AGE-SPECIFIC VARIATION IN TROPHIC NICHE OVERLAP OF DOVEKIES *ALLE ALLE*

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SUMMARY

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Stable isotope ($\delta^{15}N$, $\delta^{13}C$) analysis of primary feathers and muscle tissue of Dovekies *Alle alle* collected on Newfoundland beaches following an oil spill in early winter 2004 were used to investigate age-related variation in trophic niche during summer, fall and early winter. Observed $\delta^{15}N$ values of adults were significantly higher than those of sub-adults during fall moult and hatch-year birds during summer. Strong segregation of $\delta^{13}C$ and $\delta^{15}N$ values of hatch-year birds into two distinct groups during summer may indicate differences in the colony of origin. Similarly, a wide range of $\delta^{13}C$ values for adult and sub-adult Dovekies during fall may indicate differences in moulting areas. In early winter, the $\delta^{13}C$ values of all age classes overlapped, with relatively depleted $\delta^{13}C$ values (-20.0 ± 0.4‰) characteristic of offshore waters. Age-class overlap in $\delta^{15}N$ values (+12.2 ± 0.4‰) likely reflects a common diet of *Calanus finmarchicus*, the most abundant copepod in near-surface waters on the Newfoundland–Labrador shelf in winter. Our results suggest that Dovekies from different age classes and potentially breeding regions overlap on their wintering grounds where they rely on a common *Calanus* prey. Consequently, future climate-driven shifts in the meso-zooplankton communities in the North Atlantic have potentially large-scale population consequences for this abundant planktivore.

Key words: avian Arctic planktivore, age classes, moult, Stable isotope analysis, *Alle alle*

INTRODUCTION

Opportunities to assess the trophic niche and habitat use of non-breeding seabirds are limited by the inaccessibility of seabirds at sea after they disperse from colonies. Because seabirds are long-lived animals that exhibit delayed maturity, pre-breeding birds represent significant proportions of populations (>50% in some; Klomp & Furness 1992) but are generally under-represented in studies of marine food webs. Non-breeders are also important for the long-term persistence of populations through compensatory recruitment of individuals following mortality of adults (Votier *et al.* 2008). To enhance our understanding of seabird foraging ecology and population responses to seasonal and environmental change, further studies are needed that incorporate all demographic components.

Stable isotope studies are currently the most tractable approach to studying the foraging ecology of non-breeding seabirds. Consumers incorporate the isotopic composition of their environment and the food they consume into their body tissues (Hobson *et al.* 1994, Hodum & Hobson 2000). Stable isotope values of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) can therefore be used to indicate a consumer's trophic position and foraging location, respectively (Cherel *et al.* 2007).

Dovekies *Alle alle* are small, planktivorous auks that occur over a range of ocean current regimes throughout the North Atlantic (Brown 1988, Stempniewicz 2001). They are the most abundant seabird in the North Atlantic (>80 million individuals; Egevang *et al.* 2003) and have an extensive breeding range in the Arctic, with Greenland colonies estimated in the tens of millions (Stempniewicz 2001, Egevang *et al.* 2003). During winter, Dovekies reside in Low Arctic and boreal waters in and around Newfoundland and Labrador and the northern North Sea, where they occupy upwelling areas along shelf edges (Brown 1988, Stone *et al.* 1995, Fifield *et al.* 2009) and offshore waters (Mosbech *et al.* 2012, Fort *et al.* 2012). Dovekies feed almost exclusively on zooplankton within 40 m of the surface (Harding *et al.* 2009). They are key avian consumers in the northwest Atlantic in terms of biomass and total consumption (Mehlum & Gabrielsen 1995, Karnovsky & Hunt 2002). Stable isotope studies are revealing new information about the seasonal trophic niche of Dovekies (Karnovsky *et al.* 2008, Fort *et al.* 2010) but have yet to include non-breeders. Here we examine temporal and age-related variability in the trophic position of Dovekies in the North Atlantic using stable-isotope analysis ($\delta^{15}N$ and $\delta^{13}C$) of different tissues collected from beached birds following an oil spill off Newfoundland in late November 2004 (see Robertson *et al.* 2006 for details of sampling procedures and age-sex composition).

