



Temporal and sex-specific variability in Rhinoceros Auklet diet in the central California Current system



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ABSTRACT

We used stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and compared prey provided to chicks by each sex to evaluate seasonal and sex-specific diets in Rhinoceros Auklets (*Cerorhinca monocerata*) in the central California Current system during 2012–2013. Mixing models indicated northern anchovy (*Engraulis mordax*) were important prey for adults during fall/winter and juvenile rockfishes (*Sebastes* spp.) were important prey during incubation both years. Adult trophic level increased between incubation and chick-rearing periods in both years. During 2012, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of chick-rearing males and females differed significantly; mixing models indicated that females ate more Pacific saury (*Cololabis saira*) and less market squid (*Doryteuthis opalescens*) than males. Likewise, females delivered significantly more Pacific saury and less market squid to chicks than males during 2012. Chick growth (g d^{-1}) and chick survival to fledging were significantly lower during 2012 than 2013, likely because chicks were fed lesser quality prey or fed less frequently in 2012. Lesser body mass of females during incubation in 2012 indicated sex-specific diet differences may have been related to female energetic constraints. The observed variability in Rhinoceros Auklet diet underscores the importance of managing multiple prey populations in this system so that generalist predators have sufficient resources through changing conditions.

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1. Introduction

Many seabirds live in environments where primary productivity and prey availability vary seasonally and inter-annually (e.g., polar ecosystems and eastern boundary upwelling currents). In these environments, interactions between seasonal energetic constraints and seasonal prey availability influence the survival and reproductive success of seabirds and other marine predators (Ainley et al., 1995; Frederiksen et al., 2006; Soto et al., 2004). Often, seabird life history constraints (e.g., molt, central place foraging during breeding) result in decreased mobility and/or foraging range concurrent with increased energetic demands. Periods when changes in availability of prey coincide with life-history constraints therefore can be critical to fitness (Nelson, 1980).

During energetically demanding periods, seabirds may change the way they target and partition prey resources in response to competition (Gonzalez-Solis et al., 2000; Phillips et al., 2011) or seasonal behavioral roles (Paredes et al., 2008; Welcker et al., 2009). Additionally, sex-specific differences in chick provisioning (Quillfeldt et al., 2004; Wagner, 1997; Wiggins and Morris, 1987), foraging behavior (Lewis et al., 2002; Peck and Congdon, 2006), and diet (Bearhop et al., 2006;

Phillips et al., 2011) have been observed during the breeding season. Diet or foraging differences between sexes often occur in species with pronounced sexual dimorphism (e.g., >10% difference in body mass; Kato et al., 2000; Lewis et al., 2005; Phillips et al., 2011) and may result from competitive exclusion of the smaller sex by the larger (Forero et al., 2005; Gonzalez-Solis et al., 2000). Alternatively, sex differences may arise from morphological or physiological differences that allow one sex access to different foraging niches (e.g., larger bill size allowing one sex to handle larger prey (Koffijberg and Van Eerden, 1995) or larger body mass of one sex allowing greater dive depth and/or duration (Bearhop et al., 2006)). Sex-specific diets or behaviors among monomorphic seabirds occur less frequently (Phillips et al., 2011), and may be related to differing energetic constraints imposed by sex-specific roles during the breeding season, such as egg formation (Welcker et al., 2009) or nest defense (Fraser et al., 2002; Paredes et al., 2008). Studies reporting sex-specific differences in seabird diet and behavior were primarily conducted during the breeding season (Phillips et al., 2011). Thus, little is known about sex-specific patterns during non-breeding periods, although recent studies have found sexual segregation in foraging ranges during the pre-breeding period in some Procellariiforms (Chiu Werner et al., 2014; Hedd et al., 2014), likely driven by differing nest defense and egg production roles. Further investigation of intra-annual variation in seabird diet is necessary for understanding whether sex-specific differences in seabird diets occur outside of the breeding period.

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We studied seasonal and sex-specific diet and chick provisioning in Rhinoceros Auklets (*Cerorhinca monocerata*; Family *Alcidae*), a burrow-nesting seabird in the puffin tribe (Gaston and Jones, 1998). Male Rhinoceros Auklets are larger than females in body mass (i.e. in British Columbia, chick-rearing male body mass = 510 ± 49 SD g, $n = 20$; female body mass = 456 ± 45 SD g, $n = 25$; Vermeer, 1979) and bill depth (i.e. male bill depth = 17.1–20.1 mm, $n = 100$; female bill depth = 15.2–17.7 mm, $n = 100$; Pyle, 2008). Rhinoceros Auklets nest predominantly on islands and spend winter mainly over shelf waters in the North Pacific Ocean from California to Japan (Gaston and Jones, 1998). In central California, Rhinoceros Auklets lay and incubate eggs from April through May, and parents provision young from ~ June through August, after which birds depart breeding colonies (Hester, 1998). Females lay a single egg and both parents contribute to incubation and chick-rearing (Richardson, 1961). Parents carry whole fishes and cephalopods in their bills and deliver them to chicks (termed provisioning; Richardson, 1961). Adult males and females may consume similar prey as they provide to chicks, but results of observational and trophic studies have been mixed (Davoren and Burger, 1999; Hipfner et al., 2013; Ito et al., 2009), with no clear sex-specific differences in diet or chick provisioning patterns. Isotopic studies of blood, however, have shown a consistent pattern of adult trophic level increase after chicks hatch (Davies et al., 2009; Hipfner et al., 2013; Ito et al., 2009).

We used stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to compare Rhinoceros Auklet diet between seasons, sexes, and adult vs. chick age classes, as well as prey species delivered to chicks by each sex, at Año Nuevo Island, CA, during 2 years with differing oceanographic conditions. Our goals were to determine whether Rhinoceros Auklet diet varies according to season or sex, and to investigate the relationship between potential seasonal and sex-specific diet patterns.

2. Methods

2.1. Study site and field methods

Año Nuevo Island (ANI; $37^\circ 06' \text{N}$, $122^\circ 20' \text{W}$) is located 1 km off central California, within the central California Current upwelling system (Hayward and Venrick, 1998; Lynn and Simpson, 1987). In this system, primary productivity and prey abundance peak during spring and summer in response to wind-forced upwelling (Chavez et al., 2002). ANI is adjacent to an upwelling center at Pt. Año Nuevo, where cold, salty water is upwelled, typically during April through June, and advected equatorward (Garcia-Reyes and Largier, 2012; Schwing et al., 1991). During the spring and summer breeding period, Rhinoceros Auklets in the region typically occur from the mid-shelf to beyond the outer shelf-break, with concentrations around breeding colonies at the Farallon Islands and ANI (Santora et al., 2012).

2.2. Rhinoceros Auklet fall/winter, pre-breeding, and incubation isotopes

During the incubation period we collected blood, breast feathers, and facial plume feathers from Rhinoceros Auklet pairs nesting in artificial nest sites ($n = 42$ in 2012, $n = 34$ in 2013). These samples constituted all accessible nests and ~15% of the ANI breeding population in each year (Hester et al., 2013). We banded all birds with a metal U.S. Fish and Wildlife Service leg band, determined mass of each bird (± 5.0 g using a 600 g spring scale; Pesola, Baar, Switzerland), and sampled tissues within 7 to 14 days of egg lay (1–30 May 2012, 25 April–5 June 2013). The expected isotopic turn-over rate in blood for equivalent sized birds is ~20 days (Carleton and Martinez del Rio, 2005; Hipfner et al., 2013); therefore, isotope values of blood sampled during incubation represented adult diet in April or May (hereafter termed incubation). Blood (~1 ml per bird) was frozen at -20°C for isotope analysis, and stored on FTA cards (Fast Technology for Analysis of nucleic acids; Whatman, General Electric, Fairfield, Connecticut, USA) for DNA sex analysis.

