

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

BEAUBIER, J. & HIPFNER, J.M. 2013. Proximate composition and energy density of forage fish delivered to Rhinoceros Auklet *Cerorhinca monocerata* 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 monocerata* to nestlings at Triangle Island, British Columbia, Canada: Pacific sand lance *Ammodytes hexapterus*, Pacific saury *Cololabis saira*, juvenile rockfish *Sebastodes* 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 monocerata*, 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 monocerata* 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 *Sebastodes* 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 nestling 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 (*Sebastodes*); 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

correction factor for those not re-weighed: dessicated mass = 0.896 \times (fresh mass) - 0.233 ($R^2 = 0.993$, $P < 0.0001$).

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 \times). 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 sub-sample (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 tissue:solvent ratio, approaching levels of the high tissue:solvent Folch method, and was performed twice per sample. The average lipid measurement was recorded, unless values differed by more

than 1%, in which case a third measurement was taken and the two closest values recorded.

Protein content was determined by subtracting lipid, water and ash mass from the total mass (Lawson *et al.* 1998); fish contain virtually no carbohydrate (Hartman & Brandt 1995). As in previous studies (Anthony *et al.* 2000, Robards *et al.* 1999), we used published values for energy density of lipids (39.3 kJ · g⁻¹) and protein (17.8 kJ · g⁻¹) (Schmidt-Nielsen 1997) to estimate prey energy densities from proximate composition. While wet mass measures the energetic value of prey items more accurately than dry mass, seabird prey are subject to variable amounts of dessication while being transported from foraging areas back to the colony (Montevecchi & Piatt 1987). Therefore, following Robards *et al.* (1999), we used dry mass energy densities in all analyses and present information on proximate composition in this format.

Values for energy density and for lipid and protein content were normally distributed but of unequal variance, and this could not be remedied by transformation. 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 nestling 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 $F = 18.42$, $P < 0.0001$), mineral (Welch's $F = 12.54$, $P < 0.0001$), lipid (Welch's $F = 40.66$, $P < 0.0001$) and protein (Welch's

TABLE 1
Proximate composition and energy density (based on dry mass) of forage fish fed to Rhinoceros Auklet nestlings

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

^{a,b,c}Values marked with different letters within a column indicate statistically significant differences in post-hoc comparisons.

$F = 28.00$, $P < 0.0001$) content (Table 1). 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

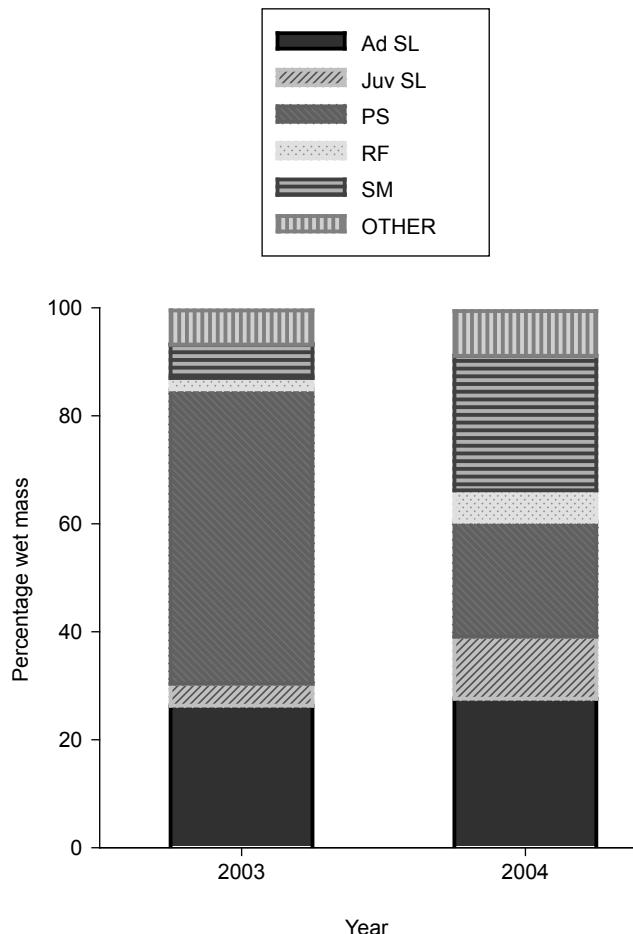


Fig. 1. Composition of the diets (as percentage wet mass) fed by Rhinoceros Auklets to their nestlings at Triangle Island, British Columbia, in 2003 and 2004. SL = sand lance; PS = Pacific saury; RF = rockfish; SM = salmon; Ad = adult; Juv = juvenile.

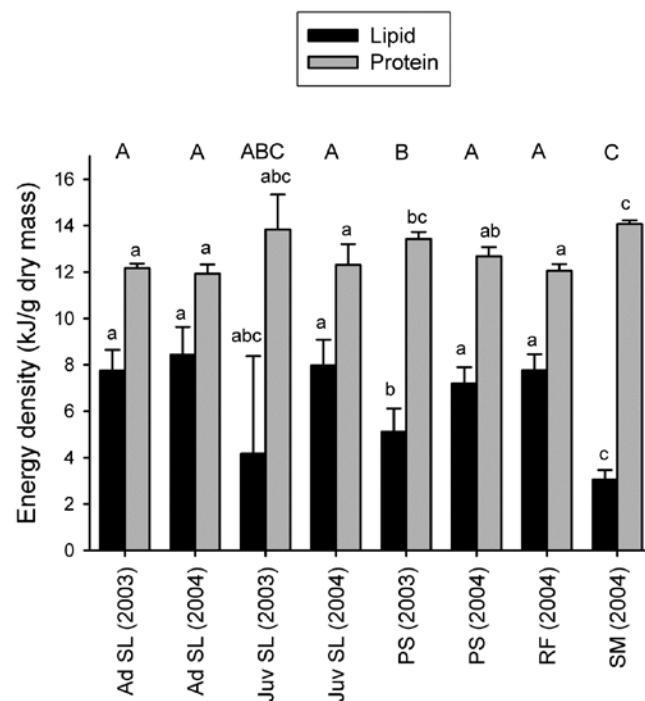


Fig. 2. Dry mass energy densities and the relative contributions of protein and lipid constituents of forage fish obtained from Rhinoceros Auklets provisioning nestlings at Triangle Island, British Columbia, in 2003 and 2004. Small letters indicate groups that are (if the same) or are not (if different) 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.

content does vary with oceanic conditions elsewhere (Robards *et al.* 2002, Wanless *et al.* 2005).

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: $20.9 \text{ kJ} \cdot \text{g}^{-1}$ for males, and $21.1 \text{ kJ} \cdot \text{g}^{-1}$ 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 $19.7 \text{ kJ} \cdot \text{g}^{-1}$ in large juveniles. Energy densities of juvenile rockfish in our study were higher than one published value ($15.9 \text{ kJ} \cdot \text{g}^{-1}$ dry mass, Van Pelt *et al.* 1997), but similar to local values reported during the 1980s ($21.8 \text{ kJ} \cdot \text{g}^{-1}$ dry mass, Vermeer & 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 (Wanless *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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