BEHAVIOR, DISTURBANCE RESPONSES AND DISTRIBUTION
OF BOWHEAD WHALES Balaena mysticetus
IN THE EASTERN BEAUFORT SEA, 1980-84

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DISCLAIMER

PROJECT RATIONALE AND DESIGN*

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INTRODUCTION

The bowhead whale, <u>Balaena mysticetus,</u> inhabits cold northern waters. All populations were exploited heavily by commercial whalers in the 18th or 19th centuries, and all were seriously reduced. Bowheads are considered endangered under U.S. legislation.

Bowheads of the Western Arctic (= Bering Sea) population, the one group occurring in U.S. waters, winter in the Bering Sea, summer in the eastern Beaufort Sea, and migrate around western and northern Alaska in spring and autumn (Fig. 1, inset). The size of this population was much reduced by intensive commercial whaling between 1848 and 1914 (Bockstoce and Botkin 1983). The extent of the summer range was apparently also much reduced (Dahlheim et al. 1980; Fraker and Bockstoce 1980). A subsistence harvest continues annually in Alaska. The International Whaling Commission's current 'best estimate' of the stock size is 3871 individuals (I.W.C. 1984).

The spring migration of Western Arctic bowheads is close to shore in the Chukchi Sea, but well offshore in the Alaskan Beaufort Sea (Braham et al. 1980, 1984; Ljungblad et al. 1982a). Thus, the eastward spring migration through the Alaskan Beaufort Sea in April–June is well north of the area of oil exploration near the coast. However, during the westward autumn migration in August – October, many bowheads occur close to shore, within or near some offshore oil leases (Braham et al. 1984; Ljungblad et al. 1984).

From June to early September, the great majority of the Western Arctic bowheads are in Canadian waters (Fraker 1979; Fraker and Bockstoce 1980; Davis et al. 1982). Intensive offshore oil exploration began several years earlier in the Canadian part of the Beaufort Sea than in the Alaskan portion. Nearshore drilling from artificial islands has been underway in the south-central part of the summering area since about 1972, with drillships in use farther offshore since 1976. Seismic exploration began there earlier and still continues. The main area of offshore drilling is north of the Mackenzie Delta and the western Tuktoyaktuk Peninsula (Fig. 1). Summering bowheads are sometimes common in and around that area (Fraker and Bockstoce 1980).

POTENTIAL FOR DISTURBANCE

The scientific literature contains few descriptions of the reactions of baleen whales to boats, aircraft, drillships, and other activities associated with offshore oil exploration. Until 1980 there had been few detailed or controlled studies of these reactions. Controlled studies are especially desirable because whale behavior is quite variable. In the absence of experimental control, it is difficult to determine whether a change in behavior is 'natural' or a response to some human activity. Long term effects of offshore industrial activities on whales are even more difficult to study. The literature on these topics has been reviewed recently by Fraker and Richardson (1980), Geraci and St. Aubin (1980), Acoustical Society of America (1981), Gales (1982), Malme et al. (1983), and Richardson et al. (1983).

Noise is one attribute of offshore oil exploration and development that may affect whales. Unlike major oil spills, noise is an ongoing component of normal offshore operations. Noise is introduced into the sea by most of the
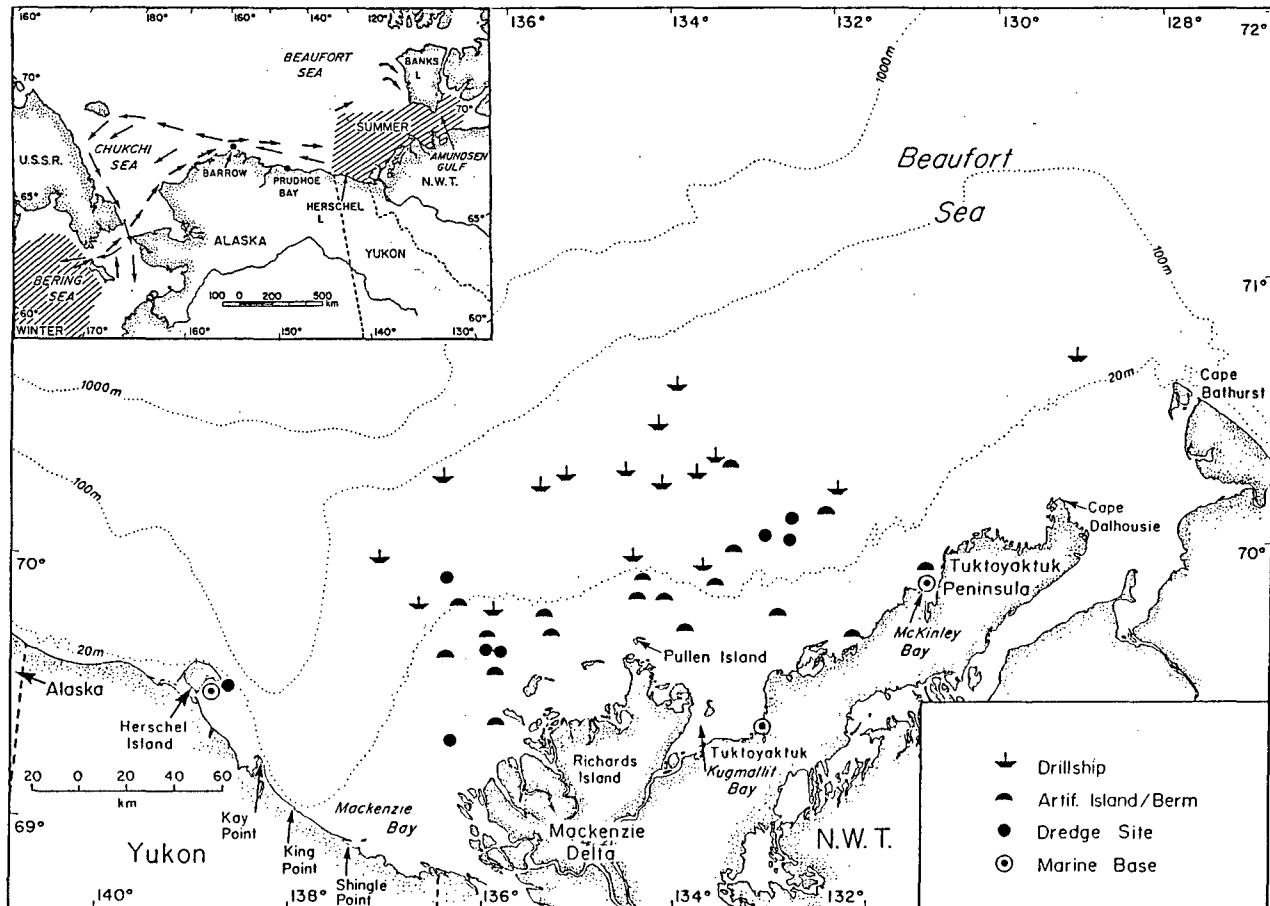
FIGURE 1. The eastern Beaufort Sea, study area for this project, showing the main sites of offshore industrial activity in August and early September, 1980-84. **Inset:** Generalized pattern of seasonal movement of the Western Arctic population of bowhead whales.

