Chapter 6

FOODS AND FEEDING ECOLOGY

Lloyd F. Lowry

Like all animals, bowhead whales must be able to locate food of the proper type and obtain adequate amounts. As a group, baleen whales have forgone pursuit and capture of individual prey and have instead developed an unusual feeding apparatus. The baleen filter, along with other morphological and behavioral modifications, allows these massive animals to feed by straining vast numbers of relatively tiny organisms from sea water. Bowheads are unique among northern hemisphere mysticetes in that they feed mostly in arctic and subarctic regions where sea ice cover may regulate oceanographic processes, productivity, and access to food. This chapter will discuss how bowheads satisfy their nutritional needs in the unusual and challenging arctic environment.

Nutritional level may influence animals such as bowhead whales in many ways. Juvenile animals that experience good feeding conditions will grow rapidly and may achieve sexual maturity at an early age (Laws 1956). Marine mammals generally give birth to a single large offspring which gains weight rapidly during the nursing period. This results in a large energy drain on adult females during the period of pregnancy and parental care. If adequately nourished, adult females may produce healthy offspring at regular intervals of 1–3 yr, the intervals depending primarily on the length of the nursing period. However, if feeding conditions are inadequate, individuals may not ovulate, may resorb or abort a developing fetus, or may be unable to feed a dependent offspring adequately.

Clearly food availability is an important ecological parameter that may limit mammal populations. This phenomenon has been well documented for terrestrial species such as white-tailed deer, *Odocoileus virginianus* (McCullough 1979), and caribou, *Rangifer tarandus* (Skogland 1985). Other factors such as disease, predation, and human harvest may also limit populations either independently or in conjunction with nutritional factors.

Marine mammals characteristically have a layer of blubber which functions as a thermal barrier, as an energy reserve, and to streamline the body (Ryg *et al.* 1988). The blubber layer in bowhead whales is particularly thick with maximum measured values reported as 43 cm (J. C. George, personal communication) to 50 cm (Tomilin 1957). The thick blubber layer is probably in part an adaptation which allows them to maintain normal body temperature in the arctic and subarctic environments in which they live year-round. To most observers it may seem that there are no thin bowheads which could lead to the conclusion that they always find an adequate supply of food. However, Eskimo whalers notice variations in blubber thickness among individual bowheads and, in fact, recognize a particularly fat variety of young whale which they call an "ingutuk" (Braham *et al.* 1980*a*). Lockyer (1986) has documented annual variability in fatness of northeast Atlantic fin whales, *Balaenoptera physalus,* which correlated with ovulation rates and food availability.

Bowhead whale stocks are presently reduced throughout most of their range (Chapter 10) and an increase in numbers is desirable. Since food potentially limits population growth, it is important to understand bowhead feeding ecology. It is necessary to know what foods are eaten, when and where, the nutritional significance of various prey species, and the relationships between prey characteristics and bowhead behavior, morphology, and energy demands. Information is also needed on how factors such as oceanographic conditions, trophic competitors, and human activities may affect prey populations and bowhead feeding patterns. This chapter reviews historical information on bowhead feeding, and results of recent studies of morphology, behavior, food habits, and oceanography that are relevant to the feeding ecology of this species.

Historical information on foods of bowhead whales is very limited. Although many thousands of bowheads were killed by commercial whalers (Ross 1979, Chapter 13; Bockstoce 1980, Chapter 14), the blubber and baleen were usually removed alongside the ship and carcasses were usually not examined. The recorded observations of whalers are therefore limited and general, as in the following from Scammon (1874, p. 54):

> When the Bowhead feeds, it moves through its native element, either below or near the surface, with considerable velocity, its jaws being open, whereby a body of water enters its capacious mouth, and along with it the animalculae (termed by the whalemen "Right Whale feed," or "brit"). The water escapes through the layers of baleen, but the insect food is retained by the fine fringes on its inner edges, and is afterward swallowed.

The reference to "Right Whale feed" suggests that Scammon considered copepods to be the main food of bowheads. In reference to what is eaten by bowheads, Scoresby (1810, pp. 584–585) states, "I have great reason to believe, that it is chiefly, if not altogether, of the squillae or shrimp tribe; for on examining the stomach of one of large size, nothing else was found in it; they were about half-an-inch long, semi-transparent, and of a pale red color." This description could very well refer to euphausiids.

Hjort and Ruud (1929) listed the following as foods of bowhead whales: *Clione limacina, Limacina helicina* (pteropods); *Balina septemtrionalis, Beroe cucumis, Mertensia ovum, Pleurobrachia pileus* (ctenophores); *Calanus finmarchicus, C. hyperboreus,* and *Hymenodosa glacialis* (copepods). However, Tomilin (1957) recognized that Hjort and Ruud (1929) had based their list of prey items on figures in Scoresby (1823) that "depicted organisms often encountered in the surroundings of the animal" (Tomilin 1957, p. 51). Based on his extensive review of cetacean morphology and ecology, Tomilin concluded that the main foods of bowheads were small organisms such as *Calanus finmarchicus* and *Limacina helicina,* and that large pteropods and ctenophores would be consumed only incidentally. Gaskin (1982) agreed with Tomilin and indicated that *Calanus glacialis* was likely to be a major food in portions of the Arctic influenced by North Pacific water.

For many centuries Alaska natives have hunted bowheads during the spring and fall migrations. In many places the landed whales are hauled up on ice or on shore to be butchered, which has allowed the examination of gastrointestinal tracts. Johnson *et al.* (1966) examined the stomachs of two bowheads taken at Point Hope, one in April 1960 and the other in May 1961. One stomach was empty. In the other they found fragments of polychaetes, crabs, snails, crustaceans, and echinoderms. Based on observations he made while working at Barrow, MacGinitie (1955) stated that bowheads ate euphausiids, mysids, pteropods, and copepods, but he presented no more specific data. Durham (1972) reported on his examinations of stomachs of 16 whales, of which 6 were empty or contained only sand. Items found in the remaining 10 stomachs included copepods, euphausiids, mysids, amphipods, isopods, tunicates, fishes, tundra vegetation, and silt. Apparently the only stomachs with appreciable quantities of food contained mysids, euphausiids, and copepods. Durham stated that whales fed sporadically while passing Point Barrow in spring and autumn. Large numbers of whales that had paused to feed were sometimes seen outside the Plover Islands during the autumn migration.

MORPHOLOGY OF THE FEEDING APPARATUS

In baleen whales the whole anterior end of the body is greatly modified for feeding (Miller 1923, Kellogg 1928, Gaskin 1982). The head is enlarged relative to the rest of the body in order to accommodate the two rows of baleen that hang from the upper jaw. Specialized processes of the maxillary bone support the enormous palate. The baleen itself consists of hardened and keratinized palatal rugosities arising from a normal mammalian palate (Pivorunas 1976). The connective tissue which attaches baleen to the skull is analagous to the tissue connecting a horse's hoof to the bones of the foot (Lambertsen *et al.* 1989).

The baleen plates themselves are made up of a large number of hair-like tubules cemented together by a matrix (Pivorunas 1976, Chapter 4). The plates are arranged along each side of the upper jaw in a transverse series (*i.e.*, perpendicular to the long axis of the body). Friction with the tongue is thought to break up the matrix along the inner edge of the plates producing a fringe of filaments or bristles that lay across the spaces between the plates forming a sieve. The plates are flexible so they can fold backward when the mouth is closed and spring into place when the mouth opens.

In the bowhead whale, the enlargement of the head region to accommodate the feeding apparatus is carried to an extreme. In adults, the head may be as much as two-fifths of the total body length (Eschricht and Reinhardt 1866). The upper jaw is strongly arched and holds a rack of baleen plates which generally number 250–350 on each side and may be up to 4.6 m long (Scoresby 1810). The surface area of the buccal side of each baleen rack was found to be about 1.75 m^2 in bowheads 7.5 and 7.8 m long (Lambertsen *et al.* 1989). Only a portion of this area may actually function in filtration (Pivorunas 1976, Lambertsen *et al.* 1989).

In bowheads, the length of baleen plates increases rapidly over the first 60 plates, reaches a maximum by about plate 120, then remains nearly constant until it begins to decrease after about plate 250 (Eschricht and Reinhardt 1866, Lambertsen *et al.* 1989). In recent years, biologists with

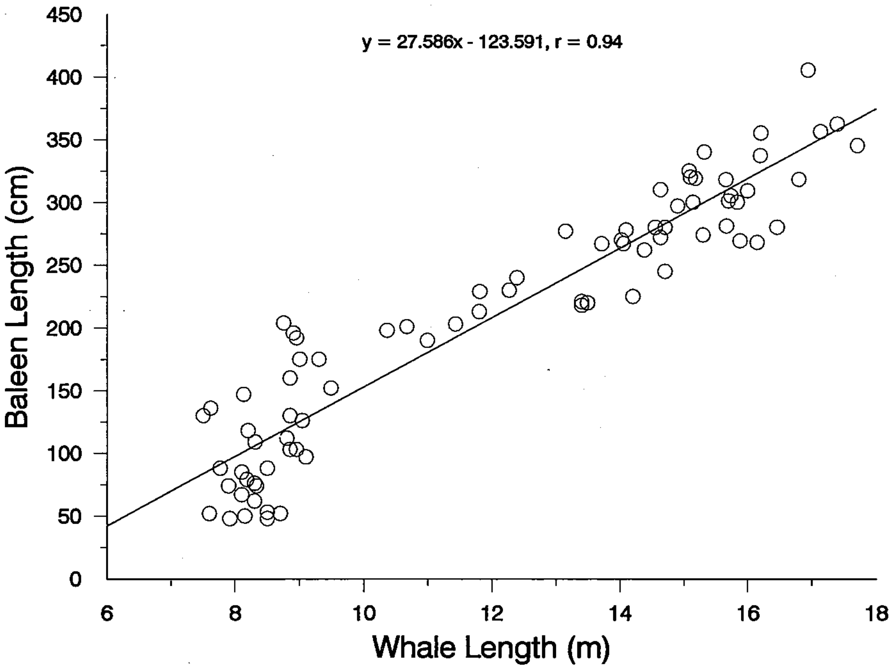

Figure 6.1. Relationship between whale length and baleen length for 80 bowhead whales taken off Alaska, 1980–1988. Data provided by J. C. George, North Slope Borough Department of Wildlife Management.

the North Slope Borough Department of Wildlife Management have measured the overall body length and one of the longer plates from each of 80 bowheads landed in Alaska. The data (Fig. 6.1) show a highly significant correlation ($r = 0.94$, $F = 596.94$, $P < 0.001$). As bowheads grow, baleen length increases by about 27.5 cm for each 1-m increase in whale length.

