

# Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density

John W. Lawson<sup>1,\*</sup>, Alexandra M. Magalhães<sup>2</sup>, Edward H. Miller<sup>1,2</sup>

<sup>1</sup>Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada

<sup>2</sup>Biology Department, Memorial University of Newfoundland, St. John's, Newfoundland A1C 3X9, Canada

**ABSTRACT:** Prey energy density values are crucial inputs to bioenergetic consumption models. Vertebrate predators in the northwest Atlantic consume a variety of prey species, but the proximate composition (PC; proportions of lipid, protein, ash and water) and energy density (ED;  $\text{kJ g}^{-1}$ ) of prey, and their variability, are known poorly. In this study, key prey species from Newfoundland and Labrador were studied: Atlantic cod *Gadus morhua*, American plaice *Hippoglossoides platessoides*, sand lance *Ammodytes dubius*, Arctic cod *Boreogadus saida*, northern shrimp *Pandalus borealis*, redfish *Sebastes* spp., Greenland halibut *Reinhardtius hippoglossoides*, squid *Illex illecebrosus* and *Gonatus fabricii*, capelin *Mallotus villosus*, Atlantic herring *Clupea harengus* and daubed shanny *Lumpenus maculatus*. PC and ED varied greatly among species and were influenced by size, season, geography and year. Herring, capelin and *G. fabricii* had the highest ED, whereas Atlantic cod, plaice, sand lance and shrimp had the lowest. Halibut and *I. illecebrosus* increased in ED with size. EDs of capelin and redfish varied seasonally; that of plaice and sand lance did not. Herring and halibut had higher ED in the early 1990s than in recent years. Such variation in prey ED has important implications for digestive efficiency, foraging energetics, and dietary preferences of vertebrate predators.

**KEY WORDS:** Proximate composition · Energy density · Capelin · Cod · Atlantic

## INTRODUCTION

Knowledge of the nutritional and energetic values of food is necessary to evaluate prey consumption of predator populations. It is also important for modeling the impact of predators on prey populations. Many consumption models require information on energy density (ED) of prey, which is commonly obtained by analysis of proximate composition (PC) or by bomb calorimetry. PC has been determined for many species of commercial importance (Stansby & Hall 1965, Stoddard 1968, Anonymous 1969, Holdway & Beamish 1984, Steimle & Terranova 1985, Krzynowek & Murphy 1987). However, almost all such analyses have been conducted only on specific body components, such as flesh or gonads, rather than on whole prey items, or on commercially significant sizes rather than sizes eaten

by marine predators (Sidwell et al. 1974, Lawson & Stenson 1995, Lawson et al. 1995). In addition, commercial samples of prey species are rarely representative of the state of that species in important areas or seasons of predation (Bowen et al. 1993). Emphasizing the ecological importance of such factors, Hislop et al. (1991) noted substantial seasonal changes in ED of prey species such as Atlantic herring *Clupea harengus* and sand lance *Ammodytes marinus*. ED of capelin *Mallotus villosus* throughout the Atlantic also varies considerably over the course of the year (Jangaard 1974, Montevecchi & Piatt 1984, Mårtensson et al. 1996). Estimates of food consumption by marine mammals in the north Atlantic have not incorporated seasonal variation in prey ED due to a paucity of data (Mårtensson et al. 1996), small sample sizes, or geographically restricted samples (Markussen & Øritsland 1991, Markussen et al. 1992, Mohn & Bowen 1996, Stenson et al. 1997).

\*E-mail: johnwl@morgan.ucs.mun.ca

In this paper we summarize ED and PC of 12 prey species that are important to vertebrate predators in the northwest Atlantic.

## METHODS

**Sampling regime.** Specimens of prey ( $n = 620$ ) were collected during a number of research cruises of the Department of Fisheries and Oceans in areas near Newfoundland and Labrador, Canada (Table 1). Although we were unable to collect samples systematically, whenever possible, samples of each species were collected from more than 1 location, season, and year. Most samples (84%) were collected in 1995 and 1996, and about half were collected more than 30 km

from the coast (designated as 'offshore'). Other samples were from 1991 to 1994.

