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COMPARISON OF BEHAVIOR OF BOWREAD WHALES OF TEE DAVIS STRAIT AND BERING/BEAUFORT STOCKS

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ABSTRACT

This report describes statistical and other comparisons between the behavior of two stocks of bowhead whales that have been studied in late summer and autumn: the Eastern Arctic or 'Davis Strait - Baffin Bay' stock and the Western Arctic or 'Bering - Chukchi - Beaufort' stock. The comparisons are based on data collected in several previous studies, including previously-unanalyzed eastern arctic data.

The behavioral repertoires of bowhead whales in the two regions were qualitatively similar in most respects. However, the comparisons revealed statistically significant quantitative differences in behavior. Such differences were evident for all three categories of whales that were compared: feeding in deep water, socializing in shallow water, and migrating. Multivariate and other analyses indicated that some but not all of these differences could be ascribed to regional differences in environmental conditions or whale activities. The report discusses possible reasons for behavioral differences that were not attributable to differences in environmental conditions or whale activities.

Sexual interactions were observed much more often at Isabella Bay in the eastern arctic than observed at any location in the western arctic during late summer or autumn. The difference was partly but not fully understandable on the basis of age segregation within the two populations. The reasons for the greater amount of sexual activity observed in autumn in the eastern arctic are not fully understood. This difference is potentially important with regard to the dynamics of the two populations.

EXECUTIVE SUMMARY

Introduction

Bowhead whales in the western arctic (Bering-Chukchi-Beaufort stock) are exposed to a variety of types of human activities in several parts of their annual range. These bowheads exhibit short-term behavioral reactions to disturbance by various human activities. However, it is not known whether such disturbances lead to any long-term changes in behavior, or to any deleterious effects on the bowhead population. Extensive data have been collected in recent years on the behavior of western arctic bowheads under presumably undisturbed as well as potentially disturbed conditions.

Bowhead whales in the eastern arctic (Davis Strait-Baffin Bay stock) are not exposed to nearly as much human activity, given the absence of bowhead hunting there and the much lower level of offshore oil exploration. Data on the behavior of eastern arctic bowheads have been collected in recent years during studies along the east coast of Baffin Island. These data had not been analyzed in any detail before the present project. MMS suggested that the eastern arctic population might serve as a virtually undisturbed 'control' population in order to assess whether the behavior of western arctic bowheads has been altered by the cumulative effects of various human activities. This overall objective has been formulated by MMS as a test of the following null hypothesis:

> H_0: There are no significant differences in normal behavior between bowhead whales of the Western Arctic and Davis Strait stocks.

To test this hypothesis and interpret the results, it is necessary to (1) analyze the existing but previously-unanalyzed data on the behavior of the Eastern Arctic bowheads, (2) compare their behavior with that of the Western Arctic stock, (3) quantify the relative amounts of human activity to which the two stocks have been exposed in recent years, and (4) evaluate whether any observed differences in behavior are attributable to differences in human activities.

The study was planned as a two-phase project. In Phase 1, the behavior of the two stocks of bowheads was to be compared (items 1 and 2 from the above list). In Phase 2, the relative exposure of the two stocks to human activity is to be determined, and behavioral similarities and differences between stocks are to be evaluated in relation to differences in human activities (items 3 and 4). The present report presents the results from Phase 1.

Data Sources and Methods

The western arctic data used for these analyses came from three studies funded by BLM/MMS or the oil industry and conducted by LGL in the 1980-86 period, plus a study conducted for MMS by the Naval Ocean Systems Center (NOSC) in 1983:

1. The LGL/MMS study of behavior and disturbance responses by bowheads summering in the Canadian Beaufort Sea in 1980-84 (Richardson [cd.] 1985).

2. The LGL/MMS study of bowheads feeding in the eastern Alaskan Beaufort Sea during September of 1985 and 1986 (Richardson et al. 1987b).

3. The LGL/Shell Western study of bowheads migrating past drillsites in the Alaskan Beaufort Sea during the autumn of 1986 (Koski and Johnson 1987).

4. The NOSC/MMS study of bowheads near seismic vessels in the Alaskan Beaufort Sea during the autumn of 1983 (Ljungblad et al. 1984b). Heavy ice conditions prevented most seismic exploration in 1983.

The data considered here were those collected when no significant source of man-made underwater noise was present. All data collected in the four western arctic studies were collected by aerial observers using a standardized observation method. The aircraft circled at an altitude of at least 1500 ft (457 m) during all observation sessions considered here. This has been shown to be high enough to avoid significant disturbance by the observation aircraft.

The eastern arctic data were collected during two LGL shore-based studies along the east coast of Baffin Island:

1. A study of bowheads migrating south past Cape Adair in the autumn of 1979. Limited additional data were available from 1978 (Koski and Davis 1979, 1980).

2. A study of bowheads summering at Isabella Bay in the late summer - early autumn periods of 1984-86. Limited additional data were available from 1983 and 1987 (Finley et al. 1986; Finley 1987, unpubl.).

In both studies, most data came from a theodolite deployed on a coastal hill or cliff. The theodolite was about 209 m above sea level at Cape Adair and 136 m above sea level at Isabella Bay--high enough to allow observations and tracking of whales several kilometers away. Aerial surveys provided supplementary data in 1978-79. At Isabella Bay, data on zooplankton and underwater sounds were acquired occasionally from boats, and whale sizes were determined in 1986 by aerial photogrammetry.

LGL's western arctic data were already available in a standardized computer-readable format prior to the present study. At the start of this project, they were converted into an improved format incorporating some additional variables. LGL's eastern arctic data, which had not previously been analyzed in detail, plus NOSC's 1983 western arctic data, were coded in the new format, entered into a computer, and validated.

The first major step of the analysis was to identify comparable subsets of the eastern and western arctic data. Preliminary analyses indicated that three categories of whale activity occurred commonly in both regions: feeding in deep (>50 m) water, socializing in shallow (≤50 m) water, and migrating. A fourth category, local travel, was commonly recognized only at Isabella Bay. Separate analyses were performed for each of these four categories of whale activities. Several other categories of activity were recognized in the western arctic, e.g. near-bottom, water-column and near-surface feeding in shallow water; socializing in deep water. The behavior of western arctic bowheads engaged in these latter activities has been reported previously, and was not analyzed further in this study because of the absence of corresponding eastern arctic data.

Bowheads Feeding in Deep Water

Most feeding activity at Isabella Bay occurred in deep water over glacial-remnant troughs several kilometers offshore. Essentially all feeding was of the type recognized in the western arctic as 'water column feeding'. There was little evidence of coordinated feeding behavior between different individual whales. However, surfacing-dive sequences of some 'paired' whales were synchronous. Near-surface feeding apparently was rare, and near-bottom feeding was not detected. Whales feeding in a trough >200 m deep several kilometers northeast of the observation site on Cape Raper moved back and forth through the area from one surfacing to the next. When at the surface, bowheads often defecated, and fecal samples (n = 2) contained remnants of large copepods. Limited zooplankton sampling indicated that concentrations of large copepods occurred at depths >100 m.

Bowheads feeding in deep water off Isabella Bay exhibited long dives and surfacings, with many respirations per surfacing. An average surfacing - respiration - dive cycle consisted of a 15.8 min dive followed by a 4.7 min surfacing during which the whale respired 17 times. This behavior is consistent with diving to great depths. The interval between successive blows within a surfacing averaged 16.9 s. Within this category of whales, surfacing - respiration - diving behavior was correlated with few of the environmental variables that we considered. Aerial activity (breaches, tail slaps, flipper slaps) was very infrequent. Most surfacings of feeding bowheads ended with a 'fluke-out' dive.

Bowheads feeding in deep (>50 m) water off Isabella Bay exhibited much longer surface times and many more blows per surfacing than did those feeding in deep waters of the Beaufort Sea ($P<0.001$). Multivariate analysis indicated that these differences could not be accounted for by differences in any of the measured environmental variables or whale activities. Thus, we conclude that there were real east-west difference in these attributes of behavior. The eastern whales also had longer intervals between successive blows ($P<0.001$) and longer dive durations ($P<0.05$), but the proportional differences were not as large. The difference in mean blow interval was probably an actual east-west difference. The cause of the slight east-west difference in mean dive durations was uncertain.

An important unknown factor is the actual depth to which the whale dove during each surfacing-dive cycle. In gray and humpback whales, depth of dive is strongly and positively correlated with most surfacing - respiration - dive variables. We suspect that an average feeding dive off Isabella Bay was considerably deeper than an average feeding dive in the Beaufort Sea. There is indirect evidence that prey concentrations tend to occur at greater average depths off Isabella Bay.

Bowheads Socializing in Shallow Water

Bowheads socializing in shallow water (≤50 m) at Isabella Bay often were engaged in very active social activity, frequently with an obvious sexual component. Groups of interacting bowheads seemed to contain a considerable proportion of large subadults, whereas pairs of interacting whales often appeared to be adults. Socializing bowheads produced many underwater calls and other sounds. High proportions of their calls were of the types that have been associated with active social interactions in western arctic bowheads and southern right whales.

Socializing bowheads at Isabella Bay tended to exhibit quite short surfacing-dive cycles with few respirations per cycle. An average cycle consisted of a 1.6 min dive and a 1.2 min surfacing with 2 blows spaced 17.7 s apart. Surfacing, respiration and dive variables were not correlated with many of the environmental variables examined. Within a given observation session, the socializing bowheads at Isabella Bay seemed to concentrate on social interactions. Within periods lasting minutes or hours, they normally did not intermix socializing with feeding, contrary to the situation in summer in the western arctic. Aerial activity and active social interactions occurred during unusually high percentages of the surfacings.

The behavior of socializing bowheads at Isabella Bay differed in several respects from that of bowheads socializing in shallow waters of the Beaufort Sea. At Isabella Bay, swimming speeds tended to be lower, aerial activities were much more frequent ($P \ll 0.001$), and fluke-out dives less frequent ($P \ll 0.001$). Harmonic calls tended to be much more prolonged than those heard in the Beaufort Sea. A mechanical 'CR-UNCH' sound was also heard near socializing bowheads at Isabella Bay but not in the western arctic. Surface times were shorter at Isabella Bay and the number of blows per surfacing lower, even after allowance for the effects of other variables ($P < 0.001$ in each case). Mean blow intervals were lower at Isabella Bay than in the west ($P < 0.001$). However, this last difference may have been attributable to regional differences in some of the corollary environmental or whale activity variables. Durations of dives did not differ significantly between regions.

The results provide clear evidence of differences in the behavior of socializing bowheads in the two study areas. However, one cannot necessarily conclude that the differences were attributable to between-population differences in socializing behavior. The socializing bowheads observed at Isabella Bay were predominantly large subadults or adults without calves, whereas those observed in shallow waters of the Beaufort were mainly smaller subadults. Presently available data on socializing whales do not allow an evaluation of the relative magnitudes of population (east-west) differences in behavior versus effects of whale size, age, or reproductive status. It is noteworthy, however, that sexual activity was common at Isabella Bay even though it has very rarely been observed anywhere in the Beaufort Sea during late summer or autumn, even in places where adult and large subadult whales were common.

Bowheads Engaged in Local Travel

Local travel was a common activity of whales at Isabella Bay, mainly involving singletons or pairs of whales. Most of these whales were traveling between the main locations where feeding and socializing took place. Swimming speeds were usually slow. Durations of surfacings and dives were intermediate between the high values of feeding whales and the low values of socializing whales. The same was true of the number of blows per surfacing. That variable, along with dive duration, was not correlated with many of the environmental variables considered. Surface times and blow intervals were correlated with several other variables; however, these results seemed to be largely a result of a relationship to one dominant variable that affected several of the others. Little active socializing occurred during local travel. Flipper and tail slaps were somewhat more common, but still infrequent. Most dives began without the flukes being raised above the surface.

Local travel undoubtedly occurred commonly in the Beaufort Sea as well. However, it was not as readily recognizable there, probably because of differences between the aerial observation method used in the west versus the coastal observation method used in the east. Too few definite cases of local travel could be isolated in the western arctic to allow comparisons with the eastern arctic data.

Bowheads Engaged in Autumn Migration

Migrating bowheads travelled consistently southeastward along the coast of Baffin Island at comparatively high speed, usually as singletons or pairs. Typical travel speeds were about 5-6 km/h. These speeds were maintained over periods of at least several hours, and in one case probably for at least 28 h. The peak of the migration past Cape Adair (250 km north of Isabella Bay) was in early October during each of the two years of observation there (1978-79). The migration corridor was within 1½ km of shore at Cape Adair and probably also at Isabella Bay.

In the eastern arctic, mean duration of surfacing, duration of dive, and number of blows per surfacing were intermediate between values for feeding and socializing whales, and generally similar to values during local travel. An average surfacing - dive cycle by a whale migrating along the Baffin Island coast consisted of a 9.3 min dive and a 1.5 min surfacing with 6 blows spaced an average of 17.1 s apart. However, migrating whales spent less time at the surface (14%) than any other category of whale in the eastern arctic. Durations of both surfacings and dives by migrating bowheads tended to be lower when sea state was high than when it was near-calm. Socializing and aerial activity were very uncommon during migration. Fluke-out dives were common, although less so than during feeding in deep water.

The physical situations, activities, behavior and (presumed) age composition of ❑igrating bowheads observed in the eastern and western arctic were similar in many respects. The main difference in circumstances was that most migrants observed in the west were many kilometers offshore over the middle-shelf region, whereas those observed in the east were <1½ km from shore. In both regions, group sizes were generally 1 or 2, and the–re was very little socializing or aerial behavior. Fluke-out dives seemed to be more common in the east.

Dive durations averaged longer in the west than in the east ($P<0.01$), whereas surface times were similar in the two regions. As a result, bowheads were at the surface for a lower percentage of the time in the west (10% vs. 14%). In both areas, bowheads were at the surface for a smaller proportion of time during migration than during the other activities that were studied. The number of blows per surfacing and the mean blow interval were similar in the east and west.

Overall, the behavior of migrating bowheads in the eastern and western arctic was more similar than was the case for either feeding or socializing bowheads. However, there was a significant difference in dive durations. The frequency of fluke-out dives apparently also differed.

Reactions to Human Activities in Eastern and Western Arctic

The primary objective of Phase 1 of this study was to determine whether there are differences in the 'normal' behavior of eastern and western arctic bowheads. Thus, all analyses summarized above were based on observations of bowheads that were not exposed to any obvious source of potential man-made disturbance at the time of the observations. A variety of regional differences in behavior have been identified. The purpose of Phase 2 of the project, to be conducted in 1988-89, will be to determine whether some of these differences can be ascribed to long-term changes in bowhead behavior in response to the cumulative effects of human activities in the western arctic.

In interpreting the possible long-term effects of disturbance in the eastern and western arctic, it would be helpful to know whether there is any evidence that bowheads of the two populations exhibit differences in their short-term responses to human activities. Limited data are available on reactions of eastern as well as western arctic bowheads to small boats, ships, and aircraft.

Bowheads reacted strongly to boats in both the eastern and western arctic. In both regions, bowheads swam rapidly away when boats approached at high speed, sometimes when the distance was as great as 4 km. In both regions, reactions to slow-moving boats were less dramatic but avoidance was still evident. In both areas, there was evidence that bowheads often resume their normal activities soon after fleeing from an approaching boat--within ½-1 hr on at least some occasions. More detailed comparisons of reactions to boats in the two regions are not possible because the data are limited and because the observation procedures and types of boats were different. However, available information suggests that sensitivity to small vessels is similar in the two regions.

Western arctic bowheads usually react strongly to direct approaches by ships, typically at distances of several kilometers. Under special circumstances, exemplified by a case of two ships approaching a cow-calf pair from opposite directions, reactions may occur at greater distances. It is uncertain whether any of the whales observed at Isabella Bay were disturbed by distant ships; if so, the disturbance was mild and infrequent.

During some low-level (e.g. 150 m) overflights by aircraft, bowheads dive hastily in both the eastern and western arctic. During other such overflights, the whales remain at the surface and seem unaffected. In both regions, there is subjective evidence that the animals are less sensitive to aircraft when actively engaged in social interactions. Although comparative data are limited, especially for the eastern arctic, sensitivity to aircraft seems generally similar in the two regions.

As a first approximation, short-term behavioral reactions of bowheads to small boats, ships and aircraft seem similar in the eastern and western arctic. However, the available data on disturbance reactions, especially in the eastern arctic, are too meagre for detailed comparisons.

Conclusions

1. The general behavioral repertoires of the eastern and western arctic populations of bowhead whales were qualitatively similar.

2. Notwithstanding (l), there were many quantitative differences between the behaviors observed in the eastern and western arctic. This was true even though east-west comparisons were restricted to whales engaged in similar activities.

3. Some of the east-west differences in behavior were attributable to differences in the environmental conditions under which bowheads occurred, or to differences in the activities of the whales. However, even after allowance for the effects of these corollary variables on behavior, several aspects of behavior remained highly significantly different between the whales observed in the eastern and western arctic.

4. The surfacing - dive cycles of whales feeding in deep (>50 m) water were much more protracted in the eastern arctic than in the west, with many more respirations per surfacing. These differences were evident even after allowance for regional differences in measured environmental variables. However, in the absence of specific data on typical depths of dives in the two regions, it is uncertain whether the differences in behavior were attributable to differences in depths of dives or to some other regional difference.

5. Behavior of bowheads socializing in shallow (<50 m) water differed strongly in many respects between the Beaufort Sea and the Isabella Bay area of the eastern arctic. Socializing was much more active at Isabella Bay, and obvious sexual interactions were much more common there. The differences were very likely attributable in part to differences in the predominant sizes and age categories of the whales whose behavior was compared. However, sexual interactions have very rarely been seen during late summer or autumn anywhere in the Beaufort Sea, including areas where there were many adults and large subadults. Thus, there may be real differences in reproductive activities between the two stocks.

6. Behavior of migrating bowheads in the two regions was generally similar. However, dive durations were considerably greater in the west, and fluke-out dives were more common in the east. Since several other behavioral variables did not differ significantly between migrants in the two regions, it is difficult to evaluate the biological significance of the two statistically significant variables.

7. Overall, the behavior of eastern arctic bowheads along the coast of Baffin Island in late summer differed quantitatively in a number of ways from that observed in the Beaufort Sea. Some but not all of these differences can be ascribed to differences in environmental conditions or the types of whales and whale activities that were observed. The apparent regional difference in the frequency of sexual interactions in late summer is potentially of particular importance. Phase 2 of this study, being done in 1989, will examine whether any of these behavioral differences can be ascribed to long-term effects of the differing levels of human activities in the two regions.

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During the present retrospective analysis, C.R. Evans and W.R. Koski organized most of the previously-unanalyzed eastern arctic data, and provided much important information about the earlier field studies. Chris Holdsworth performed the computer programming, data management, and statistical analyses. Chris Clark of Cornell University analyzed recordings of bowhead calls from Isabella Bay, and provided data on call types during spring migration at Barrow, AK. Denis Thomson assisted with interpretation of zooplankton data, and Rolph Davis provided helpful comments on the draft report. Bev Griffen produced the report. We thank all of these individuals.

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* Much of this section was prepared by Denis H. Thomson, LGL Ltd.

INTRODUCTION

The Question of Long-term Cumulative Effects of Man on Bowheads

Over the past decade much concern has been expressed about the possible effects of offshore oil and gas exploration on various species of endangered baleen whales, including the bowhead whale. One area of concern has involved questions about the effects of underwater noise and other stimuli associated with industrial activity on the behavior of whales. As a result of this concern, the U.S. Department of the Interior and other agencies--government and industrial--have funded several major studies of the short-term behavioral reactions of baleen whales to industrial sounds. Major studies of this type have been done on bowhead whales, gray whales and humpback whales. These studies have provided partial quantification of the relationships between noise levels and the short-term disturbance responses of baleen whales. However, these studies have provided little information about the significance of short-term behavioral responses to the long-term well-being of whale populations.

Studies of the possible long-term reactions of a population of whales to human activities are difficult to do, for a number of reasons. (1) A long-term study must, by definition, continue for an extended period, ideally a long period relative to the lifetimes of the animals involved. (2) Long-term experiments are generally impossible; one must rely on observations of whales in relation to year-to-year changes in actual human activities. (3) Often there are few or no quantitative data on whale activities prior to the start of the human activities that are suspected to affect the whales. (4) Data accumulate very slowly in such a study, in many cases at the rate of one observation per year, e.g. number of whales present each year. (5) It is very difficult to isolate the effects of one factor, such as human activity, from other factors, such as natural variations in the environment. Most or all of these problems have been evident in previous attempts to evaluate long-term effects of human activities on whales, e.g. for

- minke and Baird's beaked whales off Japan (Nishiwaki and Sasao 1977),
- gray whales in lagoons along Baja California (Bryant et al. 1984),
- humpback whales in Hawaii (Norris and Reeves 1978; Glockner-Ferrari and Ferrari 1985; Bauer and Herman 1986),
- humpbacks in southeast Alaska (MMC 1979/80; Dean et al. 1985), and
- bowhead whales in the Canadian Beaufort Sea (Richardson et al. 1985a, 1987a).

Bowheads in the Beaufort Sea react, at least briefly, to underwater noise from ships, seismic exploration, marine construction, and drillships (Ljungblad et al. 1985, 1988; Richardson et al. 1985b,c, 1986; LGL and Greeneridge 1987). On a longer-term basis, there are indications of reduced utilization in recent years of the part of the summering range where offshore oil exploration has been in progress over the past decade (Richardson et al. 1985a, 1987a). However, the degree of decrease in utilization of that area is controversial (Ward and Pessah in press) because there had been no systematic studies of bowhead distribution or behavior in summer before oil exploration began. It is possible that some or all of the year to year variability in use of the industrial area in recent years has been the result of responses by the whales to natural factors, especially the variable distribution of their food (ESL et al. 1986; Thomson et al. 1986; Bradstreet et al. 1987).

Rationale for Comparing Bering/Beaufort and Davis Strait Stocks

Questions about the long-term responses of endangered whales to human activities like offshore oil exploration are important despite the difficulties involved in designing and conducting effective studies. Recognizing this, MMS identified a new approach that may provide insight into the long-term, cumulative effects of human activity on bowhead whales.

The Western Arctic stock, in which the Alaska OCS Region of MMS has a particular interest, has been exposed to considerable human activity for a prolonged period. This human activity has included offshore oil exploration on part of the summering grounds since about 1976, additional oil exploration in Alaskan waters during the 1980s, other vessel traffic, and subsistence hunting pressure each spring and autumn. In contrast, the Eastern Arctic (= Davis Strait/Baffin Bay) stock has been exposed to considerably less human activity in recent decades. Behavioral and other observations have been acquired during studies of both stocks in recent years. MMS has recognized that a comparison of existing data on the behavior of these stocks might provide insight into the possible cumulative effects of human activities on bowhead behavior.

The following subsection summarizes some basic background information about the Western and Eastern Arctic stocks of bowheads.

Brief Summary of the Stocks

Historically, bowhead whales had a disjunct circumpolar distribution (Fig. 1) consisting of four or five presumably discrete stocks:

- Western Arctic (of North America) stock in the Bering, Chukchi and Beaufort Seas,

- Sea of Okhotsk stock of the eastern USSR, separated from the Western Arctic stock by the Kamchatka Peninsula,

- Northeast Atlantic or East Greenland/Spitzbergen stock,

- Davis Strait/Baffin Bay group occurring west of Greenland and in the Canadian eastern arctic, and

- the Hudson Bay group,

The degree of discreteness of the Hudson Bay and Davis Strait/Baffin Bay groups is not known. They may overlap in winter (Finley et al. 1982, p. 57; McLaren and Davis 1982; Reeves et al. 1983), in which case they may constitute a single 'Eastern Arctic' (of North America) stock.

The Western and Eastern Arctic stocks are effectively separated by a gap in bowhead distribution in the central and western part of the Canadian arctic archipelago (Fig. 1). This area is usually covered by heavy multi-year ice for most if not all of the summer. There is no reliable evidence of exchange of

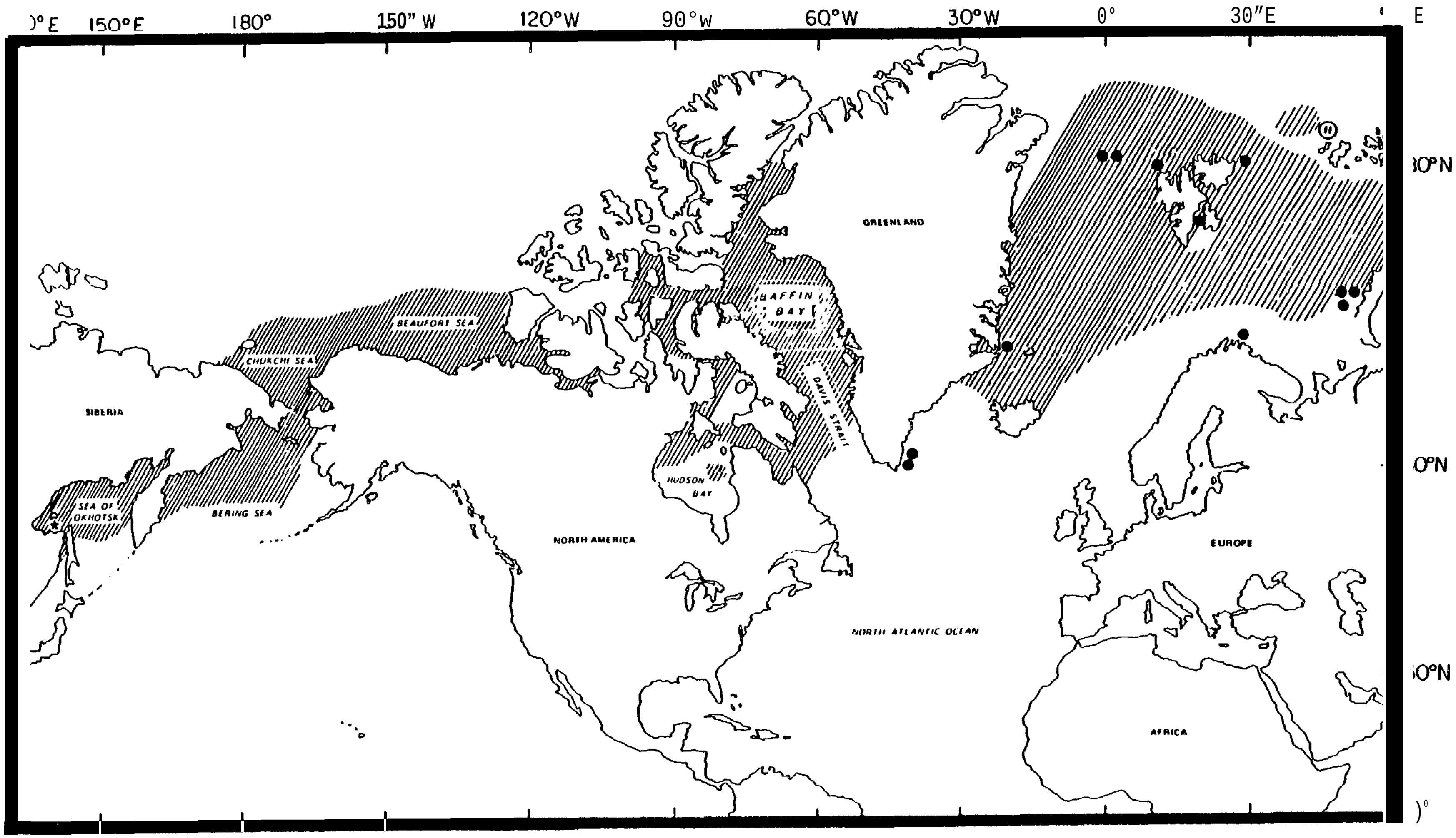

Figure 1. Approximate world distribution of bowhead whales prior to commercial whaling. Current range of each stock mav not be the same. Recent (1958-82) sightings of single bowheads in the eastern North Atlantic-are shown by dots. (From Braham 1984.)

individuals between these two stocks, although the possibility of exchange of a few individuals on rare occasions cannot be ruled out (Reeves et al. 1983b; Bockstoce 1986, p. 255).

All five groups of bowheads were hunted commercially prior to the 20th century, and were reduced to small remnants of their historical populations. The Northeast Atlantic stock was effectively extirpated. The Sea of Okhotsk, Hudson Bay and Davis Strait/Baffin Bay groups are now very small. Only the Bering/Beaufort or Western Arctic stock still exists in substantial numbers.

Western Arctic Stock

The history and present status of the Western and Eastern Arctic stocks of bowheads are quite different in several respects. The Western Arctic stock was hunted commercially primarily during the middle and latter portions of the 19th century, with limited commercial whaling continuing until about 1915 (Bockstoce 1986). A subsistence harvest by Alaskan Eskimos has continued to the present day. Nowadays, whales are hunted from unmotorized boats deployed from the landfast ice edge in spring, and from motorboats in autumn.

The Western Arctic stock is now by far the most numerous stock of bowheads. Estimates of its size have increased greatly over the past decade as censusing methods have improved. The most recent estimates for the Western Arctic stock are 7200 (IWC 1988; Zeh et al. 1988) and 7800 (IWC in press) bowheads, with a wide range of uncertainty.

Western Arctic bowheads winter in the central and northwest Bering Sea, summer in the eastern Beaufort Sea and Amundsen Gulf, and migrate around western and northern Alaska in spring and autumn. Besides the subsistence hunting pressure during parts of the spring and autumn migration, the whales are becoming increasingly exposed to offshore oil exploration in various parts of their range. The south-central part of the summer range has been an area of much offshore oil exploration since 1976. More recently, some oil exploration has begun along the autumn migration route through the Alaskan Beaufort Sea. Extensive seismic exploration preceded and accompanies this oil exploration. Oil exploration is also a possibility during the next few years along parts of the migration route through the Chukchi Sea and in parts of the winter range in the Bering Sea. Besides the oil industry activities, there is also limited ship traffic near bowheads occupying various parts of the summer and autumn range.

Eastern Arctic Stock

In comparison with the Western Arctic stock, the Davis Strait/Baffin Bay bowheads were hunted commercially for a much longer period, from the 17th to the early 20th centuries (de Jong 1978; Ross 1979, 1985; Mitchell and Reeves 1981). Ross (1979) estimated that a minimum of over 28,000 bowheads were taken from the Davis Strait/Baffin Bay stock based on available records for the period 1719-1911. This cumulative estimate of catch is known to substantially underestimate the actual harvest, but the total kill is not known. During the early years of commercial whaling the population sizes may have been about 11,000 animals for the Davis Strait/Baffin Bay group plus about 680 for the

Hudson Bay group, with considerable uncertainty (Mitchell and Reeves 1981). By the early 20th century both groups were almost extinct.

In contrast to the Bering/Beaufort stock, the Davis Strait/Baffin Bay group has not recovered to any significant degree. At present, it apparently consists of no more than a few hundred animals. The most recent data suggest a population size of at least 200-300 individuals, excluding the Hudson Bay animals (Finley et al. 1986; Finley 1987). Although there has been no routine or authorized subsistence harvest of Eastern Arctic bowheads since the end of commercial whaling about 70 years ago, bowheads are killed by Inuit on rare occasions. Mitchell and Reeves (1982) have speculated that, given the very small stock size, this occasional hunting pressure may be a significant factor in preventing population recovery. Predation by killer whales also may be a significant source of mortality (Mitchell and Reeves 1982; Finley et al. 1986; Finley 1987).

The remnant Davis Strait/Baffin Bay group presently winters in its historical wintering range in the pack ice near the ice edge in Davis Strait and perhaps Hudson Strait (Fig. 2; McLaren and Davis 1982, 1983; Born and Heide-Jorgensen 1983). The winter range of the Davis Strait/Baffin Bay group is somewhat uncertain because of the unknown degree of segregation of those whales from the Hudson Bay whales, some of which seem to winter at least as far east as eastern Hudson Strait (Finley et al. 1982).

Some whales migrate north in spring near the Greenland coast, where ice conditions are lighter than on the western side of Baffin Bay, and then travel west across Baffin Bay at about the latitude of northern Baffin Island. Others move northwest through the pack ice at more southerly latitudes later in the season when the pack ice is deteriorating and receding southward (Fig. 3). The limited available aerial survey coverage suggests that few bowheads occur in extreme northern Baffin Bay during spring (Koski and Davis 1979; Koski 1980a), although there are some 19th century records there in July (Ross and MacIver 1981).

In late spring or summer, depending on the date when landfast ice breaks up, bowheads enter various channels, bays and fiords in the Canadian arctic islands, primarily via Lancaster Sound around northern Baffin Island (Fig. 2; Southwell 1898; Mansfield 1971; Finley 1976; Greendale and Brousseau-Greendale 1976; Johnson et al. 1976; Koski and Davis 1979, 1980; Davis and Koski 1980; Koski 1980b; Ross and MacIver 1981; Reeves et al. 1983). The most southeasterly of the major late summer concentration points observed during recent years is at Isabella Bay, east-central Baffin Island (Fig. 2; Koski and Davis 1980; Reeves et al. 1983; Finley et al. 1986). During the 19th century, many bowheads were killed somewhat farther to the southeast in August and especially in September (Ross and MacIver 1981).

The old whaling literature contains many suggestions that different components of the population concentrated in different summering areas. Subadults, cows and calves were said to concentrate to the north and west, off northern Baffin Island. In contrast, whales found in late summer in fiords along eastern Baffin Island were said to be primarily large animals without calves (Eschricht and Reinhardt 1866; Brown 1868; Southwell 1898; Lubbock 1937).

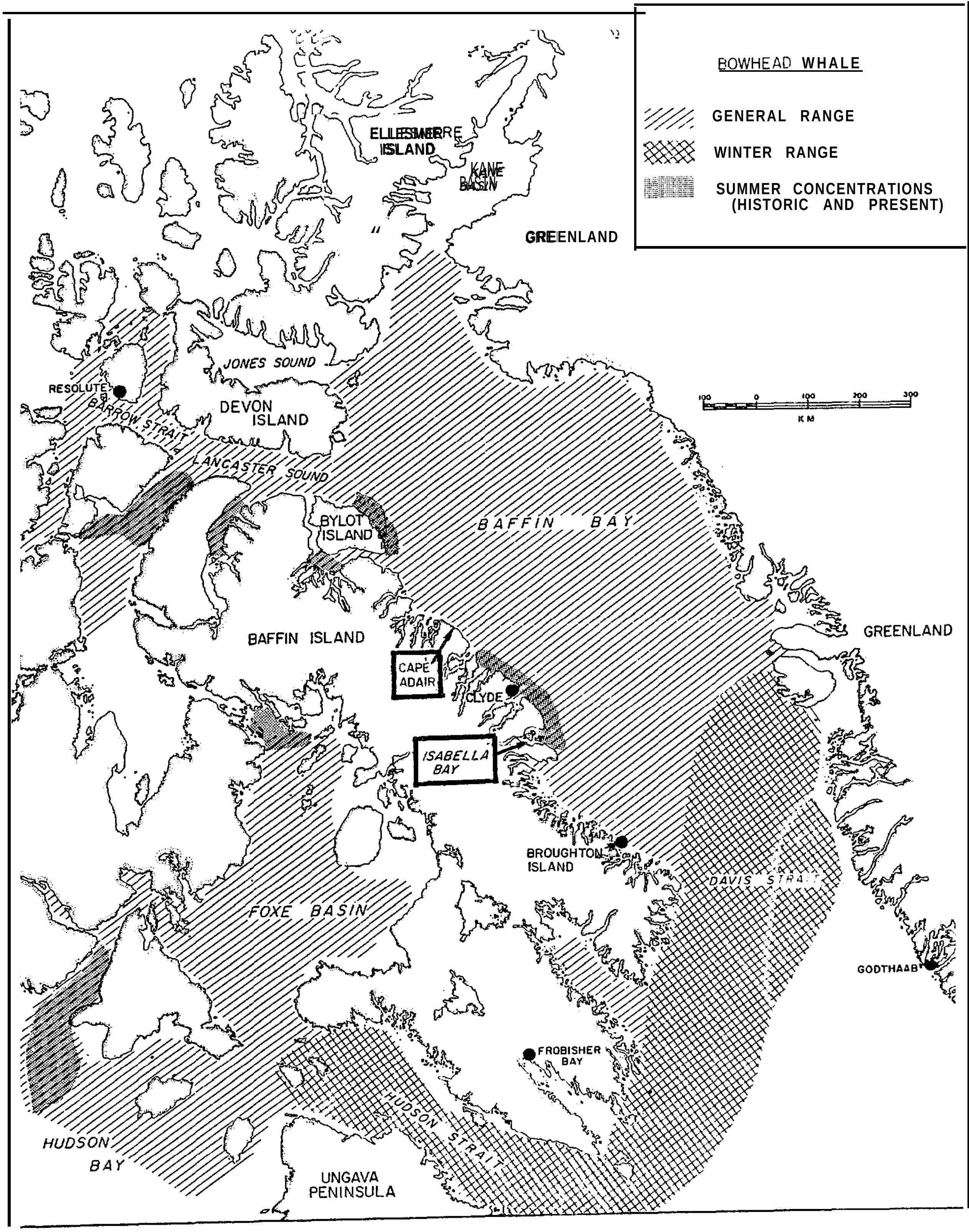

Figure 2. Distribution and important summering areas of the bowhead whale in the eastern Canadian Arctic. (From Finley et al. 1986).

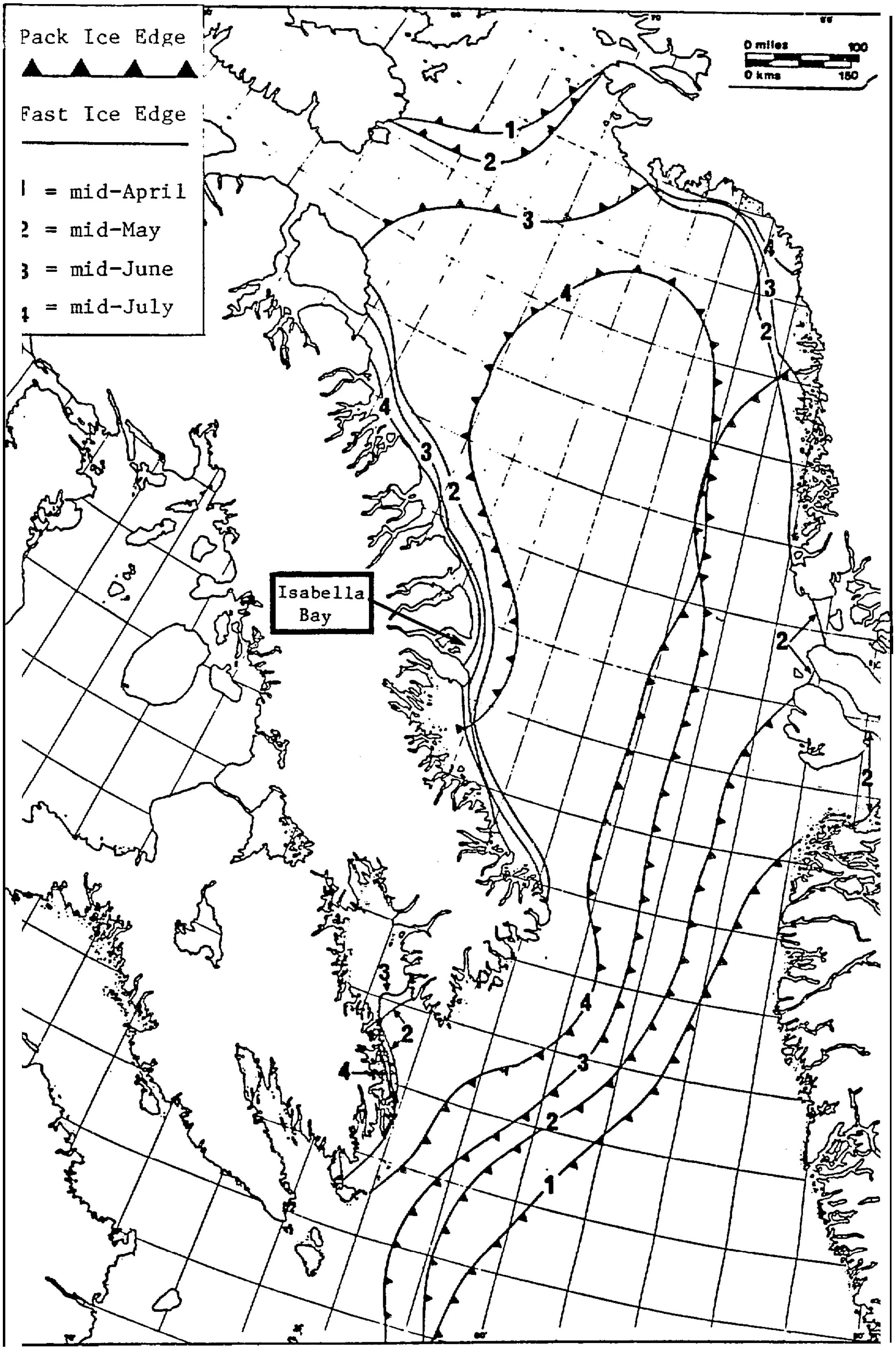

Figure 3. Average positions of fast ice and pack ice by month during spring. (From Ross and MacIver 1981, based on U.S. Navy data for 1952-71).

