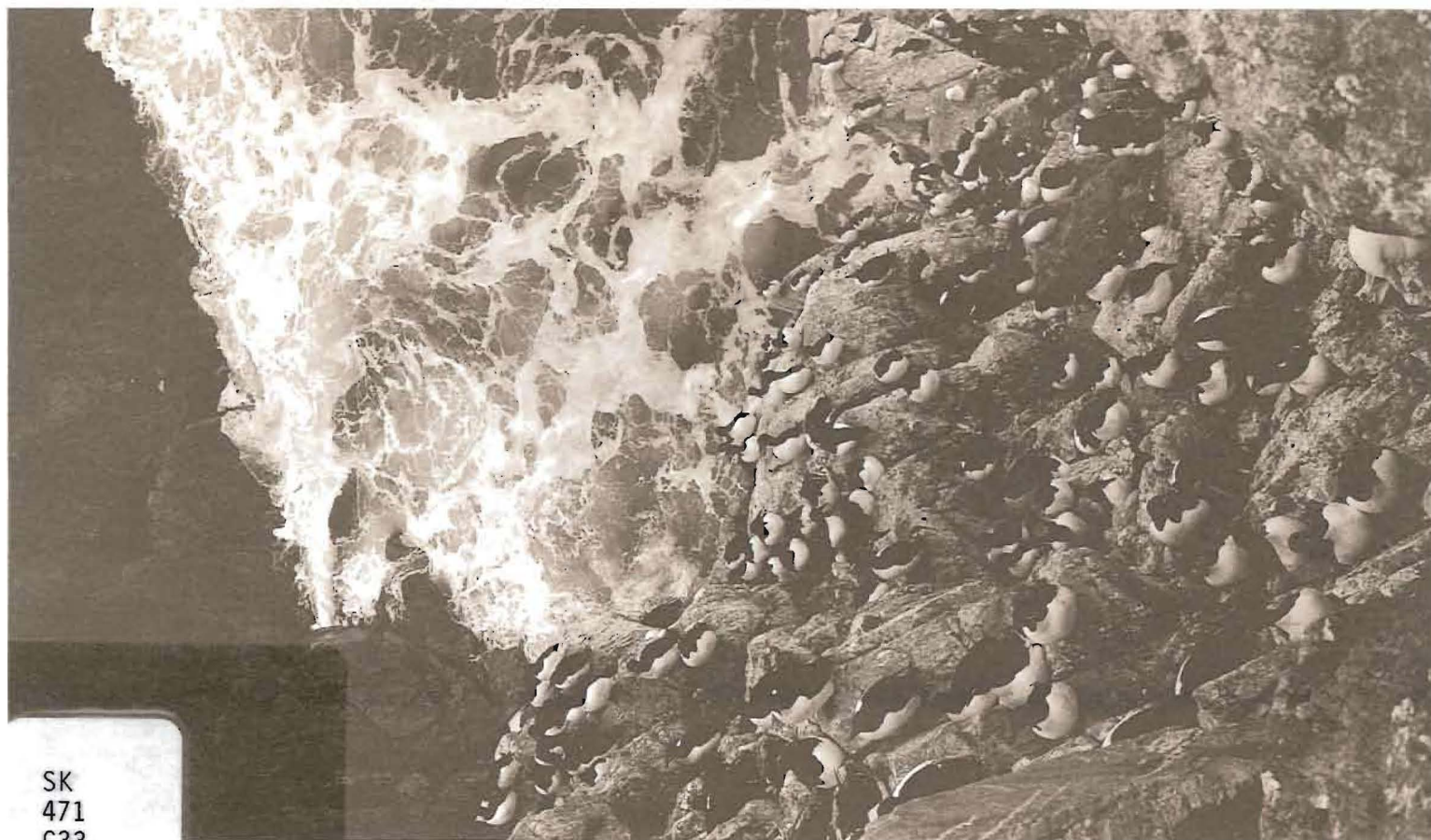


A.W. Diamond  
A.J. Gaston  
R.G.B. Brown  
(edited by W.A. Montevecchi)

# **Studies of high-latitude seabirds. 3. A model of the energy demands of the seabirds of eastern and Arctic Canada**

**Occasional Paper  
Number 77  
Canadian Wildlife Service**



SK  
471  
C33  
No. 77  
Ex. B



Environment  
Canada

Canadian Wildlife  
Service

Environnement  
Canada

Service canadien  
de la faune

A.W. Diamond<sup>1</sup>  
A.J. Gaston<sup>2</sup>  
R.G.B. Brown<sup>3</sup>  
(edited by W.A. Montevecchi)

30169566M  
0016388AS  
**Studies of high-latitude seabirds.**  
**3. A model of the energy demands**  
**of the seabirds of eastern and**  
**Arctic Canada**

**Occasional Paper**  
**Number 77**  
**Canadian Wildlife Service**

Paper presented at the Population Biology and Conservation  
of Marine Birds Symposium held at Memorial University of  
Newfoundland, St. John's, Newfoundland, in April 1989 and  
jointly sponsored by the Ocean Sciences Centre and the  
Canadian Wildlife Service

Published for the Ocean Sciences Centre by the  
Canadian Wildlife Service

OK  
471  
C33  
No. 77  
Ex. B

<sup>1</sup>CWS, Saskatoon, Sask. S7N 0X4.

<sup>2</sup>CWS, National Wildlife Research Centre, Ottawa, Ont.  
K1A 0H3.

<sup>3</sup>CWS, Dartmouth, N.S. B2Y 4A2.

A member of the Conservation and Protection family

Cover: Thick-billed Murres on Hantzsch Island. Photo by Steve Smith.

Published by Authority of the  
Minister of Environment  
Canadian Wildlife Service

*The Canadian Wildlife Service*  
The Canadian Wildlife Service of Environment Canada handles wildlife matters that are the responsibility of the Canadian government. These include protection and management of migratory birds as well as nationally significant wildlife habitat. Other responsibilities are endangered species, control of international trade in endangered species, and research on wildlife issues of national importance. The service cooperates with the provinces, territories, Canadian Parks Service, and other federal agencies in wildlife research and management.  
For more information about the Canadian Wildlife Service or its other publications, please write to:

Publications  
Canadian Wildlife Service  
Environment Canada  
Ottawa, Ontario  
K1A 0H3  
(819) 997-1095

Canadian Cataloguing in Publication Data

Main entry under title:

Studies of high-latitude seabirds

(Occasional paper, ISSN 0576-6370; no. 68, no. 69, no. 77)  
Includes abstracts in French.  
“Papers presented at the Population Biology and Conservation of Marine Birds Symposium held at Memorial University of Newfoundland, St. John’s, Newfoundland, in April 1989.”  
To be complete in 3 v.  
Contents: 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology/edited by W.A. Montevecchi and A.J. Gaston.  
2. Conservation biology of Thick-billed Murres in the Northwest Atlantic/edited by A.J. Gaston and R.D. Elliot.  
3. A model of the energy demands of the seabirds of eastern and Arctic Canada/A.W. Diamond, A.J. Gaston, R.G.B. Brown.  
ISBN 0-662-18312-6 (v. 1), 0-662-18823-3 (v. 2), 0-662-20388-7 (v. 3).  
DSS cat. no. CW69-1/68E, CW69-1/69E, CW69-1/77E.

1. Sea birds — Canada — Ecology — Congresses.  
2. Water birds — Canada — Ecology — Congresses.  
I. Montevecchi, William A. II. Gaston, A.J. III. Elliot, R.D. (Richard Donald), 1946– . IV. Diamond, A.W., 1944– . V. Brown, R.G.B. VI. Occasional paper (Canadian Wildlife Service); no. 68, no. 69, no. 77.

QL671.S78 1993      598.2971      C93-099471-X

Contents

Acknowledgements	5
Abstract	5
Résumé	6
Preface	7
1. Introduction	9
2. Methods	10
2.1 Study area	10
2.2 Study components	10
2.3 Energy expenditure by nonbreeders	11
2.3.1 Activity budgets	11
2.3.2 Energy equivalents	11
2.4 Energy expenditure by breeders	12
2.4.1 Numerical model of populations at breeding colonies	12
2.4.2 Calculating the proportion of birds at sea	13
2.4.3 Calculating energy demand for breeders	14
2.5 Creating the contour maps	14
3. Results	17
3.1 Sensitivity testing	17
3.2 Distribution of energy demand	18
3.2.1 Seasonal patterns of energy demand	18
4. Discussion	27
4.1 Deficiencies in data	27
4.1.1 Coverage	27
4.1.2 Breeding biology	27
4.1.3 Life tables	27
4.1.4 Time budgets	27
4.1.5 Energy budgets	28
4.1.6 Seabird diets	28
4.2 Spatial variation in energy consumption	28
4.3 Energy demand and the availability of prey	28
4.4 Comparisons with other studies	28
Appendix	30
Literature cited	34

List of tables	
Table 1. Equations used to calculate BMR of seabirds in relation to body weight	12
Table 2. Physiological and reproductive data for numerical model of “northern” breeding areas	14
Table 3. Physiological and reproductive data for numerical model of “southern” breeding areas	15
Table 4. Data for breeding season model: mass and energy	15
Table 5. Sensitivity tests for input parameters in energy model based on October, latitude 44–48°N, daylength 11 h	17
Table 6. Comparison of our time budget model estimates of ADEE (July, southern region, except Dovekie and Northern Fulmar, northern region) with those derived from allometric equations based on direct field measurements of ADEE	17
Table 7. Percent contributions to energy demand by selected seabirds, by oceanographic zone	24
Table 8. Energy demand of seabirds, by oceanographic zone	25
Table 9. Comparison of food requirements of seabirds in different oceanographic regions	29
Table A1. Proportion of moult occurring in each winter month	32
Table A2. Species-specific variables, input directly	32
List of figures	
Figure 1. Structure of the energetics model	10
Figure 2. Map of oceanographic zones used	13
Figure 3. An example of the model output for breeding season parameters: Atlantic Puffin in the southern area	14

Figure 4. Relationship of energy consumption to biomass estimated for each grid square, southern area, October	18
Figure 5. April: A. Distribution of data points available. B. Contour map of energy demand by seabirds	19
Figure 6. May: A. Distribution of data points available. B. Contour map of energy demand by seabirds	19
Figure 7. June: A. Distribution of data points available. B. Contour map of energy demand by seabirds	20
Figure 8. July: A. Distribution of data points available. B. Contour map of energy demand by seabirds	20
Figure 9. August: A. Distribution of data points available. B. Contour map of energy demand by seabirds	21
Figure 10. September: A. Distribution of data points available. B. Contour map of energy demand by seabirds	21
Figure 11. October: A. Distribution of data points available. B. Contour map of energy demand by seabirds	22
Figure 12. November–December: A. Distribution of data points available. B. Contour map of energy demand by seabirds	22
Figure 13. January–March: A. Distribution of data points available. B. Contour map of energy demand by seabirds	23
<b>List of appendices</b>	
Appendix 1. Input data and formulae used in the model	30

## Acknowledgements

We thank David Nettleship for supplying unpublished information and Brian Collins for helping with programming and statistics. Eric Woodsworth battled successfully to wrest the secrets of the contour-mapping procedure from the SPANS Geographic Information System in order to produce the maps of energy demand, and he also drafted Section 2.3. We are grateful to David Cairns, John Croxall, and Bob Furness for helpful comments on an earlier draft of the paper. This model was created under Department of Supply and Services Contract No. 47SS KN 107-3-4134 to A.W. Diamond (Scientific Authority A.J. Gaston).

This publication was produced by the Scientific and Technical Documents Division of the Canadian Wildlife Service. The following people were responsible: Susan Burns, Acting Chief — coordination and supervision; Sylvie Larose, Computer Publishing Specialist — layout; Marla Sheffer, Contract Editor — scientific editing; and Gilles Bertrand, Production Officer — printing. We are grateful to all of them for their time, commitment, and attention to detail in the publication process.

## Abstract

We describe a model used to estimate the energy requirements of seabirds in eastern and Arctic Canada. The model integrates data from intensive studies at breeding colonies with extensive observations at sea, using bioenergetics equations as a bridge. It is run independently for small geographic cells, then aggregated into oceanographic zones.

The basic data used in the model are as follows:

- (1) the "PIROP" shipboard counts of birds at sea used for the Canadian Wildlife Service's atlas of seabird distribution;
  - (2) breeding season counts at major colonies;
  - (3) life table estimates of nonbreeding populations;
- and
- (4) body mass measurements, from geographically appropriate sources where possible.

Sensitivity tests confirmed previous findings that exponents and multiplicands in metabolic equations are the major sources of uncertainty, followed closely by body weight. Comparisons with measurements of actual field metabolic expenditures by free-living birds using the doubly labelled water method showed that our time/energy budget methods yielded realistic values.

In most areas, year-round energy demand came mainly from nonbreeding birds, especially from populations breeding in other oceanographic regions (Northeast Atlantic, southern hemisphere). Demand peaked in August in most areas, coinciding with the chick-rearing period for breeders and the peak occurrence of nonbreeding visitors from the southern hemisphere. Among areas surveyed year-round, energy demand by seabirds per unit area was highest on the southern Labrador Banks (10.2 million kJ/km<sup>2</sup> per year) and lowest on the Scotian Shelf (2.9 million kJ/km<sup>2</sup> per year). Differences among areas were not large at the scale on which we were working. The estimate of year-round energy consumption for the Gulf of St. Lawrence was close to an estimate based on breeding birds alone, illustrating the relatively small impact of nonbreeding visitors in the gulf.

Food requirements for all seabirds averaged about 1000 kg/km<sup>2</sup> per year, which is a little lower than, but comparable with, those for Georges Bank, the eastern Bering Sea, and the North Sea. The slightly lower values obtained here may be because much of the Canadian area is covered in ice for part of the year. The general concordance of values obtained for large areas of boreal/arctic shelf seas suggests that primary productivity may be a major determinant of seabird populations.



## Résumé

Le présent document a pour but de décrire un modèle utilisé pour estimer les besoins énergétiques des oiseaux marins dans l'Est et dans l'Arctique canadiens. Le modèle intègre des données provenant d'études intensives de colonies d'oiseaux nicheurs fondées sur de vastes observations au large, à l'aide d'équations bioénergétiques. Le modèle est exécuté indépendamment pour de petites cellules géographiques, et les données sont ensuite regroupées en zones océanographiques.

Le modèle utilise les données fondamentales suivantes :

- (1) les dénombrements d'oiseaux « PIROP » au large, à bord de navires, utilisés pour l'atlas de distribution des oiseaux marins du Service canadien de la faune;
- (2) les dénombrements des principales colonies pendant la saison de nidification;
- (3) des estimations des tables de survie des populations d'oiseaux non nicheurs; et
- (4) des mesures de la masse corporelle, à partir de sources appropriées du point de vue géographique, lorsque la chose est possible.

Des tests de sensibilité ont confirmé les constatations antérieures selon lesquelles les exposants et les multiplicandes dans les équations métaboliques sont les principales sources d'incertitude, suivis de près par le poids corporel. Des comparaisons avec des mesures des dépenses métaboliques réelles d'oiseaux en liberté, sur le terrain, obtenues à l'aide de la méthode d'injection d'eau dont les molécules d'oxygène et d'hydrogène ont été marquées, ont montré que nos méthodes faisant intervenir le budget temps/énergie donnaient des valeurs réalistes.

Dans la plupart des zones, la demande énergétique annuelle provenait principalement des oiseaux non nicheurs, en particulier de populations nichant dans d'autres régions océanographiques (nord-est de l'Atlantique, hémisphère sud). La demande a atteint un sommet en août dans la plupart des zones, ce qui coïncide avec la période d'élevage des oisillons pour les nicheurs et avec la période de pointe des visiteurs non nicheurs provenant de l'hémisphère sud. Parmi les zones étudiées tout au long de l'année, la demande énergétique des oiseaux marins par unité de surface était la plus élevée sur les bancs du sud du Labrador (10,2 millions de kJ/km<sup>2</sup> par an) et la plus faible sur la plate-forme Scotian (2,9 millions de kJ/km<sup>2</sup> par an). Les différences entre les zones n'étaient pas importantes à l'échelle à laquelle nous avons travaillé. L'estimation de la consommation énergétique annuelle pour le golfe du Saint-Laurent s'approchait d'une estimation fondée sur les oiseaux nicheurs seulement, ce qui illustre l'impact relativement faible des visiteurs non nicheurs dans le golfe.

Les valeurs des besoins alimentaires pour tous les oiseaux marins étaient en moyenne d'environ 1 000 kg/km<sup>2</sup> par an, valeurs qui se comparent à celles des besoins pour le banc Georges, l'est de la mer de Béring et la mer du Nord, bien qu'elles y soient légèrement inférieures. Les valeurs légèrement inférieures obtenues ici peuvent être attribuables au fait qu'une grande partie du territoire canadien est couverte de glace pendant une partie de l'année. La concordance générale des valeurs obtenues pour de grandes superficies des mers bordières boréales/arctiques donne à penser que la productivité primaire pourrait être un déterminant important des populations d'oiseaux marins.

## Preface

W.A. Montevecchi

*Departments of Psychology and Biology and Ocean Sciences  
Centre, Memorial University of Newfoundland, St. John's,  
Nfld. A1B 3X9*

Energetics models for seabirds have for the most part been much more limited in spatial scale than the model by Diamond, Gaston, and Brown presented here. Their effort is novel in that it converts counts of birds at sea to densities (Diamond et al. 1986), allowing an estimation of energy requirements for the entire year rather than just for the reproductive period, as is usually the case. The present energetics exercise is also useful in that it indicates major research deficits that have to be addressed before the understanding of avian components of marine food webs can advance. Studies of the feeding ecology and diets of most species are needed in all seasons, but especially outside the breeding season and in winter, and shipboard and aerial surveys of birds at sea in sparsely travelled regions and in winter also need to be greatly increased. Moreover, coverages in inshore areas are lacking, although surveys in many regions (e.g., Newfoundland, Quebec North Shore, Labrador) could be made systematically and inexpensively from coastal ferries and cargo vessels. Very little is known about the life history tables of seabirds in the Northwest Atlantic, although data for some species (e.g., Thick-billed Murres) may or should soon be sufficient for such calculations. Doubly labelled water techniques and activity recorders permit direct measurements of the energy expenditures and behaviour of free-ranging individual animals at sea (e.g., Birt-Friesen et al. 1989; Cairns et al. 1990) and have eliminated much of the need to collect information on activity budgets from which to extrapolate energy requirements. However, it has not yet proven feasible to apply these techniques to nonbreeders or to birds in winter. In view of these current research needs, it is encouraging that the estimates of energy expenditures based on indirect methods reported here were in reasonable agreement with direct estimates based on doubly labelled water methods and with extrapolations from allometric equations based on studies that have used these techniques.

The temporal and spatial scales that Diamond, Gaston, and Brown have incorporated give their model a dynamism that is usually lacking in most such endeavours but that is essential for understanding large-scale ecosystems. This dynamism is vital for multispecies considerations of marine food webs that rely on understanding the trophic interactions of homeothermic

predators, large predatory fishes, small pelagic "forage" fishes, and invertebrates in a dynamic ocean environment. For the most part, ecological energetics models have had to focus on simple predator-prey interactions, and biologists have tended to consider seabirds independently of marine mammals and both these groups separately from fishes and invertebrates. Large-scale energetics models, such as this one, afford the opportunity to integrate different taxonomic groups in order to assess interspecies interactions as well as potential interactions between fisheries and marine birds and mammals (e.g., Croxall et al. 1985; Furness 1990; Furness and Barrett 1991; Montevecchi 1992; Springer 1992). Large-scale energetics models should also prove useful in long-term assessments of climatic and environmental change and their ecological consequences and in our capability to differentiate natural from human-induced perturbations (e.g., Brown 1991). Mapping energy harvests on different spatial and temporal scales will facilitate more thorough investigations of trophic interactions and of potential interactions between large predators and fisheries. For example, Cairns et al. (1991) mapped seabird consumption by Northwest Atlantic Fisheries Organization (NAFO) areas, and it is possible to directly compare avian and human harvests of fish. Geographic information systems (GIS) might greatly facilitate these analyses (Shaw and Atkinson 1990). Moreover, by incorporating marine mammals into such schemes, it would be possible to compare the harvests of fisheries, birds, and mammals relatively directly. To facilitate the incorporation of mammalian data into these models, researchers conducting surveys at sea should include sightings of mammals with avian sightings, and observations of all homeothermic predators should be analyzed concurrently.

Knowledge of the roles of seabirds in large-scale marine ecosystems is progressing rapidly. We are entering a new multispecies arena, and much exciting research will be done in collaboration with marine scientists from other disciplines. These are truly engaging times for marine ornithologists.

This publication is the third in the series Studies of high-latitude seabirds that is published as Canadian Wildlife Service Occasional Papers. This monograph and the first

two in the series (No. 68: 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology; No. 69: 2. Conservation biology of Thick-billed Murres in the Northwest Atlantic) are outgrowths of international seabird workshops cosponsored by Memorial University of Newfoundland and the Canadian Wildlife Service. All publications are available from the Canadian Wildlife Service. Future issues in this series are in preparation.

## 1. Introduction

Seabird populations in the Northwest Atlantic have fluctuated considerably during the past century. Such changes have been attributed to changes in the intensity of human disturbance and exploitation (e.g., Nettleship and Birkhead 1985; Furness and Monaghan 1987) and to natural oceanographic or climatic fluctuations (Brown 1991). The role of natural and human agencies in seabird population fluctuations is still imperfectly understood. The question of the extent to which seabird numbers are influenced by their food supplies became especially pertinent following a major decline of the capelin *Mallotus villosus* off Newfoundland in the late 1970s (Brown and Nettleship 1984) and in the Barents Sea in the 1980s (Furness and Barrett 1991) and general declines in the abundance of sand lances (*Ammodytes* spp.) around northern Great Britain in the 1980s (Heubeck 1989; Harris 1991). These fish were the principal prey of many species of seabirds and marine mammals, and their declines affected reproduction and populations of some seabird species (Monaghan et al. 1989; Harris 1991; Nettleship 1991).

