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Seasonal and sex-specific diet in rhinoceros auklets

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SEASONAL AND SEX-SPECIFIC DIET IN RHINOCEROS AUKLETS

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ABSTRACT

SEASONAL AND SEX-SPECIFIC DIET IN RHINOCEROS AUKLETS

By Ryan Carle

We used stable isotopes (δ^{15}N and δ^{13}C) and conventional chick-diet sampling methods to evaluate seasonal shifts in diets of adult male and female rhinoceros auklets (*Cerorhinca monocerata*) and prey provided to chicks by each sex in California during 2012-2013. Rhinoceros auklet isotope values underwent similar shifts in both years, which differed in environmental and prey conditions. Mixing models indicated that northern anchovy (*Engraulis mordax*) were important prey for adults during fall/winter and juvenile rockfish spp. were important prey during incubation in both years. Adult trophic level increased between the incubation and chick-rearing periods, and mixing models indicated that adults likely ate similar prey species as those fed to chicks during both years. δ^{15}N and δ^{13}C of males and females were similar ($P = > 0.05$) during most seasons. During the 2012 chick-rearing period, however, adult female diet and meals delivered to chicks by females contained more Pacific saury (*Cololabis saira*) and less market squid (*Doryteuthis opalescens*) than male diet and meals delivered to chicks by males. Chick growth and survival to fledging were less during 2012 than during 2013, likely because chicks were fed lesser quality prey or fed less frequently in 2012. Lesser body condition of females but not males during incubation in 2012 indicated that sex-specific diet and chick provisioning differences during the 2012 chick-rearing period may have been related to energetic constraints on females.

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INTRODUCTION

The interaction between seasonal energetic constraints and seasonal prey availability is critical for the fitness of predators, including seabirds (Ainley et al. 1990, Soto et al. 2004, Frederiksen et al. 2006). Many seabirds live in environments where primary productivity and prey availability vary on seasonal and inter-annual scales (e.g., polar ecosystems and eastern boundary upwelling currents). Often seabird life history constraints such as molt and central place foraging during breeding result in decreased mobility concurrent with increased energetic demands; the resulting energetic "pinch points" can be critical to fitness (Nelson 1980). For instance, communities of seabirds may suffer diminished reproductive success when prey availability is reduced during breeding (Ainley et al. 1995, Fredericksen et al. 2006), and seabird die-offs sometimes occur when quality prey is not sufficiently available to birds to fulfill energetic needs during non-breeding periods (Bodkin and Jameson 1991, Baduini et al. 2001).

In seabirds, sexes may use prey resources differently during the energetically demanding breeding period (Phillips et al. 2011). Sex-specific differences have been observed in many aspects of seabird reproduction, including chick-provisioning (Wiggins and Morris 1987, Wagner 1997, Quillfeldt et al. 2004), diet (Bearhop et al. 2006, Phillips et al. 2011), and foraging behavior (Gonzalez-Solis et al. 2000, Lewis et al. 2002, Peck and Congdon 2006). Differences between sexes occur most frequently in species with pronounced sexual dimorphism (Phillips et al. 2011) and may be the result of competitive exclusion of the smaller sex by the larger (Gonzalez-Solis et al. 2000, Forero et al. 2005) or physiological differences allowing one sex access to different foraging niches (e.g.,

deeper diving depth of the heavier sex; Bearhop et al. 2006). Sex-specific diets or behaviors in monomorphic seabirds were hypothesized to be related to differing energetic constraints on each sex during the breeding season (Fraser et al. 2002, Paredes et al. 2008, Welcker et al. 2009). The majority of studies reporting sex-specific differences in seabird diets were conducted during the breeding season (Phillips et al. 2011); thus, little is known about whether sex-specific patterns occur during non-breeding periods. Knowledge of the diet of both sexes during the entire year, as birds experience a variety of energetic constraints, would be useful for understanding why and how sex-specific differences in seabird diets occur.

The Rhinoceros auklet (*Cerorhinca monocerata*; Family *Alcidae*) is a seabird in the puffin tribe (Gaston and Dechesne 1996). Rhinoceros auklets breed on nearshore islands and spend winter mainly over shelf waters (<200 m depth) in the North Pacific Ocean from California to Japan (Gaston and Dechesne 1996). Male rhinoceros auklets are slightly larger and heavier than females (males in this study averaged 5% heavier than females), but morphometric differences are not diagnostic (Pyle 2008). Rhinoceros auklets breed in burrows, females lay single egg clutches, and both parents contribute to incubation and chick-rearing (Gaston and Dechesne 1996). Parents carry whole fishes and cephalopods in their bills and deliver them to chicks in "bill-loads" (Thayer and Sydeman 2007), with each adult averaging one bill-load delivered a night (Takahashi et al. 1999). Adults consume krill in the spring pre-breeding and incubation periods in some regions (Ito et al. 2009, Sorensen et al. 2010). Adult trophic level increases after chicks hatch, likely because adults switch at this time to eating fish with greater caloric

content, which are required by growing chicks (Ito et al. 2009, Davies et al. 2009, Hipfner et al. 2013). Adult males and females may consume similar species and size classes of prey as they provide to chicks, but results of observational and trophic studies have been mixed (Davoren and Burger 1999, Ito et al. 2009, Hipfner et al. 2013). No clear sex-specific differences in diet or in provisioning patterns have been documented in rhinoceros auklets.

To examine seasonal diet shifts and potential sex-specific patterns, we used stable isotopes (δ^{15}N and δ^{13}C) of rhinoceros auklet tissues and prey at Año Nuevo Island, CA. We also compared the frequency of occurrence and proportions of prey species delivered to chicks (termed provisioning) by males and females. To investigate the influence of inter-annual environmental variation on potential seasonal diet shifts and sex-specific patterns, we conducted the study in two years with differing oceanographic conditions. Whereas dramatic inter-annual variability in composition of rhinoceros auklet prey has been documented in this study population (Thayer and Sydeman 2007, Hester et al. 2013), potential seasonal and sex-specific differences in diet in this region remain unexamined. We hypothesized that rhinoceros auklet diet would shift seasonally and inter-annually. Specifically, rhinoceros auklet isotopes should reflect greater trophic level consumption (i.e. δ^{15}N values) during mid-summer when larger size-classes of forage fish were selected to meet greater overall energy demands (i.e., concurrent self-foraging and chick-provisioning). Due to minimal sexual dimorphism in rhinoceros auklets, we hypothesized no sex-specific differences in diet exist according to season and no sex-specific differences exist in composition of prey provided to chicks.

METHODS

Study Site and Field Methods

Año Nuevo Island (ANI; 37° 06' N, 122° 20' W) is 1 km off central California. Within the California Current upwelling system, seasonal peaks in primary productivity and prey abundance occur during spring and summer in response to wind-forced upwelling (Chavez et al. 2002). At ANI, rhinoceros auklets lay eggs from mid-April to late May, and young are provisioned by both parents from June through August (Figure 1; Thayer and Sydeman 2007).

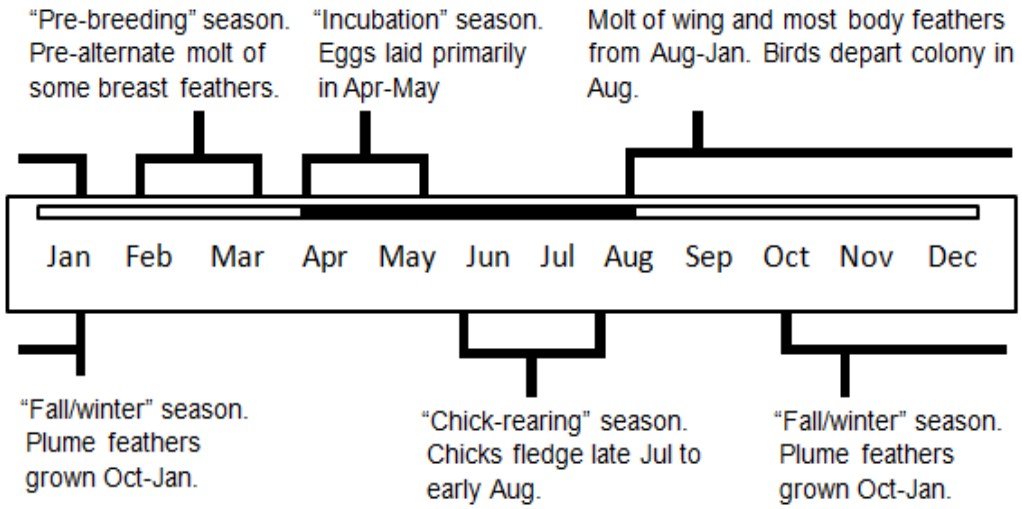

Figure 1. Reproductive and molt phenology of rhinoceros auklets at Año Nuevo Island, California. Black bar in box above months indicates breeding period; white bar indicates non-breeding period.

Approximately 260 rhinoceros auklets nested annually at ANI during the study period (Hester et al. 2013).

