

Feeding, Aerial and Play Behaviour of the Bowhead Whale, *Balaena mysticetus*, Summering in the Beaufort Sea

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Abstract

The behaviour of bowhead whales in the eastern Beaufort Sea was studied from an aeroplane during the summers of 1980–84. Much feeding and some socializing, travelling, aerial activity, and log play occurred during summer. Feeding involved surface skim feeding, feeding in the water column, and bottom feeding. Bottom feeding was indicated when whales emitted muddy water from their mouths while at the surface. Bottom feeding occurred in depths of 6–24 m, and appeared to be practiced mainly (and possibly exclusively) by subadult bowhead whales. The method of bottom feeding and types of bottom prey are not known. Aerial activity in the form of breaches, tailslaps, and flipperslaps occurred sporadically throughout the summer, was displayed by both lone and socializing whales, and may have aggressive, communicative, and possibly play functions. Lone whales also interacted with large floating logs over intervals from 5 s to at least 1.5 h. Log play involved boisterous nudging, pushing, lifting, and submerging parts of logs with some part of the whale's body. The present study enlarged the known behavioural repertory of bowhead whales, and revealed similarities in behaviour between bowhead whales, right whales, and gray whales.

Key words: bowhead whale, *Balaena mysticetus*, feeding, aerial behaviour, breaching, play, summer behaviour, Beaufort Sea.

Introduction

Bowhead whales (*Balaena mysticetus*) occur only in the northern reaches of the northern hemisphere, usually in or near arctic sea ice (Scammon, 1874). Once plentiful in both the extreme north Atlantic and in the Western Arctic near Alaska, they now number in the low hundreds in part of the former region, and between 7 and 8 thousand in the latter (International

Whaling Commission, in press). Bowheads of the Western Arctic winter in the Bering Sea, summer in the eastern Beaufort Sea, and migrate around western and northern Alaska in spring and autumn. Mating and calving appear to take place mainly during spring (Nerini *et al.*, 1984) and probably early summer (Davis *et al.*, 1983). From June to early September, many Western Arctic bowheads are in Canadian waters, which are presumed to be a main feeding area for this population (Fraker & Bockstoce, 1980; Miller *et al.*, 1986).

During the five summers of 1980–84, we studied the normal behaviour of Western Arctic bowhead whales in the eastern Beaufort Sea. This work was part of a larger study to determine the impact of offshore oil and gas exploration activities on bowhead whales. This paper describes aspects of normal behaviour not addressed in detail in a paper based on our 1980–82 data (Würsig *et al.*, 1985)—most notably bottom feeding, aerial behaviour and play—and it seeks to put our findings into context with the rapid expansion of knowledge of mysticete whale behaviour. Related data on surfacing, respiration and dive characteristics are in Würsig *et al.* (1984) and Dorsey *et al.* (in prep.). Details of disturbance reactions of bowhead whales are in Richardson *et al.* (1985, 1986, in prep.), and details of summer distribution relative to oil industry activity are in Richardson *et al.* (1987a).

Methods

Field work occurred mainly in August of 1980–84, with some additional observations in late July and early September during certain years. Work was based at Tuktoyaktuk, NWT, and the study area extended from the US–Canada border to Cape Bathurst (Fig. 1).

Most observations were from a Britten-Norman Islander aircraft, although observations from 1–12 August 1983 were from a de Havilland Series 300 Twin Otter. These aircraft have twin engines, high