This project was designed to quantify the seasonal and geographic changes in the food requirements of seabirds off eastern and Arctic Canada and to examine the relationship between seabirds and their food supplies. Information obtained on prey biomass and the consumption of competitors should make it possible to model the potential impact of seabirds on their food supplies. An understanding of the relationships among all components of the marine ecosystem will improve our ability to make realistic predictions about how seabird numbers are likely to be affected by human exploitation of marine resources. At present, we are unable to proceed beyond mapping the energy demands of seabirds. Integration of these data with other elements of the marine ecosystem awaits comparable data on food stocks and competitors.

Previous models of energy use by seabirds were made for the North Sea by Evans (1973); for Oregon and California by Wiens and Scott (1975); for waters around the Shetland Islands by Furness (1978); for waters off southwest Africa by Furness and Cooper (1982); for the Bering Sea by Hunt et al. (1981), Ford et al. (1982), and Schneider et al. (1986); for the Barents Sea by Furness and Barrett (1985); for Georges Bank by Powers and Backus (1987) and Schneider et al. (1987); for the Scotian Sea (Antarctic) by Croxall and Prince (1981, 1987); and for the Gulf of St. Lawrence by Cairns et al. (1990). The work reported here

differs from other studies in that it integrates data from the whole year and combines intensive studies at breeding colonies with an extensive data base of observations at sea to give small-scale mapping of energy use by months. None of the studies referred to above included all these elements, and none provided estimates for such a broad geographical area.

## 2. Methods

### 2.1 Study area

The study involves that part of the western North Atlantic bounded to the south by 45°N latitude and to the east by 40°W longitude, extending (in August and September) as far north as Baffin Bay and west to northeast Hudson Bay and Barrow Strait—the same area covered by the *Atlas of eastern Canadian seabirds* (Brown et al. 1975; Brown 1986). Arctic marine areas have received less coverage than boreal waters, and, because the starting point for the model is the data base of numbers of birds seen at sea, the study is most complete for areas south of 60°N. All results are based on a grid of blocks 0.5°N × 1°W (south of 65°N) or 0.5°N × 2°W (north of 65°N).

### 2.2 Study components

The study is divided into several discrete components (Fig. 1):

(1) *Seabird numbers and distribution.* Data on numbers of breeding birds at colonies are from Nettleship (1980) and, for Baccalieu Island, Montevecchi and Tuck (1987). Counts at sea from fishing and research vessels, recorded largely by volunteers, were collected from 1969 by R.G.B. Brown and others for the "Programme intégré de recherches sur les oiseaux pélagiques" ("PIROP"). The data used here are those collected up to 1984—essentially identical to those used by Brown (1986). The PIROP data

give much better coverage of offshore than coastal regions; in general, the study applies to areas at least 10 km from land and does not adequately cover areas closer inshore. The counts have been converted into estimates of absolute density by comparing shipboard counts with "expected" densities within feeding range of breeding colonies, calculated from colony counts and life table and time budget information (Diamond et al. 1986). Estimates of the proportion of nonbreeders present during the breeding season were based chiefly on life table information.

Only species that feed regularly at least 10 km from shore, and for which reliable population data were available, were considered; thus, cormorants (Phalacrocoracidae) were excluded. Gulls (*Larus* spp.) were included but were treated as nonbreeders throughout, because most remain in coastal waters while breeding and so would not be included in the PIROP data set. Black Guillemots *Cephus grylle* and Arctic Terns *Sterna paradisaea* were recorded so rarely on PIROP counts that conversion factors could not be calculated, and no further details are given for these species. Leach's Storm-Petrel *Oceanodroma leucorhoa* and Wilson's Storm-Petrel *Oceanites oceanicus* were included but were certainly underestimated by shipboard counts, as they are difficult to detect at sea.

(2) *Energy estimates.* Energy requirements were estimated from body mass derived from the literature and Canadian Wildlife Service data, corrected by time budget estimates for activities with different rates of energy expenditure. The models described by Wiens and Innis (1974) and Furness (1978) and those based on them are the most detailed in making use of data on time budgets of activities requiring different levels of energy expenditure. Rather than defining separate "activity levels" with arbitrarily assigned rates of energy expenditure as in Furness's model, we calculate energy expenditures for each major behaviour pattern (flying, swimming, etc.) using equations derived from the literature. A general review of this type of model is provided by Wiens (1984).

(3) Components (1) and (2) were combined to produce monthly or seasonal maps showing the estimated food energy required by seabirds in different areas of the western North Atlantic.

### 2.3 Energy expenditure by nonbreeders

To convert counts of seabirds into estimates of total energy expenditures, interim calculations of biomass distribution were used to make a final selection of species. Thus, Cory's Shearwater *Calonectris diomedea*, Audubon's Shearwater *Puffinus lherminieri*, Sabine's Gull *Xema sabini*, phalaropes *Phalaropus* spp., and terns *Sterna* spp. were excluded because they each contributed negligible amounts to the total biomass of seabirds in the area (<1% in all regions). Because the Common Murre *Uria aalge* and Thick-billed Murre *U. lomvia* were not separated in most observations at sea and because they have largely overlapping body weights and very similar behaviour, we have treated all murres as a single unit. However, all data pertaining to areas north of 60°N can be assumed to refer to Thick-billed Murres. The two species are intermingled farther south outside the breeding season (Brown 1986).

The Average Daily Energy Consumption (ADEC) was calculated for each species in each month; this was then

multiplied by the number of days in the month and by the numbers of that species in a given grid square to give the species' total energy demand. The totals for each species were then summed to give the total energy demand of all seabirds.

To calculate energy budgets, three separate kinds of information were needed in addition to the estimates of density derived from the counts:

- (1) activity or time budgets: these were worked out separately for daytime and nighttime, as we assumed that birds' activity patterns differ by day and by night;
- (2) the rate of energy expenditure required for each activity defined in (1); and
- (3) the energy required for moulting.

The general equation for ADEC was thus:

$$\text{ADEC} = [\sum (T_i \times E_i) + E_m] / 0.8 \quad (1)$$

where  $T_i$  is the proportion of time spent on activity "i,"  $E_i$  is the energy required by that activity,  $E_m$  is the energy cost of moulting, each parameter estimated separately for each species in each month, and 0.8 is a constant representing the efficiency of assimilation (Furness 1978). Note that ADEC = Average Daily Energy Expenditure (ADEC, the variable measured by studies of metabolism) divided by a constant (0.8).

#### 2.3.1 Activity budgets

Each bird was assumed to spend its time either flying or on the water. Flying time was divided between flapping and gliding, as these two forms of flight differ considerably in their energy demands. Time on the water was divided between resting, active swimming on the surface, and, in species that feed by chasing prey underwater (shearwaters, Northern Gannet *Sula bassanus*, auks), underwater swimming.

The proportion of time spent in air and water was estimated from the behavioural data recorded at the time the original counts were made, corrected as described by Gaston et al. (1987) and averaged over months. There are no data to guide further partitioning of the activity budget within the "flying" and "water" categories. Consequently, our assumptions were based on general knowledge of the species' behaviour. The values adopted were, as far as possible, reasonable not only in an absolute sense, but also in relation to those used for other species; for example, irrespective of the accuracy of the figure adopted for the proportion of flying time spent gliding rather than flapping, it was important that it was greater in Northern Fulmars *Fulmarus glacialis* than in gulls, and greater in gulls than in auks. We further assumed that all species rested for half the daylight hours they spent on the water. Details of the numbers attached to the variables are given in Appendix 1.

#### 2.3.2 Energy equivalents

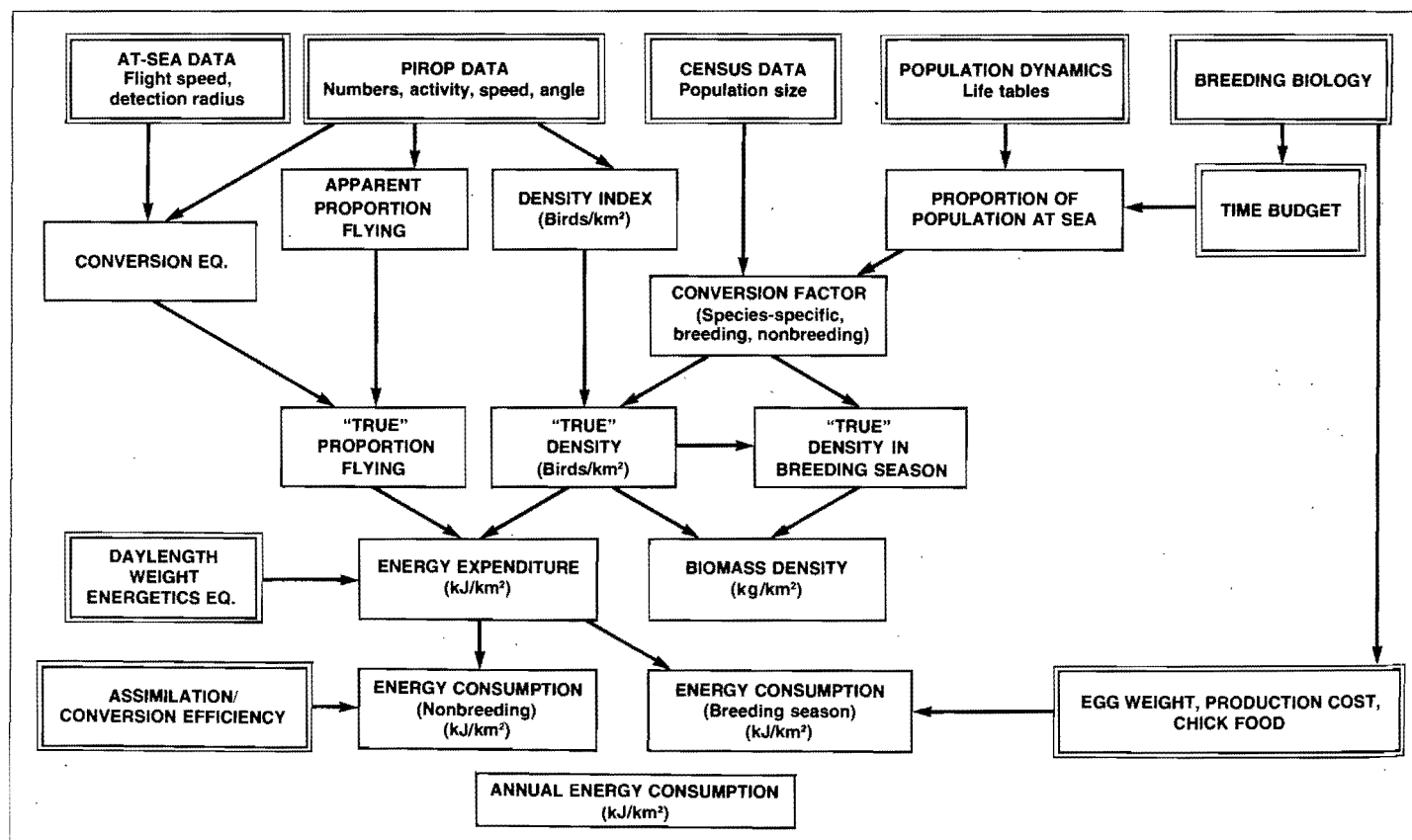
The energy demand of each activity was estimated from allometric equations of the general form

$$M = a \times W^b, \text{ or } \log M = \log a + (b \times \log W) \quad (2)$$

where  $M$  is metabolic rate and  $W$  is body mass.

Many authorities express the energy costs of various activities as multiples of Basal Metabolic Rate (BMR), using equations given by Lasiewski and Dawson (1967) or

Figure 1  
Structure of the energetics model



**Table 1**  
Equations used to calculate BMR of seabirds in relation to body weight

Equation (W in kg)	BMR of 500-g bird (kJ/d)	Reference
$327.8 \times W^{0.723}$	198.6	Lasiewski and Dawson 1967
$381.0 \times W^{0.729}$ (active phase)	229.9	Aschoff and Pohl 1970b
$307.7 \times W^{0.734}$ (passive phase)	185.0	Aschoff and Pohl 1970b
$344.9 \times W^{0.735}$	207.2	Kendeigh et al. 1977
$397.7 \times W^{0.744}$	237.5	Rahn and Whittow 1984
$381.8 \times W^{0.721}$	231.6	Ellis 1984
$428.4 \times W^{0.694}$	264.8	This study (see text)

Aschoff and Pohl (1970a, 1970b), who refer to BMR as "Standard" Metabolic Rate (SMR). Furness and Wiens and their respective co-workers used EMR (Existence Metabolic Rate) as a metabolic baseline; we have used BMR following King (1974). EMR and SMR (*sensu* Kendeigh et al. 1977) have the attraction that they contain a correction for ambient temperature, but this is less important than appears at first sight, for two reasons. First, the "ambient" temperatures normally used in bioenergetics models are standard meteorological measures likely to be very different from temperatures actually experienced by wild birds (Kendeigh 1970). Secondly, the most important metabolic rates to estimate accurately are those concerned with activity above the baseline level—i.e., those involving locomotion. For these, especially flapping flight, the heat produced by the increased activity contributes so much to maintaining a body temperature that energy expenditure is virtually independent of ambient temperature (Hart and Roy 1967; King 1974; Kendeigh et al. 1977).

Until recently, Kendeigh et al.'s (1977) general equation for BMR (combining day, night, summer, and winter [equation 5.5]) was the most generally useful, but Ellis (1984) and Rahn and Whittow (1984) showed that seabirds have higher BMRs than predicted by general equations for nonpasserines and provided equations specifically for seabirds. Their equations apply to a range of taxa, including some from the tropics; examination of their data showed that tropical species have lower BMRs than high-latitude seabirds of comparable weight. Accordingly, we used data only from nontropical species for which Ellis (1984, Table 1) gave BMR data to calculate an equation most likely to apply to the species in our study. This equation (3, below) gives a BMR for a 500-g bird about 30% higher than that predicted by the Kendeigh et al. (1977) equation. For comparison, Table 1 gives the various equations in recent use relating BMR to body weight in seabirds.

$$\text{BMR (kJ/d)} = 428.34 \times W^{0.694} \quad (W \text{ in kg}) \quad (3)$$

Since we programmed our model, Roby and Ricklefs (1986) and Birt-Friesen et al. (1989) have also shown, on the basis of measurements from doubly labelled water studies, that high-latitude seabirds have higher metabolic rates than those predicted by allometric equations.

The equations used for calculating ADEC, their justification, and the input data used in the equations are set out in Appendix 1. In this paper, we do not deal with the amounts of prey organisms consumed, because very little information on seabird diets is available over most parts of our study area except for limited periods during the year.

However, in order to make comparisons with other studies, we assumed that 1 kJ of energy ingested is equivalent to 19 mg carbon, or 0.17 g wet weight of prey (fish) (Schneider and Hunt 1982).

## 2.4 Energy expenditure by breeders

The calculation of energy demands during the breeding season is complicated by differences between the time budgets of breeders and nonbreeders and between the time budgets of breeders at different stages of the breeding cycle. We dealt with this by first identifying the grid blocks of the map that were likely to be within range of breeding birds (breeding areas, Fig. 2); birds in all other grid blocks were treated as nonbreeders not visiting a colony (including postbreeders that have dispersed). Within breeding areas, it was necessary to calculate the monthly totals of birds at each stage of the breeding cycle (including nonbreeders).

### 2.4.1 Numerical model of populations at breeding colonies

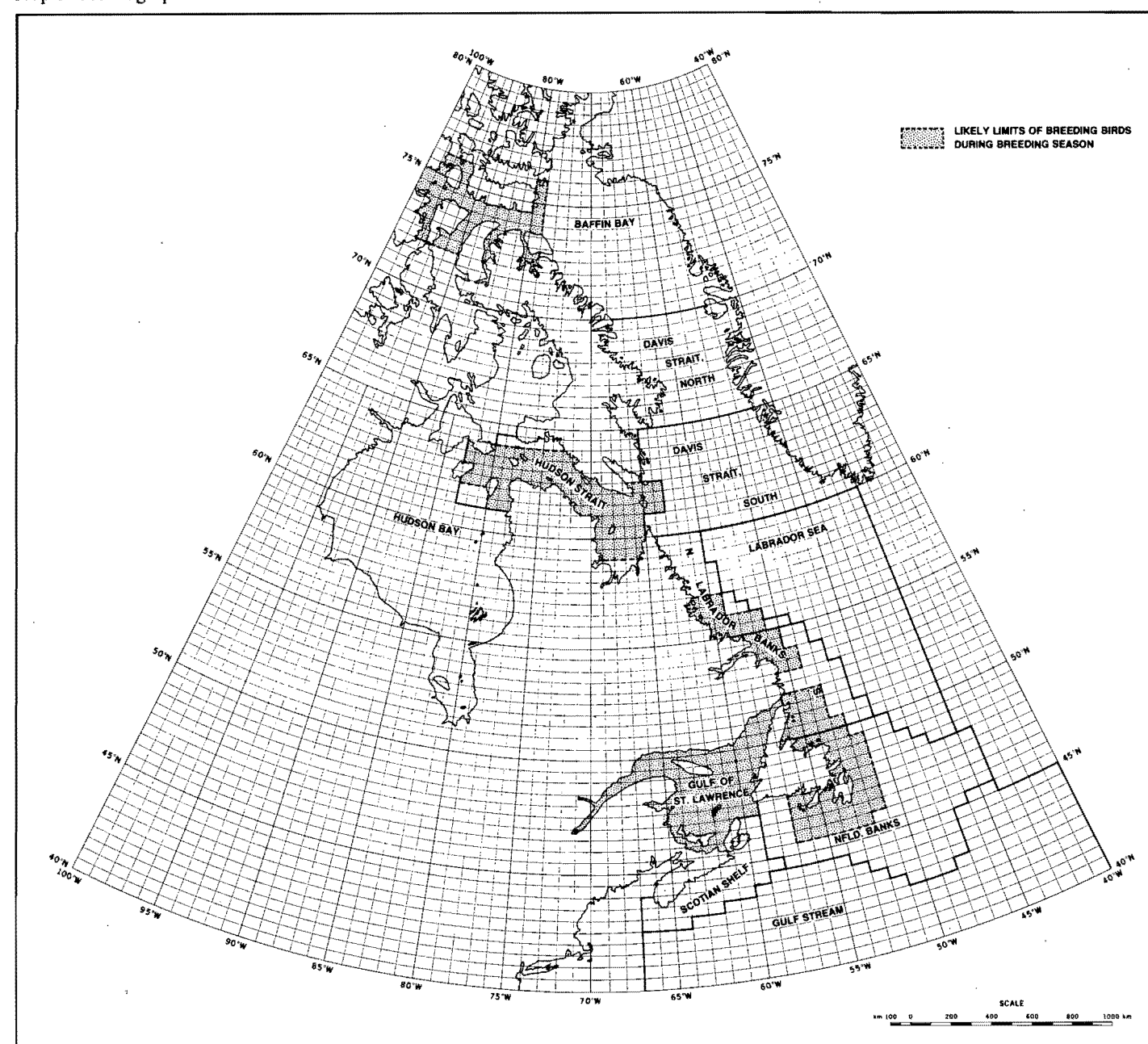
This model took standard measures of breeding phenology and biology as input variables and calculated the daily totals of birds in each of the following categories: breeder; nonbreeder; female not yet maturing an egg; female maturing an egg; member of an incubating pair; member of a pair brooding a chick; member of a pair with a chick, postbrooding; member of a pair with a fledged chick; and failed breeder. In species with a clutch size of more than one (in this study, only larids and Black Guillemot), separate totals were also calculated for numbers of eggs, chicks being brooded, postbrooding chicks, and fledged chicks.

A sample plot of the model output for one species—Atlantic Puffins *Fratercula arctica*—is given in Figure 3, which shows daily changes in numbers of different sectors of the population at a breeding colony. The energy model used a monthly total obtained by summing the number of "bird-days" in each category during the month. The model used a triangular, rather than normal, distribution of arrivals, egg laying, hatching, etc. (Ford et al. 1982). Rates of egg and chick loss were treated as constant, rather than age dependent, for ease of computation. These simplifications had a relatively slight effect on the output used in the energy model (i.e., summed by months).

The values used for the input data in this numerical model are given in Tables 2 and 3 for "northern" and "southern" breeding areas, separated at latitude 53°N on the basis of median laying dates of Black-legged Kittiwakes *Rissa tridactyla*, Common Murres, and Atlantic Puffins. Breeding seasons south of this latitude are 3–4 weeks earlier than those farther north for most species except Black Guillemot (whose breeding season shows no variation with latitude). The general constancy of timing of breeding, within a species, from the Gannet Islands at about 54°N to Coburg Island at 76°N is very striking and probably due to the influence of the cold Labrador Current.

The timing of breeding events was estimated as follows. In most cases, the median dates of laying, and often of hatching and fledging, were known; where more than one year's data existed for a colony or region, the mean of these median dates was used. We found very few records of arrival dates for breeders and virtually none for nonbreeders. In the absence of suitable data, dates were estimated using the following assumptions:

**Figure 2**  
Map of oceanographic zones used



(1) that the spread of arrival dates for both breeders and nonbreeders was equal to the spread of dates of laying (or hatching, or fledging, depending on availability, in that order of preference);

(2) that the timing of departure from the colony by both breeders and nonbreeders coincided with the timing of fledging of the chicks (likely to be true in all species except possibly Atlantic Puffins); and

(3) that nonbreeders arrived later than breeders by a period either specified or implied in the literature.