During the annual incubation period, we collected blood, breast feathers, and plume feathers from both parents of all pairs breeding in artificial nest sites (n = 42 in 2012, n = 34 in 2013). All birds were banded with a metal U.S. Fish and Wildlife Service leg band, and band numbers were recorded from birds previously banded. The mass of each bird and the bag it was weighed in were determined ± 5.0 g using a 600 or 1000 g spring scale. The mass of each bird was total mass minus mass of the bag (± 1.0 g using a 300 g spring scale). Blood was sampled within 7 to 14 days of egg lay (May 1-30 2012, April 25-June 5 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, we assumed isotope values of blood sampled from incubating birds represented the period in April or May just before egg-laying (hereafter termed incubation). Blood (~1 ml per bird) was collected in unheparinized capillary tubes and stored in glass vials for isotope analysis (frozen at -20° C) and on paper FTA cards (Fast Technology for Analysis of nucleic acids; Whatman brand, General Electric, Fairfield, CT, USA) for DNA sex analysis (Fridolfsson and Ellegren 1999).

We plucked 2 breast feathers that appeared freshly grown and clipped <1 cm of facial plume feathers from each incubating bird. Feathers are metabolically inert, and stable isotope values reflect diet at the time of feather formation (Hobson and Clark 1992). Most body feathers are molted between August and January, but some breast feathers are grown in a pre-alternate molt during February and March (Figure 1; Pyle 2008). Facial plume feathers are grown slowly between October and January (Figure 1; Pyle 2008). The isotope values of fresh breast feathers, therefore, were considered a

signal of diet from the February-March pre-breeding period (hereafter pre-breeding), whereas plume feathers were considered an integrated signal of diet during the previous October-January (hereafter fall/winter).

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

We checked and weighed (± 1.0 g using a 300 or ± 5.0 using a 600 g spring scale) all chicks in artificial nest sites every 7 days, from expected hatch date to fledging. To compare reproductive success between years, we quantified hatching success, chick growth, and chick survival to fledging. We defined hatching success as the ratio of chicks hatched to eggs laid (excluding re-lays). We calculated chick growth (g d^{-1}) for the linear growth stage from days 14 to 35 (detailed methods described in Thayer and Sydeman 2007). We defined chick survival to fledging as the ratio of chicks hatched to chicks fledged. We considered chicks fledged if they reached 40 days of age, had a mass ≥200 g, and were classified as fully-feathered on the last check before disappearance (Hester 1998).

To obtain isotope values for prey delivered and quantify a sex-specific metric of chick provisioning, we collected bill-loads from parents returning to feed chicks during 4 capture events in each year (June 26-July 24 2012, June 27-July 18 2013). We caught birds in mist nets and collected dropped prey items ($n = 164$ individual prey in 27 bill-

loads in 2012, n = 54 individual prey in 25 bill-loads 2013). We determined mass (± 0.1 g using an electronic scale) and standard length (SL, fishes) or mantle length (ML, cephalopods; both ± 1.0 mm) for each prey item. Chick meals were quantified by the bill-load— a statistically independent unit representing one load of prey carried in the bill of one adult. We measured total bill-load mass (± 0.1 g), percent mass (%M), percent number (%N), and percent frequency of occurrence (%FO) of each prey species per bill-load. The %M of prey in bill-loads reflects the likely proportions of prey consumed by chicks; it was therefore used for comparison with chick $\delta^{15}N$ and $\delta^{13}C$. The metrics %N and %FO were used to test differences in prey composition of bill-loads carried by adults. We analyzed stable isotopes of prey species that were at least 2%M of chick diet. In 2013, we also analyzed stable isotopes of prey items reported from past studies that were not present in chick diet samples (i.e., the euphausiid *Thysanoessa spinifera*, and market squid, *Doryteuthis opalescens*). Euphausiid and market squid samples were collected in May 2013 near ANI during National Marine Fisheries Service (NMFS) mid-water rockfish trawl surveys (Wells et al. 2013).

We sampled tissues from confirmed breeding adults caught in mist nets (n = 26 in 2012, n = 24 in 2013) to obtain an isotope signature during chick-rearing (whole blood) and to augment pre-breeding (breast feather) and fall/winter (plume) sample sizes. We considered birds confirmed breeders if they were carrying fish when captured or were previously sampled at a nest site during incubation and identified via leg bands. Birds carrying fish were sampled for blood, breast feathers, and plumes using methods described for birds captured at nest sites.

In each year, a small number of individuals were sampled twice for bill-loads (2 males and 2 females of 23 birds in 2012, 2 males and 1 female of 22 birds in 2013), though sampling events of individuals were always at least a week apart. We qualitatively inspected bill-loads to assess the importance of individual specialization. Eighty-six percent of double-sampled birds (6 of 7) had either no overlap in prey species or a different majority of prey species in each bill-load. Thus, individual preference appeared unlikely to be a confounding bias, so we tested differences between sexes using all bill-loads sampled.

DNA Sex Analysis

Sex was determined for all birds sampled at nest sites or mist nets (n = 90 adults, 24 chicks) using DNA extracted from blood or feathers (Fridolfsson and Ellegren 1999). Sex analysis was performed at the University of Hawai'i Center for Conservation Research and Training, Manoa, HI, USA. To assess accuracy, duplicate blood samples were tested each year (n = 6 in 2012, n = 10 in 2013). In both years, 100% of the duplicates matched the originally identified sex. In 6 instances (separate of the duplicate samples), both individuals of a breeding pair were identified as the same sex. We re-analyzed these pairs and found that 5 individuals had been incorrectly identified the first time. By re-analyzing these suspect identifications, sex-identification should be ~100% accurate.

Stable Isotope Analysis

We measured $\delta^{13}C$ and $\delta^{15}N$ in adult whole blood, breast and plume feathers, chick whole blood, and prey muscle tissue. Whole blood and prey tissues (~1 g white muscle, excluding calcified parts) were dried at 60°C for 24 hr and powdered using a mortar and pestle (Pinnegar and Pulanin 1999). Prey samples were lipid extracted by placing in a 2:1 chloroform:methanol solution and agitating in a sonicator for 30 min (Bligh and Dyer 1959, Ruiz-Cooley et al. 2011). Chemicals were decanted and this process was repeated until the solvent became clear (Logan et al. 2008). The pellet was retained and dried under a fume hood for 24 hr. Before lipid extraction, euphausiids were soaked for 3 hr in a 10% HCL solution to remove calcified parts (Jacob et al. 2005). We did not lipid extract blood because it is considered unnecessary for avian blood (Bearhop et al. 2000, Cherel et al. 2005). Feathers were rinsed in 3 subsequent baths of 2:1 chloroform:methanol and dried under a fume hood for 24 hr. Plume feathers and the distal 2 cm of each breast feather were homogenized in a grinder, including the vane and rachis.

Stable isotope analysis was performed at the Idaho State University Interdisciplinary Laboratory for Elemental and Isotopic Analysis, Pocatello, ID, USA. Aliquots of 0.5 mg of blood, feathers, and prey 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 $\delta^{13}C$ are reported as ‰ values relative to the Vienna PeeDee Belemnite scale, whereas $\delta^{15}N$ values are reported as ‰ values relative to air-N2. Based on

replicates of an in-house standard (DORM-3), instrument error (SD) was estimated to be ± 0.17‰ for $\delta^{15}N$ and ± 0.06‰ for $\delta^{13}C$.

Stable Isotope Fractionation Rates

Year-specific rates for whole blood $\delta^{15}N$ and $\delta^{13}C$ fractionation were estimated by comparing observed isotope values of chick whole blood with weighted isotope means of prey observed in chick diet during bill-load sampling (using similar methodology to Davies et al. 2009 and Hipfner et al. 2014). We used feather fractionation literature values of + 3.7‰ for $\delta^{15}N$ and + 1.0‰ for $\delta^{13}C$, from a study on Common Murres (*Uria aalge*; Becker et al. 2007).

Mixing Model

We used the mixing model Isosource (Phillips and Gregg 2003) to calculate potential contributions of each prey type to adult diet during each period. If sex-specific isotope differences occurred in a period, we also used mixing models to compare the estimated diets of males and females in that period. Using dual isotope values, Isosource accommodates up to ten sources and examines all possible combinations of each source contribution (Phillips and Gregg 2003). Solutions were considered feasible if they summed to the observed rhinoceros auklet isotope value within a tolerance level of 0.1‰. As potential diet sources, we used the year-specific mean isotope values of all prey types that were ≥5%M of chick diet in at least one year. For 2012, we included euphausiids as a potential source and used isotope values of *T. spinifera* sampled in 2013 (we did not

collect euphausiid samples in 2012). For 2013, we included market squid, euphausiids (*T. spinifera*), and Pacific sand lance (*Ammodytes hexapterus*) as potential sources although they did not appear in our chick diet sample that year. Euphausiid and market squid samples were collected during NMFS mid-water trawls near ANI in 2013 (Wells et al. 2013), and one Pacific sand lance was opportunistically collected at a rhinoceros auklet burrow. Assumptions of the mixing model were that we included all relevant prey sources, fractionation rates were accurate, and prey isotope values did not change seasonally. We report the mean and range (1^{st}-99^{th} percentile) of estimated prey contributions to adult diet for each period.

