Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic.
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INTRODUCTION

The strong link between animal energetics and individual survival has been put forward in a variety of studies (Schmidt-Hempel and Wolf, 1988; Speakman and Racey, 1989; Hobbs, 1989; Golet et al., 1998; Golet et al., 2000). During reproduction, parental care such as offspring provisioning forces adults to spend energy at a high rate, potentially threatening their own survival (Dijkstra et al., 1990; Golet et al., 2000). In temperate and polar species, the winter phase can be equally challenging. Here post-breeding individuals face extreme weather conditions with high wind speeds, elevated relative humidity, low air and water temperatures, as well as shorter days (Møller et al., 2006; Rey et al., 2007). Such environmental conditions have a profound effect on winter survival, indirectly affect future reproductive performance and ultimately shape population dynamics (Mysterud et al., 2001; Stenseth et al., 2002; Barbraud and Weimerskirch, 2003; Grosbois and Thompson, 2005; Daunt et al., 2006).

Seabirds occupy a pivotal role as top predators within marine ecosystems, but the interplay of winter environmental conditions, seabird energetics and winter survival remains largely unknown. Several techniques are available to study energy requirements and prey intake rates in free-ranging seabirds. They essentially consist of (1) daily food intake measurements using stomach content or pellet analysis (Duffy and Jackson, 1986), (2) time–energy budget analysis (Furness, 1978; Furness, 1990; Grémillet et al., 2003), (3) assessment of food intake rates via stomach temperature measurements (Wilson et al., 1995), (4) automatic weighing (Grémillet et al., 1996), and (5) biotelemetry studies using miniaturized recorders such as heart rate data loggers or accelerometers to measure energy expenditure (Wilson et al., 2006; Green et al., 2009). However, most of these techniques are inappropriate for estimating the energy needs of wintering seabirds, as birds spend this period offshore, where they are virtually inaccessible. Others are logistically extremely difficult to set up. For example, biotelemetry studies require surgery and recapture of the equipped birds and are currently only possible in large seabird species. Overall, very few studies have investigated seabird winter energy requirements (Wiens and Scott, 1975; Grémillet et al., 2003; Green et al., 2009).

To solve this problem and to be able to investigate wintering energetics of marine top predators such as seabirds, a complementary and alternative method is required. We propose the use of a new spatially and temporally explicit model, Niche Mapper™ (for details, see Porter and Mitchell, 2006; Kearney et al., 2009). This model allows energy balance calculations using the characteristics of the animals and their environment and is particularly suitable for situations where field data are scarce. Niche Mapper™ is based on the first principles of thermodynamics and on the physiological and behavioural responses of individual organisms to their environment. This refined model has been successfully employed to estimate the energy requirements of representative amphibians, reptiles, birds and mammals living in a variety of ecological contexts (e.g. seabirds, acclimatory, and mammal species) at different spatial and temporal scales.
Kearney et al., 2008; Mitchell et al., 2008; Porter et al., 2006; Natori and Porter, 2007). To date, however, it has not been deployed within marine ecosystems.

We applied Niche Mapper™ to the study of little auk (Alle alle L.) and Brünnich’s guillemots (Uria lomvia L.), which are the smallest and the largest extant alcid species living in the North Atlantic, respectively. These diving seabirds from Arctic waters are components of simple food webs. They are particularly sensitive to changes occurring at low trophic levels (Nettleship and Birkhead, 1985; Gaston and Jones, 1998) and are outstanding candidates as ecological sentinels of global change (Gjerdrum et al., 2003). They are among the most abundant seabird species in the northern hemisphere and on a worldwide scale [little auk and Brünnich’s guillemot population size is estimated to be >80 million and 20 million breeding individuals, respectively (Gaston and Jones, 1998; Kampp et al., 2000; Isaksen and Gavrilov, 2000; Egevang et al., 2003)]. Hence, they play an important role within arctic marine ecological processes, notably in terms of energy transfer. Indeed, the Brünnich’s guillemot population is the third largest seabird prey consumer worldwide (Brooke, 2004) whilst the North Water Polynya little auk population is responsible for 92–96% of the carbon flux to seabirds in that region (Karnovsky and Hunt, 2002). However, these two species are confronted with a high winter mortality, especially during events called ‘winter wrecks’, in which large numbers of seabirds cast ashore and/or are found dead inland (Gaston, 2004). The factors responsible for these wrecks are unknown and we considered it important to have a better understanding of the potential underlying mechanisms for this winter mortality.

