

Non-OCS&AP. Based on RU 83 work done in  
1975-77, submitted to Ecology.

RU-083

FILE COPY

4158

Reproductive Success of Seabirds:

The importance of colony size

George L. Hunt, Jr.

Zoe Eppley

David Schneider

Department of Ecology and Evolutionary Biology

University of California, Irvine, CA 92717

Running head - Reproductive Success of Seabirds

## ABSTRACT

A negative relation between population size and average reproductive contribution is a potentially important mechanism for regulation the population size of mobile organism, such as seabirds. Relatively few studies of nesting success have been carried out at large seabird colonies at high latitudes and there have been no systematic investigations of reproductive contribution of seabirds as a function of colony size. We compared the reproductive success of seabirds in two colonies that differed in population size by a factor of 10: St. Paul Island and St. George Island in the southeastern Bering Sea. The density and degree of aggregation of birds foraging around the more populous colony (St. George) was consistently greater than the density and aggregation of birds around the less populous colony (St. Paul). Of the five species investigated, four (Black-legged Kittiwake, Common Murre, Thick-billed Murre, and Red-faced Cormorant) had significantly lower growth rates of chicks at the larger colony. This resulted in a significant reduction in fledging weight for the two murre species at that larger colony, and a significant delay in the fledging date of Red-faced Cormorant and Red-legged Kittiwake chicks from the larger colony. There were no significant differences in clutch size or reproductive success. In an analysis of reproductive data from 22 colonies (including St. Paul and St. George) there was a consistently negative relation between colony size and several components of reproductive contribution, including clutch size, growth rate, fledging weight and chicks fledged. These results suggest that colony size may affect not only the number of chicks fledged, but also the subsequent survivorship of chicks through delayed fledging or reduced fledging weight. It is likely that large colonies will be more sensitive than small colonies to the impact of humans on fish stocks.

Key words : Density dependence; **Seabirds**; colonial nesting; Pribilof Islands;  
Bering Sea; Growth rates; **Phenology**; **Fledging weight**

Ten year index entries: Birds, colonial, density dependence of reproduction;  
Density dependence, colonial **seabird** reproduction;  
Growth rates of colonial **seabirds**, density dependence;  
Reproductive success of **colonial seabirds**, density  
dependence; **Phenology of colonial seabird** reproduction,  
density dependence; Fledging weights of colonial  
**seabirds**, density dependence.

## INTRODUCTION

The single-egg clutch and delayed maturation of many **seabirds** have been interpreted as adaptations to minimize demands on a potentially limited and irregular food supply (Wynne-Edwards 1962) and have been **cited** as evidence for the historical importance of competition among **seabird** populations (Ashmole 1963, Nelson 1966). Ashmole (1963) hypothesized that tropical populations are limited by density related pressures on food supplies **near** breeding colonies that **result** in reduced production and survivorship **of chicks**. However, Ashmole did not extend this hypothesis to colonies at **high** latitudes where food resources were thought to be **large** compared to the energetic demand **of** the seabird populations (Salomonsen 1955, Beck 1970).

If food limits seabird reproduction, then brood **size should be limited** by the ability of parents to provision their young. Students of **seabird** reproductive ecology have described reduced reproduction **due** to periodically reduced food supplies (Belopol'skii 1957, Ashmole 1963, 1971; Croxall and Prince 1979). Experimental tests have focused on the **ability of** parents to raise artificially augmented broods. Parents were **able to** raise augmented broods in some cases (Vermeer 1963, Nelson 1964, Coulson in Lack 1968, Harris 1970, Corkhill 1973, Lloyd 1977, Ward 1973) but not in **others** (Rice and Kenyon 1962, Harris 1966, Nettleship 1972). Supplemental feeding experiments (Harris 1978) and observations of broods with only one parent (Nettleship 1972) suggest limited food availability near colonies. Likewise, the existence of mechanisms facilitating brood reduction among seabirds that lay **multiple-egg clutches** suggest that frequently parents are unable to deliver **enough** food to **raise** complete broods (Nisbet and Cohen 1975, Parsons 1975, Ricklefs et al. 1978, Lundberg and Vaisanen 1979, Hahn 1981, Braun 1981, Braun and Hunt, **in press**). These experiments have not shown whether food delivery rates in the majority

of cases are limited by behavioral and physiological constraints (leading to hard selection *sensu* Wallace 1968) or by density related pressures (soft selection) as hypothesized by Ashmole (1963).

Recent estimates of the energy requirements of seabirds in the vicinity of northern colonies have shown that seabirds may take 20-30% of the annual production of forage fish (Wiens and Scott 1975, Furness 1978). Wiens et al. (1979) estimate that in the vicinity of the Pribilof Islands seabirds take 53,600 metric tons of food during the breeding season. These estimates are in marked contrast to those of modelers of marine ecosystems (Andersen and Ursin 1977, Laevastu and Favorite 1981, Walsh et al. 1981) who minimize the large-scale impact of seabird foraging. Estimates of consumption by birds in pelagic waters are generally lower than estimates from near colonies (Schneider et al. in prep. ) and suggest the local impact of seabirds on food supplies around northern colonies may be important.

At present it is difficult to demonstrate prey depletion in the vicinity of colonies because sampling methods for the fast-swimming prey of seabirds are only qualitative and because there are many other consumers using the same prey. An alternate approach is to examine reproductive achievement as a function of colony size at colonies in similar marine habitats. If density related factors do depress reproductive success, then the effects should be most pronounced at the largest colonies.

In this study, we compare reproductive achievement of seabirds in two colonies of different size. The seabird colony on St. George Island, Alaska has a population of  $2.5 \times 10^6$  birds during the breeding season, while neighboring St. Paul Island, 63 km distant, supports only one tenth as many (Hickey and Craighhead 1977). Although we have no data on food availability near the islands, we were able to obtain an index of demand for food near each colony based

on the biomass of foraging birds. We additionally compiled information on reproductive achievement and colony size for three holarctic seabirds, the Black-legged Kittiwake (Rissa tridactyla), Common Murre (Uria aalge), and Thick-billed Murre (U. lomvia) at other colonies.

## STUDY AREA AND METHODS

### The colonies

Eleven species of seabirds nest on the Pribilof Islands. These are: Thick-billed Murre  $1.6 \times 10^6$  birds, Least Auklet (Aethia pusilla)  $2.7 \times 10^5$  birds, Common Murre  $2.3 \times 10^5$  birds, Red-legged Kittiwake (Rissa brevirostris)  $2.2 \times 10^5$  birds, Parakeet Auklet (Cyclorhynchus psittacula)  $1.8 \times 10^5$  birds, Black-legged Kittiwake  $1.1 \times 10^5$  birds, Northern Fulmar (Fulmarus glacialis)  $7.1 \times 10^4$  birds, Crested Auklet (Aethia cristatella)  $3.4 \times 10^4$  birds, Horned Puffin (Fratercula corniculata)  $3.2 \times 10^4$  birds, Red-faced Cormorant (Phalacrocorax urile)  $7.7 \times 10^3$  birds, Tufted Puffin (Lunda cirrhata)  $7.0 \times 10^4$  birds (Sowls et al. 1978). Although the proportions of species change between islands (Schneider and Hunt, in press), all species are more abundant on St. George Island, where there is seven times more cliff area available for nesting (Hickey and Craighead 1977).

