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FOOD HABITS AND DIGESTIVE EFFICIENCY IN WALRUS, *Odobenus rosmarus*

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by

Kathy Irene Fisher

In Partial Fulfillment of the

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of

Master of Science

Department of Animal Science

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ABSTRACT

Fisher, Kathy Irene. M.Sc., The University of Manitoba, 1989. Food Habits and Digestive Efficiency in Walrus (Odobenus rosmarus). Major Professor; Dr. R.E.A. Stewart.

Stomach contents of 107 Atlantic walrus (Odobenus rosmarus rosmarus) from northern Foxe Basin, Northwest Territories, were examined during July 1987 and 1988. Only 20% of stomachs of adults (19/93) contained food items (>5 g). Seventeen taxa were identified in these stomachs, including bivalves, gastropods, holothurians, polychaetes and brachiopods. Total abundance ranged from 9 to 1508 individuals per stomach and weight ranged from 113 to 1447 g per stomach. The bivalve Mya truncata contributed over 86% of the total energy to the diet, while the bivalve Hiatella arctica, holothurians and the polychaete Nereis sp. contributed 8.0%, 1.9% and 1.5% respectively. The diet of males and females was similar except that females consumed more of the small bivalve H. arctica ($P<0.05$) than males and also tended to consume smaller individuals of a prey type. Walrus calves (0 to 2 years, n=12) depended largely on milk for energetic reqirements although some benthic invertebrates were found in stomachs.

The digestive efficiency in 4 captive walrus (2 males, 2 females) fed diets of herring (Clupea harengus) and clams (Spisula sp.) was determined. Energy digestion was the same on both diets ($\bar{x}=92.7\%$, n=6) but females had a significantly ($P=0.02$) higher digestive efficiency

($\bar{x}$=94.4%, n=3) than males ($\bar{x}$=91.0%, n=3). Protein digestibility was 93.8% (n=6) and did not vary (P>0.05) between diets or animals. Lipid digestibility was lower on the clam diet ($\bar{x}$=73.2, n=2) than the herring diet ($\bar{x}$=94.4%, n=4) but this is likley an artifact due to low lipid content (5.8±0.7%) and the influence of endogenous lipid loss on the clam diet.

Maintenance requirements for adult walrus in captivity were estimated to be 155 kcal/kg$^{\cdot 75}$/d. Using this estimate as minimum requirements for free-ranging walrus, an 810 kg non-pregnant, non-lactating adult would require 2000 to 4500 bivalves per day to meet energetic demands.

FORWARD

Manuscript I and II were formatted for submission to the Canadian Journal of Zoology. Both manuscripts will be submitted to this journal. Authorship will be Fisher, K.I., and Stewart, R.E.A. for Manuscript I and Fisher, K.I., Stewart, R.E.A., and Kastelein, R.A. for Manuscript II.

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I thank the many people who provided technical assistance over the two year study. Dr. M.P. Summers, Visiting Professor to the Faculty of Pharmacy, made the Cr_2O_3 tablets. B. Stewart prepared the figures, aged the walrus jaws and analysed samples for energy content. The staff of the Nutrition Laboratory, Animal Science Department, assisted with sample analyses. J.A. Fournier, National Museum of Natural Sciences in Ottawa

identified polychaetes, J.M. Topping, National Museum of Natural History in Ottawa identified gastropods and M. Curtis, Department of Fisheries and Oceans in Winnipeg identified amphipods and isopods. C. Catt prepared the tables.

I thank my colleagues and friends at the Freshwater Institute, who provided advice, rousing discussions and moral support. Thanks L.D. My parents also provided a good deal of support. Thank-you.

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LIST OF ABBREVIATIONS

ADE	Apparent Digestible Energy
BMR	Basal Metabolic Rate
Cr_2O_3	Chromic Oxide
DE	Digestible Energy
FE	Fecal Energy
GE	Gross Energy
HCl	Hydrochloric Acid
HIF	Heat Increment of Feeding
ME	Metabolizable Energy
NE	Net Energy
SCUBA	Self Contained Underwater Breathing Apparatus
UE	Urinary Energy

INTRODUCTION

Atlantic walrus (Odobenus rosmarus rosmarus) inhabit the waters of the North Atlantic and Arctic Oceans and the adjacent arctic seas (Fay 1982). Major concentrations occur in the Canadian eastern arctic in the regions of northern Hudson Bay and northern Foxe Basin and to a lesser extent in Davis Strait, Baffin Bay, and the high Arctic Islands, east of 100°W (Fig. 1) (Davis et al. 1980).

Walrus have been hunted by Inuit for centuries for food for themselves and their dogs and for the raw materials for tools and implements (Vibe 1950, Mansfield 1958). Commercial hunting in the 1800s and early and mid-1900s drastically reduced the walrus populations and in 1928, regulations were passed under the Fisheries Act which banned all commercial activities (Richard and Campbell 1988).

Very little research has been conducted on the walrus stocks in Canada (Mansfield 1973). Preliminary investigations in the late 1950s and early 1960s were broad in nature and examined methods for ageing animals, growth, reproduction and nutrition (Mansfield 1958, Loughrey 1959). The population size in Canada is unknown. Aerial surveys have been conducted at several of the major haul-out sites over the last 30 years, but these are minimum counts and do not include the number of walrus in the water or those hauled out on ice floes (Richard and Campbell 1988). Mansfield (1966) estimated that a population of 25,000 walrus would be

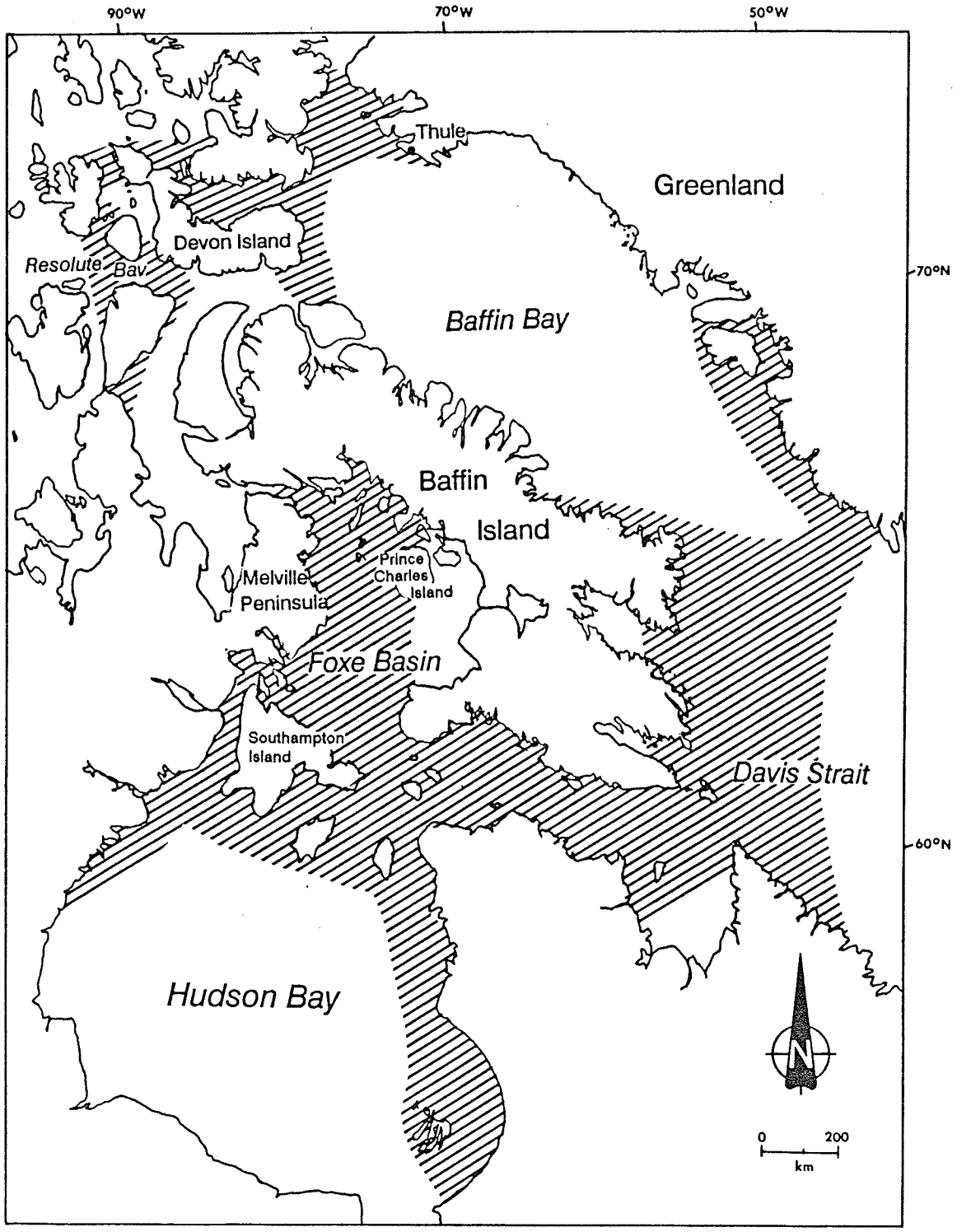

FIG. 1. Distribution of walrus in the Canadian eastern arctic (from Davis et al. 1980).

required to support the annual harvest by Inuit. Unfortunately, this number has been quoted in innumerable papers as a population estimate for Canadian stocks.

The age and sex structure of herds is also poorly understood (Reeves 1978). Female walrus reach maturity at 6 to 7 years of age (Mansfield 1958) and a single calf is produced every second or third year. Male walrus reach sexual maturity between 6 and 10 years but likely do not reproduce until they are 15 years or older when they are physically mature and able to successfully compete for females (Mansfield 1958, Fay 1982). The weight of adult male and female Atlantic walrus range from 720 to 1530 kg and 482 to 1025 kg respectively (Mansfield 1958, Fay 1985).

Habitat encroachment from non-renewable resource development projects, such as mining and oil and gas exploration, has the potential to seriously affect the walrus herds and their food resources. Walrus feed primarily on bivalve molluscs (Vibe 1950, Mansfield 1958, Fay 1982). Molluscs concentrate heavy metals such as mercury and arsenic, so walrus may be susceptible to the accumulation of pollutants (Richard and Campbell 1988). Oil spills could be detrimental to mollusc beds although the major impact of a spill would occur in the ice-scoured inter-tidal zones which are devoid of benthic life. Oil spills would be most damaging in over-wintering polynyas (Davis et al. 1980, Stirling et al. 1981) since walrus would not be able to leave the area.

Walrus are sensitive to human disturbance. Noise from airplane and boat traffic causes animals to flee into the water and swim away (Salter 1979) sometimes causing stampedes, which may kill smaller animals.

Human activity has also been reported to be the cause for abandonment of many of the haul-out sites in western Foxe Basin (Beaubier 1970). Walrus inhabit several areas near existing or proposed industrial sites or shipping routes in the high arctic. The long-term effect of vessel noise and human activity on the movement of these stocks is unknown.

Fisheries for scallops, shrimp and groundfish have recently taken place in several locations in the eastern arctic (Anonymous 1987). While not in direct conflict with walrus, these types of activities have the potential to disturb benthic fauna and alter the community structure. A commercial fishery for molluscs has recently been proposed in Arctic Bay, N.W.T. (Anonymous 1989).

Because walrus distribution is limited partly by the availability of benthic resources, any perurbation of benthic stocks could have a serious impact on the walrus population. Therefore, the main objective of this study was to examine the food habits of walrus and identify the major prey consumed. This information can be used for the eventual identification and protection of critical feeding areas to minimize the impact of resource development projects and commercial fishery ventures on the walrus stocks.

Studies on the food habits of Atlantic walrus are few. Vibe (1950) examined the stomachs of 5 walrus from the Thule District of Greenland and Loughrey (1959) collected 20 stomachs from northern Hudson Bay, although he did not report the composition of prey. Mansfield (1958) examined 111 stomachs from walrus in the Canadian eastern arctic; all but 6 of these were collected during the summer. Examination of the diet during the winter months is difficult because the drifting pack ice can

easily crush a boat and the reduced daylight hours and extreme temperatures make travelling difficult and dangerous. The summer and fall diet of Atlantic walrus consists largely of the siphons of the bivalve molluscs Mya truncata and Hiatella arctica and the feet of Serripes groenlandica/Clinocardium ciliatum (=Cardium sp.) although many other invertebrates including gastropods, polychaetes, priapulids, echinoderms, and tunicates have been identified (Vibe 1950, Mansfield 1958). Ringed (Phoca hispida) and bearded seal (Erignathus barbatus) remains have been found in several walrus stomachs in the Canadian arctic (Mansfield 1958, Loughrey 1959), Greenland (Vibe 1959), the Kara Sea (Chapskii 1936) and Franz Josef Land (Tsalkin 1937). Fish otoliths (Chapskii 1936, Mansfield 1958) and squid beaks (Mansfield 1958) have been identified in a small number of stomachs.

The food habits of Pacific walrus (Odobenus rosmarus divergens) have been studied more extensively because of the impact the estimated 200,000 animals (Fay 1982) exert on the benthic resources and the potential conflicts with other marine mammals and fisheries (Lowry and Frost 1981). The diet of Pacific walrus is similar to the Atlantic walrus and consists largely of bivalves, although over 60 genera in 10 phyla have been identified in stomachs. The bivalves Mya, Hiatella Spisula, Clinocardium and Serripes are the major prey consumed (Nikulin 1941, Brooks 1954, Fay et al. 1977, 1984).

Stomach content analysis can provide useful information on the types of prey consumed but provides no indication of the daily quantity consumed. An estimate of food intake is necessary to determine how large a benthic population is required to support the walrus population. Food intake is

most useful when expressed in terms of energy intake because it accounts for differences in energy density within and between prey types (Lavigne et al. 1982).

An alternate approach to determine the energy requirements of the walrus population is to look at the requirements of an individual walrus and apply this to the population, given knowledge of the population size, age structure and sex ratio. There have been very few attempts to construct an energy budget for pinnipeds, primarily because of major gaps in knowledge regarding individual and population parameters. No components of the energy budget of walrus have yet been experimentally determined. Estimates of gross energy (GE) intake for maintenance range from 238 to 472 kcal/$kg^{\cdot 75}$/d (Fay 1982, Gehnrich 1984). These estimates are based on the food intake levels fed to the walrus and proximate composition and energy density values from the literature. Values at the lower end of the range have been equated to maintenance requirements for non-lactating, non-pregnant females, even though changes in body weight at these feeding levels were not taken. The second objective in this study was therefore to begin to examine the energy partitioning (Fig. 2) in walrus by determining the apparent digestible energy (ADE) of 4 captive walrus. Metabolizable energy (ME) could not be determined because urine could not be collected.

Energy losses through feces (FE), urine (UE) and heat increment of feeding (HIF) have recently been measured in pinnipeds. Digestible energy (DE) in seals ranged from 90 to 98% of GE intake (Parsons 1977, Keiver 1982, Keiver et al. 1984, Ronald et al. 1984). Urinary losses ranged from 7 to 8% of DE and ME varied from 85 to 90% of GE (Keiver

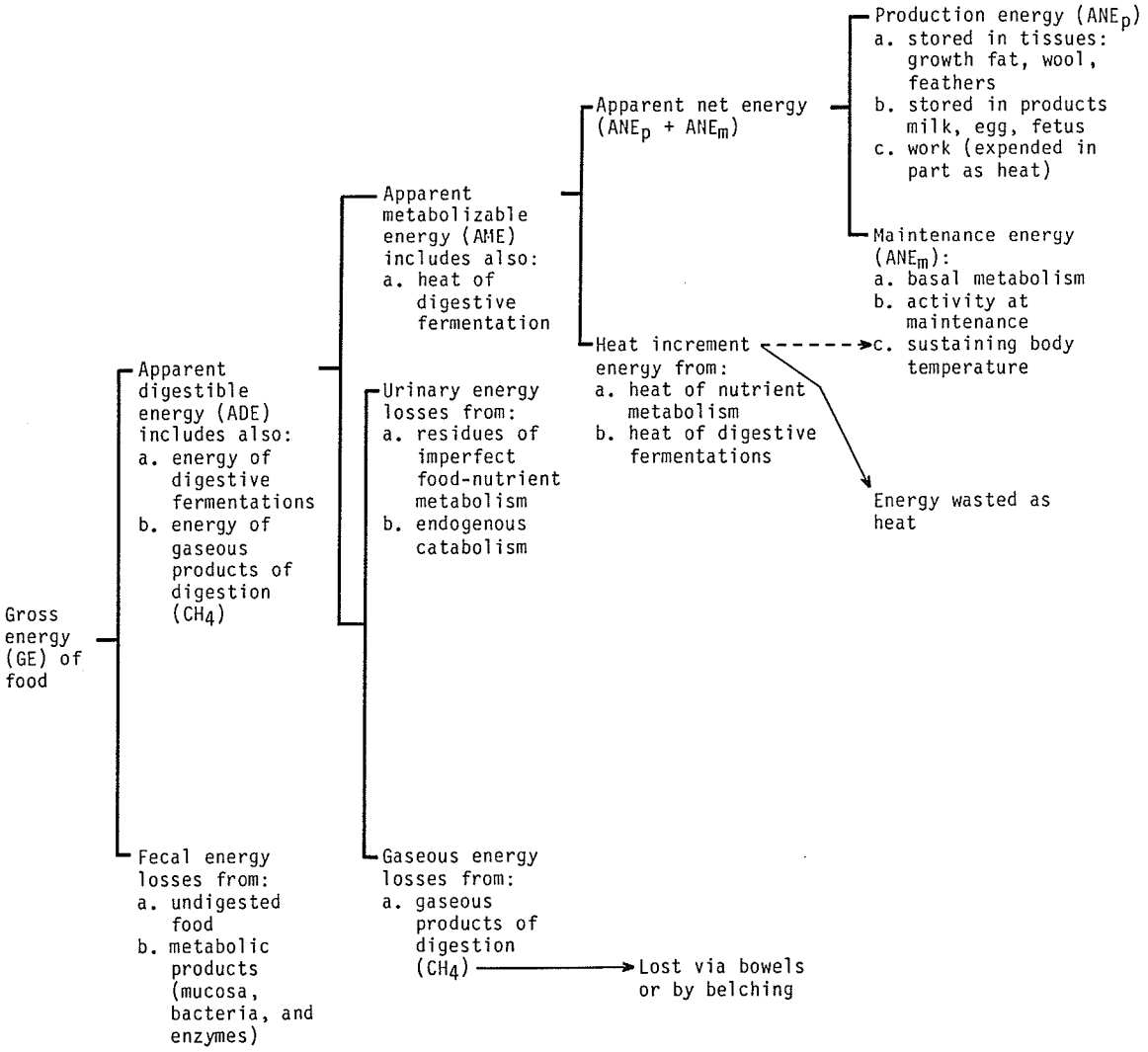

FIG 2. Apparent partitioning of energy in animals (from Crampton and Harris 1969).