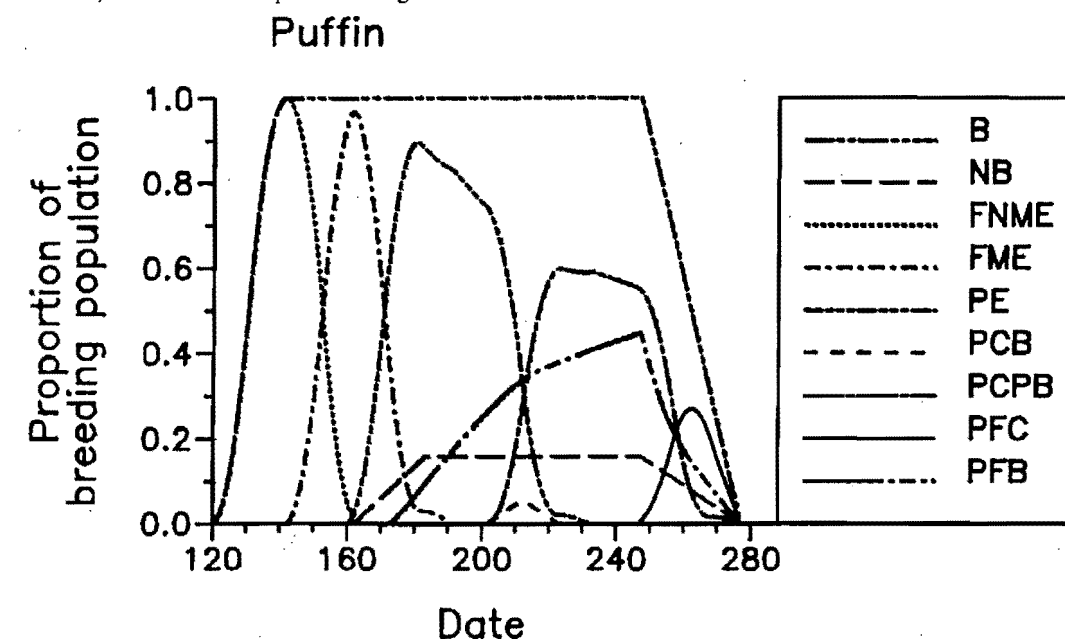
The nonbreeding population estimated to be within the breeding areas was assumed to consist of all those birds that were old enough to attend the colony (e.g., for murres, birds in their second summer and older). Numbers were estimated from the total breeding population, using the life tables in Diamond et al. (1986). These estimates were

probably larger than the proportion of nonbreeders actually coming ashore. Detailed sources are given in Appendix 1.

**2.4.2 Calculating the proportion of birds at sea**  
Breeding birds and nonbreeders that spend some time on land have a lower probability of being counted at sea because of the time they spend ashore. Consequently, the total population using the breeding area (TPA) was always greater than the countable population (CP) during the breeding season. The relation "c" between TPA and CP depended on the time budgets of each segment of the population and their proportions within the total population during a month. Its derivation was described in detail by Diamond et al. (1986). Outside the breeding season, or for birds not tied to a colony, CP was equivalent to the total population using the area, and no correction was required.



**Figure 3**  
An example of the model output for breeding season parameters: Atlantic Puffin in the southern area. B = Breeders, NB = Nonbreeders, PFB = Failed breeders, PFC = Fledged chicks, FME = Females developing egg, FNME = Females not developing egg, PE = Pairs with egg, PCB = Chicks being brooded, PCPB = Chicks postbrooding.



**Table 2**  
Physiological and reproductive data for numerical model of "northern" breeding areas

Variable	Northern Fulmar	Black-legged Kittiwake	Razorbill	Common Murre	Thick-billed Murre	Black Guillemot	Atlantic Puffin
Clutch size (CS)	1.0	1.7	1.0	1.0	1.0	1.89	1.0
First arrival, breeders (FAB) <sup>a</sup>	124	145	140	132	125	131	121
Last arrival, breeders (LAB)	130	171	160	164	147	161	141
First departure, breeders (FDB)	253	242	214	210	220	237	248
Last departure, breeders (LDB)	267	274	248	255	254	275	277
First arrival, nonbreeders (FANB)	124	175	155	140	148	201	163
Last arrival, nonbreeders (LANB)	130	201	204	172	208	212	183
First departure, nonbreeders (FDNB)	229	242	214	210	220	237	248
Last departure, nonbreeders (LDNB)	258	274	248	255	254	275	277
Egg maturation (E)	24	14	15	17	15	16	18
First laying (FL)	156	166	160	150	167	166	161
Median laying (ML)	161	179	170	166	178	181	171
First hatching (FH)	204	193	194	181	197	197	202
Median hatching (MH)	208	206	204	197	208	212	212
Age of chick at end of brooding (D4)	12	20	18	24	21	5	7
First fledging (FF)	253	243	212	205	218	237	247
Median fledging (MF)	262	254	222	221	229	252	257
Hatching success (HS)	0.62	0.80	0.63	0.89	0.73	0.54	0.63
Fledging success (FS)	0.76	0.71	0.93	0.96	0.91	0.84	0.81
Proportion re-laying (R)	0	0.05	0.13	0.06	0.08	0.12	0.03

<sup>a</sup> All dates are Julian.

#### 2.4.3 Calculating energy demand for breeders

ADEC for breeding birds and for nonbreeders attending colonies was calculated as for nonbreeders, using the appropriate time budgets for each segment of the population and adding the energy cost of egg production for females in the pre-laying period. We used the daily feeding rate and the mean meal weight to estimate the amount of food fed to each chick per day (Table 4), multiplied by a standard figure for conversion efficiency. This was then applied to the number of chicks in the population in that month as calculated by the numerical model.

#### 2.5 Creating the contour maps

To create the contour maps, the model was first run on PC SAS to generate simulated energy demand for each grid square and time period. Energy demand totals were then exported to the Tydac SPANS Geographic Information System (Tydac Corporation) together with latitude and longitude of each grid cell. Data from all time periods were combined and sorted so that roughly equal numbers of observations fell into each of six classes of energy demand.

In SPANS, a "universe" (geographic frame of reference) was created based on the geographic limits of the data, using the Lambert Conformal Conic projection.

**Table 3**  
Physiological and reproductive data for numerical model of "southern" breeding areas

Variable	Northern Gannet	Black-legged Kittiwake	Razorbill	Common Murre	Thick-billed Murre	Black Guillemot	Atlantic Puffin
Clutch size (CS)	1.0	1.85	1.0	1.0	1.0	1.88	1.0
First arrival, breeders (FAB) <sup>a</sup>	75	60	120	111	126	131	91
Last arrival, breeders (LAB)	123	100	165	131	146	161	131
First departure, breeders (FDB)	242	210	205	187	202	237	217
Last departure, breeders (LDB)	290	250	241	225	240	275	257
First arrival, nonbreeders (FANB)	105	90	150	126	141	201	133
Last arrival, nonbreeders (LANB)	153	130	200	172	187	212	173
First departure, nonbreeders (FDNB)	250	210	205	187	202	271	217
Last departure, nonbreeders (LDNB)	260	250	241	225	240	275	257
Egg maturation (E)	14	14	16	15	15	16	18
First laying (FL)	107	132	142	121	136	166	120
Median laying (ML)	131	152	165	140	155	181	140
First hatching (FH)	151	158	178	153	168	197	162
Median hatching (MH)	175	178	200	172	187	212	182
Age of chick at end of brooding (D4)	18	20	18	22	22	5	7
First fledging (FF)	242	210	196	187	202	237	217
Median fledging (MF)	266	230	218	194	209	252	237
Hatching success (HS)	0.80	0.73	0.76	0.83	0.68	0.54	0.63
Fledging success (FS)	0.90	0.79	0.88	0.92	0.91	0.84	0.66
Proportion re-laying (R)	0.05	0.06	0.06	0.09	0.09	0.12	0.03

<sup>a</sup> All dates are Julian.

**Table 4**  
Data for breeding season model: mass and energy

Species	1 EGGWT (g)	2 FEEDS (no./d/chick)	3 FEEDWT (g wet wt.)	4 FOODEN (kJ/g wet wt.)	5 MEALEN (kJ/meal)	6 DAYEN (kJ/d)
A Northern Fulmar	94	0.92	80	5.7	456	420
B Leach's Storm-Petrel	11	0.82	9	5.3	51	42
C Northern Gannet	114	2.8	95	7.6	722	2022
D Black-legged Kittiwake	52	2.1	41	5.8	237	498
E Razorbill	85	2.8	17	6.5	110	308
F Common Murre	103	4.3	10	7.3	73	314
G Thick-billed Murre	97	(PLI) 4.6 (GI) 4.5	11 12	5.9 6.0	65 72	299 324
H Black Guillemot	48	8.8	13	5.6	69	607
I Atlantic Puffin	68	3.7	14	7.2	101	374
J Dovekie	24	8.5	3.5	5.7	20	170

EGGWT = mean weight of fresh egg

FEEDS = meals/chick/day/adult

FEEDWT = mean weight of each meal fed to chick

FOODEN = mean energy density of average meal

MEALEN = FEEDWT × FOODEN

DAYEN = MEALEN × FEEDS

GI = Gannet Islands

PLI = Prince Leopold Island

Sources:

A: 1—A.J. Gaston (pers. commun.); 2,3—A. Linton and D.N. Nettleship (unpubl. data); 4—composition from Gaston and Nettleship (1981, Table 86), energy density from T.R. Birkhead and D.N. Nettleship (unpubl. data) for fish, Bradstreet (1982a) for crustacea.

B: 1—Montevicchi et al. (1983); 2,3—Ricklefs et al. 1985; 3—storm-petrel meal (Ricklefs et al. 1985) multiplied by ratio of adult weights of two species; 4—as in A.

C: 1,2—Montevicchi and Porter (1980); 3—total food intake of captive chicks (Montevicchi et al. 1984, p. 337) divided by fledging period and feeding frequency. Mean weights of meals regurgitated by adults (290 g—Montevicchi and Porter 1980) give over 3 times this measured total intake, indicating that the "meal" regurgitated by the adult is delivered to the chick in several feeds; 4—Montevicchi et al. (1984).

D: 1—Maunder and Threlfall (1972); 2,3—Galbraith (1983); 4—as in A.

E: 1—Johnson (1944); 2,3,4—T.R. Birkhead and D.N. Nettleship (unpubl. data).

F: As in E.

G: As in E for Gannet Islands (GI); Gaston and Nettleship (1981) for Prince Leopold Island (PLI).

H: 1—Asbirk (1979); 2,3,4—Cairns (1984), Gaston and Nettleship (1981, Table 86).

I: 1—Kartaschew (1960) in Lack (1968); 2—Norderhaug (1970); 3—Roby et al. (1981); 4—composition assumes all crustacea (Roby et al. 1981), energy density as in A.

A base map was digitized from the same projection and used to define the areas of the maps to be displayed. The area mapped was east of 100°W longitude, as there were relatively few data to the west (see, for example, Figs. 7, 9, and 10), and the inclusion of peripheral points can considerably distort contours drawn around areas with few data. This effect is particularly noticeable in the maps for July and August (see Figs. 8 and 9) between the southern

tip of Greenland and the area east of the Newfoundland Banks.

For each SAS output file (i.e., each month or season), the following procedure was used. The points were imported to SPANS, and a universe-oriented geographic coordinate ("Morton number") was assigned to each point based on latitude and longitude. The contour module of SPANS was used to generate contour maps using a

triangulated irregular network (TIN) algorithm. The TIN is a terrain model using a continuous sheet of interconnected triangular facets based on irregularly spaced points; it adapts to the level of complexity in the data and avoids redundancy in areas of low detail. Contours were developed from the TIN model using linear interpolation, and the resulting maps were sent to a laser printer after text labels were added. We provide maps of the distribution of the data points to allow readers to evaluate the match between distribution of data and confidence in the model output.

3. Results

3.1 Sensitivity testing

One of the most important aspects of model building is the ability to reveal which variables have the most effect on the model's output—i.e., in this study, which factors most influence a bird's energy budget. As an example, we performed sensitivity tests on the model run for October between latitudes 44°N and 48°N (daylength 11 h). We tested sensitivity simply by raising or lowering each input variable to reasonable extremes and measuring the effect on the estimate of ADEE for the two most dissimilar species in our array—Northern Fulmar and Dovekie *Alle alle* (Table 5). The results confirm the finding of Furness (1978) that variation in the exponents and multiplicands of the metabolic equations have the greatest effect on output in this type of model, followed quite closely by body weight.

Since the programming of our model, sufficient data have become available from isotopic studies of energy expenditure by free-living birds to allow Birt-Friesen et al. (1989) to calculate the allometric relationship between ADEE and body weight for breeding seabirds. To further verify the applicability of our model, we compared our estimates of ADEE for the chick-rearing period with those predicted by Birt-Friesen et al. (1989). Our estimates for all species except Northern Fulmar were higher than those predicted by the Birt-Friesen et al. (1989) equation for "cold-water seabirds" (CWSB, Table 6). For species that we assumed flapped for at least 50% of their time in flight, our estimates were lower than those predicted by their "cold-water seabirds using flapping flight" (CWSUFF) equation for Herring Gull *Larus argentatus* and Great Black-backed Gull *L. marinus*, and higher for the auks—Dovekies, murres, and Atlantic Puffins. Actual measurements for Dovekies (Gabrielson et al. 1991) and Common Murres (Cairns et al. 1991) are closer to those predicted by our model than the estimates derived from the CWSUFF equation of Birt-Friesen et al. (1989) (although the Birt-Friesen et al. equation included the data of Cairns et al. [1991]). Taken together, the recent isotopic studies suggest that our model estimates provide a reasonable approximation of energy expenditure during the breeding season. No direct estimates of ADEE for free-living birds are available for the nonbreeding period.

Estimates of energy requirements for individual grid squares were closely correlated with estimates of overall biomass. For the southern area in October, biomass

explained 97% of the variation in energy consumption (Fig. 4). Hence, it seems likely that the proportion of birds of different sizes and different flight patterns (e.g., flapping

Table 5  
Sensitivity tests for input parameters in energy model based on October, latitude 44–48°N, daylength 11 h

Input parameter	Likely extreme (%)	% change in output	
		Dovekie	Northern Fulmar
Body mass (W)	±10	6.35	6.35
Time flying (TDFLY)	±50	7.68	7.44
Proportion flapping flight (TFLAP)	±100	–	13.37
Time flying at night (TNFLY)	±100	8.25 <sup>a</sup>	4.87
Time swimming in daytime (TDSWIM)	±100	1.94	7.05
Time diving in daytime (TDDIVE)	±100	14.94	7.67 <sup>a</sup>
Flight multiplicand (FLMULT)	±50	14.68	10.09
Flight exponent (FLEXP)	±10	12.34	11.81
Gliding multiplicand (GLMULT)	±100	–	20.44
Swimming multiplicand (SSMULT)	±100	14.64	29.01
Diving multiplicand (SDMULT)	±100	25.68	–
BMR multiplicand (BMMULT)	±50	20.16	24.73
BMR exponent (BMEXP)	±10	16.99	28.93
Resting multiplicand (REMULT)	±50	15.16	15.18
Resting exponent (REEXP)	±10	9.18	12.63

<sup>a</sup> Change from 0 to 0.1.

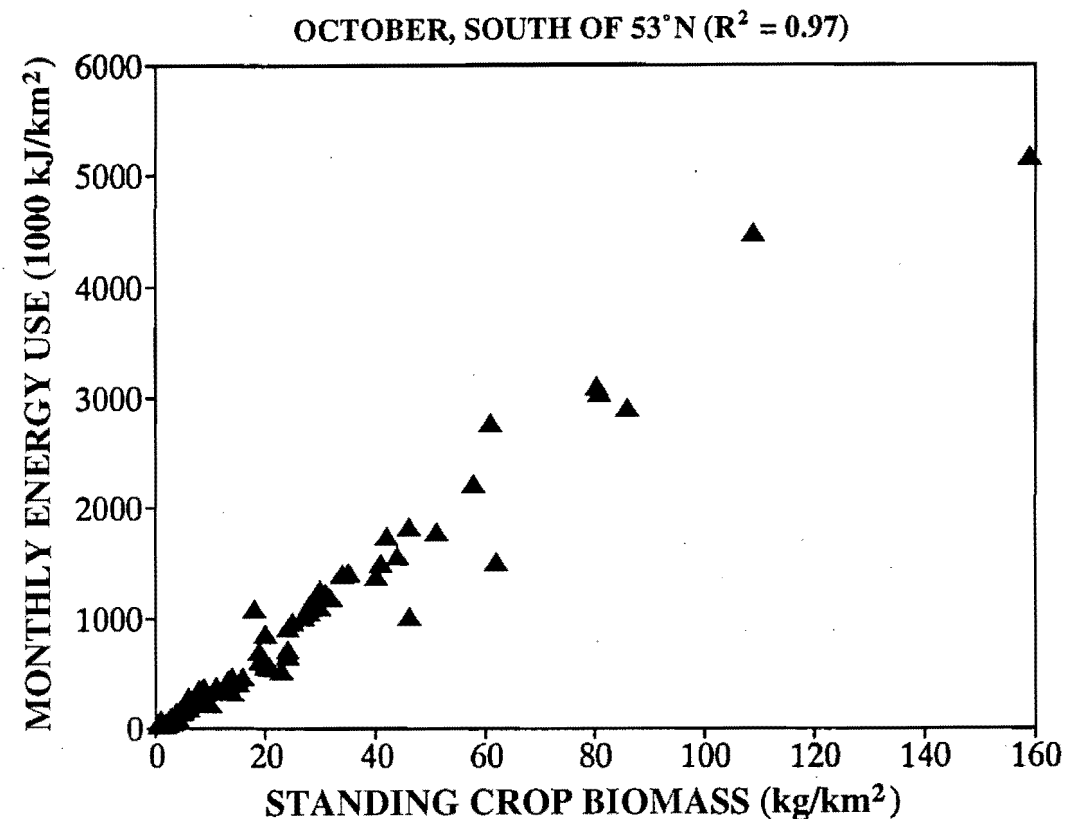
Table 6  
Comparison of our time budget model estimates of ADEE (July, southern region, except Dovekie and Northern Fulmar, northern region) with those derived from allometric equations based on direct field measurements of ADEE (Birt-Friesen et al. 1989)

Species	Time budget estimate	Allometric equation CWSB	Allometric equation CWSUFF	Direct measurement	Reference
Northern Fulmar	995	1093			
Greater Shearwater	1260	1196			
Sooty Shearwater	1530	1158			
Black-legged Kittiwake	792	710	843	794	Gabrielson et al. 1987
Herring Gull	1632	1401	1813		
Great Black-backed Gull	1954	1922	2589		
Dovekie	610	396	438	696	Gabrielson et al. 1991
Murre spp.	1910	1296	1661	1789	Cairns et al. 1991
Atlantic Puffin	1259	851	1035		

CWSB = cold-water seabirds  
CWSUFF = cold-water seabirds using flapping flight

explained 97% of the variation in energy consumption (Fig. 4). Hence, it seems likely that the proportion of birds of different sizes and different flight patterns (e.g., flapping

**Figure 4**  
Relationship of energy consumption to biomass estimated for each grid square, southern area, October



vs. gliding) was fairly constant throughout the area considered.

### 3.2 Distribution of energy demand

Figures 5–13 show (A) the distribution of data points used in the model for each time period used, and (B) the contour maps of energy demand, derived from the final output of the model; together, they illustrate the monthly distribution of the total energy required by all the seabirds. The maps include the energy demand of Dovekies and storm-petrels, which are planktivores; all the other species (which in most cases make up the bulk of the total energy demand) feed at higher trophic levels.

The percent contributions to energy demand by seabirds at different times of the year in 11 oceanographic zones are given in Table 7. Table 8 tabulates the total energy demand of seabirds in these 11 zones.

#### 3.2.1 Seasonal patterns of energy demand

In April (Fig. 5), ice limits seabird distribution south of southern Davis Strait. Peak demand ( $\text{kJ/m}^2$  per month) is in the south of the study area, where it is accounted for mainly by murres around Newfoundland and by “southern” gulls (Herring and Great Black-backed) off the Scotian Shelf and in the Gulf Stream zone (Table 7). Total energy demand was highest in the Labrador Sea (Table 8), where it was due chiefly to murres (Table 7), but data were available only for grid squares adjacent to the Labrador Shelf. Local concentrations of high energy demand near the ice edge in southern Davis Strait and on the Labrador Banks were

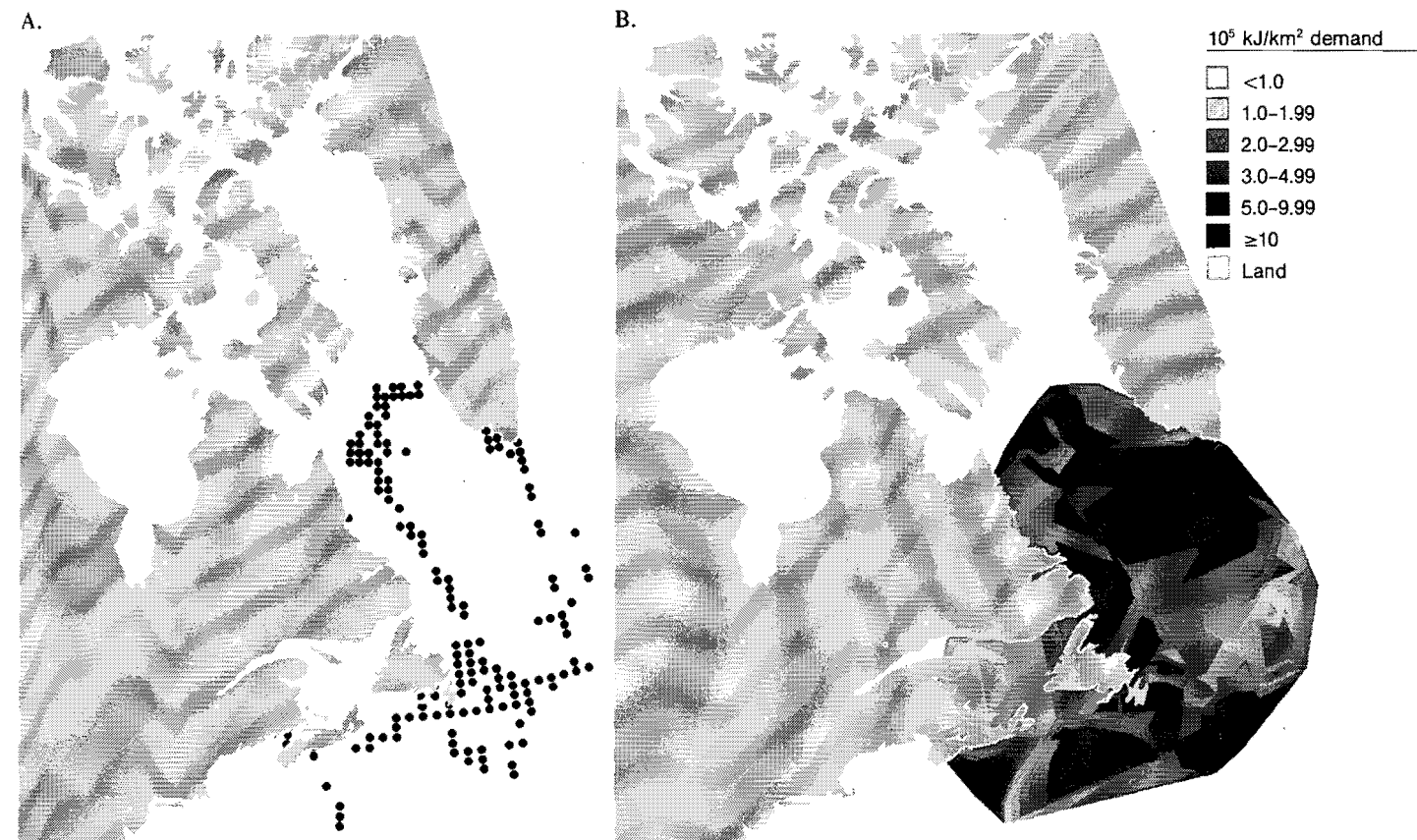
accounted for mainly by Northern Fulmars, murres, and “northern” gulls (Iceland *Larus glaucoideus*, Ivory *Pagophila eburnea*, and Glaucous *Larus hyperboreus*).

