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Converting PIROP counts of seabirds at sea to absolute densities

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Introduction

Seabirds have been counted at sea off eastern and arctic Canada since 1969 under the Programme Intégré de Recherches sur les Oiseaux Pélagiques (PIROP) (Brown *et al.* 1975, Brown 1986). The PIROP data base was designed for records gathered by many different observers, often volunteers, some of whom had limited training. Procedures for recording were therefore kept uncomplicated. All birds observed in a 10-min period were counted, irrespective of their distance from the observer. The counts were neither true belt transects, nor line transects, and thus could not be translated into estimates of density by simple multiplication or other techniques appropriate to line transects. The mapping purposes for which the PIROP system was designed do not require such density estimates, but they needed to be developed for use in a model to calculate energy demand by seabirds off eastern and arctic Canada (Diamond *et al.*, in prep.). The following analysis addresses this issue by comparing PIROP counts with densities estimated from population data. The method we use is not intended as an alternative to methods based on fixed-width transects (e.g. Briggs and Hunt 1981, Burnham *et al.* 1980, Powers 1982, Tasker *et al.* 1984, Wiens *et al.* 1978) which are obviously more appropriate when estimates of absolute density are required; rather, it is designed to address the specific characteristics of the PIROP data base.

Objectives

- (i) For selected species: to compare the densities estimated from known population sizes in different areas with the number of birds counted per linear kilometre at sea on PIROP counts.
- (ii) For all species observed: to generate a factor for converting PIROP counts to absolute densities based on the findings of (i).
- (iii) For comparable species: to generate conversion factors for species that do not breed in eastern or Arctic Canada but do occur commonly at sea using the results of (i) and (ii).

Methods

Study areas

The areas under study are the "southern" areas, which include the Gulf of St. Lawrence, east and south of Newfoundland, and southern Labrador, and the "northern" area, Lancaster Sound. In each of these areas, the seabird colonies are closer to each other than they are to either of the other areas. Also, each area can be considered to be outside the normal feeding

range of a bird that breeds in a colony in either of the other areas. Minor exceptions in Lancaster Sound are covered in the relevant species accounts. Figures 1 and 2 show the precise sea areas and the distribution of major seabird colonies within each. The whole of the Gulf of St. Lawrence is included (as far up-river as longitude 70°W); colonies are scattered around the perimeter and on islands within it, and most of the sea area within the Gulf is therefore within the foraging range of at least one colony. No point in the Gulf is more than 100 km from a seabird colony; to ensure that the sea areas covered are as closely comparable as possible, those off the coasts of Newfoundland and Labrador were chosen to be within 100 km of a major colony. The Lancaster Sound survey area is bordered north and south by coastlines 70–100 km apart. The east and west limits were chosen to include the estimated feeding ranges of major seabird colonies within Lancaster Sound, including Coburg Island (at the east end of Jones Sound), with minimal overlap between feeding zones around colonies on eastern Baffin Island and northwest Greenland. Jones Sound colonies other than Coburg Island were not included because there are no PIROP counts from there. Each of the study areas was defined in terms of the appropriate grid unit (1°W by ½°N); any such unit of which a part fell within 100 km of a major colony was included in the analysis. Areas were determined by planimeter from a 1:2 000 000 map.

Time of year

In this study we are tabulating the characteristics of the data collected over all 12 months of the year. For the calculation of the conversion factor we selected data collected in July for the three southern areas as large PIROP samples were available for that month. The activities of both breeders and non-breeders in July are most likely to be centred on the colony thus their distribution is more concentrated within the study areas than in any other month. In Lancaster Sound the counts were made in August, as ice cover inhibited the number of counts in July. The data set that we used from the PIROP data base covered the years 1969–83 inclusive.

Species selected

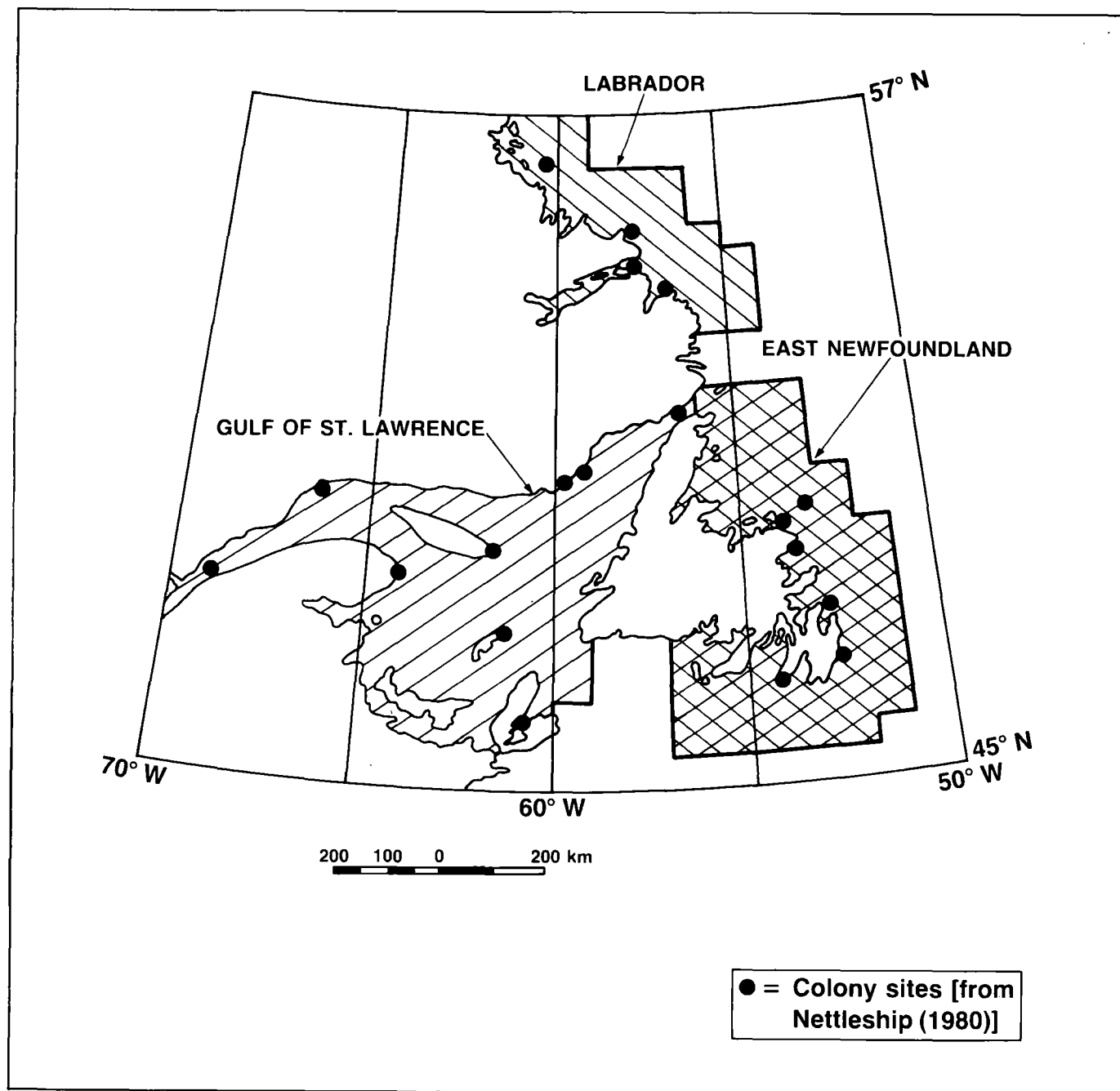
We selected species that fed regularly at least 10 km from the coast, and for which reliable population data are available, as few counts were made closer inshore. Gulls (Laridae) and cormorants (Phalacrocoracidae) are thus excluded. Black Guillemots *Cepphus grylle* and Arctic Terns *Sterna paradisaea* qualify but were so rarely recorded on PIROP counts that conversion factors could not be calculated. No further details are given for these two species.

Population sizes

Breeding populations are given by Nettleship (1980) and, for Baccalieu Island, by Montevicchi and Tuck (in press). In addition to breeding birds, substantial numbers of non-breeders attend seabird colonies during the breeding season. Most seabirds come to land rarely or not at all in their 1st year after fledging, and their attendance at the colony then

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Figure 1
Map of three southern study areas



increases until they attain breeding age, often at 5 or more years old. Thus the numbers of pre-breeding birds can actually rival those of breeders. Non-breeders are rarely counted at colonies; their numbers usually have to be estimated from life-table data, adjusted to take into account the increasing tendency, with age, to occur at or close to the colony during the breeding season. To derive the population sizes separate estimates are therefore necessary for:

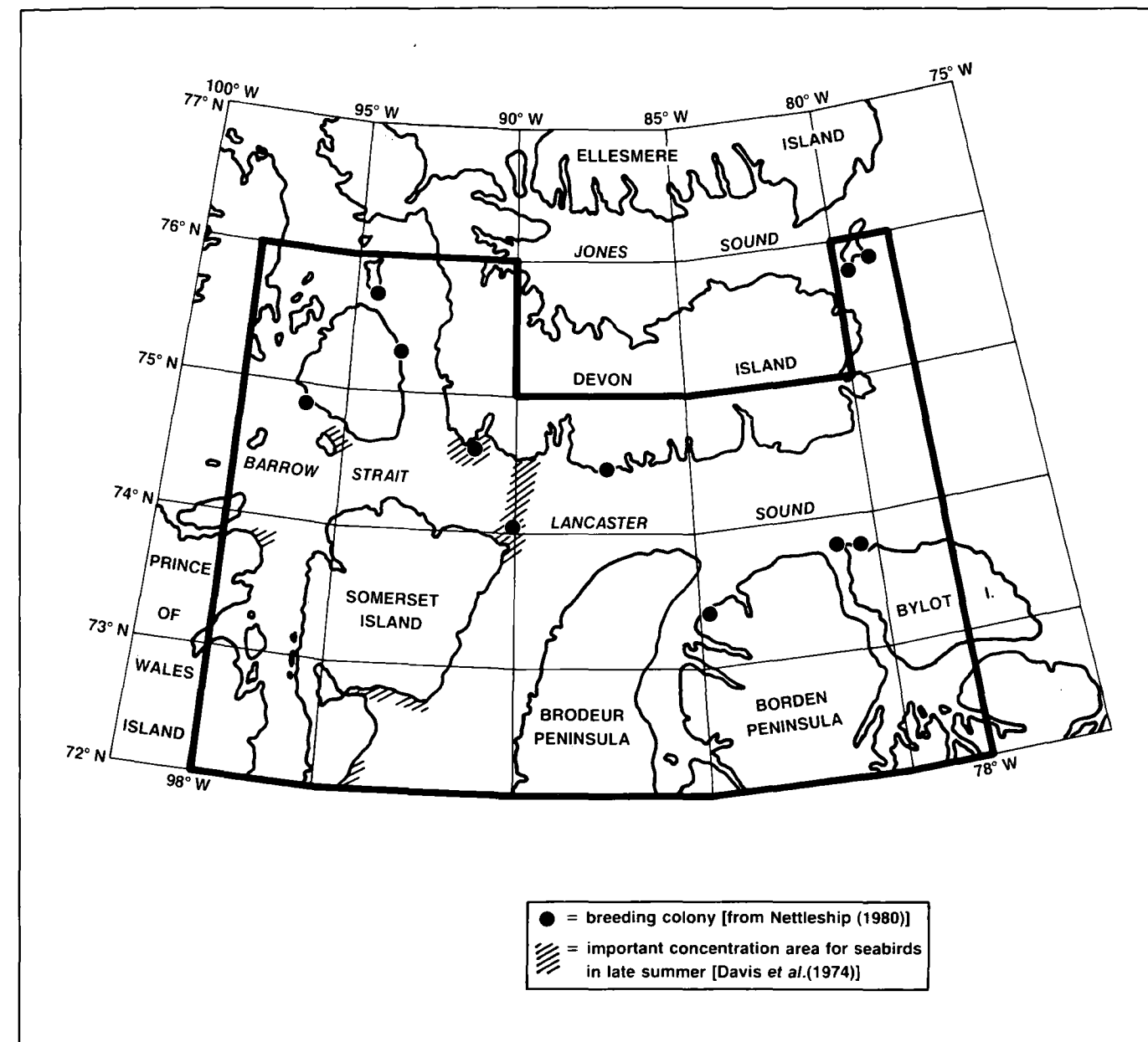
(a) the number of pre-breeding birds in the "population",

defined in relation to age-class cohorts rather than to geographical distribution;

(b) the proportion of each pre-breeding age-class which would be expected to be found within the study areas at the time concerned.

Data for (a) require the construction of a life-table. The relevant data are chiefly those on adult survival, breeding success, age of first breeding, and attendance patterns. These data can be obtained partly from banding returns of birds

Figure 2
Map of Lancaster Sound study area



marked at colonies (either as young or as breeding adults) and partly from studies at the colony itself. Band return data alone may not give reliable estimates of age-specific survival rates (Lakhani and Newton 1983), but there are no alternative methods for estimating survival of pre-breeding age-classes. We used the highest available measure of the annual survival of breeders (since most methods underestimate adult survival to some extent), derived where possible from the return of marked birds to breeding colonies in later years, rather than from recoveries of dead birds. We obtained measures of 1st-year survival from band recoveries (where available), as

there are no alternative sources.

In a stable population, adult mortality is equivalent to recruitment, i.e. to the number of birds entering the age-class at which they first breed, and the 1st-year survival applied to the cohort of fledglings (estimated from measures of clutch size and breeding success) gives the number of birds entering their 2nd year. Survival of intermediate age-classes is assumed to be constant over those age-classes, and to lie between 1st-year and adult survival, and is calculated by simple interpolation (see gannet account). If there are no suitable band recovery data for 1st-year birds, their survival

is taken to be equal to that of older immatures and calculated by interpolation between the numbers fledging and the expected number of recruits.

The expected proportion of pre-breeding birds from each age-class (b) was estimated from both attendance patterns and banding returns. Attendance patterns refer only to birds coming ashore, rather than to all those occurring within the foraging range of the colony. Banding returns for July are used to supplement and interpret observations of attendance at colonies. Both sources of data are biased, usually involve small samples, and in some cases are missing altogether.

The total population within the study area (TPA) can be expressed as follows:

$$TPA = \sum(N_i * p_i)$$

where N_i = number in i^{th} cohort

i = b for breeders (so N_b = breeding population BP)

i = f_b for failed breeders

p_i = proportion of cohort present in area (for breeders, $p_b = 1$)

If N_i is expressed in terms of the breeding population, i.e.

$$N_i = BP * x_i$$

where x_i is the size of the i^{th} cohort as a proportion of BP (so that for breeders, $x_b = 1$), then

$$TPA = BP[1 + \sum(x_i * p_i)] \quad [1]$$

Failed breeders (in this context, breeders whose eggs do not hatch) are accounted for as follows. The breeding population during the chick stage is approximated by $(BP * HS)$ where HS = hatching success. The approximation is justified because many more pairs lose eggs than lose chicks. Most of the species covered in this study lay only one egg per breeding season; the exceptions are kittiwakes, which lay up to three, and Black Guillemots, which lay one or two. The number of pairs that lose eggs are $BP(1 - HS)$; they are treated as a separate age-class, with the same time-budgets as the oldest non-breeders, and are assumed to remain within the study area throughout the month. This correction for failed breeders is included for completeness, and to allow for the modelling of those years in which breeding success can be much lower than usual. In most species average values of hatching success affect only the second decimal place of the final conversion factor. This is largely because the time-budgets of failed breeders are treated as equivalent to those of the oldest class of non-breeders, which are very similar to those of breeders.

Populations at sea

PIROP counts can be considered to be random samples of the number of birds actually at sea at the time of the count, since each count lasts only 10 min of the 16-h day. Of the "total population in area" defined above, only a proportion will be available for counting at sea during the day. This "countable

population" is determined by the size of each cohort multiplied by the proportion of the daylight hours that the average member of each cohort spends at sea. Separate estimates are necessary for breeders, non-breeders, and segments of the non-breeding population which are likely to have different patterns of attendance at the colony.

The total "countable population" thus depends not only on the size of the breeding population but also on the size of the non-breeding population, on the time-budgets of each cohort, and the proportion of each cohort likely to occur in the area. The general relationship between the "countable population" CP, the total population in the area TPA, and the breeding population BP (the form in which census results are usually expressed) can be summarized as follows:

Using the same notation as eq. [1], with the addition of T_i = proportion of day spent at sea by members of the i^{th} cohort, the general equation is

$$CP = BP[T_b + \sum(x_i * T_i * p_i)] \quad [2]$$

Making allowance for failed breeders (see above), this becomes:

$$CP = BP * [HS * T_b + (1 - HS) * T_{fb} + \sum(x_i * p_i * T_i)] \quad [3]$$

The density figures obtained by using these conversion factors do not necessarily correspond with the total numbers of birds using a particular area, because the "countable population" depends on the time-budgets of the birds involved. The "countable population" has deliberately been devised as an estimate of the number of birds *at sea*; therefore, outside the breeding season, the conversion factors given here can be used as presented. During the breeding season, in sea areas within feeding range of a breeding colony, further conversion based on attendance patterns will be necessary to estimate the total population using a particular geographical area (TPA).

Data on attendance patterns are confined almost exclusively to breeding birds; there are very few of these data for Canadian populations, and none at all for non-breeders. Some extrapolations from European data therefore have to be made for breeders. For non-breeders, a number of assumptions have to be made, sometimes on very little evidence.

In light of the above, eq. [1] can be expanded to:

$$TPA = BP * 1 + \frac{Y * S_1}{2} * \left\{ p_i + \sum_{i=2}^{A-1} (S_{nb}^{i-1} * p_i) \right\} \quad [4]$$

where Y = number of fledgelings per pair,

S_1 = survival from fledging to 1 year old,

S_{nb} = survival of older non-breeders,

i = age of cohort (2 = 2nd year, etc.),

A = age at first breeding.

The relationship between CP and TPA is assumed to be identical to that between the density of birds actually at sea (D) and the density of birds using the same area during the day (i.e. birds currently on the colony are assumed to distribute themselves at sea in the same way as those observed).

Table 1a

Categories of the ship's activity recorded during watch (% in each category)

	Jan.		Feb.		March		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.	
Zone	1	2	1	1	1	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	
Activity (PIROP Code)																						
No data (0)	19	0	16	18	1	20	0	23	0	18	0	7	30	7	30	14	44	3	0			
Non-fishing (1)	73	100	80	74	99	72	100	72	100	71	100	85	61	85	61	78	56	69	100			
Major fishing (2)	4	0	3	1	0	6	0	2	0	4	0	3	6	3	6	6	0	7	0			
Between fish stations (3)	3	0	2	6	0	1	0	2	0	7	0	5	2	5	2	2	0	21	0			
Anchored (7, 8)	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Other (9)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			

Hence, $D' = D * C_b$, where D' is the total number of birds using a unit area during 1 day and $C_b = TPA/CP$. Substituting in eq. [4];

$$C_b = \frac{1 + \left\{ \frac{Y * S_1}{2} * \left[p_i + \sum_{i=2}^{A-1} (S_{nb}^{i-1} * p_i) \right] \right\}}{(HS * T_b) + [(1 - HS) * T_{fb}] + \left\{ \frac{Y * S_1}{2} * \left[T_i p_i + \sum_{i=2}^{A-1} (S_{nb}^{i-1} * p_i * T_i) \right] \right\}} \quad [5]$$

Breeding birds at different stages of their breeding cycle spend different proportions of their time at sea, hence the term $(HS * T_b)$ can be replaced with the expansion:

$$\sum(P_{bj} * T_{bj})$$

where P_{bj} represents the proportion of breeders in the j^{th} stage of the breeding cycle (incubation, brooding chicks, etc.) and $\sum P_{bj} = HS$, and T_{bj} represents the proportion of time spent at sea by breeders in the j^{th} stage.