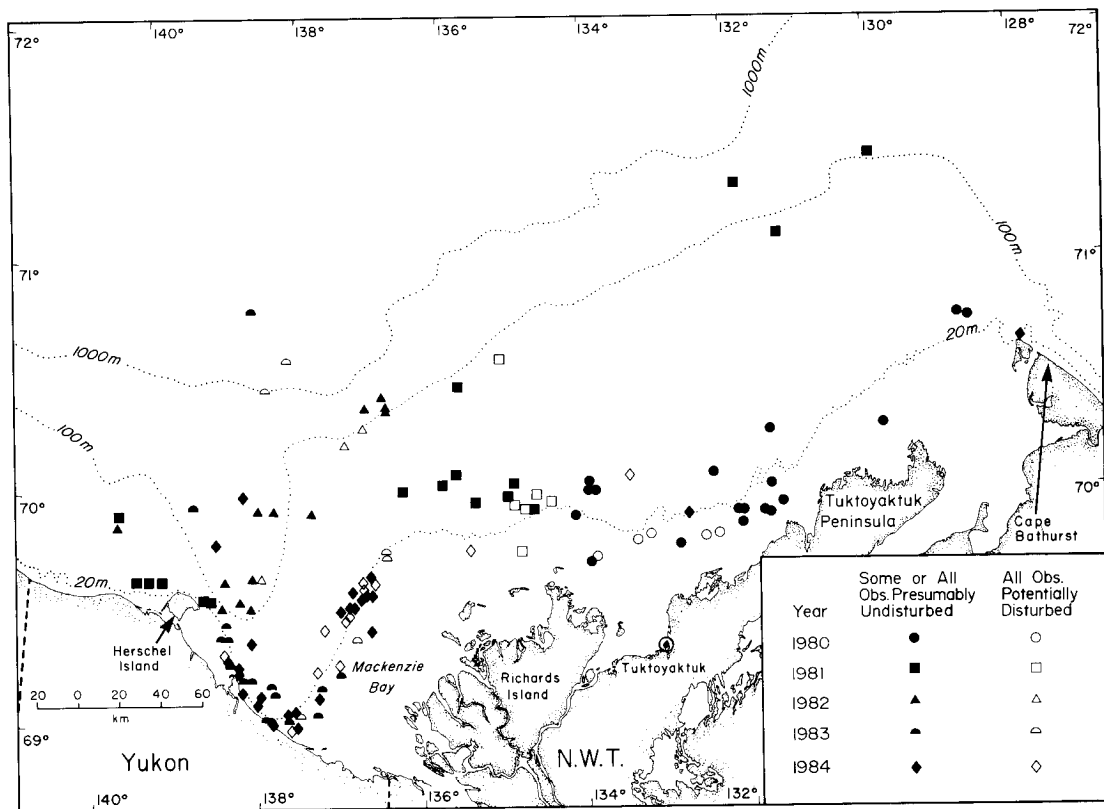


Figure 1. Eastern Beaufort Sea region showing bathymetry, locations mentioned in the text, and locations of behavioural observation sessions. Open symbols denote areas where whales may have been disturbed by human activity. The US/Canada border is represented by the dashed line west of Herschel Island.

wing configuration, low stall speed, and an endurance of about 5.5–6.0 h plus reserves.

Our usual strategy was to search until we encountered bowheads and then circle over them as long as possible while making observations. Once contact was lost, we searched for another group. We created a fixed reference point about which to circle, when bowheads were below the surface, by deploying a fluorescein dye marker. Near the start of most periods of circling above whales, a sonobuoy was dropped to record waterborne sounds. The aircraft crew usually consisted of four biologists and the pilot. Two biologists described behaviour while a third videotaped whales and a fourth operated the sonobuoy recording system. Observations were recorded onto audio cassette and, usually, onto the voice channel of the video recorder. Further details on techniques and equipment are provided in Würsig *et al.* (1985).

We made 132 offshore flights during the five seasons, and we observed bowhead whales during 85 of these flights. Most flights lasted 4 to 5.5 h. We

observed whales for a total of 186.3 h, of which 98.5 h were in the absence of sources of potential disturbance (Fig. 2). We usually did not fly when wind speed exceeded 25 km/h; whales are difficult to detect and behaviour is not reliably observable in more severe conditions. While searching for whales, we usually flew at 457 or 610 m (1500 or 2000 ft) above sea level at 185 km/h. Bowheads rarely appeared to be disturbed by the aircraft when it remained at or above 457 m (Richardson *et al.*, 1985). Most observations in 1980, 1983, and 1984 were in shallow water, usually < 50 m (Fig. 2). Most observations in 1981 were in somewhat deeper water, and those in 1982 were in still deeper water, often near the edge of the continental shelf (Fig. 1).

Results and Discussion

Feeding

We observed several types of feeding by bowheads: feeding at or just below the surface, in the water column, and at or near the bottom.

