FOODS AND FEEDING OF BOWHEAD WHALES IN WESTERN AND NORTHERN ALASKA

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ABSTRACT

Samples were collected from the gastrointestinal tracts of 20 bowhead whales taken by Eskimo whalers at several locations on the western and northern coast of Alaska. A probable total of 56 species of prey was found, including 50 species of crustaceans, 3 molluscs, and 3 fishes. Most of the prey species (23) were gammarid amphipods, which occurred in 13 of the samples examined. Of the individual prey species, the most frequently encountered were a euphausiid, *Thysanoessa raschii* (11 occurrences); a copepod, *Calanus hyperboreus* (10 occurrences); and a hyperiid amphipod, *Parathemisto libellula* (8 occurrences).

In samples from stomachs containing appreciable amounts of recognizable food, copepods were the dominant prey in nine, euphausiids in six, and gammarid amphipods in one. The latter was a whale taken at Gambell in May; the others were all taken at Barrow in May, or at Barrow or Kaktovik in September-October. Based on volumetric composition of the samples, euphausiids were the dominant (90.3% total contents) prey at Barrow in autumn (n=2). Whales taken there in May (n=4) had eaten substantial amounts of copepods (30.7%), as well as euphausiids (59.1%). Copepods (66.1%) and euphausiids (31.2%) were the dominant prey of whales taken at Kaktovik in autumn (n=8). The organisms most commonly eaten ranged from about 3 to 30 mm in length.

Based on stomach contents and other information, two important feeding areas in Alaska can at present be identified: the area between Barter Island and the U.S.-Canada demarcation line, and the region from Point Barrow to approximately Pitt Point. The organisms eaten in the Beaufort Sea in autumn are extremely high in fat and caloric content when compared to other species and more southern areas. Calculations indicate that prey densities are adequate for whales to obtain their annual energy needs during a 130-day feeding season, and that annual production in most years is probably adequate to support populations of bowheads and other consumers of zooplankton. Arctic cod are the major consumers of copepods and euphausiids in the area. Aspects of feeding ecology are obviously of great importance to the recovery of the presently reduced bowhead whale population. A major question is whether bowheads can reoccupy portions of the Bering and Chukchi seas that were once used as summer feeding areas.

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INTRODUCTION

Bowhead whales, *Balaena mysticetus*, make extensive annual migrations from wintering areas in the Bering Sea to summering grounds in Amundsen Gulf and the Beaufort and Chukchi seas (Braham *et al.* 1982). It has generally been assumed that bowheads, like other mysticete cetaceans, feed principally during the summer, and that their migration therefore is undertaken in order to reach preferred feeding areas. However, aspects of the feeding biology of bowheads are very poorly known.

The foods of most species of baleen whales are well documented since they have been the objects of commercial harvests in the 19th and 20th centuries and the contents of stomachs of harvested whales have been carefully examined (e.g., Nemoto 1957, Tomilin 1957). Bowheads were also extensively harvested by commercial whalers in the late 1800's and early 1900's. However, since they usually were processed only for baleen and sometimes for oil, the contents of stomachs were rarely, if ever, examined. Tomilin (1957) concluded based on indirect evidence that copepods (*Calanus finmarchicus*) and pteropods (*Limacina helicina*) were major food items. MacGinitie (1955) in a report based on work done at Point Barrow indicated that bowheads ate euphausiids, mysids, pteropods, and copepods. Johnson *et al.* (1966) examined the stomachs of two bowheads taken at Point Hope in April 1960 and May 1961. One stomach was empty; in the other, they found fragments of polychaetes, crabs, snails, crustaceans, and echinoderms. Mitchell (1975) stated that bowheads eat principally small and medium-sized zooplankton but sometimes also eat benthic organisms such as amphipods and mysids.

Since 1976 we have obtained and examined samples of the stomach contents of bowhead whales taken by Eskimo whalers at several locations on the western and northern coasts of Alaska. Those samples were collected for us through the cooperation of the Alaska Eskimo Whaling Commission and the National Marine Fisheries Service. Results of our analyses of the samples have been in part reported (Lowry *et al.* 1978, Lowry and Burns 1980). In this paper we will report and summarize all our observations on stomach contents of bowheads, examine the importance of various prey species in their diet, identify major feeding areas in Alaskan waters, and discuss the overall feeding strategy of bowheads in the western Arctic.

