Joel

WALRUS FEEDING: A RE-EXAMINATION

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Gay Glover Sheffield, B.S.

Fairbanks, Alaska

August 1997

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Abstract

A new approach for analyzing walrus (*Odobenus rosmarus*) diet was examined. Controlled gastric digestion experiments determined the relative rates at which different kinds of food items became unidentifiable. The ability to identify prey items varied within and among prey types. The laboratory experiments provided a new basis for examining diet data by characterizing the condition of stomach samples based on the rates at which different prey types were digested. Stomach content data acquired during 1952-1991 from 798 Pacific walruses were compiled, and interpretations about feeding habits were re-examined. Walruses regularly consumed a wider assortment of benthic prey than was previously thought. The diet of the Pacific walrus varied seasonally and regionally. Males and females consumed essentially the same food items when in the same location.

Acknowledgments

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Bud Fay envisioned this project and provided friendship, inspiration, and an opportunity for growth from its onset. Additionally, he shared his enthusiasm for, and knowledge of, walrus ecology. At the academic start of this project, my office-mate Eva said not to worry because Bud would be right there with me until the end. Though later the course of events changed, her words rang true in the encouragement, guidance, and constructive criticism received from those he called friends and colleagues. This thesis is dedicated to Bud Fay and the spirit of friendship, perseverance, and cooperation.

Table of Contents

Chapter One: Laboratory digestion of prey and the interpretation of walrus stomach contents

Chapter Two: A re-examination of Pacific walrus feeding habits

Results

Re-examination of walrus diet

Recommendations

List of Figures

Chapter One: Laboratory digestion of prey and the interpretation of walrus stomach contents

Chapter Two: A re-examination of Pacific walrus feeding habits

List of Tables

Chapter One: Laboratory digestion of prey and the interpretation of walrus stomach contents

Chapter Two: A re-examination of Pacific walrus feeding habits

List of Appendices

WALRUS FEEDING - A RE-EXAMINATION

General Introduction

Walruses (*Odobenus rosmarus*) are large pinnipeds with a northern circumpolar distribution. They eat a variety of prey, ranging in size and classification from tiny crustaceans to adult seals (Vibe 1950; Krylov 1971; Fay 1982; Lowry and Fay 1984; Fay *et al.* 1990). It has been suggested that walruses consume mainly clams, particularly *Mya* and *Serripes* (Chapskii 1936; Vibe 1950; Fay 1982; Fisher 1989), selectively consuming only the foot or siphon from each clam.

Whereas walruses usually feed in water less than 100 m deep (Fay 1982; Fay and Burns 1988) in bouts up to 36 hours (Vibe 1950; Loughrey 1959; Tomilin and Kibal'chich 1975; Nyholm 1975; Fay 1982; Irons 1983; Fay *et al.* 1986), almost all diet data have been gathered from animals killed while resting on the ice, feeding having occurred earlier. Thus, digestion had likely influenced the quantity and quality of prey in the stomachs.

There have been few studies of walrus diet. Typically, stomach samples were obtained opportunistically from hunters; consequently the sample sizes have been small. Additionally, the effects of digestion on the species composition and volume of stomach contents have never been taken into account in the interpretation of stomach contents. Prey that were rapidly digested have left no trace in the stomach, whereas the importance of digestion-resistant prey would have been exaggerated. Previous interpretations of feeding habits may have been influenced by the effects of digestion on diverse prey as much as by the actual prey ingested. A more accurate representation of diet would be possible if stomachs with contents least affected by digestion could be identified.

Pacific walrus (*O. r. divergens*) diet data were collected from the Bering and Chukchi seas from 1952-1991. As the number of stomach samples increased, initial conclusions regarding feeding habits were called into question. The concern was that digestion had affected the composition of prey in stomachs thereby biasing interpretations of stomach contents (Fay and Lowry 1981; Fay and Stoker 1982*a*; Fay 1989*a*). The objectives of this study were to 1) specify a criterion that identifies stomach data least affected by digestion, 2) then, using that criterion, account for how the composition of prey in stomachs has been affected by digestion, and 3) using the most accurate diet data available, re-examine interpretations of walrus diet.

Chapter 1: LABORATORY DIGESTION OF PREY AND THE INTERPRETATION OF WALRUS STOMACH CONTENTS

Introduction

The diet of walruses has been described almost solely from examination of stomachs collected from animals killed while resting on sea ice or land. These stomach contents had been subjected to varying amounts of digestion. Walruses feed on a broad array of prey (Appendix 1), primarily benthic invertebrates, usually at depths less than 100 m (Fay 1982; Fay and Burns 1988). They consume items representing over 12 phyla, many of which are composed solely of soft tissues (*e.g.* anemones and worms). Invertebrate prey items are consumed whole by oral suction without substantial mastication during feeding bouts lasting up to 36 hours (Tsalkin 1937; Vibe 1950; Loughrey 1959; Tomilin and Kibal'chich 1975; Nyholm 1975; Fay 1982; Irons 1983; Fay *et al.* 1986). Walruses excavate infaunal prey buried as deep as 30 cm by propelling streams of water from their mouths (Oliver *et al.* 1983). Only clams and snails are manipulated in order to (1) excavate clams from the deep sediments and (2) extract the flesh from the shells, which are then discarded (Fay 1982; Oliver *et al.* 1983). Less often, walruses consume large non-benthic organisms (*e.g.*, fishes, birds, and seals) (Freuchen 1935; Vibe 1950; Fay *et al.* 1977; Fay 1982; Lowry and Fay 1984; Gjertz 1990; Donaldson *et al.* 1995).

The diets of many pinnipeds have been reconstructed from undigested diagnostic hard parts such as bones, otoliths, opercula, and cephalopod beaks found in stomachs or feces. Walrus prey also have been identified from solid diagnostic fragments such as echiurid worm setae, clam periostraca and shell fragments, snail opercula, crustacean carapaces, bird feathers, fish bones, and seal hide or hair. Prey items composed of softer tissues (*e.g.*, anemone, worm, clam, snail, sea cucumber, or tunicate) were identified in stomachs as fragments. Such physically diverse organisms should withstand the effects of digestion and remain identifiable for varying lengths of time. Differing rates with which prey types were rendered unidentifiable in the stomach by digestion biased diet analyses of piscivorous pinnipeds (Bigg and Fawcett

1985; Murie and Lavigne 1985; Murie 1987) and fishes (Scholz *et al.* 1991). In both cases, the relative importance of prey items with the most persistent and identifiable diagnostic parts was exaggerated. Our understanding of walrus diet has been based on two assumptions: (1) identifiable food in a stomach is an unbiased representation of prey consumed, and (2) when clams and snails are eaten, only the large, muscular, exposed siphon and/or foot is ingested (Vibe 1950; Brooks 1954; Mansfield 1958; Fay *et al.* 1977; Fay 1982).

While prey representing over 100 genera from 12 phyla were found in walrus stomachs (Appendix 1), only four clam genera were considered to be the principal prey (Fay 1982). Two main lines of evidence supported this assumption. Molluscs comprised 66-99% of walrus stomach contents by volume and/or numbers (Vibe 1950; Mansfield 1958; Fay *et al.* 1977; Fay and Lowry 1981; Fay and Stoker 1982*a*; Fay *et al.* 1984; Fisher 1989), and many large infaunal clams have been found in walrus stomachs collected in regions where these molluscs were scarce (Vibe 1950; Fay *et al.* 1977). Non-molluscan prey were believed to be: (1) consumed in "less suitable" foraging areas not dominated by clams (Mansfield 1958), (2) energetically inferior to molluscs (Fay *et al.* 1977), (3) used to supplement the diet with trace elements or other nutrients not present in molluscs (Fay 1982), or, in the case of vertebrate prey, (4) hunted when benthic invertebrates were "unavailable" (Chapskii 1936; Fay *et al.* 1984).

The dominance of the siphons and feet of clams in walrus stomachs was thought to accurately reflect the walrus' diet (Vibe 1950; Brooks 1954; Fay 1955; Mansfield 1958; Fay *et al.* 1977; Fay 1982). Fay *et al.* (1977) estimated that walruses ingest only 1/4 of the wet mass of a clam. Removal of the siphon is fatal to clams (Welch and Martin-Bergmann 1990). Thus, it was reasoned, walruses destroy four times the number of clams needed to support their metabolic demands (Fay *et al.* 1977). The increase of the Pacific walrus population to or beyond the carrying capacity of their habitat in the early 1980's was thought to have been hastened by walruses removing clams at a rate nearly equal to the annual net clam production (Fay *et al.* 1977; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*).

Some investigations demonstrated, however, that walruses ingest more than just the feet and siphons of clams (Malmgren 1863; Lydekker 1916; Chapskii 1936; Tsalkin 1937; Vibe 1950). Tsalkin (1937) suggested that softer clam tissues were digested rapidly, with the more muscular foot or siphon remaining in the stomach longer. Fay and Lowry (1981) and Fay and Stoker (1982*a*) described stomachs that contained mantles, gills, viscera, and adductor muscles, as well as feet and siphons of clams. A Bering Sea walrus hunter observed intact whole clams (without shells) apparently still alive in the stomach of a walrus (C. Ozeva pers. comm.). Walruses excavate entire infaunal clams from as deep as 30 cm in sediment (Oliver *et al.* 1983). The extra effort required to remove an infaunal clam completely from deep sediments (instead of ingesting only the meaty siphon that protruded to the sediment surface) suggests the siphon is not consumed alone. Oliver *et al.* (1985) found adductor muscle and mantle tissue attached to recently discarded clam shells on the seafloor, suggesting that most of the clam flesh was consumed.

If different organisms are digested at different rates, then the species composition of prey in a stomach would vary between the time of the last meal and examination of stomach contents. Thus, organisms more resistant to digestion would be overemphasized in diet analyses. In this study, digestion trials were conducted in the laboratory to determine the relative rates at which walrus prey are rendered unidentifiable. Two hypotheses were tested: (1) All prey types are equally identifiable over time; and (2) within a prey type, individuals remain equally identifiable regardless of their initial mass.

Methods

Six groups of live walrus prey were used in digestion experiments (Table 1). Annelids were represented by the Class Polychaeta (polychaetes), echiurid and sipunculid worms were represented at the phylum level, and molluscs were represented by the Classes Gastropoda (snails) and Bivalvia (clams). Crustaceans were represented by the Class Malacostraca (hermit crabs, true crabs).

A Pyrex vessel, containing approximately 500 ml water, was heated on a stirrer/hotplate. A magnetic stirrer mixed the waterbath maintaining a constant temperature (60 rpm; 35-40° C). In order to approximate the digestive fluid of a walrus, a second Pyrex vessel containing a digestive solution of 1%

hydrochloric acid (HCl) and 2% pepsin in physiological saline (5 ml solution/g tissue) and a magnetic stirrer was placed in the heated waterbath. The digestive solution was a modified version of one used by Zimmermann *et al.* (1961) to digest samples of mammalian striated muscle over a period of 18 hours. The rate of passage of food through the digestive system of a captive walrus, however, is about 8-10 hours (Fisher 1989), more rapid than in most other pinnipeds and terrestrial carnivores (King 1983). Presumably, not more than half of that passage time is involved in gastric digestion. Therefore, the proportions of HCl and pepsin were increased to intensify the digestive action, while still maintaining an optimal pH of between 1 and 2 (Raven and Johnson 1992). Additionally, physiological saline (7.5 g NaCl/liter distilled water) was substituted for distilled water as the digestive fluid of walruses probably is somewhat salty from intake of small amounts of seawater along with prey. Furthermore, there was concern that fresh water might have some adverse effects on the isohaline tissues of the marine invertebrates, perhaps causing them to break down prematurely.

Prior to laboratory digestion, all organisms were maintained in a 90 liter tank of circulating seawater at 4°C. The selected test organism was removed from the tank, blotted on paper toweling to remove excess water, and weighed, before being placed whole into the digestive solution. Shells were removed from snails and clams. The mantle and soft parts were gently peeled "whole" from the valves. Snail shells were separated from the bodies with scissors. Care was taken to not cut through the mantle, although in some instances the digestive gland and/or testis were exposed. Opercula were left attached to the flesh of all snails.

At one hour intervals, for up to six hours, the digestive solution was removed from the waterbath and poured through a 1 mm sieve. Filtered solids were weighed to the nearest 0.1 g. The organism was inspected to determine if it was still identifiable based on the presence or absence of diagnostic tissues (Table 2). If diagnostic tissues were present, the organism scored a 1, and it was immediately returned to the digestive fluid and the waterbath. If diagnostic tissues were absent, the organism scored a 0 and digestion was halted. Because the identification tests were recorded hourly, the duration of "identifiability" of a sample organism is to the nearest hour and not an exact measure of its duration. Photographs of each food item were taken hourly during the digestion trials. For all clams, the nearest hour when the viscera and mantle tissues dissolved and were no longer identifiable also was recorded.

Statistical analyses

The sample size needed to detect a significant difference in the identifiability of several prey taxa at each hour was calculated from Sokal and Rohlf 's (1969) formula based on the arcsin transformation:

$$N^* = \frac{C}{\delta^2}$$

δ^2 = (arcsin (the square root of p_1) - arcsin (the square root of p_2))^2
p_1 = proportion 1: the proportion of population 1 exhibiting a specific characteristic
p_2 = proportion 2: the proportion of population 2 exhibiting a specific characteristic
Coefficient C = f (α, 1-β) from table in Box 16.11 (Sokal and Rohlf 1969)
N = sample size needed from each population to detect an absolute difference of $p_1 - p_2$
* when the resulting $N < 20$, the estimated sample size should be increased by 1.

