Arctic Cod (*Boreogadus saida*) as Prey: Fish Length-Energetics Relationships in the Beaufort Sea and Hudson Bay

B. BRITTEN HARTER,[1,2] KYLE H. ELLIOTT,[1] GEORGE J. DIVOKY[3] and GAIL K. DAVOREN[1]

ABSTRACT. Although Arctic cod (*Boreogadus saida*) is widely recognized as an important trophic link to top predators in Arctic marine ecosystems, the challenges of conducting fieldwork in the Arctic make this species difficult to study. We establish some basic relationships to improve prey energetics modeling when only in-field parameters (e.g., fork length) can be measured. We investigated the intraspecific relationships among energy density, fork length, mass, and water content for Arctic cod captured by Black Guillemots and Thick-billed Murres at two sites (Western Beaufort and Hudson Bay). Dry energy density was similar between sites (21.6–22.2 kJ g^{-1}) and increased with fork length (Dry ED$_{kJ/g}$ = 0.028 (± 0.01) • Fork Length$_{mm}$ + 18.12 (± 1.33). Even though fish lost some water as they were transported to the nest by avian predators, wet energy density also increased with fork length. We suggest that environmental conditions had a similar effect on growth at these two locations although they occur in very different oceanographic regimes. Arctic cod, especially large cod, is one of the most energy-rich prey species in the Arctic. Our results highlight the importance of this valuable prey to Arctic ecosystems and the utility of using seabirds opportunistically as samplers of the marine environment.

Key words: Arctic, energetics, Arctic cod, marine predators, energy density, seabirds

RÉSUMÉ. Même si la morue polaire (*Boreogadus saida*) est grandement reconnue comme un lien trophique important pour les prédateurs situés en bout de chaîne des écosystèmes marins de l'Arctique, cette espèce est difficile à étudier en raison des défis inhérents à la réalisation de travaux sur le terrain dans l'Arctique. Nous établissons des relations de base afin d'améliorer la modélisation de la valeur énergétique des proies lorsque seuls des paramètres sur le terrain (comme la longueur à la fourche) peuvent être mesurés. Nous avons étudié les relations intraspécifiques qui existent entre la densité d'énergie, la longueur à la fourche, la masse et la teneur en eau de la morue polaire capturée par le guillemot à miroir et le guillemot de Brünnich à deux sites (ouest de Beaufort et baie d'Hudson). La densité d'énergie sèche était semblable entre les sites (21,6–22,2 kJ g^{-1}) et augmentait en fonction de la longueur à la fourche (DE sèche ED$_{kJ/g}$ = 0,028 (± 0,01) • longueur à la fourche$_{mm}$ + 18,12 (± 1,33). Même si les poissons perdaient de l'eau pendant le transport jusqu'au nid par les oiseaux prédateurs, la densité d'énergie humide augmentait également en fonction de la longueur à la fourche. Nous suggérons que les conditions environnementales avaient un effet similaire sur la croissance à ces deux sites même s'ils se trouvent dans des régimes océanographiques très différents. La morue polaire, surtout celle de grande taille, est l'une des espèces proies les plus riches en énergie de l'Arctique. Nos résultats mettent en évidence l'importance de cette précieuse proie pour les écosystèmes de l'Arctique et l'utilité de se servir des oiseaux de mer de manière opportuniste en guise d'échantillonneurs de l'environnement marin.

Mots clés : Arctique, énergétique, morue polaire, prédateurs marins, densité d'énergie, oiseaux de mer

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

Arctic cod (*Boreogadus saida*) is a small (< 200 mm), short-lived (3–7 yr) marine fish (Bradstreet et al., 1986; Lønne and Gulliksen, 1989; Lawson et al., 1998). In Arctic marine ecosystems, this species represents an important trophic link between primary consumers and top vertebrate predators such as whales, seals, and seabirds (Boekelheide, 1980; Lowry and Frost, 1981; Bradstreet, 1982; Bradstreet et al., 1986; Hobson and Welch, 1992; Welch et al., 1992, 1993; Hoekstra et al., 2002). It is one of the most energy-rich prey species available in the Arctic, and when size is included, it may offer the most total calories per prey item for certain predators (Elliott and Gaston, 2008). Arctic cod is traditionally regarded as an ice-associated species, often found near the edge of the pack ice but also in schools near isolated icebergs and in open water (Lowry and Frost, 1981; Craig et al., 1982; Bradstreet et al., 1986; Moulton and Tarbox, 1987; Crawford and Jorgenson, 1993, 1996; Welch et al., 1993; Hop et al., 1997a; Gradinger and Bluhm, 2004; Elliott et al., 2008). There is a strong body of knowledge on Arctic cod, but opportunities remain to fill in gaps, particularly for