In May (Fig. 6), southern hemisphere shearwaters made a significant contribution to energy demand in the Gulf Stream and Scotian Shelf zones, whereas murres contributed most to demand off Newfoundland and on the southern Labrador Banks. Northern Fulmars continued to dominate in the Labrador Sea and northern Labrador Banks; in southern Davis Strait, demand was dominated by Dovekies (Table 7). Highest energy demand occurred on the Newfoundland Banks and in southern Davis Strait (Table 8).

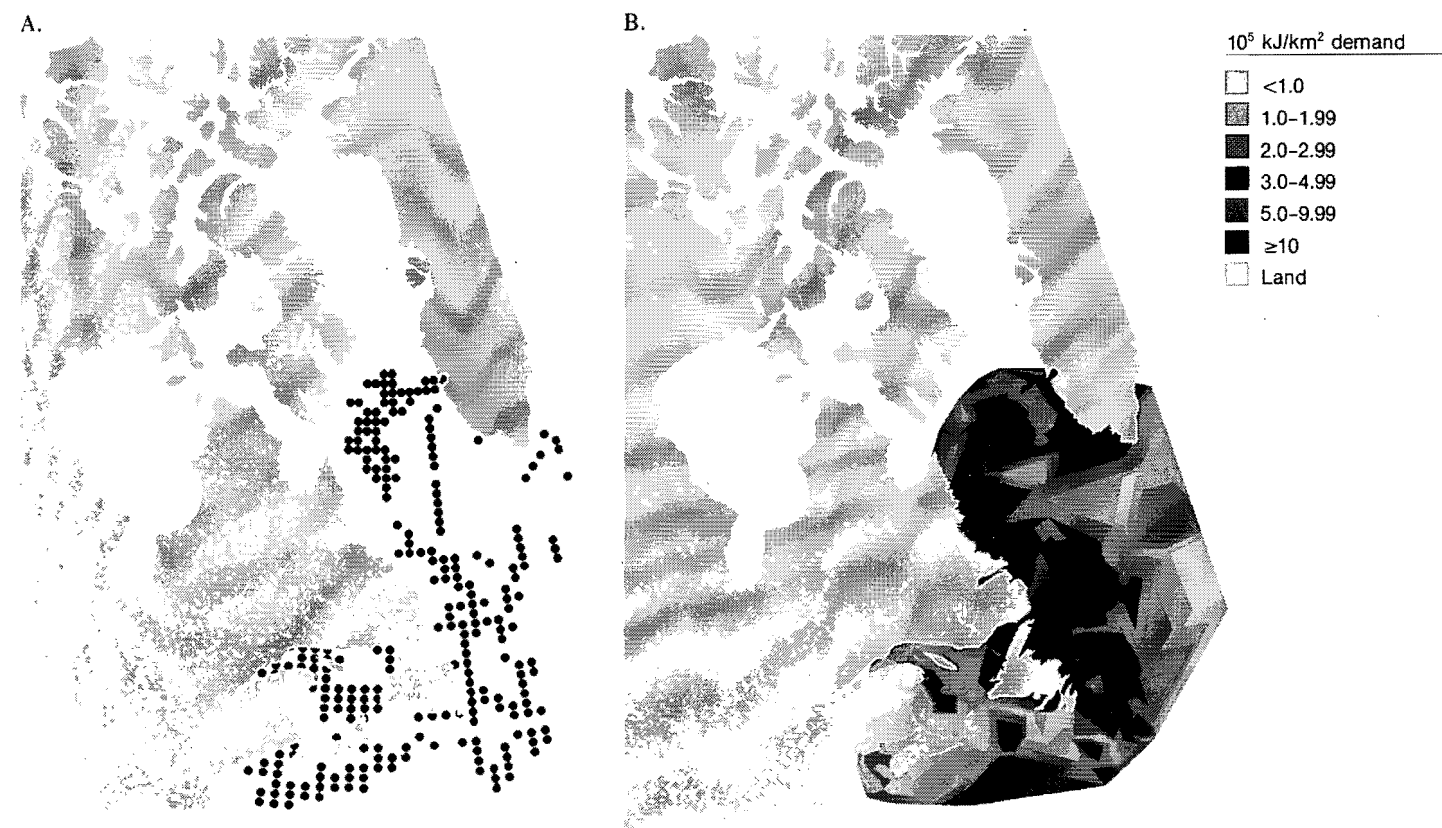
In June (Fig. 7), energy demand was concentrated close to the major breeding colonies, although there was still a peak on the Newfoundland Banks (Table 8) where murres and Northern Fulmars predominated. No data were available for northern Davis Strait or Baffin Bay/Lancaster Sound for June, and hence we were unable to model energy requirements for those areas. To estimate yearly energy use, we assumed that conditions were similar to those seen in July, as most breeding birds have arrived in these areas by early June (McLaren 1982).

July (Fig. 8) was the first month with data from northern Davis Strait, Lancaster Sound, and Baffin Bay. These zones exhibited remarkably high energy demands in both July and August—the highest estimated anywhere for any month (Table 8). This reflects the very large populations of Northern Fulmars, Dovekies, and Thick-billed Murres that breed in the area (Brown et al. 1975). In the northern part of these High Arctic zones, murres and Dovekies made up most of the energy demand, but Northern Fulmars contributed nearly two-thirds in the southern part.

**Figure 5**  
April: A. Distribution of data points available. B. Contour map of energy demand by seabirds.

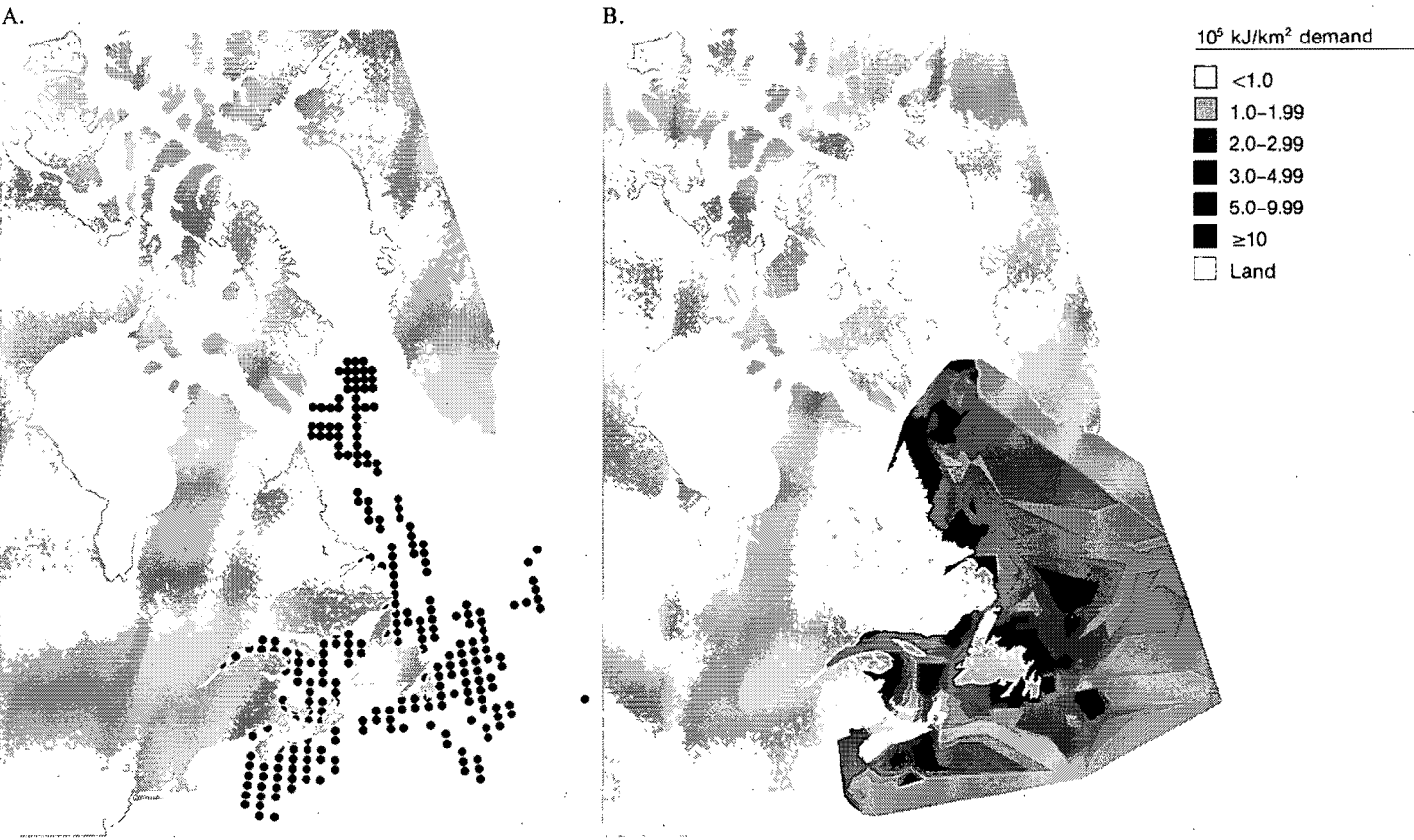


**Figure 6**  
May: A. Distribution of data points available. B. Contour map of energy demand by seabirds.

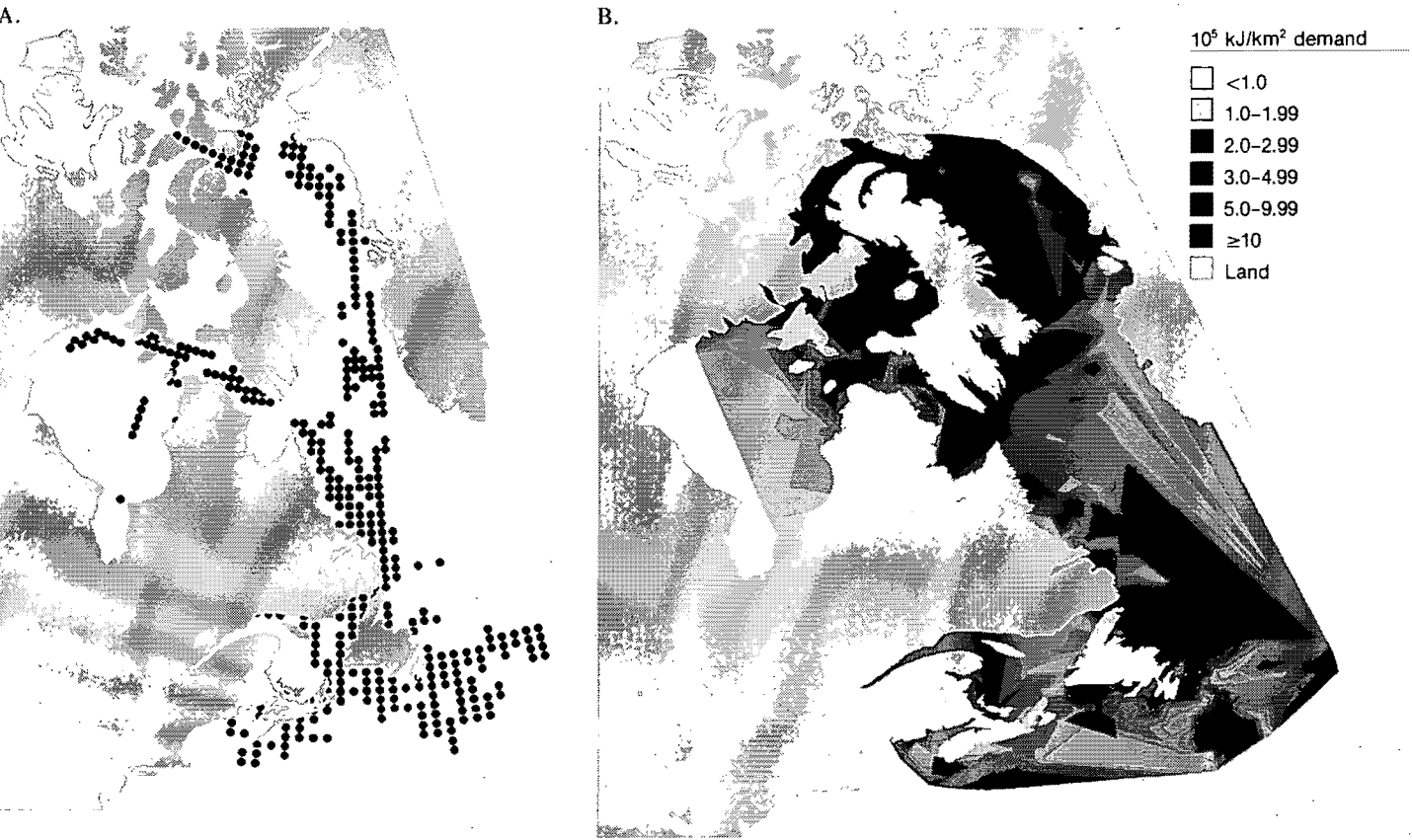




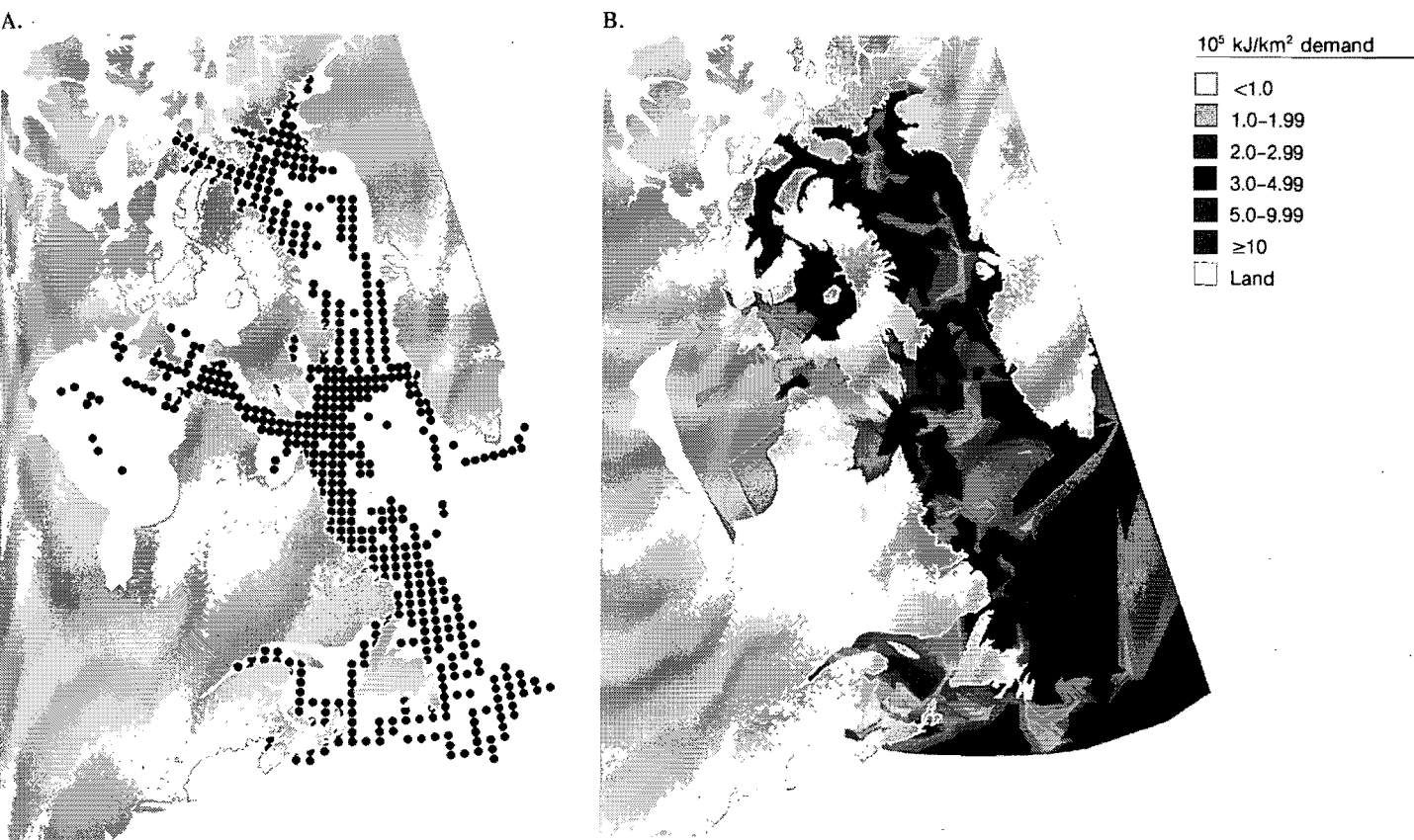
**Figure 7**  
June: A. Distribution of data points available. B. Contour map of energy demand by seabirds.



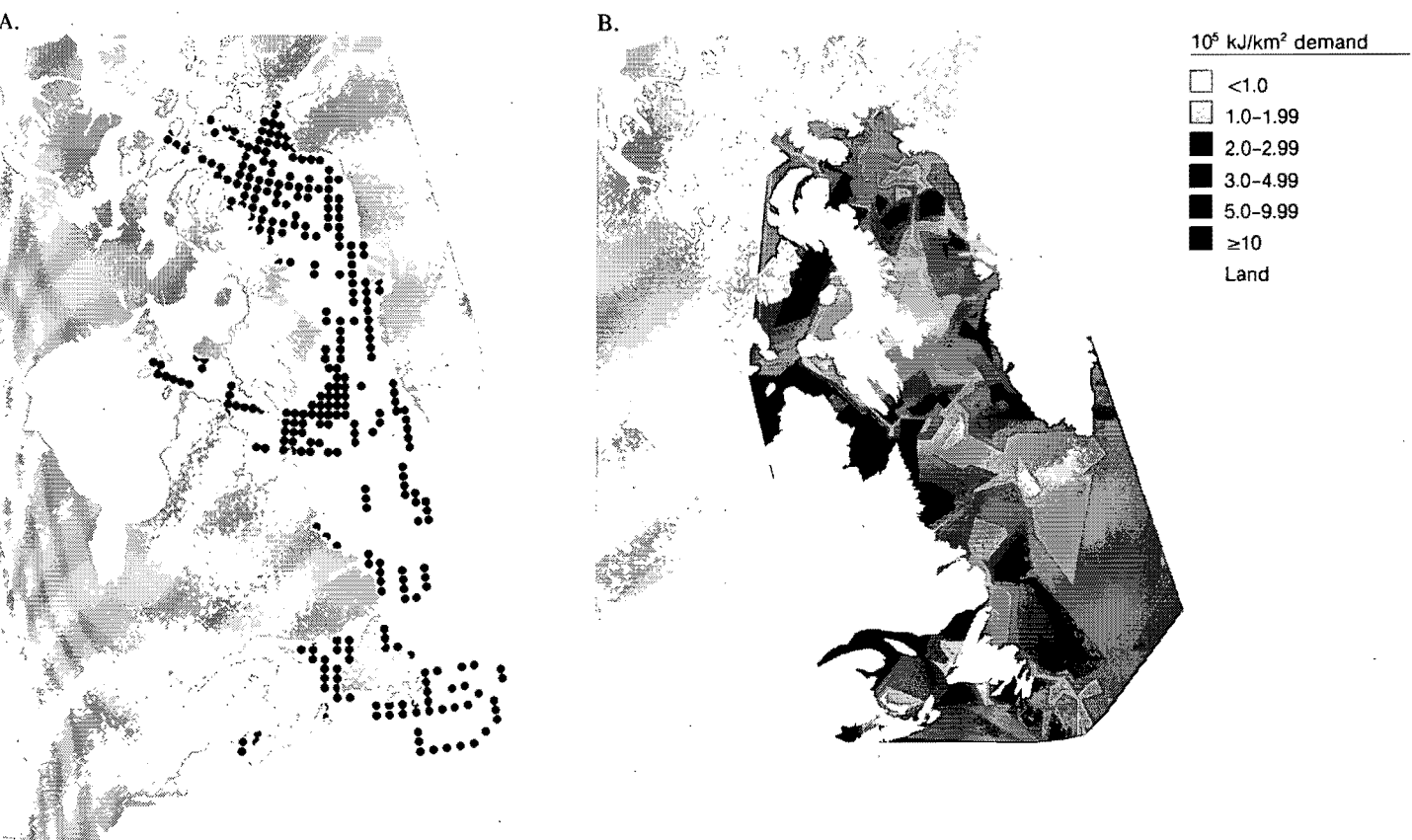
**Figure 8**  
July: A. Distribution of data points available. B. Contour map of energy demand by seabirds.