Statistics

We used the statistical package JMP (SAS Institute Inc., Cary, NC, USA) for all statistics except bootstrap tests, for which we used the program Resampling Stats for Excel (Statistics.com, Arlington, VA, USA). We tested differences between years in hatching success and chick survival using likelihood ratio χ^2 tests and differences in chick growth between years using a two-tailed *t*-test. We tested for differences in fractionation-adjusted $\delta^{15}N$ and $\delta^{13}C$ between each tissue type and year using a full-factorial MANOVA. We tested differences in $\delta^{15}N$ and $\delta^{13}C$ between sexes for each tissue using 10,000 iteration bootstrap tests. We did not quantitatively test adult vs. chick isotopes because of uncertainty in fractionation rates between age classes; instead, we visually assessed the likely similarities/differences of adult and chick diet. We tested for sex-specific differences in the %FO of commonly occurring prey species in bill-loads

delivered to chicks using likelihood ratio χ^2 tests. We tested sex-specific differences in the proportions (%N) of common prey species delivered to chicks using 10,000 iteration bootstrap tests. We log-transformed bill-load masses and tested differences between sexes and years using a full-factorial ANOVA. Finally, we tested differences among $\delta^{15}N$ and $\delta^{13}C$ of prey using full-factorial ANCOVAs, with each isotope as the dependent variable, species and year as independent variables, and prey length (fish SL or cephalopod ML) as the independent covariate. For this test, we included only prey species for which we had samples in both years and had ≥10 total isotope samples. Post-hoc two-tailed *t*-tests or *F* tests were conducted to further investigate significant effects. Residuals were tested for normalcy with Shapiro-Wilk tests and for homoscedasticity by plotting against expected values and assessing symmetry.

In several tests we made multiple comparisons. We did not use Bonferroni adjustments for multiple comparisons because recently researchers have criticized these adjustments for mathematical and logical flaws, and because they may inflate Type II error in situations with low statistical power (Perneger 1998, Moran 2003, Nakagawa 2004). Instead, for each pair-wise test (i.e. *t*-tests, paired *t*-tests, and χ^2 tests), we report the test statistic, the exact *P* value, and the absolute value of Cohen's *d* metric of standardized effect size, where a score 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). All values are reported as the $\bar{x} \pm 1$ SE unless otherwise noted.

RESULTS

Reproductive Success

Hatching success did not differ between years (82% in 2012 vs. 72% in 2013; $\chi^2_1 = 0.6$, $n = 41$, $P = 0.42$, $d = 0.30$). Average chick growth was 1.8 g d^{-1} less in 2012 than in 2013 (5.1 ± 0.55 g d^{-1} in 2012, $n = 15$, 6.9 ± 0.62 g d^{-1} in 2013, $n = 10$; $t_{23} = 2.1$, $P = 0.05$, $d = 0.87$). The percentage of chicks that survived to fledging was more than twice as great in 2013 as in 2012 (32% in 2012 vs. 75% in 2013; $\chi^2_1 = 5.8$, $n = 31$, $P = 0.02$, $d = 0.95$).

Adult Mass During Incubation

The 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; $t_{30} = 0.5$, $P = 0.62$, $d = 0.20$). The mass of females during incubation averaged 17 g less in 2012 (504 ± 8 g, $n = 23$) than in 2013 (521 ± 5 g, $n = 17$; $t_{38} = 1.7$, $P = 0.10$, $d = 0.56$). We directly compared body condition of individuals in each year by testing differences in mass of individuals that were weighed both years (i.e. serially weighed). There was no difference between years in mass of serially weighed males (1 ± 7 g heavier in 2013, $n = 8$; paired t-test, $t_7 = 0.1$, $P = 0.90$, $d = 0.05$), but serially weighed females were 19 ± 8 g heavier in 2013 than in 2012 ($n = 10$; paired t-test, $t_9 = 2.3$, $P = 0.05$, $d = 0.72$).

Chick Diet

In 2012, rhinoceros auklets provided chicks with 13 prey species (Appendix 1); Pacific saury (*Cololabis saira*; hereafter saury) comprised the majority of chick diet followed by market squid (hereafter squid) and Pacific sand lance (hereafter sand lance; Table 1). All other prey types combined were 18% of chick diet in 2012, with no individual species greater than 5% (Table 1).

Table 1. Prey $\delta^{15}N$ and $\delta^{13}C$ ($\bar{x}$ ± SD ‰), length range of individual prey sampled for isotopes (standard length: SL, mantle length: ML), and % mass (%M) and % number (%N) per bill-load of prey ($\bar{x}$ ± SE) in rhinoceros auklet chick diet (n = 27 bill-loads in 2012, n = 25 bill-loads in 2013). Bolded species comprised >10%M or %N of chick diet in a year.

Species	*n* Sampled for isotopes	SL/ML range (mm)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	%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 (*T. spinifera*)	10	----	9.62 ± 0.6	-17.33 ± 0.4	----	----

For analysis, we pooled the four species of juvenile rockfish (*Sebastes* spp.) that occurred in chick diet in 2012 (Appendix 1) as the prey type "juvenile rockfish." In 2013, rhinoceros auklets provided chicks only with juvenile shortbelly rockfish (*Sebastes*

jordani), northern anchovy (*Engraulis mordax*; hereafter anchovy), and juvenile sablefish (*Anaplopoma fimbria*; Table 1).

Prey Isotope Values

Prey types with sufficient sample sizes for testing of isotope values ($n \geq 10$) were juvenile rockfish, anchovy, and squid. $\delta^{15}N$ and $\delta^{13}C$ differed between prey types ($\delta^{15}N$ $F_{2, 42} = 9.2$, $P = < 0.001$; $\delta^{13}C$ $F_{2, 42} = 32.8$, $P = < 0.001$; Table 1). $\delta^{15}N$ of prey did not differ between years ($F_{1, 42} = 0.4$, $P = 0.56$), but prey $\delta^{13}C$ values were more positive in 2013 than in 2012 ($F_{1, 42} = 8.5$, $P = 0.006$; Table 1). Mean $\delta^{13}C$ values were 0.59‰ (anchovy), 1.08‰ (squid), and 1.42‰ (juvenile rockfish) greater in 2013 than in 2012 (Table 1). Prey length affected $\delta^{15}N$ ($F_{1, 42} = 10.4$, $P = 0.002$); visually assessing this trend it was clear that longer fish had greater $\delta^{15}N$. There also was a year*length interaction effect ($F_{1, 42} = 4.6$, $P = 0.04$). Across both years, there was no effect of prey length ($F_{1, 42} = 1.2$, $P = 0.29$), or interaction effects on $\delta^{13}C$ ($P = > 0.10$ for all).

Blood Isotope Fractionation Rates

Isotope fractionation rates of chick whole blood were + 2.0‰ in 2012 and + 1.4‰ in 2013 for $\delta^{15}N$, and - 0.2‰ in 2012 and - 0.4‰ in 2013 for $\delta^{13}C$. Growth and/or starvation in chicks can affect isotope fractionation rates, especially of $\delta^{15}N$ (Sears et al. 2009). Greater $\delta^{15}N$ fractionation in chicks in 2012 may have been related to food restriction that year (Hobson et al. 1992, Hobson et al. 1993), whereas rapid growth of healthy chicks in 2013 may have resulted in decreased $\delta^{15}N$ fractionation (Sears et al.

2009). Due to uncertainty associated with differences in chick blood fractionation between years, we chose to apply the average chick blood fractionation rates (+ 1.7‰ for $\delta^{15}N$ and - 0.3‰ for $\delta^{13}C$) to adult whole blood in both years. $\delta^{13}C$ fractionation should be similar in adults and chicks because in captive experiments, $\delta^{13}C$ fractionation of rhinoceros auklet chicks was unaffected by metabolic processes (Sears et al. 2009).

Inter-annual and Seasonal Diet Patterns

Fractionation-adjusted $\delta^{15}N$ and $\delta^{13}C$ of adults differed between 2012 and 2013 overall ($F_{2, 319} = 17.5$, $P = < 0.001$), with significant differences in adult $\delta^{15}N$ and $\delta^{13}C$ 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 breast feathers (pre-breeding period; $F_{2, 319} = 1.6$, $P = 0.20$). The greatest inter-annual differences in isotope values occurred in $\delta^{13}C$ in blood of incubating adults, chick-rearing adults, and chicks; all had ~1‰ greater $\delta^{13}C$ in 2013 vs. 2012 (Figure 2).

