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The feeding ecology of little auks raises questions about winter zooplankton stocks in North Atlantic surface waters

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Copepods are essential components of marine food webs worldwide. In the North Atlantic, they are thought to perform vertical migration and to remain at depths more than 500 m during winter. We challenge this concept through a study of the winter feeding ecology of little auks (*Alle alle*), a highly abundant planktivorous seabird from the North Atlantic. By combining stable isotope and behavioural analyses, we strongly suggest that swarms of copepods are still available to their predators in water surface layers (less than 50 m) during winter, even during short daylight periods. Using a new bioenergetic model, we estimate that the huge number (20–40 million birds) of little auks wintering off southwest Greenland consume 3600–7200 tonnes of copepods daily, strongly suggesting substantial zooplankton stocks in surface waters of the North Atlantic in the middle of the boreal winter.

Keywords: diving behaviour; energetic modelling; food requirements; marine food web; stable isotope; seabird

1. INTRODUCTION

Copepods are essential components of aquatic food webs and play an important role in marine ecosystems. Their life strategies have been extensively studied (e.g. Falk-Petersen *et al.* 2009) and their ecology is considered to be well known. At high latitudes and during winter, copepods are thought to perform vertical migration to deeper water to undergo diapause, and to become unavailable to most predators (Falk-Petersen *et al.* 2009). However, a recent study has shown that in high Arctic waters copepods maintain their synchronized diel vertical migration throughout the polar night (Berge *et al.* 2009), suggesting that further investigations are necessary to yield a complete view of copepod winter ecology.

Seabirds are powerful indicators of marine food webs (e.g. Piatt *et al.* 2007). Here we used little auks (*Alle alle*) as biosamplers of copepods, since this small Arctic species is the only seabird in the North Atlantic which feeds almost exclusively on zooplankton, essentially calanoid copepods (Stempniewicz 2001). We used isotopic tracers (Kelly 2000) and time–depth-recorders to investigate little auk diet and foraging depths during winter. It is the first study to record the winter diving behaviour of such a small seabird. We tested the hypothesis that copepods are still available in upper surface layers and consumed by little auks, even during the short winter daylight period.

2. MATERIAL AND METHODS

Little auks breed at high latitudes around the Arctic Ocean. The north-east Atlantic populations winter south of the ice edge, mainly off southwest Greenland and Newfoundland (Stempniewicz 2001). Twenty breeding little auks were caught during summer 2007 at Kap Höegh (East Greenland; 70°44′ N 21°35′ W). Blood samples (approx. 0.2 ml) were collected from the brachial vein, as well as 16 chick meals transported in adult's sublingual pouch. Twenty wintering birds were legally shot at sea off Nuuk (southwest Greenland; 64°10′ N 51°45′ W) in January 2007 and blood samples collected from the cardiac clot. Stomach contents were removed, but digestion precluded identifying the few prey items. To investigate copepod isotopic signatures, only chick meals containing more than 90 per cent copepods were analysed. Stable isotope analyses were performed following Cherel *et al.* (2007), with blood $\delta^{15}N$ ($^{15}N/^{14}N$) values reflecting the trophic position/diet (Kelly 2000). Values are mean $\pm$ s.d.

Eighteen breeding little auks from Longyearbyen (Spitsbergen; N78°13′ N 15°20′ E) and 22 from Kap Höegh were equipped with a time–depth-recorder archival tag (G5, CEFAS Technology Limited, Lowestoft, UK) during summers 2007 and 2008, respectively. Recorders were implanted into the abdominal cavity following Grémillet *et al.* (2005). Each batch of loggers was programmed to record pressure during 24-h periods at a sampling rate of 2 s; every 12th day from 6 November 2007 to 22 February 2008 and every 10th day from 1 October 2008 to 10 May 2009. Five birds from Longyearbyen were resighted in July 2008 and three of those were recaptured. Only one logger successfully recorded pressure. Thirteen birds from Kap Hoëgh were resighted and recaptured in July 2009. Only two loggers successfully recorded pressure in December–January. Stored data were analysed using MultiTrace-Dive software (Jensen Software Systems). To avoid artefacts owing to waves or tag accuracy, only dives greater than 1.5 m were analysed. To compare winter results of behavioural and isotopic analyses, only dive data recorded in December and January were used.

Individual daily energy and food requirements during December–January were calculated using the bioenergetics model Niche Mapper (Fort *et al.* 2009). The principles of Niche Mapper, its validation and all input data are detailed in the electronic supplementary material S1.

