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Seabird numbers and prey consumption in the North Atlantic

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We compared seasonal composition, abundance, and biomass of seabirds between the Northeast (ICES region) and Northwest (NAFO region) Atlantic fisheries regions to identify differences in community assemblage and prey consumption. Seabirds were more abundant in the Northwest Atlantic, but biomass was greater in the Northeast. This disparity resulted from enormous numbers of little auks *Alle alle* breeding in West Greenland and of Leach's storm-petrels *Oceanodroma leucorhoa* breeding in Newfoundland, plus large numbers of non-breeding shearwaters *Puffinus* spp. entering southern NAFO areas in summer. The Northeast Atlantic communities were dominated numerically by northern fulmars *Fulmarus glacialis*, large auks *Uria* spp., and the Atlantic puffin *Fratercula arctica*. Seabirds occupying the North Atlantic consume approximately 11×10^6 t of food annually. Overall consumption rates peak during summer as a result of increased breeding activity and seasonal movements of birds into the North Atlantic. Because of the greater biomass of birds in the northeast, consumption (mainly by piscivores) in ICES areas was approximately 20% higher than that in NAFO areas, where planktivores dominate. NAFO areas had, however, a much greater consumption rate per unit area than ICES areas. Comparative studies such as these could prove informative in assessing large predator responses to the influence of fishing and ocean-scale climate change.

Keywords: community, consumption, North Atlantic, predators, seabirds.

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Introduction

There is increasing need to integrate energy consumption by seabirds and other predators into management policies in both ICES and NAFO convention areas of the North Atlantic (ICES, 2001, 2002a; Garcia *et al.*, 2003; O'Boyle *et al.*, 2005). The need for such an ecosystem approach is amplified by increasing pressures from fisheries, mariculture, and climate change on species upon which seabirds and mammals feed (Arnott and Ruxton, 2002; Davoren and Montevecchi, 2003; Pauly *et al.*, 2003; Hjermann *et al.*, 2004; Miller and Sydeman, 2004; Wanless *et al.*, 2004).

Incorporating endothermic predators into large-scale ecosystem and foodweb approaches is an integral aspect of these initiatives (Bundy *et al.*, 2000; Camphuysen, 2005). Seabirds, in particular, being the most conspicuous and easily accessed of large marine predators, often provide useful insights into ecosystem conditions and processes (Montevecchi *et al.*, 2006). This work was initiated by the ICES Working Group on Seabird Ecology (WGSE) to collate information on North Atlantic seabird communities, to compare the seabird communities, and to estimate their prey consumption throughout the ICES (north of 36°N, east of 42°W) and NAFO (Northwest Atlantic Fisheries

Organization; north of 35°N, west of 42°W) convention areas of the North Atlantic.

The boreal and low Arctic coastal regions of the North Atlantic are highly productive and support large numbers of breeding seabirds belonging to nine families and 21 genera (Newton, 2003; Gaston, 2004). The North Atlantic seabird community is also diverse in form and feeding behaviour, and includes pelagic surface-feeders (e.g. petrels, Procellariiformes), coastal surface-feeders (e.g. terns, Sternidae), coastal omnivores (gulls, Laridae), benthic-feeders (cormorants, Phalacrocoracidae), and specialized, wing-propelled pursuit-divers (auks, Alcidae). The distribution of the last group is restricted to the northern hemisphere.

On an annual basis, many of these species exhibit varying periods of residence in different oceanographic regions and areas. Some migrate into breeding areas in spring and summer, and out of them during autumn and winter. Other visitors move into regions after breeding elsewhere. For example, in the Northwest Atlantic, trans-equatorial migrant shearwaters (*Puffinus* spp.) move onto the Grand Banks following austral summer breeding seasons in the South Atlantic. In comparison, some species do not exhibit regular migratory patterns, but rather a more diffuse dispersal (e.g. gulls and Atlantic puffin *Fratercula arctica*; Wernham *et al.*, 2002; Bakken *et al.*, 2003; Harris *et al.*, 2005).

Recent models of prey consumption have shown that seabirds consume considerable quantities of small pelagic fish and crustaceans (Montevecchi, 2002, and references therein). These levels of consumption tend to be less than those of commercial fisheries at both regional and global scales, and they are vastly exceeded by consumption by marine mammals and predatory fish (Bundy *et al.*, 2000; Barrett *et al.*, 2002; Montevecchi, 2002; Brooke, 2004).

Focal forage species (e.g. sandeels *Ammodytes* spp. in the Northeast Atlantic and capelin *Mallotus villosus* in the Northwest Atlantic) provide primary food bases for marine birds, mammals, and fish (Lavigne, 1996; Camphuysen, 2005). These fish are important as prey for many commercial fish species targeted by industrial and commercial fisheries on both sides of the Atlantic (Aikman, 1997; Carscadden and Nakashima, 1997). Owing to their pivotal roles in marine foodwebs, we pay particular attention to their consumption by different seabird communities in different oceanographic regions.

Here we draw together information on the marine bird communities and generate model estimates of their consumption throughout the North Atlantic. We make comparisons between avian communities in different oceanographic regions, and compare different feeding guilds of avian predators and their changing spatial and temporal distributions throughout an annual cycle. These comparisons aid in assessments of ocean-scale variation in seabird communities and their associated foodwebs.

Methods

Population estimates

Breeding birds

The population estimates are primarily of birds nesting in coastal regions and feeding wholly or partially at sea, but the numbers of gulls may also include a small fraction of non-marine, inland-breeding segments of the populations. Of the many species of divers (Gaviidae), ducks, and geese (Anatidae) that could also be classified as seabirds, only the common eider (*Somateria mollissima*) is included here as a breeding species owing to its total dependence on marine food, and to its very large numbers in some areas of the North Atlantic. Rare species whose numbers do not total more than a few hundred pairs (e.g. gull-billed tern *Gelochelidon nilotica* and Sabine's gull *Xema sabini*) are not included in the calculations.

