PROXIMATE COMPOSITION AND ENERGY DENSITY OF FORAGE FISH DELIVERED TO RHINOCEROS AUKLET CERORHINCA MONOCERATA NESTLINGS AT TRIANGLE ISLAND, BRITISH COLUMBIA

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Received 20 October 2012, accepted 30 December 2012

SUMMARY

We measured the proximate composition of the four main prey species delivered by adult Rhinoceros Auklets Cerorhinca moncerata to nestlings at Triangle Island, British Columbia. Marine Ornithology 41: 35–39.

We measured the proximate composition of the four main prey species delivered by adult Rhinoceros Auklets Cerorhinca moncerata to nestlings at Triangle Island, British Columbia, Canada: Pacific sand lance Ammodytes hexapterus, Pacific saury Cololabis saira, juvenile rockfish Sebastes spp., and juvenile salmon Oncorhynchus spp. We also assessed within-species variability in energy density and the variation between two years (2003 and 2004). Both the lipid content and the protein content varied significantly among prey species, causing significant interspecific variation in energy density. Energy density was consistently high in Pacific sand lance, the main prey species at Triangle Island in successful breeding years for the auklets, but variably lower in other prey types such as Pacific saury and salmon. Energy density was lower in 2003 than in 2004 in Pacific saury and, to a lesser extent, in juvenile Pacific sand lance. Our results constitute one of the few assessments of the energetic value of forage fish important in northeast Pacific marine systems and indicate that the choice of prey species can be important for predators including seabirds.

Key words: Cerorhinca moncerata, forage fish, energy density, nestling diets, proximate composition, Rhinoceros Auklet, Triangle Island

INTRODUCTION

Information on variation in the energy content of prey species is important for modeling the energetics of marine predators and understanding mechanisms driving population processes (Spitz et al. 2010). Although the species composition of seabird nestling diets is generally well described, less is known about prey quality and the energetic consequences of shifting prey availability. Variation in prey quality is likely to have significant consequences for seabirds (Whittow 2002) that rely on a small suite of prey species to provision their nestlings (Diamond & Devlin 2003).

At Triangle Island, located in British Columbia, Canada, Rhinoceros Auklets Cerorhinca moncerata provision nestlings with four primary prey species, which together constitute ~95% of biomass in most years (Hedd et al. 2006): Pacific sand lance Ammodytes hexapterus, Pacific saury Cololabis saira, juvenile rockfish Sebastes spp. and juvenile salmon Oncorhynchus spp. The representation of these four species in diets varies within and among years, but reproductive success is higher in years in which nesting diets include more young-of-year sand lance (Borstad et al. 2011). To date there has been only one cursory study of local prey energy densities (Vermeer & Devito 1986), and no studies have evaluated what these diet changes imply energetically. To fill this gap, we collected specimens of the four prey types delivered by Rhinoceros Auklets to nestlings in order to measure their proximate composition and estimate their energy densities, in two years of contrasting ocean productivity (2003 and 2004).

METHODS

Our study took place at Triangle Island, British Columbia, Canada (50°52′N, 129°05′W) in 2003, a mild El Niño year, and 2004, a year in which oceanographic conditions were more typical (Mackas et al. 2007). Adult Rhinoceros Auklets usually make a single provisioning trip to the colony each night, carrying up to 30 individual prey items (Hedd et al. 2006). Using small fishing nets, we trapped and then released seven to 12 provisioning adults and collected their bill loads at ~10-day intervals from 20 June onwards (six samples in each year). We also collected one load opportunistically late in 2003 (Table 1). All trapping was done in the same part of the colony and commenced at around 22h30.