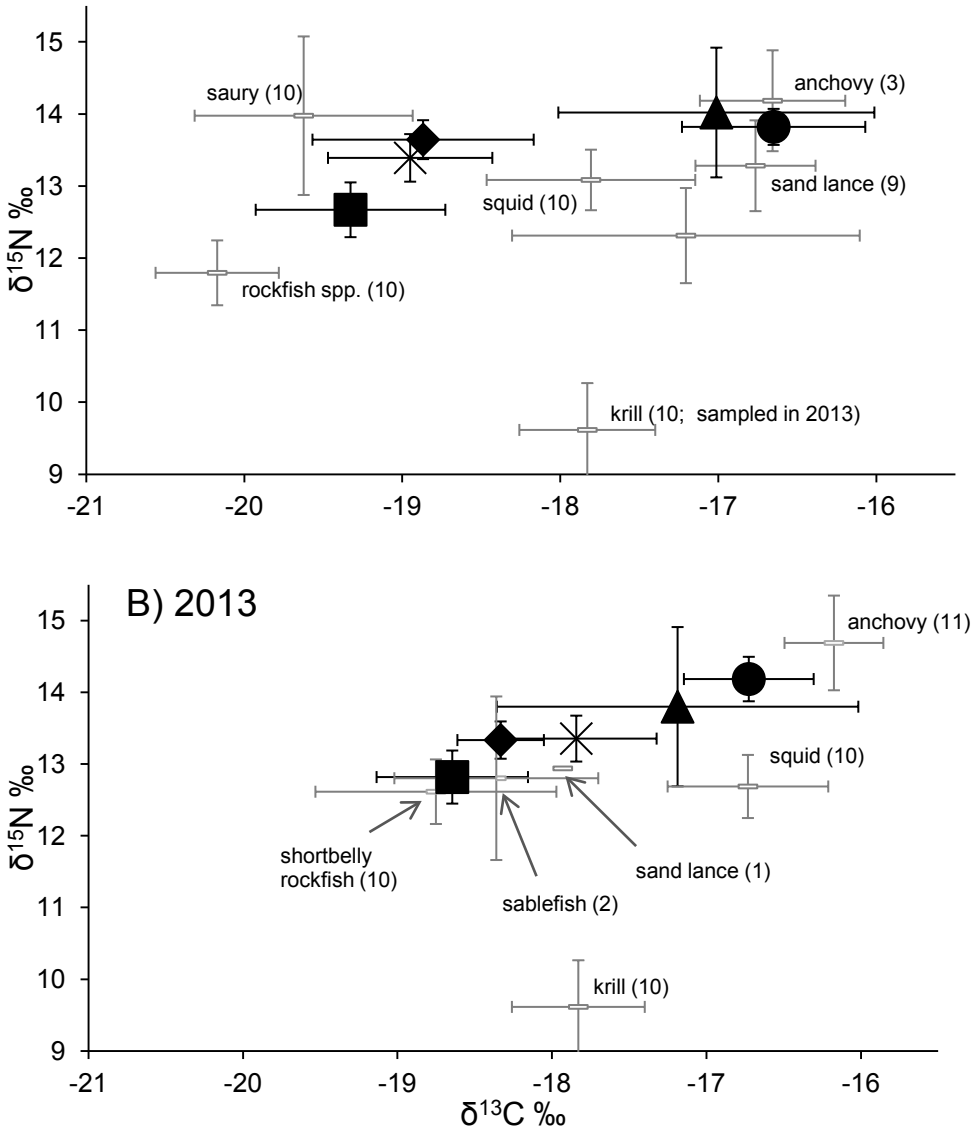

Figure 2. Fractionation-adjusted stable isotope values (δ^{15}N and δC^{13}, $\bar{x} \pm$ SE ‰) of rhinoceros auklet tissues and prey in 2012(**A**) and 2013(**B**). Circles represent fall/winter (plume feathers), triangles represent pre-breeding (breast feathers), squares represent incubation (whole blood), diamonds represent chick-rearing (whole blood), and and X represents chicks (whole blood). Prey sample sizes are in parentheses. See Table 3 for rhinoceros auklet tissue sample sizes.

This trend matched the ~1‰ average increase in prey $\delta^{13}C$ values between 2012 and 2013 (Table 1). Fall/winter and pre-breeding values differed more in $\delta^{15}N$ than $\delta^{13}C$ values between years (Figure 2).

Across both years, dual isotope values adjusted with tissue-specific discrimination factors differed by tissue type ($F_{6, 638} = 90.7$, $P = < 0.001$). We did not individually test differences between $\delta^{15}N$ and $\delta^{13}C$ of tissue types in each year because differences were visually apparent when graphed (Figure 2). Mixing model results indicated that anchovy was likely the dominant prey of adult rhinoceros auklets during fall/winter and pre-breeding periods of both years (Table 2).

Table 2. Mean and range (1^{st}-99^{th} percentile, in parentheses) of feasible solutions for prey contributions to adult diet from dual isotope ($\delta^{15}N$ and $\delta^{13}C$) mixing model IsoSource (Phillips and Gregg 2003). Results are means of both sexes pooled for fall/winter (Nov-Jan; plume feathers), pre-breeding (Feb-March; breast feathers), incubation (April-May; whole blood), and chick-rearing periods (June-July; whole blood) of 2012 and 2013. Species for which the 99^{th} percentile solution was greater than 25% in a period are bolded.

	Fall/winter	**Pre-breeding**	**Incubation**	**Chick-rearing**
2012				
Pacific saury	00 (00-01)	08 (01-13)	**44 (33-59)**	**65 (56-73)**
Market squid	00 (00-04)	04 (00-16)	06 (00-21)	**08 (00-30)**
Pacific sand lance	**24 (01-46)**	05 (00-19)	04 (00-14)	07 (00-22)
Rockfish spp.	00 (00-01)	01 (00-06)	**34 (19-45)**	03 (00-11)
Northern anchovy	**71 (52-90)**	**79 (68-89)**	04 (00-14)	09 (00-23)
Sablefish	03 (00-12)	02 (00-09)	04 (00-15)	05 (00-18)
Euphausiid (*T. spinifera*)	02 (00-05)	01 (00-03)	04 (00-16)	02 (00-07)
2013				
Market squid	03 (00-11)	03 (00-11)	03 (00-12)	00 (00-01)
Pacific sand lance	**08 (00-25)**	**19 (00-42)**	**12 (00-42)**	02 (00-05)
Shortbelly rockfish	07 (00-20)	**16 (00-36)**	**51 (06-81)**	**65 (55-70)**
Northern anchovy	**73 (68-79)**	**53 (46-60)**	05 (00-13)	**29 (28-30)**
Sablefish	08 (00-23)	**15 (00-41)**	**28 (00-85)**	04 (00-17)
Euphausiid (*T. spinifera*)	01 (00-04)	01 (00-04)	01 (00-05)	00 (00-00)

Fractionation-adjusted $\delta^{15}N$ and $\delta^{13}C$ decreased between the pre-breeding period and incubation periods (Figure 2). During incubation in 2012, likely primary prey of adults were Pacific saury (1^{st}-99^{th} percentile 33-59%) and juvenile rockfish (19-45%; Table 2).

During incubation in 2013, likely primary prey of adults were juvenile shortbelly rockfish (6-81%) and/or juvenile sablefish (0-85%; Table 2). $\delta^{15}N$ and $\delta^{13}C$ increased between the incubation and chick-rearing periods of both years (Figure 2). In 2012, saury likely was the primary prey in adult diet during chick-rearing (56-73%), with a potentially important contribution of squid (0-30%; Table 2). In 2013, the likely primary prey of adults during chick-rearing were juvenile shortbelly rockfish (55-70%) and anchovy (28-30%; Table 2). Probable primary prey in adult diet during the chick-rearing period were the same species as observed in bill-loads delivered to chicks each year (Table 1, Table 2).

Sex-specific Chick Provisioning

We tested sex-specific differences in prey provisioned to chicks using the dominant prey provided to chicks each year: saury and squid in 2012, shortbelly rockfish and anchovy in 2013. In 2012, bill-loads of females contained significantly greater %N of saury (65 ± 14%, $n = 12$) than bill-loads of males (26 ± 10%, $n = 15$; 2 sample bootstrap, $P = 0.04$, $d = 0.89$; Figure 3A, 3B).