The shortest baleen measured was 48 cm in whales 7.9 and 8.5 m long, and the longest was 405 cm in a whale 16.9 m long. There was much more individual variability in baleen length among whales 9 m or less in length. In these smaller whales, baleen length expressed as a percentage of total body length ranged from 5.6% (an 8.5-m whale with 48-cm baleen) to 23.3% (an 8.75-m whale with 204-cm baleen). Among larger whales, baleen length was usually equal to about 17–22% of total body length.

Baleen whales, in general, may feed by either engulfing prey or skimming. The rorquals mostly feed by engulfing and have short, coarse baleen, including a row of bristles joining the two main rows at the tip of the jaw (Pivorunas 1976). They have a series of ventral (throat) grooves and a specialized tongue that allow a tremendous distension of the throat region when a large volume of water and prey is engulfed (Lambertsen 1983, Orton and Brodie 1987). The ability of rorquals to skim feed may be limited because the baleen will lose contact with the lower jaw if the angle of the mouth gape exceeds 10°–15° (Pivorunas 1976).

In contrast, bowheads and right whales have long baleen with fine filaments, a space between the baleen rows at the front of the jaw, and cheek flaps extending upward from the lower jaw which provide a closure at large gape angles (Pivorunas 1979). They have no ventral grooves and have a firmer tongue than rorquals (Nemoto 1970). It is clear that they do not have the anatomical adaptations required for engulfing large volumes of water, and that they feed principally by straining small organisms from the water while swimming slowly forward with their mouths open (Pivorunas 1979, Fig. 5.3).

The density of fringes probably determines the efficiency with which various sizes of organisms are retained by the baleen. In bowheads, filaments generally number 20–120 per centimeter along the baleen plate, and are about 0.1–0.2 mm in diameter. The length of exposed fibers may exceed 50 cm in large whales (Lambertsen *et al.* 1989). There may be a limitation on the density of fringes because of inhibition of water flow through the baleen (Gaskin 1982). Braithwaite *et al.* (1983) set up an experimental filter apparatus using bowhead baleen. They found an average filtration efficiency of 97.2% in tests using brine shrimp (*Artemia salina*) that averaged 11 mm long.

Lambertsen *et al.* (1989) have conducted a detailed study of the functional morphology of the bowhead feeding apparatus. They described the size and shape of individual baleen plates, their attachment to the skull, the diameter and length of baleen bristles, and the surface contour and profile of a baleen rack. The lower jaw and lip were shown to be capable of outward rotation during feeding to form a distinct gutter for water flow along the outside of the baleen. Close-range photogrammetry demonstrated the convex shape of the anterior portion of the rack. Taken together, these findings suggested that low hydrodynamic pressures develop along the outside of the baleen rack. This would tend to draw water through the baleen filter and minimize the amplitude of pressure waves in front of the mouth that might prompt evasive action by mobile prey such as euphausiids. Other features, including the cross-sectional shape of individual baleen plates, appear specialized to increase this hydrodynamic effect.

Once food items are captured on the baleen, it is assumed that the tongue is used to move them to the entrance of the esophagus (Gaskin 1982). The tongue of a bowhead is a massive organ that may be up to 5.5 m long and 3 m wide (Reeves and Leatherwood 1985). The esophagus is short and distensible to the point that it can pass a human hand (Durham 1972). It opens into the first of four stomach chambers, which is a non-glandular sac-like structure generally believed to serve as a distensible storage compartment (Sis and Tarpley 1981, Chapter 4). Herwig *et al.* (1984) noted that the tissue lining the forestomach is analogous to that in a rumen. They found numerous bacteria and volatile fatty acids in bowhead stomach contents, and suggested that microbial fermentation occurs in the forestomach. A relatively large opening allows food to pass into the fundic chamber, from which it passes through a narrow (2.5-cm diameter) connecting chamber into the pyloric chamber. These latter three compartments are all glandular and produce digestive enzymes (Sis and Tarpley 1981). Durham (1972) measured the intestines of a 9.5-m-long female bowhead and found them to be 59.5 m.

FEEDING BEHAVIOR

Bowhead whales must use an array of sensory mechanisms and cues to detect organisms that are potential food. In order to satisfy their energy requirements, it is likely that bowheads must feed in areas with above-average concentrations of zooplankton. Furthermore, swimming with the mouth open reduces hydrodynamic efficiency, and it would therefore be advantageous for a bowhead to open its mouth only when there are sufficient prey to make it worthwhile.

How bowheads and other planktivorous mysticetes detect and evaluate prey has been the source of some speculation, but there is little evidence available to indicate what methods are actually used. The eyes are positioned behind the mouth, and it is not known whether they are useful for detecting small prey organisms. Bowheads have scattered hairs that project from epidermal depressions along the margins of the upper and lower jaw, on the chin, and behind the blowhole (Haldiman *et al.* 1981, Chapter 4). Nakai and Shida (1948) speculated that hairs on sei whales (*Balaenoptera borealis*) function like the whiskers of a cat, and morphological studies by Haldiman *et al.* (1981) confirmed that bowhead hairs are of a similar structure and are likely to have a tactile function.

Bowhead whales produce a variety of intense underwater sounds (Ljungblad *et al.* 1982; Clark and Johnson 1984, Chapter 5) but they are of relatively low frequency (mostly less than 2,000 Hz) and lack the resolution needed for detecting small individual prey items. It is, however, possible that acoustical scanning could be used to locate schools of prey (Gaskin 1982). Once food is located, vocalizations may bring other individuals to the area, as has been suggested for fin whales (Watkins and Schevill 1979).

Behavioral observations of closely related species suggest that both long- and short-distance prey detection does occur. Hamner *et al.* (1988) followed a southern right whale (*Eubalaena australis*) as it swam in a straight line for about an hour, until it reached the only large school of krill (*Euphausia superba*) that had been located during echosounder surveys in the area, and began to feed. Off Cape Cod, northern right whales (*Eubalaena glacialis*) surface feeding in a slick of plankton swam through the patches, appearing to follow the densest parts. They commonly turned away from what appeared to aerial observers to be sparser areas toward denser parts of the patch, sometimes making turns of 90° or more (Watkins and Schevill 1979).

There have been many observations of bowheads that were known, or thought, to be engaged in feeding behavior (Chapter 5). During the 1985 spring migration near Point Barrow, Alaska, groups of whales were watched closely as they circled and repeatedly dove beneath the shorefast ice (Carroll *et al.* 1987). Whales often exposed their flukes as they dove under the ice, and water was sometimes seen streaming from the baleen as they surfaced. Dives averaged 14.7 min long. Three whales, later harvested by subsistence whalers at Barrow, had copepods and euphausiids in their stomachs.

The most extensive observations of feeding behavior were made by researchers in aircraft studying bowheads in the Beaufort Sea during summer and fall. Cues such as milling and repetitive diving in one location, defecation, swimming with the mouth open, and mud streaming from the head or mouth have been used as indications that whales were feeding (Würsig *et al.* 1985, Ljungblad *et al.* 1986).

Bottom or near-bottom feeding has been inferred from observations of bowheads surfacing with mud streaming from the head or mouth, frequently with clouds of mud in the surrounding water. In the eastern Beaufort Sea, apparent bottom feeding has been seen in localized areas off the Mackenzie Delta in water 10–29 m deep (Würsig *et al.* 1985). Based on stomach contents, Frost and Lowry (1981*a*, *b*) speculated that in most cases the mud probably resulted from whales feeding near the bottom on planktonic organisms. Wartzok *et al.* (1990) conducted SCUBA observations in an area east of Point Barrow where bowheads had been diving and stirring up large quantities of mud. Benthic cores did not locate any likely prey organisms, but plankton net tows made just above the bottom caught copepods and mysids. A bowhead that was later found to have epibenthic organisms in its stomach was observed feeding prior to its capture near Saint Lawrence Island, but no mud was noted on the whale or in the water (Hazard and Lowry 1984). Perhaps the substrate was not muddy in that area.

Bowheads have been classified as water-column feeding when they dove repeatedly for long periods in the same general area. In those circumstances, whales often raised their flukes above the surface before diving. Defecation was commonly seen, which was considered an indication of prior feeding. Feeding whales often occurred in groups of 2–10 individuals in close proximity which surfaced and dove synchronously (Würsig *et al.* 1985, Ljungblad *et al.* 1986). Richardson and Finley (1989) analyzed all observations of feeding whales in the eastern and central Beaufort Sea during 1980–1986, and reported a mean dive duration of 10.8 min. The depth to which whales dove to feed has not been determined in any study, but all observations of feeding whales in the Beaufort Sea north of Alaska were in water depths $\leq$62 m (Ljungblad *et al.* 1986).

The only bowhead feeding that has been observed directly involved skimming at or near the surface. Whales usually swam upright with the rostrum just breaking the surface of the water and the lower jaw angled downward, sometimes as much as 60° (Würsig *et al.* 1985). They have also been observed to skim feed while swimming on their sides with part of their baleen rack above the surface of the water (Wartzok *et al.* 1990). Whales sometimes fed at the surface continuously for over 20 min (Würsig *et al.* 1984). Sometimes feeding whales were alone, but more often they occurred in groups of 2–10 or more. They frequently formed an echelon with each whale swimming just behind another and one-half to three body widths off to the side (Würsig *et al.* 1985, Fig. 5.3). This arrangement, which is similar to the V-formation of flying geese, may function to enhance feeding efficiency. Echelons are dynamic and the number and composition of individuals varies as whales arrive, leave, or change position. The closely related right whale has also been observed surface skimming (Watkins and Schevill 1976, 1979), and may also form echelons while feeding (Würsig *et al.* 1985).

There have been few published observations of bowhead feeding behavior in areas other than northwestern Canada and Alaska. During 1983–1988, Mr. K. J. Finley (personal communication) watched bowheads feeding in Isabella Bay on the east coast of Baffin Island. Bowheads occurred in this bay during August through October, and fed primarily over deep glacial troughs. Copepods, which were probably the primary prey, were most concentrated at a depth of 100–150 m, and bowheads showed their flukes before most dives which suggests that they were feeding deep in the water column. Feeding dives were up to 29.6 min long and averaged 15.8 min (Richardson and Finley 1989). Whales generally fed in loose groups of up to 14 individuals, surfacing and diving independently. Near-surface feeding was very rarely observed, and there was no indication of bottom feeding.