A sample size of nine from each "population" of prey provided 90% power (1-β) for detecting a 50% difference ($\alpha = 0.05$) in the proportion of each population that remained identifiable. A sample size of nine was too small for Chi-square approximations.

The hypothesis that walrus prey remain equally identifiable over time was tested using a Monte Carlo randomization (Fisher 1966). Kapplan-Meier survival estimates (Pollock *et al.* 1989) were used to calculate the probability of an organism remaining identifiable through each hour of digestion. Binomial confidence intervals were calculated for each survival estimate. Based on these calculations, a model was created that simulated the effect of digestion on the prey composition of a hypothetical walrus stomach in which equal numbers of selected prey taxa began to be digested simultaneously.

Spearman Rank Association tests (Siegel 1992) were used to determine whether there was a significant ($\alpha = 0.05$) association between mass of the organism and the last hour at which it was identifiable.

Results

The Monte Carlo randomization test indicated that the survival of prey taxa was not equal over time ($P = 0.0001$). Some prey types were rendered unidentifiable within one hour, and other types remained identifiable for six hours (Appendix 2). Sipunculid worms remained identifiable for shortest time with only 14% of the organisms identifiable after hour 1 and none identifiable after hour 2. Although 57% of the polychaetes maintained diagnostic tissues after the first hour of the experiment, none were identifiable after hour 3 of digestion. Echiurid worms maintained diagnostic tissues through hour 2, but these characteristics rapidly declined so that by hour 5 none were identifiable. All clams maintained their identifying tissues through hour 2 of the experiments, and more than 50% of the clams remained identifiable through hour 6. Snails and crustaceans were the most persistent; all specimens remained identifiable throughout the six-hour trials.

Only 12% of the clams maintained their viscera (in contrast to siphons and/or feet) through hour 1 of each experiment. In no instance did the viscera survive hour 2 of a trial. Seventy-one percent of the clams maintained a portion of their mantle, usually attached to the siphon, through hour 1 of digestion. Less than 5% of the clams maintained identifiable mantle through hour 2, and in only one case did identifiable mantle tissue persist through hour 3. The effects of digestion on the non-muscular structures of a deep dwelling clam (*Mya*) are shown in Figure 1. Typically, the soft tissues of a clam dissolved after only one hour of digestion, leaving the siphon and portions of the mantle for identification. After six hours of controlled digestion, the clam siphon was still easily identifiable.

The survival of diagnostic tissues differed within, as well as between, taxa. All snails and crustaceans were still identifiable at the end of the experiments while all sipunculid worms became unidentifiable almost immediately regardless of their mass. The larger the polychaete worm, echiurid worm, or clam, the longer it remained identifiable (Figure 2).

Kapplan-Meier survival estimates and confidence intervals were calculated (Appendix 3), and a model simulated the effect of digestion on the composition of a walrus stomach initially containing equal numbers of six prey types (Figure 3). Although prey were evenly distributed at the beginning of the model, by hour 3 sipunculid and polychaete worms were no longer represented. By hour 5, echiurid worms were no longer represented, leaving clams, snails, and crustaceans to dominate until the end of the six hour period.

Discussion

Previous studies of diet did not account for the effects of digestion on the identifiability of a variety of prey types. As a result, three biases were introduced: (1) the importance of prey with digestion-resistant tissues was exaggerated (both in frequency and volume); (2) the presence of larger polychaete worms, echiurid worms, and clams was exaggerated; and (3) entire clams (not including shells) may have been consumed more often than previously thought.

The diagnostic tissues among the walrus prey representatives varied greatly in physical composition. Some prey items consisted of more digestion-resistant material and larger structures than others (*e.g.*, the large clam foot or siphon). Consequently, volumetric ranking of prey in walrus stomachs inadequately represented the relative importance of prey types in the diet. For example, if a polychaete worm and a crustacean of similar mass were consumed simultaneously, the crustacean carapace would be identifiable longer than the worm tissue. The crustacean would not only be identifiable longer, but its heavier carapace would be more dominant in volumetric rankings.

Larger polychaetes, echiurids, and clams were identifiable longer than smaller individuals of these prey groups. Over 20 clam genera ranging in size from the tiny *Nucula* (10 mm) up to the large *Mactromeris* (140 mm) were recorded from walrus stomachs (Fay *et al.* 1977). If representatives of clam genera of varying sizes were consumed during a feeding bout, the differential rates at which prey are digested would exaggerate the relative importance of the genus comprised of larger individuals. The different rates with which prey groups become unidentifiable in a walrus stomach do not allow an accurate determination of the species composition and size of prey consumed.

The assumption that walruses are highly selective for clams stems partly from the resistance of the clam's muscular foot and siphon to digestion. Clams and snails were thought to be nutritionally superior to other prey and selectively consumed (Fay *et al.* 1977). Wacasey and Atkinson (1987), however, found no significant difference in the caloric values of polychaete worm, sipunculid worm, snail, clam, amphipod, decapod, and sea cucumber genera reported as walrus prey. The digestion experiments demonstrated that if a polychaete worm (*e.g.*, *Nephtys*) and a clam (*e.g.*, *Mya*) of similar mass were consumed, the worm would be digested faster than the clam. Thus, the worm would be more valuable to the walrus than an entire clam, because the worm's caloric energy would be more readily and completely accessible.

It is difficult to determine the foraging strategy of walruses without knowing the distribution, density, and availability of prey, or the handling times and energy values of different prey (Pyke *et al.* 1977). Additionally, the gregarious nature of feeding bouts (Tomilin and Kibal'chich 1975; Irons 1983; Taggart 1987) suggests foraging may not be independent of other activities (*e.g.*, predator avoidance) and, therefore, foraging decisions may be made within a broader realm of concerns (Zach and Smith 1981). Since the caloric value of clams and other prey are similar (Wacasey and Atkinson 1987), no apparent energy loss occurs in consuming non-clam prey. Non-clam and non-snail prey often are consumed whole (Fay 1982) with presumably less handling time than for clams or snails. Non-clam organisms which are easily ingested, rapidly digested, and of high caloric value would be energetically valuable to walruses. Thus, the optimal walrus foraging strategy might be to consume any potential prey item, including non-clam taxa, encountered while rooting along the seafloor during a feeding bout.

Clams contain a large proportion of digestion-resistant tissues (*i.e.*, the siphon and/or foot) which would seem to result in extra energy costs to a feeding walrus (*e.g.*, removal of clam from sediments and extraction of flesh from shell). Nevertheless, clams may be highly abundant and physically larger in certain areas than other potential food items, so that the additional energy benefit would outweigh additional handling costs. Whether the abundance of clams in stomachs examined in previous studies (Vibe 1950; Brooks 1954; Fay *et al.* 1977; Fay and Lowry 1981; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*; Fisher 1989) reflected 1) a foraging preference for clams, 2) the proportion of prey types available on the seafloor, or 3) the persistence of the identifiable portion of a clam during digestion, is unknown.

Contrary to previous reports (*e.g.,* Fay 1982), it appears that walruses regularly consume all of the soft tissues of clams, not solely the foot and siphon. The weight loss exhibited by adult captive walruses when fed a diet of clam feet (Fisher 1989) suggests that more than the foot of the clam is commonly consumed. Welch and Martin-Bergmann (1990) reported that the consumption of only the siphon would deprive a walrus of more than 60% of a clam's nutritional value. The experiments described in this paper demonstrated that even if clam mantle and viscera were regularly consumed, they would be underrepresented in stomach contents due to the rapid rate at which they are digested. Previously, estimates of the annual impact of walruses on clam stocks were calculated under the assumption that a walrus only uses 1/4 of the clam, destroying four times as many clams as it needs to support its metabolic demands. As a result of consuming the entire clam (except the shell), Pacific walruses might be expected to annually consume only 5% of the Bering and Chukchi sea clam stocks rather than the 20% calculated by Fay *et al.* (1977).

From the time a walrus feeds to the time its stomach is collected, many prey types can become unidentifiable. Laboratory results indicated that the ability to identify prey items varied among and within prey groups. Because the effects of digestion were not taken into account, previous diet studies did not accurately reflect the diet of walruses.

The laboratory experiments demonstrated relative rates at which diagnostic tissues of prey became unidentifiable due to digestion. Classifying stomach contents as to their relative digestive state should allow a more accurate representation of walrus diet to be developed. In future studies of walrus diet, stomach contents should be classified according to their relative state of digestion. Stomach contents that include sipunculid worms, polychaete worms, or clam mantle and viscera should be least affected by digestion and should considered most representative of the actual diet. Existing diet data and theories regarding foraging behavior of walruses need to be re-examined in light of the influence of digestion on different prey types.

Table 1. Walrus prey items used for digestion experiments.

Taxa	N
Annelida - Polychaete worms	21
Nereis	11
Nephtys	10
Sipuncula - Sipunculid worms	14
Golfingia	14
Echiura - Echiurid worms	9
Echiurus	9
Mollusca - Snails	11
Fusitriton	11
Mollusca - Clams	23
Clinocardium	7
Mya	9
Tellina	7
Arthropoda - Crustaceans	10
Pagurus	3
Cancer	5
Hyas	1
Telmessus	1

Table 2. Diagnostic tissues of walrus prey digested in the laboratory.

Taxa	Diagnostic tissue
Polychaete worm	Distinct pharynx or a segmented section of the body containing setae or parapodia.
Sipunculid worm	Body intact, held together by the retractor muscles.
Echiurid worm	Proboscis or the conical anterior and posterior ends.
Snails	Foot present.
Clams	Foot or siphon intact.
Crustacean	Cuticle from claw or carapace present.

Figure 1. The effects of controlled laboratory digestion upon the identifiable structures of a clam (*Mya*), (a) before digestion, (b) after one hour of digestion, and (c) after six hours of digestion.

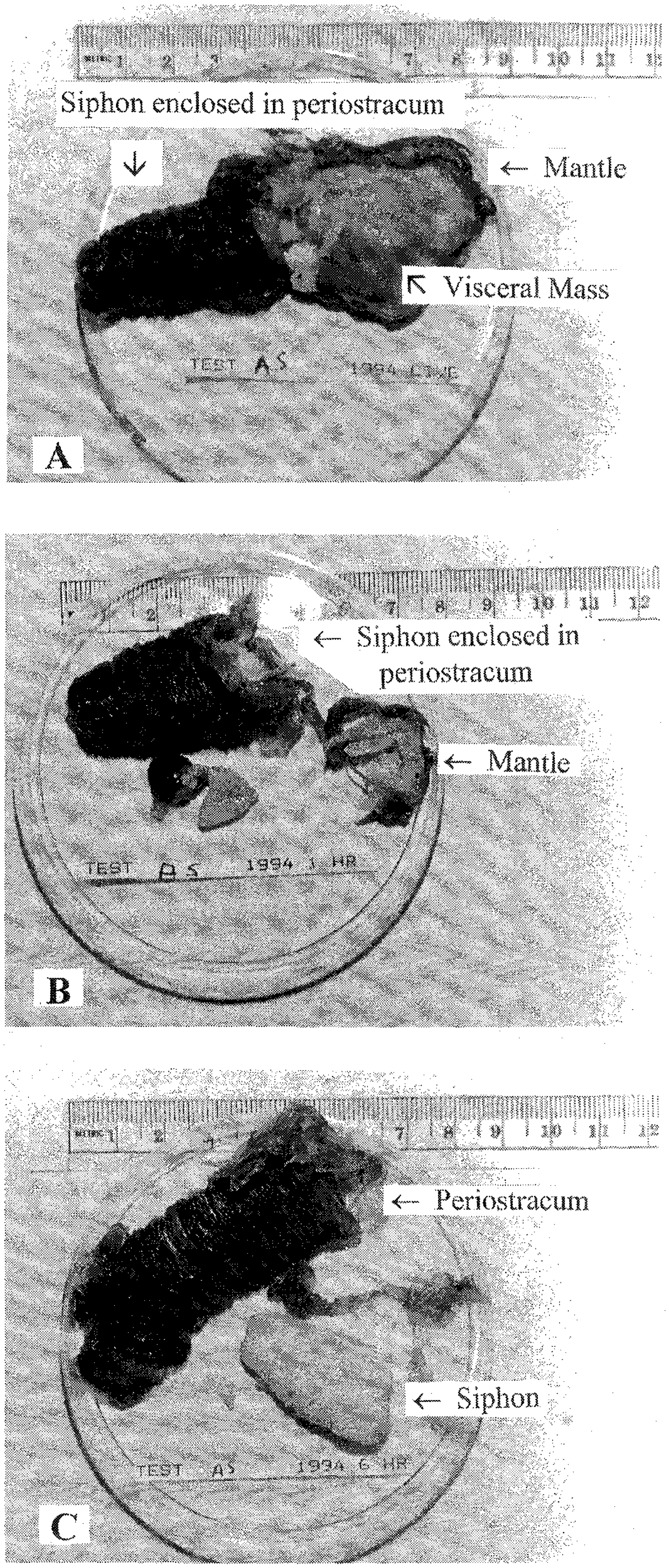
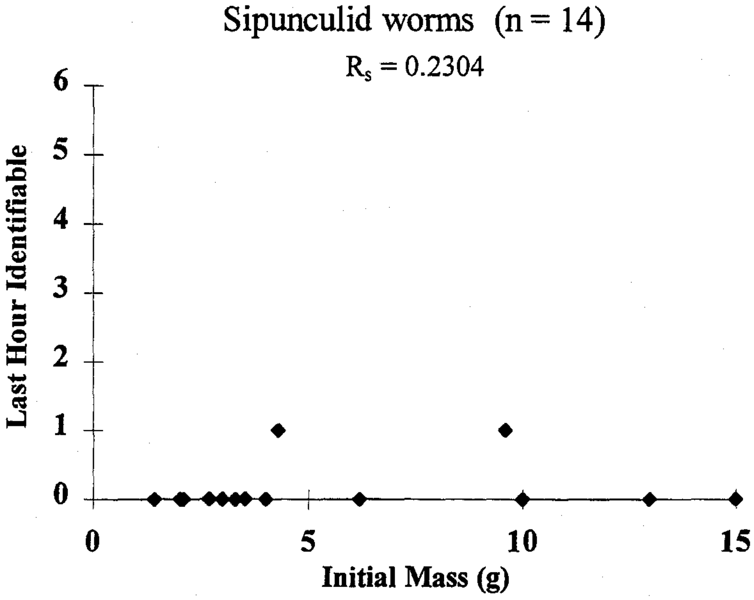