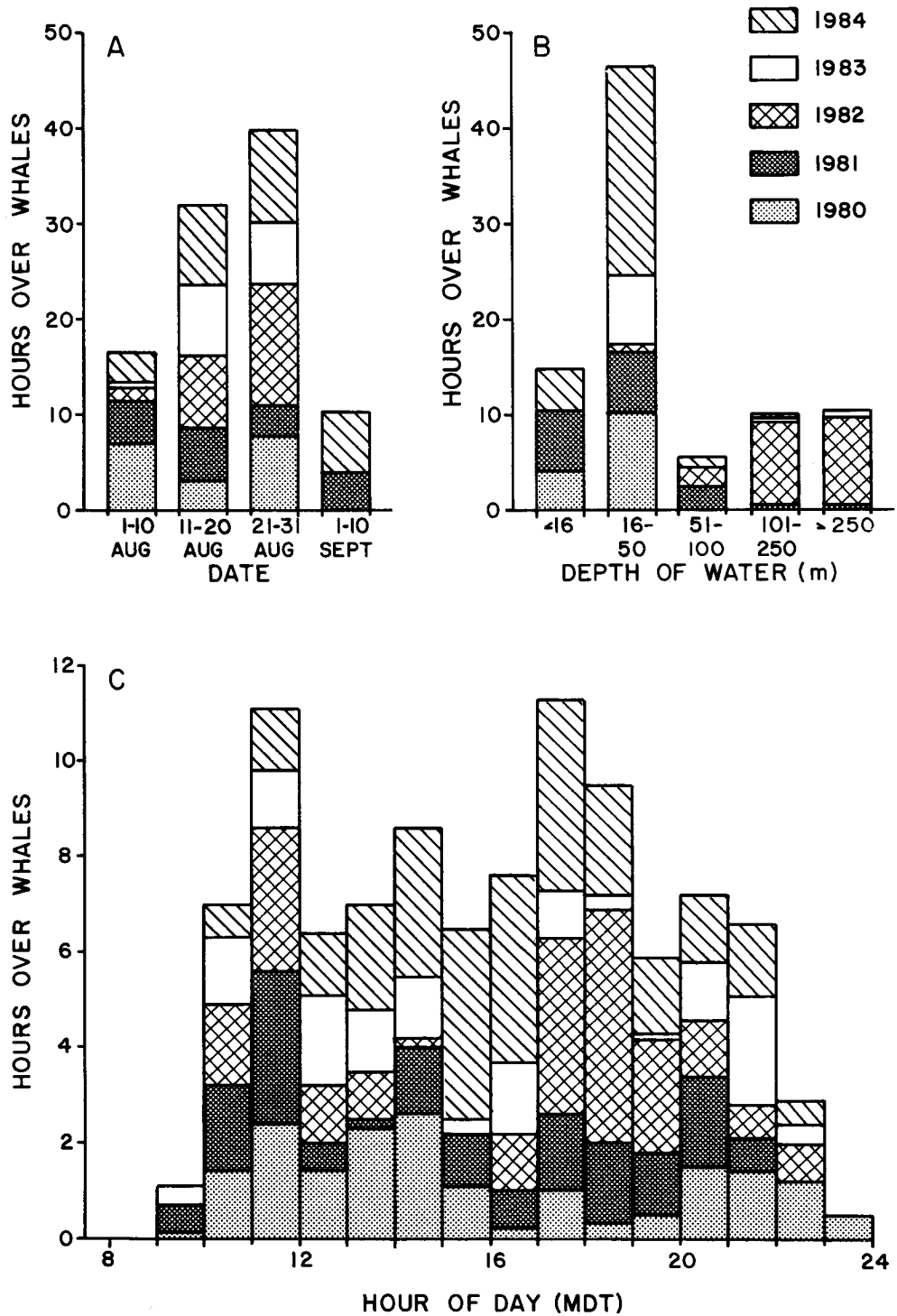


Figure 2. Distribution of behavioural observation time from the air during presumably undisturbed periods totalling 98.5 h, 1980-84, categorized by (A) date, (B) depth of water, and (C) time of day. MDT is Mountain Daylight Time.

Skim feeding occurred when whales moved forward with mouths open at or just under the surface. At times, whales skim fed alone; under such circumstances they were separated >75 m from other whales and were oriented in various directions. At other times, skim feeding occurred in coordinated echelons of up to 14 whales (Wursig et al., 1985, 1986). Skim feeding was uncommon; we saw it on only a few occasions in 1980, 1981 and 1983.

Water-column feeding probably is the dominant feeding mode in the Beaufort Sea, but because it occurs below the surface, we have not been able to ascertain its frequency. No other types of feeding were observed during 1982, when bowhead whales were generally encountered in deep water and dove for up to 0.5 h at a time. We suspect that feeding in the water column is generally not done cooperatively, unlike skim feeding in echelon. Whales believed to be water-column feeding were usually separated from each other by several hundred meters. Further details are presented in Wursig et al. (1985).

Bottom feeding had apparently occurred when whales surfaced with mud emanating from their mouths. We saw whales coming up with mud on 2 days in 1980, 1 day in 1981, 0 days in 1982, 3 days in 1983, and 12 days in 1984 (including observations near industrial activities). All evidence of bottom feeding was in quite shallow water, 6–24 m deep. Bottom feeding occurred in several different areas, including very close to the Yukon coast, about 70 km west of Richards Island, and about 60 km north of it. The most widely separated incidents of bottom feeding were about 150 km apart. Our previously unpublished 1984 observations accounted for the majority of the probable cases of bottom feeding: in 1984 we observed 96 incidents of whales with mud, from 13 August through 2 September, in water 6–24 m deep. Bottom-feeding whales were usually >75 m from each other and did not appear to be cooperating while feeding. Mud did not always emanate from the mouths of bottom feeding whales when they first surfaced. Of 14 occasions when mud emanated directly from the mouth of a whale observed from the moment it surfaced, mud was released at the start of the surfacing only 5 times. Mud came from the mouth 10 to 83 s after surfacing during the remaining 9 surfacings (mean time after surfacing was $31 \pm \text{s.d. } 28.1$ s). This indicates that the mouth may stay closed for a considerable period after surfacing.

