Re: Application by Norfolk Vanguard Limited for an Order Granting Development Consent for the Norfolk Vanguard Offshore Wind Farm

RSPB Response Submitted for Deadline 2: 30th January 2019

Comments on Applicant's Response to Written Questions

Comments on Applicant's Response to Written Questions Appendix 3.1 Red-throated diver displacement

We welcome the presentation of the displacement assessment outputs incorporating a 4km buffer and based on the displacement and mortality rates recommended by Natural England and supported by us in section 4.8 of our Written Representations. Given the levels of mortality predicted using the recommended parameters, we agree that impacts on the biogeographic/BDMPS populations should be considered to be of moderate adverse significance.

The Applicant has also provided a justification for their preferred values of 90% displacement and 1% mortality for red-throated diver with of a review of published evidence. We have provided comments on this below.

Percentage displacement

The current SNCB advice is that 90-100% displacement is assumed for red throated diver, as the evidence for displacement is high and widely acknowledged; for example Furness *et al*. (2013), gave red-throated diver the highest possible score for susceptibility to displacement. The Applicant prefers the lower end of this range, 90%. While we acknowledge that there is a range of displacement apparent from the literature, this includes, in the most recent study (Mendel *et al.,* 2019) published after the SNCB guidance, a record of 94% displacement. Therefore 90% cannot be considered the maximum possible displacement, and 100% is a suitably precautionary value.

Displacement distance

In support of the revised rates Annex 1 reviews a number of studies, the majority of which were reviewed and cited by the SNCBs in producing their guidance (SNCBs 2017). The Applicant sometimes misinterprets these studies, for example they quote Welker and Nehls (2016) as reporting asymptote at "about" 1.5km. This paper actually reported the asymptote as 1.5 - 2.0 km from the outermost wind

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turbines and so the Applicant's claim that this study suggests no displacement beyond 1.5km is inaccurate.

There is a large amount of variation in the displacement distances reported, with displacement recorded up to 12km from a wind farm. As acknowledged by the Applicant, the only noticeable trend is that larger displacement distances are recorded in large open sea areas far from the coast, whereas lower displacement distances were recorded close to the coast. As such we would expect there to be higher, rather than lower, displacement distances for Norfolk Vanguard and therefore do not accept the arguments for a low, 1.5km, displacement distance.

There is likely to be a gradient of displacement radiating out from the windfarm, the shape of which is unknown but one that can extend as far as 12km. In this context, the Applicant's preferred 1.5km seems to be just an arbitrary value and there is no evidence to change from the SNCB's recommended 4km.

Percentage mortality

In support of their preferred lower mortality percentage, the Applicant argues that as some seabirds attain higher weights during the non-breeding season, that they have little difficulty finding food at this time. Notwithstanding that the evidence presented for this weight gain is for herring gull, puffin and guillemot and it is therefore questionable whether it is applicable to red-throated divers, this review does not include other conflicting evidence that some seabirds may have an "energetic bottleneck" in the winter (Fort *et al.,* 2009). The higher weight in some non-breeding seabird reported by the Applicant is also likely to be because birds are not subject to the stresses and constraints of breeding. As such the non-breeding period can be seen as a recovery and preparatory period and it is wrong to suggest that higher weights during this period mean that the birds can be subjected to greater disturbance without consequence. Such consequences could apply by reducing condition prior to breeding and thereby decreasing breeding success.

The Applicant goes on to suggest that as current estimates of red throated diver mortality include that occurring as a consequence of shipping activity, that additional mortality arising from displacement from wind farms is likely to be small. This ignores the recent evidence from Mendel *et al.,* (2019) that the extent of displacement caused by the presence of wind farms is far greater than that arising from shipping traffic. The Applicant's argument appears to be that because the birds are already disturbed by shipping traffic that further disturbance will not matter. However, it is not known whether red-throated divers in the southern North Sea are close to a tipping point in terms of disturbance and whether any more could significantly exacerbate the mortality and lead to catastrophic impacts. The use of mortality figures that are lower than the current recommendations therefore risks underestimating the significance of the impact on this species.

