

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

Received: 12 October 2005 / Revised: 5 October 2006 / Accepted: 5 October 2006 / Published online: 8 November 2006
© Springer-Verlag 2006

Abstract Changing ocean conditions and subsequent shifts in forage fish communities have been linked to numerical declines of some piscivorous marine birds and mammals in the North Pacific. However, limited information about fish 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 fish 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 influenced by body length and we provide species-specific predictive models of total

energy based on this relationship; some models may be improved further by incorporating year and date effects. Based on observed energetic differences, we conclude that variation in fish size, quantity, and species composition of the prey community could have important consequences for piscivorous predators.

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

Introduction

Many upper trophic-level marine predators, including birds and mammals, rely on pelagic schooling fish and younger age classes of demersal fish as a food source for adults and for provisioning young (NRC 1996). The quality of prey fish is largely a function of their body composition and energetic value, attributes that vary among fish species. Pelagic schooling fish (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 flatfishes) generally have lower energy densities (Van Pelt et al. 1997; Payne et al. 1999; Anthony et al. 2000; Iverson et al. 2002). However, intraspecific variation in fish energy density can exceed interspecific differences, particularly among pelagic fishes 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 fish length, varies seasonally (Paul and Paul 1998), and varies due to sex-specific changes associated with reproduction (Montevecchi and Piatt 1984;

J. R. Ball
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, V5A 1S6 Canada

D. Esler
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, 5421 Robertson Road, Delta, BC, V4K 3N2 Canada
e-mail: desler@sfu.ca

J. A. Schmutz
Alaska Science Center, United States Geological Survey, 1011 East Tudor Road, Anchorage, AK 99503, USA
e-mail: joel_schmutz@usgs.gov

J. R. Ball (✉)
Department of Biological Sciences, CW 405,
Biological Sciences Centre, University of Alberta,
Edmonton, AB, T6G 2E9 Canada
e-mail: jball@ualberta.ca

Anthony et al. 2000). Further, energetic value of individuals within a species can vary spatially and interannually, presumably due to variation in their foraging environments (Anthony et al. 2000) or through oceanographic conditions that influence reproductive timing (Brodeur et al. 1999).

Variation in the quality of dietary fish has been demonstrated to have important effects on the performance of consumers. Experimental studies have shown that low-lipid diets result in mass loss of juvenile Steller sea lions (Rosen and Trites 2000a) and reduced deposition of energy reserves (Lance and Roby 2000), lower rates of mass gain, and elevated levels of corticosterone stress hormone in nestling birds (Kitaysky et al. 2001). Under natural conditions, declines in availability of high-quality prey can have negative repercussions for avian breeding success (Frank 1992; Crawford and Dyer 1995; Hipfner et al. 2000; Kitaysky et al. 2000; Rindorf et al. 2000; Suryan et al. 2000, 2002; Litzow et al. 2002), although reduced diet diversity alone may negatively impact survival of juvenile Steller sea lions (Merrick et al. 1997). These effects of variation in prey quality can have demographic consequences for predators by influencing postnatal growth rates, fledging success (Golet et al. 2000), and post-fledging survival (Perrins et al. 1973; Gaston 1997). Over longer time frames, the availability of high-quality prey can play an important role in the regulation of seabird (Furness and Monaghan 1987) and marine mammal (Estes 1979) populations.

During the past quarter-century, dramatic declines in many of Alaska's piscivorous predator populations in the North Pacific (Piatt and Anderson 1996; Agler et al. 1999) have been linked to a large-scale change in the composition of the prey community from one dominated by high quality pelagic schooling fishes to one composed primarily of lower quality demersal species (Decker et al. 1995; Anderson and Piatt 1999). The geographic extent of prey community change suggests that large-scale variation in the ocean environment has differentially altered the productivity and/or distribution of fish species (Anderson and Piatt 1999). However, the current knowledge of fish in the Bering Sea is limited to a few commercially important species (Loughlin et al. 1999) and relatively little is known about the important forage species which occur in the inner eastern shelf region (Springer 1999) where at least one coastal-nesting piscivore is reported to be in decline (Groves et al. 1996). Also, foraging studies of the relationship between predators and their prey rely on estimates of prey energy value, which are unavailable. Therefore, we address these data gaps by describing the proximate composition and energetic value of a

suite of marine fish in coastal waters of the eastern Bering Sea and provide predictive equations for total energetic value. We discuss relative prey value, based on variation in energy and relative abundance, along with implications for piscivorous predators.

Study area and methods

Field sampling methods

Fish were collected approximately once per week between June and August of 2002 and 2003 from several repeatedly sampled locations within the Manokinak River estuary, a large tidal river system on the Yukon-Kuskokwim Delta, Alaska, that drains into the eastern Bering Sea [N 61°12', W 165°06'; see Ball (2004) for specific sampling locations within the estuary]. Sampling was conducted across tide stages, and was primarily by otter trawl (3.1 m × 1.6 m opening; 15 mm² mesh) towed with a skiff (total number of trawls = 47, total hours trawled = 20.51 h, average trawl duration ± 1SE = 0.43 ± 0.02 h trawl⁻¹). During 2002 additional samples were collected for proximate analysis using a beach seine (36.9 m × 3.0 m; 10 mm² mesh). All sampling was performed in accordance with animal care regulations of Simon Fraser University following permitted guidelines from the Alaska Department of Fish and Game.

