Variation in assimilation efficiency and digestive efficiency of captive harp seals (*Phoca groenlandica*) on different diets

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Abstract: Digestive efficiency (DE) is influenced by many factors including food type or quality. Assimilation efficiency (AE) and DE of 12 captive harp seals (*Phoca groenlandica*) were estimated for five prey types in large outdoor seawater tanks. In trials of >9 days' duration, the seals were fed Atlantic cod (*Gadus morhua*), Arctic cod (*Boreogadus saida*), Greenland halibut (*Reinhardtius hippoglossoides*), Atlantic herring (*Clupea harengus*), and capelin (*Mallotus villosus*). Fish were marked with inert tracers so that faecal samples could be matched to individual animals. AE (digestibility of dry matter) was estimated from the relative concentration of Mn^{2+} in food and faeces. DE (digestible energy) was estimated from the relative concentrations of both Mn^{2+} and energy in food and faeces. AE and DE values were high, but varied among the fish species (DE: Atlantic cod 93.5%; Arctic cod 93.5%; halibut 94.7%; capelin 95.7%; herring 96.6%). Both estimates of digestive efficiency were positively correlated with prey energy density. For most prey, AE and DE were not correlated with meal size, number of prey in a meal, size of prey, or seal body mass. However, digestive efficiency was greater in seals fed smaller Atlantic cod, or meals of greater mass. Quantifying estimates of digestive efficiency is important for formulating energy-based population consumption models, and so should be improved. It is recommended that more pinniped species be studied in captivity, that experiments last longer, and that the number of individuals studied be increased so that individual differences can be investigated.

Résumé : L'efficacité de la digestion de la nourriture est influencée par plusieurs facteurs, notamment le type et la qualité des aliments. La digestibilité des matières sèches (AE) et l'énergie digestible (DE) de cinq types de proies ont été estimées chez 12 Phoques communs (*Phoca groenlandica*) en captivité dans de grands aquariums d'eau salée, installés à l'extérieur. Au cours des expériences, chacune d'une durée de plus de 9 jours, les phoques ont été nourris de Morue franche (*Gadus morhua*), de Saïda franc (*Boreogadus saida*), de Flétan du Groenland (*Reinhardtius hippoglossoides*), de Hareng atlantique (*Clupea harengus*) et de Capelan (*Mallotus villosus*). Les poissons ont reçu des marqueurs inertes, ce qui nous a permis d'associer les fèces à des phoques en particulier. La digestibilité des matières sèches a été estimée par mesure de la concentration relative de Mn^{2+} dans les aliments et dans les fèces. L'énergie digestible a été estimée par mesure des concentrations de Mn^{2+} et d'énergie dans les aliments et dans les fèces. Les valeurs de AE et de DE étaient élevées, mais variaient selon les espèces de poissons consommées (DE : Morue franche, 93,5%; Saïda franc, 93,5%; Flétan du Groenland, 94,7%; Capelan, 95,7%; Hareng atlantique, 96,6%). Les deux estimations de l'efficacité de la digestion étaient en corrélation positive avec la densité énergétique des proies. Dans la plupart des cas, AE et DE n'étaient pas reliées à la taille du repas, au nombre de proies dans le repas, à la taille des proies ou à la masse des phoques. Cependant, l'efficacité de la digestion était plus grande chez les phoques nourris de petites Morues franches ou de repas de masse plus élevée. Les estimations quantitatives de l'efficacité de la digestion sont importantes dans l'élaboration de modèles démographiques de consommation en fonction de l'énergie, et devraient donc être améliorées. Il serait souhaitable que l'étude des différences entre les individus soit basée sur l'examen d'un plus grand nombre d'espèces de pinnipèdes en captivité et sur des expériences de plus longue durée impliquant un plus grand nombre d'individus.
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Introduction

Animals digest food with variable efficiency, depending on such factors as food quality, meal size, time between meals, digestive tract morphology, and nutritional state (Brekke and Gabrielsen 1994; Golley et al. 1965; Heath and Randall 1985; Jackson 1986; Swart et al. 1993). Quantifying such factors is important in ecology, such as estimating the prey requirements of a predator population (Balmelli and Wickens 1994; Croxall et al. 1990; Mohn and Bowen 1996; Olesiuk 1993; Punt 1994). Estimates of prey requirements are especially needed for predator–prey systems involving managed

Table 1. Summary of data on size and proximate composition of fish species used in feeding trials.