Comments on Applicant's Response to Written Questions Appendix 3.2 Collision risk modelling: update and clarification

The RSPB welcome the additional clarification provided by Appendix 3.2. However the note itself is not clearly presented and does not answer the outstanding issues around the approach taken to collision risk modelling. In particular,

- Insufficient justification is given for using the median value for bird density in the model
- The results presented for comparison using the Band (2012) model spreadsheets use the mean of medians not the mean bird density as recommended in the guidance.
- Insufficient detail is presented with the comparison with the MSS stochastic model
- The predicted mortalities presented using means, rather than means of medians are considerably higher than those presented in the original Application documents.
- It is still impossible to check the manner in which the calculations have been carried out.

As expected, the revisions provided so far support our concerns that collision risk is likely to be higher than was presented in the Applicant's Environmental Statement Offshore Ornithology chapter [doc. 6.1.13] and Information for HRA [doc. 5.3]. We are therefore still unable to agree that adverse effects on the integrity of the following sites and features can be ruled out:

- The kittiwake population of the Flamborough and Filey Coast SPA alone and in-combination with other plans and projects;
- The gannet population of the Flamborough and Filey Coast SPA alone and in-combination with other plans and projects;
- The lesser black-backed gull population of the Alde-Ore Estuary SPA alone and in-combination with other projects.

We are also unable to agree that there are no significant impacts on:

- North Sea populations of kittiwake and great black-backed gull.

Median bird density

The Applicant argues in section 1.1 of Appendix 3.2 that their preferred measure of bird density, the median, is the more statistically correct because of the skewed nature of the data. However Figure 1 shows that the data are not skewed, rather they are binomial and in this instance it is not clear why a median is more appropriate than a mean. The fact that the data are binomial is interesting and needs further explanation as to why this is. In paragraph 6, the Applicant states there are "numerous instances when the seabird density in year 1 was very low (or indeed zero) while that in the second year was higher", but only present supporting evidence for kittiwake in January and for no other species. If, indeed, the bird density was much lower in year 1, more detail should be given and some potential explanation given. For example, were the timings of survey different in years 1 and 2? This reinforces the argument we have made in section 4.2 of our Written Representations, that full details of the survey

timings should be provided. In particular, clarity should be provided as to whether one of the years data are more representative of the site than the other. In any case, there is no reason why a median is more or less appropriate summary statistic for a bimodal distribution than a mean as both are measures of central tendency.

Band (2012) model spreadsheets

The RSPB welcome the presentation of the output spreadsheets derived from using the original version of the (deterministic) Band (2012) model. However it appears, though this is not stated clearly, that this uses the mean of medians rather than means. It would have been far more informative to have used both, so that a direct and full comparison could be made.

MSS stochastic model version

The MSS commissioned stochastic version of the Band model (McGregor *et al.,* 2018) was created to provide transparency in how it is used in assessment. The outputs are specifically designed to provide an audit trail in such a manner that they can be checked and rerun as required if there are changes or errors in the input stage. This is in contrast to the stochastic modelling carried out by the Applicant, who has consistently refused to share the code for their own stochastic model and has only provided summary outputs for the MSS stochastic model they ran in order to provide a comparison. In order to properly assess the manner in which the modelling has been carried out both must be provided, although, given the Applicant claims that the models give identical results, there is little value in having the Applicant's own model version at all.

It should also be noted that the MSS stochastic model made a number of modifications with respect to bird densities and their stochastic treatment, in line with the findings of the review by Trinder (2017), included by the Applicant as Annex 5 of The Applicant's Response to Written Questions Appendix 3.2.

Predicted mortalities comparison.