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

[2] Corresponding author: b.britten.harter@aya.yale.edu; present address: 26 Marathon Street, Arlington, Massachusetts 20474, USA

[3] Friends of Cooper Island, 652 32nd Avenue East, Seattle, Washington 98112, USA

Hudson Bay and the Beaufort Sea, about which information remains scant.

Few attempts have been made to investigate whether energy density varies with fork length or geography. Instead, studies have focused on mean energy density (kJ g⁻¹) of all Arctic cod samples collected (Cairns, 1984; Brekke and Gabrielsen, 1994; Hop et al., 1995, 1997b; Lawson et al., 1998; Ball et al., 2007; Elliott and Gaston, 2008). Some of these studies measured the mean fraction of dry mass for Arctic cod (or its complement, the mean fraction of water or moisture; Lawson et al., 1998; Ball et al., 2007), but have not examined whether this fraction changes with length. Relationships of both energy density and fraction dry mass with length are expected for Arctic cod, given their presence in other fish species (Lambert and Dutil, 1997; Lawson et al., 1998; Pothoven et al., 2006; Ball et al., 2007).

In our study, we investigated the relationships among fish size (fork length) and other biophysical parameters, such as wet and dry energy density and fraction dry mass, for Arctic cod captured by Black Guillemots (*Cepphus grylle*) and Thick-billed Murres (*Uria lomvia*), and we compared the Hudson Bay Canadian population to the Western Beaufort Alaska population. On the basis of previous work, we predicted that energy density would increase linearly with fish length, as larger animals are more likely to invest in high-energy organs (lipids and gonads) rather than growth (Lambert and Dutil, 1997; Lawson et al., 1998; Pothoven et al., 2006; Ball et al., 2007). Because of the pronounced difficulty of collection and field preservation in the Arctic, where freezing samples is impossible in many instances, establishing accurate relationships of fish length to energy density and other relevant physiological parameters will increase understanding of Arctic cod for researchers capable of measuring only length.

METHODS

At-Colony Sample Collection

We collected Arctic cod from two sites. The first was the Black Guillemot colony on Cooper Island, Alaska (71°41′ N, 155°41′ W), a barrier island in the Western Beaufort Sea near Barrow, Alaska (Divoky, 1998) during 2005–06. The second was the Thick-billed Murre colony on Coats Island (62°57′ N, 82°00′ W) in northern Hudson Bay during 2006–07. At both sites, birds carried samples back to the colony. We collected samples opportunistically during chick banding or measurement, an observed prey delivery, and a kleptoparasitic event when a Parasitic Jaegar (*Stercorarius parasiticus*) attempted to steal prey from returning parent birds in flight. All samples were collected less than two hours after delivery and during the birds' breeding season of June–August.

After collection, fish at both sites were weighed on an electronic scale accurate to ± 0.1 g (Hudson Bay) or ± 1 g

(Western Beaufort). Samples were measured from snout to the base of the fork (fork length) with ruler to ± 1 mm. After weighing and measuring, samples were immediately frozen. Fish that were missing sections, visibly dried, or otherwise incomplete were excluded from analyses.

Sampling cod from these birds, while including more complicating factors than at-sea collection, is an acceptable way to obtain samples, particularly for prey energetic studies. Bradstreet et al. (1986) proposed using animals adapted to capture these fish as sampling devices to overcome the difficulty of collecting specimens. Unlike some seabirds, which carry back partially digested prey in a gular sac to feed their chicks, alcids feed largely intact prey to their chicks. They are thus appropriate prey samplers, as prey are largely pristine and can be easily sampled at the colony. A difficult-to-test assumption is that seabirds are random samplers and are not selecting for disproportionately energy-rich fish.