The baleen whale that is best known for feeding on organisms in bottom sediment is the grey whale, *Eschrichtius robustus* (Nerini, 1984; Oliver & Slattery, 1985). The relatively short and coarsely fringed baleen of that species is particularly well adapted to bottom feeding. In contrast, bowhead whales have very long, finely fringed baleen suited for

filtering clouds of small prey from water, and seemingly not well suited for bottom feeding. Nevertheless, the amounts of mud that we have occasionally seen pouring from the mouths of bowheads appeared too great to have been picked up incidentally while bowheads fed on water-column organisms near the bottom, and we believe that at times they may feed directly on the bottom.

Pebbles and bottom-dwelling species have been found in bowhead stomachs. Lowry & Frost (1984) found that most species in the stomachs of eight bowhead whales killed off Kaktovik, Alaska, in fall were benthic amphipods. However, the benthic amphipods were an insignificant part of the overall volume of stomach contents; pelagic prey such as calanoid copepods and euphausiids were predominant. Lowry & Burns (1980) suggested that a feeding dive probably involves swimming obliquely from surface to bottom and back, feeding the entire time. This is possible, but we suspect that bowhead whales usually concentrate their feeding effort at depths where prey items are most abundant.

Stomachs of small, subadult bowheads have been found to contain some benthic prey, whereas stomachs of large adult bowheads contained only plankton (Hazard & Lowry, 1984; Lowry & Frost, 1984). Photogrammetric data collected by the methods of Davis et al. (1983) showed that the area where we observed bottom feeding in 1983 and 1984 was occupied primarily by small, subadult bowheads (Davis et al., 1986). Thus, it is possible that bottom feeding is primarily an activity of young bowheads.

We saw reddish-brown faeces near bowhead whales only sporadically (23, 11, 1, 11 and 5 times during 1980–84, respectively). We assume that much defecation occurred out of our sight below the surface of the water. It therefore does not appear possible to use incidence of defecation as an indication of relative amount of feeding.

Aerial activity

Aerial activity, consisting mainly of breaches, tail-slaps, and flipper, slaps, occurred sporadically throughout our five field seasons. General descriptions of these activities are presented in Wursig et al. (1985), and the frequency of aerial activity each summer is shown in Table 1.

Breaches were usually performed by whales that were >100 m from other whales, and occurred both as single breaches and in series of up to 19 breaches with no interruptions by other surface activity. The mean interval between breaches within a series was $31.8 \pm \text{s.d. } 9.24$ s ($n=66$). Tailslaps onto the surface of the water included single slaps and uninterrupted series of up to 148 slaps! The mean of 266 measured intervals between successive tailslaps was 4.9 s ($\pm \text{s.d. } 1.94$ s). Flipper slaps onto the surface of the water also included single slaps and up to 10 slaps in

Table 1. Frequency of aerial activity, 1980–84, based on whale-hours of observation at the surface. Both presumably undisturbed periods and periods potentially disturbed by industrial or other human activity are included

	1980	1981	1982	1983	1984
Bouts of aerial activity	6	14	9	19	7
Whale-hours at the surface	10.03	14.98	10.95	17.91	13.67
Rate (bouts/whale-h)	0.60	0.93	0.82	1.06	0.51

an uninterrupted series, with the mean of 43 measured intervals within a series being 2.9 s (\pm s.d. 1.62 s). Thus, breach intervals are longest, tailslap intervals are much shorter, and flipper slap intervals are the shortest. This ordering corresponds roughly to the amount of body mass the whale lifts above the surface of the water.

The longest bouts of aerial behaviour that we observed were by lone whales and usually consisted of alternating series of tailslaps, flipper slaps, and breaches. A particularly dramatic series involving two whales occurred on 22 August 1983. A lone whale that was aerially active before we began circling it interspersed 49 tailslaps with 6 breaches during 11.8 min of observation. Its respiration rate was 2.12 blows/min if it blew during every breach. This assumption is likely to be correct, as R. Payne (pers. comm.) found that the closely related southern right whale (*Eubalaena australis*) blows during each breach. A second whale began breaching 300 m away as the first whale surfaced after its last breach series. The second whale made 64 breaches, 36 tailslaps and 48 flipper slaps during the 75 min that we observed it. During that time, its blow rate was 2.04 blows/min (153 blows \div 75 min) if it blew during each breach. These blow rates indicate a high level of exertion; they are over double the average blow rate of non-breaching whales (0.77 blows/min, calves excluded; Dorsey *et al.*, in prep).

Some tailslaps and flipper slaps occurred in groups of whales, either as single slaps or in short series of up to 10 slaps, sometimes while the whales were actively socializing. On one occasion in 1981, the socializing appeared to include copulation between two animals (Würsig *et al.*, 1985), in addition to numerous tailslaps and flipper slaps by both animals. Bowheads of the Davis Strait stock (northwest Atlantic) have also been observed to engage in frequent aerial activity during sexual interactions in late summer (K. J. Finley, LGL Ltd., unpubl. data). On three occasions we saw a bowhead whale strike another with its tail flukes or a flipper in an apparently aggressive manner: once each in 1980 and 1981, one whale slapped its tail onto the head of another; and in 1983,

a whale slapped a flipper three times onto the back of another whale, which responded by hitting the first whale on the back with its flukes six times.