FOODS USED BY BOWHEADS

Although the foods used by bowheads may be inferred from behavioral observations, collections of feces, or sampling of potential prey in the surrounding water, the most direct indication of what is being ingested comes from the examination of stomach contents. Because bowheads of the Bering Sea stock are hunted for subsistence use, a number of whale stomachs have been made available for scientific examination through the cooperation of Alaskan whalers and the Alaska Eskimo Whaling Commission.

There are some problems associated with sampling bowhead stomachs. At some locations, whales may be processed in the water or on unsafe ice and it may be difficult or impossible to get access to the stomach. The stomach is large and complex and it may be difficult to thoroughly search and sample it. Full stomachs must be subsampled and estimates of the probable total volume of contents may be imprecise or presented in general terms. Stomachs cannot be examined until hours or sometimes even days after death. Partially digested prey may be difficult to separate, identify, and quantify. Some samples also contained clotted blood, making complete analysis difficult. The data obtained from each whale sampled are, therefore, not uniform.

Samples from 35 bowheads—14 females and 21 males—taken at Alaskan villages from 1976 to 1988 have been examined. Results of analysis of these samples have been reported in part in Lowry *et al.* (1978), Lowry and Burns (1980), Lowry and Frost (1984), Hazard and Lowry (1984), Carroll *et al.* (1987), and Lowry *et al.* (1987), and are compiled and reported, along with recent unpublished data, in this section.

The specimens examined (Table 6.1) included 32 samples from stomachs and 3 from other parts of the gastrointestinal tract. Most of the samples came from whales taken during the spring in the northeastern Chukchi Sea near Point Barrow (13 samples) and during the fall in the Beaufort Sea near Kaktovik (12 samples). Very few samples were obtained from whales taken in the Bering Sea or the Chukchi Sea south of Barrow.

A minimum of 62 species of animals have been identified from the samples (Table 6.2), broken down as follows: copepods, 11 species; euphausiids, 2; mysids, 2; hyperiid amphipods, 5; gammarid amphipods, 24; other invertebrates, 15; and fishes, 3.

Copepods occurred in 25 of the 35 samples, euphausiids in 24, mysids in 11, hyperiid amphipods in 16, gammarid amphipods in 23, other invertebrates in 18, and fishes in 7. Non-food items included detached baleen bristles which occurred in all the samples, pebbles which occurred in 12, and a bird feather and a 12-×-12-cm piece of plastic sheeting which were found in one stomach.

Table 6.1. Bowhead whale specimens from which samples of prey items were obtained. Samples were collected from the stomach unless otherwise indicated. Numbers correspond to whales shown in Table 6.2.

Number	Specimen number	Location	Date of kill	Sex	Total length (m)	Comments
1	76-B-6	Barrow	10 Sep 76	female	16.0	
2	76-B-7	Barrow	20 Sep 76	female	14.3	
3	77-B-5	Barrow	05 May 77	male	10.6	
4	79-B-3	Barrow	27 May 79	male	8.3	sample from colon
5	80-B-3	Barrow	25 May 80	male	8.5	
6	80-B-5	Barrow	25 May 80	male	10.4	
7	80-B-9	Barrow	27 May 80	female	13.6	
8	84-B-3	Barrow	21 May 84	female	8.3	
9	85-B-1	Barrow	09 May 85	male	9.0	
10	85-B-2	Barrow	10 May 85	male	12.4	
11	85-B-3	Barrow	16 May 85	male	9.5	
12	86-B-5	Barrow	04 May 86	male	8.1	
13	86-B-6	Barrow	05 May 86	female	12.3	
14	88-B-1	Barrow	24 Apr 88	female	8.8	
15	88-B-3	Barrow	25 Apr 88	female	7.8	sample mostly blood
16	88-B-9	Barrow	15 Sep 88	male	14.6	
17	88-B-10	Barrow	17 Sep 88	male	15.1	
18	88-B-11	Barrow	17 Sep 88	female	15.6	
19	79-KK-1	Kaktovik	20 Sep 79	male	12.7	recovered on 22 Sept.
20	79-KK-2	Kaktovik	06 Oct 79	female	10.5	
21	79-KK-3	Kaktovik	08 Oct 79	male	10.3	
22	79-KK-4	Kaktovik	10 Oct 79	male	10.6	
23	79-KK-5	Kaktovik	11 Oct 79	male	10.6	
24	80-KK-1	Kaktovik	14 Sep 80	male	9.1–10.7	sample from intestine
25	81-KK-1	Kaktovik	08 Sep 81	female	17.4	
26	81-KK-2	Kaktovik	11 Sep 81	male	14.0	
27	82-KK-1	Kaktovik	23 Sep 82	male	16.0	
28	83-KK-1	Kaktovik	20 Sep 83	female	14.7	
29	86-KK-1	Kaktovik	10 Sep 86	female	7.6	
30	86-KK-3	Kaktovik	26 Sep 86	male	7.3	
31	78-H-2	Point Hope	04 May 78	male	9.7	
32	79-H-3	Point Hope	06 May 79	male	9.1	
33	80-SH-1	Shaktoolik	09 May 80	male	10.1	sample from colon
34	82-G-2	Gambell	01 May 82	female	8.8	
35	88-WW-1	Wainwright	25 Apr 88	female	7.9	

A consideration of which taxa were the volumetrically dominant components of the samples shows a different picture than does the number of species consumed or the simple frequency of occurrence. Copepods were a dominant component of 17 samples, euphausiids of 13, mysids of 1, and gammarid amphipods of 2. Hyperiid amphipods, other invertebrates, and fishes were not dominant components.

Overall, these data confirm that copepods and euphausiids are the prin-

Table 6.2. Prey identified from gastrointestinal tracts of bowhead whales. Numbers correspond to individual whales described in Table 6.1. Dominant prey species are indicated by XX.

	BARROW																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
COPEPODS																		
Calanus cristatus					X													
C. glacialis			X				X	X	XX	XX	XX	XX	X	XX				X
C. hyperboreus					XX		X		X				X	X				
Calanus sp.					X													
Chiridius obtusifrons					X		X											
Euchaeta glacialis			X		XX													
Euchaeta sp.														X	X			
Heterorhabdus sp.																		
Jashnovia tolli																		
Limnocalanus grimaldi																		
Metridea longa			XX															
M. lucens																		
Metridea sp.															XX			
Pseudocalanus sp.			X															
EUPHAUSIIDS								X				X						
Thysanoessa inermis					X		X		X	X			X		X	X	X	
T. raschii	XX	XX	X		X	XX	XX		XX	X	XX		XX	X		XX	XX	XX
MYSIDS																		
Mysis litoralis							X				X						X	
Neomysis rayi					X	X	X											
HYPERIID AMPHIPODS									X									
Hyperia galba					X		X											
H. medusarum							X											
Hyperia sp.										X								
Hyperoche medusarum							X				XX							
Parathemisto abyssorum			X															
P. libellula	X	X									X							

Table 6.2. Continued.

	BARROW																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
GAMMARID AMPHIPODS								X										
Acanthostepheia behringiensis		X																
A. incarinata																		
Acanthostepheia sp.																	X	
Ampelisca macrocephala																		X
Anonyx compactus																		
A. nugax							X				X							
Apherusa glacialis																		
Atylus atlassovi																		
A. carinatus																		
Bathymedon sp.																		
Gammaracanthus loricatus																		
Gammarus zaddachi		X																
Gammarus sp.																		
Harpinia sp.														X				
Hippomedon denticulatus																		
Monoculodes zervoni		X																
Monoculodes sp.																	X	
Munnopsis sp.																		
Onisimus glacialis																		
O. litoralis																		
O. nanseni																		
Orchonome sp.																		
Pontoporeia femorata																		
Rhacotropis sp.											X							
Rozinante fragilis	X	X															X	
Weyprechtia heulgini																		
Weyprechtia pinguis																		

Table 6.2. Continued.

	BARROW																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Family Lysianassidae																		
Family Synopiidae																		
ISOPODS																		
Saduria entomon																		
SHRIMP		X																
Eualus fabricii																		
E. gaimardii																		
Pandalus goniurus																		
Sabinea septemcarinata																		
Family Crangonidae																		
CRABS																		
Chionoecetes opilio																		
Pagurid zoea																X	X	X
CUMACEANS																		
Diastylis bidentata																		
Diastylis dalli																		
Diastylis sp.																		
Leucon sp.																	X	
Family Leuconidae																		X
OSTRACODS			X															
PYCNOGONIDS																		
MOLLUSCS																		
Limacina helicina			X															
Natica clausa																		
Nuculana sp.				X														
Order Pelecypoda																		

Table 6.2. Continued.

	BARROW																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
FISHES			X														X	
Boreogadus saida																		
Myoxocephalus quadricornis																		
Pungitius pungitius																		
Family Cottidae																		
PEBBLES/SAND	X				X	X		X						X		X		X
BIRD FEATHER																		
PLASTIC																		

	KAKTOVIK												OTHER AREAS				
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
COPEPODS						XX											
Calanus cristatus																	
C. glacialis							X	X	X	X	X	X					X
C. hyperboreus	XX	XX	X	XX	X		XX	XX	XX								
Calanus sp.		X		X													
Chiridius obtusifrons				X													
Euchaeta glacialis									X								
Euchaeta sp.												X					X
Heterorhabdus sp.		X		X													
Jashnovia tolli											XX						
Limnocalanus grimaldi											XX						
Metridea longa									X								
M. lucens		X		X													
Metridea sp.																	XX
Pseudocalanus sp.							X				XX						

Table 6.2. Continued.

	KAKTOVIK												OTHER AREAS				
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
EUPHAUSIIDS											X						
Thysanoessa inermis					X												
T. raschii		X	XX	X	XX		X				X	XX					
MYSIDS																	
Mysis litoralis		X	X		X					XX	X	X					
Neomysis rayi																	
HYPERIID AMPHIPODS																	
Hyperia galba										X							
H. medusarum		X															
Hyperia sp.	X																
Hyperoche medusarum																	
Parathemisto abyssorum			X				X										
P. libellula	X	X	X	X	X				X			X					
GAMMARID AMPHIPODS																XX	
Acanthostepheia behringiensis			X		X												
A. incarinata		X															
Acanthostepheia sp.																	
Ampelisca macrocephala													X				
Anonyx compactus																X	
A. nugax												X					
Apherusa glacialis				X			X				XX						
Atylus atlassovi																X	
A. carinatus			X		X												
Bathymedon sp.																X	
Gammaracanthus loricatus			X		X												
Gammarus zaddachi																	

Table 6.2. Continued.

