

This article was downloaded by: [Simon Fraser University]

On: 18 September 2014, At: 14:28

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



## Marine Biology Research

Publication details, including instructions for authors and subscription information:  
<http://www.tandfonline.com/loi/smar20>

### Seasonal variation in the foraging ecology of a zooplanktivorous seabird assessed with stable isotope analysis

J. Mark Hipfner<sup>a</sup>, Laura Mcfarlane-Tranquilla<sup>b</sup>, Brianne Addison<sup>c</sup> & Keith A. Hobson<sup>d</sup>

<sup>a</sup> Wildlife Research Division, Environment Canada, Delta, British Columbia, Canada

<sup>b</sup> Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada

<sup>c</sup> School of Science and Health, University of Western Sydney, Penrith, Australia

<sup>d</sup> Wildlife Research Division, Environment Canada, Saskatoon, Saskatchewan, Canada

Published online: 14 Nov 2013.



[Click for updates](#)

To cite this article: J. Mark Hipfner, Laura Mcfarlane-Tranquilla, Brianne Addison & Keith A. Hobson (2014) Seasonal variation in the foraging ecology of a zooplanktivorous seabird assessed with stable isotope analysis, *Marine Biology Research*, 10:4, 383-390, DOI: [10.1080/17451000.2013.814791](https://doi.org/10.1080/17451000.2013.814791)

To link to this article: <http://dx.doi.org/10.1080/17451000.2013.814791>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>



ORIGINAL ARTICLE

## Seasonal variation in the foraging ecology of a zooplanktivorous seabird assessed with stable isotope analysis

J. MARK HIPFNER<sup>1\*</sup>, LAURA MCFARLANE-TRANQUILLA<sup>2</sup>, BRIANNE ADDISON<sup>3</sup> & KEITH A. HOBSON<sup>4</sup>

<sup>1</sup>Wildlife Research Division, Environment Canada, Delta, British Columbia, Canada, <sup>2</sup>Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada, <sup>3</sup>School of Science and Health, University of Western Sydney, Penrith, Australia, and <sup>4</sup>Wildlife Research Division, Environment Canada, Saskatoon, Saskatchewan, Canada

### Abstract

We used  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analyses on blood drawn from zooplanktivorous Cassin's auklet (*Ptychoramphus aleuticus* Pallas, 1811) on Triangle Island, British Columbia, over four years to address two questions: (1) do these seabirds systematically alter their trophic level and foraging habitat from one breeding stage to the next; and (2) do auklets select prey at the same trophic level and from the same foraging habitat to self-feed and provision offspring? Adult trophic level (inferred from  $\delta^{15}\text{N}$  values) tended to be higher prior to egg-laying than during incubation, perhaps reflecting an abundant zooplankton biomass in early spring. Season-long declines in  $\delta^{13}\text{C}$  values suggested that the auklets foraged on the continental shelf early in the season, but thereafter increasingly used habitats seaward of the continental shelf-break to obtain *Neocalanus cristatus* copepodites. Similarity in the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of provisioning adults and nestlings suggested that adults consumed the same prey from those oceanic habitats to both self-feed and to provision offspring at the nest, a behaviour that may save time and energy. The results of this study show the dynamic nature of seabird foraging ecology and the utility of stable isotope analysis for assessing seasonal variation in the foraging ecology of oceanic species.

**Key words:** *Breeding stage, carbon-13, Cassin's auklet, central-place foraging, nitrogen-15, Ptychoramphus aleuticus, provisioning, self-feeding, stable isotope analysis*

### Introduction

Animals strategically alter their foraging behaviour in response to external factors such as food availability, predators and parasites (Stephens et al. 2007). In the case of colonial seabirds, fluctuations in prey availability influence the behaviour and physiology of individuals, and ultimately their population processes (Kitaysky et al. 2010). Nutritional constraints are likely to be evident during the breeding season, when as central-place foragers (Orians & Pearson 1979), individuals regularly commute to and from feeding areas that can be tens to hundreds of kilometres from the colony (Pichgru et al. 2010). The long distances travelled are ultimately linked to the long breeding seasons and low reproductive rates that characterize the life histories of oceanic birds (Ashmole 1971). Because high adult survival rates further characterize

seabird life histories (Lack 1968), individuals that adapt effectively to a wide range of feeding conditions will achieve maximum fitness (Lescroël et al. 2010).

A further challenge arises because individuals need to forage for specific prey types to meet the nutritional demands of successive breeding stages, through a period of several months or more when oceanographic conditions such as sea-surface temperature (Ito et al. 2009), chlorophyll-*a* concentrations (Wolf et al. 2009) and the abundance of prey can fluctuate considerably. For example, females must forage to satisfy specific micronutrient requirements to produce eggs (Blount et al. 2004), while at the onset of provisioning, parents must begin to search for prey suitable for loading to deliver back to offspring at the nest site, and with which to feed themselves. Because the criteria that govern the selection of prey for the two tasks can differ, a single prey type might not be suitable

\*Correspondence: J. Mark Hipfner, Wildlife Research Division, Environment Canada, RR#1 5421 Robertson Road, Delta, British Columbia, Canada V4K 3N2. E-mail: [mark.hipfner@ec.gc.ca](mailto:mark.hipfner@ec.gc.ca)

for both tasks, and if it is not, parents will need to forage sequentially to satisfy the two requirements (Ydenberg & Davies 2010).