In Table 5 of The Applicant's Response to Written Questions Appendix 3.2, a comparison is presented of the annual predicted collisions obtained by the Applicant's favoured method (the median of summed months), the method recommended by the authors of the MSS stochastic model (the summed monthly medians) and the mean. As the Applicant makes clear, the authors of the MSS model argue that the Applicant's favoured method does not preserve the complete range of uncertainty associated with each monthly estimate. However this value is the one that is presented in the ES. In every instance, the predicted mortality preferred by the Applicant is lower than the other two values, and scant detail is given as to why this should be a preferred figure.

The RSPB welcome the presentation of collision mortalities calculated using mean densities in Annex 3 of The Applicant's Response to Written Questions Appendix 3.2 and also see Table 5 in Appendix 3.2. These predicted mortalities are considerably higher than those calculated using the median. Given that the justification provided by the Applicant for using the median is inadequate (see above) we recommend that the mean values are used in the assessments of impact significance.

<u>Model verification</u>

The RSPB welcome the presentation of the further details needed for independent verification of the collision risk modelling in Annex 1 of The Applicant's Response to Written Questions Appendix 3.2. However the only bird density figures presented are the median values. We ask that the mean bird densities are also provided. We also ask that the full outputs of the MSS stochastic model are also presented in order to provide an audit trail and verification of the calculation.

<u>Nocturnal activity rates</u>

We welcome the provision of updated collision mortality figures using the Furness *et al.* (2018) nocturnal activity rates for gannet and the NE recommended rates for kittiwake and large gulls, although these do increase concerns about levels of collision risk. There is also still a need to resolve the query regarding survey timings outlined in section 4.2 of our Written Representations. If survey timings are not known and hence it is not known whether likely peaks in activity at first and last light are accounted for, the more precautionary rates based on Garthe and Huppop (2004) and Furness *et al.,* (2013) should be used for gannet as well.

Comments on Applicant's Response to Written Questions Appendix 3.3 Operational gannet and auk displacement: update and clarification

We support the recommendations of Natural England which state that the displacement assessment for auks should incorporate a 2km buffer and be based on worst case scenario (WCS) displacement of 70% and mortality of 10%. Whilst this has been acknowledged within the report, the outputs based on these figures are not discussed. However, the tables provided indicate that at these levels, cumulative mortality is predicted to result in a rise in background mortality of over 1% for all auk species, with the rise for guillemot and razorbill being over 3%. Given the WCS levels of mortality predicted using the recommended parameters, we consider that impacts on the biogeographic/BDMPS populations should be considered to be of moderate adverse significance. We will provide further comment on the topics within this report as necessary once the further details referred to by the Applicant has been provided.

Comments on Applicant's Response to Written Questions

Our comments relate only to the Applicant's responses to questions on issues that are not covered in detail in the submissions discussed above.

Ecology Offshore – Ornithology

<u>Q.3.3 k) Gannet avoidance rate in the breeding season</u>

As pointed out in our response to written questions, Cleasby *et al.,* (2015), while not discussing avoidance rates, demonstrated that behavioural state will influence collision risk. During the breeding

season breeding birds will be constrained by central place foraging which is likely to reduce macro-avoidance. Changes in avoidance behaviour due to behavioural differences are highlighted in a recent review of avoidance behaviour (Cook *et al.,* 2018), which also points out that the figures used for the calculation of avoidance rates are largely derived from the non-breeding season for gannet. This problem (amongst others) is also true of the Skov *et al.,* (2018) study quoted by the Applicant. We maintain our recommendation of a more precautionary Avoidance Rate for gannet during the breeding season.