Specifically, we compare isotopic signatures from the primary feathers of hatch-year birds, which were grown in summer (during parental provisioning), with those of adult and sub-adult birds, which were grown during fall moult. Feather keratin is metabolically inert after synthesis, and its isotopic composition reflects diet at the time when feathers are grown (e.g. Mizutani *et al.* 1992). Adult Dovekies undergo a primary moult (Pyle 2009) and become temporarily flightless for weeks during late August after departing the colony (Montevecchi & Stenhouse 2002, Mosbech *et al.* 2012). Sub-adults are not tied to the colony in summer and consequently may begin moulting earlier than adults (Bradstreet 1982). Based on these observations, we assumed that the feather samples (primary tips) of adult and sub-adult Dovekies represent their isotopic composition during the post-breeding moult period; this period likely begins after colony departure in early August (or earlier for sub-adults) and lasts approximately one month (Gaston & Jones 1998, Mosbech *et al.* 2012). Chicks typically hatch during late July and depart the colony accompanied by the male parent by August (Bradstreet 1982), at which time they have attained approximately 70% of their adult mass (Montevecchi & Stenhouse 2002). For hatch-year birds, primary feathers grown at the colony reflect chick diet when they are being provisioned by adults during July. Chicks also have a post-breeding moult; however, the primary feathers are not replaced at that time, as is the case with the older age classes (Stempniewicz 2001).

We also assess age-specific variation in isotopic signatures from pectoral muscle, which reflects isotopic composition over the preceding 4 to 6 weeks (Hobson & Clark 1992). Pectoral muscle samples obtained from Dovekies from 28 November to 4 December 2004 therefore reflect the early winter period (from mid-October through November) when Dovekies of all age classes have arrived or are en route to their wintering areas (Mosbech *et al.* 2012). Given the evidence for nitrogen enrichment in starving birds (Williams *et al*. 2007), tissues collected from oil spill victims may not always be suitable for dietary reconstructions if the victims have suffered starvation before death. Comparing body mass with wintering birds would be useful; however, this information is currently unavailable, and the body masses of oiled birds are likely unreliable due to the additional mass of oil. However, raw δ^{15}N values (muscle) of Dovekies in our sample were within the range of wintering adults reported by Fort *et al*. 2010 (11.4–13.4‰), including East Greenland birds that are known to winter mainly off Newfoundland (Stempniewicz 2001, Mosbech *et al.* 2012).

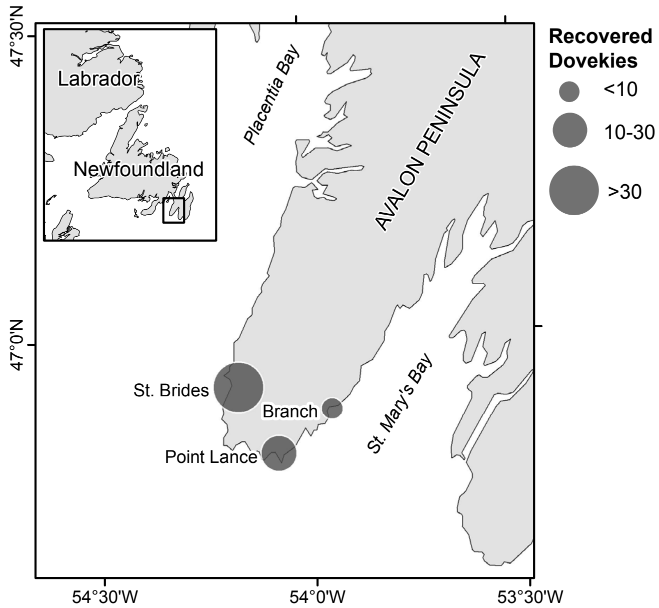

Fig. 1. Study area where samples of oiled Dovekies were collected from 28 November to 4 December 2004 on the southern Avalon Peninsula, Newfoundland.