1982, Keiver et al. 1984, Ronald et al. 1984). Heat increment of feeding (HIF) for seals was calculated as 5.5 to 17% of GE (Ashwell-Erickson and Elsner 1981, Gallivan and Ronald 1981, Innes 1984). Therefore approximately 70-75% of GE is available as net energy for seals fed fish diets.

MANUSCRIPT I

FOOD HABITS OF ATLANTIC WALRUS, *Odobenus rosmarus rosmarus*, IN NORTHERN FOXE BASIN, NORTHWEST TERRITORIES

Few studies have examined the food habits of Atlantic walrus. Vibe (1950) described the stomach contents of 5 walrus collected from the Thule District of Greenland and Mansfield (1958) examined 19 stomachs from 5 locations in the Canadian eastern arctic. Both found that the major food sources were bivalves of the genera *Mya*, *Hiatella* (=*Saxicava*) and *Serripes*/*Clinocardium* (=*Cardium*). Holothurians, gastropods, crustaceans, polychaetes and other organisms were consumed to a lesser extent. Loughrey (1959) also collected stomachs from 20 walrus taken in northern Hudson Bay but did not examine the contents of the 5 which contained food.

Inuit from the communities of Igloolik and Hall Beach rely heavily on walrus in Foxe Basin (Fig. 3) for food for themselves and their dogs (Beaubier 1970), yet little is known of the ecology and food habits of this stock (Mansfield 1966). The only documented study of the walrus diet in Foxe Basin was by Mansfield (1958) who examined 3 stomachs from the area as part of a larger study on the biology of Canadian eastern arctic walrus.

The purpose of this study was therefore to examine the diet of walrus in northern Foxe Basin and test the null hypothesis that bivalves are the

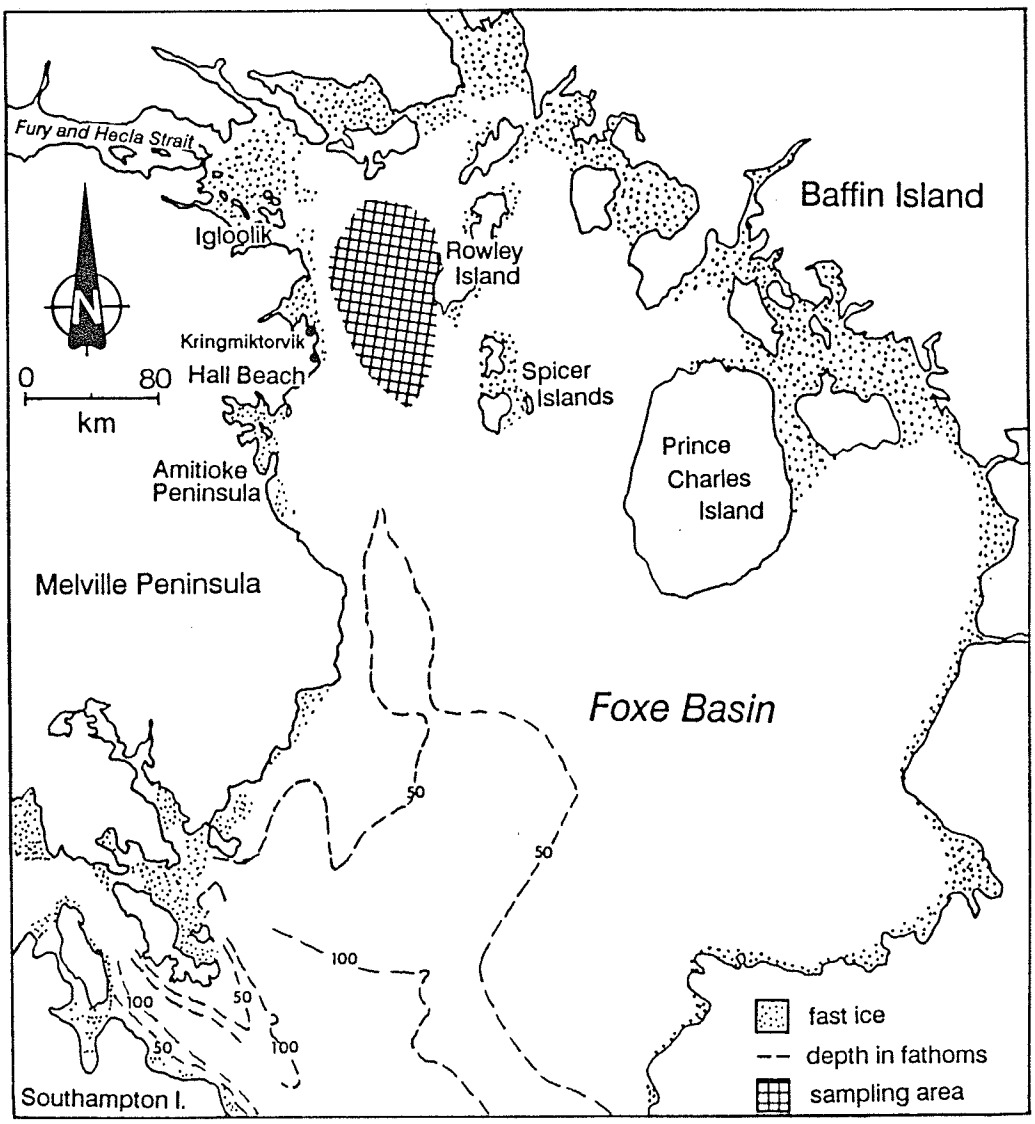

FIG. 3. Map of northern Foxe Basin showing bathymetry, limit of winter fast ice (from Mansfield 1958) and the sample collection area in this study.

major source of energy in the diet of all segments of the walrus stock. This information can then be used as the basis to identify and protect critical feeding areas for walrus in the Canadian eastern arctic.

MATERIALS AND METHODS

One hundred and seven walrus stomachs were collected from Inuit subsistence hunts in Foxe Basin, N.W.T. (Fig. 3), during July 1987, 1988 and September 1988. Samples were collected with the assistance of hunters from the communities of Igloolik and Hall Beach and by Department of Fisheries and Oceans (DFO) personnel. For each sample, the stomach and jaw (for ageing) were taken, and the sex, total length, total girth and xiphisternal blubber thickness were recorded (American Society of Mammologists, 1967). Additional data were gathered for other studies. Stomachs and jaws were frozen, usually within 24 hours of collection, and returned to Winnipeg for analysis.

Benthic invertebrates were collected as reference material for the identification of stomach contents and for energy content determinations. Most samples were obtained using SCUBA. Small epifaunal and shallow infaunal invertebrates which could not be collected by hand were gathered by divers using an underwater air lift device (Chess 1978). Benthos were also collected at the floe edge using a bottom grab and opportunistically from the beach and tidal flats. All collections were made in depths of 20 m or less and organisms were either frozen for calorimetry or preserved in 70% ethanol or 10% buffered formalin for species identification.

In the laboratory walrus stomachs were thawed, slit longitudinally and the contents sequentially washed through 4 mm and 1 mm sieves. Organisms were identified to the lowest taxonomic level possible, counted, blotted dry and weighed to ±0.1 g (Mettler PC4400, Zurich, Switzerland). Prey

items were identified using a reference collection and published keys (Shorygin 1948, Grainger 1955, Bousfield 1960, MacPherson 1971, Clarke 1974, Lubinsky 1980) or sent to invertebrate taxonomists. Polychaetes were identified by J.A. Fournier, National Museum of Natural Sciences, Ottawa; gastropod opercula by J.M. Topping, National Museum of Natural History, Ottawa; amphipods and isopods by M. Curtis, DFO, Winnipeg. Bivalves could only be identified to the level of genus because species identification is based on the shell (Keen and Coan 1974) and these are usually absent in stomachs. When bivalve genera were represented by only 1 species in Foxe Basin, genus identification was considered equivalent to species identification. The cockles, Serripes groenlandicus and Clinocardium ciliatum, which were identified in earlier literature (Lubinsky 1980) as Cardium groenlandicus and Cardium ciliatum respectively, cannot be separately identified based on fleshy parts found in the stomachs. Clinocardium shell fragments were not found in any stomachs so cockles are referred to as Serripes in the following text. Inorganic and unidentifiable organic remains on the small mesh sieve were sorted by specific gravity in a water column, drained and weighed to ±0.1 g. The volume of milk in the stomachs of calves was measured in the laboratory using a graduated cylinder and recorded to the nearest 25 ml.

Two fecal samples were incidentally collected from ice floes where walrus had recently hauled out. Samples were flushed through a 1 mm sieve and the organisms were identified, largely from diagnostic hard parts.

Walrus stomach contents were quantified using 4 methods: (1) percent occurrence of each prey type (number of stomachs in which prey type

occurred / total number of stomachs x 100) (Hyslop 1980), (2) percent abundance of each prey type (number of individuals of a prey type in all stomachs / total number of all individuals in all stomachs x 100) (Lowry and Frost 1981, Murie 1984), (3) percent weight of each prey type (weight of individuals of a prey type in all stomachs / total weight of all individuals in all stomachs x 100) (Hyslop 1980, Lowry and Frost 1981), (4) percent energy contribution (estimated energy content of individuals of a prey type in all stomachs / total energy content of all individuals in all stomachs x 100) (Murie 1984).

The criteria used for counting individual organisms depended on the prey type. Bivalve numbers were based on maximum counts of identifiable siphons, feet or bodies; gastropod, polychaete and brachiopod numbers were based on diagnostic hard parts such as opercula, jaws and shell teeth, while numbers of most other prey types were based on counts of whole individuals. The mean weights of individuals of the major prey types were determined from walrus stomachs which contained undigested representatives or from specimens in benthic collections. Polychaete weights were provided by J.A. Fournier (unpub. data).

The caloric density and percent dry matter of the major food taxa were determined from samples collected near Igloolik (Fig. 3) and Resolute Bay, N.W.T. (Fig. 1). Samples were freeze dried (Labonco Model 75018, Kansas City, Missouri) to a constant weight and energy density was measured using an adiabatic bomb calorimeter (Parr Instruments, Moline, Illinois). Dry matter and caloric density of taxa not represented in benthic collections were taken from the literature (Tyler 1973, Wacasey and Atkinson 1987, G. Atkinson, DFO, Ste. Anne de Bellevue, Quebec,

unpub. data). The percent contribution of each prey type to the total energy content of stomachs, with the exception of holothurians, was back-calculated using the number of individuals and the mean weight and energy density for each prey type or part of the item consumed. Caloric contribution of holothurians was calculated using weight and not abundance because rapid digestion prevented accurate counts from being made.

Walrus were aged according to Peterson and Born (1982). A 1 cm transverse section was cut through the right ramus mandibularis in the region of the last cheek tooth using a band saw. Sections were boiled to remove the flesh and then polished on a grinding wheel. Annual growth layers in each section were counted 3 to 5 times and the final age estimates were based on 3 identical readings. If fewer than 3 readings were identical, the 95% maximum normed residual was calculated (n=5), the outliers were removed (Snedecor and Cochrane 1980) and the median value was used as the final age estimate (Stewart and Lavigne 1979).

Differences in diet between sexes were analysed using the non-parametric Wilcoxin test for ranked data (Sokal and Rohlf 1969). The level of significance was $P<0.05$ for all analyses. Statistical comparison of the diet between age groups (immature vs adult) was not done because of the small sample size (n=5) for post-weaning immature walrus (age 3-6 years).

RESULTS

Ninety-five of the 107 walrus stomachs collected were from immature (weaned) or adult animals and 12 were from suckling calves. In immature and adult walrus, 21 (22%) of the stomachs contained food items (>5 g), 13 (14%) had trace quantities (<5 g) of food and 61 (64%) were empty. The mean weight of food items in the 21 stomachs was 1047.4±1422.1 g. The large standard deviation reflects the wide range in weights of stomach contents. The 2 stomachs from walrus taken in September 1988 had a disproportionate amount of food (5095.4±1080.1 g) and were removed from the analysis, reducing the mean weight of food in stomachs to 621.3±412.2 g (n=19). Examination of dietary composition was based on these 19 stomachs which were all collected during July 1987 and 1988.

Diet composition

The 17 taxa identified from walrus stomachs in this study are a sample of the summer walrus diet in northern Foxe Basin (Table 1). From the stomachs collected in July, two bivalve species, *Mya truncata* and *Hiatella arctica* accounted for 90.9% of all organisms ingested (Table 2). *Mya* were the most frequent (95%) and most abundant (67.2%) of all items consumed, with siphon numbers ranging from 0 to 917 per stomach. Only the siphons, sheaths and shell fragments were found in stomachs; intact bodies were absent. The red and orange tipped siphons of *Hiatella* were found in most stomachs (79%, 0 to 588 siphons) and comprised 23.7% of ingested items. Unidentified bivalve remains, which included sheaths, guts and other muscle fragments, comprised 31.5% of the total wet weight

TABLE 1. Scientific and common names of prey found in walrus stomachs in Foxe Basin, N.W.T., 1987-1988.

General taxon	Scientific name	Common name
Bivalvia	*Astarte* sp.	
	Hiatella arctica	Arctic saxicave
	Mya truncata	blunt soft shell clam
	Serripes groenlandicus[a]	Greenland cockle
Gastropoda	*Buccinum* sp.	whelk
	Natica clausa	moon snail
Polychaeta	*Eunoe* sp.[b]	scale worm
	Flabelligera affinis	
	Nereis sp.[c]	nereid worm
	Thelpus cincinnatus	terebellid worm
Holothuroidea		sea cucumber
Echinoidea	*Strongylocentrotus droebachiensis*	green sea urchin
Priapulida	*Priapulus caudatus*	priapulid worm
Amphipoda	*Anonyx sarsi*	
	Boeckosimus edwardsi	
Isopoda	*Arcturus baffini*	
Brachiopoda	*Hemithyris psittacea*	
Decapoda		

[a]Could also be *Clinocardium ciliatum*, however only shells of *S. groenlandicus* were found in stomachs.
[b]Likely *E. nodosa*, *E. oestedi* or closely related *Harmothoe imbricata* or *H. extenuata*.
[c]Likely *N. pelagica* although could be *N. zonata*.

TABLE 2. Percent occurrence, abundance, weight and estimated energy contribution of prey in stomach contents of 19 walrus in Foxe Basin, N.W.T., July 1987 and 1988.

Prey	Occurrence %	Abundance		Weight		Estimated Energy	
		No.	%	g	%	kcal	%
Bivalvia							
Mya truncata	95	5619	67.2	4719.3	40.0	29848.1	86.1
Hiatella arctica	79	1980	23.7	928.4	7.9	2772.0	8.0
Astarte sp.	79	68	0.8	13.2	0.1	19.7	0.1
Gastropoda							
Buccinum sp.	58	57	0.7	2.8	<0.1	322.4	0.9
Natica clausa	53	157	1.9	31.2	0.3	136.4	0.4
Unidentified feet	21	15	0.2	5.9	0.1	18.2	0.1
Polychaeta							
Eunoe sp.	11	39	0.5	0.2	<0.1	70.8	0.2
Nereis sp.	58	303	3.6	1.9	<0.1	513.0	1.5
Flabelligera affinis	11	10	0.1	7.6	0.1	7.6	<0.1
Thelpus cincinnatus	16	5	0.1	16.3	0.1	7.6	<0.1
Holothuroidea	63	39	0.5	1045.3	8.9	649.1	1.9
Echinoida							
Strongylocentrotus droebachiensis	11	1	<0.1	0.2	<0.1	0.1	<0.1
Priapulida							
Priapulus caudatus	21	20	0.2	121.4	1.0	312.3	0.9
Brachiopoda							
Hemithyris psittacea	47	37	0.4	5.2	<0.1	5.3	<0.1
Amphipoda							
Anonyx sarsi	16	3	<0.1	0.2	<0.1	0.1	<0.1
Boeckosimus edwardsi	5	1	<0.1	<0.1	<0.1	0.1	<0.1
Isopoda							
Arcturus baffini	5	1	<0.1	0.1	<0.1	0.2	<0.1
Decapoda	5	2	<0.1	0.1	<0.1	3.0	<0.1
Unidentified bivalve remains[a]	-	-	-	3713.8	31.5	-	-
Unidentified organic remains[b]	-	-	-	1158.9	9.8	-	-
Shell fragments	84	-	-	5.1	0.3	-	-
TOTAL	-	8357	-	11805.0	-	34685.9	-

[a]Includes sheath, guts and other remains.
[b]Mostly from the 1 mm sieve fraction.

of all stomachs. Astarte sp. were found in most stomachs (79%) but comprised <1% of the total number of individuals.

