Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses

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ABSTRACT

This study examined feeding of bowhead whales (*Balaena mysticetus*) taken by Alaska Natives at Barrow (western Beaufort Sea), Nuiqsut (central Alaskan Beaufort Sea) and Kaktovik (eastern Alaskan Beaufort Sea) during 1969-2000. The objectives were to: (1) identify the proportion of harvested whales that had been feeding; and (2) describe the diet based on stomach contents. Data used were field records for 242 whales whose stomachs were examined and laboratory analysis of samples from 123 animals. There were no significant differences in the proportions of animals that had been feeding during the autumn at Kaktovik (83%) and Barrow (75%), or in sub-adults (78%) versus adults (73%). Copepods occurred significantly more frequently in animals from Kaktovik, while euphausiids and hyperiid amphipods occurred more frequently at Barrow. During the autumn, the percent copepods by volume was greater in animals taken at Kaktovik than at Barrow, while the percent euphausiids by volume was greater in whales taken at Barrow. At Barrow, a larger proportion of animals was feeding in the autumn (76%) than the spring (34%), and copepods occurred more often in the spring. Examination of five whales taken at Nuiqsut in the autumn suggests a feeding pattern similar to that seen at Kaktovik. There were no significant differences in diets of males versus females or of sub-adults versus adults. It is concluded that in the autumn, bowheads feed regularly in the eastern, central and western Alaskan Beaufort Sea, and that feeding during the spring migration is more common than previously thought.

KEYWORDS: BOWHEAD WHALE; ARCTIC; NORTH AMERICA; FEEDING; FOOD/PREY; FEEDING GROUNDS; EUPHAUSIIDS; COPEPODS

INTRODUCTION

The bowhead whale (*Balaena mysticetus*) is the only baleen whale that spends its entire life in cold northern waters. In Alaska, bowhead whales migrate in spring from their Bering Sea wintering grounds to the Beaufort Sea. The return migration generally occurs during the late summer and autumn. The whales travel from their eastern Beaufort Sea summering grounds, westward along the coast, and into the Chukchi Sea (Fraker and Bockstoce, 1980; Moore and Reeves, 1993). At least some of them travel southwest to the northeast coast of the Chukotsk Peninsula in autumn before returning to the Bering Sea for the winter.

Examination of the stomach contents of bowhead whales harvested by Alaska Natives provides an opportunity to study their diet. Bowhead whales are harvested by hunters from three communities along the Alaskan coast of the Beaufort Sea (Fig. 1) and access varies regionally (Stoker and Krupnik, 1993). Due to whale movement patterns and ice conditions, Inupiat subsistence whalers from the community of Kaktovik, in the eastern Alaskan Beaufort Sea, hunt only during the autumn, mainly in September and early October. The same is true of whalers from Nuiqsut, in the central Alaskan Beaufort Sea, who hunt from Cross Island. However, whalers from Barrow, in the western Alaskan Beaufort Sea, have access to bowhead whales during both the spring (April-June) and autumn (September-October) migrations.

Since 1976, stomach contents samples from bowhead whales have been collected by personnel from the North Slope Borough Department of Wildlife Management (NSB-DWM), the Alaska Department of Fish and Game (ADF&G) and the National Marine Fisheries Service (NMFS). Diet data from 30 bowhead whales harvested in the Alaskan Beaufort Sea from 1976-1988 were reported by Lowry *et al.* (1978), Lowry and Burns (1980), Lowry and Frost (1984), Carroll *et al.* (1987) and Lowry (1993). Planktonic crustaceans, especially copepods and euphausiids, were the most important food items found in those studies.

Results of those scientific studies, combined with traditional knowledge of Inupiat subsistence whalers, suggested that the Alaskan Beaufort Sea was an important feeding area for bowhead whales. Concerns about plans to lease the eastern Alaskan Beaufort Sea for oil and gas exploration led the US Minerals Management Service to fund a study to assess the importance of that region for

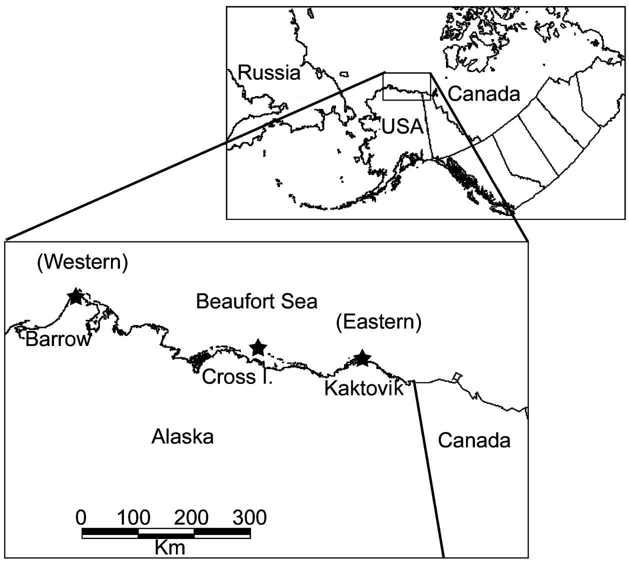

Fig. 1. Map of Alaska and the Beaufort Sea showing the three coastal whaling locations in the Beaufort Sea area: Barrow, Cross Island and Kaktovik.