**Specimen preparation.** Specimens were frozen fresh at sea and, on return to shore, were stored at  $-20^{\circ}\text{C}$  until processing. *Illex illecebrosus* squid and Atlantic herring were commercial samples that were flash frozen at sea, then stored at  $-20^{\circ}\text{C}$  in plastic-lined cardboard boxes. Species studied were Atlantic cod *Gadus morhua* ( $n = 106$ ), American plaice *Hippoglossoides platessoides* ( $n = 37$ ), sand lance *Ammodytes dubius* ( $n = 44$ ), Arctic cod *Boreogadus saida* ( $n = 52$ ), northern shrimp *Pandalus borealis* ( $n = 33$ ), redfish *Sebastes* spp. ( $n = 54$ ), Greenland halibut *Reinhardtius hippoglossoides* ( $n = 48$ ), squid *Illex illecebrosus* ( $n = 32$ ), *Gonatus fabricii* ( $n = 47$ ), capelin *Mallotus villosus* ( $n = 82$ ), Atlantic herring *Clupea harengus* ( $n = 26$ ),

Table 1. Number of prey collected from nearshore and offshore waters of Newfoundland and Labrador in 1991 to 1996, subdivided by collection area. Mean prey length  $\pm 1$  SD for each sample block shown in parentheses. Lengths are standard length for American plaice, fork length for all other fish, carapace length for shrimp, and mantle length for squid. Sum.: summer; Win.: winter

Prey species	Labrador		NE Newfoundland		E Newfoundland		S Newfoundland		Sum. <sup>a</sup>	Win. <sup>b</sup>	Total
	Nearshore	Offshore	Nearshore	Offshore	Nearshore	Offshore	Nearshore	Offshore			
Atlantic cod	82				24				106		106
<i>Gadus morhua</i>	(18.1 $\pm$ 4.94)				(27.8 $\pm$ 10.8)						
American plaice <i>Hippoglossoides platessoides</i>					24		13		24	13	37
					(27.3 $\pm$ 4.58)		(18.6 $\pm$ 2.84)				
Sand lance <i>Ammodytes dubius</i>			16			28			28	16	44
			(18.1 $\pm$ 1.89)			(17.9 $\pm$ 1.61)					
Arctic cod <i>Boreogadus saida</i>	11	5	17		16	30			11	68	79
	(14.3 $\pm$ 1.43)	(11.3 $\pm$ 1.07)	(18.1 $\pm$ 4.17)		(18.5 $\pm$ 2.07)	(14.6 $\pm$ 2.12)					
Northern shrimp <i>Pandalus borealis</i>			33						33	33	33
			(2.29 $\pm$ 0.96)								
Redfish <i>Sebastes</i> spp.					5			49	54	54	54
					(21.3 $\pm$ 2.23)		(21.9 $\pm$ 6.99)				
Greenland halibut <i>Reinhardtius hippoglossoides</i>						48			48	48	48
						(22.5 $\pm$ 6.67)					
Daubed shanny <i>Lumpenus maculatus</i>	16										16
	(14.2 $\pm$ 0.94)										
Squid <i>Illex illecebrosus</i>					32				32	47	32
					(34.0 $\pm$ 3.93)						
Squid <i>Gonatus fabricii</i>		47								47	47
		(8.46 $\pm$ 1.96)									
Capelin <i>Mallotus villosus</i>	2					82			33	51	84
	(14.8 $\pm$ 0.21)					(14.0 $\pm$ 1.09)					
Atlantic herring <i>Clupea harengus</i>			40						5	35	40
			(28.4 $\pm$ 3.11)								
Total	111	52	66		141	188	62		291	329	620

<sup>a</sup>April to September

<sup>b</sup>October to March

and daubed shanny *Lumpenus maculatus* ( $n = 16$ ) (Table 1).

Frozen specimens were thawed at room temperature for a maximum of 2 h (to reduce water loss), after which they were measured for mass (to the nearest 0.1 g) and length [fork length for fish (except standard length for plaice), dorsal carapace length for shrimp, mantle length for squid; to the nearest 0.1 cm]. Sex and maturity were ascertained by examination of the gonads. Few specimens had prey in their stomachs except Greenland halibut, *Gonatus fabricii* and shannies. These stomachs were emptied before the specimens were dried and ground.