METHODS

Samples of bowhead whale foods were collected for us by a number of different persons. All samples were from the gastrointestinal tracts, usually the forestomachs, of whales taken by Eskimo subsistence hunters and were generally obtained within a few hours of the time the whales were killed and landed. The samples which we obtained were usually preserved in buffered 10% formalin and ranged in volume from a few mL to over 2L. The total volume of food present in the stomach of each whale was usually estimated and recorded in the field.

In the laboratory, samples were drained and gently washed on a 1.00-mm mesh sieve. Food material was then sorted macroscopically into major taxonomic groups, and the water displacement volume of each group was determined. The organisms in each group were examined microscopically when necessary and identified to species if possible. Identifications were made using appropriate keys and reference specimens in collections at the Alaska Department of Fish and Game and the University of Alaska. The number of individuals and total volume of each prey species were determined, and lengths of representative specimens were measured. In the case of abundant, small organisms such as copepods, the volume and number of the various species were estimated from subsamples.

RESULTS

We examined samples of prey items from the gastrointestinal tracts of 20 bowhead whales. With three probable exceptions, all were collected from stomach contents. Seven of the samples were from whales taken near Point Barrow, nine from whales taken near Kaktovik, two from Point Hope, and one each from Shaktoolik and Gambell (Table 1). All of the samples from Kaktovik and two of those from Barrow were from whales taken in the autumn (September or October); all of the others were from whales taken in the spring (May).

TABLE 1. BOWHEAD WHALE SPECIMENS FROM WHICH SAMPLES OF PREY ITEMS WERE OBTAINED

Specimen number	Location	Date of kill	Sex	Total length (m)	Comments
76-B-6F	Barrow	10 Sep 76	female	16.0	reported to be an ingutuk
76-B-7F	Barrow	20 Sep 76	female	14.3	
77-B-5	Barrow	5 May 77	male	10.6	killed at 1600 hrs local time
79-B-3	Barrow	27 May 79	male	8.3	sample from colon
80-B-3	Barrow	25 May 80	male	8.5	killed at 0630 hrs local time
80-B-5	Barrow	25 May 80	male	10.4	killed at 0616 hrs local time
80-B-9	Barrow	27 May 80	female	13.7	killed at 1800 hrs local time
79-KK-1	Kaktovik	20 Sep 79	male	12.7	recovered on 22 September
79-KK-2	Kaktovik	6 Oct 79	female	10.5	
79-KK-3	Kaktovik	8 Oct 79	male	10.3	
79-KK-4	Kaktovik	10 Oct 79	male	10.6	
79-KK-5	Kaktovik	11 Oct 79	male	10.6	killed at 1740 hrs local time
80-KK-1	Kaktovik	14 Sep 80	male	9.1–10.7	sample probably from small intestine
81-KK-1	Kaktovik	8 Sep 81	female	17.4	killed at 1430 hrs local time
81-KK-2	Kaktovik	11 Sep 81	male	14.0	killed at 1700 hrs local time
82-KK-1	Kaktovik	23 Sep 82	male	16.0	killed at 2100 hrs local time
78-H-2	Point Hope	4 May 78	male	9.7	
79-H-3	Point Hope	6 May 79	male	9.1	
80-SH-1	Shaktoolik	9 May 80	male	10.1	sample from colon
82-G-2	Gambell	1 May 82	female	8.8	killed at 1533 hrs local time

Depending on the state of digestion of the samples, it was more or less difficult to determine the specific identity of the prey. Some prey could be identified only to phylum, family, or genus when only fragments occurred in the samples. Small, fragile organisms such as copepods were difficult to identify to species except in comparatively fresh stomach contents. Larger, more durable organisms such as amphipods and molluscs could generally be identified in mostly digested stomach or intestinal samples. The presence of euphausiids was easy to detect due to the persistent and characteristic nature of the eyes which detach from the body during digestion. Entirely soft-bodied animals such as coelenterates, salps, chaetognaths, and pteropods may not have been detected in some samples examined, although they would have been readily observed in those which were in fresh condition.