The manner in which the foraging of oceanic birds is tailored to the demands of successive breeding stages remains poorly studied. We collected blood from breeding adults of a colonial seabird, the Cassin's auklet (*Ptychoramphus aleuticus* Pallas, 1811), during the prelaying, incubation and provisioning periods of four successive breeding seasons (2002–2005). Blood was also collected from nestlings. We then performed  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  analyses on the blood samples to address two questions: (1) do Cassin's auklets systematically alter trophic level (inferred from  $\delta^{15}\text{N}$  values) and foraging habitat (inferred from  $\delta^{13}\text{C}$  values) from one breeding stage to the next; and (2) do auklet parents tend to select prey at the same trophic level and in the same foraging habitats to satisfy the overlapping demands of self-feeding and provisioning?

Cassin's auklets lay a single egg, a life-history trait that is characteristic of oceanic birds (Lack 1968), and have a long breeding season (~80 days from egg-laying to fledging) compared to their closest relatives, the *Aethia* auklets (Hipfner et al. 2010a). Like the other auklets, Cassin's auklet is adapted for zooplanktivory, with specialized mouth parts and a gular pouch in which prey are stored for delivery back to offspring in the nesting burrow (Bédard 1969). The two parents share incubation duties equally, and each usually delivers food to offspring just once per night (Adams et al. 2004). At our study site on Triangle Island, British Columbia, Canada, provisioning parents forage up to 110 km from the colony (McFarlane-Tranquilla et al. 2005).

At Triangle Island, oceanographic conditions strongly affect the auklets' breeding phenology, with the median laying date falling earlier in years with stronger primary production in the spring, and also their breeding success, which is higher in years with lower sea-surface height, when the water column holds less heat (Wolf et al. 2009). During the period of this study, Cassin's auklets bred earlier in the two years of higher primary production, 2002 and 2004, than in 2003 or 2005 (Table I). Breeding was very late and unsuccessful in 2005, during an anomalous atmospheric blocking event (Sydeman et al. 2006).

Effects of oceanography on the birds' breeding operate via the food web (Hipfner 2009), and in the four years of this study, nestling auklets received twice as much of the subarctic copepod *Neocalanus cristatus* Krøyer, 1848 in their diets in 2002 and 2004 than in 2003 and 2005 (Figure 1). Three species of euphausiids (*Thysanoessa spinifera* Holmes, 1900, *T. inspinata* Nemoto, 1963 and *Euphausia pacifica* Hansen, 1911) largely made up the difference in 2003, but diets included unusually large amounts of rarer prey types in 2005. Importantly, rates of offspring growth and survival increase very strongly with the amount of *N. cristatus* in their diets (Hipfner 2008).

## Materials and methods

### Study area

Field work was conducted on Triangle Island, British Columbia, Canada (50°52'N, 129°05'W) from late March to early July of 2002 to 2005. Triangle Island supports the largest breeding colony of Cassin's auklets in the world (Rodway 1990).

### Field sampling

Ten to 17 breeding Cassin's auklets were caught per year, in barrier nets erected between PVC poles 4 m in length in a fixed location during the prelaying (late March and early April), incubation (late April and early May), and provisioning (mid-June) periods. We assumed that all birds caught before egg-laying would breed in that year, based on observations on other auk species (Gaston 1990); during incubation and provisioning, we took blood samples only from individuals that had full or refeathering brood patches. No bird was sampled more than once during this study. Blood (0.5–1.0 ml) was drawn from the brachial vein and stored frozen at  $-10^{\circ}\text{C}$  in Eppendorf tubes. Consecutive sampling sessions were separated by at least 25 days to allow for turnover of isotopes in blood; expected half-lives for stable isotopes in blood are ~14 days for a 175 g Cassin's auklet (Carleton & Martinez del Rio 2005). Blood samples (c. 0.5 ml) were collected from 7 to 17 nestlings per year, which we extracted from earth burrows at 4–6 weeks of age. By then, elements derived from eggs should have been highly diluted by

Table I. Timing of laying and measures of breeding success for Cassin's auklets at Triangle Island, British Columbia, in 2002–2005 (from Hipfner et al. 2010b).