offshore activities associated with the oil industry, including boat and aircraft traffic, seismic exploration, dredging and drilling (Acoustical Society of America 1981; Richardson et al. 1983). Many of the sounds produced are at rather low frequencies (below 1000 Hz). This is the frequency range of most bowhead calls (Ljungblad et al. 1982b; Clark and Johnson 1984). Hearing sensitivity of baleen whales has not been measured, but the predominance of low frequency calls (Thompson et al. 1979) plus anatomical evidence (Fleischer 1976) suggest specialization for detecting low frequencies.

Sound, unlike light, can propagate long distances through water (Payne and Webb 1971; Urick 1975). With calm to moderate sea states, noise from boats, dredging and drilling is readily detectable by instruments, and

probably by bowheads, at ranges of several kilometres or more (Richardson et al. 1983). Noise from seismic exploration in open water is much more intense, and often detectable at ranges of several tens of kilometres (Ljungblad et al. 1980, 1982a; Richardson et al. 1983; Reeves et al. 1984). It is probable, therefore, that bowheads detect noise from offshore oil exploration and other offshore industrial operations at rather long distances—much longer than the distances to which vision or other sensory modalities could detect the industrial activity.

Within the often-large area around industrial activity where a bowhead could detect industrial noise, there is the potential for disturbance. This could take at least four interrelated forms: disruption of normal behavior, displacement (short- or long-term), physiological stress, or masking of natural sounds. The potential negative effects of these types of disturbance were discussed at length in the reviews cited above.

The importance of interference with detection of natural sounds is perhaps the least obvious of these types of potential disturbance. Increased noise levels reduce signal to noise ratios and, consequently, the range at which the sound signal becomes undetectable. Calls by baleen whales seem important for communication (Clark 1983), sometimes over distances of kilometres (Watkins 1981; Tyack and Whitehead 1983). Increased noise levels at frequencies similar to those of the calls will reduce the distances over which the calls can be detected. Detection of other environmental sounds may also be important to bowheads. For example, noise from ice or breaking waves may be important in finding open water within areas of heavy ice. Industrial noise may reduce the range to which bowheads can detect such noises, and consequently may delay whale movements in the presence of ice, or even increase the probability of entrapment by ice.

OBJECTIVES AND TASKS

Because of the endangered status of the bowhead whale, U.S. regulatory agencies were required, before permitting offshore hydrocarbon exploration in Alaskan waters, to assess whether that exploration would harm bowheads. After consultation among the responsible agencies, it was decided that there was insufficient information to determine the degree of jeopardy. Hence, research concerning the acoustic and non-acoustic effects of offshore hydrocarbon activities on bowheads was deemed necessary.

As part of its response, the U.S. Department of the Interior (USDI) awarded LGL Ecological Research Associates, Inc., a contract to investigate various aspects of potential industrial disturbance. The work was administered through USDI's Bureau of Land Management in 1980-81, and the Minerals Management Service in 1982-85. The general objectives were as follows:

1. "Identify and describe, qualitatively and quantitatively, the daily and seasonal behavior (e.g., feeding, breeding, calving) and activity patterns of the various age and sex classes of bowhead whales that occur in the eastern Beaufort Sea, and as it relates to the U.S. Beaufort Sea lease sale area.

2. "Determine, as possible, how and to what extent acoustic and [other] stimuli from oil and gas exploration/development activities may be expected to affect the distribution, movements, activities and activity patterns, and, ultimately, the survival and productivity of bowhead whales.

3. "Provide reliable baseline information which, in conjunction with long-term monitoring programs, can be used to detect changes in bowhead whale distribution, movements, activity patterns, etc. that may be caused by offshore oil and gas development in the Beaufort Sea.

4. "Assist ... (a) [in determining] the seasonal distribution and movements of bowhead whales in and adjacent to the Beaufort Sea Lease Sale Area; and (b) identify and characterize bowhead whale feeding areas, breeding/calving areas, or other areas of similar biological significance that may occur in or adjacent to the Beaufort Sea Lease Sale Area.

5. "Meet the study requirements of the Beaufort Sea, Endangered Species Act, Section 7 consultation..."

To address these objectives, four main tasks were defined at the start of the project, and a fifth task was defined in a subsequent contract modification:

Task 1: Prepare a literature review concerning (a) the distribution, movements, and activities, of bowhead whales; (b) the stimuli associated with offshore oil and gas exploration and development; and (c) present knowledge of the potential effects of those stimuli on bowheads. Task (1) was completed in 1980 (Fraker and Richardson 1980).

Task 2: Obtain baseline data on the activities and behavior of bowhead whales in the absence of sources of potential disturbance. This task was done because an understanding of the activities of bowheads in the absence of disturbance was necessary in order to interpret their behavior near industrial activities. There had been no previous study of the behavior of summering bowheads, and little previous study of behavior at any season. Task (2) was renewed for the entire 5-year duration of the project. However, in later years task (2) was a priority only when it provided specific control data needed for interpretation of disturbance responses.

Task 3: Conduct perturbation experiments and other studies to determine the behavioral reactions of bowhead whales to offshore oil and gas activities. Boat and aircraft traffic, seismic exploration, drilling, and construction activities were identified as the priority industrial activities. Both uncontrolled observational work and controlled experiments were required. Analysis of characteristics of waterborne sounds created by the industrial activities was considered to be part of the task. This task was renewed for all five years of the project, although priority activities changed from year to year as information accumulated about some topics.

Task 4: Determine the characteristics of bowhead feeding areas, with emphasis on zooplankton and the physical characteristics of the water masses. This task was limited in scope and was not continued after 1981. We

found that, in summer, bowheads tended to occur in areas with higher than average abundance of copepods, one of the known prey groups (Lowry and Burns 1980). The final report on this 1980-81 task was Griffiths and Buchanan (1982); the present volume does not cover this topic.

