REPRODUCTIVE PERFORMANCE OF SEABIRDS: THE IMPORTANCE OF POPULATION AND COLONY SIZE

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Abstract.—We compared reproductive performance of five species of seabirds at two colonies, St. George Island (2.5 million birds) and St. Paul Island (250,000 birds), in the southeastern Bering Sea. All species had lower chick growth rates at the larger colony, and the differences were statistically significant in four species. Fledge weights of Common Murres (*Uria aalge*) on St. George Island were 84–88% of those on St. Paul. Average fledge weights of Thick-billed Murres (*Uria lomvia*) on St. George were only 74% of those for chicks from St. Paul. We found no significant differences in clutch size or breeding success between populations breeding at the two colonies. For three species, Black-legged Kittiwakes (*Rissa tridactyla*), Common Murres, and Thick-billed Murres, we extended our analysis to include published data from other colonies. We examined breeding performance as a function of colony size, population size (suggestive of intraspecific competition), and "effective colony size," the sum of the populations of species with considerable dietary overlap (suggestive of interspecific competition for food). We found consistently negative relationships between population size and several measures of breeding performance (clutch size, growth rate, fledge weight, and breeding success). In addition to the lower breeding success at colonies that support large populations, chicks from these colonies may be subject to higher postfledging mortality because of fledging at lower weights. *Received 7 January 1985, accepted 18 October 1985.*

There is now mounting evidence that reproductive performance in seabird colonies may vary with population or colony size. Coulson et al. (1982) documented changes in reproductive performance that could be related to intraspecific competition for food. They found earlier breeding and increased egg size in a Herring Gull (*Larus argentatus*) colony after it had been culled to one-quarter of its former size. Hunt et al. (1981, 1982) suggested that colony size may affect reproductive performance in relatively stable colonies such as those of the Pribilof Islands. More recently, Gaston (in press) found a negative relationship between fledge weight and population size for Thick-billed Murres (*Uria lomvia*) and for Atlantic Puffins (*Fratercula arctica*) in data from seven colonies. Gaston et al. (1983) measured fledge weights of murre chicks at three colonies within the same year and found a negative relationship between population size and fledge weight. Furness and Birkhead (1984) examined four seabird species in Great Britain and found a negative relationship between the size of the population at a colony and the size of populations of the same species at nearby colonies. They hypothesized that this relationship was due to density-dependent depletion of prey near colonies. In a review of recent work, Birkhead and Furness (1985) concluded that negative relationships between population size and several aspects of reproductive performance support the hypothesis that intraspecific competition for food near colonies may regulate seabird populations.

Seabirds commonly breed in large, multispecies colonies and may have considerable dietary overlap with other species at the colony (Belopol'skii 1957, Pearson 1968, Croxall and Prince 1980, Hunt et al. 1982). Hence, both intra- and interspecific competition are possible. Belopol'skii (1957) attributed reduced breeding success and dietary changes in Black-legged Kittiwakes (*Rissa tridactyla*) to competition with Thick-billed Murres for food in years of low fish availability. Ashmole (1963) first suggested that competition for food around breeding colonies may regulate seabird populations.

If there are negative relationships between

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population or colony size and reproductive performance, then the greatest effects should be seen in the largest populations or colonies. St. George Island supports a seabird colony of 2.5 million birds, of which 1.5 million are Thick-billed Murres (Hickey and Craighead 1977). This colony is one of the largest in the Northern Hemisphere and is the largest for which reproductive information for several species is available. For 3 yr we compared seabird reproduction at St. George Island and at a similar but smaller colony on St. Paul Island. The latter colony, consisting of 253,800 birds, is 63 km distant and supports the same suite of species as found on St. George Island. Although the proportions of species change between the colonies (Schneider and Hunt 1984), all species are more abundant on St. George Island (Table 1). We compared reproductive performance of five species of seabirds to look for evidence of density-related depression of reproduction.

In addition, we examined reports of kittiwake and murre reproductive performance in other colonies to determine whether a density-dependent relation exists generally. To partition the possible effects of intra- and interspecific competition, we also examined reproductive performance for negative relationships with population size (indicating intraspecific competition) and "effective colony size," the sum of species with considerable dietary overlap (indicating interspecific competition for food). The results of these comparisons suggest whether reproduction in Northern Hemisphere seabirds generally shows density-dependence and the relative importance of intra-and interspecific competition.

TABLE 1. Population sizes of seabirds breeding on the Pribilof Islands (from Hickey and Craighead 1977).