Figure 2. Relationship between initial mass of walrus prey and the last hour at which the prey were identifiable. A significant association ($\alpha = 0.05$) is indicated by *. R_s = Spearman Rank correlation coefficient. N/A = not available



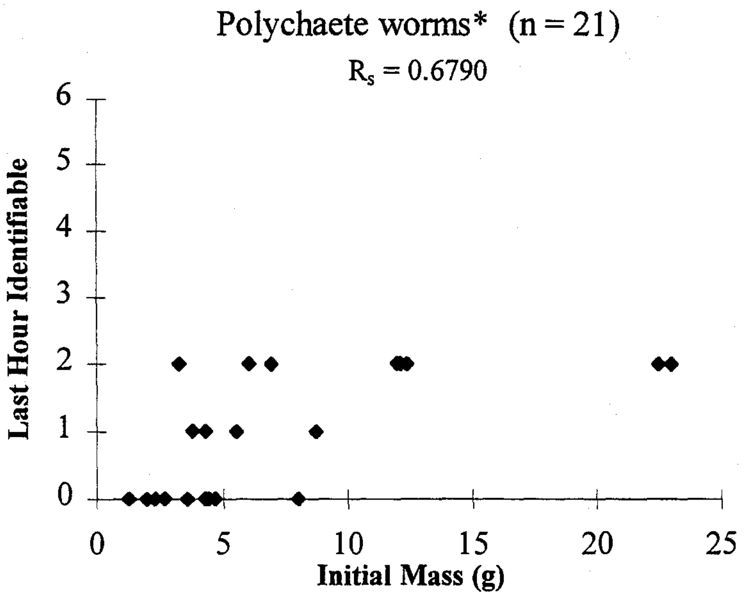
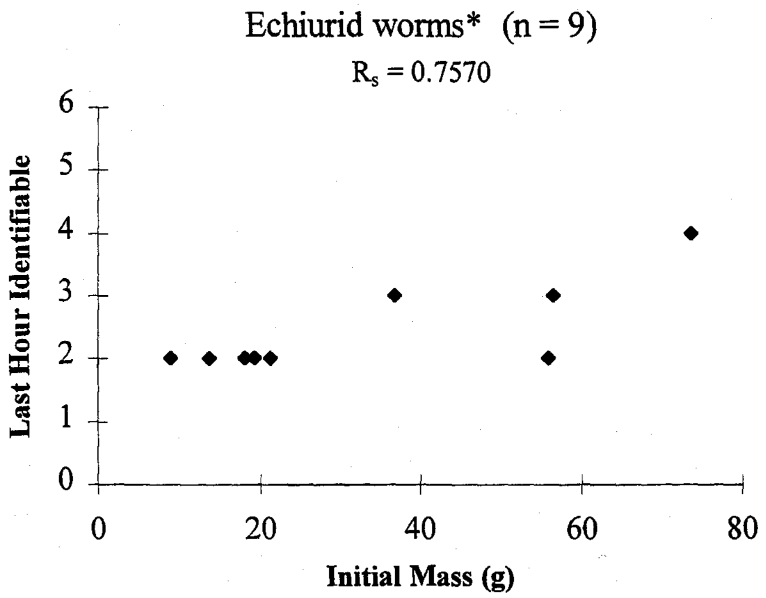
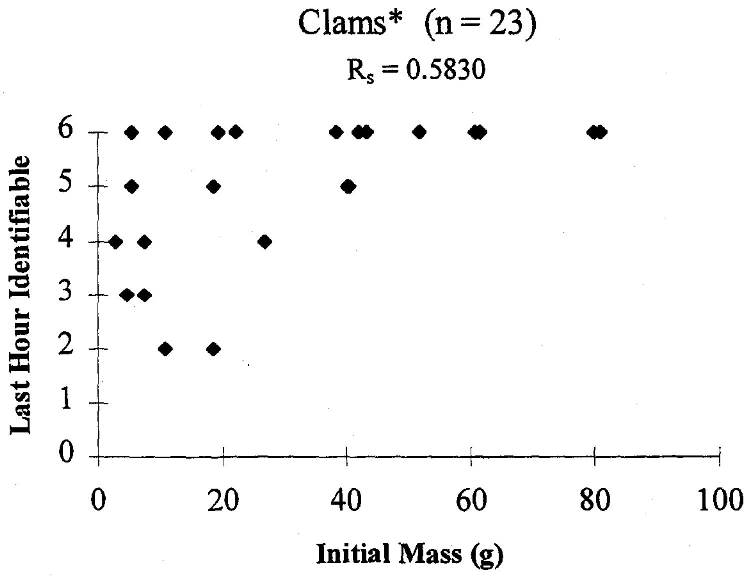


Figure 2. (continued)

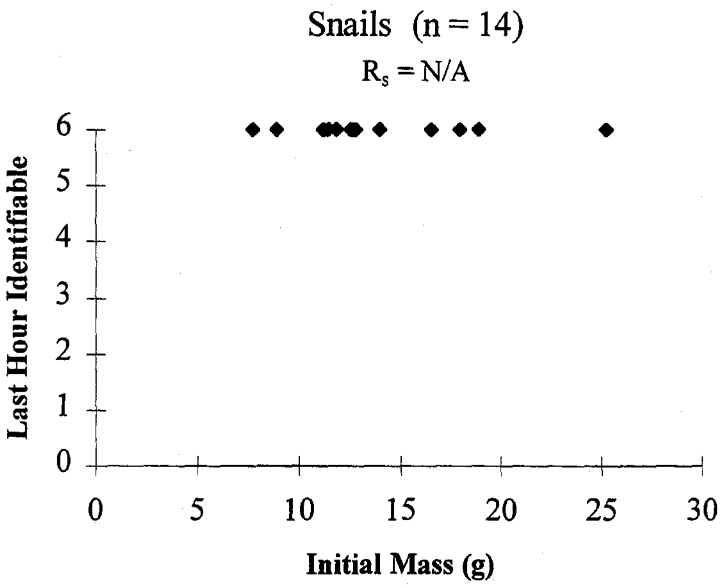

Echiurid worms* (n = 9)

$R_s = 0.7570$


Clams* (n = 23)

$R_s = 0.5830$

Figure 2. (continued)



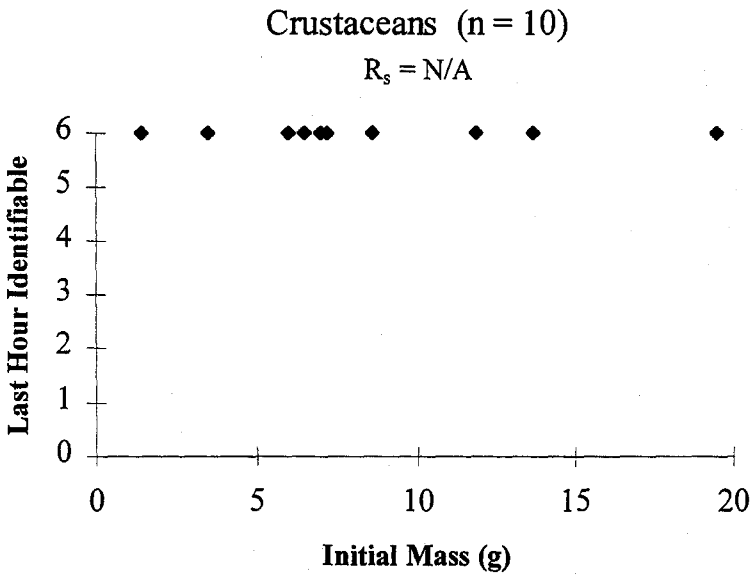
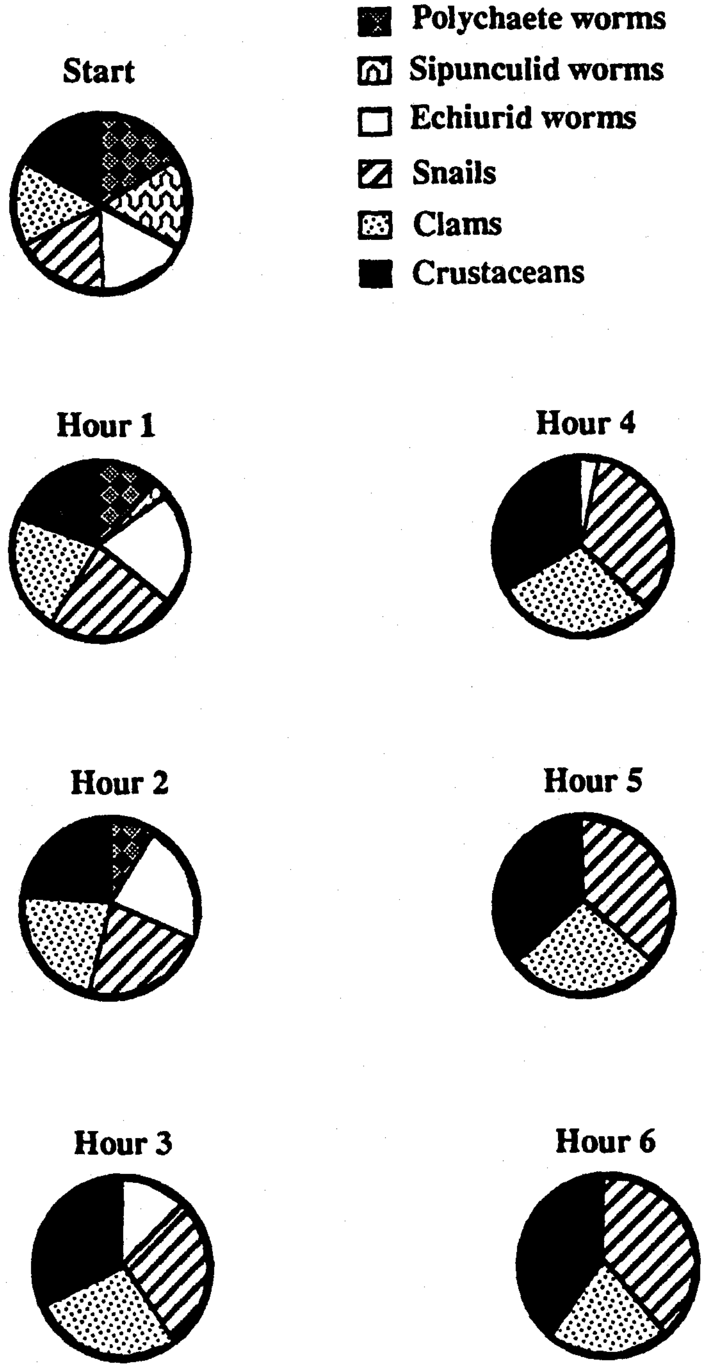


Figure 3. The effects of digestion on the contents of a hypothetical walrus stomach initially containing equal numbers of six prey taxa. The proportions of prey identified at hourly intervals after ingestion have been estimated using Kapplan-Meier estimates based upon laboratory digestion trials.



Chapter Two: A RE-EXAMINATION OF PACIFIC WALRUS FEEDING HABITS

Introduction

Pacific walruses (*Odobenus rosmarus divergens*) are large migratory pinnipeds found seasonally throughout the continental shelf of the Bering and Chukchi seas. As recently as 1990, the population was thought to be at or near the historic maximum, with not less than 200,000 animals (Gilbert *et al.* 1992). Walruses are gregarious and forage in large groups (Tomilin and Kibal'chich 1975; Fay 1982; Irons 1983; Taggart 1987) during feeding bouts lasting up to 36 hours (Vibe 1950; Loughrey 1959; Tomilin and Kibal'chich 1975; Nyholm 1975; Fay 1982; Irons 1983; Fay *et al.* 1986), usually at depths less than 100 m (Fay 1982; Fay and Burns 1988).

Food habits of walruses have been described on the basis of stomach contents collected from different time periods and areas with an emphasis on volumetric ranking of food items (Chapskii 1936; Tsalkin 1937; Fay *et al.* 1977; Fay 1982; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*; Fay *et al.* 1984; Fay *et al.* 1989*a*). The data have not been compiled or analyzed as a whole. Variation in the rates with which different prey were rendered unidentifiable have not been considered in the interpretation of stomach data. The ability to identify prey items varies among and within prey types (Chapter One). Thus, prey composition in a stomach can change between the time an animal fed and the collection and examination of its stomach. Therefore, many conclusions in the literature regarding walrus diet need to be re-examined.