Therefore, the aims of this study were (1) to highlight a new modelling approach for studying the energy balance of wintering aquatic top predators, and (2) to study the energy balance of two key species and investigate how energetic requirements potentially impact on winter survival. We hypothesize that winter conditions critically challenge the energy balance of alcids wintering in the northwest Atlantic, therefore negatively affecting their survival. To accomplish these goals we calculated little auk’s and Brünnich’s guillemots’ energy requirements and food needs during the winter off southwest Greenland and Newfoundland using Niche Mapper™.

**MATERIALS AND METHODS**

**Study sites and period**

Energy requirements and food needs were estimated for birds wintering in two areas (Fig 1) with different environmental conditions, therefore potentially affecting their energy balance. These two areas are part of the most important wintering sites for little auk and Brünnich’s guillemots (Brown, 1985; Boertmann et al., 2004). The first is situated off southwest Greenland (63–65°N, 53–55°W), while the second stretches along the northeast coast of Newfoundland (50–52°N, 52–54°W).

We defined ‘winter’ as the inter-breeding period extending from September 1st to March 1st [the latter date corresponding to the start of the spring migration towards the breeding areas (Nettleship and Birkhead, 1985)]. During this period, adults of both species are assumed to require energy only for their own maintenance. We used climate data for the winter of 2004/2005, and all modelling was assumed to require energy only for their own maintenance. We used and Birkhead, 1985). During this period, adults of both species are

**Niche Mapper™ model**

Niche Mapper™ (US Patent 7,155,377B2; wporter@wisc.edu) integrates two different sub-models to investigate individual energy balance: a microclimate model and an endotherm model (see below).

**Climate model and climate input data**

We used the latest version of the microclimate model (Micro2006c) described by Porter and colleagues (Porter et al., 2000; Porter et al., 2006; Kearney and Porter, 2004). The microclimate model uses calculated maximum and minimum shade and sunlight conditions for each location to subsequently compute the locally available coolest and hottest microhabitats for each hour of the day. Instead of using solid substrates, this climate model was modified to calculate local microclimates from 2 m above to 2 m below the water surface using a turbulent velocity profile above the surface and the temperature-dependent and solar and infrared radiation properties of salt water. Despite turbulent mixing of oceanic surface waters, birds might encounter different water temperatures when diving through the water column (e.g. Takahashi et al., 2008). However, as a sensitivity analysis (see below; Table 4) showed that the range of water temperatures naturally encountered by the birds does not radically affect their energy expenditure, we considered water temperature to be constant across the birds’ diving range (Table 2).

All climatic and environmental input values used in this model were ICOADS data provided by NOAA/OAR/ESRL PSD (Boulder, CO, USA; http://www.cdc.noaa.gov/) (Table 1).

**Endotherm model and input data**

We used an updated version (Endo2007d) of the endotherm model originally developed by Porter and Gates (Porter and Gates, 1969), upgraded and modified substantially by Porter and Mitchell (Porter and Mitchell, 2006) and described in Porter et al. (Porter et al., 2006). This endotherm model uses local environmental parameters generated by the microclimate model (see above), as well as morphological, physiological and behavioural characteristics of the animal. The model solves the coupled heat and mass balance equations for the animal–environment exchanges, and the digestive and respiratory system; heat balance (W):

\[
Q_{in} + Q_{gen} = Q_{out} + Q_{st}, \tag{1}
\]

and mass balance (g day\(^{-1}\)):

\[
m_{in} = m_{out} + m_{st}, \tag{2}
\]

where \(Q_{in}\) is heat input (sum of absorbed incoming solar and infrared radiation reaching the skin), \(Q_{gen}\) is heat produced (by all body tissues), \(Q_{out}\) depicts heat loss (by air convection, respiration, infrared
radiation emitted through the porous feathers, and conduction to the water) and \( Q_{\text{int}} \) is the stored heat (due to body temperature rising or falling); \( m_{\text{in}} \) is the mass input (food entering the gut or air entering the respiratory system), \( m_{\text{out}} \) is the mass lost (faeces or exhaled air) and \( m_{\text{st}} \) is the mass stored or absorbed (i.e. the food mass that must be absorbed by the gut, given the food type and properties, to meet the daily energy demand).