	St. George Island	St. Paul Island
Northern Fulmar (*Fulmarus glacialis*)	70,000	700
Red-faced Cormorant (*Phalacrocorax urile*)	5,000	2,500
Black-legged Kittiwake (*Rissa tridactyla*)	72,000	31,000
Red-legged Kittiwake (*R. brevirostris*)	220,000	2,200
Common Murre (*Uria aalge*)	190,000	39,000
Thick-billed Murre (*U. lomvia*)	1,500,000	110,000
Parakeet Auklet (*Cyclorrhynchus psittacula*)	150,000	34,000
Least Auklet (*Aethia pusilla*)	250,000	23,000
Crested Auklet (*A. cristatella*)	28,000	6,000
Horned Puffin (*Fratercula corniculata*)	28,000	4,400
Tufted Puffin (*F. cirrhata*)	6,000	1,000
Total	2,519,000	253,800

METHODS

Breeding seabirds were studied at St. Paul and St. George islands, Pribilof Islands, southeastern Bering Sea, during the summers of 1976, 1977, and 1978 (see Hunt et al. 1982 for a detailed account). We measured clutch size, growth rate, fledge weight, and breeding success in Red-faced Cormorants (*Phalacrocorax urile*), Black-legged Kittiwakes, Red-legged Kittiwakes (*Rissa brevirostris*), Common Murres (*Uria aalge*), and Thick-billed Murres at both colonies. Throughout the study, methods and frequency of site visits by study teams on the two islands were as similar as possible.

Clutch size and breeding success were estimated at three sites on St. George Island and at four sites on St. Paul Island. We visited each site at 3-4-day intervals to follow the progress of breeding from before egg-laying until chick departure or failure. Sample sizes are given in Table 2. Breeding success was computed for each study area, using the ratio of chicks fledged to the number of breeding attempts (defined as a defended territory or breeding site/nest construction). For comparison with published work on kittiwakes, we used chicks fledged per completed nest (= pair) as a measure of breeding success. Breeding success in murres was estimated as the number of chicks that departed successfully, divided by the average number of adults at each site during incubation and brooding. We assumed missing murre chicks to have departed successfully if their age or plumage on the previous visit indicated that they were at least 3 weeks old. We computed the number of murre chicks "fledged" per pair that laid egg(s) for comparison with other studies. Red-faced Cormorants and Black-legged Kittiwakes laid multiple-egg clutches at the Pribilof Islands. Clutch size was calculated using only nests containing eggs.

Growth rates and fledge weights were obtained at two sites accessible by ladder on St. George and at three sites on St. Paul. Study sites were visited at 3-4-day intervals, except when weather prevented. Growth rates were calculated as the difference between the initial weighing and the peak weight measured, divided by the number of days elapsed. Fledge weights were the last weights of chicks obtained before fledging, or departure in the case of murre chicks.

We used a one-way ANOVA (Sokal and Rohlf 1969) to determine whether sites and years could be pooled to compare islands. Years could not be pooled so we used t-tests to compare colonies within each year. If

TABLE 2. Sample sizes used in comparison of reproductive performance of seabirds at St. Paul (STP) and St. George (STG) islands.[a]

	Red-faced Cormorant		Black-legged Kittiwake		Red-legged Kittiwake		Common Murre		Thick-billed Murre	
	STP	STG	STP	STG	STP	STG	STP	STG	STP	STG
Clutch size					nv	nv	nv	nv	nv	nv
1976	13	10	70	19						
1977	49	17	102	70						
1978	84	37	110	39						
Growth rate										
1976	17	11	33	24	4	12	5	4	16	23
1977	4	14	22	20	3	42	9	3	17	34
1978	8	16	16	16	nd	13	nd	12	16	25
Fledge weight										
1976	nd	nd	14	8	4	28	5	4	16	23
1977	nd	nd	21	20	3	29	11	3	17	34
1978	nd	nd	15	16	nd	11	nd	12	16	25
Breeding success										
1976	93	7	127	34	76	88	70	11	96	40
1977	57	32	157	99	78	164	30	15	155	92
1978	87	66	208	136	112	187	76	38	177	131

[a] nd = no data, nv = no variation.

the difference between the two colony means reversed direction among years (e.g. greater at St. Paul one year and greater on St. George another year), we accepted the null hypothesis of no consistent difference between colonies. If the difference between colony means was consistent among years, we combined test results from all years using Fisher's (1954) method.