This study was part of a larger investigation of the provisioning behavior of red-throated loons (*Gavia stellata*), a marine piscivore, and our sampling and analysis efforts were focused on the size range of fish delivered to loon chicks, i.e., 70 to 210 mm (Norberg and Norberg 1976; Reimchen and Douglas 1984; Eriksson et al. 1990), although some fish outside this size range were included in the proximate analysis. This size range of prey is consistent with that used by many piscivores (Pearson 1968; Loughlin et al. 1999; Tasker et al. 1999), thus our data have broad implications beyond red-throated loons. Captured fish (nCAP = number captured by trawl only) were identified to species in the field using Mecklenburg et al. (2002), weighed on an electronic balance (field wet mass; ±0.1 g), and measured for total length (snout to longest caudal ray; ±1 mm). A sub-sample of fish across the size range of each species captured during each sampling event were individually bagged and frozen in a propane freezer (ca. -10°C) before being transferred to laboratory facilities where they were stored frozen (-20°C) until analysis (nCOL = numbers of fish collected by trawl, including fish outside the focal size range, and by seine for proximate analysis).

Laboratory methods

Proximate composition was determined following Van Pelt et al. (1997) and Anthony et al. (2000). Each fish 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 difference between lab and field wet masses as a percentage of field wet mass ± 1 SE was $-4.3\% \pm 0.3$; see also Montevecchi and Piatt 1987; Hislop et al. 1991), field wet mass was used in all calculations that include wet mass (see below). Frozen samples were transferred to a convection oven (60°C) to achieve a constant dry mass (± 0.0001 g). Water content was calculated as a percentage of field wet mass [%water = (field wet mass – dry mass)/field wet mass $\times 100\%$]. Dry samples were homogenized, transferred individually to extraction envelopes or thimbles depending on size, and placed in a soxhlet apparatus. Hexane/isopropanol 7:2 (v:v) was used as a lipid extraction solvent because it is non-toxic and does not dissolve proteins or other non-lipid materials, but effectively extracts storage lipids and more tightly bound structural lipids, thereby accurately indicating the lipid fraction available to a consumer (Radin 1981). Extracted lean samples were dried and weighed, and lipid content was calculated as a percentage of pre-extracted dry mass [%lipid = (dry mass – lean dry mass)/dry mass $\times 100\%$]. Lean dry samples were held in a desiccator before being incinerated at 600°C for 24 h. Ash and ash-free lean dry matter (AFLDM) (94% protein; Montevecchi et al. 1984) contents were determined as a percentage of pre-extracted dry mass [%ash = (ash mass/lean dry mass) $\times (1 - \text{\%lipid}/100\%) \times 100\%$; %AFLDM = [(lean dry mass – ash mass)/lean dry mass] $\times (1 - \text{\%lipid}/100\%) \times 100\%$].

Analyses

We used an information-theoretic approach to analyze interspecific and intraspecific variation in energetic value. This approach compares the relative support among a set of candidate models using Akaike Information Criterion, adjusted for small sample size (AIC_c) (Burnham and Anderson 2002). To aid comparisons among models, we calculated model AIC_c weights ($\text{AIC}_c w$), which sum to 1 across the model set and indicate the relative likelihood of each model, given the data. Models with higher $\text{AIC}_c w$ received greater support compared to competing models. Summed $\text{AIC}_c w$ ($\sum \text{AIC}_c w$) for each parameter, computed by summing model $\text{AIC}_c w$

across all models in the candidate set in which a given parameter occurs, indicates the relative explanatory value of each parameter given the data and the candidate model set. Parameters with $\sum \text{AIC}_c w$ approaching 1 are strongly related to variation in the dependent variable. Finally, model $\text{AIC}_c w$ were used to generate weighted parameter estimates and unconditional SE (Burnham and Anderson 2002; Eqs. 4.1 and 4.9, respectively), which incorporate model uncertainty. Details of individual model parameters and candidate model sets are provided below.

Interspecific variation in energy density

We computed dry mass energy density to compare energetic value among species. This is the most appropriate energetic measure for comparative purposes as it eliminates desiccation as a source of error (Montevecchi and Piatt 1987; Hislop et al. 1991). Dry mass energy density (kJ g^{-1}) was computed for each sample based on its lipid and AFLDM masses (%composition/100% \times dry mass) and the respective energy equivalents of 39.3 and 17.8 kJ g^{-1} [for uric acid producing vertebrates; Schmidt-Nielsen (1997), p. 171], assuming the latter consists only of protein. Carbohydrates are a negligible component of fish ($<0.6\%$ dry mass; Craig et al. 1978) and have been disregarded here, as in other studies (Van Pelt et al. 1997; Payne et al. 1999; Anthony et al. 2000). When considering transportation costs and consumption capacities, wet mass energy density is more ecologically relevant (Montevecchi and Piatt 1987). Therefore, wet mass energy density (kJ g^{-1}) was determined by multiplying dry mass energy density by the proportion of dry mass to field wet mass.