Data on the presence or absence of pre-breeding cohorts from the colony area are normally derived from two sources: (a) banding recoveries, and (b) numbers of known-age birds seen at the colony. Banding data are usually summarized by breeding season, combining recoveries in several months. Hence, a statement that "50% of 2nd-year birds are within 100 km of the colony during the breeding season" means that, over several months, an average of 50% of recoveries were within that distance. During the period when attendance by pre-breeders is highest, we can anticipate that the proportion will be much higher. Conversely, sightings of pre-breeding cohorts at the colony usually concentrate on the period of maximum attendance, and a statement that "80% of 3rd-year birds visit the colony during the breeding season" probably translates into a much lower average attendance of 3rd-years in any given month. These biases need to be considered in evaluating the resulting conversion factors.

Estimated population densities

These are calculated by dividing the countable population by the area of sea in each study area: Gulf of St. Lawrence, 225 296 km²; Newfoundland, 184 470 km²; Labrador, 105 656 km²; Lancaster Sound, 66 781 km².

PIROP counts

The PIROP data base is remarkable for its size, the length of

time over which it has been accumulated, and the size of geographic area that it covers. Inevitably, it reflects the variation of environmental factors and differences between observers, in addition to stochastic variation and the real differences in bird density that it was designed to measure. Before we use the PIROP data to determine the relative abundance of seabirds, we shall examine several factors that are likely to influence the numbers of birds recorded in the standard 10-min watches. We can then assess the categories that should be excluded from the data set to be used in calculating conversion factors, and which subsequently generate estimates for the seabird-energy model (Diamond *et al.*, in prep.). Some of the variables included in each record are tabulated, by month or species as appropriate, in Table 1, and are discussed below. We tabulate data for all months (except December, for which samples are very small), not just July and August, because we used the same criteria to sort records for use in the year-round energy model (Diamond *et al.*, in prep.) as for developing the conversion factors described here.

Each record refers to a species seen during a 10-min watch. It includes details of numbers of birds seen, position, time of day, behaviour of the birds, state of the sea, wind speed, visibility, etc. (31 variables in all, defined in detail by Brown *et al.* 1975). The records were sorted to include zero scores—where a particular species was not recorded on a watch—when calculating the mean number of birds seen per linear kilometre of sea covered.

Records were first sorted by reliability of watch (PIROP code 0 = "reliable", applied to over 90% of all watches in all months except November in Zone 2 (79%)), then by ship's activity (0 = no data, 1 = not fishing, true for over 90% of all watches (Table 1a)), and reliability of identification (0 or 2 = this or the next most similar form). Watch-types included were 00 (daytime watch, all species seen) together with seven other types of daytime watches in which different groups of species had been selected (Table 1b). The records were also sorted into geographic zones, south (45–60°N) and north (north of 60°N). Ice cover restricted observations in the northern zone to the period July–November.

1. Frequency

The frequency distribution of numbers of birds recorded per 10-min watch is shown in Table 1c. The distribution is

Table 1b
Distribution of watch-types by month and zone (zone 1 = south of 60°N, zone 2 = north of 60°N)

Month	Zone	Watch-type (species, PIROP code)						
		All spp. (00)	Only fulmars and shearwaters (20 + 22)	Only gulls (45)	Only alcids (48)	Not shearwaters or fulmars (72)	Not gulls (95)	Not auks (98)
January	1	2 841	8	2	3	0	12	0
	2	3	0	0	0	0	0	0
February	1	4 770	0	0	228	0	14	4
March	1	3 141	0	0	253	0	0	0
April	1	3 325	0	0	210	0	0	0
May	1	6 662	8	10	95	302	0	0
	2	46	0	0	0	0	0	0
June	1	7 528	0	0	21	107	0	0
	2	112	0	0	0	0	0	0
July	1	11 163	3	34	3	32	17	0
	2	2 715	0	0	208	5	0	0
August	1	15 155	24	2	92	10	0	0
	2	10 311	2	2	812	34	4	0
September	1	4 824	2	0	42	0	0	0
	2	6 507	0	6	170	0	0	116
October	1	6 933	0	0	359	1	13	193
	2	1 681	0	0	18	0	0	0
November	1	5 833	0	9	525	0	32	52
	2	27	0	0	0	0	0	0

Table 1c
Proportion of birds watch⁻¹ for which the given number of each species was recorded (%)

	1	2	3-4	5-8	9-16	17-32	33-64	65-128	129-256	257-512	513-1024	1025-2040	N
Fulmar	32	15	17	16	11	5	2	1					3 586
Greater Shearwater	19	11	15	18	15	12	5	2	1	1			2 944
Sooty Shearwater	40	18	17	10	7	3	2	1	1				1 299
Manx Shearwater	84	10	5	1									101
Storm Petrel	36	16	16	14	11	5	2						2 032
Northern Gannet	70	15	7	6	2	1							586
Phalarope	20	11	15	18	13	9	8	3	1	1			159
Jaeger spp.	74	15	7	2	1								603
Great Black-backed Gull	56	17	9	8	5	3	1						1 186
Herring Gull	46	16	14	10	7	4	2	1					1 376
Kittiwake	47	17	16	9	6	3	2						1 538
Tern spp.	59	22	9	5	3	1	1						238
Thick-billed Murre	34	14	14	13	10	7	4	2					889
Dovekie	13	10	12	14	13	10	8	7	5	4	3	1	494
Black Guillemot	59	20	11	7	2								211
Atlantic Puffin	42	19	17	12	6	3	1						485
TOTAL													19 534

Table 1d
Categories of visibility recorded during watch (% in each category)
(zone 1 = south of 60°N, zone 2 = north of 60°N)

	Jan.		Feb.		March	Apr.	May		June		July		Aug.		Sept.		Oct.		Nov.	
Zone	1	2	1	1	1	1	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Visibility (PIROP Code)																				
Good (0, 1)	89	100	87	88	88	85	61	85	88	84	81	85	86	83	79	91	78	94	83	
1/4-1 mile (2) (400-1600 m)	8	0	5	9	8	3	30	7	3	2	1	3	4	5	8	2	4	2	0	
100 yd-1/4 mile (3) (91-400 m)	1	0	1	1	1	3	10	1	8	0	0	1	1	0	1	1	1	0	0	
≤100 yd (≤91 m) (4)	0	0	0	0	0	3	0	1	0	2	5	2	0	3	0	0	0	0	17	
Glare (5)	2	0	6	2	3	1	0	4	0	2	8	8	7	7	10	5	8	3	0	
Poor + glare (6)	0	0	0	0	0	0	0	0	0	10	5	0	0	0	0	0	0	0	0	
Poor (7)	0	0	1	0	1	0	0	1	0	0	0	1	1	1	1	2	9	1	0	

Table 1e
Categories of sea state recorded during watch (% in each category)

	Jan.		Feb.		March	Apr.	May		June		July		Aug.		Sept.		Oct.		Nov.	
Zone	1	2	1	1	1	1	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Sea state (PIROP Code)																				
No data (0)	7	0	10	2	7	21	13	3	8	13	33	5	21	4	13	2	7	0	3	
Calm (1)	0	0	12	13	30	35	75	34	85	20	32	18	38	15	20	10	28	2	66	
Light (2)	57	100	46	44	44	34	11	55	7	54	25	61	34	55	59	51	48	58	31	
Medium (3)	20	0	21	27	12	7	0	7	0	5	10	11	4	13	5	30	10	28	0	
Heavy (4)	7	0	5	11	6	1	0	0	0	0	0	1	2	6	0	3	1	8	0	
Rough (5)	0	0	1	2	1	2	0	0	0	0	0	0	1	0	0	0	0	1	0	
Other (6, 7)	9	0	5	0	1	0	0	1	0	8	0	3	1	7	2	4	6	2	0	

positively skewed for most species, but the degree of skew varies considerably between species, especially in relation to flocking behaviour (compare, for example, the relatively even distributions of Great Shearwater, phalaropes, and Dovekie, all species that move in flocks, with the highly skewed distributions of the more solitary Northern Gannet, jaegers, and Black Guillemot). The distributions are not normal, nor are they consistent between species. It would thus be inappropriate to apply a uniform transformation to the raw numbers before calculating means.

2. Visibility

Most records were coded as "good visibility" (Table 1d), but in some months the next category (0.25-1 mile) (400-1600 m) contributed a significant number of records. Because most birds viewed are likely to have been well within 0.25 miles (402 m) of the ship, records in this category (PIROP visibility code 2) have been included in the calculations of the daily estimates.

3. Sea state

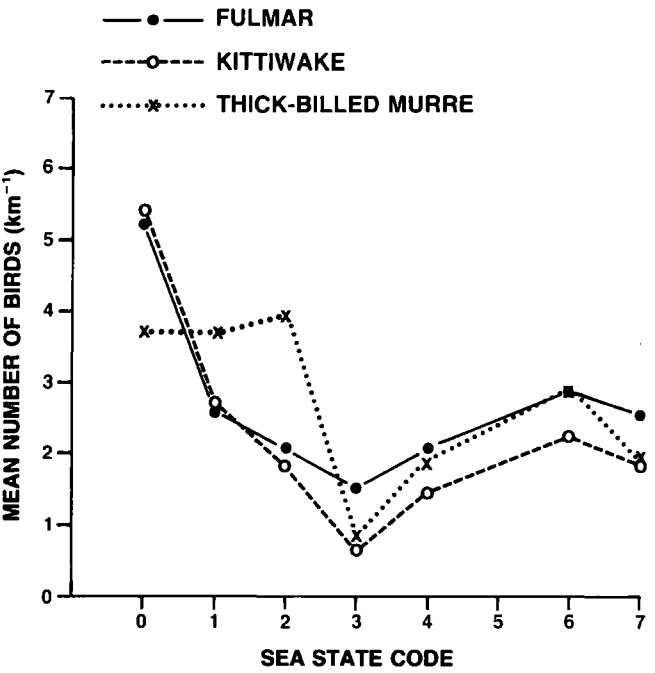
The "roughness" of the sea is recorded on a scale from 1 to 7. Codes 6 and 7 do not refer to the roughest seas, as might be expected, but to heavy swells with light waves or none at all, in which birds are probably more visible than in sea states

lower in the scale. Most records were made during calm or light sea conditions (Table 1e). We assume (supported by Fig. 3) that records with "no data" in this category were chiefly also in calm or light seas because sea state is more likely to be recorded if it is rough (see *Weather*, below). To illustrate the effect of sea state on bird numbers recorded, we sorted data from the northern zone in August for murres, fulmar, and kittiwake. All showed a declining trend in numbers until sea state 3 after which they rose again. Ideally, records from sea states 2-4 should be excluded as they seem to be the most affected by sea state, but Table 1e shows that sea state 2 is the most commonly recorded in most months, and this policy would reduce sample sizes to unusably low levels. We have therefore included all sea states except "heavy" and "rough" (codes 4 and 5, respectively), and accepted the high variance due to sea state as a property of the data for which we cannot adequately correct.