	Mean mass (g)	Mean standard length (cm)	*N*	Mean percent lipid content (wet)	*N*	Wet energy density ($kJ \cdot g^{-1}$)	Dry energy density ($kJ \cdot g^{-1}$)	Mean Mn^{2+} concn. (ppm)	*N*
Atlantic cod (*Gadus morhua*)									
Large	560 (158.0)	37.4 (4.57)	21	2.81 (1.837)	34				
Small	72.5 (16.94)	18.1 (4.73)	140	2.64 (0.866)	72				
Total				2.65 (1.260)	106	4.2 (0.60)	19.6 (1.68)	6.63 (1.436)	91
Arctic cod (*Boreogadus saida*)	23.4 (4.47)	14.4 (2.76)	40	3.98 (1.604)	34	4.8 (0.48)	21.3 (1.1)	3.74 (0.541)	17
Greeland halibut (*Reinhardtius hippoglossoides*)	52.8 (13.90)	18.3 (4.81)	69	7.15 (2.153)	25	5.4 (0.93)	24.1 (1.59)	2.19 (0.509)	11
Atlantic herring (*Clupea harengus*)	274 (70.4)	28.0 (3.40)	312	10.18 (2.987)	25	7.4 (0.98)	24.5 (1.75)	3.68 (1.546)	35
Capelin (*Mallotus villosus*)	15.9 (1.53)	12.6 (1.22)	90	19.19 (3.755)	32	10.8 (1.97)	28.0 (1.72)	2.12 (0.328)	20

Note: Values in parentheses are 1 standard deviation.

species, or in which predators are abundant, such as those involving the Atlantic harp seal (*Phoca groenlandica*).

The harp seal is widespread and abundant in the North Atlantic (Finley et al. 1990; Reijnders et al. 1993; Sergeant 1965). In the northwest Atlantic, its population is estimated at almost 5 million (Shelton et al. 1995). Harp seals eat many species of fish and invertebrates, including some of great commercial importance (Lawson and Stenson 1995; Lawson et al. 1995). This study was undertaken to quantify the assimilation efficiency (AE) and digestive efficiency (DE) of harp seals feeding on selected prey species. It is part of a larger study intended to provide inputs to a model of harp seal consumption (Stenson et al. 1995). To date, DE estimates for the model have been based on studies of other pinniped species (Ashwell-Erickson and Elsner 1981; Parsons 1977; Ronald et al. 1984), or on studies that used only a few prey species eaten by northwest Atlantic harp seals (Keiver et al. 1984; Mårtensson et al. 1994*a*).

A simple way to estimate AE (and, by using prey and faecal energy densities, DE) is to determine the ratio of inert markers in ingesta and faeces (Kleiber 1975). Naturally occurring manganese (Mn^{2+}) satisfies the requirements for an inert dietary marker, as it does not accumulate in the body even when fed in excess of requirements (Friedman et al. 1987), so changes in AE are reflected by changes in Mn^{2+} concentration in the faeces. Mn^{2+} has been used to estimate AE (digestibility of dry matter) in the northern fur seal (*Callorhinus ursinus*; Fadely et al. 1990) and ringed seal (*Phoca hispida*; Lawson et al. 1997), and DE (digestible energy) in the harp seal (Mårtensson et al. 1994*a*) and crabeater seal (*Lobodon carcinophagus*; Mårtensson et al. 1994*b*).