We plucked 2 breast feathers that appeared freshly grown and clipped <1 cm of facial plume feathers from incubating birds. Feather $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ reflect diet at the time of their formation (Hobson and Clark, 1992). Some breast feathers are grown during February and March, whereas facial plume feathers are grown slowly between October and January (Pyle, 2008). Therefore, isotope values of fresh breast feathers represented adult diet during February–March (hereafter pre-breeding), whereas plume feathers represented adult diet during the previous October–January (hereafter fall/winter).

To evaluate chick diet, we sampled chick whole blood (as described for adults; $n = 16$ in 2012, $n = 9$ in 2013) at 5 weeks of age (10–31 July 2012, 27 June–25 July 2013), when blood isotope values should reflect only the chick's post-hatching diet (Quillfeldt et al., 2008; Sears et al., 2009).

2.3. Reproductive metrics

To compare reproductive success between years, we checked artificial nest sites and natural burrows weekly during the laying and chick-rearing periods. We monitored a randomly selected subsample of natural burrows ($n = 56$ in 2012, $n = 34$ in 2013) using a burrow camera on a flexible hose (Pukamanu 2.2, Abyssal Hawaii, Kailua, Hawaii, USA). We weighed all chicks (± 1.0 g or ± 5.0 g using a 300 or 600 g spring scale; Pesola, Baar, Switzerland) in artificial nest sites every 7 days from hatch to fledging and quantified annual chick growth (g d^{-1} from the linear growth stage, days 14 to 35; methods described in Thayer and Sydeman, 2007). We quantified annual hatching success (ratio of chicks hatched to first eggs laid), chick survival to fledging (ratio of chicks hatched to chicks fledged), and total productivity (ratio of chicks fledged to first eggs laid).

2.4. Rhinoceros Auklet chick diet, chick-rearing isotopes, and prey isotopes

To obtain isotope values for prey and quantify a sex-specific metric of chick provisioning, we caught provisioning adults in mist nets and collected dropped prey items during June–July of each year. We determined mass (± 0.1 g using an electronic scale; Acculab EC-211, Data Weighing Systems, Elk Grove, Illinois, USA) and standard length (fishes) or mantle length (cephalopods; both ± 1.0 mm) of each prey item. We quantified chick meals according to bill-load – a statistically independent unit representing one load of prey carried by one adult. We measured total bill-load mass (± 0.1 g), and percent mass (%M), percent number (%N), and percent frequency of occurrence (%FO) for each prey species per bill-load. We analyzed stable isotopes of prey that were at least 2%M of chick diet. In 2013, we also analyzed stable isotopes of prey reported from past studies (Vermeer, 1980; Thayer and Sydeman, 2007; Ito et al., 2009) that were not present in chick diet samples (i.e. the euphausiid *Thysanoessa spinifera*, market squid [*Doryteuthis opalescens*], and Pacific sand lance [*Ammodytes hexapterus*]). Euphausiid and market squid samples were collected in May 2013 near ANI during National Marine Fisheries Service (NMFS) rockfish trawl surveys (Wells et al., 2013), and one Pacific sand lance was opportunistically collected outside a Rhinoceros Auklet burrow in 2013.

We sampled tissues (whole blood, breast feathers, and plume feathers, using methods described previously) from confirmed breeding adults caught in mist nets ($n = 26$ in 2012, $n = 24$ in 2013) to obtain an isotope signature during chick-rearing and to augment pre-breeding and fall/winter stable isotope sample sizes. In each year, we sampled some individuals twice for bill-loads ($n = 4$ of 23 birds in 2012, $n = 3$ of 22 birds in 2013). All repeat sampling events of individuals were at least a week apart, and 6 of 7 had differing prey species or a different majority of prey species in each bill-load. Thus, we considered individual preference an unlikely confounding bias and included all bill-loads in an analysis of sex differences.

2.5. DNA sex analysis

We determined sex for all birds sampled ($n = 90$ adults, 24 chicks) using DNA extracted from blood or feathers (Fridolfsson and Ellegren, 1999). Sex analysis was performed at the University of Hawaii Center for Conservation Research and Training, Manoa, Hawaii, USA. Duplicate blood samples were tested each year ($n = 6$ in 2012, $n = 10$ in 2013) to assess sex-identification accuracy. In both years, 100% of duplicates matched the originally identified sex.

2.6. Stable isotope analysis

We measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Rhinoceros Auklet and prey tissues. We dried whole blood and prey (~1 g white muscle) at 60 °C for 24 h and powdered them (Pinnegar and Pulanin, 1999). We soaked euphausiids for 3 h in 10% HCL to remove calcified parts before lipid extraction (Jacob et al., 2005). We lipid extracted prey by agitating in a sonicator for 30 min in repeated solutions of 2:1 chloroform:methanol (Bligh and Dyer, 1959; Logan et al., 2008; Ruiz-Cooley et al., 2011), and drying under a fume hood for 24 h. We did not lipid extract whole blood (see Bearhop et al., 2000; Cherel et al., 2005). We repeatedly rinsed feathers in 2:1 chloroform:methanol and dried them under a fume hood for 24 h. We homogenized plume feathers and the distal 2 cm of each breast feather in a grinder.

Stable isotope analysis was performed at the Idaho State University Interdisciplinary Laboratory for Elemental and Isotopic Analysis, Pocatello, Idaho, USA. Aliquots of 0.5 mg of tissues were placed in tin capsules. Samples were combusted and analyzed using Elemental Combustion System 4010 interfaced to a Delta V advantage mass spectrometer through the ConFlo IV system. Isotope ratios of $\delta^{13}\text{C}$ are reported as ‰ values relative to the Vienna PeeDee Belemnite scale, whereas $\delta^{15}\text{N}$ values are reported as ‰ values relative to air-N₂. Based on replicates of an in-house standard, instrument error (SD) was $\pm 0.17\%$ for $\delta^{15}\text{N}$ and $\pm 0.06\%$ for $\delta^{13}\text{C}$.

2.7. Stable isotope fractionation rates

We estimated year-specific rates for chick whole blood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ fractionation by comparing observed isotope values of chick whole blood with isotopes of prey observed during bill-load sampling (following Davies et al., 2009; Hipfner et al., 2014). We used feather fractionation literature values of +3.7‰ for $\delta^{15}\text{N}$ and +1.0‰ for $\delta^{13}\text{C}$, from a study on Common Murres (*Uria aalge*; Becker et al., 2007b), a close relative of Rhinoceros Auklets.

2.8. Mixing model

We used the dual isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) mixing model Isosource (Phillips and Gregg, 2003) to estimate adult diet during each period and chick diet, and to compare male vs. female diet during periods in which sex-specific isotope differences occurred. Isosource examines all possible combinations of contributions for up to 10 sources (Phillips and Gregg, 2003). We considered solutions feasible if they summed to observed Rhinoceros Auklet isotope values within a tolerance level of 0.1‰ (Phillips and Gregg, 2003). Model assumptions were that 1) we included all relevant sources, 2) fractionation rates were accurate, and 3) prey isotope values did not change seasonally. We used year-specific mean isotope values of prey that were $\geq 5\%$ of chick diet in at least one year as sources. For 2012, we included euphausiids as a source, but used isotope values of *T. spinifera* sampled in 2013. For 2013, we included prey that did not appear in our chick diet sample that year as sources (i.e. market squid, *T. spinifera*, and Pacific sand lance sampled by other means in 2013). Euphausiids were not included as a source in chick diet models because Rhinoceros Auklets feed exclusively fish to chicks (Bedard, 1969). It is possible that seasonal changes in prey isotopes affected mixing model accuracy for periods several

months from prey sampling dates (i.e. pre-breeding, fall/winter). However, the year-specific prey sampling in our study represents a finer a temporal scale than that used by many previous isotopic mixing model studies examining seasonal seabird diet (e.g., Becker et al., 2007a; Hedd et al., 2010; Sorensen et al., 2009).