Eliminating those organisms which could not be identified to species but which probably represented species found in other samples (e.g., *Calanus* sp., *Gammarus* sp., Family Lysianassidae, and Family Crangonidae), a probable total of 56 prey species was found in the 20 whales containing identifiable food remains (Table 2). With the exception of three species each of molluscs and fishes, all identified prey were crustaceans. The distribution of prey species among the major groups of crustaceans was: gammarid amphipods—23; copepods—10; hyperiid amphipods—5; shrimps—3; euphausiids, mysids, and crabs—2 each; and isopods, cumaceans, and ostracods—1 each. The number of times each of the major prey groups occurred in the samples was: gammarid amphipods—13; copepods—12; euphausiids and hyperiid amphipods—11 each; mysids and shrimps—6 each; fishes—5; molluscs—4; crabs and cumaceans—2 each; and isopods and ostracods—1 each. Of the individual prey species, the most frequently encountered were *Thysanoessa raschii* (11 occurrences), *Calanus hyperboreus* (10 occurrences), and *Parathemisto libellula* (8 occurrences). All the remaining prey species occurred in fewer than five stomachs, while 41 species occurred in only one or two samples. Pebbles, generally less than 1 cm in size, occurred in six samples.

Copepods or euphausiids were the dominant component of all except five of the samples we examined (Table 2). Two of those were from colons and contained shrimp fragments and small clams. Two others contained a single amphipod and a single snail. The fifth contained gammarid amphipods, cumaceans, and other benthic organisms. In the other 15 samples, euphausiids were the major food in six, and copepods were dominant in nine. In most of the samples, either *Thysanoessa raschii* or *Calanus hyperboreus* was the dominant prey species. At Barrow, *T. raschii* was the dominant prey in both whales taken in September, while in samples from spring *T. raschii* and copepods (*Calanus hyperboreus*, *Euchaeta glacialis*, and *Metridea longa*) each predominated in two. In samples from whales at Kaktovik, all of which were taken in late September and early October, copepods (principally *C. hyperboreus*) were dominant in seven and *T. raschii* in two.

Eliminating the samples obtained from small intestines or colons and those from stomachs which contained only a single food item, food remains were found in the stomachs of 15 whales. One of those (82-G-2) was a whale taken in the Bering Sea near Gambell on 1 May 1982. The stomach of that whale was recorded

TABLE 2. PREY IDENTIFIED FROM GASTROINTESTINAL TRACTS OF BOWHEAD WHALES. DOMINANT PREY SPECIES ARE INDICATED BY ××

	BARROW							KAKTOVIK									OTHER AREAS			
	76-B-6F	76-B-7F	77-B-5	79-B-3[1]	80-B-3	80-B-5	80-B-9	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	80-KK-1[2]	81-KK-1	81-KK-2	82-KK-1	78-H-2	79-H-3	80-SH-1[1]	82-G-2
COPEPODS													××							
Calanus cristatus					×															
C. finmarchicus											×									
C. glacialis			×				×							×	×	×				
C. hyperboreus					××		×	××	××	×	××	×		××	××	××				
Calanus sp.					×				×		×									
Chiridius obtusifrons					×		×				×									
Euchaeta glacialis			×		××											×				
Heterorhabdus sp.									×		×									
Metridea longa			××													×				
M. lucens									×		×									
Pseudocalanus sp.			×											×						
EUPHAUSIIDS																				
Thysanoessa inermis					×		×					×								
T. raschii	××	××	×		×	××	××		×	××	×	××		×						
MYSIDS																				
Mysis litoralis							×		×	×		×								
Neomysis rayi					×	×	×													
HYPERIID AMPHIPODS																				
Hyperia galba					×		×													
H. medusarum							×		×											
Hyperia sp.								×												
Hyperoche medusarum							×													
Parathemisto abyssorum			×							×				×						
P. libellula	×	×						×	×	×	×	×				×				

Continued...

TABLE 2. Continued.

	BARROW							KAKTOVIK									OTHER AREAS			
	76-B-6F	76-B-7F	77-B-5	79-B-3[1]	80-B-3	80-B-5	80-B-9	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	80-KK-1[2]	81-KK-1	81-KK-2	82-KK-1	78-H-2	79-H-3	80-SH-1[1]	82-G-2
GAMMARID AMPHIPODS																				
Acanthostepheia behringiensis		×								×		×								
A. incarnata									×											
Ampelisca macrocephala																	×			
Anonyx compactus																				×
A. nugax							×													
Apherusa glacialis											×			×						
Atylus atlassovi																				×
A. carinatus										×		×								
Bathymedon sp.																				×
Gammaracanthus loricatus										×		×								
Gammarus zaddachi		×																		
Gammarus sp.									×											
Hippomedon denticulatus																				×
Monoculodes zernovi		×																		
Monoculodes sp.										×	×									×
Munnopsis c.f. *M. typica*										×										
Onisimus glacialis									×					×	×	×				
O. litoralis								×												
O. nanseni															×					
Orchonome sp.																				×
Pontoporeia femorata																				×
Rozinante fragilis	×	×									×									
Weyprechtia heulgini											×	×								
W. pinguis													×							
Family Lysianassidae								×												
Family Synopiidae																				×

