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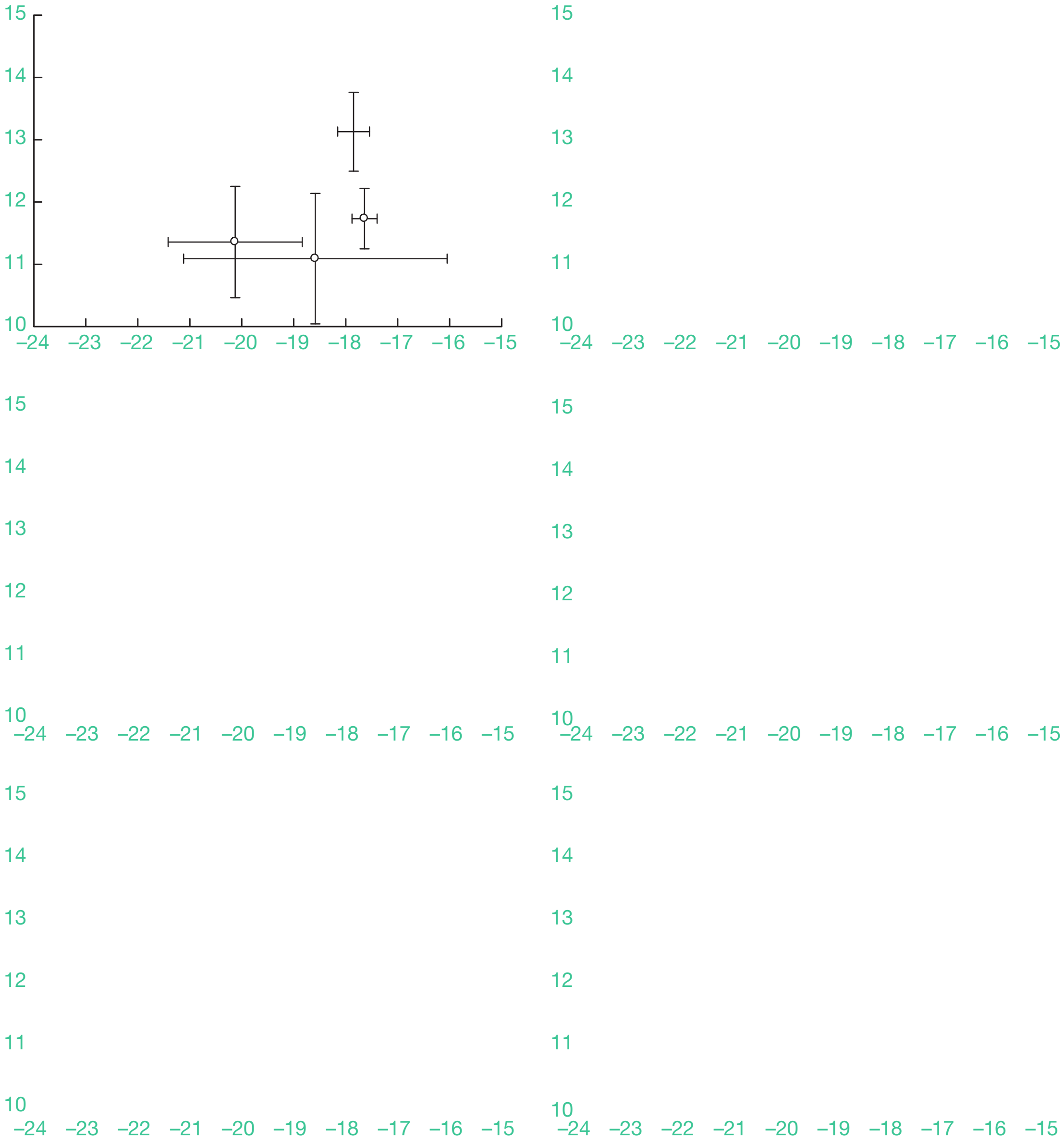
INTRODUCTION

ation found among colonies (Forero et al. 2002), subcolonies (Hipfner et al. 2007), foraging trip duration (Cherel et al. 2005), age (Hodum & Hobson 2000) and gender (Forero et al. 2005).

To date, however, few studies based on SIA have examined the extent to which marine birds alter their foraging behaviour across discrete breeding stages (but see Quillfeldt et al. 2005). Flexible foraging behaviour could be an important mechanism by which seabirds meet the unique nutritional demands of each stage and, within the larger ecological context set out by the seasonal progression of events, in the marine environment (Levinton 2001). While several SIA studies have documented the trophic relationships among the component members of seabird communities (Hobson et al. 1994, Forero et al. 2004), few have considered vials and frozen at –10°C. Squid were processed in the same way, with muscle removed from the mantle.