Members of the WGSE provided the best estimates of the numbers of seabirds currently breeding in their respective countries and regions; these data are presented in WGSE reports (ICES, 2002a, 2003 – available at http://www.ices.dk/reports/occ/). Data from the huge colonies of northern fulmars (*Fulmarus glacialis*), guillemots (*Uria* spp.), and little auks (*Alle alle*) in Canada, Greenland, Iceland, Svalbard, and the Barents Sea, and of black-legged kittiwakes (*Rissa tridactyla*) and Atlantic puffins in some areas are less precise owing to the vast numbers involved as well as difficulty of access. Moreover, while data for many species were presented to the nearest hundred, ten, or even individual pairs, others were presented as ranges, some as large as 100 000–1 000 000 pairs. For the sake of simplicity, all such ranges were entered as midpoints between the two extremes.

To simplify comparison across the Atlantic, many of the ICES and some of the NAFO areas were combined to form larger biogeographically similar regions (Figure 1, Tables 1 and 2).

Immature and non-breeding birds

Whereas the numbers of breeding adults were generally based on field data, numbers of nestlings and pre-breeders were estimated based on a classification of whether the species laid single- or multiple-egg clutches, and calculations based on numbers of breeding pairs (bp) plus the numbers of immature birds (Cairns *et al.*, 1991). Estimates of the numbers of non-breeding birds were made separately for single-egg species ($= (\text{bp} \times 0.7) + (\text{bp} \times 0.7)$) and for multi-egg species ($= (\text{bp} \times 0.6) + (\text{bp} \times 1)$). These estimates assumed that the numbers of non-breeding birds (immature birds and deferred breeders) were equivalent to 35% or 30% of the breeding population, and that the fledging success of single-egg and multi-egg clutch species was 0.7 and 1.0 chicks per pair, respectively.

These calculations are, however, very coarse, and do not take into consideration population trends of the different species. In the calculations of seasonal changes in total numbers (and hence biomass and food consumption) of

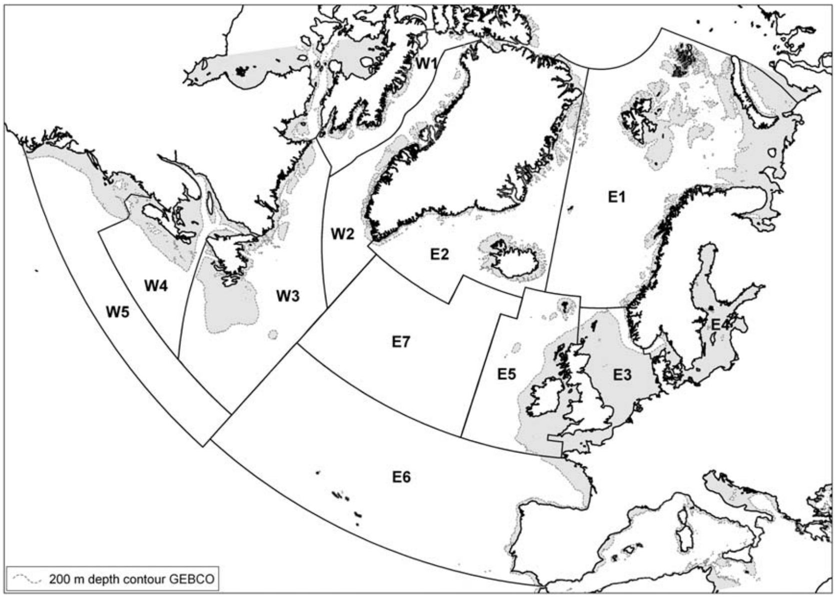

Figure 1. Boundaries of NAFO and ICES regions used in this study.

birds in a population (i.e. breeding pairs + immatures), the resulting figures were used over the entire year, and no correction was made to account for the fact that reproduction takes place in summer whereas mortality occurs during all seasons. As a result, the autumn population sizes are likely to be underestimated and the spring population sizes overestimated. For single-egg species, these under- and overestimates will each be about 10%, and for multi-egg species about 20%, based on normal survival rates of adult and immature birds.

Table 1. Relative species composition of seabirds breeding in NAFO regions as percentages of total number and total biomass (t) for each area (after ICES, 2003). Numerals in parenthesis after region number refer to NAFO areas.

Species group	NAFO W1 (0) Eastern Baffin Island	NAFO W2 (1) Western Greenland	NAFO W3 (2 and 3) Eastern Newfoundland and Labrador	NAFO W4 (4) Gulf of St Lawrence and Scotian Shelf	NAFO W5 (5 and 6) Gulf of Maine to Cape Hatteras
% By number					
Petrels	14	<1	81	9	5
Eiders	<1	0	<1	10	7
Pelecaniformes	0	0	<1	21	10
Gulls	6	<1	2	37	61
Terns	0	<1	<1	6	17
Auks	79	99	16	17	<1
Total breeding pairs (millions)	1.1	33.7	5.6	0.6	0.4
Total seabirds (millions), including immature birds	3.8	115.6	19.1	1.9	1.4
% By biomass					
Petrels	13	1	20	<1	<1
Eiders	2	<1	2	14	14
Pelecaniformes	0	<1	4	46	20
Gulls	3	4	9	26	63
Terns	0	<1	<1	<1	2
Auks	82	96	65	13	<1
Total biomass ('000 t)	3.4	20.4	3.8	2.1	1.1

Table 2. Relative species composition of seabirds breeding in six ICES regions (see Figure 1) as percentages of total number and total biomass (t) for each region (after ICES, 2003). Roman numerals in parenthesis after region number refer to ICES areas.