	KAKTOVIK												OTHER AREAS				
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Gammarus sp.		X															
Harpinia sp.																	X
Hippomedon denticulatus																X	
Monoculodes zervoni																	
Monoculodes sp.			X	X													
Munnopsis sp.			X														
Onisimus glacialis		X					X	X	X								
O. litoralis	X																
O. nanseni								X									
Orchonome sp.																X	
Pontoporeia femorata																X	
Rhacotropis sp.																	
Rozinante fragilis				X													
Weyprechtia heulgini				X	X												
Weyprechtia pinguis						X				X							
Family Lysianassidae	X																
Family Synopiidae																X	
ISOPODS																	
Saduria entomon					X												
SHRIMP		X													X		
Eualus fabricii																X	
E. gaimardii				X						X		X					
Pandalus goniurus												X					
Sabinea septemcarinata				X													
Family Crangonidae	X																
CRABS																	
Chionoecetes opilio																X	
Pagurid zoea							X				X	X					

Table 6.2. Continued.

	KAKTOVIK												OTHER AREAS				
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
CUMACEANS																	
Diastylis bidentata																X	
D. dalli										X							
Diastylis sp.				X						X							X
Leucon sp.																	
Family Leuconidae																	
OSTRACODS																	
PYCNOGONIDS										X							
MOLLUSCS																	
Limacina helicina																	
Natica clausa														X			
Nuculana sp.																	
Order Pelecypoda																X	
FISHES																	
Boreogadus saida			X			X						X					
Myoxocephalus quadricornis				X		X											
Pungitius pungitius						X											
Family Cottidae																X	
PEBBLES/SAND	X				X						X	X				X	
BIRD FEATHER												X					
PLASTIC												X					

Table 6.3. Sizes of prey organisms in stomachs of bowhead whales (adapted from Lowry and Frost 1984).

Taxon	Length (mm)[a]	Volume (ml)
Copepods	1.1–7.0	<0.001–0.02
Euphausiids	18–30	0.1–0.2
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

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

cipal foods of bowheads near the locations sampled. Organisms such as hyperiid amphipods, which are also part of the zooplankton community, are ingested incidentally but are not major dietary components. Epibenthic invertebrates such as mysids and gammarid amphipods occasionally are dominant foods, but in most cases are also consumed incidentally while whales are feeding on copepods and euphausiids. In 10 of the 12 stomachs that contained pebbles or sand, the dominant prey item was zooplankton. This may indicate that whales were foraging on copepods and euphausiids very near the bottom, although the sediment could have been consumed during earlier feeding bouts.

Sizes of representative species of the various prey are shown in Table 6.3. The organisms most commonly eaten (copepods, euphausiids, mysids, and amphipods) were usually from 3 to 30 mm long. Organisms such as isopods and fishes were considerably larger but rarely occurred in stomach contents samples. The largest item found 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 organisms found were copepods 1.1 mm in cephalothorax length that weighed about 0.1 mg.

Small copepods of the genera *Pseudocalanus* (cephalothorax length 1.1–1.6 mm), *Jaschnovia* (1.4–1.8 mm), and *Limnocalanus* (1.1–1.9 mm) are very common in the Beaufort Sea. However, in stomach samples collected through 1982, the smallest copepods that occurred in large numbers were *Calanus glacialis* (2.4–3.3 mm) and *Metridea* spp. (2.7–3.1 mm), which led to speculation that organisms smaller than 2.5 mm were not effectively retained by bowhead baleen (Lowry and Frost 1984). However, a whale taken at Kaktovik in 1986 had a full stomach, the contents of which included many *Pseudocalanus, Jaschnovia,* and *Limnocalanus.* As a group, small copepods were the dominant food item (39% of the sample volume), followed by gammarid amphipods (37%), and euphausiids (21%). The whale was a 7.6-m-long female which was noted as being very thin with baleen unusually long for such a small whale (J. C. George, personal communication).

Although this specimen confirms that bowheads can, and sometimes do, feed upon the small species of copepods, large species have dominated the majority of samples examined to date. Of 14 samples from whales taken at Barrow in the spring, larger copepods occurred in 11, small copepods in

Table 6.4. Types of prey items in stomach contents of small and large bowhead whales.

	Whales <10.5 m (n = 15)		Whales >10.5 m (n = 17)	
Prey type	Number of occurrences	Number times dominant	Number of occurrences	Number times dominant
Crustacean plankton	12	11	17	16
Soft-bodied plankton	0	0	1	0
Epibenthos	11	2	15	1
Infauna	2	1	0	0
Fish	3	0	4	0

only 1. Similarly, larger copepods occurred in all 12 samples from whales taken at Kaktovik in the fall, while small copepods were found in only 3 (Table 6.2).

Thus, analysis of stomach contents indicates that crustacean zooplankton (primarily copepods and euphausiids) are overall the most important foods of bowheads in Alaskan waters, but epibenthic organisms (mostly mysids and gammarid amphipods) are also eaten regularly and sometimes in large quantities. In order to see if size of the whale influenced the types of foods eaten, the data were separated into that from small (7.3–10.4-m-long) and large (10.5–17.4-m-long) whales. Crustacean plankton was the dominant prey in 16 of the 17 large whales as compared to 11 of the 15 small whales (Table 6.4). There was a slightly greater tendency for epibenthos and infauna to dominate in samples from small whales. These data are too limited to firmly establish whether or not there are age-related differences in feeding. A trend in carbon isotope ratios in bowhead baleen suggests that copepods become an increasingly important component in the diet of older whales (Schell *et al.* 1987, Chapter 12).

The sample of whales for which stomach contents have been examined included 14 females and 18 males. Crustacean plankton was the dominant food item both in females (11/14 = 79%) and in males (16/18 = 89%).

The first bowhead hunting off the coast of Alaska in a given year occurs in April near Saint Lawrence Island in the northern Bering Sea. Whales are often processed in the water and stomachs are usually not available for examination. In recent years, three stomachs have been recorded as empty and three as containing food. Of the latter, samples from one were collected for laboratory analysis. Stomach contents of that whale (82G2, the second whale taken at Gambell in 1982) were estimated at 20–40 liters, and consisted mostly of gammarid amphipods (92% of the sample volume) and cumaceans (7%).

From late April to early June, whales are taken at Point Hope and Wainwright. At Point Hope, three whales have been recorded as having empty stomachs and one as containing a small amount of "shrimp." At Wainwright, 10 of 12 whales examined had empty stomachs. One sample (from 88WW-1) was analyzed in the laboratory and found to consist mostly of copepods of the genus *Metridea.* No estimate was made of stomach contents volume.

The largest harvest of spring-migrating bowheads is taken near Point Barrow from late April through mid-June. From 1979 through 1988, 36

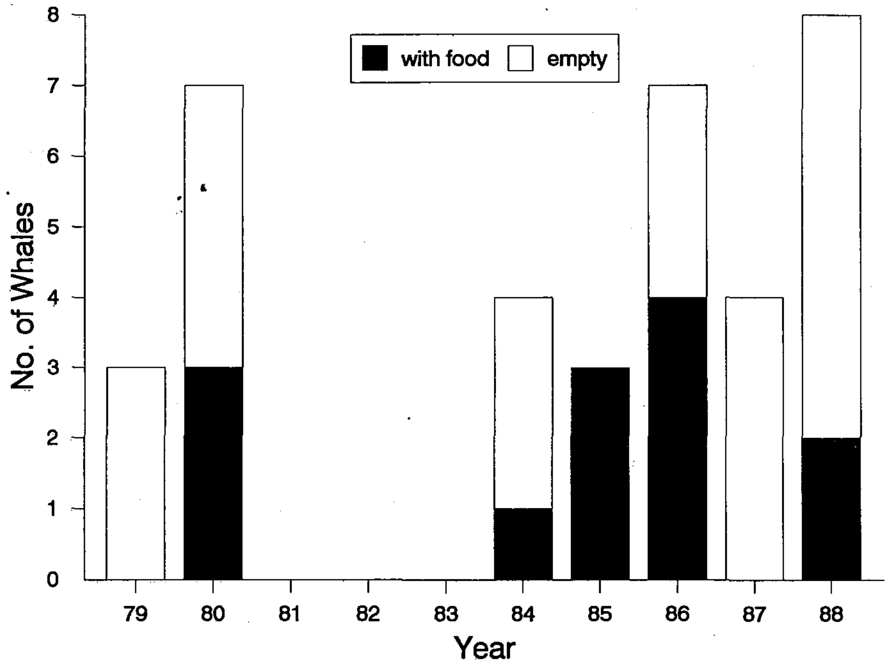

Figure 6.2. Occurrence of food in stomachs of bowhead whales taken near Point Barrow during the spring migration 1979–1988.

stomachs were examined, of which 13 were noted as containing food. The proportion of stomachs examined that have contained food has varied from year to year, ranging from 0% in 1979 and 1987 to 100% in 1985 (Fig. 6.2).

The estimated total volumes of contents in stomachs ranged from less than 1 to 60 liters, with an average of 12.2 liters in eight specimens for which volume was recorded quantitatively. Ten samples contained substantial amounts of food in conditions suitable for detailed examination (Fig. 6.3). Generally either copepods or euphausiids predominated in a given stomach, although some samples contained substantial amounts of both. Copepods and euphausiids each occurred in 9 of the 10 samples examined. The dominant prey often varied among individuals taken in the same year, although it appeared, overall, that euphausiids were a more important food item in 1980 and copepods in 1985. Mysids were a substantial component only in 1980.

It is difficult to estimate the average contribution of various prey to the overall diet in an area from the subsamples that have been available for examination. The size of the subsamples and the total volume of contents in stomachs varied greatly. Since the stomach contents volume was often not measured or estimated, it is not possible to weight results of samples from individual whales in relation to total contents. An approximation of the overall composition of the diet for bowheads near Barrow during the spring was calculated by averaging the percent contribution of prey types in the 10 individual whales shown in Figure 6.3. Based on this method of calculation the overall diet composition was as follows: copepods, 54.2%; euphausiids, 42.4%; mysids, 2.6%; and other invertebrates, 0.8%.