We observed only five spyhops, where a bowhead lifted its head more or less vertically out of the water, up to the level of its flippers at the highest, and sank back into the water tail first. All spyhops were brief. Four spyhops were performed while whales socialized, and one was interspersed with many other aerial behaviours.

We observed only two aerially active calves. One case was of a single tail slap. The second, seen from Herschel Island, was of a calf aerially active for 29 min during which it made 37 breaches or partial breaches, with up to three-quarters of the body remaining in the water. The calf breached back and forth, changing direction often, and therefore stayed within 1 km of the presumed mother, although it covered a distance of at least 3 km in its meandering course. This kind of meandering is similar to behaviour of right whale calves that breach in 'circles' near their mothers (Thomas & Taber, 1984). When the calf stopped breaching, it rapidly headed back toward the adult.

Our sonobuoy recordings showed that many breaches and tailslaps produce pulses of low-frequency underwater noise, with breach sounds concentrated at lower frequencies (mainly < 100 Hz) than tailslap sounds (up to 600 Hz, Fig. 3). We found that breach and slap sounds were not especially intense (received level \leq 107 to 118 dB re 1 μ Pa at a range of several hundred meters; Greene, 1984) as compared with bowhead calls. Some tail and flipper slaps were not detectable underwater a few hundred meters from the whale. The fact that these sounds are created at the surface rather than underwater probably limits their underwater intensity.

Aerial activity probably has several functions. Single tailslaps or flipper slaps may indicate disturbance or aggression, as when possibly precipitated by the low-level approach of an aeroplane (Richardson *et al.*, 1985) or when directed against a conspecific. Bouts of aerial activity may signal 'arousal' of some type, and may also serve to communicate to nearby

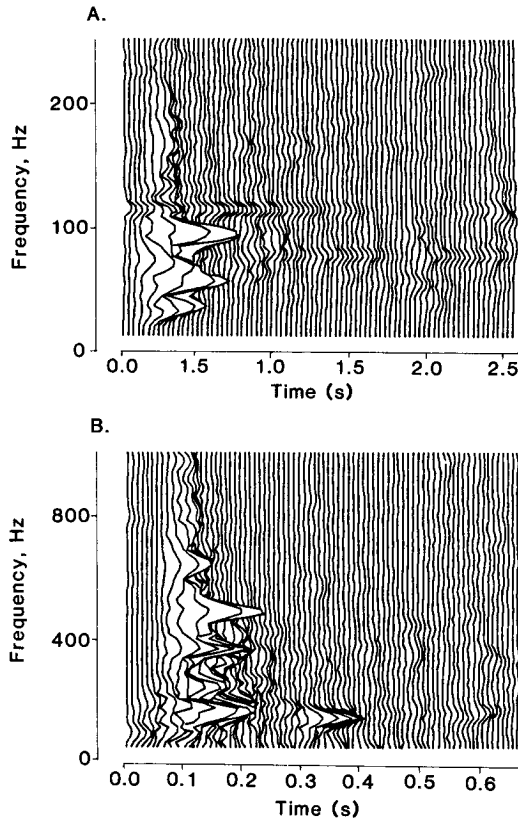


Figure 3. Waterfall spectral displays for sounds from (A) a whale breach, and (B) a whale tail slap, 22 August 1983. Note that the scales of A and B differ. The faint tones at about 70 and 110 Hz in the breach waterfall probably came from the observation aircraft. From Greene (1984).

conspecifics. Breaches, tailslaps and flipper slaps may also represent play behaviour and may not always have a function beyond play.

In other species of large whales, the function of breaching and other aerial behaviour is still a matter of speculation. Whitehead (1985) reviewed current evidence and hypotheses, particularly in hump-back whales (*Megaptera novaeangliae*). He noted that breaching is most commonly seen in species of large whales that have many close-range social interactions and that, in humpbacks, breaching is more common on winter mating and calving grounds than on summer feeding grounds. Whitehead suggested that a breach might be a display of strength in male humpbacks (directed at receptive females and/or competing males) and that play might be the main function of breaching in calves. Payne (pers. comm.) describes breaching in southern right whales on their wintering grounds and argues that it functions at times as an acoustic signal to maintain contact

