeding productivity, and overall productivity.

Fig. 4. Proportion of maximum potential young fledged (black) and components of failure in fed and unfed pairs of black-legged kittiwakes on Middleton Island, 1996–1997. Percentages calculated on a per-egg basis (n = 100 units of potential productivity), as opposed to nests built (see Methods).



tion in either year although, again following the above trend, fed pairs bred at slightly higher rates in 1997 than unfed pairs. It is possible with slightly larger sample sizes that these differences might have been both biologically and statistically significant. Fledging success and productivity were substantially augmented by feeding in both years.

In general, both fed and unfed pairs exhibited better breeding performance in 1996 than in 1997. This implies that fed kittiwakes responded to food availability in the ocean, despite having access to ample food at their nest sites. Diet composition (see below), chick survival, and chick growth parameters (Gill et al. in press) all suggested that food conditions around Middleton were relatively good in 1996. At two feedings per day (about 350 g of herring), it is unlikely that the food requirements of chick-rearing pairs were completely satisfied by supplemental feeding in 1996. Nevertheless, the fledging success of fed pairs was at least as high in 1996 as in 1997, and the fledging success of unfed pairs was also similar between years (Table 5). Thus, in the range of natural feeding conditions represented in 1996 and 1997, the difference in feeding protocols during late chick rearing had little influence on breeding performance.

Supplemental food consumption

Consumption of supplemental food per nest site was close to rates estimated for naturally foraging kittiwakes. Based on the energy density of forage fish and assimilation efficiencies measured in kittiwakes with similar weights to our study birds (see Gill et al. in press), Gabrielsen et al. (1987, 1992) calculated the food requirement during chick rearing to be 415–515 g of capelin nest^{-1} day^{-1}, depending upon brood size. The average family requirement throughout the season (assuming two-chick broods and a constant mortality rate of the second-hatched chicks) was 462 g nest^{-1} day^{-1}

Table 6. Enhancement of breeding performance achieved by supplemental feeding of black-legged kittiwakes on Middleton Island, 1996–1997.

Component of failure	1996		1997	
	Effect of feeding[a]	% of total enhancement	Effect of feeding[a]	% of total enhancement
Nonbreeding	−2.1[b]	−7.3	5.4	14.8
Reduced clutches	4.6	15.9	10.0	27.4
Egg losses	9.1	31.5	14.6	40.0
Chick losses	17.3	59.9	6.5	17.8
Total enhancement	28.9	100.0	36.5	100.0

[a] Values in column are differences between treatment groups of kittiwakes (fed – unfed) in components of failure calculated as described in Methods and illustrated in Fig. 4 (e.g. in 1996, 32.1% egg losses (fed) – 23.0% egg losses (unfed) = 9.1 percentage points improvement due to supplemental feeding).
[b] Negative value indicates unfed birds performed better than fed birds (counter to prediction).

(Gabrielsen et al. 1992). During chick rearing on Middleton in 1997, average consumption of supplemental food was 414 g nest^{-1} day^{-1}. Kittiwakes on the tower may have required a smaller quantity of food to sustain chicks than was calculated in the previous studies because the lipid content and energy density of adult Pacific herring can be higher than that of adult capelin (Anthony et al. 2000). In addition, supplemented birds probably did not need to consume as much if they were saving energy by not foraging.

The marked decrease in daily intake of supplemental food by fed birds in prelaying and early egg-laying stages was surprising because egg production is an energy-demanding period in female larids (Houston et al. 1983). We expected food consumption to increase during egg formation, which normally takes about 10 days in kittiwakes (Neuman et al. 1998). Average food consumption during incubation was lower than during any other stage of breeding in both years, consistent with the behavior of food supplemented herring gulls *Larus argentatus* (Niebuhr 1983). Supplemental food intake increased during chick rearing in 1997, as the energy demand of growing chicks was added to adult requirements.

Natural foods

The natural forage available in 1996 and 1997 may help to explain differences in breeding performance of fed and unfed kittiwake pairs. For example, reliance on sablefish during chick rearing in 1997 may have negatively affected the breeding success of unfed pairs and widened the performance gap between fed and unfed pairs. In a comparison of 12 species of forage fish consumed by seabirds (Van Pelt et al. 1997), sablefish had the lowest lipid content, and consequently was low in energy density (2.6 kJ/g wet mass). In contrast, herring had nearly the highest average lipid content (26.8% dry mass) and energy density (5.84 kJ/g wet mass) of 39 species examined in a separate study (Anthony et al. 2000). All else being equal, the energetic efficiency of foraging on sablefish would be low compared to that of foraging on high quality fish like herring. Juvenile herring were the most frequently occurring natural prey after hatching in 1996, which presumably reduced the advantage of food-supplemented pairs over unfed pairs. Nevertheless, fed pairs raised twice as many chicks as unfed pairs in 1996, indicating that food was limiting even in that relatively "good" year.