ISOPODS															
Saduria entomon											×				
SHRIMP		×						×						×	
Eualus fabricii															×
E. gaimardii										×					
Sabinea septemcarinata										×					
Family Crangonidae							×								
CRABS															
Chionoecetes opilio															×
Family Paguridae (zoea)												×			
CUMACEANS															
Diastylis bidentata															×
Diastylis sp.										×					
OSTRACODS			×												
MOLLUSCS															
Limacina helicina			×												
Natica clausa													×		
Nuculana sp.				×											
Order Pelecypoda															×
FISHES			×												
Boreogadus saida								×			×				
Myoxocephalus quadricornis									×		×				
Pungitius pungitius											×				
Family Cottidae															×
PEBBLES	×				×	×	×			×					×

[1] Sample from colon.
[2] Sample probably from small intestine.

as full and contained an estimated 30L of food. Based on the sample we examined, the prey was composed of 92% gammarid amphipods, 7% cumaceans, and 1% other benthic organisms. Four small pebbles also occurred in the sample.

The quantitative composition of stomach contents samples from the remaining 14 whales is shown in Tables 3 and 4. Euphausiids dominated in the stomach contents of whales taken at Barrow in the autumn. Whales taken at Barrow in the spring contained principally euphausiids and copepods in variable proportions, with substantial amounts of mysids in three. Total quantities of food in whales taken during spring were very small. In whales taken in the autumn at Kaktovik,

TABLE 3. QUANTITATIVE DATA (% OF TOTAL SAMPLE VOLUME) ON STOMACH CONTENTS OF BOWHEAD WHALES TAKEN AT BARROW

Prey type	AUTUMN 1976			SPRING 1977 AND 1980				
	Whale specimen number		Overall mean % of contents[1]	Whale specimen number				Overall mean % of contents[2]
	76-B-6F	76-B-7F		77-B-5	80-B-3	80-B-5	80-B-9	
Copepod	—	—	—	97.0	24.2	—	1.4	30.7
Euphausiid	97.1	86.7	90.3	1.0	48.5	95.4	91.6	59.1
Mysid	—	—	—	—	15.2	3.8	5.4	6.1
Hyperiid amphipod	2.3	3.0	2.7	<0.1	3.0	—	1.0	1.0
Gammarid amphipod	0.6	10.3	6.9	—	—	—	0.6	0.2
Other invertebrate	—	<0.1	<0.1	2.0	—	—	—	0.5
Sample volume (ml)	17.5	33.0		20.0	3.3	73.4	139.7	
Estimated total volume of contents (liters)	unknown	109		unknown	"a few invertebrates"	1	2	

[1] Calculated as the percent of combined total volume in the two samples.

[2] Calculated as the average of the percent of total volume in each of the samples.

TABLE 4. QUANTITATIVE DATA (% OF TOTAL SAMPLE VOLUME) ON STOMACH CONTENTS OF BOWHEAD WHALES TAKEN AT KAKTOVIK, AUTUMN 1979-1982

Prey type	Whale specimen number								Overall mean % of contents[1]
	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5	81-KK-1	81-KK-2	82-KK-1	
Copepod	99.7	99.0	23.4	88.3	<0.1	99.0	99.0	98.7	66.1
Euphausiid	—	0.3	67.8	4.9	97.9	0.7	—	—	31.2
Mysid	—	0.3	7.0	—	0.8	—	—	—	1.2
Hyperiid amphipod	<0.1	0.1	0.5	0.4	—	<0.1	—	<0.1	0.1
Gammarid amphipod	0.1	0.1	0.3	2.4	0.1	0.3	1.0	1.3	0.4
Other invertebrate	<0.1	<0.1	—	2.3	1.1	<0.1	—	—	0.5
Fish	<0.1	0.1	1.0	1.7	—	—	—	—	0.3
Sample volume (ml)	2406.2	545.2	399.7	131.3	357.9	145.5	19.2	95.2	
Estimated total volume of contents (liters)	44	18	22	18	36	18	3	"a few"	

[1] Calculated based on the volume and percent composition of each sample and the estimated total contents volume of stomachs from which samples were taken.