The Pribilof Islands are located in the Mid Shelf domain of the Bering Sea shelf (Fig. 1) (Iverson et al. 1979). Each island is surrounded by a water mass boundary (front) near the 50 m isobath, which appears to be a region of enhanced foraging activity for birds, particularly for murre {Kinder et al. 1983}. There is more shallow water habitat between the front and St. Paul Island than around St. George Island and bird foraging appears concentrated between each island and its surrounding front (Kinder et al. 1983). One could therefore argue that while there is a greater area of

generally good foraging available to birds at St. Paul, birds on St. George are closer to the front where foraging appears best. St. George Island is also closer to the Outer Shelf Domain and shelf-edge front, both apparently richer foraging areas for birds than the shallower waters of the Mid Shelf Domain (Iverson et al. 1979, Schneider and Hunt 1982). Since we could not measure the relative availability of prey to birds on the two islands, we compared bird abundance near one island to bird abundance near the other. We then compared the energy demand of one colony to the other.

#### Comparison of Bird Distribution in the Foraging Areas

Birds were counted at sea around both islands during the breeding seasons of 1976, 1977 and 1978. Counts were made during daylight hours from hips steaming at a minimum speed of 10 km/hr. Birds were counted in a 90° sector extending 300 m outwards from the bow and beam of the ship, on the side with the best visibility. The behavior of birds was noted and ship-following birds were excluded from the analysis. Each ten minute count was standardized by dividing it by the area surveyed during the count. Five cruises were made, yielding 309 transects within 30 km of St. Paul Island and 195 transects within 30 km of St. George Island. Standardized counts were not normally distributed so we compared mean bird density within 30 km of each of the islands using a Wilcoxon two-sample test (Sokal and Rohlf 1969). We also made an estimate of the relative energy demand of birds at the two colonies based on colony size. Miens et al. (1978, 1979) estimated the energy demand of seabirds at the Pribilof Islands, and partitioned the total demand among species groups. We further partitioned energy demand between the colonies using Hickey and Craighead's (1977) estimates of the relative population sizes of species at the two colonies.

## Comparison of Reproductive Achievement at the Two Colonies

We measured the reproductive achievement of five cliff-nesting species (Red-faced Cormorants, Black-legged Kittiwakes, Red-legged Kittiwakes, Common Murres and Thick-billed Murres) at both islands during the summers of 1976, 1977 and 1978. Species that nested in talus or crevices were not feasible to study. Phenology, clutch size and reproductive success were measured at three sites on St. George Island and four sites on St. Paul Island. At each nest, we followed the progress of nesting from before egg-laying until fledging or nesting failure; sample size was approximately 100 nesting attempts for each species in each year (see Hunt et al. 1982 for details of sampling).

Calculations of clutch size included only nests containing eggs. In species that lay multiple egg clutches, we report only the timing of first events in each nest. Reproductive success was computed for each study area, using the ratio of chicks fledged to the number of nesting attempts (a nesting attempt was defined as a defended territory or nest construction). Murres do not build nests so we estimated reproductive success as the number of chicks fledged divided by the average number of adults at each site. We assumed missing murre chicks to have fledged if their age or plumage on the previous visit indicated that they were sufficiently mature. Recomputed the number of murre chicks fledged per egg for comparison with other studies.

Growth rates and fledging weights were obtained at two sites accessible by ladder on St. George and three sites on St. Paul. Study sites were visited at two- to seven-day intervals with most sites visited every three to four days. Growth rates were calculated as the difference between initial and peak weights, divided by the number of days elapsed. Fledging weights were the last weights of chicks obtained before fledging.

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 the two islands within each year. If the difference between the two 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 islands. If the difference between means was consistent among years, we combined test results from all years using Fisher's (1954) method.

#### Comparison of Reproduction as a Function of Colony Size

To see whether reproductive achievement was related to colony size at other locations we assembled published data on Black-legged Kittiwakes (BLK), Common Murres (CM) and Thick-billed Murres (TBM) (Appendix 1). When studies presented several years of data, we used only the maximum value. Multi-year studies were more likely to report a year of poor reproduction than single year studies; the use of maximum values avoided this problem. We examined clutch size (BLK), growth rates (BLK, CM, TBM), fledging weights (CM, TBM) and reproductive success (BLK, CM, TBM). For each species we regressed each reproductive measure against the logarithm of colony size to test for a negative relation between reproductive achievement and colony size. We combined the results of the individual regressions using Fisher's (1954) method.

## RESULTS

#### Comparison of Bird Distribution in Foraging Areas

The density of all birds on the water was consistently higher around St. George than around St. Paul 1s1 and on all 15 cruises (Table 1). The weighted mean value (derived from Table 1) around St. George, 253.2 birds/km<sup>2</sup>, was

11.1 times greater than around St. Paul ( $22.9 \text{ birds/km}^2$ ) ( $p = 0.03$ , Wilcoxon two sample test based on 5 cruises). The density of murre on the water was 15.1 times greater around St. George Island ( $x = 230.5$  vs.  $15.3$ ,  $p = 0.02$  Wilcoxon test based on 5 cruises). If we compare densities for the combination of birds on the water and flying birds, we find the weighted 'mean density (derived from Table 1) to be 6.7 times greater around St. George for all species combined and 9.8 times greater for murre. Thus, around St. George there were higher densities of birds foraging close to the island and there were more birds flying further off shore to forage than around St. Paul Island.

A second measure of the differences in the densities of birds around the two islands is the pooled variance, which provides an index of crowding or aggregation. The pooled variance for murre on the water at St. George ( $2473.5$ ) was 76.3 times greater than that at St. Paul Island ( $32.4$ ) while for all birds combined, the variance differed by a factor of 14.7 ( $2478.0$  vs.  $168.6$ ). The higher densities as well as the higher degree of clumping of foraging birds near St. George Island increases the probability of interference between foraging individuals.

Energy demand, based on estimates by Wiens et al. (1978, 1979) and partitioned between colonies on the basis of population size, was 12 times greater at St. George than at St. Paul Island. The St. George Island colony accounted for 86% of the total demand; the St. Paul Island colony accounted for 7% of the total demand (Table 2). The remaining 7% was due to non-breeding procellariids (Wiens et al. 1978).

#### Comparison of Reproductive Achievement at the Two Colonies

When we compare the reproductive achievement of birds at the two colonies, we found either no significant difference or better achievement at the smaller

of the two colonies, St. Paul Island (Figs. 2, 3, Table 3). Three of the five species (Red-faced Cormorant, Red-legged Kittiwake, and Thick-billed Murre) fledged young earlier on St. Paul (Fig. 2, Table 3), while the other two species (Black-legged Kittiwake and Common Murre) were earlier on St. Paul in only two of three years. Neither Red-faced Cormorants nor Black-legged Kittiwakes showed significant differences in clutch size between the islands. This result is not unexpected in the case of the Red-faced Cormorant, as the clutch weight is a very small proportion of adult weight and may not be a sensitive indicator of food availability to the female (Hunt 1980).

Growth rates of young should be sensitive to the availability of food to the parents. All five species had lower chick growth rates on St. George Island (Fig. 3, Table 3), although the differences were not statistically significant for the Red-legged Kittiwake. The greatest difference was found in Thick-billed Murres; growth rates on St. George were only 59% of those on St. Paul. For the two kittiwake species, differences in growth rates did not translate into differences in fledging weight; kittiwake chicks remained in the nest until they were about 90% of adult weight. However, fledging was delayed for Red-legged Kittiwakes on St. George (Table 3).