Specimens were then cut into small pieces and dried to constant mass in a convection oven (Precision Scientific Inc., 3737 West Cortland Street, Chicago, IL, USA) at 100°C. Carapaces were removed from half of the shrimp specimens, but the ED data for the shelled ( $4.88 \pm 0.642 \text{ kJ g}^{-1}$  wet mass) and whole shrimp ( $4.72 \pm 0.328 \text{ kJ g}^{-1}$ ) did not differ significantly ( $F_{1,31} = 0.487$ ,  $p = 0.489$ ), so they were combined for subsequent analyses. Dried samples from the largest specimens were ground in an electric grinder to a uniform consistency. Small specimens were ground manually in a ceramic mortar. The grinder, mortar and pestle were cleaned and dried thoroughly between samples with acetone.

**PC and ED assays.** Percent moisture content was calculated using the difference between fresh and dried sample masses. Lipid content was determined for replicates of 1 to 3 g dried subsamples of each species by diethyl ether extraction in a water-cooled fat extractor (Labconco Corporation, Kansas City, MO, USA). Extraction samples were run for 16 h, after which the collection flask was dried at 100°C for 30 min, then placed in a sealed desiccator for at least 1 h to remove any diethyl ether residue and water. The mass of the lipid remaining in the flask was divided by the original sample mass to derive the % lipid content of the sample.

Percent inorganic content was determined by combusting 0.5 g samples in a muffle furnace (model FA1850, Thermolyne Corporation, Dubuque, IA, USA) at 550°C for 16 h.

Percent protein content was determined by calculation, where % protein =  $100 - (\% \text{ moisture} + \% \text{ lipid} + \% \text{ inorganic})$ . In these calculations carbohydrates were assumed to be a negligible component (Sidwell et al. 1974, Percy & Fife 1981). To verify calculated protein values, the protein content was assayed directly for random, replicate subsamples of all species using the Kjeldahl method (Chen et al. 1988). Calculated and Kjeldahl protein values did not differ significantly (paired  $t$ -test:  $t = 1.47$ ,  $p = 0.149$ ,  $df = 44$ ); calculated values are cited below.

Replicates for each lipid and protein assay were analysed. The mean of these replicates was used as the value for that specimen. Capelin and redfish data of the Department of Fisheries and Oceans, Canada (B. Nakashima & K. Kennedy unpubl. data), were analysed using identical methodologies, although each capelin data point is the average for a homogenate of 10 fish.

Coefficients of variation for moisture (2.9%), lipid (0.2% of dry replicate), protein (0.3% of dry replicate) and ash values (0.4%) obtained using these analytical techniques are low (Anonymous 1966, 1976, Hanson 1973). Percent lipid, protein and inorganic estimates were converted to percentages of the original wet sample mass and arcsine transformed [ $q = \arcsin(p^{0.5})$ , where  $p$  is a proportion] for all statistical analyses. ED was calculated assuming  $20.0 \text{ kJ g}^{-1}$  for protein and  $38.0 \text{ kJ g}^{-1}$  for lipid (Ricklefs & Schew 1994). ED values are expressed per unit wet mass, unless stated otherwise.

Persons interested in obtaining the complete database (in printed, Macintosh or DOS formats) can contact the senior author at johnwl@morgan.ucs.mun.ca or by mail.

## RESULTS

### Differences in proximate composition and energy density between species

Moisture content was similar across most species, but capelin and herring had very low values (with a concomitant increase in the relative proportion of lipids). Protein content was also similar across species, but relatively low for Greenland halibut and *Gonatus* squid. Inorganic content was highest for northern shrimp, and lowest for lipid- and energy-rich prey such as herring. There were significant differences in ED among prey types ( $F_{11,567} = 57.8$ ,  $p < 0.0001$ ; Table 2). Herring and capelin did not differ significantly from one another and had higher EDs than the other species. In contrast, Atlantic cod had the lowest ED.