Differences between species in average dry and wet mass energy density were assessed using a set of models for each that considered various groupings of the fish species, with the intent of determining which groupings explained the most variation in the data without overfitting, i.e., splitting species that were, in fact, indistinguishable in their energy density. Each model set considered 14 candidate models, including a global model (i.e., all species were different), a null model (i.e., all species were grouped), and various combinations that were plausible given the relatedness between species and our review of the data. General linear models with no intercept were used to generate AIC_c values to select the grouping combination best describing differences among species. This approach is roughly analogous to ANOVA with pairwise post-hoc tests.

Intraspecific variation in total energy content

We examined intraspecific variation in total energy content (kJ fish^{-1}) in relation to length, day of the year (Day), year, and the interaction between length and Day. For each species, total energy was calculated as dry mass energy density \times dry mass (Hislop et al. 1991). Length was included as a continuous variable and total energy and length were natural log transformed and residuals inspected to assure that the transformed data met the assumptions of the general linear models used to compute AIC_c values. Year and Day were included to account for potential inter-annual and seasonal variation, respectively (Anthony et al. 2000). The interaction term was included because seasonal changes in energy content related to reproductive condition, rather than to changes in diet, would also be related to fish length because it reflects age and therefore reproductive maturity. Our candidate model set for each species included all combinations of explanatory variables for a total of 16 models, including a null model in which the data were described by a single mean and variance, as all combinations were considered biologically feasible. $\sum \text{AIC}_{c,w}$ were calculated for each parameter to assess its contribution to total energy variation in each species. Because we expected that length would explain much of the total energy variation, we developed more general species-specific predictive equations for total energy content based on length alone.

We did not analyze interspecific variation in abundance because our trawl was likely incapable of sampling all species with equal probability due to differences in microhabitat use. We attempted to spread our sampling effort across tidal stages and locations throughout the estuary. We also attempted to sample as high in the water column as our gear would allow by towing against the tide current to increase trawl speed and by trawling in the center of the river channel, but we were unable to sample the upper water layers or the shallow waters covering the mudflats on the edge of the main river channel, and these may be important foraging locations for some marine piscivores. However, and more importantly, our trawl measures of prey abundance, i.e., the total number of each species caught, do not discriminate between prey based on features that influence search and handling time and therefore may not reflect availability from the perspective of a forager (Tasker et al. 1999), nor is it expected that all piscivores share a similar perspective of their prey environment. Therefore, we have limited our discussion of interspecific variation in abundance to only very large differences.

Results

Proximate composition and interspecific variation in energy density

We recorded 1,419 fish within our targeted size range, representing 11 species (Table 1). Rainbow smelt and arctic flounder dominated the catch, representing 49 and 31% of the fish captured, respectively, while 5% of the total number of fish captured was comprised of seven species. Proximate composition was determined for 13 fish species (Table 1). Mean water composition as percent field wet mass ranged from 75.1% in least cisco to 82.8% in unknown smelt (the single arctic cod sample contained 84.4% water). Unknown smelt also contained the greatest AFLDM component (86.7%) and the lowest ash component (5.9%). Unknown smelt were not identified to species because most were smaller than our size range of primary interest. However, they are presumed to represent young-of-the-year (YOY) pond and rainbow smelt because of their small size, high water content (Love 1970), and high protein and low lipid contents (Callow and Townsend 1981) relative to pond smelt and rainbow smelt, and because no other smelt species were identified in our trawl samples. Mean lipid composition as percent dry mass ranged between 4.2% in Bering poacher, which also contained the greatest ash component (23.3%), and 23.5% in nine-spine stickleback, which had the lowest AFLDM component (63.5%).

Mean dry mass energy density ranged from 14.5 kJ g^{-1} in Bering poacher to 20.7 kJ g^{-1} in least cisco (Fig. 1). The two models best describing variation in dry mass energy density had a cumulative support of $\text{AIC}_{c,w} = 0.77$ and differed only by whether or not Pacific herring were considered to have a different energetic value than three-spine stickleback, starry flounder, and arctic flounder. Variation in mean wet mass energy density was best described by a single model ($\text{AIC}_{c,w} = 0.63$) and ranged from 2.8 kJ g^{-1} in three-spine stickleback to 5.2 kJ g^{-1} in least cisco (Fig. 1). Arctic cod had the lowest wet mass energy density (2.6 kJ g^{-1}) owing to its high water content, but was not included in the analyses here or elsewhere because of insufficient sample size.

Intraspecific variation in total energy content

Total energy content varied as a function of the explanatory variables that we considered (length, year, Day, and length \times Day) for all fish species with a sufficiently large sample for analyses; the best fitting model for each species had an $\text{AIC}_{c,w}$ that exceeded that of the

Table 1 Numbers of each fish species between 70 and 210 mm captured (nCAP) by trawl during 2002 and 2003 combined, and total numbers collected (nCOL), including individuals outside ofthe targeted size range, for proximate composition analysis in descending order of dry mass energy density (kJ g^{-1} ; see Fig. 1)