4. Weather

Weather conditions were usually not recorded at all (78% of all watches) (Table 1f). The most common categories of recorded weather were "fog" and "high wind", which probably reflects observers' tendencies to record weather only if it was bad. However, the features of the weather during a watch that are likely to directly affect the numbers of birds

Figure 3
Influence of sea state on numbers of three species in August, northern zone

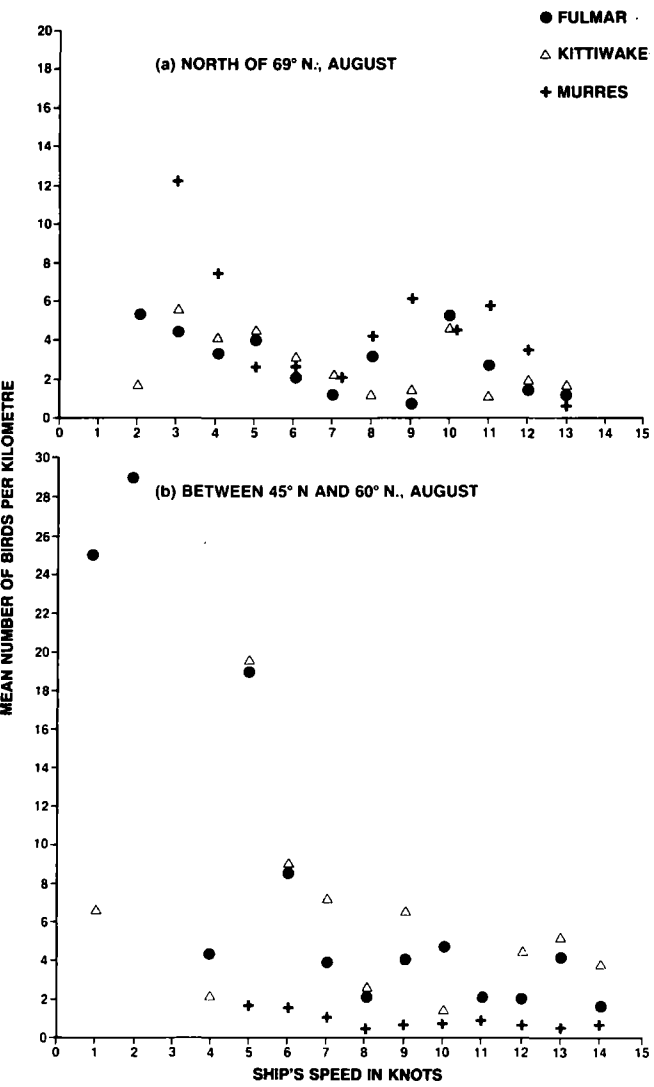


seen are visibility and the state of the sea. We have therefore selected records according to those two criteria rather than by weather.

5. Floating ice
This is recorded under "floating matter" on the PIROP record card. In the most suitable data set (July, northern zone), 61% of fulmar records and 60% of Thick-billed Murres were in the category "not recorded", and there was no clear trend in the remaining records. No further analysis was therefore warranted, nor could sorting data by ice category be justified. This is unfortunate because the proximity of ice is well known to affect seabird distributions and more assiduous recording might have shed new light on this relationship.

6. Ship's speed
The distribution of ship's speed among watches is shown in Table 1g. Brown *et al.* (1975) showed densities in terms of numbers seen per 10-min watch, but Brown (1986) divides the numbers seen by the ship's speed to give numbers per linear kilometre. Both methods involve a negative correlation between bird numbers and ship's speed, caused by birds that fly into the transect during the watch. This effect is greatest when the difference between the speed of the bird and that of the ship is greatest, i.e. at the slowest ship's speeds (see also Gaston *et al.* 1985). Examples of this trend in records of fulmar and kittiwake for July and August are shown in Figure 4. We ran 26 paired comparisons between the mean number of birds/km at speeds below 10 knots and at 10 knots or higher (Table 2). More birds were seen at the lower speeds in 24 cases, and the SE of the mean was also greater at the lower

Figure 4
Influence of ship's speed on numbers of three species



speeds in 22 cases. The trend of declining numbers with rising ship speed was steepest at speeds below 10 knots. However, only 47% of all watches overall—and even fewer in some months—were made at speeds of 10 knots or greater, so it would not be practicable to exclude all watches made at speeds below 10 knots. Inspection of Figure 4 suggests that the greatest effect of ship speed is below 5 knots, and Table 1g shows that 77% of all watches were made at speeds of 5 knots or more. We have therefore taken 5 knots as the speed below which records are excluded.

7. Following ship
Birds following or otherwise obviously associated with the ship are recorded in the "behaviour" codes 50–55 and 61 (Table 3). Fulmars, and to a lesser extent kittiwakes, are most affected, apparently more in the south than the north, no doubt because fishing activity is greater in the south. Records falling in these categories have been excluded from analysis

Table 1f
Categories of weather recorded during watch (% in each category)

Zone	Jan.		Feb.		March		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Conditions (PIROP Code)																						
No data (0)	71	100	77		58		70		80		49		79		88		81		78		80	
Drizzle (1)	1	0	1		0		2		3		0		4		0		2		3		2	
Rain (2, 3)	9	0	1		3		2		2		0		1		0		2		1		0	
High wind (4)	6	0	14		20		12		3		11		6		0		2		5		3	
Very calm (5)	0	0	0		0		1		1		0		1		0		2		8		3	
Fog (6)	0	0	1		2		6		9		39		8		12		10		5		7	
Snow (7)	7	0	6		17		7		2		0		0		0		0		0		6	
Hail (8)	0	0	0		0		0		0		0		0		0		0		0		0	

Table 1g
Number of watches recorded at each ship's speed (zone 1 = south of 60°N, zone 2 = north of 60°N)

Zone	Jan.		Feb.		March		Apr.		May		June		July		Aug.		Sept.		Oct.		Nov.	
	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Speed (knots)																						
0	15	11	18		23		14		0		14		26		6		1		9		5	
1	2	0	0		1		1		0		0		0		0		1		1		1	
2	0	1	7		5		2		0		0		0		0		1		0		1	
3	0	1	2		4		7		31		1		13		1		0		1		0	
4	6	2	3		6		7		57		3		0		3		1		2		3	
5	1	9	6		4		4		0		3		31		1		1		4		5	
6	6	6	4		2		1		0		2		0		3		7		11		19	
7	3	1	7		2		2		0		0		0		2		5		2		2	
8	5	8	4		2		8		0		8		0		13		3		6		2	
9	23	9	10		5		4		0		11		0		11		1		7		2	
10	6	5	20		26		32		11		19		30		20		52		17		27	
11	17	7	4		8		6		0		3		0		8		7		10		9	
12	5	10	5		4		3		0		5		0		9		7		6		7	
13	6	15	7		4		4		0		28		0		15		10		16		7	
14	1	4	1		2		5		0		2		0		3		6		5		0	
15	0	8	0		0		0		0		0		0		1		0		2		0	
16	0	0	0		0		0		0		0		0		0		0		0		0	
17	0	1	0		0		0		0		0		0		0		0		0		0	
18	0	0	0		0		0		0		0		0		0		0		0		0	
19	0	0	0		0		0		0		0		0		0		0		0		0	
20	3	0	0		1		0		0		0		0		3		0		0		0	

in spite of the large proportion of records involved, especially in September, as they clearly represent a strong bias between species and geographical areas.

8. Number of observers
At least 86% of watches were made by one observer, so we have made no correction for the number of observers.

9. Height of observer's eye above sea level
This variable has a considerable effect on the observer's field of view and consequently on the number of birds the observer can see. There are five PIROP categories of this variable, of which we selected those corresponding to heights of at least 15 feet (4.6 m); these account for nearly 99% of all records

in the months July–September. Samples at lower heights are too small to examine the effect of this variable in detail. It is also likely to be correlated with ship's speed since that depends on the ship's length which, in turn, will affect the height of the observation platform.

Sensitivity test of conversion factor C_b
The effect of input variables on the size of the conversion factor C_b was tested by altering each in turn and comparing their effects on the output value. Confidence limits are not available for most input parameters so we examined the most extreme case that appeared possible—for most variables, 50%. Tests were conducted for two examples, one large species that flies frequently (gannet), and one small species

Table 2
Mean numbers of birds · km⁻¹ in relation to ship speed in selected months

	June		July				August				September				November	
	South		South		North		South		North		South		North		South	
	S	F	S	F	S	F	S	F	S	F	S	F	S	F	S	F
Fulmar																
mean	2.6	0.9	16.3	1.6	3.9	1.4	12.1	3.1	3.1	2.8	8.7	1.4	2.1	0.9	2.8	2.1
SE	0.5	0.1	12.1	0.2	0.9	0.4	3.8	0.7	0.9	0.4	4.2	0.2	0.5	0.4	0.8	0.9
%F		51		82		91		65		64		61		61		50
Greater Shearwater																
mean			4.4	2.2			14.8	3.5								
SE			1.3	0.5			3.5	1.2								
%F				82				64								
Sooty Shearwater																
mean			3.4	1.1			2.6	2.2								
SE			1.1	0.3			0.7	0.6								
%F				87				75								
Kittiwake																
mean	3.7	1.8	5.1	2.4			7.8	7.1	2.9	2.4	2.9	1.5	1.8	0.9	3.1	1.2
SE	0.4	0.5	2.8	1.3			2.6	2.2	0.8	0.7	1.1	0.2	0.3	0.2	0.9	0.4
%F		54		65				67		59		72		57		49
Common Murre																
mean			1.6	0.4			0.4	0.8								
SE			0.6	0.1			—	0.3								
%F				56				84								
Thick-billed Murre																
mean							5.4	3.3			1.2	1.5				
SE							2.8	1.2			0.2	0.1				
%F								63				72				

South = south of 60°N; SE = standard error of mean; S = ship's speed less than 10 knots; F = speed 10 knots or greater; %F = % records from speed F.

that spends most of its time on the water (puffin). Results are given in Table 4.

