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 *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 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 correction factor for those not re-weighed: dessicated mass = 0.896 × (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×). 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

$F = 28.00$, $P < 0.0001$) 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.

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 kJ · g^{-1} for males, and 21.1 kJ · 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 · g^{-1} in large juveniles. Energy densities of juvenile rockfish in our study were higher than one published value (15.9 kJ · g^{-1} dry mass, Van Pelt et al. 1997), but similar to local values reported during the 1980s (21.8 kJ · 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 . 19307anH tf 1[(20),ng)-64(juv)15(eniid)-10( )]TJ 0 Tc(203664 -1.222 Td 6(r)10(o)10(c)10(k)10(f

ROBARDS, M.D., ANTHONY, J.A., ROSE