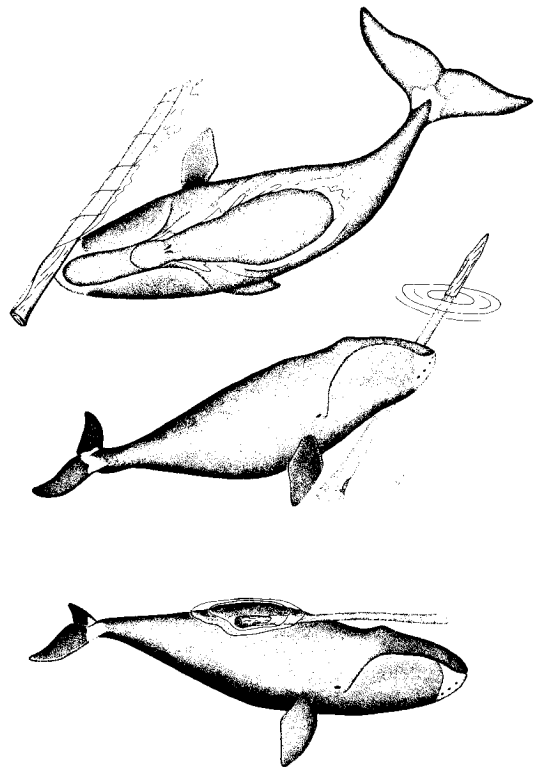


Figure 4. Bowhead whale log play, drawn from photographs and video tapes.

between animals. Since underwater sounds created by aerial activity are usually not very intense in bowhead whales, these sounds do not seem to be a very efficient method of maintaining contact over long distances.

Play

Although whales may engage in play during various social interactions, we could not separate cases of play involving more than one bowhead from possible mating activity or aggression. Therefore, we considered whales to be playing only when they associated with an object other than another whale. We saw such associations in 1981, 1982, and 1984, but not in 1980 and 1983. Play behaviour during 1981 and 1982 is summarized in Wursig et al. (1985). We present here a more detailed account of whales playing with logs.

We observed whales playing with logs up to about 10 m long on two occasions in 1981, and once each in 1982 and 1984, for 5 s, 10 min, at least 1.5 h, and 5 min, respectively. Most contact with the log consisted of the whale nudging or pushing the log with the head or body (Fig. 4). Sometimes the log was

clasped by the flippers while the whale was belly-up underneath the log, or was lifted up by the back or tailstock.

During 1981, we witnessed two incidents of whales touching logs that were floating on the water. On 10 August, a whale briefly nudged the middle of a long (about 20 m) log, propelling it 5 m forward. The whale then dove under the log and we did not see that whale again. Although the interaction lasted only 5 s, it was apparent that the whale did not simply bump into the log accidentally; it oriented toward the log and pushed. A more dramatic incident occurred on 25 August 1981, with a seismic exploration vessel only 6–8 km away. A small (possibly yearling) whale was first observed just underneath a log approximately 10 m long. The whale nudged and pushed the log and lifted it onto its back so that one end was perhaps 3–5 m above the surface for 1–2 s. This small whale was then joined by two adults that surfaced close to the log. At least one of the adult whales let the log roll over its back, and on two occasions in the 10 min during which we witnessed the behaviour, the whale rolled ventrum up underneath the log and clasped the log with its flippers. During this time, there were some nudges and close associations between the whales not touching the log. The log playing seemed to be associated with a high level of social activity.

In 1982, we witnessed log play only once, on 1 August in water approximately 300 m deep. A large whale interacted with a log approximately 10 m long for at least the 1.5 h period while we circled overhead. During that period, the seismic exploration vessel 'GSI Mariner' approached from an initial range of about 39 km to a final range of about 24 km. Either distance is close enough for noise pulses from the ship to be detectable (Richardson *et al.*, 1985, 1986), but log play was also seen in the absence of noise from seismic vessels. The whale moved as far as one whale length from the log for only 5 s during the whole 1.5 h of observation, and was in contact with the log almost all the time. It lifted one end of the log as far as 2–3 m above the water 30 separate times. Such lifting was done with the head, back, side, or ventrum, and usually lasted for only 1–2 s. On five occasions the whale rolled the log along its back by swimming under the log while touching the middle of the log with its back. On one occasion, the whale rolled the log while ventrum up beneath it. The whale pushed the log with its head 12 times and with its body while moving against the log sideways 14 times. It clasped the log with either the right or left pectoral flipper eight times, and clasped the log under both flippers while ventrum up beneath the log another three times. On eight occasions, the whale placed its chin onto the log and apparently tried to force the log beneath the surface. Each such interaction lasted about 1–10 s.

Although the whale's orientation to the log changed continually, the whale usually initiated each contact with the log by approaching head on, that is perpendicular to it. When the log was pushed by head or back, it moved through the water rapidly enough to create a white-water wake, and on two occasions the log was propelled for approximately two whale lengths.

The whale was either at or just below the surface almost the entire time, and on only two occasions did it disappear from sight, for 7 s each time. Nevertheless, blows were most frequent during 12 intervals during which the whale was mainly at the surface, with its back slightly above the water.