Some ecologically important influences on DE are food quality, meal size, and consumer age. The gastric emptying rate is generally high and the gut transit time low when food quality (e.g., energy density) is low (Best 1975; Grove et al. 1985; Hunt and Stubbs 1975). AE is also low when food quality is low (Brekke and Gabrielsen 1994; Maiorino et al. 1986). Harp seals fed herring (*Clupea harengus*) or capelin (*Mallotus villosus*) had higher DE values and consumed less food than those fed invertebrates of lower energy density (Keiver et al. 1984; Mårtensson et al. 1994*a*; no such effect of food quality in walrus (*Odobenus rosmarus*), however, was reported by Fisher et al. 1992).

An increase in meal size typically reduces the digestion rate and AE (Golley et al. 1965; Grove et al. 1985); such an effect has been documented for the harp seal (faecal energy loss increased with food intake; Keiver et al. 1984).

Finally, AE may increase with age (e.g., Heath and Randall 1985), perhaps as the gastrointestinal tract matures. No age effects on DE have been reported for pinnipeds (Fisher et al. 1992; Mårtensson et al. 1994*a*), but the age range of subjects in past studies was small.

The primary purpose of this study was to estimate AE and DE of a diversity of important prey species of the harp seal, including prey of differing quality (energy density). A second goal was to investigate the effects of meal size and age on DE. The major finding was that AE and DE values were high but varied among prey species, and were positively correlated with prey energy density. No effects of meal size or age were detected.

Methods

Twelve captive harp seals were housed in an outdoor compound at the Ocean Sciences Centre, Memorial University of Newfoundland. The seals were born at the facility or captured near Newfoundland at least 6 months prior to the experiments. Their ages, sexes, and mean body masses were as follows: two male subadults (1 and 2 years old, 57.2 and 88.9 kg, respectively), five male adults (5 and 15 years old, 133.8 and 204.7 kg, respectively, plus three seals of unknown age but captured as adults with full harp markings, 108.6, 110.9, and 114.9 kg), and five adult females (captured as adults; one was in captivity for 6 years; 66.0, 78.5, 85.1, 104.5 and 167.5 kg). Seals were cared for in accordance with the guidelines of the Canadian Council on Animal Care.

The seals had free access to a circular tank (12.2 m in diameter, 2.4 m deep) filled with seawater and surrounded by wooden decking (180 m^2 in area). Seals were weighed to the nearest 0.2 kg once per week. A mean body mass for each seal during a feeding experiment was calculated by averaging masses for those experiments lasting more than 1 week. During five of the six experiments, the seals were fed on a pure diet of one of the five fish species. Feeding was ad libitum within a 2-h period daily, usually at midday (Table 1). In the sixth experiment (the second using a diet of Atlantic cod), eight seals were fed Atlantic cod for 19 days. Four seals were fed at 50% of their previous mean ad libitum herring meal sizes. Concurrently, four were fed Atlantic cod ad libitum. After 9 days, the members of the two treatment groups were switched. Between experimental trials seals were fed a diet of herring. Seals underwent 10-day fasts before both the Atlantic cod and capelin trials as part of another experiment. Each day the total mass, number, and stan-

Table 2. Summary of estimates of dry matter assimilation efficiency (AE) and digestible energy (DE) using different fish species.

	Trial length (days)	No. of subjects	Mean meal mass (g)	No. of AE scat samples[a]	Mean AE%	Mean DE%	No. of DE scat samples
Atlantic cod							
Large	12	1	887 (453.2)	15	81.1 (3.88)		
Small	19	7	3094 (1516.0)	120[b]	84.9 (2.35)		
50% of ad libitum meal size	19	7	2183 (643.0)	37	84.1 (2.25)	93.2 (1.06)	10
Ad libitum meal size	19	7	4028 (1340.4)	48	85.3 (2.44)	94.3 (0.74)	11
Total[c]	31	7	3103 (1892.6)	63	84.3 (3.29)	93.2 (1.06)	10
Arctic cod	11	4	5625 (937.5)	47	86.9 (3.30)	93.5 (1.74)	11
Greenland halibut	11	3	5942 (1808.4)	27	88.5 (4.24)	94.7 (1.57)	9
Atlantic herring	—	10	4087 (1859.9)	172	91.0 (2.64)	96.6 (0.93)	10
Capelin	20	8	4638 (1169.8)	75	91.4 (4.15)	95.7 (1.47)	9
Overall			4679 (1031.8)	456	88.4 (2.64)	94.5 (1.97)	60

Note: Values in parentheses are 1 standard deviation.