In autumn, the bowheads that summer farthest north and west migrate east past northern Baffin Island and then south along the coast of eastern Baffin Island. They have been monitored from a clifftop observation site at Cape Adair (Fig. 2) during two autumn seasons (Koski and Davis 1979, 1980). During October, these whales migrate south past Isabella Bay and other concentration points along eastern Baffin Island, possibly intermingling with individuals that have spent the late summer there. Baffin Bay usually is largely ice-free during this period.

There has been no offshore oil drilling in the summer or early autumn range of the Davis Strait/Baffin Bay bowheads. There has been only a very limited amount of oil exploration in the winter range off the west coast of Greenland and in Davis Strait, and little of that activity was during the winter when bowheads might be present. There has been some seismic exploration in these areas. The amount of seismic exploration in the range of the Eastern Arctic bowheads has not been compiled and published, but it is undoubtedly much lower than the amount of seismic exploration in various parts of the range of the Western Arctic bowheads. There is commercial and subsistence fishing off the west coast of Greenland, although very little of this would be in winter when bowheads are present in those waters. There is limited summer shipping in various parts of the range, along with local movements of small boats around communities. As noted above, there is no hunt for Eastern Arctic bowheads.

It is apparent that, in recent decades, the Davis Strait/Baffin Bay bowheads have been exposed to much less human activity than have the Western Arctic bowheads, although the ratio has not yet been quantified. Thus, the former group might be considered a control population against which the behavior of Western Arctic bowheads can be compared. This provides a possible approach for evaluating whether the increasing human activity in the range of the Western Arctic stock has led to long-term changes in behavior.

Available Behavioral Data

Many data on the behavior of Western and Eastern Arctic bowheads have been collected in recent years. Thus, a comparison of the behavior of these two stocks can be done using existing data.

Western Arctic Stock

Several major studies since 1980 have provided a large quantity of data on the behavior of Western Arctic bowheads in spring, summer and autumn. In spring, the behavior of migrating bowheads has been documented systematically for several years during the census along the ice edge near Barrow (e.g. Carroll et al. 1987). There have been additional incidental aircraft-based observations of behavior during spring. In late summer, behavior of bowheads in the Canadian Beaufort Sea was studied systematically from 1980 to 1984 during the LGL/MMS bowhead behavior and disturbance study (Würsig et al. 1984a, 1985a,b, 1986, Dorsey et al. in press). In autumn, behavior of bowheads feeding and migrating in the Alaskan Beaufort Sea has been studied systematically during projects funded by MMS (Ljungblad et al. 1984b, 1985; Richardson et al. 1987b) and industry (Koski and Johnson 1987).

Taken together, these studies provide a large amount of data, some systematic and some not, on the behavior of Western Arctic bowheads during three of the main phases of the annual cycle. Many of the data collected in each of these seasons pertain to 'presumably undisturbed' bowheads, i.e. to whales that were not exposed to noise from human activity at the time of the observations[1] Behavior of the Western Arctic bowheads has not been studied during late autumn in the Chukchi Sea, during winter in the Bering Sea, or during early summer in Amundsen Gulf and offshore in the Beaufort Sea.

Eastern Arctic Stock

The behavior of bowheads has not been studied as intensively in the eastern as in the western arctic. However, a significant amount of information has been collected by LGL Ltd. during two situations:

1. Bowheads spending the late summer at Isabella Bay, eastern Baffin Island, were studied for four years (1983-87) as part of a study funded primarily by the World Wildlife Fund Canada (Finley et al. 1986; Finley 1987, unpubl.). Detailed behavioral observations were collected, in many cases using the theodolite tracking method. However, many of the behavioral data were not analyzed in detail, since this was not one of the main study objectives. Limited data on oceanographic conditions, food availability, etc., were obtained at Isabella Bay in 1983-87.

2. Behavioral observations on migrating bowheads, including surfacing-respiration-dive cycles and swimming speeds, were collected by theodolite from a clifftop at Cape Adair, Baffin Island, during the autumns of 1978 and 1979 (Koski and Davis 1979, 1980). This work was part of the industry-funded Eastern Arctic Marine Environmental Study.

Almost all data from these two studies pertain to undisturbed whales.

In addition, other data on the distribution, movements and other aspects of the biology of Eastern Arctic bowheads were collected by LGL during various aircraft-, shore-, and ice-based studies in spring, summer, autumn and winter from 1975 to 1982 (Finley 1976; Johnson et al. 1976; Koski and Davis 1979, 1980; Davis and Koski 1980; Koski 1980a,b; McLaren and Davis 1981, 1982, 1983).

Thus, detailed behavioral observations of 'presumably undisturbed' bowheads from both stocks have been collected during two situations: (1) on late summer feeding grounds, and (2) during autumn migration. These data provide a basis for comparing the normal behavior of the two stocks at corresponding phases of their annual cycles.

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[1] Behavioral observations from circling aircraft are counted as 'presumably undisturbed' only if the aircraft was at an altitude of at least 1500 ft (457 m), which has been found to be high enough to avoid significant aircraft disturbance (Richardson et al. 1985b,c).

Objectives

The overall objective of the present study is to determine whether there is any evidence of differences in the behavior of the Western and Eastern Arctic stocks of bowheads that can be attributed to cumulative, long-term effects of the greater degree of exposure of Western Arctic bowheads to human activities. This overall objective has been formulated by MMS as a test of the following null hypothesis:

> H_0: There are no significant differences in normal behavior between bowhead whales of the Western Arctic and Davis Strait stocks.

In order to test this hypothesis and interpret the results, it is necessary to analyze the existing but previously-unanalyzed data on the behavior of the Eastern Arctic bowheads, compare their behavior with that of the Western Arctic stock, quantify the relative amounts of human activity to which the two stocks have been exposed in recent years, and evaluate whether any observed differences in behavior are attributable to differences in human activities.

MMS has formulated the specific objectives in the following way:

1. Analyze recently collected raw data on the normal behavior of bowhead whales on their summer feeding grounds in the fiords of eastern Baffin Island.

2. Relate observed behaviors to natural features including depth, turbidity' nearness to shore, time of year, weather, and ice conditions. Compare these observations with those from the Beaufort Sea feeding areas. [Observations along fall migration-routes were also compared.]

3. Quantify and describe the similarities and differences in observed normal behavior of Davis Strait bowheads vs. comparable bowheads in the Beaufort Sea.

4. Quantify the differences in degree of exposure to offshore oil and gas activities, and other human activities, between the Western Arctic and Davis Strait bowhead stocks.

5. Perform appropriate statistical analyses to identify statistical significance and for hypothesis testing.

6. Search for correlations between observed behaviors and degree of exposure to human caused activities.

Approach

The study was planned as a two-phase project. In Phase 1, the behavior of the two stocks of bowheads was to be compared. Phase 1 encompasses objectives

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[2] Specific data on this point are not available.

1-3 and (in part) 5 from the above list. In Phase 2, the relative exposure of the two stocks to human activity is to be determined, and behavioral similarities and differences between stocks are to be evaluated in relation to differences in human activities (objectives 4, part of 5, 6). The present report presents the results from Phase 1 of the project.

Phase 1

During Phase 1, we used behavioral data collected in the absence of known sources of potential disturbance during previous studies to compare normal behavior of Davis Strait/Baffin Bay (control) vs. Bering/Beaufort bowheads. Two main approaches were used to distinguish within-stock from between-stock variation.

1. The behavior of Eastern Arctic bowheads was examined relative to environmental variables (e.g. water depth, sea state, ice cover, distance from shore, date, time of day) and whale activities (e.g. feeding, socializing, local travel, migration) to identify sources of within-population variation. Analyses of these types have already been done on many of the Western Arctic data--Würsig et al. 1984a, 1985a,b, 1986; Koski and Johnson 1987; Richardson et al. 1987b; Dorsey et al. in press).

2. Appropriate subsets of the Western and Eastern Arctic data were selected to provide the maximum possible degree of comparability. For example, behavior of Eastern Arctic bowheads that were feeding in the water column in deep water (a common situation at Isabella Bay) was compared with behavior of Western Arctic bowheads feeding in the water column at deep locations.

After identifying comparable sets of data for the two stocks, we compared behavior in three ways: univariate statistical analyses of individual behavioral variables (e.g. surface times, dive times, number of blows per surfacing, etc.), multivariate statistical analyses of a variety of variables considered simultaneously, and qualitative and quantitative examination of types of activities and vocalizations exhibited by the two stocks of bowheads under comparable conditions. Based on these analyses, we assessed the validity of the null hypothesis of no difference between the behavior of the two bowhead populations. These topics are all dealt with in the present report.

Phase 2

In Phase 2, human activity information will be compiled for the various areas occupied by Eastern and Western Arctic bowheads in different seasons. We assume that the overall behavior of a population of whales could be influenced by human activities encountered at seasons other than those when the whales are observed. Therefore, we will consider human activities during the parts of the Eastern and Western Arctic ranges used through the year. Many of the necessary western data have already been compiled (Richardson et al. 1985a, 1987a; Norton and McDonald 1986; Norton et al. 1987; Brouwer et al. 1988). More effort will be needed to compile corresponding data for the Davis Strait/Baffin Bay bowheads, since no related work has been done previously.

Based on these human activity data, we will--for each stock--develop an overall measure of the human activities encountered during each season, and during the year as a whole. Available data on noise levels and sensitivity of bowheads to each type of activity will be used in ranking activities. Eastern and Western Arctic results will be compared to quantify the relative exposure of the two stocks to potentially disturbing activities. We will then assess whether any of the between-stock differences in behavior demonstrated in Phase 1 (this report) can be attributed to differences in the cumulative effects of human activities.

The remainder of this report deals with the Phase 1 objectives--documentation of the behavior of the Eastern Arctic bowheads and comparisons of their behavior with that of the Western Arctic stock.

STUDY AREAS, PERIODS, AND ICE CONDITIONS

Western Arctic

Many bowheads feed and socialize over the broad continental shelf in the southeastern (Canadian) Beaufort Sea during August and early September, after most ice has receded from that area. Their distribution varies widely from year to year (Richardson et al. 1985a, 1987a). In some years, including 1983-86, large numbers of small subadult whales occur in very shallow (<20 m) nearshore waters during late August and early September. In other years, these nearshore concentrations are not so evident, although there is still some shoreward movement late in the summer (Richardson et al. 1985a, 1987a). The year 1982 was unusual in that most whales remained in deep water during late summer. Also, during 1982 large whales, including mothers accompanied by calves, comprised a larger than normal fraction of the observed whales (Davis et al. 1983; Koski et al. 1988). Large whales tend to be proportionally more common east of Cape Bathurst in Franklin Bay and Amundsen Gulf than they are over the continental shelf of the southeastern Beaufort Sea.

During late summer, the western edge of the range is normally near the Alaska/Yukon border, with only a small (and variable) proportion of the whales being in Alaskan waters. Those that are off Alaska during August tend to be in deep water over the continental slope (Ljungblad et al. 1987; Moore et al. 1988).

Some westward movement, interspersed with feeding, occurs during August and early September. However, from mid September onward westward migration becomes more pronounced, feeding becomes less frequent, and bowheads become common in the Alaskan Beaufort Sea (Ljungblad et al. 1987; Richardson et al. 1987b). When traveling through Alaskan waters, they tend to be over the mid-shelf area, closer to shore than in August. The last bowheads do not leave Canadian waters until October and sometimes November, when ice cover is usually quite extensive.

All Western Arctic data considered here were collected from an observation aircraft circling at an altitude of 457 m or more--high enough to avoid significant disturbance by the observation aircraft (Richardson et al. 1985b,c). Many other bowheads may have been disturbed by an observation aircraft below 457 m altitude or by a nearby vessel, an industrial site, or another human activity. All such ‘potentially disturbed' observations have been excluded from all analyses in this report, with the exception of the brief section ‘Comparison of Reactions to Human Activities’. The potentially disturbed data were excluded because our objective is to see whether the ‘normal’ behavior of whales in the Western Arctic differs in any basic way from that in the Eastern Arctic.

The largest of the four Western Arctic datasets came from the LGL/MMS study of bowhead behavior and disturbance responses in the Canadian Beaufort Sea during the late summers of 1980-84 (Richardson, cd., 1985). Behavioral observations were obtained from 1 August to 8 September, but mostly in August. Locations where presumably undisturbed bowheads were observed were widely distributed (Fig. 4), but varied from year to year following year-to-year variations in the concentration areas of the whales (Richardson et al. 1985a, 1987a). Water depths at observation locations varied from less than 10 m to about 1700 m. Distances from shore varied from about 100 m to 148 km. In 1980-81 and 1983-84, most observations were in relatively shallow (<50 m) waters, but in 1982 almost all observations were over outer shelf and continental slope waters 50-500 m deep. The great majority of these 1980-84 data were collected under open water conditions. However, a small percentage were collected in or close to drifting pack ice whose percentage cover ranged from <1% to 85%. Information about the individual observation sessions in 1980-83 can be found in Table 1 within each of Würsig et al. (1982, 1983, 1984b).

The second Western Arctic dataset came from the LGL/MMS study of bowhead feeding near the Alaska/Yukon border from 3 to 29 September of 1985 and 1986 (Richardson et al. 1987b). Water depths at observation locations usually were 5 to 50 m, with a single exceptional case over water 280 m deep (Fig. 5). During September 1985, very few whales occurred west of the Alaska/Yukon border until after mid September, by which time pack ice covered most of the study area and new ice was forming rapidly. In 1985, ice cover at observation locations ranged from O to 50%, plus 100% ‘grease’ ice on a few occasions. In contrast, during September 1986 the late summer feeding range of Western Arctic bowheads extended slightly into Alaskan waters, and the ice edge was unusually far offshore. There was no ice at any of the behavioral observation locations in 1986. For information about the individual observation sessions in 1985-86, see Richardson et al. (1986, p. 196; 1987b, p. 334).

The third Western Arctic study whose data are considered here was an LGL/Shell Western study of bowheads near the Alaska/Yukon border and migrating past drillsites in the Alaskan Beaufort Sea (Koski and Johnson 1987). Their 14 behavioral observation sessions extended from 4 September to 6 October 1986. Some of the data from this study were believed to represent the behavior of undisturbed whales, and are considered here. For more details about the individual observation sessions, see Davis (1987, p. 37) and Koski and Johnson (1987).

The fourth Western Arctic study that provided some data for the analysis was the behavioral observation project conducted by the Naval Ocean Systems Center and SEACO Inc. in 1983 for MMS (Ljungblad et al. 1984b). Most of their data were collected in the absence of potentially disturbing human activities. We considered NOSC’S 1983 data on ‘presumably undisturbed’ migrating whales in

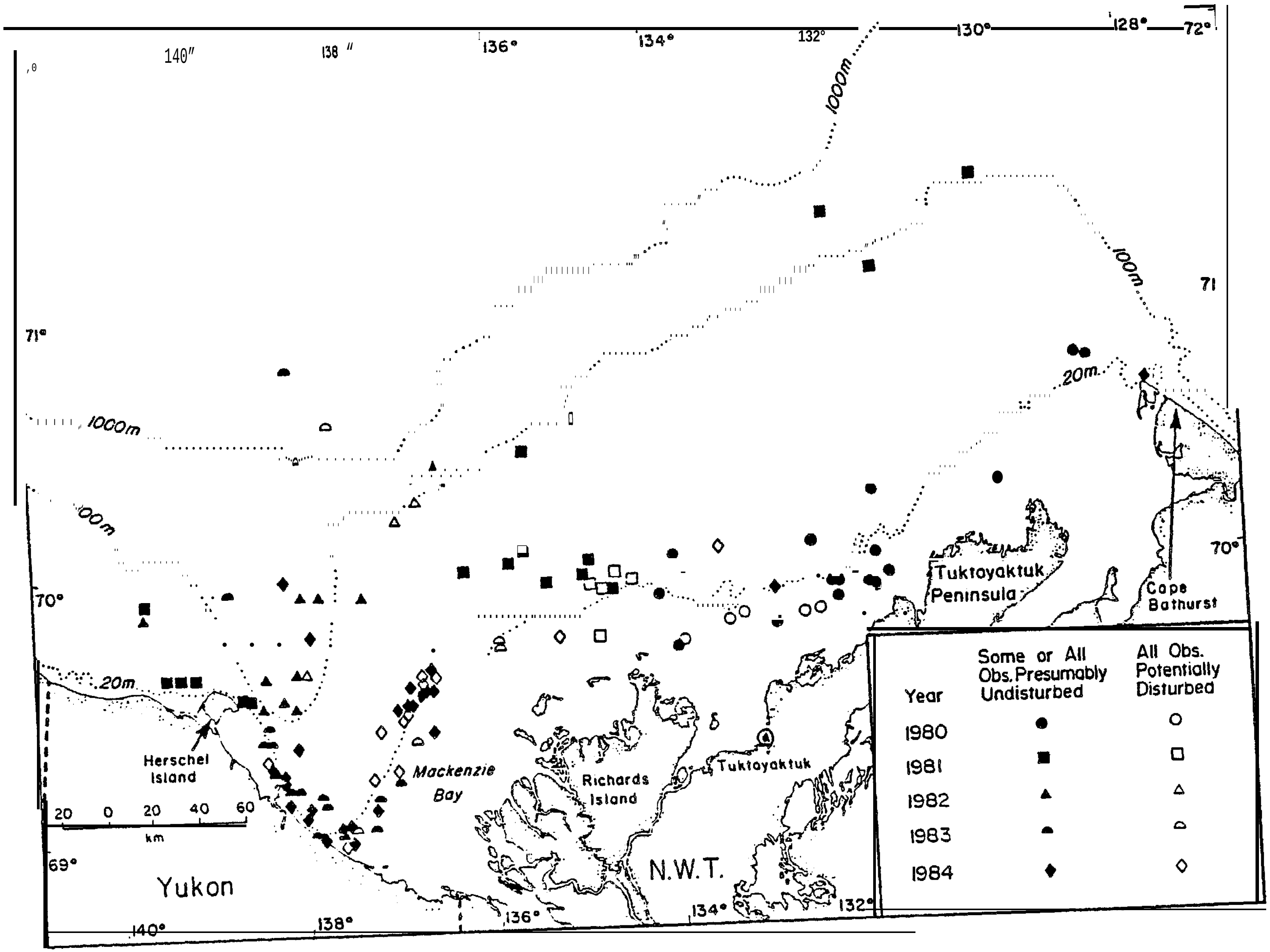
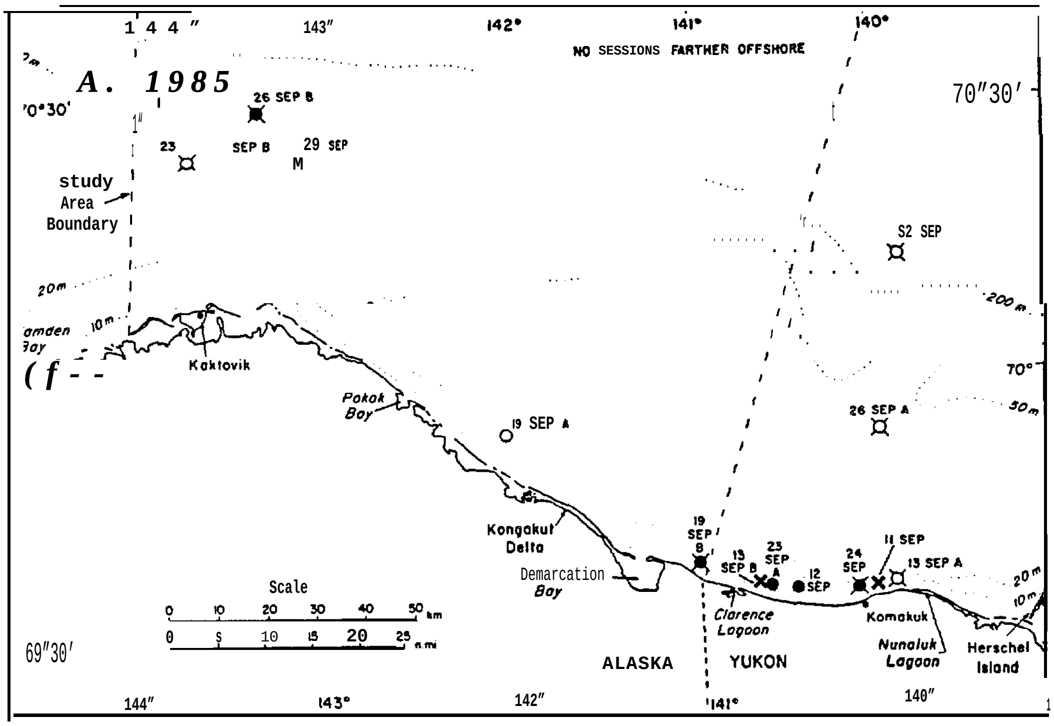


Figure 4. Eastern Beaufort Sea region showing bathymetry and locations of behavioral observation sessions. (From Würsig et al. 1985b).



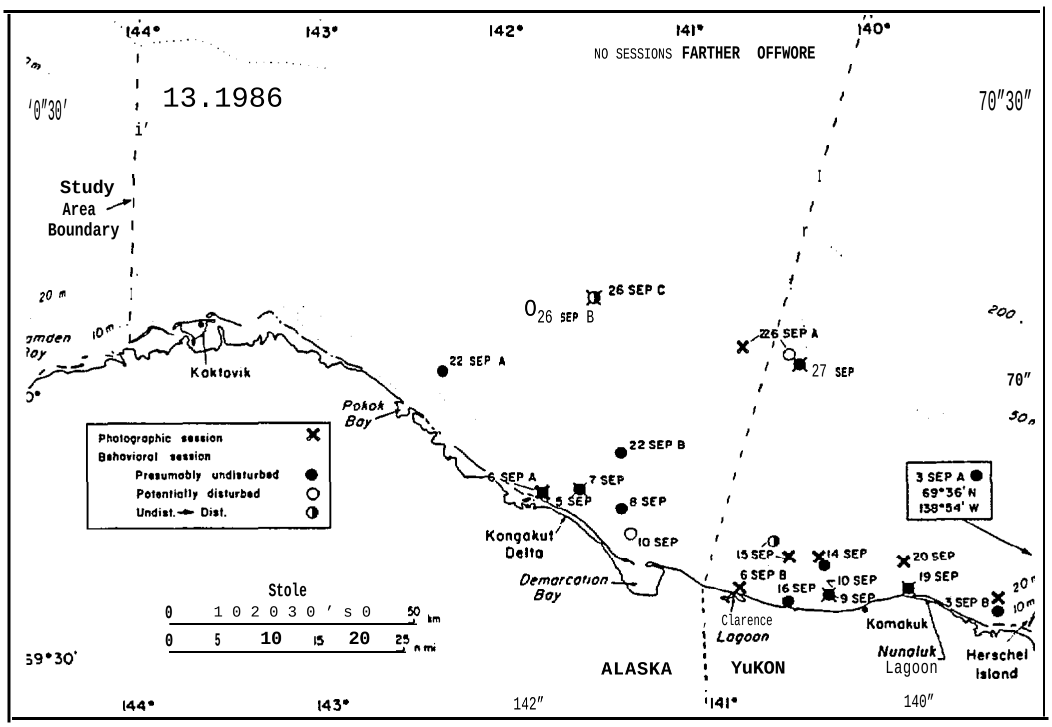


Figure 5. Locations where behavior of bowheads was observed, and where calibrated vertical photographs were acquired, during LGL/MMS bowhead feeding study, September 1985-86. When there was >1 behavioral or photo session on one date, the sessions are designated A, B and C. (From Richardson et al. 1987b).

order to supplement the rather small LGL dataset concerning migrating whales in the Beaufort Sea. The NOSC data used in the present project were collected in the Alaskan Beaufort Sea on six dates from 12 to 30 September 1983. There was extensive pack ice in the areas through which these whales were migrating. We did not consider NOSC's data on other categories of whales aside from actively migrating whales. We also did not use NOSC's data from years other than 1983, since their observation procedures differed from LGL's in earlier years, and since most whales observed by NOSC in 1984 were 'potentially disturbed'.

Eastern Arctic

The seasonal movements of bowhead whales within the Davis Strait and Baffin Bay region were summarized in the Introductions earlier. Behavioral data were collected in late summer and autumn at two locations along eastern Baffin Island: Cape Adair and Isabella Bay.

Cape Adair

Observations of the autumn migration of bowheads were conducted in 1978 and 1979 from Cape Adair, a coastal cliff over 200 m high along the coast of northeast Baffin Island (Fig. 2). Cape Adair is a promontory located midway between two fiords, Scott and Patterson Inlets. The continental shelf slopes gently to the 200 m isobath, which is about 25 km offshore from the cape. Observations from Cape Adair were conducted from a vantage-point about 209 m above sea level. Observation periods totalled

- 260.0 h from 13 Sept to 7 Ott 1978, and

- 277.4 h from 20 Sept to 16 Ott 1979 (hours when visibility <1 km excluded).

The current off Cape Adair is predominantly south-flowing with small scale perturbations induced by glacial troughs that cut across the continental shelf and temporary reversals due to countervailing wind events. Current flows vary from 12-24 cm/s (0.43-0.86 km/h) in nearshore areas to faster flows (24-40 cm/s) at the edge of the continental shelf (Fissel et al. 1982). The area was essentially ice free during the periods of observation.

Isabella Bay

Observations of bowheads in Isabella Bay have been obtained from Cape Raper, the coastal headland at the northeast corner of the bay (Fig. 6). Most data were obtained from the top of a 136 m hill about 2 km west of the tip of Cape Raper, now officially known as Balaena Lookout. Some data were obtained from Cape Raper itself. Observation periods were as follows:

- 14 Aug-18 Sept 1983 (Finley et al. 1983),
- 18 Aug-15 Sept 1984 (Finley et al. 1984, 1986),
- 17 Aug-23 Sept 1985 (Finley et al. 1986), and
- 6 Sept-9 Ott 1986 (Finley 1987).

Additional observations were obtained from 30 hug to 3 Ott 1987 (Finley in prep.). However, in 1987 the bowheads were often too far away to allow reliable shore-based observations of behavior. The 1987 data are not considered in the quantitative analyses of behavior presented in this report.

Isabella Bay is the outer extension of McBeth Fiord, a typical deeply-incised Baffin Island fiord. Maximum depths reach 560 m near the head of the fiord west of Isabella Bay, and gradually become shallower toward the mouth where there is a sill. Depths at the mouth of the fiord in Isabella Bay do not exceed 250 m. The 200 m isobath at the outer edge of the continental shelf is located about 55 km offshore from Cape Raper.

Three local bathymetric features are important in relation to the local distribution of bowheads at Isabella Bay. The first is an extensive, shallow (<30 m) bank, Isabella Bank, immediately adjacent to the observation site just inside the bay (Fig. 6). The other two features are glacial troughs that cut across the continental shelf, one located to the northeast of Cape Raper (hence NE Trough) and the other located in southeastern Isabella Bay off Henry Kater Peninsula (hence Kater Trough, Fig. 6). These troughs reach depths of 250 m. From Balaena Lookout, bowheads are readily observable when they are on Isabella Bank, and less readily observable by telescope when in the Northeast Trough. In 1986-87, bowheads were most common over the Kater Trough far from Balaena Lookout. Surprisingly, blows of whales over Kater Trough sometimes were detectable at ranges of 30 km or more when visibility and lighting conditions were ideal. On one date (6 Ott 1986) tail flukes of whales over Kater Trough were visible from Balaena Lookout. However, observations of blows or of whales at these long ranges were very incomplete and are not used in this study.

The marine system at Isabella Bay is dominated by the southward flowing Baffin Current. Interactions of the Baffin Current with the bathymetry and the tidal currents of the fiords establish ephemeral small-scale circulation features such as eddies observed at the mouth of Isabella Bay. Although the tidal amplitude is low (1.2 m) at Isabella Bay, the tidal bore characteristics of the fiord basin enhance the flooding and ebbing regime.

The highly variable wind regime also affects surface currents, and possibly the availability of zooplankton to bowheads. Intermittent wind-induced changes in surface currents may occur over a period of a day or several days. Wind trajectories and storm tracks are hi-directional--either northerly or southerly, depending on the specific position of a quasi-stationary, upper atmospheric trough that tends to be situated over Baffin Island (Maxwell 1982). The alignment of the shallow continental shelf parallel to the prevailing wind enhances wind forcing. The prevailing southward-flowing surface current may be enhanced by northerly winds or retarded by southerlies (Fissel et al. 1982). The average surface flow rate varies considerably between years, e.g. 0.57 km/h in 1985 vs. 0.95 km/h in 1986, depending on prevailing wind regimes (Finley et al. 1986).

Generally the last of the Baffin Bay pack ice fields disintegrate in late summer in the coastal region between 68° and 70°N. In some years, such as 1983, the pack ice fields can remain throughout the year. In other years such as 1985 the pack ice may be gone by early August. In most years the pack ice is

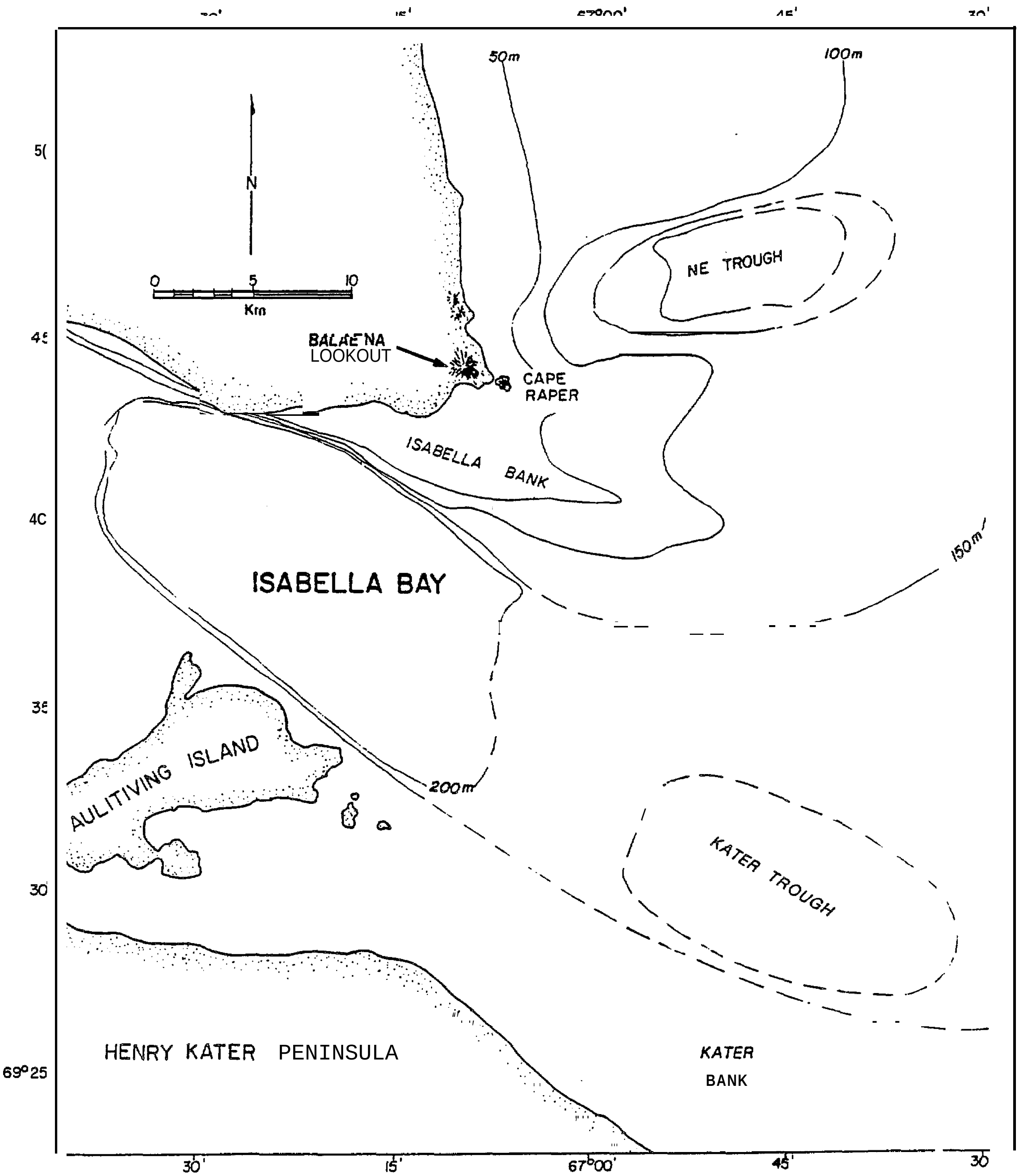


Figure 6. Isabella Bay study area showing bathymetric contours (50 m intervals). The extent of the Kater Trough is not well known. (From Finley 1987).

gone by late August. After the pack ice has disappeared, high waves and swells are common at Isabella Bay. New ice usually begins forming in mid October. Icebergs are always present in the area, either drifting southward or grounded. Icebergs grounded on the tip of Kater Bank create a distinctive 'berg patch'.

METHODS

Western Arctic

Similar aerial observation methods were employed during all four of the studies whose data are considered here. The specific details of the observation procedures employed during each study and each year are given in the previously-cited reports of the individual studies. The following is a general summary of the standard procedures.

Bowheads were located by aerial reconnaissance techniques. While searching for bowheads to observe, we usually flew at 457 m (1500 ft) above sea level to avoid or at least minimize aircraft disturbance as the aircraft arrived over whales. In a few cases the aircraft was at a lower altitude when whales were first encountered, but climbed to ≥457 m for observations. If the aircraft flew over or near the whales while below 457 m, the subsequent observational data were not considered to be 'presumably undisturbed' until the aircraft had been at >457 m for 30 min.

All Western Arctic data considered here were acquired from twin-engine high-wing aircraft that could circle tightly and continuously for several hours at low speeds. Almost all 1980-84 summer data were acquired from a Britten-Norman 'Islander' aircraft, which has piston engines. A few 1983 summer data plus all 1985-86 autumn data were acquired from de Havilland Canada DHC-6 'Twin Otter' aircraft, which have turboprop engines. The NOSC autumn 1983 data on migrating whales were collected from a Grumman Goose re-engined with turboprop engines and from a Twin Otter. All aircraft were equipped with Very Low Frequency navigation systems with latitude-longitude readouts.

Observations were concentrated on a focal group of whales in order to obtain detailed information on the behavior of one or more specific individuals over as long an observation period as possible. Although we collected some information on other whales in the area, especially when the focal whales were below the surface, much effort was given to remaining over the focal group for as long as possible.

Observation procedures during the four studies were very similar; there was considerable overlap in the field crews between years and studies to provide continuity and standardization. In the absence of distinctive ice pans and other natural markers of position, we dropped a fluorescein dye marker to create a fixed reference point about which to circle when bowheads were below the surface. From 1981 onward, there were almost always four observers in the aircraft: two to describe behaviors, a third to videotape whales for a permanent record and to provide supplementary direct observations, and a fourth to operate sonobuoy receivers and other equipment. When one or more whales of the focal group was at the surface, one of the two primary observers observed them through binoculars to obtain detailed data on respiration and other behaviors. The second primary observer observed without binoculars to obtain a broader perspective, e.g. to record distances from other whales, directions of movement, etc. All observers plus the pilot were in continuous communication via intercom, and behavioral information was recorded onto audio and video tape recorders by taping the intercom signal.

Behavioral and related data dictated by the observers included the following:

1. Location, from which approximate water depth was determined later from charts;
2. Time (to the second);
3. Number of individual bowheads visible in area; number of calves;
4. Individually distinguishing features (if any) on focal whales;
5. Heading (°True), turns, and estimated swimming speed of focal whales;
6. Distances between focal whales (estimated in adult whale lengths);
7. Durations of time at surface and of dives for focal whales;
8. Timing (to the second) and number of respirations (blows) of focal whales;
9. Indications of feeding, e.g. open mouth, mud streaming from mouth, defecation;
10. Socializing; probable mating;
11. Probable nursing (cow-calf pairs);
12. Play with logs or surface debris;
13. Underwater blow (release of a large burst of air bubbles underwater);
14. Aerial activity: breaches, tailslaps, flipper slaps, lunges, rolls;
15. Behavior at start of dive: fluke out? peduncle arch? pre-dive flex?

Stringent criteria for acceptability of data were applied during all four studies[3]. For example, durations of surfacings were counted only when the whale was actually seen surfacing and diving. We did not assume that the first and last blows of a surfacing represented the times of surfacing and diving,

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[3] The 1983 NOSC data on migrating whales were re-evaluated by LGL so that criteria for inclusion of these data in the present analyses were the same as those applied during the three LGL studies.

since bowheads are often at the surface for a few seconds before the first blow and after the last one. Often it is uncertain how long a whale has been at the surface before it is first seen. When the time of 'first surfacing' was not known with certainty, the duration of the surfacing was not estimated. The duration of the preceding dive was estimated only if the dive was long enough and the uncertainty small enough to ensure that the dive duration could be estimated within ± 5%. The number of respirations per surfacing was recorded only when the whale was in clear view throughout the surfacing, without any possibility that a blow was missed when the 'line' of reflected sun glare swept across the animal as the observation aircraft circled overhead.

During all four studies, naval sonobuoys (AN/SSQ-41B or -57A) were dropped into the water during most observation sessions. Sonobuoys detected the calls of the bowheads as well as any sounds from distant industrial activities (e.g. seismic exploration) that might be affecting the animals. The acoustic data were telemetered by the sonobuoys to the observation aircraft, where they were recorded onto a continuously running tape recorder. When there were strong sounds from industrial activities, the whales were categorized as 'potentially disturbed' and the associated data are not considered here.

Behavioral data were transcribed from audio tape onto data sheets either between flights or after the field season. After the audiotapes were transcribed, the videotapes were reviewed to provide supplementary data on points not noticed or dictated in real time. During the three LGL studies, the combined transcribed data were then coded into a standard numerical format containing one line of data (one record) for each surfacing or dive of a focal whale. The format of the records differed slightly among years, increasing in length from 42 fields of data in 1980-81 to 45 fields in 1983-86. The coded data were entered into Apple II microcomputers, proofread, and checked for impossible or implausible data by range-checking and validation programs. The validation program performed many checks within and between records to identify any inconsistencies in identification data, time sequences, heading/turn data, and various other variables. All questionable items identified by the validation program were hand checked and corrected where necessary.

During the 1980-84 LGL/MMS study, there were a total of 132 offshore flights totalling 593 h. We circled over bowheads for 186.3 h during 85 of those flights. Of this observation time, about 98.5 h was under presumably undisturbed conditions (Fig. 4; Würsig et al. 1985b; Dorsey et al. in press). During that study, we collected at least partial data on 4337 surfacings and 958 dives, of which 2129 and 475, respectively, were from presumably undisturbed periods.[4]

During the 1985-86 LGL/MMS feeding study, we circled over whales and observed their behavior on 28 occasions totalling 32.5 h from 3 to 29 September. Part or all of 20 observation sessions was considered to represent 'presumably undisturbed' whales (Fig. 5; Richardson et al. 1987b). of the 679

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[4] This undisturbed/disturbed breakdown represents the numbers as originally recorded. A few borderline cases were reclassified during the present study.

surfacings and 69 dives for which data were obtained, 472 and 33 (respectively) were considered 'presumably undisturbed'[4].