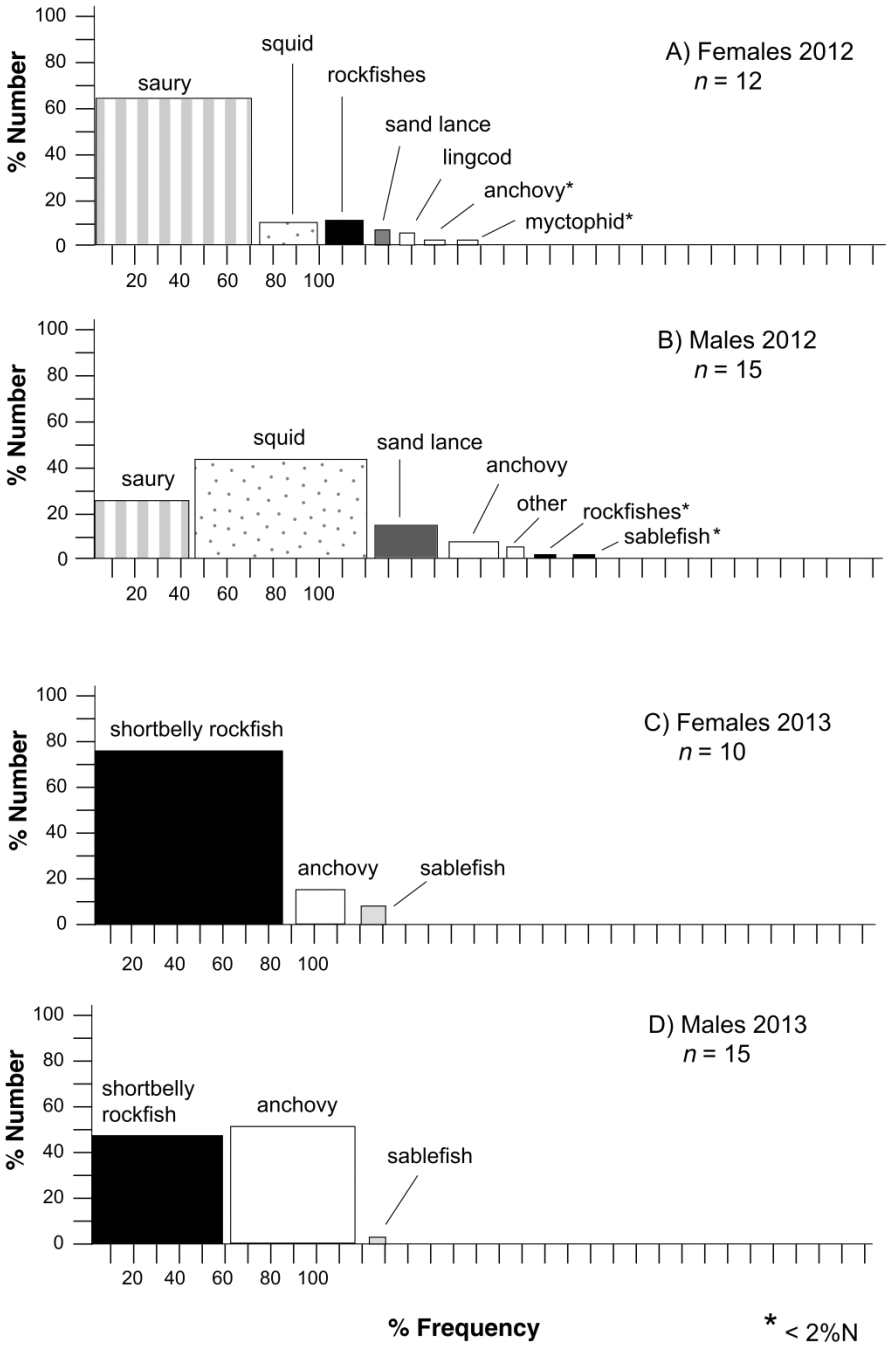

Figure 3. Prey provided to chicks by male and female rhinoceros auklets, calculated as $\bar{x}$ % number and % frequency of occurrence of species per bill-load for **A**) females in 2012, **B**) males in 2012, **C**) females in 2013, and **D**) males in 2013.

Saury occurred in 66% of female bill-loads vs. 40% of male bill-loads, but this difference was not strong statistically ($\chi^2_1 = 1.9$, $n = 27$, $P = 0.17$, $d = 0.56$; Figure 3A, 3B). In 2012, bill-loads of females contained less %N of squid (10 ± 6%) than bill-loads of males (42 ± 10%; 2 sample bootstrap, $P = 0.02$, $d = 1.01$; Figure 3A, 3B). Squid occurred less frequently in bill-loads of females (%FO = 25%) than in those of males (%FO = 73%; $\chi^2_1 = 6.5$, $n = 27$, $P = 0.02$, $d = 1.13$; Figure 3A, 3B). In 2013, bill-loads of females ($n = 10$) had a lesser %N of anchovy than those of males ($n = 15$; 15 ± 11% females vs. 50 ± 13% males; 2 sample bootstrap, $P = 0.05$, $d = 0.82$; Figure 3C, 3D). Bill-loads of females also contained anchovy less frequently than bill-loads of males, but this difference was not as strong statistically as the difference in %N (females %FO = 20% vs. males %FO = 53%; $\chi^2_1 = 2.9$, $n = 25$, $P = 0.09$, $d = 0.73$; Figure 3C, 3D). In 2013, bill-loads of females had greater %N and %FO of shortbelly rockfish than bill-loads of males, but these differences were not strong statistically (females %N = 75 ± 13% vs. males %N = 48 ± 12%; 2 sample bootstrap, $P = 0.15$, $d = 0.60$; females %FO = 80% vs. males %FO = 53%; $\chi^2_1 = 1.9$, $n = 25$, $P = 0.16$, $d = 0.58$; Figure 3C, 3D).

Bill-load mass 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; $F_{1, 48} = 0.3$, $P = 0.61$, $d = 0.16$) or within years (2012 $t_{48} = -0.8$, $P = 0.42$, $d = 0.28$; 2013 $t_{48} = 1.5$, $P = 0.14$, $d = 0.60$). Bill-load mass of both sexes together was greater in 2012 (28.6 ± 3.0 g, $n = 27$) than in 2013 (21.5 ± 2.3 g, $n = 25$; $F_{1, 48} = 6.0$, $P = 0.02$, $d = 0.53$). This trend was driven by heavier bill-loads of females in 2012 (31.1 ± 9.0 g, $n = 12$) than in 2013 (17.6 ± 2.8 g, $n = 10$; $t_{48} = -2.7$, $P = 0.01$, $d = 1.53$), whereas mass of males' bill-loads 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 = 0.20).

Male vs. Female Isotope Values

During most seasons, isotope values of male and females were similar (i.e. $P > 0.10$), and in some cases the means of males and females were virtually identical (Table 3, Figure 4).

Table 3. $\delta^{15}N$ and $\delta^{13}C$ of male and female rhinoceros auklet tissues ($\bar{x} \pm$ SE ‰), and results of 10,000 iteration bootstrap tests (*P* value) and Cohen's *d* comparing values of sexes during each period. Bolded values represent differences between sexes in the same tissue and year with $P \geq 0.05$ and $d \geq 0.8$. Tissue type sampled and months represented for each period are in parentheses.

	2012			**2013**		
	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	*n*	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	*n*
Fall/winter (*plume feather*; *Oct-Jan*)						
Male	**17.62 ± 0.05**	-15.25 ± 0.14	24	17.90 ± 0.07	-15.26 ± 0.07	26
Female	**17.43 ± 0.04**	-15.06 ± 0.09	28	17.86 ± 0.05	-15.18 ± 0.10	22
Test Result	***P* = 0.003** ***d* = 0.86**	*P* = 0.27 *d* = 0.33		*P* = 0.71 *d* = 0.13	*P* = 0.53 *d* = 0.19	
Pre-breeding (*breast feather; Feb-Mar*)						
Male	17.74 ± 0.19	-15.49 ± 0.20	25	17.55 ± 0.21	-15.55 ± 0.19	27
Female	17.71 ± 0.16	-15.53 ± 0.18	30	17.40 ± 0.25	-15.88 ± 0.29	22
Test result	*P* = 0.97 *d* = 0.03	*P* = 0.90 *d* = 0.04		*P* = 0.56 *d* = 0.13	*P* = 0.34 *d* = 0.28	
Incubation (*whole blood; Apr-May*)						
Male	14.41 ± 0.10	-19.13 ± 0.15	18	14.59 ± 0.08	-18.18 ± 0.11	15
Female	14.33 ± 0.07	-19.13 ± 0.14	20	14.48 ± 0.10	-18.16 ± 0.14	16
Test result	*P* = 0.52 *d* = 0.21	*P* = 0.98 *d* = 0.0		*P* = 0.40 *d* = 0.30	*P* = 0.90 *d* = 0.04	
Chick-rearing (*whole blood; Jun-Jul*)						
Male	15.36 ± 0.04	**-18.37 ± 0.16**	13	**15.14 ± 0.06**	-17.78 ± 0.08	13
Female	15.32 ± 0.10	**-18.97 ± 0.19**	13	**14.91 ± 0.07**	-17.96 ± 0.07	11
Test result	*P* = 0.71 *d* = 0.15	***P* = 0.02** ***d* = 0.95**		***P* = 0.02** ***d* = 1.0**	*P* = 0.12 *d* = 0.68	
Chicks (*whole blood*; *Jun-Jul*)						
	15.39 ± 0.08	-18.47 ± 0.13	16	14.76 ± 0.11	-17.54 ± 0.18	9