Q.3.3 m) Predation at the Alde-Ore Estuary SPA

The Applicant cites Mavor *et al.* (2001) in saying that fox predation resulted in the failure of 75% of nests in 2000. This is based on a pers. comm. reference, rather than a published study. Whilst the Applicant is correct in that there is not currently a predator fence in place, regular fox control has been carried out in recent years. On Havergate Island, the population has declined in the last few years despite there being no evidence of fox presence. It should also be noted that there are various constraints to the use of predator fencing in the parts of the SPA used by nesting gulls, including potential for impacts on the landscape, historic features and SAC vegetated shingle of the site. However, our key point remains that whilst we do not agree that adverse effects on the integrity of the Alde-Ore Estuary can be ruled out at this stage, that predator management within the SPA would not be an acceptable form of mitigation.

Habitats Regulations Assessment

Q.23.35 Apportioning to lesser black-backed gulls of the Alde-Ore Estuary SPA

The Applicant gives further justification for their apportioning approach for the lesser black-backed gulls from the Alde-Ore Estuary. They state that tracking data indicate that a figure of 3.5% would be more realistic than their figure of 25%, although it is not entirely clear how the 3.5% has been derived from the data, and the population figure of 2000 pairs quoted for the years in question is not accurate (it would average around 1700 pairs – see Annex II to our Written Representations). We also disagree with the assertions that the diet of birds from urban and rural coastal colonies would be similar (see our Written Representations and Response to the Examining Authority's Written Questions) and our position regarding apportionment therefore remains unchanged from these responses.

Q.23.36 Use of migration-free breeding season for gannets

For the definition of breeding season, the most appropriate information is site specific data for the Flamborogh and Filey Coast SPA as this is the colony most likely to be affected. RSPB reserve managers advise that numbers of gannet inshore start to increase from mid-January, with birds prospecting on the cliffs from February onwards, with the majority returning by late March. The majority of birds have departed the colony by the end of September, though some presence on the cliffs is expected in October. The last juveniles on the cliffs are usually in early November.

We note that a calculation based on the full breeding season is presented, which we welcome in principle, however, as it is not clear whether these calculations use mean or median monthly bird densities, we are not certain that these outputs are correct.

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

Jérôme Fort[1,2,*], Warren P. Porter[3] and David Grémillet[1,4]

[1]CNRS-CEFE – UMR 5175, 1919 Route de Mende, 34 293 Montpellier cedex 5, France, [2]CNRS-DEPE-IPHC, 23 rue Becquerel, 67087 Strasbourg cedex 02, France, [3]Department of Zoology, University of Wisconsin, 250 N. Mills Street, Madison, WI 53706, USA and [4]Percy FitzPatrick Institute, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa

*Author for correspondence (e-mail: jerome.fort@cefe.cnrs.fr)

SUMMARY

Studying the energetics of marine top predators such as seabirds is essential to understand processes underlying adult winter survival and its impact on population dynamics. Winter survival is believed to be the single most important life-history trait in long-lived species but its determinants are largely unknown. Seabirds are inaccessible during this season, so conventional metabolic studies are extremely challenging and new approaches are needed. This paper describes and uses a state-of-the-art mechanistic model, Niche Mapper^{TM}, to predict energy expenditure and food requirements of the two main seabird species wintering in the northwest Atlantic. We found that energy demand increased throughout the winter phase in both species. Across this period, mean estimated daily energy requirements were 1306 kJ day^{-1} for Brünnich's guillemots (*Uria lomvia*) and 430 kJ day^{-1} for little auks (*Alle alle*) wintering off Greenland and Newfoundland. Mean estimated daily food requirements were 547 g wet food day^{-1} for Brünnich's guillemots, and 289 g wet food day^{-1} for little auks. For both species and both wintering sites, our model predicts a sharp increase in energy expenditure between November and December, primarily driven by climatic factors such as air temperature and wind speed. These findings strongly suggest the existence of an energetic bottleneck for North Atlantic seabirds towards the end of the year, a challenging energetic phase which might explain recurrent events of winter mass-mortality, so called 'seabird winter wrecks'. Our study therefore emphasizes the relevance of thermodynamics/biophysical modelling for investigating the energy balance of wintering marine top predators and its interplay with survival and population dynamics in the context of global change.