2.9. Statistics

We used the statistical package JMP (SAS Institute, Cary, North Carolina, USA) for all statistical tests except bootstrap tests, for which we used Resampling Stats for Excel (Statistics.com, Arlington, Virginia, USA). We used likelihood ratio χ^2 tests to test differences between years in hatching success, chick survival, total productivity, and sex-specific differences in the %FO of common prey species in bill-loads. We tested differences in chick growth between years using two-tailed *t*-tests. We tested differences in fractionation-adjusted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between each tissue and year using a full-factorial MANOVA. We used 10,000 iteration bootstrap tests to test differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between sexes for each tissue, and to test sex-specific differences in the proportions (%N) of common prey species in bill-loads. We tested differences in log-transformed bill-load masses between sexes and years using a full-factorial ANOVA. We tested differences among $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of prey using full-factorial ANCOVAs, with species and year as independent variables and prey length as an independent covariate. Finally, we tested correlations between prey proportions in adult mixing model estimates vs. chick bill-loads and chick mixing model estimates vs. chick bill-loads using linear regressions. We conducted post-hoc two-tailed *t*-tests or *F* tests to investigate significant effects. We tested residuals for normality with Shapiro–Wilk tests and for homoscedasticity by plotting residuals vs. expected values and assessing symmetry.

Following the advice of Nakagawa (2004) and others (Garamszegi, 2006; Moran, 2003; Perneger, 1998), we did not use Bonferroni corrections for multiple comparisons. Instead, for each pair-wise test we report the test statistic, the exact *p* value, and the absolute value of Cohen's *d* metric of standardized effect size, where a *d* of ≤ 0.2 is considered a “small effect,” ≥ 0.5 is considered a “medium effect,” and ≥ 0.8 is considered a “large effect” (Cohen, 1988). We defined statistical significance as $p \leq 0.5$ with $d \geq 0.5$ for pair-wise tests and as $p \leq 0.5$ for multivariate tests. Values are reported as $\bar{x} \pm 1$ SE unless otherwise noted.

3. Results

3.1. Reproductive success

Hatching success did not differ between years (90% in 2012, $n = 78$; 86% in 2013, $n = 66$; $\chi^2_1 = 0.4$, $n = 144$, $p = 0.53$, $d = 0.1$). Chick growth was significantly lower during 2012 (5.1 ± 0.6 g d^{-1} , $n = 15$) than during 2013 (6.9 ± 0.6 g d^{-1} , $n = 10$; $t_{23} = 2.1$, $p = 0.05$, $d = 0.9$). Chick survival to fledging was significantly lower during 2012 (65%, $n = 66$) than during 2013 (86%, $n = 43$; $\chi^2_1 = 6.2$, $n = 109$, $p = 0.01$, $d = 0.5$). Overall productivity was lower during 2012 (54%, $n = 79$) than during 2013 (73%, $n = 51$; $\chi^2_1 = 4.4$, $n = 130$, $p = 0.04$, $d = 0.4$).

3.2. Adult mass during incubation

Mass of males during incubation did not differ between years (540 ± 26 g in 2012 vs. 546 ± 34 g in 2013, $n = 16$ both years; $t_{30} = 0.5$, $p = 0.62$, $d = 0.2$). Mass of females during incubation was 17 g less in 2012 (504 ± 8 g, $n = 23$) than in 2013 (521 ± 5 g, $n = 17$; $t_{38} = 1.7$, $p = 0.10$, $d = 0.6$), though this trend was not significant. As a metric of body condition, we compared the mass of individuals that were weighed both years. There was no difference between years in mass of serially weighed males (% change in mass = $0.0008 \pm 1\%$, 1 ± 7 g heavier in 2013, $n = 8$; paired *t*-test, $t_7 = 0.1$, $p = 0.90$, $d = 0.1$), but serially weighed females were significantly heavier in 2013

than in 2012 (by $4 \pm 2\%$, 19 ± 8 g, $n = 10$; paired t -test, $t_9 = 2.3$, $p = 0.05$, $d = 0.7$).

3.3. Chick diet

We collected 164 individual prey in 27 bill-loads in 2012, and 54 individual prey in 25 bill-loads in 2013. In 2012, Rhinoceros Auklets provided chicks with 13 prey species; Pacific saury (*Cololabis saira*; hereafter saury) comprised the majority of chick diet ($43 \pm 9\%$) followed by market squid (hereafter squid; $28 \pm 7\%$) and Pacific sand lance (hereafter sand lance; $13 \pm 6\%$; Table 1). All other prey types combined were 18% of chick diet in 2012 (Table 1). For analysis, we pooled the 4 species of juvenile rockfishes (*Sebastes* spp.) that occurred in chick diet in 2012 as the prey type “juvenile rockfishes.” In 2013, chicks were provided solely with juvenile shortbelly rockfish (*Sebastes jordani*; $59 \pm 9\%$), northern anchovy (*Engraulis mordax*; hereafter anchovy; $36 \pm 9\%$), and juvenile sablefish (*Anaplopoma fimbria*; $5 \pm 4\%$; Table 1).

3.4. Prey isotope values

Prey with sufficient sample sizes for testing of isotope values ($n \geq 10$) included juvenile rockfishes, anchovy, and squid. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differed significantly among prey ($\delta^{15}\text{N}$ $F_{2,42} = 9.2$, $p < 0.001$; $\delta^{13}\text{C}$ $F_{2,42} = 32.8$, $p < 0.001$; Table 1, Fig. 1). $\delta^{15}\text{N}$ of prey did not differ between years ($F_{1,42} = 0.4$, $p = 0.56$), but prey $\delta^{13}\text{C}$ values were significantly higher in 2013 than in 2012 ($F_{1,42} = 8.5$, $p = 0.006$; Table 1, Fig. 1). $\delta^{15}\text{N}$ was significantly affected by prey length ($F_{1,42} = 10.4$, $p = 0.002$); longer fish had greater $\delta^{15}\text{N}$. There also was a significant year*length interaction effect, with longer prey in 2013 than in 2012 ($F_{1,42} = 4.6$, $p = 0.04$), whereas other interaction effects (i.e. year*length, year*species, species*length, or year*species*length) were not significant ($p > 0.10$ for all). Across years, $\delta^{13}\text{C}$ was unaffected by prey length ($F_{1,42} = 1.2$, $p = 0.29$) or interaction effects ($p > 0.10$ for all).

3.5. Blood isotope fractionation rates

Isotope fractionation rates of chick whole blood were $+2.0\%$ in 2012 and $+1.4\%$ in 2013 for $\delta^{15}\text{N}$, and -0.4% in 2012 and -0.2% in 2013 for $\delta^{13}\text{C}$. Growth and/or starvation in chicks can increase or decrease isotope fractionation rates, especially for $\delta^{15}\text{N}$ (Sears et al., 2009). Due to uncertainty associated with differences in chick blood fractionation between years, we applied the average chick blood fractionation rates ($+1.7\%$ for $\delta^{15}\text{N}$ and -0.3% for $\delta^{13}\text{C}$) to adult whole blood for both years.