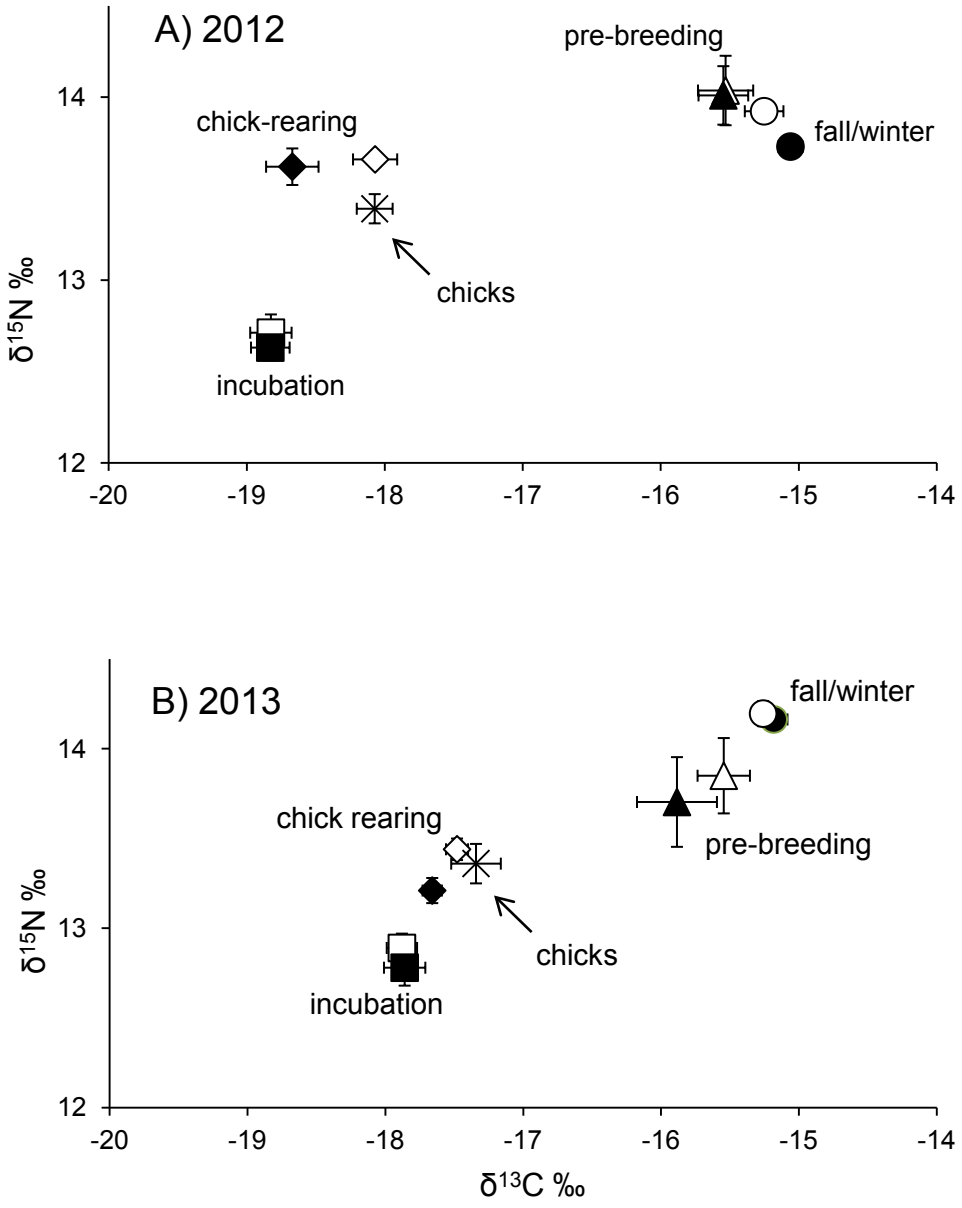

Figure 4. Fractionation-adjusted stable isotope values (δ^{15}N and δC^{13}, $\bar{x}$ ± SE ‰) of adult male and female rhinoceros auklet and chick tissues in 2012(**A**) and 2013(**B**). Black shapes represent adult female values, white shapes represent adult male values, and an X represents chick values. See Table 2 for sample sizes.

$\delta^{15}N$ and $\delta^{13}C$ of males and females did not differ during the incubation or pre-breeding periods in either year, or during fall/winter 2012-13 (P = > 0.10, d = < 0.5 for all; Table 3 and Figure 4). The greatest magnitude difference between sexes occurred during the 2012 chick-rearing period, when the $\delta^{13}C$ of males (-18.37 ± 0.16‰) was 0.60‰ greater than that of females (-18.97 ± 0.19‰; P = 0.02, d = 0.95), whereas there was no difference between sexes in $\delta^{15}N$ during the same period (P = 0.71, d = 0.15; Table 3 and Figure 4, 5).

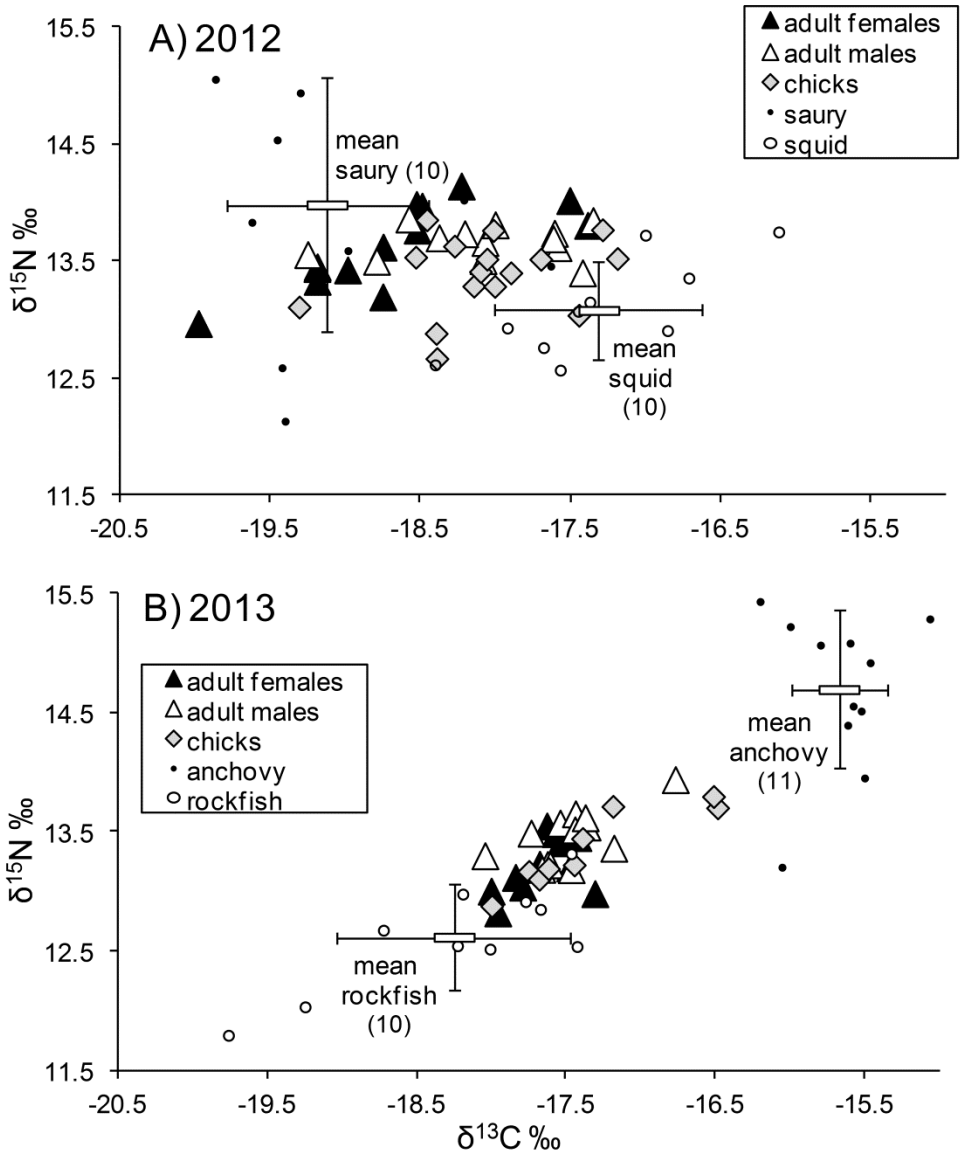

Figure 5. Fractionation-adjusted isotope values ($\delta^{15}N$ and $\delta^{13}C$) of individual adult male and female rhinoceros auklets and chicks, and individual and mean values of dominant prey during the 2012(**A**) and 2013(**B**) chick-rearing periods. Error bars are ± 1 SD.

The $\delta^{13}C$ of the primary prey types provided to chicks in 2012 (saury and squid) differed by 1.81‰ (Table 1 and Figure 5). Mixing models indicated that adults of both sexes were feeding on a mixture of saury, squid, and other prey during the 2012 chick-rearing period (Table 4).

Table 4. Mean and range (1st-99th percentile, in parentheses) of feasible solutions for prey contributions to the diet of adult female and male rhinoceros auklets from dual isotope ($\delta^{15}N$ and $\delta^{13}C$) mixing model IsoSource (Phillips and Gregg 2003). Results are shown for periods during which mean $\delta^{15}N$ or $\delta^{13}C$ values differed ($P \geq 0.05$ and $d \geq 0.80$) between sexes. Species for which the 99th percentile solution was greater than 25% in a period are bolded. Pacific saury was not included as a potential diet source in 2013 models.

	Fall/winter 2012 females	Fall/winter 2012 males	Chick-rearing 2012 females	Chick-rearing 2012 males	Chick-rearing 2013 females	Chick-rearing 2013 males
Pacific saury	00 (00-01)	01 (00-04)	**75 (66-83)**	**56 (46-63)**	-----	-----
Market squid	01 (00-04)	03 (00-12)	06 (00-21)	**08 (00-32)**	03 (00-10)	02 (00-07)
Pacific sand lance	**27 (01-63)**	**10 (00-30)**	04 (00-14)	**09 (00-31)**	**13 (00-48)**	**09 (00-32)**
Rockfish spp.	00 (00-01)	01 (00-03)	05 (00-12)	03 (00-11)	**39 (01-70)**	**40 (03-63)**
Northern anchovy	**67 (34-90)**	**80 (64-92)**	04 (00-15)	**17 (01-33)**	**18 (10-26)**	**29 (23-35)**
Sablefish	03 (00-13)	04 (00-14)	02 (00-08)	02 (00-07)	**27 (00-76)**	**21 (00-67)**
Euphausiid (*T. spinifera*)	02 (00-06)	00 (00-05)	04 (00-15)	05 (00-18)	01 (00-04)	00 (00-02)

The 1st and 99th percentile mixing model estimates for saury in diet of adults were 20% greater for females than males (females 66-83% vs. males 46-63%; Table 4). The 1st and 99th percentile solutions for squid during chick-rearing 2013 were 0-22% for females vs. 0-31% for males (Table 4). The estimated differences in diet of males and females were

similar in direction to those seen in bill-loads in 2012, when females provided more saury and males more squid to chicks (Figure 3A, 3B).