**Figure 9**  
August: A. Distribution of data points available. B. Contour map of energy demand by seabirds.

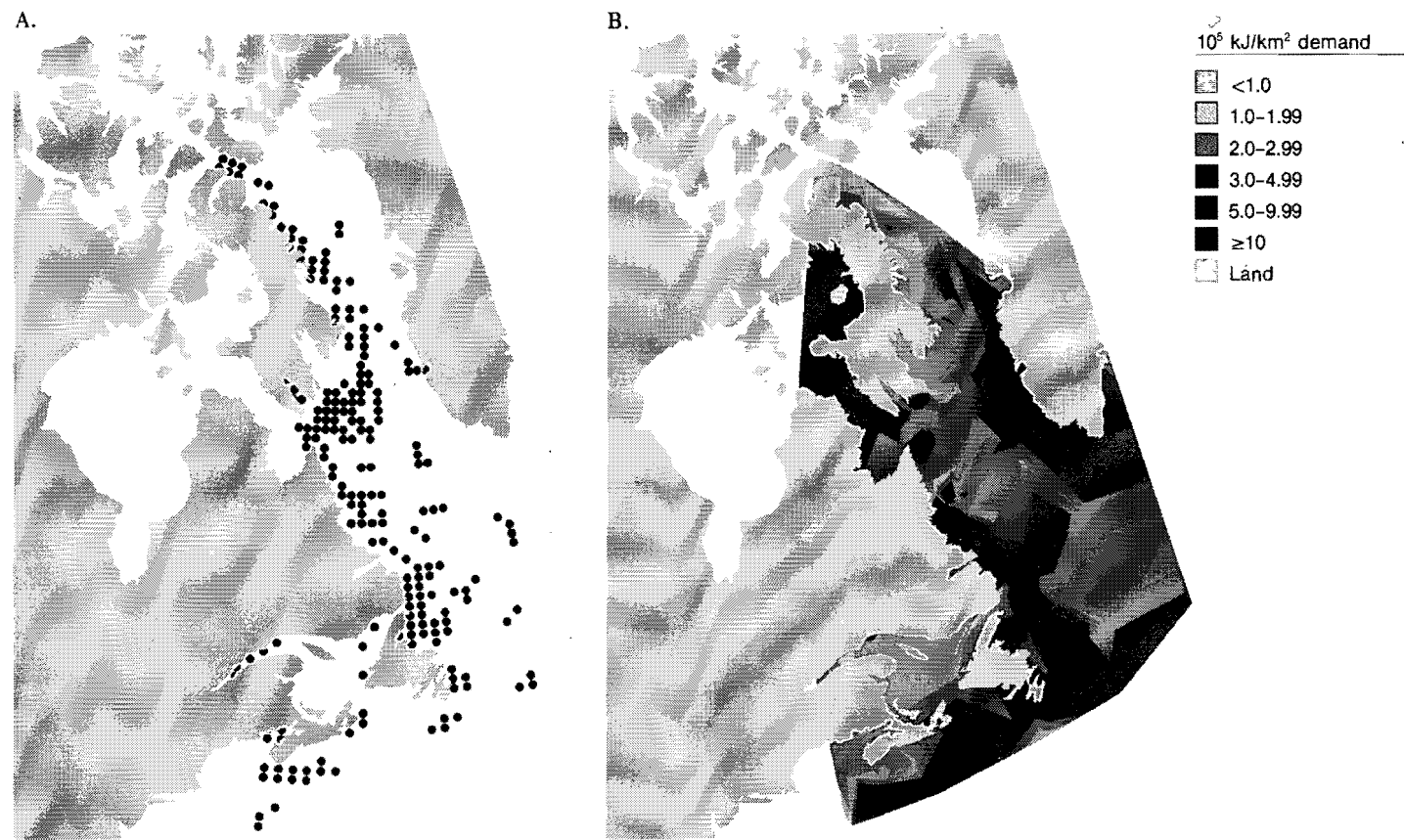


**Figure 10**  
September: A. Distribution of data points available. B. Contour map of energy demand by seabirds.

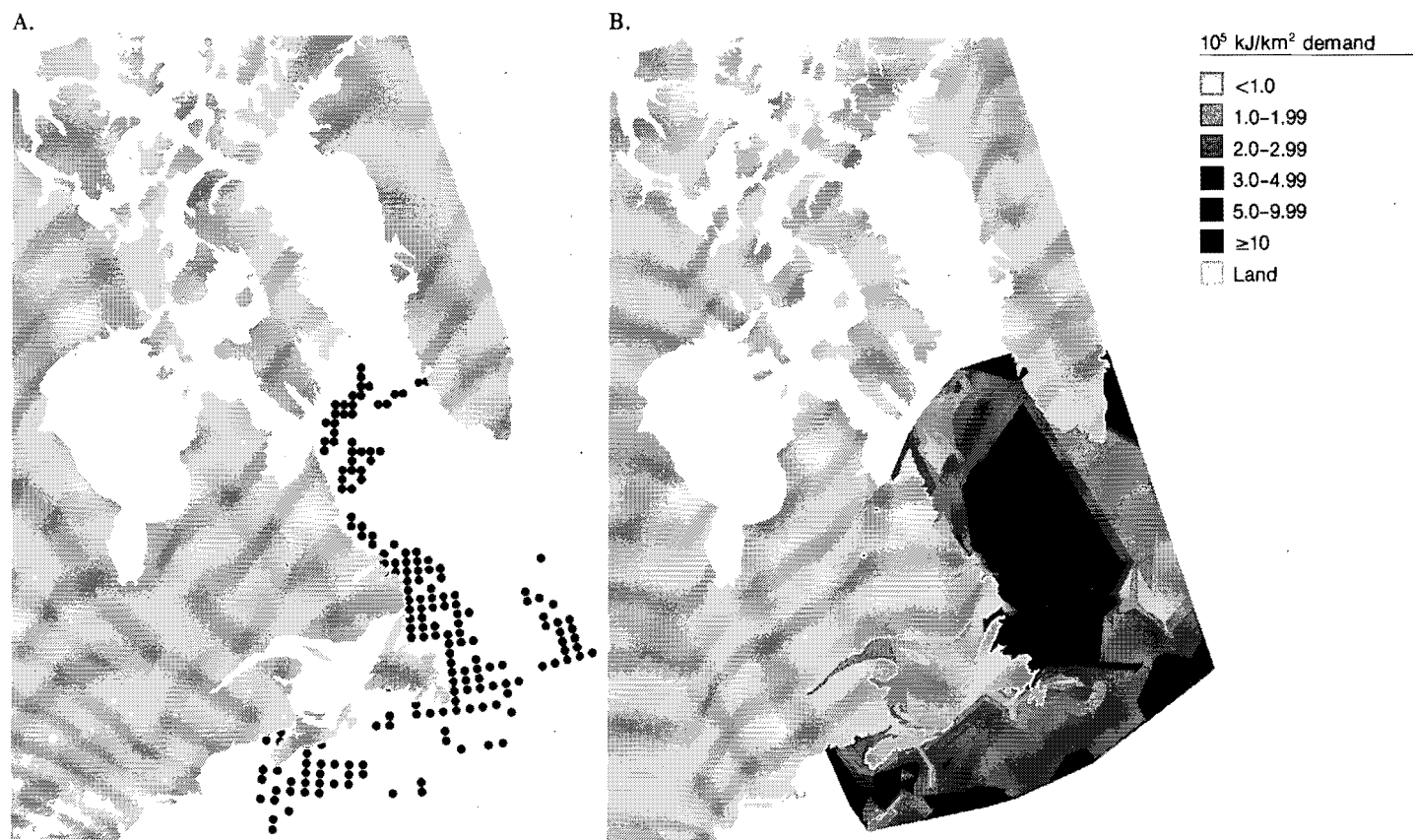




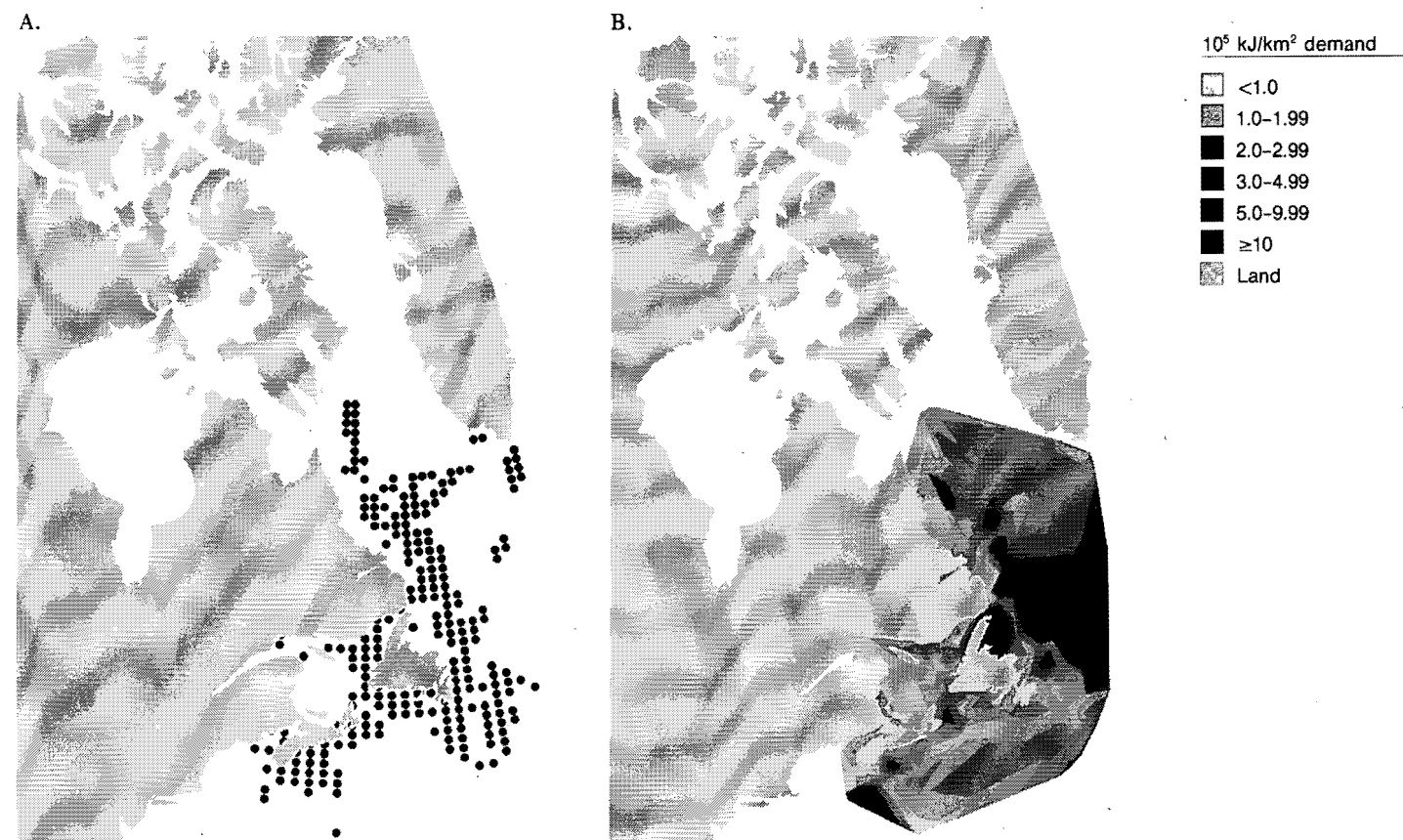
**Figure 11**  
October: A. Distribution of data points available. B. Contour map of energy demand by seabirds.



**Figure 12**  
November–December: A. Distribution of data points available. B. Contour map of energy demand by seabirds.



**Figure 13**  
January–March: A. Distribution of data points available. B. Contour map of energy demand by seabirds.



July was the month of highest energy demand in Hudson Strait, and the peak areas within this zone reflect the large colonies of Thick-billed Murres on Digges and Akpatok islands. South of 60°N, Northern Fulmars and migrant southern hemisphere shearwaters predominated, the shearwaters contributing most demand in the south and Northern Fulmars in the north (Table 7). Most of the Northern Fulmars here, like the shearwaters, must be nonbreeding migrants, because there are no large breeding colonies south of Baffin Island.

Data were most complete for August (Fig. 9), when energy requirements reached the highest values of the year in several zones (Table 8) but were patchily distributed. In Baffin Bay and Lancaster Sound, Dovekies contributed most energy demand, followed by Northern Fulmars and Thick-billed Murres, which each contributed about twice as much as Black-legged Kittiwakes (Table 7). In northern Davis Strait, murres greatly predominated; Northern Fulmars were the only other species to contribute more than 10% of the total energy demand. In the southern strait, demand was divided more evenly between Northern Fulmars, Black-legged Kittiwakes, and murres. On the northern Labrador Banks, Northern Fulmars contributed more than a third of the energy demand and shearwaters less than a third; on the southern banks, shearwaters made up nearly half and Northern Fulmars again over a third. Shearwaters dominated all zones to the south, except the Gulf of St. Lawrence and Scotian Shelf, where “southern” gulls predominated.

In September (Fig. 10), energy demand was lower overall than in August (Table 8), due as much to the

eastward movement of shearwaters after their moult as to the exodus of breeding birds from their colonies. Major changes from August included the predominance of Black-legged Kittiwakes, rather than auks, in Baffin Bay and Lancaster Sound; the predominance of Northern Fulmars in southern Davis Strait and the Labrador Sea; and a major withdrawal of shearwaters from the Labrador Sea concurrent with their greatest impact on the Gulf of St. Lawrence (Table 7).

By October (Fig. 11), Northern Fulmars predominated throughout the High Arctic and northern Davis Strait, followed by “northern” gulls in Baffin Bay/Lancaster Sound and murres and Dovekies in northern Davis Strait. Murres accounted for most energy demand in southern Davis Strait and northern Labrador Banks, but the southern Labrador Banks were still dominated by Northern Fulmars, Black-legged Kittiwakes, and gulls. Shearwaters were still of major importance on the Newfoundland Banks and the Scotian Shelf, and especially in the Gulf Stream region, where they accounted for over 90% of total energy demand. October was the first month in which murres did not predominate in Hudson Strait, where they were replaced by Northern Fulmars, but data were available only from the extreme eastern end of the strait (Table 7).

Winter data were sparse, so they have been grouped into early winter (November and December) and late winter (January through March). In early winter (Fig. 12), Northern Fulmars, Black-legged Kittiwakes, and gulls accounted for most energy demand in most zones; murres and dovekies made significant contributions only on the Newfoundland Banks (Table 7). By late winter (Fig. 13),

**Table 7**  
Percent contributions to energy demand by selected seabirds, by oceanographic zone (see Fig. 2)

Species	Jan.-Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.-Dec.
<b>Zone 1 (Northern Davis Strait [S] and Baffin Bay/Lancaster Sound [N])</b>									
Northern Fulmar	S	-	-	-	61.5	12.9	20.6	42.3	-
	N	-	-	-	6.6	23.2	34.5	32.5	-
Shearwaters	S	-	-	-	0	0.1	0	0	-
	N	-	-	-	0	0	0	0	-
Kittiwake	S	-	-	-	10.6	2.7	12.5	9.6	-
	N	-	-	-	4.0	12.2	43.2	11.6	-
Southern gulls <sup>a</sup>	S	-	-	-	0	0.2	0	0	-
	N	-	-	-	0	0	0	0	-
Northern gulls <sup>b</sup>	S	-	-	-	1.5	1.5	0.6	8.9	-
	N	-	-	-	0.6	0.6	0.5	25.6	-
Murres	S	-	-	-	18.4	80.2	27.8	20.8	-
	N	-	-	-	50.1	22.0	10.4	7.1	-
Dovekie	S	-	-	-	4.7	2.6	33.5	17.4	-
	N	-	-	-	38.0	34.6	2.3	12.1	-
Auks <sup>c</sup>	S	-	-	-	25.6	83.0	61.8	38.3	-
	N	-	-	-	88.7	63.9	13.1	30.3	-
<b>Zone 2 (Southern Davis Strait)</b>									
Fulmar		15.2	34.8	11.3	37.8	62.9	29.8	26.5	40.3
Shearwaters		0	0	0	0.4	2.5	6.4	1.6	0
Kittiwake		1.4	8.4	7.8	25.6	17.8	23.8	20.9	10.3
Southern gulls		0.6	1.0	0.9	0	0.7	0.4	1.8	1.7
Northern gulls		67.0	23.1	11.3	3.2	0.7	0.5	5.6	25.3
Murres		4.3	29.5	7.6	26.4	4.7	26.2	40.4	19.1
Dovekie		11.3	3.0	60.9	2.6	5.5	3.9	3.0	3.2
Auks		15.9	32.7	68.5	29.1	5.2	30.4	14.7	22.4
<b>Zone 3 (Northern Labrador Banks)</b>									
Fulmar		7.7	18.0	44.6	63.3	49.2	34.1	0	13.2
Shearwaters		0	0	0	0	19.3	30.9	0	0.1
Kittiwake		2.4	6.3	15.2	0.8	9.4	13.6	11.5	6.9
Southern gulls		0	0.6	24.1	0	3.0	2.4	9.6	1.7
Northern gulls		5.7	48.3	3.3	0	0.2	5.6	19.8	2.8
Murres		0.3	49.0	12.8	35.9	8.6	4.5	0	73.5
Dovekie		83.9	0.1	0	0	0	0.3	0	1.5
Auks		84.2	49.1	12.8	35.9	10.7	10.4	41.1	75.2
<b>Zone 4 (Southern Labrador Banks)</b>									
Fulmar		70.0	79.5	28.8	4.8	35.5	35.7	17.1	28.2
Shearwaters		0	0	0	12.7	45.8	44.8	46.2	2.4
Kittiwake		5.5	2.7	1.0	5.7	4.4	7.1	14.6	32.7
Southern gulls		4.2	2.7	11.1	3.9	1.8	2.0	11.4	26.5
Northern gulls		19.5	15.2	3.7	0.3	0	0	0.1	2.4
Murres		0.4	0	42.8	53.3	5.7	2.3	7.9	3.0
Dovekie		0.3	0	10.6	0.1	0	0	0	4.3
Auks		0.9	0	53.6	71.5	9.2	6.2	14.6	7.3
<b>Zone 5 (Labrador Sea)</b>									
Fulmar		82.0	7.4	45.5	63.1	35.8	30.4	62.9	71.5
Shearwaters		0	0	0	20.2	32.6	50.0	4.3	0.6
Kittiwake		4.6	6.9	11.3	0.4	23.4	7.6	18.7	14.1
Southern gulls		0.2	0.2	17.0	8.6	0.4	0.6	0.5	1.6
Northern gulls		10.6	1.2	7.2	0	0	0	0	2.4
Murres		0.4	84.3	17.0	8.6	0.4	0.6	6.9	1.6
Dovekie		2.1	0	11.0	1.8	0	0	1.3	4.7
Auks		2.5	84.3	27.9	13.7	2.1	1.0	8.7	6.4
<b>Zone 6 (Gulf of St. Lawrence)</b>									
Fulmar		2.4	-	1.7	2.8	7.7	1.1	6.1	1.7
Shearwaters		0	-	0	0.3	14.1	9.6	23.0	0
Kittiwake		10.0	-	7.3	6.5	11.5	5.5	4.5	9.1
Southern gulls		23.3	-	34.5	28.0	46.2	51.0	61.1	72.5
Northern gulls		18.5	-	0.8	0	0	0	0.3	10.5
Murres		11.6	-	39.4	38.2	10.5	0.9	0	4.2
Dovekie		0.9	-	0	0	0	0	0	0
Auks		45.7	-	39.7	38.3	11.5	1.2	0.2	4.2
<b>Zone 7 (Newfoundland Banks)</b>									
Fulmar		26.2	10.0	13.8	2.4	4.5	11.4	7.4	17.8
Shearwaters		0	0.2	8.2	26.6	59.3	76.0	63.1	53.5
Kittiwake		12.4	9.0	3.4	1.9	0.8	0.9	3.1	8.2
Southern gulls		18.4	12.8	1.9	6.8	9.4	1.4	10.9	15.1
Northern gulls		2.5	0.4	0.2	0	0	0	0	0.2
Murres		21.2	62.6	59.0	56.7	14.3	0.5	0.1	1.7
Dovekie		18.0	1.0	8.1	0.3	0	0	0	0.4
Auks		40.6	65.7	68.9	58.4	17.5	3.9	2.1	2.1

**Table 7 (continued)**  
Percent contributions to energy demand by selected seabirds, by oceanographic zone (see Fig. 2)

Species	Jan.-Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.-Dec.
<b>Zone 8 (Scotian Shelf)</b>									
Fulmar	6.9	2.0	15.3	2.3	0.4	0	0.8	4.3	5.3
Shearwaters	0	0	29.0	63.8	38.0	10.8	2.7	48.6	10.1
Kittiwake	4.8	0.1	0.2	0.4	0	1.8	1.8	4.1	1.9
Southern gulls	61.4	82.2	30.6	23.4	55.2	80.4	42.9	20.1	80.4
Northern gulls	4.7	0.2	0	0	0	0	0	6.1	0
Murres	7.8	2.4	4.6	0.1	0	0	0	0.1	0.2
Dovekie	14.1	0	0.1	0	0	0	0	0	0.2
Auks	22.2	2.4	4.6	0.1	0	0	0	0	0.5
<b>Zone 9 (Gulf Stream)</b>									
Fulmar	5.6	1.8	6.2	2.8	0.6	0	0	0.4	1.2
Shearwaters	0	0	41.5	48.5	47.4	78.7	58.1	90.9	13.5
Kittiwake	9.1	0	0	0	0	0	6.1	2.3	3.8
Southern gulls	73.6	83.0	40.7	18.6	45.8	11.0	18.5	4.5	78.5
Northern gulls	0.7	0.3	0	0	0	0	0	0	0
Murres	2.3	0	0.2	0	0	0.8	0.1	0.2	1.0
Dovekie	7.9	2.0	7.4	0	0	0	0	0	0.4
Auks	10.7	2.0	8.2	0	1.8	7.2	0.7	0.3	1.7
<b>Zone 10 (Hudson Strait)</b>									
Fulmar	-	-	-	30.9	0.4	16.1	26.8	55.2	86.1
Shearwaters	-	-	-	0	0	3.3	0	0	0
Kittiwake	-	-	-	0.4	0	6.7	13.1	5.7	0
Southern gulls	-	-	-	13.0	0.4	0.6	1.2	0.3	0
Northern gulls	-	-	-	0	0.5	0.9	0.6	11.9	6.7
Murres	-	-	-	44.6	95.1	66.2	52.8	17.9	0
Dovekie	-	-	-	0	0	2.0	2.0	8.5	7.2
Auks	-	-	-	46.1	96.1	71.1	58.2	26.5	7.2
<b>Zone 11 (Hudson Bay)</b>									
Fulmar	-	-	-	-	0	3.3	-	-	-
Shearwaters	-	-	-	-	0	0	-	-	-
Kittiwake	-	-	-	-	0	0.1	-	-	-
Southern gulls	-	-	-	-	8.1	11.2	-	-	-
Northern gulls	-	-	-	-	0	17.1	-	-	-
Murres	-	-	-	-	70.9	44.0	-	-	-
Dovekie	-	-	-	-	0	0	-	-	-
Auks	-	-	-	-	89.3	56.7	-	-	-

<sup>a</sup> Southern gulls = Herring and Great Black-backed gulls.