METHODS

Study area and sample acquisition

Dovekie carcasses were collected from beaches on the southern shore of the Avalon Peninsula, Newfoundland (Fig. 1), from 28 November to 4 December 2004 (Robertson *et al.* 2006). After information on the degree of oiling, age and sex classification, and morphometric data were recorded for all individuals, the intact carcasses were made available by the Canadian Wildlife Service at Mount Pearl, Newfoundland, to sample primary feather and pectoral muscle for stable isotope analysis (n = 72). Sex and age classes were determined (n = 68 birds) using the criteria outlined by Bradstreet (1982): birds classed as adult were fully-grown with no bursa; sub-adults were morphologically smaller with bursa; and hatch-year birds (collected in the calendar year of hatch) were smaller than sub-adults, had poorly ossified intra-orbital skeletal ridges, as well as having a bursa. Feather samples were not analyzed for all Dovekies (n = 49) as oil compromised the integrity of some feathers.

Stable isotope tissue sampling and processing

Feathers were cleaned of surface contaminants using a 2:1 ratio solution of chloroform:methanol, air-dried under a fume hood and cut into fragments, avoiding the quill and shaft. Muscle was oven-dried to a constant mass at 60 °C. Dried samples were then coarsely ground and lipids were removed using a 2:1 ratio solution of chloroform:methanol. Muscle samples were ground when re-dried, and a 1 mg subsample of each tissue was weighed in a tin cup and crushed. Instruments were cleaned with acetone between samples to prevent cross-contamination. Isotope values were determined by the Stable Isotope Facility, University of California, Davis. Results

TABLE 1
Stable isotopic values from feathers of Dovekies (corrected for discrimination factors)

			Mean ± standard deviation	
Age	**Season**	**n**	**δ^{15}N (‰)**	**δ^{13}C (‰)**
Adult	Fall	28	+11.4 ± 0.3^{a}	-21.4 ± 1.0^{a}
Sub-adult	Fall	7	+9.2 ± 0.8^{b}	-21.3 ± 1.1^{a}
Hatch year	Summer	14	+9.3 ± 0.7^{b}	-19.5 ± 1.3^{b}
ANOVA			$F_{2,46}$ =99.8, $P < 0.001$	$F_{2,46}$ =13.5, $P < 0.01$

[a,b] Values in the same column not sharing a common superscript are significantly different (post-hoc Tukey HSD multiple comparison test, $P < 0.05$).

are reported in delta notation (δ) in parts per thousand (‰) relative to air (δ^{15}N) and PeeDee Belemnite (δ^{13}C). Replicate measurement of laboratory standards (two standards for every 12 unknowns) indicated measurement errors of approximately 0.16‰ for nitrogen and 0.03‰ for carbon.

Discrimination factors

Isotopic values of food fractionate when that food is integrated into the tissues of a consumer vary across species, tissues, diet, nutritional status, age and geographic area (Vanderklift & Ponsard 2003, Williams *et al.* 2007). To allow comparisons between hatch-year Dovekies during the summer—when they are still growing—with sub-adult and adult birds during fall moult, we apply average (±SD) discrimination factors for the feather tissues of fish-eating seabirds. For adult and sub-adult Dovekies, we used values reported by Becker *et al.* (2007) for adult Common Murres *Uria aalge*, a close relative of Dovekies: 3.7 ± 0.2 ‰ for δ^{15}N and 1.9 ± 0.3 ‰ for δ^{13}C. For hatch-year birds we used values reported by Hobson & Clark (1992) for 14 juvenile Ring-billed Gulls *Larus delawarensis* raised on a diet of fish: 3.0 ± 0.2‰ for δ^{15}N and 0.2 ± 1.3‰ for δ^{13}C. For early winter (pectoral muscle) we assume that hatch-year birds that have completed their growth and development (Montevecchi & Stenhouse 2001) are not physiologically different from sub-adult and adult birds. We therefore present the raw isotopic values, not corrected for fractionation, for all age classes in early winter.