To test whether reproductive achievement showed density-dependence at other locations (see Appendix), we assembled published data on Black-legged Kittiwakes (BLK), Common Murres (CM), and Thick-billed Murres (TBM). When studies presented several years of data, we used only the maximum value, as this provides a measure of how well pairs in a colony of a particular size can do. Additionally, multiple-year studies were more likely to report a year of reproductive failure than single-year studies; these failures often were due to stochastic factors (e.g. weather). The use of maximum values reduced the bias different lengths of study (years) introduced to estimates of average breeding success. We examined clutch size (BLK), growth rates (BLK, CM, TBM), fledge weights (CM, TBM), and breeding success (BLK, CM, TBM). For each species we calculated Pearson partial correlation coefficients for each reproductive measure against colony size, population size, and effective colony size. The partial correlations represent the unique effects of colony size, population size, and effective colony size; the intercorrelation between these variables has been removed. The partial correlation coefficients were tested using t-tests, and probabilities were calculated for one-tailed tests.

Effective colony size was calculated for a colony by summing the populations of species whose diets were likely to overlap those of kittiwakes and murres. Species included in the calculation of effective colony size are listed in the Appendix. We used overlap in a very broad sense and excluded only species that fed very far offshore (Manx Shearwater, *Puffinus puffinus*), on different-size prey (cormorants), or on different prey (planktivores).

RESULTS

Comparison of reproductive performance at the Pribilof Islands.—We found no significant differences in clutch size or breeding success of seabird populations at St. Paul and St. George (Table 3). There were significant differences in chick growth rates and fledge weights that, although not affecting reproductive success directly, may affect later survivorship of chicks.

All five species had lower chick growth rates at the larger colony (Fig. 1, Table 3), although the difference was not statistically significant for Red-legged Kittiwakes. The largest difference in growth rate was in Thick-billed Murres, with growth rates at the larger colony only 59% of those at the smaller colony. Murre chicks leave the colony when they are three weeks

TABLE 3. Differences in reproductive parameters of seabirds breeding on St. Paul (P) and St. George (G) islands.[a] Probability levels based on Fisher's (1954) method to combine tests (years). RFC = Red-faced Cormorant, BLK = Black-legged Kittiwake, RLK = Red-legged Kittiwake, CM = Common Murre, TBM = Thick-billed Murre.

	RFC	BLK	RLK	CM	TBM
Clutch size	$P < G^{ns}$	$P > G^{ns}$	nv	nv	nv
Growth rate	$P > G^{**}$	$P > G^{*}$	$P > G^{ns}$	$P > G^{*}$	$P > G^{**}$
Fledge weight	nd	flips	flips	$P > G^{*}$	$P > G^{***}$
Breeding success	flips	flips	flips	flips	flips

[a] nd = no data, nv = no variation in clutch size, flips = direction not consistent from year to year; ns = not significant at $P = 0.05$, * = $P < 0.05$, ** = $P < 0.005$, *** = $P < 0.001$.

old and about 20% of adult weight. Murre chicks of both species departed St. George Island at substantially lower weights than chicks from the smaller colony; mean fledge weight of Thick-billed Murre chicks from St. George was only 74% of that of chicks from St. Paul. Lower growth rates in the two kittiwake species and Red-faced Cormorants at St. George did not result in lower fledge weights. These chicks remain in the nest until nearly adult size, and birds on St. George Island completed growth before fledging.

Density-dependence of kittiwake and murre reproduction.—When we examined the effect on reproductive performance of population size, colony size, and effective colony size, reproductive measures showed the most consistently negative relationships with population size (Fig. 2). Partial correlations for population size were negative in 9 of 9 cases (4 significant, $P < 0.05$). We combined probabilities (Fisher 1954) for the partial correlations for measures we thought were independent (BLK growth rate, breeding success; CM breeding success, fledge weight; TBM breeding success, fledge weight) and obtained a significant negative relationship between population size and reproductive performance ($P = 0.0076$, $\chi^2 = 27.0501$, 12 df). Partial correlations between colony size and reproductive performance were negative in 1 of 9 cases (none statistically significant), and those for effective colony size were negative in 4 of 9 cases (again, none statistically significant). The generally positive partial correlations for colony size (8 of 9 cases) were suggestive of a positive relationship, but a two-tailed t-test showed no statistically significant relationship between colony size and reproductive performance.

We considered the possibility that the negative correlation between population size and growth rates or fledge weights of murres might be the result of subspecies differences in adult size. We had sufficient data to examine growth rates for two subspecies of Thick-billed Murre (*U. l. lomvia* and *U. l. arra*; Fig. 3) and found negative correlations with population size in both cases. It seems unlikely that the negative correlations found in the combined analyses (Fig. 2) are the result of our inclusion of data from more than one subspecies.