### Relationships of energy density to size and sex

ED differed with body size in some prey species, and was unrelated to body size in others. For example, ED increased with body size in halibut ( $r^2_{\text{adj}}$  length = 0.595,  $r^2_{\text{adj}}$  mass = 0.631), but was independent of body size in Atlantic cod ( $r^2_{\text{adj}}$  length = 0.070,  $r^2_{\text{adj}}$  mass = 0.110; Fig. 1). ED tended to increase with body length in other prey species, but the relationships were weak ( $r^2_{\text{adj}} = 0.350$ , or less).

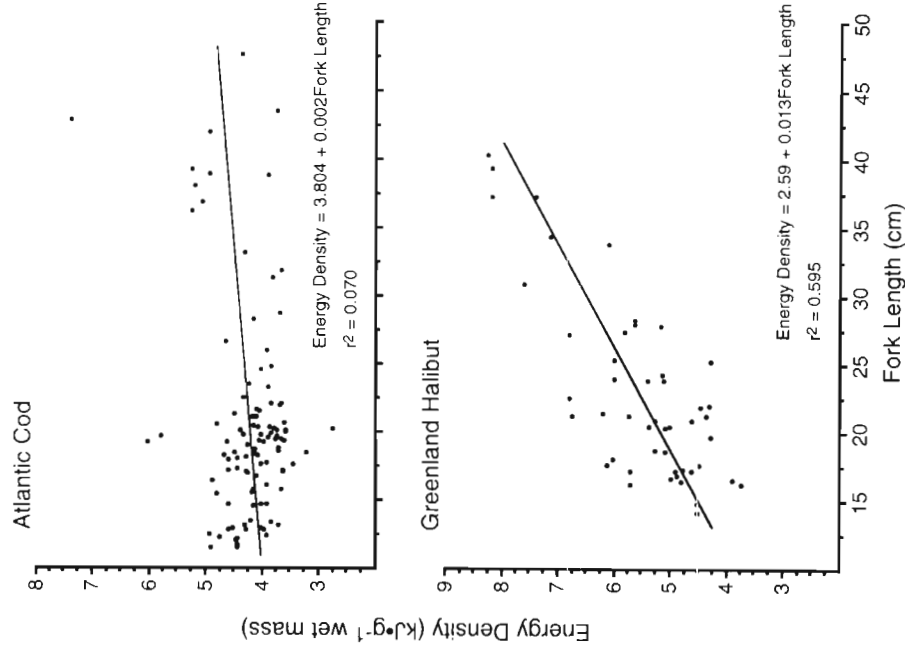


Fig. 1. Relationship between prey size and ED for Atlantic cod (weak relationship) and for Greenland halibut (strongly positive relationship). Size ranges of these fish consumed commonly by harp seals are delineated by grey rectangles

Halibut and northern shrimp exhibited sex differences in ED. Female halibut had a higher ED ( $6.00 \pm 0.947 \text{ kJ g}^{-1}$ ) than males ( $5.17 \pm 0.738 \text{ kJ g}^{-1}$ ;  $F_{1,31} = 4.95$ ,  $p < 0.034$ ), whereas the converse was true for shrimp (females:  $4.57 \pm 0.410 \text{ kJ g}^{-1}$ ; males:  $5.19 \pm 0.528 \text{ kJ g}^{-1}$ ;  $F_{1,32} = 9.16$ ,  $p < 0.005$ ).

### Seasonal and geographic differences in energy density of prey

Significant differences in EDs of some species were detected, depending on where and when they were collected. For example, capelin had significantly lower EDs during the summer ( $4.71 \pm 0.810 \text{ kJ g}^{-1}$ ) than winter ( $10.7 \pm 0.66 \text{ kJ g}^{-1}$ ;  $F_{1,83} = 375$ ,  $p < 0.0001$ ). When we compared these data from similar locations with values from the Department of Fisheries and Oceans (Nakashima & Kennedy unpubl. data), this seasonal difference held true for offshore capelin (summer:  $3.99 \pm 0.911 \text{ kJ g}^{-1}$ , winter:  $6.30 \pm 3.832 \text{ kJ g}^{-1}$ ;  $F_{1,181} = 20.3$ ,  $p < 0.0001$ ), but not for those collected in nearshore areas (summer:  $3.38 \pm 0.257 \text{ kJ g}^{-1}$ , winter:  $3.33 \pm 0.238 \text{ kJ g}^{-1}$ ;  $F_{1,339} = 0.164$ ,  $p = 0.686$ ).