Year	Median laying date	No. of eggs	No. hatched (%)	No. fledged (%)	% Breeding success	Fledging mass (mean $\pm$ SD, g)
2002	31–4 Apr	63	41 (65)	38 (93)	60	160 $\pm$ 19
2003	9–13 Apr	45	31 (69)	27 (87)	60	146 $\pm$ 21
2004	2–6 Apr	70	56 (80)	49 (88)	70	166 $\pm$ 18
2005	20–24 Apr	63	42 (67)	5 (12)	8	120 $\pm$ 16

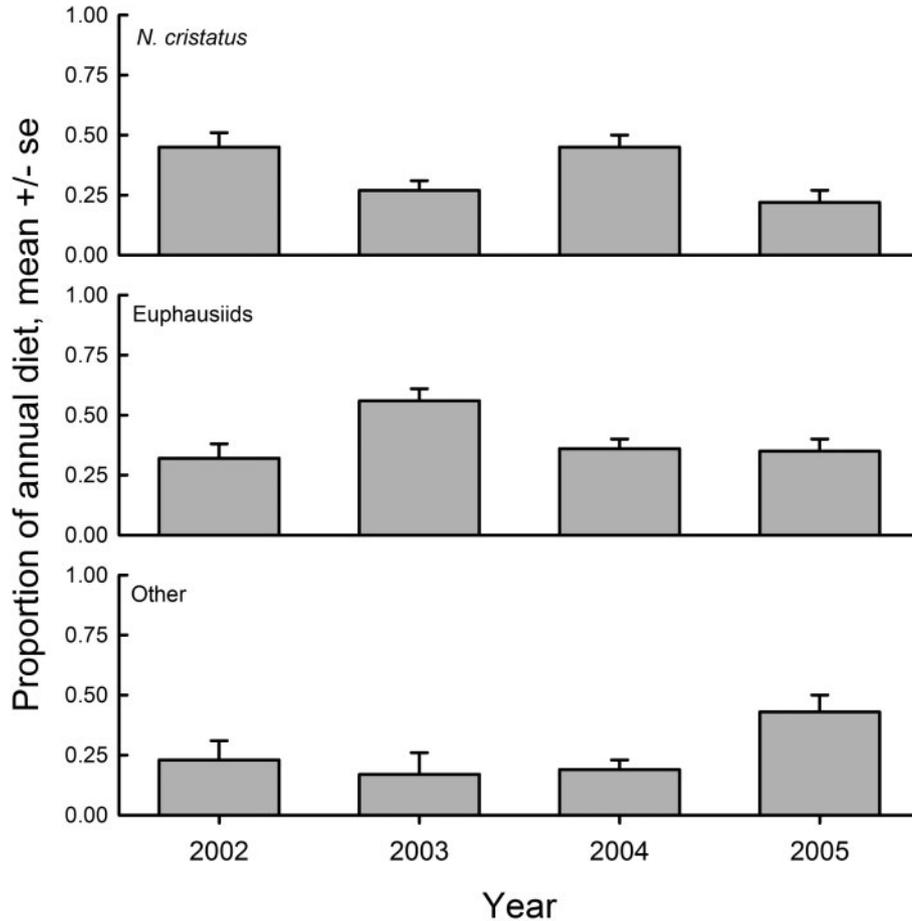


Figure 1. Annual percentage biomass of major prey types (*Neocalanus cristatus*, euphausiids and other) fed to Cassin's auklet nestlings in the period from 18 May to 27 June in each year from 2002 to 2005 on Triangle Island.

those in prey, as the avian yolk sac is generally used up by 5 days post-hatching (Romanoff 1944).

#### Stable isotope analyses

Blood samples were freeze-dried and powdered, and lipids extracted 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 subsamples of powdered material at the Department of Soil Science, University of Saskatchewan. Samples were first loaded into tin capsules and combusted in a Robo-Prep elemental analyser at 1200°C. The resultant CO<sub>2</sub> and N<sub>2</sub> gases were separated and analysed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer, with every fifth sample separated by two (albumin) laboratory standards. Results were reported in delta notation in parts per thousand (‰) relative to Air ( $\delta^{15}\text{N}$ ) and VPDB ( $\delta^{13}\text{C}$ ). Based on replicate measurements of albumin standards, measurement precision (SD) for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values was estimated to be  $\pm 0.1\text{‰}$  and  $\pm 0.3\text{‰}$ , respectively.

#### Statistical analysis

To test whether the foraging behaviour of Cassin's auklets varied systematically from one breeding stage to the next, we built a set of three candidate models for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  measurements: (1) a null model; (2) Year (1–4); and (3) Year + Stage (1–3), with Year and Stage as categorical variables. The dataset for these ANOVA models included  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for 172 adults. To address whether provisioning adults tended to feed themselves and their offspring with prey from the same trophic level taken in the same habitats, we built a set of three candidate models for both isotopes: (1) a null model; (2) Year (1–4); and (3) Year + Age Class (2), as categorical variable. The data set for these models included isotope values for 55 provisioning-stage adults and 47 nestlings. We expected  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values to vary among years, largely due to unexplained variation in the prey base (Rau et al. 2003). Our research questions thus focus on whether the Stage and Age Class terms are additive to the Year term. All analyses were run with the Fit Model function of JMP (SAS Institute).

All models within each candidate set were ranked using Akaike's information criterion corrected for

Table II. Results of AIC model selection to explain variation in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Cassin's auklets (1) during three breeding stages (prelaying, incubation, provisioning) and (2) provisioning adults and nestlings, in four years.