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bowhead whale feeding. The report from that 1985-1986 study concluded that feeding in the eastern Alaskan Beaufort Sea region was not significant to the annual nutrition of bowheads (Richardson, 1987), but the design of and conclusions from that study were criticised by the North Slope Borough Science Advisory Committee (1987). Partly to resolve that controversy, a multidisciplinary study entitled 'Bowhead whale feeding in the eastern Alaskan Beaufort Sea' was conducted during 1997-2000 (Richardson and Thomson, 2002). As part of that study stomach contents samples were collected from bowheads harvested at Kaktovik; field records and previously-unanalysed stomach contents samples from other bowheads taken in the Beaufort Sea were also acquired and analysed (made available by the NSB-DWM and other sources). The objectives of this study were to: (1) evaluate the frequency of bowhead whale feeding in this region by examining the field records and stomach contents samples from harvested whales; and (2) to quantify the composition of the diet of bowhead whales in the Alaskan Beaufort Sea based on analysis of stomach contents from harvested whales.

METHODS

Field records and feeding status

Bowhead whales harvested in the Beaufort Sea by Alaskan native subsistence whalers during 1969-2000 were classified as either 'feeding', 'not feeding' or 'uncertain' based on descriptive field records and laboratory data on stomach contents. If field records indicated that a substantial amount (i.e. at least 10 items or 1 litre) of prey was present in the stomach, the whale was classified as feeding. If field records indicated that the stomach was empty, the whale was classified as not feeding. If field records recorded the presence of only a small amount of prey (i.e. less than 10 items or less than 1 litre), or that food was present but no quantity was indicated, the feeding status of the whale was recorded as uncertain. For some whales field records did not provide any information about stomach contents, but collected samples were available for laboratory analysis. In those instances, a whale was classified as feeding if the sample contained 10 or more identifiable prey items, not feeding if there were no identifiable prey items, and uncertain if the sample contained fewer than 10 prey items. Items such as algae, feathers and pebbles were not considered to be food items. Data were grouped by harvest location and harvest season. The proportions of feeding whales from different harvest locations and seasons were compared using chi-square tests. Whales with feeding status classified as uncertain were not included in these comparisons.

Collection and analysis of stomach contents samples

A biologist was stationed in Kaktovik to sample bowhead whales taken during September 1997, 1998, 1999 and 2000. The stomach of each whale landed was examined as soon as possible, usually within a few hours after the animal was brought to shore. An estimate was made of the total stomach contents volume and a sample of contents was collected from the forestomach, when possible. Stomach contents samples were kept frozen until examined in the laboratory.

Additional stomach contents samples were provided from bowhead whales harvested at Barrow and Kaktovik during 1986-2000, and by Nuiqsut hunters based at Cross Island in 1999-2000. Those samples were either preserved in 70% isopropyl alcohol, 10% buffered formalin, or were frozen.

In the laboratory, samples were gently rinsed in freshwater on a 1.0mm screen with a 0.42mm screen layered underneath. Prey items were sorted macroscopically into major taxonomic groups, examined microscopically, and identified to the lowest taxonomic level possible by the authors and species taxonomy experts at the University of Alaska. Voucher specimens of prey items were stored in 70% isopropyl alcohol. The water displacement volume of sorted prey items was measured to the nearest 0.1ml in graduated cylinders. Volumes were recorded as measured with no correction for state of digestion. These methods were similar to those used in the collection and analysis of bowhead whale stomach contents in previous years (e.g. Lowry and Frost, 1984).

Stomach contents data analyses

Data were entered into an electronic database that also contained all previously existing data on stomach contents of bowhead whales harvested in Alaska. Prey data from individual whales were grouped into major prey types (e.g. copepod, euphausiid, etc.), and comparisons were carried out for whales harvested in autumn at Kaktovik versus autumn at Barrow, for whales harvested at Barrow in spring versus autumn, for males versus females, and for whales <13m versus ≥13m in length. The division into size categories was based on the length at which bowhead whales reach sexual maturity, which is approximately 13m (Koski *et al.*, 1993).

Bowhead whale prey data were analysed in two ways. First, when a group of whales included at least five animals, the frequency of occurrence of major prey types was calculated as the number of samples containing that prey divided by the total number of samples examined. Then, the frequencies of all prey types consumed were compared using 2×2 contingency tables with an experiment wise error rate of $\alpha = 0.05$ using Bonferroni's procedure (Neter *et al.*, 1990). All whale stomachs for which ≥10 prey items were enumerated were used in the frequency of occurrence analysis. Second, principal components analysis with varimax rotation (Johnson and Wichern, 1982) was used to define diet indices, and multiple regression analysis was then applied to those indices to test for possible simultaneous effects of the following covariates on diet: location, season, whale sex, whale length and collection year. Principal components analysis was applied to data on the rank order of prey importance in each individual bowhead stomach, considering 16 identified prey groups (Appendix 1). For each prey group, importance was defined as the ratio of the volumetric contribution of that prey type to the total volume of the sample examined. Therefore, only specimens with quantitative data on prey composition were used in this analysis. For each stomach used in the analysis, principal component scores after varimax rotation ('dietary indices') were computed for the three principal components that explained the greatest amount of variance in the dataset. Those dietary indices were then used as the dependent variables in multiple regression analyses to assess relationships between the covariates and diet. Type 3 sums of squares were used to compute p values for the significance of each covariate. Type 3 sums of squares for each covariate were computed by including all other covariates in the model before computing that covariate's sum of squares.

RESULTS

Data and specimen collection

Field records were obtained from 444 bowheads harvested in the Beaufort Sea during 1969-2000, of which 242 had their stomachs examined. Thirteen bowheads were harvested during the 1997-2000 whaling seasons at Kaktovik, and stomach contents samples were collected from 12 of them. Additional samples not described in previous papers were obtained from 73 bowheads harvested during 1986-2000 at Barrow (69), Kaktovik (1) and Cross Island (3). Further details on whales and stomach samples examined are given in Lowry and Sheffield (2002).