Energetic Analysis

A subset of fish spanning the length range of Arctic cod, as described by Bradstreet (1986) (Western Beaufort: n = 15; Hudson Bay: n = 20), was selected for detailed energetic analysis. We selected approximately two fish from each 10 mm length bin, with the Coats Island samples having more bins because of their wider range of sample lengths. In the laboratory, each frozen fish was freeze-dried for 36 hours in a Labconco freeze drier. The freeze-dried samples were weighed whole and then homogenized using a blade grinder. We prepared pellets ranging from 0.3 to 0.6 g using a Parr pellet press. If the fish was large enough, up to three pellets were made to ensure accurate energy density values. The pellets were dried at 55°C for 24 hours and weighed to the nearest 0.0001 g. The pellets were combusted in a Parr adiabatic calorimeter, calibrated using a benzoic acid standard. The procedures for operating the equipment and making standard corrections for energetic calculations including fuse wire and acid formulation are available in the equipment manual (Parr Instrument Company, n.d.). We calculated total kJ per fish as the mean energy density of all pellets made from the sample multiplied by the total dry mass (g) of the sample after freeze drying.

We calculated a series of parameters based on laboratory and at-colony data. We defined dry energy density (kJ g⁻¹) as the sample's calculated total energy (kJ) divided by the total dry mass (g). The other two parameters are derived from the total wet mass measured at the colony. Wet energy density is the sample's calculated total kJ divided by its at-colony wet mass (g). Fraction dry mass is the mass of the sample after freeze-drying divided by the at-colony wet mass.

Fish Drying in Transit

Transit by birds back to the colony causes drying that decreases the measured mass of fish (Montevecchi and

Piatt, 1987) and therefore also slightly increases their calculated fraction dry mass and wet energy density. Transit time will not affect any measurements related to dry energy density, but different transit times do create a small source of potential error for fraction dry mass and wet energy density. Murre transit times when delivering Arctic cod averaged 25 minutes (± 12 min. SD) (Elliott et al., 2008), while guillemot transit times averaged 12 minutes (± 5 min. SD) (B.B. Harter, G.J. Divoky, and G.K. Davoren, unpubl. data). As murres make longer trips with more variable duration, it would be expected that fish obtained by murres would be slightly (less than one gram) drier and have higher apparent wet energy density and fraction dry mass than fish acquired by guillemots. Owing to potential different trip durations and drying prior to collection at the colony, we provide all measurements (Table 1) but focus on energy densities calculated from dry weight.

Statistical Analyses

We compared mean values for parameters (e.g., length, dry energy density, and fraction dry mass) between sites using Student's t-test. We tested for normality and equal variance between sites using histogram plotting and Bartlett's test. To test for linear relationships between parameters (e.g., length and dry energy density), we performed ANCOVA to see if data could be pooled. We then performed linear regression to investigate the relationships between parameters.

RESULTS

For parameters unaffected by drying in transit, fish from Hudson Bay and the Western Beaufort were indistinguishable. The samples analyzed did not differ in length ($t_{33} = -0.513$, $p > 0.61$) and had nearly identical dry energy densities (Table 1). For dry energy density vs. length relationships, data from both sites could be pooled for further analysis (Table 2), and dry energy density (kJ g^{-1}) was significantly predicted by fork length ($r^2 = 0.20$, $t_{33} = 2.84$, $p < 0.008$, Fig. 1).

For parameters potentially affected by drying in transit, data for all parameters could also be pooled for further analyses on the basis of indistinguishable relationships (Table 2) and the assumption of similar drying per unit time under similar temperatures and conditions. For the pooled data from the two locations, fraction dry mass ($r^2 = 0.21$, $t_{33} = 2.93$, $p < 0.007$, Fig. 2) and at-colony wet energy density ($r^2 = 0.27$, $t_{33} = 3.17$ $p < 0.002$, Fig. 3) increased with fork length. At-colony wet energy density also increased with fraction dry mass for pooled data ($r^2 = 0.84$, $t_{33} = 13.2$, $p < 0.0001$, Fig. 4). For data from each individual site, most regressions were significant as well (Table 2). As expected from differences in transit drying, fish from Hudson Bay had higher observed fraction dry mass when collected at the colony (Hudson Bay: 20.9 ± 0.01%; Western Beaufort:

17.2 ± 0.01%, $t_{33} = -4.49$, $p < 0.0001$), as well as higher wet energy density at the colony (Table 1).