During the 2013 chick-rearing period, $\delta^{15}N$ and $\delta^{13}C$ of males were greater than those of females by 0.23‰ (2 sample bootstrap, $P = 0.02$, $d = 1.0$) and 0.18‰ respectively (2 sample bootstrap, $P = 0.12$, $d = 0.68$; Figure 4 and Table 3). Mixing models indicated that during the 2013 chick-rearing period adult females were consuming 1-70% rockfish and 10-26% anchovy, whereas adult males were consuming 3-63% rockfish and 23-35% anchovy (Table 4). This trend matched the pattern in bill-loads in 2013 in which males provided chicks more anchovy and females more shortbelly rockfish (Figure 3C, 3D). However, due to the small magnitude of the difference in isotope values and uncertainty of mixing model estimates, we considered differences in male and female diet during the 2013 chick-rearing period inconclusive.

During the fall/winter of 2011-2012, the $\delta^{15}N$ and $\delta^{13}C$ of males were greater than those of females by 0.19‰ (Figure 4 and Table 3). This difference was significant for $\delta^{15}N$ (2 sample bootstrap, $P = 0.003$, $d = 0.86$) but not for $\delta^{13}C$ ($P = 0.27$, $d = 0.33$). Mixing models indicated a 30% difference in the 1st percentile solution proportions of anchovy in the diet of females, but there was overlap in the 99th percentile solution proportions of anchovy in each sex's diet (females 34-90% vs. males 64-92%; Table 4). Thus, males may have taken up to 30% more anchovy than females in fall/winter 2011-12, but this result was inconclusive given the small magnitude of the difference in isotope values and the uncertainty associated with the mixing model estimates.

DISCUSSION

Using stable isotope techniques, we found that the diet of adult rhinoceros auklets underwent similar seasonal shifts in consecutive years with differing environmental conditions. Stable isotopes of adult male and female rhinoceros auklets were similar ($P = \geq 0.10$) or virtually identical during most seasons. Sex-specific differences were most pronounced during the 2012 chick-rearing period, when bill-loads delivered to chicks by females contained more saury and less squid than those delivered by males, as did the estimated diet of females vs. males.

Rhinoceros auklet reproductive success was poor in 2012 compared with 2013. Hatching success did not differ significantly between years, whereas chick growth (g d^{-1}) and survival to fledging were less in 2012 than in 2013. These results indicated that the chick-rearing period was critical to determining the differences in overall reproductive success between these years. Chick growth and survival in rhinoceros auklets have been linked with the abundance and quality of prey available during chick-rearing (Vermeer 1980, Takahashi et al. 2001, Thayer and Sydeman 2007). Poor chick growth and survival to fledging in 2012 may have been a result of chicks being fed mainly saury and squid that year. Saury and squid are considered lesser quality prey for rhinoceros auklet chicks compared with juvenile rockfish and anchovy, which have greater caloric and lipid content (Vermeer 1980, Hester 1998, Thayer and Sydeman 2007, Beaubier and Hipfner 2013). Previous researchers of rhinoceros auklets at ANI (Thayer and Sydeman 2007) found that chick growth rate was positively correlated with the annual proportions of juvenile rockfish and anchovy, and negatively correlated with the annual proportion of

saury, in chick diet. They also found that chick survival to fledging was positively correlated with the overall mass of bill-loads delivered to chicks. In our study, however, bill-loads were significantly heavier in 2012 than 2013, whereas the percentage of chicks that survived to fledging was much less (32%) in 2012 than 2013 (75%). This may be an indication that despite receiving larger meals in 2012, chicks still had poor growth and survival to fledging on a diet comprised mainly of lesser quality prey (i.e. saury and squid). Alternatively, adults may have fed chicks less frequently in 2012, so that chicks received less food despite being fed larger meals.

Adult rhinoceros auklets may have selected saury and squid for chicks in 2012 because more preferred prey were not available in the environment. Thayer and Sydeman (2007) found that the composition of bill-loads fed to chicks each year at ANI reflected actual abundance of prey in the environment. NMFS mid-water trawl surveys conducted in the central CA coastal region indicated that the abundance of juvenile rockfish was near the long-term average (1990-2013) in 2012, but was the greatest on record in 2013 (Wells et al. 2013). Data from the same trawls indicated that the abundance of anchovy was well below average in 2012 and slightly below average in 2013, whereas the abundance of squid was above average in both years, especially 2012 (Wells et al. 2013). However, abundance estimates of anchovy and squid from these trawls must be taken only as a general estimate because the trawls specifically target only juvenile rockfish. No data exists on the abundance of saury in the environment during the study. Upwelling and chlorophyll-a around ANI were greater in spring of 2013 than 2012, which was potentially related to the greater abundance of preferred rhinoceros

auklet prey during the 2013 chick-rearing period (Bjorkstedt et al. 2012, Wells et al. 2013).

The diet of adult rhinoceros auklets underwent similar shifts each year despite differing environmental conditions. $\delta^{15}N$ and $\delta^{13}C$ were more positive during fall/winter and pre-breeding of both years than during incubation or chick-rearing (Table 4 and Figure 4). Mixing model results indicated that adult diet in fall/winter of both years was comprised primarily of anchovy and secondarily of sand lance (Table 2). In a previous study, the stomachs of adult rhinoceros auklets sampled in winter in Monterey Bay, CA, contained primarily squid and anchovy (Baltz and Morejohn 1977), whereas squid was not an important fall/winter diet item in our study (1^{st}-99^{th} percentile 0-4% in fall/winter 2011-2012, 0-11% in fall/winter 2012-2013; Table 2). The differences between our findings and Baltz and Morejohn's (1977) may be related to differences in methodology (i.e. stomach sampling vs. stable isotopes), or may indicate that rhinoceros auklets change their fall/winter diet in response to inter-annual variability in prey resources, as they have done during the chick-rearing period (Thayer and Sydeman 2007). Anchovy are energetically rich (Becker et al. 2007), and may be an important prey during the fall/winter period when rhinoceros auklets undergo an energetically costly pre-basic molt of body feathers (Pyle 2008).

Rhinoceros auklet $\delta^{13}C$ values were more negative during the incubation and chick-rearing periods than during fall/winter and pre-breeding in both years. Based on mixing model estimates, this was a reflection of adults switching from eating anchovy and sand lance in fall/winter and pre-breeding to prey with lesser $\delta^{13}C$ values such as

juvenile rockfish and/or saury during incubation and chick-rearing (Table 2). Juvenile shortbelly rockfish were the most frequently occurring rockfish in chick diet (Appendix 1). 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). Adult rhinoceros auklets probably fed heavily on juvenile rockfish during the incubation period (Figure 2 and Table 2); therefore, the heavier mass of incubating females during 2013 could have been related to the greater abundance of juvenile rockfish available in 2013 (Wells et al. 2013).

$\delta^{13}C$ has been used as an indicator of nearshore vs. offshore feeding, with lesser $\delta^{13}C$ values representing a more "offshore" signal (Hobson et al. 1994, Burton and Koch 1999). Rhinoceros auklet $\delta^{13}C$ was lesser during the breeding season, when birds at ANI are constrained to return to the nearshore breeding colony. It is possible that anchovies, which move offshore in the winter (Mais 1974), maintain a relatively greater $\delta^{13}C$ signal acquired when they were located nearshore in summer (Santora et al. 2012). Alternatively, baseline shifts in isotopes may occur seasonally in relation to upwelling or other environmental factors (Michener and Kaufman 2007). We found significant inter-annual shifts in prey isotope values (Figure 2), but assumed that prey isotope values did not change significantly within years. The significant inter-annual differences we found in prey isotopes underscore the necessity of using up-to-date prey samples (i.e. at least from the same year that predator tissues are sampled) to ensure accurate results for stable isotope food web studies involving forage fish.

Contrary to results from other regions that euphausiids are an important pre-breeding diet item for adult rhinoceros auklets (Hobson et al. 1994, Davies et al. 2009, Ito et al. 2009, Sorensen et al. 2010), our mixing models indicated that euphausiids were not an important component of adult diet during any period sampled (mean < 5% for all periods; Table 2). Rhinoceros auklets at ANI may not have fed as heavily on euphausiids as in other regions, but it is also possible that the isotope values of the breast feathers did not accurately reflect diet during the pre-breeding period. The latter explanation should be seriously considered because the variability of isotope values in breast feathers was greater than in other tissues (Table 3 and Figure 2), and rhinoceros auklets molt only a portion of breast feathers during the February-March pre-breeding period. Isotope values during the pre-breeding periods were most similar to those of the fall/winter periods (Table 3 and Figure 2), indicating that some of the breast feathers sampled may have been grown during the pre-basic molt (August-January), rather than during the pre-alternate molt (February-March, described by Pyle 2008 as "absent/limited"; Figure 1). We propose that breast feather isotopes should be used cautiously as an indicator of seasonal diet in rhinoceros auklets because of the limited extent of the pre-alternate molt and the difficulty of visually selecting breast feathers by age in the field due to variable mechanisms causing feather wear.