Fish were daubed dry of excess water, weighed on an electronic balance (± 0.1 g), and their fork and standard lengths measured (± 1 mm). Rockfish were classified only to genus (Sebastes); species previously identified in Rhinoceros Auklet bill loads at Triangle Island include yellowtail S. flavidus and widow rockfish S. entomelas (Vermeer & Westrheim 1984). Fish over 6 g were frozen individually in Whirlpaks, or in species-specific bundles in Ziploc bags. Smaller specimens (juvenile rockfish and sand lance) were frozen in bundles of 8 g, keeping bill loads together where possible. Specimens were stored in a propane freezer at -10°C in the field and then at -20°C in the laboratory. Because they thawed at least partially in transport, and again in the lab while being processed, we re-weighed a subset of all specimens to determine total loss of water since the time of capture on the colony and thereby establish a
We classified sand lance as adults (1+) or young-of-year juveniles (0+) based on otolith measurements. Sagittal otoliths were removed, cleaned of tissue using a damp cloth and patted dry. Each otolith was then cross-sectioned along the transverse plane using nail-clippers and burnt to a light brown over an alcohol flame. The sectioned otolith was then mounted in modeling cement and examined under mineral oil using a dissecting scope (40×). Individuals with no annuli outside of the nucleus were recorded as 0+ fish; individuals with one annulus outside of the nucleus were counted as 1+ fish; and so on. All saury were classified as juveniles (0+) because they were under the minimum knob length reported for mature adults (~253 mm; Suyama et al. 1994). All rockfish and salmon were classified as 0+ and 1+ (new smolts), respectively, based on morphology and size (Woodbury & Ralston 1991, Moser & Boehlert 1991).

We used proximate composition analysis to measure total lipid, protein, water and ash content in individual prey items. Prey above 6 g in mass were processed individually, while juvenile sand lance and rockfish were processed in 8 g batches. Whole fish were homogenized using a stainless steel mortar and pestle, and a subsample (2 g) of the resulting homogenate placed in a dried ceramic crucible, dessicated in a drying oven at 100 °C for 24 hours to determine water content, weighed and then ashed in a 600 °C muffle furnace for two hours to determine ash content by subtraction. Crude lipid content was determined using a modified Bligh and Dyer method (Higgs et al. 1979), in which 2 g of wet tissue is extracted using 40 mL of 1:1 chloroform methanol and 8 mL of distilled water. This method (Crossin 2003) greatly increases the extracted lipid (Welch’s F = 11.71, P < 0.001), mineral (Welch’s F = 12.54, P < 0.001) and protein (Welch’s F = 40.66, P < 0.001) content. We therefore assessed interspecific variation in these parameters using Welch’s approximation and Tamhane’s T2 post-hoc comparisons (Tamhane 1979). Otherwise, we used ANOVA and Bonferroni post-hoc multiple comparisons.

Results

Pacific saury dominated Rhinoceros Auklet nesting diet at Triangle Island in 2003, but there was a more even mix of Pacific sand lance, rockfish, saury and salmon in 2004 (Fig. 1). The proximate composition of rockfish and salmon was analyzed only in 2004, because of their scarcity in 2003.

Significant interspecific variation was found in water (ANOVA F = 18.42, P < 0.001), mineral (Welch’s F = 12.54, P < 0.001), lipid (Welch’s F = 40.66, P < 0.001) and protein (Welch’s F = 47.56, P < 0.001) for forage fish fed to Rhinoceros Auklet nestlings.

Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>N</th>
<th>Water</th>
<th>Ash</th>
<th>Lipid</th>
<th>Protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>Saury</td>
<td>2003</td>
<td>16</td>
<td>74.63 ± 1.57 (2.1)a</td>
<td>11.70 ± 1.68 (14.4)ab</td>
<td>13.04 ± 4.36 (33.4)b</td>
<td>75.45 ± 3.67 (4.9)bc</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>14</td>
<td>73.09 ± 2.10 (2.1)b</td>
<td>10.47 ± 0.98 (9.3)b</td>
<td>18.32 ± 3.71 (20.2)a</td>
<td>71.21 ± 3.69 (5.2)ab</td>
</tr>
<tr>
<td>Sand lance, adult</td>
<td>2003</td>
<td>35</td>
<td>76.12 ± 1.80 (2.4)a</td>
<td>12.01 ± 3.17 (25.8)ab</td>
<td>19.74 ± 5.83 (29.5)a</td>
<td>68.38 ± 5.17 (7.6)a</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>27</td>
<td>74.57 ± 2.12 (2.8)a</td>
<td>11.47 ± 2.99 (26.0)ab</td>
<td>21.48 ± 6.95 (32.4)a</td>
<td>67.05 ± 6.84 (10.2)a</td>
</tr>
<tr>
<td>Sand lance, juvenile</td>
<td>2003</td>
<td>3</td>
<td>76.12 ± 0.81 (1.05)a</td>
<td>11.71 ± 2.00 (17.1)ab</td>
<td>10.62 ± 5.02 (47.2)abc</td>
<td>77.80 ± 3.38 (4.3)abc</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>16</td>
<td>76.18 ± 1.50 (2.0)a</td>
<td>10.51 ± 0.43 (0.4)b</td>
<td>20.31 ± 2.82 (13.9)a</td>
<td>69.18 ± 3.10 (4.5)a</td>
</tr>
<tr>
<td>Rockfish</td>
<td>2004</td>
<td>16</td>
<td>75.57 ± 1.61 (2.1)b</td>
<td>12.62 ± 1.06 (8.4)b</td>
<td>19.75 ± 3.15 (15.9)a</td>
<td>67.70 ± 3.39 (5.0)a</td>
</tr>
<tr>
<td>Salmon</td>
<td>2004</td>
<td>12</td>
<td>80.22 ± 0.85 (1.0)b</td>
<td>13.09 ± 1.10 (8.4)b</td>
<td>7.78 ± 1.78 (22.9)b</td>
<td>79.13 ± 2.05 (2.6)c</td>
</tr>
</tbody>
</table>

Values marked with different letters within a column indicate statistically significant differences in post-hoc comparisons.

Marine Ornithology 41: 35–39 (2013)
As a result of the differences in lipid and protein content, energy density varied among species (Fig. 2). Salmon (in 2004) and saury (in 2003) had the lowest total energy density, although not significantly lower than juvenile sand lance in 2003. The differences in energy density were due to lower lipid-derived energy in those two species-year combinations; salmon and saury (in 2003, but not 2004) actually had the highest protein-derived energy of all prey types, matched only by juvenile sand lance in 2003 (Fig. 2).

Pacific saury had lower energy densities in 2003 than in 2004 (Fig. 2). There was some indication that juvenile sand lance also had lower energy densities in 2003 than in 2004, although there was no suggestion that adult sand lance differed in energy density between the two years.

**DISCUSSION**

Our study provides estimates of variation in proximate composition and energy density in several important forage fish species of northeast Pacific waters and should be useful in studies investigating local food web dynamics. We found that water, mineral, lipid and protein content varied among at least some of the four primary prey types delivered by adult Rhinoceros Auklets to nestlings at Triangle Island. As a result of interspecific differences in proximate composition, energy densities also varied among species, as found in other interspecific comparisons (Anthony et al. 2000). In this study, energy densities were high in adult Pacific sand lance (in both years) and in rockfish (in the one year this species was examined), but lower in Pacific saury (in one of two years) and Pacific salmon (in one year) and perhaps juvenile sand lance (one of two years). Because variation in energy density and water content skews energetic comparisons based on biomass alone, our results suggest that biomass is unlikely to accurately gauge the energetic content of whole bill loads.

The most plausible cause of interannual variation in the energy density of fish, as found in Pacific saury and to less extent juvenile sand lance (lower in 2003 in both cases), is food availability. Independent marine sampling showed higher densities of shelf copepods in 2004 than in 2003 in the region of Triangle Island (Mackas et al. 2007), shelf copepods being the primary prey of Pacific saury and Pacific sand lance (Blackburn and Anderson 1997, Watanabe et al. 2003). There is evidence that growth rate and lipid deposition decrease in both of these fish if feeding conditions are poor (Robards et al. 2002, Watanabe et al. 2003). Although adult sand lance did not differ in energy density or other constituents between the two years, we caution that interannual variation in this species should still be considered, because sand lance energy

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**Fig. 1.** Composition of the diets (as percentage wet mass) fed by Rhinoceros Auklets to their nestlings at Triangle Island, British Columbia, in 2003 and 2004. SL = sand lance; PS = Pacific saury; RF = rockfish; SM = salmon; Ad = adult; Juv = juvenile.