Changes in the values of population-dynamics variables had little effect on the value of C_b , nor did changes in the proportions of pre-breeders in the colony area. The proportion of breeders at different stages of the breeding cycle had an important effect in both species. This effect was greater in the case of the puffin, where post-brooding birds spend most of their time at sea, than for the gannet where post-brooders continue to attend their chick until fledging. The proportion of time the birds spent on the colony had a big effect in incubating and brooding birds, whose time spent at sea can be fairly accurately measured.

It appears that C_b provides a fairly robust conversion factor as long as the timing of breeding of the species concerned is known with reasonable accuracy. However, if the timing of breeding, or the duration of different breeding states, is so poorly known that the proportion of breeders at a given stage of their cycle in any month is not known within $\pm 50\%$, the

value of C_b is subject to considerable inaccuracy. In the case of our model, we have every reason to believe that data on timing of breeding are adequate.

Results

Species accounts — Southern areas

The full details of assumptions, interpolations, and calculations are given in the Northern Gannet species account; the same methods are used for the other species unless otherwise stated.

(i) Northern Gannet *Sula bassanus*

(a) *Breeding population*: Gulf, 45 550 birds; Newfoundland, 19 960.

(b) *Life-table*: A cohort of 1000 breeding pairs produces an average of 720 fledgelings per year; this breeding success of 72%, reported from Newfoundland by Montevecchi *et al.*

Table 3
Percentage of birds following or circling the ship in selected months

	June	July	August		September		November
	South	South	South	North	South	North	South
Northern Fulmar	36	16	18	4	55	10	43
Kittiwake	11	14	13	13	59	15	38
Common Murre	1	3	0		0		0
Thick-billed Murre				0.2		0	

Table 4
Sensitivity tests for the conversion factor C_b , relating numbers observed at sea during the breeding season to total numbers using the same area

Input parameter	Selected value, June		Change in value	% Change in output (C_b)	
	N. Gannet	Puffin		N. Gannet	Puffin
Adult survival	0.94	0.955	−50%	+52.0	+ 0.5
1st year survival	0.58	0.35	−50%	− 6.7	− 0.7
Chicks fledged/pair	0.72	0.42			
Age at first breeding	5	5	−25%	− 0.3	− 0.4
Proportion at breeding stage:					
Pre-laying	0.01	0.01	Increase each value to 1.0	−25.3	−25.2
Incubating/breeding	0.66	0.71		+ 5.4	+13.6
Post-brooding	0.23	0.06		−10.0	−64.0
Failed	0.10	0.22		−10.0	−25.2
Proportion present in colony area:					
First year	0.77	0.25	−50%	+ 6.3	+ 1.1
Second year	0.90	0.75	−50%	0.1	0.1
Other pre-breeders	1.00	1.00	−50%	0.1	0.1
Proportion of time at sea:					
Pre-layers	0.60	0.75	−50%	~ 0	~ 0
Incubating/brooding	0.40	0.50	−50%	+20.3	+27.6
Post-brooding	0.50	1.00	−50%	+ 8.8	+ 4.7
Failed	0.50	0.75	−50%	+ 3.8	+12.8
First year	1.00	1.00	−50%	+ 6.2	+ 1.4
Second year	0.75	0.90	−50%	0.1	0.1
Other pre-breeders	0.75	0.80	−50%	0.1	0.1
"True" value of C_b	1.896	1.660			

(1984), is similar to figures from the eastern Atlantic (Nelson 1978), though lower than that of the 81% reported from Newfoundland by Montevecchi and Porter (1980). Data from Bonaventure Island, Quebec, showed much lower breeding success (38%, Poulin 1969), due probably to a combination of toxic chemical pollution and human disturbance (Montevecchi and Tuck, in press; Montevecchi *et al.* 1984).

Adult mortality averages 6% · yr⁻¹ (Nelson 1978). Assuming a stable population, adult mortality is balanced by recruitment which, to simplify calculation, is taken to occur in one age-class only, that in which first breeding usually occurs (i.e. the modal age of first breeding or AFB). Nelson (1978, Table 18) gives this as 5, so 6% of 2000 birds = 120 birds are required in year-class 5. No figures are available for survival of the age-classes between 2 and 5, and those for

1st-year mortality are conflicting; Nelson (1978) assumes 65% in his Table 18 but quotes banding returns indicating about 54% in Table 25. Moisan and Scherrer (1973) give banding returns of birds from the Gulf of St. Lawrence that suggest a 1st-year mortality of 42%, which is the figure used here. When we apply this to the 720 fledgelings the result is 418 1st-year birds. Numbers of 2-, 3-, and 4-year-olds are derived by interpolation between this figure and the number of 5-year-old recruits calculated, assuming a constant mortality rate, by the formula

$$S = (F_b/N_1)^{1/x}$$

where S = annual survival rate between 1st-year and age of first-breeding, F_b is the number of birds at age of first breeding (b years), N_1 is the number of 1st-years, and $x = (b - 1)$.

Table 5
Northern Gannet life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	94	2000	100
Fledgelings	72	720	36.0
1st Year	58	418	20.9
2nd Year	73	306	15.3
3rd Year	73	224	11.2
4th Year	73	164	8.2
5th Year = recruitment	73	120	6.0

This gives an annual survival rate over years 2–5 of 73%, and a total pre-breeding population of 1112 birds or 56% of the breeding population, apportioned to the various age-classes as in Table 5. This method of estimating pre-breeding mortality is preferred to the direct use of banding returns because such returns are known to be biased in a number of ways, particularly by the propensity of younger birds to die, directly or indirectly, at the hand of man. Thus banding recoveries are only used to estimate mortality where no other method is possible, especially for 1st-year mortality.

(c) *Proportion in study area*: Banding returns (Moisan and Scherrer 1973) show that in July about 77% of the bands from yearlings, about 80% of the bands from 2-year-olds, and 100% of adult bands are recovered within 100 km of the colony. Assuming a similar pattern for 3- and 4-year-olds to that of 2-year-olds, the total proportion of birds within the study area in July is estimated by:

$$\text{for 1st years, } x_1 * p_1 = 0.21 \times 0.77 = 0.161$$

$$\text{for 2nd to 4th years } \sum_{i=2}^4 (x_i * p_i) = 0.347 \times 0.80 = 0.278$$

$$\sum_{i \neq b} (x_i * p_i) = 0.439$$

or 44% of the breeding population present as pre-breeders in the study area.

(d) *Time spent at sea*: Attendance-shifts average about 7.5 h in July (Montevecchi and Porter 1980) which, in a 16-h day, suggests that each adult spends about half its time at sea. There are no quantitative data on attendance patterns of immatures, but Nelson (1978) suggests that 1st-years never come ashore and older young spend progressively more time ashore at the colony between the 2nd and 5th years. We assume that 1st-years spend all their time at sea, and other immatures average 75% at sea. So, $T_1 = 1.0$, $T_{2-4} = 0.75$, $T_b = 0.5$.

The countable population can, therefore, be finally estimated, using a hatching success of 80% (Montevecchi *et al.* 1984 (cf. 85% of Montevecchi and Porter 1980)), as follows:

Table 6
Black-legged Kittiwake life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	83.5	2000	100
Fledgelings	58	1073	53.7
1st Year	79	848	42.4
2nd Year	79	670	33.5
3rd Year	79	529	26.5
4th Year	79	418	20.0
(5th Year = recruitment	79	330	16.5

$$CP = BP (HS * T + \sum (x_i * T_i * p_i))$$

$$CP = BP [(0.80 * 0.5) + 0.162 + (0.278 * 0.75) + (0.20 * 0.75)] = 0.92 BP$$

breeders 1st year 2nd–4th yr failed breeders

(ii) Black-legged Kittiwake *Rissa tridactyla*

(a) *Breeding population*: Gulf, 82 580 birds; Newfoundland, 123 260; Labrador, 100.

(b) *Life-table*: Newfoundland birds have an average clutch size of 1.85 and breeding success (chicks fledged per egg laid) of 58% (Maunder and Threlfall 1972). The breeding success of 80% recorded by Nettleship *et al.* (1982) is probably atypical, coming from a very small and rapidly increasing colony. First-year survival is 79% in European birds (Coulson and White 1959); adult mortality, averaging the two sexes, which have slightly different rates, is 16.5% (Wooller and Coulson 1977), and mean age of first breeding, again pooling the sexes, averages 5 years (Wooller and Coulson 1977, Salomonsen 1967). Assuming a constant survival rate between the end of year 1 and the start of year 5, and working from the calculated proportion of 1st-years, the mean immature survival works out to 79%, i.e. equal to 1st-year survival. The proportion of the breeding population of each age-class (1–4), can be calculated as 42, 34, 27, and 20%, respectively (Table 6).

(c) *Proportion in study area*: Banding returns from large numbers of kittiwakes marked in northwest Greenland (Salomonsen 1967) show that, in July, virtually no 1st-year birds would be found within 100 km of their colony, but almost all birds of older age-classes would be. We assume that the entire population of kittiwakes, with the exception of 1st-year birds, are within 100 km of the colony in July. The number of non-breeders present can therefore be taken directly from the life-table as the number of all 2-, 3-, and 4-year-old birds, i.e. 81% BP.

(d) *Time spent at sea*: Adults feeding chicks have been documented as spending about 82% of their daylight hours at sea

Table 7
Common Murre life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	94	2000	100
Fledgelings	76	760	38.0
1st Year	40	304	15.2
2nd Year	79	240	12.0
3rd Year	79	190	9.5
4th Year	79	150	7.5
(5th Year = recruitment	79	120	6.0

in the Pribilofs (Hunt *et al.* 1982), and 56% of their day at sea in the North Sea (Hodges 1974, per J. Porter, pers. commun.). The Pribilofs data are from a very large colony, the North Sea data from a small one, so the mean of the two values (69%) is used here. Four-year-old birds are assumed to spend the same proportion of the day at sea as adults, and for 2- and 3-year-olds we used 90%.