Gastropods were recognized primarily by the opercula, but in some stomachs which contained less digested contents, the opercula were still attached to the bodies. Buccinum sp. and Natica clausa occurred in over half the stomachs (58%, 53% respectively) and comprised 2.6% of all organisms; Natica were 2.7 times as abundant as Buccinum.

Four taxa of polychaetes were found in walrus stomachs. The most frequently occurring was Nereis sp. (58%) followed by Thelpus cincinnatus (16%), Harmothoe sp. (11%) and Flabelligera affinis (11%). Polychaetes comprised 4.8% of all organisms but contributed <1% to the total weight of the stomachs. Nereis was the most abundant polychaete (3.6%) and ranged from 0 to 123 individuals per stomach.

Holothurians were found in 12 of 19 stomachs (63%), but could not be accurately counted or further identified because of rapid digestion and a lack of diagnostic hard parts. Holothurians contributed 8.9% to the total wet weight but 85% (884.7/1045.3 g) of the biomass was found in 3 stomachs.

Priapulus caudatus was found in 21% of all stomachs and represented 0.2% of total abundance. All priapulids were swallowed whole and showed no sign of mastication. Brachiopods occurred in 47% of stomachs but contributed <0.5% to total abundance or weight, while amphipods, isopods, sea urchins and decapods each occurred in less than 20% of stomachs and contributed little to abundance (<0.5%) or weight (<0.5%).

An average of 85.7±124.8 g of stones was found in all stomachs containing food and the largest amount (501.5 g) was found in the stomach

of a 9 year old male which had fed on bivalves. Shell fragments occurred in small quantities (0 to 10 g) in 84% of the stomachs sampled.

Prey size and percent energy contribution of prey types

Stomachs generally contained large numbers of relatively small food items, most being less than 10 g. Average Mya and Hiatella siphons (with sheath) weighed 8.4 g (n=1312) and 2.2 g (n=30) respectively, and Serripes feet and bodies weighed 6.8 g (n=180) and 4.0 g (n=269) respectively (Table 3). Intact holothurians weighed 2.0-22.3 g and priapulids weighed 4.0-23.3 g. The caloric content of the more frequently consumed larger prey (Mya, Buccinum and holothurians) ranged from 5000 to 6000 cal/individual. The caloric content of Serripes feet was also near 6000 cal/individual but if the foot and body were consumed, the energy intake nearly doubled ($\bar{x}$=8961 cal/indiv.). There is no indication that the body of Mya is consumed by walrus, but if it were, the energetic returns would also be 2 times higher than for the siphon and sheath alone. The caloric density of Hiatella was similar to other bivalves but the caloric content was lower ($\bar{x}$=1400 cal/indiv.) because of the smaller siphon (Table 3). The highest caloric content of prey was for Priapulus caudatus (15613 cal/indiv.) (Appendix 1). Other worms, which are generally much smaller, had lower caloric contents (1600 to 1800 cal/indiv.).

Mya contributed 86.1% of all energy in stomachs of immature and adult walrus (Fig. 4). Hiatella, holothurians, Nereis, Buccinum and Priapulus contributed 8.0%, 1.9%, 1.5%, 0.9% and 0.9% respectively and all other organisms contributed less than 1%. Mya was the dominant taxon in terms

TABLE 3. Mean wet weight (g), percent dry matter (% DM), caloric density (cal/g, dry matter basis) and caloric content per individual (cal/indiv., wet weight basis) for major prey found in walrus stomachs in Foxe Basin, N.W.T., 1987 and 1988.

Prey		$\bar{X}$ ± 1 S.D.	n	Source
Mya truncata				
body	wet weight(g)	11.03 ± 7.79	98	a
	%DM	14.77 ± 3.68	98	a
	cal/g	4284.4 ± 350.1	27	a
	cal/indiv.	6979.8		
siphon	wet weight(g)	4.32	1312	b
	%DM	15.72 ± 3.4	156	a
	cal/g	3972.6 ± 232.8	23	a
	cal/indiv.	2697.8		
sheath	wet weight(g)	4.05	-	c
	%DM	25.82 ± 5.99	130	a
	cal/g	2500.3 ± 352.2	10	a
	cal/indiv.	2614.6		
total (sheath + siphon)	cal/indiv.	5312		
Hiatella arctica				
siphon	wet weight(g)	1.14	30	b
	%DM	15.72	-	d
	cal/g	3956	4	e
	cal/indiv.	709		
sheath	wet weight(g)	1.07	-	c
	%DM	25.82	-	d
	cal/g	2500.3	-	d
	cal/indiv.	690.8		
total	cal/indiv.	1400		
Serripes groenlandicus				
foot	wet weight(g)	6.8	180	b
	%DM	20.3 ± 3.0	11	a
	cal/g	4290.1 ± 62.0	11	a
	cal/indiv.	5922.1		
body	wet weight(g)	4.0	269	b
	%DM	16.9 ± 2.5	11	a
	cal/g	4495 ± 184.6	11	a
	cal/indiv.	3039		
total	cal/indiv.	8961		
Nereis sp.	wet weight(g)	2.0 ± 1.0	2	f
	%DM	22	-	g
	cal/g	3848	-	e
	cal/indiv.	1693		
Buccinum sp.	wet weight(g)	5.7 ± 0	2	a
	%DM	21.0 ± 1.8	3	a
	cal/g	4723.9 ± 7.4	3	a
	cal/indiv.	5655		
Holothurians	wet weight(g)	8.4 ± 6.7	2	a
	%DM	14.9 ± 1.9	2	a
	cal/g	4168.1 ± 122.8	2	a
	cal/indiv.	5217		

[a]Specimens from benthic collections.
[b]Specimens from stomach contents.
[c]Estimated as 94% of mean siphon wet weight, based on 74 *Mya truncata* from benthic collections.
[d]Value for *Mya truncata*.
[e]Wacasey and Atkinson, 1987.
[f]J.A. Fournier, National Museum of Natural Sciences, Ottawa, unpub. data.
[g]G. Atkinson, Department of Fisheries and Oceans, Ste. Anne de Bellevue, Quebec, unpub. data, after preservation in 10% formalin then 70% ethanol.

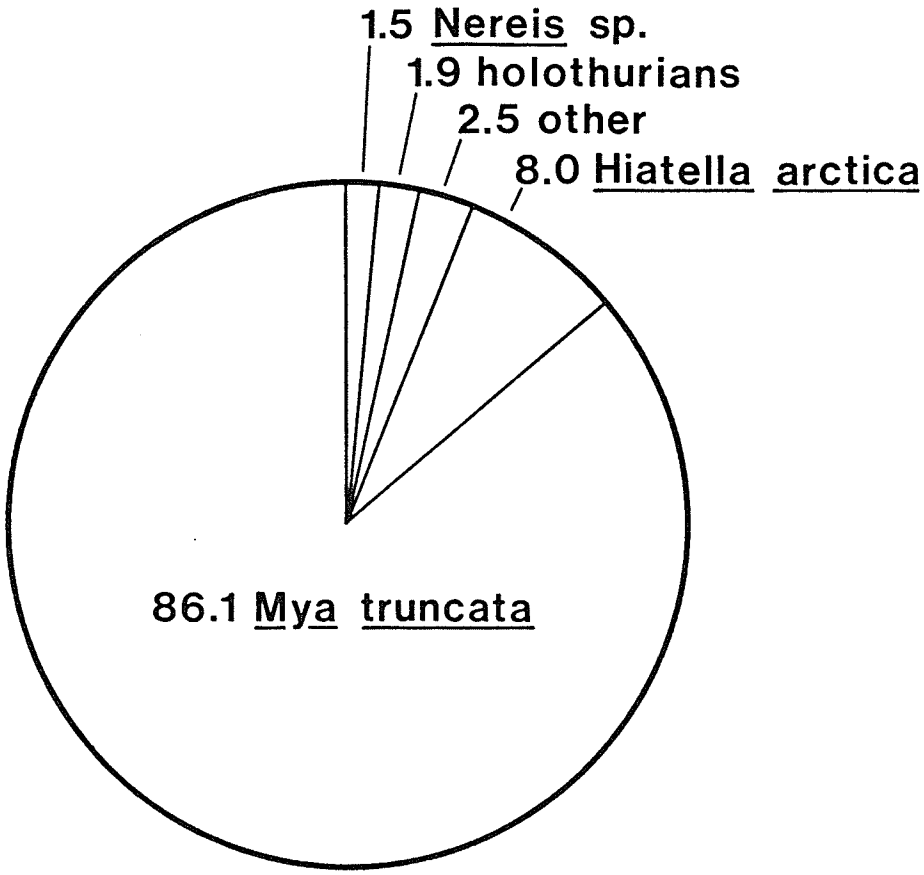

FIG. 4. Estimated percent contribution of the major prey to the total energy content of the walrus diet in Foxe Basin, N.W.T., July 1987 and 1988.

of percent energy contribution in 16 of 19 stomachs, while holothurians, Nereis and Buccinum were each dominant in 1 of 19 stomachs.

Sex, age, seasonal and depth differences in diet

Few significant differences were found in the stomach contents of male and female walrus. Both had similar proportions of stomachs containing food (females, 9 of 42; males, 10 of 45). Females tended to consume more food items ($P<0.10$) and have larger quantities of food ($P<0.20$) and energy ($P<0.10$) in their stomachs compared to males, although these differences were not significant (Table 4). Mya contributed the same percent to the total energy content of stomachs in male and female walrus, but females received significantly more energy (greater % contribution) from Hiatella than did male walrus ($P<0.05$). There was no significant difference between sexes in the percent contribution of holothurians to the total energy content, although 3 of the 10 males were feeding extensively on holothurians (>40% of total energy of each stomach).

Obvious differences in stomach contents between immature (3-6 years) and adult walrus were not apparent. Stomachs from immature animals had similar total weights of food items (219.7-1447.2 g) as adults (112.9-1370.4 g) and similar ranges of energy content (immatures, 634.9-5695.0 kcal; adults, 202.4-4804.5 kcal). Diversity of taxa was the same in adults (n=14 taxa), and immatures (n=14 taxa) with Mya being dominant in all stomachs of immature animals.

TABLE 4. Comparison between sexes of the abundance, weight and energy content ($\bar{X}$ ± 1 S.D., range) of prey in stomachs with food and the energy contribution of Mya, Hiatella and holothurians ($\bar{X}$, range) to the diet of walrus in Foxe Basin, N.W.T., July 1987 and 1988.

	Males $\bar{X}$ ± S.D. (range) n=10	Females $\bar{X}$ ± S.D. (range) n=9	Significance
Number (abundance) of prey items	223.8 ± 173.3 (9-725)	679.8 ± 516.9 (72-1508)	P>0.05
Weight of prey items (g)	446.1 ± 304.4 (112.9-959.3)	793.7 ± 463.3 (366.8-1447.2)	P>0.05
Energy content of prey items (kcal)	994.1 ± 755.4 (202.4-2385.7)	2746.1 ± 2028.2 (324.4-5695.0)	P>0.05
Contribution of Mya to total energy content (%)	83.9 (0-97.5)	86.9 (66.2-95.9)	P>0.05
Contribution of Hiatella to total energy content (%)	2.5 (0-9.7)	10.2 (3.9-14.5)	P<0.05
Contribution of holothurians to total energy content (%)	6.2 (0-95.0)	0.1 (0-2.0)	P>0.05

Twelve stomachs of calves were examined (Table 5). Three of 8 newborns (age 0 years) had empty stomachs and 5 contained 100-1650 ml of milk, 2 of which had small quantities of benthic organisms. The stomach of one yearling contained only milk while that of another (age estimate based on total length) contained milk, several bivalves, polychaetes and stones. The stomach of one two-year old contained 75 ml of milk while another contained no milk but several bivalves.

Water depth was measured at 5 sampling locations in 1988. Seven stomachs from adults taken on ice floes in depths of 38 to 70 m were empty and 2 stomachs from walrus taken in 12 m of water had only trace amounts (<5 g) of food items (Table 6).

Fecal samples contained hard parts from bivalves, gastropods, polychaetes and brachiopods as well as bivalve siphon and sheath remains (Table 7). No taxa were identified that had not previously been found in walrus stomachs.

Only 2 stomachs were collected outside of July, so seasonal differences in feeding could not be assessed in detail. The 2 stomachs collected in September contained an average of 3.5 times more food than the fullest stomach in July. Mya was again dominant in terms of number (79.4%) and contribution to energy content of stomachs (75.1%) (Table 8). The stomachs from September contained large numbers ($\bar{x}$=134.5±23.3, n=2) of the cockle Serripes, representing 24.1% of the energy content of the stomachs. Not only were the feet of Serripes found, but also large numbers of bodies (n=269) and fragments of adductor muscle and mantle, indicating that all of the fleshy parts of the cockle were eaten.

TABLE 5. Volume of milk and numbers of benthic invertebrates from stomach contents of 12 walrus calves in Foxe Basin, N.W.T., July 1987 and 1988.

Age[a] (years)	Milk[b] (ml)	Benthic invertebrates
0	1650	
0	500	
0	200	
0	850	1 *Natica clausa*
0	100	1 *Hemithyris psittacea*
0	0	
0	0	
0[c]	0	
1	25	
1[c]	200	5 *Mya truncata*, 2 *Nereis* sp., 1 *Eunoe* sp., 1 *Thelpus cincinnatus*
2	75	
2	0	5 *M. truncata*, 1 *Astarte* sp., shell fragments

[a]Based on counts of growth layers in jaws. Actual age of a calf at age 0 is 1 to 3 months, age 1 is 25-27 months, age 2 is 49-51 months.
[b]Measured to the nearest 25 ml.
[c]Age estimate based on total length.

TABLE 6. Stomach contents of walrus in relation to water depth.

Depth (m)	n	Empty %	Trace (<5g) %	Food (>5g) %
12	2	-	100	-
38	2	100	-	-
41	1	100	-	-
61	2	100	-	-
70	2	100	-	-

TABLE 7. Percent occurrence and abundance of prey in 2 fecal samples from walrus in Foxe Basin, N.W.T., July 1988.

Prey	Occurrence (%)	Abundance (No.)
Bivalvia		
Astarte sp.	100	7
Gastropoda		
Buccinum sp.	100	11
Natica clausa	50	14
Polychaeta		
Nereis sp.	100	2
Brachiopoda		
Hemithyris psittacea	50	1
Unidentified bivalve remains[a]	50	-
Shell fragments	100	-
Stones	100	-
TOTAL		35

[a]Includes sheath and siphons.

TABLE 8. Percent occurrence, abundance, weight and estimated energy contribution of prey in stomach contents of 2 walrus in Foxe Basin, N.W.T., September 1988.

Prey	Occurrence %	Abundance No.	Abundance %	Weight g	Weight %	Estimated Energy kcal	Estimated Energy %
Bivalvia							
Mya truncata	100	1414	79.4	5772.7	56.7	7511.2	75.1
Hiatella arctica	100	30	1.7	34.2	0.3	42.0	0.4
Serripes groenlandicus	100	269	15.1	2518.7	24.7	2410.5	24.1
Gastropoda							
Buccinum sp.	50	14	0.8	0.7	<0.1	79.1	0.8
Natica clausa	50	2	0.1	0.1	<0.1	1.7	<0.1
Polychaeta							
Nereis sp.	50	1	0.1	<0.1	<0.1	1.7	<0.1
Flabelligera affinis	100	47	2.6	56.4	0.6	27.6	0.3
Holothuroidea	50	2	0.1	10.4	0.1	6.5	0.1
Echinoida							
Strongylocentrotus droebachiensis	50	1	0.1	0.6	<0.1	0.1	<0.1
Unidentified bivalve remains[a]	-			1729.2	17.0		
Unidentified organic remains[b]	-			57.6	0.6		
Shell fragments	-			9.5	0.1		
TOTAL		1780		10190.1		10008.4	

[a]Includes sheath, guts and other remains.
[b]Mostly from the 1 mm sieve fraction.

Hiatella were found in small numbers (7 and 23 siphons) and contributed 0.4% to the total energy content of stomachs.

DISCUSSION

Biases in stomach content analyses

The analysis of stomach contents has been used for many years to describe the diet of marine mammals (Lowry and Frost 1981). These studies provide information on the types of prey consumed but it is difficult to accurately assess the relative importance of prey types in the diet because of potential errors resulting from the differential digestion and retention of prey types (Bigg and Fawcett 1985).

In this study, percent occurrence, abundance, weight and estimated energy contribution of prey species were used to describe the diet of walrus. Percent occurrence provides a qualitative picture of what is eaten but over-estimates the contribution of relatively unimportant prey types (Berg 1979). Astarte, Natica and Hemithyris were found in over half the walrus stomachs in this study, yet combined, they provided less than 1% of the total weight or energy of prey represented by stomach contents. Measurements of abundance are accurate for the most part, but differential digestion rates of prey species and the retention of hard parts obscure the true relative contribution of different species (Bigg and Perez 1985). Prey such as holothurians and some polychaete species are digested rapidly and lack diagnostic hard parts so they are under-represented in counts, while the retention of hard parts, such as squid beaks leads to over-estimation of the importance of these taxa (Bigg and Fawcett 1985). The extent to which polychaete jaws and gastropod opercula are retained is unknown and their representation in the stomachs in this study therefore may or may not reflect the true contribution of

these species to the walrus diet. However, polychaetes and gastropods represent only 3.1% of the total energy of the diet so they would have to be massively under-estimated to have any impact on the conclusions.