Table 1
Prey $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($\bar{x} \pm \text{SD}\%$), length range of individual prey sampled for isotopes (standard length: SL, mantle length: ML), Species in bold composed $>10\%$ M or %N of chick diet in a year.

Species	n Sampled for isotopes	SL/ML range (mm)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	%M chick diet	%N chick diet
2012						
Pacific saury	10	84–145	13.98 ± 1.1	-19.12 ± 0.7	43 ± 9	43 ± 9
Market squid	10	37–63	13.08 ± 0.4	-17.31 ± 0.7	30 ± 7	28 ± 7
Pacific sand lance	9	85–121	13.28 ± 0.6	-16.27 ± 0.4	12 ± 6	13 ± 6
Northern anchovy	3	81–123	14.18 ± 0.7	-16.16 ± 0.5	5 ± 4	6 ± 4
Rockfish spp.	10	35–63	11.80 ± 0.5	-19.67 ± 0.4	5 ± 3	5 ± 4
Pacific sanddab	4	37–41	11.52 ± 1.3	-21.13 ± 1.0	2 ± 2	3 ± 3
Lingcod	5	63–72	13.22 ± 0.2	-18.08 ± 0.7	2 ± 2	2 ± 2
Sablefish	2	107–144	12.31 ± 0.7	-16.71 ± 0.4	1 ± 1	1 ± 1
2013						
Shortbelly rockfish	10	70–86	12.62 ± 0.5	-18.25 ± 0.8	58 ± 9	59 ± 9
Northern anchovy	11	85–119	14.69 ± 0.7	-15.67 ± 0.3	36 ± 9	36 ± 9
Sablefish	2	108–133	12.80 ± 1.2	-17.86 ± 0.7	7 ± 5	5 ± 4
Market squid	10	34–52	12.69 ± 0.4	-16.23 ± 0.5	–	–
Krill (<i>T. spinifera</i>)	10	–	9.62 ± 0.6	-17.33 ± 0.4	–	–

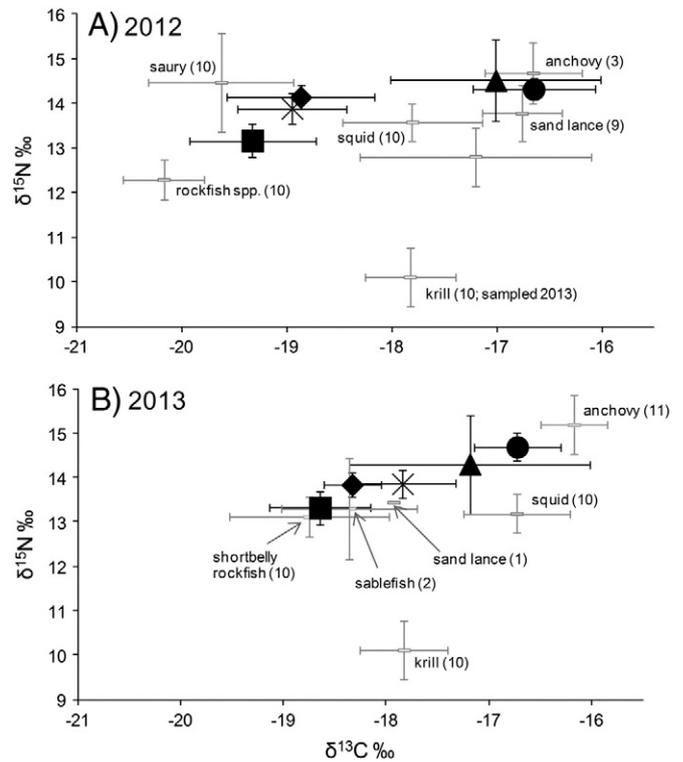


Fig. 1. Fractionation-adjusted stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, $\bar{x} \pm \text{SE}\%$) of Rhinoceros Auklet tissues and prey ($\bar{x} \pm \text{SD}\%$) in 2012 (A) and 2013 (B). Circles represent fall/winter, triangles represent pre-breeding, squares represent incubation, diamonds represent chick-rearing, and an X represents chicks. Prey sample sizes are in parentheses. See Table 2 for Rhinoceros Auklet tissue sample sizes.

3.6. Inter-annual and seasonal diet patterns

There were significant differences in fractionation-adjusted (hereafter adjusted) adult $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ between years for all tissues (fall/winter $F_{2,319} = 10.0$, incubation $F_{2,319} = 20.5$, chick-rearing $F_{2,319} = 24.3$, $p < 0.001$ for all) except for breast feathers (pre-breeding period $F_{2,319} = 1.6$, $p = 0.20$). The greatest inter-annual isotope differences occurred in $\delta^{13}\text{C}$ in blood of incubating adults, chick-rearing adults, and chicks; all had $\sim 1\%$ greater $\delta^{13}\text{C}$ in 2013 vs. 2012 (Fig. 1). This trend matched the $\sim 1\%$ average increase in prey $\delta^{13}\text{C}$ values between 2012 and 2013 (Table 1).

Across years, adjusted dual isotope values differed significantly by tissue type ($F_{6,638} = 90.7$, $p < 0.001$). We did not individually test differences between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of tissue types in each year because

Table 2

Mean and range (1st–99th percentile, in parentheses) of feasible solutions for prey contributions to adult Rhinoceros Auklet diet from dual isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) mixing model IsoSource (Phillips and Gregg, 2003). Results are for both sexes pooled for fall/winter, pre-breeding, incubation, and chick-rearing periods of 2012 and 2013. Values for which the 99th percentile solution was greater than 25% are bolded. Euphausiids were not included as a potential source in chick diet models.

	Fall/winter <i>n</i> = 52	Pre-breeding <i>n</i> = 55	Incubation <i>n</i> = 38	Chick-rearing <i>n</i> = 26	Chicks <i>n</i> = 16
Pacific saury	0 (0–1)	8 (1–13)	44 (33–59)	65 (56–73)	42 (30–55)
Market squid	0 (0–4)	4 (0–16)	6 (0–21)	8 (0–30)	15 (0–49)
Pacific sand lance	24 (1–46)	5 (0–19)	4 (0–14)	7 (0–22)	10 (0–33)
Rockfish spp.	0 (0–1)	1 (0–6)	34 (19–45)	3 (0–11)	7 (0–23)
Northern anchovy	71 (52–90)	79 (68–89)	4 (0–14)	9 (0–23)	11 (0–34)
Sablefish	3 (0–12)	2 (0–9)	4 (0–15)	5 (0–18)	10 (0–30)
Euphausiid (<i>T. spinifera</i>)	2 (0–5)	1 (0–3)	4 (0–16)	2 (0–7)	–
2013	<i>n</i> = 49	<i>n</i> = 55	<i>n</i> = 34	<i>n</i> = 24	<i>n</i> = 9
Market squid	3 (0–11)	3 (0–11)	3 (0–12)	0 (0–1)	1 (0–4)
Pacific sand lance	8 (0–25)	19 (0–42)	12 (0–42)	2 (0–5)	7 (0–21)
Shortbelly rockfish	7 (0–20)	16 (0–36)	51 (6–81)	65 (55–70)	39 (10–58)
Northern anchovy	73 (68–79)	53 (46–60)	5 (0–13)	29 (28–30)	33 (30–35)
Sablefish	8 (0–23)	15 (0–41)	28 (0–85)	4 (0–17)	20 (0–57)
Euphausiid (<i>T. spinifera</i>)	1 (0–4)	0 (0–4)	1 (0–5)	0 (0–0)	–