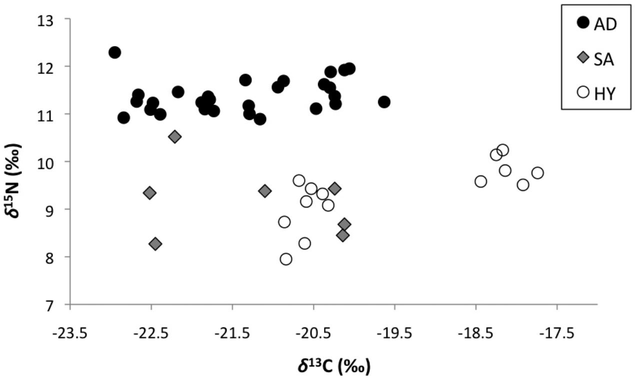

Fig. 2. Stable carbon δ^{13}C and nitrogen δ^{15}N isotope values, corrected for discrimination factors, of adult (AD), and sub-adult (SA) Dovekies grown in fall and of hatch-year (HY) Dovekies grown in summer. Data are isotopic values, corrected for discrimination factors, of individual birds (n = 49).

Data analyses

Analysis of variance (ANOVA) was used to examine age-specific differences in the δ^{15}N and δ^{13}C values of Dovekies within each time period followed by post-hoc range tests (Tukey's multiple comparison test for unequal sample sizes) for statistically significant outcomes. All statistics were computed using Cran R. The statistical significance for all analyses was assumed at $P < 0.05$. We present the isotopic signatures of individual birds in addition to the mean ± SD isotopic values for each age class within the distinct time periods.

RESULTS

There were no significant sex differences in δ^{15}N ($F_{1,99} = 0.2$; $P = 0.6$) or δ^{13}C ($F_{1,99} = 0.01$; $P = 0.9$) isotopic values (uncorrected). The δ^{15}N values of adult males (+15.1 ± 0.4‰) that attend their offspring at sea during the post-breeding period were not significantly different ($F_{1,25} = 0.6$; $P = 0.5$) than independent post-breeding females (+15.0 ± 0.4‰). Nor did we find any sex differences ($F_{1,25} = 0.4$; $P = 0.6$) in the post-breeding δ^{13}C values of adult males (-19.6 ± 0.9‰) and females (-19.3 ± 1.1‰). Therefore, sexes were pooled in all other analyses.

Age-specific variation in trophic niche

There was significant age-specific variability in the mean δ^{15}N values (corrected) from Dovekie feathers (Table 1). Mean δ^{15}N values of adult Dovekies during fall were significantly higher ($F_{2,\,46} = 99.8$, $P < 0.001$) than those of sub-adults over the same period and of hatch-year birds during summer, when they are provisioned by parents at the colony (Table 1). Mean δ^{15}N values of sub-adult birds in fall were not different from hatch-year birds in summer (Table 1, Fig. 2). Mean δ^{13}C values of adults and sub-adults in fall overlapped and were significantly different from hatch-year birds in summer ($F_{2,\,46} = 13.5$, $P < 0.01$). The δ^{13}C values of individual hatch-year birds were separated into two distinct groups (Fig. 2). Birds in the more carbon-enriched group (mean -17.9 ± 0.2‰) had significantly higher ($F_{1,12} = 11.9$, $P = 0.004$) δ^{15}N values (+9.8 ± 0.1‰) than birds in the more carbon-depleted group (-20.4 ± 0.2‰, mean δ^{13}C and +8.9 ± 0.2‰, mean δ^{15}N values).

In early winter, there was strong overlap in the δ^{15}N and δ^{13}C values of Dovekies (Table 2, Fig. 3) with no statistical differences between age classes for δ^{15}N ($F_{2,65} = 0.0$, $P < 0.9$) or δ^{13}C ($F_{2,65} = 2.3$, $P < 0.1$; Fig. 3). Higher variation in δ^{15}N values of sub-adults indicates a more variable diet relative to adults and hatch-year birds, although sample sizes were also relatively small.