<sup>b</sup> Northern gulls = Iceland, Ivory, and Glaucous gulls.

<sup>c</sup> Auks = murres, Razorbill, Dovekie, and Atlantic Puffin.

**Table 8**  
Energy demand of seabirds, by oceanographic zone<sup>a</sup>

Zone	Energy demand (kJ/m <sup>2</sup> per period)									Total energy demand (kJ/m <sup>2</sup> per year)
	Jan.-Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.-Dec.	
1 Baffin Bay/Lancaster Sound (N)	-	-	[1.91]	[3.82]	3.82	4.55	0.30	0.11	-	14.51
Northern Davis Strait (S)	-	-	[0.17]	[0.34]	0.34	4.61	0.41	0.14	-	6.01
2 Southern Davis Strait	(0.12)	0.93	1.44	0.48	0.23	1.40	0.72	0.55	0.18	6.05
	[0.18]									[6.11]
3 Northern Labrador Banks	1.89	(0.74)	1.02	(0.22)	0.43	0.99	(0.46)	2.04	0.48	8.27
		[1.45]		[0.72]			[0.98]			[10.00]
4 Southern Labrador Banks	1.29	0.44	1.10	0.75	0.97	1.55	0.44	1.24	2.43	10.21
5 Labrador Sea	0.50	(3.15)	0.46	0.23	0.46	0.96	(0.19)	0.38	(1.14)	7.47
		[0.48]					[0.67]		[0.50]	[4.64]
6 Gulf of St. Lawrence	0.16	[0.33]	0.51	0.59	0.33	0.43	0.50	0.11	(<0.01)	2.96
								[0.16]		[3.12]
7 Newfoundland Banks	0.26	1.33	1.44	1.07	0.72	1.67	0.34	0.98	0.39	8.20
8 Scotian Shelf	0.21	0.28	0.17	0.34	0.41	0.29	(0.28)	0.35	0.58	2.91
							[0.32]			[2.95]
9 Gulf Stream	(0.24)	(0.57)	(0.33)	(0.18)	(0.32)	(0.45)	(2.11)	(0.70)	(0.51)	5.41
10 Hudson Strait	-	-	[0.23]	(0.46)	1.08	0.50	0.80	0.39	(0.05)	3.51
				[0.79]						[3.84]
11 Hudson Bay	-	-	[0.10]	[0.20]	(0.21)	0.05	[0.05]	-	-	0.61
Mean, excluding Hudson Bay, Labrador Sea, Gulf Stream, and areas N of 65°N (Zones 1, 5, and 9)										[6.35]

<sup>a</sup> Figures in boldface are based on more than 25% of grid squares for the zone. Figures in regular type are based on 10-25% of grid squares for the zone.

Figures in parentheses are based on less than 10% of grid squares for the zone. Figures in square brackets are interpolated or estimated; totals in square brackets include interpolations.

Northern Fulmars dominated most zones, but there were large concentrations of Dovekies on the northern Labrador Banks, and "southern" gulls predominated on the Scotian Shelf and in the Gulf Stream zone. Murres contributed more than 10% of total energy demand only in the Gulf of St. Lawrence and on the Newfoundland Banks (Table 7); at this time of year, many murres were probably too close inshore to be detected by PIROP counts.

## 4. Discussion

### 4.1 Deficiencies in data

One of the most useful results of constructing a model is the light that it can shed on the quality and coverage of the relevant data. Accordingly, we summarize here the major gaps in relevant aspects of the biology of seabirds in eastern and Arctic Canada, as they became evident during this study.

#### 4.1.1 Coverage

The data base on which our maps were based consists of more than 350 000 10-minute counts. Despite this impressive size, the coverage was still inadequate in many areas. In the High Arctic, we had no data for May or June, although aerial surveys have shown that many birds are present by mid-May (McLaren 1982). In Hudson Strait, data were adequate (>10% of grid squares) only from July to October, whereas observations in Hudson Bay never achieved a better than 10% coverage except in August. Data for the northern Labrador Banks were inadequate for April, June, and September, and for the Labrador Sea for April, September, and early winter. Moreover, records in the Labrador Sea in April, June, and August were highly concentrated along the edge of the Labrador Banks. Hence, estimated energy demand for those months was probably characteristic of the continental slope zone, rather than of the Labrador Sea as a whole. Data were poor for the Gulf of St. Lawrence in early winter and for the Scotian Shelf in September. Practically all the data from the Gulf Stream zone came from areas close to the southern edge of the Scotian Shelf or the southern edge of the Newfoundland Banks. As with those for the Labrador Sea, overall estimates for this zone probably gave values characteristic of the continental slope, rather than of the whole area, as defined in Figure 2. For these two zones, we shall not discuss estimates of annual energy demand further because of the uncertainty regarding which areas they actually represent. In the High Arctic (Zone 1), extensive areas are covered by pack ice during the summer, especially along the east coast of Baffin Island (Brown 1986). Ships used for the surveys necessarily concentrated their activities in open water areas where most of the birds would also have concentrated. Hence, extrapolation of observed densities to the whole area may be misleading, and the very high total energy demand for this zone in July and August may be

overestimated by up to 20% in July and 10% in August (based on ice maps in Lancaster Sound Regional Study 1980).

#### 4.1.2 Breeding biology

Several detailed studies have been carried out—many of them either by, or associated with, the Canadian Wildlife Service—on a broad range of species from the Gulf of St. Lawrence to the High Arctic. A significant proportion of this work has not yet been published, and only some parts of it have been available to this project. Enough data are available to enable comparisons to be made between different colonies of one species, notably for Thick-billed Murres but also for Black-legged Kittiwakes, Atlantic Puffins, Common Murres, and Razorbills *Alca torda*. Notable exceptions are the *Larus* gulls, for which much basic information remains to be gathered or published.

Harris (1985) warned that energy models that apply data from one colony to others may be seriously flawed because of considerable intraspecific differences in some aspects of breeding biology. We are aware of this difficulty, and our model allows such differences to be taken into account, if necessary colony by colony, at the price of some tedious but straightforward programming at various intermediate stages of the model. However, aside from the division into northern and southern areas, we have made no attempt to incorporate a colony by colony approach in the present study.

#### 4.1.3 Life tables

Life table data are unsatisfactory, because there have been no long-term banding studies in Canada from which reliable survival data can be obtained. For these important parameters, it has been necessary to use European data (e.g., Dunnet et al. 1979; Hudson 1985; Coulson and Thomas 1985). The lack of comparable studies in eastern North America is one of the most glaring deficiencies in the material at our disposal.

#### 4.1.4 Time budgets

Apart from those for the two murre species (Gaston 1985; Cairns et al. 1987), there are very few data either from Canada or from Europe, although again the latter source has been used more than is desirable. In particular, there is

virtually no information on the behaviour of nonbreeders, which make up a substantial proportion of the populations concerned. Activity budgets of birds at sea are nonexistent, and much of this void in the data could be filled relatively simply by observations (e.g., of time spent flapping vs. time spent gliding) at little cost.

#### 4.1.5 Energy budgets

We relied almost entirely on equations published by physiologists. Early values were based on nonseabird species in artificial conditions, but rapid strides have been made in measuring these parameters in the field (e.g., Birt-Friesen et al. 1989). This work should be extended across as wide a taxonomic and structural range of species as possible. However, direct measurement of energy consumption outside the breeding season is not yet technically feasible.

#### 4.1.6 Seabird diets

Dietary information is sparse, both geographically and temporally, and much of it is presented as numbers of prey items or frequency of occurrence; neither form allows biomass estimates to be made. Diets of seabirds in winter off Canada—apart from recent data on Thick-billed Murres off Newfoundland (Elliot et al. 1990)—are virtually unknown.

#### 4.2 Spatial variation in energy consumption

The lowest values for year-round energy consumption were estimated for Hudson Bay, the Gulf of St. Lawrence, and the Scotian Shelf. Hudson Bay is well known to have low productivity as a result of a strong vertical stratification of water, resulting in little mixing of surface water with deeper waters (Roff and Legendre 1986). In the Gulf of St. Lawrence, marine bird populations are known to be much smaller than formerly, probably because they have still not recovered from overharvesting during the 18th and 19th centuries (Nettleship and Evans 1985). The dearth of breeding seabirds along the coast of Nova Scotia, although affected by human persecution, may also reflect a shortage of suitable breeding sites. The fact that this area is less attractive to nonbreeding visitors than the continental shelf areas farther north presumably reflects differences in the availability of food. Predictably, the highest energy demand was estimated for the Baffin Bay/Lancaster Sound area, which supports very large populations of seabirds during the summer, and on the Labrador and Newfoundland banks, long known as areas of high productivity.

Compared with studies carried out at smaller scales (e.g., Brown 1980; Hunt and Schneider 1987; Schneider et al. 1987; Piatt 1990), the amount of variation in year-round energy consumption by seabirds among our oceanographic zones appears small. If we omit the enclosed waters of Hudson Bay, where strong vertical stratification causes low primary productivity over a uniquely large area (Roff and Legendre 1986), then the highest and lowest estimates differ by a factor of 4.9 (2.9–14.1 kJ/m<sup>2</sup> per year). This is similar to the variation found among different parts of Georges Bank, adjacent to the southern edge of our area and oceanographically similar to our Scotian Shelf zone (3.6–19.9 kJ/m<sup>2</sup> per year; Schneider et al. 1987). The total

area of Georges Bank is smaller than that of any one area that we considered. Likewise, Cairns et al. (1991) found large variations in the harvest of prey by seabirds among different fisheries zones within the Gulf of St. Lawrence. It is possible that variation within some of our zones would be greater than that observed among zones. Also, as explained above, the energy demand in the oceanic zones of the Labrador Sea and Gulf Stream may have been exaggerated by the uneven distribution of grid squares for which information was available.

#### 4.3 Energy demand and the availability of prey

Mapping the impact of seabirds on particular species of prey is not possible at present because the data on fish stocks and distribution are not available at a sufficiently fine resolution. Several attempts have been made to assess the impact of seabirds on capelin around Newfoundland (Threlfall 1983; Brown and Nettleship 1984); these have used unpublished figures on the diets of many seabird species and address a region, rather than the grid square approach employed in this model. The major problem lies with the fish stock data. These were reviewed (for capelin, the best known of the species that are a major prey of seabirds) by Carscadden (1984), whose best figures for one stock (Div. 2J3K) varied by a factor of seven over nine of the years covered by PIROP data, and who showed elsewhere (Carscadden et al. 1981) that Russian and Canadian results from the most up-to-date technique (acoustic scanning) could differ in the same year by an order of magnitude. Further "guesstimates" of the impact of seabirds on capelin stocks can hardly be justified in this situation, although refinement of techniques for estimating the seabirds' energy demands—as in the model presented here—will enable such estimates to be made when more reliable fisheries data become available.

#### 4.4 Comparisons with other studies

Estimates of the amount of food taken by seabirds in a variety of oceanographic regions are now available. The results of these studies have been converted into common units for comparison (Table 9). Figures from the present study are at the bottom end of the range, which is not surprising in view of the large proportion of the region covered by ice for much of the year. Nevertheless, the mean food requirements of seabirds in all zones except Hudson Bay are close to those estimated for Georges Bank, the eastern Bering Sea, and waters adjacent to the Shetland Islands, all continental shelf areas in boreal or arctic waters.

The numbers in Table 9 depend critically on the assumed energy density of prey; we have used 6 kJ/g in deriving our food requirements, but this conversion factor is derived from prey taken during the breeding season, which may be richer in energy than the annual average. A more conservative value of 4 kJ/g (which is the average, for example, of prey available to Antarctic seabirds in the Scotia Sea; Croxall et al. 1985) raises the mean food requirements off eastern and Arctic Canada to 1.6 g/m<sup>2</sup>, essentially identical with the estimates for Georges Bank and the eastern Bering Sea.

Our estimate of energy consumption for the Gulf of St. Lawrence (3.12 kJ/m<sup>2</sup> per year) is equivalent to 112 000 t

**Table 9**  
Comparison of food requirements of seabirds in different oceanographic regions

Location	Food requirements (g/m <sup>2</sup> ) <sup>a</sup>	Reference
Peru	11–45	Schaeffer 1970
Oregon	8	Wiens and Scott 1975
Georges Bank	1.6	Powers and Backus 1987
Eastern Bering Sea	0.5–2.5	Schneider and Hunt 1982
Shetland Islands waters	1.9	Furness 1978
Scotia Sea (Antarctic)	6.5	Croxall et al. 1985
Southern Davis Strait	1.0	This study
Hudson Strait	0.6	This study
Hudson Bay	0.1	This study
Northern Labrador Banks	1.7	This study
Southern Labrador Banks	1.7	This study
Newfoundland Banks	1.4	This study
Gulf of St. Lawrence	0.4	Cairns et al. 1990
Gulf of St. Lawrence	0.5	This study
Scotian Shelf	0.5	This study
Eastern Canada (mean)	1.1	This study

<sup>a</sup> Mean wet weight of food taken calculated for this study by assuming 1 g wet weight = 6 kJ.

of food over the entire 214 000 km<sup>2</sup> (1 g/m<sup>2</sup> = 1 t/km<sup>2</sup>). Cairns et al. (1991), using a similar energy modelling approach but basing their estimates on the Birt-Friesen et al. (1989) regression for free-living seabirds, estimated 80 000 t for the breeding population alone. Nonbreeding visitors have a relatively small presence in the gulf compared with other waters. Hence, the small difference between the two figures emphasizes the convergence of estimates obtained by different means as techniques are refined and allometric equations are improved.

Our figures tend to support the suggestion of Schneider et al. (1987) that areas of comparable size and oceanography in the northern hemisphere (boreal/arctic shelf ecosystems) support seabird populations that harvest similar amounts of energy from the marine environment. Such figures are substantially lower than those from areas of enhanced marine productivity, such as major wind-driven upwellings and the Southern Ocean. The concordance of figures derived from comparable ecosystems suggests that marine productivity and the consequent supplies of food available to seabirds are the main determinants of seabird populations at a regional scale.

A large proportion of energy consumed by marine birds in eastern Canadian waters is accounted for by nonbreeding visitors from the eastern Atlantic and the southern hemisphere, and it is interesting to speculate why this is so. Considering the great importance of the Labrador Banks to seabirds throughout the year, the breeding populations of seabirds in the area are surprisingly small (Brown et al. 1975). The same applies to southern Davis Strait, where summer energy use is higher than in any area outside the Labrador and Newfoundland banks. Conversely, nonbreeding summer visitors do not penetrate north of 65°N, the area where the intensity of use by breeding seabirds is highest. It may be that there is a causal relationship between the low breeding populations of seabirds in these areas and their importance as feeding areas for staging and wintering populations. To discover which can be regarded as cause and which as effect will require further study.



## Appendix 1: Input data and formulae used in the model

### Time budgets

#### Time spent flapping and gliding

In all species, the partitioning of flying between flapping and gliding was assumed to be the same by day and by night. Northern Fulmars and shearwaters make extensive use of gliding flight, and we assumed that they glided for 75% of flying time. Gannets and larids were assumed to flap for 50% and storm-petrels for 75% of flying time, and auks were assumed to flap all the time.

#### Time on the water in the daytime

Time on the water was divided into resting and swimming on the surface and swimming underwater. Phalaropes, storm-petrels, jaegers, and gulls do not swim underwater to any significant extent. Their time on the water was divided equally between surface swimming and resting. Northern Fulmars feed almost entirely on the surface, swimming underwater only occasionally; 5% of time on the water was allocated to underwater diving, 45% to surface swimming, and 50% to resting. Northern Gannets feed underwater, but only after diving from high above the surface, so that most of the energy they use derives from kinetic energy developed in flight. They rarely submerge from the surface. Underwater swimming is allotted 5% of their time on the water, and the other 95% is allocated to resting. Auks pursue prey underwater after diving from the surface, and Thick-billed Murres in summer spend about the same time on the surface and under the surface (Gaston 1985); therefore, in the daytime, 25% of their time on the water is allotted to swimming underwater, 25% to swimming on the surface, and 50% to resting. Shearwaters feed at and below the surface, pursuing prey underwater more often than Northern Fulmars but less frequently than auks. We allotted 15% of their time on the water to swimming below the surface, 35% to swimming on the surface, and 50% to resting.

#### Activities at night

Partitioning activities at night is particularly difficult, because the assumption that birds rest at night, which is often made in summer (e.g., Gaston 1985 for Thick-billed

Murres), is unlikely to apply at these latitudes in winter, when nights are very long. Some Ivory Gulls and Black Guillemots overwinter in the High Arctic (Brown and Nettleship 1981), where there is practically no daylight for several months. These birds must be able to feed at night, as storm-petrels are known to. Further, birds may not cease flying at night; dusk and dawn observations of birds at sea show no obvious signs of birds settling down on the water or rising from it, as would be expected if they spent the night on the water (R.D. Elliot, pers. commun.). To allow for the possibility that seabirds both feed and fly to some extent at night, all species except auks are assumed to fly 10% of the night. While the seabirds are on the water, it is assumed that they spend 25% of their time swimming at the surface and the remainder resting, except for auks and shearwaters, which we assume spend 5% of the time swimming underwater and 20% swimming on the surface.

### Moult period

Most species have a complete postnuptial moult, beginning for some during the breeding period, and an incomplete prenuptial body moult—often mostly or entirely the head feathers. The postnuptial moult presumably makes a significant addition to energy expenditure. As the postnuptial moult involves the flight feathers, whose growth can be scored numerically, quantitative data are more likely to be available for it. The prenuptial moult, which involves a smaller proportion of the feathers than the postnuptial moult and does not include the flight feathers, is not included in our model.

The cost of postnuptial moult in each month is estimated by dividing the total energy cost of the moult by the number of months over which it is spread. The duration is taken to be the entire period from the first to last months given in the literature. As the distribution of moult scores within a population is approximately normal during most of the moult, this method will tend to overestimate the energy required for moult at the beginning and end of the moult period and underestimate it during the peak.

### Energy equivalents

#### Flapping flight

Use of a multiple of BMR to estimate the energy used in flapping flight (EFF) is unsound, because the different components of the equation describing power requirements scale differently to body weight (Pennycuik 1982). Instead, we used the Kendeigh et al. (1977) equation 5.43, which is based on a number of species of nonpasserines with body weights ranging from less than 4 g to more than 1 kg.

$$\text{EFF (kJ/d)} = 3939.02 \times W^{0.698} \quad (\text{W in kg}) \quad (4)$$

#### Gliding flight

The energy demand of gliding flight (EGF) has been determined only for the Herring Gull (Baudinette and Schmidt-Nielsen 1974), which uses 50 kJ/h—3.1 times the BMR of the species, as measured by Lustick et al. (1978, in Ellis 1984). EGF is therefore estimated as 3.1 times BMR. Using equation (3) (Section 2.1.2), this gives:

$$\text{EGF (kJ/d)} = 1327.85 \times W^{0.694} \quad (\text{W in kg}) \quad (5)$$

Croxall and Prince (1981) pointed out that calculating EGF by applying the same coefficient to BMR for all species would give a greater cost of gliding to large birds than to small ones, which contradicts theoretical predictions. They used a multiple of  $1.85 \times \text{EER}$  (=EMR) instead, on the grounds that this gives a smaller bias than using a multiple of BMR. Unfortunately, EMR contains a correction for ambient temperature, which, as explained in Section 2.1.2, may be inappropriate when estimating energy requirements for locomotion in birds. The species considered by Croxall and Prince (1981) were mostly much larger than those with which we are dealing, so the effect of overestimating the cost of gliding flight to large birds should not be very great.

#### Resting

Gaston's (1985) use of EMR as the most appropriate description of the energy demand of a resting seabird (ER) is followed here. For nonpasserines in winter at these latitudes, the appropriate equation is equation 5.31 in Kendeigh et al. (1977) (nonpasserines at 0°C, 10-h photoperiod):

$$\text{ER (kJ/d)} = 697.68 \times W^{0.5316} \quad (\text{W in kg}) \quad (6)$$

#### Swimming on the surface

Prange and Schmidt-Nielsen (1970) found that a Mallard *Anas platyrhynchos* averaged 3.2 times BMR measured on the same bird while swimming at the speed that minimized its cost of transport (0.55 m/s). We have adopted this value here. It is very close to the value of  $3.1 \times \text{BMR}$  suggested by Ellis (1984) as typical of surface swimming in birds.