Stomachs collected from animals that had fed shortly before death would contain prey less affected by digestion. The data from such stomach samples should provide a more accurate representation of walrus diet and insights into foraging behavior. This chapter (1) compiles stomach data collected from Pacific walruses between 1952 and 1991 in the Bering and Chukchi seas, (2) examines how digestion may have biased previous stomach content analyses and (3) re-examines previous interpretations regarding diet.

Original interpretations of walrus food habits

The large number and volume of clams frequently found in walrus stomachs led to the conclusion that walruses are highly selective for clams (Fay *et al.* 1977; Fay and Lowry 1981; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*). Fay *et al.* (1977) postulated that walruses forage by locating and feeding selectively upon clam patches until the clam supply is exhausted or the animal satiated. Non-clam prey were considered of minor importance and assumed to be eaten when 1) clams were scarce, or 2) nutrients were lacking in clam tissues, or 3) ingested accidentally while feeding on clams (Chapskii 1936; Nikulin 1941; Krylov 1971; Fay 1982; Fay *et al.* 1984).

Males and females were presumed to prefer different sizes of clams. Males were thought to consume large clams such as *Mya* and *Clinocardium* (Brooks 1954; Fay *et al.* 1977), whereas, females were thought to consume small-sized clams such as *Astarte* and *Macoma*. Subsequently, Fay and Stoker (1982*a*) found that males and females ate clams of similar genera and sizes in the northern Bering Sea. They suggested that males and females were competing for the same types and sizes of prey as the increasing walrus population reduced overall prey availability (Fay and Stoker 1982*a, b*).

Walruses were reported to be at or near the carrying capacity of their habitat in the 1980's based on an estimated increase from 50,000 animals to over 200,000 between 1960 and 1985 (Fedoseev 1962; Gilbert 1985) as well as on density-dependent population responses including leanness (Fay and Kelly 1980), decreased productivity (Lowry *et al.* 1980*c*; Fay *et al.* 1989*b*; Fay *et al.* 1997), and an age composition skewed toward older animals (Fay *et al.* 1989*b*). Additionally, reports of an increased frequency of non-molluscan prey items in stomachs collected in the northern Bering Sea between 1975-1985 were thought to reflect a food limited walrus population compelled to consume more "alternate" prey (Fay *et al.* 1977; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*; Fay *et al.* 1989*b*).

Clams were not the predominant prey and stomachs did not contain large quantities of food in the western Chukchi Sea. Fay *et al.* (1986) suggested that this region was not a critical feeding area. They concluded that walruses occupied the Chukchi Sea primarily in summer during the annual molt when energy demands and feeding were likely to be low.

I re-examined available stomach content data to determine if the different rates at which prey are rendered unidentifiable by digestion affected the reported prey composition in stomachs. Using the historical records of walrus stomachs least affected by digestion, four hypotheses were tested: (1) the frequency of prey types consumed is not different between the Bering Sea and the Chukchi Sea, (2) the frequency of prey types consumed is not different regionally within the Bering Sea or the Chukchi Sea, (3) the frequency of clam genera consumed is not different between males and females, and (4) the frequency of non-molluscan prey use did not change between 1975 and 1985 in the northern Bering Sea.

Methods

Stomach content data were collected in the Bering and Chukchi seas by Native subsistence hunters, Russian professional hunters, and staff from the University of Alaska Fairbanks, the Alaska Department of Fish and Game, the Eskimo Walrus Commission, and the U.S. Fish and Wildlife Service. Data were entered into a computerized database (Foxpro 2.5b). Included in the database were the age and sex of the animal, date, and location of collection. Walrus ages were determined previously (Fay unpublished; Hills unpublished; Frost and Lowry unpublished; Fay and Lowry 1981; Lowry and Fay 1984; Fay *et al.* 1989*a*; Fay 1993). Walruses were classified as calves (0-2 yr.), juveniles (3-7 yr.), and adults ($\geq$8 yr.). Reported collection locations were considered exact for walruses harvested from Russian and American research vessels. Walruses collected by Native subsistence hunters were assumed to be within 75 km of a hunter's village.

Records of stomach samples from individual animals were used in the analyses. Diet data reported as summary statistics from groups of samples (Nikulin 1941; Brooks 1954; Krylov 1971; Tomilin and Kibal'chich 1975) were not used. Data were taken from the original data sheets, when possible. If an original stomach record was not available, then data from unpublished reports or published literature were entered. No records of food remains in intestines or feces were used. A food item was identified either by the description of a whole organism, or by the description of a diagnostic fragment of soft tissue (*i.e.,* molluscan foot or siphon) or mud tube, operculum, shell fragment, beak, seta, carapace, feather, bone, or hair sample. Macroalgae were not considered food items in this study as suggested by some previous investigators (Allen 1880). Prey data were entered into the database at generic or higher taxonomic levels. Current taxonomic nomenclature was used in the database regardless of the nomenclature in the original records. The nomenclature is that of Anonymous (1984) and Kozloff (1990).

Seven groups identified and categorized only at the phylum level were Cnidaria (cnidarians), Rhynchocoela (ribbon worms), Priapula (priapulid worms), Echiura (echiurid worms), Sipuncula (sipunculid worms), Brachiopoda (brachiopods), and Bryozoa (bryozoans). Annelids were represented by the Class Polychaeta (polychaete worms). Molluscs were represented by three classes: Gastropoda (snails), Bivalvia (clams), and Cephalopoda (octopus). Five crustacean orders were categorized including: Thoracica (barnacles), Cumacea (cumaceans), Amphipoda (amphipods), Isopoda (isopods), and Decapoda (crabs/shrimp). Echinoderms categorized at the class level were the Holothuroidea (sea cucumbers) and Ophiuroidea (brittle stars). Urochordates and vertebrates were represented by the Classes Asciidiacea (tunicates), Osteichthyes (bony fishes), Aves (birds), and Mammalia (mammals).

Records of stomach data were separated into Bering Sea or Chukchi Sea data sets. Stomach records were sorted as to their relative digestive state. If a sipunculid worm or a polychaete worm, or the soft viscera and mantle tissues of clams were present in a stomach, the stomach record was labeled "fresh" as these prey tissues were digested beyond recognition in 1-3 hours (Chapter 1). It was assumed that the animal had fed recently prior to collection. Stomach records that did not contain these prey types or tissues were considered to be of an unknown digestive state. Furthermore, sipunculid or polychaete worms, or clams with mantle or viscera were excluded in all subsequent analyses because these taxa were present in all stomachs labeled as "fresh".

The frequencies with which different prey types were represented in stomach records labeled "fresh" and "unknown" were calculated for both the Bering and Chukchi seas. The frequencies of prey types consumed by at least 10 animals were compared between stomach record types using 2 by 2 contingency tables with an experiment wise error rate < 0.05 (using Bonferroni's procedure). The mean number of prey types present in stomach records labeled "fresh" and "unknown" were compared using a *t*-test.

Using fresh stomach records only, the frequencies of prey types were compared between stomach records of the Bering Sea and the Chukchi Sea, from each region of the Bering and Chukchi seas, and between males and females. Additionally, the four most frequently identified snail, clam, amphipod, and decapod genera were compared between the Bering and Chukchi seas. The frequency of non-molluscan prey use in the northern Bering Sea was examined with records collected between 1975-1985. Fresh stomach records from this region were sorted into two subsets: "molluscan" (only clams or snails occurred) and "non-molluscan". One non-molluscan prey type was allowed to occur in "molluscan" stomachs. Stomachs in which two or more non-clam or non-snail prey types occurred were classified "non-molluscan" regardless of the possible presence of clams or snails. The frequencies of molluscan and non-molluscan stomachs from 1975 to 1985 were compared in a 4x2 Chi-square test.

Results

Compilation of stomach content data: 1952-1991.

Records from the stomachs of 798 walruses were obtained from the Alaskan coastal villages of Barrow, Nome, Shishmaref, Wainwright, and Wales, from villages on Diomede, King, Nunivak, and St. Lawrence islands, and from eight oceanographic cruises in the Bering and Chukchi seas between 1952-1991 (Table 3). Previously, no standard protocol was used in the collection or recording of walrus stomach contents. Methods for handling stomach samples often were not described, and criteria for prey identification were not detailed. Over 100 types of organisms from 11 phyla were identified as walrus prey including 11 genera from 4 phyla not previously recorded in the literature (Appendix 1). Brooks (1954) and Krylov (1971) identified additional prey including the polychaete genus *Onuphis*, the crustacean Order Mysidacea, the decapod Genus *Pandalus*, and fishes from the Lumpenidae and Blennidae families, but these data were not used in the following analyses because information regarding the individual animals was unavailable.

Contents of fresh and unknown stomachs.

Stomachs from 224 walruses collected in the Bering Sea, mainly from March-June 1952-1991, were classified as fresh based on the presence of either a polychaete worm, a sipunculid worm, or clams for which the mantle and viscera tissues had been noted (Table 4). In the same period 387 stomachs taken from the Bering Sea were classified as being in an unknown digestive state.

The percent occurrence of each taxon was typically higher in fresh stomachs than in stomachs in unknown stages of digestion (Table 5). The mean number of taxa present was significantly higher in fresh (3.83, SD = 1.45) than in unknown stomachs (2.73, SD = 1.37) ($t = 9.23$; $P < 0.00001$). Twelve percent of fresh stomachs contained more than 5 prey types each. Only 4% of the unknown stomachs contained more than 5 prey types each. The soft coral *Gersemia*, the snail *Velutina*, three clam genera (*Musculus*, *Cardita*, *Mactra*), brachiopods, the King crab (*Paralithodes*), the tunicate *Halocynthia*, a bird (*Cepphus*), two species of seals (*Erignathus barbatus*, *Phoca largha*), and one unidentified seal, were found only in "unknown" stomachs.

Stomach records from 92 walruses collected in the Chukchi Sea, mainly between July and October 1966-1987, were classified as fresh (Table 4). The stage of digestion was unknown for 95 stomachs. Typically, the percent occurrence of each prey type was higher in fresh stomachs than in stomachs in unknown stages of digestion (Table 5). The mean number of prey types present in fresh (5.30, SD = 1.78) and in unknown stomachs (2.34, SD = 1.75) was significantly different ($t = 11.46$; $P < 0.00001$). Thirty-eight percent of the fresh stomachs contained more than 5 prey types each. Thirteen percent of the unknown stomachs contained representatives of more than 5 prey types each. The clam *Tellina*, the brittle star *Ophiura*, and unidentified fishes occurred in "unknown" stomachs but were not present in fresh stomachs from the Chukchi Sea.

Re-examination of walrus diet.

Bering Sea *vs.* Chukchi Sea

A higher percentage of cnidarians, priapulid worms, snails, octopus, amphipods, decapods, and tunicates occurred in the Chukchi Sea stomachs, while more echiurid worms, clams, sea cucumbers, and fishes were identified in Bering Sea stomachs ($P < 0.05$) (Table 5). Large-sized clam genera such as *Serripes*, *Mya*, and *Mactromeris* were recorded more often in the Bering Sea stomachs, while small-sized clam genera, such as *Yoldia* and *Astarte*, were recorded more often in stomachs from the Chukchi Sea (Table 6). Clams and snails were the most frequently identified prey in fresh stomachs from the Bering and Chukchi seas.

Regional diets

Stomachs were collected from four regions of the Bering Sea and four regions of the Chukchi Sea (Figure 4). The stomach contents from all Bering Sea regions were dominated by clams and snails (Table 7). Priapulid and echiurid worms, snails, and decapods were rare in records from the western Bering Sea. Sea cucumbers were observed most frequently in the western region. The sample from the central Bering Sea was too small for meaningful comparisons.

Stomach records from the Chukchi Sea were dominated by snails, clams, priapulid worms, decapods, amphipods, and tunicates (Table 8). Priapulid worms, octopus, and amphipods occurred more often in records from the northeastern Chukchi Sea, while tunicates were most frequent in records from the northwestern Chukchi Sea. The sample from the southeastern Chukchi Sea was too small for any meaningful comparisons.

Diet of males *vs.* females

Echiurid worms and the clam genus *Mya* were more common in the stomachs of males than females (Table 9) from the Bering Sea. The frequencies of occurrence of all other clam genera were not significantly different between males and females of the Bering Sea. No differences were detected between the frequency of occurrence of prey types, including clam genera, identified in the stomachs of males and females of the Chukchi Sea (Table 9).

Consumption of molluscan and non-molluscan prey

One hundred and seventy-seven fresh stomachs from the northern Bering Sea were collected between 1975 and 1985. One hundred and eight of these records were classified as molluscan stomachs and 69 were classified as non-molluscan. Due to small sample sizes, records from 1979 were combined with those collected in 1980. No difference ($\chi^2 = 2.00$; $P = 0.5720$) was detected between the ratio of molluscan and non-molluscan stomachs for each sampling year between 1975 and 1985 (Figure 5).