Task 5: Document occurrence and intensity of industrial activity in the Beaufort Sea during 1980-84 and, as possible, relate such patterns to recent trends in behavior and distribution of bowheads. This task was first identified in 1982; it included a retrospective analysis of existing 1980-81 data plus accumulation of additional data in 1982-84. The main intent was to assess whether there was any evidence of change in the distribution of summering bowheads with respect to the main area of offshore oil exploration in the eastern Beaufort Sea.

The present report summarizes the results pertaining to tasks (2), (3), and (5). Results from task (2) are covered in the 'Normal Behavior of Bowheads' section of this report (Würsig et al. 1985). Results from task (3) are covered in the 'Disturbance Responses of Bowheads' section (Richardson et al. 1985c) and in the 'Characteristics of Waterborne Industrial Noise' section (Greene 1985). Task (5) is covered in the 'Distribution of Bowheads and Industrial Activity' section (Richardson et al. 1985a). The present report is a self-contained account of the main results from all five years of the study, including previously unreported results from 1984. Additional details for 1980-81, 1982 and 1983 can be found in earlier reports (Richardson [ed.] 1982, 1983, 1984).

The present report excludes certain aspects of the project. Tasks (1) and (4) ended with the submission of the aforementioned reports by Fraker and Richardson (1980) and Griffiths and Buchanan (1982). A joint effort by Naval Ocean Systems Center and LGL to study bowhead behavior and reactions to seismic vessels in the Alaskan Beaufort Sea in autumn 1981 is reported separately (Fraker et al. in prep.). Plans to conduct spring sound propagation tests in Alaska in 1982, and artificial island noise measurements in Alaska or Canada in 1983, could not be implemented because of logistical constraints; funds allocated for these two efforts were redirected to task (3) in 1984.

APPROACH IN THIS STUDY

Study Area

The study area was the same in each year of the study: the southeastern Beaufort Sea, including the area of offshore oil exploration and surrounding waters to the west, north and east (Fig. 1). Observation sites were between 127°W and 141°W, and from the shore to 190 km offshore. The study period each year has been from late July or early August to late August or early September. This area and season were chosen (1) to take advantage of summer weather, light and ice conditions, (2) because bowheads travel less and thus are easier to study when feeding in summer than when migrating in spring or autumn, and (3) because this is the part of the bowheads' range where offshore oil exploration is furthest advanced. The presence of extensive offshore oil exploration provided opportunities for observation that did not exist in the Alaskan Beaufort Sea. Because this study was conducted in the eastern (Canadian) Beaufort Sea, site-specific information about reactions of bowheads to industrial activities in the Alaskan lease areas was not

obtained. However, we believe that most data collected in the eastern Beaufort Sea are applicable to the Alaskan situation.

The eastern Beaufort Sea is largely ice covered from October to June, but by July there is usually open water south and east of a line from Herschel Island northeast to Banks Island (Fig. 1). However, wind shifts can blow much ice back into this area at any time. Most of our work was on whales in open water, but some was near or in pack ice. In most parts of the study area, water depths increase very gradually out to the shelf break near the 100 m contour, and then increase more rapidly to >1000 m (Fig. 1). The 100 m contour ranges from 15 to 150 km from shore.

Bowhead distribution in summer is variable within and between years. Whales occur in both open water and pack ice, both beyond the shelf break and in water as shallow as 10 m (Fraker and Bockstoce 1980; this study). August and early September are times of peak abundance in shallow areas. Feeding, socializing and travelling are the main activities.

Offshore drilling in the eastern Beaufort Sea began in 1972, initially from artificial islands built in a few metres of water off the Mackenzie River Delta, but after 1976 in deeper water. Each summer from 1976 to 1984, 3-5 drillships operated inside the 100 m contour, and artificial islands and caissons for drilling were completed in waters as deep as 31 m (Fig. 1). Dredges were widely used in constructing islands. By 1983-84, five drillships, 5-6 seagoing dredges, four icebreakers, 8-10 helicopters, and over 30 support vessels were in use offshore. Offshore seismic exploration occurs in the study area each summer. At most times in recent open water seasons, 2-4 seismic boats using airgun arrays or other high-energy noise sources have operated in the eastern Beaufort Sea. Each seismic boat produces an intense noise pulse every 6-15 s.

Approach and Logistics

Behavior of undisturbed bowheads (Task 2) was studied before and after disturbance experiments, thereby providing control data, and on other occasions when experiments were not possible. When logistical difficulties prevented us from conducting experiments, we collected data on undisturbed behavior.

Whenever possible in all years of the study, we conducted experimental tests of reactions of bowheads to industrial activities (Task 3). In these tests, we compared behavior of a specific group of bowheads before, during and after exposure. This method is more sensitive than uncontrolled observations of some whales in the presence of the industrial activity and others in its absence. Many factors aside from industrial activity may differ between groups of whales observed at different places and times. However, the uncontrolled observations were also of interest. For example, they showed that some bowheads approached full-scale industrial sites that could not be simulated adequately during experiments.

No field work specifically directed at determining bowhead distribution in relation to industrial activities (Task 5) was funded under this project. However, many distributional data were obtained incidental to our behavioral work. When task (5) was initiated in 1982, we compiled these distributional

data, along with results from other studies of bowheads conducted in the same study area during 1980-84.

Our observations were obtained from three types of 'platforms'--aircraft, boats, and shore:

Aircraft: Most behavioral observations were from an aircraft circling high
enough above whales to avoid aircraft disturbance. The aircraft crew had
the advantages of great mobility and a good vantage point for
observations. The aircraft crew could drop sonobuoys near bowheads to
record the underwater sounds to which whales were exposed, as well as
the calls that they emitted. An Islander aircraft was used in all years,
although a Twin Otter was also used for part of the 1983 field season.

Boat: A boat, usually a 12.5-m fishing vessel, was chartered for at least
part of each field season. The main functions of the boat were to
conduct disturbance experiments, to record underwater sounds near whales
and near industrial sites, and (in 1980-81 only) to conduct the
'characteristics of bowhead feeding areas' task.

Shore: Shore based observations were attempted at Herschel Island and
King Point (Fig. 1) in 1980-81 but not in 1982-84. Many whales had been
seen close to shore at these locations in some earlier years (Fraker
and Bockstoce 1980). Virtually none were near King Point in 1980-81,
and those near Herschel Island were too far offshore for effective
shore-based observations or experiments. No shore based work was
attempted in 1982-84. In 1983 and 1984 bowheads did occur close to
shore at King Point, and much of our aircraft- and boat-based work in
1983 was in that area.