Key words: alcids, bioenergetics, daily energy requirement, Niche Mapper^{TM}, winter wrecks.

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^{TM} (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^{TM} 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.

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^{TM} to the study of little auks (*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 Gavrilo, 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 auks' and Brünnich's guillemots' energy requirements and food needs during the winter off southwest Greenland and Newfoundland using Niche Mapper^{TM}.

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 auks 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 consequently performed for the time period between September 1st 2004 and March 1st 2005.

Niche Mapper^{TM} model

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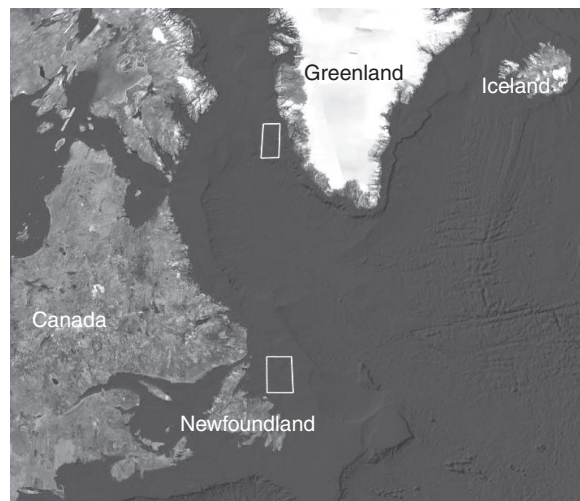

Fig. 1. Map of the two study sites off Greenland and off Newfoundland.

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

Table 1. Climate data used for modelling daily energy requirements of Brünnich's guillemots and little auks off Greenland and Newfoundland between September 2004 and March 2005

	Year	Month	Air temperature (°C)		SST (°C)		Relative humidity (%)		Scalar wind speed (m s^{-1})		Cloud cover (%)	
			Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Newfoundland	2004	September	11.3	6.6	12.1	8.0	88.0	66.6	12.4	5.3	100	0
	2004	October	11.5	2.0	9.5	4.4	100.0	76.7	20.6	0.0	100	0
	2004	November	10.0	−1.5	5.9	1.6	100.0	83.4	18.4	3.6	100	0
	2004	December	5.3	−10.5	5.0	0.1	99.7	70.4	17.3	4.1	100	0
	2005	January	4.9	−7.0	0.3	−1.3	98.8	88.4	19.9	8.0	100	0
	2005	February	0.9	−9.0	−0.1	−1.5	98.6	66.4	13.9	5.9	100	0
	2005	March	0.4	−5.9	−1.6	−1.6	96.0	71.1	15.3	7.3	100	0
Greenland	2004	September	6.4	4.0	6.3	4.3	83.8	75.5	14.2	4.8	100	0
	2004	October	5.5	0.0	4.3	1.9	97.2	68.6	16.0	4.0	100	0
	2004	November	3.5	−0.3	4.5	1.7	89.8	74.2	12.1	2.4	100	0
	2004	December	−5.7	−9.9	2.3	−1.2	64.8	64.4	8.6	6.4	100	0
	2005	January	1.5	−10.3	4.0	−1.3	93.2	63.6	17.5	2.0	100	0
	2005	February	−0.6	−10.7	0.9	−1.3	95.3	55.0	14.0	6.0	100	0
	2005	March	3.2	−4.6	0.1	−1.3	69.1	69.1	12.7	8.0	100	0

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™ (ICOADS data provided by NOAA/OAR/ESRL PSD, Boulder, CO, USA; http://www.cdc.noaa.gov/).

radiation emitted through the porous feathers, and conduction to the water) and Q_{st} is the stored heat (due to body temperature rising or falling); m_{in} is the mass input (food entering the gut or air entering the respiratory system), m_{out} is the mass lost (faeces or exhaled air) and m_{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 usually occurs in the second half of June (Stempniewicz, 2001). We consequently assumed that the energy requirements and energy budget of females in March are still not affected by reproductive preparations.