Discussion

For over 20 years, information regarding walrus diet was based on data from only a small number of individuals: 29 from the Bering Sea, 12 from the Chukchi Sea, and a small, undisclosed number from the Bering Strait/Chukchi Peninsula region (Fay unpublished; Burns unpublished; Nikulin 1941; Brooks 1954; Kenyon 1958). Initial interpretations from these data became the basis for prevailing theories regarding walrus feeding habits. When large numbers of stomach samples were collected between 1975 and 1991, however, many previously unrecorded non-clam taxa were identified as prey. Nonetheless, non-clam organisms were still considered less preferred prey as well as an inferior energy source (Fay *et al.* 1977; Fay and Stoker 1982*a*; Fay and Stoker 1982*b*; Fay *et al.* 1986; Fay *et al.* 1989*b*). Furthermore, western scientists did not have the benefit of stomach data collected by Russians, primarily from animals of the western Chukchi Sea where many non-clam prey were consumed (Nikulin 1941; Krylov 1971; Tomilin and Kibal'chich 1975), until the late 1970's and 1980's (Fay 1989*b*).

Much of the data concerning the diet of walruses were collected opportunistically and, therefore, temporally, geographically, and seasonally fragmented. As a result of selective harvesting of females by hunters, the sex composition of walruses in the database was not random (Merrick and Hills 1988; Fay and Stoker 1982*b*; Fay 1982; Fay *et al.* 1989*b*; Fay *et al.* 1997). Any seasonal change in prey availability during the collection years is unknown. There are almost no data concerning temporal changes in prey availability. One exception is a reported decline in 1993 of two shallow-dwelling, small-sized clam species, *Macoma calcarea* and *Nucula belloti*, southwest of St. Lawrence Island (Grebmeier and Cooper 1995).

Polychaete worms, sipunculid worms, and clam soft tissues are digested rapidly, and their presence in a stomach indicates that a walrus had fed shortly before collection (Chapter One). The rapid digestion of polychaete and clam soft tissues combined with their ubiquitous distribution in the Bering and Chukchi seas (Fay *et al.* 1977; Stoker 1981; Feder *et al.* 1994), make worms and clams ideal for characterizing the condition of stomach samples throughout the range of the Pacific walrus.

Quantifying the condition of stomach samples, based on the rates at which different prey types were digested, enables investigators to more accurately describe the diet of walruses. I recommend that future analyses of diet use stomachs containing indicators of recent feeding. The diet of walruses is more diverse than previously thought, and the importance of non-clam prey in the diet was underestimated. Fresh stomachs contained more occurrences of each prey type identified and more prey types per stomach than did stomachs labeled "unknown", indicating less discriminating prey selection than previously thought.

The frequent occurrence of clams in stomachs from the Bering and Chukchi seas is consistent with estimates that clams make up half the benthic biomass on the continental shelf of the Bering and Chukchi seas (Zenkevitch 1963; Stoker 1978). Clams were present in most fresh stomachs, yet clams represented only one of at least four prey types present in each fresh stomach. The widespread occurrence of non-clam prey in fresh stomachs suggests that, although walruses frequently consume clams, they also commonly eat many other benthic organisms. The frequent occurrence of non-clam taxa in the walrus diet suggests that the impact of walruses on the standing stock of clams is far less than the 20% estimated by Fay *et al.* (1977).

The walrus population has recovered rapidly from severe exploitation by commercial hunters on three occasions during the last 150 years (Fay *et al.* 1986; Fay *et al.* 1989*b*). The impact walruses have on benthic community structure is unknown, but the rapid recoveries of the walrus population have been attributed to large stocks of clams that accumulated in the absence of walruses (Fay *et al.* 1989*b*). Yet, clams are the most frequently consumed benthic organisms in the Bering Sea (Feder and Jewett 1981) and have many predators in addition to walruses including crabs, sea stars, bottom fishes, and bearded seals (*Erignathus barbatus*) (Burns 1967; Feder and Jewett 1981; Lowry *et al.* 1980*c*; Fukuyama and Oliver 1985). It is possible that populations of other clam predators expanded when the walrus population was depleted. Thus, when the walrus population recovered from over-exploitation, large clams may not have been unusually abundant. The repeated, rapid recoveries of the walrus population from severe exploitation without an apparent "warehouse" of accumulated clams suggests that walruses are not dependent solely upon clam populations. Instead, they also eat a variety of other foods.

Fay *et al.* (1989*b*; 1997) suggested that the Pacific walrus population became food limited in the early 1980's. Reports of an increased frequency of prey items other than clams and snails (*e.g.*, sea cucumbers, bottom fishes) in stomachs were thought to reflect a food limited walrus population that was compelled to consume "alternate" prey (Fay and Stoker 1982*b*). The presence of non-molluscan prey in stomachs, however, is not necessarily an indicator of reduced prey availability. The analysis of fresh stomachs indicated that non-molluscan prey were a common and important part of the walrus diet. The reported increased occurrence of non-molluscan prey in the northern Bering Sea between 1975-1985 likely reflected the greater number of stomachs collected rather than changes in prey availability. Ten times the number of stomachs containing food were collected between 1975-1985 than had been collected during the previous 20 years. The additional data provided an opportunity to examine stomachs in varying degrees of digestion from regions containing diverse benthic communities (Stoker 1981).

Sea stars, brittle stars, and sea urchins are found throughout the Bering and Chukchi seas (Jewett and Feder 1981), but they apparently are a poor food for walruses. Walruses rarely eat these echinoderms, presumably because too much effort is required to separate soft tissue from the substantial skeletal parts. An increase in the occurrence of sea stars, brittle stars, and sea urchins in the stomachs of walruses may indicate a food-limited walrus population.

The suggestions by Brooks (1954) and Fay *et al.* (1977) that males and females typically select for different types and sizes of clams and that "convergent predation" among sexes for similar clam types occurred as the walrus population increased (Fay and Stoker 1982*a*; Fay and Stoker 1982*b*) were not supported by this study. The more frequent consumption of echiurid worms and the clam, *Mya*, by males than females may be due to a bias in sampling location rather than differences between male and female diet. Many stomachs from males were taken from the western Bering Sea, a region used predominately by summering adult males. Whether echiurid worms or the clam *Mya* were more common in the western Bering than in other Bering Sea regions, or selected for more often by males than females is not known. Results from the present study supported Fay's (1989*a*) later hypothesis that male and female walruses eat essentially the same food items when in the same location.

The western Chukchi Sea is an important feeding area for walruses, especially females, between April and October. Females occupy the Chukchi Sea primarily in summer when many females are pregnant, lactating, or both and have increased energy demands (Gehnrich 1984). The scarcity of clams reported in stomachs from the western Chukchi Sea probably mirrors low clam densities in that region; other benthic prey apparently are abundant (Nerini 1984). Typically, non-clam prey consumed in the Chukchi Sea were soft bodied and small (*e.g.,* priapulid worms). The rapid digestion of those prey, combined with longer haulout times associated with the walrus' annual molt, may account for the small amounts of food found in stomachs from the Chukchi sea. Some prey in the western Chukchi Sea, however, are large. Up to 11% of stomach samples collected there contained seal remains (Chapskii 1936, Krylov 1971; Fay *et al.* 1983; Lowry and Fay 1984), further indicating the importance of the Chukchi Sea as a feeding area.

Deep-dwelling clams frequently were found in walrus stomachs but not in sediment grabs, leading Fay *et al.* (1977) and Stoker (1981) to conclude that walruses prey selectively on the large deep-dwelling clams. The benthic samples were collected, however, with shallow sediment sampling equipment inadequate to capture many species of walrus prey. Thus, prey availability was not accurately addressed.

Walrus diet varied seasonally. Although males and females shared a common diet when in the same location, they spent much of the year in different areas, and energy needs varied between the sexes and with reproductive status (Fay 1982; Gehnrich 1984). The composition of prey in a stomach reflects local benthic communities probably more than selection for a particular prey type. Overall, the wide shelf of the Bering and Chukchi seas is a shallow, highly productive, detritus based ecosystem with little or no apparent seasonal fluctuation in benthic biomass or standing stock, but the benthic communities are regionally diverse (Zenkevitch 1963; Stoker 1978; Stoker 1981; Feder *et al.* 1994; Grebmeier *et al.* 1995; Grebmeier and Cooper 1995). Benthic faunal composition and biomass vary regionally due to heterogeneous food availability, depth, and substrate types and because of physical disturbances such as ice gouging or predation (Stoker 1978; Stoker 1981; Grebmeier *et al.* 1995). Consequently, the diet of walruses varies with their annual movements.

The central Bering Sea is an area inhabited by walruses of both sexes throughout the winter in most years (Fay 1982). Large concentrations of walruses overwinter in polynyas and the unstable pack ice southwest of St. Lawrence Island and in Kuskokwim Bay, as well as near the leading edge of the pack ice (Fay 1982; Fay *et al.* 1986). Females feed throughout the winter, but adult males mostly fast while rutting in December-March (Gehnrich 1984). Snails and crabs were important in the diet of female walruses feeding in deep offshore water (80-117 m) in winter (Tikhomirov 1964; Fay *et al.* 1984; Fay and Burns 1988). Whether the importance of crabs and snails reflected the proportion of benthic fauna available in deeper water or the selectivity of female walruses for decapods and gastopods during the winter is unknown.

The northern Bering Sea is an area inhabited by walruses of both sexes during the spring and fall in most years (Fay 1982). The diet of walruses during the spring and fall comprised a wide assortment of prey. Clams and snails were the two most frequently consumed organisms in the northern Bering Sea. Priapulid worms, echiurid worms, decapods, and sea cucumbers also commonly occurred in stomachs from the northern Bering Sea. The most varied assortment of prey genera, and the greatest number of prey unique to one region, were found in stomachs taken from this region.

Most females and young occupy the Chukchi Sea during May-October, while most adult males summer along the ice-free coasts of the southeastern and western Bering Sea (Fay 1982). The females in the Chukchi Sea frequently consumed an assortment of snails, small-sized clam genera, decapods, priapulid worms, amphipods, and tunicates. Conversely, relatively fewer non-clam prey were ingested by males summering in the southern Bering Sea, with the exception of echiurids in the western Bering Sea and sea cucumbers in the southeastern Bering Sea. These regional differences probably reflected differences in the composition of benthic communities.

All available stomach data were used to investigate the suggestions by Fay and Lowry (1981), Fay and Stoker (1982*b*), Fay *et al.*(1984) and Fay *et al.* (1989*a*) that walrus diet analyses should consider the effects of digestion on the prey composition of a stomach sample and variation in the composition of benthic communities. Walruses regularly consumed a wider assortment of benthic prey items than was previously thought, and the importance of non-clam prey in the walrus diet had been underestimated. The diet of walruses is now known to vary regionally. Therefore, diet varies seasonally as walruses move through different regions. Males and females eat essentially the same food items when in the same location. Sex-specific diets nonetheless are observed, because adult males and females inhabit different regions seasonally. Regional differences most likely result from patchy distributions of diverse prey items and benthic communities within both the Bering and Chukchi seas.

Table 3. Date, location, sample size, handling protocol, and sources of Pacific walrus stomach samples collected between 1952-1991 in the Bering (n = 611) and Chukchi (n = 187) seas. 1 = Diomede (Diomede Island), 2 = Gambell (St. Lawrence Island), 3 = Savoonga (St. Lawrence Island).

Year	Month	Sea/Region	*N*	Collection or handling protocol	Literature Cited
		BERING SEA			
1952	May	N	5	Unknown	Fay (unpublished)
1954	May	N	2	Unknown	Fay (unpublished)
1956	May	N	1	Unknown	Fay (unpublished)
1957	January	N	1	Unknown	Fay (unpublished)
1958	May-June	N	8	Unknown	Fay (unpublished.); Kenyon 1958
1959	May	N	1	Unknown	Fay (unpublished)
1967	May	N	1	Unknown	Burns (unpublished)
1970	May	N	4	Unknown	Burns (unpublished)
1971	Jan.-Feb.	SE	3	Unknown	Fay *et al.* 1984; Fay (unpublished)
1974	May-June	N	3	Unknown	Fay *et al.* 1984; Fay (unpublished)
1975	May-June	N	102	Unknown	Fay *et al.* 1977; Fay (unpublished)
1979	May-June	N[1]	22	"About 1/4 of the contents collected on avg. from each stomach, if a walrus had eaten a seal then 1/2 of the contents were collected".	Lowry *et al.* 1980*b*; Lowry (unpublished)
1979	May-June	N[2]	14	"1/3 of the stomach contents from each animal were collected".	Lowry *et al.* 1980*b*; Lowry (unpublished)
1979	May-June	N[3]	15	"All contents collected, including seal eaters, early in the collection, more clams saved - random at end".	Lowry *et al.* 1980*b*; Lowry (unpublished)
1979	May-June	N	2	Unknown	Lowry *et al.* 1980*b*; Lowry (unpublished)
1980	May-June	N	96	Stomach contents were thoroughly mixed before subsamples were taken.	Fay and Stoker 1982*a*; Fay (unpublished)
1981	April	SE	19	Contents "thoroughly washed and drained" in seawater.	Fay and Lowry 1981; Fay *et al.* 1981; Fay (unpublished)
1982	Apr.-June	N, SE	76	"Most" were 5 lb. subsamples from the cardiac end of the stomach; contents unmixed.	Fay and Stoker 1982*b*; Fay (unpublished)
1984	Nov.-Dec.	N	14	Not all samples weighed.	Sease 1984; Fay (unpublished)
1985	Apr.-June	N, W, C	108	Contents placed in buckets, weighed, washed in muslin bags, and drained.	Lowry *et al.* 1986; Burns *et al.* 1985; Fay and Burns 1988; Fay *et al.* 1989*a*; Fay (unpublished),
1991	Mar.-May	W, SE, C	114	Samples were rinsed in sea water.	Hills *et al.* 1991; Hills (unpublished)
		CHUKCHI SEA			
1966	"winter"	NE	1	Unknown	Fay (unpublished)
1976	September	NE	1	Unknown	Burns (unpublished)
1977	October	SE	3	Unknown	Lowry *et al.* 1980*a*; Lowry (unpublished)
1979	May-June	NE	1	Unknown	Lowry *et al.* 1980*b*; Lowry (unpublished)
1983	July-Sept.	SW, NW	47	Samples were rinsed in sea water.	Fay *et al.* 1983; Lowry and Fay 1984; Fay *et al.* 1986; Fay (unpublished)
1987	Sept.-Oct.	NE, SW, NW	134	Samples were rinsed in sea water.	Merrick and Hills 1988; Fay *et al.* 1993; Feder *et al.* 1991

Table 4. Date, location, sample size, sex, age, and sample type for "fresh" walrus stomachs collected in the Bering and Chukchi seas between 1954 and 1991 (M = male, F = female, U = unknown sex, S = a subsample of contents collected, W = entire contents of stomach collected).