Results from the various tasks, platforms and years of the study were
complementary. Detailed results from all five years are presented in the
following four sections on normal behavior, disturbance responses,
characteristics of waterborne industrial noise, and summer distribution
relative to industrial activities. Results concerning zooplankton
composition and biomass in some locations where bowheads were and were not
observed in August 1980 and 1981 were presented in an earlier final report
(Griffiths and Buchanan 1982). A summary of the entire study appears in a
separate volume (Richardson, Greene and Würsig 1985b).

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NORMAL BEHAVIOR OF BOWHEADS, 1980-84*

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ABSTRACT

Behavior of bowheads was observed during August and early September of 1980-84, mainly during 98.5 h while an observation aircraft circled at altitude $\geq$457 m above 'presumably undisturbed' whales. In 1980, 1983 and 1984, most whales studied were in waters 10-30 m deep, although not in the same areas during various years. In 1981 they were often in water about 50 m deep, and in 1982 most were in water >100 m deep. Year to year variation in distribution and behavior may have been attributable to changes in zooplankton availability, although this is unproven.

Surfacing, Respiration and Dive Cycles.--Intervals between successive blows were relatively stable, averaging 13.5 $\pm$ s.d. 8.88 s (n = 5161, calves excluded) over the five years. Number of blows per surfacing (4.34 $\pm$ 3.254, n = 626) and duration of surfacing (1.19 $\pm$ 1.137 min, n = 715) were positively correlated. Dives averaged 4.42 $\pm$ 6.319 min in duration (n = 333), with a skewed distribution and a maximum of 31 min. Blow rate, averaged over surface plus dive time, was 1.10 $\pm$ 0.873 blows/min (n = 156). Surfacing-respiration-dive variables were not strongly related to time of day or date in season but were different for mothers and calves than for other whales.

Feeding occupied much of the time of bowhead whales in summer. Whales sometimes skim fed at the surface either alone or in coordinated echelons of up to 14 animals. Bottom feeding was indicated when whales surfaced with mud emanating from their mouths, usually in water 6-24 m deep and with whales >75 m apart. Near bottom feeding was suspected on other occasions when mud streamed from the body but not the mouth. We suspected that whales fed in the water column on the many occasions when they dove repeatedly in an area without making forward progress, and did not surface with mud.

Social behavior, including nudging, chasing, or orienting toward one another when $\leq\frac{1}{2}$ body length apart, was more frequent in early August than later in summer. Apparent mating was seen only twice. Bowheads in groups often surfaced and dove in rough synchrony, and those within 3 km of one another did so at times.

Other behaviors.--On four occasions, we saw whales play with logs up to about 10 m long. Two cases of calf play consisted of orientation toward suspended or floating particles. Aerial activity consisted mainly of breaches, tail slaps, and flipper slaps. One whale breached 64 times, tailslapped 36 times, and flipperslapped 49 times in 75 min. Pre-dive flexes, consisting of a concave bending of the back, and raised flukes as the whale dove, were most common before long dives. Underwater blows occurred irregularly, but often during socializing.

INTRODUCTION

Several early authors--notably Scoresby (1820), Scammon (1874) and Bodfish (1936)--discussed behavior of bowheads, mainly of whales that were under stress during capture. Systematic observations of undisturbed behavior commenced only recently. Braham et al. (1979) and Rugh and Cubbage (1980) gathered information about durations of dives, surface times and swimming speeds for bowheads migrating past Cape Lisburne, Alaska, and Davis and Koski (1980) and Koski and Davis (1980) did similar work on bowheads migrating in the eastern Canadian arctic. Everitt and Krogman (1979) described six whales that were apparently involved in mating activity during the spring migration past Point Barrow, and there are other accounts of bowheads engaging in precopulatory behavior in the Bering and Chukchi Seas in spring. It has been known since commercial whaling days in the 19th century that feeding is the predominant activity of bowheads in the Beaufort Sea in summer.

Our study of behavior of undisturbed bowhead whales in the Canadian Beaufort Sea was conducted along with a study of disturbance responses (Richardson et al. 1985c) during the summers of 1980 through 1984. Results of these studies were described in yearly reports to the U.S. Minerals Management Service, and data for 1980-1982 are published in Würsig et al. (1984a, in press). The present report summarizes data for all five years of research. In 1982-84, a study similar to ours has been conducted on bowhead whales feeding and migrating in the Alaskan Beaufort Sea later in the season, in September. The behavioral findings of this Alaskan work for 1982 and 1983 are in Reeves et al. (1984) and Ljungblad et al. (1984b), respectively.

Objectives and Approach

The two main objectives of the 'Normal Behavior' task were (1) to provide a description of presumably undisturbed behavior immediately before and after experimental disturbance trials, against which the results of these trials could be compared, and (2) to provide general information on the normal behavior of bowhead whales. The first task is essential to an interpretation of how whales react to potential disturbance, and we attempted to obtain information on the behavior of the same individual animals immediately before and after the period of potential disturbance. The second main objective of the normal behavior study is also essential to a study of potential disturbance, because we must have a basic knowledge of undisturbed behavior patterns in order to properly assess disturbance reactions. There was considerable variability in behavior from year to year, and an ongoing study of normal behavior allows us to address whether whales might be more susceptible to disturbance in some situations or years than in others. Normal behavior studies were carried out (1) in association with experimental disturbance trials, and (2) when studies of disturbance effects were not possible.

Background information concerning the rationale and design of the study, and the choice of the eastern Beaufort Sea as the study area, is given in the previous section 'Project Rationale and Design' (Richardson et al. 1985b).