Common name	Species	nCAP	nCOL	Length (mm)	Mass (g)	%Water	%Lipid	%AFLDM	%Ash
Least cisco	<i>Coregonus sardinella</i>	3	3	178.7 ± 10.5	52.4 ± 10.3	75.1 ± 0.9	21.1 ± 2.4	69.5 ± 1.9	9.3 ± 0.5
Nine-spine stickleback	<i>Pungitius pungitius</i>	0	4	58.0 ± 1.5	1.1 ± 0.1	77.2 ± 1.6	23.5 ± 1.7	63.5 ± 1.5	13.0 ± 0.5
Pond smelt	<i>Hypomesus olidus</i>	22	40	88.5 ± 2.8	4.8 ± 0.6	78.5 ± 0.4	16.5 ± 0.9	73.4 ± 0.8	10.1 ± 0.4
Unknown smelt	Osmeridae spp.	1	12	56.6 ± 1.4	0.8 ± 0.1	82.8 ± 0.8	7.4 ± 0.9	86.7 ± 1.1	5.9 ± 1.2
Rainbow smelt	<i>Osmerus mordax dentex</i>	689	289	146.4 ± 2.4	22.1 ± 1.1	80.0 ± 0.1	8.7 ± 0.3	80.2 ± 0.2	11.1 ± 0.1
Pacific herring	<i>Clupea pallasii</i>	18	22	126.6 ± 5.8	14.6 ± 2.9	80.5 ± 0.4	7.3 ± 1.1	79.8 ± 0.9	13.0 ± 0.3
Three-spine stickleback	<i>Gasterosteus aculeatus</i>	0	3	62.3 ± 6.7	2.5 ± 0.6	82.2 ± 4.1	11.3 ± 6.3	69.5 ± 0.5	19.3 ± 6.8
Starry flounder	<i>Platichthys stellatus</i>	8	10	94.6 ± 7.1	10.5 ± 2.1	80.1 ± 0.5	7.1 ± 1.1	78.5 ± 0.8	14.4 ± 0.7
Arctic flounder	<i>Pleuronectes glacialis</i>	443	114	117.0 ± 4.0	26.1 ± 2.4	79.9 ± 0.2	7.9 ± 0.3	76.9 ± 0.3	15.3 ± 0.3
Arctic cod	<i>Boreogadus saida</i>	1	1	116.0	10.0	84.4	4.5	82.5	13.0
Saffron cod	<i>Eleginus gracilus</i>	149	151	146.6 ± 2.2	25.2 ± 1.6	81.7 ± 0.1	5.1 ± 0.1	78.7 ± 0.2	16.1 ± 0.2
Belligerent sculpin	<i>Megalocottus platycephalus</i>	65	51	135.6 ± 6.2	39.3 ± 5.0	82.0 ± 0.2	6.6 ± 0.5	75.2 ± 0.5	18.2 ± 0.4
Bering poacher	<i>Occella dodecaedron</i>	20	23	144.4 ± 6.1	17.8 ± 2.1	79.5 ± 0.4	4.2 ± 0.4	72.5 ± 0.3	23.3 ± 0.5

Water composition presented as percent field wet mass; lipid, ash-free lean dry matter (AFLDM), and ash compositions presented as percent dry mass

null model by a factor of $>1 \times 10^4$. Length was consistently an important explanatory variable (Table 2), having a strong, positive effect 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 saffron cod, and was nearly as important as length in belligerent sculpin (Table 2), all of which had higher total energy contents for a given length and Day in 2002 compared to 2003 (Table 3). Year was not an important factor in the remaining species. Day alone and the length \times Day interaction were both relatively unimportant to variation in total energy content for all species with the exception of Pacific herring (Table 2). Weighted parameter estimates indicate that total energy content of Pacific herring increased with increasing Day, and that longer fish did not increase as rapidly with increasing Day as smaller fish (Table 3). However, the inclusion of zero in the 95% confidence interval (CI; $1.96 \times \text{SE}$) of the interaction term parameter estimate suggests this latter effect was not significant.

Discussion

This study is the first from the eastern Bering Sea to describe energy value and abundance of nearshore marine fishes that are potentially important prey for piscivorous predators. Prey fishes in this system differ across species in proximate composition, energy density and total energy content, and relative abundance. This likely plays an important role during prey selection, and may ultimately limit productivity and population growth of local piscivore populations.

Interspecific variation in energy density

The dry mass energy densities for fishes reported here ($14.5\text{--}20.7 \text{ kJ g}^{-1}$) conform to the general pattern of low energetic values for demersal fishes (arctic and starry flounder, arctic and saffron cod, belligerent sculpin, and Bering poacher) and higher values for pelagic species (least cisco, pond and rainbow smelt, and Pacific herring; Fig. 1). The ranking of species based on dry mass energy density reflects the dominating contribution of lipid content, although variation in AFLDM and ash content were also important (Table 1). The

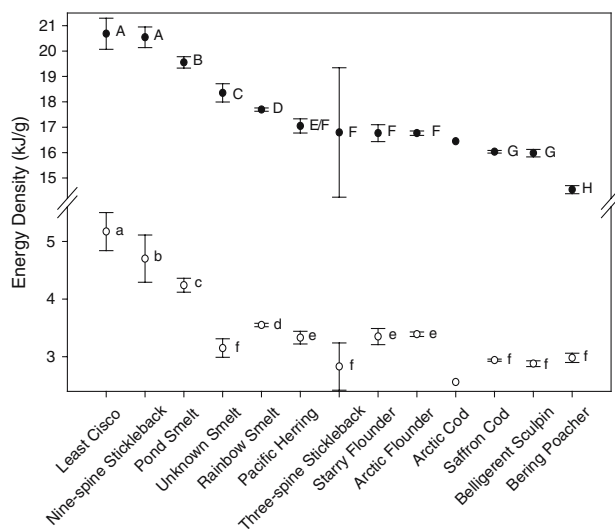


Fig. 1 Mean dry mass (closed circles) and field wet mass (open circles) energy densities of all fish processed (years combined; ± 1 SE). Upper and lower case lettering represents groupings of species with similar dry and wet mass energy densities, respectively, based on the best fitting model(s) using AIC_c as the selection criterion. For dry mass, the two top models had a cumulative $AIC_{c,w} = 0.77$, with the only difference between those models being the definition of Pacific herring as a separate category (E) or grouped with other species (F). The best fitting wet mass model had an $AIC_{c,w} = 0.63$. Arctic cod is represented by a single sample and therefore was not included in the grouping analyses