Given the isotopic results (see below), birds were assumed to feed on copepods during winter. We then estimated the daily food intake for the whole little auk population wintering off southwest Greenland. This population is composed, to a large extent, of birds breeding in northwest Greenland, east Greenland and Svalbard (Stempniewicz 2001). The number of little auks wintering off southwest Greenland is therefore estimated as 20–40 million birds (Karnovsky & Hunt 2002; Barrett *et al.* 2006).

3. RESULTS

During summer, the $\delta^{15}N$ value of chick meals (which correspond to copepod prey, Harding *et al.* 2009) averaged 8.4 $\pm$ 0.5‰ (figure 1). Summer and winter bird blood $\delta^{15}N$ values were almost identical (figure 1), yet statistically different (11.4 $\pm$ 0.1 and 11.7 $\pm$ 0.4‰,

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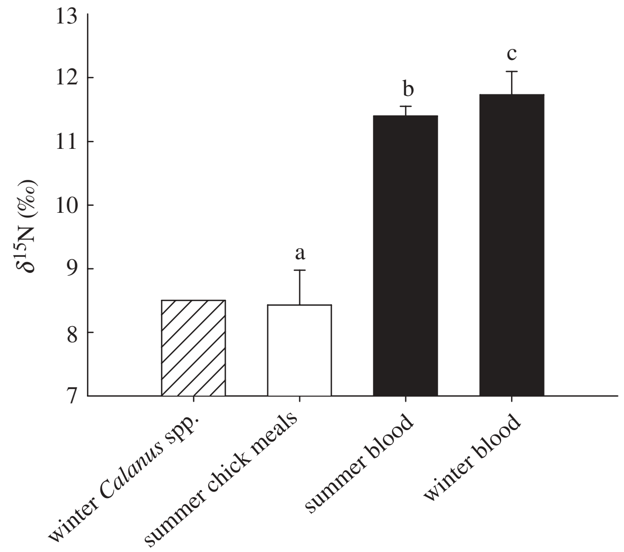

Figure 1. Stable nitrogen isotope values for chick meals ($n = 9$) and for little auks blood samples ($n = 20$) collected at Kap Höegh (east Greenland) during the summer, and for little auks blood samples ($n = 21$) collected at sea off Nuuk (southwest Greenland) during winter. Values are means ± s.d. Values not sharing the same superscript letters are significantly different (see §3). Winter value for *Calanus* spp. is from Sato *et al.* (2002).

respectively; *t*-test, $t = 3.75$, $p < 0.001$). During summer, adult bird blood was 3‰ enriched in δ^{15}N compared with copepod prey, as expected for an increase of one trophic level (figure 1). During winter, measured bird blood was also 3‰ enriched in δ^{15}N compared with copepods (figure 1, Sato *et al.* 2002).

During winter (December–January), the mean depth of dives was 12 ± 11 m, with a maximum dive depth of 50 m ($n = 6056$ dives). The mean dive duration was 45 ± 25 s. On average, birds spent 24 per cent of their time diving, an activity which was equally performed during the daylight and night periods (48% and 52% of time diving, respectively; figure 2). Dives were mostly concentrated during the daylight period and the first part of the night (figure 2; detailed results in electronic supplementary material S2).

During January, Niche Mapper predicted an individual daily energy expenditure of 438 ± 41 kJ d^{-1}, and a food requirement necessary to meet this expenditure of 180 ± 17 g zooplankton per day (wet mass). Consequently, we estimate that the southwest Greenland wintering population of 20–40 million little auks consumes 3600–7200 tonnes of zooplankton per day (wet mass).

4. DISCUSSION

Using a multidisciplinary approach combining stable isotope analysis, biotelemetry and energetic modelling, this study presents indirect evidence that during winter daylight periods copepods are still numerous in surface waters less than 50 m off southwest Greenland. Little auks are known to feed almost exclusively on copepods in summer (e.g. Karnovsky *et al.* 2008), and blood δ^{15}N values found here are in agreement with birds preying upon copepods during this period (Karnovsky *et al.* 2008). Isotopic δ^{15}N signatures are also similar for summer and winter copepods (Sato *et al.* 2002; figure 1), as well as for summer and winter adult blood samples (figure 1). This strongly suggests that little auks feed predominantly on copepods in winter. During this period, birds may also consume other prey, but in a minor proportion since amphipods, euphausiids or fish larvae have higher isotopic signatures than copepods (Tamelander *et al.* 2008) and would thus lead to higher blood δ^{15}N values. Winter blood values slightly higher than those measured in summer might reflect such minor amphipod/euphausiid/fish consumption, as well as the general food web enrichment from summer to winter (Rolff 2000).