DISCUSSION

We show that, for Arctic cod, dry energy density is significantly predicted by fork length, suggesting that researchers can gain valuable information about this crucial prey item using only a ruler. Despite small potential differences from drying during transit, wet energy density and fraction dry mass are also both predicted by fork length. The increases with fork length in energy density and fraction dry mass, observed in this study and in studies of other fishes (e.g., Pothoven et al., 2006; Rodgveller et al., 2007), are likely driven by a physiological change, with older fish investing proportionally more in lipid-rich organs such as energy stores (adipose tissue) and gonads rather than in growth as they enlarge and age (Benoit et al., 2010). Similar relationships between length and energy density have been found in other species in multiple ecosystems (Lawson et al., 1998; Payne et al., 1999; Wuenschel et al., 2006; Ball et al., 2007; Rodgveller et al., 2007), but we believe this is the first such relationship published for Arctic cod. The strength of the linear relationship, while not extremely high ($r^2 = 0.20$), is similar to those published for other species (Lawson et al., 1998).

On the basis of similar dry energy densities and indistinguishable relationships with length, we suggest that Arctic cod from Hudson Bay and the Western Beaufort Sea are similar biophysically, despite their different oceanographic regimes. More northern fish tend to have higher body-fat content (Garvey and Marschall, 2003; Tocher, 2003), but the variation in latitude between these two sites does not appear to be great enough to generate a meaningful difference.

The data for the Western Beaufort Sea and Hudson Bay (some of which were published previously by Elliott and Gaston, 2008) are similar to data from other studies, fitting within the high and low values of data for mean wet and dry energy density and mean fraction dry mass of other Arctic cod studies (Table 1). Among sites of similar latitude (including the Bering Sea and the northwest Atlantic), discrepancies among studies appear to be related to the age class sampled, as the mean energy density and fraction dry mass generally agreed with our length-based regressions (Figs. 2, 3). Correcting for transit drying (i.e., slightly lowering the fraction dry mass and wet energy density) would bring our data on wet energy density and fraction dry mass and comparable data from external studies into even closer concurrence. Fish sampled from Svalbard (79° N) during February and June (Brekke and Gabrielsen, 1994) had higher energy densities than predicted by our equation. Those sampled in February had notably higher densities, which could be attributed to differences in breeding condition (Craig et al., 1982). Those sampled in June were much closer in energy density to samples from Hudson Bay and the Western Beaufort Sea, falling within the high and low

TABLE 1. Basic statistics (mean ± SE) for body size, wet and dry energy density, wet mass, and fraction dry mass for samples of Arctic cod from the Western Beaufort and Hudson Bay, as well as those from other studies.

Sample location	n_{fish}	Fish length (mm)	Dry energy density (kJ g⁻¹)	At-colony wet mass (g)	At-colony wet energy density (kJ g⁻¹)	Fraction dry mass	Source
Western Beaufort	15	129.4 ± 8.4 (87–181)	22.2 ± 0.42	17.2 ± 2.68[1] (5–33)	3.9 ± 0.21[1]	17.2 ± 0.67[1]	This study
Hudson Bay	20	134.9 ± 6.86 (88–191)	21.6 ± 0.48	19.7 ± 2.75[1] (3.3–47.8)	4.5 ± 0.19[1]	20.9 ± 0.48[1]	This study
Labrador and Newfoundland	52	159 ± 0.25	–	36.6 ± 0.63	4.4 ± 0.12	21.1 ± 0.22	Lawson et al. (1998)
Eastern Bering	1	116	~16.6	10	~2.6	15.6	Ball et al. (2007)
Svalbard (1985)[3]	–	132 ± 13[2]	–	14.2 ± 4.3[2]	7.4 ± 0.1	28 ± 0.0	Brekke and Gabrielsen (1994)
Svalbard (1986)	–	99 ± 22[2]	–	7.7 ± 4.3[2]	4.9 ± 0.0	23 ± 0.1	Brekke and Gabrielsen (1994)
Resolute and Allen Bays (1990)[4]	8	–	26.415 ± 0.24	13.46 ± 0.70	6.269 ± 0.20	16.3 ± 0.52	Hop et al. (1997b)

[1] Data that may be affected by drying in transit to colony.
[2] Parameters with SD rather than SE.
[3] Samples captured in February and assumed to be reproducing.
[4] Samples fed *Calanus* in captivity with unknown changes to body parameters.