[a]Each scat sample comprised two replicates (see the text).

[b]Includes data for unidentified seals fed meals of unknown meal size.

[c]Excluding data for seals fed 50% of ad libitum meal size.

dard length of fish consumed by each seal were recorded. Before the seals were fed each day, at least 10 fish were set aside and frozen for analysis of Mn^{2+} concentration and proximate composition (water, lipid, protein, and ash content).

For identification of individual seals' faeces, unique markers were added to each seal's meal. Markers included coloured Microgrits (Micro Tracers Inc., 1370 Van Dyke Avenue, San Francisco, Calif.), unpopped popcorn, whole dried kernel corn, dried Indian corn, and short pieces of silicon tubing 0.3 cm in diameter.

Faecal samples were collected from the deck and tank daily and during weekly tank cleaning. Date, time, and seal identity (if a seal was observed defecating) were recorded for each sample. Faecal samples collected from individual seals on the same day were analysed separately if they differed in colour, size, or texture; otherwise, only one of the samples was analysed (the same criterion was used for faeces identified by markers; see below). Samples from subadults were not obtained for Arctic cod and Greenland halibut. The 15-year-old male contributed six faecal samples. Total faecal collections were impractical, since these seals would have altered their food-consumption patterns and ceased to defecate for prolonged periods unless they were allowed access to water in which to swim.

Faecal samples were frozen in a sealed plastic bag at −20°C soon after collection. Frozen faecal and prey samples were later thawed and the faeces were checked for the presence of markers. Both sample types were dried to constant mass in 13 cm diameter aluminum pans in a mechanical convection oven (Precision Scientific Inc., 3737 West Cortland Street, Chicago, Ill.) at 100°C. Moisture contents of faeces collected in the water ($\bar{x}$ = 56.9%, SD = 21.62) and on deck ($\bar{x}$ = 58.3%, SD = 23.29) were not significantly different overall ($F_{[1,442]} = 0.27$, $p = 0.601$), or when subdivided by food type, so a correction factor for desiccation was not applied. After markers were removed, the dried samples were manually ground to uniform consistency in a large ceramic mortar and stored in 50-g plastic vials. The mortar and pestle were cleaned and dried thoroughly between grindings.

Mn^{2+} analyses were carried out on 174 fish and 456 seal faecal samples (Tables 1 and 2). Subsamples (0.5 g) of ground faeces or fish were placed in ceramic crucibles and ashed at 550°C in a muffle furnace (Model FA1850, Thermolyne Corporation, Dubuque, Iowa) for 15 h. Concurrently, a 0.5-g reference sample of oyster tissue (12.3 ± 1.5 ppm; National Bureau of Standards 1566a, U.S. Department of Commerce, Washington, D.C.) was ashed. The ashed samples were then digested using 2 mL of nitric acid (68% pure, trace metal grade; Fisher Scientific, 112 Colonnade Road, Nepean, Ont.) and diluted to a total volume of 50 mL (faeces) or 25 mL (fish) with dionized water. Mn^{2+} concentrations were determined using an atomic absorption spectrophotometer (Perkin–Elmer 2380; 279.5 nm wavelength, slit width 0.2 nm, oxidizing air–acetylene flame; Perkin–Elmer, 5349 Ferrier Street, Montreal, Que.). Duplicate aliquots were processed on all faecal and most fish samples to derive variance estimates of Mn^{2+} concentration. The differences between replicate values for faeces and fish were small ($\bar{x}$ = 2.5%, SD = 1.1, and $\bar{x}$ = 2.4%, SD = 0.7, respectively) and not significant (paired t test, $t = -1.2$, $p = 0.4$, and $t = -1.0$, $p = 0.329$, respectively), so replicate values were averaged for each sample.