Eight redfish collected offshore of southern Newfoundland in July had significantly lower ED than the combined winter samples ( $4.52 \pm 0.986 \text{ kJ g}^{-1}$ ,  $F_{1,60} = 7.85$ ,  $p = 0.007$ ; Kennedy unpubl. data). Redfish collected in offshore areas of eastern Newfoundland in October ( $4.51 \pm 0.778 \text{ kJ g}^{-1}$ ) had lower ED than those from southern Newfoundland in January ( $5.51 \pm 0.682 \text{ kJ g}^{-1}$ ,  $F_{1,52} = 7.58$ ,  $p = 0.008$ ).

American plaice (summer, eastern Newfoundland:  $4.31 \pm 0.302 \text{ kJ g}^{-1}$ ; winter, southern Newfoundland:  $4.22 \pm 0.668 \text{ kJ g}^{-1}$ ;  $F_{1,35} = 0.360$ ,  $p = 0.554$ ) and

Table 2. Proximate composition of prey species. Mean (SD) moisture, lipid, protein, and inorganic content and energy density (ED) for the 12 species studies. Values are expressed for wet mass

Species	Mass (g)	Length (cm) <sup>a</sup>	% moisture content	% lipid content	% protein content	% inorganic content	ED (kJ g <sup>-1</sup> )
Atlantic cod	131 (184.5)	20.2 (7.85)	78.5 (2.17)	2.6 (1.19)	16.1 (1.68)	2.9 (0.47)	4.2 (0.60)
American plaice	153 (104.3)	24.2 (5.57)	78.2 (1.96)	3.0 (1.14)	15.6 (1.61)	3.1 (0.56)	4.3 (0.46)
Sand lance	15.1 (3.30)	17.9 (1.70)	77.9 (2.69)	2.9 (1.88)	16.7 (1.52)	2.5 (0.51)	4.4 (0.82)
Arctic cod	36.6 (20.44)	15.9 (3.36)	78.9 (2.47)	3.7 (1.60)	15.0 (1.84)	2.3 (0.39)	4.4 (0.77) <sup>b</sup>
Northern shrimp	11.5 (2.04)	2.3 (0.10)	74.6 (1.90)	3.6 (0.85)	17.2 (1.26)	4.6 (0.41)	4.8 (0.51)
Redfish	204 (143.8)	21.9 (6.68)	74.4 (1.99)	6.0 (1.93)	16.0 (1.77)	3.8 (0.76)	5.4 (0.83) <sup>b</sup>
Greenland halibut	84.4 (55.98)	22.6 (6.71)	78.1 (2.40)	7.5 (2.25)	12.2 (1.06)	2.2 (0.40)	5.5 (1.13) <sup>b</sup>
Daubed shanny	11.6 (1.99)	14.3 (1.01)	72.2 (6.14)	5.0 (1.67)	19.9 (4.33)	2.9 (0.65)	5.9 (1.38)
Squid ( <i>Illex</i> )	136 (35.6)	34.0 (3.93)	75.1 (1.45)	6.6 (1.55)	17.0 (0.65)	1.4 (0.14)	5.9 (0.56)
Squid ( <i>Gonatus</i> )	22.0 (13.81)	8.5 (0.20)	73.5 (5.95)	10.9 (3.80)	13.7 (2.70)	1.9 (0.56)	6.9 (1.76)
Capelin	19.4 (4.92)	14.0 (1.09)	68.2 (10.06)	13.7 (7.87)	16.1 (4.97)	2.1 (0.44)	8.4 (3.28) <sup>b</sup>
Atlantic herring	280 (85.7)	28.2 (3.13)	65.0 (3.43)	13.7 (3.90)	20.1 (1.28)	0.8 (0.07)	9.4 (1.40)

<sup>a</sup>Fork length for fish (except standard length for American plaice), carapace length for shrimp, and mantle length for squid

<sup>b</sup>Value is an average of 2 samples of significantly different energy density

sand lance (summer, eastern Newfoundland:  $4.56 \pm 0.732 \text{ kJ g}^{-1}$ ; winter, northeastern Newfoundland:  $4.20 \pm 0.941 \text{ kJ g}^{-1}$ ;  $F_{1,42} = 2.06$ ,  $p = 0.158$ ) did not exhibit seasonal or geographic differences in ED.