Comparison	Supported models	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		$R^2$	$\Delta\text{AIC}_c$	$\text{AIC}_{c,w}$	$k$	$R^2$	$\Delta\text{AIC}_c$	$\text{AIC}_{c,w}$	$k$
1. Adults at three stages	Year + Stage	0.58	0.00	1.00	6	0.76	0.00	1.00	6
	Year	0.51	19.60	0.00	4	0.53	109.42	0.00	4
	Null	–	137.15	0.00	1	–	240.24	0.00	1
2. Adults vs. nestlings	Year	0.66	0.00	0.54	4	0.48	0.00	0.75	4
	Year + Age	0.68	0.31	0.46	5	0.47	2.24	0.25	5
	Null	–	107.97	0.00	–	–	61.60	0.00	1

small sample size ( $\text{AIC}_c$ ), based on the difference between each model's  $\text{AIC}_c$  and the lowest  $\text{AIC}_c$  from among the candidate set. In addition to selecting a single most parsimonious model ( $\Delta\text{AIC}_c = 0.0$ ), any models with  $\Delta\text{AIC}_c$  scores  $\leq 10.0$  can be considered to have received support (Burnham & Anderson 2002). We also report  $\text{AIC}_{c,w}$ , which measures the weight of evidence in favour of a particular model on a scale from 0 to 1, given the data and candidate model set.

## Results

### *Are trophic level and foraging habitat adjusted to breeding stage?*

The top-ranked model for  $\delta^{15}\text{N}$  values in the blood of adult Cassin's auklets included the Stage term in addition to Year. That model had good explanatory power, and it received all of the AIC model weight (Table I). Mean  $\delta^{15}\text{N}$  values were higher prior to laying than during incubation, with an overall seasonal range of variation of about 0.4‰ (Table III), although that pattern was not repeated in all four years (Figure 1). Overall,  $\delta^{15}\text{N}$  values were lower in 2002 and 2004 than in 2003 and 2005 (Table III).

For  $\delta^{13}\text{C}$ , the top-ranked model again included the Stage term in addition to Year, had strong explanatory power, and received all of the AIC model weight (Table II). Mean  $\delta^{13}\text{C}$  values declined from the prelaying to incubation periods, and declined again from the incubation to provisioning periods (Table III). That occurred in all four years, with the season-long decline in  $\delta^{13}\text{C}$  values averaging  $\sim 1.6\text{‰}$  (Figure 1). Overall,  $\delta^{13}\text{C}$  values were lowest in 2005, moderate in 2002, and highest in 2003 and 2004 (Table III). The  $\delta^{13}\text{C}$  values were lowest in 2005, moderate in 2002, and highest in 2003 and 2004 (Table III).

### *Do adults self-feed and load from similar trophic levels and habitats?*

The top-ranked model for  $\delta^{15}\text{N}$  values in self-feeding adults and nestlings included Year but not Age Class, and had good explanatory power. The model that included Year and Age Class received nearly equal support (Table II). Mean  $\delta^{15}\text{N}$  values were higher in nestlings than in adults in all four years (Figure 1), although the 95% confidence intervals around the parameter estimates bounded zero (Table III).

The top-ranked model for  $\delta^{13}\text{C}$  also included Year but not Age Class (Table II). While the model that

Table III. Parameter estimates (mean, 95% confidence bounds) for the Breeding Stage and Age Class terms for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in Cassin's auklet adults during three breeding stages and in adult provisioners and their nestlings in four years. In the case of the adult vs. nestling comparison, note that Age Class was not included in the top model for either isotope, and that the 95% confidence intervals substantially bound zero.

Comparison	Top model	Parameter	$\delta^{15}\text{N}$		$\delta^{13}\text{C}$	
			Mean	(95% CI)	Mean	(95% CI)
1. Adults at three stages	Year + Stage	Prelaying	0.15	(0.09)	0.79	(0.09)
		Incubation	–0.21	(0.09)	–0.15	(0.09)
		Provisioning	0.08	(0.10)	–0.64	(0.09)
		2002 (Y1)	–0.61	(0.09)	0.01	(0.10)
		2003 (Y2)	0.56	(0.11)	0.39	(0.11)
		2004 (Y3)	–0.34	(0.10)	0.25	(0.10)
		2005 (Y4)	0.39	(0.11)	–0.64	(0.11)
2. Adults vs. nestlings	Year	Adults	–0.074	(0.106)	0.003	(0.092)