Year	Month	Region	*N*	Vessel/Location	Adults	Juvenile	Calf	Unknown age	Type
				BERING SEA					
1954	May	N	1	St. Lawrence Island	-	-	-	1U	1W
1956	May	N	1	St. Lawrence Island	-	-	-	1U	1W
1974	May	N	1	St. Lawrence Island	-	-	-	1U	1U
1975	May-June	N	55	Diomede I., St. Lawrence I., Nome	7F, 26M	1M, 3F	-	2F, 14M, 2U	30U, 1S, 24W
1979	May	N	11	Diomede I., St. Lawrence I.	1F, 5M	-	-	3M, 2U	10U, 1W
1980	May-June	N	37	Diomede I., St. Lawrence I.	12F, 12M	-	-	5F, 8M	36S, 1W
1982	May-June	N	30	Diomede I., St. Lawrence I., King I., Nome, Wales	12F, 12M	-	-	2F, 4U	28S, 2W
1984	Nov.-Dec.	N	3	ZAKHAROVO	2F, 1M	-	-	-	3W
1985	Apr.-June	N	30	Diomede I., St. Lawrence I., King I., Nome	16F, 9M	1M	-	2M, 1F, 1U	26U, 4S
1985	April	W	7	ZAKHAROVO	1M	-	-	6M	7W
1991	April	W	14	ZASLONOVO	14M	-	-	-	4W, 10S
1981	April	SE	3	RESOLUTION	3M	-	-	-	3W
1981	April	SE	9	ZVYAGINO	6F	1M, 2F	-	-	9W
1982	May	SE	2	Nunivak Island	-	-	-	2M	2S
1991	Mar.-Apr.	SE	15	ZASLONOVO	15F	-	-	-	15W
1985	March	C	5	ZAKHAROVO	5F	-	-	-	5W
		Totals	**224**		**159**	**8**	**0**	**57**	
				CHUKCHI SEA					
1976	September	NE	1	Barrow	-	-	-	1U	1U
1979	May-June	NE	1	Wainwright	-	-	-	1 U	1U
1987	September	NE	21	ZAKHAROVO	18F, 1M	2M	-	-	21W
1983	July-Aug.	NW	15	ZYKOVO	14F, 1M	-	-	-	15W
1987	Sept.-Oct.	NW	22	ZAKHAROVO	18F, 3M	-	1M	-	22W
1983	July-Aug.	SW	17	ZYKOVO	14F, 3M	-	-	-	17W
1987	October	SW	14	ZAKHAROVO	11F, 3M	-	-	-	14W
1977	October	SE	1	Shishmaref	-	-	-	1U	1U
		Totals	**92**		**86**	**2**	**1**	**3**	

Table 5. Percent occurrence of prey identified in "fresh" walrus stomachs and stomachs in unknown stages of digestion from the Bering Sea ("fresh": $n = 224$; unknown: $n = 387$) and Chukchi Sea ("fresh": $n = 92$, unknown: $n = 95$). A significant ($\alpha = 0.05$) difference in the frequency of occurrence is indicated by *.

	Bering Sea			**Chukchi Sea**	
	fresh	unknown		fresh	unknown
Clams	98	96	Snails *	99	94
Snails *	83	62	Clams	89	38
Echiurid worms *	44	15	Decapods *	67	20
Priapulid worms *	40	22	Priapulid worms *	61	31
Decapods *	38	28	Amphipods *	52	15
Sea Cucumbers	36	33	Tunicates *	50	8
Amphipods *	15	5	Cnidarians *	35	7
Cnidarians *	11	4	Echiurid worms *	26	2
Tunicates	7	5	Octopus *	23	7
Fish *	7	2	Sea Cucumbers	12	4
Octopus *	6	3			

Table 6. Percent occurrences of snail, clam, amphipod, and decapod genera in "fresh" walrus stomachs from the Bering Sea ($n = 224$) and the Chukchi Sea ($n = 92$). A significant ($\alpha = 0.05$) difference in the frequency of occurrence is indicated by *.

	Bering Sea	**Chukchi Sea**
Snails		
Polinices *	55	96
Natica *	42	96
Neptunea *	48	90
Buccinum *	4	33
Clams		
Serripes *	80	64
Mya *	80	37
Hiatella *	28	6
Mactromeris *	20	1
Yoldia *	15	31
Astarte *	4	40
Amphipods		
Ampelisca *	< 1	37
Anonyx	9	17
Decapods		
Hyas	14	25
Argis *	4	20
Sabinea *	< 1	16
Pagurus	13	13

Figure 4. Oceanographic regions where fresh stomachs were collected from Pacific walruses taken in the Bering and Chukchi seas between 1952-1991.

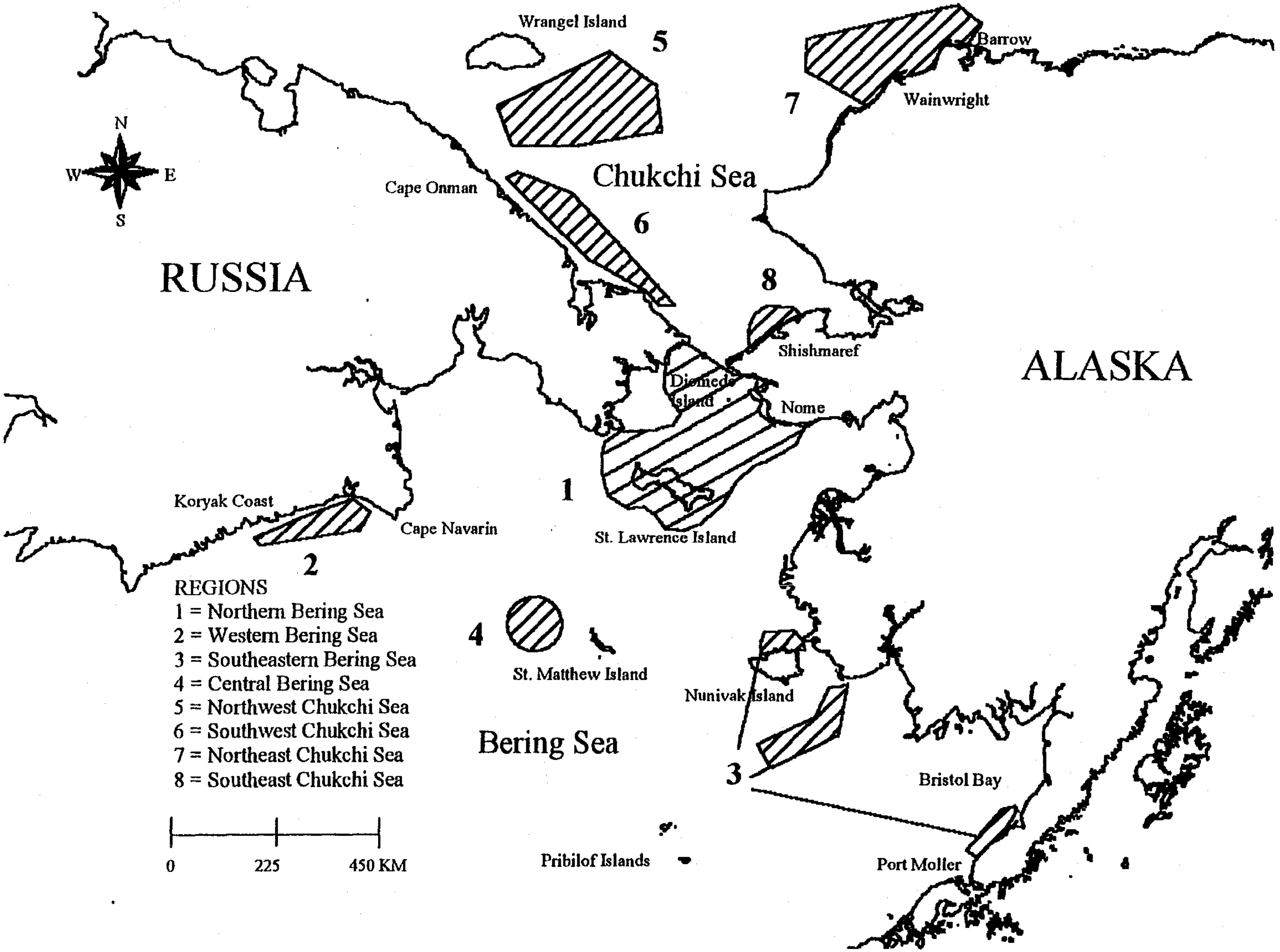


Table 7. Percent occurrence of prey identified in "fresh" walrus stomachs in the northern ($n = 169$), western ($n = 21$), southeastern ($n = 29$), and central ($n = 5$) regions of the Bering Sea. A significant ($\alpha = 0.05$) difference in the frequency of occurrence is indicated by *. Central region not included in statistical testing.

Bering Sea	N	W	SE	C
Cnidarians	10	10	14	0
Priapulid worms *	50	10	3	40
Echiurid worms *	45	0	72	60
Snails *	88	38	79	100
Clams	99	100	97	60
Octopus	8	0	0	40
Amphipods	14	5	24	0
Decapods *	41	5	41	100
Sea cucumbers *	42	57	7	0
Tunicates	5	5	17	0
Fish	5	14	3	0

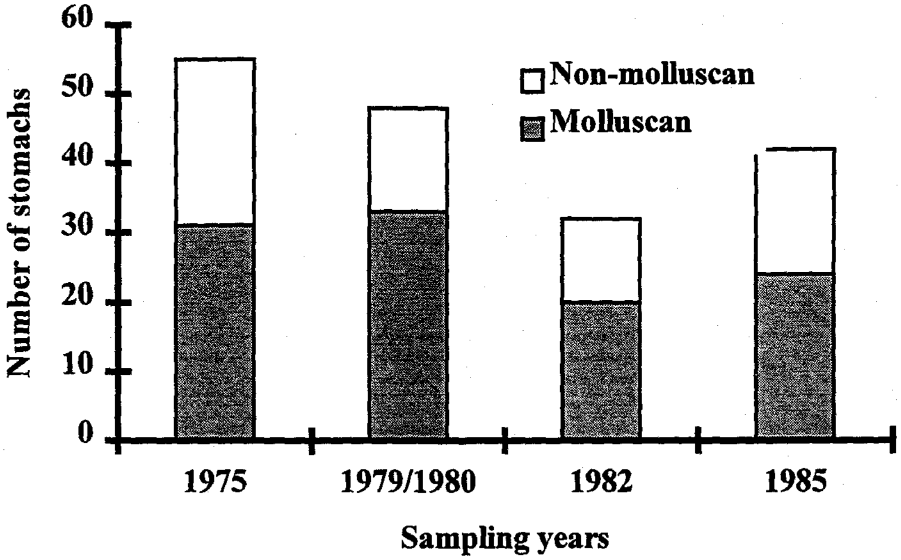
Table 8. Percent occurrence of prey identified in "fresh" walrus stomachs from the northeastern ($n = 23$), northwestern ($n = 37$), southwestern ($n = 31$), and southeastern ($n = 1$) regions of the Chukchi Sea. A significant ($\alpha = 0.05$) difference in the frequency of occurrence is indicated by *. The southeastern region is not included in statistical testing.

Chukchi Sea	NE	NW	SW	SE
Cnidarians	39	46	19	0
Priapulid worms *	91	35	71	0
Echiurid worms	17	19	42	0
Snails	100	100	100	100
Clams	87	89	90	100
Octopus *	48	22	6	0
Amphipods *	78	27	65	0
Decapods	48	76	71	100
Sea cucumbers	22	11	6	0
Tunicates *	26	65	52	0

Table 9. Percent occurrence of major prey taxa identified in "fresh" walrus stomachs of males and females collected in the Bering Sea (males $n = 130$; females $n = 91$) and the Chukchi Sea (males $n = 15$; females $n = 74$). A significant ($\alpha = 0.05$) difference in the frequency of occurrence of prey between males and females is indicated by *.