Feeding status and diets

Of 32 bowhead whales sampled or examined at Kaktovik during the autumn harvest (1979-2000), 24 were considered to have been feeding, 5 were categorised as not feeding while the feeding status of 3 was uncertain. Stomach contents samples were available from 21 whales; at least 46 prey taxa were identified in the samples (Appendix 1). Copepods occurred in all 21 samples, and euphausiids, amphipods (both gammarid and hyperiid) and mysids each occurred in more than half (Table 1). Copepods were the dominant prey by volume in 62% of the 21 samples with volumetric data; euphausiids were dominant in 24% (Fig. 2). The most commonly eaten species of copepods were *Calanus hyperboreus* and *C. glacialis*. The most commonly eaten euphausiid was *Thysanoessa raschii* (Table 2).

Of 5 bowheads sampled or examined at Cross Island during the autumn harvest (1987-2000), 4 were considered to have been feeding and 1 was not feeding. At least 9 prey taxa occurred in the 3 stomach contents samples examined (Appendix 1). Copepods occurred in all 3 samples; gammarid amphipods, hyperiid amphipods and decapods each occurred in 2; and euphausiids and cumaceans each occurred in 1 (Table 1). Only one of the samples from Cross Island was in suitable condition for sorting and volumetric analysis; it contained >99% copepods. *C. hyperboreus* occurred in all 3 Cross Island stomach samples, and *C. glacialis* occurred in 2 (Table 2).

Table 1

Percent frequency of occurrence of major prey types identified from bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomach contents samples examined).

Prey type	Kaktovik autumn (n=21)	Cross Island autumn (n=3)	Barrow autumn (n=69)	Barrow spring (n=30)
Copepod	100	100	20	80
Euphausiid	62	33	94	93
Gammarid amphipod	81	67	55	23
Hyperiid amphipod	67	67	28	33
Mysid	57	0	49	20
Fish	48	0	26	3
Decapod	52	67	29	7
Isopod	24	0	19	0
Cumacean	24	33	13	3

Of 105 bowhead whales sampled or examined at Barrow during the autumn harvest (1976-2000), 77 were considered to have been feeding, 26 were categorised as not feeding while the feeding status of 2 was uncertain. Stomach contents samples were available from 69 whales, and at least 54 prey taxa were identified in the samples (Appendix 1).

Table 2

Number of identified occurrences of copepod and euphausiid species in stomach contents samples from bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomach contents samples examined).

Prey species	Kaktovik autumn (n=21)	Cross Island autumn (n=3)	Barrow autumn (n=69)	Barrow spring (n=30)
Copepod				
Calanus cristatus	-	-	-	2
C. finmarchicus	1	-	-	-
C. glacialis	10	2	8	20
C. hyperboreus	15	3	4	5
Chiridius obtusifrons	1	-	-	2
Derjuginia tolli	1	-	-	-
Euchaeta glacialis	2	1	1	4
Heterorhabdus sp.	2	-	-	-
Limnocalanus grimaldi	3	-	-	-
Metridea lucens	2	-	-	-
M. longa	4	-	-	4
Pseudocalanus sp.	4	-	-	1
Euphausiid				
Thysanoessa inermis	2	-	7	8
T. raschii	6	-	26	14

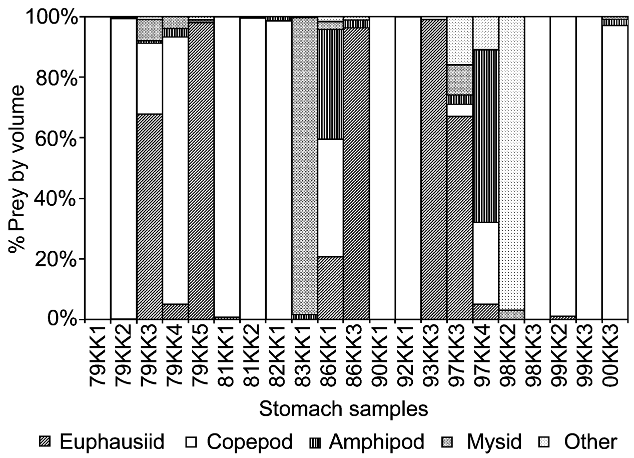

Fig. 2. Percent prey by volume for 21 individual bowhead whales harvested in the eastern Alaskan Beaufort Sea near Kaktovik, Alaska, during the autumn (1979-2000).

Euphausiids were the main prey item, occurring in 94% of the samples; copepods occurred in 20% (Table 1). Euphausiids were the dominant prey by volume in 88% of the 64 samples with volumetric data whereas copepods were dominant in only 5% (Fig. 3). The predominant species of euphausiid eaten was *T. raschii*; *C. glacialis* and *C. hyperboreus* were the most commonly eaten copepods (Table 2).

Of 99 bowhead whales sampled or examined at Barrow during the spring harvest (1969-2000), 31 were considered to have been feeding, 60 were categorised as not feeding while the feeding status of 8 was uncertain. Stomach contents samples were available from 30 whales, and at least 40 prey taxa were identified in the samples (Appendix 1). Euphausiids occurred in 93% of the samples and copepods in 80% (Table 1). Euphausiids were the dominant prey by volume in 63% of the 28 samples with volumetric data and copepods were dominant in 27% (Fig. 4). Copepods were the dominant item in 6 of 11 whales taken in 1977-1988 but only 1 of 17 taken in 1993-1998. *T. raschii* was the most commonly eaten species of euphausiid, and *C. glacialis* was the most commonly eaten copepod (Table 2).