Three week old young of both species of murres go to sea at about 20% of adult weight. In both Common Murres and Thick-billed Murres, chicks from St. George departed at lower weights than on St. Paul (Fig. 3, Table 3). Thick-billed Murre chicks from St. George fledged at only 74% of the weight of chicks from St. Paul Island.

While we found no difference in reproductive success between seabird populations on the two islands, we did find significantly lower growth rates, fledging weights and delayed fledging for some species at the larger colony. The magnitude of the difference in reproductive achievement between seabird

populations at the two colonies was greatest for the most abundant species, the Thick-billed Murre (Fig. 3, Table 3). These findings suggest that seabird reproduction is affected by density related factors and that chicks fledged from the larger colony may suffer higher mortality rates than chicks produced at the smaller colony.

#### Reproduction as a Function of Colony Size

Clutch size (BLK), growth rates (BLK, TBM, CM), fledging weights (TBM, CM) and reproductive success (BLK, TBM, CM) varied inversely with colony size for (Fig. 4) in colonies for which there were reports of colony size and reproductive measures (Appendix 1). The correlations were significant in four of the nine regressions (Fig. 4). The combined probability (Fisher 1954) for the entire analysis was  $<0.005$  ( $\chi^2=64.405$ , 18 df). It is noteworthy that the growth rates for all three species (BLK, CM, TBM) on St. George Island (b in Fig. 4) were among the lowest reported in any study, as were the weights of murre chicks when they left the colonies.

There also appears to be a negative relation between colony size and the ability of pairs to raise extra chicks (Table 4). This comparison involves many different species with different foraging patterns and methods of provisioning chicks, and conclusions must be drawn with extreme caution. However, there is one species, the Common Puffin (*Fratercula arctica*) which was examined at two colonies of different size (Table 4). The results of this comparison are consistent with our hypothesis of a negative relationship between colony size and reproductive achievement.

## DISCUSSION

At the Pribilof Islands, we found reduced growth rates, delayed fledging, and reduced fledging weights for young of several seabirds at the larger of two colonies, but we found no direct effects on the numbers of chicks produced (clutch size or net reproductive success). In comparing reproduction among several northern hemisphere colonies we found that clutch size and reproductive success, as well as growth rates and fledging weights were all reduced in larger colonies. These results are consistent with the conclusions of Coulson et al. (1982) who attributed increased size of individuals and increased egg size in a Herring Gull (Larus argentatus) colony to reduced competition after the population was culled to 1/4 its former size.

Other studies have demonstrated a close correlation between the growth rates of young and food supplies [Bryant 1975, 1979 House Martins (Delichon urbica); van Balen 1973 Great Tits (Parus major)]. In Common Terns, the quality and quantity of food available to the females was found to affect both the number of young produced (clutch size and reproductive success) and potentially reduce post-fledging survival (due to delayed phenology) (Nisbet 1978).

Reduced post-fledging survivorship in seabirds has been associated with low fledging weights (Perrins et al. 1973, Jarvis 1974) and with late fledging (Harris 1966, Perrins 1966, Nisbet and Drury 1972). However, two studies of alcids failed to show lower survivorship in late fledging or low fledging weight birds. Lloyd (1979) found no significant difference in survivorship of early (heavy) and late (light) fledging razorbills. However, he worked at a colony with only 1000 Razorbills. In a study of post-fledging survivorship of Common Murres at Stora Karlsö [population size about 13,000 birds (Hedgren 1979)] Hedgren (1981) also found no relation between survivorship and the timing of fledging or fledging weight. However, the mean weight of Stora Karlsö

murres was  $253.9 \pm 35.3$  g and the upper limit for smallest size class Hedgren used in his analysis ( $<215$  g) was 47 g heavier than the mean fledging weight of Common Murres on St. George Island ( $\bar{x} = 168 + 20.2$  g, Hunt et al. 1982). Hedgren did find a 19% lower return rate (survival) of low fledging weight birds, but this was not statistically significant. A 31% lower return rate would have failed significance because of his small sample size. Because St. George birds are almost all at or below the upper bound of Hedgren's lowest weight category, we believe that the considerably reduced fledging weights of murres on St. George Is1 and may result in decreased post-fledging survival.

Thus far most studies of post-fledging mortality and experimental manipulations of brood size have been done at relatively small colonies. If chicks at large colonies depart underweight as our data suggest, many estimates of post-fledging survival may be too high. The possibility that results from experimental manipulations of brood size are sensitive to colony size raises doubts about the interpretation of past tests of Lack's (1954) hypothesis concerning the evolution of clutch size. We now need a series of brood size supplements across a wide range of colony sizes within a single species. Additionally, if birds at large colonies are incapable of raising extra chicks, then a species requiring large colony size (for lack of alternate sites, avoidance of predators or information sharing, see Wittenberger and Hunt, in press) may lose the option of having larger broods.

Competition implies resource depletion. At large seabird colonies the potentially limited resources are nest sites, food, or access to food without interference. Competition for nest sites is important at the Pribilof Islands (Squibb and Hunt, in press) but occurs primarily early in the season when nests are being established. Competition for nest sites does not explain the depression of growth rates, fledging weights or the delay in fledging found at St. George

1s1 and. Although we have no measures by which to compare nesting interference at the two colonies, there are neither indications of differences in nesting density (Hickey and Craighead 1977), nor did we see obvious differences in the amount of interference at the nest sites.

It is likely that reduced food delivery rates were responsible for reduced growth rates on St. George. Reduction in food delivery may result either from interference among foraging birds or from prey depletion. Interference during feeding may be important because birds feed in large aggregations, especially around St. George Island. The energetic demand of birds at the St. George colony is 12 times greater than the demand at the St. Paul colony. Walleye Pollock (Theragra chalcogramma) is the most important prey of four of the five seabirds (BLK, RLK, CM, TBM) we studied (Hunt et al. 1981, Schneider and Hunt, in press). Pollock are also the principal food of Northern Fur Seals (Callorhinus ursinus) which have large colonies on the Pribilof Islands. Prey consumption of seabirds at moderate sized colonies appears to be a substantial portion of the fish production (Furness 1978), and resource depression at St. George Isl and is a possibility.

We have demonstrated density dependence of reproduction for three dominant species in northern hemisphere seabird colonies. Our results from the Pribilof Islands suggest that competition for food reduces food delivery rates to chicks. We attribute the consistently lower growth rates, fledging weights and delayed fledging on St. George Island to the demonstrably greater demands placed on the food supplies around this colony. While we have not determined whether increased interference in feeding or prey depletion exist, both types of competition are likely and may be important. An important implication of our results is that large seabird colonies will be particularly sensitive to reduction in their food resources by man.

## ACKNOWLEDGMENTS

We thank the Aleut communities of St. Paul and St. George for their permission to work on their lands, the Pribilof Island Program of the National Marine Fisheries Service (in particular, J. Adams, K. Dzimbel, A. Groves, R. Hajny, J. R. Mercurief, J. Scordino and 1-1. Thayer), and the captains and crews of the Discover, Moana Wave, Surveyor and T. G. Thompson. The following people helped with fieldwork: B. Braun, O. Forsell, J. Francis, J. Johnson, J. Koelling, B. Mayer, D. Mercurief, G. McGlashon, P. Mercurief, M. Naughton, L. Philemonoff, M. Pitts, A. Prokopiou, W. Rodstrom, M. Roelke, D. Schwartz, S. Sharr, D. Siegal-Causey, R. Squibb, and M. Warner. Data management was aided by G. Bush, M. Crane, J. Kaiwi, J. Mershman and H. Petersen. This work was supported in part by the National Oceanic and Atmospheric Administration (NOAA), [through interagency agreement with the Bureau of Land Management under which a multi-year program responding to the needs of petroleum development of the Alaskan continental shelf is managed by the Outer Continental Shelf Environmental Assessment Program (OCSEAP)] and by NSF grants DPP 79-10386 and DPP 82-06036 to G. L. Hunt, Jr.