Weight measurements of stomach contents are also affected by differential digestion rates of prey taxa, resulting in an under-representation of easily digested prey (Berg 1979) such as holothurians and polychaetes. This error increases with time after feeding and is significant in this study because many of the stomachs contained well digested contents. The contribution of each prey type based on weight measurements therefore is unlikely to be a good indicator of the relative importance of different prey species in the walrus diet.

Back-calculation of the actual energy contribution of various prey types provides a good estimate of the relative importance of each prey type because it is based on abundance and the original size of items. Although it is subject to the same errors as abundance measurements, as well as errors inherent in estimating mean size, energy and dry matter content for each prey type, these errors do not affect the relative importance of prey species in energetic terms. Errors are minimal for bivalves because siphons and feet were easily counted and the sample size for back-calculating actual siphon and foot size and determining energy density was large. For minor prey such as holothurians, which were likely under-represented in all estimates, even a tripling of their energetic contribution would not significantly affect their rank as the third most important prey in the diet in July. Similarly, the potential retention of gastropod opercula and polychaete jaws do not alter their standing as minor prey types in terms of energy contribution to the diet.

Therefore, although several prey types are under- or over-represented in abundance, weight or energy contribution measurements, these are relatively minor prey and do not influence the overall findings, that bivalves are the major energy source in the diet.

The walrus diet

This study provides further documentation that Atlantic walrus are stenophagus feeders and rely heavily on a small number of prey species to meet their energetic requirements. The bivalves, Mya, Hiatella and Serripes provided over 94% of the total energy of the walrus diet in this study, therefore the null hypothesis cannot be rejected. Mansfield (1958) examined 3 stomachs from walrus taken in Foxe Basin and similarly concluded that these 3 bivalves were the dominant food types (by abundance) in the walrus diet. Taxa identified by Mansfield (1958) from Foxe Basin samples, but not found in this study were the holothurian Thyonidium, the isopod Mesidotea sabini and ascidaceans (tunicates). Polychaetes, brachiopods, amphipods, echinoids and the isopod Arcturus baffini found in this study were not reported by Mansfield. In other locations in the eastern Canadian arctic, Mansfield (1958) identified pagurid crabs (hermit crabs), shrimp, squid, fish and seal flesh, but again, bivalves were dominant in 12 of 19 stomachs.

Atlantic walrus in the waters near Thule Greenland and Pacific walrus in the Bering and Chukchi Seas also rely heavily on bivalves. In a limited sample (n=5) from the Thule district, the diet was found to consist largely of Serripes, Clinocardium, Mya and Hiatella (Vibe 1950), while in the Bering Sea Mya, Spisula, Hiatella, Serripes and

Clinocardium comprised 60 to 80% of identifiable food items of the diet, although over 60 genera of benthic organisms were reported (Fay et al. 1977, 1984).

Whether walrus in this study are selecting certain prey species or consuming a representative sample of benthic invertebrates on the sea floor is unknown because there are no available estimates of the abundance or distribution of benthic invertebrates in Foxe Basin. However, qualitative information suggests that selection of prey items is occurring, since certain species such as asteroids (starfish), crinoids (feather stars, sea lilies) and ophiuroids (basket stars and brittle stars) have not been found in walrus stomachs, yet were identified in taxonomic surveys from Foxe Basin (Grainger 1955) and would be within the foraging capabilities of walrus. Selective feeding has been reported in both Atlantic (Vibe 1950) and summering Pacific (Fay et al. 1977) walrus. In these studies, the relative proportions of benthic invertebrate species collected from the sea floor were significantly different from proportions of invertebrate taxa found in stomach contents. Fay (1982) suggested that walrus selectively feed on bivalves, but other preferred food items may be opportunistically ingested when travelling between patches of bivalves, accounting for the large numbers of prey species found in stomachs.

Seasonal feeding patterns of Atlantic walrus are not well documented, largely due to the inaccessibility of walrus populations during the winter. Results from this study indicate that walrus are not feeding extensively during July since food items were found in only 34% of stomachs (32/93) and the amount in those stomachs with food was small

compared to gut capacity or samples from September. It is possible that sample collection did not coincide with daily feeding rhythms - a factor that might account for the high proportion of empty stomachs found in this study. Also, the gastro-intestinal clearance rate in pinnipeds is rapid (5-9 hours, Parsons 1977) so that evidence of recent feeding would be quickly removed. Haul-out patterns and feeding rhythms in Atlantic walrus are virtually unknown (Loughrey 1959, Richard and Campbell 1988), but it is unlikely that the small quantities of food found in stomachs are totally due to sampling biases since stomachs were collected throughout the 24-hour day over several weeks. Mansfield (1958) similarly reported that only 18% (7/39) of stomachs collected in July in the Canadian eastern arctic contained food. In contrast, Atlantic walrus off Greenland are reported to feed throughout the summer and fall months (Vibe 1950).

Why Foxe Basin walrus do not feed extensively throughout the summer is unclear. Water depths are less than 100 m throughout the basin (Canadian Hydrographic Service 1984), within the known diving capabilities of walrus (Fay and Burns 1988). Regardless of the reason, these data indicate that walrus consume sufficient energy throughout the year to be able to survive for several weeks at a time largely on their energy reserves.

Information on feeding in Foxe Basin during the fall and winter is scant. Samples collected by Mansfield (1958) (n=39) in September indicate that about 25% of stomachs contained food, although both stomachs collected in September in this study were partially full. All

samples collected by Mansfield (1958) during October (n=2) and November (n=1) contained food.

Seasonal differences in the types of food eaten by walrus seem to be related to herd movements and bivalve distribution. In this study, Serripes was not consumed during July but contributed 24.1% of the dietary energy in September, while the energy contribution by Hiatella decreased from 8% in July to 0.4% in September. Mya and Hiatella inhabit depths down to 80 m while Serripes are rarely found in waters greater than 40 m (Vibe 1950). In July and August, walrus in Foxe Basin are found on ice floes in deeper waters near Rowley and Spicer Islands (Fig. 3), feeding primarily on Mya and Hiatella. In September-October, the herds move closer to the western shores (Orr et al. 1986) into shallower waters, where they feed on Serripes and other bivalves. Mansfield (1958) similarly found that when walrus fed in the shallow waters near Amitoke Peninsula, Serripes was dominant in stomachs, but in deeper waters at Kringmiktorvik, Mya and Hiatella were dominant. The limited depth data in this study were collected only during July and none of the 9 samples contained significant quantities of food.

Walrus of both sexes and all ages (≥ 3 years) consume the same types of prey items. Fay et al. (1977, 1984) reported that the diet of male and female Pacific walrus is similar, except that females consumed more Hiatella and smaller individuals of a prey type than males. In this study, females also obtained a larger percent of energy in their diet from Hiatella than males, but other differences were not statistically significant. Similarity in diet among walrus likely reflects the fact

that the major prey types are relatively small and sedentary and are effectively located and consumed by all segments of the population.

The quantities of milk and benthic invertebrates found in the stomachs of newborns, yearlings and two-year old calves in this study are similar to those reported in other studies (Freiman 1941, Nikulin 1941, Mansfield 1958, Loughrey 1959 and Fay 1982). Newborns rely heavily on milk during the first year, although small numbers of invertebrates are eaten (Fay 1982, this study). The dependancy on milk is decreased as foraging skills are acquired and most calves are fully weaned by 2 years of age (Fay 1982). Some however continue to suckle. A 25-27 month old calf in this study had only milk in its stomach. Nikulin (1941) found two 26-27 month old calves containing only milk while Freiman (1941) reported another containing both milk and invertebrates. Suckling into the third summer most likely occurs when females do not produce a subsequent calf to supplant the older one (Fay 1982).

Studies on the food habits of walrus in the Canadian eastern arctic, Greenland and the Pacific indicate that bivalves are the major food types consumed by all segments of the walrus populations, except for calves. Further studies on the diet of walrus during the spring, fall and winter seasons may provide further insight into which prey types are the major contributors of energy to the diet throughout the entire year.

MANUSCRIPT II

DIGESTIVE EFFICIENCY IN WALRUS, *Odobenus rosmarus*

An understanding of the food requirements of the Atlantic walrus population is necessary to identify and protect feeding areas from exploitation by commercial fishery and non-renewable resource development projects. It is difficult to determine the amount of food consumed by walrus because direct observation of feeding is rarely possible. Stomach content analysis can provide information regarding the type of prey eaten, but provides no indication of the quantity of food consumed (Bagenel 1978).

An alternate approach is to look at the energetic requirements of individual walrus. These requirements can then be applied to the population, with knowledge of parameters such as the age structure and sex ratio, to estimate the annual energy budget for the population (Lavigne et al. 1982). Studies on the energetic requirements of walrus in captivity have not been done, primarily because animals are kept at public aquaria where limited research is carried out. The only component of the energy budget (Fig. 2) which has been estimated in captive walrus is gross energy intake. Estimates of the amount of energy required to

maintain healthy walrus range from 22,000 to 70,000 kcal per day (Fay 1982, Gehnrich 1984).

In this study, the apparent digestive efficiency of energy and nutrients in 4 captive Pacific walrus (Odobenus rosmarus divergens) was determined. Studies with other pinnipeds indicate that the digestive efficiency of energy ranges from approximately 90% to 98% of gross energy intake (Parsons 1977, Ashwell-Erickson and Elsner 1981, Keiver 1982, Ronald et al. 1984, Worthy and Fadley 1987) and is similar to those values reported for other marine and terrestrial carnivores (Inman 1941, Roberts and Kirk 1964, Fausett 1976, Moors 1977, Davison et al. 1978). Therefore, the null hypothesis being tested was that the digestive efficiency of walrus was similar to that reported for other carnivores consuming flesh-based diets.

MATERIALS AND METHODS

This research was conducted at the Harderwijk Marine Mammal Park, Harderwijk, the Netherlands, during November and December 1988. The 4 walrus (Table 9) used in this study have lived in captivity since being stranded as pups on the Alaskan coast. The adult male and female (14 years old) were housed separately from the immature male and female (5 years old) (Fig. 5) to reduce aggressive behavior (Kastelein and Wiepkema 1989). Animals had access to an outdoor freshwater pool with a dry ledge and an indoor covered area. Pools were 4 m deep, with a water turnover rate of 175 m^3/hr and a volume of 185 m^3 (Pool A) or 280 m^3 (Pool B). The indoor areas were 3.5 by 5.0 m and had a concrete tile floor and concrete walls. Each area had access doors to the adjacent pool and the weighing room (Area C). Throughout the study period, the water temperature ranged from 8°C to 12°C and the mid-day air temperature was -0.5°C to 13.0°C. The photoperiod was natural (latitude 52°23'N).

The walrus were routinely fed a diet of herring (Clupea harengus), squid (Illex sp.), mackerel (Scomber scomber), sprat (Sprattus sprattus) and whiting (Merlangius merlangus). The 2 diets used in this study were herring and clams (Spisula sp.). Only the feet of the clams were fed to the walrus to simulate the natural diet, which consists largely of feet and siphons of several clam species (Vibe 1950, Fay et al. 1977, Manuscript I).

The herring were obtained as a single lot from a local fish company in Holland. Fish weighed 84.4±12.6 g ($\bar{x}$±S.D., n=20) and ranged from 65 to

TABLE 9. Biological data for the four walrus at Harderwijk Marine Mammal Park, Harderwijk, the Netherlands, November-December 1988.

Walrus Code Number	Maturity	Age (years)	Sex	Initial Weight (kg)
ZHOr001	adult	14	M	1383
ZHOr002	adult	14	F	1193
ZHOr003	immature	5	M	794
ZHOr004	immature	5	F	550

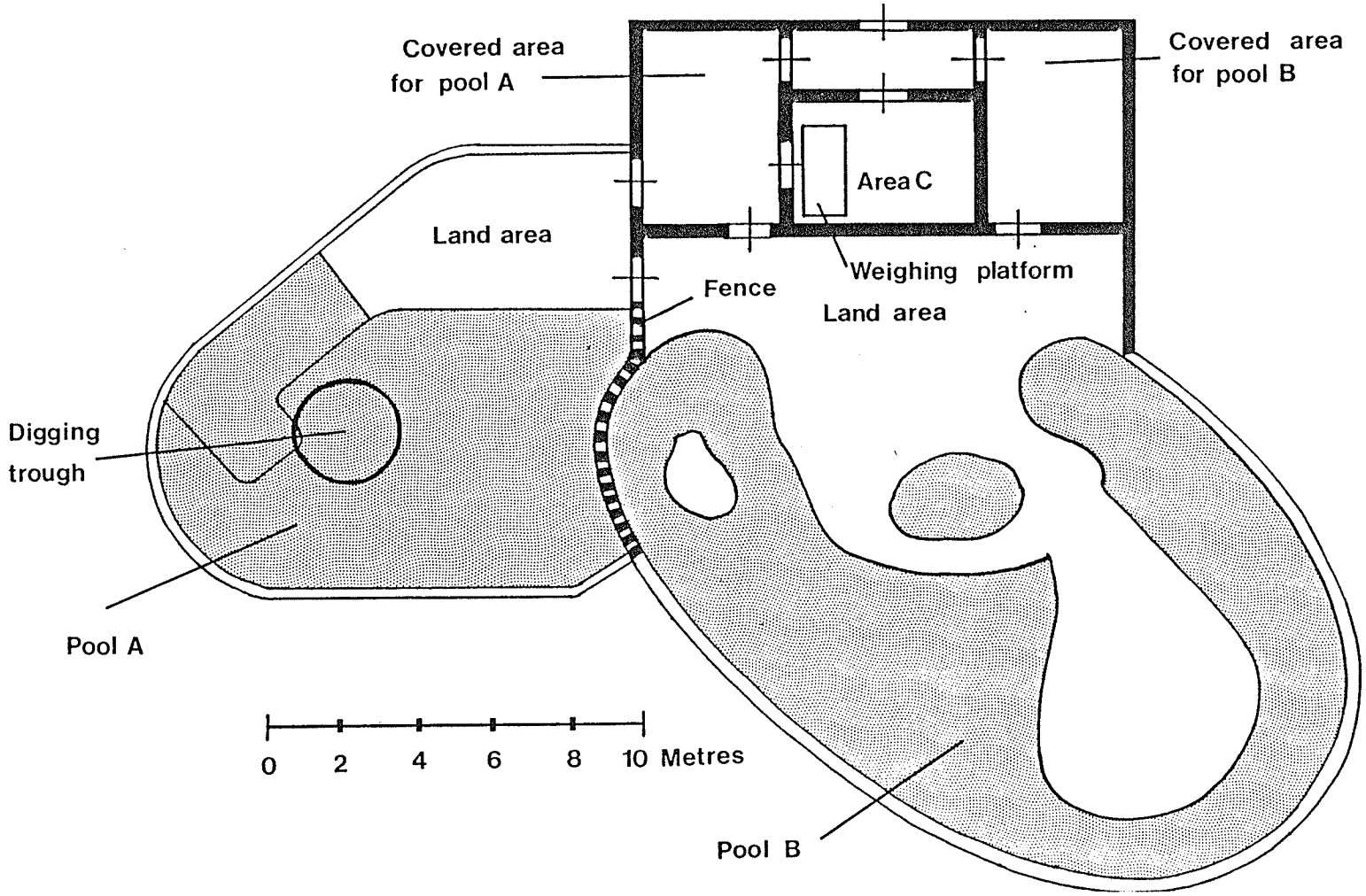

Fig. 5. Housing facilities for the four walrus at the Harderwijk Marine Mammal Park, Harderwijk, the Netherlands, 1988. Adult and immature walrus were housed in Area A and B respectively (Kastelein and Wiepkema 1989).

120 g. The clams were obtained from Nova Scotia, where they were quickly blanched to remove the feet, frozen and shipped via air to the Marine Mammal Park. The feet weighed 27.2±8.8 g (n=100) and ranged from 8 to 60 g. The fish and clams were kept at -20°C and daily rations were thawed in water overnight prior to feeding.

Feeding rates were adjusted to maintenance level prior to each experiment, where maintenance is defined as that level of food intake at which the animal neither gains nor loses weight (Kleiber 1975). The amount of herring each walrus required for maintenance was estimated from historical food intake records and recommendations from the trainers. The amount of clams was estimated from the weight change of the adult male when fed 23.0 kg of clams per day during the 10 day period between experiments. Both adult and immature walrus were fed the herring diet but only the adults were fed the clams.

The indicator method was used to determine the digestibility of the diets because total fecal collection was not possible. Chromic oxide (Cr_2O_3) was used as the inert marker (Schneider and Flatt 1975) and was added randomly to the diet in tablet form (Appendix 2) at 0.25% (clam) or 0.26% (herring) of the wet weight of the diet. Tablets were inserted into the herring's thoracic cavity through the opercular opening and into the clam's foot through the proximal opening.