Field work occurred mainly in August, with some additional observations in late July and early September during certain years. Work was based at Tuktoyaktuk, Northwest Territories (Fig. 1). Observations of behavior were conducted from the air, from a boat, and--in 1980 and 1981 only--from shore
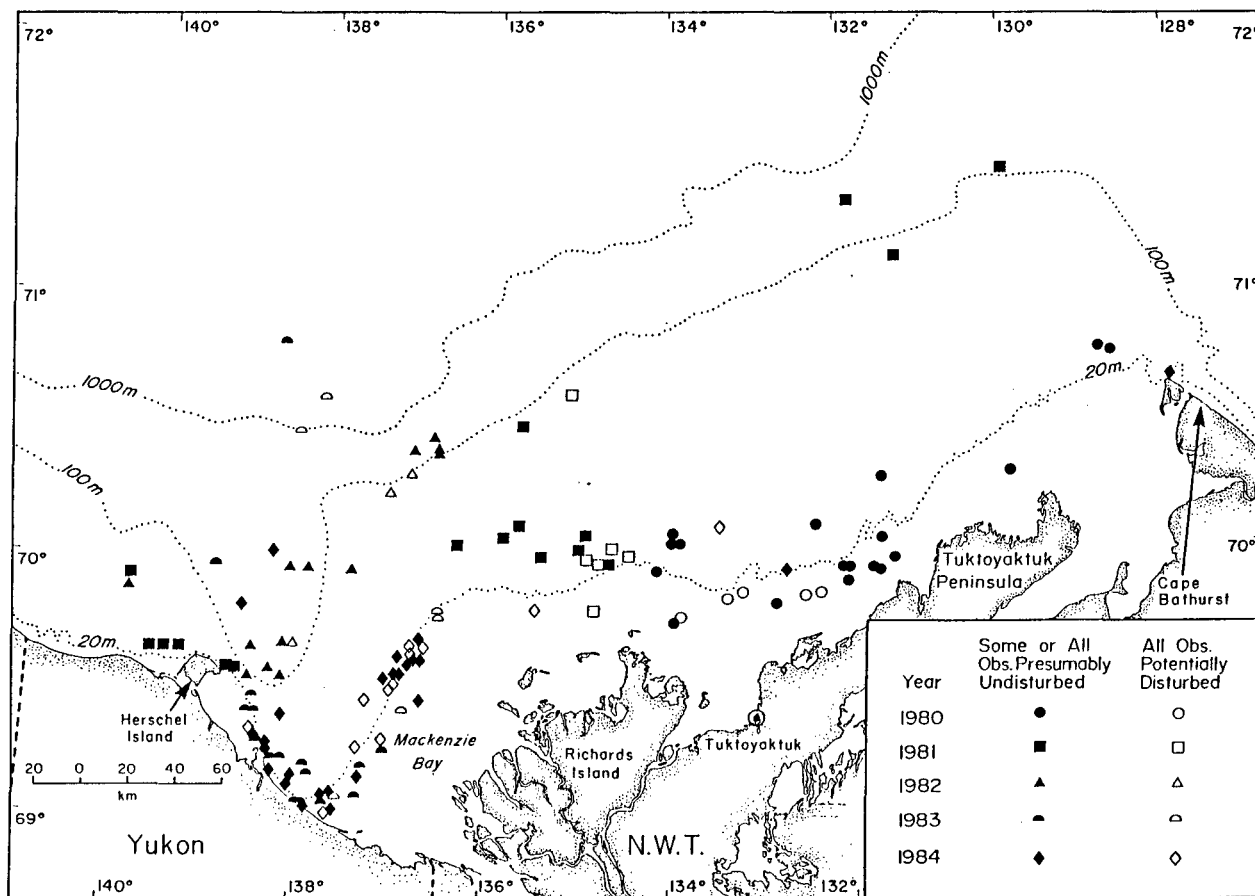
FIGURE 1. Eastern Beaufort Sea region showing bathymetry, locations mentioned in the text, and locations of behavioral observation sessions.

at Herschel Island, Yukon. Aircraft-based observers had the advantage of high mobility and a good vantage point and consequently collected most of the behavioral data. When whales were observed, sonobuoys were often dropped from the aircraft to allow us to hear and record bowhead sounds. Sonobuoys also allowed us to determine when industrial noises were present in the water. Boat-based observers used hydrophones for this purpose. Observations of bowheads in the presence of strong industrial noise may not represent undisturbed behavior, and were excluded from this section on 'Normal Behavior'.

METHODS AND DATA BASE

Aerial Observations

Most behavioral observations were made from a Britten-Norman Islander aircraft, although observations from 1-12 August 1983 were from a deHavilland Series 300 Twin Otter. These aircraft have twin engines, high wing configuration, and low stall speed. Both aircraft were equipped with radar altimeters and Very Low Frequency (VLF) navigation systems. Positions

and flight tracks were recorded manually from the VLF systems. Both aircraft had an endurance of about 5.5-6.0 h plus reserves. The Islander had a forward-looking radar useful for determining distances to industrial sites, shore, etc. Sonobuoys (AN/SSQ-57A or AN/SSQ-41B) were deployed and monitored from both aircraft in order to record waterborne sounds from bowheads and industrial sources (details in Greene 1985). A hand-held color video camera (JVC-CV-0001 or Sony HVC-2000) connected to a portable videocassette recorder (Sony SLO-340 or SL-2000) was used through a side window to record oblique views of bowheads.

Our usual strategy was to search until we encountered bowheads and then circle over them as long as possible while making observations. Once contact was lost, we searched for another group. We created a fixed reference point about which to circle when bowheads were below the surface by deploying a dye marker (1-2 teaspoons of fluorescein dye in about 1 litre of water in a plastic 'freezer' bag, which burst on impact with the water). Near the start of most periods of circling above whales, a sonobuoy was deployed.

We made 132 offshore flights during the five seasons, and we gathered behavioral observations of bowheads during 85 of these flights. Most flights lasted 4 to 5.5 h, and we observed bowhead whales for a total of 186.3 h. We usually did not fly when wind speed exceeded 25 km/h; whales are difficult to detect and behavior is not reliably observable in more severe conditions. While searching for whales, we usually flew at 457 or 610 m (1500 or 2000 ft) above sea level (a.s.l.), and at 185 km/h. Bowheads rarely appeared to be disturbed by the aircraft when it remained at or above 457 m (Richardson et al. 1985c).

The aircraft crew usually consisted of four biologists and the pilot. In the Islander, from which most behavioral observations were obtained, three biologists were seated on the right side of the aircraft, which circled to the right when we were obtaining behavioral observations. Biologists seated in the right front (co-pilot's) seat and in the seat directly behind it were responsible for describing whale behavior. This information was recorded onto audiotape and also, on most occasions, onto the audio channel of the videotape recorder. A third biologist in the right rear seat operated the video camera during most periods while we circled above whales visible at the surface. That individual was also responsible for some record keeping, radar measurement of distances to industrial activities, and overall direction of the work. A fourth biologist, in the left rear seat, searched for bowheads outside of the area being circled, launched sonobuoys and dye markers, and operated sound recording equipment. The biologists and pilot were in constant communication via intercom. The Twin Otter circled to the left during behavioral observations; three biologists were seated on the left side behind the pilot and one in the right front (co-pilot's) seat.