TABLE 2. Individual regression statistics for characteristics of Arctic cod in the Western Beaufort Sea and Hudson Bay and ANCOVA results comparing homogeneity of regressions between these two areas. Because none of the relationships were significantly different, data were pooled for later analysis. Bold text indicates significant results.

Independent	Dependent	Western Beaufort Sea only			Hudson Bay only			ANCOVA homogeneity comparison	
		n	p	r^2	n	p	r^2	$F_{1,33}$	p
Fork length	Dry energy density	15	> 0.27	0.09	20	**< 0.01**	0.33	1.74	0.20
Fork length	Fraction dry mass[1]	15	**< 0.003**	0.51	20	> 0.15	0.11	2.26	0.14
Fork length	Wet energy density[1]	15	**< 0.02**	0.37	20	**< 0.04**	0.22	0.07	0.79
Fraction dry mass[1]	Wet energy density[1]	15	**< 0.001**	0.94	20	**< 0.001**	0.85	1.14	0.29

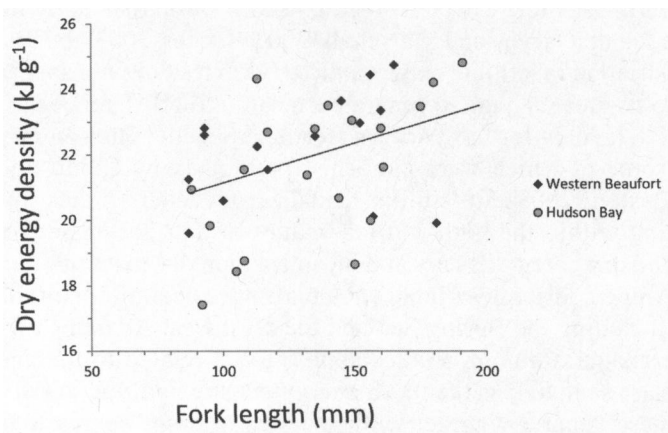[1] Parameters that may be affected by drying in transit to colony.

FIG. 1. The relationship between fork length (mm) and dry energy density (kJ g⁻¹) for the pooled data from both sites (parameter SE in parentheses). Dry $ED_{kJ/g} = 0.028$ (± 0.01) • Fork $Length_{mm} + 18.12$ (± 1.33).
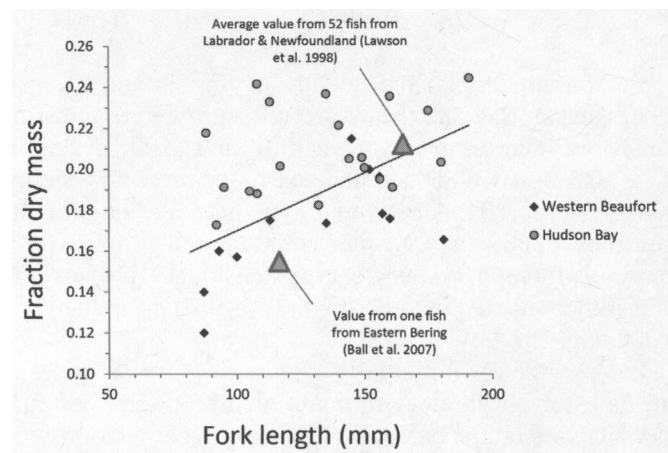

FIG. 2. The relationship between fork length (mm) and fraction dry mass for the pooled data from both sites (parameter SE in parentheses). Fraction Dry Mass = 0.0004 (± 0.0001) • Fork $Length_{mm} + 0.136$ (± 0.02). The relationship for fraction body water would be the complement (1 – (fraction dry mass)). Mean values from fish sampled in two other studies with similar conditions are also plotted on this graph (Δ) to show general concordance.

values of our sample. Latitude differences could explain the variance (Garvey and Marschall, 2003; Tocher, 2003). Other records of energy densities of laboratory-manipulated Arctic cod (Hop et al., 1997b) are useful for general corroboration, but suffer from uncertainty around the effects of captive feeding.