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).

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).

Behavioural properties

Conduction, convection, evaporation, and solar and infrared radiation all affect heat loss, heat gain and energy expenditure. These processes are affected by the physical characteristics of the media surrounding the bird's body during its different activities (flying in air, diving under water or resting at the water surface). We therefore incorporated bird behavioural parameters (flying, diving and resting) into Niche Mapper™, as well as air and water temperatures, flight altitude, dive depth and flight speed. Winter time budgets (i.e. proportions of time spent flying, diving and resting) were estimated using published data concerning breeding Brünnich's guillemots (Falk et al., 2000; Falk et al., 2002). According to this information, Brünnich's guillemots were assumed to spend 7% of the time flying,

Table 2. Parameters used in the energetic model for both alcid species

	Brünnich's guillemot	Little auk	References
Morphological properties			
Body mass (max.–min.) (kg)	0.75–1.00	0.14–0.17	Schreiber and Burger, 2002
Plumage depth (dorsal–ventral) (mm)	5.6–16.0	7.4–12.8	This study
Plumage reflectivity (dorsal–ventral) (%)	38.0–74.4	40.4–65.0	This study
Feather length (dorsal–ventral) (mm)	32.4–25.0	20.0–19.2	This study
Feather diameter (dorsal–ventral) (μm)	33.0–33.0	33.0–33.0	This study
Wing span (m)	0.72	0.39	Croll et al., 1991; Elliot and Gaston, 2005, A. M. A. Harding, unpublished
Wing area (cm^2)	550	180	Croll et al., 1991; Elliot and Gaston, 2005, A. M. A. Harding, unpublished
Physiological properties			
Body core temperature (max.–min.) (°C)	39.6–40.3	40.1	Gabrielsen et al., 1988; Gabrielsen et al., 1991
Flesh thermal conductivity (W m^{-1}°C^{-1})	0.5	0.5	Cheng and Plewes, 1992
Oxygen extraction efficiency (%)	35	35	Hainsworth, 1981; Arens and Cooper, 2005
Digestive efficiency (%)	70	80	Wiens and Scott, 1975; Harding et al., 2009
Core temperature–skin temperature (°C)	0.1	0.1	W.P.P., unpublished
Exhaled air temperature–local air temperature (°C)	2	2	Porter et al., 2000
Bird density (kg m^{-3})	932.9	932.9	Porter et al., 2006
Flight metabolism (W)	88.00	10.57	Pennycuick, 1989; A. M. A. Harding, unpublished; this study
Behavioural properties			
Ventral area contacting substrate (%)	25	25	This study
Flight speed (m s^{-1})	18.1	13.0	Nettleship and Birhead, 1985
Dive depth (m)	48.0	27.3	Falk et al., 2000; Mori et al., 2002
Flight altitude (m)	5	5	Gaston, 2004, see methods
Proportion of time spent flying per day (%)	7	7	Our estimate based on Falk et al., 2000; Falk et al., 2002, J.F., unpublished
Proportion of time spent diving per day (%)	17	17	Our estimate based on Falk et al., 2000; Falk et al., 2002; J.F., unpublished