Seabird blood samples: Blood (0.5 to 1.0 ml) was drawn from the brachial veins of adults of each of the 5 species caught by a variety of standard methods (in nets and noose carpets, or with noose poles) during each of the prelaying, incubation and provisioning periods. Adults were released immediately after being sampled. Blood samples (ca. 0.5 ml) were collected from nestlings at approximately 3 wk of age. By that age, nestlings in all species weighed about 3 to 6 times their hatching mass, and elements derived from eggs should have been highly diluted by those in prey delivered by adults and should represent a very small fraction of the elemental composition of blood. Blood was placed into vials and frozen at –10°C.

Stable isotope analyses. ***Sample processing***: All samples were shipped frozen to the Environment Canada laboratory of KAH. Blood and prey samples were freeze-dried and powdered. Lipids were extracted from prey samples by successively rinsing in a 2:1 chloroform:methanol solution, then air-drying under a fume hood. Stable-carbon and -nitrogen isotope assays were performed on 1 mg sub-samples of powdered material at the stable isotope facility of the Department of Soil Science, University of Saskatchewan. Samples were first loaded into tin cups and combusted in a Robo-Prep elemental analyzer at 1200°C. The resultant CO_2 and N_2



nestlings late in the breeding season, after the more zooplanktivorous Cassin's auklet had completed its breeding season (Fig. 2). In contrast, there was no seasonal shift towards either more inshore or offshore habitats across the community. A detailed statistical analysis is precluded by the many possible factors (species, stages and tissues) and interactions.

We sampled blood from nestlings of all 4 of these late-season, high-trophic level species within a relatively narrow time period (<10 d; Fig. 2) and found highly significant differences among them in their combined δ^{15}N and δ^{13}C values (Wilks' lambda = 0.08, $F_{2,3,27} = 40.45$, $p < 0.0001$). Overlap only appeared between nestlings of the 2 puffin species, rhinoceros auklet and tufted puffins.

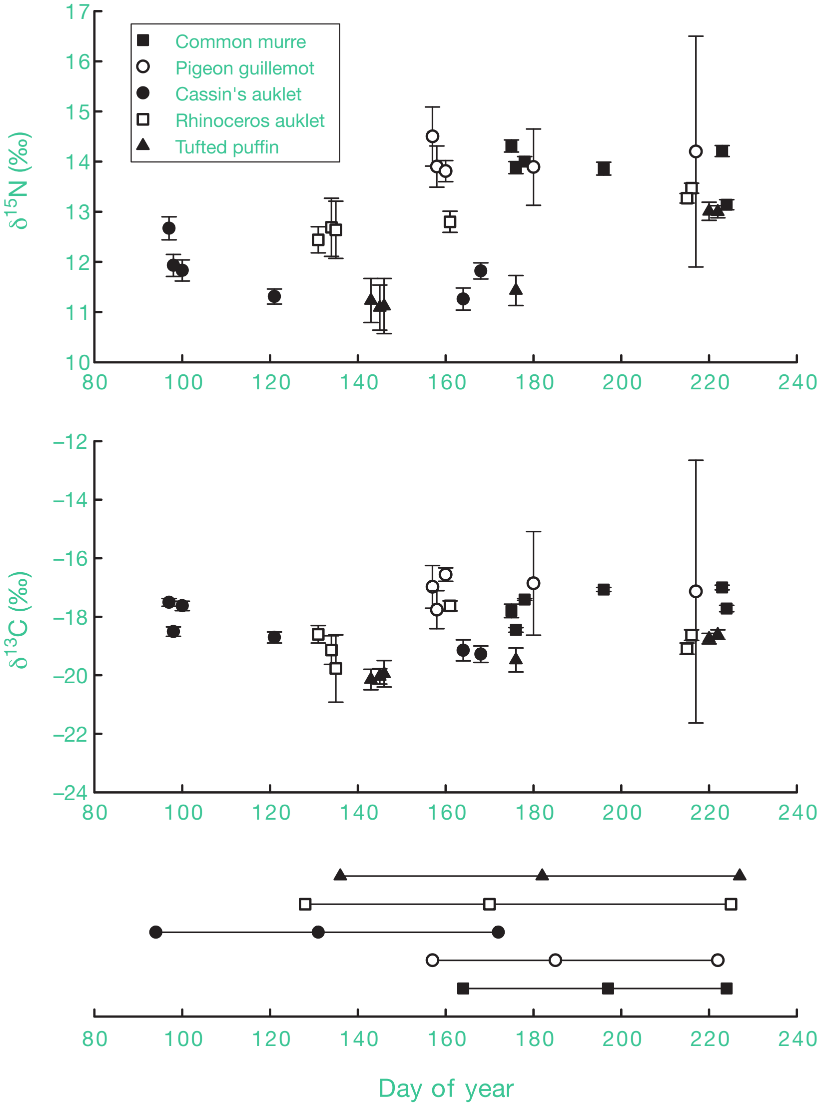


Fig. 2. Diet-tissue discrimination-corrected stable isotopic values ($\delta^{15}N$, upper panel; $\delta^{13}C$, lower panel) of tissues from all 5 alcid species (for taxonomic names see Table 1) in relation to the day of the year on which they were collected. Data points below panels are median dates of egg-laying, hatching and fledging for the 5 alcids in 2002; lines thus represent the incubation periods and the offspring-provisioning periods