Species group	ICES E1 (I, II) Barents and Norwegian Seas	ICES E2 (Va, XIV) East Greenland and Iceland	ICES E3 (IV, VIId, e) North Sea and English Channel	ICES E4 (III) Baltic Sea, Skagerrak, and Kattegat	ICES E5 (Vb, VI, VII) Faroes and western UK	ICES E6 (VIII, IX, X) France, Iberia, and the Azores
% By number						
Petrels	10	15	12	0	41	63
Pelecaniformes	<1	<1	4	7	5	1
Eiders	2	3	2	40	<1	0
Gulls	18	7	41	41	14	32
Terns	1	2	4	8	<1	4
Auks	69	73	37	4	39	<1
Total breeding pairs (millions)	7.4	11.3	2.5	1.1	3.8	0.3
Total seabirds (millions), including immature birds	25.5	38.6	8.8	3.9	13.1	1.0
% By biomass						
Petrels	12	20	12	0	30	60
Pelecaniformes	2	2	16	13	22	3
Eiders	9	12	4	67	<1	0
Gulls	15	6	32	18	12	36
Terns	<1	<1	1	1	<1	<1
Auks	62	60	36	2	36	<1
Total biomass ('000 t)	16.4	20.6	6.9	5.1	9.5	0.9

Seasonal movements of birds into and between areas

In addition to those populations that breed in NAFO and ICES areas, there are large numbers of seabirds and waterfowl that breed outside these areas (including inland), but enter them at certain times of the year as migratory or wintering populations. The most abundant species were accounted for in the appropriate season in the model through rough estimates of the numbers of birds likely to have entered the respective areas along known migration and dispersal routes, based on the experience of the authors, consultation with experienced researchers who have worked at sea, published at-sea distribution atlases (Huettmann and Diamond, 2000; Stone *et al.*, 1995), and published consumption models (Montevecchi, 2000; Appendices 1 and 2).

Furthermore, birds breeding in a given ICES and NAFO area may also move through or to other areas during migration or to spend the winter (Merkel *et al.*, 2002; Wernham *et al.*, 2002; Bakken *et al.*, 2003). We attempted to account for these movements by estimating the numbers of each species present in each area each season (Appendices 3 and 4). These attempts were limited to the most abundant species breeding within a given area, i.e. species whose biomass constituted >2% of an exploratory estimate of the total biomass of seabirds breeding in that area (based on Tables 2.1–2.5 of ICES, 2002a and Table 3.1 of ICES, 2003).

No attempt was made, however, to quantify attendance in the large, central North Atlantic ICES XII area. No useful (in this context) estimates of bird numbers have been published for that area but, while extensive, these deep waters are relatively poor in nutrients (Shealer, 2002) and therefore probably also in seabird numbers. It is consequently unlikely that any estimates of seabird consumption in ICES XII will substantially affect the total. Moreover, being in the middle of the North Atlantic, this caveat will not preclude any east–west comparison of results.

Owing to differences in ocean climate regimes in the eastern and western North Atlantic, the seasons were defined differently, i.e. for NAFO areas, spring = April–June, summer = July–September, autumn = October–December, and winter = January–March; for ICES areas, spring = February–April, summer = May–July, autumn = August–October, and winter = November–January.

Consumption and energy expenditure

The annual consumption by seabirds in a given area was estimated using calculated species-specific energy demands, numbers of individuals of that species within that area, number of days present, and a mean energy density of food (see below). Consumption was modelled separately for each season, then summed to give an annual total.

Field metabolic rates during the breeding season were estimated using Ellis and Gabrielsen's (2002) allometric equations for different orders of seabirds. For seaducks, the equations for "all seabirds" were used. The length of the breeding season was set as the incubation period plus the fledging period (in days, as given in Cramp and Simmons, 1977, 1983; Cramp, 1985) plus 20 days (see Barrett *et al.*, 2002, for examples from ICES I and II).

For the non-breeding component of the breeding population (chicks, immatures, and deferred breeders) during the breeding season and for all birds outside the breeding season, FMR (field metabolic rate) was set as $2.5 \times$ BMR (basal metabolic rate; Gales and Green, 1990; G. W. Gabrielsen, pers. comm.). BMR was calculated using Ellis and Gabrielsen's (2002) allometric equations. FMR values for breeders and non-breeders were summed to give the overall energy expenditure for a given species within a given season.

Because diet composition is largely unknown in many species in most of the ICES and NAFO areas, a fixed energy density of prey of $5.5\ \mathrm{kJ\,g^{-1}}$ wet mass was chosen after an exploratory study comparing a model using fixed densities with one using species-specific diet composition and energy densities (fatty fish, lean fish, or invertebrates) from the Norwegian and Barents Seas (Barrett *et al.*, 2002). Digestion efficiency was set at 75% (Hilton *et al.*, 2000).

Results

Breeding populations

Approximately 68×10^6 pairs of seabirds breed in the North Atlantic, with approximately 60% (41×10^6 pairs, equivalent to ca. 141×10^6 seabirds) in the NAFO areas and ca. 40% (26×10^6 pairs, or 91×10^6 seabirds) in the ICES areas (Tables 1 and 2). Note that these totals do not include the ca. 3.5×10^6–4×10^6 pairs (mostly Brünnich's guillemots, *Uria lomvia*) that breed in the eastern Canadian Arctic, west of NAFO 0 (Nettleship and Evans, 1985; Gaston and Jones, 1998).