This endotherm model ultimately estimates daily energy and food requirements for an adult individual for the Julian day at the centre of each month throughout the winter period. However, the current version can accommodate daily simulations for the entire year, if sufficient climate data are available. Because Brünnich’s guillemots and little auks are monomorphic and because males and females presumably seek the same wintering areas (Gaston and Jones, 1998) (J.F., unpublished), they face similar environmental conditions. We therefore assumed that energy requirements were the same for males and females in both species. Moreover, egg laying for both species therefore assumed that energy requirements were the same for males and females in March are still not affected by reproductive preparations.

Resting metabolic rates were estimated using heat production required to maintain a body core temperature of 40.1°C for little auks (Gabrielsen et al., 1991) and between 39.6 and 40.3°C for Brünnich’s guillemots (Gabrielsen et al., 1988) according to their morphological properties, the physical environment available to them, and their behavioural choices.

Water loss rates from the respiratory system were based on the calculated air volume passing through the lungs on a daily basis to meet metabolic demands. We assumed that the air was saturated with water vapour in the lungs at the average body temperature integrated radially from the core to the skin. Exhaled air was assumed to be 2°C warmer than local air temperature at each hour (Porter et al., 2000; Welch, 1980). The minimum core–skin temperature difference under which the bird could not dissipate the heat efficiently enough to maintain homeostasis was set at 0.1°C (Porter et al., 2000).

Flight costs were estimated for each species using Pennycuick’s model and software Flight 1.18 (Pennycuick, 1989). We used default model parameters and different literature values (Table 2) for body mass, wingspan and wing area (Croll et al., 1991; Elliott and Gaston, 2005) (A. M. A. Harding, personal communication). For a body mass of 0.15 kg, little auk flight costs were estimated to be 10.57 W, whereas flight costs for a 1 kg Brünnich’s guillemot were estimated to be 88 W. Variability of these flight costs linked to body mass variations of the birds during the winter period (Pennycuick, 1989; Croll et al., 1991) were taken into account by Niche Mapper™ (see Porter and Mitchell, 2006).

### Morphological properties

An ellipsoid body shape was assumed following Porter et al. (Porter et al., 2000). Plumage properties were measured on bird carcasses for five little auks and five Brünnich’s guillemots from the Field Museum of Natural History in Chicago. All birds were from the northwest Atlantic waters and in winter plumage. Plumage depth, feather length, diameter and reflectivity were measured mid-dorsally and mid-ventrally for each species. The reflectivity was measured using a portable ASD spectrometer (Analytical Spectral Devices FieldSpec Pro ASD, Boulder, CO, USA) with grating-based optics, using a contact probe with a 10 nm resolution for all wavelengths between 350 and 2500 nm. This range covers approximately 97% of the solar spectrum that reaches the earth’s surface. All morphological properties measured and used for this study are presented in Table 2.

### Physiological properties

Physiological properties for both species are presented in Table 2. The effective flesh thermal conductivity was based on in vivo measurements of muscle tissue (Cheng and Plewes, 2002).