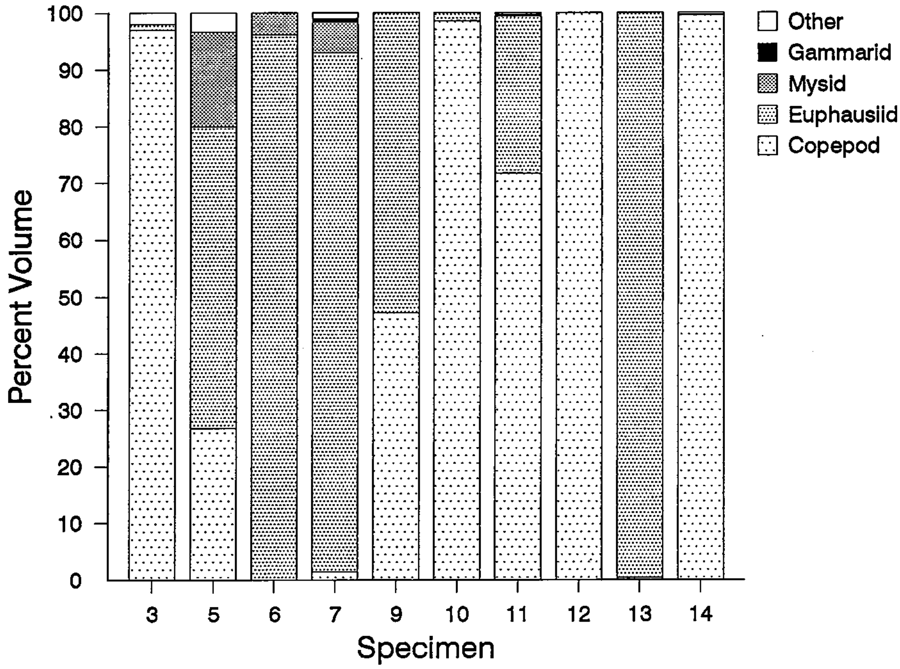

Figure 6.3. Composition of stomach contents samples from 10 bowhead whales taken near Point Barrow during spring 1977–1988. Specimen numbers refer to whales shown in Table 6.1.

In September and October, bowheads are harvested near the village of Kaktovik on Barter Island. Stomachs of 15 whales taken during 1979–1988 have been examined, and 13 of those contained food. The two that did not were retrieved more than a day after being struck. During that time any food would have been completely digested, and the data therefore suggest that all or nearly all bowheads taken at Kaktovik had been feeding prior to capture. Total estimated volumes of contents ranged from 3 to 48 liters, with an average of 25.9 liters in eight specimens for which volume was recorded quantitatively.

In 11 samples that were suitable for detailed examination, either copepods or euphausiids were usually the dominant component of stomach contents, although some contained mixtures of the two (Fig. 6.4). Copepods occurred in at least trace amounts in every sample, while euphausiids were not detected in four samples. Two specimens were notably different. The sample from whale 83KK-1 contained mostly mysids (98.1%) and some gammarid amphipods (1.4%). This whale had the largest volume of stomach contents recorded at Kaktovik (48 liters). Whale 86KK-1 had eaten almost equal amounts of copepods (38.6%) and gammarid amphipods (36.8%) along with substantial amounts of euphausiids (21.1%). This was the only sample that contained almost exclusively small species of copepods. It was noted as having a full stomach.

The approximate overall composition of the diet of whales taken at Kaktovik, based on percentage of contribution of prey types in the 11 whales

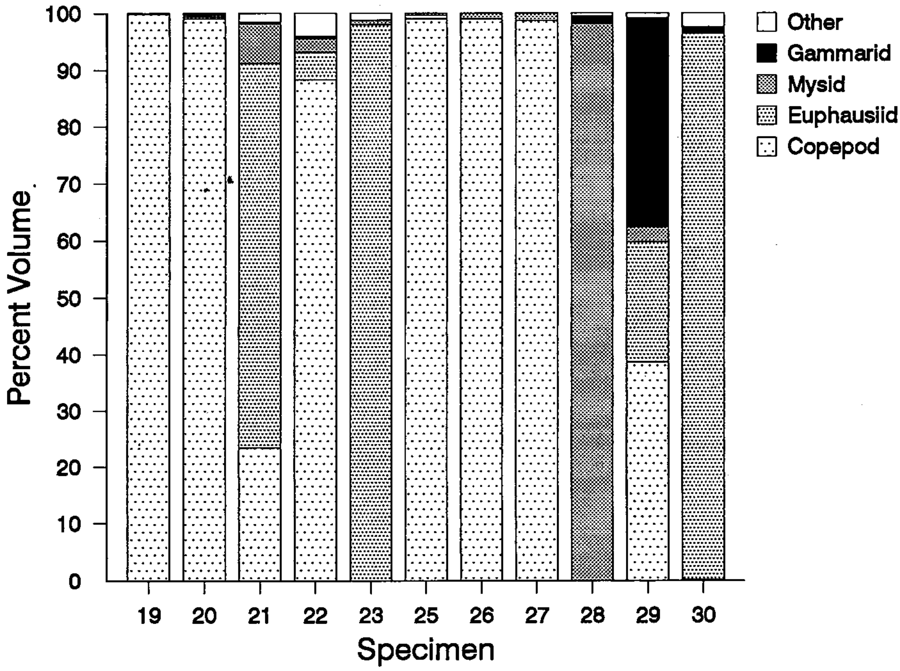

Figure 6.4. Composition of stomach contents samples from 11 bowhead whales taken near Kaktovik during fall 1979–1986. Specimen numbers refer to whales shown in Table 6.1.

shown in Figure 6.4 was as follows: copepods, 58.7%; euphausiids, 26.3%; mysids, 10.1%; gammarid amphipods, 3.9%; and other invertebrates, 1.0%. The relatively high value for mysids is due mostly to specimen 83KK-1, although mysids occurred in 7 of the 11 samples examined. Gammarid amphipods occurred in every sample, but made up a large proportion only in whale 86KK-1.

Fall-migrating bowheads are also taken at Point Barrow. Five of six whales whose stomachs were examined during 1976–1988 contained food. The total volume of contents of one whale (76B-7) was estimated as 109 liters, and three others were recorded at 8 liters. Samples suitable for analysis were received from all five whales. Euphausiids were the dominant item in all the samples (Fig. 6.5). Copepods occurred in only one sample in trace amounts. The approximate overall composition of the diet was as follows: euphausiids, 96.0%; mysids, 0.3%; gammarid amphipods, 2.6%; and other items, 1.1%.

ANNUAL FEEDING CYCLE OF THE BERING SEA STOCK

The observations described in the previous section suggest that bowheads feed occasionally while migrating northward in the spring off the west coast of Alaska. The region west of Point Barrow seems to be of particular importance for feeding, at least in some years, but whales may feed oppor-

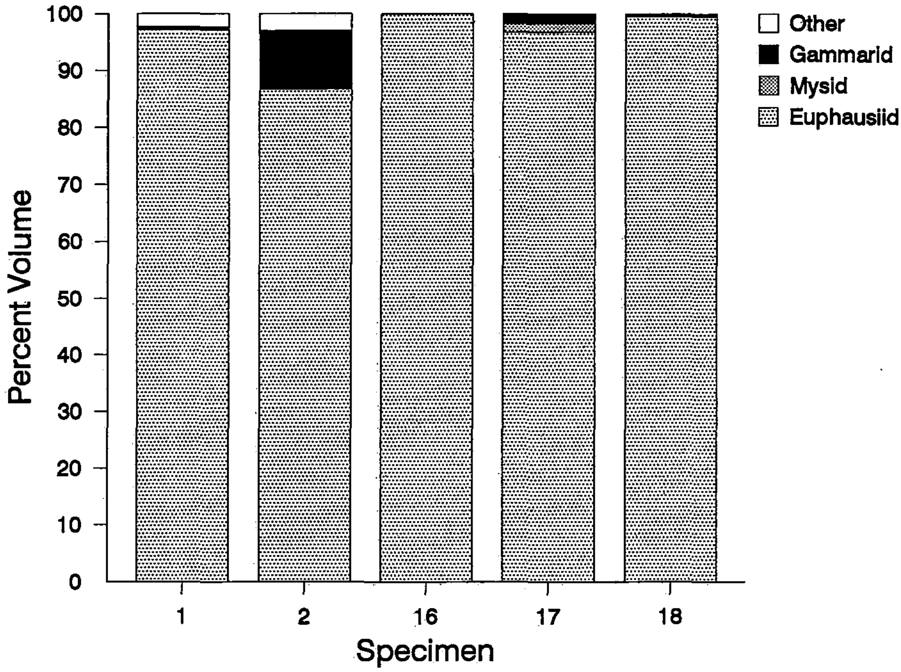

Figure 6.5. Composition of stomach contents samples from five bowhead whales taken near Point Barrow during fall 1976–1988. Specimen numbers refer to whales shown in Table 6.1.

tunistically at other locations in the lead system where oceanographic conditions produce locally abundant food (Carroll *et al.* 1987).

After passing Point Barrow, bowheads swim eastward through a system of offshore leads until they reach the west coast of Banks Island (Braham *et al.* 1980*b*). Whales observed in this Arctic Ocean lead system have not been recorded as feeding, although it is possible that they may sometimes feed below the surface or under the ice (D. K. Ljungblad and W. J. Richardson, personal communications).

From mid-June through October, many bowheads are in the eastern Beaufort Sea and the Amundsen Gulf region, and it is assumed that they spend much of this 4-mo period feeding (Fraker and Bockstoce 1980). Behavioral observations have confirmed that feeding is a predominant activity of whales summering in this area (Würsig *et al.* 1985), but the proportion of time spent feeding, and the types of prey being consumed, are unknown. Griffiths and Buchanan (1982) sampled zooplankton near whales feeding north of the Mackenzie Delta in 1980–1981. They found the copepods *Calanus hyperboreus* and *C. glacialis* to be more common near feeding whales than elsewhere. The copepod *Limnocalanus macrurus* was the dominant component of the zooplankton in a bowhead feeding area off the Yukon coast. Whales seen feeding in this area were mostly subadults, and calculations incorporating data on zooplankton density and theoretical bowhead feeding rates suggested they could consume as much as 26% of their annual energy requirement by feeding in the area for a 6-wk period

(Bradstreet *et al.* 1987). Some whales may summer and feed off the north coast of Alaska rather than migrating all the way to the eastern Beaufort Sea. Whales that were probably feeding have been seen in early August north of Kaktovik (Ljungblad *et al.* 1983) and east of Point Barrow (Lowry and Frost 1984).

Whales that summer in Canadian waters continue to feed as they move westward into the Alaskan portion of the Beaufort Sea in late August, September, and October. Based on stomach contents, reports from Eskimo whalers, and aerial observations by whale researchers, Lowry and Frost (1984) identified two feeding areas north of Alaska, one extending from Barter Island to the U.S./Canada border and the second from Point Barrow east to approximately Pitt Point. The incidence of feeding and types of prey used in these areas were described in the previous section based on stomach contents of whales taken at Kaktovik and Barrow. A study of the eastern feeding area concluded that the bowhead population as a whole obtained about 1% of its annual energy needs in that region in 1985 and 1986 (Richardson 1987). Subadult whales that spent about 10 d in the area may have obtained as much as 6% of their annual nutritional needs.