DISCUSSION

Our study provides strong inferential evidence for density-related depression of reproductive achievement in seabirds. At the Pribilof Islands, we found significantly lower growth rates in four species, and, for murres, lower fledge weights at the larger colony. Using published data for other colonies, we found negative relationships between population size and clutch size, growth rates, and breeding success in Black-legged Kittiwakes, and growth rates, breeding success, and fledge weight in Common and Thick-billed murres. We used partial correlation analysis to determine that population size, rather than colony size or the size of potential competitor populations, is the most important factor. We have not eliminated the possibility that population size covaries with some undetermined causal factor, nor have we determined the mechanism by which population size effects reproductive performance, although we have suggestive evidence.

Competition for nest sites is important at seabird colonies (Squibb and Hunt 1983) and may affect the species composition of colonies (Whittam and Siegel-Causey 1981). Nest-site defense in the face of strong competitive pressure could increase the energy expenditure of pairs and might potentially influence the energy allocated to eggs. However, site competi-

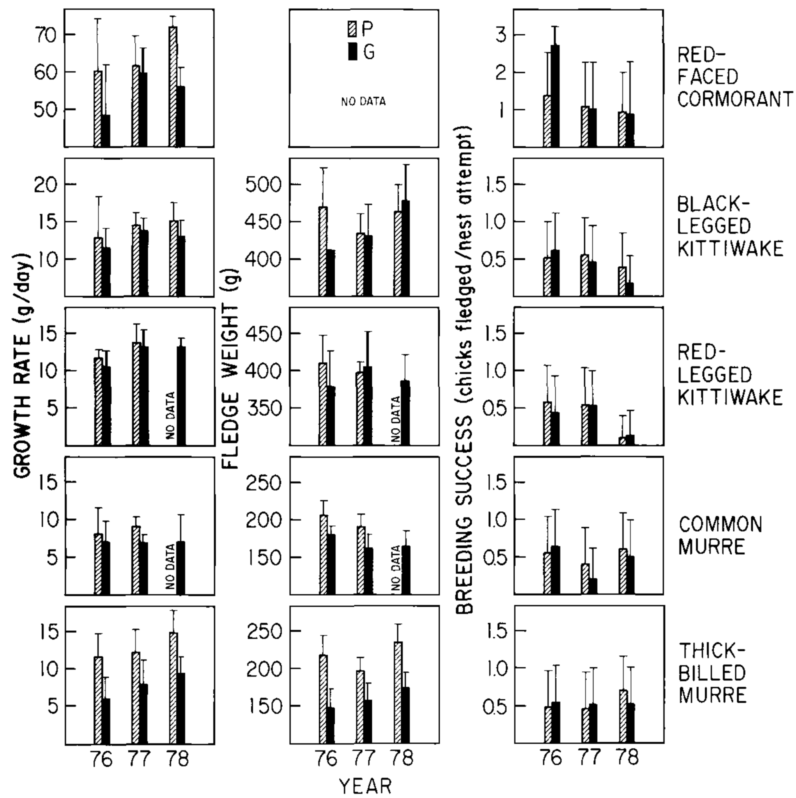

Fig. 1. Comparison of reproductive performance of seabird populations on St. Paul (hatched bars) and St. George (solid bars) islands for five species of cliff-nesting seabirds, 1976–1978. Figures show mean ± 1 SD.

tion is most intense early in the breeding season when sites are being established and declines thereafter. It is difficult to envision how nest-site competition directly could cause the differences in chick growth rates and fledge weights that we found correlated with population size.

Competition for food may affect directly chick growth rates by reducing food delivery rates, if not the total amount delivered to chicks. Competition may depress the resource base, or birds competing for prey may interfere with others during prey capture. Large numbers of birds feeding in an area might reduce the resource base, thereby decreasing prey availability. Seabirds breeding at moderate-size colonies may reduce fish standing stocks in the area (Furness 1978, Furness and Cooper 1982). There has been no direct demonstration, however, of resource depletion around seabird colonies. If resource depletion occurs, it should affect all species using the depleted prey. However, our analysis shows no effect of effective colony size on reproductive performance. In contrast, interference during foraging should affect only those species that feed together and should be greatest within a species or a foraging type. Kittiwakes feeding on ephemeral prey that school at the surface may easily interfere with each other or may cause the prey to disperse. Likewise, interference among murres during feeding seems likely where they feed in dense aggregations (e.g. >1,000 birds/km^2), as has been found at St. George Island (Ford et al. 1982, Schneider and Hunt 1984). The negative correlations between population size and reproductive performance are consistent with an interference mechanism.