Adult $\delta^{15}N$ and $\delta^{13}C$ values increased between incubation and chick-rearing, indicating a pattern observed in other populations of rhinoceros auklets and puffins (Figure 2; Davies et al. 2009, Ito et al. 2009, Hedd et al. 2010, Hipfner et al. 2013). This pattern may be a result of adults optimizing foraging efficiency after chicks hatch by

switching from self-feeding on low trophic level prey to larger, energetically rich fish that chicks require (Hipfner et al. 2013). Our results supported this hypothesis, indicating that during the chick-rearing period, adults likely ate the same species of prey in potentially similar proportions that they delivered to chicks (Figure 2 and Table 2). In Japan, adults switched from eating euphausiids during incubation to eating Japanese anchovy (*Engraulis japonicus*) during chick-rearing, possibly because of seasonal changes in prey availability (Ito et al. 2009). At ANI, proportions of each species in adult diet shifted between incubation and chick-rearing (Table 3), which could have been related to shifting prey availability. However, in both years the dominant prey item during incubation (saury in 2012, juvenile shortbelly rockfish in 2013) continued to be dominant during chick-rearing (Table 2). Prey $\delta^{15}N$ also increased with prey length, so it is likely that rhinoceros auklet trophic level increased because they ate larger individuals of the same prey species later in the breeding season. Thus, a combination of parental prey selection, changing prey availability, and prey growth was likely responsible for the increasing trophic level of adults between incubation and chick-rearing. Our understanding of why adult trophic level increases during the breeding season in rhinoceros auklets and other puffins would benefit from closer examination of how prey isotopes change seasonally.

The diet of adult males and females was remarkably similar overall, and both sexes' isotope values changed seasonally in similar directions and magnitudes (Figure 4 and Table 3). Thus, males and females likely used similar habitats and exploited similar niches during most of the year. An interesting exception to the similarity of male and

female isotope values occurred during the chick-rearing period of 2012, when females had significantly lesser $\delta^{13}C$ values than males (Figure 4, 5). The difference in $\delta^{13}C$ between sexes was likely due to diet and not metabolic processes, because $\delta^{13}C$ was not affected by growth or starvation in a captive study of rhinoceros auklet chicks (Sears et al. 2009). In mixing models, this $\delta^{13}C$ difference corresponded to a greater contribution of saury and a lesser contribution of squid in the diet of females compared with males (Table 4). During the same period, females provisioned chicks with more saury and less squid than males (Figure 3A, 3B). These results together indicated males and females were targeting different prey during the chick-rearing period of 2012. Notably, similar but inconclusive trends occurred in the chick-rearing period of 2013, when female bill-loads contained less anchovy and more juvenile rockfish than male bill-loads (Table 3 and Figure 3C, 3D).

The scope of this study did not allow us to determine with certainty why sex-specific differences occurred during the 2012 chick-rearing period. Physiological differences between males and females leading to niche separation seems an unlikely reason, because of the relatively small differences in male and female body size (males in this study averaged 5% heavier than females), and because sex-specific diet differences did not occur during most seasons. Competitive exclusion also seems unlikely because of the small size of the colony at ANI (~260 breeding birds). Our results indirectly support the hypothesis that sex-specific differences observed during the 2012 chick-rearing period were related to differing energetic constraints for each sex during reproduction. In this hypothesis, which has been offered as a potential explanation for sex-specific

differences in other alcids (Bradley et al. 2002, Adams et al. 2004, Welcker et al. 2009), males and females behave differently during chick-rearing because females must recover body condition lost during egg formation and/or incubation. Females consequently need to self-feed more than males during the late breeding season and may take greater duration or distance foraging trips than males (Adams et al. 2004, Welcker et al. 2009) to more productive or reliable foraging locations (Weimerskirch 1998). Examples of alcids in which this hypothesis may apply are marbled murrelets (*Brachyramphus marmatus*), in which males visited nests more often than females during the chick-rearing period (Bradley et al. 2002), dovekies (*Alle alle*), in which females provisioned chicks less frequently and made more long-duration foraging trips than males (Welcker et al. 2009), and Cassin's auklets (*Ptychoramphus aleuticus*), in which females foraged an average 10 km further from the breeding colony than males during the late breeding period (Adams et al. 2004).

Several of our results provide indirect support for an energetic-constraint driven hypothesis to explain sex-specific differences during the 2012 chick-rearing period: 1) the natural history and $\delta^{13}C$ of prey taken during chick-rearing 2012, 2) female body condition in 2012, and 3) the bill-load mass of females in each year. The natural history and $\delta^{13}C$ of saury and squid indicated that males and females took different prey because they may have foraged in different habitats. Although saury can sometimes be found nearshore, they generally occur in waters 65-160 km offshore (Leet et al. 1992). Market squid typically occurs in shelf and shelf break habitat in the immediate vicinity (i.e. <10 km) of ANI in spring and summer (Santora et al. 2012). Furthermore, $\delta^{13}C$ of saury was

1.8‰ less than squid in 2012 (Figure 5), indicating a possibly more offshore distribution of saury than squid (Hobson et al. 1994, Burton and Koch 1999). Thus, squid may have been available to rhinoceros auklets a short distance from ANI in summer 2012, whereas birds may have had to travel over 60 km to obtain saury. The average foraging trip length of rhinoceros auklets in Japan was 87 km (Kato et al. 2003); presumably rhinoceros auklets at ANI can travel similar distances. Based on these generalizations, female rhinoceros auklets may have taken more saury than males because they foraged further offshore.

Female body condition during the 2012 breeding season also provides indirect support for the hypothesis that energetic constraints caused sex-specific differences in diet and chick provisioning. The body condition of females during incubation (as evidenced by serial mass measurements) was significantly less in 2012 than 2013, whereas the body condition of males did not differ between years. This may have been a result of the need for females to expend more energy during the early breeding period in order to produce the egg. A typical rhinoceros auklet egg (77.7 ± 6.4 SD g; Wilson 1977) is equivalent to 15% of the average body mass (504 ± 8 g SE, n = 23) of incubating females at ANI in 2012. Like the poor growth and survival to fledging of chicks, poorer female body condition in 2012 may have been related to the lesser quality of prey available that year. The poorer body condition of females in 2012 may have necessitated taking prey with different nutritional values, or foraging in more predictable or productive areas further from the colony to gain body condition during the energetically demanding chick-rearing period.

Finally, the mass of bill-loads provided to chicks by females in 2012 also supports the hypothesis that females made more distant foraging trips that year. Bill-loads delivered to chicks by females in 2012 were significantly heavier than bill-loads delivered by males that year, or bill-loads delivered by females in 2013. In the extreme example of long-distance travelling Procellariiform seabirds such as sooty shearwaters (*Puffinus griseus*), adults gained body condition and provided chicks with more food after long-duration foraging trips. Chicks were provided more food overall, however, if adults only took short trips (Weimerskirch 1998, Weimerskirch 2007). Rhinoceros auklets travel lesser distances than Procellariiforms, so heavier bill-loads of females in 2012 only hypothetically indicated longer foraging trips that year. However, poor chick growth and survival to fledging in 2012, despite heavier bill-loads, indicated that chicks may have been fed infrequently. Thus, we hypothesize that because females had lesser body condition during the 2012 breeding period, they prioritized feeding themselves over their chicks and foraged further from the colony than males. This hypothetically would explain our observed results of females taking more offshore prey (i.e. saury) and males more nearshore prey (i.e. squid), and could have been a factor in poor chick growth and survival during 2012. Differences may have been less pronounced during 2013 because preferred prey were abundant and females were in superior body condition. This hypothesis is supported only indirectly by our results, so further study on sex-specific foraging areas, dive behavior, and chick-feeding frequency during years with differing prey availability is needed.

In conclusion, we found that the diets of adult rhinoceros auklets underwent consistent seasonal shifts across 2 years with differing environmental conditions. Rhinoceros auklets used different prey species in different seasons and years, underscoring the importance of conserving a diversity of prey species for this species and other generalist seabirds. Pronounced sex-specific differences in diet and in prey species delivered to chicks occurred when females were in lesser body condition while exerting energy to feed chicks and preferred prey appeared to be unavailable. Prey isotope signals changed based on prey size and sampling year, and we caution that predator and prey tissues should be sampled during the same year to ensure accurate interpretation of results in stable isotope food web studies. Our results underscore the value of examining the entire seasonal cycle during multiple years when attempting to understand the ecology of a species.

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Appendix 1. Prey species provided to rhinoceros auklet chicks in 2012-2013, with size ranges (mm, SL = standard length, ML = mantle length).

Common name	**Latin name**	**Length range (mm; SL or ML)**	***n* fish measured**
2012			
Pacific saury	*Cololabis saira*	59-170	52
Market squid	*Doryteuthis opalescens*	35-90	41
Northern anchovy	*Engraulis mordax*	81-123	3
Pacific sand lance	*Ammodytes hexapterus*	84-121	23
Sablefish	*Anoplopoma fimbria*	107	1
Lingcod	*Ophiodon elongatus*	63-72	4
Shortbelly rockfish	*Sebastes jordani*	35-64	10
Widow rockfish	*Sebastes entomelas*	42	1
Yellowtail rockfish	*Sebastes flavidus*	37	1
Chilipepper rockfish	*Sebastes goodei*	38	1
Pacific sanddab	*Citharichthys sordidus*	37, 41	2
Northern lampfish	*Stenobrachius leucopsarus*	67	1
2013			
Shortbelly rockfish	*Sebastes jordani*	68-86	36
Northern anchovy	*Engraulis mordax*	85-128	12
Sablefish	*Anoplopoma fimbria*	108, 133	2