Ljungblad *et al.* (1986) plotted 692 sightings made during fall 1979–1984 of bowheads that appeared to be feeding. Feeding whales were seen from off the Yukon coast (139°W longitude) to west of Point Barrow (158°40′W). Numerous sightings of feeding whales were made east of Barter Island, north of Camden Bay, north of Prudhoe Bay, and east of Point Barrow. Ljungblad *et al.* (1986) concluded that bowheads feed over a period of 8–25 d as they migrate westward through the Beaufort Sea north of Alaska.

After passing Point Barrow, bowheads are presumed to move across the northern Chukchi Sea to the northeast coast of Siberia (Bogoslovskaya *et al.* 1982, Miller *et al.* 1986). It has been assumed that they feed, at least opportunistically, in these areas. Concentrations of potential prey including *Calanus, Thysanoessa,* and *Mysis* have been documented to occur in the southern and southwestern Chukchi Sea in September (Sleptsov 1961). Miller *et al.* (1986) recorded large numbers of bowheads off Cape Vankarem in September–October 1979 and 1980, and concluded that conditions in that area might be particularly suitable for feeding.

Bowheads appear to winter mostly in the marginal ice zone of the central Bering Sea (Brueggeman 1982, Ljungblad 1986). There is no direct information on whether or not whales feed in this area. All of the bowheads seen in January 1986 were either resting, mating, or swimming slowly at the surface (Ljungblad 1986). Based principally on characteristics of prey populations, Lowry and Frost (1984, p. 14) speculated that "winter feeding in the Bering Sea, if it occurs, is of little significance in the annual nutrition of bowheads." Richardson (1987) considered it likely that at least some opportunistic feeding does occur during winter months.

Schell and co-workers (1987, Chapter 12) examined the ratios of stable carbon isotopes in bowhead baleen and tissues as part of a study to determine the importance of the eastern Beaufort Sea as a feeding area for bowheads. Carbon isotope ratios, which in zooplankton vary geographically and between trophic levels, were also found to vary along the length of the baleen and in tissues. Results from muscle and blubber analyses suggested that young whales obtained a large amount of their annual food intake from areas other than the eastern or central Beaufort Sea. The pattern of isotope variation in large whales was different from that in small whales, which may reflect feeding in different areas or on different prey types. The longer-term records contained in the baleen indicated that whales feed on herbivorous zooplankton (*e.g.*, copepods) in the eastern Beaufort Sea, and eat more omnivorous and carnivorous species (*e.g.*, euphausiids and amphipods) in the western Beaufort, Chukchi, and Bering seas.

FOOD AVAILABILITY AND CHARACTERISTICS

Once the diet of bowhead whales is reasonably well understood, it becomes possible to examine the availability of its food in the environment. Some knowledge of the amounts of food available and the factors that control food availability are important for explaining, and perhaps predicting, the distribution of whales during the feeding season. Data on abundance and distribution of prey are also needed to understand ecological aspects of bowhead nutrition.

A detailed consideration of oceanography, phytoplankton productivity, and invertebrate ecology is beyond the scope of this chapter. Water mass characteristics and movements, light availability and penetration, and nutrient availability and utilization are all important factors that need to be taken into account. Bowheads often occur in oceanographically complex areas where arctic and subarctic marine water masses interact with terrestrial runoff. There is great seasonal variability in sunlight which is further modified in the water column by sea ice cover and turbidity from rivers and other sources (Chapter 2). Nutrients may come from terrestrial runoff in rivers or marine sources where processes such as upwelling bring deep water up to near the surface.

Most studies of bowhead food availability have focused on areas thought to be of particular importance for feeding, especially the eastern Beaufort Sea where the majority of the Bering Sea population is presumed to feed during June–October. Grainger (1975) conducted oceanographic studies off the Mackenzie River Delta and Tuktoyaktuk Peninsula. In this region, a plume of low-salinity water carrying a heavy load of particulate material and nutrients flows northward and meets a colder, more saline, and generally nutrient-poor mass of Arctic Basin water. This produces a two-layered system with the arctic water mass below the Mackenzie plume, the latter becoming less distinct farther offshore. Grainger (1975) thought that turbidity probably limited productivity in the plume, while nutrients were the limiting factor in the arctic water. Productivity of both phytoplankton and zooplankton was relatively low in his study area. However, as noted by Fraker and Bockstoce (1980), Grainger (1975) found the highest standing stocks of zooplankton in an area north of the Tuktoyaktuk Peninsula where bowheads commonly occur.

Characteristics of bowhead feeding areas in the southeastern Beaufort Sea were further explored in 1980–1981 by Griffiths and Buchanan (1982). Two distinct water layers were again documented in the study area. Hydromedusae and copepods accounted for most of the biomass in zooplankton net samples. Highest biomass generally occurred below the thermocline (10 m or deeper) or just above the sea floor. In both years, the biomass of copepods was higher where bowheads were seen than in other areas. However, average copepod biomass in the water column near whales was not particularly high (0.1 g/m^3 in 1980 and 0.3 g/m^3 in 1981), leading Griffiths and Buchanan (1982) to speculate that bowheads might also eat hydromedusae. Dropnet samples indicated that mysids, isopods, and to a lesser extent, copepods were the most abundant organisms near the bottom. The biomass of mysids was 1.0 g/m^3 adjacent to the bottom at a shallow water station off King Point.

The accumulation of data on zooplankton and bowhead distributions, in conjunction with remote sensing of oceanographic and meteorologic conditions, allowed a detailed examination of the relationships among these factors (Thomson *et al.* 1986). The location of the Mackenzie River plume, which is clearly identifiable in satellite imagery, was presumed to influence bowhead distribution since zooplankton biomass tended to be lower in water influenced by the plume. The area influenced by the Mackenzie discharge was largely controlled by wind speed and direction. Under prolonged westerly winds the plume occurred close to shore, along the Tuktoyaktuk Peninsula. Easterly winds caused it to spread to the north and west. Data on bowhead distribution were generally consistent with the hypothesis that bowheads avoid the plume. Other factors may also be important since, in some years, whales apparently were absent from previously used areas that were not being influenced by the Mackenzie plume. Thomson *et al.* (1986) identified several processes that could be important for producing concentrations of food in various areas including (1) an estuarine front (resulting from the Mackenzie plume) in Mackenzie Bay, north of Richards Island and the Tuktoyaktuk Peninsula, and off King Point and Herschel Island; (2) upwelling in areas off the Yukon coast; (3) turbulence which occurs off Herschel Island and Cape Bathurst; and (4) oceanographic phenomena occurring at the shelf break, perhaps especially in Herschel Canyon.

In late summer and early fall 1985 and 1986, studies were conducted in bowhead whale feeding areas in both the Canadian and Alaskan portions of the Beaufort Sea. These studies used hydroacoustic and other techniques to delineate and sample zooplankton layers in a more realistic fashion than previous studies that had usually measured average biomasses in the entire water column.

Studies in Canadian waters (Bradstreet and Fissel 1986, Bradstreet *et al.* 1987) verified previous conclusions that bowheads do not usually feed in areas influenced by the Mackenzie plume because of a lower biomass of zooplankton. High zooplankton biomass tended to occur in areas where easterly or southerly winds caused upwelling of Arctic Ocean water. Interfaces between the Arctic Basin water and the Mackenzie plume caused formation of elongated zooplankton patches along inclined subsurface fronts. Zooplankton biomass, which was dominated by the small copepod *Limnocalanus macrurus,* was highest near feeding whales. Maximum observed values in net tows were 2.3 g/m^3 in 1985 and 1.5 g/m^3 in 1986. Although euphausiids contributed little to the total biomass found in zooplankton samples, their apparent biomass was 16–20 times greater in tows taken near bowheads than in areas where no whales were seen.

The bowhead feeding study area north of Alaska, between 141°W and

144°W longitude, was to the west of the region strongly influenced by Mackenzie River water. Zooplankton biomass during August and September was highest in the area between shore and the 50-m isobath, and was on average similar to that found over the continental shelf of the Canadian portion of the Beaufort Sea (Griffiths *et al.* 1987). Zooplankton distribution was patchy in both 1985 and 1986. Hydroacoustics detected patches that were as much as several kilometers long and were usually 5–10 m thick, although they sometimes extended from just below the surface to the bottom. Copepods dominated the zooplankton with *Calanus* spp. most common offshore, and *Limnocalanus macrurus* most abundant in nearshore waters. In 1986, bowheads were seen feeding nearshore in an area where, based on net samples, the zooplankton biomass in the highest density layers was 2–3 g/m^3, with *L. macrurus* the dominant species. Within the eastern Beaufort Sea study area north of Alaska, mysids and euphausiids were not major contributors to the total biomass of potential bowhead prey, but they were found to be more abundant near the bottom in nearshore waters.

In October 1986, Griffiths *et al.* (1987) also collected net samples of zooplankton in the central and western Beaufort Sea. In contrast to results from the eastern Beaufort Sea, euphausiids comprised a substantial proportion of the sample biomass (catches up to 0.3 g/m^3) and copepods were relatively scarce.

In September 1989, Wartzok *et al.* (1990) sampled zooplankton in conjunction with bowhead whale studies conducted in the Beaufort Sea. Midwater bongo net tows documented high densities of copepods (up to 1.5 g/m^3) where whales were feeding in the water column, and surface tows found high densities of euphausiids (up to 2.8 g/m^3) where whales were skim feeding. The combined biomass of euphausiids, copepods, and mysids was significantly greater near feeding whales than in areas where whales were not feeding.

Comparisons of results from zooplankton surveys with bowhead stomach contents suggest some correlations and some discrepancies. The preponderance of euphausiids in the zooplankton of the western Beaufort Sea correlates well with observations indicating that whales taken near Barrow in the fall had fed almost exclusively on euphausiids. Whales taken in the Beaufort Sea near Kaktovik often had fed on copepods which also predominated in zooplankton samples. These whales, however, had also eaten large amounts of euphausiids, which comprised a very small proportion of the apparent zooplankton biomass. Copepods found in stomach contents from bowheads taken in Alaskan waters have usually been of the larger species. While larger species of copepods have been relatively common in zooplankton samples taken in the Beaufort Sea, the dominant species, especially in nearshore waters east of Kaktovik, has been a small copepod *Limnocalanus macrurus*.

In the only study that has specifically addressed bowhead feeding in the eastern portion of the North American Arctic, K. J. Finley (personal communication) sampled zooplankton near feeding bowhead whales in Isabella Bay, Baffin Island. The dominant component of the zooplankton over the glacial troughs where bowheads fed was copepods of the genus *Calanus*. Zooplankton biomass averaged over 50-m-depth ranges was as high as 0.8 g/m^3 and may have been higher in patches on which whales actually fed.