We obtained consistent data of 15 types:

1. Location of sighting (and therefore approx. water depth from charts);
2. Time of day;
3. Number of individuals visible in area; number of calves;
4. Individually distinguishing features (if any) on whales;
5. Heading in degrees true, turns, and estimated swimming speed of each whale;

6. Distances between individuals (estimated in adult whale lengths);
7. Durations of time at surface and sometimes duration of dive;
8. Timing and number of respirations, or blows;
9. Indications of feeding: e.g., open mouth, defecation, mud streaming from mouth;
10. Socializing; probable mating;
11. Probable nursing;
12. Play with surface debris or logs;
13. Underwater blow (releasing a large burst of bubbles underwater);
14. Aerial activity: breaches, tailslaps, flipper slaps, lunges, rolls;
15. Behavior at start of dive: fluke out, peduncle arch, pre-dive flex.

Descriptions of these behaviors appear later in this report and, in more detail, in Würsig et al. (in press).

We were at times able to identify whales by sight, within an observation flight, based on distinctive chin patch shapes or white marks on the back or tail, and we were then able to determine dive durations for these individuals. Davis et al. (1983) showed that smaller bowheads tend to have fewer such white marks than do larger whales.

Water depths were determined by consulting Canadian Hydrographic Service chart #7650 (1980 printing) and Dome Petroleum Ltd. chart E-BFT-100-03. The distributions of behavioral observations by 10-day period, depth of water, and hour of day are presented in Figure 2. Most observations in 1980, 1983, and 1984 were in shallow water. Most observations in 1981 were in somewhat deeper water, and those in 1982 were in still deeper water, often near the edge of the continental shelf (Fig. 1).

In this section of the report, with rare exceptions that are specifically indicated, we describe only the behavior observed with no known potential disturbances. Data collected during periods of potential disturbance are described separately in the 'Disturbance' section (Richardson et al. 1985c). Whales were classified as 'presumably undisturbed' only if the observation aircraft was at an altitude of at least 457 m (1500 ft) a.s.l., no vessels were underway within 4 km, and no other industrial activities were close enough to create waterborne sounds prominent to the human ear. Observations in the presence of noise impulses from distant seismic vessels were treated as potentially disturbed and were excluded. Some observations were collected when our 12.5 m boat was nearby; the whales were considered to be presumably undisturbed if the boat had been anchored or drifting quietly with engine off for at least 30 min. Of 186.3 h spent observing bowheads, 98.5 h were during presumably undisturbed periods.

Behavioral observations were transcribed from audiotape onto data sheets during periods of poor weather between observation flights. The videotape was also examined at this time to provide additional details not noted in real time. After the field season, transcriptions were checked again with the audiotape and converted into a standardized numerical format with one record per surfacing or dive of each whale that was under detailed observation. These records were hand-checked by a different individual and entered into a microcomputer for subsequent computer validation, tabulation, and statistical analysis. The standardized data files contain the following:
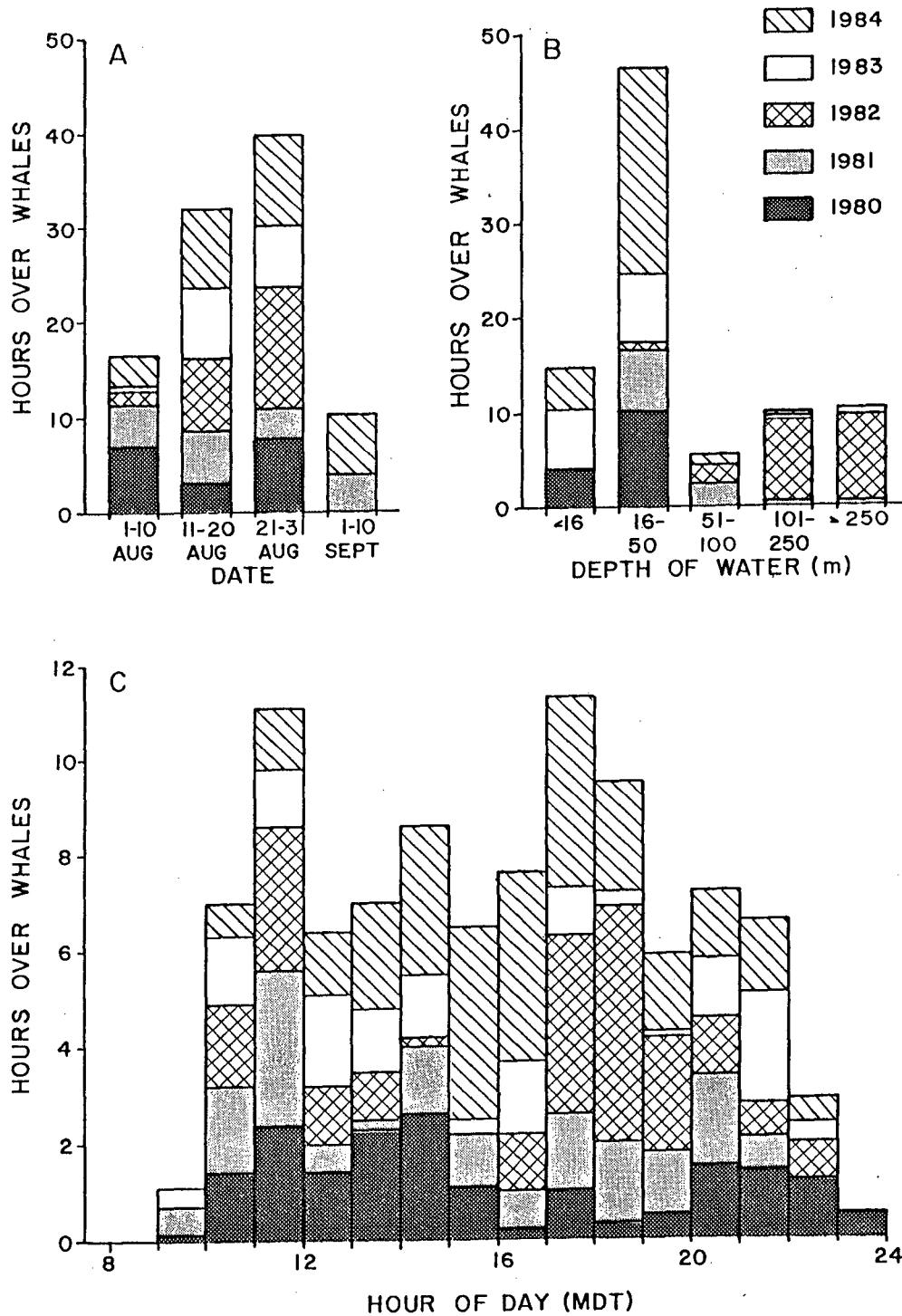
FIGURE 2.   Distribution of behavioral observation time (98.5 h) from the air during presumably undisturbed periods, 1980-84, categorized by (A) date, (B) depth of water, and (C) time of day.