Table 2 Relative contribution ($\sum AIC_{c,w}$) of each global model parameter in predicting total energy content for each species

Species ^a	$\sum AIC_{c,w}$			
	ln(Length) (mm)	Year	Day	ln(Length) \times Day
Pond smelt	1.00	0.52	0.44	0.43
Unknown smelt	1.00	^b	0.51	0.51
Rainbow smelt	1.00	1.00	0.67	0.64
Pacific herring	1.00	0.34	0.95	0.95
Starry flounder	1.00	0.06	0.35	0.36
Arctic flounder	1.00	0.25	0.57	0.56
Saffron cod	1.00	1.00	0.73	0.63
Belligerent sculpin	1.00	0.97	0.23	0.23
Bering poacher	1.00	0.25	0.54	0.62

^a An insufficient number of samples were collected to perform analyses on the four species omitted from this table

^b Zero unknown smelt were captured in 2003. Therefore, a model including year was not included in the model set for this species

inverse relation between lipid and water contents magnified the discrepancy between minimum and maximum mean wet mass energy density among species to nearly twofold ($2.8\text{--}5.2\text{ kJ g}^{-1}$ wet mass) and had important consequences for the ranking of species, although there were fewer differences between species overall (Fig. 1). Species that were particularly affected in their wet mass energy density ranking include Ber-

ing poacher, which had low amounts of both lipid and water, and three-spine stickleback, arctic cod, and unknown smelt, all of which contained a high percentage of water (Table 1).

Intraspecific variation in total energy content

We found strong positive relationships between length and total energy content for all species with the exception of nine-spine stickleback. Total energy content increased by more than a factor of three with increasing length for all species except Bering poacher, and exceeded a factor of four for least cisco and Pacific herring (Table 3). The increase in total energy with length is explained by an associated increase in body size, and by an increase in energy density due to a reduction in body water stores with growth (Love 1970), and a shift in the allocation of resources from growth (i.e., AFLDM) to storage (i.e., lipid) (Callow and Townsend 1981). Hislop et al. (1991) reported a similar finding for lesser sandeel (*Ammodytes marinus*) and sprat (*Sprattus sprattus*). We were unable to provide a predictive equation for nine-spine stickleback as the model suggested a biologically implausible negative effect of length on total energy. We believe this results from a small sample size ($n = 4$), small difference in length between the smallest and largest sample (7 mm), and a low energy value for the largest fish.

We also detected temporal variation in the total energy content of some fish species (Table 3). The effect of year on the total energy content of rainbow smelt, saffron cod, and belligerent sculpin likely reflects better foraging conditions in nearshore waters for these fishes in 2002 compared to 2003. Anthony et al. (2000) drew similar conclusions with respect to Pacific herring. Although we did not find an interannual difference in total energy content of Pacific herring, this was the only species we sampled in which a seasonal effect was detected. We did not find support for an interaction between length and day of the year suggesting this seasonal variation was unrelated to physiological changes associated with changing reproductive condition of longer and presumably sexually mature fish compared to smaller fish. Similar to findings elsewhere (Paul and Paul 1998; Iverson et al. 2002), we suggest the seasonal variation in Pacific herring total energy content reflects the seasonal fasting and feeding foraging behavior of this species (Paul et al. 1998). The lack of a seasonal effect for most species in our study is in contrast to findings elsewhere and likely reflects the comparatively short duration of our investigation: late June to mid-August v. ≥ 5 months (Hislop et al. 1991), 4 months (Anthony et al. 2000), three seasons (Iverson

Table 3 Parameter estimates for predicting total energy content ($\text{kJ fish}^{-1} = e^{\ln(\text{Total energy})}$) of each fish species