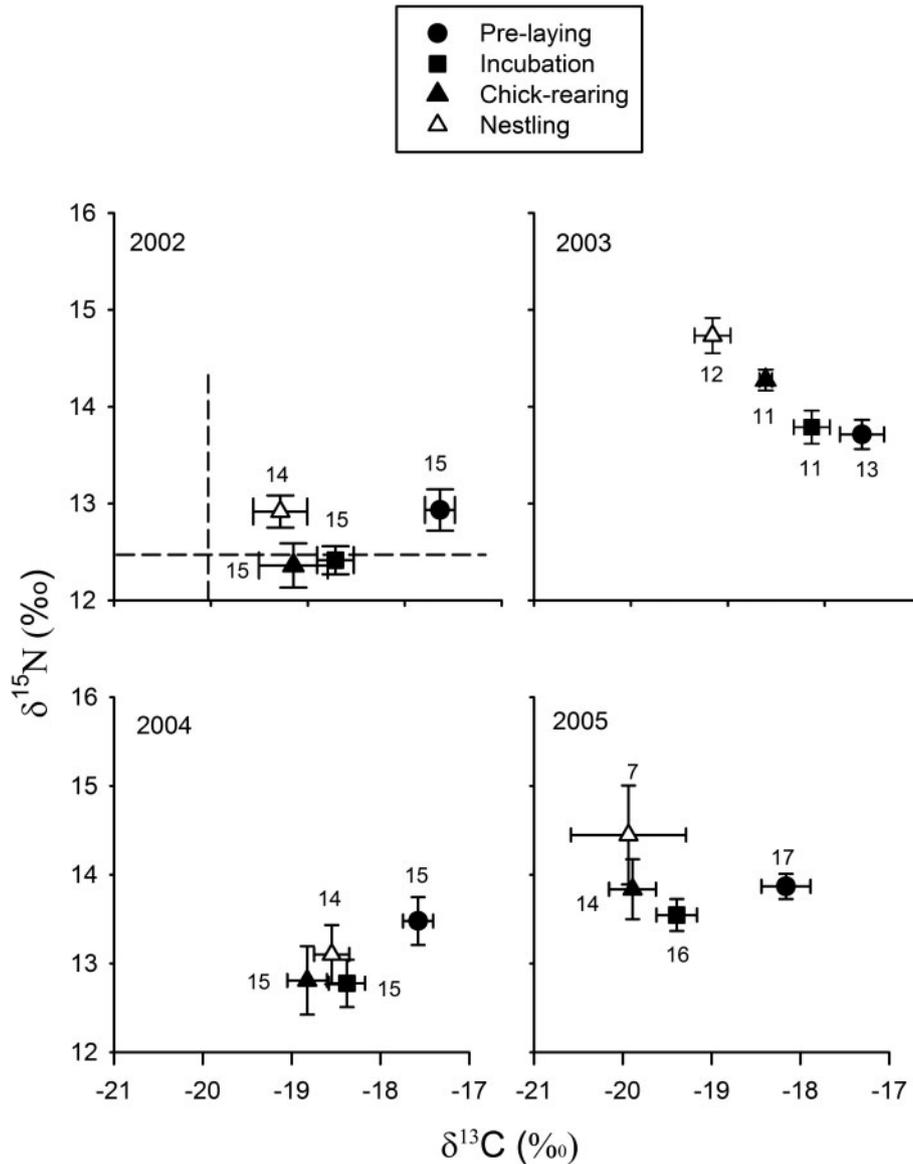


Figure 2. Bivariate plot showing the mean  $\pm$  95% confidence interval trophic level ( $\delta^{15}\text{N}$ ) and inshore/offshore location ( $\delta^{13}\text{C}$ ) of the diets of adult Cassin's auklets during three breeding stages, and of nestlings, in 4 years at Triangle Island. In the 2002 panel, the dashed lines represent the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values expected from diets consisting solely of the copepod *Neocalanus cristatus*, based on discrimination factors calculated directly from nestling diets (see Davies et al. 2009).

included Year and Age Class was also supported, it received only one-third of the weight of the Year-alone model, and the 95% confidence intervals around the parameter estimates for Age Class again bounded zero (Table III).

## Discussion

Zooplanktivorous Cassin's auklets breeding on Triangle Island substantially altered their foraging behaviour from one breeding stage to the next across the wide range of marine environmental conditions that prevailed during the four years of this study (Wolf et al. 2009). Overall, trophic level (inferred

from  $\delta^{15}\text{N}$  values) tended to be higher at the start of the season (prior to egg-laying) than at mid-season (during incubation), although that was not the case in all four years. There was greater consistency across years in the auklets' seasonal choice of foraging habitat (inferred from  $\delta^{13}\text{C}$  values), with declining  $\delta^{13}\text{C}$  values suggesting an inshore-to-offshore pattern of movement to capture prey in all four years. As with other studies that used stable isotope analysis to infer seabird diets, we cannot discount that seasonal and yearly variation in the isotopic baseline played some role. Although direct comparisons of adult to nestling stable isotope values need to be made cautiously (Bearhop et al. 2000;

Sears et al. 2009), our results also suggest that adult auklets tended to take prey from similar trophic levels and foraging habitats to feed themselves and to deliver to offspring at the nest.