Arctic colonies tend to be large, supporting large populations. If reproduction in arctic colonies tends to be less successful than reproduction in subarctic or temperate colonies due to a latitudinal effect, then our correlations may be misleading. Most of the colonies we used in this analysis are subarctic, as they occur in the area between the 5°C and 15°C August sea sur-

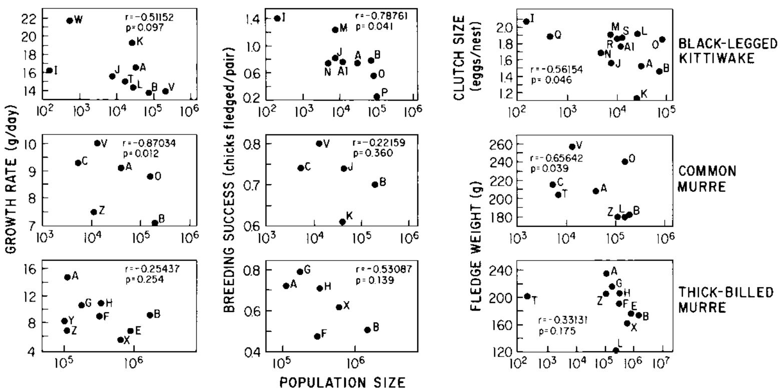

Fig. 2. Relationship between reproductive performance and population size for Black-legged Kittiwakes, Common Murres, and Thick-billed Murres. Letters designate colonies listed in the Appendix. Partial correlations and probabilities are given.

face isotherms (Tuck 1961). Four colonies (Akpatok Island; Cape Hay, Bylot Island; Prince Leopold Island; Coburg Island) are arctic colonies and have large Thick-billed Murre populations. No substantial differences were evident, however, in the reproductive performance of subarctic and arctic colonies of similar size (Fig. 2). Independently, Gaston et al. (1983) found a negative relationship between fledge weight of Thick-billed Murres and population size in these four colonies. Thus, habitat differences that potentially covary with population size are not a factor.

Mahoney and Threlfall (1981) suggested that slower chick growth rates at arctic colonies may be due simply to lower ambient temperatures, requiring chicks to allocate more energy to thermoregulation and less to growth (but see Birkhead and Nettleship 1984 for a critique of their results). Ordinarily, brooding would protect chicks from the high costs of thermoregulation. At arctic colonies with large populations, however, parents may spend more time foraging and leave chicks exposed longer or at an earlier age, exacerbating temperature effects. In our analysis, the majority of colonies with small populations of kittiwakes or murres are in warmer ocean areas or at lower latitudes than the largest colonies. Nevertheless, low temperature alone cannot account for Gaston et al.'s (1983) observation of a negative relationship between feeding rates for chicks and population size at nearby arctic colonies, nor does it explain negative correlations for clutch size or breeding success in our results.

Density-dependent depression of reproductive success (a bird's lifetime achievement) may be even more profound than our results suggest, through the production of underweight young. Low fledge weight has been associated with decreased postfledging survival rates in seabirds (Perrins et al. 1973, Jarvis 1974), although studies of Atlantic Puffins (Harris 1982), Razorbills (*Alca torda;* Lloyd 1979), and Common Murres (Hedgren 1981) failed to show an effect of fledge weight on survivorship. These three studies were done on colonies with increasing populations (D. N. Nettleship pers. comm.). In Razorbills and Common Murres, parental feeding of young at sea may compensate for low fledge weight. However, body size profoundly affects thermoregulatory costs of precocial chicks, and large body size is critical for chicks' thermal defense in water (Eppley 1984). Large chick size and relatively mild sea temperatures may be the reason Hedgren (1981) found no effect of fledge weight on survivorship in Common Murres. The smallest size class of chicks used in Hedgren's analysis was 28%

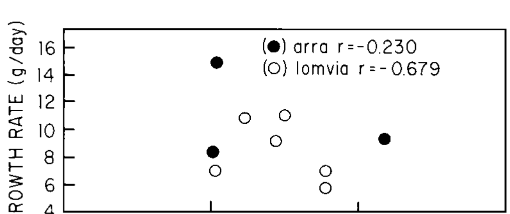

Fig. 3. Growth rates for subspecies of Thick-billed Murres as a function of population size.

heavier than the average fledge weight of the same species on St. George Island.

Previous attempts to determine limits to seabird reproductive performance have tested the abilities of pairs to raise artificially increased broods. However, the ability to raise additional young also appears to be negatively related to population size. Among Atlantic Puffins, pairs at Skomer (16,000 puffins) raised extra young (Corkhill 1973a), while pairs from Great Island (480,840 puffins) failed to raise extra young (Nettleship 1972).