Species	Global model					Length model	
	Intercept	ln(Length) (mm)	Year (1×10^{-2})	Day (1×10^{-2})	ln(Length) \times Day (1×10^{-3})	Intercept	ln(Length) (mm)
Least cisco	–	–	–	–	–	-18.71 ± 0.29	4.68 ± 0.06
Pond smelt	-12.87 ± 0.83	3.51 ± 0.26	4.89 ± 3.84	-2.19 ± 2.35	4.70 ± 5.17	-13.18 ± 0.64	3.58 ± 0.14
Unknown smelt	-13.48 ± 1.01	3.47 ± 0.25	–	1.75 ± 1.50	0.69 ± 5.10	-13.62 ± 1.28	3.58 ± 0.32
Rainbow smelt	-12.66 ± 0.36	3.35 ± 0.07	14.36 ± 2.11	-1.05 ± 0.94	1.88 ± 1.69	-12.61 ± 0.18	3.35 ± 0.04
Pacific herring	-18.78 ± 2.10	4.61 ± 0.44	4.52 ± 4.23	32.37 ± 9.60	-66.02 ± 72.04	-13.39 ± 1.22	3.53 ± 0.25
Three-spine stickleback	–	–	–	–	–	-12.53 ± 0.13	3.50 ± 0.03
Starry flounder	-11.16 ± 1.48	3.17 ± 0.33	1.67 ± 2.45	0.30 ± 0.26	0.73 ± 0.64	-11.29 ± 1.72	3.23 ± 0.38
Arctic flounder	-10.73 ± 0.22	3.10 ± 0.05	0.10 ± 0.80	0.22 ± 0.31	0.42 ± 0.68	-10.78 ± 0.19	3.13 ± 0.04
Saffron cod	-13.32 ± 0.71	3.47 ± 0.14	25.35 ± 3.20	1.80 ± 1.82	-2.66 ± 3.66	-13.64 ± 0.44	3.57 ± 0.09
Belligerent sculpin	-12.22 ± 0.49	3.37 ± 0.10	21.07 ± 6.78	0.11 ± 0.26	-0.24 ± 0.50	-12.32 ± 0.49	3.40 ± 0.10
Bering poacher	-10.31 ± 1.33	2.78 ± 0.27	2.11 ± 2.72	-1.13 ± 2.85	5.03 ± 5.02	-10.71 ± 0.91	2.93 ± 0.18

Global model [$\ln(\text{Total energy}) = \text{intercept} + \ln(\text{Length}) + \text{Day} + \text{Year} + \ln(\text{Length}) \times \text{Day}$] parameters (± 1 unconditional SE) represent model AIC_c averaged estimates across the entire candidate set of models: year is a categorical variable with 2003 being the reference level and the parameter estimate representing the difference in total energy content due to year 2002 relative to 2003; Day is a continuous variable rescaled with 1 representing 20 June and the parameter estimate indicating the effect of increasing Day on total energy content. Length model [$\ln(\text{Total energy}) = \text{intercept} + \ln(\text{Length})$] parameter estimates (± 1 SE) are unweighted

– No parameter estimate computed

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 effect 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 offset the cost of roundtrip travel if the energy and time costs associated with handling larger fish 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 brood. Nine-spine stickleback and pond smelt are typically small [Mecklenburg et al. (2002) report typical maximum lengths of 65 and 150 mm, respectively] compared to most species in this study. A forager

selecting one or a few prey solely on total energy content would likely reject these small species in favor of large, energetically valuable fish such as least cisco.

Prey abundance also affects the rate at which energy can be acquired. Based on our capture data, least cisco are likely inconsequential to predators in this system, despite their high energy value, because they are relatively rare compared to arctic flounder and rainbow smelt. For example, a forager focusing on least cisco would encounter almost 150 arctic flounder and more than 200 rainbow smelt on average before encountering its target prey. This does not mean that a least cisco would be rejected if encountered, but by including arctic flounder and rainbow smelt in the diet a higher rate of energy acquisition could be achieved compared to a diet that only included least cisco. Comparing profitability between arctic flounder and rainbow smelt, we would predict the latter to be preferentially selected, despite the former possibly being easier to capture (Bowen et al. 2002). This is because total energy content increases more rapidly with length in rainbow smelt compared to arctic flounder, whose body shape likely increases handling time (personal observation, Bowen et al. 2002) and may limit consumption to smaller individuals of lower total energy value. Our sampling protocol does not address the abundance of the small, energetically valuable pond smelt and nine-spine stickleback. If these species are abundant and have low handling costs, they may be profitable to predators that deliver multiple prey or when self-feeding.

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 flounder, had low lipid components and energy densities compared to many fish 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 significantly less benefits compared to a high-lipid diet (Rosen and Trites 2000a; Kitaysky et al. 2001) due to the lower assimilation efficiency 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. 1996; Ball 2004), future studies are needed to determine if the local prey regime has shifted similarly to other locations in Alaska in response to climatic and oceanographic variation.

Recommendations for future prey studies

We join other researchers in encouraging future studies to report proximate composition values and energy density on a dry mass basis for comparative purposes (Montevecchi and Piatt 1987; Hislop et al. 1991). In this study, the significant mass lost due to desiccation between collection and initiation of lab procedures would result in over-estimation of wet mass energy density if water loss were not accounted for. Similarly, energy density estimates derived from the relationship between lipid and water contents (Hislop et al. 1991; Anthony et al. 2000) are prone to bias if there is unaccounted water loss. By using dry mass energy density as the comparative standard, variation in energetic content resulting from variable desiccation rates between species, and between studies, would be minimized.

We also encourage researchers to develop species-specific models relating total energy content to length using proximate analysis. Estimates of total energy content based on the energy density values of prey items fails to account for potential effects of length on energy density and total energy content reported here and elsewhere (Hislop et al. 1991; Anthony et al. 2000). In contrast, length is highly correlated to total energy content, can be easily and accurately assessed in the field, either by direct observation, or by collecting unconsumed items, and is unaffected by desiccation (Montevecchi and Piatt 1987). Estimates of total

energy content may be further improved by incorporating both seasonal and interannual variation in the predictive model.