## Literature Cited

- Andersen, K. P. and E. Ursin. 1977. A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddelelser Danmarks fra Fiskeri-og Havundersøgelser* N. S. 7: 319-435.
- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103b: 458-473.
- \_\_\_\_\_. 1971. Seabird ecology and the marine environment. Pages 112-286 in D. S. Farner and J. R. King, editors. *Avian biology*. Volume 1. Academic Press, New York, New York, USA.
- Baird, P. A. and M. A. Hatch. 1979. Breeding biology and feeding habits of seabirds of Sitkalidak Strait, 1977-1978. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2: 107-186.
- Barrett, R. T. and O. J. Runde. 1980. Growth and survival of nestling Kittiwakes Rissa tridactyla in Norway. *Ornis Scandinavica* 11: 228-235.
- Beck, J. R. 1970. Breeding seasons and moult in some smaller Antarctic petrels. Pages 542-550 in M. W. Holgate, editor. *Antarctic Ecology*. Academic Press, London, England.
- Belopol'skii, L. O. 1957. Ecology of sea colony birds of the Barents Sea. Israel Program for Scientific Translations 1961.
- Birkhead, T. R. 1977. Adaptive significance of the nestling period of Guillemots (Uria aalge). *Ibis* 199: 544-549.
- Birkhead, T. R. and D. N. Nettleship. 1981. Reproductive biology of Thick-billed Murres (Uria lomvia): an inter-colony comparison. *Auk* 98: 258-269.
- Braun, B. M. 1981. Siblicide, the mechanism of brood reduction in the Black-leg Kittiwake, Rissa tridactyla. Thesis, University of California, Irvine,

California, USA.

- Braun, B. M. and G. L. Hunt, Jr. In press. Brood reduction in Black-legged Kittiwakes. *Auk* 100:
- Brown, R. G. B., Nettleship, D. N., Germain, P., Tull, C. E. and T. Davis. 1975. Atlas of eastern Canadian seabirds. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Brun, E. 1979. Present status and trends in populations of seabirds of Norway. Pages 289-302 in J. C. Bartonek and D. N. Nettleship, editors. Conservation of marine birds of northern North America. Wildlife Research Report 11. United States Fish and Wildlife Service, Washington, District of Columbia, USA.
- Bryant, D. M. 1975. Breeding biology of the House Martin (Delichon urbica) in relation to aerial insect abundance. *Ibis* 117:180-216.
- \_\_\_\_\_. 1979. Reproductive costs in the House Martin (Delichon urbica). *Journal of Animal Ecology* 48:655-675.
- Corkhill, P. 1973. Food and feeding ecology of Puffins. *Bird Study* 20:207-220.
- Coulson, J. C. 1963. The status of the Kittiwake in the British Isles. *Bird Study* 10:147-179.
- Coulson, J. C. and E. White. 1961. An analysis of factors influencing the clutch size of the Kittiwake. *Proceedings of the Zoological Society of London* 136:207-217.
- Coulson, J. C., Duncan, N. and C. Thomas. 1982. Changes in the breeding biology of the Herring Gull (Larus argentatus) induced by reduction in the size and density of the colony. *Journal of Animal Ecology* 51:739-756.
- Cramp, S., Bourne, W. R. P. and P. Saunders. 1974. The seabirds of Britain and Ireland. Collins, London, England.
- Croxall, J. P. and P. A. Prince. 1979. Antarctic seabird and seal monitoring

- studies. *Polar Record* 19:573-595.
- Drury, W. H., Ramsdell, C. and J. B. French, Jr. 1981. Ecological studies in the Bering Strait region. *Environmental Assessment of the Alaskan Continental Shelf. Biological Studies* 11:175-488.
- Fisher, R. A. 1954. *Statistical methods for research workers*. Twelfth edition. Oliver and Boyd, Edinburgh, Scotland.
- Furness, R. W. 1978. Energy requirements of seabird communities: a bioenergetics model. *Journal of Animal Ecology* 47:39-53.
- Gaston, A. J. and D. N. Nettleship. 1981. The Thick-billed Murres on Prince Leopold Island - a study of the breeding biology of a colonial, high arctic seabird. Monograph Number 6. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Hahn, D. C. 1981. Asynchronous hatching in the Laughing Gull: cutting losses and reducing rivalry. *Animal Behaviour* 29:421-427.
- Harris, M. P. 1966. Breeding biology of the Manx Shearwater Puffinus puffinus. *Ibis* 108:17-33.
- \_\_\_\_\_. 1970. Breeding ecology of the Swallow-tailed Gull, Creagus furcatus. *Auk* 87:215-243.
- \_\_\_\_\_. 1978. Supplementary feeding of young Puffins Fratercula arctica. *Journal of Animal Ecology* 47:15-23.
- Hatch, S. A., T. W. Pearson and P. J. Gould. 1979. Reproductive ecology of seabirds at Middleton Island, Alaska. *Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators* 2:233-308.
- Hedgren, S. 1979. Seasonal variation in fledging weight of Guillemots Uria aalge. *Ibis* 121:356-361.
- \_\_\_\_\_. 1981. Effects of fledging weight and timing of fledging on the

- survival of Guillemot (Uris aalge) chicks. *Ornis Scandinavica* 12:51-54.
- Hedgren, S. and A. Linman. 1979. Growth of guillemot Uris aalge chicks in relation to time of hatching. *Ornis Scandinavica* 10:29-36.
- Hickey, J. J. and F. L. Craighead. 1977. A census of seabirds on the Pribilof Islands. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2: 96-195.
- Hunt, G. L. Jr. 1980. Mate selection and mating systems in seabirds. Pages 113-168 In J. Burger, B. L. Olla and H. E. Winn, editors. The behavior of marine animals, Volume 4. Plenum Press, New York, New York, USA.
- Hunt, G. L. Jr., B. Burgeson and G. A. Sanger. 1981. Feeding ecology of seabirds of the eastern Bering Sea. Pages 629-648 in D. W. Hood and J. A. Calder, editors. The eastern Bering Sea shelf: oceanography and resources. Volume 2. University of Washington Press, Seattle, Washington, USA.
- Hunt, G. L. Jr., Z. Eppley, B. Burgeson, and R. Squibb. 1982. Reproductive ecology, foods and foraging areas of seabirds nesting on the Pribilof Islands, 1975-1979. Environmental Assessment of the Alaskan Continental Shelf. Biological Studies 12:1-258.
- Iverson, R. L., L. K. Coachman, R. T. Cooney, T. S. English, J. J. Goering, G. L. Hunt, M. C. Macauley, C. P. McRoy, W. R. Reeburg, and T. E. Whitledge. 1979. Ecological significance of fronts in the southeastern Bering Sea. Pages 437-466 in R. J. Livingston, editor. Ecological processes in coastal marine ecosystems. Plenum Press, New York, New York, USA.
- Jarvis, M. J. F. 1974. The ecological significance of clutch size in the South African gannet (Sula capensis (Lichtenstein)). *Journal of Animal Ecology* 43:1-18.
- Kinder, T. H., G. L. Hunt, D. Schneider, and J. D. Schumacher. 1983.