The countable population, using a hatching success of 73% (Maunder and Threlfall 1972) is thus:

$$CP = BP [(0.69 * 0.73) + (0.21 * 0.69) + (0.60 * 0.90) + (0.27 * 0.69)]$$

breeders 4th year 2nd–3rd year failed breeders

$$= 1.38 BP$$

(iii) Common Murre *Uria aalge*

(a) *Breeding population*: Gulf, 46 240 birds; Newfoundland, 977 160; Labrador, 112 300.

(b) *Life-table*: Breeding success from the clutch of one averaged 76% in Newfoundland (McLagan and Piatt 1982, Birkhead and Nettleship 1982). First-year survival is 38% from both Helgoland (Mead 1974) and Canadian banding recoveries (A.J. Gaston and D. Noble, unpubl.); this is likely to be too low, but by how much is unclear. We adopted a conservative value of 40% in this study, chiefly to smooth out the otherwise very sharp jump required between 1st-year and adult survival. Average age of first breeding is 5 years (Birkhead and Hudson 1977). Estimates of adult survival range from 87% in Helgoland (Mead 1974) and 88% in eastern Canada (Gaston and Noble, unpubl.) from straight banding recoveries, to 91.5% from resightings on Skomer Island (Birkhead and Hudson 1977), 93.5% from British banding recoveries, selected to minimize the various biases inherent in band recovery data (Mead 1974), and 94% from changes in composition of pairs including a bridled bird in Labrador (T.R. Birkhead, pers. commun.). Since most sources underestimate adult survival, the highest of them (94%) is used here. Interpolating, as before, between 1st-year and adult survival, we obtain an estimate of 79% mean annual survival of immatures from 1 to 4 years old. This agrees well

with the 77% survival of 2- and 3-year-olds from returns of birds banded on Helgoland (Mead 1974). The life-table (Table 7) gives a slightly lower estimate of survival to age of first breeding (16%) than that of 20% suggested by Birkhead and Hudson (1977).

(c) *Proportion in study area*: Recoveries of known-age banded birds in July suggest that about 60% of immatures would be within 100 km of the colony (Mead 1974).

(d) *Time spent at sea*: Birkhead (1978) found that pairs with eggs were together at the site, on average, 30% of the day-time, and pairs with chicks (estimated from Birkhead 1978, Fig. 6), about 20%. Each adult was therefore, on average, at sea $70/2 = 35\%$ of the time in the incubation period, 40% while raising the chick. Three- and 4-year-olds are assumed here also to spend 35% of their time at sea in July, and 1-year-olds 100%, as they are not seen on land. Birkhead (1978) saw only 20% of the 2-year-olds that the life-table suggests should be present in the population, in the “club” of non-breeders on Skomer Island; here, 80% is used as an estimate of the average time spent at sea by 2-year-olds.

The above figures, together with a hatching success of 89% (Birkhead and Nettleship 1982), yield the following estimate of the countable population:

$$CP = BP [(0.89 * 0.38) + (0.60) + (0.60 * 0.12 * 0.80) + (0.17 * 0.60 * 0.35) + (0.11 * 0.35)] = 0.56 BP$$

breeders 1st year 2nd year 3rd–4th year failed breeders

(iv) Thick-billed Murre *Uria lomvia*

(a) *Breeding population*: Gulf, 1400 birds; Newfoundland, 3700; Labrador 18 740.

(b) *Life-table*, (c) *proportion in study area*: There are no local data, thus we assume these data to approximate those of the Common Murre. The West Greenland breeding population probably behaves similarly to southern Canadian birds, since both areas are “Low Arctic”; Kampp (1982) estimated adult survival there as 90% (known to be an underestimate) and survival to first breeding (5 years) as 18% (page 49 in Kampp, 1982) or ca. 20% (abstract in Kampp, 1982). These figures are comparable with the values used here for Common Murres of 94% and 16%, respectively.

(d) *Time spent at sea*: Gaston (1985) gave figures for the time spent at sea by breeders and non-breeders at Digges Island and Prince Leopold Island. We used the former figures here since Digges is the closer colony to those considered in this report. In July, there are about 4 h of darkness at Digges, 2 of which are spent on the colony by each breeder. Thus, of available daylight, each breeder spends 10 h on the colony each day and 10 h at sea. Non-breeders spend on average 6.3 h on the colony in July, all of it by day, thus spend 68% of the daylight hours at sea. First-year birds are assumed to spend all of the time at sea.

Table 8
Razorbill life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	92	2000	100
Fledgelings	67	670	33.5
1st Year	49	328	16.4
2nd Year	83.5	274	13.7
3rd Year	83.5	229	11.5
4th Year	83.5	191	9.6
(5th Year = recruitment	83.5	160	8.0

Hatching success averages 68% in Labrador (Birkhead and Nettleship 1982), so

$$CP = BP [(0.50 * 0.68) + (0.6 * 0.29 * 0.68) + (0.6 * 0.15) + (0.32 * 0.68)]$$

breeders
2nd-4th
year
1st
year
failed
breeders

$$= 0.77 RP$$

(v) Razorbill *Alca torda*

(a) *Breeding population*: Gulf, 6740 birds (Chapdelaine and Laporte 1982); Newfoundland, 1480; Labrador, 38 584.

(b) *Life-table*: Clutch size is one and breeding success averaged 67% in the Gulf of St. Lawrence (Bedard 1969). First-year survival, from banding returns, is 49% in eastern Canada (Bedard 1969), which agrees well with the 45% from British banding recoveries (Lloyd 1974). Adult survival, from resightings of breeding birds at Skokholm Island, Europe, is 90–92% (Lloyd and Perrins 1977); the higher figure is used here. The modal age of first breeding is 5 years in Britain (Lloyd and Perrins 1977). Average annual survival between years 1 and 5, by interpolation, is estimated at 83.5% (Table 8).

(c) *Proportion in study area*: British recoveries between May and July showed 20% of 1st-years within 200 km of the colony (Mead 1974); by interpolation, 10% are estimated to be within 100 km of the colony. Adults and immatures older than one year showed similar distribution patterns to each other; accordingly, all birds older than 1 year are assumed to be within 100 km of land in July.

(d) *Time spent at sea*: Lloyd (1982) found that off-duty breeding razorbills spent 20–34% of their time on land at Great Saltee Island, and 37% on Skokholm; these figures are very similar to those for Common Murres (discussed previously). There are no other data on time-budgets, so these are assumed to be the same as Common Murres.

Hatching success averaged 76% in the Gulf (Bedard 1969), 70% in Norway (Barrett 1984) and 64% on Skokholm, Wales (Lloyd 1977); the mean of these figures (70%) is used here.

Table 9
Atlantic Puffin life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	96	2000	100
Fledgelings	71	710	35.5
1st Year	35	249	12.8
2nd Year	75	187	9.4
3rd Year	75	140	7.0
4th Year	75	106	5.3
(5th Year = recruitment	75	80	4.0

The countable population is therefore:

$$\begin{aligned} \text{CP} = & \text{BP} [(0.35 * 0.70) + (0.10) + (0.13 * 0.80) + (0.21 * 0.35) \\ & \text{breeders} \qquad \text{1st} \qquad \text{2nd} \qquad \text{3rd-4th} \\ & \qquad \text{year} \qquad \text{year} \qquad \text{year} \\ & + (0.30 * 0.35)] = 0.63 \text{ BP} \\ & \text{failed} \\ & \text{breeders} \end{aligned}$$

(vi) Atlantic Puffin *Fratercula arctica*

(a) Breeding population: Gulf, 14 740; Newfoundland 495 000; Labrador, 153 460.

(b) *Life-table*: Breeding success in Newfoundland (33% (Nettleship 1972*a*)) is substantially lower than breeding successes measured elsewhere (e.g. 64% on Skomer (Ashcroft 1979), 87% and 93% on Funk and Small Islands, Newfoundland (Nettleship 1972*a*), 80% on Isle of May, Scotland (Harris 1983), 77% on St. Kilda (Harris 1980)). Here we use an overall mean figure, from all these studies, of 71%.

First-year survival was 35% in banding returns of British puffins (Mead 1974). The same data estimated adult survival at 95.5%, close to the 96% from resightings recorded by Harris (1983) in Scotland and 95% by Ashcroft (1979) in Wales. Age of first breeding is widely given as 5 years on average (e.g. Ashcroft 1979; Harris 1981, 1983) and that figure is used here, although Harris' data suggest that the modal age of first breeding may be nearer 6; 26 of his sample of 54 first bred at 7 or older. The average annual survival rate between years 1 and 5, by interpolation, is 75% (Table 9).

The life-table deserves comment. It is based on such Canadian data as are available, and on the assumption that the population is stable. More likely, puffin populations are declining as Nettleship (1980, 1985) has claimed. However, they might be declining because of low breeding success (which would be likely if the very low breeding output measured by Nettleship (1972a) in Newfoundland was typical of Canadian puffins), or because of low survival of immatures, or from a higher adult mortality than that used here (which is inferred from British figures). Without knowing at which point in the life-cycle there is excess mortality, the life-table

cannot be adjusted to reflect the apparent steep decline in the population.

Alternative life-tables can be constructed using different values for breeding success. The most recent and detailed studies are by Harris (1980, 1983) in Scotland where breeding success averaged nearly twice the Newfoundland figure, for example. This figure, applied to Table 9, implies an increasing population, which is true of many British colonies but not of the Canadian population which is at best stable but more likely declining (Nettleship 1980, 1985). Alternatively, setting recruitment constant at replacement rate with 80% breeding success gives a 2–4 year survival of 73%, which is substantially lower than the figure in Table 9.

It is important to note that breeding success as reported in the literature refers to chicks fledged per pair that laid an egg; in some British colonies, 20–30% of “breeding” pairs may occupy burrows without laying. Puffins in Canada are censused by “occupied burrows”, but this category includes burrows in which no egg is laid (Nettleship 1972*b*). Hence, these figures for breeding success, low as they are, may seriously overestimate the breeding output of a population counted by this method. Counteracting this bias is the tendency for research on puffin breeding biology to cause losses and so underestimate the breeding success of undisturbed colonies. This has been suggested by Pierotti (1983) and Birkhead and Nettleship (1982), though Harris (1980, 1983) suggested that the methods used in such research (including Nettleship’s (1972*a*), which Pierotti addressed specifically) do not seriously lower breeding success in puffins.