TABLE 5. SIZES OF PREY ORGANISMS IN STOMACHS OF BOWHEAD WHALES

	Length (mm)[1]	Volume (mL)
Copepods	3.5–7.0	0.002–0.02
Euphausiids	18–30	0.1–0.15
Mysids	23–33	0.1–0.2
Hyperiid amphipods	8–21	0.05–0.1
Gammarid amphipods	7–55	0.02–4.0
Isopods	52–86	3.4–5.7
Fishes	31–83	0.1–2.9

[1] Measurements are total length for all groups except copepods, which are cephalothorax length.

copepods and euphausiids in aggregate comprised 91.2–99.7% of the contents of individual samples and 97.3% of the overall prey in all samples combined. The stomach contents in individual whales varied from 99.7% copepods to 97.9% euphausiids; overall, copepods comprised about twice as much of the stomach contents as did euphausiids. The total volume of stomach contents in the whales varied from 3 to 44L, with an average of 23L.

Sizes of representative species of the major prey groups eaten by bowheads are shown in Table 5. The organisms most commonly eaten (copepods, euphausiids, mysids, and amphipods) range from about 3 to 30 mm in length and have a volume of 0.002 to 0.2 mL. Organisms such as isopods and fishes are considerably larger but were rarely found in stomach contents samples. The largest item we found in bowhead stomach contents was the shell of a snail (*Natica clausa*), 3.4 cm high and 2.6 cm in basal diameter, weighing 8.0 g. The smallest items were *Pseudocalanus* copepods, which are approximately 1.3 mm in cephalothorax length and weigh about 0.1 mg.

In addition to the whales from which samples were collected, some additional animals were examined in the field and the presence or absence of food in their stomachs recorded. Of whales taken in the Bering Sea in spring, two had prey in the stomach: one taken at Gambell (82-G-2) contained gammarid amphipods, cumaceans, and other benthic organisms; the other (78-S-1) taken at Savoonga was reported to contain "a few euphausiid-like creatures." Three had empty stomachs: two of those reportedly had material in the intestines, and the third had crustaceans in the baleen. Of four whales taken in the Chukchi Sea in spring, two had empty stomachs, one contained a snail, the other a single gammarid amphipod. Four whales taken at Barrow in spring have contained food remains, and seven have been recorded as having empty stomachs. Three of the latter had some food residues in the intestines. All whales that have been taken and examined in the autumn (2 at Barrow and 10 at Kaktovik) have contained substantial quantities of food.

We examined the relationship between whale size and the principal type of prey found in samples based on 18 animals of known length which contained recognizable prey. Whales that had eaten principally copepods ranged from 10.5 to 17.4 m, with a mean length of 13.1 m (n=7). Those that contained mostly euphausiids ranged from 8.5 to 16.0 m, with a mean of 12.0 (n=7). Five whales in which we found only benthic organisms were 8.3—10.1 m, with a mean length of 9.2 m. Only one of the whales that had eaten copepods or euphausiids was less than 10.3 m in length.

DISCUSSION

We identified a wide array of organisms from samples taken from the gastrointestinal tracts of bowhead whales. Most of the prey species (53/56) were invertebrates, and most of those (35/53) were primarily benthic organisms. However, with few exceptions, benthic species composed a very small proportion of the overall stomach contents. Four of the five exceptions were whales taken in spring in the Bering and Chukchi seas; the fifth was a whale taken at Barrow in spring whose colon contained three small clams. The two taken in the Chukchi Sea each contained single items. One of those taken in the Bering Sea had an empty stomach but shrimp fragments in the colon; the other had a stomach filled with benthic invertebrates. The five whales were all small, the largest being 10.1 m long, and were undoubtedly subadult animals (Marquette 1978). We conclude, based on the samples we examined and field records, that some bowheads feed while passing through the northern Bering Sea in May. The incidence of feeding during the northward migration appears to be less in the Chukchi Sea than in the Bering. Feeding whales may be predominantly juveniles, and their prey are mostly benthic invertebrates.

Four of 11 whales taken and examined at Barrow in the spring have contained food in their stomachs, generally a few liters or less of copepods and euphausiids. We conclude that some feeding occurs near Barrow during the spring migration and that planktonic organisms are the main prey. However, based on the high proportion of empty stomachs and the small volumes of contents in those containing food, it appears that the main feeding season has not yet commenced.