<table>
<thead>
<tr>
<th>Year</th>
<th>Month</th>
<th>Air temperature (°C)</th>
<th>SST (°C)</th>
<th>Relative humidity (%)</th>
<th>Scalar wind speed (m s⁻¹)</th>
<th>Cloud cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newfoundland 2004 September 11.3</td>
<td>6.6</td>
<td>12.1</td>
<td>8.0</td>
<td>88.0</td>
<td>66.6</td>
<td>12.4</td>
</tr>
<tr>
<td>2004 October 11.5</td>
<td>2.0</td>
<td>9.5</td>
<td>4.4</td>
<td>100.0</td>
<td>76.7</td>
<td>20.6</td>
</tr>
<tr>
<td>2004 November 10.0</td>
<td>–1.5</td>
<td>5.9</td>
<td>1.6</td>
<td>100.0</td>
<td>83.4</td>
<td>18.4</td>
</tr>
<tr>
<td>2004 December 5.3</td>
<td>–10.5</td>
<td>5.0</td>
<td>0.1</td>
<td>99.7</td>
<td>70.4</td>
<td>17.3</td>
</tr>
<tr>
<td>2005 January 4.9</td>
<td>–7.0</td>
<td>0.3</td>
<td>–1.3</td>
<td>98.8</td>
<td>88.4</td>
<td>19.9</td>
</tr>
<tr>
<td>2005 February 0.9</td>
<td>–9.0</td>
<td>–0.1</td>
<td>–1.5</td>
<td>98.6</td>
<td>66.4</td>
<td>13.9</td>
</tr>
<tr>
<td>2005 March 0.4</td>
<td>–5.9</td>
<td>–1.6</td>
<td>–1.6</td>
<td>96.0</td>
<td>71.1</td>
<td>15.3</td>
</tr>
<tr>
<td>Greenland 2004 September 6.4</td>
<td>4.0</td>
<td>6.3</td>
<td>4.3</td>
<td>83.8</td>
<td>75.5</td>
<td>14.2</td>
</tr>
<tr>
<td>2004 October 5.5</td>
<td>0.0</td>
<td>4.3</td>
<td>1.9</td>
<td>97.2</td>
<td>68.6</td>
<td>16.0</td>
</tr>
<tr>
<td>2004 November 3.5</td>
<td>–0.3</td>
<td>4.5</td>
<td>1.7</td>
<td>89.8</td>
<td>74.2</td>
<td>12.1</td>
</tr>
<tr>
<td>2004 December –5.7</td>
<td>–9.9</td>
<td>2.3</td>
<td>–1.2</td>
<td>64.8</td>
<td>64.4</td>
<td>8.6</td>
</tr>
<tr>
<td>2005 January 1.5</td>
<td>–10.3</td>
<td>4.0</td>
<td>–1.3</td>
<td>93.2</td>
<td>63.6</td>
<td>17.5</td>
</tr>
<tr>
<td>2005 February –0.6</td>
<td>–10.7</td>
<td>0.9</td>
<td>–1.3</td>
<td>95.3</td>
<td>55.0</td>
<td>14.0</td>
</tr>
<tr>
<td>2005 March 3.2</td>
<td>–4.6</td>
<td>0.1</td>
<td>–1.3</td>
<td>69.1</td>
<td>69.1</td>
<td>12.7</td>
</tr>
</tbody>
</table>

For each parameter (air temperature, sea surface temperature (SST), relative humidity, scalar wind speed and cloud cover), maximum and minimum monthly values are taken into account by Niche Mapper™ (ICODS data provided by NOAA/OAR/ESRL PSD, Boulder, CO, USA; http://www.cdc.noaa.gov/).
physiological properties and behavioral properties. Rowe et al., 2000). This diet was composed of fish (capelin Mallotus villosus and cod Gadus spp.), squid, euphausids and amphipods, in variable proportions.

Diet

The relative proportions of different prey items within the diet of Brünnich’s guillemot was estimated across the wintering season using published data (Elliot et al., 1990; Falk and Durinck, 1993; Rowe et al., 2000). This diet was composed of fish (capelin Mallotus villosus and cod Gadus spp.), squid, euphausids and amphipods, in variable proportions.

There is little information about the winter diet of little auks, but Karnovsky and Hunt (Karnovsky and Hunt, 2002) found that post-breeding adults consume approximately 50% fish (juvenile Arctic cod Boreogadus saida) and 50% amphipods. This trend was confirmed by opportunistic winter observations (Stempniewicz, 2001). We consequently assumed that wintering little auks fed half on fish (Arctic cods) and half on amphipods. Nonetheless, additional simulations using different ratios of cod/amphipods showed that energy density values for cod and amphipods are not different enough to significantly affect our results.