Year	Surfacing Records	Dive Records	Total Records
1980	563	223	786
1981	778	223	1001
1982	312	141	453
1983	1401	242	1643
1984	1283	129	1412
Total	4337	958	5295

Of these, 2129 surfacing and 475 dive records were from presumably undisturbed periods.

Methods of analysis of bowhead sounds recorded via sonobuoys are described in the 'Bowhead Sounds' section of the results, below.

Shore and Boat-Based Observations

Most behavioral observations were made from the air, but observations from shore and a boat at times helped us to understand activity patterns when the airplane was not present, and allowed us to obtain some data (precise speed information, for example) that we could not obtain from the air. Our limited theodolite tracking information appears in Würsig et al. (in press) and is not repeated here. Because our observations from boats pertain mostly to disturbance trials, these data are detailed in the 'Disturbance' section.

RESULTS

Respiration, Surfacing and Dive Characteristics

Four characteristics of a surfacing lend themselves to repeated quantitative sampling: the interval between blows in a surfacing (blow interval), the number of blows per surfacing, the duration of surfacing (surface time) and the duration of dive between surfacings (dive time). Because these variables are comparatively easy to assess quantitatively, they are suitable for use in analysis of responses to disturbances. A detailed understanding of respiration, surfacing and dive behavior under undisturbed conditions is a prerequisite for interpretation of disturbance responses.

Definition of Terms

The measurement of each of these four quantities depends on how a surfacing and dive are defined. Bowheads that are migrating or travelling for relatively long distances· usually make two distinguishable types of dives--brief, shallow dives between successive respirations, and long, deeper dives between these groups of respirations. Rugh and Cubbage (1980) called the two types of dives series dives and sounding dives, respectively. Most bowheads observed in this study, however, remained at the surface between successive respirations. Moreover, from our aerial vantage point we could not always determine whether a whale was at the surface or slightly below it. As a result, we defined only one type of dive, the sounding dive, during which the whale was out of sight underwater. We defined a surfacing as the period of time during which the whale was at the surface or, from our aerial vantage point, visible just below the surface. Thus any shallow 'dives' that

occurred for a few seconds between respirations were not counted as dives, or as interruptions of a surfacing.

Observers working from low vantage points on ice, shore or a boat would treat such shallow dives differently, because the whale would usually be out of their sight as soon as it went below the surface. Thus the definitions of surfacings and dives used in this study are in part a function of our aerial vantage point, and one must use caution when comparing our data with those collected from low vantage points.

On rare occasions a whale remained visible just under the surface of the water for periods of up to several minutes; these were considered dives if they exceeded an arbitrary minimum of 60 s. We used an additional convention in 1983 and 1984, when the water at observation sites was usually more turbid than in previous years; in these cases, whales were less easily visible while underwater. Periods of submergence lasting less than 15 s were not counted as dives in 1983-84 unless, before submerging, the whale lifted its flukes out of the water, arched strongly or performed a pre-dive flex.

A blow is an exhalation of air by a whale. It can occur either above or below the surface. Surface blows are usually visible as a misty white cloud. We calculated blow intervals only for successive blows within a single surfacing when our view of the whale was not interrupted between the blows. Underwater blows become visible at the surface as a white circular burst of bubbles that may grow to 15 m in diameter. They are discussed in a later section.

Calves, because of their small size, are much more difficult to observe when just under the surface of the water than are adults under similar conditions. We analyzed our observations of calves separately and will present that analysis following the non-calf observations. The remainder of this section considers undisturbed whales excluding calves, i.e. all adults and subadults that we observed.

Blow Interval

In 1980-84, we measured 5161 blow intervals for undisturbed non-calves. The frequency distributions were very similar in all five years; the modal category of blow intervals was 10-13 s in each year. The year 1984 had the shortest mean blow interval of the five years, and 1983 had the longest. Table 1 presents the summary statistics for blow intervals for the five years of this study. The overall mean blow interval for presumably undisturbed non-calves observed in 1980-84 was 13.5 ± 8.88 s (n = 5161, range = 1-173 s).

We wondered whether the first blow interval in a surfacing might be shorter than subsequent blow intervals, i.e., whether a whale tends to breathe more quickly at the start of a surfacing than for the remainder of a surfacing. For each year, we compared the first blow interval and the mean of the subsequent blow intervals in all surfacings that had three or more blows (two or more blow intervals) and for which all blows were timed. Only presumably undisturbed non-calves were considered. On average, the first blow interval was significantly shorter only in 1982 (paired t = 2.40, df = 43, $0.02 < p < 0.05$), which was the year with the longest dives and longest surfacings. In 1981 and 1983, the first blow interval averaged shorter than the mean of the subsequent blow intervals, but not significantly so, while in

Table 1. Summary statistics for the principal surfacing, respiration and dive variables in presumably undisturbed bowheads in 1980-84. Calves are excluded from every line except that labelled 'calves'.