In terms of total biomass, however, the balance is reversed, with seabirds breeding in the western North Atlantic (ca. 31 000 t) weighing approximately 60% of those breeding in the eastern North Atlantic (ca. 59 000 t; Tables 1 and 2). This difference is due to the huge numbers of small little auks (>100×10^6 birds, body mass ≈160 g) and Leach's storm-petrels *Oceanodroma leucorhoa* (>15×10^6 birds, body mass ≈50 g) that dominate the breeding communities in NAFO 1 and NAFO 2 + 3, respectively.

Auks dominate the communities breeding in the northern regions on both sides of the Atlantic, constituting 80% and 99% of those breeding along eastern Baffin Island and western Greenland, respectively, in the NAFO areas, and about 70% of those breeding in the Barents and Norwegian Seas, eastern Greenland, and Iceland in the ICES areas (Tables 1 and 2). In western Greenland, 33×10^6 pairs of little auks comprise ca. 80% by number and ca. 60% of total biomass of the total NAFO summer population. Atlantic puffins, little auks, common guillemots (*Uria aalge*), and Brünnich's guillemots make up, respectively, 22%, 18%, 9%, and 9% (by number) of the total ICES populations. In biomass, the contribution by little auks falls to 5%, whereas that of the larger species is between 13% and 16%.

The petrels are also very unevenly distributed and numerically dominate the Newfoundland and Labrador community (80% by number, but just 20% by biomass because of the small size of Leach's storm-petrel), and the southern ICES areas (60–65% by number and biomass in region E6, mostly Cory's shearwaters, *Calonectris diomedea*). Northern fulmars and Manx shearwaters (*Puffinus puffinus*) also make up large proportions by number (41%) and biomass (30%) of the seabirds breeding in the Faroes and along the western borders of the UK. Northern fulmars are also numerous at Iceland (estimated to be 1.5×10^6 pairs).

The Pelecaniformes (great cormorants, *Phalacrocorax carbo*, European shags, *P. aristotelis*, and northern gannets, *Morus bassanus*) constitute more of the seabird community in the three southern NAFO areas (10–20% by number, 20–46% by biomass, Table 1) than in any other NAFO area or any ICES region. In the eastern North Atlantic, they attain only 5–7% by number and 13–22% by biomass in regions around the UK and in the Baltic Sea (Table 2).

The shallow, inland Baltic Sea and its approaches are dominated by common eiders and gulls, constituting 40% and 41% by number and 67% and 18% by biomass of the total breeding population, respectively. Approximately 45% of ca. 1×10^6 pairs of common eiders that nest in all ICES areas breed in the Baltic. Common eiders also attain their highest proportions (7–10% by number, 14% by biomass) in the inshore NAFO areas 4–6.

The only subarea in the NAFO and ICES areas where gulls dominate the seabird breeding community is NAFO 5 and 6. Of the approximately 380 000 pairs of seabirds breeding in that subarea, 60% are gulls (mainly laughing gulls, *Larus atricilla* and herring gulls, *L. argentatus*). Together with terns (Sternidae), they make up a large majority of the community (65% of the total biomass). In the ICES areas, breeding gulls are more evenly spread (except in eastern Greenland and Iceland, where they are relatively few), and constitute 14–40% by number and 12–36% of the biomass in the different regions, and nowhere do terns constitute >10% by number or >1% of the biomass.

Seasonal changes in numbers and biomass of seabirds

Overall, the seabird community in the NAFO areas is dominated by huge numbers of individual birds feeding at low trophic levels, including three small planktivorous species (little auk in NAFO 1, Leach's storm-petrel in NAFO 2 + 3, and Wilson's storm-petrel, *Oceanites oceanicus*, migrating into and through NAFO 4–6).

Owing to temporary movements of birds from the southern Atlantic into northwestern waters, and the migration of North Atlantic seabirds across fishing areas, there are, however, considerable seasonal changes in numbers and biomasses of seabirds occupying the various parts of the North Atlantic (Tables 3 and 4). Such movements include those of large numbers of birds migrating south out of Arctic Canada and the northernmost NAFO areas, and those moving southwestward from the northern ICES areas into the southern NAFO areas in autumn and winter (Appendices 1–4). For example, the large increase in numbers and biomass off eastern Newfoundland and Labrador in autumn and winter is due to the influx of millions of common eiders, auks (including probably $>10 \times 10^6$ Brünnich's guillemots and $>100 \times 10^6$ little auks), and black-legged kittiwakes (*Rissa tridactyla*) from colonies northwest of the NAFO areas (in the eastern Canadian Arctic), Baffin Island, and western Greenland, and from ICES regions (the Barents Sea, Norwegian Sea, and Iceland; Appendices 1 and 3). Farther south, 4.5×10^6–5×10^6 non-breeding birds (mostly greater shearwaters, *Puffinus gravis*, sooty shearwaters, *P. griseus*, and Wilson's storm-petrels) enter southern NAFO areas from the southern oceans in summer, and 1.5×10^6 inland-breeding ring-billed gulls (*L. delawarensis*) move out to the coast in the same areas in winter (Appendix 1). Similarly, in the eastern North Atlantic, nearly 7×10^6 seaducks winter in the Baltic Sea, but leave again in spring to breed inland. These include 4.3×10^6 long-tailed ducks (*Clangula hyemalis*), 1.2×10^6 common scoters (*Melanitta nigra*), and 1×10^6 velvet scoters (*M. fusca*; Appendix 2).

Table 3. Approximate maximum numbers of seabirds (millions) occupying NAFO and ICES regions in winter, spring, summer, and autumn. Birds passing through a given area during a season may therefore be counted in several areas within that season.