Comparisons of diets between sexes, sizes, regions and seasons

There was no significant difference in the proportion of bowhead whales feeding in the autumn at Kaktovik and Barrow (Table 3; χ^2=0.69; df=1; p>0.1). For whales harvested near Barrow, a larger proportion was feeding in the autumn than in the spring (χ^2=35.77; df=1; p<0.001). The proportions of whales <13m and ≥13m long that were feeding were virtually identical for all seasons and locations (Table 3), and for all samples combined there was no significant difference (91/160 versus 42/67; χ^2=0.52; df=1; p>0.1).

There were significant differences in the frequency of occurrence of prey types between bowhead whales harvested in autumn at Kaktovik and Barrow (Table 1); copepods occurred more often in whales harvested near

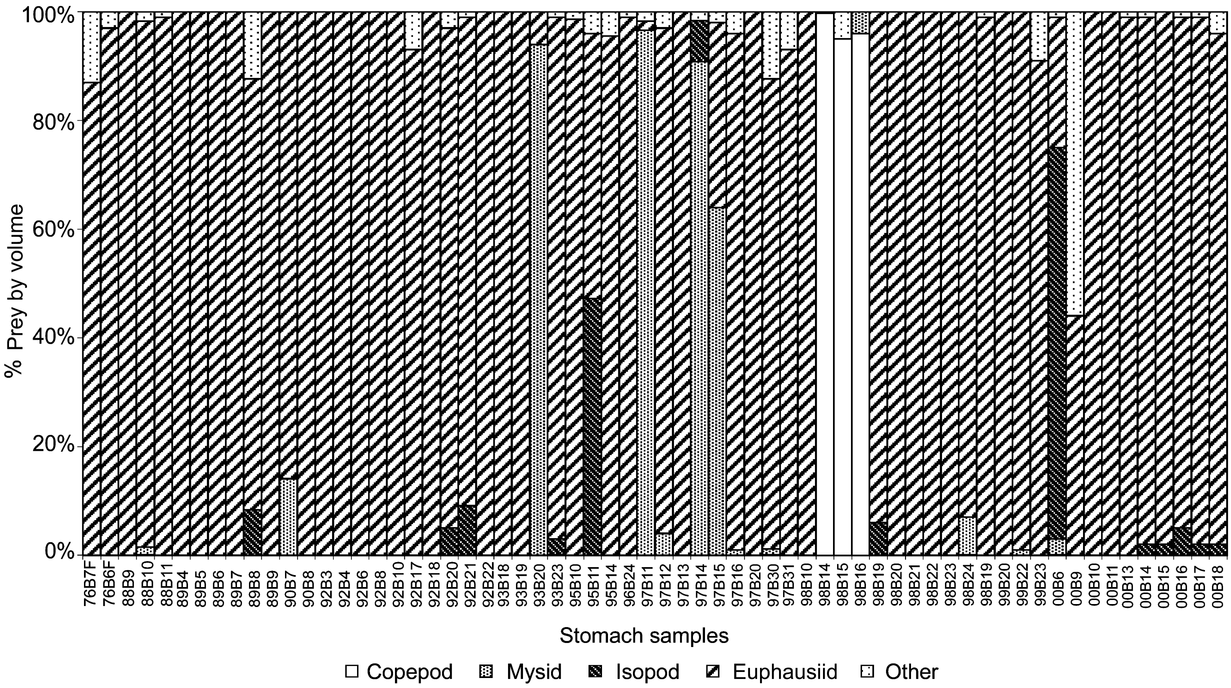

Fig. 3. Percent prey by volume for 64 individual bowhead whales harvested in the western Alaskan Beaufort Sea near Barrow during the autumn (1976-2000).