The diminished response to supplemental food in 1996 may also be attributed to differences in diet prior to hatching. Lanternfish, an exceptionally lipid-rich fish (Van Pelt et al. 1997, Anthony et al. 2000), were found in half of the early regurgitations in 1996, but were not present in 1997. Capelin, another energy-rich species (Van Pelt et al. 1997, Anthony et al. 2000), were also present in 1996 only. About half the early season diet in 1997 was composed of lower-energy prey such as copepods, amphipods, and sablefish. It seems likely that the higher-quality food supply prior to hatching in 1996 reduced the differences in clutch size and hatching success between fed and unfed pairs. Unfed pairs apparently were food stressed even before laying in 1997.

Carryover effects of food supplementation

We hypothesized that birds fed at the beginning of the season would do better in subsequent stages than they would have done had they not been fed at all. This is based on the assumption that supplemental feeding improves the body condition and/or motivation to breed among fed birds, resulting in better breeding performance even after a bird has been cut off from the additional food. That was not the case in this study. Kittiwakes responded detectably only to their immediate food supply, thus the timing of failure in kittiwake colonies probably corresponds closely to failures of the local food supply. The absence of carryover effects further suggests that winter foraging conditions may have little influence on subsequent breeding performance in kittiwakes. Similar results have been obtained in other supplemental feeding studies of larids (Niebuhr 1983, Bolton et al. 1992, Bukaciński et al. 1998, but see Wernham and Bryant 1998).

Effects of food supplementation on components of productivity

Laying success

Although laying success was not significantly improved by providing food in either year the percentage of fed pairs breeding in 1997, the poorer food year, was markedly higher (6%) than unfed pairs. The lack of a very strong food effect on laying success was surprising because female birds in general tend not to breed or lay fewer eggs when nutritionally stressed (Drent and Daan 1980, Houston et al. 1983). The effect of food supplementation on laying success in seabirds has not been examined previously because of the relative difficulty of doing so. Experimental studies on other taxa have produced results both consistent (Simmons 1993) and inconsistent (Newton and Marquiss 1981) with our results.

Kittiwake laying success in the North Pacific averages only 65% (Hatch et al. 1993a). In the most productive years the mean increases to 80%, and the highest single rate observed was 97% (Hatch et al. 1993a). In the present study, laying success exceeded 90% in all groups in both years, and fed birds in 1997 achieved a rate of 97%. It appears that laying success on Middleton was already at or near the maximum rate, with all pairs responding to adequate foraging conditions that could not be radically enhanced with extra food in 1996 or 1997. Evidently, about 3% of site-holding kittiwake pairs cannot be induced to breed no matter how good the conditions. This is consistent with breeding performance in a highly productive colony in Britain, where an average of 3.1% of mature birds failed to breed annually (Wooller and Coulson 1977).

Clutch size

Kittiwake clutches in North Pacific colonies, including Middleton, average about 1.5 eggs per nest (Hatch et al. 1993a). In relatively productive years, the average increases to about 1.6 eggs. The largest mean clutch observed in this experiment (fed pairs, 1996) was 1.94 eggs per nest, which is close to the largest single value (1.98 eggs per nest) previously observed in North Pacific colonies (Hatch et al. 1993a). Apparently, this is about the maximum level attainable by kittiwakes on Middleton and elsewhere in Alaska.

Kittiwake clutches containing three eggs are common in Britain (Coulson and White 1961, Coulson and Thomas 1985), uncommon in Alaskan colonies (Hatch et al. 1993a), and extremely rare on Middleton (S. A. Hatch and V. A. Gill unpubl. data). We expected some experimental pairs to lay three eggs given an unlimited food supply. None did so, despite being fed for up to 4 weeks prior to egg laying. Middleton kittiwakes have experienced breeding failures so persistently that they may be conditioned to lay smaller than maximum clutches, even when food is abundant during egg laying. Birds had no assurance that additional food would be available to them during the nestling period. That outcome is consistent with Lack's (1947) view that clutch size is constrained by the capability of parents to provide food for nestlings rather than by females' laying ability.

Hatching success

Hatching success was notably improved by supplemental food in both study years although only significantly so in 1997, probably because of more unfavorable natural conditions that year. In an average year, about 57% of the kittiwake eggs hatch in Alaskan colonies (Hatch et al. 1993a). Unfed pairs did slightly better than that in 1996 and slightly poorer in 1997, but fed pairs exceeded the Alaska average in both years. The highest hatching rate observed (76% among fed pairs in 1996) agrees with the 76% mean recorded in productive years in the North Pacific (Hatch et al. 1993a).