The lipid and caloric content of zooplankton may be as, or more, important than biomass for considerations of bowhead energetics. Some species of arctic marine zooplankton accumulate lipids during the summer that are used for maintenance and reproduction during winter months (Lee 1975). This results in very high caloric values, especially for copepods in late summer (Percy and Fife 1980).

After reviewing data from the eastern Canadian Arctic, Lowry and Frost (1984) noted that, when expressed as calories/g wet weight, the most important prey of bowheads (copepods and euphausiids) have high caloric values while organisms that are rarely, if ever, eaten (*e.g.*, ctenophores and hydromedusae) have very low values. Recent samples collected within bowhead feeding areas in the eastern Beaufort Sea have confirmed this relationship and provided detailed data on caloric and lipid content of bowhead prey species (Bradstreet *et al.* 1987). On a wet-weight basis, copepods and euphausiids had caloric values four to five times higher than hydromedusae and ctenophores.

ENERGY REQUIREMENTS

Large whales pose particular problems for determining energy demands since they cannot be held and studied in captivity and may be difficult to observe in the wild. Even when animals are available for examination, such as from subsistence hunts, it can be difficult to make detailed observations and take needed measurements. For these reasons, a variety of approaches have been used to take advantage of available data and generate approximations of energy requirements (*e.g.*, Lockyer 1981, Thomson 1987).

Brodie (1981) published the first analysis of bowhead whale energetics. He estimated that heat loss from the metabolically active surface area and the lungs amounted to 95×10^3 Kcal/d for a bowhead 13.72 m long weighing about 46 mt, and doubled this value to 190×10^3 Kcal/d to account for reproduction, growth, and other energy demands. To supply this amount of energy on an annual basis would require the metabolism of about 4,000 kg of lipids, which would amount to a blubber layer 10 cm thick on top of the 18-cm-thick layer that is needed for insulation. If a bowhead could capture the 100 mt of crustaceans needed to acquire this amount of blubber in a 6-mo feeding season, it could afford to fast for 6 mo over the winter. Brodie calculated that, if a bowhead's mouth had a cross-sectional area of 1 m^2 and it swam at 5 km/h while feeding, prey densities would have to be 30 g/m^3 if a whale fed for 5 h/d or 7.5 g/m^3 if feeding extended over 20 h/d. These values greatly exceed what has been measured in zooplankton net samples.

Lowry and Frost (1984) made similar calculations, again assuming, as did Brodie (1981), that a 13.7-m-long bowhead would have to ingest 4,000 kg of lipids to maintain itself throughout the year. If lipid comprised 16.8% of the wet weight of arctic copepods (Percy and Fife 1980) a whale would need to consume 23,810 kg of copepods during a feeding season. Based on copepod biomasses of 0.6–0.9 g/m^3 (Griffiths and Buchanan 1982) and assuming 100% filtering efficiency (efficiency measured in the laboratory by Braithwaite *et al.* [1983] was 97.2%) this would require filtering of 26–38 $\times 10^6$ m^3 of water. A whale with a mouth opening of 3.6 m^2 swimming at

Table 6.5. Estimated metabolic rates for bowheads and fin whales. Estimates for bowheads are from Thomson (1987) for a 35-mt whale. Fin whale estimates are from Lockyer (1981) and are based on a 43.5-mt animal. Adapted from Thomson (1987).

Species	Assumptions	Metabolic rate Kcal/kg/d
Bowhead	basal metabolism	4.3
	migrating at 5 km/hr	5.0–5.8
	average summer	6.4
Fin whale	basal metabolism	4.0
	maintenance	8.9
	yearly average	10.8

4.2 km/h could filter that volume of water in 1,720–2,513 h of feeding, less than the 3,120 h available in a 130-d feeding season. However, Bradstreet *et al.* (1987) found that lipids in arctic copepods account for only 5–8% of the wet weight. If that correction is taken into account, these calculations again suggest that bowheads must locate and feed in areas where prey are very concentrated.

Brodie (1981) and Lowry and Frost (1984) used very different estimates of the cross-sectional area of a bowhead's mouth in their calculations of the rate at which prey could be captured. The estimate used by Lowry and Frost (1984) was based on the assumptions that the height of the mouth opening is equal to the baleen length (approximately 2.4 m for a bowhead 13.7 m long), and that the width is about 1 m at the top and 2 m at the bottom. Brodie did not explain how his estimate was derived. The actual size and shape of a bowhead's mouth opening when feeding is not well known. In any event, other parameters and processes may be more important than cross-sectional area in determining filtering rates and efficiency (see Lambertsen *et al.* 1989).

Thomson (1987) used a variety of techniques to estimate the energy requirements of bowheads. Calculations utilized data on bowhead morphology, physiology, and behavior, where available, supplemented with information from other species of cetaceans. Consideration was given to energy required for basal metabolism and swimming, as well as energy costs of growth, pregnancy, and lactation. Estimates of basal metabolic rate for bowheads were similar to those for fin whales (Table 6.5). Although activities and seasons included in the bowhead and fin whale studies were not entirely comparable, it appears that estimates of active metabolic rates for bowheads were considerably lower. Metabolic rates were used to estimate daily food requirements, which were lowest for subadult animals and highest for lactating females (Table 6.6). If it is assumed that no feeding occurs during winter or early spring, individual whales would require 433–2,102 kg of food per day. Thomson (1987) concluded that in order to acquire this amount of food, bowheads would have to feed in areas where average prey biomass exceeds 2.0–2.5 g/m^3.

Using these data and information on age structure and productivity, Thomson (1987) calculated that a population of 4,417 bowheads would

Table 6.6. Estimated amounts of food (kg/day) required by bowhead whales of different sex and age classes. Values shown assume that no feeding occurs other than during the indicated feeding season. Adapted from Thomson (1987).

	Length of feeding season		
Sex/age class	105 d	130 d	165 d
Subadult	681	550	433
Adult male	1,352	1,092	860
Non-reproductive female	1,387	1,120	883
Pregnant female	1,408	1,138	896
Lactating female	2,102	1,698	1,337

consume about 4.2×10^5 mt per year, or an average of about 95 mt of food per individual per year. Considering the differences in methods of calculation, this value is remarkably close to Brodie's (1981) estimate that a bowhead would need to eat 100 mt of crustaceans per year.

In spite of differences in approaches and assumptions, all studies of bowhead energetics point out that whales must feed in areas where prey are concentrated. Studies on North Atlantic right whales have produced the same conclusion (Kenney *et al.* 1986). Although sampling of zooplankton and epibenthos has become increasingly sophisticated in recent years, adequate prey densities are seldom located, which suggests that researchers are still not sampling as effectively as are the whales. Before realistic comparisons can be made of energy needs and food availability, further refinements are needed in techniques for catching fast-swimming organisms and in locating and sampling discrete concentrations, especially those occurring near the sea floor (Brodie *et al.* 1978). Also, assumptions about the length of the feeding season and location of feeding areas are based on incomplete data. These assumptions need to be verified and changed, where necessary, to reflect accurately the actual feeding patterns of bowheads.

TROPHIC RELATIONSHIPS

The data that have been collected on food habits of bowhead whales and other arctic and subarctic marine organisms have allowed a preliminary evaluation of trophic relationships among major species (*e.g.*, Lowry and Burns 1980, Bradstreet and Cross 1982, Frost and Lowry 1984). Such relationships can be represented in a simplified, non-quantitative fashion as a food web (Fig. 6.6). The food web indicates pathways through which energy flows to reach a particular species, as well as competitive and predatory relationships. Bowheads feed almost entirely on primary consumers which generally eat primary producers, and are therefore at the third trophic level of the food web. Humans are the primary predator of bowheads, although bowheads are occasionally attacked by killer whales, *Orcinus orca* (J. C. George and K. J. Finley, personal communications).

Other species also feed on organisms that are the principal prey of bowheads. Lowry *et al.* (1978) found that both bowheads and ringed seals, *Phoca hispida,* ate mostly euphausiids in the western Beaufort Sea near

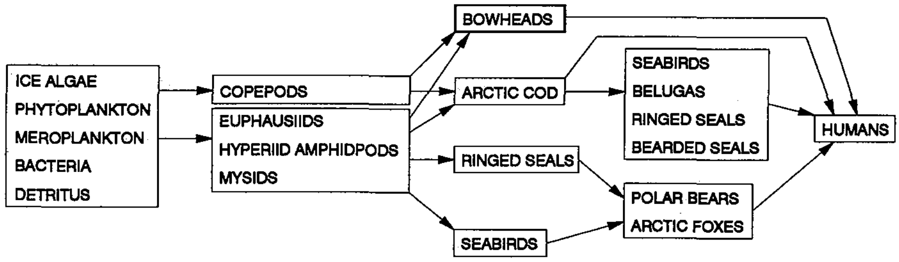

Figure 6.6. Simplified food web showing trophic relationships of bowhead whales in the Beaufort Sea (adapted from Lowry and Burns 1980).

Point Barrow. Copepods are a major component of the diet of arctic cod, *Boreogadus saida,* throughout the Beaufort Sea (Lowry and Frost 1981, Lacho 1986). Arctic cod are a major source of food for ringed seals and other vertebrate consumers in the Beaufort Sea and elsewhere (Bradstreet *et al.* 1986). A study conducted in the eastern Beaufort Sea found that both bowheads and arctic cod ate mostly copepods and euphausiids, while ringed seals ate mostly arctic cod and euphausiids (Frost and Lowry 1981*a*). These results indicate that bowheads and arctic cod have a similar position in the food web while ringed seals may feed at two distinct trophic levels (Fig. 6.6).

The relative simplicity of the food web of which bowheads are a part has allowed a preliminary quantification of trophic relationships. Frost and Lowry (1984) used data on biomass and food habits of major vertebrate consumers to estimate the quantities of prey consumed on the continental shelf of the Beaufort Sea north of Alaska. Results (Fig. 6.7) suggest that arctic cod were, overall, the major consumers of zooplankton (93.1%) with lesser amounts eaten by bowheads (5.9%), ringed seals (1.0%), and seabirds (<0.1%). Since large arctic cod are sometimes cannibalistic, they also accounted for most of the arctic cod consumed (76.7%), followed by ringed seals (17.3%), belukha whales (4.8%), and seabirds (1.3%). When types of zooplankton are considered individually (Fig. 6.8), arctic cod is the major predator in all instances (97.8% of the biomass of copepods eaten, 65.8% of the euphausiids, and 70.7% of the hyperiid amphipods). Bowheads eat a substantial portion of the total amount of euphausiids consumed (31.5%), and much smaller portions of hyperiid amphipods (2.6%) and copepods (2.2%). Ringed seals consume a substantial portion of the total hyperiid amphipods (26.7%) and some of the euphausiids (2.6%).