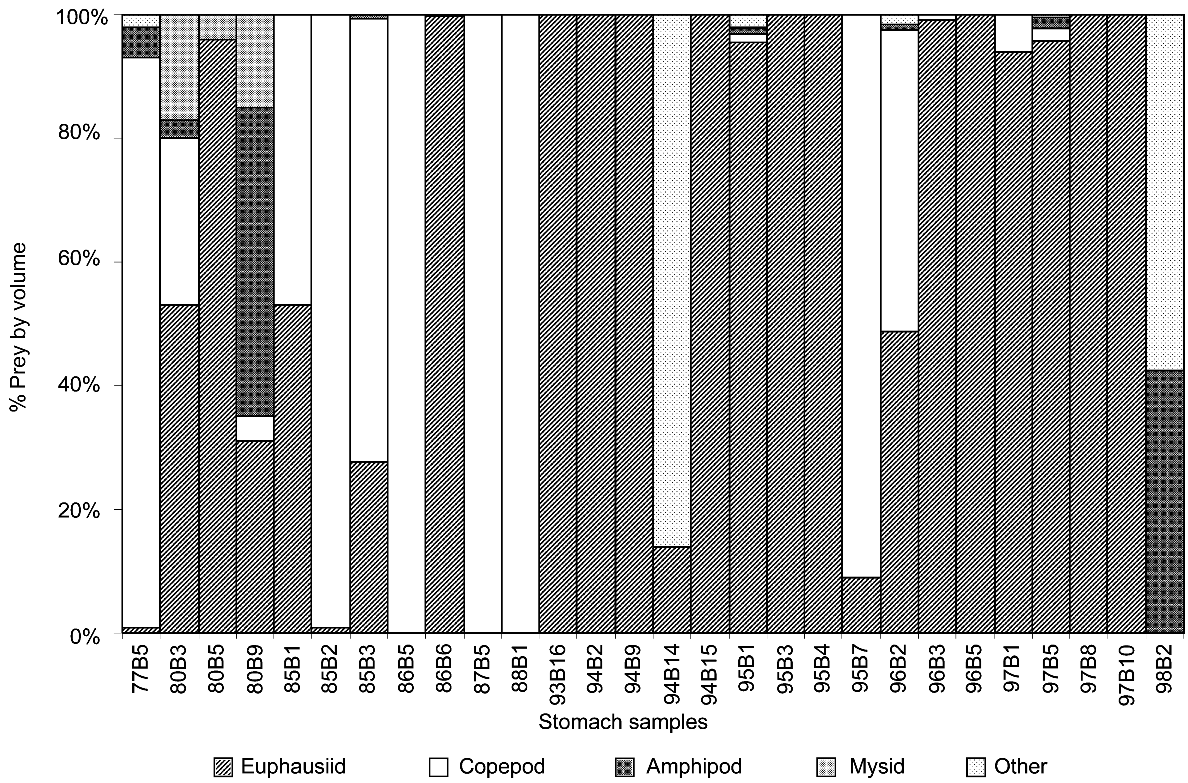

Fig. 4. Percent prey by volume for 28 individual bowhead whales harvested in the western Alaskan Beaufort Sea near Barrow during the spring (1977-98).

Kaktovik (χ^2=43.04; df=1; p<0.001), whereas euphausiids (χ^2=10.61; df=1, p<0.005) and hyperiid amphipods (χ^2=12.39; df=1; p<0.001) occurred more often in whales harvested near Barrow.

Bowhead whales harvested at Barrow showed seasonal differences in the frequency of occurrence of prey types (Table 1), with copepods occurring significantly more often in whales harvested in the spring (χ^2=31.52; df=1; p<0.001). Euphausiids occurred with similar frequency in autumn and spring (χ^2=0.01; df=1; p>0.1).

Within each location and season there were no significant differences in the frequency of occurrence of prey types in male and female bowhead whales (Bonferonni-adjusted χ^2 tests; p>0.1). Likewise, there were no significant differences in whales <13m and ≥13m long (p>0.05), although during autumn at Barrow mysids and fish occurred with a marginally greater (0.05<p<0.1) frequency in whales <13m long. When all samples were considered in aggregate (Table 4), the frequency of occurrence of prey types was virtually identical in males and females (p>0.1 for all tests). There were some small differences between length classes, with copepods, mysids, fishes, and isopods occurring more frequently in small whales, but the differences were not statistically significant (p>0.1 for all tests).

Table 3

Percentages of bowhead whales taken in the Alaskan Beaufort Sea (1969-2000) that were categorised as feeding, by location, season and length class. Numbers in parentheses are total sample sizes. Whales of uncertain feeding status were not included in calculations.

	Length <13m	Length ≥13m	All lengths
Kaktovik autumn	85 (20)	78 (9)	83 (29)
Cross Island autumn	100 (2)	67 (3)	80 (5)
Barrow autmun	75 (67)	75 (36)	75 (103)
Combined autumn	78 (89)	75 (48)	77 (137)
Barrow spring	34 (71)	32 (19)	34 (91)

Table 4

Percent frequency of occurrence of major prey types identified in bowhead whales taken in the Alaskan Beaufort Sea (1969-2000) separated by sex and size (n = the number of stomach contents samples examined).

Prey type	Males (n=61)	Females (n=58)	Length <13m (n=83)	Length ≥13m (n=36)
Copepod	49	50	55	36
Euphausiid	87	88	88	86
Gammarid amphipod	49	55	53	50
Hyperiid amphipod	39	33	35	39
Mysid	43	45	51	28
Fish	23	26	30	11
Decapod	28	28	27	31
Isopod	15	16	18	8
Cumacean	10	16	12	14

In the principal components analysis, the three most important 'dietary indices' accounted for 48.9% of the variance in the ranked volumetric data on prey. Multiple regression analysis was applied, in turn, to each of these three indices to determine whether that measure of diet differed with location, season, whale length, or whale sex. All three dietary indices showed a significant effect of season, while location was significant for one index (Table 5). There was no evidence for effects of sex, length class, or year on diet (p≥0.1 in all cases). The index that showed a difference for both location and season (Factor 1) was one that strongly contrasted the ranking of copepods and euphausiids in the diet.

Estimates of the volume of stomach contents were available for 46 bowhead whales harvested at Kaktovik and Barrow. The estimates are imprecise and often given as ranges, and are therefore not suitable for rigorous analysis. However, a summary of those observations (Table 6) shows that at both Kaktovik and Barrow autumn stomachs frequently contained 20 litres or more, and sometimes had over 100 litres of contents. In the latter case, stomachs were often described as 'full' in field records. Estimated contents volumes at Barrow in the spring were generally lower and never exceeded 60 litres.

Table 5

P values from multiple regression analyses testing for differences in three indices of bowhead whale diet according to location, season, whale sex and length class and year. Diet indices ('factors') are based on a principal components analysis of the rank order of volumetric importance of major prey types identified in 123 bowhead whale stomachs from the Alaskan Beaufort Sea.

Variable	Factor 1	Factor 2	Factor 3
Location	<0.01	0.16	0.22
Season	<0.01	<0.01	0.01
Sex	0.52	0.92	0.62
Length class	0.33	0.19	0.23
Year	0.06	0.60	0.10
% variance in diet explained by this factor:	18.0	15.4	15.5

Table 6

Estimates of volume of stomach contents in bowhead whales taken in the Alaskan Beaufort Sea, 1969-2000 (n = the number of stomachs for which contents volume was estimated).