The 10-min incident observed in 1984 was similar to that of 1982, but of shorter duration. No seismic exploration noise was present. The 1982 log play sequence is the longest one described for bowheads to date.

Our observations do not represent isolated instances. Other investigators saw lone bowheads apparently playing with logs in the summering grounds on at least three other occasions in 1981 and 1983 (William Koski, pers. comm.; J. Cubbage, pers. comm.). We have also seen log play during the early autumn off northern Alaska (Richardson *et al.*, 1987b).

Association with objects other than conspecifics has been described for many marine mammals and for at least four other species of large whales (right whales, Payne, 1972; gray whales, Swartz, 1977; a humpback whale, Couch, 1930; and a sperm whale *Physeter catodon*, Nishiwaki, 1962). Specific elements of the log play that we have observed in bowhead whales are strikingly similar to play with seaweed observed in southern right whales (Payne, 1972); both involved lifting the object with the head, moving the object along the back, and patting it with the flippers. The attempt to push the log under water with the head is also reminiscent of a motion commonly made by male right whales when attempting to mate with uncooperative females (Payne, pers. comm.). In 1981, one of the log-playing bowheads was also associating with two other whales at the time; in the 1982 and 1984 examples, the whale was alone. It appears, therefore, that log play may occur under a variety of situations.

In 1982, we observed two incidents of calves playing with suspended material near the surface. They repeatedly oriented toward the material. In both cases, the calves were alone at the surface, while their mothers were apparently feeding in the water column. Details of this activity are found in Würsig *et al.* (1985).

Concluding remarks

Variations in feeding and other activities

In our study, two of the main attributes that varied from year to year were bowhead whale distribution

in the eastern Beaufort Sea (Richardson *et al.*, 1987a) and the frequency and type of feeding (Wursig *et al.*, 1985). In 1980, we saw indications of bottom feeding, skim feeding, and water column feeding close to shore off the Mackenzie Delta and Tuktoyaktuk Peninsula. From 1980 to 1982, there was a progressive increase in the depth of water in which bowheads were observed. In 1981, we saw skim-feeding and apparent water-column feeding. In 1982 most whales appeared to be water column feeding far from shore. In 1983 and 1984, some whales were again closer to shore but along the Yukon coast, west of where they had been in 1980. Feeding activity in 1983 was probably most like that in 1980, as the feeding behaviour observed near shore was bottom feeding and skim-feeding. In contrast to 1980 and 1981, none of the skim-feeding observed in 1983 was by whales in echelon formation. In 1984, bottom feeding but no skim feeding was observed. In 1983 and 1984, most whales near shore were subadults (Davis *et al.*, 1986), indicative of widespread age segregation in the population. Most bottom feeding that we observed was by subadults, and it is possible that feeding mode is at least in part influenced by age.

Bowhead distribution and feeding types probably reflect changes in prey distribution, abundance, or species composition. We do not have sufficient data on the prey of these bowheads to test such a relationship. Stomach contents of bowheads have not been collected in the Canadian Beaufort Sea, and factors affecting zooplankton dynamics in that area were not studied in detail until after our study ended (*cf.* Bradstreet *et al.*, 1987). There are indications, however, that some of the variability in bowhead distribution is related to variability in water mass characteristics (Borstad, 1985), some of which reflect differences in prey availability (Bradstreet *et al.*, 1987). The most impressive case of near-surface skim feeding that we observed (18 August 1981) was at a location where copepod abundance in near-surface waters was unusually high (Griffiths & Buchanan, 1982). Recently, copepod concentrations at depth have been shown to be far above average at several locations where bowheads were feeding below the surface (Bradstreet *et al.*, 1987; Griffiths *et al.*, 1987).

Studies of some other baleen whales provide more direct evidence for changes in geographic distribution in response to changes in their prey. Humpback whales feed on different kinds of prey in different areas, and have been studied intensively in recent years. On Stellwagen Bank near Cape Cod, where sand lance (*Ammodytes americanus*) were present in large concentrations, individual humpback whales returned in consecutive years (Mayo, 1982, 1983). Their movements within each summer were quite predictable even to the extent of which points on the bank (separated by only 25 km) they occupied early and late in the season. In contrast,

humpback whales that feed farther north near Newfoundland utilize mainly capelin (*Mallotus villosus*). Sighting rates for humpbacks in one small nearshore area roughly quadrupled over three years, while humpbacks disappeared from a second area farther offshore (Whitehead & Carscadden, 1985). Capelin stocks offshore collapsed at the same time that humpbacks and spawning schools of capelin became plentiful inshore. Whitehead concluded that summer distribution of humpbacks changed in direct response to the failure of offshore capelin stocks. Similarly, Bryant *et al.* (1981) found that the disappearance of humpbacks from Glacier Bay, Alaska, in 1980 was accompanied by a low krill population in that year, and Wing & Krieger (1983) showed that humpbacks aggregated in areas of high krill concentrations in south-eastern Alaska in the summer of 1981 and 1982. Where prey species remained in the same place in high abundance, humpback whales returned each year to the same area. When the prey moved dramatically, the whales also moved.