differences were visually apparent when graphed (Fig. 1). Anchovy likely was the dominant prey of adult Rhinoceros Auklets during fall/winter and pre-breeding periods of both years (Table 2). Adjusted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ was lesser during incubation than during pre-breeding of both years (Fig. 1). During incubation in 2012, primary prey of adults likely were Pacific saury (1st–99th percentile 33–59%) and juvenile rockfishes (19–45%; Table 2). During incubation 2013, primary prey of adults likely was juvenile rockfishes (6–81%) and/or juvenile sablefish (0–85%; Table 2). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were greater during chick-rearing than during incubation in both years (Fig. 1). In 2012, saury likely was the primary prey of chick-rearing adults (56–73%), with a potentially important contribution of squid (0–30%; Table 2). During 2013, juvenile shortbelly rockfish (55–70%) and anchovy (28–30%) likely were the primary prey of chick-rearing adults (Table 2). Mixing model estimates of mean prey proportions in chick-rearing adult diet (Table 2) were significantly correlated with prey proportions in chick diet (%M) observed in bill-loads in 2012 ($\beta = 1.16$, $p = 0.05$, $r^2 = 0.66$) and 2013 ($\beta = 1.06$, $p = 0.003$, $r^2 = 0.97$; Table 1). Likewise, chick diet mean prey proportions estimated by mixing models (Table 2) were significantly correlated with chick diet prey proportions (%M) observed in bill-loads in 2012 ($\beta = 0.68$, $p = 0.02$, $r^2 = 0.76$) and 2013 ($\beta = 0.59$, $p = 0.02$, $r^2 = 0.87$; Table 1).

3.7. Sex-specific chick provisioning

In 2012, bill-loads of females contained significantly more saury (%N = $65 \pm 14\%$, $n = 12$) than bill-loads of males (%N = $26 \pm 10\%$, $n = 15$; 2 sample bootstrap, $p = 0.04$, $d = 0.9$; Fig. 2A, B). Saury also occurred more frequently in bill-loads of females (%FO = 66%) than males (%FO = 40%), but the difference was not significant ($\chi^2_1 = 1.9$, $n = 27$, $p = 0.17$, $d = 0.6$; Fig. 2A, B). In 2012, bill-loads of females contained significantly less squid (%N = $10 \pm 6\%$) than those of males (%N = $42 \pm 10\%$; 2 sample bootstrap, $p = 0.02$, $d = 1.0$; Fig. 2A, B). Squid also occurred significantly less frequently in bill-loads of females (%FO = 25%) than males (%FO = 73%; $\chi^2_1 = 6.5$, $n = 27$, $p = 0.02$, $d = 1.1$; Fig. 2A, B). In 2013, bill-loads of females ($n = 10$) contained significantly less anchovy than those of males ($n = 15$; %N = $15 \pm 11\%$ females vs. $50 \pm 13\%$ males; 2 sample bootstrap, $p = 0.05$, $d = 0.8$; Fig. 2C, D). Bill-loads of females also contained anchovy less frequently than those of males in 2013, but the difference was not significant (females %FO = 20% vs. males %FO = 53%; $\chi^2_1 = 2.9$, $n = 25$, $p = 0.09$, $d = 0.7$; Fig. 2C, D). In 2013, bill-loads of females had greater %N and %FO of shortbelly rockfish than bill-loads of males, but these differences were not significant (%N, 2 sample bootstrap, $p = 0.15$, $d = 0.6$; %FO, $\chi^2_1 = 1.9$, $n = 25$, $p = 0.16$, $d = 0.6$; Fig. 2C, D).

Bill-load masses of females ($n = 22$) and males ($n = 30$) did not differ across years (females = 25.0 ± 3.5 g vs. males = 25.4 ± 0.4 g; $F_{1, 48} = 0.3$, $p = 0.61$, $d = 0.2$) or within years (2012 $t_{48} = -0.8$, $p = 0.42$, $d = 0.28$; 2013 $t_{48} = 1.5$, $p = 0.14$, $d = 0.6$). Bill-load masses of both sexes together were significantly greater in 2012 (28.6 ± 3.0 g, $n = 27$) than in 2013 (21.5 ± 2.3 g, $n = 25$; $F_{1, 48} = 6.0$, $p = 0.02$,

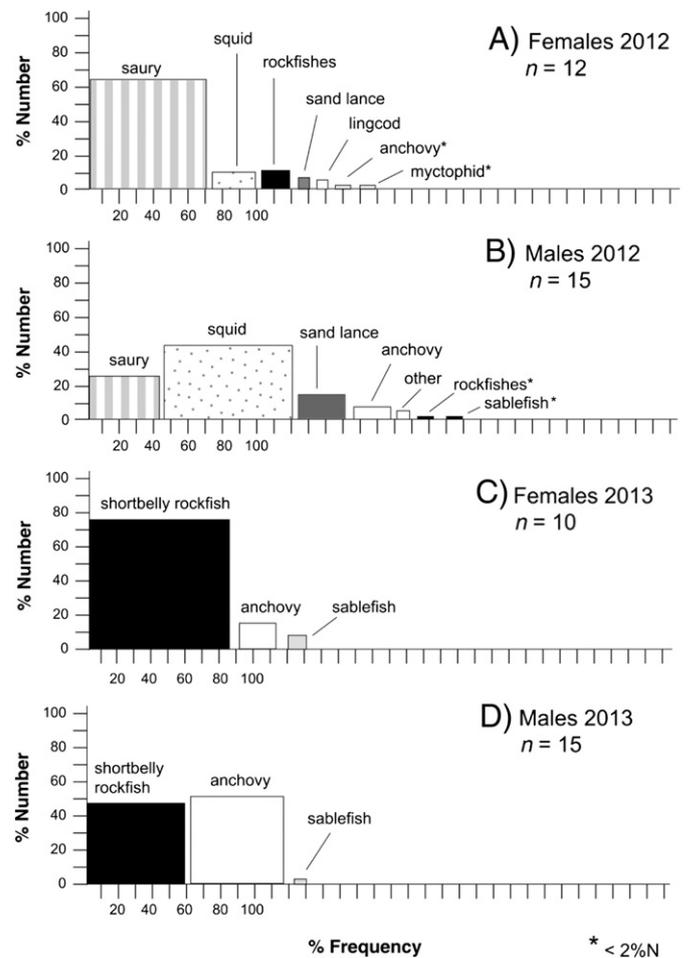


Fig. 2. Prey provided to chicks by male and female Rhinoceros Auklets, calculated as $\bar{x}\%$ number (y axes) and % frequency of occurrence (scaled on x axes) of species per bill-load for A) females in 2012, B) males in 2012, C) females in 2013, and D) males in 2013.

$d = 0.5$). This trend was driven by significantly heavier bill-loads of females in 2012 (31.1 ± 9.0 g, $n = 12$) than in 2013 (17.6 ± 2.8 g, $n = 10$; $t_{48} = -2.7$, $p = 0.01$, $d = 1.5$), whereas bill-load masses of males did not differ between years (26.6 ± 3.1 g in 2012, $n = 15$; 24.1 ± 3.2 g in 2013, $n = 15$; $t_{48} = -0.7$, $p = 0.53$, $d = 0.2$).