We suggest that many facets of seabird reproductive performance are negatively related to population size, and that these in turn may influence postfledging survivorship. We need to use caution in modeling population dynamics of large seabird populations based on parameters obtained in small populations. If management models for large seabird populations use survivorship values obtained from small populations, and ignore density-dependent influences, then predictions concerning population recovery rates are likely to be misleading.

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APPENDIX. Colony and population sizes (no. of birds) for colonies used in analysis (Fig. 2). "+" indicates species included in calculating "effective colony size." BLK = Black-legged Kittiwake, CM = Common Murre, TBM = Thick-billed Murre. Numbers in parentheses refer to sources.

	Colony and population sizes
A. St. Paul Island, Bering Sea	253,800
+ Northern Fulmar (*Fulmarus glacialis*)	700
Red-faced Cormorant (*Phalacrocorax urile*)	2,500
+ Black-legged Kittiwake (*Rissa tridactyla*)	31,000
+ Red-legged Kittiwake (*R. brevirostris*)	2,200
+ Common Murre (*Uria aalge*)	39,000
+ Thick-billed Murre (*U. lomvia*)	110,000
Parakeet Auklet (*Cyclorrhynchus psittacula*)	34,000
Crested Auklet (*Aethia cristatella*)	6,000
Least Auklet (*A. pusilla*)	23,000
+ Horned Puffin (*Fratercula corniculata*)	4,400
+ Tufted Puffin (*F. cirrhata*)	1,000
Source: Sowls et al. 1978 (map 38, site 2); reproductive measures from Hunt et al. 1982 (BLK, CM, TBM)	
B. St. George Island, Bering Sea	2,519,000
+ Northern Fulmar	70,000
Red-faced Cormorant	5,000
+ Black-legged Kittiwake	72,000
+ Red-legged Kittiwake	220,000
+ Common Murre	190,000
+ Thick-billed Murre	1,500,000
Parakeet Auklet	150,000
Crested Auklet	28,000
Least Auklet	250,000
+ Horned Puffin	28,000
+ Tufted Puffin	6,000
Source: Sowls et al. 1978 (map 38, site 1); reproductive measures from Hunt et al. 1982 (BLK, CM, TBM)	

APPENDIX. Continued.

	Colony and population sizes
C. Skomer Island (including Skokholm and Middleholm colonies), Irish Sea	331,732
+ Manx Shearwater (*Puffinus puffinus*)	260,000 (1, 2)
+ Northern Fulmar	224 (4)
Storm-Petrels	12,920 (3)
Shags	30 (4)
Cormorants	28 (4)
+ Great Black-backed Gull (*Larus marinus*)	314 (4)
+ Lesser Black-backed Gull (*L. fuscus*)	20,000 (4)
+ Herring Gull (*L. argentatus*)	7,600 (4)
+ Black-legged Kittiwake	5,000 (4)
+ Razorbill (*Alca torda*)	4,296 (3, 4)
+ Common Murre	5,320 (3, 4)
+ Atlantic Puffin (*Fratercula arctica*)	16,000 (4)
Sources: (1) Corkhill 1973b, (2) Perrins et al. 1973, (3) Cramp et al. 1974, (4) T. R. Birkhead in litt.; reproductive measures from Birkhead 1977 (CM), Birkhead and Hudson 1977 (CM)	
D. Farne Islands, North Sea	50,000[a]
Source: Cramp et al. 1974; reproductive measures from Cullen 1957 (BLK), Pearson 1968 (BLK, CM)	
E. Akpatok Island, eastern Canadian Arctic	840,000
+ Thick-billed Murre	840,000
Source: A. J. Gaston in litt.; reproductive measures from Gaston et al. 1983 (TBM)	
F. Cape Hay, Bylot Island, eastern Canadian Arctic	320,350
+ Glaucous-winged Gull (*Larus glaucescens*)	150 (1)
+ Black-legged Kittiwake	40,000 (2)
+ Thick-billed Murre	280,000 (2)
+ Black Guillemot (*Cepphus grylle*)	200 (1)
Sources: (1) Birkhead and Nettleship 1981, (2) Gaston and Nettleship 1981; reproductive measures from Birkhead and Nettleship 1981 (TBM)	
G. Prince Leopold Island, eastern Canadian Arctic	362,400
+ Northern Fulmar	124,000
+ Glaucous-winged Gull	400
+ Black-legged Kittiwake	58,000
+ Thick-billed Murre	172,000
+ Black Guillemot	8,000
Source: Gaston and Nettleship 1981; reproductive measures from Gaston and Nettleship 1981 (TBM)	

APPENDIX. Continued.