	Winter	Spring	Summer	Autumn
NAFO				
W1	0	4.6	4.6	3.8
W2	19.7	123.6	115.6	17.7
W3	125.2	25.7	22.7	130.1
W4	1.7	5.4	4.4	4.3
W5	2.8	19.7	4.3	10.6
Total	149.4	179.0	151.5	166.5
ICES				
E1	15.0	21.5	25.5	26.0
E2	21.4	33.9	38.6	33.1
E3	8.9	8.3	8.8	8.8
E4	10.2	9.8	3.9	5.8
E5	10.3	12.6	13.2	13.6
E6	1.3	2.1	1.0	1.4
Total	67.1	88.2	91.1	88.8

Table 4. Approximate biomass of seabirds ('000 t) occupying NAFO and ICES regions in winter, spring, summer, and autumn.

	Winter	Spring	Summer	Autumn
NAFO				
W1	0	4.7	4.7	3.4
W2	8.1	24.2	20.8	7.8
W3	33.2	9.9	7.0	25.2
W4	1.1	4.9	3.1	3.5
W5	2.3	4.7	3.2	3.2
Total	44.8	48.4	38.8	43.1
ICES				
E1	10.5	14.6	16.4	16.4
E2	15.3	20.3	20.6	19.9
E3	7.1	6.8	6.9	7.0
E4	11.2	11.1	5.1	7.0
E5	7.6	9.3	9.5	9.5
E6	2.2	1.3	0.9	0.9
Total	53.9	63.4	59.4	60.8

It should be noted, however, that our quantifications of these movements of seabirds across the fishing areas were based on few data collected in the 1970s and 1980s, such that very little is known about the actual numbers of the different species in the various areas during a given period. Many of the values used here are based on best guesses fitting the estimated population numbers, known migration routes, and at-sea distributions gleaned from the literature.

The total biomasses of seabirds occupying NAFO and ICES waters (Table 4) in different seasons vary little (39 000–48 000 t in NAFO waters, 54 000–64 000 t in ICES waters). This low variability in overall numbers and biomass in NAFO waters is due to the large influx of non-breeding birds from the South Atlantic compensating for the large numbers of birds returning to their breeding colonies in Arctic Canada and the eastern North Atlantic. Similarly, the numbers and biomass of ducks entering and leaving the Baltic nearly compensate for the birds moving westward from the northern ICES to winter in NAFO areas.

Our calculations are based only on estimates of the maximum number for any given species and season, and do not consider how long individual birds stay within each area. Thus, short stays in two or more areas, e.g. during migration in spring and autumn, will result in a slight overrepresentation of those species in the total numbers and biomasses across those areas.

Consumption estimates

Seabirds occupying the NAFO and ICES areas of the North Atlantic consume an estimated 11×10^6 t of food annually, with 46% being taken in the western sector and 54% in the east (Table 5).

Table 5. Approximate food consumption ('000 t) by seabirds occupying NAFO and ICES regions in winter, spring, summer, and autumn.

	Winter	Spring	Summer	Autumn	Total
NAFO					
W1	0	94	121	58	274
W2	223	601	948	203	1 974
W3	1 073	190	193	792	2 248
W4	38	95	72	52	257
W5	55	72	100	44	271
Total	1 389	1 052	1 434	1 149	5 024
ICES					
E1	257	335	533	533	1 547
E2	358	453	680	504	1 996
E3	178	167	217	176	738
E4	204	188	116	123	630
E5	188	210	294	235	927
E6	41	23	26	21	112
Total	1 227	1 375	1 866	1 481	5 950

While numbers (Table 3) and biomass (Table 4) of seabirds in a given area in a given season are based on maximum numbers in that season (see above), the food consumption of seabirds occupying the NAFO and ICES areas (Table 5) is based on the number of days each species stays in a given subarea and therefore does not correspond directly with the numbers and biomass in Tables 3 and 4.

Of the 11×10^6 t consumed, about 2×10^6 t was eaten annually in each of areas W2 (West Greenland), W3 (East Newfoundland and Labrador), and E2 (East Greenland and Iceland), and 1.5×10^6 t in E1 (Barents and Norwegian Seas). Consumption in these four areas accounts for 70% of the annual total consumption of food in the northern North Atlantic (Table 5).

There are also large seasonal differences, especially in the northern NAFO regions. In West Greenland, consumption is four times greater in summer than in winter, whereas in eastern Newfoundland and Labrador, winter consumption is five times greater than in summer (Table 5). In the Northeast Atlantic (E1 and E2), consumption increases by a factor of two from winter to summer, whereas in the Baltic Sea it increases by the same factor from summer to winter (Table 5).

Discussion

Seabird numbers

Considering the large oceanographic differences between the cold low Arctic waters of the Northwest Atlantic and the warmer boreal waters of the Northeast Atlantic, there are significant differences in the avian communities and foodwebs across the North Atlantic (ICES, 2002b, 2003, 2004).

Most strikingly, planktivores dominate the breeding community in the Northwest Atlantic, especially in areas W2 and W3, whereas piscivores play dominant trophic roles in the Northeast Atlantic. The dominance by planktivorous species in the Northwest Atlantic is almost entirely a consequence of the vast number ($>30 \times 10^6$ pairs) of little auks nesting in northwestern Greenland. In Newfoundland, the community of breeding seabirds is dominated numerically, but not in terms of biomass, by Leach's storm-petrels. In the Northeast Atlantic, the avian communities are dominated by large alcids (mainly guillemots and Atlantic puffins), which feed primarily on small schooling fish (sandeels, capelin, young herring (*Clupea harengus*), young gadoids). The Northwest Atlantic community is further supplemented by high numbers and a large biomass of trans-equatorial migrant shearwaters that are predominantly planktivorous and breed in the south Atlantic Ocean (Brown *et al.*, 1981; Cairns *et al.*, 1991). These shearwaters also occur in the Northeast Atlantic, but not nearly in the numbers that move into the Northwest Atlantic. Non-breeding seabirds play a more dominant role in the Northwest than in the Northeast Atlantic, and even with the uncertainties associated with these estimates, the relative differences between the two areas appear striking and robust.