The total amount of zooplankton estimated to be consumed annually in the Beaufort Sea north of Alaska exceeded 1×10^6 mt. Based on estimates of primary production, production of zooplankton could range from 0.3–4.4×10^6 mt (Frost and Lowry 1981*a*). This suggests that food for animals such as bowheads may be either plentiful or limited. Stirling *et al.* (1977) speculated that a decrease in the numbers and productivity of ringed seals in the eastern Beaufort Sea in 1974–1975 could have been due to sea ice conditions influencing primary productivity. Annual variations in caloric content of copepods (Bradstreet *et al.* 1987) and in growth rates of arctic cod (Lowry and Frost 1981) also suggest annual variations in energy availability.

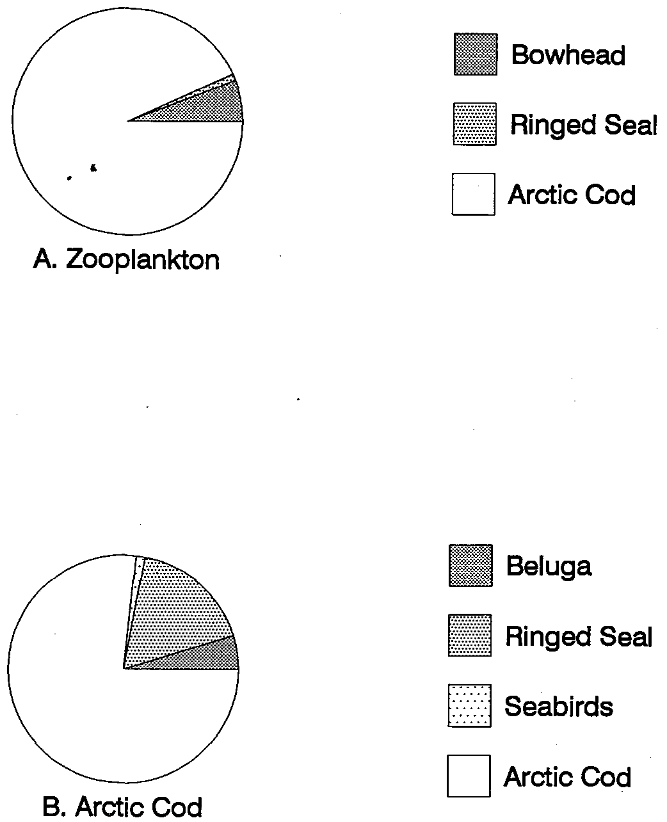

Figure 6.7. Relative amounts of zooplankton and arctic cod eaten by vertebrate consumers in the Beaufort Sea north of Alaska (adapted from Frost and Lowry 1984).

While the potential for trophic competition is obvious, especially between bowheads and arctic cod, specific aspects of feeding ecology may ameliorate this somewhat. For example, arctic cod consume large numbers of small copepods (Frost and Lowry 1981*a*, Lacho 1986, Bradstreet *et al.* 1986) which have only occasionally occurred in bowhead stomachs. Since different-sized copepods may feed on various diatom species in different proportions (Bradstreet and Cross 1982), the trophic sub-systems used by arctic cod and bowheads may be partially isolated.

All evidence suggests that arctic cod play a central role in the trophic ecology of the Beaufort Sea, as they probably do throughout much of the summer range of bowheads. It is possible that when bowhead stocks were decimated by commercial whalers, the numbers of arctic cod and ringed seals increased and took advantage of increased availability of zooplankton (Frost and Lowry 1984). Such a competitive relationship was suggested by Kenney *et al.* (1986) for North Atlantic right whales which may compete for food with planktivorous fishes, especially sand lance, *Ammodytes americanus*.

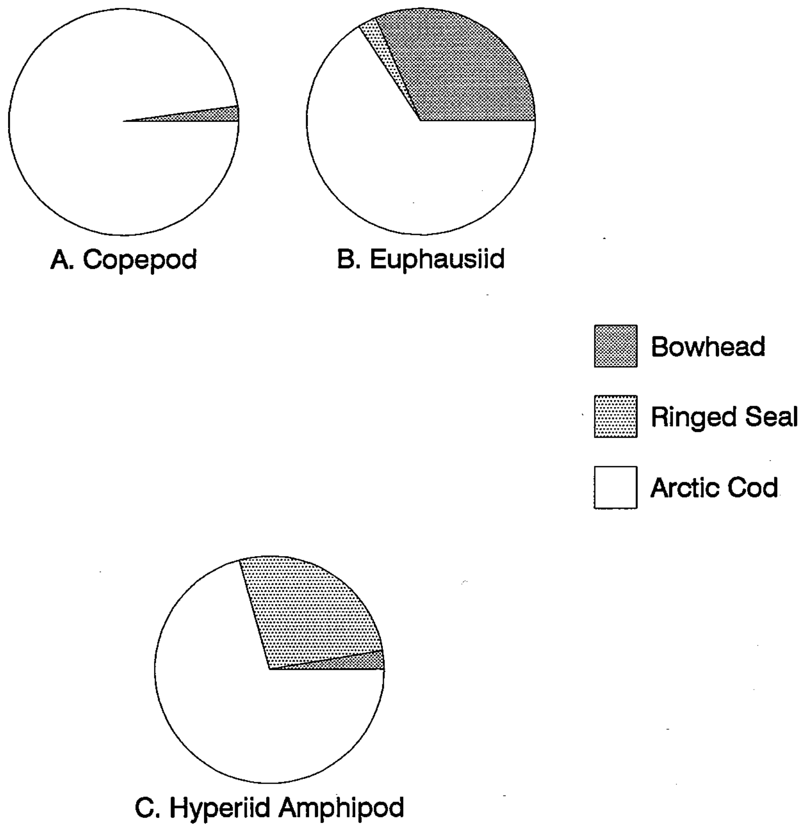

Figure 6.8. Relative amounts of copepods, euphausiids, and hyperiid amphipods eaten by vertebrate consumers in the Beaufort Sea north of Alaska (adapted from Frost and Lowry 1984).

Ringed seals, in conjunction with other marine mammals and seabirds, may play a role in limiting arctic cod abundance. Polar bears, *Ursus maritimus,* which prey on ringed seals throughout their range, may play a key role in this system. It is worth noting, however, that humans utilize all the major species of vertebrate consumers and therefore may influence the ecological relationships of bowheads in a variety of ways.

CONCLUSIONS

Although recent studies have contributed greatly to our understanding of bowhead feeding ecology, the picture is still incomplete and in many ways enigmatic. It is, however, clear that bowhead feeding involves more than a mass of muscle forcing a fine-mesh plankton net through the water. The bowhead is at one end of a spectrum of feeding adaptations in mysticetes. Specializations that allow baleen whales to filter small organisms efficiently from large amounts of water are likely to be more finely developed in bowheads than in most other species. The extremely long baleen and associated modifications of the head region are the most obvious indications, but more subtle hydrodynamic features may be equally important. The variation in characteristics of bowhead baleen, especially among small individuals, is interesting but of unknown significance.

Sampling of stomach contents has produced a long list of prey species for bowhead whales feeding off Alaska. Those samples indicate that the primary foods are copepods and euphausiids, usually 3–30 mm long. Other invertebrates in this general size range are also eaten. It is reasonable to assume that similar organisms are the main foods of bowheads throughout their present range, but it is unlikely that samples of stomach contents will become available to verify this. Observations of whales and their stomach contents suggest a considerable degree of adaptability in feeding behavior which allows bowheads to exploit relatively fast-swimming zooplankton and epibenthic organisms, in addition to the copepods that are usually considered to be the normal food of balaenids.

Only some of the areas used by bowheads for feeding have been studied. Satellite telemetry and research on stable isotope ratios may help identify feeding areas, describe feeding behavior, and allow a more accurate assessment of the significance of different regions for the energetics of various age and sex classes of whales. Until a comprehensive picture of the annual feeding cycle is obtained, evaluations of the significance of particular areas for feeding, or of the potential effects of displacement from those areas, will be tenuous.

Although the mechanisms used by bowheads to detect and evaluate prey have not been identified, it is obvious that they must feed in areas where food is concentrated at well-above-average levels. There are discrepancies between estimates of energy needs and apparent prey availability. Estimates that have been made of energy requirements of large whales are crude and based on few actual data, and may be excessive. Some of this discrepancy may also be due to problems with sampling fast-swimming prey such as euphausiids which are an important food of bowheads. However, even in the case of right whales, which feed mostly on copepods and juvenile euphausiids, it is difficult to reconcile prey availability with energy needs. The possible behavioral and physiological responses of bowheads to food limitation are unknown. The principal prey of bowheads accumulate storage lipids and have a high caloric content in mid to late summer, which may help whales secure and store an adequate supply of energy.

The mechanisms that regulate productivity and distribution of copepods and euphausiids in arctic and subarctic waters are poorly known and require much additional research. Factors that could enhance production or create dense concentrations of prey include upwelling, fronts, ice edge effects, and nutrient input from non-marine sources.

Although bowheads may rarely die of starvation, nutrition is probably a factor that can limit population growth, as is known to happen in other animals. The relation between nutrition and the growth and reproductive output of individual bowheads is not known and will be difficult to investigate. In any event, the prey used by bowheads are also eaten by other species, especially arctic cod, and the total amount of food available may be limiting, at least in some years.

Prior to their decimation by commercial whalers, bowheads of the Bering Sea population summered, and presumably fed, in the Bering and Chukchi seas, as well as the Beaufort Sea. In those areas, especially in the Bering Sea, they were part of a very complex food web involving many species of invertebrates, fishes, seabirds, and marine mammals, including several other species of planktivorous baleen whales (Frost and Lowry 1981*b*). Presently, bowheads do not share their primary summer feeding grounds with any other species of baleen whale. If bowheads are to regain their former abundance, it is likely that they will have to reoccupy portions of their summer feeding grounds that were abandoned decades ago. Why do bowheads leave the highly productive Bering Sea each year, just prior to the spring bloom, and migrate 3,000 km to the less productive Beaufort Sea for the summer feeding season? This is but one of the many important questions about bowhead feeding ecology that remain to be answered, and that should be addressed by future studies of bowhead whales and the ecosystems in which they live.

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Editors
John J. Burns
J. Jerome Montague
Cleveland J. Cowles

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