On the other hand, Atlantic cod collected in nearshore areas of eastern Newfoundland in August ( $4.40 \pm 1.008 \text{ kJ g}^{-1}$ ) had similar EDs to those collected in southern Labrador in July ( $4.16 \pm 0.618 \text{ kJ g}^{-1}$ ;  $F_{1,104} = 2.98$ ,  $p = 0.087$ ).

While Arctic cod from offshore Labrador ( $4.13 \pm 0.167 \text{ kJ g}^{-1}$ ) had lower EDs than those collected offshore of northeastern Newfoundland ( $4.85 \pm 0.436 \text{ kJ g}^{-1}$ ;  $F_{4,74} = 42.81$ ,  $p < 0.0001$ ), those collected during the winter in nearshore northeastern Newfoundland ( $3.19 \pm 0.331 \text{ kJ g}^{-1}$ ) had lower EDs than in any other location or season.

### Interannual differences in energy density of prey

There were significant interannual differences in ED of 2 species for which we had sufficient samples across a number of years and which were collected at the same time of year. Herring, collected in October for 5 yr, had significantly higher ED during 1992 and 1993 (which did not differ) than in following years ( $F_{4,30} = 30.0$ ,  $p < 0.0001$ ). Similarly, halibut collected in 1992 had significantly higher ED than those collected in 1995 ( $F_{1,46} = 12.5$ ,  $p = 0.001$ ).

## DISCUSSION

For an improved understanding of the relationship between marine predators and their prey requirements, factors affecting prey quality, such as season, location and maturity, must be documented. If not, descriptions of sampling regimes must be adequate to permit others to determine the degree to which results of PC analyses can be used in other research.

Capelin caught in the winter offshore of Newfoundland had the highest lipid and energy content of the species we analysed, or that have been reported for the north Atlantic (e.g. Anonymous 1969, Steimle & Terranova 1985, Nakashima & Kennedy 1990, Brekke & Gabrielsen 1994, Mårtensson et al. 1996). As in previous studies (Steimle & Terranova 1985, Mårtensson et al. 1996), Atlantic herring was also high in energy content. The high abundance, schooling behaviour (Jangaard 1974), relatively high ED, and high digestibility (Mårtensson et al. 1994, Lawson et al. 1997b) of these species may explain why they are predominant items in the diet of many northwest Atlantic predators (Brown & Nettleship 1984, Monteverchi & Piatt 1984, Whitehead & Carscadden 1985, Cairns et al. 1990,

Fahrig et al. 1993, Fontaine et al. 1994), including harp seals in portions of this seal species' range (Murie & Lavigne 1991, Beck et al. 1993, Lawson & Stenson 1997). The relatively high ED for capelin and herring (Hodder et al. 1973, this study) in the fall coincides with a period when harp seals are feeding heavily and gaining mass prior to the breeding season. Since harp seals must satisfy an increased energy demand during this time, it is not surprising that capelin are a preferred prey item offshore, when these seals have prey choices (Lawson et al. 1998).

Traditionally, capelin has been reported as the predominant prey of harp seals in the western Atlantic (Fisher & Mackenzie 1955, Sergeant 1973, Murie & Lavigne 1991, Beck et al. 1993). However, the diet of these seals from nearshore northeastern Newfoundland since 1986 has been dominated by Arctic cod instead (Lawson & Stenson 1995). This may be a response to the apparent increase in the biomass of these fish off southern Labrador and eastern Newfoundland since the mid 1980s (Lilly et al. 1994). Although harp seals digest Arctic cod less efficiently than capelin (Lawson et al. 1997b), this dietary shift in nearshore areas does not entail a significant reduction in diet quality since capelin and Arctic cod have similar EDs there. A similar dietary change in response to prey availability may have occurred when common murres *Uria aalge* breeding in Labrador switched from a reliance on capelin in the early 1980s (Birkhead & Nettleship 1987) to a diet dominated by daubed shannies (R. Bryant unpubl. data). The difference in ED between nearshore capelin and daubed shannies is not significant. These examples emphasize that understanding of predators' foraging ecology requires estimates of prey ED for the specific seasons, prey sizes, and regions of interest.