During the 1986 LGL/Shell Western study (Koski and Johnson 1987), 'presumably undisturbed' data were collected during part or all of seven observation sessions. Of the 250 surfacings and 109 dives for which data were obtained, 125 and 54 were considered 'presumably undisturbed'[4].

During the two LGL studies in 1985-86, calibrated vertical photographs of many whales whose behavior had been observed were taken immediately after most behavioral observation sessions, using the photogrammetric methods of Davis et al. (1983). This provided data on the sizes and individual identities of many of the whales. Photogrammetry was not attempted after observation sessions in 1980-84, but sizes of whales in some parts of the study area were determined during separate photogrammetry projects in 1981-84 (Koski et al. 1988).

During the 1983 NOSC study (Ljungblad et. al. 1984b), field procedures were similar to those in the three LGL studies; B. Würsig supervised the collection of behavioral data in the NOSC study as well as during 2 of 3 LGL studies. NOSC's behavioral data were transcribed onto the same type of datasheet as used by LGL.

Eastern Arctic

Cape Adair

Autumn migration of bowhead whales along the northeast coast of Baffin Island was observed from a coastal cliff (elevation about 209 m asl) at Cape Adair (71°30'N, 71°35'W, see Fig, 2) in 1978 and 1979. Observations extended from 13 Sept to 7 Ott 1978 (total of 260.0 h observation--Koski and Davis 1979) and from 20 Sept to 16 Ott 1979 (total of 277.4 h observation when visibility exceeded 1 km--Koski and Davis 1980). In both years observations extended throughout most hours of daylight when visibility exceeded 1 km. Observations were made with the aid of binoculars, telescopes and a theodolite. The vantage point allowed good visibility for up to 3 or 4 km offshore, 0.5 km to the northwest, and 2+ km along the coast to the southeast.

When migrating bowheads were seen, the numbers, presence of calves, swimming directions, durations of surfacings and durations of dives were noted. In 1979, the times of most respirations were also noted, from which the number of blows per surfacing and intervals between successive blows could often be determined. The theodolite was used to determine whale positions during surfacings. From these data, distances from shore, distances travelled underwater> and net speeds of travel were determined for the 1979 migration.

During both years, the primary purpose of the Cape Adair study was to assess the routes and timing of the bowhead migration and the numbers of whales involved. Behavioral observations were collected incidentally to these main objectives. The behavioral data were not always recorded in a systematic way, especially in 1978. Based on a re-examination of the original field data, we decided that the 1979 behavioral data could be compared with the data collected elsewhere in later years, but that the 1978 data were not comparable.

Accordingly, only the 1979 data from Cape Adair are used in this retrospective analysis. The 1979 data on migrating whales at Cape Adair were coded into a standard numerical format[5] during the present study, based on the original field data. The coded 1979 data included information on 143 surfacings and 131 dives, all collected under 'presumably undisturbed' conditions.

Isabella Bay

Shore-based Observations.--Most observations of bowheads and oceanographic phenomena at Isabella Bay were made from the peak of Balaena Lookout, a large hill 2 km west of Cape Raper at the northeast corner of Isabella Bay (69°44'N, 67°07'W). This site provided a strategic, wide range of view (280°) over most of Isabella Bay and north along the coast of Baffin Island (Fig. 5). During the four years considered here, observations began on dates ranging from 14 August to 6 September, and ended between 15 September and 9 October, for an average duration of 34 days (range 29-38 days).[6]

Observations were made with the aid of binoculars and a theodolite (usually a Wild T16). The theodolite was mounted on Balaena Lookout at an elevation of 136.2 m above sea level either on a tripod or, in 1985-86, on a permanent concrete pillar. The theodolite was used to determine positions of whales, oceanographic features, zooplankton and bathymetric stations, and kayak-based observers during underwater recording sessions. There were usually two, and sometimes three, observers. Observations with the theodolite usually were dictated into a tape recorder (1983-84) or to the other observer(s) who recorded them in field notebooks (1985-86).

Two behavioral sampling techniques were employed: focal-animal and scan sampling (Altmann 1974). During focal-animal sampling, the activities and positions of a recognizable individual, pair or group of whales were described for as long as possible (usually 3-8 h). Scan-sampling was conducted on an opportunistic basis depending on other sampling priorities but usually once a day. During scans we determined the positions of all visible whales and observed them for a sufficient period (generally ½-1 rein) to assign them to one of the following general behavioral categories:

1. directed swimming, including direction,
2. resting,
3. socializing, including group size, type of display (e.g. contact, tail loft, tail slap, etc.),
4. feeding, including orientation to surface features, and avian associations.

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5 See 'Quantitative Analyses of Behavior', below, for coding format.

6 See 'Study Area, Periods & Ice' section for specific dates.

During scan sampling, two positions were usually taken for each moving whale to determine its bearing and speed.

Boat-based Observations.--Occasionally observations were conducted in close proximity to bowheads from a kayak equipped with a compact 2-channel audio recorder (Pioneer PK-R7AW) that recorded signals from a hydrophore (modified from AN/SSQ-57A sonobuoy) on one channel and voice input on the other. When possible during underwater recording sessions, the positions of the kayak and whales were determined from the shore-based theodolite.

Zooplankton Sampling.--Zooplankton was sampled by vertical and horizontal net tows. Sampling was conducted at various locations in the Isabella Bay area at the beginning of the study, but became focussed in one area, the NE Trough, when the feeding patterns of the bowhead became known. Sampling also was conducted in a control area where bowheads did not feed. Weather and other priorities permitting, zooplankton sampling was conducted from a 7.5 m 'Lake Winnipeg' boat, which was directed to sampling stations by establishing positions with a theodolite and relaying messages via two-way radios.

Horizontal tows were obtained with Miller samplers (0.5 mm mesh) at depths between 5 and 75 m at various locations in Isabella Bay. Tows generally were conducted for 10 min at about 0.9 m/s. The volume filtered was estimated using mouth area (0.008 m^2) and readings from a flow meter.

Vertical hauls were obtained with a 0.5 m diameter plankton net (0.5 mm mesh) hand-winched at about 0.6 m/s to the surface. In 1986, samples were stratified into two depth layers, usually 0-100 m and 100-200 m, by means of net release messengers. For comparison, samples were collected in a known feeding area (the NE Trough) and in a deep area of Isabella Bay where feeding was seldom observed. Volume of water filtered was estimated using the mouth area of the net (0.1963 m^2) and depth of haul.

Aerial Photogrammetry.--Bowhead whales were photographed at Isabella Bay in 1986 using the vertical photographic technique of Davis et al. (1983). [Additional vertical photographs were obtained in 1987, but the results are not yet available.] Aerial photographs were taken through a camera port in the floor of DHC-6 'Twin Otter' aircraft. The camera was a hand-held, medium-format (6x7 cm) Pentax camera equipped with a 105 mm f2.4 lens and Kodak Ektachrome 200 color reversal film. An altitude as close as possible to 145 m was maintained by radar altimeter during photographic sessions.

Previous Analyses of Isabella Bay Data.--The objectives of the Isabella Bay project emphasized conservation issues, involvement of local Inuit, and the present and historic utilization of the study area by bowhead whales (Finley et al. 1983, 1984, 1986; Finley 1987). Those reports contain considerable information on the numbers of bowheads present, their local distributions and general activities in the area, their speeds of movement during various activities, the zooplankton data, and the approximate sizes and age-classes of the whales. Some of those types of information are summarized in this report based on the results already presented by Finley et al. (1983-86) and Finley (1987).

Only a limited analysis of the behavioral and acoustic observations was possible within the scope of the original Isabella Bay study. The behavioral data from Isabella Bay were not coded into a standard numerical format until the present study (see next section). The total numbers of records (surfacings and dives) now coded for the years 1983-86 were 28, 1278, 284 and 119, respectively (total 1709). The low number in 1983 reflected the fact that only two whales were seen, both on one day, during 1983. Many whales were present close to the observation site in 1984. Many whales were also present in 1985, but less emphasis was placed on collection of detailed surfacing, respiration and dive data that year. The low sample size for 1986 reflects the fact that most of the whales present spent most of their time too far away from the observation site to be observed in detail during 1986.

Quantitative Analyses of Behavior

Standardized Behavioral Data Format

At the start of this project, the existing behavioral data files for the three LGL projects in the Western Arctic were transferred via serial interface from an Apple 11 to an IBM-compatible microcomputer. All subsequent manipulations and analyses were done on the latter type of computer.

For purposes of statistical analysis, it was necessary that the numerical data from both bowhead stocks be organized into a consistent and suitable format. The data format used previously by LGL for the Western Arctic data met many but not all of the requirements. Besides behavioral data, the existing Western Arctic data files included date, time, disturbance situation, water depth, and whale status (e.g. large, small, mother, calf). However, the files did not include the exact location of each observation, distance from shore, sea state, ice cover, number of whales in the area, size composition of the whale group (subadults, adults, mixture), or predominant group activity. Most of these types of data are either constant for each observation session or change only at infrequent intervals. Most of this information was available in unpublished files from the original Western Arctic projects. These data were compiled and added to the behavioral data files as additional variables.

The same program that merged the additional data into the existing behavioral data files also converted the files into a more workable, versatile and logical format (Table 1). The Western Arctic data were almost all acquired via aerial observation techniques. In contrast, the unanalyzed Eastern Arctic data were almost all acquired from clifftop observation sites, often via theodolite tracking. Theodolite methods sometimes provided data on swimming speeds and net distances travelled during surfacings and dives. To make maximum use of those data, the revised data format includes provision for these additional variables when known. Thus, the new file type can be used without further changes in future studies of bowhead behavior, whether aircraft-, shore- or ice-based.

In contrast to the already-coded LGL data from the Western Arctic, the NOSC data on migrating whales seen in 1983 and the LGL Eastern Arctic behavioral data had to be compiled and coded during the present project. These data were coded directly into the new data format (Table 1). For the Eastern Arctic, some previously-untranscribed audiotapes of behavioral dictation had

Table 1. Variable list--new coding format for bowhead behavioral data.

First Record Format (RECTYP 0): Includes fields that are constants (or change infrequently) within an observation session.

Field	Width	Meaning
RECTYP	1	RECord TYPe: always 0 on header records of this format
DATE 1	6	Local DATE
TIME1	6	Local TIME when these RECTYP 0 data begin to apply
GROUP 1	2	Lowest whale GROUP number for this RECTYP 0
ID	3	Whale Identification no.: always 000 on RECTYP 0
TIME2	6	Local TIME when these RECTYP 0 data cease to apply
GROUP2	2	Highest whale GROUP number for this RECTYP 0
PROJ	2	PROJect no.
PLATF	1	Observation PLATForm type
FLIGHT	2	FLIGHT number (within YR and PROJ)
OB.SES	3	Observation SESsion no. (within YR and PROJ)
PHOTOS	1	High-resolution PHOTOS taken?
TZONE	2	Time ZONE correction, in hours behind GMT
LAT	4	LATitude of ohs. site
LONG	6	LONGitude of ohs. site
AREA	2	Project-specific AREA for this RECTYP 0
SEA. ST	1	SEA STate, 0-8 scale. 9=unknown
ICE.PC	3	Ice cover in percent within about 1 km
GR. ICE	1	GRease ICE within 1 km
G. CALF	1	Group/CALF composition
G.NONC	1	Group NONCalf composition
G.ACT	1	Group's predominant ACTivity
G.FEED	1	Group's predominant FEEDing mode
N, 1KM	2	No. whales within approx. 1 km
N. AREA	3	No. whales within approx. 10 km
ALT	3	ALTitude of observer (or aircraft) in metres
DISTUR	1	Overall Disturbance situation
D.AIRC	1	Potential AIRCraft disturbance
D.BOAT	1	Potential BOAT disturbance; exclude seismic boats
D.SEIS	1	Potential SEISmic disturbance
D.SITE	1	Potential disturbance from stationary SITE
D. OTHR	1	Other potential disturbance types
PLBKTY	1	Playback Type
PLBKPH	1	Playback Phase

Second Record Format (RECTYP 1-5): Used to code individual surfacings, dives and indications of whale presence (mud spots, defecations, underwater blows).

Field	Width	Meaning
RECTYP	1	RECord TYPe: 1 = surfacing, 2 = dive, etc.
DATE	6	DATE: yr (last 2 digits), mon (01-12), day (01-31)
TIME	6	TIME: Hr (00-23), Min (00-59), Sec (00-59)
GROUP	2	Whale GROUP number within OB.SES
ID	3	Whale Identification number within OB.SES
SEQNUM	2	SEQuence NUMber in sfcing/ dive sequence by known whale

Continued. . .

Table (Concluded).

Field	Width	
STATUS	1	Whale STATUS (calf, mother, small, large, etc.)
LENGTH	3	Whale LENGTH as determined by photogrammetry
NBLOWS	2	Number of BLOWS during surfacing
LENSFC	4	LENgth of SurFaCing, in sec.
HEAD	2	HEADing
TURN	1	Occurrence and type of TURN during surfacing
DEGTUR	2	DEGree of TURn during surfacing
MOTION	1	Generalized speed of MOTION during surfacing
W.ACT	1	Whale ACTivity
W.FEED	1	Type(s) of whale FEEDing indications
W.BEH1	2X2	Behavioral events during this sfcing or dive.
W.BEH2	1	Code first event as W.BEH1; if 2 events occurred, code second in W.BEH2
GRPSIZ	2	GRouP SIZe (within 5 whale-lengths)
SOCIAL	1	SOCIAL interaction?
AERIAL	1	AERIAL behaviour?
FLEX	1	Pre-dive FLEX at end of sfcing/start of dive?
FLUKES	1	FLUKES out at end of sfcing/start of dive?
LENPRE	4	LENgth of PREceding dive by this individual
LENSUB	4	LENgth of SUBsequent dive by this individual or, on dive records, LENgth of this Submergence
KMSHOR	3	Distance of whale from SHORe
DEPTH	4	Water DEPTH, in m
W.BEAR	3	BEARing of whale from observation site
W.KM	3	Distance of whale from observation site
NETSPE	1	NET SPEed during surfacing or dive, in km/hr
NETDIS	2	NET DIStance travelled during surfacing or dive
D.BEAR	2	BEARing from predom. source of Disturbance to whale
D.KM	3	km from predom. source of potential disturbance

Additional RECTYP 1 Variables Generated by Computer from RECTYP 6-7

Field	Width	Meaning
INITBI	3	INITial Blow Interval of the surfacing, in sec
LASTBI	3	LAST Blow Interval of the surfacing, in sec
MEANBI	4	MEAN Blow Interval during surfacing
BISUM	4	SUM of all Blow Intervals during surfacing
BISS	6	Sum of Squares of all Blow Intervals during sfcing
BIN	2	Number of Blow Intervals measured during this sfcing

Third Record Format (RECTYP 6,7) Blow intervals during whale surfacings; follows the RECTYP 1 (surfacing record) with which it is associated

Field	Width	Meaning
RECTYP	1	RECord TYPe: 6 for BI 1-20; 7 FOR BI 21-...
DATE	6	DATE, as on immediately preceding RECTYP 1
TIME	6	TIME, as on immediately preceding RECTYP 1
GROUP	2	Whale GROUP number, as on immed. preceding RECTYP 1
ID	3	Whale Identification no., as on immed. preced. RECTYP 1
BI1-BI20	20x3	Blow Intervals: spaces to record up to 20 BIs

to be transcribed. Other data were collated from previous reports, field notebooks, dataforms, computer printouts of whale positions and speeds as determined from theodolite data, and bathymetric charts.

The newly-coded Eastern Arctic and NOSC data were entered into an IBM-compatible microcomputer, proofread, and subjected to a range-checking and validation program. The validation program was an improved version of the Apple II program developed during an earlier project for MMS, with major revisions

- to allow operation on IBM-compatible computers,
- to accommodate the revised and expanded data format, and
- to include additional cross-checks that are possible and desirable given the new format.

Apparent discrepancies detected by the computer were reviewed manually and necessary corrections were made.

The new validation program was also applied to the converted LGL Western Arctic data. This confirmed that the format conversion and addition of new data had been done as planned.

Selection of Compatible Data Subsets

Previous analyses of the behavior of Western Arctic bowheads in summer and autumn have shown that the surfacings respiration and diving cycles as well as other aspects of behavior are quite variable. Much of this variability is attributable to inherent variability of behavior among individual whales and within individuals over time. However, many aspects of behavior are correlated with

- the environmental circumstances (water depth, ice cover, date, etc),
- the activities of the whales (e.g. feeding at depth vs. at surface, socializing, traveling), and
- the size and status of the whales (e.g. subadults, adults, mothers, calves).

The main studies in which these relationships have been investigated are Ljungblad et al. (1984b), Würsig et al. (1984a, 1985b), Richardson et al. (1987 b), and Dorsey et al. (in press). Behavior can also be affected by proximity to various human activities.

In this project, it was important to compare the normal behavior of the two stocks of bowheads under conditions when environmental circumstances, whale activities, and whale status were as similar as possible. Only by standardizing the data in this way is it possible to examine the possibility that the overall behavior of the two stocks differs. Thus, it was necessary to select subsets of the Western and Eastern Arctic data that would be as comparable as possible.

Review of data from the two regions indicated that meaningful samples from ‘presumably undisturbed’ whales might be available for four circumstances:

whales feeding in deep water,
whales socializing in shallow water,
- whales engaging in local travel, and
whales migrating in early autumn.

For each of these four activities, we defined a tentative selection procedure based on the variables available in the behavioral data files (Table 1). At this stage, we purposely kept the selection criteria broad to ensure that sample sizes were as large as possible. Despite this, the sample size for local travel in the Western Arctic was negligible. However, there was a considerable quantity of information about whales engaged in local travel at Isabella Bay. Hence, we decided to analyze the local travel subset from the Eastern Arctic as well as the other three subsets from both regions.

Next we summarized the distributions of all behavioral and environmental variables for each of the four Eastern Arctic and three Western Arctic subsets of data. This provided information about the comparability of the eastern and western data for each category of whales. Based on these preliminary comparisons, we made minor refinements in the criteria for selecting data subsets. The final criteria were as follows:

Whales feeding in deep water:

- no known disturbance source nearby,
- water depth >50 m (since feeding was rare in shallower water at Isabella Bay),
- mothers and calves excluded (since neither occurred at Isabella Bay),
- group activity = feeding, travel + feeding, or socializing + feeding,
- not actively socializing during current surfacing or dive,
- predominant feeding mode = water column feeding (i.e. exclude near-surface and near-bottom feeding cases, which did not occur at Isabella Bay).

Whales socializing in shallow water:

- no known disturbance source nearby,
- water depth ≤50 m (since socializing was rare in deeper water at Isabella Bay),
- mothers and calves excluded,
- group activity = socializing, travel + socializing, or socializing + feeding.

Whales engaged in local travel (Isabella Bay only):

- no known disturbance source nearby,
- mothers and calves excluded (neither occurred at Isabella Bay),
- group activity = travel,
- exclude traveling whales seen at Isabella Bay on 5-7 Ott 1986, which were migrating.

Whales engaged in migration:

- no known disturbance source nearby,
- mothers and calves excluded,
- group activity = travel,
- dates restricted to those when all traveling whales were engaged in long-distance travel. In east, this included all Cape Adair observations plus traveling whales seen at Isabella Bay on 5-7 Ott 1986. In west, this included all traveling whales seen after 11 September.

Once these final criteria for the data subsets were determined, we summarized the behavior of the whales engaged in each activity in the Eastern Arctic and, separately, the Western Arctic. For each of the seven subsets of data (4 eastern, 3 western), we re-summarized the data for each variable and determined the correlation matrix among variables. Also, for each of the seven data subsets, multiple regression analysis was performed to investigate the factors affecting durations of surfacings and dives, number of respirations (blows) per surfacing, and intervals between successive blows. All analyses were performed with BMDP statistical software running on an IBM-compatible microcomputer and working directly with the behavioral data files.

Blow interval data were analyzed in a slightly different fashion during this study than during most previous analyses for bowheads. A blow interval is the time in seconds between two successive respirations within a single surfacing. Depending on the number of blows during a surfacing, there can be no blow intervals (if zero or one blow), one blow interval (if 2 blows), or >1 blow intervals (if >2 blows). In this study, regardless of the number of blows during a surfacing, each surfacing with >1 blow interval contributed one value--the mean of all blow intervals docume-nted during the surfacing--to the analysis. During previous studies, most analyses of blow intervals treated each blow interval individually. (The multiple regression analyses of Würsig et al. 1985b, p. 50; Richardson et al. 1985b, p. 138; 1986; and Dorsey et al. in press were exceptions; they were based on the same 'mean blow interval' method used here.) The present approach has the advantage of reducing the 'lack of independence' problem associated with multiple observations on the same individual animal (Machlis et al. 1985; Hoekstra and Jansen 1986). Because the mean blow interval values analyzed here are means, their standard deviations are expected to be lower than would be the case based on individual blow intervals. Also, the sample size will be considerably smaller.

During multiple regression analyses of surface times, dive times, mean blow intervals, and number of blows per surfacings all four of these dependent variables as well as two of the predictor variables (water depth and distance from shore) were log-transformed to avoid statistical problems associated with the skewed distributions. Skewing was less severe for feeding whales than for other categories of whales. However, for consistency, the log transformation was applied in all cases. We examined scatter plots of residuals vs. all predictor variables (Draper and Smith 1981) to ensure that the transformation procedure was appropriate and successful.

Collectively, the various types of analysis were used to characterize the behavior of the whales engaged in feeding in deep water, socializing in shallow water, local travel (Eastern Arctic only), and migration. No such analyses have been done previously for either the Eastern or Western Arctic stock. Most previous analyses of Western Arctic data have considered all 'presumably undisturbed' whales without distinguishing the subsets of whales identified above.[7] Also, no previous analysis of Western Arctic data has combined the results from the three different behavioral studies conducted by LGL over the 1980-86 period.

Comparison of Behavior in Eastern and Western Arctic

For each of the three data subsets available from both the Eastern and the Western Arctic, we compared various behavioral variables using univariate and multivariate methods. The multivariate approach had the advantage of allowing us to take account, to some extent, of differences in environmental conditions between the two regions. We used a multiple regression approach to determine the significance of differences in durations of surfacings or dives between the two regions after allowing for any differences attributable to water depth, ice cover, and so on. This approach provided a way to allow, at least in part, for unavoidable differences between environmental conditions between the Eastern and Western arctic. Again, BMDP software was used for all analyses, and the transformation and 'analysis of residuals' procedures mentioned above were applied.

Data On Bowhead Calls

Data on the call types and call rates of Western Arctic bowheads on the summer range in the Canadian Beaufort Sea were obtained during 1980-84. Many of these data pertain to undisturbed whales (Würsig et al. 1985b, p. 58-67). For each behavioral observation session when calls were recorded via sonobuoy, the number of calls of each of seven standard call types was determined by C.W. Clark following his standard system for categorizing bowhead call types (Clark and Johnson 1984).

For comparison, bowhead calls and other bowhead sounds recorded opportunistically at Isabella Bay in 1984-87 were analyzed by C.W. Clark and KJF during the present study. Four recording sessions totalling 3.0 h in duration provided tapes containing large numbers of sounds--one session in 1984, one in 1985, and two in 1987. (These 1987 acoustic data are the only 1987 data considered in this report.) Tapes were converted into continuous hardcopy spectrographs with an overall frequency range of 0-3500 Hz. Thereafter all tapes were listened to twice at normal speed while following the details of the hardcopy spectrographs. By this procedure, all bowhead sounds were noted, and each sound was judged as being either a call or a physical sound (slap, blow or 'cr-unch'; see Results). Whenever a call was heard, it was categorized into one of the seven call types recognized in previous Western Arctic studies. In general, signal levels for the bowhead

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7 Calves or mothers + calves usually have been treated separately in earlier studies; they are excluded altogether here, since they were rarely present at our observation sites in the Eastern Arctic.

sounds at Isabella Bay were relatively high due to the close proximity of the hydrophore to the vocalizing whale(s). In several cases many of the very loud sounds saturated the recording system and were partially distorted.

RESULTS

Behavior in Eastern Arctic

General Utilization of Isabella Bay

Seasonal Utilization.--During the late summers of 1984-86, bowheads were seen in Isabella Bay on virtually every day of adequate visibility (Fig. 7). In 1983 only two bowheads were seen; this was thought to be due to the unusual presence of the Baffin Bay pack-ice offshore from Isabella Bay throughout the 1983 season (Finley et al. 1983). In 1984-85, when observations began in mid August, a few whales were present by the date observations began. Small numbers of bowheads were present on most if not all days in the latter half of August 1984-85 (usually <10 on any day; never >15). More bowheads arrived in September. In September 1984-86, 20-45 whales typically could be seen on days of good visibility. Larger numbers were counted during systematic scans of the bay on two occasions: 66 whales on 14 Sept 1984 and 68 whales on 23 Sept 1985. Those were the last dates of observation in 1984 and 1985, so it is possible that even larger numbers appeared later in those years. In 1986, when observations extended to 9 October, the maximum number counted from shore was 34 bowheads on 26 September, but this is a minimum because the whales were usually near the Kater Trough, too far away to be counted accurately. In 1986, whales were present until at least 9 October, the last day of observations. At least 23 were present as late as 7 October, the last observation date with good visibility (Fig. 7C).

It is suspected that the bowheads arriving at Isabella Bay in mid-late September were whales that had spent the late summer period nearby. There is no evidence that they were autumn migrants from summering areas around northern Baffin Island. The only evidence of active southward migration recorded at Isabella Bay during the study periods in 1983-86 involved five whales that were swimming steadily southward past the bay on 5-7 October 1986; 1986 was the only year (in the 1983-86 period) when the Isabella Bay study extended into October. Similarly, aerial surveys around north Baffin Island and shore-based studies at Cape Adair during 1975-79 indicated that there is little southward migration of bowheads until around 1 October (Johnson et al. 1976; RRCS 1977; Koski and Davis 1979, 1980).

Population Segregation.--Aerial photogrammetry conducted on 28-29 Sept 1986 showed that Isabella Bay is used primarily by large adult bowheads not attended by calves (Fig. 8). The mean length was 14.4 m (n = 83). Fully 89% of the whales were >13 m long, which is about the minimum size of mature females --at least in the western arctic population. The few whales smaller than 13 m present in 1986 were mostly large subadults (11½-13 m), but one small subadult was photographed (Fig. 8). Similarly, the whales present in other years were believed to be mainly adults or large subadults. One cow (15 m) attended by a 6 m calf was photographed in 1986. This was the only cow-calf pair seen at Isabella Bay during the 1983-86 study period.

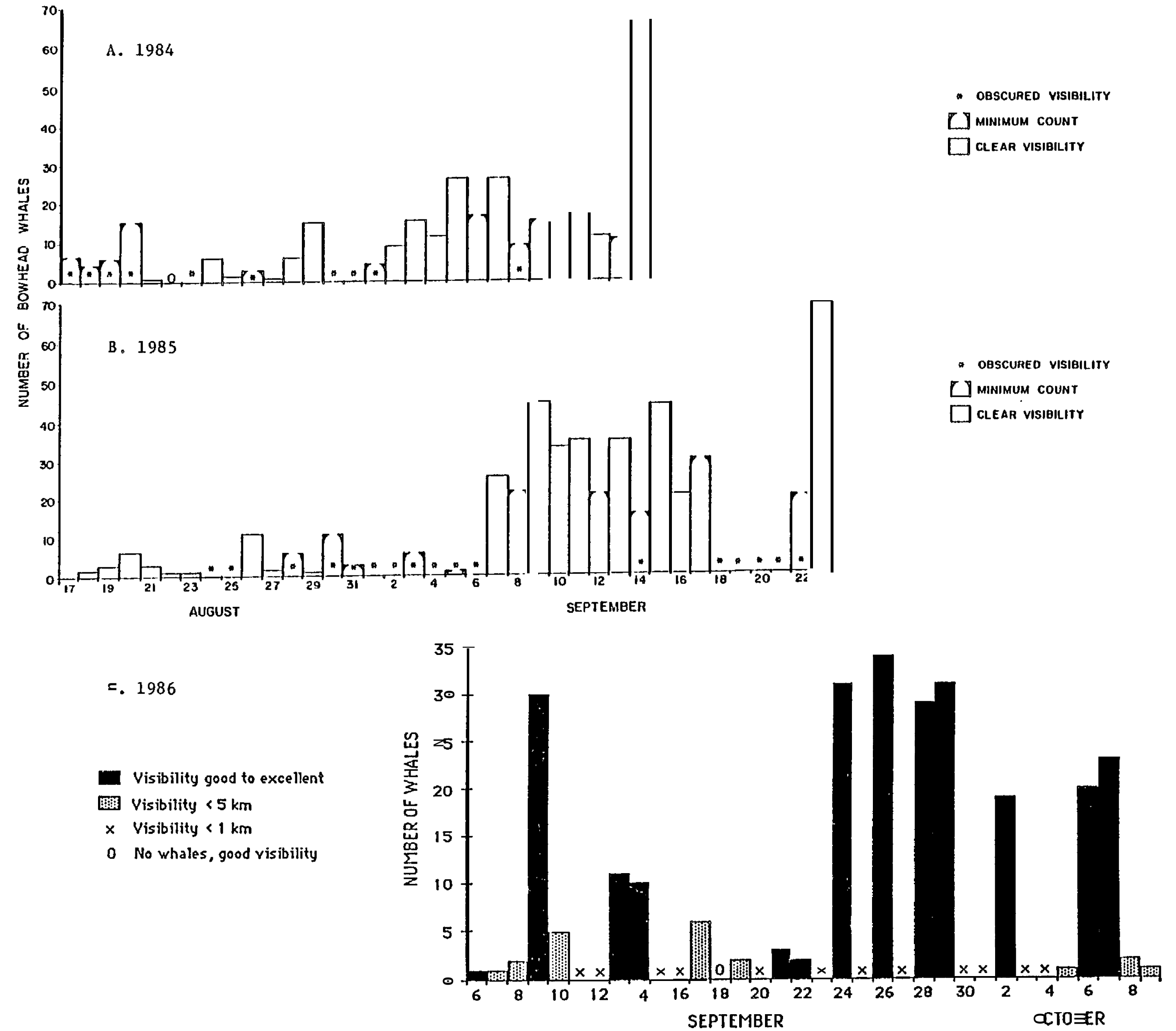

Figure 7. Daily maximum numbers of bowheads observed at Isabella Bay in 1984-86. In 1986, numbers observed after 22 September are based mostly on blow sources and probably underrepresent the total numbers present. (From Finley et al. 1986 and Finley 1987).

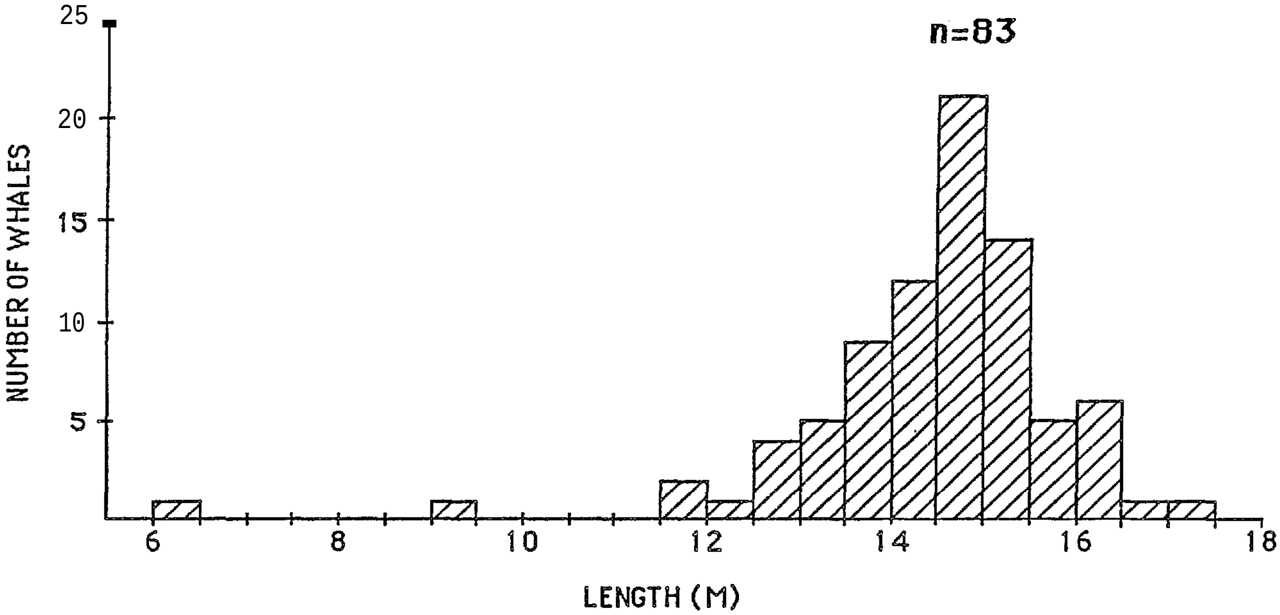

Figure 8. Length-frequency distribution of bowheads photographed at Isabella Bay, 28-29 September 1986. (From Finley 1987).

The high proportion of adults not attended by calves is consistent with reports from the 19th century whalers, who recognized the whales along eastern Baffin Island in late summer as a distinctive sub-population (Guerin 1845; Eschricht and Reinhardt 1866; Brown 1868). In contrast, during late summer most of the maternal component of the population was believed to occur farther north and west on the 'nursery grounds' around northern Baffin Island and as far west as Prince Regent Inlet in the high arctic archipelago (Eschricht and Reinhardt 1866; Finley et al. 1983). The 19th century whalers also indicated that small subadults concentrated in these northerly areas, at least during the early part of the summer,

Although a few calves have been seen north of Isabella Bay in recent years, extensive aerial and shore-based surveys of these areas in the late 1970s failed to find a high proportion of calves in any part of the range (Davis and Koski 1980; Koski 1980a,b; Koski and Davis 1980). The size composition of the bowheads summering farther north around northern Baffin Island has not been determined photogrammetrically. Hence, there is no modern-day information about the percentage of subadults summering farther north in relation to the low percentage at Isabella Bay.

Both male and female bowheads were at Isabella Bay during recent years, based on direct visual observations as some whales rolled ventrum up. However, the proportions of males and females are not known (Finley in prep.).

The high proportion of adults at Isabella Bay and the very low proportion of mothers attended by calves represents a different situation than that encountered in most nearshore waters of the southeastern Beaufort Sea during late summer. Along the coasts of the Mackenzie Delta, northern Yukon and northeastern Alaska, most bowheads occurring close to shore in shallow waters are subadults, predominantly shorter than 10 m (Koski et al. 1988). The Western Arctic bowheads found farther east, in the deep waters of Franklin Bay east of Cape Bathurst, may be more similar to the Eastern Arctic bowheads at Isabella Bay. In Franklin Bay, most bowheads present in late summer are adults without calves, although small numbers of subadults and cow-calf pairs have been photographed (Koski et al. 1988). Unfortunately, almost no behavioral data have been collected in Franklin Bay, so it is not possible to compare behavior of Eastern Arctic bowheads in Isabella Bay vs. that of Western Arctic bowheads in Franklin Bay.

<u>Local Distribution Patterns and Associated Activities</u>.--The local distribution of bowheads at Isabella Bay was not uniform. In all years when whales were present in substantial numbers, they concentrated in a few areas corresponding to major underwater topographic features (Fig. 9-11). In turn, the behavioral activities of the bowheads tended to vary with their location in the Isabella Bay area. In general, almost all deep foraging activity took place in one of two deep glacial troughs: NE Trough located 6+ km northeast of the observation point, and the Kater Trough located 25+ km southeast. In contrast, almost all social-sexual activity took place on Isabella Bank, a shallow bank at the northeast corner of Isabella Bay close to the observation site. Bowheads also used Isabella Bank for behavior that KJF has termed 'grooming/rubbing' and for resting.

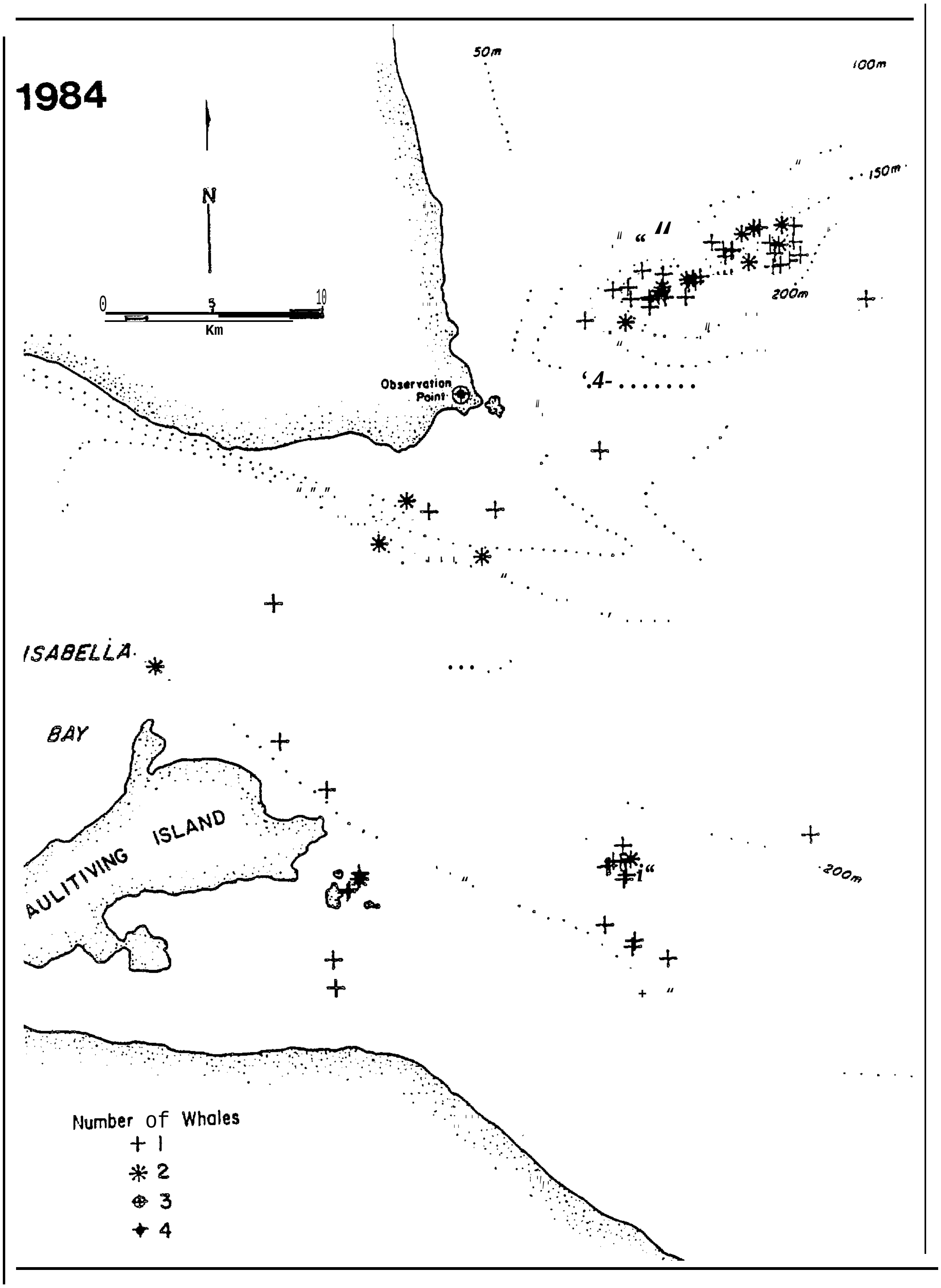

Figure 9. Distribution of bowheads at Isabella Bay during six daily scans on 3-12 September 1984. (From Finley et al. 1986). Bathymetric contours shown here are based on data available , n 1986; . see Figure 11 for more detailed bathymetric data. The positions s of whales >20 km from the observation point are approximate; their bearings are correct but distances are likely scattered over too broad a range due to refraction.