- Correlation between fronts and seabirds around the Pribilof Islands, Alaska. *Estuarine, Coastal and Shelf Science* 16:309-319.
- Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford, England.
- \_\_\_\_\_. 1968. Ecological adaptations for breeding in birds. Chapman and Hall, London, England.
- Laevastu, T., and F. Favorite. 1981. Ecosystem dynamics in the eastern Bering Sea. Pages 611-625 in D. W. Hood, J. A. Calder, editors. The eastern Bering Sea shelf: oceanography and resources. Volume 1. University of Washington Press, Seattle, Washington, USA.
- Lloyd, C. S. 1977. The ability of the Razorbill Alca torda to raise an additional chick to fledging. *Ornis Scandinavica* 8:155-159.
- \_\_\_\_\_. 1979. Factors affecting breeding of Razorbills Alca torda on Skokholm. *Ibis* 121:165-176.
- Lundberg, C. A., and R. A. Vaisanen. 1979. Selective correlation of egg size with chick mortality in the Black-headed Gull (Larus ridibundus). *Condor* 81:146-156.
- Mahoney, S. P., and W. Threlfall. 1981. Notes on the eggs, embryos and chick growth of Common Guillemots Uria aalge in Newfoundland. *Ibis* 123:211-218.
- Maunder, J. E., and W. Threlfall. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. *Auk* 89:789-816.
- Nelson, J. B. 1964. Factors influencing clutch-size and chick growth in the North Atlantic Gannet, Sula bassana. *Ibis* 106:63-77.
- \_\_\_\_\_. 1966. The breeding biology of the Gannet Sula bassana on the Bass Rock, Scotland. *Ibis* 108:584-626.
- Nettleship, D. N. 1972. Breeding success of the Common Puffin (Fratercula

- arctica L. ) on different habitats at Great Island, Newfoundland. **Ecological Monographs** 42:239-268.
- Nisbet, I. C. T. 1978. Dependence of fledging success on egg-size, parental performance and egg-composition among Common and Roseate Terns, Sterna hirundo and S. dougallii. **Ibis** 129:207-215.
- Nisbet, I. C. T., and M. E. Cohen. 1975. Asynchronous hatching in Common and Roseate Terns, Sterna hirundo and S. dougallii. **Ibis** 117:374-379.
- Nisbet, I. C. T., and W. H. Drury. 1972. Post-fledging survival in Herring Gulls in relation to brood-size and date of hatching. **Bird-banding** 43:161-172.
- Nysewander, D. R., and D. B. Barbour. 1979. The breeding biology of marine birds associated with Chiniak Bay, Kodiak Island. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2:21-106.
- Parsons, J. 1975. Asynchronous hatching and chick mortality in the Herring Gull Larus argentatus. **Ibis** 117:517-520.
- Pearson, T. H. 1968. The feeding biology of seabird species breeding on the Fame Islands, Northumberland. **Journal of Animal Ecology** 37:521-552.
- Perrins, C. M. 1966. Survival of young Manx Shearwaters Puffinus puffinus in relation to their presumed date of hatching. **Ibis** 108:132-135.
- Perrins, C. M., M. P. Harris, and C. K. Britton. 1973. Survival of Manx Shearwaters Puffinus puffinus. **Ibis** 115:535-548.
- Petersen, M. R., and M. J. Sigman. 1977. Population dynamics and trophic relationships of marine birds in the Gulf of Alaska and southern Bering Sea. Part XII: field studies at Cape Peirce, Alaska--1976. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 4:633-693.

- Rice, D. W. , and K. W. Kenyon. 1962. Breeding cycles and behavior of Laysan and Black-footed Albatrosses. *Auk* 79:517-567.
- Ricklefs, R. E. , D. C. Hahn, and W. A. Montevecchi. 1978. The relationship between egg size and chick size in the Laughing Gull and Japanese Quail. *Auk* 95:135-144.
- Salomonsen, F. 1955. The food production of the sea and the annual cycle of Faeroese marine birds. *Oikos* 6:92-100.
- Schneider, D. , and G. L. Hunt, Jr. 1982. Carbon flux to seabirds in waters with different mixing regimes in the southeastern Bering Sea. *Marine Biology* 67:337-344.
- \_\_\_\_\_, and \_\_\_\_\_. In press. A comparison of seabird diets and foraging distribution around the Pribilof Islands, Alaska. Occasional Reports. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Sokal , R. R. , and F. J. Rohlf. 1969. Biometry. Freeman, San Francisco, California, USA.
- Sowls, A. L. , S. A. Hatch and C. J. Lensink. 1978. Catalog of Alaskan seabird colonies. United States Fish and Wildlife Service, Washington, District of Columbia, USA.
- Springer, A. , and D. Roseneau. 1978. Ecological studies of colonial seabirds at Cape Thompson and Cape Lisburne, Alaska. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2:839-960.
- Springer, A. , D. Roseneau, D. , and M. Johnson. 1979. Ecological studies of colonial seabirds at Cape Thompson and Cape Lisburne, Alaska. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2:516-574.

- Squibb, R. and G. L. Hunt, Jr. In press. A comparison of nesting-edges used by seabirds on St. George Island. Ecology.
- Tuck, L. 1960. **The Murre**s. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- van Bal en, J. H. 1973. A comparative study of the breeding ecology of the Great Tit Parus major in different habitats. Ardea 61:1-93.
- Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gull (Larus glaucescens) on Mandarte Island, B.C. British Columbia Provincial Museum, Occasional Papers 13:1-64.
- Ward, J. D. 1973. Reproductive success, food supply, and the evolution of clutch-size in the Glaucous-winged Gull. Dissertation, University of British Columbia, Vancouver, Canada.
- Walsh, J. J., G. T. Rowe, R. L. Iverson, and C. P. McRoy. 1981. Biological export of shelf carbon is a neglected sink of the global CO<sub>2</sub> cycle. Nature 291:196-201.
- Wallace, B. 1968. Topics in population genetics. Norton, New York, New York, USA.
- Wiens, J. A., and J. M. Scott. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.
- Wiens, J. A., G. Ford, D. Heinemann, and C. Fieber. 1978. Simulation modeling of marine bird population energetic, food consumption, and sensitivity to perturbation. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 2:1-83.
- \_\_\_\_\_, \_\_\_\_\_, and \_\_\_\_\_. 1979. **Simulation** modeling of marine bird population energetic, food consumption, and sensitivity to perturbation. Environmental Assessment of the Alaskan Continental Shelf. Annual Reports of Principal Investigators 1:217-270.

Wittenberger, J. and G. L. Hunt, Jr. In press. The adaptive significance of coloniality in birds. In D. S. Farner and J. R. King, editors. Avian biology. Volume VII. Academic Press, New York, New York, USA.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Hafner, New York, New York, USA.