Hence, the energy demand of surface swimming (ESS) is given as follows:

$$\text{ESS (kJ/d)} = 1370.69 \times W^{0.694} \quad (\text{W in kg}) \quad (7)$$

#### Swimming underwater

Furness and Cooper (1982) and Gaston (1985) predicted that wing-propelled birds swimming underwater would use energy at a rate similar to that required by

flapping flight. Evidence presented by Birt-Friesen et al. (1989) is consistent with this prediction. Nagy et al. (1984) measured the energy demand of a Jackass Penguin *Spheniscus demersus* swimming underwater at  $9.8 \times \text{BMR}$ , not far below the multiple usually accepted for flapping flight. We have adopted their value here for the calculation of the energy demand of swimming underwater (ESU):

$$\text{ESU (kJ/d)} = 4197.73 \times W^{0.694} \quad (\text{W in kg}) \quad (8)$$

#### Moult

There are few data assessing the metabolic cost of moult. Here we follow Furness (1984) in using the Kendeigh et al. (1977) equation 5.64 for the *total* cost of moult; the daily cost is then obtained by dividing by the number of days over which moult extends (Table A1).

$$\text{MOLTCOST (kJ)} = 26\,423.193 \times W^{0.959} \quad (\text{W in kg}) \quad (9)$$

This equation has a very high exponent—much closer to 1.0 than in any other equation used here—so that the cost of moult is not scaled to body weight but is almost directly proportional to it. Further data are needed to test whether this is really the case.

### Breeding colony data (for acronyms, refer to Tables 2 and A2)

#### Northern breeding area

*Northern Fulmar*. Linton and Nettleship (1977). LAB and LANB are the dates by which breeders and nonbreeders, respectively, have returned from the pre-laying exodus.

*Black-legged Kittiwake*. D.N. Nettleship and T.R. Birkhead (unpubl. data). FANB from Salomonsen (1967), who suggested that nonbreeders arrive one month after breeders. For D4, Barrett (1978, in Barrett and Runde 1980) found that chicks were attended constantly by at least one parent, but Hodges (1974) did not. We used 20 d, as implied by Hodges (1974).

*Razorbill*. Chiefly Birkhead and Nettleship (1982). FAB estimated as 30 d before ML. R from Bedard (1969). FANB and LANB from Lloyd and Perrins (1977); FANB estimated as 15 d after FAB, and LANB = MH.

*Common Murre*. Birkhead and Nettleship (1982). FAB 20 d before FL. Arrival of nonbreeders as in Razorbill. *Thick-billed Murre*. Gaston and Nettleship (1981), except ML, MH, MF, HS, which are means of values given there and by Birkhead and Nettleship (1982).

*Black Guillemot*. Asbirk (1979) and Cairns (1984). FAB taken as 50 d before ML. NB is arbitrary, as no data exist; the proportions of nonbreeders at colonies evidently differ widely from place to place.

*Atlantic Puffin*. FAB assumes the same delay between FAB and ML as in Newfoundland (Nettleship 1972) and that the laying peak in Labrador is 30 d later than that in Newfoundland, as suggested by fledging dates in Birkhead and Nettleship (1982). FANB is taken as (FAB + 42 d) from Nettleship (1972). FDNB = FDB and LDNB = LDB (Nettleship 1972; Harris 1983). E from Ashcroft (1979). HS is assumed to be the same as in Newfoundland (Nettleship 1972); FS is calculated from HS and "breeding" success in Labrador (Nettleship and Birkhead 1981).

Table A1

Proportion of moult occurring in each winter month

Species	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Northern Fulmar	0.17	0.17	0.17	0.17	0.08	0.08	0.08
Sooty Shearwater	0.10	0	0	0	0	0	0
Greater Shearwater	0	0	0	0	0	0	0
Storm-petrels	0.05	0.15	0.15	0.15	0.15	0.15	0.15
Northern Gannet	0.13	0.13	0.13	0.13	0	0	0
Black-legged Kittiwake	0.25	0.25	0	0	0	0	0
Great Black-backed Gull	0.10	0.10	0.10	0.10	0.05	0	0
Herring Gull	0.13	0.13	0.13	0.13	0	0	0
Ivory Gull	0.11	0.11	0	0	0	0.11	0.11
Glaucous Gull	0.10	0.10	0.10	0.10	0.10	0.10	0.10
Iceland Gull	0.14	0.14	0.14	0	0	0	0
Skuas	0.13	0.13	0.13	0.13	0.13	0.13	0.13
Jaegers	0.13	0.13	0.13	0.13	0.13	0.13	0.13
Thick-billed Murre	0.50	0.40	0	0	0	0	0
Common Murre	0.35	0.15	0	0	0	0	0
Atlantic Puffin	0	0	0	0.25	0.25	0.25	0.25
Dovekie	0.50	0	0	0	0	0	0
Black Guillemot	0.20	0.20	0.20	0	0	0	0
Phalaropes	0.05	0	0.03	0.05	0.05	0.05	0.05

Sources: Northern Fulmar, shearwaters, storm-petrels, skuas, jaegers, gulls, phalaropes, and Black Guillemot—Ginn and Melville (1983), Cramp and Simmons (1983); where they disagree, Cramp and Simmons (1983) were followed. Northern Gannet—Nelson (1978). Thick-billed Murre—Gaston and Nettleship (1981). Common Murre—Birkhead and Taylor (1977). Atlantic Puffin—Harris and Yule (1977). Dovekie—Bradstreet (1982b).

Table A2

Species-specific variables, input directly

Species	Day (DAYLIGHT)			Night (1 - DAYLIGHT)		
	TFLAP	TDSURF	TDDIVE	TNFLY	TNSURF	TNDIVE
Northern Fulmar	0.25	0.50	0	0.10	0.25	0
Shearwaters	0.25	0.35	0.15	0.10	0.20	0.05
Storm-petrels	0.75	0.50	0	0.10	0.25	0
Northern Gannet	0.50	0	0.05	0.10	0.25	0
Gulls	0.50	0.50	0	0.10	0.25	0
Auks	1.0	0.25	0.25	0	0.20	0.05
Jaegers/skuas	0.50	0.50	0	0.10	0.25	0
Phalaropes	1.0	0.50	0	0.10	0.25	0

Southern breeding area  
 Methods, sources, and assumptions are as for northern areas, except as specified below.  
*Northern Gannet.* FAB is eight weeks before ML (Montevocchi and Porter 1980). Spread of laying is from Nelson (1978). Arrival of nonbreeders is 30 d after breeders (Wanless 1983). E and R are from Poulin (1969). LDNB is 30 d before LDB (Montevocchi et al. 1984).  
*Black-legged Kittiwake.* Maunder and Threlfall (1972).  
*Razorbill.* R is from Lloyd and Perrins (1977), timing and spread of breeding from Bedard (1969).  
*Common Murre.* R. McLagan and J. Piatt (unpubl. data).  
*Thick-billed Murre.* All dates 15 d later than Common Murre (Tuck 1961, Tables 15 and 16). HS and FS from Birkhead and Nettleship (1982) for Labrador, as there are no Newfoundland data.

Input values  
 EFU = 1.25 = efficiency of food conversion (Furness 1978)  
 MONTHDAY = number of days in month  
 DAYLIGHT = number of hours of daylight (proportion of 24 h)

TFLAP = proportion of flying time spent flapping  
 TDSURF = proportion of daylight swimming time spent on surface  
 TDDIVE = proportion of daylight swimming time spent underwater  
 TNFLY = proportion of nighttime spent flying  
 TNSURF = proportion of nighttime swimming time spent on surface  
 TNDIVE = proportion of nighttime swimming time spent underwater  
 MOLTPROP = proportion of moult carried out in month

Values calculated from the PIROP data  
 TDFLY = proportion of daytime spent flying

Values calculated from other input  
 TGLIDE = (1 - TFLAP) = proportion of flying time spent gliding  
 TDSWIM = (1 - TDFLY) = proportion of daytime spent in/on water

TDREST = (1 - [TDSURF + TDDIVE]) = proportion of daylight swimming time spent resting

Calculation of monthly energy requirement  
 All energy units are kilojoules per day (kJ/d).  
*Daytime flying ("DAYFLY"):*  
 TDFLY [(TFLAP × EFF) + (EGF × {1 - TFLAP})]  
*Daytime in/on water ("DAYSWIM"):*  
 (1 - TDFLY) × [(TDSURF × ESS) + (TDDIVE × ESU) + (ER × {1 - TDSURF - TDDIVE})]  
*Night flying ("NIGHTFLY"):*  
 TNFLY [(TFLAP × EFF) + (EGF × {1 - TFLAP})]  
*Night in/on water ("NIGHTSWIM"):*  
 (1 - TNFLY) × [(TNSURF × ESS) + (TNDIVE × ESU) + (ER × {1 - TNSURF - TNDIVE})]

Thus, excluding moult:  
 ADEE = [DAYLIGHT × (DAYFLY + DAYSWIM)] + [(1 - DAYLIGHT) × (NIGHTFLY + NIGHTSWIM)]  
 and Monthly Energy Requirement (MER), including moult, is given by:  
 MER = EFU [(MONTHDAY × ADEE) + (MOLTPROP × MOLTCOST)]

## Literature cited

- Asbirk, S. 1979. The adaptive significance of the reproductive pattern in the Black Guillemot, *Cephus grylle*. Vidsk. Medd. Dan. Naturhist. Foren. Kobenhavn 141:29-80.
- Aschoff, J.; Pohl, H. 1970a. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. J. Ornithol. 111:38-46.
- Aschoff, J.; Pohl, H. 1970b. Rhythmic variations in energy metabolism. Fed. Proc. Fed. Am. Soc. Exp. Biol. 29:1541-1552.
- Ashcroft, R.E. 1979. Survival and breeding biology of Puffins on Skomer Island, Wales. Ornis Scand. 10:100-110.
- Barrett, R.T. 1978. The breeding biology of the Kittiwake *Rissa tridactyla* (L.) in Troms, North Norway. PhD thesis, Univ. of Troms, Troms, Norway.
- Barrett, R.T.; Runde, O.J. 1980. Growth and survival of nestling Kittiwakes *Rissa tridactyla* in Norway. Ornis Scand. 11:228-235.
- Baudinette, R.V.; Schmidt-Nielsen, K. 1974. Energy cost of gliding in Herring Gulls. Nature (London) 248:83-84.
- Bedard, J. 1969. Histoire naturelle du Gode, *Alca torda*, L., dans le golfe Saint-Laurent, province de Québec, Canada. Can. Wildl. Serv. Study No. 7, Ottawa.
- Birkhead, T.R.; Nettleship, D.N. 1982. Studies of alcids breeding at the Gannet Clusters, Labrador, 1981. Can. Wildl. Serv. Manuscr. Rep. 144 pp.
- Birkhead, T.R.; Taylor, A.M. 1977. Molt of the Guillemot *Uria aalge*. Ibis 119:80-85.
- Birt-Friesen, V.L.; Montevecchi, W.A.; Cairns, D.K.; Macko, S.A. 1989. Activity-specific metabolic rates of free-living Northern Gannets and other seabirds. Ecology 70:357-367.
- Bradstreet, M.S.W. 1982a. Occurrence, habitat use and behaviour of seabirds, marine mammals, and arctic cod at the Pond Inlet ice edge. Arctic 35:28-40.
- Bradstreet, M.S.W. 1982b. Pelagic feeding ecology of Dovekies *Alle alle* in Lancaster Sound and western Baffin Bay. Arctic 35:126-140.
- Brown, R.G.B. 1980. Seabirds as marine animals. Pages 1-38 in J. Burger, B.L. Olla, and H.E. Winn (eds.). Behavior of marine animals. Vol. 4. Plenum Press, New York.
- Brown, R.G.B. 1986. Revised atlas of eastern Canadian seabirds. Canadian Wildlife Service, Ottawa.
- Brown, R.G.B. 1991. Marine birds and climatic warming in the northwest Atlantic. Pages 49-54 in W.A. Montevecchi and A.J. Gaston (eds.). Studies of high-latitude seabirds. 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology. Can. Wildl. Serv. Occas. Pap. No. 68.
- Brown, R.G.B.; Nettleship, D.N. 1981. The biological significance of polynyas to arctic colonial seabirds. Pages 59-65 in I. Stirling and H. Cleator (eds.). Polynyas in the Canadian Arctic. Can. Wildl. Serv. Occas. Pap. No. 45.
- Brown, R.G.B.; Nettleship, D.N. 1984. Capelin and seabirds in the northwest Atlantic. Pages 184-194 in D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.). Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.
- Brown, R.G.B.; Nettleship, D.N.; Germain, P.; Tull, C.E.; Davis, T. 1975. Atlas of eastern Canadian seabirds. Canadian Wildlife Service, Ottawa.
- Cairns, D.K. 1984. The foraging ecology of the Black Guillemot (*Cephus grylle*). Unpubl. rep., Canadian Wildlife Service.
- Cairns, D.K.; Bredin, K.A.; Montevecchi, W.A. 1987. Activity budgets and foraging ranges of breeding Common Murres. Auk 104:218-224.
- Cairns, D.K.; Montevecchi, W.A.; Birt-Friesen, V.L.; Macko, S.A. 1990. Energy expenditures, activity budgets and prey harvest of breeding Common Murres. Stud. Avian Biol. 14:84-92.
- Cairns, D.K.; Chapdelaine, G.; Montevecchi, W.A. 1991. Prey exploitation by seabirds in the Gulf of St. Lawrence. Pages 277-291 in J.-C. Theriault (ed.). The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.
- Carscadden, J.E. 1984. Capelin in the northwest Atlantic. Pages 170-183 in D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.). Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.
- Carscadden, J.E.; Winters, G.H.; Miller, D.S. 1981. Assessment of the Division 3L capelin stock 1967-1980, using SCAM. Northwest Atlantic Fisheries Organization SCR Doc. 81/3, Ser. No. N267. 13 pp.
- Coulson, J.C.; Thomas, C. 1985. Changes in the biology of the Kittiwake *Rissa tridactyla*: a 31-year study of a breeding colony. J. Anim. Ecol. 54:9-26.
- Cramp, S.; Simmons, K.E.L. (eds.). 1983. The birds of the western Palearctic. Vol. 3. Oxford Univ. Press, Oxford.
- Croxall, J.P.; Prince, P.A. 1981. A preliminary assessment of the impact of seabirds on marine resources at South Georgia. CNFRA (Com. Natl. Fr. Rech. Antarct.) 51:501-509.
- Croxall, J.P.; Prince, P.A. 1987. Seabirds as predators on marine resources, especially krill, at South Georgia. Pages 347-368 in J.P. Croxall (ed.). Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.
- Croxall, J.P.; Prince, P.A.; Ricketts, C. 1985. Relationships between prey life-cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea. Pages 516-533 in W.R. Siegfried, P.R. Condy, and R.M. Laws (eds.). Antarctic nutrient cycles and food webs. Springer, Berlin.
- Diamond, A.W.; Gaston, A.J.; Brown, R.G.B. 1986. Converting PIROP counts of seabirds at sea to absolute densities. Can. Wildl. Serv. Prog. Note No. 164. 21 pp.
- Dunnet, G.M.; Ollason, J.C.; Anderson, A. 1979. A 28-year study of breeding Fulmars *Fulmarus glacialis* (L.) in Orkney. Ibis 121:293-300.
- Elliot, R.D.; Ryan, P.C.; Lidster, W.W. 1990. The winter diet of Thick-billed Murres in coastal Newfoundland waters. Stud. Avian Biol. 14:125-138.
- Ellis, H.I. 1984. Energetics of free-ranging seabirds. Pages 203-234 in G.C. Whittow and H. Rahn (eds.). Seabird energetics. Plenum Press, New York.
- Evans, P.R. 1973. Avian resources of the North Sea. Pages 400-412 in E.D. Goldberg (ed.). North Sea science. MIT Press, Cambridge, Mass.
- Ford, R.G.; Wiens, J.A.; Heinemann, D.; Hunt, G.L. 1982. Modelling the sensitivity of colonially breeding marine birds to oil spills: guillemot and kittiwake populations on the Pribiloff Islands, Bering Sea. J. Appl. Ecol. 19:1-31.
- Furness, R.W. 1978. Energy requirements of seabird communities: a bioenergetics model. J. Anim. Ecol. 47:39-53.
- Furness, R.W. 1984. Modelling relationships among fisheries, seabirds, and marine mammals. Pages 117-126 in D.N. Nettleship, G.A. Sanger, and P.F. Springer (eds.). Marine birds: their feeding ecology and commercial fisheries relationships. Can. Wildl. Serv. Spec. Publ., Ottawa.
- Furness, R.W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. Ibis 132:205-217.
- Furness, R.W.; Barrett, R.T. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16:305-313.
- Furness, R.W.; Barrett, R.T. 1991. Ecological responses of seabirds to reductions in fish stocks in North Norway and Shetland. Proc. Int. Ornithol. Congr. 20:2241-2245.
- Furness, R.W.; Cooper, J. 1982. Interactions between seabird and pelagic fish populations in the southern Benguela region. Mar. Ecol. Prog. Ser. 8:243-250.
- Furness, R.W.; Monaghan, P. 1987. Seabird ecology. Blackie, Glasgow.
- Gabrielson, G.W.; Mehlum, F.; Nagy, K.A. 1987. Daily energy expenditure and daily energy utilization of free-living Black-legged Kittiwakes. Condor 89:126-132.
- Gabrielson, G.W.; Taylor, J.R.E.; Konarzewski, M.; Mehlum, F. 1991. Field and laboratory metabolism and thermoregulation in Dovekies (*Alle alle*). Auk 108:71-78.
- Galbraith, H. 1983. The diet and feeding ecology of breeding Kittiwakes *Rissa tridactyla*. Bird Study 30:109-120.
- Gaston, A.J. 1985. Energy invested in reproduction by Thick-billed Murres (*Uria lomvia*). Auk 102:447-458.
- Gaston, A.J.; Nettleship, D.N. 1981. The Thick-billed Murres of Prince Leopold Island. Can. Wildl. Serv. Monogr. No. 6, Ottawa.
- Gaston, A.J.; Collins, B.T.; Diamond, A.W. 1987. Estimating densities of birds at sea and the proportion in flight from counts made on transects of indefinite width. Can. Wildl. Serv. Occas. Pap. No. 59. 14 pp.
- Ginn, H.; Melville, D.S. 1983. Molt in birds. British Trust for Ornithology Guide No. 19, Tring, U.K.
- Harris, M.P. 1983. Biology and survival of the immature Puffin *Fratercula arctica*. Ibis 125:56-73.
- Harris, M.P. 1985. Morphology and breeding of Puffins at Isle of May and St. Kilda, Scotland. Biol. Conserv. 32:81-97.
- Harris, M.P. 1991. Population changes in British Common Murres and Atlantic Puffins, 1969-88. Pages 52-58 in A.J. Gaston and R.D. Elliot (eds.). Studies of high-latitude seabirds. 2. Conservation biology of Thick-billed Murres in the Northwest Atlantic. Can. Wildl. Serv. Occas. Pap. No. 69.
- Harris, M.P.; Yule, R.F. 1977. The molt of the Puffin *Fratercula arctica*. Ibis 119:535-541.
- Hart, J.S.; Roy, O.Z. 1967. Temperature regulation during flight in pigeons. Am. J. Physiol. 213:1311-1316.
- Heubeck, M. (ed.). 1989. Seabirds and sandeels: proceedings of a seminar in Lerwick, 15-16 October 1988. Shetland Bird Club, Lerwick, U.K.
- Hodges, A.F. 1974. A study of the biology of the Kittiwake *Rissa tridactyla*. PhD thesis, Univ. of Durham, Durham, U.K.
- Hudson, P.J. 1985. Population parameters for the Atlantic Alcidae. Pages 233-261 in D.N. Nettleship and T.R. Birkhead (eds.). The Atlantic Alcidae. Academic Press, London.
- Hunt, G.L.; Schneider, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. Pages 7-41 in J. Croxall (ed.). Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.
- Hunt, G.L.; Burgeson, B.; Sanger, G.A. 1981. Feeding ecology of seabirds of the eastern Bering Sea. Pages 629-647 in D.W. Hood and J.A. Calder (eds.). The eastern Bering Sea shelf: its oceanography and resources. Vol. 2. U.S. Government Printing Office, Washington, D.C.
- Kartaschew, N.N. 1960. Die Alkenvögel des Nord Atlantiks. A. Ziemsen, Wittenberg (Lutherstadt).
- Kendeigh, S.C. 1970. Energy requirements for existence in relation to size of bird. Condor 72:60-65.
- Kendeigh, S.C.; Dol'nik, V.R.; Gavrilov, V.M. 1977. Avian energetics. Pages 127-204 in J. Pinowski and S.C. Kendeigh (eds.). Granivorous birds in ecosystems. Cambridge Univ. Press, Cambridge.
- King, J.R. 1974. Seasonal allocation of time and energy resources in birds. Pages 4-85 in R.A. Paynter (ed.). Avian energetics. Publ. Nuttall Ornithol. Club No. 15.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lancaster Sound Regional Study. 1980. Preliminary data atlas. Department of Indian and Northern Affairs, Ottawa.
- Lasiewski, R.C.; Dawson, W.R. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13-23.
- Linton, A.; Nettleship, D.N. 1977. Biological investigations of Northern Fulmars (*Fulmarus glacialis*) at Prince Leopold Island, N.W.T., summer 1976. Unpubl. rep., Can. Wildl. Serv. 152 pp.
- Lloyd, C.S.; Perrins, C.M. 1977. Survival and age of first breeding in the Razorbill (*Alca torda*). Bird-Banding 48:239-252.
- Lustick, S.; Battersby, B.; Kelly, M. 1978. Behavioural thermo-regulation: orientation toward the sun in herring gulls. Science 200:81-83.
- Maunder, J.E.; Threlfall, W. 1972. The breeding biology of the Black-legged Kittiwake in Newfoundland. Auk 89:789-816.
- McLaren, P.L. 1982. Spring migration and habitat use by seabirds in eastern Lancaster Sound and western Baffin Bay. Arctic 35:88-111.
- Monaghan, P.; Uttley, J.D.; Burns, M.D.; Thalne, C.; Blackwood, J. 1989. The relationship between food supply, reproductive effort and breeding success in arctic terns *Sterna paradisaea*. J. Anim. Ecol. 58: 261-274.
- Montevecchi, W.A. 1992. Seabird indication of marine fish conditions. In R.W. Furness and J.J.D. Greenwood (eds.). Seabirds as monitors of environmental change. Chapman Hall, London (in press).
- Montevecchi, W.A.; Porter, J.M. 1980. Parental investments by seabirds at the breeding area with emphasis on Northern Gannets, *Morus bassanus*. Pages 323-365 in J. Burger, B.L. Olla, and H.E. Winn (eds.). Behavior of marine animals. Vol. 4. Plenum Press, New York.
- Montevecchi, W.A.; Tuck, L.M. 1987. Newfoundland birds: exploitation, study and conservation. Publ. Nuttall Ornithol. Club No. 28. 273 pp.
- Montevecchi, W.A.; Kirkham, I.R.; Roby, D.D.; Brink, K. 1983. Size, organic composition and energy content of Leach's Storm-Petrel eggs. Can. J. Zool. 61:1457-1465.
- Montevecchi, W.A.; Ricklefs, R.E.; Kirkham, I.R.; Gabaldon, D. 1984. Growth energetics of nestling Northern Gannets (*Sula bassanus*). Auk 101:334-341.
- Nagy, K.A.; Siegfried, W.R.; Wilson, R.P. 1984. Energy utilization by free-ranging Jackass Penguins, *Spheniscus demersus*. Ecology 65:1648-1655.
- Nelson, J.B. 1978. The Gannet. Buteo, Vermillion, S. Dak.
- Nettleship, D.N. 1972. Breeding success of the Common Puffin (*Fratercula arctica*) on different habitats at Great Island, Newfoundland. Ecol. Monogr. 42:239-268.
- Nettleship, D.N. 1980. A guide to the major seabird colonies of eastern Canada. Unpubl. rep., Canadian Wildlife Service, Dartmouth.
- Nettleship, D.N. 1991. The diet of Atlantic Puffin chicks in Newfoundland before and after the initiation of an international capelin fishery, 1967-1984. Proc. Int. Ornithol. Congr. 20:2263-2271.
- Nettleship, D.N.; Birkhead, T.R. 1981. Alcid studies in Labrador: Gannet clusters June-September 1981. Unpubl. rep., Can. Wildl. Serv.
- Nettleship, D.N.; Birkhead, T.R. (eds.). 1985. The Atlantic Alcidae. Academic Press, London.
- Nettleship, D.N.; Evans, P.G.H. 1985. Distribution and status of the Atlantic Alcidae. Pages 53-154 in D.N. Nettleship and T.R. Birkhead (eds.). The Atlantic Alcidae. Academic Press, London.
- Norderhaug, M. 1970. The role of the Little Auk, *Plautus alle* (L.), in arctic ecosystems. Pages 558-560 in M.W. Holdgate (ed.). Antarctic ecology. Vol. 1. Academic Press, London.
- Pennycuik, C.J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil. Trans. R. Soc. London, Ser. B 300:75-106.
- Piatt, J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. Stud. Avian Biol. 14:36-51.
- Poulin, J.M. 1969. Reproduction du Fou de Bassan (*Sula bassana*), Ile Bonaventure (Québec) (Perspective écologique). MSc thesis, Univ. Laval, Quebec City.
- Powers, K.D.; Backus, R.H. 1987. Energy transfer to seabirds. Pages 372-374 in R.H. Backus (ed.). Georges Bank. MIT Press, Cambridge, Mass.
- Prange, H.D.; Schmidt-Nielsen, K. 1970. The metabolic cost of swimming in ducks. J. Exp. Biol. 53:763-777.
- Rahn, H.; Whittow, G.C. 1984. Introduction. Pages 1-32 in G.C. Whittow and H. Rahn (eds.). Seabird energetics. Plenum Press, New York.
- Ricklefs, R.E.; Day, C.H.; Huntington, C.E.; Williams, J.B. 1985. Variability of feeding rate and meal size of Leach's Storm-Petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54:883-898.
- Roby, D.; Ricklefs, R.E. 1986. Energy expenditure in adult Least Auklets and Diving Petrels during the chick-rearing period. Physiol. Zool. 59:661-678.