Seasonal variation in the foraging behaviour of breeding seabirds has rarely been assessed, because relatively few studies have considered the stages prior to provisioning (Quillfeldt et al. 2005; Ronconi & Burger 2008; Williams et al. 2008; Hedd et al. 2009). Mean blood  $\delta^{15}\text{N}$  values in adult Cassin's auklets tended to be higher prior to laying than during incubation, with the overall yearly variation across stages averaging about 0.4‰. To the extent that it represents a true reduction in trophic level through the early part of the season, when Cassin's auklets have only themselves to feed, the decline in  $\delta^{15}\text{N}$  values could occur because zooplankton biomass increases through this time of year in waters off the British Columbia coast (Mackas 1992). However, that pattern was not evident in all years. In 2003,  $\delta^{15}\text{N}$  values differed little between the prelaying and incubation periods and then increased at provisioning, perhaps because zooplankton timing was earlier than normal during that year's weak El Niño event (Mackas et al. 2007). Interestingly,  $\delta^{15}\text{N}$  values were higher overall in 2002 and 2004, two years of strong primary production, than in 2003 and 2005, two years of weaker primary production (Wolf et al. 2009) – consistent with the observations of Rau et al. (2003), who found that  $\delta^{15}\text{N}$  values in the copepod *Calanus pacificus* Brodsky, 1948 were negatively correlated with an index of upwelling intensity.

Mean  $\delta^{13}\text{C}$  values in Cassin's auklets declined in all years from the prelaying to incubation stages, and again from the incubation to provisioning stages. A decline in  $\delta^{13}\text{C}$  values from late incubation to late provisioning was observed previously in the little auk (*Alle alle* Linnaeus, 1758), a zooplanktivorous seabird of Arctic waters (Harding et al. 2008). Because nearshore habitats in the northeast Pacific are enriched in  $^{13}\text{C}$  relative to offshore habitats (Kline 2009), the declines suggest that this population of breeding Cassin's auklets engaged in a season-long, nearshore-to-offshore movement in search of prey.

The  $^{13}\text{C}$ -depleted habitats used late in the season almost certainly were located seaward of the continental shelf break up to 110 km northwest of Triangle Island, where provisioning-stage adults forage for late-stage (C5) *Neocalanus cristatus* copepodites (Boyd et al. 2008). Among prey collected from Cassin's auklets in 2002 (Davies et al. 2009), the oceanic *N. cristatus* was more depleted in  $^{13}\text{C}$  (95% CI  $-20.95$  to  $-19.31$ ‰) than was the shelf-resident euphausiid *Thysanoessa spinifera* ( $-19.40$  to  $-17.76$ ‰), and the difference in mean  $\delta^{13}\text{C}$  values

between them (1.5‰) closely matched the overall extent of decline in adult auklets (1.4‰). Therefore, we propose that the birds foraged mainly for euphausiids on the continental shelf early in the season, but thereafter made increasing use of waters seaward of the shelf-break to forage for *N. cristatus*, a seasonally available (Miller et al. 1984), spatially predictable (Boyd et al. 2008) and nutritious (Hedd et al. 2002) prey type. Further, the absence of the Age Class term in the top models for both  $\delta^{15}\text{N}$  and especially  $\delta^{13}\text{C}$  suggests that Cassin's auklets used those oceanic habitats and that prey type both for self-feeding and loading, irrespective of yearly environmental variation. For central-place foragers, depending on the spatial distribution of different prey types, self-feeding and loading on the same prey type in the same patch can save significant amounts of time (Ydenberg & Davies 2010). Previously, Adams et al. (2010) showed how repeatedly exploiting predictable prey patches enabled Cassin's auklets to reduce the time they spent searching for prey.

Although differences in the  $\delta^{15}\text{N}$  values of adults and nestling Cassin's auklets were slight overall, the values were higher in nestlings in all four years, contrary to the pattern seen in zooplanktivorous little auks in a single year (Harding et al. 2008), but consistent with observations on magellanic penguins (*Spheniscus magellanicus* Forster, 1781; Forero et al. 2002). Experimental studies have shown that blood  $\delta^{15}\text{N}$  values of piscivorous nestling rhinoceros auklets (*Cerorhinca monocerata* Pallas, 1811) were depleted by  $\sim 0.5$ ‰ due to growth, and that nutritional stress can lower those values by a further  $\sim 0.3$ ‰ (Sears et al. 2009). However, there was no suggestion in our study that values in nestling Cassin's auklets were reduced relative to adult values in the two years of lower fledging masses, 2003 and 2005. Like others (Harding et al. 2008; Williams et al. 2007; Sears et al. 2009), we believe further experimental study of factors that affect discrimination factors in nestling seabirds are needed in order to fully interpret results such as ours (Karnovsky et al. 2012).

In summary, we found that the foraging behaviour of Cassin's auklets breeding on Triangle Island was considerably altered from one breeding stage to the next. This probably reflects general features of the species' life history, such as differences in the energetic demands of different breeding stages (Elliott et al. 2010) and the need to obtain suitable prey with which to provision offspring (Boyd et al. 2008), as well as processes operating in the marine ecosystem surrounding Triangle Island (Mackas 1992). We also found that the auklets tended to self-feed and load prey for delivery to offspring from similar trophic levels and habitats. In contrast to most studies which have focused on diets and at-sea

distributions of provisioning birds (Abraham & Sydeman 2006; Adams et al. 2010), our results are significant from a conservation standpoint in demonstrating that the auklets use a variety of habitat types over several breeding stages in the course of a breeding season.