(c) *Proportion in study area:* First-year birds rarely come ashore; Mead (1974) gives one banding return of a yearling 70 km from its natal colony. Twenty-five percent of 1st-years are here assumed to spend July within 100 km of shore. Few 2nd-year birds land (though more than 1st-years), but all the returns of banded 2-year-olds from eastern North America are at the natal colony (CWS unpubl. rep., Ottawa). We assume that 75% of 2-year-olds are within 100 km of the colony in July. Three- and 4-year-olds are assumed to be entirely within the area, as are adults. Ashcroft's (1979) finding that 20% of adult puffins in a Welsh colony could not breed because of competition with rabbits and Manx Shearwaters *Puffinus puffinus*, and that a further 2% were away from the colony each year, has not been shown to apply in Canadian colonies.

(d) *Time spent at sea*: There are no time-budgets for this species. The single chick is not brooded or attended (as, for example, in murres and Razorbills), so an estimated 75% of time spent at sea for each adult in July seems reasonable. First-years are assumed to spend 100% of their time at sea. Few 2nd-year birds land (though more than 1st-years); they are treated here as spending 90% of their time at sea. Three- and 4-year-olds are assumed to spend the same amount of time at sea as adults.

The mean of all figures for hatching success given by Harris (1984) is 77%; this figure is used here.

The countable population is therefore:

$$CP = BP [(0.75 * 0.77) + (0.13 * 0.25) + (0.09 * 0.75 * 0.9) + (0.12 * 0.75) + (0.23 * 0.75)] = 0.93 BP$$

Species accounts — Northern area

(i) Northern Fulmar *Fulmarus glacialis*

(a) *Breeding population*: This species breeds commonly in arctic Canada, but rarely in the Maritimes (Nettleship and Montgomerie 1974). The breeding population in the Lancaster Sound study area (Fig. 2) is 344 000, with an additional 6000 birds on Coburg Island of which 25% probably feed within the study area in August; the total BP for the purposes of this exercise is thus 345 000 birds.

(b) *Life-table*: The only quantitative data (apart from Salomonsen (1967—see below)) are from a Scottish colony in an expanding population (Dunnet *et al.* 1979). Direct application of these figures for age at first breeding (9 years), and annual survival of breeders (97%) and non-breeders (91%), to the Canadian breeding output of 47% (Linton and Nettleship 1977), produces a life-table with a surplus of recruits equivalent to 268% of the number needed to keep the population stable. The Canadian population is probably stable, and certainly shows no evidence of increase on the scale shown by eastern Atlantic populations (Nettleship 1980), so the Scottish data cannot be applied wholesale to Canadian populations. The problem with adjusting the data to yield a life-table more likely to reflect the state of the Canadian population, as with the Atlantic Puffin, is that there are a number of different ways to make adjustments but no Canadian data to guide which one is chosen.

Perhaps the feature of the Scottish data least likely to apply to the Canadian Arctic is the high pre-breeding survival. The age of first breeding is probably also over-estimated, even for the Scottish population (Dunnet *et al.* 1979). A small decrease in adult survival can also have a marked effect on the rest of the life-table. Accordingly, the following changes to the Scottish data are suggested for the Canadian Arctic population:

- (i) age of first breeding 8 years, rather than 9;
- (ii) adult survival 95%, rather than 97%;
- (iii) using these two changes, the mean annual survival of pre-breeders is calculated by interpolation between the number of fledgelings and the number of 8-year-old recruits required in a stable population (see Northern Gannet).

Pre-breeding survival works out to 82.4%, compared with the 91% of the Scottish population. The calculated life-table is shown in Table 10.

Salomonsen (1967) gives a graph of the age distribution of banded birds recovered off Greenland, which differs quite markedly from that in Table 10. Among several possible reasons for this are probable higher chick production in the Low Arctic colonies of West Greenland, compared with those

Table 10
Northern Fulmar life-table, based on cohort of 1000 breeding pairs

Age-class	% Survival (for fledgelings, = breeding success)	Number in population	% Breeding population
Adult	95	2000	100
Fledgelings	47	470	23.5
1st Year	82.4	387	19.4
2nd Year	82.4	319	16.0
3rd Year	82.4	263	13.2
4th Year	82.4	217	10.9
5th Year	82.4	179	9.0
6th Year	82.4	147	7.4
7th Year	82.4	121	6.1
(8th Year = recruitment	82.4	100	5.0

of the Canadian High Arctic, and possible distortions through hunting of fulmars in Greenland.

(c) *Proportion in study area*: Salomonsen (1967) and Macdonald (1977), referring to Greenland and British populations, respectively, both suggested that most birds older than 4 years, and many 3-year-olds, come to land regularly at the colony during the breeding season. Birds between 3 and 7 years old in the calculated life-table (Table 10) account for about 47% of the breeding population. Linton and Nettleship (1977) found that non-breeders attending the colony at Prince Leopold Island, Lancaster Sound, numbered about 61% of the breeding population. Non-breeders of 1- and 2-years-old account for a further 35% of the breeding population. Banding recoveries from Disko Bay in Northwest Greenland (Salomonsen 1967) suggest that 1- and 2-year-old birds account for about 13% of the local population in the summer; Salomonsen (1967) implies that these birds had been banded elsewhere and that 1- and 2-year-old birds do not visit the vicinity of breeding colonies. However, if they do visit land in similar proportions to their numbers in Disko Bay, they would raise the proportion of non-breeders very close to that obtained in Lancaster Sound (Linton and Nettleship 1977). This would mean—contrary to Salomonsen's suggestion—that there are negligible numbers of non-breeders within the feeding range of the colony that do not come to land. Here we use the figure of 61% of the breeding population present as non-breeders, from Linton and Nettleship's (1977) field data from Lancaster Sound itself, but point out that this is not consistent with the calculated life-table.

Fulmars are known to have a large potential feeding range while breeding, but authorities differ sharply on the actual ranges involved. Dunnet and Ollason (1982) quoted band recoveries of breeding birds, in the breeding season, averaging 232 km from the colony; these could be split into separate means ($n = 3$ each) for incubation (296 km) and chick-rearing (176 km). However, Furness (1983) and Furness and Todd (1984) use very different foraging ranges; these authors misquote Dunnet and Ollason (1982) as giving

"no clear evidence for ranges of breeding adults", and calculates a maximum potential foraging range of 120 km for a 6-hour departure. Furness (1983) based his figures on sightings of dyed birds—not necessarily feeding when sighted, though he did not mention this—at a time when small chicks were present, being constantly brooded, and with a small food demand. He dyed 21 birds with eggs or small chicks; "several" of the eggs were lost before the study was completed. Of 10 sightings in July and August, the furthest was 120 km, the median 35 km; nine birds failed to rear chicks and all but one of the sightings could in theory have been from these birds. The birds studied by Furness made much shorter foraging trips than those on Prince Leopold Island, which are therefore likely to forage at least as far from land as suggested by Dunnet and Ollason's (1982) figures. Furness and Todd (1984) found that the diets of fulmars breeding on Foula and St. Kilda were very different, suggesting that there was very little overlap in the feeding ranges of the two colonies and thus, since the islands are 445 km apart, that their foraging ranges are less than 220 km. The limits chosen for the Lancaster Sound study area are about 250 km from the nearest fulmar colony, except for the small one at Coburg Island which is less than 50 km inside the study area limits. Here it is assumed that only 25% of Coburg birds forage within the study area. Further, the few birds from other Lancaster Sound colonies which might feed outside the study area are probably balanced by birds entering it from colonies in northwest Greenland and northeast Baffin Island.

(d) *Time spent at sea*: Breeding birds spend, on average, 8 h of the day at sea while the chick is being brooded (for the 1st week of August), and 96% of the day at sea for the rest of the month (Linton and Nettleship 1977); on average, therefore, breeders spend 81% of the day at sea during August in Lancaster Sound. Linton and Nettleship's (1977) data suggest that non-breeders attending the colony follow similar attendance patterns to breeders; but non-breeders attending a particular site surely cannot be assumed to be the same individuals as can birds attending a chick, so that the data on non-breeders—with regards to both their numbers and their time-budgets—are less reliable than the data for breeders.

The countable population is therefore calculated using a proportion of non-breeders of 0.61 BP, a hatching success of 62% (Linton and Nettleship 1977), and assuming all 1.61 BP birds are in the area and spend 81% of their time at sea. From these figures,

$$CP = BP [(0.62 * 0.81) + (0.61 * 0.81) + (0.38 * 0.81)] = 1.3 \text{ BP}$$

breeders non- failed
 breeders breeders

(ii) Black-legged Kittiwake *Rissa tridactyla*

(a) *Breeding population*: Lancaster Sound, 207 500 birds (assuming 75% of colonies at Coburg Island and Baillie-Hamilton Island feed within the survey area).

(b) *Life-table*: Clutch-size in Lancaster Sound averages 1.7, hatching success 80%, and fledging success 57% (Nettleship and Birkhead, ND).

(c) *Time spent at sea*: Taken as 82% for breeders (figures for Pribilofs, from Hunt *et al.* 1982) and 4-year-olds, others as for southern areas.

The countable population is therefore:

$$CP = BP [(0.82 * 0.80) + (0.20 * 0.82) + (0.60 * 0.90) + (0.20 * 0.82)]$$

breeders 4th 2nd-3rd failed
 year years breeders

$$= 1.52 \text{ BP}$$

(iii) Thick-billed Murre *Uria lomvia*

(a) *Breeding population*: 740 000 birds.

(b) *Life-table*, (c) *proportion in study area*: Assumptions as for southern areas, except for the population of 2- to 4-year-old non-breeders. This is taken as 19% BP from the counts of non-breeders attending the colony (Gaston and Nettleship 1981), rather than the 17% BP suggested by the Common Murre life-table (29% BP 2- to 4-year-olds, of which 60% were estimated to be in the study area). Band recoveries in the Canadian arctic suggest that few, if any, 1- or 2-year-old birds are in the vicinity of the colony in July (A.J. Gaston, pers. commun.).

(d) *Time spent at sea*: Gaston's (1985) figures for Prince Leopold Island suggest that breeders spend 50% of their time at sea and non-breeders 47%.