TABLE 2
Stable isotopic values from muscle (uncorrected) of Dovekies

			Mean ± standard deviation	
Age	**Season**	**n**	**δ^{15}N (‰)**	**δ^{13}C (‰)**
Adult	Early winter[a]	41	+12.1 ± 0.3	-19.9 ± 0.3
Sub-adult	Early winter[a]	7	+12.2 ± 0.8	-19.9 ± 0.3
Hatch year	Early winter[a]	20	+12.2 ± 0.3	-20.1 ± 0.4
ANOVA			$F_{2,65} = 0.0$, $P < 0.9$	$F_{2,65} = 2.3$, $P = 0.1$

[a] Approximately 4 to 6 weeks before collection from 28 November to 4 December 2004.

DISCUSSION

We document age-related variation in the trophic position and relative foraging locations of Dovekies on their breeding and moulting grounds in the Arctic and extensive overlap in winter, with reliance on a common prey. Interrogation of seasonal shifts in trophic position within and across age classes was, unfortunately, outside the scope of this study: reliable tissue-discrimination factors for planktivores were lacking and baseline marine isoscapes for the North Atlantic were poorly resolved. Improved resolution of tissue-specific discrimination factors for different species, age classes and foraging guilds, particularly planktivores, and fine-scale information on marine isoscapes, are needed to advance our use of stable isotopes to answer questions regarding the seasonal foraging ecology of migratory seabirds (Bond & Jones 2009).

Isotopic niche of Dovekies during breeding and moult

Dovekies exhibited age-related variation in the trophic position and relative foraging locations on their breeding and moulting grounds in the Arctic. Dovekie chick diet has been well studied across their range, and is typically composed of calanoid copepods; there are regional differences in species composition and size associated with distinct oceanographic regimes (Bradstreet 1982, Karnovsky *et al.* 2003, Jakubas *et al.* 2007). Here, δ^{13}C values of individual hatch-year birds fell into two distinct groups with significantly different δ^{15}N values. Fort *et al*. (2010) documented differences in the isotopic signatures of adult Dovekies from the East Greenland and Spitsbergen colonies; the Arctic-influenced Greenland birds had higher δ^{15}N and signatures relative to the Atlantic-influenced Spitsbergen colonies. Presumably this pattern reflected differences in the availability of *Calanus* species within the different oceanographic regimes. The observed isotopic separation of hatch-year Dovekies in this study, although limited by sample size, could similarly reflect differences in prey availability within contrasting oceanograhic regimes (Karnovsky *et al.* 2011).

Adult Dovekies during fall moult had the highest δ^{15}N values of any age class or period. Previous isotopic studies of adult Dovekies support this finding. The highest trophic position of the annual cycle appears during fall moult, explained as a dietary shift from calanoid copepods during the breeding season to a mixed diet of amphipods (e.g. *Themisto libellula, Apherusa glacialis*) and fish (e.g. Arctic Cod *Boreogadus saida*) in fall (Karnovsky & Hunt 2002, Karnovsky *et al.* 2008, Fort *et al.* 2010). Higher relative occurrences of amphipods and fish in the stomachs of Dovekies in fall provide further evidence that Dovekies target higher-trophic-level prey during fall moult (Bradstreet 1982, Karnovsky *et al.* 2008). Information from tracking data, ship-based surveys and ringing recoveries indicate that Dovekies concentrate near sea-ice-covered waters during moult (Bradstreet 1982, Stempniewicz 2001, Mosbech *et al.* 2012). The relatively high δ^{15}N values of adult Dovekies observed here during fall moult could reflect a diet of ice-associated Arctic Cod, which have among the highest δ^{15}N of the prey species targeted by Dovekies (Hobson & Welsh 1992, Moller 2006). High-quality prey may be a neccessity for post-breeding adults regardless of where they moult, given the need to recover the high energetic costs incurred during chick-rearing (Harding *et al.* 2009) and the need to increase energy stores in preparation for winter shortages.