Protein, lipid and carbohydrate content, as well as dry matter proportions, were estimated for each month after Lawson, Magalhaes and Miller (Lawson et al., 1998) and Percy and Fife (Percy and Fife, 1981) (Table 3). Protein, lipid and carbohydrate content were estimated as a percentage of dry matter.

Sensitivity analysis

A sensitivity analysis was performed to examine the robustness of the model and to identify key input parameters affecting the birds’ daily energy requirements. To this end, we used selected microclimate and endotherm parameters, focusing on parameters that could vary substantially between individuals and/or across the winter period. These input values were modified according to standard variability of 10% of the average, when minimum and maximum recorded values, or they were set to a standard variability of 10% of the average, when minimum and maximum values were not available (Grémillet et al., 2003).

RESULTS

Little auks

Niche Mapper™ predicts little auk daily energy requirements to increase throughout the winter period (September–March), from 353 to 470 kJ day⁻¹ off Newfoundland and from 385 to 484 kJ day⁻¹ off southwest Greenland. At both sites, this increase is not significant.
constant through the winter; birds face a strong and sudden rise in daily energy requirements between November and December (+16.4% off Newfoundland and +19.5% off Greenland) (Fig. 2). Before and after this rise, energy requirements are on average 397±6.4 and 468±9.7 kJ day–1 (means±s.e.m.), respectively, off Greenland and 377±12.5 and 457±5.3 kJ day–1, respectively, off Newfoundland.

Little auk daily energy requirements before this sudden rise (from September to November) are similar at the two wintering sites, with values slowly increasing from 385 to 405 kJ day–1 off Greenland, and from 353 to 396 kJ day–1 off Newfoundland. During this period, the overall increase in daily energy demand is nonetheless stronger off Newfoundland (+5.9±1.1%), than off Greenland (+2.6±2.1%).

Predicted energy expenditure between December and March remains high, yet constant, with a mean variation of –2.9±3.3% off Greenland (min. 444, max. 470 kJ day–1) and of +0.1±2.8% off Newfoundland (min. 444, max. 470 kJ day–1).

Predicted individual daily food requirements follow similar trends, with values between 258 and 322 g wet food day–1 off Greenland (mean 297±8.6 g), and between 256 and 313 g wet food day–1 off Newfoundland (mean 280±8.1 g). Off Greenland, the beginning of the winter period is marked by a slight diminution in daily food requirements until November, followed by a general increase throughout the rest of the season. Off Newfoundland, despite minor variations, food requirements generally increase throughout the season (Fig. 2).

### Brünnich’s guillemots

Predicted daily energy requirements during winter for Brünnich’s guillemots show an overall increase from 1156 to 1473 kJ day–1 off southwest Greenland and from 1061 to 1417 kJ day–1 off Newfoundland (Fig. 2). As for little auks, this increase is not constant throughout the wintering period but is characterized by a sharp rise between November and December (+19.5% and +16.5% off Greenland and Newfoundland, respectively). Before and after this rise, energy requirements are on average 1202±23.8 and 1440±12.6 kJ day–1, respectively, off Greenland and 1127±40.4 and 1381±16.1 kJ day–1, respectively, off Newfoundland.

Before this phase (i.e. from September to November), predicted energy requirements are similar at the two sites (between 1156 and 1233 kJ day–1 off Greenland, and between 1061 and 1201 kJ day–1 off Newfoundland). However, while energy requirements are relatively constant until November off Greenland (+3.3±2.2%), they increase off Newfoundland (+6.4±0.9%).

After December, energy requirements stay high and relatively constant at both sites with a mean monthly variation of –1.2±1.7% off Greenland (min. 1420, max. 1449 kJ day–1) and –0.7±3.0 off Newfoundland (min. 1346, max. 1417 kJ day–1).