	Bering Sea			**Chukchi Sea**	
Major Taxa	Males	Females	**Major Taxa**	Males	Females
Clams	98	97	Snails	100	100
Snails	79	89	Clams	87	89
Priapulid worms	45	33	Decapods	67	69
Sea cucumber	45	27	Amphipods	67	51
Decapods	42	36	Tunicates	60	50
Echiurid worms *	35	60	Priapulid worms	47	62
Amphipods	13	16	Cnidarians	20	39
Cnidarians	10	2	Echiurid worms	20	27
Fish	9	2	Octopus	13	26
Tunicates	5	10	Sea cucumber	7	12
Octopus	3	12			
Clam Genera			**Clam Genera**		
Mya *	89	70	*Serripes*	73	64
Serripes	84	76	Unid. Tellinidae	60	50
Unid. Tellinidae	30	47	*Astarte*	40	42
Hiatella	28	26	*Mya*	47	35
Mactromeris	16	23	*Yoldia*	33	31

Figure 5. Numbers of "molluscan" and "non-molluscan" walrus stomachs recorded between 1975 and 1985 in the northern Bering Sea.



Recommendations

The following recommendations are intended for future investigators of walrus diet. Recommendations are listed in 3 separate categories: data collection, management, and feeding habit studies.

Data collection:

1) Undertake future studies of food habits based on clearly established hypotheses and objectives.
2) Standardize the collection, handling, and recording methods of stomachs and their contents.
3) Enclose an individual stomach content sample in a fine meshed bag (*i.e.*, paint strainer bag), and gently rinse the sample in a manner that will not destroy delicate diagnostic tissues.
4) Record exact kill locations in order to assess the benthic conditions at sampling locations.
5) Record whether a walrus was killed while hauled out on ice or land, or while in the water.
6) Record the proportion of stomach contents removed for each sample.
7) Document the criteria used to identify prey items (*e.g.,* clam foot, siphon, visceral mass, periostracum, or shell fragment).
8) Identify food items to the lowest taxonomic level possible.
9) Note the state of digestion of the stomach contents. Though contents from all stomachs should be examined for qualitative data, classify stomachs based upon the relative condition of the contents. Use the presence of either a sipunculid worm, a polychaete worm, or a clam with mantle and viscera present to determine which samples are least affected by digestion. Previous stomach data were sampled opportunistically, with the sampling secondary to subsistence or commercial harvesting purposes. Future walrus harvests inevitably will be carried out under similar conditions, and it is important that the relative state of digestion of the stomach contents be identified and taken into account during analyses.
10) Document the presence, quantity, and condition of non-food items (*e.g.,* sediment, mollusc shells).

Management:

11) Re-establish stomach collecting programs in villages where walruses are frequently hunted (ex. Diomede, Gambell, Nome, Savoonga, Shishmaref, Wainwright, Wales), and monitor for local trends and/or apparent shifts in regional prey consumption. Interview hunters for historical and present-day trends in walrus diet and for feeding observations. Collect walrus morphological, reproductive, and productivity data in order to further enhance the interpretation of diet data.

12) Report diet study results to Native subsistence hunters, especially in villages where walrus stomachs were collected. The study of walrus diet has regularly involved cooperative efforts. Biological samples usually are provided by subsistence hunters, and the analysis of these samples is done by biologists. Both parties are equally interested in the condition and status of the walrus population.

13) Determine important feeding locations for walruses.

Feeding habits studies:

14) Determine relationships between the frequency and duration of feeding bouts and the distance from haulout sites for the different sex and age class of walruses.

15) Investigate walrus prey selection. Obtain data on the composition, age classes, and densities of benthic prey taxa, including deep-dwelling clams, in locations where Pacific walrus diet data will be collected. Determine if the prey composition consumed in the western Bering Sea during the 1970's, a period of re-colonization by walruses (J. Burns pers. comm.), has changed with time or reflect local benthic community populations.

16) Determine if the community structure of benthic prey is driven by the local physical oceanographic conditions or by predation. Investigate the effect bioturbation by feeding walruses and gray whales (*Eschrichtius robustus*) has on benthic communities. Estimate the potential impact of walruses feeding on certain regional benthic communities during their annual migrations. Estimate the potential impact of walruses feeding throughout the winter in concentrated areas.

17) Investigate the degree to which the diets of bearded seals and walruses overlap. Investigate the impact other benthic competitors, such as brittle stars and bearded seals, have upon walrus prey.
18) Investigate whether it is local oceanographic conditions, nutritional needs, or a behavioral preference that motivates predation on seals by walruses.

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Appendix 1. Summary of prey and other items consumed by walruses. Atlantic walrus (*Odobenus rosmarus rosmarus*) references denoted in bold type. All other references refer to Pacific walruses. Taxonomic names updated from original notation indicated by ♣ (Anonymous 1994).

CNIDARIA
Scyphozoa
Jellyfish [32, 37]
Anthozoa
Anemone [28, 31, 32, 37]
Gersemia [30♣]
Sea Pen [35]
Hydrozoa [29]

RHYNCHOCOELA [32♣]

PRIAPULA [35]
Priapulus [16, 17, 18, 19, 21, 26, 27, 28, 31, 32, 33, 36, 37, 38, 42]

ANNELIDA
Polychaeta [2, 21, 29, 34, 35, 36]
Eunoe [38]
Phyllodoce [16, 31, 32]
Nereis [38]
Nephtys [17, 19, 28, 31, 32, 37]
Onuphis [26]
Lumbrineris [28, 31, 32, 37]
Flabelligera [37, 38, 42]
Brada [31, 32]
Aphrodite [45]
Arenicola [31, 32, 37]
Unid. Maldanidae [37]
Maldane [17]
Unid. Terebellidae [45]
Terebella [45]
Pectinaria [28, 31]
Thelepus [38]
Owenia [45]

SIPUNCULA [19, 35, 37]
Golfingia [28, 31, 32]

ECHIURA [29, 35]
Echiurus [17, 26, 28, 31, 32, 33, 36, 37]

MOLLUSCA [23]
Gastropoda [16, 29, 34, 35]
Margarites [26, 28, 31, 32, 37]
Solariella [17, 31]
Turritella [32]
Boreoscala [31♣]
Onchidiopsis [31, 37]
Velutina [30]
Unid. Naticidae [37, 42]
Natica [17, 21, 28, 31, 32, 33, 36, 37, 38]
Polinices [28, 31, 32, 33, 36, 37]
Unid. Buccinidae [37]
Buccinum [13, 16, 17, 21, 28, 31, 32, 33, 36, 37, 38, 43]

Unid. Neptunidae [33]
Neptunea [17♣, 19, 28, 31, 32, 33, 36, 37]
Colus [21♣]
Clinopegma [36]
Nudibranch [28]
Bivalvia [1, 16, 33, 34]
"Cockles" [2, 35]
Nucula [17, 26, 28, 32, 33, 35]
Nuculana [35]
Yoldia [26, 28, 31, 32, 35, 36, 37]
Mytilus [45]
Musculus [30]
Chlamys [43]
Patinopecten [21♣]
Thyasira [26, 31]
Unid. Caridean [28]
Cyclocardia [30]
Astarte [17, 18, 19, 21, 28, 29, 31, 35, 37, 38]
Clinocardium [19, 28, 31, 36]
Serripes [12♣, 16♣, 17, 28, 29, 31, 32, 33, 36, 37, 38]

Mactromeris [28♣, 29♣, 31♣, 32♣]
Mactra [26]
Siliqua [29, 32]
Unid. Tellinidae [31, 32, 35, 36, 37, 42]
Macoma [17, 18, 19, 26, 30]

Bivalvia (cont.)
Tellina [28, 29]
Liocyma [30, 31]
Cardium [18, 21]
Mya [3, 4, 11, 13, 16, 17, 18, 19, 21, 26, 27, 28, 29, 31, 32, 33, 35, 37, 38, 39, 43]

Hiatella [3♣, 13♣, 16♣, 18♣, 19, 21♣, 28, 31, 32, 35, 37, 38]

Panomya [36]
Cephalopoda
Rossia [18]
Squid [21]
Octopus [28, 31, 32, 34, 35, 36, 37]
Benthoctopus [17♣]
Octopus [26]

BRACHIOPODA [32]
Hemithyris [38]

BRYOZOA [28, 31]

CRUSTACEA [29]
Thoracica
Balanus [28]
Mysidacea [26]
Cumacea [35]
Diastylis [45]
Amphipoda [34, 35, 42]
Ampelisca [27, 28, 32, 37]
Byblis [31, 32]
Lembos [28]
Unid. Gammaridae [26]
Gammarus [11]
Maera [33]
Protomedeia [31]
Anonyx [28, 31, 32, 33, 37, 38]
Onissimus [45]
Acanthostephia [45]
Boeckosimus [38]
Hippomedon [28, 31]

Isopoda [15]
Arcturus [38]
Saduria [21♣]
Decapoda [2, 16, 34, 35, 38]
Unid. Hippolytidae [21, 26]
Spirontocaris [21]
Eualus [21]
Pandalus [26]
Unid. Crangonidae [31]
Crangon [45]
Sclerocrangon [12, 19, 21, 28, 37]
Argis [26♣, 28, 31, 32, 33, 37]
Sabinea [37]
Unid. Paguridae [21, 37]
Pagurus [21♣, 28, 31, 32, 34, 36]
Labidochirus [45]
Unid. Brachyuran [28]
Paralithodes [23]
Hyas [19, 26, 28, 31, 32, 33, 37]
Chionoecetes [17, 26, 28, 33, 36, 37]

ECHINODERMATA
Holothuroidea [29, 34, 35, 38]
Psolus [18, 28, 37]
Stolus [45]
Cucumaria [17, 18, 21, 26, 28, 31, 32, 37]
Molpadia [19]
Duasmodactyla [21♣, 28♣, 31♣]
Echinoidea [43]
Strongylocentrotus [38]
Ophiuroidea [2]
Ophiura [45]

UROCHORDATA
Ascidiacea [21, 33, 35]
Pelonaia [17, 26, 28, 31, 32, 33, 42]
Boltenia [30]
Halocynthia [26♣, 28♣, 30♣, 33♣]

VERTEBRATA
Osteichthyes [4, 21, 32]
Boreogadus [8]
Ammodytes [31, 32]
Unid. Lumpenidae [26]
Unid. Blenniidae [26]
Aves
Fulmarus [8, 10♣]
Somateria [40]
Uria [24, 44]
Cepphus [39]
Mammalia (Cetacea) [4]
Monodon monoceros [5, 14]
Mammalia (Pinnipedia)
Odobenus rosmarus [14]
Unid. Phocidae [5, 6, 10, 22, 14, 35]
Phoca largha [25, 34]
Phoca hispida [6, 7, 12♣, 15, 16, 17, 18, 19, 21, 34, 39, 43]

Phoca groenlandica [41]
Erignathus barbatus [9, 19, 20, 28, 34]

PHAEOPHYCEAE [16♣, 17♣]
Laminaria [28]
Fucus [1]

OTHER
Phalacrocorax feathers [45]
gastropod eggs [37]
crab egg clusters [21, 37]
wood [31]
shells [2, 3, 16, 19, 21, 28, 29, 31, 32, 35, 37, 38, 43]

sediments [1, 4, 12, 14, 15, 18, 27, 28, 31, 32, 33, 35, 37, 43]

glass [28]
nylon line [37]
engine gasket material [28]

Appendix 1 (continued)

1 **Von Baer (1838)**
2 **Lamont (1861)**
3 **Malmgren (1863)**
4 **Brown (1868)**
5 **Buckland (1886)**
6 **Gray (1889)**
7 **Pike (1897)**
8 **Römer and Schaudinn (1900)**
9 **Kolthoff (1901)**
10 **Bidenkap (1904)**
11 **Orleans (1907)**
12 **Johansen (1912)**
13 Gapanovitch (1923)
14 **Freuchen (1935)**
15 Chapskii (1936)
16 **Tsalkin (1937)**
17 Nikulin (1941)
18 **Vibe (1950)**
19 Brooks (1954)
20 Breshin (1958)
21 **Mansfield (1958)**
22 **Pedersen (1962)**
23 Tikhomirov (1964)
24 Nelson (1969)
25 Shustov (1969)
26 Krylov (1971)
27 Tomilin and Kibal'chich (1975)
28 Fay *et al.* (1977)
29 Fay and Lowry (1981)
30 Fay (1982)
31 Fay and Stoker (1982*a*)
32 Fay and Stoker (1982*b*)
33 Fay *et al.* (1984)
34 Lowry and Fay (1984)
35 Fay *et al.* (1986)
36 Fay and Burns (1988)
37 Fay *et al.* (1989*a*)
38 **Fisher (1989)**
39 Fay *et al.* (1990)
40 **Gjertz (1990)**
41 **Timoshenko and Popov (1990)**
42 Feder *et al.* (1991)
43 **Gjertz and Wiig (1992)**
44 **Donaldson *et al.* (1995)**
45 Fay (unpublished)

Appendix 2. Hourly identification scores (1 = identifiable, 0 = unidentifiable) for walrus prey during laboratory digestion. Flesh weight of each specimen at the start of each digestion trial in grams.