Losses during the egg stage may be attributed to inadequate care and incubation of the eggs. Egg predation was non-existent on the tower, and addled eggs accounted for only 15% of the eggs that failed to hatch in 1997. Some unfed pairs quit incubating eggs in both years, and fed pairs also experienced their greatest loss of potential productivity during incubation. It is possible that hatching rates for both fed and unfed pairs were reduced on the tower by competition for nest sites. Fighting occasionally resulted in eggs rolling out of nests.

Fledging success

In contrast to components of productivity measured prior to chick rearing, fledging success was substantially improved by supplemental feeding in both years of the study. The quality and availability of natural foods may have decreased after hatching in 1996 to levels close to those in 1997, or the chick stage may be inherently more sensitive to food limitation because of the higher energy demand during that stage. Based on collected regurgitations and the growth rates of chicks (Gill et al. in press), it appeared unlikely that food availability declined after hatching in 1996 relative to 1997. It seems more probable that the chick-rearing stage is highly food limited.

Kittiwakes in the North Pacific generally fledge about 50% of their chicks (Hatch et al. 1993a) – similar to unfed pairs in this study. Even in the most productive years, mean fledging rates are only 71%, which is lower than rates (85% and 81%) exhibited by fed pairs on Middleton in this study. However, fed pairs did not achieve the maximum fledging rate (95%) reported from other Pacific colonies (Hatch et al. 1993a), a value that is possibly inflated by sampling error. The present study indicates that kittiwakes can fledge more chicks than is normal for North Pacific colonies if adequate food is available.

Productivity

Mean kittiwake productivity in Alaska was only 0.32 chicks fledged per nest in a long-term data set accumulated prior to 1990 (Hatch et al. 1993a). This corresponds to productivity of unfed pairs on Middleton in 1997. The productivity of unfed kittiwakes in 1996 was double the productivity of unfed pairs in 1997. In both years, the productivity of fed birds surpassed the average of 0.72 chicks per nest in even the most productive years in North Pacific colonies. In 1996 it approximated the highest productivity recorded in Alaska (1.23 chicks per nest; Hatch et al. 1993a).

In contrast to cliff-nesting kittiwakes on Middleton, which were unable to fledge any young before and during the two years of this study, unfed pairs on the tower were able to fledge young (albeit at a much reduced rate relative to fed pairs). Apparently this was because of the predator-free environment provided by the vertical walls of the tower. Since 1991, productivity has been higher on the tower than on the cliffs, even without supplemental feeding (S. A. Hatch and V. A.

Gill unpubl. data). In simple terms, our experiment showed that Middleton kittiwakes protected from gull predation can rear about 0.3 young per nest built (more in an exceptionally good year like 1996), similar to the Alaska average. When abundant food is also available, their productivity increases to more than one offspring per nest.

Timing of failure and enhancement of breeding performance

Most of the unrealized potential for fledgling production on Middleton – about 60–70% of total losses in both fed and unfed kittiwakes – was attributable to failures that occurred prior to chick rearing (Fig. 4). This agrees with averages from other North Pacific colonies, where productivity is largely determined before hatching, and the ability of kittiwakes to meet the food requirements of nestlings is of secondary importance (Hatch et al. 1993a). Fed and unfed pairs lost most of their potential productivity through the inability to hatch eggs, and secondarily because of their poor success at raising chicks. Depressed egg production (including reduced clutch sizes and failure of pairs to breed) was third in importance in reducing productivity. Based on observational data from other colonies, Hatch et al. (1993a) concluded that, on average, the productivity of Alaskan kittiwakes is limited primarily by the inability of many pairs to produce eggs, secondarily by their poor success at hatching eggs, and thirdly by their incapability to rear young. Both approaches establish the lesser role of chick rearing in determining overall productivity.

In 1996, chick rearing was more responsive to supplemental food than earlier stages (60% versus 40% of total enhancement of breeding performance), whereas the reverse was true in 1997 (18% of total enhancement occurred during chick rearing versus 82% before hatching; Table 6). It is important to recognize the distinction between "enhancement" – the increase in breeding performance of fed birds at any stage over that which occurred under no treatment – and the absolute number of losses incurred per stage. Because losses are cumulative over all stages, it is possible for chick rearing to be highly responsive to supplemental food in relative terms, but less important than other stages in determining overall productivity, as occurred in 1996. The timing of food shortages apparently differed between years, such that the shortfall between what the birds had naturally available (quantity and quality of food in the ocean) and what they needed to perform optimally (supplemental food provided by us) was greatest during chick rearing in 1996 and before hatching in 1997.