DISCUSSION

We found that combined $\delta^{15}N$ and $\delta^{13}C$ values differed significantly among breeding stages in adult common murres *Uria aalge*, Cassin's auklets *Ptychoramphus aleuticus*, rhinoceros auklets *Cerorhinca monocerata* and tufted puffins *Fratercula cirrhata*. These species demonstrably altered their diets and habitats through the season. Diets of provisioning adults differed from those fed to nestlings they provisioned in all species except the tufted puffin. There was no pattern in the trophic and habitat shifting common to all species, but the alcid community at Triangle Island as a whole exhibited a seasonal trophic shift, from low to mid-trophic level feeding early (zooplankton and mixed zooplankton and fish diets), to mid- to high trophic level feeding late (fish diets), though with no corresponding shift in foraging habitat.

Our field-derived estimates of diet-tissue $\delta^{15}N$ discrimination factors were +1.5‰ for Cassin's auklets and +0.6‰ for rhinoceros auklets, values considerably smaller than the 2 to 4‰ typically reported for birds (Dalerum & Angerbjörn 2005). There is increasing awareness that many factors affect isotopic diet–tissue discrimination factors (Quillfeldt et al. 2008). As such, a single discrimination factor applied to all seabirds of both age groups is almost certainly unrealistic. Nonetheless, we consider our approach using contemporary data of diet and blood isotope values at our study site to be the most appropriate option available to us and certainly better than application of 'textbook' values.

Species-level analyses

Common murre and pigeon guillemot

At all breeding stages, common murres *Uria aalge* and pigeon guillemots *Cepphus columba* fed on high trophic level prey (fish) captured in inshore or benthic habitats. They were the only species to display such general consistency in diet and foraging habitat. Adult common murres provisioned nestlings with prey from a lower mean trophic level than they ate themselves, although this pattern is not universal in murres. Of note, diets fed to common murre nestlings inferred from SIA corresponded quite well with observed diets at Triangle Island, which consist mainly (70 to 80%) of adult Pacific sandlance and juvenile rockfish (Hipfner & Greenwood 2008). Likewise, isotopic values in pigeon guillemot nestlings at Triangle Island were consistent with those from diets at the Farallon Islands, California, which consist of juvenile rockfish and benthic fish (Ainley & Boekelheide 1990).

benthic habitats. The upward trophic shifting appears to be a regular occurrence in this species at Triangle Island (Hipfner et al. 2007).

Tufted puffin was the only species of the 5 alcid species in our study to show close correspondence in δ^{15}N and δ^{13}C values in adults and nestlings. Interestingly, Piatt & Kitaysky (2002) concluded that squid were very important in adult, but not in nestling, diets across Alaska, while Baird (1991) proposed that adult puffins delivered larger, more energy-rich items to nestlings than they ate themselves. Likewise, Hobson et al. (1994) placed adult tufted puffins at a relatively low trophic level during the breeding season despite evidence that nestlings were fed fish. The δ^{15}N values in nestlings were consistent with their observed diets at Triangle, which consisted largely of Pacific sandlance and juvenile rockfish (Vermeer 1979).

Community-level stable isotopic analyses

Our alcid community exhibited a clear temporal trophic shift: early in the season (March through May), foraging was directed at low (by tufted puffin) or low to mid- (by Cassin's auklet, rhinoceros auklet) trophic level prey, but later (June through August) at mid- to high trophic level prey (by common murre, pigeon guillemot, rhinoceros auklet and tufted puffin). Even in the more zooplanktivorous Cassin's auklets, fish often becomes important in nestling diets late in their breeding season (June and July; Ainley & Boekelheide 1990). However, the community shift in trophic level occurred without a corresponding shift towards either more inshore or offshore feeding, consistent with the lack of strong association between δ^{15}N and δ^{13}C values in prey items. This suggests that any trophic level increase in δ^{13}C values was swamped by the much larger spatial effect of inshore (benthic) versus offshore (pelagic) signals.

The tendency to converge on fish feeding late in the breeding season occurs in other alcid-based seabird communities (Ainley & Boekelheide 1990, Hatch & Hatch 1990). Our study complements those studies because it includes concurrent isotopic measurements of adult and nestling trophic position, which indicate that both nestlings and adults fed on high trophic level prey late in the breeding season. That general pattern: relying on lower trophic levels early and higher trophic levels late, likely mirrors the temporal flow of energy through the marine ecosystem, whereby the pulse in lower trophic level biomass progressively results in later pulses in higher trophic level biomass (Levinton 2001).

A high degree of trophic overlap has been reported in other seabird communities (Forero et al. 2004). Given that many species in these communities time their breeding so that they raise nestlings on the same