**Fig. 2.** Dry mass energy densities and the relative contributions of protein and lipid constituents of forage fish obtained from Rhinoceros Auklets provisioning nestlings at Triangle Island, British Columbia, in 2003 and 2004. Small letters indicate groups that are (if the same) or are not (if different) statistically significantly different in energy density for lipid or protein; capital letters indicate groups that are or are not statistically significantly different in total energy density (Tamhane’s T2 multiple comparisons, P < 0.0001). Error bars represent 95% confidence intervals for each of lipid and protein. SL = sand lance; PS = Pacific saury; RF = rockfish; SM = salmon; Ad = adult; Juv = juvenile.
Energy densities of adult Pacific sand lance from the vicinity of Triangle Island were similar to those derived from dry mass and reported for the species in the early summer in Kachemak Bay, Alaska: 20.9 kJ \cdot g^{-1} for males, and 21.1 kJ \cdot g^{-1} for females (Robards et al. 1999). Values for juvenile sand lance were also similar in the two studies, with Robards et al. (1999) reporting peak energy densities of 19.7 kJ \cdot g^{-1} in large juveniles. Energy densities of juvenile rockfish in our study were higher than one published value (15.9 kJ \cdot g^{-1} dry mass, Van Pelt et al. 1997), but similar to local values reported during the 1980s (21.8 kJ \cdot g^{-1} dry mass, Vermeir & Devito 1986). Lipid content was also similar to that reported in California during years of good food availability (Rau et al. 2001). While the physiology of settling juveniles is not well understood (Love et al. 2002), juvenile rockfish raised in aquaculture environments store lipids when food is in excess and diets have high ratios of lipid to protein (Lee et al. 2002), and this may also occur in natural systems (Rau et al. 2001). In 2004, juvenile rockfish numbers were high along the Pacific coast (Baltz 2004), and rockfish were abundant in common murre Uria aalge diets at Triangle Island (Hipfner & Greenwood 2008).

**Implications for Rhinoceros Auklets**

Based on our assessment of variation in prey quality, differences in prey quality could contribute to the marked interannual variation in Rhinoceros Auklet breeding success at Triangle Island (Borstad et al. 2011), as in seabirds elsewhere (Vanless et al. 2005). For instance, to achieve equal energy delivery, Rhinoceros Auklets provisioning with salmon would have to deliver 150% of the wet mass of those provisioning with adult Pacific sand lance (calculated from water content and dry biomass energy densities of the two species). The energetic deficit could be significant if salmon were exploited for any significant amount of time, and may explain why salmon tend to be rare in auklet diets at Triangle Island (Thayer et al. 2008). Yet the high prevalence of lower-quality Pacific saury in diets in 2003, suggests that Rhinoceros Auklets may have to rely on inferior prey during some periods — perhaps especially in years when a late spring bloom reduces the availability of juvenile sand lance to the population at Triangle Island (Borstad et al. 2011).

**ACKNOWLEDGEMENTS**

We thank the 2003 and 2004 Triangle Island field crews for assistance with field work and Judy Myers, Glen Crossin, Bart van der Kamp, John Shurin and Lisa Cassidy for lab support. This research was supported through funding from the Centre for Wildlife Ecology (Simon Fraser University and the Canadian Wildlife Service), facilities support from the University of British Columbia, and an NSERC grant to the lead author. We received invaluable ship and helicopter support from the Canadian Coast Guard. Methods complied with the laws of Canada and were carried out under permits from Environment Canada (Scientific) and Simon Fraser University (Animal Care).

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