Many bowhead whales summer in the eastern Beaufort Sea (Fraker and Bockstoce 1980), where they are presumed to feed extensively (Griffiths and Buchanan 1982). Whales that have been taken and examined while moving westward through the Alaskan Beaufort Sea in autumn have all contained food. Whales taken at Barrow have contained mostly euphausiids, while in those taken near Kaktovik both copepods and euphausiids occur, with copepods overall predominating in the samples. Benthic organisms are quantitatively unimportant near Kaktovik but comprised a small and perhaps significant proportion of the samples examined from Barrow. Feeding of whales in autumn is obviously directed primarily at organisms in the water column, with benthic organisms being taken incidentally during near-bottom feeding.

Several lines of evidence point to the existence of at least two areas of the Alaskan Beaufort Sea where bowheads regularly feed during September-October. First, of course, is the occurrence of substantial quantities of food in the stomachs of all the whales taken and examined at Kaktovik and Barrow during autumn hunts. Whalers from Kaktovik have indicated that they regularly find bowheads feeding in the area to the east of Barter Island (D. Ljungblad, pers. commun.; G. Jarrell, pers. commun.). In discussing bowheads in the area to the east of Point Barrow, Durham (1979) stated that " the hunters sometimes encounter herds of 50 to 60 whales along the Plover Islands (Thomas Brower, pers. commun.). This area may be a rest stop for the whales and provide an opportunity for them to feed, judging from stomach contents."

The feeding area east of Barrow appears to extend to approximately Pitt Point. On 18 September 1974, 57 whales were counted in this area (Braham *et al.* 1982), while on 20 September counts ranged from 81 to 136 (Ray and Wartzok 1980). On 8 August 1976, a single whale was seen just offshore from the Plover Islands (Lowry, unpublished). Two ringed seals (*Phoca hispida*) collected in the immediate area within minutes of sighting the bowhead had been actively feeding on euphausiids (Lowry *et al.* 1980). On 19 August 1976, four bowheads were seen northeast of Point Barrow, and on 21 September 47 whales were counted in the area (Braham *et al.* 1982). As indicated in this report, whales taken at Barrow on 10 and 20 September 1976 had both been feeding on euphausiids. A group of 20 whales which appeared to be feeding was seen north of Point Barrow on 22 October 1978 (Braham *et al.* 1982).

The feeding area in the eastern Beaufort Sea extends from Barter Island east to at least the U.S.-Canada demarcation line (141°W longitude). In 1979, 35 whales were seen milling east of Beaufort Lagoon on 24 September, and 37 were observed north of Demarcation Bay on 26 September (Ljungblad *et al.* 1980). In 1980, single whales that appeared to be feeding were sighted north of Beaufort Lagoon on several occasions from 9 to 21 September, and a group of nine was seen east of Barter Island on 14 September (Frost and Lowry 1981, Ljungblad 1981). On 22 September 1982, 128 bowheads were counted in the area north of Demarcation Bay. Most of the animals were milling around near the surface (S. Johnson, pers. commun.).

Although bowheads may feed regularly or occasionally in other parts of the Alaskan Beaufort Sea, such occurrences cannot be verified by observations of stomach contents since very few whales are taken elsewhere than the areas discussed above. Ljungblad (pers. commun.) has seen bowheads engaged in behavior that might indicate feeding in the areas north of Flaxman Island and northeast of Pingok Island.

The smallest organisms which are regular foods of bowheads are the copepods *Metridea* spp. (cephalothorax length 2.7–3.1 mm) and *Calanus glacialis* (2.4–3.3 mm). The most commonly eaten species of copepod, *Calanus hyperboreus*, is much larger, ranging in length from 3.6 mm (copepodite stage IV) to 6.4 mm (adult). The smaller copepods, *Pseudocalanus* sp. (1.1–1.6 mm long) and *Derjuginia tolli* (1.4–1.8 mm long), although very abundant in the Beaufort Sea (Frost and Lowry 1981), virtually never occur in bowhead stomach contents. It appears, therefore, that organisms smaller than about 2.5 mm are not effectively retained by bowhead baleen. The largest prey regularly consumed appear to be about 30 mm long and

TABLE 6. CALORIC VALUES OF REPRESENTATIVE SPECIES OF ARCTIC ZOOPLANKTON AND BENTHOS, ARRANGED IN ORDER OF DECREASING CALORIC VALUE. ALL VALUES ARE FROM SAMPLES TAKEN IN SEPTEMBER UNLESS OTHERWISE INDICATED. (ADAPTED FROM PERCY AND FIFE 1980.)