- Roby, D.D.; Brink, K.L.; Nettleship, D.N. 1981. Measurements, chick meals and breeding distributions of Dovekies (*Alle alle*) in northwest Greenland. *Arctic* 34:241-248.
- Roff, J.C.; Legendre, L. 1986. Physico-chemical and biological oceanography of Hudson Bay. Pages 265-292 in I.P. Martini (ed.). Canadian inland seas. Elsevier, Amsterdam.
- Salomonsen, F. 1967. Fuglene på Grønland. Rhodos, Copenhagen.
- Schaeffer, M.B. 1970. Men, birds and anchovies in the Peru current—dynamic interactions. *Trans. Am. Fish. Soc.* 99: 461-467.
- Schneider, D.; Hunt, G.L. 1982. Carbon flux to seabirds in waters with different mixing regimes in the southeastern Bering Sea. *Mar. Biol.* 67:337-344.
- Schneider, D.C.; Hunt, G.L.; Harrison, N.M. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. *Cont. Shelf Res.* 5:241-257.
- Schneider, D.C.; Hunt, G.L., Jr.; Powers, K.D. 1987. Energy flux to pelagic birds: a comparison of Bristol Bay (Bering Sea) and Georges Bank (N.W. Atlantic). Pages 259-278 in J.P. Croxall (ed.). Seabirds: feeding ecology and role in marine ecosystems. Cambridge Univ. Press, Cambridge.
- Shaw, D.M.; Atkinson, S.F. 1990. An introduction to the use of geographic information systems for ornithological research. *Condor* 92:564-570.
- Springer, A.M. 1992. A review: walleye pollack in the North Pacific—how much difference do they really make? *Fish. Oceanogr.* 1:80-96.
- Threlfall, W. 1983. Seabirds. Pages 467-508 in G.R. South (ed.). Biogeography and ecology of the island of Newfoundland. Junk, The Hague.
- Tuck, L.M. 1961. The murre. *Can. Wildl. Serv. Monogr. Ser. No. 1.*
- Wanless, S. 1983. Seasonal variation in the numbers and condition of Gannets *Sula bassana* dying on Alisa Craig, Scotland. *Bird Study* 30:102-108.
- Wiens, J.A. 1984. Modelling the energy requirements of seabird populations. Pages 255-284 in G.C. Whittow and H. Rahn (eds.). Seabird energetics. Plenum Press, New York.
- Wiens, J.A.; Innis, G.S. 1974. Estimation of energy flow in bird communities: a population bioenergetics model. *Ecology* 55:730-746.
- Wiens, J.A.; Scott, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. *Condor* 77:439-452.

## Other publications in the Occasional Papers series

- No. 1  
Birds protected in Canada under the Migratory Birds Convention Act/Oiseaux protégés au Canada en vertu de la Loi concernant les oiseaux migrateurs. 1991 edition. Bilingual.  
Cat. No. CW69-1/1-1991.
- No. 2  
Canadian bird names, French, English and scientific. Bilingual.  
Cat. No. CW69-1/2. Publ. 1957, rev. 1972.
- No. 3  
Use of aerial surveys by the Canadian Wildlife Service, by D.A. Benson.  
Out of print.  
Cat. No. CW69-1/3. Publ. 1963, repr. 1966.
- No. 4  
Queen Elizabeth Islands game survey, 1961, by J.S. Tener.  
Cat. No. CW69-1/4. Publ. 1963, repr. 1972.
- No. 5  
Age determination in the polar bears, by T.H. Manning.  
Cat. No. CW69-1/5. Publ. 1964, repr. 1973.
- No. 6  
A wildlife biologist looks at sampling, data processing and computers, by D.A. Benson. Out of print.  
Cat. No. R69-1/6. Publ. 1964.
- No. 7  
A preliminary report on the effects of phosphamidon on bird populations in New Brunswick, by C.D. Fowle. Out of print.  
Cat. No. R69-1/7. Publ. 1965.
- No. 8  
Birds of Nova Scotia-New Brunswick border region, by G.F. Boyer.  
Cat. No. CW69-1/8. Publ. 1966, repr. 1981.
- No. 9  
Effects of dietary methylmercury on Ring-necked Pheasants, with special reference to reproduction, by N. Fimreite.  
Cat. No. R69-1/9. Publ. 1971.
- No. 10  
Trends in populations of barren-ground caribou over the last two decades: a re-evaluation of the evidence, by G.R. Parker.  
Cat. No. CW69-1/10. Publ. 1971, repr. 1972.
- No. 11  
The Canada migratory game bird hunting permit and related surveys, by D.A. Benson.  
Cat. No. R69-1/11. Publ. 1971.
- No. 12  
Observations on duck hunting in eastern Canada in 1968 and 1969, by H. Boyd.  
Cat. No. R69-1/12. Publ. 1971.
- No. 13  
Evaluation of ecological effects of recent low water levels in the Peace-Athabasca Delta, by H.J. Dirschl.  
Cat. No. CW6-1/13. Publ. 1972.
- No. 14  
The Great Cormorants of eastern Canada, by A.J. Erskine.  
Cat. No. CW69-1/14. Publ. 1972.
- No. 15  
Distribution of barren-ground caribou harvest in north-central Canada, by G.R. Parker.  
Cat. No. CW69-1/15. Publ. 1972.
- No. 16  
Bird migration forecasts for military air operations, by H. Blokpoel.  
Cat. No. CW69-1/16. Publ. 1973.
- No. 17  
Waterfowl populations on the Peace-Athabasca Delta, 1969 and 1970, by D.J. Neiman and H.J. Dirschl.  
Cat. No. CW69-1/17. Publ. 1973.
- No. 18  
Gammarus predation and the possible effects of Gammarus and Chaoborus feeding on the zooplankton composition in some small lakes and ponds in western Canada, by R.S. Anderson and L.G. Raasveldt.  
Cat. No. CW69-1/18. Publ. 1974.
- No. 19  
A summary of DDE and PCB determinations in Canadian birds, 1969 to 1972, by M. Gilbertson and L. Reynolds.  
Cat. No. CW69-1/19. Publ. 1974.
- No. 20  
Development of a simulation model of Mallard Duck populations, by C.J. Walters, R. Hilborn, E. Oguss, R.M. Peterman and J.M. Stander.  
Cat. No. CW69-1/20. Publ. 1974.
- No. 21  
Use of museum specimens in toxic chemical research, by A.M. Rick.  
Cat. No. CW69-1/21. Publ. 1975.
- No. 22  
Impoundments for waterfowl, by W.R. Whitman.  
Cat. No. CW69-1/22. Publ. 1976.
- No. 23  
Minimizing the dangers of nesting studies to raptors and other sensitive species, by R.W. Fyfe and R.R. Olendorff.  
Cat. No. CW69-1/23. Publ. 1976.
- No. 24  
Waterfowl damage to Canadian grain: current problems and research needs, by L.G. Sugden.  
Cat. No. CW69-1/24. Publ. 1976.
- No. 25  
Census techniques for seabirds of arctic and eastern Canada, by D.N. Nettleship.  
Cat. No. CW69-1/25. Publ. 1976.
- No. 26  
The present status of the polar bear in James Bay and Belcher Islands area, by Charles Jonkel, Pauline Smith, Ian Stirling and George B. Kolenosky.  
Cat. No. CW69-1/26. Publ. 1976.
- No. 27  
Limnological and planktonic studies in the Waterton Lakes, Alberta, by R. Stewart Anderson and Roderick B. Green.  
Cat. No. CW69-1/27. Publ. 1976.
- No. 28  
Birds and mammals of the Belcher, Sleeper, Ottawa, and King George Islands, Northwest Territories, by T.H. Manning.  
Cat. No. CW69-1/28. Publ. 1976.



No. 29

Developments in PPS sampling — Impact on current research, by A.R. Sen. Cat. No. CW69-1/29. Publ. 1976.

No. 30

Dynamics of snowshoe hare populations in the Maritime Provinces, by Thomas J. Wood and Stanley A. Munroe. Cat. No. CW69-1/30. Publ. 1977.

No. 31

Migration and population dynamics of the Peace-Athabasca Delta goldeye population, by D.B. Donald and A.H. Kooyman. Cat. No. CW69-1/31. Publ. 1977.

No. 32

The effects of fire on the ecology of the Boreal Forest, with particular reference to the Canadian north; a review and selected bibliography, by John P. Kelsall, E.S. Telfer and Thomas D. Wright. Cat. No. CW69-1/32. Publ. 1977.

No. 33

The ecology of the polar bear (*Ursus maritimus*) along the western coast of Hudson Bay, by Ian Stirling, Charles Jonkel, Pauline Smith, Richard Robertson and Dale Cross. Cat. No. CW69-1/33. Publ. 1977.

No. 34

Canvasback habitat use and production in Saskatchewan parklands, by Lawson G. Sugden. Cat. No. CW69-1/34. Publ. 1978.

No. 35

The diets of muskoxen and Peary caribou on some islands of the Canadian High Arctic, by Gerald R. Parker. Cat. No. CW69-1/35. Publ. 1978.

No. 36

Observations of Mallards in the parkland of Alberta, by Michael F. Sorensen. Cat. No. CW69-1/36. Publ. 1978.

No. 37

The wildlife valuation problem: A critical review of economic approaches, by William A. Langford and Donald J. Cocheba. Cat. No. CW69-1/37. Publ. 1978.

No. 38

Spatial changes in waterfowl habitat, 1964–74, on two land types in the Manitoba Newdale Plain, by G.D. Adams and G.G. Gentle. Cat. No. CW69-1/38. Publ. 1978.

No. 39

Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories, in August and September 1976, by D.N. Nettleship and A.J. Gaston. Cat. No. CW69-1/39. Publ. 1978.

No. 40

Responses of Peary caribou and muskoxen to turbo-helicopter harassment, Prince of Wales Island, Northwest Territories, by Frank L. Miller and Anne Gunn. Cat. No. CW69-1/40. Publ. 1979.

No. 41

Avian community structure of six forest stands in La Mauricie National Park, Quebec, by J.-L. DesGranges. Disponible également en français. Cat. No. CW69-1/41E. Publ. 1979.

No. 42

Population ecology studies of the polar bear in northern Labrador, by Ian Stirling and H.P.L. Kiliaan. Disponible également en français. Cat. No. CW69-1/42E. Publ. 1980.

No. 43

Census methods for murre, *Uria* species; a unified approach, by T.R. Birkhead and D.N. Nettleship. Disponible également en français. Cat. No. CW69-1/43E. Publ. 1980.

No. 44

Population ecology studies of the polar bear in the area of southeastern Baffin Island, by Ian Stirling, Wendy Calvert, and Dennis Andriashek. Disponible également en français. Cat. No. CW69-1/44E. Publ. 1980.

No. 45

Polynyas in the Canadian Arctic, by Ian Stirling and Holly Cleator, eds. Disponible également en français. Cat. No. CW69-1/45E. Publ. 1981.

No. 46

The Lesser Snow Geese of the eastern Canadian Arctic, by H. Boyd, G.E.J. Smith, and F.G. Cooch. Disponible également en français. Cat. No. CW69-1/46E. Publ. 1982.

No. 47

The distribution and abundance of seals in the eastern Beaufort Sea, 1974–79, by Ian Stirling, Michael Kingsley, and Wendy Calvert. Disponible également en français. Cat. No. CW69-1/47E. Publ. 1982.

No. 48

Foraging behaviour of Peary caribou in response to springtime snow and ice conditions, by F.L. Miller, E.J. Edmonds, and A. Gunn. Disponible également en français. Cat. No. CW69-1/48E. Publ. 1982.

No. 49

A review of some important techniques in sampling wildlife, by A.R. Sen. Disponible également en français. Cat. No. CW69-1/49E. Publ. 1982.

No. 50

Intensive regulation of duck hunting in North America: its purpose and achievements, by Hugh Boyd. Disponible également en français. Cat. No. CW69-1/50E. Publ. 1983.

No. 51

Human dimensions of migratory game-bird hunting in Canada, by Shane A.D. Parker and Fern L. Filion. Disponible également en français. Cat. No. CW69-1/51E. Publ. 1984.

No. 52

Components of hunting mortality in ducks, by G.S. Hochbaum and C.J. Walters. Disponible également en français. Cat. No. CW69-1/52E. Publ. 1984.

No. 53

The interpretation of aerial surveys for seabirds: some effects of behaviour, by A.J. Gaston and G.E.J. Smith. Disponible également en français. Cat. No. CW69-1/53E. Publ. 1984.

No. 54

Waterfowl studies in Ontario, 1973–81, by S.G. Curtis, D.G. Dennis, and H. Boyd, eds. Disponible également en français. Cat. No. CW69-1/54E. Publ. 1985.

No. 55

The reported kill of ducks and geese in Canada and the USA, 1974–82, by Hugh Boyd. Disponible également en français. Cat. No. CW69-1/55E. Publ. 1985.

No. 56

Population dynamics of the Common Loon (*Gavia immer*) associated with mercury-contaminated waters in northwestern Ontario, by J.F. Barr. Disponible également en français. Cat. No. CW69-1/56E. Publ. 1986.

No. 57

The Ring-billed Gull in Ontario: a review of a new problem species, by H. Blokpoel and G.D. Tessier. Disponible également en français. Cat. No. CW69-1/57E. Publ. 1986.

No. 58

The birds of the Creston Valley and southeastern British Columbia, by R.W. Butler, B.G. Stushnoff, and E. McMackin. Disponible également en français. Cat. No. CW69-1/58E. Publ. 1986.

No. 59

Estimating densities of birds at sea and the proportion in flight from counts made on transects of indefinite width, by A.J. Gaston, B.T. Collins, and A.W. Diamond. Disponible également en français. Cat. No. CW69-1/59E. Publ. 1987.

No. 60

Waterfowl breeding population surveys, Atlantic Provinces, by A.J. Erskine, ed. Disponible également en français. Cat. No. CW69-1/60E. Publ. 1987.

No. 61

A survey of Lesser Snow Geese on Southampton and Baffin islands, NWT, 1979, by A. Reed, P. Dupuis, and G.E.J. Smith. Disponible également en français. Cat. No. CW69-1/61E. Publ. 1987.

No. 62

Studies of the effects of acidification on aquatic wildlife in Canada: waterfowl and trophic relationships in small lakes in northern Ontario, by D.K. McNicol, B.E. Bendell, and R.K. Ross. Disponible également en français. Cat. No. CW69-1/62E. Publ. 1987.

No. 63

Bison ecology in relation to agricultural development in the Slave River lowlands, NWT, by H.W. Reynolds and A.W.L. Hawley, eds. Cat. No. CW69-1/63E. Publ. 1987.

No. 64

A simulation model for the Greater Snow Goose population, by J. Gauvin and A. Reed. Disponible également en français. Cat. No. CW69-1/64E. Publ. 1987.

No. 65

The birds of the Fraser River delta: populations, ecology and international significance, by Robert W. Butler and R. Wayne Campbell. Cat. No. CW69-1/65E. Publ. 1987.

No. 66

Mortality of migratory barren-ground caribou on the calving grounds of the Beverly herd, Northwest Territories, 1981–83, by Frank L. Miller, Eric Broughton, and Anne Gunn. Cat. No. CW69-1/66E. Publ. 1988.

No. 67

Studies of the effects of acidification on aquatic wildlife in Canada: Lacustrine birds and their habitats in Quebec, by Jean-Luc DesGranges, ed. Disponible également en français. Cat. No. CW69-1/67E. Publ. 1989.

No. 68

Studies of high-latitude seabirds. 1. Behavioural, energetic, and oceanographic aspects of seabird feeding ecology, by W.A. Montevecchi and A.J. Gaston, eds. Cat. No. CW69-1/68E. Publ. 1991.

No. 69

Studies of high-latitude seabirds. 2. Conservation biology of Thick-billed Murres in the Northwest Atlantic, by A.J. Gaston and R.D. Elliot, eds. Cat. No. CW69-1/69E. Publ. 1991.

No. 70

Habitats of the northeast coast of James Bay, by N. Dignard, R. Lalumière, A. Reed, and M. Julien. Disponible également en français. Cat. No. CW69-1/70E. Publ. 1991.

No. 71

Key migratory bird terrestrial habitat sites in the Northwest Territories (2nd edition), by Stuart A. Alexander, Robert S. Ferguson, and Kevin J. McCormick. Cat. No. CW69-1/71E. Publ. 1991.

No. 72

Atlas of pelagic birds of western Canada, by K.H. Morgan, K. Vermeer, and R.W. McKelvey. Cat. No. CW69-1/72E. Publ. 1991.

No. 73

The Red-throated Loon as an indicator of environmental quality, by D. Lynne Dickson. Disponible également en français. Cat. No. CW69-1/73E. Publ. 1992.

No. 74

Aerial radio-tracking of Whooping Cranes migrating between Wood Buffalo National Park and Aransas National Wildlife Refuge, 1981–84, by E. Kuyt. Cat. No. CW69-1/74E. Publ. 1992.

No. 75

The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island, by K. Vermeer, R.W. Butler, and K.H. Morgan, eds. Cat. No. CW69-1/75E. Publ. 1992.

No. 76

Declines in Canadian amphibian populations: designing a national monitoring strategy, by C.A. Bishop, K.E. Pettit, eds. Cat. No. CW69-1/76E. Publ. 1992.



CANADA'S GREEN PLAN



Over 50% recycled  
paper including  
10% post-consumer  
fibre.

M – Official mark of Environment Canada

Canada