	Colony and population sizes
H. Coburg Island, eastern Canadian Arctic	380,350
+ Glaucous-winged Gull	150 (1)
+ Black-legged Kittiwake	60,000 (2)
+ Thick-billed Murre	320,000 (2)
+ Black Guillemot	200 (1)
Sources: (1) Birkhead and Nettleship 1981, (2) Gaston and Nettleship 1981; reproductive measures from Birkhead and Nettleship 1981 (TBM)	
I. North Shields, North Sea	
+ Black-legged Kittiwake (1963)	150[b]
(1983)	200[b]
Source: Coulson and Thomas 1985; reproductive measures from Coulson and White 1958, 1961 (BLK); Coulson and Thomas 1985 (BLK)	
J. Bluff, Norton Sound, Bering Sea	53,834
Pelagic Cormorant (*Phalacrocorax pelagicus*)	518
+ Glaucous-winged Gull	274
+ Black-legged Kittiwake	7,550
+ Common Murre	41,800
+ Thick-billed Murre	400
Parakeet Auklet	65
+ Horned Puffin	3,186
+ Tufted Puffin	41
Source: Sowls et al. 1978 (map 95, sites 2–6); reproductive measures from Drury et al. 1981 (BLK, CM)	
K. Cape Lisburne, Chukchi Sea	126,768
Pelagic Cormorant	78
+ Glaucous-winged Gull	50
+ Black-legged Kittiwake	25,000
+ Common Murre	70,000
+ Thick-billed Murre	30,000
+ Black Guillemot	170
+ Horned Puffin	1,450
+ Tufted Puffin	20
Source: Sowls et al. 1978 (map 128, site 17); reproductive measures from Springer and Roseneau 1978 (BLK), Springer et al. 1979 (BLK)	
L. Cape Thompson, Chukchi Sea	417,695
Pelagic Cormorant	46
+ Glaucous-winged Gull	300
+ Black-legged Kittiwake	26,500
+ Common Murre	155,719[c]
+ Thick-billed Murre	233,578[c]
+ Black Guillemot	4
+ Pigeon Guillemot (*Cepphus columba*)	14
+ Horned Puffin	1,494

APPENDIX. Continued.