The relationships between size and energy density would be even more broadly applicable if we could more accurately compare colony-collected samples to those collected at sea. The equation in Montevecchi and Piatt (1987) that corrects for drying during parent bird flight to the colony
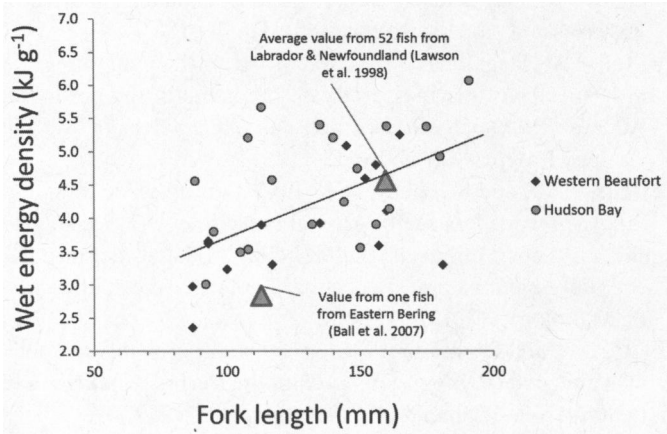
FIG. 3. Relationship between fork length (mm) and at-colony wet energy density (kJ g⁻¹) with data from both sites (parameter SE in parentheses). Wet $ED_{kJ/g} = 0.015$ (± 0.0004) • Fork Length$_{mm}$ + 2.25 (± 0.58). Mean values from fish sampled in two other studies with similar conditions are also plotted on this graph (Δ) to show general concordance.

FIG. 4. The relationship between fraction dry mass and at-colony wet energy density (kJ g⁻¹) for pooled data from both sites (parameter SE in parentheses). Wet $ED_{kJ/g} = 27.458$ (± 2.08) • Fraction Dry Mass − 1.072 (± 0.41).

gives us confidence that the total amount of water loss in transit is small, making fish collected at the colony similar to those from other studies collected at sea. However, the transit dehydration equation lacks a term for fish body size, which may correlate with total water loss. Because we are attempting to understand the relationship between body size and energy density, we cannot risk using the equation and possibly producing spurious correlations, as it is likely that body size does affect total water loss. A more robust correction equation could allow us a more accurate picture of the prey.

CONCLUSION

The relationships established in this study suggest the possibility of estimating energy density from field-based measures of fish length for Arctic cod, an important prey species for marine predators, thereby eliminating the difficulty and expense of freezing and transporting samples as well as the time- and infrastructure-intensive calorimetry process. Our findings also confirm that large Arctic cod constitute a "double bonus" for marine predators. Not only do predators receive exponentially increasing mass of food from longer fish (Hop, 1994; Elliott and Gaston, 2008), but larger fish are also more energy-rich per unit mass than smaller individuals. This fact is particularly noteworthy because younger, smaller cod have sometimes been associated with brackish, open water habitats while older, larger cod have been associated with ice (Lowry and Frost, 1981; Bradstreet et al., 1986; Jarvela and Thorsteinson, 1999; Thedinga and Johnson, 2006). Arctic pack ice retreat may therefore have a particularly strong influence on the foraging efficiency of nesting seabirds and other marine predators (Orians and Pearson, 1976; Lessells and Stephens, 1983; Elliott et al., 2009). Similar studies could continue to provide insight into the basic ecology of Arctic cod and
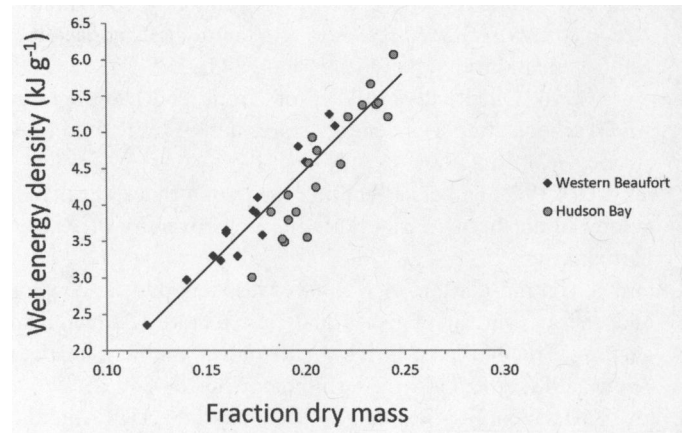
how to estimate prey energy accurately, such as more conclusive research on changes to fish caused by bird transit (Montevecchi and Piatt, 1987), as well as changes to Arctic cod body condition that may be due to seasonality or breeding (Lawson et al., 1998).