3.8. Sex-specific diet

Stable isotope values of males and females did not differ (2 sample bootstraps, $p = >0.10$, $d = <0.5$ for all; Fig. 3), except during the chick-rearing periods of both years and fall winter 2011–12. The greatest magnitude difference between sexes occurred during the 2012 chick-rearing period, when $\delta^{13}\text{C}$ of males (-18.37 ± 0.16) was significantly greater than that of females (-18.97 ± 0.19 ; 2 sample bootstrap, $p = 0.02$, $d = 1.0$, Figs. 3, 4). There was no difference in $\delta^{15}\text{N}$ between sexes during the same period (2 sample bootstrap, $p = 0.71$, $d = 0.2$; Figs. 3, 4). Mixing model mean estimates of prey proportions in female diet during the 2012 chick-rearing period were significantly correlated with %N of prey delivered to chicks by females that year ($\beta = 1.15$, $p = 0.0001$, $r^2 = 0.98$), with saury being the dominant prey item in both metrics (Fig. 2A, Table 3). Whereas mixing models estimated that saury made up the majority of male diet (mean 56%; Table 3) during the 2012 chick-rearing period, the dominant prey in males' bill-loads that year was squid (42%N; Fig. 2B). Mixing model estimates of prey proportions in male diet during this period and %N of prey delivered by males were not correlated ($\beta = 0.46$, $p = 0.48$, $r^2 = 0.13$). However, mixing model estimates of males and female diet during the 2012 chick-rearing period (Table 3) were consistent with the trend observed in bill-loads of females delivering more saury and males more squid to chicks (Fig. 2A, B).

During the 2013 chick-rearing period, $\delta^{15}\text{N}$ of males was significantly greater than that of females (by 0.23‰; 2 sample bootstrap, $p = 0.02$,

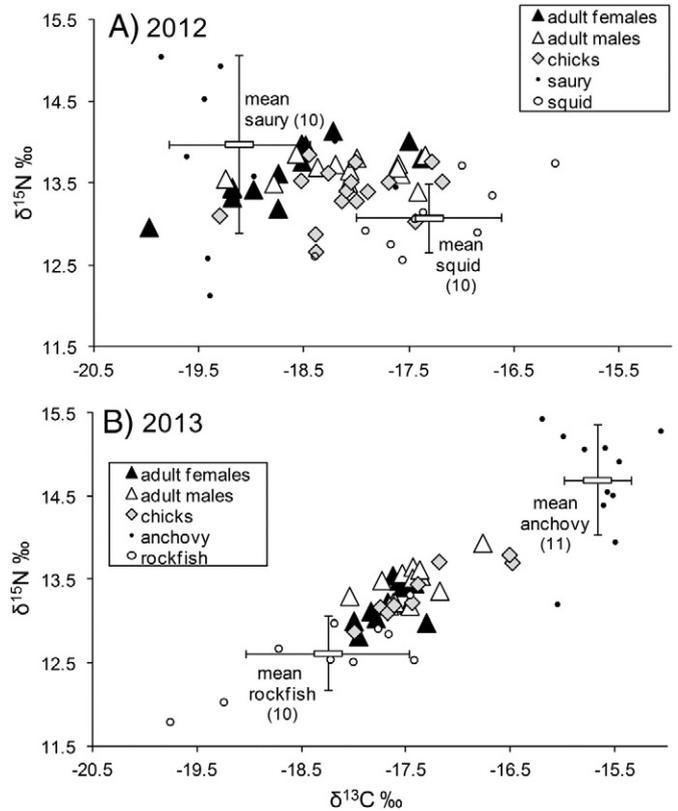


Fig. 4. Fractionation-adjusted chick-rearing period isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, ‰) of individual adult male and female Rhinoceros Auklets and chicks, and individual and mean values (± 1 SD‰) of dominant prey during the 2012 (A) and 2013 (B). Prey sample sizes are in parentheses.

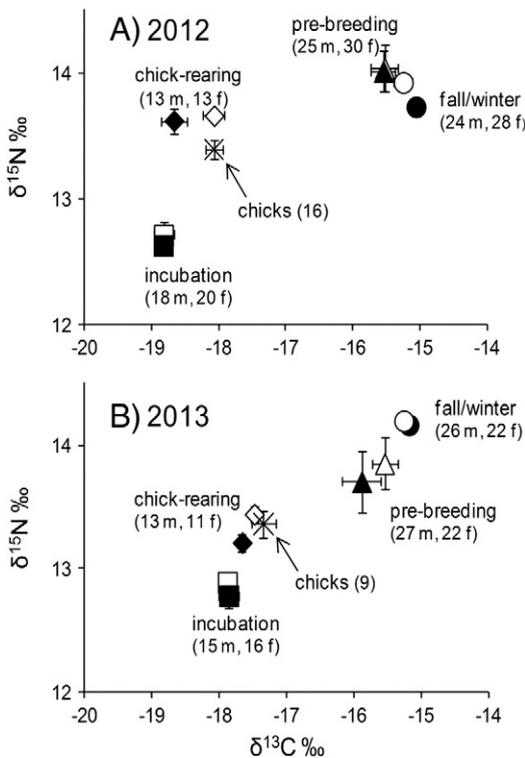


Fig. 3. Fractionation-adjusted stable isotope values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, $\bar{x} \pm \text{SE}$ ‰) of Rhinoceros Auklet adult male and female and chick tissues in 2012 (A) and 2013 (B). Black shapes represent adult females, white shapes represent adult males, and an X represents chicks. Sample sizes are in parentheses (m = male, f = female).

$d = 1.0$), whereas $\delta^{13}\text{C}$ did not differ between sexes (2 sample bootstrap, $p = 0.12$, $d = 0.7$; Figs. 3, 4). Mixing models indicated that during the 2013 chick-rearing period females consumed 1–70% shortbelly rockfish and 10–26% anchovy, whereas males consumed 3–63% shortbelly rockfish and 23–35% anchovy (Table 3). This was consistent with bill-loads in 2013, when males delivered more anchovy and females delivered more shortbelly rockfish (Fig. 2C, D). During fall/winter of 2011–2012, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of males were greater than those of females by 0.19‰ (Fig. 3). This difference was significant for $\delta^{15}\text{N}$ (2 sample bootstrap, $p = 0.003$, $d = 0.9$) but not $\delta^{13}\text{C}$ ($p = 0.27$, $d = 0.3$). Mixing models indicated that males may have taken up to 30% more anchovy (99th percentile) than females during fall/winter 2011–12 (Table 3). However, we considered diet differences between sexes during the 2013 chick-rearing and 2011–12 fall/winter periods inconclusive given the small magnitude differences in isotope values and the uncertainty inherent in mixing model estimates.

4. Discussion

Using stable isotopes, we found both seasonal and sex-specific patterns in Rhinoceros Auklet diet. Rhinoceros Auklet adult diet underwent similar seasonal shifts in 2 consecutive years with different oceanographic conditions. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of adult male and female Rhinoceros Auklets did not differ ($p \geq 0.10$) except during the chick-rearing period both years and fall/winter 2011–12. Sex-specific diet and chick provisioning differences were significant and conclusive only during the 2012 chick-rearing period. During this period, female diet and bill-loads contained proportionally more saury and less squid than male diet and bill-loads.