The importance of analysing PC of prey of the same consistency (whole animals) and condition as those normally found in predators' diets is further illustrated by our analyses of squid. The ED of squid, particularly *Gonatus fabricii*, is higher than reported previously (except for similar values in Perez 1994), and this is likely a function of this study's inclusion of the entire animal, rather than just the muscular, low-fat mantle (e.g. Croxall & Prince 1982). While there appears to be a slight increase in ED with body mass for most species in this study, this trend is significant only for *Illex illecebrosus* and halibut. This may explain why predators like harp seals *Phoca groenlandica* eat small prey (Beck et al. 1993, Lawson et al. 1995); there may be no energetic advantage to searching for rarer and potentially harder-to-handle large prey. In fact, captive harp seals' digestive efficiency was greater when fed small Atlantic cod than larger cod (Lawson et al. 1997b), even though the ED of cod does not correlate well with size.



Possible effects of sampling must be documented when reporting analyses of species that potentially undergo seasonal or geographic variation in PC. Jan-gaard (1974) reported that the fat content of Barents Sea capelin declined by as much as 80% during spring spawning, with a return to high levels in the fall. Canadian herring exhibit a similar pattern (Stoddard 1968). We also found seasonal differences in ED where, as in a previous study (Nakashima & Kennedy unpubl. data), capelin (and redfish) have greater fat content and ED in winter and in offshore areas. That plaice and sand lance did not exhibit these sorts of differences may be due to a confounding of seasonal and geographic influences.

Most PC and ED determined previously for marine species from the northwest Atlantic were usually not of the species or size commonly consumed by marine predators (many analyses have been conducted on specimens larger than those eaten) or not collected in the appropriate season or location. Measures of prey quality are critical inputs to bioenergetic models of predator consumption (Markussen et al. 1992, Olesiuk 1993, Mohn & Bowen 1996, Stenson et al. 1997). Given the apparent seasonal and geographic variability in ED for prey such as capelin and herring, which can be more profound than interspecific differences, models which do not account for this may be too simplistic to adequately estimate predator impacts on prey stocks (Nordøy et al. 1995).

Another factor to consider is the potential for inter-annual differences in ED of prey (Mårtensson et al. 1996). Nilssen et al. (1994) reported significant changes in the liver index of prespawning cod in Lofoten during 1947 to 1988. In addition to the inter-annual changes in ED reported for herring and halibut in this study, several other studies of fish in the Atlantic have shown long-term changes in body condition (Shelton et al. 1996, Lambert & Dutil 1997) or size-at-age (Hansen 1987). This will have significant impacts on consumption rates, and perhaps prey choice, of many predators, and should be examined more closely—particularly for important prey species such as capelin and Arctic cod.

Differences in prey quality have implications for digestive efficiency (Nordøy et al. 1993, Brekke & Gabrielsen 1994, Mårtensson et al. 1994, Lawson et al. 1997a, b), energetics, and perhaps predators' food preferences. These preferences, when coupled with the high mobility, relatively long life and learning abilities of predators such as cetaceans, seals and seabirds, may even influence where predators travel to feed. Ecologically relevant analysis of PC, which correlates levels and variation of PC with processes such as digestive efficiency and food preferences, will further help to explain predators' prey choices. Also, while dif-

ferent to obtain in the field, observational data on the behaviour of fish and the handling mechanics of the predators should be considered. Comparisons of the results of this study and diets of predators in the northwest Atlantic suggest that predators may not be choosing prey strictly on the basis of their energy yield. Temporal and spatial dissimilarity in abundance for different prey species may have as large an influence as prey quality.

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