Predicted daily food requirements of Brünnich’s guillemots wintering off Newfoundland remain constant throughout the study period, with an average of 550±7.5 g wet food day–1 (min. 540.7, max. 584.2 g). Off Greenland, food requirements are more variable and increase throughout the winter period (from 443 g

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### Table 3. Protein, lipid and carbohydrate content, and dry matter proportion for each prey consumed by little auks and Brünnich’s guillemots during the winter

<table>
<thead>
<tr>
<th>Prey</th>
<th>Protein (% dry matter)</th>
<th>Lipid (% dry matter)</th>
<th>Carbohydrate (% dry matter)</th>
<th>Dry matter proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euphausiids</td>
<td>43.9</td>
<td>52.4</td>
<td>0.7</td>
<td>26.1</td>
</tr>
<tr>
<td>Amphipods</td>
<td>47.5</td>
<td>26.4</td>
<td>1.2</td>
<td>22.4</td>
</tr>
<tr>
<td>Fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capelin</td>
<td>50.6</td>
<td>43.1</td>
<td>0.0</td>
<td>31.8</td>
</tr>
<tr>
<td>Arctic cod</td>
<td>71.1</td>
<td>17.5</td>
<td>0.0</td>
<td>21.1</td>
</tr>
<tr>
<td>Squid</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gonatus sp.</td>
<td>51.7</td>
<td>41.1</td>
<td>0.0</td>
<td>26.5</td>
</tr>
</tbody>
</table>

---

Table 4. Sensitivity analysis for the daily energy requirements of little auks and Brünnich’s guillemots wintering off southwest Greenland

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Brünnich’s guillemots</th>
<th>Variation of seasonal energy requirements (%)</th>
<th>Little auks</th>
<th>Variation of seasonal energy requirements (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endotherm</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plumage depth: dorsal, ventral (mm)</td>
<td>5.0, 14.4</td>
<td>±10%</td>
<td>6.7, 11.5</td>
<td>±10%</td>
</tr>
<tr>
<td>Plumage reflectivity: dorsal, ventral (%)</td>
<td>0.34, 0.67</td>
<td>±10%</td>
<td>0.36, 0.58</td>
<td>±10%</td>
</tr>
<tr>
<td>Feather length: dorsal, ventral (mm)</td>
<td>29.2, 22.5</td>
<td>±10%</td>
<td>18.0, 17.3</td>
<td>±10%</td>
</tr>
<tr>
<td>Feather diameter (μm)</td>
<td>29.7</td>
<td>±10%</td>
<td>29.7</td>
<td>±10%</td>
</tr>
<tr>
<td>Plumage density (1 cm⁻³)</td>
<td>4114.8</td>
<td>±10%</td>
<td>4114.8</td>
<td>±10%</td>
</tr>
<tr>
<td>Body core temperature (°C)</td>
<td>39.6</td>
<td>±10%</td>
<td>36.1</td>
<td>±10%</td>
</tr>
<tr>
<td>Digestive efficiency (%)</td>
<td>0.83</td>
<td>±10%</td>
<td>0.72</td>
<td>±10%</td>
</tr>
<tr>
<td>Exhaled air temperature–local air temperature (°C)</td>
<td>1.8, 2.2</td>
<td>±10%</td>
<td>1.8, 2.2</td>
<td>±10%</td>
</tr>
<tr>
<td>Flight metabolism (W)</td>
<td>79.2</td>
<td>±10%</td>
<td>9.513</td>
<td>±10%</td>
</tr>
<tr>
<td>Ventral area contacting substrate (%)</td>
<td>0.225</td>
<td>±10%</td>
<td>0.225</td>
<td>±10%</td>
</tr>
<tr>
<td>Flight speed (m s⁻¹)</td>
<td>16.25</td>
<td>±10%</td>
<td>11.7</td>
<td>±10%</td>
</tr>
<tr>
<td>Dive depth (m)</td>
<td>43.3</td>
<td>±10%</td>
<td>24.57</td>
<td>±10%</td>
</tr>
<tr>
<td>Flight altitude (m)</td>
<td>4.5</td>
<td>±10%</td>
<td>4.5</td>
<td>±10%</td>
</tr>
<tr>
<td>Climate</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Air temperature (°C)</td>
<td>−7.80</td>
<td>±10%</td>
<td>−7.80</td>
<td>±10%</td>
</tr>
<tr>
<td>Sea surface temperature (°C)</td>
<td>−0.60</td>
<td>±10%</td>
<td>−0.60</td>
<td>±10%</td>
</tr>
<tr>
<td>Relative humidity (%)</td>
<td>55.0</td>
<td>±10%</td>
<td>55.0</td>
<td>±10%</td>
</tr>
<tr>
<td>Wind speed (m s⁻¹)</td>
<td>2.0</td>
<td>±10%</td>
<td>2.0</td>
<td>±10%</td>
</tr>
<tr>
<td>Cloud cover (%)</td>
<td>0</td>
<td>±10%</td>
<td>0</td>
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</table>