Rhinoceros Auklet chick growth (g d^{-1}), survival to fledging, and overall productivity were lower in 2012 than in 2013, whereas hatching success did not differ between years. Rhinoceros Auklet chick growth

Table 3

Mean and range (1st–99th percentile, in parentheses) of feasible solutions for prey contributions adult female and male Rhinoceros Auklet diets from dual isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) mixing model IsoSource (Phillips and Gregg, 2003). Results are shown for periods during which male and female $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ mean values differed significantly (2 sample bootstraps, $p \leq 0.02$ and $d \geq 0.80$ for all). Values for which the 99th percentile solution was greater than 25% are bolded. Pacific saury was not included as a potential source in 2013 models.

	Fall/winter 2012		Chick-rearing 2012		Chick-rearing 2013	
	Females <i>n</i> = 28	Males <i>n</i> = 24	Female <i>n</i> = 13	Males <i>n</i> = 13	Females <i>n</i> = 11	Males <i>n</i> = 13
Pacific saury	0 (0–1)	1 (0–4)	75 (66–83)	56 (46–63)	–	–
Market squid	1 (0–4)	3 (0–12)	6 (0–21)	8 (0–32)	3 (0–10)	2 (0–7)
Pacific sand lance	27 (1–63)	10 (0–30)	4 (0–14)	9 (0–31)	13 (0–48)	9 (0–32)
Rockfish spp.	0 (0–1)	1 (0–3)	5 (0–12)	3 (0–11)	39 (1–70)	40 (3–63)
Northern anchovy	67 (34–90)	80 (64–92)	4 (0–15)	17 (1–33)	18 (10–26)	29 (23–35)
Sablefish	3 (0–13)	4 (0–14)	2 (0–8)	2 (0–7)	27 (0–76)	21 (0–67)
Euphausiid (<i>T. spinifera</i>)	2 (0–6)	0 (0–5)	4 (0–15)	5 (0–18)	1 (0–4)	0 (0–2)

and survival to fledging have been linked with the abundance and quality of prey available during chick-rearing (Vermeer, 1980; Takahashi et al., 2001; Thayer and Sydeman, 2007). Poorer chick growth and survival to fledging in 2012 may have resulted from chicks being fed mainly saury and squid, which typically have lower nutritional quality than juvenile rockfishes or anchovy (Beaubier and Hipfner, 2013; Becker et al., 2007a; Thayer and Sydeman, 2007). In a previous study in central California, Rhinoceros Auklet chicks grew faster when they were fed more juvenile rockfishes and anchovy and slower when they were fed more saury (Thayer and Sydeman, 2007). Furthermore, chick survival to fledging depended more strongly on the overall mass of bill-loads than the species of prey provided to chicks (Thayer and Sydeman, 2007). In our study, however, bill-loads were significantly heavier in 2012, when chick survival to fledging was significantly less (65% in 2012 vs. 86% in 2013). Therefore, adults may have fed chicks less frequently in 2012, so that chicks received less food overall despite being provided larger meals.

Thayer and Sydeman (2007) found that annual bill-load composition of Rhinoceros Auklets at ANI reflected actual abundance of juvenile rockfishes and anchovy in the environment. NMFS trawl surveys conducted near ANI indicated that juvenile rockfish abundance was near the long-term average (1990–2013) in 2012, but was the greatest on record in 2013 (Wells et al., 2013). Trawls also indicated that anchovy abundance was well below average in 2012 and slightly below average in 2013, whereas squid abundance was above average in both years, particularly 2012 (Wells et al., 2013). Thus, Rhinoceros Auklets may have selected saury and squid for chicks in 2012 because high-quality alternate prey was unavailable that year. However, abundance estimates for anchovy and squid from these night trawls must be interpreted with caution because both species are fast and patchy and thus able to avoid sampling gear designed for juvenile rockfishes. No direct survey data exist on saury distribution or abundance in the region during the study. Saury are often associated with warm (i.e. 15–17 °C), deep waters (Hughes, 1974; Smith et al., 1970), but distribution and abundance is highly variable (Hughes, 1974; Tian et al., 2004; Tseng et al., 2013). Sea surface temperature, upwelling, and chlorophyll-*a* concentrations around ANI were greater in spring of 2013 than 2012 (Bjorkstedt et al., 2011; Wells et al., 2013), potentially creating better environmental conditions for juvenile rockfishes during 2013 (Ralston et al., 2013).

Mixing models indicated that adult diet in fall/winter of both years was composed primarily of anchovy with lesser contributions by sand lance (Table 2). Whereas Rhinoceros Auklet stomachs sampled during winter in Monterey Bay in the 1970s contained primarily squid and anchovy (Baltz and Morejohn, 1977), squid was not an important fall/winter diet item during our study (99th percentile 4% in 2012, 11% in 2014; Table 2). Although this difference could be related to methodology (i.e. stomach sampling vs. stable isotopes), it seems more likely that Rhinoceros Auklets responded to inter-annual variability in prey

resources during fall/winter, as has been shown during the chick-rearing period (Vermeer, 1980; Thayer and Sydeman, 2007). Anchovy are energetically rich (Becker et al., 2007a), and may be important prey during fall/winter, when Rhinoceros Auklets undergo an energetically costly molt to replace most body feathers (Pyle, 2008). Whereas sand lance was an important prey for breeding and non-breeding Rhinoceros Auklets in Washington state and British Columbia (Vermeer, 1980; Bertram and Kaiser, 1993; Lance and Thompson, 2005), sand lance have historically been absent from Rhinoceros Auklet adult and chick diet in California (Baltz and Morejohn, 1977; Thayer and Sydeman, 2007). Rhinoceros Auklets are typically found in offshore waters in California during winter (Briggs et al., 1987), but sand lance are found in shallow (<60 m), nearshore waters (Ostrand et al., 2005). Thus, it seems unlikely that Rhinoceros Auklets preyed heavily on sand lance during fall/winter, and the 1st percentile mixing model estimates for sand lance (1% in 2012, 0% in 2013) may be most accurate.

Adults appeared to switch from eating primarily anchovy during non-breeding periods to prey with lesser $\delta^{13}\text{C}$ values (i.e. juvenile rockfishes and/or saury) during the breeding season (Fig. 1). Juvenile shortbelly rockfish were the most frequently occurring rockfish in chick diet during both years. Shortbelly rockfish are born in winter and early spring (Wylie Echevarria, 1987) and probably become large enough for seabirds to eat around March–April (Ainley et al., 1990). It appeared that adults fed heavily on juvenile rockfishes during incubation in both years (Fig. 1 and Table 2). Therefore, the heavier body mass of incubating females during 2013 could have been related to the greater availability of juvenile rockfishes that year (Wells et al., 2013).

$\delta^{13}\text{C}$ has been used as an indicator of nearshore vs. offshore feeding, with lesser $\delta^{13}\text{C}$ values representing a more “offshore” signal (Burton and Koch, 1999; Hobson et al., 1994). It was therefore unexpected that Rhinoceros Auklet $\delta^{13}\text{C}$ was lesser during the breeding season, when birds at ANI regularly return to the nearshore breeding colony. Rhinoceros Auklets may have acquired greater $\delta^{13}\text{C}$ during winter by eating anchovies. Anchovies move offshore in the winter (Mais, 1974), but might maintain a relatively greater $\delta^{13}\text{C}$ signal acquired when they were located nearshore during summer (Santora et al., 2012). Alternatively, baseline isotopic shifts may occur seasonally in relation to upwelling or other environmental factors (Michener and Kaufman, 2007). We found inter-annual shifts in prey $\delta^{13}\text{C}$ of ~1‰ (Fig. 1 and Table 1), but assumed for mixing models that prey isotope values did not change significantly within years. These inter-annual differences in prey isotopes underscore the necessity of sampling predator and prey tissues in the same year or concurrently to ensure accurate results for stable isotope studies involving forage fish.