The oceanographic rationales for these differences need to be explored. For example, what are the oceanographic conditions off western Greenland that support a vast abundance of plankton-eating seabirds (plus historically large numbers of fish-eating guillemots)? For seabirds, the presence of suitable nesting sites may limit population size (Ashmole, 1963; Olsthoorn and Nelson, 1990), and that limitation may be relevant here. Western Greenland may contain an especially large number of little auk nest sites, or perhaps the islands off Newfoundland provide especially abundant burrow sites for Leach's storm-petrels. More likely, however, is that differences in seabird species composition between regions reflect differences in the prey base. In terms of numbers, the little auks in northwest Greenland deserve special consideration. This is an Arctic community, located near a polynya system, where a high primary production, an extraordinarily long growth season, and a close coupling of primary and secondary production at the planktonic level translates across the regional foodweb to support the largest population of marine birds known in the Arctic (Deming *et al.*, 2002; Hobson *et al.*, 2002; Karnovsky and Hunt, 2002). Little auks in northwest Greenland eat copepods, amphipods, and small polar cod (*Boreogadus saida*; Nettleship and Birkhead, 1985; Gaston and Jones, 1998; Egevang and Falk, 2001; Karnovsky and Hunt, 2002; Montevecchi and Stenhouse, 2003).

The superabundance of Leach's storm-petrels in Newfoundland may be explained by a combination of nest-site and foraging opportunities. This species requires remote and mammal-free islands, suitable soil in which to dig nest burrows, and sufficient night-time in which to access burrows without being preyed upon by diurnal predators.

Sufficient soil for burrowing disappears a short distance north of Newfoundland, and summer daylength increases too. Moreover, secondary productivity is considerably higher around Newfoundland and on the Grand Banks than it is a short distance to the south (Backus and Bourne, 1987).

The piscivorous birds that dominate the bird communities of the Northeast Atlantic are primarily guillemots and Atlantic puffins that feed almost exclusively on schooling forage fish such as sandeels, herring, pilchard (*Sardina pilchardus*), young gadoids, and sprat (*Sprattus sprattus*; Mitchell *et al.*, 2004). These fish are found in shallow shelf waters (defined here as a depth < 200 m; Daan *et al.*, 1990). The North Sea, for example, is 89% shelf waters (by comparison, the average proportion of shelf waters overall in the North Atlantic is about 20%). Therefore, part of the dominance by piscivores in the northeast (ICES I–VII) could be due to the high proportion of shelf waters there. However, a similar extent of the shelf waters of W3 not only supports large numbers of piscivorous auks, which breed in the area, but also larger numbers of planktivorous storm-petrels and shearwaters, many of which feed in deep water and along the shelf edge and consume an almost equal biomass of food.

Consumption

Total estimated consumption by seabirds in the North Atlantic of 11×10^6 t is approximately 10–20% of the total consumption by the world's seabirds (maximum CI range = $56–133 \times 10^6$ t) estimated by Brooke (2004). Although this percentage seems relatively high, it may reflect both the elevated consumption by seabirds at high latitudes and the conservative approach of Brooke's estimate.

Although still relatively crude in its construction (with regard to numbers of birds, the time they spend in each area, and estimates of energy requirements), we are confident that our consumption estimates are in the correct order of magnitude. This statement is, for example, corroborated by Lilliendahl and Solmundsson's (1997) estimate of summer consumption by six seabird species in Iceland (442 000 t), only 14% lower than that estimated using our model (513 000 t). In waters off eastern Canada, Diamond *et al.* (1993) estimated seabird food requirements to be 1.1 g m^{-2} (or 1.1 t km^{-2}), similar to our figure of 0.8 t km^{-2} (Table 6). Our estimates also corroborate those of Diamond *et al.* (1993), who found a maximum food requirement off the coasts of Labrador and Newfoundland (W3, Figure 1). Similarly, while our estimate for the Northeast Atlantic (5.9×10^6 t y^{-1}) is ca. 20% higher than Furness' (1994) 4.9×10^6 t y^{-1}, and for the North Sea (680 000 t y^{-1}) is 13% higher than Tasker and Furness' (1996) 600 000 t y^{-1}, the lower figures were based on counts of breeding birds made in the early 1980s, since when the numbers of many species have increased considerably (Mitchell *et al.*, 2004).

Taking seasonal movements of birds between and into NAFO and ICES areas into account increased the model output in the NAFO areas by 63% (from 2.9×10^6 to 5.0×10^6 t), and in the ICES areas by 15% (from

Table 6. Surface areas of ICES and NAFO regions based on the GEBCO 1-min global bathymetric grid, approximate total annual seabird consumption, and the consumption rate per km^2.