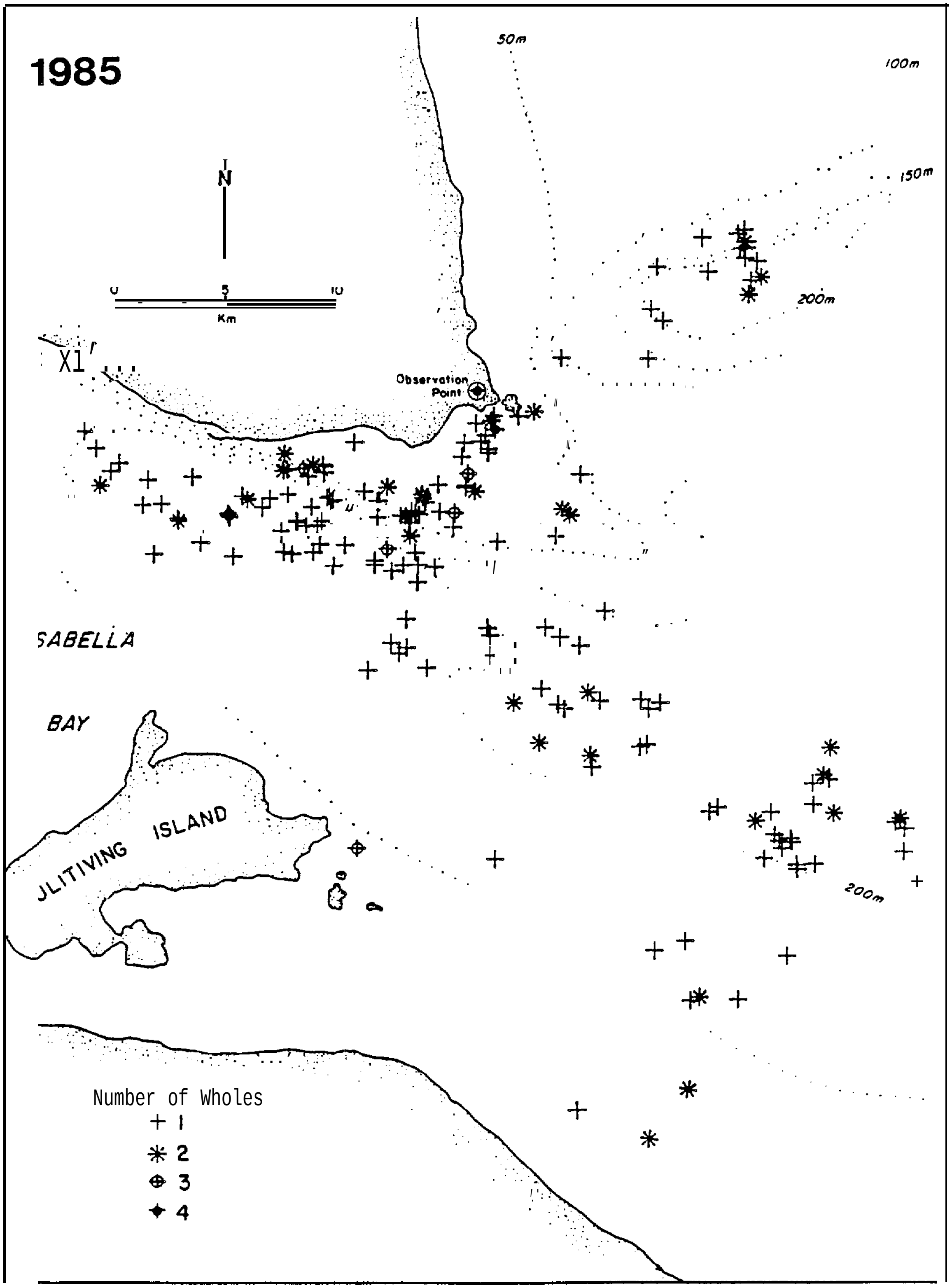

Figure 10. Distribution of bowheads at Isabella Bay during seven daily scans on 7-16 September 1985. (From Finley et al. 1986). Bathymetric contours shown here are based on data available in 1986; see Figure 11 for more detailed bathymetric data. The positions of whales >20 km from the observation point are approximate; their bearings are correct but distances are likely scattered over too broad a range due to refraction.

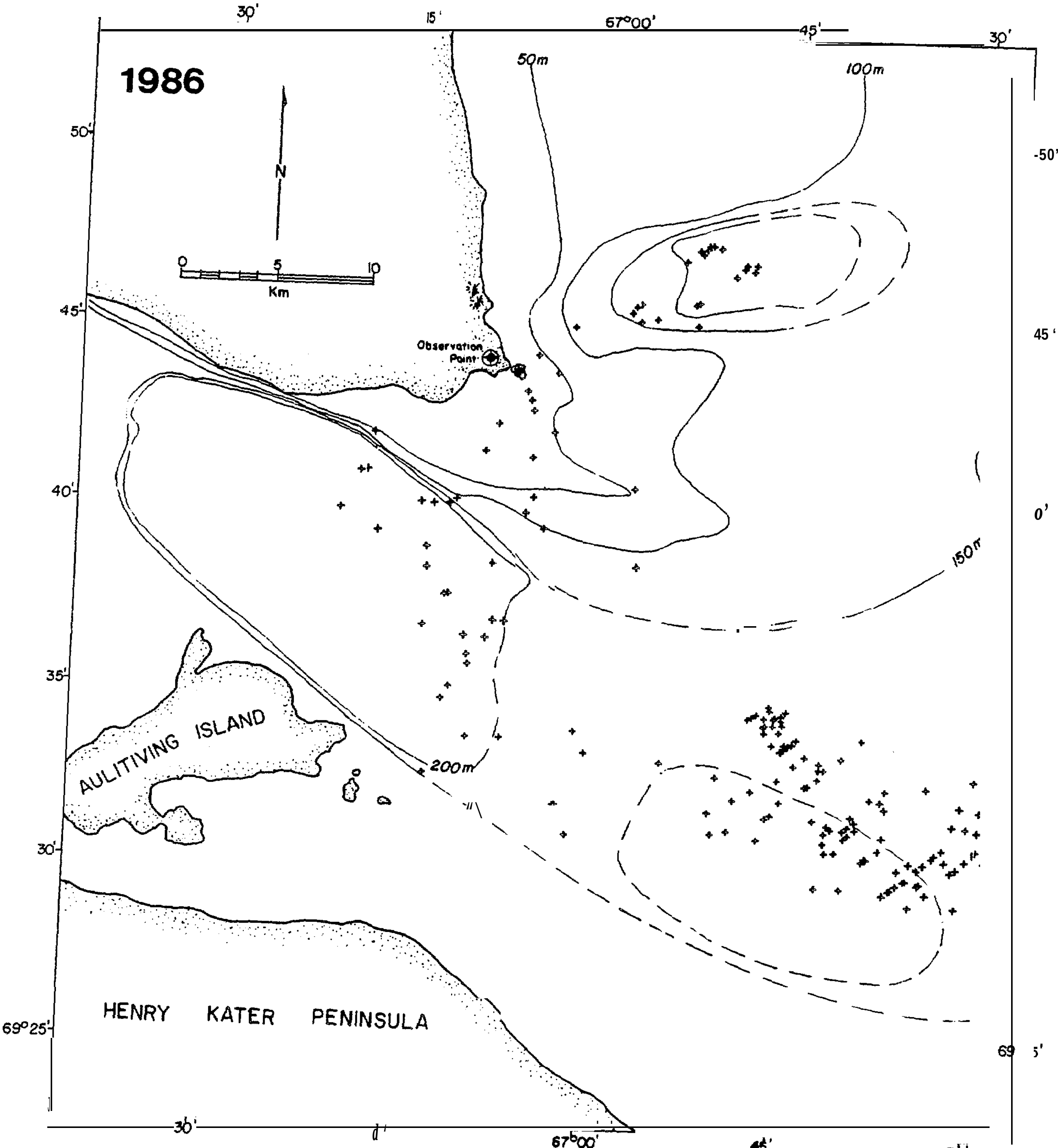

Figure 11. Distribution of bowheads at Isabella Bay during 10 daily scans on 9 September-6 October 1986. The positions of whales >20 km from the observation point are approximate; their bearings are correct but distances are likely scattered over too broad a range due to refraction. (From Finley 1987).

Whales observed at locations between the three major concentration areas noted above were generally involved in directed **local** movements. The five whales observed moving strongly south along the outer coast late in the 1986 season were presumed to be migrating.

Table 2 summarizes, for each of these four categories of whales, the dates, times, distances from shore, water depths and ice cover. Comparative data for corresponding categories of whales in the western arctic are also shown. Table 3 gives, for each category of whales, information about the frequencies of different group sizes and group activities. Table 4 summarizes activities of individual whales during each surfacing that was observed. These data are discussed in subsequent sections of this report.

Behavior of Feeding Bowheads at Isabella Bay

Types and Locations of Feeding.--Almost all bowhead feeding activity observed at Isabella Bay took place several kilometers offshore (Table 2C) in two deep (>200 m) glacial troughs. The proportions of the deep feeding activity that occurred in the NE Trough vs. the Kater Trough differed markedly between years, possibly in response to changing currents and resultant changes in prey densities (Finley et al. 1986; Finley 1987). Feeding was common in the NE Trough in 1984 and less so in 1985 (Fig. 9, 10). In 1986 (and 1987), most feeding was in the Kater Trough (Fig. 11). Bowheads were seen over the NE Trough during 13 of 18 days with good visibility in 1984 (11 of 12 d in Sept 1984) but during only 7 of 20 such days in 1985 (5 of 11 d in Sept 1985) (Finley et al. 1986, p. 40). Bowheads were seen over the NE Trough during 5 of 16 days in 1986, but most of the feeding seen there in 1986 was on only two dates (Finley 1987, p. 41). Feeding was observed commonly during all daylight hours (Table 2B).

Deep foraging typically was characterized by long dive durations, long surfacings, stereotyped surface postures (including pre-dive flexes), and flukes raised above the surface as the whale dove. Foraging patterns of individual whales involved crisscross movements back and forth through a feeding area. In 1984-86, 84% of the dives in the NE Trough occurred within a 3 km^2 area. Surface movements usually were random in orientation (Finley 1987, p. 50).

There were frequent defecations by the feeding whales. Bowheads in the NE Trough feeding area often were attended by foraging Northern Fulmars (*Fulmarus glacialis*). On at least some of these occasions, the fulmars were consuming bowhead feces. Attendance by seabirds was not seen when the whales were outside the NE Trough. (When whales were over Kater Trough, they were too far away for seabirds to be seen.)

Other types of feeding activity have been observed very infrequently at Isabella Bay (Table 3D). On four occasions in 1984-87 whales were observed feeding in shallow-water eddies created by a coastal prominence, Cape Raper. On these occasions feeding behavior was deduced from short surface-dive sequences (which did not involve a fluke-out posture) that were oriented in characteristic ways relative to surface features (slick bands and lines of flotsam) associated with the eddy.

Table 2. Circumstances of observations of bowhead whales in the eastern and western arctic. Four categories of whales (three in western arctic) are represented in different columns.

The values in the table represent numbers and percentages of surfacings. Because a given whale is counted more than once if more than one surfacing is observed, the contingency data for some variables are not all independent of one another, and statistical analysis is not justified in these cases. For a given category of wha les, the tota L number of cases differs among variables because not all variables could be determined for each surfacing.

	Eastern Arctic								Western Arctic							
	Feeding in deep water		Socializing in shallow water		Local travel		Migrat ion		Feeding in deep water		Socializing in sha llow water		Migrat ion***			
													Number			
	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%	LGL	NOSC	'Cot.	%
A. DATE																
1-15 Aug		0		0		0		0	57	39	262	34	**	**	**	0
16-31 Aug	74	30	91	40	L32	39		0	77	52	258	33	**	**	**	0
1-15 Sept	166	68	L 36	60	203	60		0	14	9	L27	16	**	13	13	1
16-30 Sept	4	2		0	1	0	6	4		0	L25	16	38	115	L53	S5
1-16 Ott		0		0		0	138	96		0		0	15	0	15	8
Total	244	100	227	100	336	99	L44	L00	148	L00	772	99	53	L28	181	100
B. HOUR (Local time)																
6-S h	10	4		0		0	17	12		0		0				0
9-1 L	67	27	73	32	55	16	22	15	23	16	222	29	4	35	39	22
12-14	56	23	39	17	141	42	60	42	16	11	194	25	26	65	91	50
15-17	74	30	95	42	103	31	43	30	43	29	198	26	23	28	51	28
18-20	37	15	20	9	37	11	2	1	57	39	102	13				0
21-23		0		0		0		0	9	6	56	7				0
Total	.244	99	227	100	336	L00	144	L00	148	101	772	100	53	128	1s1	100

Continued . . .

Table 2 (Concluded).

	Eastern Arctic								Western Arctic							
													Migration***			
	Feeding		Socializing		Local Travel		Migration		Feeding		Socializing		Number			
	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%	LGL	NOSC	Tot.	%
C. KM FROM SHORE																
0-2 km	6	3	97	43	124	39	130	96		0	81	10				0
2-4	9	4	129	57	57	18	3	2		0	73	9	9		9	5
4-10	61	26	1	0	103	32	2	1		0	202	26				0
10-20	162	68		0	35	11		0	23	16	73	9				0
20-40		0		0		0		0	36	24	117	15	21		21	12
40-80		0		0		0		0	6	4	226	29	23	116	139	77
80+		0		0		0		0	83	56		0		12	12	7
Total	238	101	227	100	319	100	135	99	148	100	772	98	53	128	181	101
D. WATER DEPTH (m)							*									
<10 m	**	0		0		0		0	**	0	79	10				0
10-19	**	0	129	57	51	18	5	22	**	0	203	26	9	1	10	6
20-49	**	0	98	43	102	36	13	57	**	0	490	63	39	111	150	83
50-99	16	7	**	0	63	22	3	13	45	30	**	0	5	4	9	5
100-250	228	93	**	0	71	25	2	9	53	36	**	0				0
>250		0	**	0		0		0	50	36	**	0		12	12	7
Total	244	100	227	100	287	101	23	101 *	148	100	772	99	53	128	181	101
E. ICE COVER (%)																
None	232	98	175	79	245	81	24	17	80	54	669	89	21	1	22	12
1-9 %	4	2	46	21	21	7	120	83	29	20	58	8	19		19	11
10-29		0		0	28	9		0	39	26		0	13		13	7
30-59		0		0		0		0		0	25	3				0
60-79		0		0	8	3		0		0		0		30	30	17
80-90		0		0		0		0		0		0		94	94	53
Total	236	100	221	100	302	100	144	100	148	100	772	100	53	125	178	100

* Data missing for a high proportion of surfacings.
** This combination was excluded based on the definition of this category of whales (see Methods, p. 29).
*** Migration data are presented separately for LGL 1985-86 observations and 1983 NOSC observations.

Table 3. Frequencies of various group sizes and activities of bowhead whales in the eastern and western arctic. Presentation as in Table 2.

	Eastern Arctic								Western Arctic							
	Feeding		Socializing		Local Travel		Migration		Feeding		Socializing		Migration- Number			
	Number	Z	Number	%	Number	%	Number	Z	Number	Z	Number	Z	LGL	NoSC	Tot.	z
A. GROUP SIZE (within 5 body lengths)																
1	142	60	57	28	190	58	104	73	113	85	368	53	33	80	113	62
2	74	31	68	33	116	36	29	20	5	4	202	29	20	14	34	19
3	21	9	61	29	10	3	9	6	2	2	75	11		34	34	19
4		0	12	6	4	1		0	13	10	35	5				0
5		0	9	4		0		0		0	6	1				0
>5		0		0	6	2		0		0	7	1				0
Total	237	100	207	100	326	100	142	99	133	101	693	100	53	128	181	100
B. NO. BHD WITHIN 1 KM *																
1	14	16		0	72	30	84	58	14	9		0	21	2	23	13
2	16	18	38	18	117	49	41	28	19	13	10	2	18		18	10
3	14	16	87	41	33	14	19	13	3	2	1	0		7	7	4
4	6	7	53	25	16	7		0	14	9	34	5	9	3	12	7
5	33	37	27	13		0		0	1	1	90	14				0
6	7	8		0	3	1		0	6	4	64	10	5	14	19	10
7		0	7	3		0		0	29	20	253	38		72	72	40
8		0		0		0		0	14	9	55	8				0
> 8		0		0		0		0	48	32	151	23		30	30	17
Total	90	102*	212	100	241	101	144	99	148	99	658	100	53	128	181	101
C. GROUP ' S PREDOMINANT ACTIVITY																
1 Travel	**	0	**	0	336	100	144	100	**	0	**	0	53	128	181	100
2 Socialize	**	0	216	95	**	0	**	0	**	0			**	**	**	0
3 Feed	227	93	**	0	**	0	**	0	50	34	**	0	**	**	**	0
& Trav + Social	**	0	11	5	**	0	**	0	**	0	25	3	**	**	**	0
5 Trav + Feed	9	4	**	0	**	0	**	0	38	26	**	0	**	**	**	0
6 Social + Feed	8	3		0	**	0	**	0	60	41	747	97	**	**	**	0
Total	244	100	227	100	336	100	144	100	148	101	772	100	53	128	181	100
0. GROUP ' S PREDOMINANT FEEDING MODE													*			
0 None		0	227	100	308	100	144	100	**	0	10	1	14	119	133	100
1 Water-Column	228	94		0		0		0	148	100	522	69				0
2 Bottom		0		0		0		0	**	0	37	5				0
3 Near-Surface	9	4		0		0		0	**	0	67	9				0
5 Wat-Col + Sfc	5	2		0		0		0	**	0	121	16				0
Total	242	100	227	100	308	100	144	100	148	100	757	100	14*	119	133	100*

* Data ❑issing for a high proportion of surfacings.
** This combination was excluded based on the definition of this category of whales (see Methods, p. 29).
*** Migration data are presented separately for LGL 1985-86 observations and 1983 NOSC Observations.

Table 4. Frequencies of various individual activities of bowhead whales in the eastern and western arctic. Four categories of whales (three in western arctic) are represented in different columns. Presentation as in Table 2.

	Eastern Arctic								Western Arctic							
	Feeding		Socializing		Local Travel		Migration		Feeding		Socializing		Migration- Number			
	Number	%	Number	%	Number	%	Number	%	Number	%	Number	%	LGL	NOSC	Tot.	%
A. SPEED OF MOTION																
0 None	18	10	104	55	22	7		0	26	27	85	20		1	1	1
1 slow	26	14	23	12	78	26	5	4	2S	29	123	28	11	4	15	9
2 Moderate	26	14	3	2	9	3		0	24	25	122	28	32	2S	57	33
3 Fast	8	4	2	1	15	5	19	14	1	1	9	2	1	31	32	19
4 Mov. @ Unk Sp	96	53	48	25	168	55	110	81	2	2	20	5	2	57	59	34
6-8 Speed Change	6	3	9	5	13	4	1	1	16	16	74	17	2	6	8	5
Total	180	98	189	100	305	100	135	100	97	100	433	100	48	124	172	101
B. SOCIAL ACTIVITY BY THIS INDIVIDUAL DURING THIS SURFACING																
None	242	99	115	53	331	99	133	99	143	97	546	72	51	102	153	91
Passive ***	2	1	58	27		0		0	5	3	41	5	2	11	13	8
Active	**	0	43	20	2	1	2	1	**	0	170	22		3	3	2
Total	244	100	216	100	333	100	135	100	148	100	757	99	53	116	169	101
C. AERIAL ACTIVITY BY THIS INDIVIDUAL DURING THIS SFC/DIVE SEQ																
None	238	98	114	52	317	95	135	99	141	95	727	94	50	115	165	98
Roll/Flip .Slap	2	1	36	16	3	1	2	1	1	1	7	1	1		1	1
Flipper Slap	2	1	22	10	3	1		0		0		0				
Tail Slap	2	1	16	7	8	2		0		0	13	2				
Fl + Tail Slap		0	15	7	2	1		0		0	6	1				
Breach		0	14	6		0		0	3	2	10	1	2		2	1
Breach + Other		0	4	2		0		0	3	2	9	1				
Total	244	101	221	100	333	100	137	100	148	100	772	100	53	115	168	100
D. FLUKES OUT AT END OF SURFACING							*		*					*		
No	38	22	172	86	232	88	20	62	9	60	189	52	41	2S	69	73
Yes	138	78	27	14	32	12	28	58	6	40	176	48	9	16	25	27
Total	176	100	199	100	264	100	4S	100*	15	100*	365	100	50	44	94	1 00*

* Data missing for a high proportion of surfacings.
** This combination was excluded based on the definition of this category of whales (see Methods, p. 29).
*** Within ½ body length of, and parallel to, another whale, but not actively interacting or orienting toward one another.
**** Migration data are presented separately for LGL 1985-S6 observations and 1983 NOSC observations.

Near-surface (skim) feeding by whales was suspected on only two occasions. In each case, only a single whale was involved, and the behavior occurred during a storm (Finley et al. 1986, p. 42). This behavior was quite different from the near-surface feeding sometimes observed in the Beaufort Sea, which commonly involved structured groups of whales that sometimes appeared to be feeding cooperatively (Würsig et al. 1985a,b, 1986).

There was no evidence of bottom feeding of the type observed by Würsig et al. (1985a,b, 1986, in press) in shallow portions of the Beaufort Sea.

Thus, almost all feeding activity at Isabella Bay involved feeding in the deep waters over the NE Trough or Kater Trough. Feeding activity there was qualitatively similar to the water-column feeding that has been described as being the most common feeding mode for Western Arctic bowheads in the Beaufort Sea (Würsig et al. 1984a, 1985a,b; Richardson et al. 1987b). However, in the Beaufort Sea--unlike Isabella Bay--water column feeding has been observed commonly in shallow as well as deep water.

Prey Organisms.--As noted above, bowheads frequently defecated at the surface while feeding in the NE Trough. Two samples of feces collected in the NE Trough consisted primarily of the chitinous segments of large copepods, presumably *Calanus glacialis* and *C. hyperboreus* (Finley et al. 1986).

The highest concentrations of zooplankton found by zooplankton sampling at Isabella Bay occurred at depths >100 m in the NE Trough (Fig. 12; see also Finley et al. 1986). The NE Trough was one of the main areas where bowheads fed. Copepods were the dominant zooplankters and two large species, *Calanus glacialis* and *C. hyperboreus*, predominated at depths >100 m. At these depths, the larger lifestages--copepodite V and adult female--were most abundant numerically and thus contributed most of the total biomass.

Although zooplankton sampling efforts were limited, the proportions and biomasses of mature copepods seemed to decrease from 1984 through 1987 in the NE Trough, consistent with the decrease in whale feeding activity there. In 1986-87 most bowhead feeding in the Isabella Bay area shifted to the Kater Trough, presumably in response to more favorable feeding conditions there. Due to limited logistic capabilities it was not possible to sample zooplankton in the Kater Trough.

Group Sizes.--Bowheads in the NE Trough usually fed independently of each other (Table 3A). Occasionally only one feeding individual was present, but usually there were other whales within 1 km (Table 3B). As many as 14 whales have been observed scattered through the area feeding individually. Occasionally pairs of whales whose diving activities tended to be synchronous fed in the NE Trough. 'Paired' whales generally remained within a few whale-lengths of one another. Except in the case of paired whales, there was no evidence of synchronous diving by various whales feeding simultaneously in the NE Trough.

Rates of Movement.--During dives in the NE Trough, the net horizontal movements of bowheads seldom exceeded ½ km in absolute terms, or a net speed of 2 km/h. Net rates of movement while at the surface (probably influenced by currents) averaged only 1.6 km/h and the whales often paused, apparently to

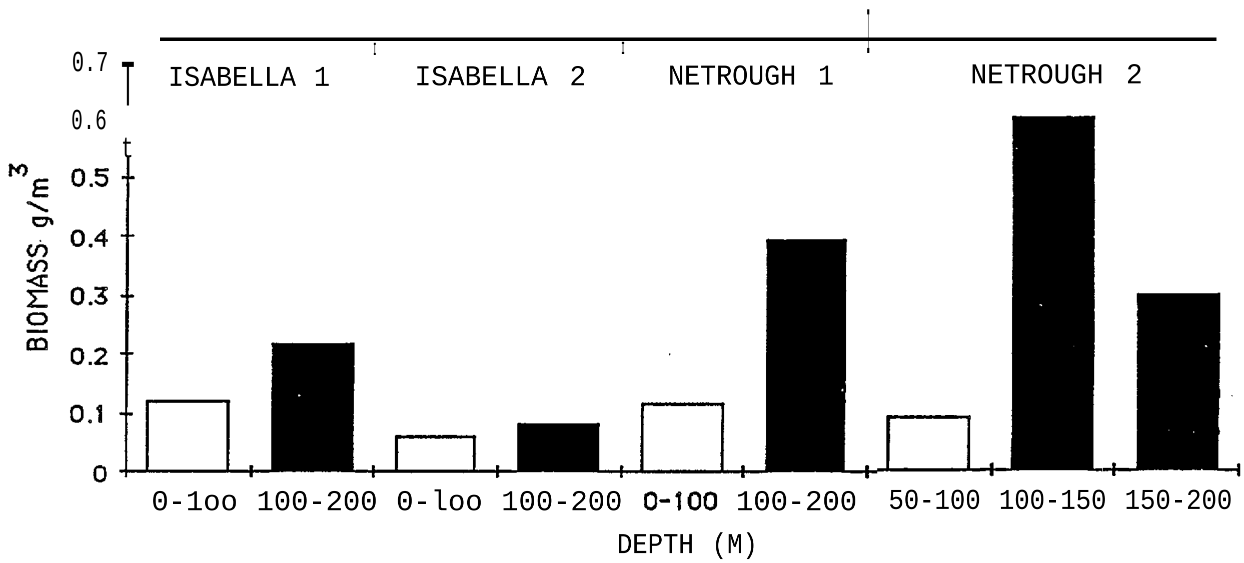

Figure 12. Mean zooplankton biomass at various depth ranges and stations in Isabella Bay and NE Trough, mid-September 1986. Based on n = 5 vertical hauls except at station NE Trough 2, which was based on n = 3 (50-100 m) and n = 2 (100-150, 150-200 m). (From Finley 1987).

rest between dives (Table 4A). Distances travelled at the surface between feeding dives were typically 100-150 m (Finley 1987, p. 50). On one occasion when a bowhead foraged along slick lines created by an eddy in the lee of Cape Raper, its rate of movement slowed to 2.1 km/h compared to its traveling rate of 5.2 km/h.

Surfacing-Dive Cycle.--Selected quantitative data on surfacing, respiration and diving behavior of feeding bowheads at Isabella Bay have been reported previously by Finley et al. (1986, p. 35, 39) and Finley (1987, 51). However, there has been no previous comprehensive analysis of the surfacing-dive cycles of feeding bowheads in the Eastern Arctic. This section is based on an analysis during the present project of all data on whales feeding in deep (>50 m) water at Isabella Bay over the 1983-86 period. Most of these data pertain to whales in or near the NE Trough. (Whales feeding in the Kater Trough were too far away to allow detailed observations.) The criteria for including observations in the 'Whales feeding in deep water' category are listed in the Methods section. To ensure that we were considering a relatively homogeneous set of observations, we excluded the few data on bowheads feeding in water <50 m deep. There were no mothers, calves, or actively socializing whales in this 'feeding' dataset.

The durations of surfacings and dives of the feeding whales, and the number of blows (respirations) per surfacing, all tended to be very high (Fig. 13). During an average surfacing-dive cycle, a whale feeding in deep water off Isabella Bay dove for 15.8 rein, surfaced for 4.7 rein, and respired 17 times during the surfacing. These values were high relative to the three other categories of whales studied in the eastern arctic ($P<0.001$ in each case), and relative to previously reported values for the western arctic (cf. Würsig et al. 1984a, 1985b; Dorsey et al. in press).

The mean duration of surfacing and mean number of respirations per surfacing were each at least 2.4x higher for feeding whales than for any one of the other three categories of whales in the eastern arctic. Previous western arctic studies have indicated that longer surfacings with more respirations per surfacing are to be expected when whales are in deep water. However, previous studies have not shown such high values for whales feeding in deep water, or such a wide disparity between feeding whales and other categories of whales. For example, Würsig et al. (1985b) found mean surface times of 1.63 min in water 101-250 m deep, and 2.29 min in water >250 m deep, in contrast to the 4.7 min for whales feeding in deep water at Isabella Bay. Würsig et al. found means of 6.3 and 7.9 blows per surfacing in these two ranges of water depth, as opposed to the mean of 17.3 blows per surfacing for feeding whales off Isabella Bay.

The mean dive duration for feeding whales off Isabella Bay, 15.8 rein, was high. However, the difference relative to previously reported values for whales in deep water was not as great as that for surface times and number of blows per surfacing. Previous studies in the western arctic have shown that dives tend to be longer when bowheads are in water deeper than 100 m. For whales summering in the Beaufort Sea in 1980-84, Würsig et al. (1985b) found a mean dive duration of 10.7 min when water depth was 101-250 m, and 12.0 min for depths >250 m. Similarly, when we isolated the observations of feeding whales in deep (>50 m) waters of the Beaufort Sea in 1980-86, we found a mean

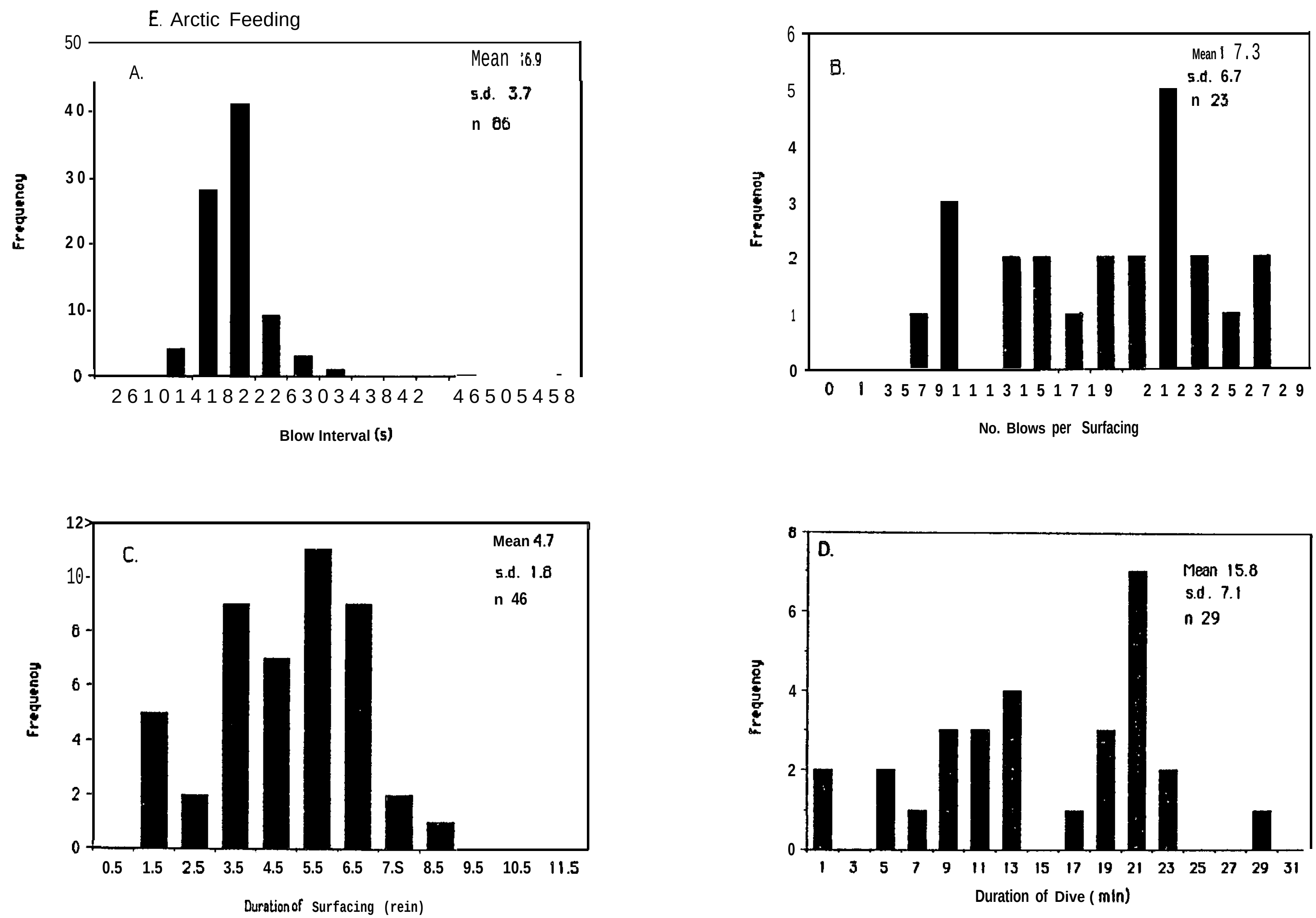

Figure 13. Frequency distributions of surfacing, respiration and dive variables for undisturbed bowheads feeding in deep water (>50 m) at Isabella Bay, eastern arctic.

dive duration of 10.8 min (this study). The range of dive durations found for feeding whales off Isabella Bay, 2.0 to 29.6 rein, was similar to the range found during summer in the western arctic, where dives as long as 31 min have been documented in deep water (Würsig et al. 1984a, 1985b).

The above results are based on the total water deptha. The actual depths to which the eastern and western arctic bowheads were diving were not known. In the cases of humpback and gray whales diving to known depths, dive times are strongly correlated with the actual depth of dive (Würsig et al. 1986b; Dolphin 1987a,b). Assuming that a similar pattern holds for bowheads, the long dive times, exceptionally long surface times, and high number of blows per surfacing suggest that the feeding whales observed off Isabella Bay were diving deeper than those observed in the Beaufort Sea.

For feeding whales, the mean interval between successive blows within a surfacing[8] was 16.9 ± s.d. 3.7 s (n = 86 surfacings). The range was from 10 to 28.5 s (Fig. 13A). The mean value for. feeding whales was similar to corresponding means for other categories of whales in the eastern arctic (F' = 0.899 df = 3,97, P>0.1). The similarity of the blow intervals for eastern arctic bowheads engaged in a wide variety of activities was consistent with summer results from the western arctic. There, blow intervals during summer are less dependent on environmental conditions and whale activities than are number of blows per surfacing, surface times, and dive times (Würsig et al. 1984a, 1985b; Dorsey et al. in press). However, blow intervals during autumn migration through the Beaufort Sea tend to be longer than those for whales engaged in various summer activities (see later).

Factors Affecting the Surfacing-Dive Cycle.--Table 5 summarizes the correlations of the four surfacing, respiration and dive variables discussed above with various environmental and whale activity variables. These interrelationships are important in understanding whether the eastern arctic data are comparable to corresponding western arctic data. If the behavior of feeding whales were strongly affected by environmental variables that differ between the two areas, comparisons between the two stocks would be severely confounded by the environmental differences. Conversely, if behavior is not strongly affected by a particular environmental variable, eastern and western arctic results may be comparable even if the environmental variable differs greatly between the two areas.

Table 5 is consistent in format with our previous presentation of corresponding results for Western Arctic bowheads (Würsig et al. 1985b, p. 50; Dorsey et al. in press). This format needs to be understood, partly because

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[8] Each 'mean blow interval' analyzed here represents the mean of all blow intervals within a single surfacing. Each surfacing contributes 1 case to this analysis, and to Fig. 13. This procedure differs from that used in most previous analyses of bowhead blow intervals (see Methods).

[9] F' represents results from the Brown-Forsythe modification of ANOVA, which tolerates unequal variances in the different categories being compared (Dixon et al. 1985). Results were similar when the analysis was repeated based on log transformed data.

Table 5. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables bowheads feeding in deep (>50 m) water in Eastern Arctic, 1984-1986.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 84	0-1[b]	St[g]		St		St		St	
Year = 85	"	ns		ns		ns			
Year = 86	"	ns						+	+++
Date	1-76[c]	ns		ns		ns		ns	---
Date²	(1-76)²	na		ns		ns	--	ns	
Time	0-24[d]	ns		++		ns		ns	
Time²	(0-24)²	ns		+++	+++	ns		ns	
Sea State	Bf	ns		ns		ns		na	
Ice Cover	%								
>5% Ice Cover?[b]	0-1[b]								
Disc. from Shore	log (km)	ns		ns		ns		ns	
Water Depth	log (m)	ns		ns		ns		ns	
Group Activ - Trav. + .%x.	0-1[b]								
" " = Trav. + Feed	"	ns		ns		ns		ns	+
" " = Sot. + Feed	"					ns			
No. Bhd. Within 1 km	No.								
Group Size	1-3	ns		+		---	---	ns	
Active Socializ.?[b]	0-1[b]								
Passive Socializ.?	"								
Aerial Behav.?	"								
Pre-dive Flukes?		ns		++		ns		ns	
Sample Size		35	35	19	19	69	69	19	19
Multiple Correlation					0.772		0.563		0.905
% Variance Explained					48.4		31.7		81.9
Adjusted % Var. Expl.					45.4		29.7		76.7
Overall Significance					***		***		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships
***, +++ or --- means P<0.001   *, + or - means 0.05>P>0.01
**, ++ or -- means 0.01≥P>0.001   ns means P>0.05
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so for feeding whales, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for chose variables significant (nominal P≤0.05) according to stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Ott = 62.

[d] All Eastern Arctic data in EDT.

[e] In degrees and decimal degrees.

[g] 'St' denotes 'Standard' year against whose results other years were compared by dummy 'year' variables.

several similar tables appear later in this report. Both simple and partial correlations are shown. The simple correlation columns show the significance of correlation between individual predictor and dependent variables. The analyses summarized here considered only the surfacings or dives for which all of the listed variables were known, since only those surfacings or dives could be considered in the associated multiple regression analyses. For simple correlations that were significant ($P \leq 0.05$), *the* direction of correlation is shown as +, ++ or +++ for positive relationships and -, -- or --- for negative relationships. The number of + or - symbols represents the significance level of the correlation: $p \leq 0.05$, 0.01 or 0.001, respectively.

Each partial correlation column in Table 5 summarizes the results of a stepwise multiple regression analysis to assess which environmental and whale activity variables seemed to affect the dependent variable, i.e. duration of surfacing, number of blows per surfacing, etc. The significance and direction of the relationship are shown for those variables that showed a significant partial correlation with the dependent variable, i.e. a significant relationship after the effects of other environmental and whale activity variables were 'taken into account'. The last several rows of the table give the sample sizes and the usual summary statistics for multiple regression analyses.

In general, we place little emphasis on correlations significant at the marginal $0.01 < p \leq 0.05$ level. Given the large number of tests done, a few of these apparent relationships would be expected by chance even if there were no true relationship. Also, in the case of partial correlations, the nominal significance levels are known to overstate the real significance levels. The precise values cannot be calculated (Draper and Smith 1981, p. 310-2), Thus, some or all of the partial correlations designated as '+' or '-' are undoubtedly non significant ($P > 0.05$) and not indicative of real effects on whale behavior.

The simple correlation analyses indicated that durations of surfacings and dives by whales feeding in deep water were not strongly related to any of the environmental or whale activity variables considered (Table 5). The only relationship significant at even the marginal $0.01 < P \leq 0.05$ level was a tendency for dive duration to be greater in 1986 than in other years. Multiple regression analysis suggested that this was a real effect, and that there was also a tendency for shorter dives late in the season. However, the multiple regression results for dive times are of very doubtful reliability because of the low sample size (n = 19).

The number of blows per surfacing was not strongly correlated with many variables, but did tend to be higher late in the day ($P \leq 0.001$). Also, the number of blows per surfacing tended to be higher when the surfacing was terminated by a 'fluke-out dive', i.e. the tail flukes were raised above the surface as the whale submerged. Only the time of day effect was significant when all variables were considered together via multiple regression. Again, however, the sample size (n = 19) was too low for reliable multivariate analysis.