AE was calculated using the formula $AE\% = [1 - (C_i/C_f)] \times 100$, where C is the concentration (dry mass basis) of Mn^{2+} in the ingesta (i) or faeces (f; Kleiber 1975). AE%, DE%, and percent lipid estimates were arcsine-transformed ($q = \arcsin(p^{0.5})$, where p is a proportion) for all statistical analyses. DE was calculated using the formula in Mårtensson et al. (1994*a*, 1994*b*).

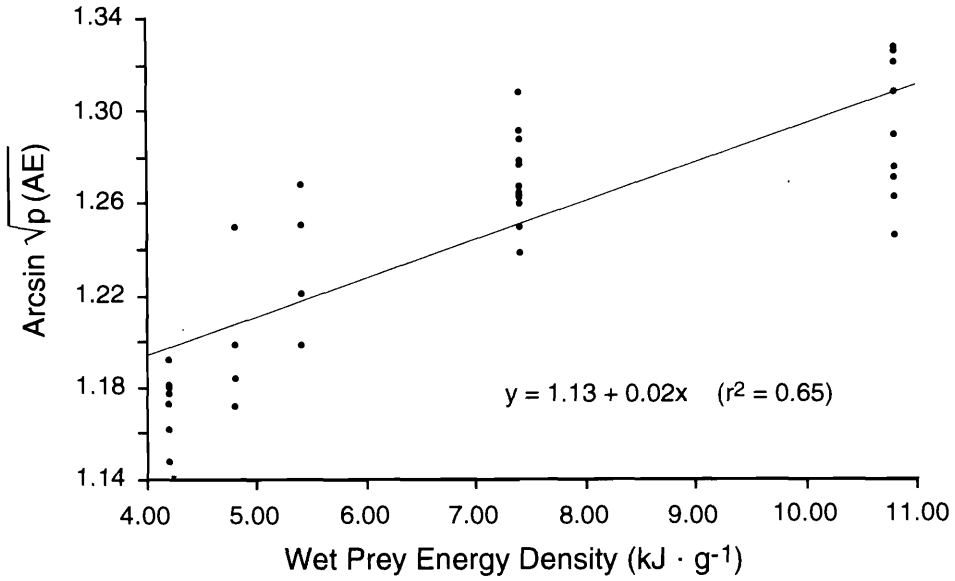
Proximate composition of prey was estimated using whole fish that had been dried and ground (see above). The lipid content of prey and faecal samples was measured using diethyl ether extraction, and protein content was derived by subtracting lipid, water, and ash masses from the total wet mass and assuming negligible carbohydrates. Energy density was calculated assuming 20 and 38 kJ · g^{-1} for protein and lipid, respectively.

Results

Prey characteristics

Prey lengths and masses varied among feeding trials. The largest fish fed to the harp seals were Atlantic cod (''large'' trial) and the smallest were capelin (Table 1). Lipid contents varied significantly among prey types, with Atlantic cod being lowest (more than 16% lower than capelin, $F_{[4,217]} = 385.1$, $p < 0.0001$; Table 1). Similarly, energy density (wet mass) ranged from 4.2 kJ · g^{-1} (19.6 kJ · g^{-1} dry mass) for Atlantic cod to 10.8 kJ · g^{-1} (28.0 kJ · g^{-1} dry mass) for capelin. Mn^{2+} concentrations also varied, with capelin being the lowest and Atlantic cod the highest ($F_{[4,167]} = 66.2$, $p < 0.0001$). The mean Mn^{2+} concentration for all five prey species was 2.92 ppm (wet mass).