### Acknowledgements

Many people assisted us with data collection, and we thank them all. For logistical support, we thank the Canadian Coast Guard and West Coast Helicopters for safe transport; BC Parks for permits to conduct research on the Anne Vallée Ecological Reserve; Monica Court, Judy Higham, Moira Lemon and Connie Smith for keeping us well organized; and Bob Elner, Elsie Krebs and Ron Ydenberg for support. Primary funding was provided by the *Nestucca* Oil Spill Trust Fund, The World Wildlife Fund Canada, Environment Canada, and the Centre for Wildlife Ecology at Simon Fraser University.

### References

- Abraham CL, Sydeman WJ. 2006. Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera*. *Marine Ecology Progress Series* 313:271–83.
- Adams J, Takekawa JY, Carter HR. 2004. Foraging distance and home range of Cassin's auklets nesting at two colonies in the California Channel Islands. *The Condor* 106:618–37.
- Adams J, Takekawa JY, Carter HR, Yee J. 2010. Factors influencing the at sea distribution of Cassin's Auklets (*Ptychoramphus aleuticus*) that breed in the Channel Islands, California. *Auk* 127:503–13.
- Ashmole NP. 1971. Seabird ecology and the marine environment. Chapter 6 in: Farner DS, King JR, editors. *Avian Biology*. New York: Academic Press, p 223–86.
- Bearhop S, Teece MA, Waldron S, Furness FW. 2000. The influence of uric acid upon  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of avian blood: implications for trophic studies. *Auk* 117:504–07.
- Bédard J. 1969. Adaptive radiation in Alcidae. *Ibis* 111:189–201.
- Blount JD, Houston DC, Surai PF, Møller AP. 2004. Egg-laying capacity is limited by carotenoid pigment availability in wild gulls *Larus fuscus*. *Proceedings of the Royal Society of London Series B* 271:S79–S81.
- Boyd WS, McFarlane-Tranquilla L, Ryder JL, Shisko SG, Bertram DF. 2008. Variation in marine distributions of Cassin's Auklets (*Ptychoramphus aleuticus*) breeding at Triangle Island, British Columbia. *Auk* 125:158–66.
- Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. New York: Springer. 496 pages.
- Carleton SA, Martinez del Rio C. 2005. The effect of cold induced increased metabolic rate on the rate of  $^{13}\text{C}$  and  $^{15}\text{N}$  incorporation in house sparrows (*Passer domesticus*). *Oecologia* 144:226–32.
- Davies WE, Hipfner JM, Hobson KA, Ydenberg RC. 2009. Seabird seasonal trophodynamics: Isotopic patterns in a community of Pacific alcids. *Marine Ecology Progress Series* 382:211–19.
- Elliott KH, Shoji A, Campbell KA, Gaston AJ. 2010. Oxygen stores and foraging behavior of two sympatric, planktivorous alcids. *Aquatic Biology* 8:221–35.
- Forero MG, Hobson KA, Bortolotti GR, Donazar JA, Bertelotti M, Blanco G. 2002. Food resource utilization by the Magellanic penguin evaluated through stable isotope analysis: Segregation by sex and age and influence on offspring quality. *Marine Ecology Progress Series* 234:289–99.
- Gaston AJ. 1990. Population parameters of the Ancient Murrelet. *Condor* 92:998–1011.
- Harding AMA, Hobson KA, Walkusz W, Dmoch K, Karnovsky NJ, Van Pelt TI, Liffield JT. 2008. Can stable isotope measurements of little auk (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine food webs? *Polar Biology* 31:725–33.
- Hedd A, Ryder JL, Cowen LC, Bertram DF. 2002. Inter-annual variation in the diet, provisioning and growth of Cassin's Auklets at Triangle Island, BC: Responses to variation in ocean climate. *Marine Ecology Progress Series* 229:221–32.
- Hedd A, Fifield DA, Burke CM, Montevecchi WA, McFarlane-Tranquilla L, Regalar PM, et al. 2009. Seasonal shift in the foraging niche of Atlantic puffins *Fratercula arctica* revealed by stable isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analyses. *Aquatic Biology* 9:13–22.
- Hipfner JM. 2008. Matches and mismatches: Ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series* 368:295–304.
- Hipfner JM. 2009. Euphausiids in the diet of a zooplanktivorous seabird: Seasonal and annual variation and the role of ocean climate. *Marine Ecology Progress Series* 390:277–89.
- Hipfner JM, Gorman KB, Vos RA, Joy JB. 2010a. Evolution of the embryonic developmental period in the marine bird families Alcidae and Spheniscidae: Roles for nutrition and predation? *BMC Evolutionary Biology* 10:179.
- Hipfner JM, McFarlane-Tranquilla LA, Addison B. 2010b. Experimental evidence that both timing and parental quality affect breeding success in a zooplanktivorous seabird. *Auk* 127:195–203.
- Ito M, Minami H, Tanaka Y, Watanuki Y. 2009. Seasonal and interannual oceanographic changes induce diet switching in a piscivorous seabird. *Marine Ecology Progress Series* 393:273–84.
- Karnovsky, NJ, Hobson KA Iverson SJ. 2012. From lavage to lipids: Innovations and limitations in estimating diets of seabirds. *Marine Ecology Progress Series* 451:263–84.
- Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredericks ZM, Shultz MT, et al. 2010. Food availability and population processes: Severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Functional Ecology* 24:625–37.
- Kline Jr TC. 2009. Characterization of carbon and nitrogen stable isotope gradients in the northern Gulf of Alaska using terminal feedstage copepodite-V *Neocalanus cristatus*. *Deep-Sea Research II* 56:2537–52.
- Lack D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Clarendon Press. 409 pages.
- Lescroël A, Ballard G, Toniolo T, Barton KJ, Wilson RP, Lyver PB, et al. 2010. Working less to gain more: When breeding quality relates to foraging efficiency. *Ecology* 91:2044–55.
- Mackas DL. 1992. Seasonal cycle of zooplankton off southwestern British Columbia: 1979–1989. *Canadian Journal of Fisheries and Aquatic Sciences* 49:903–21.
- Mackas DL, Batten S, Trudel M. 2007. Effects on zooplankton of a warmer ocean: Recent evidence from the Northeast Pacific. *Progress in Oceanography* 75:223–52.
- McFarlane-Tranquilla L, Ryder JL, Boyd WS, Shisko SG, Amey K, Bertram DF, et al. 2005. Diurnal marine distributions