In other regions (i.e. Alaska, British Columbia, and Japan), euphausiids were an important pre-breeding diet item for adult Rhinoceros Auklets (Davies et al., 2009; Hobson et al., 1994; Ito et al., 2009). Euphausiids, however, were not a major component of adult diet at

ANI during any period sampled (mean <5% for all periods; Table 2). Rhinoceros Auklets at ANI may not have fed heavily on euphausiids, or it is possible that breast feather isotopes did not accurately reflect pre-breeding diet. Breast feathers had the greatest isotopic variability of any tissue sampled (Fig. 1), and Rhinoceros Auklets do not molt all breast feathers during the February–March pre-alternate molt (Pyle, 2008). Pre-breeding and fall/winter isotope values were relatively similar (Fig. 1), indicating that some sampled breast feathers may have been grown during the pre-basic molt (August–January, Pyle, 2008). Therefore, we recommend caution when using breast feather isotopes to estimate seasonal Rhinoceros Auklet diet, because of the limited pre-alternate molt and difficulty of visually selecting breast feathers by age in the field.

Adult $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased between incubation and chick-rearing (Fig. 1), reinforcing a pattern observed in other populations of Rhinoceros Auklets and puffins (Hedd et al., 2010; Hipfner et al., 2013; Ito et al., 2009). Increasing trophic level may result from adults switching after chicks hatch from self-feeding on low trophic level prey to larger, energetically rich fish required by chicks (Hipfner et al., 2013). Our results support this theory, indicating that chick-rearing adults and chicks had relatively similar diets (Fig. 1). At ANI, shifting proportions of prey species in adult diet between incubation and chick-rearing (Table 2) could have been related to seasonal changes in prey availability (Ito et al., 2009). However, the dominant prey species during incubation (saury in 2012, shortbelly rockfish in 2013) continued to be dominant during chick-rearing in both years (Table 2). Prey $\delta^{15}\text{N}$ increased with prey length; therefore, Rhinoceros Auklet trophic level likely increased because birds ate larger individual prey later in the breeding season. Thus, a combination of selection, seasonal prey availability, and prey growth was likely responsible for observed increases in adult trophic level between incubation and chick-rearing.

Adult male and female isotopes values did not significantly differ, or differences were inconclusive, during all periods except the 2012 chick-rearing period, and both sexes' isotope values changed seasonally in similar directions and magnitudes (Fig. 3). Therefore, males and females likely used similar habitats and exploited similar niches during most of the year. Females, however, had significantly lesser $\delta^{13}\text{C}$ values than males during the chick-rearing period of 2012 (Figs. 3, 4). The sex-specific difference in $\delta^{13}\text{C}$ likely was due to diet, because $\delta^{13}\text{C}$ was not affected by metabolic processes in a captive study of Rhinoceros Auklet chicks (Sears et al., 2009). The $\delta^{13}\text{C}$ difference corresponded to a greater proportion of saury and a lesser proportion of squid in female vs. male diet (Table 3). During the same period, females provisioned chicks with more saury and less squid than males (Fig. 2A, B). Together, these results suggested that males and females targeted different prey during the chick-rearing period of 2012. Similar but weaker trends occurred during chick-rearing in 2013, when female bill-loads contained less anchovy and more juvenile rockfish than male bill-loads (Fig. 2C, D).

While this study was not designed to determine the mechanism driving sex-specific differences, multiple metrics provided clues to potential causes of differences during the 2012 chick-rearing period. Niche separation deriving from physiological differences between sexes seems unlikely, because male and female diet was similar during other seasons. Intra-specific competitive exclusion also seems unlikely because of the small breeding population at ANI (~260 breeding birds; Hester et al., 2013). However, the biogeography of prey taken during the 2012 chick-rearing period indicated that males and females may have foraged in different locations. Saury most frequently occur from 40–160 km offshore (Leet et al., 1992; Smith et al., 1970), and are typically associated with relatively warm (i.e. 15–17 °C), deep waters and thermal fronts (Hughes, 1974). Market squid typically occur in the immediate vicinity (i.e. <10 km) of ANI during spring and summer (Santora et al., 2012). Average foraging trip length of Rhinoceros Auklets in Japan was 87 km (Kato et al., 2003) and presumably Rhinoceros Auklets at ANI travel similar distances. Thus, females may have taken more saury than males because they foraged farther offshore more

often. In British Columbia, Rhinoceros Auklets foraged over a larger area and spent more time engaged in solitary foraging and less time in foraging flocks when prey was in lesser densities (Davoren, 2000). Thus, it is plausible that females foraged over greater distances in 2012 in response to lesser availability of preferred prey that year.

In other alcids such as Cassin's Auklets (*Ptychoramphus aleuticus*), and Dovekies (*Alle alle*), chick-rearing females foraged farther from the breeding colony than males, which may have been related to sex-specific energetic constraints (Adams et al., 2004; Welcker et al., 2009). Hypothetically, females need to recover body condition lost during egg formation and/or incubation and consequently may take longer foraging trips than males in order to self-feed (Adams et al., 2004; Bradley et al., 2002; Welcker et al., 2009). Serially-weighed females in our study weighed less during incubation in 2012 than 2013, whereas males displayed no difference. Thus, females in poorer body condition during incubation in 2012 may have invested greater effort to self-feed in more predictable or productive areas farther from the breeding colony that year (Jakubas et al., 2012; Weimerskirch, 1998, 2007).

Heavier bill-load masses of females in 2012, compared with those of males during both years and females in 2013, may also have indicated more distant foraging trips by females that year. Many seabirds, including bill-loading species that deliver frequently (e.g., Common Murres [*Uria aalge*; Uttely et al., 1994] and Common Terns [*Sterna hirundo*; Burness et al., 1994]), increased food-loads for chicks and decreased meal frequency when foraging farther from the colony (Granadeiro et al., 1998; Gray and Hamer, 2001; Weimerskirch, 1998). However, Rhinoceros Auklets in Japan maintained consistent bill-load masses despite changes in foraging distance (Deguchi et al., 2010). In our study, greater bill-load masses of females in 2012 indicated that Rhinoceros Auklets did adjust meal sizes, though the relationship with foraging distance is not known. However, poor chick growth and survival to fledging despite heavier bill-loads in 2012 indicated that chicks may have been fed less frequently. Thus, we hypothesize that because females had lesser body condition during the 2012 breeding season, they prioritized feeding themselves and foraged farther from the colony than males, potentially influencing observed poorer overall reproductive success during 2012. Diet and provisioning differences between sexes may have been less pronounced during 2013 because energetically sufficient prey were abundant and females were in superior body condition. Further study on sex-specific foraging areas, dive behavior, and chick-feeding frequency is needed to better resolve sex-based differences in foraging strategies.

In conclusion, we found that the diets of adult Rhinoceros Auklets underwent consistent seasonal shifts across 2 years with differing environmental conditions, and that sex-specific differences in diet and prey delivered to chicks were likely related to energetic constraints, prey availability, or both. Furthermore, Rhinoceros Auklet diet was composed of a mixture of commercially fished and un-fished species, of both the classic "forage" category (i.e. anchovy, squid, saury) and juvenile ground-fishes (i.e. shortbelly rockfish, sablefish, lingcod). The observed temporal and demographic variability in Rhinoceros Auklet diet underscores the importance of understanding and managing multiple prey populations in the central California Current region so that generalist marine predators have sufficient resources through changing energetic and oceanic conditions.

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