Fig. 1. Relationship between assimilation efficiency of adult harp seals fed different diets and wet energy density of prey. Each point is the mean AE value for an individual in one feeding trial.



Variation in AE by prey type

AE of harp seals varied among prey species ($F_{[4,451]} = 100.83$, $p < 0.0001$). Atlantic cod was digested least efficiently; capelin and herring were digested most efficiently (Table 2). A similar pattern was observed for DE values ($F_{[4,54]} = 10.11$, $p < 0.0001$), which were greater than AE values in all cases (paired t test; $t = 26.35$, $p < 0.0001$).

AE was strongly related to the energy density of prey. AE for adult seals increased linearly with prey energy density ($r^2 = 0.65$; Fig. 1). DE was also related to prey energy density ($r = 0.51$, $p = 0.006$, $N = 28$ samples from 10 seals). In contrast, meal mass was weakly correlated with energy content of prey ($r = 0.29$, $p = 0.0004$, $N = 321$).

For Atlantic cod, harp seals had higher AE and DE values when on an ad libitum diet than when they were restricted to 50% of ad libitum meal mass (AE: $F_{[1,83]} = 5.61$, $p = 0.02$; DE: Mann–Whitney U test, $U = 20.5$, $N = 20$, $p = 0.026$; Table 2). Further, AE was greater when seals were fed more, and smaller, Atlantic cod ($F_{[1,37]} = 10.3$, $p = 0.003$; Table 2). For other prey types, the relationship of AE to the number of prey consumed was weak ($r = 0.39$, $p < 0.0001$, $N = 101$).

Individual variation in AE

AE values varied among individual study animals, but differences were not significant overall ($F_{[9,332]} = 1.45$, $p = 0.23$) or for separate prey species.

Subadults exhibited higher AE values than adults for Atlantic cod (paired t test, $t = 2.433$, $p = 0.0168$) and capelin (paired t test, $t = -2.613$, $p = 0.0122$) but not for herring (paired t test, $t = -1.782$, $p = 0.0767$). Despite these age differences, AE was weakly correlated with body mass ($r = 0.15$, $p = 0.004$, $N = 339$). DE did not differ between age groups either overall (Mann–Whitney U test, $U = 90.5$, $N = 45$ $p = 0.088$) or for any prey type. Male and female harp seals did not differ in AE (paired t test, $t = 0.34$, $p = 0.734$) or DE (Mann–Whitney U test, $U = 183.5$, $n = 45$, $p = 0.129$).

Discussion

AE and DE values for captive harp seals in this study were generally high but varied among prey species (Table 2). This is consistent with findings from other pinniped studies, and is somewhat surprising, given the short retention time of food reported for seals (e.g., Markussen 1993) compared with other carnivores (Warner 1981). In this study one harp seal passed faeces containing Atlantic cod otoliths only 7 h after being fed. Published estimates are similar for ringed seals (*Phoca hispida*, 5.8–8.5 h; Parsons 1977), southern elephant seals (*Mirounga leonina*, 9 h; Krockenberger and Bryden 1994), and harbour seals (*Phoca vitulina*, 2.5–6.25 h; Helm 1984; Markussen 1993). Seals with rapid passage rates were likely to pass faeces with a high water content (e.g., Helm 1984); in our study, faeces averaged 57.3% water (SD = 22.3%).

Differences in AE and DE among prey species were due predominantly to variation in prey energy density. The proportions of lipid, and energy density, in the fish varied (Table 1), and were strongly related to AE (Fig. 1) and DE, so the observed differences in DE were not unexpected. The AE value for herring is close to that reported in previous studies of northern fur seals (Fadely et al. 1990) and ringed seals (Lawson et al. 1997). The DE value for herring is similar to values reported in previous studies of harp seals (92.5–95%; Keiver et al. 1984) and harbour seals (92.1%; Ashwell-Erikson and Elsner 1981).