## Appendix 1. Colonies used in Fig. 4 and sources for data.

Colony	Size	Location	Sources
a. St. Paul Is.	253,800	Bering Sea	Hunt et al. 1982 <b>Sowls et al. 1978</b>
b. St. George Is.	2,519,000	Bering Sea	Hunt et al. 1982 <b>Sowls et al. 1978</b>
c. Skomer Is.	220,384	Irish Sea	<b>Birkhead 1977</b> Cramp et al. 1974
d. Fame Islands	50,000	North Sea	Pearson 1968 <b>Cramp et al. 1974</b>
e. Akpatok Is.	1,200,000	N. Atlantic	Tuck 1960 <b>Brown et al. 1975</b>
f. Cape Hay	350,000	Baffin Bay	<b>Birkhead and Nettleship 1981</b> Brown et al. 1975
g. Prince Leopold Is.	362,400	Baffin Bay	<b>Gaston and Nettleship 1981</b> Brown et al. 1975
h. Coburg Is.	350,000	Baffin Bay	<b>Birkhead and Nettleship 1981</b> Brown et al. 1975
i. North Shields	150	North Sea	<b>Coulson and White 1961</b>
j. Bluff	60,000	Bering Sea	<b>Drury et al. 1981</b> <b>Sowls et al. 1978</b>
k. Cape Lisburne	127,000	Chukchi Sea	Springer and <b>Roseneau 1978</b> Springer et al. 1979 Sowls et al. 1978
l. Cape Thompson	417,695	Chukchi Sea	Springer and <b>Roseneau 1978</b> Springer et al. 1979 <b>Sowls et al. 1978</b>

m.	Kulichoff Is.	1,327	N. Pacific	Nysegander and Barbour 1979
n.	Sitkalidak Strait	23,453	N. Pacific	Baird and Hatch 1979
O.	Gull Is.	138,380	N. Atlantic	Mahoney and Threlfall 1981 Maunder and Threlfall 1972 Brown et al. 1975
p.	Cape Peirce	1,230,000	Bering Sea	Petersen and Sigman 1977 Sowls et al. 1978
q.	Dunbar	451	North Sea	Coulson and White 1961
r.	Brownsman	50,000	North Sea	Coulson and White 1961 Coulson 1963
S.	St. Abbs	50,000	North Sea	Coulson and White 1961
t.	Middleton Is.	172,000	North Pacific	Hatch et al. 1979 Sowls et al. 1978
u.	Runde	300,000	North Sea	Barrett and Runde 1980 Brun 1979
v.	Stora Karlsö	28,800	Baltic	Hedgren and Linnman 1979
w.	Hekkingen	1,000	North Sea	Barrett and Runde 1980

Table 1. Abundance of birds within 30 km of St. George Island and St. Paul Island. Abundance does not include ship-following birds. N is the number of ten minute counts,  $\bar{x}$  is the average density (birds/km<sup>2</sup>), sd is the standard deviation around the mean, and NR is not recorded separately.

<u>Cruise</u>	St. George Island			St. Paul Island		
	<u>n</u>	<u><math>\bar{x}</math></u>	<u>sd</u>	<u>n</u>	<u><math>\bar{x}</math></u>	<u>sd</u>
a. Birds in the air and on water combined.						
August 1975	13	320.6	352.8	63	<b>115.9</b>	<b>291.7</b>
June 1976	13	274.6	337.6	14	20.8	25.0
July 1976	35	1936.7	6635.2	92	111.0	129.6
July 1977	<b>40</b>	330.1	582.6	47	81.9	84.7
August 1977	39	211.3	240.1	44	45.4	32.6
August 1978	55	179.0	<b>331.3</b>	49	36.4	47.0
b. Birds on water only.						
August 1975	<b>13</b>	NR	NR	13	NR	NR
June 1976	<b>13</b>	4.2	7.9	14	1.5	3.9
July 1976	35	<b>1056.0</b>	5627.6	92	38.1	80.9
July 1977	40	158.4	360.3	47	27.4	29.8
August 1977	39	18.3	45.1	44	<b>11.1</b>	<b>11.5</b>
August 1978	55	36.6	139.2	49	6.9	<b>11.8</b>

Table 2. Energy demand of the seabird colonies at St. George Island and St. Paul Island. Estimate is based on Wiens et al. (1978) figures for species groups and Hickey and Craighead's (1977) estimates of population sizes of species on the two islands. Energy demand for species groups is given in  $10^{10}$  kcals and as percent of the total demand.

	Energy demand ( $10^{10}$ kcals)			
	St. George Island		St. Paul Island	
	kcals	%	kcals	%
<b>Murres</b>	4.400	68.0	0.383	6.0
Auk? ets	0.147	2.0	0.022	0*3
Puffi ns	0.039	0.6	0.006	0.1
Ful mars	0.599	9.0	0.006	<b>0.1</b>
<b>Kittiwakes</b>	0* 374	6.0	0.042	<b>0.6</b>
Total	5.559	86.0	0.459	7.0

**Total** Energy Demand

St. George/St. Paul

**12 : 1**

Table 3. Differences in reproductive parameters of seabirds nesting on St. Paul (P) and St. George (G) Islands. 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
LAYING Date <sup>a</sup>	p < G**	flips	flips	n. d.	flips
HATCHING Date <sup>a</sup>	P < G**	flips	flips	flips	p < G*
FLEDGING Date <sup>a</sup>	p < G**	flips	p < G**	flips	p < G** (.005)
CLUTCH SIZE	P < G n. s.	p > G n. s.	n. v.	n. v.	n. v.
GROWTH RATE	p > G**	p > G*	P > G n. s.	P > G*	p > G** (.005)
FLEDGING WEIGHT	n. d.	flips	flips	P > G*	P > G**
PRODUCTIVITY	flips	flips	flips	flips	flips

a: < for date means earlier in season  
n. s. : not significant at p = .05  
n. d. : no data  
n. v. : no variation in clutch size  
flips: direction of difference not consistent from year to year; not combined