- of radio-tagged Cassin's Auklets and Rhinoceros Auklets breeding at Triangle Island, B.C. Canadian Wildlife Service Technical Report Series No. 423. 77 pages.
- Miller CB, Frost BW, Batchelder HP, Clemons MJ, Conway RE. 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii* in the Northeast Pacific. *Progress in Oceanography* 13:201–43.
- Orians G, Pearson NE. 1979. On the theory of central place foraging. Chapter 8 in: Horn DJ, Stairs GR, Mitchell RD, editors. *Analysis of Ecological Systems*. Columbus, OH: Ohio State University Press, p 155–77.
- Pichegru L, Ryan PG, Crawford RJM, van der Lingen CD, Grémillet D. 2010. Behavioural inertia places a top marine predator at risk from environmental change in the Benguela upwelling system. *Marine Biology* 157:537–44.
- Quillfeldt P, McGill RAR, Furness RW. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: Review and study of Wilson's storm-petrel. *Marine Ecology Progress Series* 295:295–304.
- Rau GH, Ohman MD, Pierrot-Bults A. 2003. Linking nitrogen dynamics to climate variability off central California: A 51-year record based on N-15/N-14 in CalCOFI zooplankton. *Deep-Sea Research II* 50:2431–47.
- Rodway MS. 1990. Status and conservation of breeding seabirds in British Columbia. Chapter 3 in: Croxall JP, editor. *Supplement to the Status and Conservation of the World's Seabirds*. Cambridge: International Council for Bird Preservation, p 43–102.
- Romanoff AL. 1944. Avian spare yolk and its assimilation. *Auk* 61:235–41.
- Ronconi RA, Burger AE. 2008. Limited foraging flexibility: Increased foraging effort by a marine predator does not buffer against scarce prey. *Marine Ecology Progress Series* 366: 245–58.
- Sears J, Hatch SA, O'Brien DM. 2009. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. *Oecologia* 159:41–48.
- Stephens DW, Brown JS, Ydenberg RC. 2007. *Foraging: Behavior and Ecology*. Chicago, IL: University of Chicago Press. 608 pages.
- Sydeman WJ, Bradley RW, Warzybok P, Abraham CL, Jahncke J, Hyrenbach KD, et al. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters* 33: L22S09. 5 pages.
- Williams CT, Buck CK, Sears J, Kitaysky AS. 2007. Effects of nutritional restriction on nitrogen and carbon stable isotopes in growing seabirds. *Oecologia* 153:11–18.
- Williams CT, Iverson SJ, Buck CL. 2008. Stable isotopes and fatty acid signatures reveal age- and stage-dependent foraging niches in tufted puffins. *Marine Ecology Progress Series* 363:287–98.
- Wolf SG, Sydeman WJ, Hipfner JM, Abraham CL, Tershy BR, Croll DR. 2009. Range-wide reproductive consequences of ocean climate variability for the seabird Cassin's Auklet. *Ecology* 90:742–53.
- Ydenberg RC, Davies WE. 2010. Resource geometry and provisioning routines. *Behavioral Ecology* 21:1170–78.

*Editorial responsibility: Leandro Bugoni*