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Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: implications for piscivorous predators

Jeffrey R. Ball · Daniel Esler · Joel A. Schmutz

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Abstract Changing ocean conditions and subsequent shifts in forage Wsh communities have been linked to numerical declines of some piscivorous marine birds and mammals in the North PaciWc. However, limited information about Wsh communities is available for some regions, including nearshore waters of the eastern Bering Sea, where many piscivores reside. We determined proximate composition and energetic value of a suite of potential forage Wsh collected from an estuary on the Yukon-Kuskokwim Delta, Alaska, during 2002 and 2003. Across species, energy density ranged from 14.5 to 20.7 kJ g ^{1} dry mass and varied primarily as a function of lipid content. Total energy content was strongly inXuenced by body length and we provide species-speciWc predictive models of total energy based on this relationship; some models may be improved further by incorporating year and date eVects. Based on observed energetic diVerences, we conclude that variation in Wsh size, quantity, and species composition of the prey community could have important consequences for piscivorous predators.

Keywords Calorimetry · Eastern Bering Sea · Energetics · Forage Wsh · Foraging ecology · Proximate composition · Yukon-Kuskokwim Delta

Introduction

Many upper trophic-level marine predators, including birds and mammals, rely on pelagic schooling Wsh and younger age classes of demersal Wsh as a food source for adults and for provisioning young (NRC 1996). The quality of prey Wsh is largely a function of their body composition and energetic value, attributes that vary among Wsh species. Pelagic schooling Wsh (e.g., Ammodytidae, Clupeidae, and Osmeridae) are typically high in lipid content and energy density (kJ g ^{1}), whereas demersal species (e.g., Cottidae, Gadidae, and XatWshes) generally have lower energy densities (Van Pelt et al. 1997; Payne et al. 1999; Anthony et al. 2000; Iverson et al. 2002). However, intraspeciWc variation in Wsh energy density can exceed interspeciWc diVerences, particularly among pelagic Wshes compared to demersal species, making generalizations about relative prey value by species unreliable (Hislop et al. 1991; Anthony et al. 2000). Energy density generally increases with Wsh length, varies seasonally (Paul and

Laboratory methods

Proximate composition was determined following Van Pelt et al. (1997) and Anthony et al. (2000). Each Wsh was transferred to an individual tray and weighed frozen on an electronic balance (lab wet mass; 0.0001 g). Because samples lost mass from desiccation during processing and freezing (mean diVerence between lab and Weld wet masses as a percentage of Weld wet mass 1SE was 4.3% 0.3; see also Montevecchi and Piatt 1987; Hislop et al. 1991), Weld wet mass was used in all calculations that include wet mass (see below). Frozen samples were transferred to a convec-

null model by a factor of $>1 \cdot 10^4$. Length was consistently an important explanatory variable (Table 2), having a strong, positive eVect on total energy content for all species with the exception of nine-spine stickleback (see below).

The importance of year for explaining variation in total energy content varied considerably by species. Year was of equal importance to length in explaining total energy variation in rainbow smelt and saVron cod, and was nearly as important as length in belligerent sculpin (Table 2), all of whti s ET7 TJ E.5(t) g7 TJ E.3(gy1)7(tal)5(h.8(l)6.5(o)7..6(er E.3(gy1)1.2 ET 0.0062 Tc 0.1

inverse relation between lipid and water contents magniWed the discrepancy between minimum and maximum mean wet mass energy density among species to nearly twofold (2.8–5.2 kJ g ^{1}

et al. 2002). This must be taken into consideration if our energy estimates are to be applied outside of the summer months.

Implications of prey energy value and relative abundance for predators

Variation in energetic value of prey and the frequency at which prey-types are encountered are the two factors that, in combination, likely have the greatest eVect on energy acquisition and productivity in piscivorous predators. If we consider energy density alone, a predator would gain the greatest energy intake per gram by selecting least cisco, nine-spine stickleback, and pond smelt over the other species in this community. This may be an important criterion when self-feeding (Davoren and Burger 1999), or if multiple prey are delivered at once and small, energy-dense items with lower handling costs can increase the total energetic value of the bill load (Orians and Pearson 1979). For piscivores that deliver one or a few prey items to their young, selecting longer prey that contain more total energy may oVset the cost of roundtrip travel if the energy and time costs associated with handling larger Wsh are low. Longer prey items would enable a provisioning adult to increase net energy gain and reduce the number of trips required to meet energetic needs of

The range of dry mass energy densities reported here are within the range reported in other multi-species studies. However, the two species present in the greatest abundance in our study, rainbow smelt and arctic Xounder, had low lipid components and energy densities compared to many Wsh species (Van Pelt et al. 1997; Anthony et al. 2000). In addition to a potentially lower net rate of energy acquisition, individuals consuming a diet low in lipids may gain signiWcantly less beneWts compared to a high-lipid diet (Rosen and Trites 2000a; Kitaysky et al. 2001) due to the lower assimilation eYciency and higher processing costs associated with diets of lower lipid content (Brekke and Gabrielsen 1994; Rosen and Trites 2000b). While it is tempting to conclude that this seemingly poor quality prey community has had negative demographic consequences for local piscivorous populations such as red-throated loons (Groves et al.

Crawford RJM, Dyer BM (1995) Responses by four seabird species to a X