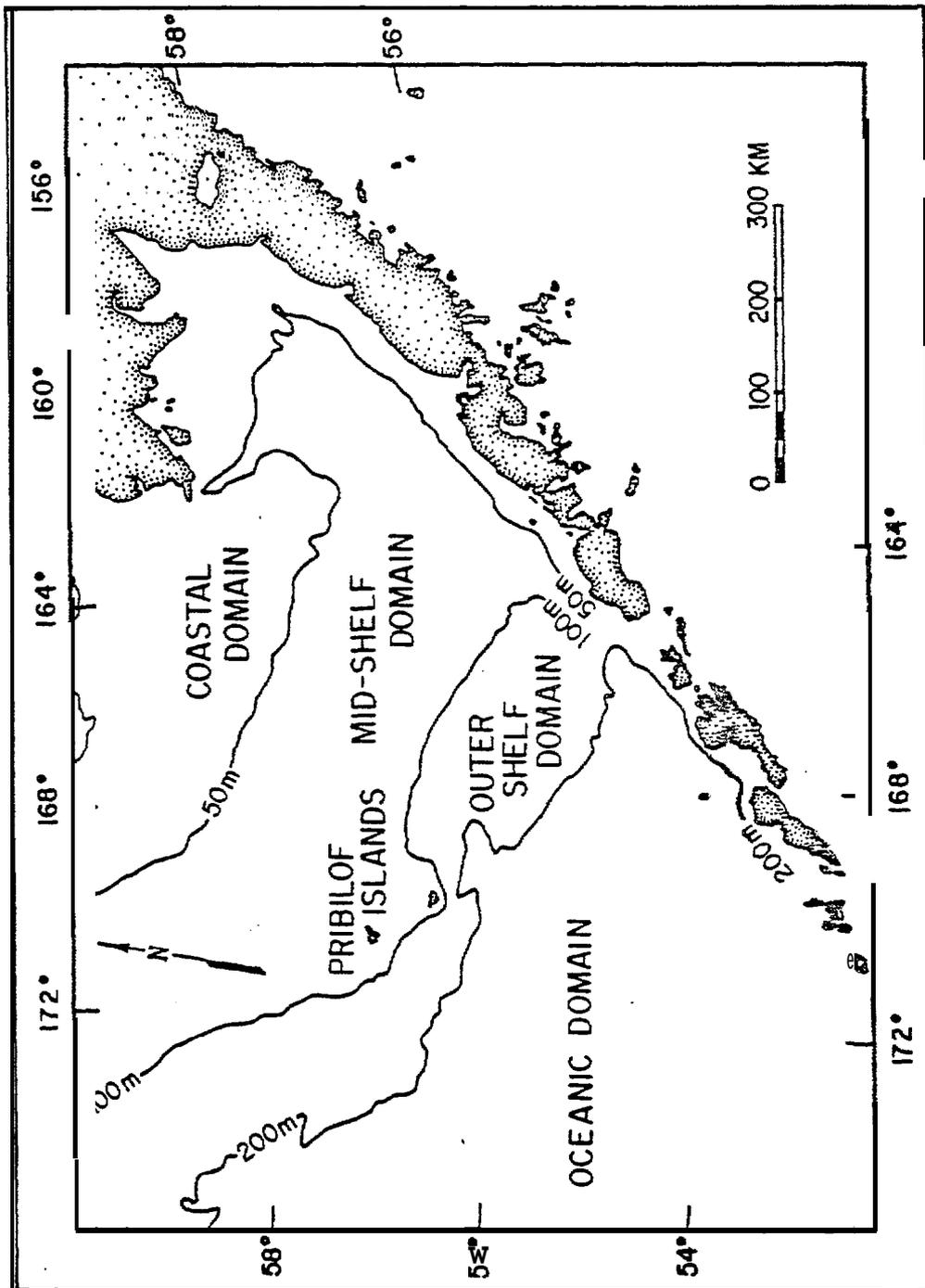
\* p < .05  
\*\* p < .001

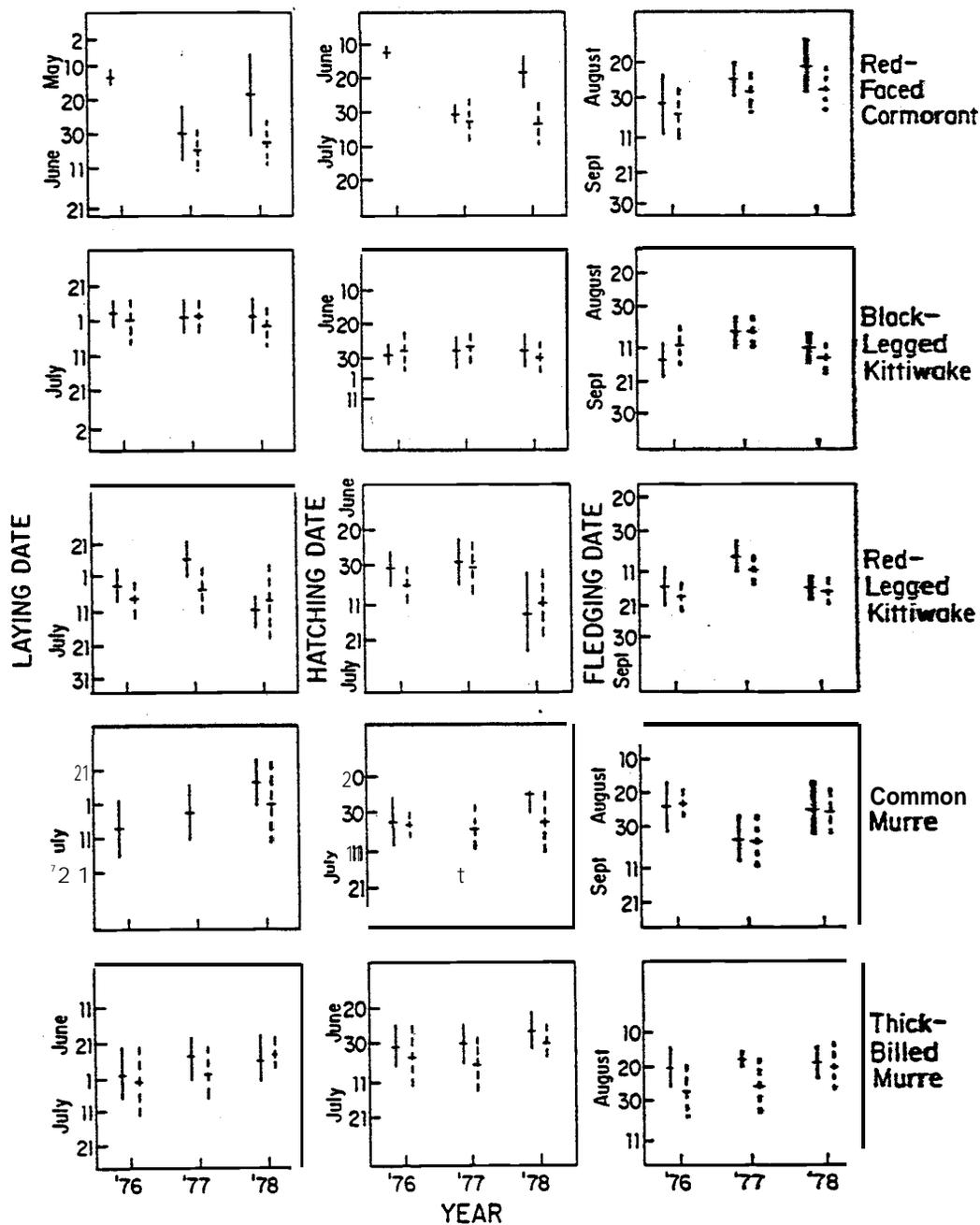
Table 4. Ability of seabirds to raise artificially supplemented broods as a function of colony population size of all species combined (order of magnitude, listed in increasing size).