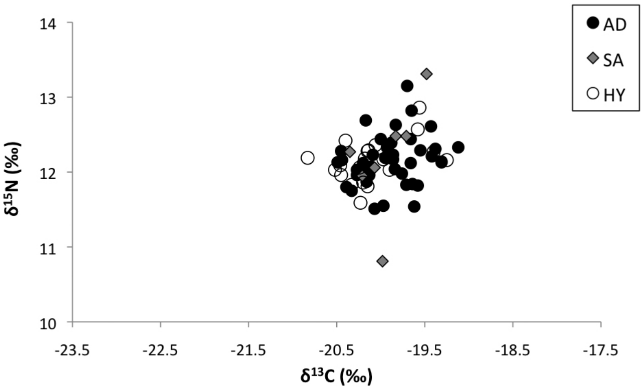

Fig. 3. Stable carbon δ^{13}C and nitrogen δ^{15}N isotope values, uncorrected, of pectoral muscle from adult (AD), sub-adult (SA) and hatch-year (HY) Dovekies in early winter. Data are isotopic values, uncorrected, of individual birds.

While sub-adult Dovekies occupied a similar range of δ^{13}C values to adults, significantly lower δ^{15}N values could indicate either differences in the location of moult and associated prey base or differences in the timing of moult. For example, although *Calanus* copepods in the Greenland Sea descend to depth in late summer, the total copepod biomass in the upper 60 m of the water column remains the same because of the concurrent seasonal increase in the biomass of smaller, non-*Calanus* copepods such as *Pseudocalanus* spp., *Oncaea* spp. and *Oithona* spp. (Moller *et al.* 2006). Sub-adult Dovekies may take advantage of an abundant food source, while post-breeding adult birds that incur high energetic costs during chick-rearing (Harding *et al.* 2009) may seek out higher-trophic-level prey. Alternatively, sub-adults, which are not tied to the breeding colony, likely have greater flexibility in the timing of moult. If sub-adults moult earlier in the season, they may take advantage of the seasonal abundance of calanoid copepods, possibly explaining the observed overlap in the δ^{15}N values of hatch-year and sub-adult Dovekies.

Isotopic niche of Dovekies during winter

In early winter, there was strong overlap of all age classes in relatively carbon-depleted, offshore waters and a corresponding overlap in δ^{15}N values. The latter overlaps were likely associated with consumption of *C. finmarchicus,* a ubiquitous copepod in Atlantic waters that is relatively abundant in near-surface waters on the Newfoundland–Labrador shelf in winter (Planque *et al*. 1997; Fort *et al*. 2010). Fort *et al.* (2012) showed a strong, positive correlation between *C. finmarchicus* abundance and the density of adult Dovekies in an offshore region of the Newfoundland shelf during winter, when other calanoid copepod species (*C. hyperboreus* and *C. glacialis*) are unavailable. It is therefore possible that multiple populations and age classes take advantage of this important area during winter, when productivity is lower elsewhere and daily food requirements are high in cold and harsh weather (Fort *et al*. 2009).

Conservation implications

Profound and rapid changes in ocean circulation and the hydrologic regimes in Arctic regions (IPCC 2007, Hurrell 2003) are triggering dramatic shifts in the phenology, biology and distributions of North Atlantic meso-zooplankton communities (Beaugrand 2009, Beaugrand *et al.* 2002). These changes could significantly alter the foraging environments of Dovekies and other planktivores. Changes in hydrological regimes at lower latitudes in the western North Atlantic (Greene & Pershing 2007) could similarly disrupt the foraging environment of Dovekies through shifts in the distribution and seasonal timing of meso-zooplankton. While there is evidence that reproductive and population consequences of Dovekies may be partly mediated by flexible foraging strategies during the breeding season (Grémillet *et al.* 2012, Karnovsky *et al.* 2011, Kwasniewski *et al.* 2010, Welcker *et al.* 2009), further studies of the seasonal foraging ecology of all age classes outside the breeding season are warranted to predict how populations will cope with predicted, climate-mediated changes in the North Atlantic.

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