Taxon	Cal/g wet weight	% of maximum
Copepod (*Calanus* sp.)		
September	2,983	100
mid-late August	2,660	90
late July-early August	2,018	69
Euphausiid (*Thysanoessa inermis*)	1,974	67
Hyperiid amphipod (*Parathemisto libellula*)	1,364	46
Gammarid amphipod (*Anonyx nugax*)	1,299	44
Chaetognath (*Sagitta elegans*)	517	18
Isopod (*Saduria* (=*Mesidotea*) *sabini*)	367	12
Pteropod (*Clione limacina*)	296	10
Ctenophora (*Mertensia ovum*)	98	3
Cnidaria (*Aglantha digitale*)	89	3

include euphausiids, mysids, and amphipods.

The fact that bowheads migrate several thousands of kilometers annually to summer and feed in the Beaufort Sea implies that the quantities and kinds of food available to them there are adequate, and also perhaps that feeding conditions are superior to those found in other areas. The abundance of copepods in the Beaufort Sea is not remarkably high (Griffiths and Buchanan 1982). The abundance of euphausiids is extremely difficult to quantify (Brodie *et al.* 1978), but observations of predator stomach contents indicate that they may be locally abundant (Frost and Lowry 1981). One way in which arctic marine zooplankton are remarkable is their tendency to accumulate storage lipids during the summer which are used for maintenance and reproduction during winter months (Lee 1975). In samples of *Calanus hyperboreus* collected from Fletcher's Ice Island in October, lipids comprised 64% of the dry weight (Lee 1975). In samples collected in September at Frobisher Bay, lipids comprised 52.4% of the dry weight of *Thysanoessa inermis* and 57.4% of *Calanus* spp. (Percy and Fife 1980). Caloric values of representative species of arctic marine zooplankton and benthos are shown in Table 6. Values are expressed in terms of calories per gram wet weight, which is the most appropriate consideration from the perspective of a consumer. Organisms which are the primary foods of bowheads (copepods and euphausiids) have very high caloric values. Those eaten with some frequency (hyperiid and gammarid amphipods) have intermediate values. Those organisms which are rarely or never consumed have very low caloric values. Of interest also is the fact that copepods in September contain almost 50% more calories than those sampled in late July and early August. Therefore, given equivalent prey densities, late summer feeding may be of greater value to the whales than that which occurs earlier in the year.

Although it is probably true in general that arctic zooplankton are richer in calories than those in more southern latitudes (Percy and Fife 1981), there are few data available with which to verify this hypothesis. Nishiyama (1977) sampled zooplankton in Bristol Bay, Alaska and determined the caloric value of *Calanus* and *Thysanoessa* to be 5,512 and 5,554 cal/g ash-free dry weight. Those values are 44% and 19% lower than comparable measurements for the same species collected at Frobisher Bay (Percy and Fife 1980). The values for caloric content of Frobisher Bay copepods are the highest published values for any marine organism (e.g., see Braun *et al.* 1968, Tyler 1973, Laurence 1976).

Several authors have attempted to assess the relationship between availability of food in the marine environment and the food requirements of whales. Studies dealing with fin whales (*Balaenoptera physalus*) have concluded that either whales swim exceedingly fast, or densities of prey are much greater than those found using standard sampling techniques (Klumov 1961, Brodie *et al.* 1978). Similar results were derived by Brodie (1980) and Griffiths and Buchanan (1982), dealing with bowheads. However, those studies did not take into account the energetic richness of prey available in the Arctic.

We have made similar calculations, starting with the energetic assumptions used by Brodie (1980), who concluded that a bowhead 13.72 m long would need to ingest approximately 4,000 kg of lipids during the feeding season in order to maintain itself throughout the year. Based on data in Percy and Fife (1980), 16.8% of the wet weight of *Calanus* copepods collected in late July and August is lipid; therefore, a whale would need to consume 23,810 kg of copepods during the feeding season. A bowhead 13.72 m long would have baleen approximately 2.4 m long (Alaska Eskimo Whaling Commission, unpubl. data). We assume that while feeding the mouth opening is 2.4 m high and tapers from 2.0 m wide at the bottom to 1.0 m at the top and a whale swims at about 4.2 km/hour (2.8–5.6 km/hr in Ljungblad *et al.* 1981). Using those assumptions, 15,120 m^3 of water would be filtered each hour. Griffiths and Buchanan (1982) observed biomasses of *Calanus* ranging from 0.623–0.903 g/m^3 at certain depths in areas of the Canadian Beaufort Sea where bowheads appeared to be feeding on organisms in the water column. To acquire 23,810 kg of copepods would require filtering 26,367,000–38,218,000 m^3 of water (assuming the above prey densities and 100% filtering efficiency), which would involve 1,744–2,528 hours of feeding. Frost and Lowry (1981) estimated a feeding season of 105 days in the Canadian Beaufort and 25 days in the Alaskan Beaufort Sea, which suggests 3,120 hours available for feeding. Therefore, it appears that bowheads can obtain their annual food requirements with a 130-day feeding season in the Beaufort Sea, if they feed for somewhat over half the time they are on the feeding grounds and concentrate their efforts in areas where prey are relatively abundant. Based on the above assumptions and an average weight for copepods of 0.004 g (Bain *et al.* 1977), the ingestion rate of copepods would be approximately 50,000 individuals per minute.