Minimum and maximum input values from Micro2006c and Endo2007d are the minimum and maximum values recorded for each parameter or ±10% of the average. As body mass is highly correlated with field metabolic rate (FMR) in most animals (Ellis and Gabrielsen, 2002), a strong variation in energy requirements is expected when body mass varies, independently of the model. Therefore, this parameter does not appear in the sensitivity analysis. The maximum variation of calculated energy requirements is marked in bold. It highlights the fact that air temperature is the critical parameter affecting the energy balance of wintering alcids. However, it is also important to note that plumage depth is the second most important parameter.

### Discussion

We used Niche Mapper™ to estimate the daily energy expenditure and food requirements of little auks and Brünnich’s guillemots wintering in northwest Atlantic waters. As in all bioenergetics studies, even the most elaborate model is incapable of fully grasping nature’s complexity. We ran the most refined and extensively field-tested energetic model currently available, and also took great care in compiling accurate input values. Nonetheless, we wish to stress that all results presented here are theoretical in nature, and that the values provided are therefore estimates.

Beyond these limitations, Niche Mapper™ is currently the only tool available to accurately study heat exchange mechanisms associated with porous media (fur and feathers), climatic conditions, and their impact on the energy balance of seabirds wintering offshore, where direct metabolic studies are impossible. It therefore appears to be a good complementary method to biotelemetry, especially for small-sized species, which cannot be easily caught and fitted with internal data loggers recording heart rate. Furthermore, our sensitivity analysis supports the robustness of Niche Mapper™, with few parameters critically affecting the predicted energy requirements (Table 4). These are mainly environmental parameters, such as air temperature or wind speed, which can be measured in situ or via remote sensing. Other important factors are morphological parameters, such as plumage depth, a parameter particular to each species.

The most important outcome of our study is the sharp increase in energy expenditure between November and December, which occurs for both species at both study sites. Similar patterns have been found for great cormorants (Phalacrocorax carbo) wintering in Greenland (Grémillet et al., 2005). The end of the year therefore

**Sensitivity analysis**

For the sake of simplicity, the results of the sensitivity analysis are only presented for little auks and Brünnich’s guillemots wintering off southwest Greenland (Table 4). The results and the most important factors influencing the individual daily energy demand are nonetheless identical at the two sites (Greenland and Newfoundland). Taking into account the variability of single input parameters, the sensitivity analysis shows that air temperature is a key factor influencing daily energy requirements. Plumage depth and wind speed also substantially affect energy requirements (Table 4).
appears to be a particularly challenging phase of the annual cycle for North Atlantic seabirds, with decreasing air temperatures being the main driving force (Table 4).

In most situations, species confronted with fluctuating environmental conditions maintain an energetic steady state and ensure their survival via physiological and/or behavioural plasticity (Komers, 1997; Dawson and O’Connor, 1999). Alcids wintering in the North Atlantic carry very limited body reserves and cannot survive longer than 3–4 days without foraging, even at the best of their body condition (Gaston et al., 1983; Gaston and Jones, 1998). They are therefore bound to increase their energy intake rates substantially in November and December, if they are to survive (as observed in other wintering seabird species) (e.g. Grémillet et al., 2005).

On the other hand, this critical period is characterized by harsh storms (Arctic Climate Impact Assessment, 2004), which are known to have a negative impact on seabird flying and diving performance (Finney et al., 1999). Storms also increase wind-driven water turbidity and affect prey availability and distribution (Schreiber, 2001), thus decreasing the birds’ predatory efficiency. November and December storms therefore affect seabird foraging performance and their ability to acquire energy at a time of peak energy demand. This critically challenges their energy balance and creates an energetic bottleneck. Our results, which strongly suggest such a bottleneck, might explain the timing of seabird winter wrecks, during which large numbers of seabirds cast ashore and/or are found dead inland (Gaston, 2004). During the past 50 years, major wrecks of little auks and Brünnich’s guillemots have more or less always occurred in late November and December in the North Atlantic (Gaston and Jones, 1998; Gaston, 2004). Gaston (Gaston, 2004) explained this timing by the abundance of inexperienced and vulnerable juvenile birds, which is higher in November and December than in late winter. This might well be the case, but we argue that the energetic bottleneck identified in this study is most probably the major determinant of the magnitude and of the timing of winter mortality in adult and juvenile seabirds wintering in the North Atlantic.