Mean blow interval was not correlated with many of the environmental or whale activity variables. However, blow intervals tended to be shorter when several whales were feeding together than for single whales. After this effect was taken into account, there was also evidence of shorter blow intervals late in the day. Because of the larger sample size (n = 69), results for blow intervals are more reliable than those for other variables. Interestingly, Würsig et al. (1985b, p. 50) also found evidence for slightly shorter blow intervals late in the day in the Beaufort Sea after effects of other variables were taken into account.

In general, the analyses summarized in Table 5 indicate that the surfacing, respiration and diving cycles of bowheads feeding in deep water at Isabella Bay were not strongly related to many environmental or whale activity variables. This lack of strong correlations was probably largely due to the narrow range of feeding circumstances considered, as defined in the Methods, p. 29. Whatever the reason, this result is encouraging with respect to the likely comparability of data from feeding whales in the eastern and western arctic.

Other Behavioral Variables.--Whales that were actively interacting at close range were excluded from the 'feeding in deep water' category. However, there were virtually no such cases at Isabella Bay. Furthermore, there were very few cases (1% of surfacings) in which two feeding whales were swimming $\leq \frac{1}{2}$ body length apart and parallel to one another, which we call a 'passive social interaction'. Similar results were obtained for whales feeding in deep water in the western arctic (Table 4B).

Aerial activity--breaches, tail slaps, flipper slaps and rolls--was infrequent among feeding whales at Isabella Bay (2% of surfacings, Table 4C). The corresponding percentage for whales feeding in deep waters of the western arctic was 6%.

Bowheads feeding in deep water at Isabella Bay raised their flukes above the surface at the onset of 78% of their dives. This is a high percentage relative to other categories of whale activities in the eastern arctic (Table 4D). Similarly, in the western arctic, fluke-out dives seem to be more common for whales water-column feeding in deep water than for those in shallower water (e.g. Richardson et al. 1987b, p. 356).

Summary.--Most feeding activity at Isabella Bay occurred in deep water over glacial-remnant troughs several kilometers offshore. Essentially all feeding was of the type recognized in the western arctic as 'water column feeding'. There was little evidence of coordinated feeding behavior between different individual whales. However, surfacing-dive sequences of some 'paired' whales were synchronous. Near-surface feeding apparently was rare, and near-bottom feeding was not detected. Whales feeding in the trough NE of Cape Raper moved back and forth through the area from one surfacing to the next; in 1984-86, 84% of the dives in the NE Trough were within a 3 km^2 area. When at the surface, bowheads often defecated, and fecal samples (n = 2) contained remnants of large copepods. Limited zooplankton sampling indicated that concentrations of large copepods occurred at depths >100 m. Bowheads feeding in deep water exhibited unusually long dives and surfacings, with many respirations per surfacing. This behavior is consistent with diving to great depths. Within this category of whale activity, surfacing - respiration - diving behavior was correlated with few of the environmental variables that we considered. This reflects the narrow environmental context in which water-column feeding was observed at Isabella Bay. Aerial activity was very infrequent. Most surfacings of feeding bowheads ended with a 'fluke-out' dive.

Behavior of Socializing Bowheads at Isabella Bay

Socializing bowheads at Isabella Bay were found primarily in the shallow waters of Isabella Bank, near the observation site (Fig. 9-11; Table 2c). Socializing was common in both late August and early September, and was observed intermittently at all times of day (Table 2A,B). Whether it continued at night is unknown. The most common situation was for 2 or 3 whales to be located close together, often with additional whales within 1 km (Table 3A,B).

During many individual surfacings by whales classified as socializing, there was no overt social interaction with a nearby whale. However, active interactions were much more common during surfacings when the group activity was classified as socializing (20% of surfacings) than for feeding, local travel, or migration (Table 4B).

It is difficult to discern the maximum range of acoustic communication among bowheads and, hence, of their social interactions. Although the whales were often spread over a large area at Isabella Bay, it was often apparent from their co-ordinated activity patterns that they formed a diffuse herd. Activities probably were coordinated via long-range acoustic exchange. Würsig et al. (1985a) noted that in the Beaufort Sea, 'There was often an impressive degree of synchrony of basic behaviors among members of quite widely spaced groups.' They noted 'apparent synchronization of behaviors on time scales ranging from seconds to days', and that general activities sometimes differed among locations. Similar synchrony of herd activity patterns was observed at Isabella Bay. Within this loose social framework, it was apparent that (aside from the individual), there were two basic social units: pairs and larger groups (generally 3-6 whales).

Pairs.--Scan data from Isabella Bay indicated that, on the average, a minimum of 36% of the animals were members of obvious pairs (Finley et al. 1986, p. 47). Obvious pairs were usually seen within a few body-lengths of each other, and exhibited co-ordinated behavior. Pairs commonly remained together over periods of hours. Judging from the amount of white pigmentation on their peduncles[10], it appears that pairs usually involved adult whales. Although there was no direct evidence, Finley et al. (1986, p. 58) suggested, based on behavioral evidence, that pairs represented male-female associations. Pairs occurred throughout the range of the herd at Isabella Bay whereas most of the larger social groups occurred in one area (see below).

Larger Groups.--Social groups of 3-6 (or more) whales were transitory and involved high levels of activity and behavioral interaction. These larger groups occurred almost exclusively on the shallow Isabella Bank. These groups

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10 In the western arctic, the amount of white tends to increase with increasing whale size (Davis et al. 1983).

almost always included a 'central' whale and a number of attendant whales. Their conspicuous activities included tail lofts[11] (Plate 1), tail and flipper slaps, rolls, chases, caresses, sexual conduct, and much vocalization. Except for tail lofts, all of these activities have been recorded in sexually-active groups of bowheads in the western arctic (Everitt and Krogman 1979; Ljungblad 1981, p. 11; Ljungblad et al. 1982, p. 22; 1984a, p. 25, 83; Würsig et al. 1985a,b). This activity was similar to the breeding behavior of southern right whales (Saayman and Tayler 1973; Payne and Dorsey 1983). Judging from the lack of white pigmentation on their peduncles[10], most of the whales involved in group sexual activity on Isabella Bank may have been large subadults.

In all cases, group sexual activity was directed at one animal that frequently rolled belly-up. Similar behavior has often been seen in southern right whales and in Western Arctic bowheads, and has been interpreted as female abstinence. However, on 2 of 3 occasions when the sex of the 'central' animal in such a group was determined at Isabella Bay, it was a male. The attendant animals also were males, as evident from their unsheathed penises, in all cases when their sex could be determined. Similar homosexual behavior has been observed in adolescent right whales (C.W. Clark pers. comm.) and may be quite common among cetaceans in general (Saayman and Tayler 1973; Würsig 1988).

Würsig et al. (1985a,b) observed that the amount of social-sexual activity of bowheads in the Beaufort Sea declined from early August to early September. They suggested that this trend may have been part of a continuing decline from a (presumed) spring breeding season. The amount of social-sexual activity in Isabella Bay declined after mid September, but this may have been due to more favorable feeding opportunities rather than waning sexual inclination. It appears that at least some bowheads engage in sexual activities throughout much of the year (see review by Nerini et al. 1984), as do right whales (Payne and Dorsey 1983). For this reason, there is some doubt about the timing of the true mating season and of conception. In any case, sexual interactions are common at Isabella Bay in late summer. It would be valuable to learn whether the bowheads that engage in sexual activity at Isabella Bay during late summer are sexually mature.

Underwater Sounds.--Bowhead sounds recorded in Isabella Bay on four dates in 1984-87 were analyzed by C.W. Clark during the present project. The Isabella Bay material consisted of 3 h of cassette tapes (Table 6). All recordings were made in the presence of socially (often sexually) active whales in shallow (<50 m) waters on Isabella Bank. Figure 14 shows examples of seven of these sound types as they appear on spectrographs.

In Table 6, # WHALES was the number of bowheads within the estimated recording range of the kayak. DURATION was the length of the recording session. The call types labelled UPsweep, DOWNsweep, CONStant, and INFLected

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11 Tail loft (Plate 1): From a stationary or near-stationary position, the tail was lifted high, the back arched, and the whale slowly sank vertically. Occasionally the tail fell to one side during a loft, or barely cleared the surface. The flukes did not slap the surface sharply.

Table 6. Summary of the total number of different sound types recorded from bowhead whales in Isabella Bay (see text for details}.

Date	# Whales	Duration (h)	Calls								Other Sounds	
			UP	DOWN	CONS.	INFL.	HIGH	HARM,	PUL.	SLAP	BLOW	CR-UNCH
6 Sep 84	3	0.86	14	9	4	5	1	324	1	127	0	47
23 Sep 85	68	0.75	12	4	2	11	22	131	100	136	6	0
3 Sep 87	4-6	0.70	9	1	0	21	26	0	124	36	18	0
10 Sep 87	3-5	0.69	7	0	0	2	5	0	55	17	2	0
TOTALS		3.00	42	14	6	39	54	455	280	316	26	47

Plate 1. Tail-loft posture by a bowhead on Isabella Bank, 14 September 1987. The object directly behind the whale's peduncle is a researcher's kayak.

refer to frequency-modulated (FM) calls with FM contours approximated by the name of the call type. HIGH refers to any FM call that was above 400 Hz (e.g. Fig. 14). HARM refers to a harmonic or pulsed tone call, characterized by its rich harmonic spectrum (Fig. 14). On spectrographs, harmonic sounds often appear similar to the discrete pulsed calls produced by killer whales (see Ford 1987), except that the fundamental for bowheads is between 25 and 100 Hz. PUL refers to a complex pulsive call with broadband, complex spectral energy distribution.

The remaining sound types listed in Table 6 are not calls. A SLAP is a short-duration, wideband sound with a sharp onset (Fig. 14). A slap sound is usually, but not always, produced by a whale striking the surface of the water with its pectoral flipper or flukes, or with its entire body during a breach. BLOW refers to a sound produced by the exhalation and/or inhalation of air during respiration. Blow sounds are typically broadband, noisy sounds with some underlying frequency emphasis and of variable duration. CR-UNCH refers to a pair of noisy, broadband sounds, each lasting around 0.2-0.4 s and separated by c. 0.5 s (Fig. 14). To the human ear, the second part of the CR-UNCH sound has a distinctive recoil-like quality. The sound is not a vocalization and is not associated with any visible surface activity. It is, however, associated with the presence of bowhead whales near the recording site.

During the 6 Sept 1984 session there were three whales, a pair and an 'escort', engaged in vigorous social activity that included much tail lofting and slapping. Occasionally the whales came into close contact although there was no evidence that they engaged in sexual contact. There was a wide variety of harmonic (pulsed-tone) calls and slap sounds (Table 6), plus many CR-UNCH sounds.

The 23 Sept 1985 recording was made amidst a scattered herd of 68 whales, most of which were within 3 km of the recording kayak. Most of these whales were resting or engaged in mild social activities. However, two or three groups were engaged in intensive social-sexual activities 2-3 km from the kayak. The kayak approached within 20-40 m of several individuals, and on two occasions individual whales approached and dove beneath the kayak. The underwater recording contained a wide variety of FM calls, pulsive and harmonic (pulsed tone) calls, and slaps. Interestingly, despite the many whales in the immediate area, no more than two whales seemed to call at one time.

During the 3 Sept 1987 session, 4-6 whales were engaged in intensive homosexual activity in one general location within 100 m of the recording kayak. One whale was the focus of the sexual activity. Based on the morphology and position of its genital slit, it was a male. It frequently rolled belly up while the others attempted to copulate with it. The underwater record was dominated by complex pulsive calls emitted in sporadic clusters.

During the 10 Sept 1987 session, 3-5 whales were engaged in transient homosexual activity. The 'central' animal, a subadult male, frequently changed location and was pursued by the males. Again, the underwater recording was dominated by complex pulsive calls. The proportions of the various types of calls were similar to the proportions on 3 Sept 1987 (Table 6).

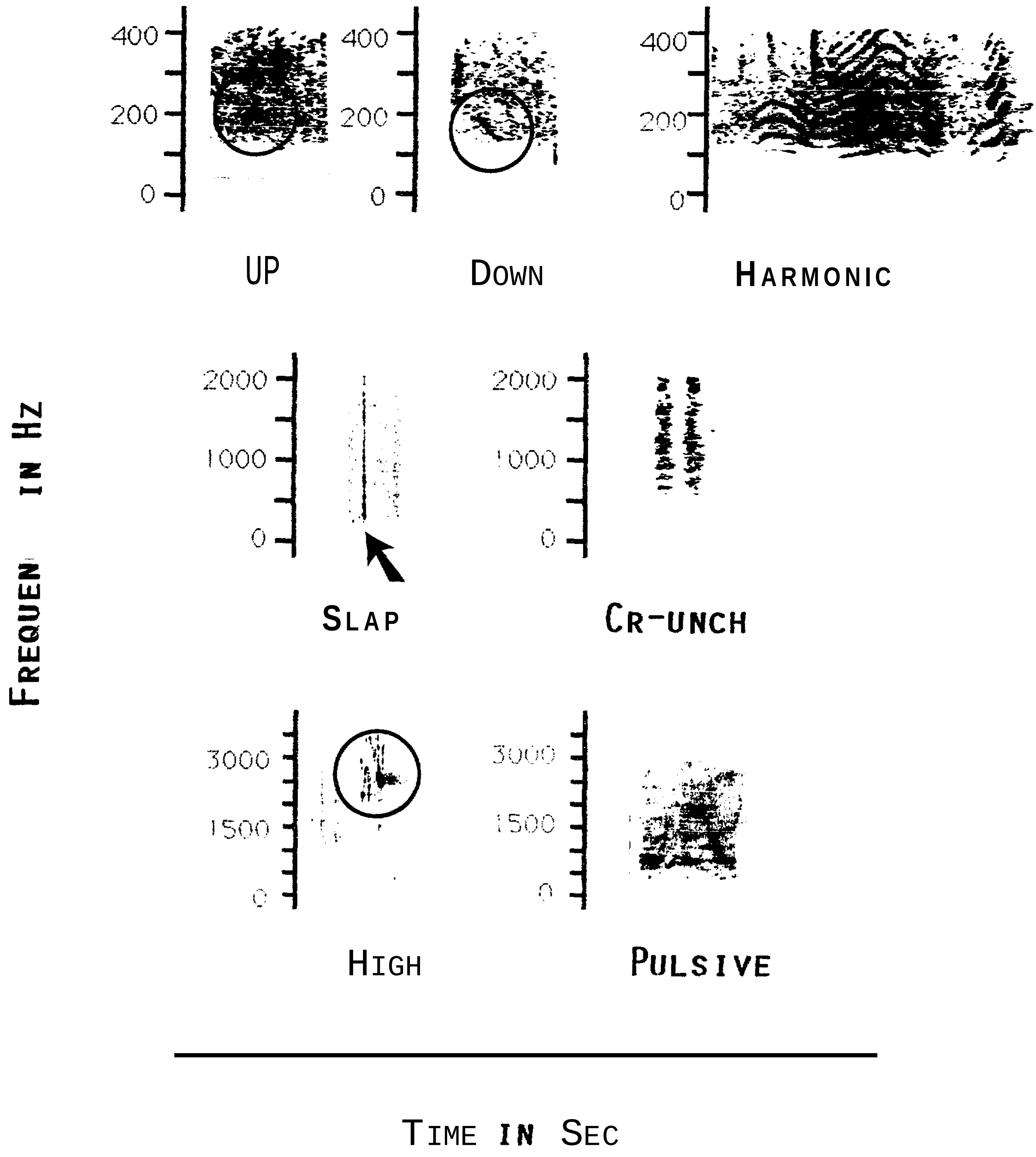

Figure 14. Spectrographs of several call types and physical sounds produced by bowhead whales at Isabella Bay. All simple FM calls recorded were weak, accounting for the low signal-to-noise ratio for the examples of 'Up' and 'Down' calls shown here.

Overall, the Isabella Bay recordings consisted mostly of complex pulsive calls and harmonically rich (pulsed tone) calls plus slaps. Sounds were usually produced in clusters having similar acoustic qualities, giving the impression that all sounds in the cluster came from the same individual. These sounds were produced by socially (and often sexually) active whales. Hence, the recording situations were quite different from those when most data on calls of Western Arctic bowheads have been recorded. Therefore, comparisons of Eastern and Western Arctic call data should be done with caution.

The harmonic or pulsed tone calls recorded at Isabella Bay were often 3-9 s in duration (Fig. 14). They were longer than the harmonic calls recorded in the Western Arctic, which were generally only 1-2 s in duration. Harmonic (pulsed tone) calls comprised a high proportion of the calls recorded at Isabella Bay (51%, or 455 of 890). All of these calls were recorded during two recording sessions, and the majority occurred on 6 Sept 1984. Fully 91% of the calls recorded on that occasion (324 of 358) were harmonic calls. During that session, a trio of whales involving a pair and an escort engaged in intensive interactions, including much tail lofting and slapping.

Pulsive sounds accounted for 31% of the calls recorded at Isabella Bay (280 of 890). The pulsive sounds were similar to the roars, trumpeting and screams heard occasionally during the spring and summer seasons in the western arctic (Clark and Johnson 1984; Ljungblad et al. 1982, 1987; Würsig et al. 1985b). These pulsive sounds were also very reminiscent of the sequences of complex pulsive calls produced by sexually active groups of southern right whales (Clark 1983).

High FM calls accounted for 6% of all calls recorded at Isabella Bay (54 of 890). All high FM calls were associated with complex pulsive calls, as has been observed for Western Arctic bowhead calls from other seasons. This further substantiates the conclusion that high FM calls are associated with socially and sexually active whales.

All of the simple FM calls (UP, DOWN, CONStant, and INFLected) recorded in Isabella Bay were of very weak intensity, as indicated by the poor signal to noise ratio in Fig. 14. This strongly implies that they were produced by distant whales and not by any of the socially active whales under visual observation near the recording sites. Also, simple FM calls comprised only 11% of all calls recorded at Isabella Bay (101 of 890). These simple FM calls were essentially identical to the simple FM calls recorded from Western Arctic bowheads during spring and summer.

A comparison of the types and proportions of the bowhead sounds recorded at Isabella Bay vs. in the Western Arctic appears later in this report.

Surfacing-Dive Cycle.--Most active social interactions observed in detail at Isabella Bay involved bowheads in shallow waters over the Isabella Bank. To obtain a relatively homogeneous dataset for analysis, we selected observations of bowheads engaged in social interactions in water ≤50 m deep. (See 'Methods', p. 29, for more specific selection criteria.)

The durations of surfacings and dives of the socializing whales, and the number of blows per surfacing, all tended to be low (Fig. 15). During an average surfacing-dive cycle, a whale socializing in shallow water at Isabella Bay dove for 1.6 rein, surfaced for 1.2 rein, and respired 2 times during the surfacing. Corresponding average values for feeding whales in deep water were 15.8 min for dives, 4.7 min for surfacings, and 17 blows per surfacing (Fig. 13). As shown later, values of these three variables for whales engaged in local travel and migration in the eastern arctic were intermediate between those of socializing and feeding whales. For all three variables, the differences among categories of whales in the eastern arctic were highly significant ($P<0.001$).

The mean duration of surfacing for socializing whales at Isabella Bay, 1.2 ± s.d. 1.8 min (n = 78, range 0.02-12.1 rein), was similar to the 1.2 ± 0.8 min (n = 76) reported by Würsig et al. (1985b) for actively socializing whales summering in the western arctic. We counted all surfacings of bowheads whose general activity during the observation session as a whole was socializing, Active socializing occurred during only about 20% of these surfacings (Table 4)* In contrast, Würsig et al. considered only whales that were actively socializing during the surfacing in question. However, the western arctic results proved to be about the same (1.1 + 0.7, n = 276) when we recomputed the mean based on the same procedures used for the Isabella Bay data. For socializing whales at Isabella Bay, surfacings <30 s in duration were by far the most common. Of the 78 surfacings depicted in Fig. 15C, 38 were <30 s in duration. The '<30 s' category was not the modal category for any of the other three whale activities examined in the eastern arctic.

Given the short surfacings (and dives) of socializing whales, it is not surprising that the number of blows per surfacing also tended to be low. The mean of 2.1 ± s.d. 2.9 blows per surfacing (n = 35, range 0-11) at Isabella Bay was low not only relative to other categories of bowheads in the eastern arctic, but also relative to results from the Beaufort Sea. Würsig et al. (1985b) observed 3.9 ± 2.2 blows/surfacing (n = 61) for actively socializing bowheads in the Beaufort Sea in summer. Our reanalysis of the Beaufort data showed 4.6 ± 3.0 blows/surfacing (n = 224) when based on the same criteria as applied at Isabella Bay. The east-west difference was highly significant ($t = 4.67$, $df = 257$, $P<0.001$).

The mean dive duration at Isabella Bay, 1.6 ± s.d. 1.7 min (n = 45, range 0.1-7.8 rein), was very short--not much longer than the mean duration of surfacing (1.2 rein). This result, coupled with the shallow water at the locations of the socializing whales, indicates that they spent most or all of their time close to the surface, and almost half (42%) of their time at the surface. Forty-two percent is an unusually high proportion of time at the surface for bowheads--higher than for other categories of whales in the eastern arctic, and higher than has been found in the western arctic.

The interval between successive blows within a surfacing averaged 17.7 ± 11.6 s (n = 50 surfacings, range 8-84 s) for socializing whales in shallow water at Isabella Bay (Fig. 15A). This mean was very similar to the means for feeding whales (Fig. 13) and for whales engaged in local travel and migration (Fig. 16, 17, later) ($F' = 0.89$, $df = 3,97$, $P>0.05$).

Table 7. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables bowheads socializing in shallow (≤50 m) water in Eastern Arctic, 1984.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Date	1-76[c]	ns		ns		ns		---	
Date[2]	(1-76)^2	ns		ns		ns		---	
Time	0-24[d]	ns		ns		+		na	
Time^2	(0-24)^2	na		ns		++	++	ns	
Sea State	Bf	ns		ns		ns		---	---
Ice Cover	%								
>5% Ice Cover?[b]	0-1[b]								
Dist. from Shore	log (km)	ns		ns		ns		---	
Water Depth	log (m)	+++	+++	ns		ns		++	
Group Activ = Trav. + Soc.	0-1[b]	ns		ns		+		++	
" " = Trav. + Feed	"								
" " = Sot. + Feed	"								
No. Bhd. Within 1 km	No.	--		ns		ns		---	
Group Size	1-3	ns		ns		ns		ns	
Active Socializ.?[b]	0-1[b]	ns		ns		ns		ns	
Passive Socializ.?	"	+				ns		+	
Aerial Behav.?	"	ns		ns		ns		ns	
Pre-dive Flukes?	"	ns		ns		ns		ns	
Sample Size		53	53	26	26	37	37	38	38
Multiple Correlation			0.519				0.428		0.623
% Variance Explained			26.9				18.3		38.8
Adjusted % Var. Expl.			24.0				15.9		37.1
Overall Significance			***				**		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships
***, +++ or --- means P≤0.001   *, + or - means 0.05≥P>0.01
**, ++ or -- means 0.01≥P>0.001   ns means P>0.05
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so for socializing whales, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables significant (nominal P≤0.05) according to stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Ott = 62.

[d] All Eastern Arctic data in EDT.

[e] In degrees and decimal degrees.

Factors Affecting the Surfacing-Dive Cycle.--Durations of surfacings by socializing whales at Isabella Bay were strongly correlated with only two of the variables examined (Table 7). Even though all data that were considered were from water ≤50 m deep, surface times tended to increase with increasing water depth ($P<0.001$). Also, the larger the number of bowheads within about 1 km, the shorter the surfacings, on the average ($P<0.01$). Multiple regression analysis indicated that once the correlation of surface times with water depth (log transformed) was taken into account, there was no significant partial correlation with number of whales within 1 km. However, the number of bowheads within 1 km was correlated with water depth to a sufficient extent ($r = -0.17$) that it was not possible to determine which of these two variables actually affected surface times.

The number of blows per surfacing was not significantly correlated with any of the variables examined. Mean blow interval was strongly correlated only with time of day ($P<0.01$; Table 7). Blow intervals tended to be somewhat longer late in the day.

Durations of dives by socializing whales showed strong ($P<0.001$) negative correlations with several variables: date, sea state, distance from shore, and number of bowheads within 1 km (Table 7). There were also somewhat weaker ($P<0.01$) positive correlations with water depth and the occurrence of traveling as well as socializing. However, these variables were all interrelated. The strongest simple correlation was with sea state. Once that relationship was taken into account, there was no significant partial correlation with any other variable. It is not possible to determine whether sea state actually affected dive times, or whether the apparent effect was attributable to one of the other interrelated variables.

Thus, for socializing whales three of the four surfacing, respiration and dive variables were strongly related to few or none of the environmental variables. One variable, the dive duration, was correlated with a suite of interrelated factors. However, it is possible that only one of these variables had a causal influence.

Other Behavioral Variables.--Almost all socializing bowheads whose swimming speed was estimated were either stationary or traveling slowly (Table 4A). Moderate and fast swimming was very uncommon during social interactions.

Active interactions with another nearby whale occurred during 20% of the surfacings--a much higher percentage than for whales engaged in other activities. In addition, during another 27% of the surfacings (also a very high percentage), one or more additional whales were <½ body length away, but without any active interaction (Table 4B).

Aerial behavior was very frequent during socializing. One or more aerial activities occurred during 48% of the surfacings--a very high percentage in comparison with other situations in the eastern or western arctic (Table 4C). Flipper slaps were especially common, but tail slaps and breaches also occurred more commonly among socializing whales than among other whales in the eastern arctic (Table 4C).

E. Arctic Local Travel

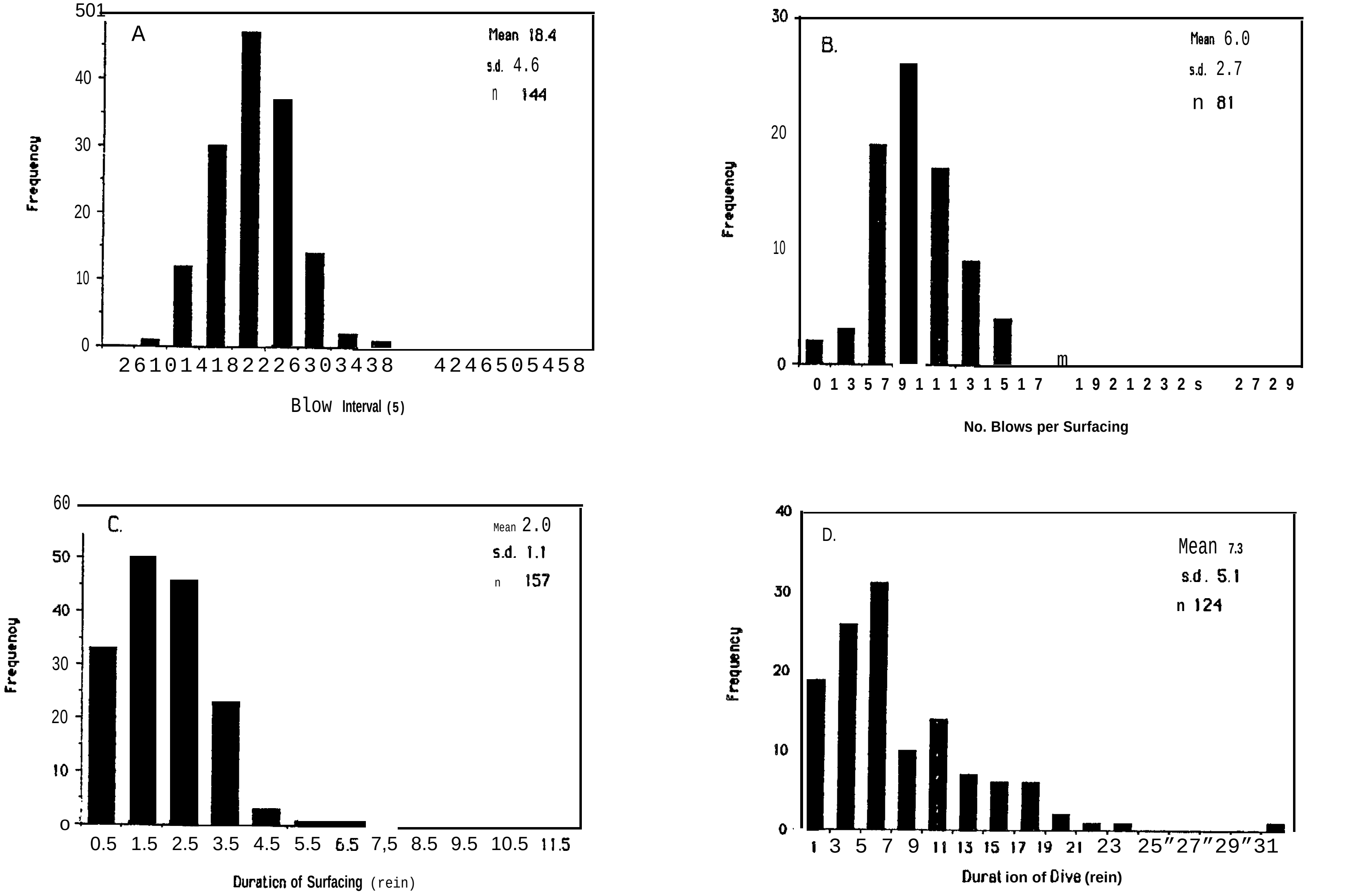

Figure 16. Frequency distributions of surfacing, respiration and dive variables for undisturbed bowheads engaged in local travel at Isabella Bay, eastern arctic.

During local travel, an average cycle consisted of a 7.3 min dive and a 2.0 min surfacing with 6 respirations. Based on the average surface and dive durations, eastern arctic bowheads were at the surface about 21% of the time during local travel, as opposed to 23% during feeding, 42% during socializing and 14% during migration.

Intervals between successive blows within a surfacing averaged 18.4 s (Fig. 16A). This was the highest average for any of the four categories of whales studied in the eastern arctic, but differences among those categories were slight and not statistically significant ($F' = 0.89$, $df = 3,97$, $P>0.05$).

Because few of the western arctic data could be assigned specifically to whales engaged in local travel, no comparisons with western arctic data are possible.

Factors Affecting the Surfacing-Dive Cycle.--During local travel, the duration of surfacing was strongly correlated with several environmental and other variables (Table 8). Surface times tended to be low for the two whales observed briefly in 1983 and low in the presence of ice. Surface times tended to be higher late in the season, for whales far from shore over deep water, and for whales in larger groups. Most of these apparent relationships seemed to be a result of the few 1983 observations, when ice cover was greater than average, the observation date was relatively early in the season, and the whales passed close to shore in shallow water. Once the unusually low surface times observed in 1983 were taken into account by multiple regression, only the correlation between long surface times and larger group sizes remained significant at the $P<0.01$ level.

The number of blows per surfacing was not strongly related to any of the variables considered but the mean blow interval was positively correlated with several variables (Table 8). Blow intervals tended to be longer late in the season, with higher sea states, well offshore over deeper water, and with larger group sizes. Blow intervals also tended to be shorter during surfacings that ended with a fluke-out dive. The 'distance from shore' effect was strongest, and was probably responsible for the simple correlations with several related variables. Once 'distance from shore' was taken into account, most of the other partial correlations were not significant.[12]

Dive durations during local travel were not strongly correlated with many variables. Only a negative correlation with the number of bowheads within 1 km was significant at the $P\leq0.01$ level (Table 8).

Other Behavioral Variables.--Whales engaged in local travel were most commonly singletons; for 58% of the surfacings there was no other whale within 5 body lengths. Pairs were also common (36%, Table 3A). Active socializing was rare during local travel (only 1% of surfacings, Table 4B). Flipper and tail slaps were slightly more common, with one or the other occurring during 5% of

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[12] A strong negative partial correlation between mean blow interval and water depth was a spurious result associated with the strong positive correlation of blow intervals with the closely-related 'distance from shore' variable ($r = 0.82$ for log water depth vs. log distance from shore).

Table 8. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables bowheads engaged in local travel in Eastern Arctic, 1983-1985.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (*l)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 83	0-1[b]	---	---					ns	
Year = 84	"	St[g]		St		St		St	
Year = 85	"	+						ns	+
Date	1-76[c]	+++		ns		+++		ns	
Date[2]	(1-76)[2]	+++		ns		+++	+	ns	
Time	0-24[d]	ns		na		ns			
Time[2]	(0-24)2	ns		ns		ns			
Sea Stare	Bf	ns		ns		++		ns	
Ice Cover	%	---		ns		ns		ns	
>5% Ice Cover?[b]	0-1[b]	---		ns		ns		ns	
Dist. from Shore	log (km)	+++		ns		+++	+++	ns	
Water Depth	log (m)	++		na		++	---	ns	
Group Activ = Trav. + Sot.	0-1[b]								
" " = Trav. + Feed	"								
" " = Sot. + Feed	"								
No. Bhd. Within 1 km	No.	ns		ns		ns	--	--	--
Group Size	1-2	+++	++	+	+	++		na	
Active Social iz.?[b]	0-1[b]								
Passive Social iz.?	"								
Aerial Behav.?	"	ns		ns		ns			
Pre-dive Flukes?	"	ns		ns		--		ns	
Sample Size		110	110	62	62	90	90	67	67
Multiple Correlation			0.544		0.268		0.647		0.444
% Variance Explained			29.6		7.2		41.9		19.7
Adjusted % Var. Expl.			27.6		5.6		39.1		17.2
Overall Significance			***		*		***		***

a The four dependent variables were all logarithmically transformed to avoid skewness.

Pluses indicate positive and significant correlation or partial correlations; minuses indicate negative relationships

***, +++ or --- means P<_0.001   *, + or - means 0.05>_P>0.01

**, ++ or -- means 0.01>P>0.001   ns means P>0.05

Blanks in the simple correlation columns denote variablea that were not analyzed because they were constant or nearly so for whales engaged in local travel, or because the value waa unknown for a considerable proportion of the otherwise-usable cases. Partial correlation are shown only for those variables significant (nominal P<0.05) according to stepwise multiple regression.

b 0 = False, 1 = True.

c In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Ott = 62.

d All Eastern Arctic data in EDT.

e In degrees and decimal degreea.

g 'St' denotes 'Standard' year againat whose results other years were compared by dummy 'year' variables.

the surfacings (Table 4C). No breaches were noted during local travel. Most surfacings (88%) terminated without the flukes being raised above the surface (Table 4D).

Summary. --Local travel was a common activity of whales at Isabella Bay, mainly involving singletons or pairs of whales. Swimming speeds were usually slow. Durations of surfacings and dives were intermediate between the high values of feeding whales and the low values of socializing whales. The same was true of the number of blows per surfacing. That variable, along with dive duration, was not correlated with many of the environmental variables considered. Surface times and blow intervals were correlated with several other variables; however, these results seemed to be largely a result of a relationship to one dominant variable that affected several of the others. Little active socializing occurred during local travel. Flipper and tail slaps were somewhat more common, but still infrequent. Most dives began without the flukes being raised above the surface.

Behavior of Migrating Bowheads in Eastern Arctic

Timing. --During late September and early October the component of the eastern arctic bowhead population that summers in the high arctic archipelago migrates southward along the east coast of Baffin Island. These whales may include many immatures plus most of the females with calves, although there is little direct evidence on this point.

The timing of this southward migration appears to be quite consistent. In both 1978 and 1979 the bulk of the migration occurred during the first week of October (Table 9). Similar numbers of bowheads were recorded in both years: 41 were seen going south past Cape Adair in 1978, 44 in 1979. When periods with no observations were taken into account, at least double these numbers were estimated to have passed. When sightings during aerial surveys were also taken into account, it was estimated that about 140 bowheads may have migrated south past Cape Adair during the autumn of 1979 (Koski and Davis 1980).

Observations at Isabella Bay, 240 km south of Cape Adair, were extended as late as 9 October during 1986 in an attempt to document the continuation of the southward migration. However, only 5 migrant whales were seen, on 5-7 October (Finley 1987). In 1987 observations continued until 3 Ott and only 2 migrants were seen (Finley in prep.). It appears that the bulk of the southward migration past Isabella Bay occurs later in October even though it would be theoretically possible for whales to travel the distance between Cape Adair and Isabella Bay (Fig. 2) in 40-48 h if they sustained a rate of 5-6 km/h. It is possible that the migration at the latitude of Isabella Bay is less restricted temporally and spatially than that at Cape Adair because of the proximity of Isabella Bay to the bowheads' wintering grounds in Davis Strait.

Almost all of the available data on migrating Eastern Arctic bowheads were collected during early October (Table 2A). Most of the observations were of singletons (73% of surfacings), with some data on pairs (20%) and a few observations (6%) of a group of three (Table 3A).

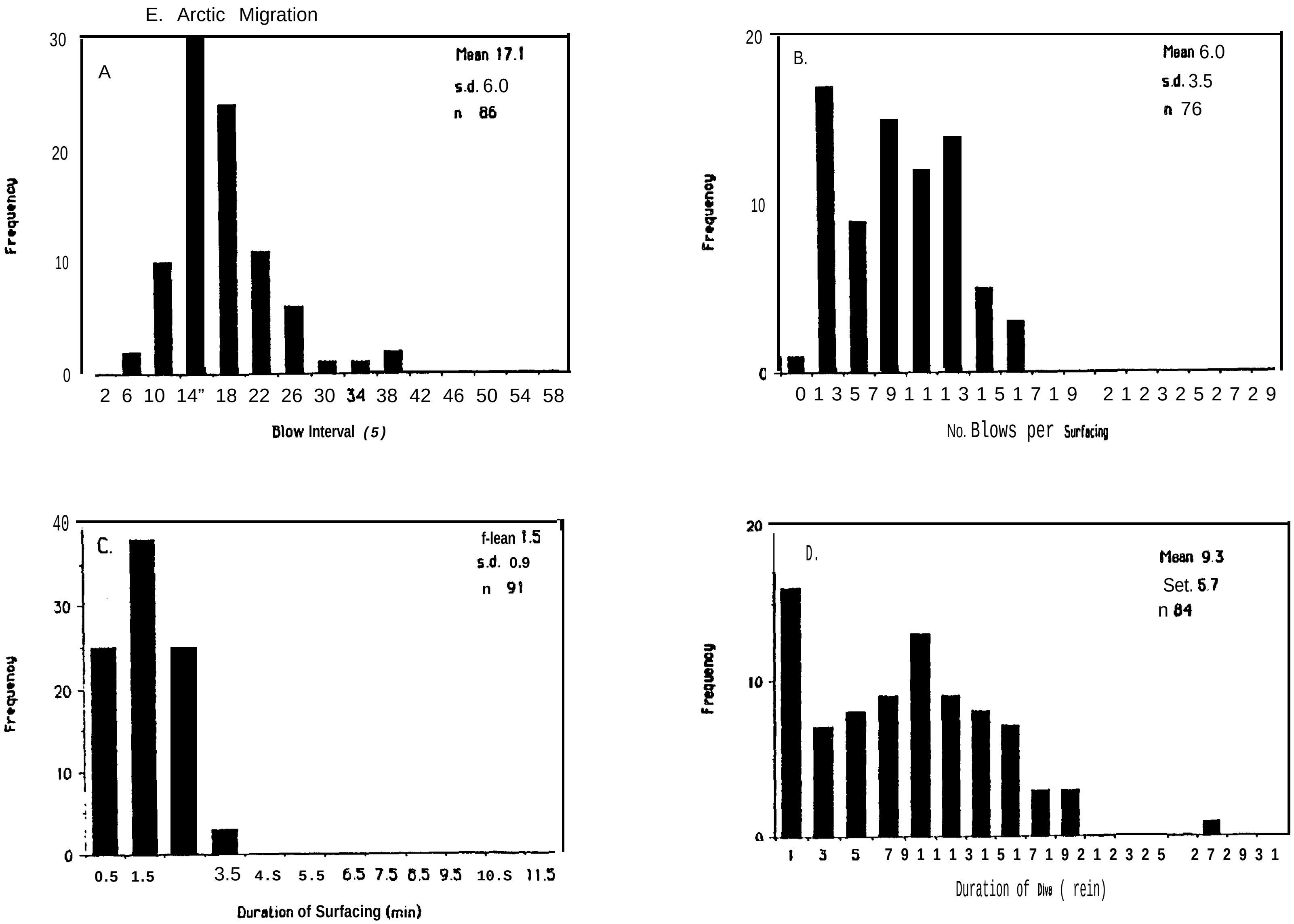

Figure 17. Frequency distributions of surfacing, respiration and dive variables for migrating bowheads at Cape Adair and Isabella Bay, eastern arctic.