17% of the time diving (submerged under water), and the rest of the time resting on the water surface. In the absence of any comparable behavioural information for little auks, we assumed that the proportion of time spent diving and flying was the same for the two species during the winter period (J.F., unpublished). The model takes into account the fact that the bird cannot dive and fly at the same time, and that birds resting at the water surface are one-quarter submerged. Most seabirds at sea remain less than 100 m above the sea surface in flight (Gaston, 2004). However, this altitude varies with weather and wind conditions. For wing flapping seabirds such as alcids, flying close to the sea surface is advantageous when wind speed is high. However, this is probably not the case during periods of little wind. As these variations are extremely difficult to consider in our model, we assumed that both species studied fly at an altitude of 5 m above the sea throughout the winter. In any case, pressure and temperature variations between 0 and 100 m are very low [pressure: 196 Pa difference at 0°C air and salt water temperature; vertical temperature: less than 2°C difference because of cloudy conditions, high winds, a turbulent velocity profile and sea surface evaporation (Tracy et al., 1980), Niche Mapper^{TM}]. Thus, we considered that neither variable significantly affected the birds' energetics. Both little auks and Brünnich's guillemots were assumed to be diurnal and crepuscular during winter, and also to stay inactive at the water surface during darkness (Birkhead and Nettleship, 1981; Gaston and Jones, 1998) (J.F., unpublished).

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 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^{TM} 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

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

	Protein (% dry matter)	Lipid (% dry matter)	Carbohydrate (% dry matter)	Dry matter proportion
Euphausiids[a]	43.9	52.4	0.7	26.1
Amphipods[a]	47.5	26.4	1.2	22.4
Fish				
Capelin[b]	50.6	43.1	0.0	31.8
Arctic cod[b]	71.1	17.5	0.0	21.1
Squid				
Gonatus sp.[b]	51.7	41.1	0.0	26.5

[a]Percy and Fife, 1981. [b]Lawson et al., 1998.

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. 442, max. 481 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
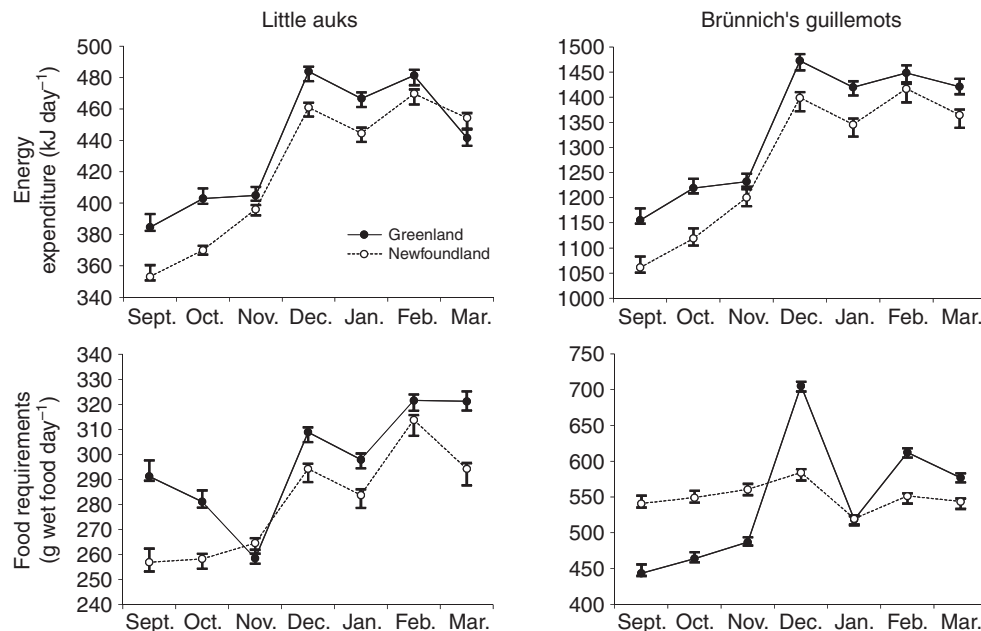

Fig. 2. Energy and food requirements predicted by the model Niche Mapper^{TM} for little auks and Brünnich's guillemots wintering off southwest Greenland and Newfoundland. Error bars were calculated using average maximum ranges for all parameters as estimated in the sensitivity analysis (Table 4).