The end of the winter (December to March) may also play a crucial role for seabird energetics, with a 4 month plateau of maximum energy expenditure. This plateau stands at an average of 463kJ day$^{-1}$ for little auks and 1411kJ day$^{-1}$ for Brünnich’s guillemots. During the breeding season, when provisioning chicks, different studies have shown that these two species cope with energy expenditures as high as 696 and 1860kJ day$^{-1}$, respectively (Ellis and Gabrielsen, 2002). These values are noticeably higher than those predicted by Niche Mapper$^\text{TM}$ for the winter period. However, breeding energy expenditures occur in a favourable energetic context, with mostly good weather conditions and maximum prey abundance [e.g Arnkværn et al. for copepods (Arnkværn et al., 2005)], and they occur for a limited time period only [the nesting period lasts for 28.3 days on average in Greenland (Evans, 1981)]. In contrast, the winter energy requirements predicted in our study occur in a demanding and unpredictable environment, when storms make prey capture challenging for seabirds (Finney et al., 1999). This phase lasts for a third of the annual cycle, causing an enormous total energy demand compared with that of the short breeding period.

Current climate models predict drastic changes in the North Atlantic, with rising air and water temperatures, as well as more frequent winter storms (Arctic Climate Impact Assessment, 2004; Corell, 2006). From this study, we could expect that higher temperatures will have a positive effect upon the energy budget of seabirds wintering in this region, as it would potentially widen the November/December energetic bottleneck. However, indirect effects of global warming on prey availability and distribution might counterbalance the positive effect of higher temperatures on seabird energetics. More frequent winter storms might also critically perturb seabird foraging conditions, and changing water temperatures are already causing major ecosystem shifts in the North Atlantic (Beaugrand et al., 2002; Sandvik et al., 2005). Therefore, additional energetic studies, combining multi-year climate data and climate change scenarios, as well as data on energetics, behaviour and the distribution of birds and prey stocks are now necessary on larger temporal and spatial scales. From these it might be possible to predict fundamental niches of species in the future and to investigate and foresee the impact of climate change on seabird energetics and distribution during their wintering season (see Kearney et al., 2008) (for a review, see Kearney and Porter, 2009).

Outlook
Our study highlights the relationship that exists between harsh environmental conditions and the energy balance of alcids wintering in the northwest Atlantic. Predicting the existence of an energetic bottleneck in December, it provides important insights into the determinants of winter mass-mortality in these marine top predators.

Furthermore, our work presents and emphasizes the importance of a generic thermodynamic/biophysical/behavioural model to understand energy limitations in wintering marine animals. This algorithm, here applied at the individual level, also appears to be a powerful tool to define energetic constraints on population dynamics, and is of considerable applied interest. Indeed, with the ability to calculate daily energetics and food requirements from simple biotic and abiotic information, Niche Mapper$^\text{TM}$ can be used to estimate the food requirements of warm-blooded marine predators at the population and community level, to predict their impact on economically valuable fish stocks, and to evaluate their capacity to adapt to global change (e.g. overfishing and climate change).

Niche Mapper$^\text{TM}$ can be obtained and used for free in collaboration with Warren Porter (http://www.zooology.wisc.edu/faculty/Por/Port.html) or purchased in its present form by contacting Warren Porter (wporter@wisc.edu). We are grateful to the Field Museum of Natural History in Chicago and to Paula Holahan from the University of Wisconsin Zoological Museum for their help in examining bird tissue. We thank A. Harding, H. Sandvik and M. Enstipp. J.F. is supported by a grant from the University Louis Pasteur (Strasbourg, France).

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