Using the 79% hatching success recorded by Gaston and Nettleship (1981) at Prince Leopold Island, the countable population is therefore:

$$CP = BP [(0.50 * 0.79) + (0.19 * 0.47) + (0.15) + (0.21 * 0.47)] = 0.73 \text{ BP}$$

breeders 2nd-4th 1st failed
 year year breeders

Conversion factors

(i) Breeding species

Table 11 shows the calculated densities at sea for all species in each study area, together with the mean number of birds seen per linear kilometre on PIROP counts in July and a conversion factor C, obtained by dividing the PIROP index into the calculated mean density. The two murre species (*Uria*) are so difficult to distinguish at sea that in the southern areas, where the two species overlap, they are commonly recorded as "murre spp." on PIROP counts; samples of individual species are inadequate, so the figures for "murre spp." have been used here, using breeding biology data for Common Murres (which far outnumber Thick-billed Murres here). The two species are likely to have similar conversion factors because these depend chiefly on visibility and behaviour at sea, in which the two species are clearly very similar. The two values of C for Northern Gannets differ by more than an order of magnitude. There is no real alternative to using the mean of the two values (1.27) and accepting—however reluctantly—the large margins of error involved.

The two C values calculated for southern Black-legged Kittiwakes are very close. That for Lancaster Sound is much higher, apparently because kittiwakes there are highly concentrated in coastal waters too close inshore to be sampled

by the survey vessels on which PIROP counts are made. Nettleship and Gaston (1978) found that only 21% of kittiwakes in Lancaster Sound in August were further than 4 km from shore. Applying this correction to C for Lancaster Sound gives a revised estimate of $5.05 * 0.21 = 1.06$, almost identical to C for southern areas. This is lower than C for gannets, which at first seems anomalous as gannets are so much bigger than kittiwakes, but immature gannets are much darker (and thus less visible) than young kittiwakes.

The single value of C obtained for Northern Fulmars (in Lancaster Sound) is rather higher than might be predicted from those obtained for gannets and kittiwakes. Nettleship and Gaston (1978) found in aerial surveys of western Lancaster Sound in August that over 40% of fulmars were in the coastal zone (defined as within 4 km of the shore). Applying this "coastal correction"—as for northern Black-legged Kittiwakes (above)—lowers C to 1.02.

The conversion factors obtained for "murre spp." are similar to those for puffins, although murres are larger than puffins (23% longer-winged using wing lengths in Birkhead and Nettleship (1982)) and would be expected to be more easily visible. Razorbill C values are very variable, but derive from much lower densities than other auks. The figures for Thick-billed Murres in Lancaster Sound yield an anomalously low value of C, suggesting that the calculated value of D underestimates the real density of birds. The expected density is much higher than for any other species (except fulmars in Lancaster Sound—see above). The low value of C may be due partly to the few PIROP samples available from Lancaster Sound and partly to the tendency—evident also in murres and puffins—for C to be lower at higher densities. Applying a "coastal correction" as for fulmars and kittiwakes (above), using 30% of birds found in the coastal zone on aerial surveys (Nettleship and Gaston 1978) lowers C still further, as the anomaly here lies in the very high PIROP counts rather than in high expected densities. We cannot satisfactorily explain this anomalous result.

The values of C for expected densities of auks of less than 0.5 birds·km⁻² are particularly variable and, because the sample sizes involved are small, we have omitted these data. The mean of the values of C for all alcids corresponding to expected densities of at least 0.5 birds·km⁻² is 1.8, with 95% confidence intervals of 1.2–2.3. We have applied this value to alcids in general.

(ii) Implications of the conversion factors

It is possible to check on the absolute and relative values of C, by reference to the distances from the ship at which the different species are likely to be visible. Because the PIROP counts are expressed as birds per linear kilometre, a conversion factor (to birds·km⁻²) of 1.0 would imply that the birds were detected up to a distance of 500 m either side of the ship. Gannets and kittiwakes (and fulmars after correcting for coastal effects) each have a C of about 1; though gannets are larger, many of them are in immature plumage, with varying amounts of brown rendering them less conspicuous, whereas even 1st-year kittiwakes appear largely white so it is reasonable to expect these two species to share a similar C. It is also reasonable to expect them to be detected up to

Table 11
Breeding and countable populations, calculated densities at sea, PIROP counts, and conversion factors for seabirds in the four study areas

Species	Region	BP	CP	D	PIROP		C
					\bar{x}	SE	
Northern Fulmar	Lanc. Sound	344 000	577 280	8.345	4.923	0.705	1.695
	Lanc. Sound (coastal correction)†			5.007			1.020
Northern Gannet	Gulf	45 550	41 906	0.186	0.073	0.016	2.372
	E. Nfld.	19 960	16 343	0.089	0.514	0.195	0.172
	Labrador	0	0	—	0.047	0.012	—
Black-legged Kittiwake	Gulf	82 580	167 377	0.743	0.707	0.106	1.051
	E. Nfld.	123 260	168 866	0.915	0.880	0.327	1.041
	Labrador*	100	—	—	0.520	0.119	—
	Lanc. Sound	207 500	315 400	4.723	0.935	0.117	5.050
	Lanc. Sound (coastal correction)†			0.992			1.060
Razorbill	Gulf	6 750	3 718	0.017	0.040	0.034	0.413
	E. Nfld.	1 480	814	0.004	0.018	0.007	0.550
	Labrador	38 584	21 221	0.201	0.067	0.019	2.678
Thick-billed Murre	Lanc. Sound	740 000	614 200	9.197	10.597	1.382	0.868
	Lanc. Sound (coastal correction)†			6.438			0.558
	Hudson Strait	1 650 000	1 204 500	4.208	3.224		1.305
Murre spp.	Gulf	47 640	35 249	0.112	0.035	0.013	3.397
	E. Nfld.	980 860	519 856	2.818	1.294	0.292	2.179
	Labrador	131 044	69 453	0.657	0.347	0.092	1.896
Atlantic Puffin	Gulf	14 740	13 747	0.061	0.017	0.007	3.211
	E. Nfld.	495 000	470 250	2.549	1.493	0.215	1.707
	Labrador	153 460	145 787	1.380	0.708	0.345	1.949

* Many non-breeding kittiwakes from Greenland visit Labrador waters in July.
† See text for explanation.
Note: Gulf = Gulf of St. Lawrence; E. Nfld. = eastern Newfoundland;
BP = breeding population (no. of birds); CP = countable population; D =
calculated density (birds per square kilometre); PIROP = mean no. of birds
per linear kilometre recorded on 10-min PIROP watches; C = conversion
factor (D/PIROP). See text for details.

500 m from the ship, as Dixon (1977) found that gannets, kittiwakes, and fulmars were first seen on average 363 m, 216 m, and 352 m (respectively) from the ship when sitting on the water, and they would be visible in flight substantially further away. The conversion factor of 1.8 for alcids suggests that they were visible up to 277 m; Dixon (1977) first saw Common Murres and Atlantic Puffins at mean distances of 217 and 218 m, respectively.

The values of C are thus reasonable in relation to the little available information known about these species' visibility at sea.

Conversion factors have been calculated to three decimal places to minimize rounding errors, but it would give a misleading impression of precision to express them to more than a single decimal place; they are therefore rounded accordingly.

(iii) Other species

Conversion factors are also needed for other species, but cannot be calculated directly either because they do not breed in this area (Greater and Sooty Shearwaters *Puffinus gravis* and *P. griseus*, respectively, phalaropes *Phalaropus* spp., Great Skua *Catharacta skua*); because they feed so close to land while breeding that very few breeders would be detected on PIROP counts (*Larus* gulls, jaegers *Stercoraria* spp.); or because their breeding populations have yet to be determined (Leach's Storm Petrel *Oceanodroma leucorhoa*, which is also hard to distinguish at sea from non-breeding migrants of Wilson's Storm Petrel *Oceanites oceanicus*, and Dovekie *Alle alle*, of which the first breeding population known in Canada was described in 1984 (Finley and Evans 1984)). Conversion factors for these species have to be estimated by comparison with the most similar of the species for which

they can be calculated:

Dovekies 1.8; they present difficulties because, although their colouring is much the same as the other auks, they are very much smaller (wing length 69% of Atlantic Puffin, 56% of Common Murre, using Dovekie wing length in Norderhaug (1970)). Dovekies typically move in flocks, which are easier to detect than scattered birds but are also invariably underestimated, so the biases introduced by flocking are at least opposing even if they do not cancel each other out. There seems no alternative to using the same conversion factor for Dovekies as for the other auks. Sooty and Great Shearwater 1.4 (the detectability of both shearwaters is likely to be intermediate between that of fulmars and auks because, though they behave like fulmars, they are much darker; a C midway between 1.0 of fulmars and the 1.8 of murres is therefore appropriate). Storm petrels and phalaropes 2.0 (this is the highest as they are the smallest species, thus we feel it is reasonable to suggest that they are twice as hard to see as Northern Fulmars). Skua 1.8 (similar size to Great Black-backed Gull, but dark at all ages). Jaegers 1.6 (between Great Black-backed Gull and Skua). *Larus* gulls, other than Great Black-backed, 1.2 (slightly more than Black-legged Kittiwake to allow for less conspicuous immatures). Great Black-backed Gull 1.4 (slightly more than Northern Gannet, corresponding to smaller size, and slightly higher than other *Larus* gulls because of the darker back of adults).

Conclusions

(i) Conversion factors for translating the mean numbers of birds seen per linear kilometre on PIROP 10-min watches to the mean number of birds · km⁻² at ship speeds of 5 knots and over, for observations made from at least 4.6 m above the sea, are suggested as follows: Northern Fulmar 1.0; Northern Gannet 1.3; Black-legged Kittiwake 1.1; Common Murre, Thick-billed Murre, Razorbill, and Atlantic Puffin 1.8. These species breed in the areas under study and consequently the conversion factors are based on acceptable data from population sizes available for counting.

(ii) By comparison with the most similar of the above species, the following conversion factors are suggested for species that do not breed in the areas under study, and those that breed in numbers either too small or too poorly known to allow conversion factors to be calculated: Sooty and Great Shearwater 1.4; storm petrels and phalaropes 2.0; Great Black-backed Gull 1.4; other *Larus* gulls 1.2; Skua 1.8; jaegers 1.6; Dovekie 1.8.

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