	Total area (10^6 km^2)	Area of waters <200 m deep	% <200 m deep	Total consumption ('000 t)	Consumption rate (t km^{-2})	Consumption rate (t km^{-2}) in waters <200 m deep
ICES						
E1	3.8	0.99	26	1.55	0.41	1.57
E2	1.6	0.27	17	2.00	1.25	7.47
E3	0.7	0.61	89	0.74	1.06	1.22
E4	0.4	0.43	96	0.63	1.42	1.47
E5	1.3	0.39	31	0.93	0.72	2.37
E6	3.9	0.14	4	0.11	0.03	0.81
E7	2.1	0	0	—	—	—
All ICES regions	13.9	2.83	20	5.95	0.43	2.10
Total excluding E6 and E7	7.8	2.69	34	5.84	0.74	2.40
NAFO						
W1	0.6	0.09	15	0.27	0.46	2.92
W2	1	0.14	14	1.97	1.97	13.66
W3	2.1	0.42	20	2.25	1.07	5.36
W4	1	0.32	32	0.26	0.26	0.79
W5	1.6	0.24	15	0.27	0.17	1.15
Total for all NAFO areas	6.2	1.21	20	5.02	0.81	4.12

5.2×10^6 to 6.0×10^6 t; Table 7). In the ICES areas, this is most evident in the Baltic, Skagerrak, and Kattegat, where adding the population of wintering seaducks nearly doubled the annual consumption estimate for that subarea. The most striking differences in the NAFO areas are attributable to the huge seasonal influxes of birds to and from the southern oceans into NAFO 5 and 6, and the exchanges between northern ICES areas, the eastern Canadian Arctic, and NAFO 0, 1, 2, and 3.

The total food consumption estimate for NAFO areas is similar in summer and winter (Table 5), whereas in ICES areas consumption peaks in summer at levels about 50% higher than in winter. The elevated energy demand in summer is primarily due to increased reproductive activity, but also partly to a larger number of birds (and hence higher biomass) in summer than in winter in the northeastern Atlantic. In the ICES areas there are 37% more birds (and 11% higher biomass) as a result of large numbers moving out of the areas in winter and returning in summer. In the NAFO areas, the numbers and biomasses of seabirds are similar in summer and winter.

As for the numbers of seabirds, there is also considerable spatial variation in consumption rate across the ICES and NAFO areas. The apparent paradox of 20% greater total consumption by seabirds in the ICES areas despite the fact that 50–100% more birds occupy the NAFO areas (Table 3) is due to (i) the smaller size of NAFO birds and hence their lower total biomass (Table 4) and energy demand and (ii) the large numbers of planktivores in the NAFO areas. The seabird community of the Northwest Atlantic is dominated by planktivorous seabirds that breed there (Leach's storm-petrels), migrate into the region trans-equatorially in summer (shearwaters), or move into the region in winter (little auks; Brown, 1986; Montevecchi, 2000). Because the energy density of planktonic prey may be approximately 20% lower than the 5.5 kJ g^{-1} used in the present model, consumption by these planktivores will actually be slightly higher than that calculated here, so reducing this paradox. Moreover, when the surface areas of the NAFO and ICES regions are considered, the consumption rate per unit area in the eastern sector is only approximately half that in the west (Table 6). The greatest harvest rate (2.0 t km^{-2}) was calculated for the area off western Greenland, where the planktivorous little auks dominate the community, and rates >1.0 t km^{-2} were also apparent off Labrador and Newfoundland, around Iceland, and in the North and Baltic Seas. The lowest rates (0.03 t km^{-2}) were in the deep seas off France and Iberia, and around the Azores.

Many seabirds, however, forage over the rich, inshore shelf areas (Shealer, 2002), and an exploratory analysis taking only shelf areas (here defined as waters <200 m deep) into consideration showed intense feeding off west Greenland, Labrador and Newfoundland, and around Iceland, and a minimum in the deepwater southeastern sector of ICES (the Azores), and in the Gulf of St Lawrence and the Scotian Shelf (W4; Table 6). Such analyses taking into account physical (sea temperature, extent of frontal systems, length of coastline/continental shelf, etc.) and biological parameters (production, etc.) should, however, be investigated further.

Table 7. Estimates of food consumption ('000 t) by seabirds in ICES and NAFO regions (a) when not considering seasonal movements of birds into, out of, and through the regions, and (b) when doing so.

		Total (a)	Total (b)
ICES			
E1	Barents and Norwegian Seas	1 440	1 547
E2	Eastern Greenland and Iceland	1 740	1 996
E3	North Sea and English Channel	690	738
E4	Baltic, Skagerrak, and Kattegat	380	630
E5	Faroes and western UK	860	927
E6	France, Iberia, and the Azores	70	112
Total ICES		5 180	5 950
NAFO			
W1	Eastern Baffin Island	220	274
W2	Western Greenland	1 650	1 974
W3	Eastern Newfoundland and Labrador	700	2 248
W4	Gulf of St. Lawrence and Scotian Shelf	180	257
W5	Gulf of Maine to Cape Hatteras	100	271
Total NAFO		2 910	5 024

Summary

The comparisons presented here are useful in increasing our understanding of mega-scale oceanic processes and fluxes. Such comparisons will be useful in assessing trends as well as more abrupt changes in oceanography and climate. Considerations of changing trophic interactions will facilitate assessments of shifts in coastal and pelagic foodwebs and how these might be related to the oceanography. It is these biophysical associations between marine birds, their prey, and physical oceanographic variation that are needed for comprehensive engagement of questions about the biological effects of climate change, and about upper trophic level consequences of human fishing practices.

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Appendix 1

Approximate numbers of seabirds and waterfowl that breed outside NAFO region, but which enter or pass through NAFO regions before or after breeding. Sources: Huettmann and Diamond (2000), Montevecchi (2000), ICES (2003), Lyngs (2003), and Huettmann (pers. comm.).