The energy density of Atlantic cod in this study was greater than that of the crustaceans (*Thysanoessa* sp. and *Parathemisto libellula*) fed to young harp seals by Mårtensson et al. (1994*a*). Most seals eating Atlantic cod in this study did not lose weight, in contrast to the latter study. This difference occurred despite smaller cod meal mass (1.9 kg · d^{-1}) in this study than shrimp meal mass (2.8 kg · d^{-1}) in the study of Mårtensson et al. (1994*a*), and was likely due to the higher DE value of Atlantic cod that we report. Pup weight loss reported by Mårtensson et al. (1994*a*) may also have resulted from energy requirements for growth in these young

Table 3. Studies of digestive efficiency of various seal species estimated using inert marker techniques.

	Age and sex of seals	No. of seals	Duration of study	No. of experiments	Prey types used	No. of faecal samples analysed	Sources
Harp seal (*Phoca groenlandica*)	Weaned pups Subadults (2–4 yr)	2 4	2 weeks for age comparisons on capelin diet; otherwise 2 months	2	Capelin, *P. libellula*, and *Thysanoessa* sp.	16 capelin (6 pup and 10 subdult), 15 *Thysanoessa*, and 5 *P. libellula*	Mårtensson et al. 1994*a* (study of DE)
	Subadult males (5–24 months)	4	9–35 d	?	Herring	Unstated sample size	Keiver et al. 1984 (study of DE)
Ringed seal (*Phoca hispida*)	1 subadult male and 3 subadult females (2–4 yr)	4	24 h	3 herring and 1 capelin	Herring and capelin	Unstated sample size	Parsons 1977 (study of DE)
Crabeater seal (*Lobodon carcinophagus*)	Males (2.5, 3.5, 7.5, and 19.5 yr) and females (4.5 and 8.5 yr)	6	—	—	*Euphausia superba*	1 of each faecal sample per seal (total unstated)	Mårtensson et al. 1994*b* (study of DE)
Pacific harbour seal (*Phoca vitulina richardsi*)	Subadults (1 yr) Adults (4 yr)	2 4 (2 fed herring and 2 fed pollock)	10 d	1 herring and 1 pollock	Herring and pollock (*Theragra chalcogramma*)	Unstated sample size	Ashwell-Erickson and Elsner 1981 (study of DE)
Grey seal (*Halichoerus grypus*)	Subadults (1, 1, and 2 yr) and adults (7.5 and 12 yr) (sex unstated)	5	5–18 d per level of food intake	≥three 24-h collections per level of intake	Herring	Unstated sample size	Ronald et al. 1984 (study of DE)
Northern fur seal (*Callorhinus ursinus*)	Subadult males (2 yr)	3	3 d	3	Herring	9 per seal	Fadely et al. 1990 (study of AE); Miller 1978
	Subadult males and females (0.4–5 yr) and adult females (4 and 5 yr)	13 (unclear)	Herring 5–12 d and pollock 11 d	2 herring and 1 pollock	Herring and pollock	8 herring and 4 pollock	
Walrus (*Odobenus rosmarus*)	Adult male and female (14 yr) and subadult male and female (5 yr)	4	5–7 d	2	Herring and clams (*Spisula* sp.)	3 per sex and 6 per diet[a]	Fisher et al. 1992 (study of DE)

[a]Pooled results from an unstated number of scat samples.

animals, or from high activity as the pups searched their pool and consumed many small crustaceans.