A further consideration with respect to the bowhead whale stock in the western Arctic is whether the total annual production of prey in the feeding areas is sufficient to supply the energetic requirements of all the whales summering in the area. Although the summer feeding range of the bowhead once included much of the Bering and Chukchi seas as well as the Beaufort Sea (Bockstoce and Botkin 1980), at present the Beaufort Sea is the primary feeding area, although some late season feeding may occur in the Chukchi Sea (Frost and Lowry 1981). Calculations such as those done for an individual whale feeding on copepods cannot be expanded to the entire population because euphausiids, a major prey species, have not been quantitatively sampled properly in the Beaufort Sea (see Frost and Lowry 1981 and Griffiths and Buchanan 1982) and bowhead prey are also eaten by other consumers in the Beaufort Sea. Frost and Lowry (1983) estimated the quantities of prey eaten on an annual basis by populations of major vertebrate consumers in the Alaskan Beaufort Sea. They considered only species which feed primarily on organisms connected to the pelagic/planktonic food web—bowhead whales, white whales (*Delphinapterus leucas*), ringed seals, seabirds, and arctic cod (*Boreogadus saida*). Results indicated that arctic cod are by far the major consumer of zooplankton. They were estimated to eat 97.8% of the total copepod and 65.8% of the total euphausiid biomass consumed annually by all species of predators combined. Estimates for bowhead consumption were 2.2% of the total copepod biomass and 31.5% of the total euphausiid biomass consumed. Although these results suggest the possibility of considerable competition for food, some resource partitioning occurs since many of the copepods eaten by arctic cod are small forms (*Derjuginia* and *Pseudocalanus*), which are not major foods of bowheads (Frost and Lowry in press). Based on extrapolations from measurements of primary production, Frost and Lowry (1981) estimated that 0.3–4.4 million t of zooplankton are produced annually in the Alaskan Beaufort Sea. When compared to the estimated total amount of zooplankton consumed annually (approximately 1.1 million t (Frost and Lowry in press)), this suggests that food availability may be limiting in years of low production, while in other years a surplus of food may be available. Causes of annual variations in productivity and their effects on consumer populations are largely unknown.

What then is the feeding strategy of western arctic bowhead whales? Bowhead whales are robust-bodied animals, possessing long baleen with fine fringes capable of efficiently retaining very small prey. Although our study has shown that some feeding occurs in the northern Bering and Chukchi seas during the spring northward migration, the major known summer feeding grounds are in the Beaufort Sea. The quantities and kinds of organisms there are adequate, and the extraordinarily high fat content (and caloric value) of prey facilitates accumulation of blubber reserves necessary to maintain the animals during periods of fasting. Extensive blubber reserves may help sustain animals through years of low summer productivity which may occasionally occur.

Some late summer and early autumn feeding may occur in the Chukchi Sea. There is no direct information to indicate whether bowheads feed on their wintering grounds in the Bering Sea. However, based on considerations such as the seasonal distribution and abundance of prey, and their probable caloric content, we speculate that winter feeding in the Bering Sea, if it occurs, is of little significance in the annual nutrition of bowheads. Bowhead whales swim from the Bering Sea to the Beaufort Sea to feed because of the high-energy foods available there, and perhaps also because competition for food from other organisms occurs at tolerable levels. No other baleen whale penetrates northward into what is presently the principal feeding grounds for bowheads. In years past, bowheads mingled with other species in the Bering Sea in summer until they were eliminated by predation from commercial whalers. Whether the portions of their feeding range that were lost decades ago will ever be regained is a most interesting question, and one of great significance when contemplating the ability of the western arctic bowhead population to regain its former abundance.

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