REFERENCES

Ball, J.R., Esler, D., and Schmutz, J.A. 2007. Proximate composition, energetic value, and relative abundance of prey fish from the inshore eastern Bering Sea: Implications for piscivorous predators. Polar Biology 30(6):699–708.

Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., and Fortier, L. 2010. From polar night to midnight sun: Photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. Polar Biology 33(11):1505–1520.

Boekelheide, R.J. 1980. Arctic terns: Breeding ecology and sea-ice relationships on an Arctic barrier island. MSc thesis, University of California, Davis.

Bradstreet, M.S.W. 1982. Occurrence, habitat use, and behavior of seabirds, marine mammals, and Arctic cod at the Pond Inlet ice edge. Arctic 35(1):28–40.

Bradstreet, M.S.W., Finley, K.J., Sekerak, A.D., Griffiths, W.B., Evans, C.R., Fabijan, M.F., and Stallard, H.E. 1986. Aspects of the biology of Arctic cod (*Boreogadus saida*) and its importance in Arctic marine food chains. Canadian Technical Report of Fisheries and Aquatic Sciences 1491.

Brekke, B., and Gabrielsen, G.W. 1994. Assimilation efficiency of adult kittiwakes and Brunnich's Guillemots fed capelin and Arctic cod. Polar Biology 14:279–284.

Cairns, D.K. 1984. Foraging ecology of the Black Guillemot. PhD thesis, Carleton University, Ottawa, Ontario.

Craig, P.C., Griffiths, W.B., Haldorson, L., and McElderry, H. 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 39:395–406.

Crawford, R.E., and Jorgenson, J.K. 1993. Schooling behaviour of Arctic cod, *Boreogadus saida*, in relation to drifting pack ice. Environmental Biology of Fishes 36(4):345–357.

———. 1996. Quantitative studies of Arctic cod (*Boreogadus saida*) schools: Important energy stores in the Arctic food web. Arctic 49(2):181–193.

Divoky, G.J. 1998. Factors affecting growth of a Black Guillemot colony in northern Alaska. PhD thesis, University of Alaska Fairbanks.

Elliott, K.H., and Gaston, A.J. 2008. Mass-length relationships and energy content of fishes and invertebrates delivered to nestling Thick-billed Murres *Uria lomvia* in the Canadian Arctic, 1981–2007. Marine Ornithology 36:25–34.

Elliott, K.H., Woo, K., Gaston, A.J., Benvenuti, S., Dall'Antonia, L., and Davoren, G.K. 2008. Seabird foraging behaviour indicates prey type. Marine Ecology Progress Series 354:289–303.

———. 2009. Central-place foraging in an Arctic seabird provides evidence for Storer-Ashmole's halo. Auk 126(3):613–625.

Garvey, J.E., and Marschall, E.A. 2003. Understanding latitudinal trends in fish body size through models of optimal seasonal energy allocation. Canadian Journal of Fisheries and Aquatic Sciences 60(8):938–948.

Gradinger, R.R., and Bluhm, B.A. 2004. In-situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the High Arctic Canada Basin. Polar Biology 27(10):595–603.

Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a High Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series 84:9–18.

Hoekstra, P.F., Dehn, L.A., George, J.C., Solomon, K.R., Muir, D.C.G., and O'Hara, T.M. 2002. Trophic ecology of bowhead whales (*Balaena mysticetus*) compared with that of other Arctic marine biota as interpreted from carbon-, nitrogen-, and sulfur-isotope signatures. Canadian Journal of Zoology 80(2):223–231.

Hop, H. 1994. Bioenergetics and trophic relationships of Arctic cod (*Boreogadus saida*) in the Canadian High Arctic. PhD thesis, University of Alberta, Edmonton. 181 p.