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

	Brünnich's guillemots				Little auks			
Parameters	Min. value	Max. value	Range	Variation of seasonal energy requirements (%)	Min. value	Max. value	Range	Variation of seasonal energy requirements (%)
Endotherm								
Plumage depth: dorsal, ventral (mm)	5.0, 14.4	6.2, 17.6	±10%	±7.16	6.7, 11.5	8.1, 14.1	±10%	±5.34
Plumage reflectivity: dorsal, ventral (%)	0.34, 0.67	0.42, 0.82	±10%	<±0.01	0.36, 0.58	0.44, 0.71	±10%	±0.02
Feather length: dorsal, ventral (mm)	29.2, 22.5	35.6, 27.5	±10%	±0.21	18.0, 17.3	22.0, 21.1	±10%	±1.45
Feather diameter (μm)	29.7	36.3	±10%	±2.18	29.7	36.3	±10%	±0.48
Plumage density (1 cm^{-2})	4114.8	5029.2	±10%	±0.66	4114.8	5029.2	±10%	±0.89
Body core temperature (°C)	39.6	40.3	Min.–max.	±1.83	36.1	40.1	±10%	±2.02
Digestive efficiency (%)	0.63	0.77	±10%	<±0.01	0.72	0.88	±10%	±0
Exhaled air temperature–local air temperature (°C)	1.8	2.2	±10%	0.01	1.8	2.2	±10%	0.01
Flight metabolism (W)	79.2	96.8	±10%	±0.84	9.513	11.627	±10%	±0.31
Ventral area contacting substrate (%)	0.225	0.275	±10%	±0.06	0.225	0.275	±10%	±0.17
Flight speed (m s^{-1})	16.25	19.87	±10%	±0.23	11.7	14.3	±10%	±0.28
Dive depth (m)	43.3	52.8	±10%	<±0.01	24.57	30.03	±10%	<±0.01
Flight altitude (m)	4.5	5.5	±10%	<±0.01	4.5	5.5	±10%	<±0.01
Climate								
Air temperature (°C)	**−7.80**	**5.17**	**Min.–max.**	**±8.52**	**−7.80**	**5.17**	**Min.–max.**	**±8.87**
Sea surface temperature (°C)	−0.60	5.27	Min.–max.	±0.04	−0.60	5.27	Min.–max.	±0.03
Relative humidity (%)	55.0	97.2	Min.–max.	±1.20	55.0	97.2	Min.–max.	±1.44
Wind speed (m s^{-1})	2.0	17.5	Min.–max.	±2.57	2.0	17.5	Min.–max.	±2.70
Cloud cover (%)	0	100	Min.–max.	<±0.01	0	100	Min.–max.	<±0.01

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.

wet food day^{-1} in September to 577 g wet food day^{-1} in March), with a sharp increase between November and December (from 487 to 705 g wet food day^{-1}). After this sharp increase food requirements decrease between December and January (from 705 to 518 g wet food day^{-1}) (Fig. 2). Note that differences between energy and food requirements at the different locations are due to differences in the calorific value of the preferred diet (Table 3). For instance, guillemots off Newfoundland progressively shift from a fish to a crustacean diet across the winter (Elliot et al., 1990; Rowe et al., 2000), which explains why food requirements remain more or less constant over this period. Off Greenland, a similar shift occurs for guillemots (Falk and Durinck, 1993). However, in December and February, birds primarily consume Arctic cod, whereas they mostly eat capelin during other months (Falk and Durinck, 1993). Cod are energetically less profitable than capelin (essentially because of a lower lipid content; see Table 3), which results in an increase in food requirements for these 2 months.

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).

DISCUSSION
We used Niche Mapper^{TM} 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^{TM} 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^{TM}, 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

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, 1996). 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 behaviour 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 $463\,\mathrm{kJ\,day^{-1}}$ for little auks and $1411\,\mathrm{kJ\,day^{-1}}$ 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 $1860\,\mathrm{kJ\,day^{-1}}$, respectively (Ellis and Gabrielsen, 2002). These values are noticeably higher than those predicted by Niche Mapper[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 nestling 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[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).

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