Our DE estimate for capelin was similar to that reported by Mårtensson et al. (1994*a*) for young harp seals, although we found significantly lower AE values during the first week of the feeding trial. During the first week of the capelin trial, we noted that faeces were extremely oily and many had such a high lipid content that they floated. During the subsequent 2 weeks the lipid content of the faeces decreased substantially. We excluded AE values from this apparent acclimation period (the first week of the experiment) from analyses, as they were significantly lower than estimates from the subsequent 2 weeks ($F_{[2,90]} = 15.3$, $p < 0.0001$). The 10-day pretrial fast for capelin may have resulted in the loss of intestinal digestive capacity, which required a week of feeding to recover. Alternatively, the intestinal mucosa may have required several days to develop the large surface area necessary to absorb the higher lipid content (Gross et al. 1985; Lloyd et al. 1994). This same increase in AE over time was not seen during the Atlantic cod trial begun after a 10-day fast, and little lipid was noted in the scats. Apparently, the low lipid content of Atlantic cod did not challenge the seals' ability to digest it. Temporal changes in AE during the capelin trial highlight the importance of conducting feeding trials for long enough to allow seals to adjust physiologically. Brief trials may not allow documentation of changes in digestive processes or appetite when the diet is changed, particularly when diet quality varies.

Furthermore, longer trials may be necessary to allow enough data to be gathered to determine ad libitum meal masses for prey of different quality. Although we found that meal mass was weakly correlated with lipid content of prey, we predicted that seals would consume more prey if the prey were digested less efficiently. This prediction was not supported, probably because of small differences in AE among prey types, large variance in meal mass, and perhaps insufficient data to measure the predicted effect if it was minor.

The relationship of AE and DE to prey energy density was linear rather than curvilinear. We expected that the gastrointestinal system of harp seals would not be able to absorb all of the lipid in prey above a certain lipid level. After 2 weeks of eating capelin, which had the highest lipid content of the fish we analysed, or that has been reported for the northwest Atlantic (e.g., Anonymous 1969; Brekke and Gabrielsen 1994; Steimle and Terranova 1985), it was clear that the seals had not reached the limit of their digestive capability.

Harp seals had higher AE and DE values when they consumed Atlantic cod ad libitum than when they were restricted to 50% of ad libitum meal mass (Table 2). This is similar to the results of a study of grey seals (*Halichoerus grypus*; Ronald et al. 1984) in which the digestibility of energy and lipid increased as seals were fed greater proportions of their maintenance food level. Since the harp seals had been fasted or fed ad libitum, their digestive systems may not have been prepared to digest only partial meals.

Further evidence of a partial meal effect is seen in the first Atlantic cod experiment, where the seal ate smaller meals when offered larger cod (Table 1). Compared with the second cod trial, the AE value was higher when seals were fed many small than fewer larger Atlantic cod. Alternatively, smaller cod might have been easier to fractionate before passage of the digesta to the intestine.

The Mn^{2+} concentration in fish in this study was more variable and, on average, lower than in prey from the Pacific analysed by Fadely et al. (1990). If other harp seal prey in the northwest Atlantic are as variable in Mn^{2+} concentration, then Mn^{2+} should be measured directly rather than estimating AE using the mean value suggested by Fadely et al. (1990), particularly for seals eating mixed diets. On the other hand, the strong relationship of AE to prey energy density means that we can be more confident about predicting the amounts of prey required by harp seals to satisfy their daily energy requirements, without having to collect faecal samples from wild seals.

Captive studies have severe limitations in terms of sample size and age representation. To date, AE and DE estimates derived using methods like those in this study are available for only 7 of 33 extant pinniped species (Table 3), therefore it is impossible at present to draw general conclusions about digestive efficiency and feeding ecology, annual cycle, etc. We recommend that researchers take advantage of ecologically divergent species that are in captivity, such as leopard seals (*Leptonyx hydrurga*) and bearded seals (*Erignathus barbatus*), to draw general conclusions. It is also invalid to infer sex or age differences in DE based on existing information. Although Fisher et al. (1992) reported a difference in AE between two male and two female walruses, the study involved a typically small captive sample. In this case, one cannot deduce that a general sex difference occurs, only that there was a significant difference between the two classes of individuals studied. We believe that no studies of captive pinnipeds have documented sex or age differences in DE. Only with sufficiently detailed experimental documentation can we be sure that any reported differences in pinniped digestive efficiency are not artifacts of sample size or experiment duration, or reflect inappropriate statistical treatment.

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