Comparative breeding performance of Pacific and Atlantic kittiwakes

In contrast to the poor productivity of kittiwakes on Middleton and in the Pacific region generally, kittiwakes in Britain have high breeding success. In the late 1980s, British and Irish colonies averaged 0.77–0.83 chicks per breeding pair (Harris and Wanless 1990) – two and a half times the mean productivity of Pacific kittiwakes. At a colony in northeast England (North Shields), kittiwakes commonly reared more than one young per nest (Thomas 1983, Coulson and Porter 1985, Coulson and Thomas 1985), which represents the high end of the range in Atlantic colonies (Walsh and McGrath 1989, Harris and Wanless 1990). Kittiwakes at North Shields nested on window ledges of an abandoned warehouse, a situation similar to the tower on Middleton with respect to absence of predation and uniform quality of the nest sites (Coulson and Thomas 1985). As predicted, feeding birds on Middleton increased their productivity to values comparable to those observed at North Shields. Fed pairs had clutch sizes similar to those observed in later years of the North Shields study but slightly smaller than the mean clutch recorded there since observations began in 1949 (Coulson and Thomas 1985). Fed pairs had hatching success 7–10 percentage points higher than North Shields kittiwakes (Thomas 1983, Coulson and Thomas 1985) but achieved the same or slightly lower fledging rates (Thomas 1983, Coulson and Wooller 1984, Coulson and Porter 1985). Mean productivity per fed pair on Middleton was similar to long-term averages recorded at North Shields (Coulson and Thomas 1985). As noted, a conspicuous difference in breeding performance between the two colonies was the absence of three-egg clutches among fed pairs on Middleton. Similar to our findings, studies in Britain have also identified hatching success as a key determinant of overall productivity (Coulson and Wooller 1984).

Our study provides benchmark values of breeding performance attainable by kittiwakes in Alaska under optimal conditions. Maximum values of the main components of productivity were 97% laying success, 76% hatching success, and 85% fledging success. When food is plentiful and predators are absent, pairs should be able to lay an average of 1.9 eggs per nest and fledge 1.26 chicks per nest built, or 1.32 chicks per egg-laying pair. Those values are comparable to highly productive colonies in the eastern Atlantic and suggest that differences in life-history characteristics between Pacific and Atlantic kittiwakes (Table 1) are primarily controlled by environment, not genes.

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Appendix. Frequency of occurrence and mass of prey species in regurgitations of black-legged kittiwakes prior to, and during, chick rearing on Middleton Island, 1996–1997.

Breeding stage and prey species	1996		1997			
	Number	% frequency	Number	% frequency	Mass (g)	% mass
Prior to chick rearing[a]						
Amphipods (Gammaridae)	–	–	1	12.5	0.1	0.1
Capelin *Mallotus villosus*	4	20.0	–	–	–	–
Copepods	–	–	2	25.0	2.2	3.0
Isopods	1	5.0	–	–	–	–
Pacific herring *Clupea pallasi*[b]	1	5.0	1	12.5	15.0	20.0
Pacific sand lance *Ammodytes hexapterus*	1	5.0	3	37.5	30.0	40.0
Sablefish *Anoplopoma fimbria*	–	–	1	12.5	1.0	1.3
Squid (Gonatidae)	1	5.0	–	–	–	–
Unidentified fish	2	10.0	2	25.0	28.0	37.3
Unidentified lanternfish (Myctophidae)	10	50.0	–	–	–	–
Unidentified smelt (Osmeridae)	3	15.0	–	–	–	–
Chick rearing[c]						
Amphipods (Gammaridae)	2	3.8	6	4.0	0.5	0.02
Capelin	2	3.8	10	6.7	179.0	7.2
Euphausiids *Thysannoessa* spp.	–	–	9	6.0	225.0	9.0
Flatfishes (Pleuronectidae)	–	–	2	1.3	10.0	0.4
Fish B[d]	–	–	8	5.4	29.0	1.1
Pacific herring[b]	24	46.2	4	2.7	50.0	1.7
Pacific sandfish *Trichodon trichodon*	1	1.9	–	–	–	–
Pacific sand lance	5	9.6	77	51.7	857.0	34.4
Sablefish	10	19.2	52	34.9	1039.0	41.7
Unidentified fish	4	7.7	9	6.0	66.0	2.6
Unidentified lanternfish (Myctophidae)	5	9.6	–	–	–	–
Unidentified sculpin (Cottidae)	–	–	1	0.7	5.0	0.2
Unidentified smelt (Osmeridae)	3	5.8	3	2.0	29.0	1.2
Walleye pollock *Theragra chalcogramma*	–	–	1	0.7	15.0	0.6

[a] n = 20 regurgitations in 1996, n = 8 regurgitations (76.3 g total mass) in 1997; biomass estimates not obtained for 1996 samples.
[b] Small herring obtained naturally from the ocean distinguished from supplementally fed herring by size.
[c] n = 52 regurgitations (50 chicks, 2 adults) in 1996, n = 149 regurgitations (141 chicks, 8 adults; 2504.5 g total mass) in 1997; biomass estimates not obtained for 1996 samples.
[d] Unidentified species distinguishable from remainder of unidentified fish.