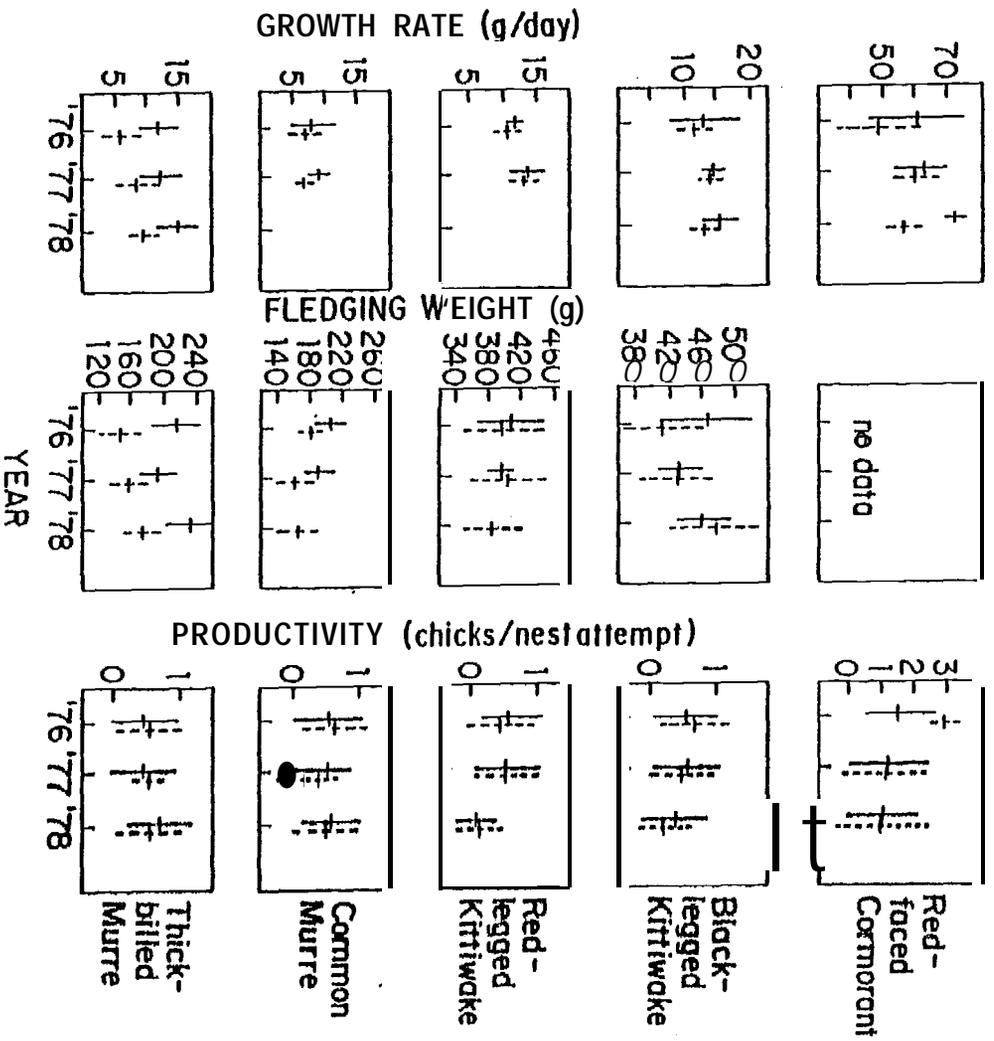
Study	Species	Able to <b>raise</b> larger broods?
Colonies with $10^3$ birds		
Marsden Bay		
<b>Coulson</b> in Lack 1968	Black-legged Kittiwake	yes
Mandarte Island		
Vermeer 1963	Glaucous-winged Gull	yes
Ward 1973	Glaucous-winged Gull	yes
Colonies with $10^4$ birds		
Bass Rock		
Nelson 1964	Gannet	yes
<b>Skokholm</b>		
Lloyd 1979	Razorbill "	<b>yes</b>
	(pop. size 1000)	
Harris 1966	Manx Shearwater	no
	(pop. size 70,000)	
Skomer Island		
<b>Corkhill</b> 1973	Common Puffin	yes
Colonies with $>10^5$ birds		
Great Island		
Nettleship 1972	Common Puffin	<b>no</b>
Midway Atoll		
Rice and Kenyon 1962	Laysan Albatross	no

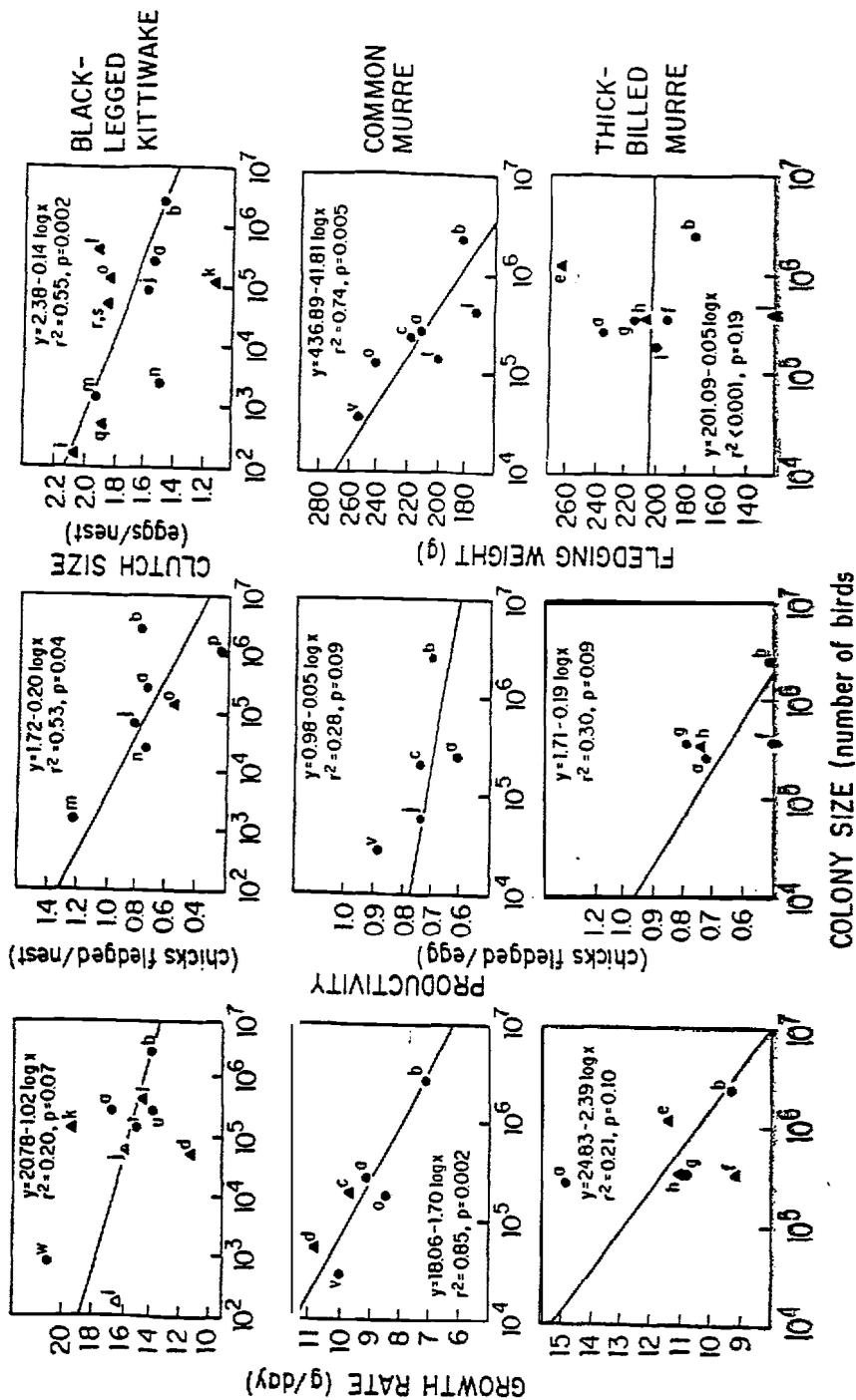
## FIGURE LEGENDS

- Fig. 1. Location of the Pribilof Islands in the southeastern Bering Sea.
- Fig. 2. Comparison of the breeding **phenology** of seabird populations on St. Paul (solid line) and St. George (dashed line) Islands for five species of cliff-nesting seabirds, 1976-1978. Figures show mean  $\pm 1$  standard deviation.
- Fig. 3. Comparison of reproductive achievement of seabird populations on St. Paul (solid line) and St. George (dashed line) Islands for five species of cliff-nesting seabirds, 1976-1978. Figures show mean  $\pm 1$  standard deviation.
- Fig. 4. Relation between reproductive achievement and colony size for Black-legged Kittiwakes, Common **Murres** and Thick-billed **Murres**. Letters designate colonies listed in Appendix 1. Lines are least squares regression lines; regression coefficients and probabilities are given.









COLONY SIZE (number of birds)