Each experiment consisted of a 5 day pre-trial period and a 5 to 7 day collection period. Each day was considered to begin at 0900 hours and run for 24 hours. The pre-trial period ensured the diet and marker equilibriated in the digestive tract and passed at a uniform rate (Schneider and Flatt 1975). Animals were fed daily at 0900, 1200 and

1600 hours on the herring diet and 1000, 1300 and 1600 hours on the clam diet. One-third of the daily ration was given at each meal. Vitamin and salt supplements (Appendix 3) were added in the morning meal and Cr_2O_3 tablets were added to all meals throughout the experiment.

Fecal samples were obtained during the collection period when the animals were kept in the covered areas, from approximately 1600 hours to 0900 hours the next morning. During the daytime (0900-1600 hours) when the walrus had access to the pools, fecal samples were opportunistically collected from the dry ledge. Samples were collected within 30 minutes of defecation, weighed to 0.1 g (Mettler PC4400, Zurich, Switzerland) and individually frozen at -20°C for analysis. Ten herring and 10 samples of 5 clams each were taken twice during each experiment and individually analyzed for proximate composition and energy content.

The walrus were weighed 3 times during each experiment using a 1500 kg scale with 0.1 kg graduations (Mettler ID2, Zurich, Switzerland). Weights were taken on the first day of the pre-trial period, and at the beginning and end of the collection period. The animals were weighed in the morning before feeding to reduce the influence of gutfill.

All fecal and diet samples were returned to Canada for analysis where samples were freeze dried to a constant weight (Labonco Model 75108, Kansas City, Missouri) and then ground in a Braun coffee grinder. All analyses were performed in duplicate. Energy content was measured using an adiabatic bomb calorimeter (Parr Instruments, Molline, Illinois). Total nitrogen was determined using micro-Kjeldahl procedures and a Kjeltec Auto 1030 Analyser (Teactor, Herdon, Virginia) (Association of Official Analytical Chemists 1965) and crude protein was calculated as

6.25 x % total nitrogen. In the food samples, crude protein was a measure of true protein plus a small amount of non-protein nitrogen and in the fecal samples, it was a measure of all nitrogenous compounds in which ammonia was the endproduct of chemical analysis (Schneider and Flatt 1975). Total lipid content of the diet and fecal samples was analyzed using the Folch et al. (1957) and Marchello et al. (1971) methods respectively. Fecal samples and the chloroform:methanol:HCl solution were centrifuged at 1500 RPM for 10 minutes to reduce chloroform evaporation during filtration. The concentration of Cr_2O_3 in fecal samples and tablets was analyzed according to Williams et al. (1962). Samples were ashed at 550^{o}C for 24 hours. Unless otherwise specified, all results are expressed on a dry matter basis and mean values are reported ± 1 standard deviation (S.D.).

Fecal losses and digestive efficiency were calculated according to Kleiber (1975). Analysis of variance was used to test for differences in digestion coefficients between diets and animals. The analysis was based on the daily digestion coefficients (replicates) for the 4 walrus on the herring diet and the 2 walrus on the clam diet. Sex and age were treated as blocks and tested against the interaction term between treatment (tmt), sex and age (tmt*sex*age). The level of significance was $P<0.05$ for all analyses.

RESULTS

Fecal excretion patterns

During the collection periods, females usually defecated only once each night while the males defecated 2 to 3 times nightly. Therefore, only the males provided sufficient data for the establishment of daily fecal excretion patterns. The Cr_2O_3 concentration in samples from the adult male fed the herring diet were highest in the first defecation following 1600 hours (4 of 5 nights) (Fig. 6a). The first defecation usually occurred from 1930 to 2330 hours, approximately 4 to 8 hours after the last meal. The Cr_2O_3 concentration was lower in the second defecation and higher in the third each day. Lipid excretion followed a similar pattern to Cr_2O_3 excretion for 4 of the 5 nights and protein excretion showed no consistent pattern with Cr_2O_3 excretion.

On the herring diet, the immature male exhibited less pattern in daily Cr_2O_3 excretion than the adult male (Fig. 6b). Most peak concentrations occurred in the late evenings (2100 to 0200 hours) and early mornings (0500 to 0700 hours), 5 to 10 hours and 13 to 15 hours post prandial and they did not necessarily occur during the first defecation. The Cr_2O_3 concentrations in 2 samples on Day 5 were approximately 50% higher than the mean concentration ($\bar{x}$=7.1±2.1, n=17), even though food and Cr_2O_3 intake remained constant and no apparent changes in routine were noted. The fecal lipid pattern on Day 1, 2 and 5 was opposite that of Cr_2O_3, unlike patterns observed for the adult male. Fecal protein showed no visible pattern throughout the study.

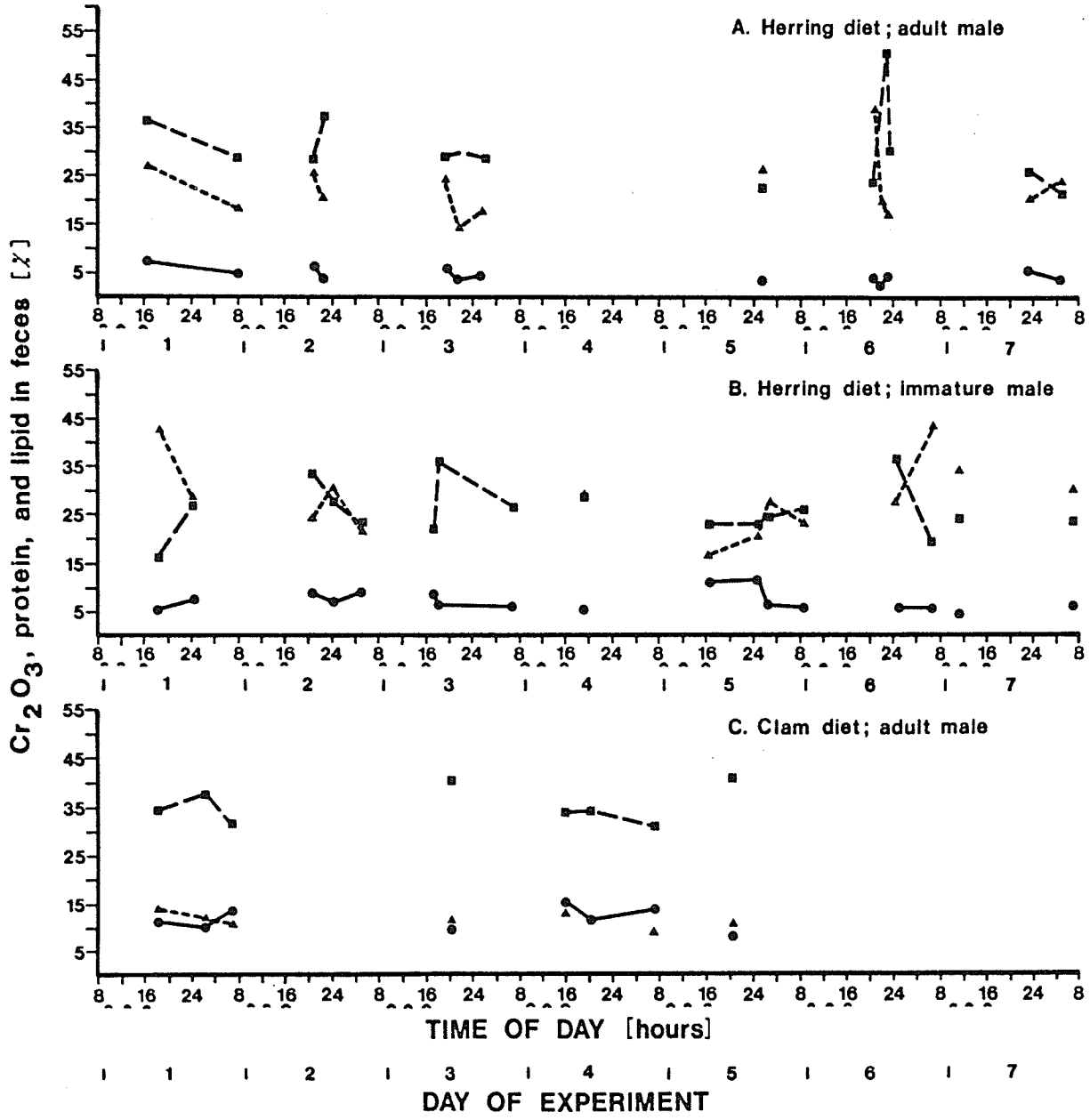

FIG. 6. Fecal Cr_2O_3 ●——●, protein ■– –■, and lipid ▲---▲ patterns for (a) the adult male fed the herring diet, (b) the immature male fed the herring diet and (c) the adult male fed the clam diet. Each 24-hour day started at 0900 hours. ^ indicates feeding times. (Lines drawn between points within a day are for visual aid only, and do not indicate continuity between samples.)

On the clam diet (Fig. 6c) the Cr_2O_3 excretion pattern of the adult male was similar to that observed on Day 3 and 6 on the herring diet, except that the peak Cr_2O_3 concentrations occurred in the early evenings (1600 to 1800 hours) and early mornings (0600 to 0700 hours), unlike the late evening peaks on the herring diet. Protein excretion showed an opposite pattern to Cr_2O_3 excretion, unlike in the herring diet.

The only fecal sample collected between 0900 and 1600 hours (herring diet, immature male, Day 2, 1130 hours) was similar in composition to other fecal samples (Fig. 6b).

Energy balance and maintenance requirements

Weight change in the 4 walrus on the herring diet was measured only in the collection period, and not over the entire experiment since food intake was altered on the second day of the pre-trial period. Food intake on the clam diet was held constant throughout the experiment and weight change was measured over the entire 10 day period. Walrus on the herring diet consumed 12.0 to 19.5 kg of fish per day and maintained body weight within 0.5% per day (Table 10). Feeding level therefore approximated maintenance requirements. On the clam diet, the male and female walrus were fed 24.0 and 18.0 kg/d respectively. The adult male lost 0.7% of body weight per day while the female's weight remained constant.

Food intake for maintenance on the herring diet was higher in the adult walrus than in the immature animals as expected, but in mass-specific terms, the immature female had the highest daily intake rate (222.7 kcal/$kg^{.75}$/d). The adult male had a higher specific ingestion

TABLE 10. Weight changes, food and energy intake for walrus fed herring and clam diets.

Diet	Walrus	Walrus weight (kg)			Change in weight[c]		Food intake (kg/d)	Energy intake (kcal/kg.$^{.75}$/d)
		Beginning of pre-trial period	Beginning of collection period[a]	End of collection period[b]	%/d	kg/d		
Herring	adult male	1383	1385	1363	-0.3	-4.4	19.5	180.6
	adult female	1193	1184	1188	+<0.1	+0.8	15.0	155.1
	immature male	794	791	784	-0.2	-1.4	12.0	168.7
	immature female	550	551	537	-0.5	-2.8	12.0	222.7
Clam	adult male	1363	1320	1289	-0.7	-10.3	24.0	109.8
	adult female	1151	1151	1152	+<0.1	+0.3	18.0	90.5

[a]Day 1 on the herring diet, Day 2 on the clam diet.
[b]Day 6 on the herring diet, Day 5 on the clam diet.
[c]Measured over the collection period on the herring diet and over the pre-trial and collection periods on the clam diet.

rate than the adult female on both the herring (male 180.6 kcal/kg$^{\cdot 75}$/d, female 155.1 kcal/kg$^{\cdot 75}$/d) and clam (male 109.8 kcal/kg$^{\cdot 75}$/d, female 90.5 kcal/kg$^{\cdot 75}$/d) diets.

Proximate composition

The proximate composition and energy density of the herring did not change during the study ($P>0.05$) (Table 11). The lipid and protein content of the clams also remained constant, however the dry matter and energy content varied significantly ($P<0.05$). The mean dry matter content of clam samples was 21.1% and 19.8% respectively and calculations of nutrient intake on a dry matter basis were therefore based on the overall mean of the 2 samples (20.4%). The mean energy content of the second sample (4.92 kcal/g) was 2% higher ($P<0.05$) than the first (4.81 kcal/g), with an overall mean for the 2 samples of 4.87 kcal/g. The mean ash content of the first sample (6.2%) was 17% higher than the second (5.3%) ($P<0.05$), with an overall mean of 5.8%. The lipid content of the clams was only 10.7% that of the herring, resulting in a 24.4% lower caloric density in clams. The carbohydrate content of the clams was not measured, but is represented in the energy measurements.

Energy and nutrient digestion

Energy intake on the herring diet ranged from 25083.2 kcal/d for the 2 immature walrus to 40760.6 kcal/d for the adult male walrus (Table 12). Mean energy intake for the 2 adult walrus on the clam diet was 42.2% lower ($\bar{x}$=20852.9 kcal/d) than on the herring diet ($\bar{x}$=36057.3 kcal/d) (Table 13). Fecal energy losses relative to intake were higher for

TABLE 11. Proximate composition (%) and energy density (kcal/g) ($\bar{X}$ ± 1 S.D.) of the herring and clams fed to walrus.

Diet	Sample No.	n	Moisture (%)	Dry matter (%)	Protein (%)	Total lipid (%)	Ash (%)	Energy (kcal/g)
Herring	1	10	67.9 ± 1.6	32.1 ± 1.6	48.1 ± 2.7	49.5 ± 4.2	6.2 ± 0.5	6.36 ± 0.24
	2	10	66.4 ± 2.7	33.6 ± 2.7	46.8 ± 4.1	47.7 ± 4.1	6.4 ± 0.4	6.37 ± 0.27
	pooled	20	67.2 ± 2.3	32.8 ± 2.3	47.5 ± 2.9	49.6 ± 4.1	6.3 ± 0.5	6.37 ± 0.25
Clam	1	10	78.9 ± 0.6*	21.1 ± 0.6*	75.7 ± 1.5	5.1 ± 0.8	6.2 ± 0.3*	4.81 ± 0.03*
	2	10	80.2 ± 0.6*	19.8 ± 0.6*	76.6 ± 1.2	5.5 ± 0.6	5.3 ± 0.3*	4.92 ± 0.05*
	pooled	20	79.6 ± 0.9	20.4 ± 0.9	76.1 ± 1.4	5.3 ± 0.7	5.8 ± 0.5	4.87 ± 0.07

*Significant differences at $P<0.05$ within a column, see text for details.

TABLE 12. Daily gross nutrient and energy intake, mean fecal loss, number of fecal samples, fecal loss relative to intake and apparent digestion coefficients ($\bar{X} \pm 1$ S.D.) for walrus fed the herring diet.

	Walrus	Intake ($\cdot d^{-1}$)	Fecal loss ($\cdot d^{-1}$)	n	Fecal loss/ intake x 100 (%)	Apparent digestion coefficient (%)
Energy (kcal)	adult male	40760.6	3895.9 ± 699.8	13	9.6 ± 1.7	90.4 ± 1.7
	adult female	31354.0	1743.9 ± 762.0	5	5.6 ± 2.4	94.4 ± 2.4
	immature male	25083.2	2041.6 ± 575.2	17	8.1 ± 2.3	91.8 ± 2.3
	immature female	25083.2	1108.1 ± 109.6	5	4.4 ± 0.4	95.6 ± 0.4
Dry matter (g)	adult male	6398.0	989.9 ± 149.0	13	15.5 ± 2.3	84.5 ± 2.3
	adult female	4921.5	521.7 + 166.2	5	10.6 ± 3.4	89.4 ± 3.4
	immature male	3937.2	485.9 ± 103.6	17	12.3 ± 2.6	87.7 ± 2.6
	immature female	3937.2	418.5 ± 43.5	5	10.6 ± 1.1	89.4 ± 1.1
Protein (g)	adult male	3036.5	293.0 ± 64.0	13	9.6 ± 2.1	90.4 ± 2.1
	adult female	2335.7	125.5 ± 37.4	5	5.4 ± 1.6	94.6 ± 1.6
	immature male	1868.6	126.1 ± 33.7	17	6.7 ± 1.8	93.3 ± 1.8
	immature female	1868.6	106.4 ± 20.4	5	5.7 ± 1.1	94.3 ± 1.1
Total lipid (g)	adult male	3174.0	233.8 ± 56.3	13	7.4 ± 1.8	92.6 ± 1.8
	adult female	2441.6	112.0 ± 59.8	5	4.6 ± 2.4	95.4 ± 2.4
	immature male	1953.2	150.6 ± 49.2	15	7.7 ± 2.5	92.3 ± 2.5
	immature female	1953.2	56.8 ± 8.1	4	2.9 ± 0.4	97.1 ± 0.4
Ash (g)	adult male	401.2	353.0 ± 47.4	13	88.0 ± 11.8	-
	adult female	308.6	235.5 ± 91.9	5	76.2 ± 29.5	-
	immature male	248.7	150.6 ± 49.2	17	61.0 ± 19.9	-
	immature female	248.7	220.8 ± 26.0	5	89.4 ± 10.5	-

TABLE 13. Daily gross nutrient and energy intake, mean fecal loss, number of fecal samples, fecal loss relative to intake and apparent digestion coefficients ($\bar{X} \pm 1$ S.D.) for walrus fed the clam diet.