It is not surprising that annual changes in prey distribution can cause changes in whale distribution. Baleen whales can probably obtain enough food only by feeding selectively in areas of concentrated prey (Nemoto, 1970; Brodie *et al.*, 1978; Brodie, 1981; Griffiths & Buchanan, 1982; Thomson, 1987). Year-to-year or other variations in the types and vertical distribution of prey could presumably affect the relative frequencies of surface, water-column, and near-bottom feeding in bowhead whales.

Given the above, we suspect that the observed annual variation in bowhead distribution and behaviour is principally a reflection of varying horizontal and vertical distribution of their prey. To understand for any given year where bowheads are likely to concentrate and how they are likely to feed, it will be necessary to understand factors affecting prey distribution. There is increasing evidence that the distribution of the prey of bowheads in the eastern Beaufort Sea is affected by factors such as (1) timing and amount of spring run-off from the Mackenzie River, (2) distribution of ice during spring and summer, (3) wind patterns and paths of major storms, and (4) the variable distribution of the plume of turbid brackish water from the Mackenzie River. Any or all of these interrelated factors could affect prey distribution and, therefore, the distribution and behaviour of bowheads (Borstad, 1985; Thomson *et al.*, 1986; Bradstreet *et al.*, 1987).

A further uncertainty is the degree to which the present Western Arctic bowhead stock is food-limited. The total size of this stock is clearly lower than before commercial exploitation, so the present stock might not be food-limited. If so, details of summer distribution of bowheads might not be predictable even with a detailed understanding of prey distribution. However, the number of bowheads now

summering in the eastern Beaufort Sea may be a high proportion of the number that summered in that part of the ancestral range before commercial exploitation (Fraker, 1983). Also, populations of potential food competitors (e.g., arctic cod, *Boreogadus saida*; Lowry & Frost, 1981; Frost & Lowry, 1984) may have increased since the beginning of commercial whaling. Thus, bowheads summering in the eastern Beaufort Sea may be food-limited at present. Also, the important limitation is probably not the total amount of food available. Since bowheads concentrate their feeding in areas with dense patches of zooplankton and patch locations vary, bowhead distribution is also likely to vary. An understanding of prey variability is critical in understanding the variable activities and distribution of bowhead whales during summer.

Comparisons with bowheads in Alaskan waters

Bowhead whales of the Western Arctic spend the winter near the edge of the sea ice in the Bering Sea, migrate to the eastern Beaufort Sea in spring, and migrate back to the Bering Sea in fall. During spring migration, bowhead whales appear to do little feeding; most bowheads taken in Alaskan waters in spring have empty stomachs (Marquette *et al.*, 1982), although some contain food (Hazard & Lowry, 1984; Lowry & Frost, 1984; Carroll *et al.*, 1987). In September, considerable feeding occurs in the Alaskan Beaufort Sea, especially between Kaktovik (144°W longitude) and the Alaska-Yukon border (Ljungblad *et al.*, 1984; Lowry & Frost, 1984). Prior to the onset of active westward migration, behaviour in Alaskan waters in September is usually similar to that in Canadian waters in August (Richardson *et al.*, 1987b).

Much mating and other social activity occurs during spring migration (Everitt & Krogman, 1979; Carroll & Smithhisler, 1980; Johnson *et al.*, 1981; Ljungblad, 1981). There is a waning of social activity during the summer (Würsig *et al.*, 1985), and by fall it is uncommon (Ljungblad *et al.*, 1984). Aerial activity is also greatest in spring (Carroll & Smithhisler, 1980; Rugh & Cabbage, 1980), and occurs only sporadically during summer and fall in the Western Arctic. In contrast, the component of the Eastern Arctic (Davis Strait) stock that summers along eastern Baffin Island exhibits considerable aerial and sexual activity in late summer (K. J. Finley, unpubl. data). It is not clear whether this represents a difference between stocks or the presence of a particular age/sex component of the Eastern Arctic population along Baffin Island.

In general, bowhead whales on their Western Arctic summering grounds, including the eastern part of the Alaskan Beaufort Sea up to mid- or late September, have the same basic repertory of behaviours as do migrating bowheads. However, summer-

ing and migrating bowheads differ in the relative amounts of time spent in different activities—feeding, socializing, breaching and other aerial behaviour, and travelling. At least some of the differences appear to occur as a continuum between seasons rather than an abrupt change. Travelling is the predominant activity during spring and fall migrations, while feeding is the predominant activity during summer. The average length of stay in any one area is therefore longer in summer, but considerable travelling occurs in summer and some feeding occurs during migration, especially in fall. The differences in behaviour between seasons are not as clear-cut and dramatic as once thought.

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