		Numbers of individuals (×1 000)			
Region	Species	Winter	Spring	Summer	Autumn
W2	Northern fulmar	50	100	100	50
	Greater shearwater			200	
	Common eider	400	400		400
	King eider	300	300	50	300
	Long-tailed duck	80	80		80
	Black-legged kittiwake	200			200
	Brünnich's guillemot*	500	500		1 500
	Brünnich's guillemot†	1 450	500		500
	Atlantic puffin	200			
	Little auk	7 000	6 000		

(*continued on next page*)

Appendix 1 (*continued*)

Region	Species	Numbers of individuals (×1 000)			
		Winter	Spring	Summer	Autumn
W3	Wilson's storm-petrel			50	50
	Northern fulmar	200	200	300	300
	Greater shearwater			2 750	2 750
	Sooty shearwater			500	500
	Common eider	200	200		200
	Scoter species		40	75	40
	Long-tailed duck	150	150		150
	Iceland gull	100	100		100
	Glaucous gull	50	50		100
	Black-legged kittiwake	1 150	500		500
	Brünnich's guillemot	1 550	500		
	Atlantic puffin	2 000			
W4	Greater shearwater		1 000	850	1 500
	Sooty shearwater		1 000	35	
	Wilson's storm-petrel			600	50
	Common eider	91	91		
	Scoter species		100	40	160
	Long-tailed duck	50	50		
	Red phalarope			870	850
W5	Greater shearwater		1 500	1 900	1 900
	Sooty shearwater		300	410	410
	Wilson's storm-petrel		600	600	600
	Common eider	190			
	Long-tailed duck	230			
	Scoter species	160	180		
	Red-breasted merganser	60			
	Red-necked phalarope	250			
	Red phalarope	240			
	Bonaparte's gull	60			

*From Canadian Arctic.
†From ICES areas.

Appendix 2

Estimates of the numbers of waterfowl that breed outside ICES regions, but which enter or pass through ICES regions before or after breeding. Sources: Nygård *et al.* (1988), Anker-Nilssen *et al.* (2000), Delany and Scott (2002), Kershaw and Cranswick (2003), Hagemeijer and Blair (1997), and Durinck *et al.* (1994).

Region	Species	Numbers of individuals (×1 000)		
		Winter	Spring	Autumn
E1	Long-tailed duck	80	50	
	King eider	120	80	
	Velvet scoter	25	15	
E2	Long-tailed duck	145		
E3	Long-tailed duck	31		
	Common scoter	220		

Appendix 2 (*continued*)

Region	Species	Numbers of individuals (×1 000)		
		Winter	Spring	Autumn
E4	Great cormorant (*Phalacrocorax carbo carbo*)	20	10	
	Greater scaup	145	70	
	Long-tailed duck	4 300	4 000	1 000
	Common scoter	1 200	1 200	500
	Velvet scoter	950	900	500
	Common goldeneye	120	50	60
	Red-breasted merganser	44	31	30
	Goosander	75	20	10
E5	Common scoter	40		
	Common eider	8		
E6	Common scoter	50		

Appendix 3

Estimates of numbers of staging birds that breed in NAFO regions and move into or pass through other NAFO regions outside the breeding season.

Region	Species	Numbers of individuals (×1 000)			
		Winter	Spring	Summer	Autumn
W2	Northern fulmar	55[1]	100[1]	100[1]	50[1]
	Common eider	27[1]	27[1]		27[1]
	Brünnich's guillemot	900[1]	900[1]		900[1]
W3	Northern fulmar	300[1,2]	300[1,2]	300[1,2]	300[1,2]
	Herring gull*	152[1,2]			
	Iceland gull*	100[1,2]			100[1,2]
	Glaucous gull*	50[1,2]			50[1,2]
	Black-legged kittiwake*	500[1,2]			500[1,2]
	Brünnich's guillemot*	10 000[1,2]	5 000[1,2]		1 500[1,2]
	Little auk	20 000[2]	5 000[2]		10 000[2]
W4	Northern fulmar	170[1,2]	100[1,2]	100[1,2]	50[1,2]
	Herring gull	350[1–3]	350[1–3]		
	Black-legged kittiwake	550[1,2]	550[1,2]		
	Razorbill	50[3]	20[3]		
	Little auk	370[2]	200[2]		
W5	Leach's storm-petrel		15 000[3]		6 000[3]
	Northern gannet		270[3]		
	Common eider	190[3,4]			190[4]
	Herring gull	150[3,4]			
	Ring-billed gull	1 500[3,4]			
	Little auk	100[2]			

*Includes birds from Canadian Arctic, [1,2,3,4]from W1, W2, W3, and/or W4, respectively.

Appendix 4

Estimates of the numbers of seabirds that breed in ICES regions and move or pass through other ICES regions outside the breeding season.

		Numbers of individuals (×1 000)		
Region	Species	Winter	Spring	Autumn
E1	Black-legged kittiwake	100[5]		
	Common guillemot	500[2]		
E2	Northern fulmar	50[1]		
	Northern gannet	40[2]		
	Common eider	20[1]		
	Black-legged kittiwake	550[1,5]	200[1]	200[1]
	Brünnich's guillemot	1 100[1]	600[1]	125[1]
	Atlantic puffin	1 400[1,5]		
	Little auk	500[1]	500[1]	
E3	Northern fulmar	50[1]		
	Northern gannet	50[3]		
	Common eider			50[1]
	Herring gull	220[1]		
	Great black-backed gull	40[1]		
	Black-legged kittiwake	200[1]	46[1]	
	Common guillemot	500[1,2]		
	Atlantic puffin	500[1]		
E4	Common eider	100[1]		
	Herring gull	50[1]		
E5	Northern gannet	65[2,3]		
	Great black-backed gull	35[2]		
	Black-legged kittiwake	320[1,3,5]	50[1]	
	Arctic tern		400[2]	400[2]
	Razorbill	500[2]		
	Atlantic puffin	1 500[1,2]		
E6	Northern gannet	400[2,3,5]		
	Lesser black-backed gull	450[3,5]	150[3,5]	
	Black-legged kittiwake	200[1,3,5]		
	Arctic tern		400[2]	400[2]

[1,2,3,5]From E1, E2, E3, and/or E5.