Further, we infer from little auk diving behaviour that copepods remain abundant in winter surface waters, even during the daylight period when they are supposed to perform vertical migration to greater depths (figure 2; Fortier *et al.* 2001; Berge *et al.* 2009). Even though our dive depth results are consistent with summer recordings (Harding *et al.* 2009), further studies are now needed to confirm the first winter dive data for little auks. Their performance is impressive, with hundreds of dives conducted daily, over 1 minute and to depths of up to 50 metres (see electronic supplementary material S2). However, this maximum dive depth is extremely shallow when compared with the depths greater than 500 metres at which copepods are assumed to occur in winter.

Copepods are classically thought to enter diapause in the autumn and to spend all winter in deeper water (Falk-Petersen *et al.* 2009). During early spring, and mostly synchronized with the phytoplankton spring bloom, they are supposed to migrate back to surface waters (Falk-Petersen *et al.* 2009). However, a recent acoustic study has shown that even in winter and during the high-latitude polar night, some copepods perform a synchronized diel vertical migration in the epipelagic layer (Berge *et al.* 2009), whereby they migrate to the food-rich surface layers during darkness and move to deeper water during daylight, where they are out of reach from predators (Fortier *et al.* 2001). Our study strongly suggests that during winter, swarms of copepods are still present in surface waters (*sensu* Berge *et al.* 2009), where they are targeted by little auks both during the daylight and the dark period.

Using a bioenergetic model, we estimated that the amount of copepods available to little auks wintering off southwest Greenland is substantial, since the daily intake of the little auk population wintering off southwest Greenland is estimated to amount to 3600–7200 tonnes. This result is based on a diet composed only of copepods and it might be slightly overestimated since little auks probably also consume a few other prey items such as amphipods and euphausiids. The standing stock of copepods is currently unknown and it is impossible to estimate the proportion of the population caught per day by wintering birds. However, a range of 3600–7200 tonnes of copepods caught per day during the winter off southwest Greenland is larger than the daily amount of copepods consumed during summer by the breeding population of the North Water Polynya (i.e. 3450–6900 tonnes of wet food consumed per day, including 2340–4680 tonnes of copepods; Karnovsky &

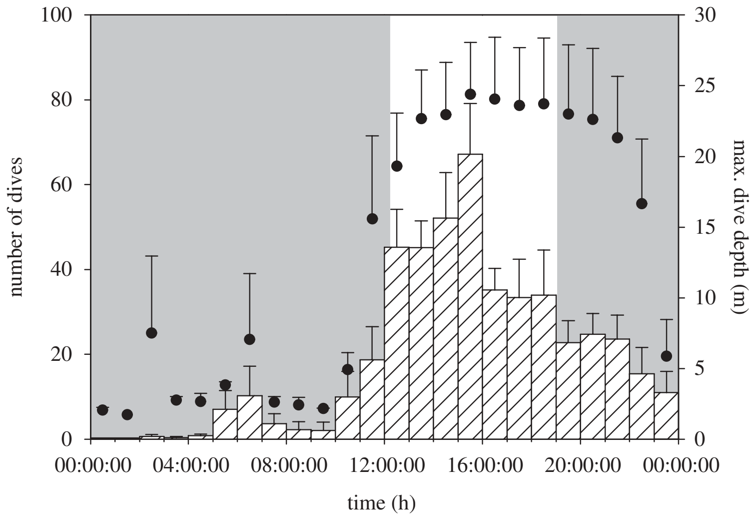

Figure 2. Average number of dives (bars with cross lines) and maximum depth reach for any dive (filled circles) recorded for little auks ($n = 3$) at each hour of day during winter (December–January) (±s.e.). The grey background represents the night/darkness period, while the white background represents the daylight period off Nuuk, southwest Greenland (64°10′ N 51°45′ W). Sunrise and sunset hours were converted to GMT hours. They correspond to the earliest sunrise and latest sunset observed during the study period.

Hunt 2002). Therefore, this suggests that the daily presence of copepods in the upper layer of the water column throughout the winter is much more important than usually assumed, with far-ranging consequences for regional food webs and energy flow.

Fieldwork led in Greenland was conducted under permits of the IPEV Ethics Committee (MP/12/24/05) and with the permission of the Greenland Home Rule Government (Danish Polar Center permit 512-240). Fieldwork led in Spitsbergen was conducted under permits 234 Forsøksdyrutvalget, Mattilsynet, Norway.

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