	Walrus	Intake ($\cdot d^{-1}$)	Fecal loss ($\cdot d^{-1}$)	n	Fecal loss/ intake x 100 (%)	Apparent digestion coefficient (%)
Energy (kcal)	adult male	23831.9	2211.0 ± 747.6	8	9.3 ± 3.1	90.7 ± 3.1
	adult female	17873.9	1221.1 ± 374.1	4	6.8 ± 2.1	93.2 ± 2.1
Dry matter (g)	adult male	4898.4	588.1 ± 141.3	8	11.9 ± 2.9	88.1 ± 2.9
	adult female	3673.8	304.5 + 71.0	4	8.3 ± 1.9	91.7 ± 1.9
Protein (g)	adult male	3729.6	224.3 ± 73.3	8	6.1 ± 2.0	94.0 ± 1.9
	adult female	2797.2	101.3 ± 40.3	4	3.6 ± 1.4	95.9 ± 2.3
Total lipid (g)	adult male	260.1	70.4 ± 11.8	7	27.1 ± 4.5	73.2 ± 4.5
	adult female	195.1	52.2 ± 10.8	4	26.7 ± 5.5	73.1 ± 5.4
Ash (g)	adult male	283.1	204.2 ± 74.3	8	72.1 ± 26.2	-
	adult female	212.4	100.3 ± 38.2	4	47.2 ± 18.0	-

males than females (Table 12 and 13) resulting in a significantly greater (3.5%, P=0.02) mean digestive efficiency for female ($\bar{x}$=94.4%, n=3) than males ($\bar{x}$=91.0%, n=3) (Table 14). There was no difference (P>0.05) in energy digestion between diets ($\bar{x}$=92.7%, n=6) (Table 15).

Dry matter intake on the herring and clam diets ranged from 3937.2 to 6398.0 g/d and 3673.8 to 4898.4 g/d respectively. Fecal loss of dry matter ranged from 10.6% to 15.5% of intake on the herring diet and 8.3% to 11.9% of intake on the clam diet (Table 12 and 13). Average dry matter digestion of both diets was 3.8% greater (P=0.07) for females ($\bar{x}$=90.2%, n=3) than males ($\bar{x}$=86.6%, n=3). There was no difference (P>0.05) in dry matter digestion between diets.

Protein intake for the adult walrus was similar in both diets (Table 12 and 13). Mean digestibility for all walrus was 93.8% (n=6) and did not vary (P>0.05) between diets or sexes (Table 14 and 15).

Lipid intake on the herring and clam diets ranged from 1953.2 to 3174.0 g/d and 195.1 to 260.1 g/d respectively. Mean lipid intake for the adult walrus was 12.3 times greater on the herring diet ($\bar{x}$=2807.8 g/d, n=2) than the clam diet ($\bar{x}$=227.6 g/d, n=2) while the mean fecal lipid loss in the adults was only 2.8 times greater on the herring diet ($\bar{x}$=172.9 g/d) than the clam diet ($\bar{x}$=61.3 g/d) (Table 12 and 13). Lipid digestion was significantly higher (P<0.01) on the herring diet ($\bar{x}$=94.4%, n=4) than the clam diet ($\bar{x}$=73.2%, n=2). No differences in lipid digestion between sexes were found.

Fecal loss of ash relative to intake was high for both diets, ranging from 47.2% to 89.4% (Table 12 and 13). Because these values represent

TABLE 15. Differences between diets in apparent digestion coefficients for energy and nutrients ($\bar{X}$ ± 1 S.D.) for walrus fed herring and clam diets.

	Herring (n=4)	Clams (n=2)	Significance
Energy	93.1 ± 2.4	92.0 ± 1.7	P = 0.48
Dry matter	87.8 ± 2.3	89.9 ± 2.6	P = 0.14
Protein	93.2 ± 1.9	95.0 ± 1.3	P = 0.16
Total lipid	94.4 ± 2.3	73.2 + 0.1	P < 0.01

TABLE 14. Differences between sexes in apparent digestion coefficients in energy and nutrients ($\bar{X}$ ± S.D.), for walrus fed herring and clam diets.

	Male (n=3)	Female (n=3)	Significance
Energy	91.0 ± 0.8	94.4 ± 1.2	P = 0.02
Dry matter	86.6 ± 2.0	90.2 ± 1.3	P = 0.07
Protein	92.6 ± 1.9	94.9 ± 0.9	P = 0.12
Total lipid	86.0 ± 11.1	88.5 ± 13.4	P = 0.21

not only dietary and endogenous ash but intake of ash from Cr_2O_3 tablets and vitamin supplements, the digestibility of ash was not determined.

DISCUSSION

Fecal excretion patterns

The indicator method for determining digestibility using Cr_2O_3 assumes that the marker passes through the digestive tract at the same rate as the nutrients and this rate is constant throughout the 24-hour day (Schneider and Flatt 1975). Many researchers have shown that there is diurnal variation in nutrient and Cr_2O_3 excretion (Kane et al. 1952, Clawson et al. 1955, Moore 1957) although Keiver (1982) found no difference in the Cr_2O_3 concentration among fecal samples from harp seals (Phoca groenlandica). In this study, the Cr_2O_3 concentration varied throughout the day and fecal nutrient excretion patterns did not consistently follow Cr_2O_3 excretion patterns. This could indicate that the pre-trial period was not sufficiently long for Cr_2O_3 to reach equilibrium with the nutrients, however periods of 3 days or less have been used successfully for pre-trial periods in other pinniped studies (Keiver 1982, Ronald et al. 1984, Worthy and Fadley 1987).

Information on the passage of indicator substances, relative to nutrient passage in monogastrics is scarce. Moore (1957) described excretion patterns in swine, but unfortunately samples collected at hourly intervals were combined for 4 consecutive days so that the daily variability at each interval was obscured. In general, Moore (1957) found that diurnal variation in protein and Cr_2O_3 excretion patterns corresponded quite closely and were opposite that of crude fibre. Patterns were characteristic for each pig and largely dependant on the length of time between feedings.

In this study, the time between meals was constant, however Cr_2O_3 in feces seemed to vary between individuals. Each meal fed to the walrus consisted of 40 to 80 fish or 650 to 900 clam feet with 45 to 73 Cr_2O_3 tablets added randomly in the fish or clams. In the initial stages of digestion, only nutrients would be released as the digestive fluids acted on the fish or clams, primarily on the outside of the meal (Bigg and Perez 1975). Cr_2O_3 would be released after the digestive fluids penetrated the gut cavity of the fish or the muscle layers of the clam foot. Cr_2O_3 levels would remain fairly constant until all the tablets were liberated. Since the gut cavity of fish is digested faster than the muscle bands (Bigg and Perez 1985), there would be a final stage in digestion, after all the Cr_2O_3 was gone, when only nutrients would be released. Depending on when defecation occurred, relative to the stage of digestion, variable amounts of nutrients and Cr_2O_3 would occur in the feces. Also, since digestive efficiency is high and few nutrients are lost in the fecal material, metabolic lipid and protein from the digestive tract may obscure the relationship between the marker and dietary nutrients.

Fecal excretion patterns from this study indicate that daily variation in Cr_2O_3 concentration exists and that the ratio of indicator to nutrients was inconsistent throughout the 24-hour period. Because several fecal samples per day were collected, variability was reduced and an accurate estimate of digestibility was obtained.

Energy balance and maintenance requirements

Most digestibility studies have been done at maintenance feeding levels so that comparisons between diets can be made (National Research Council 1981). Maintenance levels should be determined over a period of weeks so that several measurements of body weight are taken. In this way, short-term variations in weight, due to the influence of gut or bladder fullness, changes in the size of the metabolic water pool or the effect of hormones can be minimized (Robbins 1983). An accurate determination of maintenance requirements for walrus, as reflected by changes in body weight could not be obtained in this study due to time restrictions. Energy intake on the clam diet was 42% less than on the herring diet, therefore weight loss was expected. The adult male lost 74 kg of weight on the clam diet, however the adult female did not lose any weight. The female's weight remained constant when energy intake was 31354.0 kcal/d (herring) and 17873.9 kcal/d (clam). Perhaps compensatory changes in body composition masked tissue depletion (Robbins 1983) in the female on the clam diet. If body protein was being catabolized as found by Worthy (1982) in fasting harp seal pups, significant quantities of metabolic water would be required for urea excretion (Pike and Brown 1967). Under normal conditions, marine animals do not consume water (Pilson 1970, Depocas et al. 1971), but drinking has been observed in fasting males otarid seals and common dolphins (Delphinus delphis) (Gentry 1981, Hui 1981). The walrus may have ingested water to eliminate nitrogenous wastes and maintain a positive water balance. Also, the catabolism of lipid from blubber and core

reserves would yield 1.07 g of water per g of lipid (Prosser and Brown 1965). This water may be used for the elimination of nitrogenous compounds or retained in the total body water pool.

Weight change data from the herring diet, although limited, suggest that the walrus were near maintenance feeding reqirements. The specific ingestion rate for immature walrus was 1.17 times higher than for adult walrus consuming fish. It has been recognized for many years that immature animals which are growing or kept at maintenance consume more energy per unit body size per day than fully mature adults. Innes et al. (1987) found that immature phocid seals required 1.40 times more energy for maintenance than adult phocids of a similar body size and that growing immature seals required an additional 1.38 times more energy than immature seals at maintenance.

The specific ingestion rate of the adult male was 1.16 times higher than the adult female suggesting that the adult male was still growing. Gehnrich (1984) determined that daily food intake in captive male and female walrus increased until approximately age 7 and then remained constant. Between the age of 11 and 16 years, the food consumption rate in males increased again before levelling off at age 17. Growth data from the Pacific walrus population also indicate that this period of secondary growth occurs in males from age 10 to 16 years (Fay 1982). Therefore, if the adult female is the only walrus in this study which is considered fully grown, the specific ingestion rate of the immature walrus is actually 1.26 times higher than for adult walrus. This value is closer to that reported by Innes et al. (1987). Maintenance requirements for the adult female walrus consuming herring are therefore

considered to approximate maintenance requirements for adult non-pregnant, non-lactating walrus in captivity.

The level of food intake may affect energy digestibility in many herbivores (Brown 1966, Robbins 1983). In swine fed various grain-based meals, some researchers have found no differences in digestibility as intake level varied (Cunningham et al. 1962, De Goey and Ewan 1975) while others report small differences (Haydon et al. 1984). In carnivores, Inman and Smith (1941) found no difference in digestibility in silver foxes (Vulpes vulpes) fed 175 to 325 g of fresh beef per day. In the only study in pinnipeds which examined the effect of level of nutrient intake on digestibility, Keiver (1982) found no differences in digestibility when harp seals were fed herring at 0.5 to 1.3 times maintenance level. The above data suggest that level of food intake does not affect digestibility in carnivores, therefore comparisons of digestibility between herring and clam diets can be considered to be valid, although intake levels were different.

Energy and nutrient digestion

The main objective of this study was to determine the apparent digestive efficiency of walrus fed herring and clam diets. Currently there is only 1 other facililty in Europe and North America which houses more than 4 walrus (Kastelein, pers. comm.) because they are difficult and expensive to maintain in captivity. Therefore, although the sample size of 4 used in this study is small for statistical comparisons between diets and groups, the absolute values are important in determining the energetic requirements of free-ranging walrus.

The digestive efficiency of energy for walrus fed herring and clam diets in this study is within the range reported for other pinnipeds and flesh eating carnivores (Table 16). Energy digestibility in pinnipeds fed fish diets is greater than 90% of gross energy intake. Digestive efficiencies of marine animals fed non-fish diets are lower. Keiver (1982) found that the digestibility of energy in harp seals fed shrimp (Pandalus borealis) was 72.2% of gross energy intake. Poor digestibility was due to chitin in the shrimp exoskeleton. Energy digestion in sea otters (Enhydra lutris) fed clams (Spisula solidissima), black abalone (Haliotis cracherodii), crabs (Cancer antennerius) and squid (Loligo opalescens) was similar in all diets, averaging 80.9% (Fausett 1976). The digestibility of clams and abalone seem relatively low since only the fleshy parts of the food items were consumed. Fausett (1976) offered no physiological reasons for low digestibility but hypothesized that because sea otters have a catholic diet and abundant food resources, there may be no evolutionary advantage in maximizing digestive efficency. In this study, walrus digested over 90% of energy intake on both herring and clam diets. This is not surprising since marine fats and proteins are highly digestible (Geraci 1975).

Sex differences in energy digestion are not common in most species. Literature on farm and laboratory animals indicate that males and females digest energy equally as well (Skitsko and Bowland 1970, Eggum and Pederson 1983). However Moors (1977) found that male weasels (Mustela nivalis) fed diets of voles (Microtus), mice (Apodemus), rabbits

TABLE 16. Digestive efficiencies for carnivores fed flesh-based diets.

Species	Diet	Energy (%)	Dry matter (%)	Protein (%)	Total lipid (%)	Reference
Walrus (*Odobenus rosmarus*)	atlantic herring (*Clupea harengus*)	90.4- 95.6	84.5- 89.4	90.4- 94.6	92.3- 97.1	Table 12
	clams (*Spisula* sp.)	90.6- 93.1	88.1- 91.7	94.0- 95.9	73.1- 73.2	Table 13
Northern fur seal (*Callorhinus ursinus*)	atlantic herring	83.9- 97.3				Worthy and Fadley 1987
Grey seal (*Halichoerus grypus*)	atlantic herring	92.6	87.6	93.1	92.7	Ronald et al. 1984
Harp seal (*Phoca groenlandica*)	atlantic herring	92.5- 95.0	83.3- 90.3	93.2- 95.0	94.3- 96.1	Keiver 1982
	shrimp (*Pandalus borealis*)	72.2	60.0	81.8	89.2	
Harbour and spotted seal (*Phoca vitulina* and *P. largha*)	pollock (*Theregra chalcogramma*)	96.7				Ashwell-Erickson and Elsner 1981
	pacific herring (*C. pallasi*)	91.2				
Ringed seal (*Phoca hispida*)	atlantic herring	96.3- 97.9	96.2- 97.9	99.0- 99.6	87.1- 92.5	Parsons 1977
	capelin (*Mallotus villosus*)	97.9	98.1	99.3	90.1	
Sea otter (*Enhydra lutris*)	clam (*S. solidissima*)	80.3				Fausett 1976
	crab (*Cancer antennarius*)	79.6				
	squid (*Loligo opalescens*)	76.6				
	black abalone (*Haliotis cracherodii*)	87.6				

TABLE 16. Continued

Species	Diet	Energy (%)	Dry matter (%)	Protein (%)	Total lipid (%)	Reference
Fisher (*Martes pennanti*)	snowshoe hare (*Lepus americanus*) white-tailed deer (*Odocoileus virginianus*) small mammals (*Microtus pennsylvanicus*, *Blarnia brevicauda*, *Peromyscus leucopus*, *P. maniculatus*) Coturnix quail, (*Coturnix coturnix*)	80.9- 92.6	72.3- 92.0	78.9- 93.5	80.9- 99.4	Davison et al. 1978
Weasel (*Mystela nivalis*)	vole (*Microtus* sp.) mice (*Apodemus* sp.) rabbit (*Oryctolagus cuniculus*), starling (*Sturnus vulgaris*)	81.6- 96.0				Moors 1977
Mink (*Mustela vison*)	sucker (*Catostomus commersoni*), ling (*Lota maculosa*), sunfish (*Aplodintus grunniens*)	90.1- 93.5			97.0- 98.8	Roberts and Kirk 1964
Silver fox (*Vulpes vulpes*)	beef organs		93.4- 97.4	94.4- 97.8	95.5- 98.8	Inman 1941
	beef and horsemeat		93.3- 96.4	91.9- 96.1	97.1- 98.8	Inman and Smith 1941
Red fox (*Vulpes vulpes*)	snowshoe hare, white-tailed deer, apple/deer mix	85.4- 97.0	77.9- 96.9			Litvaitis and Mautz 1976
	rabbit	91				Vogtsberger and Barrett 1973
Bobcat (*Lynx rufus*)	white-tailed deer, rabbit, chicken	91				Golley et al. 1965
Coyote (*Canis latrans*)	white-tailed deer, snowshoe hare, mice (*Mus musculus*)	88.2- 96.8	81.5- 96.8	87.9- 98.3	95.7- 97.3	Litvaitis and Mautz 1980.

(Oryctolagus cuniculus) and starling (Sturnus vulgaris) (Table 16) had higher fecal energy losses than females, resulting in significantly different digestive efficiencies between sexes. Differences in the digestion of energy between males and females have not previously been reported for pinnipeds, largely because studies to date have used animals of the same sex (Keiver et al. 1984, Worthy and Fadley 1987) or have not indicated that differences in sex were tested for (Parsons 1977, Ashwell-Erickson and Elsner 1981, Ronald et al. 1984). Data from this study suggest that the digestive efficiency of males may be lower than that of female walrus, however the small sample size prevents definitive conclusions from being drawn.

The digestibility of protein by walrus fed herring and clams was similar to values reported for other carnivores (Table 16). Efficiencies are generally high in carnivores because of the easily digestible nature of animal proteins (Robbins 1983). Protein digestibility in fish flesh is particularly high because of the low amount of connective tissue (Geraci 1975). Significant differences in protein digestibility were not found between diets in this study although digestibility is usually lower in carnivore diets when whole prey items are eaten because of the non-digestible residues, such as bones, teeth, hair, feathers, etc. (Robbins 1983). For example, Davison et al. (1978) found that protein digestion was significantly lower in fishers fed diets of small mammals and coturnix quail (78.9% and 81.4% respectively) which contained a higher proportion of non-digestible protein than in the snowshoe hare and white-tailed deer diets (92.6% and 93.5% respectively) (Table 16). Protein digestibility in this study did not appear to be

affected by bones in the herring diet, likely because these were quickly digested.