Estimated contents volume	Kaktovik autumn (n=18)	Barrow autumn (n=16)	Barrow spring (n=14)
% with ≥ 20 litres	39	56	29
% with ≥ 100 litres	11	31	0
Range (litres)	2-150	1-189	1-60

DISCUSSION

Prior to this study, our understanding of the diet composition of bowhead whales in the Alaskan Beaufort Sea was based on samples collected from 30 animals (Lowry, 1993). As a result of this project, quantitative diet data based on laboratory analysis of stomach samples are now available for a total of 123 animals. The frequency of feeding and types of food that were eaten are now reasonably well described for whales taken in the eastern Alaskan Beaufort Sea (Kaktovik) in autumn and the western Beaufort Sea (Barrow) during both autumn and spring. This paper also describes the first diet samples collected from bowhead whales in the central Alaskan Beaufort Sea (Cross Island).

Previous studies (Lowry and Burns, 1980; Lowry and Frost, 1984; Lowry, 1993) have shown that bowhead whales taken in the Alaskan Beaufort Sea during the autumn commonly have food in their stomachs. Using field records and laboratory results this study concluded that 105 bowhead whales taken in the Alaskan Beaufort Sea during September-October had been feeding and 32 had not (Table 3). The estimate of 77% overall frequency of feeding in autumn bowheads is likely to be an underestimate for several reasons. For some of the whales that were recorded as not feeding, stomachs could not be examined until many hours after the initial strike during which time contents could have been completely digested. The three Kaktovik whales assigned uncertain feeding status each had small amounts of prey in their stomachs. In addition, some stomach contents samples were received in such poor condition (e.g. filled with congealed blood) that locating and identifying prey was difficult or impossible.

Copepods and euphausiids were the main bowhead whale prey items in the eastern Alaskan Beaufort Sea near Kaktovik, which agrees with previously presented results for this area (Lowry and Burns, 1980; Lowry and Frost, 1984; Lowry, 1993). Of the two groups, copepods were the most important as they were present in every stomach sample and were essentially the only item in 12 of the 21 samples. However, euphausiids were also an important prey item and dominated the contents of five whale stomachs. Other crustaceans and fishes also were eaten, but they generally were minor components of samples that consisted mostly of copepods or euphausiids.

In the western Beaufort Sea near Barrow, bowhead whale diet during September-October was dominated by euphausiids, which made up almost the entire contents of 54 of the 64 samples examined. These results confirm the importance of euphausiids in the autumn diet of bowhead whales in this region, a conclusion that had previously been based on samples from only five stomachs (Lowry, 1993). Copepods were the predominant prey in 3 stomachs and mysids in 4. Interestingly, the only whales with copepods dominant were taken on the same day in 1998, and 2 of the 4 with mysids dominant were taken on the same day in 1997. This may be indicative of temporal/spatial patches of prey that are found and exploited by the whales.

Regional differences in diets of autumn-harvested bowheads may be explained by regional differences in prey availability. Copepods are known to dominate the zooplankton of the Canadian Beaufort Sea and eastern Alaskan Beaufort Sea and euphausiids are not considered abundant there (Bradstreet and Fissel, 1986; Griffiths and Thomson, 2002). In that region, bowhead whales often occur at locations where copepods dominate the biomass (Griffiths and Buchanan, 1982; Griffiths *et al.*, 2002). In contrast, euphausiids have been found in substantial quantities in the western Beaufort Sea, where copepods were less abundant (Griffiths *et al.*, 1987).

Previous studies (Lowry and Frost, 1984; Carroll *et al.*, 1987; Lowry, 1993) concluded that bowhead whales fed only occasionally while migrating northward along the west coast of Alaska in spring. This study estimated the overall frequency of feeding at Barrow during spring at 34%. This frequency was significantly less than at either Barrow or Kaktovik in the autumn, and estimated quantities of contents in the stomach were considerably smaller. Fourteen of 28 spring samples were comprised almost entirely of euphausiids and 6 had nearly all copepods, but several contained mixtures of different crustacean groups. Copepods occurred significantly more often in whales that fed near Barrow in spring than in autumn. This difference could be partly due to the locations where whales are taken as spring hunting occurs in the Chukchi Sea to the west of Point Barrow whereas autumn whales are taken in the Beaufort Sea mostly to the north and east of the Point (J.C. George, unpubl. data). There are essentially no data available on zooplankton distributions in this region during spring. In contrast with previous studies that found that copepods were the dominant prey of bowhead whales taken during the spring migration in 1980-88 (Carroll *et al.*, 1987; Lowry, 1993), this study suggests that euphausiids overall have been the more important prey in the western Beaufort Sea in spring as well as autumn. It appears that there may have been a change in the spring diet of bowheads in this area, with euphausiids being more important in the 1990s than in pre-1990s samples (Fig. 4). It is unknown whether this apparent change in diet is due to changes in oceanic conditions that may have altered abundance patterns of copepods or euphausiids, differences in specific locations where whales were harvested or where they were feeding, or some other factor.

The frequencies of occurrence of various prey types in stomachs of male and female bowhead whales were nearly identical, and indications of slight age/size effects on diet were not statistically significant. Lowry (1993) examined size-related differences in diet based on samples from 32 bowhead whales and concluded there was a slightly greater tendency for benthic taxa to occur in whales <10.5m long. The analysis here of a larger number of samples also suggests slight differences in the diet of small (<13m) versus larger (≥13 m) whales. Prey groups such as mysids, fish and isopods that occurred relatively infrequently in larger whales were found more commonly in small whales, but those differences were small and not statistically significant. If real, the differences may reflect size-related differences in feeding abilities (probably as a function of baleen length) or in feeding areas, as has been suggested for bowhead whales in the eastern Canadian Arctic (Finley, 2001).