A low percentage of time at the surface has also been noted during migration through the Alaskan Beaufort Sea (Fraker et al. 1985; Richardson et al. 1987b, p. 300). Based on our reanalysis of western arctic data, whales were at the surface only 10% of the time during autumn migration through the Alaskan Beaufort Sea, as opposed to 13% during feeding in deep water and 30% during socializing in shallow water.

The intervals between successive blows during migration averaged 17.1 ± s.d. 6.0 s (n = 86, Fig. 17). This mean was similar to the means for other categories of whales in the eastern arctic (cf. Fig. 13, 15, 16). This mean also was nearly identical to the corresponding value for migrating whales in the western arctic, 17.2 ± 7.5 s (n = 148).

Factors Affecting the Surfacing-Dive Cycle.--During migration along Baffin Island, surfacings tended to be short when sea state was high, and long when whales were in groups rather than singletons (Table 10). These two effects both remained significant when considered simultaneously via multiple regression.[14]

The number of blows per surfacing tended to be lower late in the migration season, but was not strongly ($P<0.01$) related to any other variable. Mean blow interval showed no strong simple correlation to any variable, although there was evidence of somewhat longer blow intervals late in the season (Table 10).

Dive durations tended to be reduced late in the migration season based on the simple correlation analysis (Table 10). However, there was no significant partial correlation between dive duration and date. There was evidence of reduced dive durations (as well as surface times) with high sea states.[15]

Other Behavioral Variables.--There was virtually no evidence of active socializing during migration. Aerial behavior was rare. About 58% of the surfacings ended with a fluke-out dive; this was a higher percentage than during local travel or socializing, but lower than during feeding in deep water (Table 4).

Summary.--Migrating bowheads travelled consistently southward at comparatively high speed, usually as singletons or pairs. Typical travel speeds were about 5-6 km/h. These speeds can be maintained over periods of several hours, and in one case probably for at least 28 h. The peak of the

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14 Multiple regression also revealed a negative partial correlation to the number of bowheads within 1 km. Since that variable was strongly related to group size (r = 0.74), and "group size was positively related to surface time, the negative partial correlation of surface time with 'no. bowhead within 1 km' was undoubtedly spurious.

15 Dive duration also may have been related to group size and/or the number of whales in the area (Table 10). However, the inconsistent directions of partial correlation, together with the lack of a strong simple correlation with either variable, suggests that these effects were spurious.

Table 10. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables bowheads migrating in Eastern Arctic, 1979 and 1986.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 79	0-1[b]	St[g]		St		St		St	
Year = 86	"	ns		ns		ns		ns	
Date	1-76[c]			--		+		--	
Date²	(1-76)²			--	--	+	++	--	
Time	0-24[d]	ns				ns			
Time²	(0-24)²	ns				ns			
Sea State	Bf		---			ns			---
Ice Cover	%	ns		ns		ns		ns	
>5% Ice Cover?[b]	0-1[b]								
Dist. from Shore	log (km)								
Water Depth	Log (m)								
Group Activ = Trav. + Soc.	0-1[b]								
" " = Trav. + Feed	"								
" " = Soc. + Feed	"								
No. Bhd. Within 1 km	No.	ns	---	Its		ns		ns	---
Group Size	1-3	++	+++	ns		ns	+	+	+++
Active Socializ.?[b]	0-1[b]								
Passive Socializ.?	"								
Aerial Behav.?	"								
Pre-dive Flukes?	"								
Sample Size		89	89	74	74	82	82	86	86
Multiple Correlation			0.545		0.496		0.371		0.624
% Variance Explained			29.7		24.6		13.8		38.9
Adjusted % Var. Expl.			27.2		21.3		11.6		36.7
Overall Significance			***		***		**		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships
***, +++ or --- means P≤0.001   *, + or - means 0.05≥P>0.01
**, ++ or -- means 0.01≥P>0.001   ns means P>0.05
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so for migrating whales, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables significant (nominal P≤0.05) according to stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Oct = 62.

[d] All Eastern Arctic data in EDT.

[e] In degrees and decimal degrees.

[g] 'St' denotes 'Standard' year against whose results other years were compared by dummy 'year' variables.

migration past Cape Adair was in early October during each of the two years of observation there (1978-79). The migration corridor was within 1½ km of shore at Cape Adair and probably also at Isabella Bay (observations at the latter location usually have not 'extended late enough into the autumn to document the peak of migration). Mean duration of surfacing, duration of dive, and number of blows per surfacing were intermediate between values for feeding and socializing whales, and generally similar to values during local travel. However, migrating whales spent less time at the surface (14%) than any other category of whale. Durations of both surfacings and dives by migrating bowheads tended to be lower when sea state was high than when it was near-calm. Socializing and aerial activity were very uncommon during migration. Fluke-out dives were common, although less so than during feeding in deep water.

Comparison of Behavior in Eastern vs. Western Arctic

Feeding Bowheads

Comparability of Data.--At Isabella Bay, most of the feeding that could be observed in detail was in one specific location--in the deep water over the NE Trough (Fig. 6). As discussed earlier, most of these whales fed in ice-free water 100-250 m deep several kilometers from shore (Table 2C-E). Their feeding mode was generally consistent with the water column feeding described previously in the western arctic (Würsig et al. 1985a,b). Several types of indirect evidence suggested that these whales were usually feeding at considerable depths on concentrations of large copepods:

- The surfacings and dives were long, with many respirations per surfacing; in gray and humpback whales, these parameters tend to increase with increasing depth of dive.

- Fecal samples (n = 2) contained large copepods.

- The maximum zooplankton concentration consisted of large copepods at depths exceeding 100 m.

The bowheads at Isabella Bay, presumably including those feeding over the NE Trough, consisted mainly of adults and large subadults (Fig. 8).

Feeding in the Beaufort Sea during summer was a much more variable phenomenon. This is not surprising, considering the wide variety of locations within the Beaufort Sea where whales were observed (Fig. 4). Water-column feeding was inferred to have occurred very commonly at most locations where bowheads were observed, including shallow as well as deep sites. In addition, bowheads in shallow waters of the Beaufort Sea sometimes fed near the bottom or near the surface. Whale sizes were rarely determined at the specific times and places where behavior was observed. However, the bowheads found over the outer shelf and shelf break (about 50-500 m deep) were predominantly large subadults and adults in the years when photogrammetry projects were conducted in these areas. In contrast, the bowheads feeding in shallow water were predominantly small subadults (Koski et al. 1988).

Thus , the whales and whale activities over and beyond the outer shelf of the Beaufort Sea were similar in several ways to those over the NE Trough at Isabella Bay. In contrast, the many observations of whales feeding in shallow waters of the Beaufort Sea had no counterparts at Isabella Bay. For this reason, the feeding whales considered in this report were restricted to those feeding in waters >50 deep, exclusive of mothers and calves (which were absent at Isabella Bay). We also excluded whales that, at the time of observation, were engaged in active socializing, bottom feeding, or near-surface feeding. Whales that were potentially disturbed by nearby industrial activities were also excluded (see Methods).

Application of these criteria resulted in more directly comparable data from the east and west, although at the expense of a great reduction in the sample size for feeding bowheads in the western arctic. Even then, however, there were some differences in the situations in which feeding bowheads were observed in the two regions, Feeding bowheads were observed at a wide range of times of day in both regions (Table 2B). However, the majority (68%) of the eastern observations were in early September, whereas in the west almost all observations were in August (91%, Table 2A). Because of the gentler slope of the bottom in the Beaufort Sea, whales feeding in water >50 m deep tended to be much farther from shore in the west than in the east (Table 2C). Even after the observations in water ≤50 m deep were excluded, depths at feeding locations were more variable in the Beaufort Sea than at Isabella Bay. In the Beaufort Sea, there were similar numbers of observations over 50-99 m of water, 100-250 m, and >250 m. At Isabella Bay, almost all cases were over 100-250 m (Table 2D). Ice cover near feeding whales at Isabella Bay was almost always zero, whereas whales feeding in deep waters of the Beaufort often were in light ice conditions (Table 2E).

Besides these unavoidable differences in physical conditions at observation locations, there were also differences in the typical numbers and activities of the whales present (Table 3). At Isabella Bay, feeding whales were most commonly singletons (60%) or pairs (31%). In the Beaufort, singletons were more common (85%) and pairs much less common (4%). For this comparison, whales within 5 body-lengths of one another were counted as being members of the same group. On a larger scale, the approximate number of whales within 1 km never exceeded 6 for the systematic observations at Isabella Bay, whereas it was 7 or more 61% of the time in the Beaufort (Table 3B). This seemingly large difference is probably not particularly important for the present comparisons of feeding whales, since whales feeding in the water column seem to feed largely independently of one another both at Isabella Bay and in the Beaufort.

Differences in overall activities were probably more important as confounding factors. In the Beaufort Sea, whales that were classed as feeding often intermixed their feeding with local travel or socializing (26% and 41% of observations, respectively--Table 3C). Only 34% of the observations of whales feeding in deep water in the Beaufort were of whales whose general activity was classed as feeding only, with no travel or socializing. In contrast, at Isabella Bay 93% of the observations of feeding whales came from whales whose general activity was classed as feeding only. It would have been desirable to consider only the 'feeding only' cases. However, this was impractical because, in deep waters of the western arctic, the sample of 'feeding only' observations was too small to be useful. As noted later, multiple regression analysis was used to take account of the potentially confounding effects of east-west differences in the frequency of socializing or local travel by feeding whales.

Univariate Comparisons.--Several aspects of the behavior of whales feeding in deep water were similar in the eastern vs. western arctic. In both areas, swimming speeds while at the surface between feeding dives were commonly zero, slow or moderate, and rarely fast (Table 4A). Close social interactions were very infrequent in both areas. Passive interactions (whales $\leq \frac{1}{2}$ body-length apart and parallel to one another) occurred during only 1% of the surfacings in the east and 3% in the west (Table 4B). Active interactions, in which the whales touched or oriented toward one another at close range, were rare among feeding whales, and in any event these few cases were excluded from consideration. Aerial activities were also infrequent in both areas, occurring during only 3% of the surfacings in the east and 5% in the west (Table 4C). The flukes were commonly raised above the surface at the onset of a feeding dive in both areas, although the sample size from the western arctic was too low for statistical analysis (Table 4D).[16]

There were highly significant east-west differences in the surfacing - respiration - dive cycles of bowheads feeding in deep water. Durations of surfacings averaged 4.74 min in the east vs. 1.66 min in the west ($P<0.001$, Table 11C). The 4.74 min value is very long relative to the surface times not just for feeding whales in the western arctic, but for any other category of bowhead in the western (or eastern) arctic. Similarly, the mean number of respirations per surfacing was much higher in the eastern arctic (17.3) than in the west (6.9, $P<0.001$, Table 11B). Again, the 17.3 figure for feeding whales in the eastern arctic is much higher for any other whale category in either the west or the east.

The intervals between successive blows were more similar in the east and west, averaging 16.9 vs. 15.0 s, respectively. However, after a logarithmic transformation to reduce the effects of rightward skew, especially in the western data, the difference was significant ($P<0.001$, Table 11A).

Durations of dives in the eastern arctic also tended to be greater than those for whales in >50 m of water in the west. However, the difference was only marginally significant ($0.05>P>0.01$). The average dive durations were 15.8 min in the east vs. 11.1 min in the west (Table 11D).

Overall, the surfacing-dive cycles of whales feeding off Isabella Bay tended to be longer than those for whales feeding in deep water of the Beaufort Sea. As discussed earlier, these results probably mean that bowheads were feeding deeper in the water column off Isabella Bay (see 'Results--Feeding at Isabella Bay').

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16 The low sample size from the western arctic occurred because the FLUKES variable was not coded in 1980-82. Most observations of western arctic bowheads feeding in deep water came from 1981-82.

Table 11. Summary statistics and comparisons for surfacing, respiration and dive variables. 'Western Arctic Migration' column includes LGL (1985-86) and NOSC (1983) data; see Table 17 for separate 1985-86 and 1983 results.

F represents results of simple l-way ANOVA among whale categories. E vs. W comparisons are based on t-tests. Where the ' symbol appears, the variances differed and a modified t-test or ANOVA not assuming equal variances was used.

*** p < 0.001   ** 0.001 < p < 0.01   * 0.01 < P < 0.05   ns P > 0.05

	Eastern Arctic						Western Arctic			
	Feeding in deep water	Social in shallow water	Local travel	Migration	Comparison of four E arctic categories		Feeding in deep water	Social in shallow water	Migration	Comparison of three W arctic categories
A. MEAN BLOW INTERVAL (S)										
Mean	16.936	17.660	18.385	17.092	F' = .89	Mean	15.032	12.902	17.184	F = 15.63
SD	3.697	11.623	4.607	6.006	df = 3, 97	SD	13.289	7.186	7'.472	df = 2, 801
N	86	50	144	86	ns'	N	131	525	148	***
Min.	10	8	7	6		Min.	7.6	2	3	
Max.	28.5	84	32.3	38		Max.	158	113	68	
E/W	[ns][b]	***'		ns						
LOGMBI[a]										
Mean	1.219	1.203	1.250	1.209	F' = 2.51	Mean	1.136	1.073	1.203	F = 37.28
SD	.091	.171	.115	.145	df = 3, 182	SD	.149	.172	.166	df = 2, 801
E/W	***'	***		ns	(*)'					***
B. NUMBER OF BLOWS PER SURFACING										
Mean	17.304	2.143	5.963	5.961	F' = 56.74	Mean	6.892	4.585	6.534	F' = 13.44
SD	6.718	2.861	2.704	3.542	df = 3, 47	SD	4.545	2.969	3.266	df = 2, 150
N	23	35	81	76	***'	N	65	224	73	***'
Min.	6	0	0	0		Min.	1	0	1	
Max.	27	11	15	14		Max.	19	13	14	
E/W	***'	***		ns						
LOGNBL[a]										
Mean	1.227	.359	.804	.772	F' = 53.29	Mean	.810	.677	.829	F' = 12.79
SD	.191	.340	.204	.271	df = 3, 114	SD	.298	.259	.219	df = 2, 176
E/W	***'	***'		ns	***'					***'

Continued. . .

Table 11 (Concluded).

	Eastern Arctic						Western Arctic			
	Feeding in deep water	Social in shallow water	Local travel	Migration	Comparison of four E arctic categories		Feeding in deep water	Social in shallow water	Migration	Comparison of three W arctic categories
C. DURATION OF SURFACING (rein)										
Mean	4.741	1.185	1.969	1.488	F' = 63.44	Mean	1.663	1.120	1.680	F' = 16.36
SD	1.770	1.806	1.143	.858	df = 3, 169	SD	1.058	.660	.952	df = 2, 173
N	46	78	157	91	*** '	N	73	276	78	*** '
Min.	1.033	.017	.033	.017		Min.	.133	.033	.033	
Max.	8.183	12.117	6.833	3.517		Max.	5.267	3.517	4.800	
E/W	*** '	[ns'][b]		ns						
LOGSFC[a]										
Mean	.636	-.508	.175	-.015	F' = 45.31	Mean	.104	-.087	.114	F = 11.07
SD	.208	.845	.410	.572	df = 3, 183	SD	.364	.425	.401	df = 2, 424
E/W	*** '	***'		(*)'	*** '					***
D. DUNATION OF DIVE (rein)										
Mean	15.799	1.639	7.323	9.330	F' = 44.77	Mean	11.050	2.654	14.560	F' = 35.40
SD	7.093	1.663	5.091	5.672	df = 3, 89	SD	9.947	3.817	8.455	df = 2, 90
N	29	45	124	84	***'	N	43	94	42	*** '
Min.	2.05	.13	.52	1.03		Min.	.10	.05	1.50	
Max,	29.62	7.82	31.60	27.50		Max.	30.98	17.50	29.95	
E/W	*	[*'][b]		[***'][b]						
LOGSUB[a]										
Mean	1.133	.043	.753	.862	F = 76.71	Mean	.664	.040	1.041	F' = 45.02
SD	.281	.389	.340	.347	df = 3, 278	SD	.761	.591	.384	df = 2, 99
E/W	[***'][b]	ns		**	***					*** '
E. % TIME AT SURFACE[c]										
	23	42	21	14			13	30	10	

[a] Mean ± s.d. for logarithmically transformed values. In the case of number of blows per surfacing, for which the value was occasionally zero, LOGNBL = $\log_{10}$ (NBLOWS + 1).

[b] Of the two tests on untransformed and log transformed data, the one whose significance level is shown in brackets appeared to be less reliable based on the shapes of the distributions.

[c] % time at surface estimated from 'mean surface time' divided by 'mean surface time' + 'mean dive time'

Multivariate Comparisons.--In evaluating the biological significance of the above differences, it is important to assess whether they can be accounted for by differences in the environmental situations or activities of the feeding whales. Whales feeding in deep water in the Beaufort Sea were farther offshore, and in a greater variety of water depths and ice cover conditions, than were those off Isabella Bay. The western data were also collected slightly earlier in the summer. Furthermore, group sizes and group activities of feeding whales differed somewhat between east and west.

Relationships between these corollary variables and the surfacing - respiration - diving behavior of feeding whales were examined by multiple regression analysis. The general approach, along with results for the eastern arctic, was presented and discussed earlier (see Table 5). Corresponding results for the western arctic are in Table 12. In the west, surfacing - respiration - diving variables of bowheads feeding in deep water were not strongly correlated with most potential predictor variables. A major exception was the 'Travel + Feed' variable. Western arctic bowheads that intermixed local travel with feeding tended to have longer surfacings and dives, with more blows per surfacing, than did whales whose activity was recorded as 'feeding only' ($P<0.001$ in each case). Bowheads engaged in 'traveling + feeding' contributed a much higher proportion of the 'feeding' data in the west than in the east (26% vs. 4%, Table 3C). Thus, we need to allow for this difference when comparing surfacing - respiration - diving cycles in the eastern and western arctic.

Table 13 compares the surfacing - respiration - diving cycles of bowheads in the eastern vs. western arctic before and after allowance for differences in these types of corollary variables. The top row of the table shows the significance of the east-west differences before allowance for corollary variables (simple correlation columns) and after such an allowance (partial correlation columns). The technique used was to merge the eastern and western arctic datasets, and to add a 'dummy' predictor variable distinguishing eastern from western arctic cases. To test the null hypothesis of no east-west difference in whale behavior, we examined the significance of the partial correlation of the dependent (behavior) variable with the dummy 'east vs. west' variable after allowance for partial correlations with other predictor variables.

The most important result is that the duration of surfacing and number of blows per surfacing were highly significantly greater in the eastern arctic (nominal $P<0.001$) even after allowance for the confounding effects of other variables. As expected, the 'travel + feed' effect discussed above was the most notable confounding variable. When local travel was interspersed with feeding, as often occurred in the western arctic, surface times and number of blows per surfacing tended to be high. However, the partial correlation columns show that even after this effect was taken into account, surface times and the number of blows per surfacing were highly significantly greater in the eastern arctic than in the west.

The east-west difference in blow intervals did not seem to be significant after the effects of other variables (mainly date) were taken into account. However, closer examination of the data shows that there almost certainly was a real east-west difference in mean blow intervals. There was overlap between

Table 12. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables bowheads feeding in deep (>50 m) water in Western Arctic, 1981-1984. (No suitable data in 1980, 1983, 1985-86.)

Predictor Variable		Duration Of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration Of Preceding Dive (min)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 81	0-1[b]	ns				ns		---	--
Year = 82	"	St[g]		St		St		St	
Year = 84	"	ns		ns		ns		ns	+++
Date	1-76[c]	ns		ns		ns		ns	
Date[2]	(1-76)[2]	ns		ns		ns		ns	
Time	0-24[d]	ns		ns				ns	
Time[2]	(0-24)	ns		ns				ns	
Longitude	°W[e]	ns		Its		ns		+	
Sea State	Bf	as		ns		ns		ns	
Ice Cover	%	ns		ns		Its		Its	
>5% Ice Cover?[b]	0-1[b]	ns		ns		ns		ns	
Disc. from Shore	Log (km)	ns		ns		ns		ns	
Water Depth	log (m)	ns		ns		ns		·	
Group Activ = Trav. + Soc.	0-1[b]								
" " = Trav. + Feed	"	++	+++	+++	+++	ns		+++	+++
" " = Soc. + Feed	"	ns		-		ns		---	++
No. Bhd. Within 1 km	No.	ns	+	ns		ns			
Speed of Motion	0-3 f								
Group Size	1-4	ns		ns		ns			
Active Socializ.?[b]	0-1[b]								
Passive Socializ.?	"	ns		ns		ns			
Aerial Behav.?	"	ns		ns		ns		ns	
Pre-dive Flukes?	"								
Sample Size		58	58	50	50	107	107	33	33
Multiple Correlation			0.494		0.546		0.199		0.895
% Variance Explained			24.4		29.8		4.0		80.1
Adjusted % Var. Expl.			21.7		28.4		3.0		76.4
Overall Significance			***		***		*		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships
***, +++ or --- means P≤0.001   *, + or - means 0.05≥P>0.01
**, ++ or -- means 0.01≥P>0.001   ns means P>0.05
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables significant (nominal P≤0.05) according to stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Oct = 62.

[d] All Western Arctic data converted to Pacific Standard Time in hours and decimal hours.

[e] In degrees and decimal degrees.

[f] 0 = No motion, 1 = slow, 2 = moderate, 3 = fast.

[g] 'St' denotes 'Standard' year against whose results other years were compared by dummy 'year' variables.

Table 13. Comparison of the surfacing, respiration and diving behavior of feeding bowheads in the eastern and western arctic after allowance for effects of environmental variables and whale activities.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Part ial	Simple	Partial
East (1) vs. West (0)	0-1	+++	+++	+++	+++	+++		ns	
Date	1-76[c]	+++		+++		+++	+++	+	
Date^2	(1-76)^2	+++		+++		+++		+	
T ime	0-24[d]	ns		ns				ns	
Time^2	(0-24)^2	ns		ns				ns	
Sea State	Bf	++		+++		++		ns	
Ice Cover	z	ns		ns		ns			---
>5z Ice Cover?[b]	0-1[b]	ns		ns		ns		ns	
Disc. from Shore	Log (km)					ns		ns	
Water Depth	log (m)	ns		ns		ns		ns	
Group Activ = Trav. + Sot.	0-1[b]								
" " = Trav. + Feed	"	ns	++	+	+++	ns		+++	++
" " = Sot. + Feed	"	---		---				---	---
No. Bhd. Within 1 km	No.								
Group Size	1-4	ns		ns		ns		---	
Active Social iz.?[b]	0-1[b]								
Passive Social iz.?	"	ns				ns			
Aerial Behav.?	"	ns		ns				ns	
Sample Size - E Arctic		36	36	19	19	80	80	20	20
W Arctic		58	58	50	50	107	107	33	33
Multiple Correlation			0.643		0.668		0.336		0.762
% Variance Explained			41.3		44.6		11.3		5s.1
Adjusted % Var. Expl			40.0		43.0		10.3		55.5
Overall Significance			***		***		***		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; ❑inuses indicate negative relationships
***, +++ or --- means $P \leq 0.001$ *, + or - means $0.05 > P > 0.01$
**, ++ Or -- means $0.01 \geq P > 0.001$ ns means $P > 0.05$
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables recognized as significant (nominal $P \leq 0.05$) by stepwise ❑ultiple regression.

b O = False, l = True.

c In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Ott = 62.

d All Western Arctic data converted to Pacific Standard Time in hours and decimal hours. All Eastern Arctic data in Eastern Daylight Time.

[e] In degrees and decimal degrees.

the eastern and western arctic field seasons, but most eastern data were collected somewhat later than most western data (Table 2A). Given this, plus the typically larger mean blow intervals in the east, it is not surprising that there was a strong positive correlation between mean blow interval and date when the eastern and western datasets were merged (Table 13). There was no significant correlation between blow intervals and date when either the eastern or the western arctic data were considered separately (Tables 5, 12). This strongly suggests that the mean blow interval vs. date correlations (simple and partial) in the pooled data represent an east-west difference rather than a real date effect.

Dive durations in the eastern arctic averaged somewhat longer than those in the west, but the difference was not as significant as for the three surfacing and respiration variables (Table 11D). Multiple regression analysis failed to identify a significant east-west difference in dive times (Table 13).

Summary.--Bowheads feeding in deep (>50 m) water off Isabella Bay exhibited much longer surface times and many more blows per surfacing than did those feeding in deep waters of the Beaufort Sea. Multivariate analysis indicated that these differences could not be accounted for by differences in any of the measured environmental variables or whale activities. Thus, we conclude that there were real east-west difference in these attributes of behavior. The eastern whales also had longer intervals between successive blows and longer dive durations, but the proportional differences were not as large. The difference in mean blow interval was probably an actual east-west difference, The cause of the slight east-west difference in mean dive durations was uncertain.

An important unknown factor is the actual depth to which the whale dove during each surfacing-dive cycle. In gray and humpback whales, depth of dive is strongly and positively correlated with most surfacing - respiration - dive variables (Würsig et al. 1986b; Dolphin 1987a,b). We suspect that an average feeding dive off Isabella Bay was considerably deeper than an average feeding dive in the Beaufort Sea. Prey concentrations probably occur at greater average depths off Isabella Bay. The evidence for this, and its implications with regard to the interpretation of east-west differences in behavior, are treated in the 'Discussion', later.

Socializing Bowheads

Comparability of Data.--At Isabella Bay, most of the socializing that was observed in detail was over the shallow 'Isabella Bank' close to the observation site (Fig. 6). Active social interactions were common, including considerable aerial activity, raucous underwater calling, and some obvious sexual interactions. Large subadult whales are believed to have been involved in most of the interactions among small groups of whales over Isabella Bank. In addition to these groups of socializing whales at Isabella Bank, 2-whale groups were more widely distributed in the Isabella Bay area. These 'pairs' are suspected to have consisted mainly of adult whales.

Socializing in the Beaufort Sea occurred widely in both shallow and deep waters. Although boisterous interactions similar to those noted commonly at Isabella Bay were seen in the Beaufort, most social interactions in the latter area were less dramatic. Whales in shallow water were predominantly small subadults (at least in the years when measured), whereas those farther offshore tended to be predominantly larger subadults and adults (Koski et al. 1988).

Based on previous analyses of western arctic data as well as preliminary analyses of eastern and western data during this project, we expected that most behavioral variables would be correlated with water depth. Most observations of socializing whales at Isabella Bay were in water ≤50 m deep. Thus, for east-west comparisons of socializing bowheads, we considered only the whales in ≤50 m of water. This criterion considerably reduced the sample size in the western arctic. Nonetheless the sample size for 'socializing bowheads in shallow waters of the western arctic' was larger than that for any of the other categories of whales in either the east or the west (Table 11). A more detailed listing of the case selection criteria for socializing bowheads is given in the 'Methods' (p. 29).

Even after restricting the data to observations in ≤50 m of water, there were several differences in the circumstances where socializing bowheads were observed. In the west, 67% of the observations of socializing were in August and only 32% in September, whereas in the east the percentages were more or less reversed--40% and 60% (Table 2A). Given the east-west differences in bottom slope, almost all (99%) of the eastern observations in ≤50 m of water were of whales <4 km from shore. In contrast, 81% of the western observations were >4 km offshore (Table 2C). Although all whales considered here were in ≤50 m of water, depths were less variable in the east than in the west. In the east 57% of the cases were in 10-19 m of water and 43% in 20-49 m. In the west 10% of the observations were in <10 m, 26% in 10-19 m, and 63% in 20-49 m (Table 2D). In both areas, most observations of socializing bowheads were in ice-free water, and observations were widely distributed throughout the daylight hours (Table 2B,E).

There were also some differences in the typical numbers and activities of the whales present (Table 3). Group size (i.e. number of whales within 5 body-lengths) was usually 1-4 in both regions. However, it was more commonly one in the west (53% of observations) than in the east (28%). This was probably indicative of the lower intensity of social activity during most observation sessions in the western arctic. On the other hand. the estimated number of bowheads within 1 km was usually greater in the west. For example, the approximate number within 1 km exceeded 5 only 3% of the time at Isabella Bay, but 79% of the time in the Beaufort Sea.

Within a given observation session at Isabella Bay, whales classified as socializing rarely interspersed their socializing with other activities such as local travel or feeding. In contrast, whales socializing in shallow waters of the Beaufort Sea were almost always believed to be feeding during part of the observation session (97% of cases; Table 3C). This difference might have important implications with regard to expected surface and dive times, number of blows per surfacing, etc. Unfortunately, there were too few cases of mixed socializing plus feeding in the east, or of 'pure socializing in the west, to permit separate analyses of these two situations. When bowheads in the Beaufort Sea intermixed socializing with feeding, water-column feeding was most common, but near-bottom and near-surface feeding were occasionally seen (Table 3D).

Thus, there were considerable differences in the circumstances, sizes (ages) and activities of bowheads socializing in shallow waters at Isabella Bay and in the Beaufort Sea. It is important to take these differences into account insofar as possible while evaluating east-west differences in behavior. To some extent this can be done using multivariate methods. However, some differences cannot be taken into account in any quantitative way because of insufficient overlap between circumstances in the eastern and western arctic, or because of lack of information, For example, differences in the predominant sizes (ages) of the whales observed in the two regions cannot be treated quantitatively because we lack information about the sizes of the individual socializing whales whose behavior was observed.

Univariate Comparisons.--For socializing whales in shallow water, frequencies of several individual behaviors differed between the eastern and western arctic. (In contrast, for whales feeding in deep water, there were few differences of these types--see above.) In the east, net forward swimming speed was most commonly recorded as zero (55% of cases), whereas in the west it was commonly zero, slow or moderate (20, 28 and 28%, respectively; Table 4A). Swimming speed was judged in a somewhat subjective fashion, with only limited overlap in observers between east and west.[17] Hence, these percentages probably do not warrant statistical comparison. However, they are suggestive of an east-west difference.

Active social interactions occurred during similar percentages of the surfacings in the two regions--20% in the east and 22% in the west (Table 4B). However, 'passive' interactions (whales $\leq \frac{1}{2}$ body length apart and parallel) were more common in the east (27% vs. 5% of surfacings). Consequently, the 'no active or passive interaction this surfacing' category was less common in the east (53% vs. 72%). Active social interactions often involved aerial activities in the eastern arctic (most commonly flipper or tail slapping). This was less common in the west. Overall, aerial activities occurred during 48% of the surfacings in the east vs. 6% in the west ($chi^2 = 240$, $P \ll 0.001$; Table 4C). The 48% figure for bowheads socializing in the eastern arctic is a much higher value than found for any other category of bowheads in either the east or the west.

Fluke-out dives were considerably more common among socializing bowheads in shallow waters of the western arctic (48% of dives) than in the east (14%; $chi^2 = 67$, $P \ll 0.001$; Table 4D). The difference may be related to the much greater frequency of water-column feeding interspersed with socializing in the

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17 Although overlap between field observers in the east and west was limited, numerical coding of the eastern data was all either done or checked by individuals with observation experience in both regions and coding experience in the west.

west. Fluke-out dives are common when whales are feeding in the water column (Table 4D).

All of the available data on underwater sounds of bowheads at Isabella were recorded in the presence of socializing whales (see 'Results--Socializing at Isabella Bay' section, earlier). In contrast, in the western arctic bowhead sounds have been recorded in a wide variety of locations and seasons, and during a variety of whale activities. The types and characteristics of most bowhead sounds at Isabella Bay were very similar to those recorded in the Western Arctic, but there were two exceptions. The exceptions involved harmonic (pulsed tone) calls and CR-UNCH sounds. The harmonic calls from Isabella Bay in late summer were much longer (usually 3-9 s, Fig. 14) than those from the western arctic during spring or summer (typically 1-2 s). The CR-UNCH sounds recorded at Isabella Bay (Fig. 14) have not been reported from the western arctic during the spring or summer.

A third difference between the calls heard in the east and west was that pulsive, harmonic and high FM calls comprised much higher proportions of the calls at Isabella Bay (Table 14). Much if not all of this difference was undoubtedly attributable to differences in the activities of the whales rather than to any regional effect. Most western arctic data came from migrating or feeding whales, which most commonly emit simple FM calls. However, very active social interactions occurred during two recording sessions in the Beaufort Sea

Table 14. Relative frequencies (%) of three classes of bowhead calls from Pt. Barrow, Alaska, during the spring migration (C.W. Clark, unpubl. data); from the Canadian Beaufort Sea in the summer during presumably undisturbed conditions (Würsig et al. 1985b); and at Isabella Bay in the late summer (this study). All acoustic analyses and call categorizations were by C.W. Clark.

	Simple FM	Harmonic	Pulsive or High FM
PT. BARROW, SPRING			
1984	85.4%	11.5%	3.2%
1985	77.7	15.9	6.4
1986	76.8	13.5	10.4
E BEAUFORT, SUMMER			
1980-81	44.3	11.5	44.3
1982	84.9	5.6	9.5
1983	73.1	17.0	9.9
1984	86.1	10.2	3.7
ISABELLA BAY, LATE SUMMER[a]			
1984-87	11.3	51.1	37.5

[a] See Table 6 for more details.

during the summer of 1981. On those occasions, only 24% of the 484 calls were simple FM calls, 26% were harmonic, and 51% were pulsive or high FM (Würsig et al. 1982, p. 113). These percentages were much closer to those observed in the presence of actively socializing bowheads at Isabella Bay (11%, 51%, 38%, respectively). However, statistical comparison of these percentages is probably not warranted because of the small numbers of recording sessions involved (4 in east, 2 in west).

Bowheads socializing in shallow water exhibited short surfacings and dives with few blows per surfacing. This was true in both the eastern and the western arctic, but the eastern values were especially low. The mean durations of surfacings in the east and west were similar (1.2 vs. 1.1 rein, respectively). However, surface times in the eastern arctic were highly skewed. Surfacings <30 s long accounted for 49% of the surfacings in the east as opposed to only 24% in the west (chi^2 = 17.4, P<0.001). When a logarithmic transformation was used to compensate for the skewing, the mean duration of surfacing in the western arctic was highly significantly greater than that for the east (P<0.001, Table 11C). Similarly, the mean number of blows per surfacing was higher in the west than in the east (4.6 vs. 2.1 blows/ surfacing, P<0.001, Table 11B). The mean durations of dives were low in both regions--2.7 min in the west and 1.6 min in the east. The east-west difference was not significant, based on log-transformed data (Table 11D). One additional difference between east and west was that mean intervals between successive blows were shorter in the west (12.9 vs. 17.7 s; P<0.001, Table 11A).

Overall, the surfacing-dive cycles of bowheads socializing in shallow water were short in both regions, but especially so at Isabella Bay. There also were differences in swimming speed, calls, and frequencies of social interactions., aerial activities, and fluke-out dives. Taken together, these quant"itative differences in individual measures of behavior indicate that there were extensive east-west differences in behavior among whales socializing in shallow water.

Multivariate Comparisons.--Multivariate comparisons can provide some information" about the possible reasons for the observed east-west differences in individual behavioral variables. In comparison with Isabella Bay, bowheads socializing in shallow waters of the Beaufort Sea tended to be observed earlier in the season, farther from shore, and in more variable water depths. There also were differences in whale sizes, group sizes, and the occurrence of interspersed activities> especially feeding. Possible effects of these differences on behavior must be considered while evaluating the quantitative differences between behavior in the eastern and western arctic.

Factors affecting the surfacing - respiration - dive cycles of socializing bowheads in the eastern arctic were evaluated in Table 7 and the associated text. Each surfacing and respiration variable was strongly related to no more than one or two of the many variables considered. Surface times tended to be higher as water depth increased (within the 0-50 m range considered). Mean blow intervals tended to be higher late in the day. Number of blows per surfacing was not strongly related to any of the measured variables. In contrast, dive durations at Isabella Bay were correlated with several interrelated environmental variables, and it was not possible to determine how many of these correlations represented real causal linkages (see 'Results--Socializing at Isabella Bay').

Table 15 presents corresponding analyses of the data on socializing whales in shallow waters of the western arctic. Each of the three measurements of surfacing and respiration had significant simple correlations with several variables. For surface times, the partial correlations with date, time of day and sea state were all significant ($P<0.01$). However, number of blows per surfacing showed significant partial correlation with any other variable after a correlation with date was taken into account. Mean blow interval showed significant partial correlations with sea state, group size, and occurrence of aerial activity during the surfacing. Durations of dives tended to be slightly longer late in the day. The environmental variables that were significantly related to behavior in the western arctic (Table 15) were not the same as those significantly related to the corresponding measures of behavior in the eastern arctic (Table 7).

The surface times and number of blows per surfacing remained notably lower in the eastern arctic than in the west even after allowance for other measured variables ($P<0.001$, Table 16). Mean blow interval, in contrast, did not seem to be significantly higher in the east after other variables (sea state, group size, occurrence of aerial activity) were considered. This result does not prove the lack of a regional difference in blow intervals. However, it does show that the simple east-west difference in blow intervals demonstrated earlier might be a spurious result of regional differences in corollary variables that may affect blow intervals. Dive times did not differ significantly between regions in either a univariate or multivariate sense.

<u>Summary</u>.--The behavior of bowheads socializing in shallow water (<50 m) at Isabella Bay differed in several respects from that of bowheads socializing in shallow waters of the Beaufort Sea. At Isabella Bay, swimming speeds tended to be lower, aerial activities were much more frequent, and fluke-out dives less frequent. Certain underwater sounds also differed. Surface times were shorter at Isabella Bay and the number of blows per surfacing lower, even after allowance for the effects of other variables. Mean blow intervals were lower at Isabella Bay than in the west. However, this difference may have been attributable to regional differences in some of the corollary environmental or whale activity variables. Durations of dives did not differ significantly between regions.

The results provide clear evidence of differences in the behavior of socializing bowheads in the two study areas. However, one cannot necessarily conclude that the differences were attributable to between-population differences in socializing behavior. The socializing bowheads observed at Isabella Bay were predominantly large subadults or adults without calves, whereas those observed in the Beaufort were mainly smaller subadults. Presently available data on socializing whales do not allow an evaluation of the relative magnitudes of population (east-west) differences in behavior versus effects of whale size, age, or reproductive status.

Such a comparison might be possible if data were available on the social behavior of the large whales, most without calves, that summer in Franklin Bay (Koski et al. 1988). Franklin Bay is located east of Cape Bathurst, just east

Table 15. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables: bowheads socializing in shallow (<50 m) water in Western Arctic, 1980-1986. (No suitable data in 1982.)

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (min)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 80	0-1[b]	ns		ns		ns		ns	
Year = 81	"	ns		ns		ns		ns	
Year = 83	"	St[g]		St		St		St	
Year = 84	"	—.		ns		ns		ns	
Year = 85	"	++		++		ns		ns	
Year = 86	"	++		+++				ns	
Date	1-76[c]	+++	+++	+++		---		ns	
Date²	(1-76)²	+++		+++	+++	---		ns	
Time	0-24[d]	ns	++	ns		ns		+	++
Time²	(0-24)	ns		ns		ns		+	
Longitude	°W[e]	++		++		ns		ns	
Sea State	Bf	ns	+++	ns		++	++	ns	
Ice Cover	%	ns		++		ns		ns	
>5% Ice Cover?[b]	0-1[b]	ns		++		ns			
Dist. from Shore	log (km)	ns		ns		+++		ns	
Water Depth	log (m)	ns		ns		ns		ns	
Group Activ = Trav. + Sot,	0-1[b]	ns		+		ns		ns	
" " = Trav. + Feed	"								
" " = Sot. + Feed	"								
No. Bhd. Within 1 km	No.	ns		ns		+++		ns	
Speed of Motion	0-3[f]								
Group Size	1-7	ns		ns		+++	+++	ns	--
Active Socializ. ?[b]	0-1[b]	ns		ns		ns		ns	
Passive Socializ. ?	"	ns		ns		ns		ns	
Aerial Behav. ?	"	ns				+++	+++	ns	
Pre-dive Flukes?	"								
Sample Size		210	210	177	177	405	405	65	65
Multiple Correlating			0.424		0.398		0.354		0.470
% Variance Explained			17.9		15.9		12.6		22.1
Adjusted % Var. Expl.			16.8		15.4		11.9		18.3
Overall Significance			***		***		***		**

[a] The four dependent variables were all logarithmically transformed to avoid skewness. Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships

***, +++ or --- means $P \leq 0.001$ *, + or - means $0.05 \geq P > 0.01$

**, ++ or -- means $0.01 \geq P > 0.001$ ns means $P > 0.05$

Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables significant (nominal $P \leq 0.05$) according to stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Oct = 62.