The digestibility of lipids in the diet of carnivores has been studied primarily in commercial fur-bearing species. Lipid digestibility is high in carnivores since animal fats in the diet are easily digested (Leoschke 1959). However some dietary lipid is passed in feces as are non-lipid extract soluble materials of food origin and endogenous lipid, such as residues of digestive juices. In this study, lipid digestibility on the herring diet was significantly greater than on the clam diet. This is likely an artifact because apparent digestibility measurements include endogenous losses, unlike measurements of true digestibility. The herring diet is high in fat, therefore dietary lipid loss was high relative to endogenous lipid loss. However in the clam diet, the lipid content was only one tenth of that in the herring diet, and even though fecal loss of dietary lipid was low, fecal loss relative to intake appeared high due to the constant endogenous loss. This resulted in a lower apparent digestibility. Similarly, when fishers were fed diets with a lipid content of 3.7% (hares) the apparent digestibility of lipid was 80.9%, but when the lipid content was 14.2 to 39.2% (small mammals, quail and deer), apparent digestibility ranged from 91.5 to 99.4% (Davison et al. 1978). It is likely that the true lipid digestibility of both herring and clam diets in this study is similar, since all marine fats are highly digestible (Geraci 1975).

Overall, energy and nutrient digestibility in walrus was similar to that of other carnivores, therefore the null hypothesis cannot be rejected. The indicator method using Cr_2O_3 was useful in determining

energy and nutrient digestibility, providing several fecal samples were collected to reduce daily variability. Future studies on the energetic requirements of captive walrus require a larger sample size to determine if sex differences in digestive efficiency exist and to serve as a basis for extrapolation to wild populations.

GENERAL DISCUSSION

Food intake estimates for pinniped populations in the wild are often based on intake levels for animals in captivity (Sergeant 1973). These estimates are frequently too high (Lavigne et al. 1982, Innes et al. 1987) because energy intake is estimated from the quantity of food consumed and literature values for proximate composition and caloric density (Fay 1982, Gehnrich 1984). Using an average caloric density can cause significant errors in the estimate of energy intake because of large seasonal changes in the proximate composition of the diet. For instance, the fat content of Atlantic herring can range from 1% to 28% throughout the year (Varga et al. 1977). In addition, many estimates of energy intake for populations are extrapolated from requirements for immature growing pinnipeds, which are significantly higher than requirements for adult pinnipeds (Innes 1984, Innes et al. 1987). Also, many captive animals are obese and consume more food than required out of boredom with their environment (Geraci 1972, Gaskin 1982).

Energy requirements for 6 captive walrus in Marineland California were estimated as 238 to 472 kcal/kg$^{\cdot 75}$/d GE, with the lower value representing maintenance requirements for adult animals and the higher value representing requirements for immature growing animals (Gehnrich 1984). Maintenance requirements (238 kcal/kg$^{\cdot 75}$/d) were higher than those estimated in this study (155 kcal/kg$^{\cdot 75}$/d), probably because the walrus at Marineland were fed ad libitum and weight changes were not

monitored. In addition, proximate composition and caloric content of food items were taken from the literature (Gehnrich 1984).

The estimated mass-specific energy intake for maintenance in adult walrus in this study (155 kcal/kg$^{\cdot 75}$/d) is similar to phocid seals in general (131 kcal/kg$^{\cdot 75}$/d, Innes et al. 1987), but higher than adult ringed seals (104-126 kcal/kg$^{\cdot 75}$/d, n=5, Parsons 1977) and adult grey seals (Halichoerus grypus) (109 kcal/kg$^{\cdot 75}$/d, n=1, Ronald et al. 1984). In these studies, the level of energy intake for maintenance is 1.5 to 2 times that for basal metabolism, assuming basal metabolic rate (BMR)=70W$^{\cdot 75}$ (Kleiber 1975). Although earlier studies (Hart and Irving 1959, Schmidt-Nielson 1975) indicated that BMR was significantly higher in marine mammals than terrestrial animals, the requirements for measurement of BMR were not always met. In studies involving mature seals that are post-absorptive, at rest and in the thermoneutral zone, there is no indication that BMR is significantly different between marine and terrestrial mammals (Lavigne et al. 1986). Energy intake for maintenance in pinnipeds is also consistent with average daily metabolic rates for other mammals, which are about 1.5 to 3 times BMR (Gessaman 1973, McNab 1980, Lavigne et al. 1982, Peters 1983).

Assuming FE is 7.3% of GE (this study), UE is 7 to 8% of DE (Keiver 1982) and HIF is 17% of GE (Gallivan and Ronald 1981), 108 kcal/kg$^{\cdot 75}$/d of NE would be available from the 155 kcal/kg$^{\cdot 75}$/d of GE for basal metabolism, thermoregulation and activity. It is unlikely that maintenance costs above basal metabolism are the same in captive and wild walrus and therefore it is necessary to understand the ecology and

feeding behavior of walrus before extrapolating energy requirements to wild populations.

The foraging and feeding behavior in walrus is not well known since it is impossible to directly observe animals when they are feeding. Based on surface activities, it appears that a large portion of the day is spent feeding. A regular feeding pattern does not seem to exist in the Pacific, although walrus were observed in the water more often during the morning and evening and contained more food in the stomachs during the early morning and late evening than at other times (Fay 1982). In Greenland, feeding appears to be dependant on the tides. Walrus move in to shallow waters on flood tides and feed for 4 to 6 hours and then retreat at ebb to deeper waters, thereby spending 8 to 12 hours a day feeding (Vibe 1950). Walrus often feed in 80 m of water (Vibe 1950) although depths of 102 to 113 m have been recorded (Fay and Burns 1988). Although there is no estimate of the time spent swimming and diving in captivity, energy expended on activity is almost certainly lower than in the wild.

Thermoregulatory costs may be similar in both environments, although captive walrus are not frequently exposed to extremes in temperature. The thermoneutral zone in walrus has not been determined but based on observations in the wild, animals appear 'comfortable' in air temperatures of -20^{o}C with a light wind blowing. Also walrus are often observed asleep in the water, presumably without thermoregulatory stress (Ray and Fay 1968). Increased thermoregulatory costs are therefore unlikely to occur unless access to water is denied, such as when the

drifting pack ice solidifies or polynyas freeze-over (Lavigne et al. 1982).

Net energy requirements for reproduction and lactation in walrus are unknown. Data on the composition and quantity of milk produced and the length of the lactation period are neccesary prior to estimating the energetic costs of lactation. In captive walrus, energy intake in lactating females was estimated to be 50% higher than non-pregnant, non-lactating females of comparable age (Gehnrich 1984).

An estimate of the number of bivalves required to support the walrus population cannot be made at this time since the population size and the energy requirements for various segments of the population, especially pregnant and lactating females are unknown. However, a minimum estimate of bivalve consumption by mature adults can be approximated if energy requirements for maintenance are assumed to be similar to those of captive animals. Unfortunately, it is difficult to estimate the energetic returns per bivalve because conflicting evidence exits with regard to how much of the soft fleshy parts of the bivalves are consumed. Divers in the Bering Sea have recently found pits and furrows in the sea-floor from walrus feeding which indicate that in soft sediments, the deep burrowing bivalves such as Mya and Spisula are excavated using hydraulic jetting and the soft parts are removed by suction. The shells are left empty beside the excavated pit (Oliver et al. 1983). Stomach content analysis however indicates that usually only the siphon or foot is consumed, although sometimes small shell fragments and parts of adductor muscles are found (Vibe 1950, Fay et al. 1977, Manuscript I). Whether walrus consume all of the fleshy parts in these instances or only the

siphon or foot is unknown. Perhaps the bodies are left in the shells when excavated and consumed by other fauna prior to retrieval by divers. In rocky areas, Mya are firmly embedded in the substrate (Vibe 1950, Fay 1982) and walrus likely bite off the siphons.

Based on the estimated maintenance requirement for an adult walrus (155 kcal/kg$^{\cdot 75}$/d) and the species and proportion of bivalves consumed, an average 810 kg walrus would need to consume 2035 to 4430 bivalves per day for maintenance (Table 17). The highest energetic return per bivalve would occur if a walrus consumed whole Mya. If only the siphons were consumed, twice as many Mya would be required to meet energy requirements. Based on an excavation rate of 6 bivalves per minute for walrus in the Bering Sea (Oliver et al. 1983), foraging times would also increase from 5.7 to 12.3 hours when only siphons are consumed.

Immature animals require significantly more energy for maintenance and growth of tissues (Brody 1945). Immature growing phocid seals require 1.38 times more energy than immature phocids at maintenance and the latter requires 1.40 times more energy than adult phocids at maintenance (Innes et al. 1987). Based on these data, an immature growing 400 kg walrus would require 299 kcal/kg$^{\cdot 75}$/d (155 kcal/kg$^{\cdot 75}$/d x 1.38 x 1.40) or 2316 to 5042 bivalves per day and would need to forage for 6.4 to 14.0 hours per day. The calculated foraging times for adult and immature walrus are similar to those observed in walrus feeding off the Greenland coast (Vibe 1950).

Many questions remain to be answered before feeding areas can be adequately identified and protected. Results from this study indicate that walrus rely heavily on bivalves, especially Mya, Hiatella and

TABLE 17. Estimated daily bivalve consumption and foraging times for adult and immature walrus.

Species	Composition	Adult		Immature	
		No.	Time (hr)	No.	Time (hr)
Mya	100% siphons (with sheath)	4430	12.3	5042	14.0
	100% whole	2035	5.7	2316	6.4
Serripes	100% feet	3974	11.0	4523	12.6
	100% whole	2626	7.3	2989	8.3
Mya + Serripes	75% siphons (with sheath) + 25% feet	3322 +993	12.0	3781 +1131	13.6
Mya + Serripes	75% whole +25% whole	1526 +626	6.1	1737 +747	6.9

NOTE: Foraging times are based on an excavation rate of 6 bivalves per minute, from Oliver et al. 1983.

Serripes to meet their energetic requirements. Adult walrus require approximately 2000 to 4500 bivalves per day for maintenance while immature, pregnant and lactating females require significantly greater intakes to meet their energetic demands.

SUMMARY

Studies on the food habits of walrus in northern Foxe Basin during the summer and fall season indicated that walrus are stenophagus feeders, and rely almost exclusively on bivalves to meet their energetic requirements. Mya and Hiatella supplied over 90% of the gross energy intake in July while other invertebrates were frequently consumed but provided little energy to the diet. Male and female walrus consumed the same types of prey but females received a larger percent of the energy in their diet from Hiatella than males. During September, species composition of the diet changed and the cockle Serripes, which was not eaten during July, contributed over 24% of the energy to the diet.

The apparent digestive efficiency of energy in walrus fed herring and clam diets was 92.7%, similar to values for other pinnipeds and flesh eating carnivores. Digestive efficiency in females was slightly higher than in males. Estimated maintenance requirements for adult walrus were 155 kcal/$kg^{.75}$/d. At this level, an adult 810 kg walrus would require approximately 2000 to 4500 bivalves per day to meet energy demands.

Additional information is required prior to the identification and protection of walrus feeding areas in the Canadian eastern arctic. Priorities in field research should center on estimating the size, sex ratio and age structure of Canadian walrus stocks as well as the distribution and biomass of bivalve populations in arctic waters. Future studies on captive walrus should focus on determining the energy requirements for immature, pregnant and lactating walrus.

LITERATURE CITED

AMERICAN SOCIETY OF MAMMOLOGISTS. 1967. Standard measurements of seals. J. Mammal. 48: 459-462.

ANONYMOUS. 1987. Renewable resource development subsidiary agreement. Decision guidelines. Main report. Don Ference and Associates, Management Consultants, 505-475 W Georgia, Vancouver, B.C.

ANONYMOUS. 1989. Department of Fisheries and Oceans work plan in support of the Government of the Northwest Territories renewable resource development strategy. Central and Arctic Region, Winnipeg, Manitoba.

ASHWELL-ERICKSON, S.M., and ELSNER, R. 1981. The energy cost of free existence for Bering Sea harbor and spotted seals. Abstracts of the Fourth Biennial Conference on the Biology of Marine Mammals. Dec. 14-18, 1981, San Francisco, CA.

ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1965. Official methods of the Association of Analytical Chemists. Washington, D.C.

BAGENEL, T. 1978. Methods for assessment of fish production in fresh waters. IBP Handbook No. 3. Blackwell Scientific Publications, Oxford.

BEAUBIER, P.H. 1970. The hunting pattern of the Igluligmiut with emphasis on the marine mammals. M.Sc. thesis, McGill University, Montreal.

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of Gobiusculus flavescens (Gobidae). Mar. Biol. 50: 263-273.

BIGG, M.A., and FAWCETT, I. 1985. Two biases in diet determination of northern fur seals (Callorhinus ursinus). In Marine mammals and fisheries. Edited by J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen and Unwin Publishers, London. pp. 284-291.

BIGG, M.A., and PEREZ, M.A. 1985. Modified volume: a frequency-volume method to assess marine mammal food habits. In Marine mammals and fisheries. Edited by J.R. Beddington, R.J.H. Beverton, and D.M. Lavigne. George Allen and Unwin Publishers, London. pp. 273-282.

BOUSFIELD, E.L. 1960. Canadian Atlantic sea shells. Nat. Mus. of Canada, Ottawa.

BRODY, S. 1945. Bioenergetics and growth. Hafner Press, London.

BROWN, L.D. 1966. Influence of intake on feed utilization. J. Dairy Sci. 49: 223-230.

BROOKS, J.W. 1954. A contribution to the life history and ecology of the Pacific walrus. Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks, Spec. Rep. 1. 103 pp.

CANADIAN HYDROGRAPHIC SERVICE. 1984. Minister of Supply and Services, Ottawa.

CHAPSKII, K.K. 1936. The walrus of the Kara Sea. Trudy Vsesoiuz. Arkt. Inst., Leningrad. 67: 1-124.

CHESS, J.R. 1978. Some procedures for assessing organisms associated with rocky substrata. Gutshop '78. Fishfood habits studies. Proc. of the Second Pacific Northwest Technical Workshop, Oct. 10-13, 1978. Maple Valley, Wash. pp. 25-38.

CLARKE, A.H. 1974. Molluscs from Baffin Bay and the northern North Atlantic Ocean. Nat. Mus. of Nat. Sci. Publ. Biol. Oceanography, No. 7. Ottawa.

CLAWSON, A.J., REID, J.T., SHEFFY, B.E., and WILLMAN, B.E. 1955. J. Anim. Sci. 14: 700-715.

CRAMPTON, E.W. and HARRIS, L.E. 1969. Applied animal nutrition. W.H. Freeman and Company, San Francisco.

CUNNINGHAM, H.M., FRIEND, D.W., and NICHOLSON, J.W.G. 1962. Efficiency of conversion of protein, energy and carbon in pigs restricted late in the fattening period. Can. J. Anim. Sci. 42: 176-182.

DAVIS, R.A., FINLEY, K.J., and RICHARDSON, W.J. 1980. The present status and future management of arctic marine mammals in Canada. Science Advisory Board of the Northwest Territories. Report 3. Yellowknife, Northwest Territories.

DAVISON, R.P., MAUTZ, W.W., HAVEN, H.H., and JAMES, B.H. 1978. The efficiency of food utilization and energy requirements of capture female fishers. J. Wildl. Manage. 42(4): 811-821.

DE GOEY, L.W., and EWAN, R.C. 1975. Effect of level of intake and diet deletion on energy metabolism in the young pig. J. Anim. Sci. 40: 1045-1051.

DEPOCAS, F., HART, J.S., and FISHER, H.D. 1971. Sea water drinking and water flux in starved and fed Harbor seals, Phoca vitulina. Can. J. Physiol. Pharmacol. 49: 53-62.

EGGUM, B.O., and PEDERSON, B. 1983. The effect of sex on protein utilization in rats. Acta. Agric. Scand. 33: 201-203.

FAUSETT, L.L. 1976. Assimilation efficiency of captive sea otters Enhydra lutris (Carnivora: Mustelidae). M.A. thesis, California State University, Long Beach, CA.

FAY, F.H. 1982. Ecology and biology of the Pacific walrus. North American Fauna No. 74 U.S. Fish and Wildlife Service, Washington. 279 pp.

_____ 1985. Odobenus rosmarus. Mammalian species. The American Society of Mammalogists. No. 238.

FAY, F.H., BUKHTIYAROV, Y.A., STOKER, S.W., and SHULTZ, L.M. 1984. Foods of the Pacific walrus in winter and spring in the Bering Sea. NOAA Tech. Rep. Nat. Mar. Fish. Service No. 12. 104 pp.

FAY, F.H., and BURNS, J.J. 1988. Maximal feeding depth of walruses. Arctic. 41(3): 239-240.

FAY, F.H., FEDER, H.M., and STOKER, S.W. 1977. An estimate of the impact of the Pacific walrus population on its food resources in the Bering Sea. U.S. Dep. Commer., Nat. Tech. Inf. Serv., Springfield, Va. PB-273-505. 38 pp.

FOLCH, J., LEE, M., and STANLEY, G.H.S. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497-509.

FREIMAN, S. 1941. Materials on the biology of the Chukchi walrus. Izv. TINRO,Vladivostok. 20: 3-20.

GALLIVAN, G.J., and RONALD, K. 1981. Apparent specific dynamic action in the harp seal (Phoca groenlandica). Comp. Biochem. Physiol. 69: 579-581.

GASKIN, D.E. 1982. The ecology of whales and dolphins. Heinemann, London.

GEHNRICH, P.H. 1984. Nutritional and behavioral aspects of reproduction in walruses. M.Sc. thesis, University of Alaska, Fairbanks, Alaska.