Hop, H., Graham, M., and Trudeau, V.L. 1995. Spawning energetics of Arctic cod (*Boreogadus saida*) in relation to seasonal development of the ovary and plasma sex steroid levels. Canadian Journal of Fisheries and Aquatic Sciences 52:541–550.

Hop, H., Welch, H.E., and Crawford, R.E. 1997a. Population structure and feeding ecology of Arctic cod schools in the Canadian High Arctic. In: Reynolds J.B., ed. Fish ecology in Arctic North America. American Fisheries Society Symposium 19. Bethesda, Maryland. 68–80.

Hop, H., Tonn, W.M., and Welch, H.E. 1997b. Bioenergetics of Arctic cod (*Boreogadus saida*) at low temperatures. Canadian Journal of Fisheries and Aquatic Sciences 54:1772–1784.

Jarvela, L.E., and Thorsteinson, L.K. 1999. The epipelagic fish community of Beaufort Sea coastal waters, Alaska. Arctic 52(1):80–94.

Lambert, Y., and Dutil, J.-D. 1997. Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)? Canadian Journal of Fisheries and Aquatic Sciences 54(S1):104–112.

Lawson, J.W., Magalhães, A.M., and Miller, E.H. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: Proximate composition and energy density. Marine Ecology Progress Series 164:13–20.

Lessells, C.M., and Stephens, D.W. 1983. Central place foraging: Single-prey loaders again. Animal Behaviour 31(1):238–243.

Lønne, O.J., and Gulliksen, B. 1989. Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biology 9(3):187–191.

Lowry, L.F., and Frost, K.J. 1981. Distribution, growth, and foods of Arctic cod (*Boreogadus saida*) in the Bering, Chukchi, and Beaufort Seas. Canadian Field-Naturalist 95:186–191.

Montevecchi, W.A., and Piatt, J.F. 1987. Dehydration of seabird prey during transport to the colony: Effects on wet weight energy densities. Canadian Journal of Zoology 65(11):2822–2824.

Moulton, L.L., and Tarbox, K.E. 1987. Analysis of Arctic cod movements in the Beaufort Sea nearshore region, 1978–79. Arctic 40(1):43–49.

Orians, G.H., and Pearson, N.E. 1976. On the theory of central place foraging. In: Horn, D.J., Stairs, G.R., and Mitchell, R.D., eds. Analysis of ecological systems. Columbus: Ohio State University Press. 154–177.

Parr Instrument Company. n.d. Operating instructions for the 1241 Oxygen Bomb Calorimeter. Moline, Illinois: Parr Instrument Company. http://www.parrinst.com/wp-content/uploads/downloads/2012/06/203M_Parr_1241-Oxygen-Bomb-Calorimeter-Inst_Rev-0888.pdf.

Payne, S.A., Johnson, B.A., and Otto, R.S. 1999. Proximate composition of some north-eastern Pacific forage fish species. Fisheries Oceanography 8(3):159–177.

Pothoven, S.A., Nalepa, T.F, Madenjian, C.P., Rediske, R.R., Schneeberger, P.J., and He, J.X. 2006. Energy density of lake whitefish *Coregonus clupeaformis* in Lakes Huron and Michigan. Environmental Biology of Fishes 76:151–158.

Rodgveller, C., Moss, J.H., and Feldman, A.M. 2007.The influence of sampling location, timing, and hatching origin on the prediction of energy density in juvenile pink salmon. NOAA Technical Memorandum NMFS-AFSC-170. Juneau, Alaska: Auke Bay Laboratory, Alaska Fisheries Science Center.

Thedinga, J.F., and Johnson, S.W. 2006. Fish assemblages near Barrow, Alaska–August 2005. Juneau, Alaska: Auke Bay Laboratory, Alaska Fisheries Science Center. 10 p.

Tocher, D.T. 2003. Metabolism and functions of lipids and fatty acids in teleost fish. Reviews in Fisheries Science 11(2):107–184.

Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., and Hop, H. 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. Arctic 45(4):343–357.

Welch, H.E., Crawford, R.E., and Hop, H. 1993. Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. Arctic 46(4):331–339.

Wuenschel, M.J., Jugovich, A.R., and Hare, J.A. 2006. Estimating the energy density of fish: The importance of ontogeny. Transactions of the American Fisheries Society 135:379–385.