[d] All Western Arctic data converted to Pacific Standard Time in hours and decimal hours.

[e] In degrees and decimal degrees.

[f] 0 = No motion, 1 = slow, 2 = moderate, 3 = fast.

[g] 'St' denotes 'Standard' year against whose results other years were compared by dummy 'year' variables.

Table 16. Comparison of the surfacing, respiration and diving behavior of socializing bowheads in the **eastern and western arctic** after allowance for effects of environmental variables and whale activities.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
East (1) vs. West (0)	0-1		---	---	---	++		ns	
Date	1-76[c]	ns	+++	+++		---		ns	
Date[2]	(1-76)[2]	+		+++	+++	---		ns	
Time	0-24[d]	ns		ns		ns		+	
Time[2]	(0-24)[2]	ns		ns		ns		+	
Sea State	Bf	---				+++	++		
Ice Cover	%	ns		++		ns		ns	
>s% Ice Cover?[b]	0-1[b]	ns		++		ns			
Dist. from Shore	log (km)	++		+		++		ns	
Water Depth	log (m)	ns		ns		ns		ns	
Group Activ = Trav. + Soc.	0-1[b]	ns		ns		ns		++	++
" " = Trav. + Feed	"								
" " = Soc. + Feed	"	+++		+++				ns	
No. Bhd. Within 1 km	No.	++		+		ns		ns	
Group Size	1-7	++		ns		+++	+++	ns	
Active Socializ.?[b]	0-1[b]	++	+	ns		ns		ns	
Passive Socialize?	"	ns	+	ns		ns		ns	
Aerial Behav.?	"			--		+++	+++	ns	
Sample Size - E Arctic		54	54	27	27	39	39	39	39
W Arctic		210	210	177	177	405	405	65	65
Multiple Correlation			0.426		0.500		0.340		0.338
% Variance Explained			18.1		25.0		11.6		11.5
Adjusted % Var. Expl.			16.9		24.3		11.0		9.7
Overall Significance			***		***		***		**

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships

***, +++ or --- means P<0.001 *, + or - means 0.05≥P>0.01

**, ++ or -- means 0.01≥P>0.001 ns means P>0.05

Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables recognized as significant (nominal P≤0.05) by stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Oct = 62.

[d] All Western Arctic data converted to Pacific Standard Time in hours and decimal hours. All Eastern Arctic data in Eastern Daylight Time.

[e] In degrees and decimal degrees.

of the area mapped on Fig. 4. That group of western arctic bowheads appears to be similar, at least in size composition and with respect to the scarcity of calves, to the group of eastern-arctic bowheads occurring at Isabella Bay. Unfortunately, there has been no opportunity to collect systematic data on the behavior of the large bowheads summering in Franklin Bay.

Migrating Bowheads

Comparability of Data.--In the eastern arctic, most observations of migrating bowheads were from Cape Adair in 1979. A few additional data on migrants passing Isabella Bay were collected in 1986. These whales were traveling consistently southward within 1½ km of shore, mainly during early October. Ice cover was always less than 10%, and the majority of the migrating whales were observed in the afternoon (72% from 12:00-17:59). Water depths at the locations of the whales passing Cape Adair were not determined. The few migrants passing Isabella Bay were in a wide variety of water depths (Table 2).

In the western arctic, observations of whales that were actively traveling west were obtained in the Alaskan Beaufort Sea during mid-late September 1983 (NOSC data) and during late September and early October of 1985-86 (LGL data). In 1985-86, ice cover was usually <10%, but occasionally 10-29%. In 1983, ice cover was almost always 60-90% (Table 2E). As in the eastern arctic, the majority of the observations of migrating whales were in the afternoon (78% from 12:00-17:59). Most migrating whales were in water 20-49 m deep 20-80 km from shore (Table 2).

Thus, the dates and times of observations were quite similar in the eastern and western arctic, as were the majority of the physical conditions on occasions when migrants were seen. The two major exceptions were distance from shore and ice cover. (1) Migration occurred <1½ km from shore in the east but mainly over the middle-shelf region 20-80 km offshore in the west. However, because of the steeper bottom slope in the east, water depths at observation locations were similar in the east and west. No depth criterion was applied to restrict the observations considered in the analyses of migrating bowheads. (2) Ice cover was zero or light in the east and in 1985-86 in the west, but was heavy in 1983 in the west.

The general activities and group sizes of the migrating bowheads observed in the two regions were also quite similar. In both regions, most whales were singletons, i.e. no other bowhead within 5 whale lengths, and the remainder were pairs or triples (Table 3A). However, the estimated number of whales within a 1 km radius around the focal whale did not exceed 3 in the eastern arctic, but often did so in the west (Table 3B). In both regions, the only whales considered in the analysis were those whose group activity was identified as 'migration only' (see list of selection criteria in 'Methods').

Another important similarity was in the size and age composition of the migrating whales. Whales migrating south along the coast of Baffin Island past Cape Adair and Isabella Bay are suspected to include most of the smaller subadults in that population, as well as most mothers with calves and some other adults (see Introduction). This is a similar mix of individuals as has been observed and measured via photogrammetry during migration through the Alaskan Beaufort Sea (Koski and Johnson 1987; Richardson et al. 1987b).

Thus, the observations of migrating bowheads in the two regions appeared to be generally comparable, with the exception of the 'distance from shore', 'ice cover', and 'number of whales within 1 km' variables. Given the similarities in the types and activities of the migrating whales observed in the two regions, there was less potential for confounding by environmental and other differences than was the case for bowheads feeding in deep water or, especially, those socializing in shallow water.

Univariate Comparisons.--The behavior of migrating bowheads in the two regions was similar in most respects. In both areas, most individuals traveled steadily in a single direction, typically southeast or south parallel to the coast of Baffin Island, and west or northwest parallel to the coast (but farther offshore) in the Alaskan Beaufort Sea. Travel speeds in the eastern arctic were measured by theodolite or 'time and distance' methods. The usual swimming speed in the east was 5-6 km/hr; a southward-flowing current accounted for as much as 1 km/hr of this (see 'Results--Migration in E Arctic', p. 68). In the western arctic, travel speeds have been estimated via 'time and distance' in a variety of autumn studies and via theodolite at Point Barrow in spring. Estimates of migration speeds there were comparable to those in the eastern arctic.

Social interactions and aerial activity were infrequent during migration in both the eastern and western arctic (Table 4). Fluke-out dives appeared to be more common during migration in the east than in the west (58% vs. 27% of all dives, $chi^2 = 13.68$, $df = 1$, $P<0.001$, Table 4D). However, sample sizes were small, and the number of different individual whales contributing to the samples was even smaller, so this result must be treated with some caution (Machlis et al. 1985).

Western Arctic, 1983 vs. 1985-86: Before comparing surfacing, respiration and dive variables for migrating bowheads in the eastern vs. western arctic, we first compared these variables for western arctic whales observed by NOSC in 1983 (heavy ice cover) vs. LGL in 1985-86 (little or no ice). Mean blow intervals and number of blows per surfacing did not differ appreciably from 1983 to 1985-86 (Table 17A,B). Durations of surfacing averaged slightly shorter in 1983 than in 1985-86; the difference was at most only marginally significant (Table 17C).

Dive duration was the one variable that did differ markedly in the Alaskan Beaufort Sea between 1983 (mean 5.48 min) and 1985-86 (mean 18.19 rein: $P<0.001$). Whether this difference was real or artefactual is not known. The consistently heavy ice cover in the Alaskan Beaufort during 1983 (Table 2E) may have resulted in shorter dives during the periods while whales were observable in relatively open areas. We speculate that longer but unmeasured dives may have occurred in 1983 while the whales traversed areas of heavier ice separating the more open areas where they could be observed. Also, the larger number of whales within 1 km during many of the 1983 observation sessions than in 1985-86 (Table 3B) could also have tended to reduce the apparent dive durations in 1983. When the number of whales in the area increases, it becomes more difficult to reidentify whales after long dives,

Table 17. Surfacing, respiration and dive variables for undisturbed bowheads migrating west in the Beaufort Sea in September-October of 1985-86 (LGL data) and September 1983 (unpubl. NOSC data, from study of Ljungblad et al. 1984b). Mothers and calves are excluded. Values given are mean ± s.d. and, in parentheses, minimum and maximum. Mean ± s.d. values are given for logarithmically transformed data as well as data *per se*.

	LGL 1985-86		Nose 1983		1985-86 VS. 1983 Comparison[a]		1983/85/86 Combined	
A. Mean Blow Interval (s)								
per se	17.0 ± 4.95 (9-39)	n = 45	17.2 ± 8.36 (3-68)	n = 103	t' = 0.19 df = 136	ns	17.2 ± 7.47 (3-68)	n = 148
LogMBI	1.22 ± 0.112	n = 45	1.20 ± 0.184	n = 103	t' = 0.77 df = 133	ns	1.20 + 0.17	n = 148
B. Number of Blows per Surfacing								
per se	7.1 ± 3.14 (1-13)	n = 30	6.1 ± 3.33 (1-14)	n=43	t = 1.32 df = 71	ns	6.5 ± 3.27 (1-14)	n = 73
Log(NBL+1)	0.87 ± 0.226	n = 30	0.80 ± 0.213	n = 43	t= 1.17 df = 71	ns	0.83 ± 0.219	n = 73
C. Duration of Surfacing (min)								
per se	1.94 ± 1.05 (0.03-4.80)	n = 32	1.50 ± 0.84 (0.03-3.73)	n = 46	t = 2.04 df = 76	*	1.68 ± 0.95 (0.03-4.80)	n = 78
LogSFC	0.16 ± 0.47	n = 32	0.08 ± 0.35	n = 46	t = 0.81 df = 76	ns	0.11 ± 0.40	n = 78
D. Duration of Dive (min)								
per se	18.19 ± 6.63 (1.63-29.95)	n = 30	5.48 ± 4.97 (1.50-19.32)	n= 12	t = 5.99 df = 40	***	14.56 ± 8.46 (1.50-29.95)	n = 42
LogSUB	1.21 ± 0.25	n = 30	0.62 ± 0.33	n=12	t = 6.37 df = 40	***	1.04 ± 0.38	n = 42

[a] t' is t-test adjusted such that it does not assume equal population variances.
ns means P>0.1; * means 0.05≥P>0.01; *** means p<0.001.

thereby causing a bias against the long dives. Whatever the reason, observed dive durations by bowheads migrating through the Alaskan Beaufort in 1983 tended to be much shorter than those in 1985-86. Hence, comparisons of pooled Beaufort Sea data on dive durations by migrating whales versus corresponding eastern arctic data need to be treated with caution.

Eastern vs. Western Arctic: In contrast to the results for feeding and socializing bowheads, surfacing and respiration parameters were similar for migrating whales in the two regions (Table 11). The mean number of blows per surfacing was 6.0 in the east and 6.5 in the west ($t = 1.03$, df = 147, $P>0.1$). The mean blow intervals in the two regions were almost identical (17.1 s in east vs. 17.2 s in west). Likewise, the mean duration of surfacing was similar in the two areas: 1.5 min in the east and 1.7 min in the west ($t = 1.38$, df = 167, $P>0.1$). The x1.13 and non-significant difference in mean surface times of migrating whales between east and west was much less than the corresponding differences for feeding whales (x2.85, $P<0.001$) or socializing whales (x2,64[18], $p<0.001$[19]).

Duration of dive was the variable that differed most between east and west. The mean dive times were 9.3 min in the east and 14.6 min in the west (Table 11D; $t = 2.63$[19], df = 124, $P<0.01$). As noted above, dive times in the western arctic were longer in 1985-86 (little or no ice) than in 1983 (much ice). Since there was little or no ice near the migrating whales observed in the east, the 1983 western arctic data perhaps should be excluded. If this is done, the east-west difference becomes even greater; the mean dive times then are 9.3 min in the east and 18.2 min in the west ($t' = 5.87$[19], df = 73, $P<0.001$). The east-west difference in dive durations was more pronounced (x1.56 including 1983 data; x1.95 excluding them) than that in surface times (x1.13). As a result, the percentage of time spent at the surface during migration was lower in the west than in the east (10% vs. 14%). In both areas, the whales were at the surface for a smaller percentage of the time during migration than during any of the other activities examined (Table 11E). The low percentage of time spent at the surface during migration through the Alaskan Beaufort Sea has been noted previously (Fraker et al. 1985; Richardson et al. 1987b, p. 300).

Multivariate Comparisons.--The relationships between environmental variables and the surfacing - respiration - dive cycles of bowheads migrating in the eastern arctic were shown in Table 10 and discussed in text adjacent to that table. Surfacings and dives both tended to be short when sea state was high. Surfacings were longer for bowheads migrating in groups than for singletons. The number of blows per surfacing tended to be reduced late in the season, and mean blow intervals were somewhat longer late in the season (Table 10).

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18 Based on back-transformed mean LOGSFC (Table 11C).

19 Based on log-transformed data (LOGSFC or LOGSUB).

Western Arctic: Corresponding analyses for migrating bowheads in the Alaskan Beaufort Sea are summarized in Table 18. Several different environmental and group size variables appeared to be related to one or more of the behavioral variables. However, sample sizes were low in relation to the number of predictor variables (15) that were considered: 30-93 cases, depending on the dependent variable being analyzed. Thus, the results of the multiple regression analyses of behavior during migration in the western arctic are tentative. In the case of dive durations for which n = **30,** the multiple regression results should probably be ignored because of the very small sample size.

Eastern vs. Western Arctic: Table 19 shows the results of multivariate analyses to assess whether surfacing, respiration and dive variables for migrating bowheads differed between the eastern and western populations after allowance for nine potentially confounding variables. Sample sizes were adequate for all four surfacing respiration and dive variables.

There was no evidence of significant east-west differences in number of blows per surfacing, mean blow interval or duration of surfacing by migrating bowheads. This was true in both a univariate sense (Table 11A,B) and after allowance for several potential confounding variables (Table 19).

Durations of dives tended to be considerably longer for migrating whales in the western arctic than in the east ($P<0.001$, Table 11D). The multiple regression approach suggested that this difference was not significant after allowance for correlations with several environmental and whale activity variables (Table 19). However, more detailed examination of the stepwise multiple regression results showed that the analysis could not reliably determine whether dive durations differed between the eastern and western arctic after allowance for other variables[20].

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20 Inspection of the step-by-step results showed that the partial correlations with the East-West dummy variable became non-significant when the $Date^2$ term was taken into account. Dive durations tended to decrease as the autumn progressed in the eastern arctic (Table 10), the western arctic (Table 18), and both areas pooled (Table 19). Thus, it is likely that dive duration is directly related to date. However, it is possible that part of the apparent date effect on dive durations in the pooled data (Table 19) was actually the result of an east-west difference in dive durations. Because most observations of migrating whales were in late September in the west and early October in the east (Table 2A), the date and east-west variables were strongly interrelated. The multiple regression analysis could not distinguish any east-west difference that may exist from the date effect.

Thus, the apparent lack of a significant east-west difference after allowance for other variables is not conclusive. One possibility is that the strong univariate difference in dive times between the east (shorter dives) and west (longer) is an artefact of the tendency for dives to become shorter late in the autumn. Alternatively, the lack of a significant east-west difference after allowing for date effects may be an artefact of the interrelationship of date and dive time, and the inability of any analysis procedure to separate their effects.

Table 18. Summary of simple and partial correlations between (a) environmental and activity variables vs. (b) four surfacing, respiration and dive variables: bowheads migrating in Western Arctic, 1983 and 1985-1986.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (rein)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
Year = 83	0-1[b]	ns		ns		ns		0s	
Year = 85	"	ns		ns		ns			
Year = 86	"	St[g]		St		St		St	
Date	1-76[c]	0s		ns		ns			
Date[2]	(1-76)[2]	ns		ns		ns			
'i ime	0-24[d]	++	++	+		ns		++	+++
Time[2]	(0-24)	++		.		ns		++	
Longitude	°we	+		++	++	ns		+	
Sea State	Bf								
Ice Cover	%	ns		ns		ns		ns	
>5% Ice Cover?[b]	0-1[b]	ns		ns		ns		ns	
Dist. from Shore	log (km)	ns		ns		ns			+++
Water Depth	log (m)	ns		ns		ns		—	---
Group Activ = Trav. + Sot.	0-1[b]								
" " = Trav. + Feed	"								
" " = Sot. + Feed	"								
No. Bhd. Within 1 km	No.			ns		ns			
Speed of Motion	0-3[f]	ns		ns		ns		ns	
Group Size	1-3	ns		ns		+++	+++	+	
Active Socializ.?[b]	0-1[b]								
Passive Socialize?	"								
Aerial Behav.?	"	ns		ns		ns		ns	
Pre-dive Flukes?	"								
Sample Size		51	51	49	49	93	93	30	30
Multiple Correlation			0.391		0.396		0.426		0.856
% Variance Explained			15.3		15.7		18.1		73.3
Adjusted Z Var. Expl.			13.6		13.9		16.3		70.2
overall Significance			**		**		***		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships

***, +++ or --- means $P<0.001$ *, + or - means $0.05 \geq P>0.01$

**, ++ or -- means $0.01 \geq P>0.001$ ns means $P>0.05$

Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for chose variables significant (nominal $P \leq 0.05$) according to stepwise multiple regression.

[b] 0 = False., 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Oct = 62.

[d] All Western Arctic data converted to Pacific Standard Time in hours and decimal hours.

[e] In degrees and decimal degrees.

[f] 0 = No motion, 1 = slow, 2 = moderate, 3 = fast.

[g] 'St' denotes 'Standard' year against whose results other years were compared by dummy 'year' variables.

Table 19. Comparison of the surfacing, respiration and diving behavior of migrating bowheads in the eastern and western arctic after allowance for effects of environmental variables and whale activities.

Predictor Variable		Duration of Surfacing (min)[a]		No. Blows per Surfacing (+1)[a]		Mean Blow Interval (sec)[a]		Duration of Preceding Dive (min)	
Name	Scale	Simple	Partial	Simple	Partial	Simple	Partial	Simple	Partial
East (1) vs. West (0)	**0-1**	ns		ns		ns			
Date	1-76[c]	---				ns		---	
Date²	(1-76)²	---	---	---	---	ns		---	---
Time	0-24[d]	ns		ns		ns		ns	
Time²	(0-24)²	ns		ns		ns		ns	
Sea State	Bf								
Ice Cover	%	ns		ns		ns			
>5% Ice Cover?[b]	0-1[b]	ns		ns		ns		ns	
Dist. from Shore	log (km)								
Water Depth	log (m)								
Group Activ = Trav. + Sot.	0-1[b]								
" " = Trav. + Feed	"								
" " = Sot. + Feed	"								
No. Bhd. Within 1 km	No.	ns		ns		ns		--	---
Group Size	1-3	++	+	ns		+++	+++	ns	
Active Socializ.?[b]	0-1[b]								
Passive Socializ.?	"								
Aerial Behav.?	"	ns		ns		ns		ns	
Sample Size - E Arctic[f]		89	89	74	74	84	84	86	86
W Arctic		7s	78	73	73	140	140	43	43
Multiple Correlation			0.372		0.354		0.307		0.531
Z Variance Explained			13.9		12.5		9.5		28.2
Adjusted Z Var. Expl.			12.3		11.3		9.0		27.0
Overall Significance			***		***		***		***

[a] The four dependent variables were all logarithmically transformed to avoid skewness.
Pluses indicate positive and significant correlat ions or partial correlat ions; minuses indicate negative relationships
***, +++ or --- means P≤0.001   *, + or - means 0.05≥P>0.01
**, ++ or -- means 0.01≥P>0.001   ns means P>0.05
Blanks in the simple correlation columns denote variables that were not analyzed because they were constant or nearly so, or because the value was unknown for a considerable proportion of the otherwise-usable cases. Partial correlations are shown only for those variables recognized as significant (nominal P≤0.05) by stepwise multiple regression.

[b] 0 = False, 1 = True.

[c] In days after 31 July, i.e. 1 Aug = 1, 1 Sept = 32; 1 Ott = 62.

[d] All Western Arctic data converted to Pacific Standard Time in hours and decimal hours. All Eastern Arctic data in Eastern Daylight Time.

[e] In degrees and decimal degrees.

[f] Sample sizes exceed those in Tables 10, 18 because fewer predictor variables are considered here. This allowed inclusion of some additional cases for which some variables were unknown.

Some other potentially confounding environmental and whale activity variables were omitted from these four multiple regression analyses because their values were not known for significant fractions of the cases. These additional variables included sea state, distance from shore, water depth, speed of motion, and occurrence of turns, social interactions and pre-dive 'flukes out'. Residuals from each of the four multiple regression analyses were plotted against these seven additional variables considering only the cases where the additional variables were known. These plots indicated that none of the four surfacing, respiration and dive variables that we analyzed was appreciably related to any of the seven additional variables. Thus, the exclusion of those variables from the formal multiple regression analyses did not affect the evaluation of possible east-west differences in behavior.

Summary. --The physical situations, activities, behavior and (presumed) age composition of migrating bowheads observed in the eastern and western arctic were similar in many respects. The main difference in circumstances was that most migrants observed in the west were much farther offshore, although water depths may have been comparable. Also, migrating whales observed in the east were in light or zero ice conditions, whereas those observed in the west were in widely variable ice conditions; heavy in 1983 but light or zero in 1985-86. In both regions, group sizes were generally 1 or 2, and there was little socializing or aerial behavior. Fluke-out dives seemed to be more common in the east.

Dive durations averaged significantly longer in the west than in the east ($P<0.001$), whereas surface times were not significantly different. As a result, bowheads were at the surface for a lower percentage of the time in the west (10% vs. 14%). In both areas, bowheads were at the surface for a smaller proportion of time during migration than during the other activities that were studied. The number of blows per surfacing and the mean blow interval were similar in the east and west.

Overall, the behavior of migrating bowheads in the eastern and western arctic was more similar than was the case for either feeding or socializing bowheads. However, there was a highly significant difference in dive durations, especially when the comparison was restricted to zero or light ice situations. As discussed above, there is some doubt as to whether this difference represented a real east-west difference in diving behavior or an artefact associated with the tendency for dives to become shorter late in the autumn. The frequency of fluke-out dives may also have differed between east and west.

Comparison of Reactions to Human Activities

The primary objective of Phase 1 of this study was to determine whether there are differences in the 'normal' behavior of eastern and western arctic bowheads. Thus, all of the analyses discussed previously were based on observations of bowheads that were not exposed to any obvious source of potential man-made disturbance at the time of the observations. A variety of regional differences in behavior have been identified in the preceding section. The purpose of Phase 2 of the project, which is being conducted in 1989, is to determine whether some of these differences can be ascribed to long-term changes in bowhead behavior in response to the cumulative effects of human activities in the western arctic.

In interpreting the possible long-term effects of disturbance in the eastern and western arctic, it would be helpful to know whether there is any evidence that bowheads of the two populations exhibit differences in their short-term responses to human activities, For western arctic bowheads, data exist regarding the short-term reactions to ships, aircraft, seismic vessels, drillships and dredging (Richardson et al. 1985a,b, 1986, MS; Ljungblad et al. 1985, 1988; Koski and Johnson 1987). In each case, there are limited experimental results as well as opportunistic observations of reactions of whales to actual disturbance incidents. However, for the eastern arctic bowheads, there are only a few opportunistic observations of responses to aircraft and motorboats (Degerbøl and Freuchen 1935; Finley et al. 1986; Finley 1987). Thus, aircraft and motorboats are the only disturbance sources for which a comparison of disturbance reactions in the eastern and western arctic can be attempted.

Boats

Eastern Arctic.--Steam-powered whaleships began operating in the Davis Strait/Baffin Bay area in 1859. However, during the 1870s the ships remained fully rigged for-sailing because "The Greenland whale, with its acute hearing especially while under water, made the working of engines on the fishing grounds impossible if whales were to be approached, thus the fishing was always carried out entirely under sail" (Lubbock 1937, p. 401).

Degerbøl and Freuchen (1935) indicated that eastern arctic bowheads in northern Hudson Bay were very sensitive to motorboats in 1923: '... a [bowhead] whale again came into the [Repulse Bay] harbour, but soon turned shy and fled when a motorboat was started. [Five days later] a whale in Repulse Bay, once more [was] frightened away by the thudding of a motorboat, although it was so far away that it could not possibly have heard it.' The latter sentence of the quotation is internally inconsistent, but one would expect a motorboat to be detectable much farther away via underwater sound than via any other sensory modality. Degerbøl and Freuchen provided no additional information about the radius of responsiveness or type of motorboat.

Observations at Isabella Bay, Baffin Island, in 1984-87 provided additional information about the sensitivity of eastern arctic bowheads to motorboats (Finley et al. 1986; Finley 1987 and unpubl.). Isabella Bay is remote from most human and industrial activities during the open-water season. The difficulty of boat travel along the exposed coast and lack of hunting opportunities have discouraged use of the area by hunters from the nearest communities, which are Clyde (about 110 km by sea to the north) or Broughton Island (about 250 km south). However, hunters with outboard-powered (75-110 hp) boats occasionally visited the study camp and caused some reactions by bowheads. In 1985 and 1986, poor weather and high sea states curtailed boat travel and the camp was visited only by a single party of hunters in each year. In 1984 and 1987, traveling conditions were more favorable, and the camp was visited by as many as five different parties of hunters. Hunters usually attempted to restrict their boating activities when whales were present. However, this was not always possible, and some interactions between motorboats and bowheads were observed.

The best documented case occurred on 26 August 1985 when a hunter departed from camp in a 90-hp 7.5-m boat and travelled toward a single bowhead on Isabella Bank (Fig. 18). Although there were too few data on surfacing - respiration - diving cycles to warrant numerical analysis, the sequential theodolite data provided information about distances and speeds of travel. For 40 min prior to the boat's departure the whale had remained in one position in shallow (12 m) water, frequently rolling and submerging. When the boat departed from shore at a range of 3.7 km, the whale submerged and moved directly away. During its first dive the whale travelled 0.75 km at a speed of 7.7 km/h. As the boat approached (at a speed of 39 km/h) to its closest point of approach within 2 km of the whale, it undertook a long (1.8 km) dive at a speed of 10.3 km/h. This was the fastest documented speed of any whale at Isabella Bay, about double the normal traveling speed. The whale's course veered to its left as the boat passed on the right (Fig. 18). When the boat stopped at a point 4.2 km from the whale, the whale's movement slowed to 3.7 km/h. When the boat resumed traveling at about 11:55, the whale's speed increased to 6.2 km/h. During this last dive the whale travelled the remarkably long distance of 2.2 km underwater. The whale continued to veer left, away from the boat (Fig. 18).

Similar strong avoidance reactions caused by rapidly moving boats were observed opportunistically from the boats on two other occasions. Twice during travel between Clyde Inlet and Isabella Bay bowheads were encountered close to shore in water <20 m deep. In one of these cases the boat passed 7 different whales. The whales were first seen about 1-2 km ahead of the boat, moving rapidly away parallel to shore. The range when they first started to swim away was not known. Their rapid movement was evident from strong upwellings. As the boat came abreast of the whales about 1 km from shore, those inshore reversed direction and then appeared to slow down or stop. The two whales that were on the seaward side did not appear to react as strongly as those on the shoreward side. One of the 'seaward' animals reversed direction as the boat approached within 300 m and surfaced 100 m behind the boat, first facing it and then moving slowly toward shore.

On the second occasion, the boat overtook a pair of whales that were moving south (presumably migrating) within 1 km of shore. The passage of the boat caused them to reverse direction. However it appeared that their migration was only briefly interrupted as two whales (presumed to be the same individuals) appeared at Cape Raper at a time consistent with their measured rate of movement past the observation site (6.7 km/h).

Bowheads were also encountered during zooplankton sampling cruises in the deep (>200 m) waters of the NE Trough off Isabella Bay. The boat was powered by a 90 hp outboard engine, either operating intermittently at slow speeds (usually <5 km/h) or stopped. The whales appeared wary of the boat, seldom approaching closer than 300-500 m. However, they continued to undertake fluke-out dives while the boat operated slowly in the feeding area. These observations are consistent with earlier evidence that bowheads and other baleen whales are most sensitive to vessels that move rapidly and change

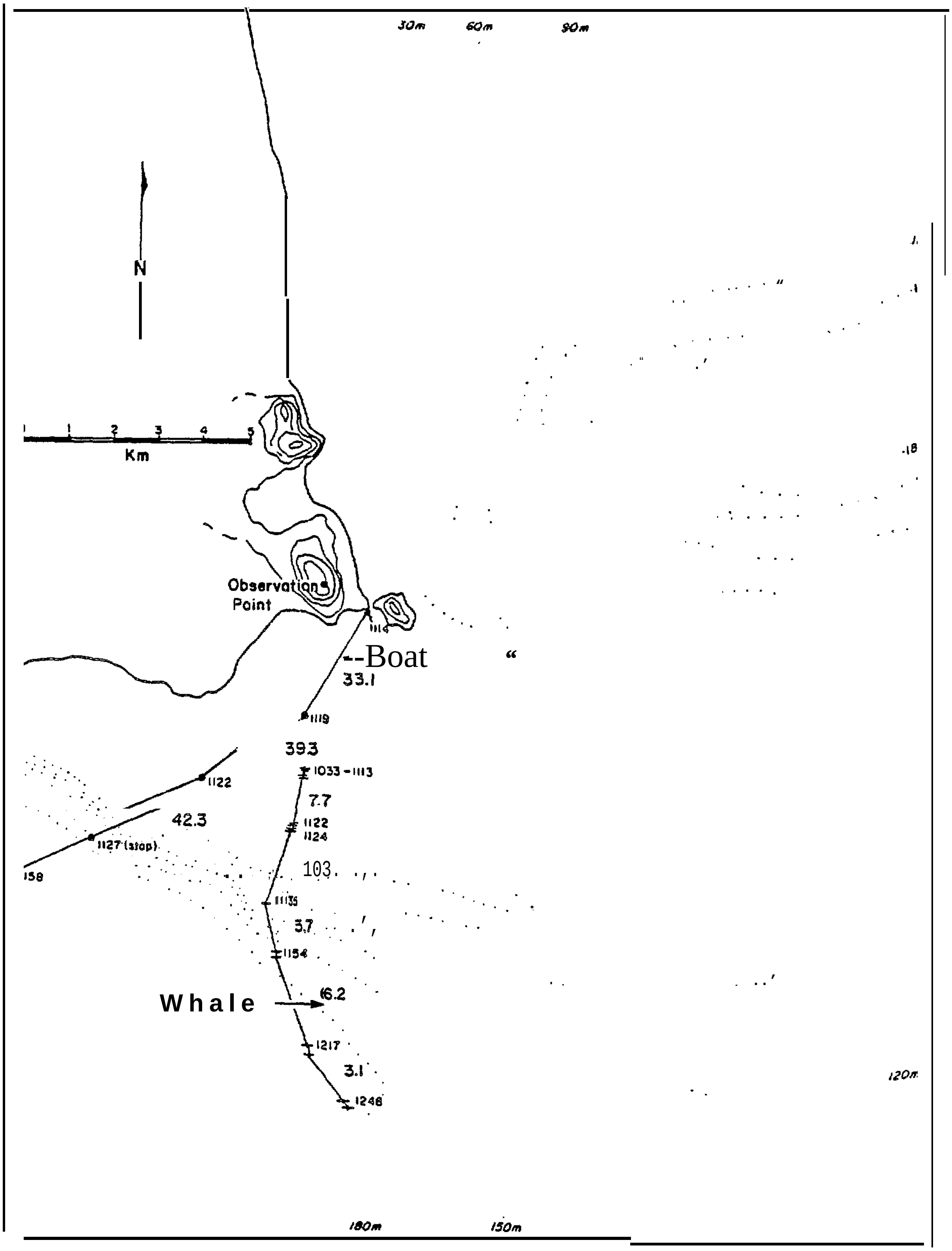

Figure 18. Track of a single bowhead showing response to an outboard-powered boat on 26 August 1985 at Isabella Bay. Larger-type numbers are speeds (km/h); smaller-type numbers are times. (From Finley et al. 1986).

course and speed, and less sensitive to vessels that travel slowly in a consistent pattern (see review by Richardson et al. 1983 and bowhead data in Richardson et al. 1985a,b).

Western Arctic.--In the western arctic, it is well known that bowheads are sensitive to outboard motor noise. This is one of the reasons that the spring hunt is still conducted without using motors on the boats. Detailed observations of the reactions of bowheads to outboard-powered boats have not been made. However, incidental observations were made of single radio-tagging attempts via motorboats in each of 1980, 1985 and 1986. By the time that the motorboat had approached to within 500 m, the whales were swimming rapidly away, changing course to avoid the approaching boat (W.J. Richardson and B. Würsig, unpubl. data).

More extensive and systematic observations have been made of the reactions of bowheads to small diesel-powered vessels in the Canadian and Alaskan Beaufort Sea (Richardson et al. 1985a,b; Thomson and Richardson 1987). Among other observations, there were four controlled disturbance tests with the 13-m 115-hp diesel-powered 'Sequel', whose underwater sound is dominated by components at and above 400 Hz (Greene 1985, p. 224; Miles et al. 1987, p. 225ff). Bowheads oriented randomly when 'Sequel' was >4 km away, but tended to head away from the boat when it was underway **2-4** km way ($P<0.05$) or <2 km away ($P<0.005$). Significantly more of the bowheads moved at moderate or fast speed when the boat was within 4 km ($P<0.001$). Considering all tests and all whales together, the increase in speeds was already evident when the boat was 2-4 km away ($P<0.05$), and was especially evident when the boat was within 2 km ($P<0.001$). However, sensitivity varied among individuals; some reacted when the boat was still about 4 km away; others allowed it to approach to 1 or 2 km before they began swimming rapidly. When an approaching boat was within 4 km, surfacings tended to be short ($P<0.01$) and there were unusually few respirations per surfacing ($P<0.02$, Richardson et al. 1985b).

'Sequel' has also been used to sample zooplankton near bowhead whales (Griffiths and Buchanan 1982; Bradstreet and Fissel 1987). During zooplankton tows, the boat normally moved on a steady course at slow speed. In addition, on several occasions 'Sequel' approached bowheads slowly in order to get close enough for subsequent underwater sound playback tests. During some of these zooplankton sampling efforts and slow-speed approaches, whale behavior was observed from a circling aircraft as well as from the boat itself. In general, bowheads reacted considerably less strongly to 'Sequel' when it was moving slowly while doing zooplankton tows or attempting to approach whales than when it moved rapidly toward whales during disturbance tests. However, bowheads 1-2 km ahead of 'Sequel' sometimes swam away even when the boat approached at idling speed, about **5** km/h. Our subjective impression is that swimming speeds when bowheads were avoiding the slow-moving boat were slower than those when they avoided a rapidly-approaching boat.

During slow-speed zooplankton sampling with another 13-m boat, bowheads exhibited strong avoidance reactions and were displaced by several kilometers. The boat involved in these observations, 'Annika Marie', had engines with about four times as much power as 'Sequel' (436 vs. 115 hp). Although this boat displaced feeding bowheads, repeated photography of individually recognizable animals revealed that at least some of the whales returned to the feeding area after the boat had left (p. 475 in Thomson and Richardson 1987).

In summary, bowheads reacted strongly to boats in both the eastern and the western arctic. In both regions, bowheads swam rapidly away when boats approached at high speed, sometimes when the distance was as great as 4 km. In both regions, reactions to slow-moving boats were Less dramatic but avoidance was still evident, There was evidence from both areas that bowheads often resume their normal activities soon after fleeing from an approaching boat--within ½-1 hr on at least some occasions. More detailed comparisons of reactions to boats in the two regions are not possible because the data are limited and because the observation procedures and types of boats were different. However, available information suggests that. sensitivity to small vessels is similar in the two regions.

Ships

Larger ocean-going vessels were seldom seen during the five-year study at Isabella Bay. Commercial freighters were seen on four different occasions (10 Sept 1985, 21 Sept 1986, 7 and 13 Sept 1987), but all of them passed south at least 30 km offshore. On all of these occasions bowheads were present, but it was sometimes equivocal whether they showed responses to the distant vessels.

On 10 Sept **1985,** about 37 bowheads were over or near Isabella Bank when a freighter was seen. Although many of the whales were engaged in social activities throughout the ship's passage, two whales were observed moving rapidly southward along the outer coast, possibly in response.

On 13 Sept 1987 a passing ship was observed between 09:30 and 12:45 an estimated 30-40 km offshore. It was clearly audible at 10:30 in air (calm at the time) as it passed due east of the observation site >30 km offshore. Presumably it was also audible underwater, although there was no confirmation of this. At about the same time, at least 11 different bowheads moved strongly into Isabella Bay along its southern coast. This westward movement continued until at least 13:00. It is uncertain whether the whales reacted to the ship or simply undertook a coordinated movement as a herd.

On two other occasions, a single bowhead and a pair of bowheads feeding 7-9 km offshore in the NE Trough showed no apparent response as ships passed. The whales continued to undertake fluke-out dives during and after the passage of the ship.

Aside from the supply vessels noted above, only one other large vessel, the oceanographic research ship 'Pandora', was seen at Isabella Bay during the study. This vessel entered Isabella Bay on 17 Sept 1985. However, it passed at night so no observations of whale responses were possible.

In the Canadian Beaufort Sea, bowheads have been observed to react to an oil-industry supply vessel and a transiting seismic vessel in much the same manner as to the smaller boats discussed above (Richardson et al. 1985a,b). Reactions were not noticed at distances exceeding about 2.8 km. However, during more detailed observations in the Alaskan Beaufort Sea, similar types of reactions to supply vessels were noticed at distances up to 4-6 km (Koski and Johnson 1987). In addition, a cow-calf pair appeared to react strongly at considerably greater distances when two vessels approached them simultaneously from opposite directions. The closest points of approach of the two vessels were about 15 and 20 km from the whales (Koski and Johnson 1987).

In general, it is clear that western arctic bowheads usually react strongly to direct approaches by ships, typically at distances of several kilometers. Under special circumstances, exemplified by the cow-calf observation noted above, reactions may occur at greater distances. It is uncertain whether any of the whales observed at Isabella Bay were disturbed by distant ships; if so, the disturbance was mild and infrequent.

Aircraft

Coastal communities on eastern Baffin Island are served regularly by a scheduled aircraft, a twin turboprop Fokker F-27. It normally passed over Isabella Bay 4-6 times/week at an altitude of about 1800-2400 m (6000-8000 ft). However on one occasion, 6 Sept 1984, this aircraft passed at an altitude <136 m and circled twice over a group of 3 bowheads engaged in sexual activities in shallow (17 m) water over Isabella Bank (Finley et al. 1986). During the first circle, the aircraft passed directly over the whales and caused them to dive rapidly. This created considerable white water. During the second circle the aircraft passed close to (but not directly over) the whales and did not cause a notable reaction although the whales had ceased interacting. Within 5 min they had regrouped and continued to engage in sexual activities for more than 2 h.

Similar startle responses were noted during aerial photogrammetric surveys of the bowheads at Isabella Bay in 1987 (Finley unpubl.). During these flights the aircraft (a DeHavilland Twin Otter) circled at an altitude of 150 m over bowheads located in deep (>200 m) water of the Kater Trough. Often the same groups of whales were photographed repeatedly. On about half of the occasions when the aircraft passed directly over the whales, they appeared startled and dove with a noticeable flurry of white water. However during one survey (30 Sept 1987) the aircraft passed directly over a group of 8-10 sexually-active whales 6 times in 2 h without causing any notable change in their activities.