GENTRY, R.L. 1981. Sea water drinking in eared seals. Comp. Biochem. Physiol. 68: 81-86.

GERACI, J.R. 1972. Experimental thiamine deficiency in captive harp seals, Phoca groenlandica, induced by eating herring, Clupea harengus, and smelt, Osmorus mordax. Can. J. Zool. 57: 2256-2263.

GERACI, J.R. 1975. Pinniped nutrition. Rapp. P.-V. Reun. Cons. int. Explor. Mer. 169: 312-323.

GESSAMAN, J.A. 1973. Ecological energetics of homeotherms. A view compatible with ecological modeling. Utah State University Press, Utah.

GOLLEY, F.B., PETRIDES, G.A., RAUBER, E.L., and JENKINS, J.H. 1965. Food intake and assimilation by bobcats under laboratory conditions. J. Wildl. Manage. 29(3): 442-447.

GRAINGER, E.H. 1955. Echinoderms of Ungava Bay, Hudson Strait, Frobisher Bay and Cumberland Sound. J. Fish. Res. Bd. Can. 12(6): 899-916.

HART, J.S., and IRVING, I. 1959. The energetics of Harbor seals in air and in water with special consideration of seasonal changes. Can. J. Zool. 37: 447-457.

HAYDON, K.D., KNABE, D.A., and TANKSLEY, T.D., JR. 1984. Effect of level of feed intake on nitrogen, amino acid and energy digestibilities measured at the end of the small intestine and over the total digestive tract of growing pigs. J. Anim. Sci. 59(3): 717-724.

HUI, C.A. 1981. Sea water consumption and water flux in the common dolphin Delphinus delphis. Physiol. Zool. 54(4): 430-440.

HYSLOP, E.J. 1980. Stomach content analysis - a review of methods and their application. J. Fish. Biol. 17: 411-429.

INMAN, W.R. 1941. Digestibility studies with foxes. II. Digestibility of frozen beef tripe, frozen lip meat, frozen beef hearts and frozen cow udders. Sci. Agr. 22: 33-37.

INMAN, W.R., and SMITH, G.E. 1941. Digestibility studies with foxes. I. Effect of the plane of nutrition upon the digestibility of meats. Sci. Agr. 22: 18-27.

INNES, H.S. 1984. Swimming energetics, metaboloic rates and hind limb muscle anatomy of some phocid seals. Ph.D. thesis, University of Guelph, Guelph, Ont.

INNES, S., LAVIGNE, D.M., EARLE, W.M., and KOVACS, K.M. 1987. Feeding rates of seals and whales. J. Anim. Ecol. 56: 115-130.

KANE, E.A., JACOBSON, W.C., MOORE, L.A. 1952. Diurnal variations in the excretion of chromium oxide and lignin. J. Nut. 47: 263-270.

KASTELEIN, R.A., and WIEPKEMA, P.R. 1989. A digging trough as occupational therapy for Pacific walrusses (Odobenus rosmarus divergens) in human care. Aquatic Mammals. 15(1): 9-17.

KEEN, A.M., and COAN, E. 1974. Marine molluscan genera of western North America: an illustrated key. Stanford University Press, Stanford, California.

KEIVER, K.M. 1982. Apparent digestible and metabolizable energy in harp seals (Phoca groenlandica). M.Sc. thesis, University of Guelph, Guelph, Ont.

KEIVER, K.M., RONALD, K., and BEAMISH, W.H. 1984. Metabolizable energy requirements for maintenance and faecal and urinary losses of juvenile harp seals (Phoca groenlandica). Can. J. Zool. 62: 769-776.

KLEIBER, M. 1975. The fire of life. An introduction to animal energetics. R.E. Krieger Publishing Co., Huntington, N.Y.

LAVIGNE, D.M., BARCHARD, W., INNES, S., and ORITSLAND, N.A. 1982. Pinniped bioenergetics. FAO Fish. Ser. 5: 191-235.

LAVIGNE, D.M., INNES, S., WORTHY, G.A.J., KOVACS, K.M., SCHMITZ, O.J., and HICKIE, J.P. 1986. Metabolic rates of seals and whales. Can. J. Zool. 64: 279-284.

LEOSCHKE, W.L. 1959. The digestibility of animal fats and proteins by mink. Am. J. Vet. Res. 20: 1086-1089.

LITVAITIS, J.A., and MAUTZ, W.W. 1976. Energy utilization of three diets fed to a captive red fox. J. Wildl. Manage. 40(2): 365-368.

_____. 1980. Food and energy use by captive coyotes. J. Wildl. Manage. 44(1): 56-61.

LOUGHREY, A.G. 1959. Preliminary investigtion of the Atlantic walrus, Odobenus rosmarus rosmarus (Linnaeus). Can. Wildl. Ser., Wildl. Manage. Bull. 14, Ser. 1. 123 pp.

LOWRY, L.F., and FROST, K.J. 1981. Feeding and trophic relationships of phocid seals and walruses in the Eastern Bering Sea. In The eastern Bering Sea shelf: oceanography and resources, Vol. 2. Edited by D.W. Hood and J.A. Calder. Office of Marine Pollution Assessment, NOAA, BLM.

LUBINSKY, I. 1980. Marine bivalve molluscs of the Canadian Central and Eastern Arctic: faunal composition and zoogeography. Cdn. Bull. of Fish and Aquat. Sci. No. 207. Ottawa.

MACPHERSON, E. 1971. The marine molluscs of Arctic Canada. Nat. Mus. of Nat. Sci. Publ. Biol. Oceanography, No. 3. Ottawa.

MANSFIELD, A.W. 1958. The biology of the Atlantic walrus, Odobenus rosmarus rosmarus (Linnaeus) in the eastern Canadian Arctic. Fish. Res. Board Can., Manuscr. Rep. Ser. (Biol.) 653. 146 pp.

_____. 1966. The walrus in Canada's Arctic. Can. Geog. J. 72(3): 88-95.

_____. 1973. Tha Atlantic walrus Odobenus rosmarus in Canada and Greenland. International Union for the Conservation of Nature Publications New Series, Supplemental Paper. 39: 69-79.

MARCHELLO, J.A., DRYDEN, F.D., and HALE, W.H. 1971. Bovine serum lipids. I. The influence of added animal fat to the ration. J. Anim. Sci. 1008-1015.

McNAB, B.K. 1980. Food habits, energetics, and the population biology of mammals. Am. Nat. 116: 106-124.

MOORE, J.H. 1957. Diurnal variation in the composition of the faeces of pigs on diets containing chromium oxide. Br. J. Nutr. 11: 273-288.

MOORS, P.J. 1977. Studies on the metabolism, food consumption and assimilation efficiency of a small carnivore, the weasel (Mustela nivalis L.). Oecologia.27: 185-202.

MURIE, D.J. 1984. Estimating food consumption of free-living seals Phoca groenlandica (Erxleben 1777). M.Sc. thesis, University of Guelph, Guelph, Ont.

NATIONAL RESEARCH COUNCIL. 1981. Nutritional energetics of domestic animals and glossary of energy terms. National Academy Press, Washington.

NIKULIN, P.G. 1941. The Chukchi walrus. Izv. TINRO, Vladivostok. 20: 21-59.

OLIVER, J.S., SLATTERY, P.N., O'CONNOR, E.F., and LOWRY, L.F. 1983. Walrus, Odobenus rosmarus, feeding in the Bering Sea: a benthic perspective. Fisheries Bulletin 81(3): 501-512.

ORR, J.R., RENOOY, B., and DAHLKE, L. 1986. Information from hunts and surveys of walrus (Odobenus rosmarus) in Northern Foxe Basin, Northwest Territories,1982-1984. Can. Manuscr. Rep. of Fish. and Aquat. Sci. No. 1899. 24 pp.

PARSONS, J.L. 1977. Metabolic studies on ringed seals (Phoca hispida). M.Sc. thesis, University of Guelph, Guelph, Ont.

PETERS, R.H. 1983. The ecological implications of body size. Cambridge University Press, London.

PETERSON, S., and BORN, E.W. 1982. Age determination of the Atlantic walrus, Odobenus rosmarus rosmarus (Linnaeus), by means of mandibular growth layers. Z. Saugetierkunde 47: 55-62.

PIKE, R.L., and BROWN, M.L. 1967. Nutrition: an integrated approach. John Wiley and Sons, Inc., New York.

PILSON, M.E.Q. 1970. Water balance in California sea lions. Physiol. Zool. 43:257-269.

PROSSER, C.L., and BROWN, F.A.Jr. 1965. Comparative animal physiology. W.B. Saunders W., Philadelphia.

RAY, C., and FAY, F.H. 1968. Influence of climate on the distribution of walruses, Odobenus rosmarus (Linnaeus). II. Evidence from physiological characteristics. Zoologica. 53: 19-31.

REEVES, R.R. 1978. Atlantic walrus (Odobenus rosmarus rosmarus): a literature survey and status report. U.S. Fish Wildl. Serv. Res. Rep. 10. 41 pp.

RICHARD, P.R., and CAMPBELL, R.R. 1988. Status of the Atlantic walrus, Odobenus rosmarus rosmarus in Canada. Can. Field Nat. 102(2): 337-350.

ROBBINS, C.T. 1983. Wildlife nutrition and feeding. Academic Press, New York.

ROBERTS, W.K., and KIRK, R.J. 1964. Digestibility and nitrogen utilization of raw fish and dry meals by mink. Am. J. Vet. Res. 109: 1746-1750.

RONALD, K., KEIVER, K.M., BEAMISH, F.W.H., and FRANK, R. 1984. Energy requirements for maintenance and faecal and urinary losses of the grey seal (Halichoerus grypus). Can. J. Zool. 62: 1101-1105.

SALTER, R.E., 1979. Site utilization, activity budgets, and disturbance responses of Atlantic walruses during terrestrial haul-outs. Can. J. Zool. 57(6): 1169-1180.

SCHMIDT-NIELSON, K. 1975. Animal physiology. Adaptation and environment. Cambridge University Press, New York.

SCHNEIDER, B.H., and FLATT, W.P. 1975. The evaluation of feeds through digestibility experiments. The University of Georgia Press, Athens.

SERGEANT, D.E. 1973. Feeding, growth, and productivity of Northwest Atlantic harp seals (Pagophilus groenlandicus). J. Fish. Res. Bd. Can. 30: 17-29.

SHORYGIN, A.A. 1948. Opredelitel' fauny i flory severnykh morei SSSR (Guide to the fauna and flora of the northern waters of the USSR). Fish. and Marine Ser. Transl. Series No. 3865.

SKITSKO, P.J., and BOWLAND, J.P. 1970. Energy and nitrogen digestibility and retention by pigs as influenced by diet, sex, breeding group and replicate. Can. J. Anim. Sci. 50: 685-691.

SNEDECOR, G.W., and COCHRAN, W.G. 1980. Statistical methods, seventh edition. The Iowa State University Press, Ames, Iowa.

SOKAL, R.R., and ROHLF, J.F. 1969. Biometry. The priciples and practice of statistics in biological research. W.H. Freeman and Co., San Francisco.

STEWART, R.E.A., and LAVIGNE, D.M. 1979. Age determination in harp seals. International Workshop on Biology and Management of Northwest Atlantic Harp Seals, Guelph, Ont., Canada. Dec. 3-6, 1979. Working paper. HS/WPIO. 8 p.

STIRLING, I., CLEATOR, H., and SMITH, T.G. 1981. Marine mammals. In Polynyas in the Canadian Arctic. Edited by I. Stirling and H. Cleator. Can. Wildl. Serv. Occasional Paper No. 45. pp. 45-58.

TSALKIN, V.I. 1937. Materials on the biology of the walrus of the Franz Josef Archipeligo. Biul. Mosk. Obsch. Isp. Prirody, otd. biol. 46: 43-51.

TYLER, A.V. 1973. Caloric values of some North Atlantic invertebrates. Mar. Biol. 19: 258-261.

VARGA, S., SIMS, G., and ILES, T.D. 1977. The fat and moisture contents of herring populations in the waters of the Canadian Maritime Provinces. Fish and Marine Ser. Tech. Rep. No. 723.

VIBE, C. 1950. The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939-41. Medd.om Gronl. 150(6): 1-115.

VOGTSBERGER, L.M., and BARRETT, G.W. 1973. Bioenergetics of captive red foxes. J. Wildl. Manage. 37(4): 495-500.

WACASEY, J.W., and ATKINSON, E.G. 1987. Energy values of marine benthic invertebrates from the Canadian Arctic. Mar. Ecol. Prog. Ser. 39: 243-250.

WILLIAMS, C.H., DAVID, D.J., Iisma, O. 1962. The determination of Cr_2O_3 in feed and excreta samples by atomic absorption spectrophotometry. J. Agr. Sci. 59: 381-385.

WORTHY, G.A.J. 1982. Energy sources of harp seals, Phoca groenlandica, during the post-weaning period. M.Sc. thesis, University of Guelph, Guelph, Ont.

WORTHY, G.A.J., and FADELY, B.S. 1987. A new technique for the measurement of assimilation efficiency in free-ranging marine mammals. Second Workshop on Pinniped Energetics, Dec. 5, 1987. Miami, FL.

APPENDIX 1. Mean wet weight (g), percent dry matter (% DM), caloric density (cal/g, dry matter basis) and caloric content per individual (cal/indiv., wet weight basis) for minor prey found in walrus stomachs in Foxe Basin, N.W.T., 1987 and 1988.

Prey		$\bar{X}$ ± 1 S.D.	n	Source
Priapulus caudatus	wet weight(g)	20.6	1	a
	%DM	15.2	1	a
	cal/g	4986.1	1	a
	cal/indiv.	15613		
Amphipod	wet weight(g)	0.03 ± 0	2	a
	%DM	19	-	b
	cal/g	3596	-	c
	cal/indiv.	21		
Isopod	wet weight(g)	0.5	1	a
	%DM	19	-	b
	cal/g	2478	5	c
	cal/indiv.	235	-	
Decapod	wet weight(g)	4.0	1	d
	%DM	19	-	b
	cal/g	3886	-	f
	cal/indiv.	2953	-	
Hemithyris psittacea	wet weight(g)	0.34 ± 0.12	6	d
	%DM	14	-	e
	cal/g	3002	3	c
	cal/indiv.	143		
Natica clausa	wet weight(g)	0.9 ± 0.5	20	a
	%DM	21.0	-	f
	cal/g	4697	2	c
	cal/indiv.	869		
Eunoe sp.	wet weight(g)	1.8 ± 1.4	8	g
	%DM	25	-	e
	cal/g	4036	1	c
	cal/indiv.	1816		
Flabelligera affinis	wet weight(g)	1.3	13	a
	%DM	20	-	e
	cal/g	2263	1	c
	cal/indiv.	588		
Astarte sp.	wet weight(g)	0.34 ± 0.4	11	d
	%DM	19	-	e
	cal/g	4486	-	c
	cal/indiv.	290	-	
Thelpus cincinnatus	wet weight(g)	2.0	-	h
	%DM	17	-	e
	cal/g	4487	-	c
	cal/indiv.	1526		

[a]From stomach contents.
[b]Tyler, 1973, value for average amphipod.
[c]Wacasey and Atkinson, 1987.
[d]From benthic collections.
[e]G. Atkinson, Department of Fisheries and Oceans, Ste. Anne de Bellevue, Quebec, unpubl. data, after preservation in 10% formalin then 70% ethanol.
[f]Value for Buccinum sp.
[g]J.A. Fournier, National Museum of Natural Sciences, Ottawa, unpubl. data.
[h]Value for Nereis sp.

APPENDIX 2. Composition of chromic oxide (Cr_2O_3) tablets fed to the four captive walrus at the Harderwijk Marine Mammal Park, Harderwijk, the Netherlands, 1988.

Constituent	Amount (mg)	Manufacturer
Chromic oxide	250	Mobay Chemical Corp. Pittsburg, PA
Starch 1500	250	Colorcon Inc., Indianapolis
Avicel	125	F.M.C., Philadelphia
Magnesium Stearate	6	Mallinkrodt, Canada
	631	

APPENDIX 3. Vitamin and salt tablets fed to the four walrus at the Harderwijk Marine Mammal Park, Harderwijk, the Netherlands, 1988.

Name	Constituent	Amount	Number per day	Supplier
Sodium chloride	NaCl	0.6 g	30 (adults) 20 (immatures)	Brocacef bv, maarssen, Holland
Sea Tabs	Vitamin A (Acetate)	12,500 I.U.	10 (adults) 8 (immatures)	Pacific Research Laboratories, El Cajun, California
	Vitamin D_3 (Cholecalciferol)	400 I.U.		
	Vitamin E (dl-a Tocopheryl Acetate)	50 I.U.		
	Vitamin C (ascorbate)	125 mg.		
	Vitamin B_1 (Thiamine)	250 mg.		
	Vitamin B_2 (Riboflavin)	5.0 mg.		
	Niacin	10 mg.		
	Vitamin B_6 (Pyridoxine)	3.0 mg.		
	Vitamin B_{12} (Cyancobalamin)	10 mcg.		
	Pantothenic Acid (d-Calcium)	5 mg.		
	Biotin	5 mcg.		
	Iron (Sulfate)	25 mg.		
	Iodine	150 mcg.		
	Magnesium (MnO)	25 mg.		
	Copper ($CuSO_4$)	1.5 mg.		
	Zinc ($ZnSO_4$)	250 mcg.		
	Manganese ($MgSO_4$)	trace		
	Folic Acid	trace		
	Inositol	trace		
	Kelp	trace		