Polychaete worms							
(n = 21)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Nephtys	1.3	0	0	0	0	0	0
Nephtys	2.0	0	0	0	0	0	0
Nereis	2.3	0	0	0	0	0	0
Nereis	2.7	0	0	0	0	0	0
Nephtys	3.3	1	1	0	0	0	0
Nereis	3.6	0	0	0	0	0	0
Nereis	3.8	1	0	0	0	0	0
Nereis	4.3	0	0	0	0	0	0
Nereis	4.3	1	0	0	0	0	0
Nereis	4.4	0	0	0	0	0	0
Nereis	4.7	0	0	0	0	0	0
Nereis	5.5	1	0	0	0	0	0
Nereis	6.0	1	1	0	0	0	0
Nephtys	6.9	1	1	0	0	0	0
Nereis	8.0	0	0	0	0	0	0
Nephtys	8.7	1	0	0	0	0	0
Nephtys	12.0	1	1	0	0	0	0
Nephtys	12.1	1	1	0	0	0	0
Nephtys	12.4	1	1	0	0	0	0
Nephtys	22.5	1	1	0	0	0	0
Nephtys	23.0	1	1	0	0	0	0

Echiurid worms							
(n = 9)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Echiurus	8.9	1	1	0	0	0	0
Echiurus	13.7	1	1	0	0	0	0
Echiurus	18.1	1	1	0	0	0	0
Echiurus	19.3	1	1	0	0	0	0
Echiurus	21.2	1	1	0	0	0	0
Echiurus	36.9	1	1	1	0	0	0
Echiurus	56.0	1	1	0	0	0	0
Echiurus	56.5	1	1	1	0	0	0
Echiurus	73.6	1	1	1	1	0	0

Appendix 2. (continued)

Sipunculid worms							
(n = 14)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Golfingia	1.4	0	0	0	0	0	0
Golfingia	2.0	0	0	0	0	0	0
Golfingia	2.1	0	0	0	0	0	0
Golfingia	2.7	0	0	0	0	0	0
Golfingia	3.0	0	0	0	0	0	0
Golfingia	3.3	0	0	0	0	0	0
Golfingia	3.5	0	0	0	0	0	0
Golfingia	4.0	0	0	0	0	0	0
Golfingia	4.3	1	0	0	0	0	0
Golfingia	6.2	0	0	0	0	0	0
Golfingia	9.6	1	0	0	0	0	0
Golfingia	10.0	0	0	0	0	0	0
Golfingia	13.0	0	0	0	0	0	0
Golfingia	15.0	0	0	0	0	0	0

Snails							
(n = 14)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Fusitriton	7.7	1	1	1	1	1	1
Fusitriton	8.9	1	1	1	1	1	1
Fusitriton	11.2	1	1	1	1	1	1
Fusitriton	11.4	1	1	1	1	1	1
Fusitriton	11.8	1	1	1	1	1	1
Fusitriton	12.5	1	1	1	1	1	1
Fusitriton	12.6	1	1	1	1	1	1
Fusitriton	12.6	1	1	1	1	1	1
Fusitriton	12.8	1	1	1	1	1	1
Fusitriton	14.0	1	1	1	1	1	1
Fusitriton	16.5	1	1	1	1	1	1
Fusitriton	17.9	1	1	1	1	1	1
Fusitriton	18.9	1	1	1	1	1	1
Fusitriton	25.2	1	1	1	1	1	1

Appendix 2. (continued)

Clams (n = 23)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Clinocardium	2.9	1	1	1	1	0	0
Clinocardium	4.7	1	1	1	0	0	0
Mya	5.3	1	1	1	1	1	1
Mya	5.4	1	1	1	1	1	0
Clinocardium	7.5	1	1	1	0	0	0
Mya	7.6	1	1	1	1	0	0
Mya	10.7	1	1	0	0	0	0
Tellina	10.7	1	1	1	1	1	1
Mya	18.5	1	1	1	1	1	0
Mya	18.6	1	1	0	0	0	0
Clinocardium	19.4	1	1	1	1	1	1
Mya	22.1	1	1	1	1	1	1
Mya	26.2	1	1	1	1	0	0
Mya	38.4	1	1	1	1	1	1
Clinocardium	40.2	1	1	1	1	1	0
Tellina	40.4	1	1	1	1	1	0
Tellina	42.1	1	1	1	1	1	1
Clinocardium	43.4	1	1	1	1	1	1
Tellina	51.8	1	1	1	1	1	1
Tellina	60.8	1	1	1	1	1	1
Tellina	61.5	1	1	1	1	1	1
Clinocardium	79.8	1	1	1	1	1	1
Tellina	80.9	1	1	1	1	1	1

Crustaceans (n = 10)	weight (g)	hr 1	hr 2	hr 3	hr 4	hr 5	hr 6
Pagurus	1.4	1	1	1	1	1	1
Pagurus	3.5	1	1	1	1	1	1
Telmessus	6.1	1	1	1	1	1	1
Cancer	6.5	1	1	1	1	1	1
Pagurus	7.0	1	1	1	1	1	1
Cancer	7.2	1	1	1	1	1	1
Hyas	8.6	1	1	1	1	1	1
Cancer	11.9	1	1	1	1	1	1
Cancer	13.7	1	1	1	1	1	1
Cancer	19.5	1	1	1	1	1	1

Appendix 3. Kapplan-Meier survival estimates (KME), expressed as percentages, with lower 95% (LCL) and upper 95% (UCL) binomial confidence limits, based on hourly examination of specimens digested in the laboratory.

Polychaete worms *n* = 21	KME	LCL	UCL
Hour 1	57	34	78
Hour 2	38	18	62
Hour 3	0	0	16
Hour 4	0	0	0
Hour 5	0	0	0
Hour 6	0	0	0

Snails *n* = 11	KME	LCL	UCL
Hour 1	100	72	100
Hour 2	100	72	100
Hour 3	100	72	100
Hour 4	100	72	100
Hour 5	100	72	100
Hour 6	100	72	100

Sipunculid worms *n* = 14	KME	LCL	UCL
Hour 1	14	02	42
Hour 2	0	0	23
Hour 3	0	0	0
Hour 4	0	0	0
Hour 5	0	0	0
Hour 6	0	0	0

Clams *n* = 23	KME	LCL	UCL
Hour 1	100	85	100
Hour 2	100	85	100
Hour 3	91	72	99
Hour 4	83	61	95
Hour 5	70	47	87
Hour 6	52	31	73

Echiurid worms *n* = 9	KME	LCL	UCL
Hour 1	100	66	100
Hour 2	100	66	100
Hour 3	33	07	70
Hour 4	11	03	48
Hour 5	0	0	34
Hour 6	0	0	0

Crustaceans *n* = 10	KME	LCL	UCL
Hour 1	100	---	---
Hour 2	100	---	---
Hour 3	100	---	---
Hour 4	100	---	---
Hour 5	100	---	---
Hour 6	100	---	---

Appendix 4. Taxa identified from all walrus stomachs collected in the Bering Sea by region: northern ($n = 415$), western ($n = 137$), southeastern ($n = 51$), and central ($n = 8$). Highlighted taxa are summaries. (U = unidentified).

	N	W	SE	C		N	W	SE	C		N	W	SE	C		N	W	SE	C
CNIDARIA	x	x	x		*Onchidiopsis*	x				*Hiatella*	x	x	x		*Paralithodes*		x		
Anemone	x	x	x		*Velutina*	x				**Cephalopoda**	x	x		x	*Hyas*	x	x		
Jellyfish	x				U. Naticidae	x		x	x	Octopus	x	x		x	*Chionoecetes*	x	x	x	
Soft coral	x				*Natica*	x	x	x	x						Crab egg clusters	x			x
					Polinices	x	x	x	x	**BRACHIOPODA**			x						
RHYNCHOCOELA	x				*Buccinum*	x		x	x						**ECHINODERMATA**				
					Neptunea	x	x	x	x	**BRYOZOA**	x				**Holothuroidea**	x	x	x	
PRIAPULA	x	x	x	x	*Clinopegma*		x		x						U. Holothuroidean	x	x	x	
					Margarites	x		x	x	**CRUSTACEA**	x	x	x	x	*Cucumaria*	x	x	x	
ANNELIDA					*Solariella*	x				U. Crustacean	x	x	x		*Psolus*	x			
Polychaeta	x	x	x	x	*Turritella*	x				**Thoracica**	x				*Stolus*	x		x	
U. Polychaete	x	x	x	x	Egg clusters	x			x	*Balanus*	x								
Lumbrineris	x	x	x		Nudibranch	x				**Amphipoda**	x	x	x		**UROCHORDATA**				
Nephtys	x	x	x		**Bivalvia**	x	x	x	x	U. Amphipod	x	x	x		**Asciidiacea**	x	x	x	
Arenicola	x		x		Nucula	x				*Ampelisca*	x				U. Tunicates	x		x	
U. Maldanidae	x				*Yoldia*	x			x	*Byblis*	x				*Pelonaia*	x	x	x	
Maldane	x				*Musculus*	x				*Anonyx*	x	x	x		*Halocynthia*			x	
U. Terebellidae		x			*Thyasira*	x				*Hippomedon*	x								
Terebella			x		*Cardita*	x			x	*Protomedeia*	x				**VERTEBRATA**				
Pectinaria	x				*Astarte*	x	x	x		*Lembos*	x				**Osteichthyes**	x	x	x	
Flabelligera	x	x	x		U. Carditae	x				**Isopoda**	x				U. Fish	x		x	
Brada	x	x	x		U. Cardiidae	x	x	x	x	*Saduria*	x				*Ammodytes*	x	x		
Phyllodoce	x		x		*Clinocardium*	x			x	**Decapoda**	x	x	x	x	**Aves**	x		x	
					Serripes	x	x	x	x	U. Decapod	x	x	x		*Cepphus*	x			
ECHIURA	x	x	x	x	*Mactra*	x				U. Crangonidae	x		x		*Phalacrocorax*			x	
					Mactromeris	x	x	x		*Crangon*	x		x		**Mammalia**	x		x	
SIPUNCULA	x	x			*Siliqua*	x		x		*Argis*	x		x		U. Seals	x			
					U. Tellinidae	x	x	x	x	*Sabinea*	x				*Erignathus barbatus*	x		x	
MOLLUSCA	x	x	x	x	*Macoma*	x				*Sclerocrangon*	x				*Phoca hispida*	x			
Gastropoda	x	x	x	x	*Tellina*	x		x		U. Paguridae	x	x	x		*Phoca largha*	x			
U. Gastropod	x		x		*Liocyma*	x				*Pagurus*	x		x						
Boreoscala	x				*Mya*	x	x	x		*Labidochirus*	x								

Appendix 5. Taxa identified from all walrus stomachs collected in the Chukchi Sea by region: northeastern ($n = 70$), southwestern ($n = 56$), northwestern ($n = 58$), southeastern ($n = 3$). Highlighted taxa are summaries. (U. = unidentified).

	NE	SW	NW	SE		NE	SW	NW	SE		NE	SW	NW	SE		NE	SW	NW	SE
CNIDARIA	x	x	x		*Buccinum*	x	x	x		*Gammarus*		x			**VERTEBRATA**	x	x	x	
Anemone	x	x			*Neptunea*	x	x	x		*Anonyx*	x	x	x		**Osteichthyes**	x			
Sea pen	x	x	x		*Clinopegma*			x		*Onissimus*		x			U. Fish	x			
U. Anthozoan		x			*Margarites*	x	x	x	x	*Acanthostephia*			x		**Mammalia**	x	x	x	
					Egg clusters	x	x	x		*Lembos*		x			U. Seals	x			
RHYNCHOCOELA			x		**Bivalvia**	x	x	x	x	**Decapoda**	x	x	x	x	*Phoca hispida*		x	x	
					U. Bivalve	x			x	U. Decapod	x	x	x						
PRIAPULA	x	x	x	x	*Nucula*	x	x	x		*Eualus*		x							
					Nuculana		x	x		U. Crangonidae	x		x						
ANNELIDA					*Yoldia*	x	x	x		*Crangon*				x					
Polychaeta	x	x	x	x	*Mytilus*	x				*Argis*	x	x	x						
U. Polychaete	x	x	x		*Cyclocardia*	x				*U. Paguridae*	x	x	x						
Lumbrineris		x	x	x	*Astarte*	x	x	x		*Pagurus*	x	x	x	x					
Nephtys		x	x		*Serripes*	x	x	x		*Hyas*	x	x	x						
Aphrodite		x	x		*Mactromeris*	x				*Chionoecetes*		x	x						
Arenicola			x		*Siliqua*				x	Crab egg clusters			x						
U. Maldanidae	x	x	x		U. Tellinidae	x	x	x											
Maldane		x	x		*Macoma*		x	x		**ECHINODERMATA**									
Owenia	x				*Tellina*				x	**Holothuroidea**	x	x	x						
U. Terebellidae			x		*Mya*	x	x	x		U. Holothurian	x		x						
Flabelligera	x	x	x		*Hiatella*	x	x	x		*Cucumaria*	x	x	x						
Brada		x			**Cephalopoda**	x	x	x		*Stolus*		x							
					Octopus	x	x	x		**Ophiuroidea**		x							
ECHIURA	x	x	x							*Ophiura*		x							
					BRYOZOA		x	x											
SIPUNCULA	x	x	x							**UROCHORDATA**									
					CRUSTACEA	x	x	x	x	**Asciidiacea**	x	x	x						
MOLLUSCA	x	x	x	x	U. Crustacean		x	x		U. Tunicates		x	x						
Gastropoda	x	x	x	x	**Cumacea**		x			*Pelonaia*	x	x	x						
U. Gastropod	x	x	x		*Diastylis*		x												
Onchidiopsis	x	x	x		**Amphipoda**	x	x	x											
U. Naticidae	x	x	x		U. Amphipod	x	x	x											
Natica	x	x	x	x	*Ampelisca*	x	x	x											
Polinices	x	x	x	x	*Byblis*		x												