In the western arctic, overt reactions of bowheads to a circling observation aircraft were sometimes conspicuous when it was below 457 m altitude (1500 ft), uncommon at 457 m, and generally undetectable at 610 m (2000 ft). The usual reaction to an aircraft at 305 m (1000 ft) or below was a hasty dive when the aircraft first approached, with little or no detectable effect thereafter (Richardson et al. 1985a,b). On rare occasions, bowheads seemed to move away in response to an aircraft circling at ≤457 m. Reactions were most common in nearshore waters <15 m deep, where lateral propagation of aircraft noise was greatest (Greene 1985). Sensitivity to aircraft seemed to be reduced when bowheads were engaged in active social interactions and perhaps feeding (Ljungblad 1981; Richardson et al. 1985a,b). When the same bowheads were circled at high (457 m and/or 610 m) and lower (305 m) altitudes, blow intervals tended to be shorter when the aircraft was low. During photogrammetry flights in the western arctic, many bowheads overflown by a Twin Otter at about 150 m altitude dove hastily, but many others remained at the surface as the aircraft flew over and away.

In summary, during some low-level (e.g. 150 m) overflights by aircraft, bowheads dive hastily in both the eastern and western arctic. During other such overflights, the whales remain at the surface and seem unaffected. In both regions, there is subjective evidence of reduced sensitivity to aircraft when the whales are actively engaged in social interactions. [Payne et al. (1983) obtained a similar result for southern right whales.] Although comparative data are limited, especially for the eastern arctic, sensitivity to aircraft seems generally similar in the two regions.

DISCUSSION

General Similarities and Differences in Behavior

Most aspects of the behavioral repertoires of bowhead whales are very similar in the eastern and western arctic. Almost all of the general activities and specific behaviors seen in the east have also been seen in the west. The few behaviors detected commonly in the east but not the west are (a) tail lofting, (b) mechanical 'CR-UNCH' sounds heard underwater near socializing whales, and (c) 'rock-nosing'. Rock-nosing involves a whale that is close to shore and floating motionless with the head below the surface. The 19th century whalers recognized that this behavior occurred commonly along eastern Baffin Island in early autumn (e.g. Guerin 1845). Rock-nosing was described briefly by Finley et al. (1986, p. 59):

> "On several occasions we saw single whales remaining head down most of the time over long periods (1.5 h) in shallow (<10 m) water with a substrate of smooth uniformly-sized boulders. This fits Guerin's (1845) description of the 'rock-nose' whale, that is 'it frequently places the extremity of its head, or nose as the whalers call it, close to the shore, upon a rock'. Donnelly (1967) described a similar nose-down posture of the southern right whale, thought to be a courtship display of males. We have not yet been able to determine the sex of such posturing individuals at Isabella [Bay.]"

Finley et al. (1986) suspected that rock nosing is a component of breeding behavior. However, its significance is not known for certain.

A larger number of activities and behavioral events seen in the west have not been noticed in the east, probably because of the much narrower range of observation sites and seasons investigated in the east. All eastern arctic data came from observations at two coastal locations--Isabella Bay and Cape Adair. In contrast, the western data were collected at many distances from shore across the entire eastern and central Beaufort Sea. All eastern observations were collected from mid August to mid October. The systematic observations from the western arctic were collected from early August to early October, only slightly different than the dates of observations in the eastern arctic. However, other workers have observed the behavior of western arctic bowheads in spring (e.g. Everitt and Krogman 1979; Ljungblad 1981; Carroll et al. 1987), when there have been no systematic observations of the behavior of eastern bowheads. Given the much more extensive observational coverage from the western arctic, it is not surprising that some whale activities and individual behaviors observed in the west have not been noticed in the east.

The main activities and behaviors that are reasonably common in the west but not at Isabella Bay or Cape Adair included near-surface echelon feeding, near-bottom feeding, and log play (Würsig et al. 1985a,b, in press). The steeply-sloping shorelines of much of the eastern arctic provide less shallow water than occurs in the western arctic, reducing the extent of the areas where near-bottom feeding might occur. Drifting logs are very common in the Beaufort Sea, presumably arriving via the Mackenzie River which drains vast forested areas. There is no comparable source of logs in the Baffin Bay area.

Aside from these few apparent differences in behavioral repertoire, the behaviors of the separate populations of bowheads in the eastern and western arctic are qualitatively similar. However, this study has demonstrated that, during the late summer - early autumn period, there are many quantitative differences between behaviors along the Baffin Island coast and in the Beaufort Sea. When evaluated by statistical methods, many of these differences proved to be highly significant.

In the case of bowheads feeding in deep water, the most noticeable differences were the longer dives and surfacings, with more respirations per surfacing, in the eastern arctic.

For bowheads socializing in shallow water, there were many quantitative differences in behavior. In the eastern arctic there were lower swimming speeds, more frequent aerial activities, less frequent fluke-out dives, more prolonged harmonic (pulsed tone) calls, occurrence of the CR-UNCH sound, shorter surface times with fewer blows per surfacing, and possibly shorter blow intervals. Many of these differences seemed to be related to the occurrence of more vigorous social interactions, including sexual interactions, at Isabella Bay. In contrast, most social interactions observed in the Beaufort Sea were less boisterous, and overtly sexual interactions were rarely seen there in late summer. A further difference was that socializing whales in the Beaufort Sea usually intermixed their social activities with feeding, whereas whales socializing over Isabella Bank rarely fed while socializing.

Many of these differences may have been related to the different sizes and ages of the socializing whales in shallow waters of the Beaufort Sea (mainly small subadults) and Isabella Bay (mainly large subadults or adults), based on their sizes. However, the possibility of differences in reproductive activities between the two populations, as suggested by the results of this study, warrants close scrutiny because of the potential direct connection with the well-being of the populations. (See further discussion on p. 111-113.)

For **migrants**, there were few obvious differences in behavior between the east and west. The most noteworthy difference was the longer average duration of dives in the western arctic. Also, the flukes were raised above the surface at the onset of a higher proportion of the dives in the eastern than in the western arctic.

The null hypothesis established at the outset of this project was that there are no differences in normal behavior between bowhead whales of the western and eastern arctic stocks. If the behavioral data considered in this report were representative of the eastern and western arctic populations, we could clearly reject the null hypothesis in the case of whales feeding in deep water and for those socializing in shallow water. The situation is less clear cut for migrants, for which only two of the many behavioral variables considered--dive duration and occurrence of fluke-out dives--differed markedly between east and west.

While evaluating the null hypothesis, it is important to consider the representativeness and comparability of the observations. For bowheads feeding in deep water, the main confounding factor is possible east-west differences in zooplankton availability, especially differences in the typical depths of zooplankton concentrations. If zooplankton tend to concentrate at different depths in the east and west, this would presumably affect the typical depths of dives, which could in turn affect many aspects of behavior. For socializing whales, there are several potential confounding factors, most or all of which may be related to population segregation, including differences in the ages of the whales observed in the east and west. A discussion of these confounding factors is needed before evaluating the null hypothesis.

Bowhead Feeding Behavior vs. East-West Differences in Zooplankton[21]

In summer, bowhead whales must consume enough food to sustain themselves through the winter and for a portion of their migration. Lactation, pregnancy and growth all put additional energetic demands on the whales. Based on theoretical considerations and very limited data, an average subadult bowhead may require about 444 kg/d for the 130 d spent on the summer feeding grounds (Thomson 1987b). Based on the estimated size of the mouth opening and swimming speed while feeding, Thomson (1987b) estimated that consumption of this amount by an average subadult bowhead[22] would necessitate feeding in concentrations of zooplankton that had an average biomass of 2.1 g/m^3.

Western arctic bowheads, like other baleen whales, are known to concentrate their feeding at locations where zooplankton is concentrated (Griffiths and Buchanan 1982; Bradstreet and Fissel 1987; Bradstreet et al. 1987; Griffiths et al. 1987). Furthermore, bowheads are believed to feed at the depths where the zooplankton is most concentrated, provided that this depth is within the diving capabilities of the whales.

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21 Much of this section was prepared by Denis H. Thomson, LGL Ltd., King City, Ont.

22 Calculated requirements of subadults are listed here because most of the bowheads feeding at the stations where zooplankton was studied were subadults. See Thomson (1987b) for corresponding estimates for adults at various stages of the reproductive cycle.

Observed zooplankton biomasses at locations in the Beaufort Sea where bowheads feed are consistent with the calculated requirements of the whales. The mean biomass of zooplankton found within all layers of concentrated zooplankton evident via echosounder near feeding bowheads in the Canadian and Alaskan Beaufort Sea was 1.5 g/m^3 (n = 17; Griffiths et al. 1987; Bradstreet et al. 1987). The mean biomass within the densest 'layer' of zooplankton found at each whale feeding location was 2.0 g/m^3 (n = 8; Bradstreet et al. 1987). These values are much higher than the average biomass found in the water column as a whole. Even so, they probably underestimate actual prey biomass at the specific locations where bowheads feed, given the various methodological problems in finding the densest zooplankton patches available to whales and measuring the biomass within those patches.

Regional or other differences in the vertical distribution of zooplankton concentrations could have a pronounced effect on the feeding modes and surfacing - respiration - dive cycles of bowheads. In the cases of gray and humpback whales diving to known depths, surfacing, respiration and diving behaviors are correlated with the depths of dives (Würsig et al. 1986b; Dolphin 1987a,b). Surfacings and dives tend to be longer, and the number of respirations per surfacing greater, when these species of whales dive deeply. These correlations are related to physiological demands and maximization of feeding efficiency during dives to different depths. If the best available prey concentration is deep, feeding will be most efficient if the feeding dives are comparatively long, minimizing the proportion of the time spent in descending or ascending. If feeding dives are longer than average, the whale must respire more times than average after the dive. Since intervals between successive respirations tend to be less variable than other aspects of the surfacing - respiration - dive cycle, a high number of respirations during a surfacing requires a relatively lengthy surfacing.

Thus, significant differences in depths of prey concentrations are likely to result in significant differences in surfacing - respiration - dive cycles. This study has shown that the surfacing - respiration - dive cycles of bowheads feeding in deep water off Isabella Bay tend to be longer than those of bowheads feeding in deep waters of the Beaufort Sea (Table 11). These differences would be understandable if there were significant differences in the vertical distributions of zooplankton in the eastern and western arctic. The following subsections review present knowledge about relevant aspects of zooplankton biology, emphasizing relative abundances, vertical distributions, and seasonal variations in the two regions.

Productivity of Baffin Bay and the Beaufort Sea

Platt et al. (1987) estimated that primary productivity in the Baffin Bay region is about 35-70 g C/m^2/y, but could be as high as 100 g C/m^2/y. Primary productivity in shallow waters of the Beaufort Sea is about 15-40 g C/m^2/y (D. Schell in Subba Rao and Platt 1984; Macdonald et al. 1987). In northern areas, primary production is strongly pulsed. Much of the plant material produced during the pulse of production during the open water season is not consumed by the zooplankton. This material sinks to the bottom where it provides food for the benthos (Longhurst et al. 1984; Thomson 1987a). Regional differences in the standing crop of benthos may be a measure of regional differences in primary productivity--perhaps a better measure than is the standing crop of zooplankton. The relatively small over-wintering populations of zooplankton cannot consume more than a small fraction of the pulse of primary production that occurs during the spring bloom.

Zooplankton standing crop in the southern Beaufort Sea is about half that in the more productive Eastern Arctic or Bering Sea. However, the standing crop of benthos is much lower in the Beaufort Sea than in Baffin Bay or the Bering Sea (Table 20).

Table 20. (imprison of primary productivity, zooplankton biomass in the upper 50 m, and mean benthic biomass at depths of 5 to 50m in three regions.

Region	Primary Productivity (g $C/m^2/y$)	Zooplankton Biomass (mg/m^3)	Benthic Biomass (g/m^2)	References
E. Cdn Arctic	35-70	400	319	Sekerak et al. 1979; Thomson 1982; Platt et al. 1987
Beaufort Sea	15-40	100-200	41	Carey 1977; Subba Rao and Platt 1984; Griff iths et al. 1987; Macdonald et al. 1987
Bering Sea	75-150	400	475	Alton 1974; Ikeda and Motoda 1978; Thanson and Martin 1984; Thomson 1987a

When compared to differences among other oceanic areas, the average biomass of zooplankton in the eastern arctic is not very different from that found in the southern Beaufort Sea. However, it is the biomass of zooplankton that occurs in dense concentrations that is relevant to feeding whales. Very little information is available about the peak biomasses available in zooplankton concentrations in the eastern arctic.

Characteristics of Arctic Zooplankton

The species compositions of the zooplankton communities found in the upper 50 m of the Beaufort Sea, Northwest Passage, and Baffin Bay are similar. In these regions, the zooplankton communities are dominated by copepods, specifically Calanus hyperboreus, C. glacialis, Pseudocalanus minutus, Euchaeta norvegica, Metridia longs, Microcalanus pygmaeus, and Oithona similis (Grainger 1965; Shih and Laubitz 1978; Buchanan and Sekerak 1982; Longhurst et al. 1984). In the eastern arctic, Calanus finmarchicus can be abundant in areas where there is a pronounced Atlantic influence (Longhurst et al. 1984). In the Beaufort Sea, Eucalanus bungii, Calanus cristatus and others may be abundant where there is an intrusion of Bering Sea water (Johnson 1956). The brackish water species Limnocalanus macrurus can be abundant in areas with estuarine influences such as off the Mackenzie River and in some high arctic bays (Sekerak et al. 1976b; Thomson et al. 1978; Bradstreet et al. 1987; Griffiths et al. 1987).

Most of these copepods have a two year life cycle in most areas (Grainger 1965; Cairns 1967; Dunbar 1968). Depending on food supply and other conditions , the life cycle may be longer or shorter than two years (Cairns 1967). Species that require two years to reach maturity generally overwinter as stage II or III copepodites during their first winter and as stage IV or V copepodites during their second winter.

During the short arctic summer, copepods must store energy for the long winter when food is scarce. This energy is stored in the form of lipids. In spring, lipid content of arctic copepods is low, averaging about 29% of dry weight (Lee 1974). Lipid content is highest in fall when it can amount to 74% of dry weight. Given the high caloric content of lipid, caloric content also increases over the summer and is highest in fall (Percy and Fife 1981; Harris 1985). Thus, the bowhead feeding that occurs at Isabella Bay and in the Beaufort Sea during late summer and fall occurs at a season when the lipid and caloric content of the copepods is highest. Feeding is probably more efficient then than at other times of year.

In early summer, copepods concentrate in the upper part of the water column where most of the primary productivity occurs (Longhurst et al. 1984). In late summer and early fall, most of the herbivorous copepods migrate down to their over-wintering depths. In the Baffin Bay area, copepods overwinter at depths >200 m (Longhurst et al. 1984; Head and Harris 1985). Copepods descend to these depths when they have accumulated sufficient lipid and protein reserves for over-wintering (Head and Harris 1985). In late summer, those copepods that had not accumulated sufficient reserves and were still feeding in the upper 50 m were lighter and had a lower lipid content than animals from >200 m depth (Head and Harris 1985). Copepods from deep water in Swedish and Norwegian fjords were also heavier than those from surface waters and had large oil sacs (Hirche 1983). This seasonal vertical migration of copepods has been noted in other areas including the Bering Sea (Smith and Vidal 1986), North Pacific Ocean (Cooney 1986), and Arctic Ocean (Dawson 1978).

Vertical Distribution of Zooplankton in Baffin Bay

The vertical distribution of copepods in Baffin Bay varies with season. The main factors associated with these vertical distribution patterns are the timing of seasonal migration and the vertical distribution of temperature and salinity (Longhurst et al. 1984). These variations in vertical distribution of copepods and other zooplankton likely have a strong influence on bowhead feeding.

Finley et al. (1986) saw a few bowheads skim feeding at the surface of Isabella Bay in late summer. The potential food of these surface feeding whales was not investigated. However, several zooplankton species sometimes concentrate near the surface at this time of year. Longhurst et al. (1984) found a near-surface concentration of zooplankton in Baffin Bay, usually in the upper 5 m. At some of their stations, copepods within this near-surface concentration had large oil sacs compared with individuals immediately below it. In addition, pteropods and hyperiid amphipods are sometimes very abundant in eastern arctic surface waters (Sekerak et al. 1976a,b; Thomson et al. 1978; Longhurst et al. 1984). Hyperiids sometimes appear to swarm at the surface (Dunbar 1946; Sekerak et al. 1976b).

Longhurst et al. (1984) investigated the vertical distribution of zooplankton in the northern Baffin Bay area in August. Continuous vertical profiles showed that most species and life stages of copepods were concentrated in layers. Only a small fraction of the total zooplankton biomass was near the surface. The layer containing maximum numbers of zooplankton was usually about 15 m shallower than the base of the thermocline. The base of the thermocline was located at an average depth of 36 m. Below the thermocline, there usually was another layer of copepods near the interface between the Arctic Ocean Water and the deeper Atlantic Water. This second layer with copepods usually occurred in the upper 50 m of the Atlantic water some 200-250 m below the surface. Younger copepodite stages were generally found higher in the water column than the older stages. The copepods found within the lower layers tended to be larger and have a higher lipid content than copepods found higher in the water column (Head and Harris 1985).

In the Baffin Bay region, there are areal differences in the depth distributions of copepods. In Lancaster Sound the timing of breakup and appearance of open water determine the timing of biological spring and summer (Sameoto et al. 1986). Differences in the timing of breakup were associated with differences in the timing of copepod life cycles within various parts of Lancaster Sound (Sameoto et al. 1986). Sekerak et al. (1979) also noted regional differences in the development schedule of copepods in the Baffin Bay area. During Longhurst et al.'s (1984) sampling in August, there was still a considerable amount of ice in Kane Basin. Unlike the usual situation in Baffin Bay, zooplankton in Kane Basin was concentrated near the surface. Longhurst et al. (1984) speculated that this represented the early spring condition. The remainder of their study area was ice free and copepods were found at deeper depths. As the summer progresses, copepods (particularly the larger life stages) tend to be found deeper in the water column (Longhurst et al. 1984; Head and Harris 1985). In Fram Strait, an absence of ice, stratification, and the onset of the spring bloom are all necessary for reproduction in *Calanus glacialis* (Hirche and Bohrer 1987). Since the timing of breakup can vary among years and among areas, the timing of life cycles and of the downward seasonal migration can vary among years and areas.

In Isabella Bay, Finley et al. (1986) and Finley (1987) found that zooplankton biomass was high in the deep water (>100 m) of the NE Trough, which was used intensively by foraging bowheads during some years. In 1986 zooplankton biomass was higher at depths >100 m within the trough than at shallower depths above the trough, or at shallow or deep (>100 m) depths in other areas. However, the mean biomass detected at depths >100 m within the trough (0.43 g/m^3) was comparable to that in the upper 50 m of Lancaster Sound and Baffin Bay (0.4 g/m^3; Sekerak et al. 1979). The deep tows in the NE Trough were vertical tows, which average the high biomass within zooplankton 'layers' with the low biomass between layers. The whales presumably fed at a depth with higher than average biomass. There was a higher proportion of adult female copepods and stage V copepodites at depths of 100-200 m within the trough than in waters <100 m over the trough or in other areas. These older stages probably represented copepods that had descended to overwintering depths.

There were striking differences in use of the NE Trough by bowheads over the four years of the study (see 'Results'). Although some zooplankton sampling was done each year, depth-stratified samples were taken below 100 m only in 1986. Thus, there is little information with which to compare food availability in years when bowheads used the NE Trough heavily, sparsely, or not at all.

Vertical Distribution of Zooplankton in the Beaufort Sea

The seasonal pattern of vertical migration of copepods in the Beaufort Sea itself has not been studied in detail. In the Arctic Ocean farther north, Calanus hyperboreus copepodites over-winter at depth's of 300-500 m and rise to near-surface waters in summer (Dawson 1978). Newly moulted females are found near the surface in summer and winter at depths of about 150 m. The other adult females sink from 100 to 300 m in spring. Calanus glacialis in the Arctic Ocean winter at depths of about 200 m and rise to near-surface depths in July and August (Geinrikh et al. 1980). In October 1986, Griffiths et al. (1987) found few copepods in the upper 50 m of the eastern Alaskan Beaufort Sea. Copepods had dominated the zooplankton of this area in September of that year. Griffiths et al. speculated that copepods had migrated downward to their over-wintering depths by October.

Vertical Distributions in the Beaufort Sea and Baffin Bay Compared

The composition of the zooplankton of the Beaufort Sea is similar to that of Baffin Bay, the Arctic Ocean and other areas where a seasonal vertical migration has been studied. The depths to which these migrations may occur in the western arctic likely are similar to those recorded in other areas. In deep waters of the Beaufort Sea, the depth of the interface between Arctic Surface Water and the Atlantic layer below it is similar to that in Baffin Bay. However, there are differences in the ice regimes in the two areas, and these differences could cause differences in the timing of the seasonal migration of copepods. Another difference is the presence of a broad and shallow continental shelf in the Canadian Beaufort Sea, contrasting with the narrow shelf in northwest Baffin Bay.

In the eastern arctic, biological spring and the subsequent descent of copepods to overwintering depths occurs later in areas where the ice cover persists longer (Longhurst et al. 1984; Sameoto et al. 1986). During all but one of the years from 1980 to 1986, heavy ice cover persisted until early or mid August over most deep waters of the Beaufort Sea where copepods may overwinter. In contrast, deep waters of northern Baffin Bay are generally open by mid July. Concentrations of pack ice can often be found off the east coast of Baffin Island, including Isabella Bay, until September (Marko 1982 and 'Study Area' section). However, areas to the north are generally open much earlier (Marko 1982). Currents along eastern Baffin Island flow to the south. Thus, the copepods found off Isabella Bay in late summer originate farther north in areas where open water occurs early. Thus, these copepods would have begun summer reproductive and feeding activities early in the summer.

In the Beaufort Sea, summer feeding by copepod populations overwintering in deep water off the shelf may tend to occur later in the summer, given the heavy ice cover usually present over deep water for much of the summer. If summer feeding is delayed for this reason, the descent of copepods to over-wintering depths probably would also be delayed relative to that in Baffin Bay. A regional difference in the timing of the downward migration of copepods might cause differences in the vertical distribution of copepods in two areas during late summer. This could account for differences in the typical depths of feeding dives by bowheads. The hypothesized earlier descent of copepods off Isabella Bay could result in deeper feeding dives in that region, with correspondingly longer surfacing - respiration - diving cycles,

We emphasize that this hypothesis is speculative. There is strong suggestive evidence that bowheads were feeding very deep in the water column at Isabella Bay: the large copepods found in their feces (n = 2 samples) were concentrated at deep depths, and the surfacing - respiration - dive cycles were consistent with deep dives. However, this evidence for deep dives is indirect. A seasonal vertical migration of Calanus copepods has been demonstrated in the Baffin Bay area, the Arctic Ocean, and some other areas. However, the evidence of a corresponding seasonal vertical migration in the southern Beaufort Sea is only suggestive. In the eastern arctic there is evidence that the timing of ice breakup affects the timing of the summer feeding period for copepods, and the timing of their subsequent downward migration. It is reasonable to suppose that the typically later ice breakup in most of the deep waters of the Beaufort Sea[23] causes a later date of downward migration there, but there is no direct evidence on this point.

Thus, these arguments suggest a plausible hypothesis for the occurrence of feeding at deeper depths in Baffin Bay than in the Beaufort Sea during late summer. However, information about the vertical migration of copepods and other zooplankton in the Beaufort Sea is needed. Also, more detailed information about the vertical distribution of zooplankton off Isabella Bay in late summer would be helpful in understanding the feeding behavior of bowheads there.

Direct measurements of the depths of dives by bowheads, as determined by telemetry or echosounding, would be very useful in understanding many aspects of their behavior and physiology. Depths of bowhead dives have not been measured. On a few occasions, the depths of prey concentrations on which bowheads were feeding have been determined at the specific locations and times where whale behavior was observed (Richardson et al. 1987b VS. Griffiths et al. 1987). However, all of these data came from shallow water (≤25 m). Hence, it is not possible to establish relationships between surfacing - respiration - dive variables of bowheads versus prey depth.

As noted earlier, the behavior of bowheads feeding in deep water was quantitatively different in several respects off Isabella Bay from that in the Beaufort Sea. These differences could not be accounted for by relationships between behavior and any of the environmental or whale activity variables that were measured. However, depths of dives could not be measured, and there was little specific information about depths of prey concentrations (from which depths of dives could be inferred). Thus, a key corollary variable that may

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23 There is open water early in the summer in western Amundsen Gulf and near Banks Island--the direction from which the current typically flows. This open area is typically less extensive than the open deep waters in Baffin Bay in early summer.

have differed substantially between regions was not measurable. In the absence of information about depths of dives, it is impossible to determine whether the observed differences in behavior of whales feeding in deep water represented a population difference between the eastern and western arctic stocks, or a difference attributable to food availability at the times and places of observation.

Behavior of Socializing Bowheads vs. Population Segregation

The behavior of bowheads socializing in shallow water at Isabella Bay, eastern Arctic, during late summer and autumn was quite different than at most observation locations in shallow portions of the Beaufort Sea (see Results). At Isabella Bay, socializing was typically quite active and boisterous, with much aerial activity and few fluke-out dives. In the Beaufort, social interactions in late summer rarely were this intense, aerial activity was less common, and fluke-out dives were more common. There often was a clear sexual component to the social interactions at Isabella Bay; this was rarely evident in the Beaufort. There also were significant differences in surface times and number of blows per surfacing, even after allowance for corollary variables.

Thus there were strong differences in social behavior between the eastern and western arctic, including a near absence of overt reproductive behavior in the Beaufort in late summer as opposed to considerable reproductive behavior in the east. The apparent difference in reproductive activities between populations is of special interest, given its possible direct connection to the 'health' of the population. It is important to develop an understanding of the reason(s) for the seemingly lower reproductive activity in the western arctic during late summer.

One possibility might be a regional difference in the timing of the annual cycle of bowheads. The season when zooplankton is suitable for feeding may begin somewhat earlier in the east according to the evidence (largely indirect) discussed in the previous section. If so, the annual cycle of activities might be slightly advanced in the east relative to the west, and the presumed 'winter' reproductive season might commence earlier in the autumn in the eastern arctic than in the west. This idea is highly speculative, given the scarcity of relevant data on zooplankton, bowhead reproduction, and other aspects of the annual cycle of bowheads in the eastern arctic. Also, the timing of autumn migration in the eastern and western arctic is quite similar (see 'Results--Migration in E Arctic'). Obvious sexual interactions were seen frequently at Isabella Bay before autumn migration began, whereas such behaviors were very infrequent in the Canadian and Alaskan Beaufort Sea during late summer and autumn migration. Thus, the regional difference in reproductive activities did not seem to be simply a minor difference in the timing of the annual cycles of bowheads in the two areas.

A more likely explanation is the probable segregation of bowheads according to age, sex, or reproductive status. The bowheads socializing and engaging in sexual behavior at Isabella Bay in late summer may represent a component of the eastern population whose western arctic counterpart spends the late summer outside the area where behavior has been observed. Size segregation of bowheads on the summering grounds in the Canadian Beaufort Sea is well documented (Davis et al. 1983, 1986a,b; Cubbage and Calambokidis 1987;

Koski et al. 1988). The whales observed socializing in shallow waters of the Beaufort Sea were mainly small subadults, whereas those at Isabella Bay were mainly large subadults and adults. Thus, it is perhaps not surprising that more sexual activity was observed among the socializing whales at Isabella Bay. Unfortunately, it was not possible to isolate the western arctic data on large subadults or adults from the overall dataset on socializing whales. We rarely had useful data on the sizes of the specific socializing whales whose behavior was observed.

However, it is curious that overt sexual interactions have almost never been seen anywhere in the Beaufort Sea during late summer or fall. This is true despite the fact that observations in the western arctic have been much more wide-ranging, and over more years, than those in the east. Many behavioral observation sessions have been conducted in areas of the Beaufort Sea where most of the whales present were large subadults or adults. In a few cases the specific whales whose behavior was observed were photographed and measured at the end of the observation session, and confirmed to be large (Koski and Johnson 1987; Richardson et al. 1987b). Thus, the rarity of observations of sexual activity by bowheads in the Beaufort Sea during late summer is not just the result of a paucity of observations of large bowheads.

One area where adult and large subadult bowheads are known to concentrate during late summer is Franklin Bay and (in at least some years) other parts of Amundsen Gulf such as DeSalis Bay along southern Banks Island (Davis et al. 1982; Koski et al. 1988). Systematic behavioral observations have not been collected in these easternmost parts of the summer range of western arctic bowheads. However, casual observations during photogrammetric work suggested that many of the whales in Franklin Bay were water column feeding in deep water (W.R. Koski, LGL Ltd., pers. comm.). It is perhaps important that few of the large whales found in Franklin Bay and DeSalis Bay were accompanied by calves. Calves were also almost totally absent from the Isabella Bay area in the eastern arctic. Water depth increases rapidly with distance from shore in Franklin Bay, as in Isabella Bay. Behavioral observations in Franklin Bay and Amundsen Gulf could be very useful in evaluating whether, during late summer, there really is much less reproductive activity among bowheads in the western than the eastern arctic. More generally, any future observations of all aspects of behavior in those areas should be compared with behavior of the large whales occurring at Isabella Bay.

The 19th century whalers in the eastern arctic believed that small subadult bowheads and cow-calf pairs summered well to the northwest of Isabella Bay in the Bylot Island area and in the channels of the Canadian arctic archipelago accessible via Lancaster Sound (Fig. 2). During recent years a few cow-calf pairs have been seen in these areas, or migrating south from them in autumn. However, there has been no photogrammetric study to confirm the sizes of the bowheads summering in these northwestern areas, and no study of bowhead behavior in those areas during late summer. The size composition and behavior of bowheads that summer northwest of Isabella Bay may be similar to sizes and behaviors of bowheads studied in the Beaufort Sea, but this prediction remains to be tested.

In conclusion, behavior of bowheads socializing in shallow water at Isabella Bay is clearly different in many respects than that of bowheads socializing in shallow water of the Beaufort Sea. It may be of special importance that overt sexual activities are rare in the Beaufort Sea in late summer, but common at Isabella Bay. This might be symptomatic of a difference in reproductive activities between the two regions. The null hypothesis of no difference in behavior of socializing whales observed in the two regions can be rejected. However, it is unlikely that the samples, especially the data from a single area of the eastern arctic, are fully representative of the two populations. Hence, the available data on socializing bowheads in the eastern and western arctic probably are not directly comparable. To provide a more meaningful comparison, more information would be needed about behavior of bowheads summering in the Amundsen Gulf region of the western arctic, or from areas northwest of Isabella Bay in the east, or ideally from both of these areas.

In the absence of additional fieldwork in these areas, it could also be useful to conduct a more intensive analysis of existing data on the sexual interactions observed at Isabella Bay, for which there were no counterparts in the western arctic. This analysis should attempt to evaluate the functions of the sexual interactions to determine whether they represented actual reproductive activity, behavior facilitating reproduction later in the winter, or perhaps a form of behavioral maturation in subadults nearing the age of sexual maturity. This question could be approached through' further analysis of existing data on these interactions and a detailed comparison with the spring reproductive behavior of western arctic bowheads (e.g. Everitt and Krogman 1979; Ljungblad 1981). A detailed comparison of sexual behavior at Isabella Bay with the better-known reproductive behavior of the right whale (cf. Donnelly 1967, 1969; Saayman and Tayler 1973; Payne and Dorsey 1983; Kraus et al. 1986; Payne 1986) would also be valuable in interpreting the significance of the social activities at Isabella Bay, and the apparent scarcity of similar activities in the Beaufort Sea.

Overall Statistical Significance of Differences, Especially for Migrating Bowheads

It is obvious that the overall behavior of the **feeding** bowhead whales and especially the **socializing** whales differed significantly between the two regions. For both of those categories of whale activity, statistical analysis revealed highly significant differences in a number of variables. Some of these differences remained significant after the potentially confounding effects of many temporal, environmental and whale-activity variables were taken into account by multivariate analysis.

Thus, for feeding and socializing whales, there is no question that the behavior of the observed animals differed. Instead, the main questions involve the possible explanations for the obvious behavioral differences. For feeding whales, the differences in behavior might represent real differences between populations, but might also result from the presumed greater average depth of feeding dives in the eastern arctic study area. For socializing whales, the observed differences in behavior were probably largely a result of differences in the age (and possibly sex) composition of the animals observed in the eastern vs. western arctic.

Migrating bowheads observed in the two regions were more directly comparable than were socializing or feeding whales. The conditions under which migrants were observed were similar in most respects, with the main exceptions being distance from shore and (in 1983) ice conditions. The size and age compositions of the whales observed in the two regions were also suspected to be more similar in the case of migrants than for socializing bowheads.

In the case of migrating bowheads, only a few of the numerous behavioral variables that we examined were significantly different between regions. The flukes were raised above the surface at the onset of a larger proportion of the dives in the east than in the west, based on a small sample ($P<0.001$, Table 4). Dive durations tended to be notably longer in the western arctic ($P<0.001$; Table 11). However, a multiple regression analysis to assess whether dive durations remained significantly different after allowance for other environmental and whale activity variables produced inconclusive results. Because average dive durations were shorter in the east while average surface times were similar in the east and west, the percentage of time at the surface was higher in the east. Directions of travel in the two areas were very different (mainly W or NW in Beaufort; SE or S in Baffin Bay). However, this was an inevitable consequence of differences in the geography of the two regions, and should not be counted as a meaningful difference in behavior. Other variables that did not seem to differ appreciably between bowheads migrating in the two regions were duration of surfacing, number of blows per surfacing, mean interval between successive blows, swimming speeds, and frequencies of social interactions and aerial behaviors.

One possible way to evaluate the overall significance of differences in behavior of migrating bowheads in the two regions would be to combine the probabilities associated with the various statistical tests. Rosenthal (1978) summarizes several methods for combining probabilities from independent tests of one null hypothesis. For each behavioral variable, our statistical test for an east-west difference was a test of a subsidiary null hypothesis to the general null hypothesis posed in the Introduction. At first glance, one might propose to combine the probabilities from the tests of various behavioral variables to obtain a single test of the overall east-west difference in behavior. However, this would not be legitimate because a single surfacing of one whale can contribute data on several different variables. Thus that surfacing can be represented in several different statistical tests. In that situation, there is a real concern that the various tests are not statistically independent, which is essential for obtaining a meaningful pooled probability. Thus, we can only conclude that, for migrating bowheads, at least two specific aspects of behavior--dive durations and frequency of fluke-out dives--appear to differ significantly between the eastern and western arctic,

The possible relationships of behavioral differences to differences in human activities will be evaluated in Phase 2 of this study, to be done in 1989. One can speculate, for example, that the longer dive durations of migrating whales in the western arctic would make them less accessible to hunters; this difference in behavior might be related to the continuing bowhead hunt in the western arctic. Likewise, the lower frequency of fluke-out dives by migrants might be related to the fact that this behavior increases the conspicuousness of a whale to hunters.

CONCLUSIONS

1. The general behavioral repertoires of the eastern arctic (Davis Strait/Baffin Bay) and western arctic (Bering/Beaufort) populations of bowhead whales are qualitatively similar. Almost all behaviors observed during late summer and autumn in the eastern arctic (along the east coast of Baffin Island) have also been seen in the west. Likewise, most of the behaviors seen during the more extensive western studies have also been seen in the east.

2. Notwithstanding conclusion (l), there were many quantitative differences between the behaviors observed in the eastern and western arctic. This was true even though east-west comparisons were restricted to whales engaged in similar activities i.e.

   - feeding in the water column in deep water,
   - socializing in shallow water, and
   - migrating in autumn.

   There were statistically significant regional differences in the behavior of bowhead whales engaged in all three of these activities (Table 21).

3. Environmental conditions in the Beaufort Sea and along the east coast of Baffin Island are very different. Some of the east-west differences in behavior appeared to be attributable to differences in the environmental conditions under which bowheads occurred. Other differences seemed to be attributable to differences in the activities in which the whales were engaged at the time of observation, e.g. 'pure' socializing in one area at Isabella Bay, Baffin Island, vs. intermixed socializing plus feeding in the Beaufort. However, even after allowance for the effects of these corollary variables on behavior, several aspects of behavior remained highly significantly different between the whales observed in the eastern and western arctic.

4. The surfacing - dive cycles of whales feeding in deep (>50 m) water were much more protracted in the eastern arctic than in the west, with many more respirations per surfacing (Table 21). These differences were evident even after allowance for regional differences in measured environmental variables. However, one potentially relevant corollary variable that could not be measured was depth of dives. It is suspected that the behavioral differences were at least partially attributable to a greater average feeding depth in the east. In the absence of specific data on depths of dives, it is uncertain whether the observed strong east-west differences in behavior among feeding whales were attributable to differences in depths of dives or to some other regional difference.

5. Behavior of bowheads socializing in shallow (<50 m) water differed strongly in many respects between the Beaufort Sea and the Isabella Bay area of the eastern arctic (Table 21). Socializing was much more active at Isabella Bay, and obvious sexual interactions were much more

Table 21. Summary of the observed behavior of bowhead whales in the Baffin Bay (eastern arctic) area relative to that in the Beaufort Sea (western arctic). See Tables 3, 4, 11 for details. Boldface type highlights the main E-W differences.

	While Feeding in Deep (>50 m) Water	While Socializing in Shallow (<50 m) Water*	While Migrating in Autumn
Distance from Shore	**Closer in E**	**Closer in E**	**Much closer in E**
Group Size	Similar, but pairs more common in E	**>1 more often in E than in W**	Slightly smaller in E
No. bhd within 1 km	**Fewer in E**	**Fewer in E**	**Fewer in E**
Interspersed Activities	**None in E; travel or social in W**	**None in E; feeding in W**	None in either area
Predominant Feeding Mode	Water-column in E; mainly wat.-col. in W	None in E; wat.-column most common in W	
Speed of Motion	Zero to moderate in both areas	Zero to moderate; more often zero or low in E	Moderate to fast in both areas
Social Activity	Little in either area	**Much more active in E**	Rare in either area
Aerial Activity	Rare in both areas	**More common in E (P<0.001)**	Rare in both areas
Flukes Out at End of Surfacing	Common in both areas; low n in West	**Less common in E (P<0.001)**	**More common in E (P<0.001)**
Mean Blow Interval	**Slightly longer in E (P<0.001)**	**Much longer in E (P<0.001)**	Similar
No. Blows per Surfacing	**Much larger in E (P<0.001)**	**Much smaller in E (P<0.001)**	Similar
Duration of Surfacing	**Much longer in E (P<0.001)**	**Shorter in E (P<0.001)**	Similar
Duration of Dive	**Longer in E (P<0.001)**	Similar; short in both areas	**Shorter in E (P<0.01)**
% of Time at Surface	**Higher in E**	**Higher in E**	**Higher in E**

* See p. 83 for discussion of differences in calls produced by socializing bowheads in the two regions.

common during late summer there than in the Beaufort Sea. The differences were very likely attributable in part to differences in the predominant sizes and age categories of the whales whose behavior was compared. Most bowheads socializing in shallow waters of the Beaufort Sea were small subadults, whereas most of those in shallow water at Isabella Bay were adults and large subadults. However, sexual interactions have very rarely been seen during late summer or autumn anywhere in the Beaufort Sea, including areas where there were many adults and large subadults. Given the high frequency of such behavior at Isabella Bay, there may be real differences in reproductive activities between the two stocks.

6. Bowheads engaged in autumn migration in the eastern and western arctic were the most directly comparable of the three categories of whales considered. Behavior of migrants in the two regions was generally similar. However, dive durations were considerably greater in the west, and fluke-out dives were more common in the east. Given that most of the behavioral variables examined did not differ significantly between migrants in the two regions, it is difficult to evaluate the biological significance of the two statistically significant differences that were detected.

7. Overall, it is apparent that the behavior of eastern arctic bowheads along the coast of Baffin Island in late summer differs quantitatively in a number of ways from that observed in the Beaufort Sea. Some of these differences can be ascribed to differences in environmental conditions or the types of whales and whale activities that were observed in the two regions. However, other east-west differences in behavior cannot be accounted for in this way. The apparent regional difference in the frequency of sexual interactions in late summer is potentially of particular significance. Phase 2 of this study, being done in 1989, will examine whether any of these behavioral differences can be ascribed to long-term effects of the differing levels of human activities in the two regions.

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