It is difficult to use bowhead stomach contents data to estimate the overall diet composition for a location/season for a number of reasons. Those include variation in the state of digestion of samples, the wide range in the volumes of collected samples, and the frequent lack of data on total volume of stomach contents. Nonetheless, preliminary estimates of diet composition based on the data shown in Figs 2, 3 and 4 were calculated using two methods: (1) averaging the percent volumes of contents for each prey type found in individual whales; and (2) calculating the percent of times that a prey type was the dominant component of a stomach contents sample. The two methods produced remarkably consistent estimates (Table 7), in agreement with the patterns of regional and seasonal importance of copepods and euphausiids described above.

There are other sources of information on feeding of bowhead whales in the Beaufort Sea. One is the traditional knowledge of local subsistence whalers. While much of the Inupiat knowledge on bowhead whale feeding has not been recorded in written form, personal observations of the authors and other sources show that hunters are quite aware that bowhead whales feed in certain parts of the Alaskan Beaufort Sea. Whalers at Kaktovik have described feeding areas in the eastern Alaskan Beaufort Sea (Galginaitis and Koski, 2002), and at Barrow they have long known about autumn feeding areas and tend to focus their hunting activities in those areas (Minerals Management Service, 1997). Hunters are also aware of the types of behaviours whales exhibit when feeding, and have described weight gain of bowheads over the summer feeding season and a seasonal change in the taste of the muscle (Puiguitkaat, 1981). Another source is sightings and behavioural observations made during aerial surveys and systematic behavioural studies. Sightings of feeding bowhead whales, when accumulated over many late summer/autumn seasons, have been widely distributed across the Alaskan Beaufort Sea (Ljungblad *et al.*, 1986; Miller *et al.*, 2002; Treacy, 2002), and in the eastern Alaskan Beaufort Sea feeding is the most commonly observed activity (Würsig *et al.*, 2002). Such observations support the conclusions of this paper. Information on feeding also comes from the analysis of stable isotope ratios in bowhead whale tissues. Such studies by Schell *et al.* (1989) and Hobson and Schell (1998)

Table 7

Estimates of bowhead whale diet composition in the Alaskan Beaufort Sea (1969-2000) based on: (1) averaging the percent composition by volume in individual stomach contents samples; and (2) the percent of times a prey type was the dominant component of stomach contents samples (*n* = the number of stomach contents samples that were suitable for volumetric analysis).

	Kaktovik (*n*=21)		Barrow autumn (*n*=64)		Barrow spring (*n*=28)	
	Mean % volume	% times dominant	Mean % volume	% times dominant	Mean % volume	% times dominant
Copepod	61	62	5	5	28	27
Euphausiid	22	24	84	88	61	63
Amphipod	5	5	1	0	4	4
Mysid	6	5	6	6	1	0
Other	6	5	4	1	5	7

concluded that in terms of total annual nutrition, the eastern and central Beaufort Sea is a relatively unimportant feeding ground for bowhead whales, especially for adult animals. However, Hoekstra *et al.* (2002), also using isotopic methods, concluded that the Beaufort Sea is an important feeding area for bowhead whales of all sizes. The direct evidence of feeding presented in this paper more closely agrees with the conclusions of Hoekstra *et al.* (2002).

CONCLUSIONS

Results of this study change our previous understanding of the feeding ecology of bowhead whales in two important ways. First, bowhead whales feed regularly in the nearshore waters of the eastern, central and western Alaskan Beaufort Sea during September-October. With food found in more than three-quarters of the animals examined, this entire region should be considered an integral part of the summer-autumn feeding range of bowhead whales. Results of stomach contents analysis, aerial observations, and traditional knowledge suggest that reference to the passage of bowhead whales through this region as a 'westward autumn migration' is misleading. At the least, it is a very incomplete description of their activities in the region. In fact, a major activity of bowhead whales in the Alaskan Beaufort Sea during autumn is feeding, with whales moving west when prey are not available in sufficient numbers (Griffiths *et al.*, 2002), or when the whales choose not to feed, or when they combine feeding with simultaneous westward travel (Würsig *et al.*, 2002). Second, feeding near Barrow during the spring migration is not just occasional, but rather a relatively common event as evidenced by the fact that approximately a third of the animals sampled there had been feeding. However, the amount of food in the stomachs tends to be lower in spring than in autumn.

The conclusions drawn from this study appear to contradict those of Richardson (1987, p.485) who concluded that 'Food resources consumed in the Eastern Alaskan Beaufort Sea do not contribute significantly to the annual energy needs of the Western Arctic bowhead stock'. However, examination of stomach contents only showed whether or not bowhead whales had fed and what prey were eaten, and it does not directly address the relative significance of feeding in various regions. Nonetheless, for the conservation of these whales and their habitats it seems inappropriate to dismiss areas where the majority of animals show evidence of having fed as being unimportant to their nutrition. This unresolved issue remains important in the evaluation of possible cumulative effects of oil and gas development on bowhead whales, and additional studies are warranted (National Research Council, 2003).

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Appendix 1

Prey and other items consumed by bowhead whales harvested in the Alaskan Beaufort Sea (1969-2000). Locations and seasons where whales were harvested are indicated after each taxon (BS = Barrow/spring; BF = Barrow/autumn; K = Kaktovik; C = Cross Island). Numbers identify taxa used in the principal components analysis.