Acknowledgments This study forms part of the research submitted by JRB for the Master of Science degree at Simon Fraser University. The authors gratefully acknowledge the collection assistance of P. Fontaine, C. Eldermire, E. Bohman, B. Lake, E. Harrington, and S. Rhoades. Sampling was conducted under the authority of the Simon Fraser University Animal Care Committee (permit 625B) and the State of Alaska Department of Fish and Game (permits CF-02-052, CF-03-042). Special thanks to K. Gorman for initiating the laboratory protocol and to S. Maclean for conducting much of this work. T.D. Williams and the Centre for Wildlife Ecology, Simon Fraser University, provided laboratory equipment and space. N. Pingayak, J. Ayuluk, R. Ayogan, the staff and pilots of the Yukon Delta NWR, and the staff of the Alaska Science Center, Anchorage, provided logistic support. Funding was provided by: USGS, Alaska; B. Leedy, Division of Migratory Bird Management, USFWS, Alaska; Northern Scientific Training Program, Canada; LoonWatch, Sigurd Olson Environmental Inst., Wisconsin. The comments of J. F. Piatt, L. M. Dill, R. C. Ydenberg, and two anonymous reviewers improved previous drafts of this manuscript.

References

- Agler BA, Kendall SJ, Irons DB, Klosiewski SP (1999) Declines in marine bird populations in Prince William Sound, Alaska coincident with a climate regime shift. *Waterbirds* 22:98–103
- Anderson PJ, Piatt JF (1999) Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Mar Ecol Prog Ser* 189:117–123
- Anthony JA, Roby DD, Turco KR (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *J Exp Mar Biol Ecol* 248:53–78
- Ball JR (2004) Effects of parental provisioning and attendance on growth and survival of red-throated loon pre-fledglings: a potential mechanism linking marine regime shifts to population change. MSc Thesis, Department of Biological Sciences, Simon Fraser University
- Bowen WD, Tully D, Boness DJ, Bulheier BM, Marshall GJ (2002) Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar Ecol Prog Ser* 244:235–245
- Brekke B, Gabrielsen GW (1994) Assimilation efficiency of adult kittiwakes and Brunnich's guillemots fed capelin and arctic cod. *Polar Biol* 14:279–284
- Brodeur RD, Wilson MT, Walters GE, Melnikov IV (1999) Forage fishes in the Bering Sea: distribution, species associations, and biomass trends. In: Loughlin TR, Ohtani K (eds) *Dynamics of the Bering Sea*. Alaska Sea Grant College Program, Fairbanks, pp 509–536
- Burnham KP, Anderson DR (2002) *Model selection and multimodal inference: a practical information-theoretic approach*, 2nd edn. Springer, Berlin Heidelberg New York
- Calow P, Townsend CR (1981) Resource utilization in growth. In: Townsend CR, Calow P (eds) *Physiological ecology: an evolutionary approach to resource use*. Sinauer Associates, Sunderland, pp 220–244
- Craig JF, Kenley MJ, Talling JF (1978) Comparative estimations of the energy content of fish tissue from bomb calorimetry, wet oxidation and proximate analysis. *Freshw Biol* 8:585–590