	Colony and population sizes
Source: Sowls et al. 1978 (map 129, sites 1-5); reproductive measures from Swartz 1966 (CM, TBM), Springer and Roseneau 1978 (BLK), Springer et al. 1979 (BLK)	
M. Kulichoff Island and nearby colonies in Kodiak Bay, Kodiak Island, North Pacific	25,942
Pelagic Cormorant	1,377
Red-faced Cormorant	738
+ Glaucous (*Larus hyperboreus*) and Glaucous-winged gulls	2,428
+ Mew Gull (*L. canus*)	450
+ Black-legged Kittiwake	7,477
+ Terns	881
+ Common Murre	480
+ Pigeon Guillemot	314
+ Horned Puffin	441
+ Tufted Puffin	11,386
Source: Sowls et al. 1978 (map 34, sites 15-18, 22, 47, 85-90, 99-101); reproductive measures from Nysewander and Barbour 1979 (BLK)	
N. Sitkalidak Strait, Kodiak Island, North Pacific	22,743
Pelagic Cormorant	252
Red-faced Cormorant	137
+ Glaucous-winged Gull	940
+ Mew Gull	20
+ Black-legged Kittiwake	4,766
+ Terns	2,340
+ Pigeon Guillemot	520
+ Horned Puffin	184
+ Tufted Puffin	13,584
Source: Baird and Hatch 1979; reproductive measures from Baird and Hatch 1979 (BLK)	
O. Gull Island and nearby colonies in Witless Bay (Green, Pebble, and Great islands), North Atlantic	2,691,210
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	2,000,000 (2)
+ Northern Fulmar	12 (1)
Double-crested Cormorant (*Phalacrocorax auritus*)	500 (1)
+ Black-legged Kittiwake	83,070 (1)
+ Razorbill	640 (1)
+ Common Murre	154,960 (1)
+ Thick-billed Murre	1,200 (1)
+ Atlantic Puffin	480,840 (1)
Sources: (1) Brown et al. 1975, (2) A. J. Gaston in litt.; reproductive measures from Maunder and Threlfall 1972 (BLK), Mahoney and Threlfall 1981 (CM)	
P. Cape Peirce and nearby colonies, Bristol Bay, Bering Sea	576,809
Cormorants	2,315 (1, 2)
+ Glaucous-winged Gull	5,715 (1, 2)
+ Black-legged Kittiwake	100,460 (1, 2)
+ Common Murre	381,590 (1, 2)
+ Pigeon Guillemot	300 (1, 2)
Parakeet Auklet	100 (1, 2)
+ Horned Puffin	1,184 (1, 2)
+ Tufted Puffin	85,145 (1, 2)
Sources: (1) Sowls et al. 1978 (map 39, sites 3-11), (2) S. R. Johnson pers. comm. (revised estimate for Cape Peirce); reproductive measures from Petersen and Sigman 1977 (BLK)	
Q. Dunbar, North Sea	450
+ Black-legged Kittiwake	450[b]
Source: Coulson 1963; reproductive measures from Coulson and White 1961 (BLK)	
R. Brownsman, North Sea	50,000 (2)
+ Black-legged Kittiwake	10,000 (1)
Sources: (1) Coulson 1963, (2) Cramp et al. 1974; reproductive measures from Coulson and White 1961 (BLK)	
S. St. Abbs, North Sea	50,000 (2)
+ Black-legged Kittiwake	13,000 (1)
Sources: (1) Coulson 1963, (2) Cramp et al. 1974; reproductive measures from Coulson and White 1961 (BLK)	
T. Middleton Island, North Pacific	167,935
Pelagic Cormorant	4,682
+ Glaucous-winged Gull	1,140
+ Black-legged Kittiwake	150,494
+ Common Murre	6,596
+ Thick-billed Murre	207
+ Rhinoceros Auklet (*Cerorhinca monocerata*)	1,316
+ Tufted Puffin	3,500
Source: Sowls et al. 1978 (map 48, site 1); reproductive measures from Hatch et al. 1979 (BLK, CM, TBM)	
U. Runde, North Sea	278,588
+ Northern Gannet (*Sula bassanus*)	988 (1)
+ Black-legged Kittiwake	200,000 (2)
+ Razorbill	5,600 (1)
+ Common Murre	12,000 (1)
+ Atlantic Puffin	60,000 (1)
Sources: (1) Brun 1979, (2) Barrett and Runde 1980; reproductive measures from Barrett and Runde 1980 (BLK)	

APPENDIX. Continued.

	Colony and population sizes
V. Stora Karlso, Baltic Sea	17,100
+ Lesser Black-backed Gull	1,300
+ Herring Gull	600
+ Razorbill	2,400
+ Common Murre	12,800
Source: Hedgren and Linnman 1979; reproductive measures from Hedgren and Linnman 1979 (CM); Hedgren 1980, 1981 (CM)	
W. Hekkingen, North Sea	?
+ Black-legged Kittiwake	520
Source: Barrett and Runde 1980; reproductive measures from Barrett and Runde 1980 (BLK)	
X. Digges Sound (including Cape Wolstenholme), eastern Canadian Arctic	607,000
+ Thick-billed Murre	600,000
+ Black Guillemot	5,000
+ Arctic Tern (*Sterna paradisaea*)	1,000[d]
Source: A. J. Gaston in litt.; reproductive measures from Gaston et al. 1983 (TBM)	
Y. Hantzsch Island, eastern Canadian Arctic	110,000
+ Black-legged Kittiwake	10,000
+ Thick-billed Murre	100,000
Source: A. J. Gaston in litt.; reproductive measures from Gaston et al. 1983 (TBM)	

APPENDIX. Continued.

	Colony and population sizes
Z. Kongkok Bay and nearby colonies, St. Lawrence Island, Bering Sea	763,050
Pelagic Cormorant	300
+ Black-legged Kittiwake	1,800
+ Murres	216,000[e]
Parakeet Auklet	1,600
Crested Auklet	181,000
Least Auklet	361,000
+ Horned Puffin	600
+ Tufted Puffin	750
Source: Sowls et al. 1978 (map 93, sites 1, 12); reproductive measures from Johnson and West 1975 (CM, TBM)	
A1. Commander Islands, Bering Sea	?
+ Black-legged Kittiwake	12,000
Source: Firsova 1978; reproductive measures from Firsova 1978 (BLK)	

[a] Colony size 10,000–100,000; no population estimates.

[b] Population estimates based on the number of active nests, rather than the number of birds on the colony.

[c] Obtained using Sowls et al.'s (1978) figure for murres and Swartz's (1966) estimate of 60% Thick-billed Murres.

[d] Gaston reports "several hundred pair"; assume 500 pairs here.

[e] Assume 50% Thick-billed Murres.