1. Cnidaria		**Copepoda (cont.)**		**Gammarid amphipods (cont.)**		**Gammarid amphipods (cont.)**		**Decapoda (cont.)**	
Scyphozoa	BS, BF	*Euchaeta* sp.	BS, K	*Acanthostepheia behringiensis*	BF, K	*Onissimus nanseni*	K	*Sabinea septemcarinata*	BF, K
2. Annelida		*Euchaeta glacialis*	BS, BF, K, C	*Acanthostepheia incarinata*	K	Podoceridae	BF	*Sclerocrangon* sp.	BF
Polychaeta	BF	*Heterorhabdus* sp.	K	*Acanthostephia malmgreni*	BF	*Pontoporeia femorata*	BF	*Sclerocrangon boreas*	BF
Mollusca		*Limnocalanus grimaldii*	K	*Aceroides latipes*	K	*Protomedeia* sp.	BF	Decapod zoea	BF, K, C
3. Gastropoda	K	*Metridea* sp.	BS, K	*Anonyx* sp.	BS, BF, K, C	*Rhacotropis* sp.	BS, BF, K	**15. Echinodermata**	
Limacina helicina	BS	*Metridea lucens*	K	*Anonyx nugax*	BS	*Rozinante fragilis*	BF, K	Ophiuroidea	BS
Margarites sp.	BS	*Metridea longa*	BS, K	*Ampelisca macrocephala*	BF	*Weyprechtia* sp.	BF, K, C	**16. Vertebrata**	BF, K
Natica sp.	BS	*Pseudocalanus* sp.	BS, K	*Apherusa glacialis*	K	*Weyprechtia heuglini*	BF, K	*Ammodytes* sp.	BF
Natica clausa	BS	**8. Mysidacea**	BS, BF, K	*Arrhis* sp.	BF	*Weyprechtia pinguis*	BF, K	Agonidae	BF
Neptunea sp.	BS	*Mysis* sp.	BF, K	*Atylus carinatus*	BF, K	**12. Hyperiid amphipods**	BS, BF, K	Gadidae	C
4. Bivalvia	BF	*Mysis litoralis*	BS, BF, K	*Boeckosimus affinis*	BF	*Hyperia* sp.	BS, K	*Boreogadus* sp	BF
Astarte sp.	BS	*Mysis occulata*	BF, K	*Boeckosimus krassini*	BF	*Hyperia galba*	BS, K	*Boreogadus saida*	BS, K
Liocyma fluctuosa	BS	*Neomysis* sp.	BS, BF	*Boeckosimus litoralis*	K	*Hyperia medusarum*	BS, K	Cottidae	BF
Nuculana sp.	BS	*Neomysis rayii*	BS, BF	*Byblis* sp.	BS, BF	*Hyperoche medusarum*	BS	*Icelinus* sp.	BF
Tellinidae	BS	**9. Cumacea**	K, C	*Erichthonius* sp.	BS	*Parathemisto* sp.	BS	*Lepidopsetta bilinicata*	BF
Yoldia sp.	BS, BF	*Brachydiastylis resima*	BS	*Eusirus cuspidatus*	BS, BF	*Parathemisto abyssorum*	BS, K, C	*Lycodes* sp.	BF
5. Chelicerata		*Diastylis* sp.	BF, K	*Gammarus* sp.	BS, BF, K	*Parathemisto libellula*	BF, K, C	*Myxocephalus* sp.	BF
Pycnogonidae	K	*Diastylis dalli*	K	*Gammarus zaddachi*	BF	**13. Euphausiacea**	BS, BF, K, C	*Myxocephalus quadricornis*	K
Crustacea		*Diastylis galbra*	K	*Gammaracanthus* sp.	BF	*Thysanoessa* sp.	BS, BF, K	Pleuronectidae	BF
6. Ostracoda	BS	*Diastylis sulcata*	BF	*Gammaracanthus loricatus*	BF, K	*Thysanoessa inermis*	BS, BF, K	*Pungitius pungitius*	K
7. Copepoda	BS, BF, K, C	Leuconidae	BF	*Harpinia* sp.	BS	*Thysanoessa raschii*	BS, BF, K	Stichaeidae	BF
Aetideidae	BF	*Leucon* sp.	BF	Lysianassidae	BF, K	**14. Decapoda**	BF, K, C	Zoarcidae	BF
Calanus sp.	BS, BF, K	*Leucon nasica*	BS	*Melita* sp.	BF	Crangonidae	K	**17. Phaeophyceae**	
Calanus cristatus	BS	**10. Isopoda**	K	*Melita quadrispinosa*	BF	*Argis* sp.	BS, BF	Plant material	BF
Calanus finmarchicus	K	*Munnopsis* sp.	K	*Monoculodes* sp.	BF, K	*Eualus* sp.	BS, BF	**18. Other**	
Calanus glacialis	BS, BF, K, C	*Saduria* sp.	BF, K	*Monoculodes zervoni*	BF	*Eualus gaimardi*	BF, K	Baleen	BS, BF, K, C
Calanus hyperboreus	BS, BF, K, C	*Saduria entomon*	BF, K	Oedicerotidae	BF	*Heptacarpus* sp.	BF	Bird feathers	BF, K
Chiridius obtusifrons	BS, K	Amphipoda	BS, K, C	*Onissimus* sp.	BF, K	Hippolytidae	BF	Plastic sheeting	BF, K
Derjuginia tolli	K	**11. Gammarid amphipods**	BS, BF, K, C	*Onissimus glacialis*	K	*Pandalus goniurus*	K	Wood	BF, K
Euchaetidae	K	*Acanthostepheia* sp.	BS, BF, K	*Onissimus litoralis*	K	*Sabinea* sp	BF	Sediments	BS, BF, K