- Crawford RJM, Dyer BM (1995) Responses by four seabird species to a fluctuating availability of cape anchovy *Engraulis capensis* off South Africa. *Ibis* 137:329–339
- Davoren GK, Burger AE (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Anim Behav* 58:853–863
- Decker MB, Hunt GL Jr, Byrd GV Jr (1995) The relationships among sea-surface temperature, the abundance of juvenile walleye pollock (*Theragra chalcogramma*), and the reproductive performance and diets of seabirds on the Pribilof Islands, southeastern Bering Sea. In: Beamish RJ (ed) Climate change and northern fish populations. *Can Spec Publ Fish Aquat Sci*, No. 121, pp 425–437
- Eriksson MOG, Blomqvist D, Hake M, Johansson OC (1990) Parental feeding in the Red-throated Diver *Gavia stellata*. *Ibis* 132:1–13
- Estes JA (1979) Exploitation of marine mammals: *r*-selection of *K*-strategists? *J Fish Res Board Can* 36:1009–1017
- Frank D (1992) The influence of feeding conditions on food provisioning of chicks in common tern *Sterna hirundo* nesting in the German Wadden Sea. *Ardea* 80:45–55
- Furness RW, Monaghan P (1987) Seabird ecology. Chapman and Hall, New York
- Gaston AJ (1997) Mass and date at departure affect the survival of ancient murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* 139:673–678
- Golet GH, Kuletz KJ, Roby DD, Irons DB (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *Auk* 117:82–91
- Groves DJ, Conant B, King RJ, Hodges JI, King JG (1996) Status and trends of loon populations summering in Alaska, 1971–1993. *Condor* 98:189–195
- Hipfner JM, Adams PA, Bryant R (2000) Breeding success of black-legged kittiwakes, *Rissa tridactyla*, at a colony in Labrador during a period of low capelin, *Mallotus villosus*, availability. *Can Field Nat* 114:413–416
- Hislop JRG, Harris MP, Smith JGM (1991) Variation in the caloric value and total energy content of the lesser sandeel (*Ammodytes marinus*) and other fish preyed on by seabirds. *J Zool* 224:501–517
- Iverson SJ, Frost KJ, Lang SLC (2002) Fat content and fatty acid composition of forage fish and invertebrates in Prince William Sound, Alaska: factors contributing to among and within species variability. *Mar Ecol Prog Ser* 241:161–181
- Kitaysky AS, Hunt GL Jr, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296
- Kitaysky AS, Kitaiskaia EV, Wingfield JC, Piatt JF (2001) Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-legged kittiwake chicks. *J Comp Physiol B* 171:701–709
- Lance BK, Roby DD (2000) Diet and postnatal growth in red-legged and black-legged kittiwakes: an interspecific cross-fostering experiment. *Auk* 117:1016–1028
- Litzow MA, Piatt JF, Prichard AK, Roby DD (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia* 132:286–295
- Loughlin TR, Sukhanova IN, Sinclair EH, Ferrero RC (1999) Summary of biology and ecosystem dynamics in the Bering Sea. In: Loughlin TR, Ohtani K (eds) Dynamics of the Bering Sea. Alaska Sea Grant College Program, Fairbanks, pp 387–407
- Love RM (1970) The chemical biology of fishes. Academic, New York
- Mecklenburg CW, Mecklenburg TA, Thorsteinson LK (2002) Fishes of Alaska. American Fisheries Society, Bethesda
- Merrick RL, Chumbley MK, Byrd GV (1997) Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. *Can J Fish Aquat Sci* 54:1342–1348
- Montevecchi WA, Piatt JF (1984) Composition and energy content of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators. *Comp Biochem Physiol* 78A:15–20
- Montevecchi WA, Piatt JF (1987) Dehydration of seabird prey during transport to the colony: effects on wet weight energy densities. *Can J Zool* 65:2822–2824
- Montevecchi WA, Ricklefs RE, Kirkham IR, Gabaldon D (1984) Growth energetics of nestling northern gannets (*Sula bassanus*). *Auk* 101:334–341
- National Research Council (1996) The Bering Sea ecosystem. National Academy Press, Washington
- Norberg RA, Norberg UM (1976) Size of fish carried by flying Red-throated Divers *Gavia stellata* (Pont.) to nearly fledged young in nesting tarn. *Ornis Fenn* 53:92–95
- Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Stairs GR, Mitchell RD (eds) Analysis of ecological systems. Ohio State University Press, Columbus, pp 155–177
- Paul AJ, Paul JM (1998) Spring and summer whole-body energy content of Alaskan juvenile Pacific herring. *Alaska Fish Res Bull* 5:131–136
- Paul AJ, Paul JM, Brown ED (1998) Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasii* Valenciennes 1847) relative to age, size and sex. *J Exp Mar Biol Ecol* 223:133–142
- Payne SA, Johnson BA, Otto RS (1999) Proximate composition of some north-eastern Pacific forage fish species. *Fish Oceanogr* 8:159–177
- Pearson TH (1968) The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. *J Anim Ecol* 37:521–552
- Perrins CM, Harris MP, Britton CK (1973) Survival of manx shearwaters *Puffinus puffinus*. *Ibis* 115:535–548
- Piatt JF, Anderson P (1996) Response of common murrelets to the Exxon Valdez oil spill and long-term changes in the Gulf of Alaska marine ecosystem. In: Rice SD, Spies RB, Wolfe DA, Wright BA (eds) Proceedings of the Exxon Valdez Oil Spill Symposium, American Fisheries Society Symposium No. 18. American Fisheries Society, Bethesda, pp 720–737
- Radin NS (1981) Extraction of tissue lipids with a solvent of low toxicity. *Methods Enzymol* 72:5–7
- Reimchen TE, Douglas S (1984) Feeding schedule and daily food consumption in red-throated loons (*Gavia stellata*) over the pre-fledging period. *Auk* 101:593–599
- Rindorf A, Wanless S, Harris MP (2000) Effects of changes in the sandeel availability on the reproductive output of seabirds. *Mar Ecol Prog Ser* 202:241–252
- Rosen DAS, Trites AW (2000a) Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. *Can J Zool* 78:1243–1250
- Rosen DAS, Trites AW (2000b) Digestive efficiency and dry-matter digestibility in Steller sea lions fed herring, pollock, squid, and salmon. *Can J Zool* 78:234–239
- Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment, 5th edn. Cambridge University Press, Cambridge
- Springer AM (1999) Summary, conclusions, and recommendations. In: Loughlin TR, Ohtani K (eds) Dynamics of the Bering Sea. Alaska Sea Grant College Program, Fairbanks, pp 777–799
- Suryan RM, Irons DB, Benson J (2000) Prey switching and variable foraging strategies of black-legged kittiwakes and the effect on reproductive success. *Condor* 102:374–384

- Suryan RM, Irons DB, Kaufman M, Benson J, Jodice PGR, Roby DD, Brown ED (2002) Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser* 236:273–287
- Tasker ML, Camphuysen CJ, Fossum P (1999) Variation in prey taken by seabirds. In: Furness RW, Tasker ML (eds) Diets of seabirds and consequences of changes in food supply. ICES Cooperative Research Report, no. 232. International Council for Exploration of the Sea, Copenhagen, pp 18–28
- Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some north Pacific forage fishes. *Comp Biochem Physiol* 118A:1393–1398