		Blow interval (s)			Number of blows per surfacing			Length of surfacing (min)			Length of dive (min)		
		mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
All non-calves	1980	12.9	8.61	915	4.8	2.91	70	1.25	0.723	94	2.25	3.549	25
	1981	13.0	8.08	1113	4.2	2.91	194	1.06	0.764	204	3.80	4.986	80
	1982	14.9	8.66	795	7.4	5.11	58	2.05	1.320	70	12.08	9.153	51
	1983	17.0	13.49	866	3.2	2.37	229	1.05	1.484	248	1.88	2.357	140
	1984	11.6	4.66	1472	5.5	2.97	75	1.10	0.559	99	6.27	7.195	37
	1980-84	13.5	8.88	5161	4.3	3.25	626	1.19	1.137	715	4.42	6.319	333
Calves	1980	15.1	10.30	30	3.3	2.06	4	0.71	0.472	5	1.80	1.958	3
	1981	11.6	7.65	34	0.8	1.47	11	0.70	0.569	16	1.02	1.503	6
	1982	18.6	16.05	100	4.0	2.49	19	1.66	1.459	21	6.82	5.715	29
	1983	11.5	5.07	4	1.1	0.90	7	0.36	0.478	8	1.98	2.720	7
	1984	8.4	2.01	10	—	—	0	1.20	0	1	—	—	0
	1980-84	16.0	13.58	178	2.6	2.45	41	1.05	1.131	51	4.96	5.358	45
Adults with calf	1980	14.1	6.65	49	3.2	3.13	6	0.91	0.683	9	0.96	1.692	5
	1981	15.1	5.30	91	3.9	2.98	11	1.38	1.065	13	9.99	7.707	10
	1982	18.6	9.45	178	6.4	4.77	20	2.30	1.593	23	8.62	5.862	22
	1983	18.0	9.29	7	5.0	—	1	1.45	0.259	2	12.18	1.002	2
	1984	—	—	0	—	—	0	—	—	0	—	—	0
	1980-84	16.9	8.27	325	5.1	4.16	38	1.74	1.387	47	8.17	6.485	39
All other non-calves	1980	12.8	8.71	866	4.9	2.87	64	1.29	0.722	85	2.57	3.842	20
	1981	12.8	8.26	1022	4.2	2.91	183	1.04	0.738	191	2.92	3.791	70
	1982	13.8	8.11	617	8.0	5.25	38	1.93	1.164	47	14.70	10.361	29
	1983	17.0	13.52	859	3.2	2.37	228	1.05	1.489	246	1.73	2.015	138
	1984	11.6	4.66	1472	5.5	2.97	75	1.10	0.559	99	6.27	7.195	37
	1980-84	13.3	8.88	4836	4.3	3.19	588	1.15	1.108	668	3.92	6.138	294

Table 1. Continued.

		Blow interval (s)			Number of blows per surfacing			Length of surfacing (min)			Length of dive (min)		
		mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Skim-feeding whales	1980	13.7	11.36	30	—	—	0	—	—	0	—	—	0
	1981	16.4	12.90	48	2.8	2.05	13	0.70	0.702	12	3.34	4.258	9
	1982	—	—	0	—	—	0	—	—	0	—	—	0
	1983	31.7	23.79	120	6.9	3.99	10	5.20	3.636	15	0.93	1.001	16
	1984	—	—	0	—	—	0	—	—	0	—	—	0
	1980-84	25.3	21.58	198	4.6	3.63	23	3.19	3.549	27	1.80	2.840	25
Bottom-feeding whales	1980	—	—	0	—	—	0	—	—	0	—	—	0
	1981	—	—	0	—	—	0	—	—	0	—	—	0
	1982	—	—	0	—	—	0	—	—	0	—	—	0
	1983	11.5	5.39	6	3.0	2.65	3	0.13	0.130	2	0.42	0.024	2
	1984	11.9	5.13	133	7.0	3.42	7	1.43	0.480	10	12.31	14.555	2
	1980-84	11.9	5.12	139	5.8	3.61	10	1.21	0.668	12	6.36	10.851	4
All other non-calves (not skim or bottom feeding)	1980	12.8	8.51	885	4.8	2.91	70	1.25	0.723	94	2.25	3.549	25
	1981	12.8	7.77	1065	4.3	2.94	181	1.09	0.668	192	3.86	5.095	71
	1982	14.9	8.66	795	7.4	5.11	58	2.05	1.320	70	12.08	9.153	51
	1983	14.6	8.97	740	3.0	2.14	216	0.79	0.600	231	2.03	2.466	122
	1984	11.6	4.62	1339	5.3	2.91	68	1.06	0.557	89	5.93	6.806	35
	1980-84	13.1	7.66	4824	4.3	3.23	593	1.10	1.051	676	4.61	6.427	304
Socializing whales (including only whales that were actively interacting)	1980	13.6	9.10	127	4.7	2.08	3	1.40	0.488	10	0.25	0.186	3
	1981	14.2	11.60	223	3.8	2.17	41	1.15	0.868	43	3.07	3.195	24
	1982	14.2	8.01	74	3.8	2.75	4	1.34	0.796	5	0.58	0	1
	1983	15.6	9.70	85	4.3	2.46	13	1.22	0.711	14	0.62	0.235	3
	1984	14.0	5.56	44	—	—	0	1.42	0.309	4	8.35	0	1
	1980-84	14.2	9.93	553	3.9	2.23	61	1.22	0.766	76	2.66	3.139	32

Table 1. Continued.

		Blow interval (s)			Number of blows per surfacing			Length of surfacing (min)			Length of dive (min)		
		mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Non-socializing whales	1980	12.8	8.63	760	4.7	2.94	65	1.22	0.745	82	2.52	3.707	22
(excluding whales <8 m	1981	12.5	6.67	861	4.4	3.07	146	1.05	0.736	154	4.12	5.578	56
apart that were not	1982	14.9	8.72	721	7.7	5.15	54	2.10	1.341	65	12.31	9.096	50
actively interacting)	1983	17.3	13.92	766	3.1	2.36	215	1.04	1.527	231	1.90	2.381	135
	1984	11.6	4.62	1428	5.5	2.97	75	1.10	0.557	93	6.51	7.399	34
	1980-84	13.4	8.75	4536	4.4	3.35	555	1.19	1.181	625	4.65	6.577	297
Single whales	1980	13.3	10.20	324	5.2	3.20	32	1.32	0.955	33	1.26	2.154	7
(excluding skim-feeders)	1981	12.1	5.08	394	5.4	3.07	51	1.24	0.684	56	3.89	4.709	20
	1982	13.7	8.22	530	8.6	5.09	31	2.10	1.190	40	15.82	9.844	27
	1983	14.0	7.89	521	3.0	2.15	151	0.71	0.540	151	2.12	2.466	74
	1984	11.6	4.66	1331	5.5	2.95	66	1.13	0.558	83	6.14	7.075	30
	1980-84	12.6	6.82	3100	4.6	3.40	331	1.10	0.822	363	5.41	7.474	158
Whales in groups	1980	12.8	7.18	401	4.7	3.04	23	1.30	0.592	41	1.31	2.243	9
(excluding skim-feeders)	1981	14.3	10.55	415	3.7	2.55	85	1.09	0.833	88	4.00	5.439	44
	1982	17.2	9.06	265	6.0	4.86	27	1.98	1.496	30	7.87	6.139	24
	1983	15.9	10.93	225	3.0	2.12	68	0.91	0.683	82	1.83	2.451	50
	1984	11.9	4.80	126	5.3	3.35	9	0.96	0.558	16	6.83	8.261	7
	1980-84	14.5	9.25	1432	4.0	3.05	212	1.16	0.904	257	3.85	5.200	134
Depth (m) <16	1980	12.6	7.13	89	2.7	1.67	19	0.70	0.403	24	0.76	1.236	9
	1981	—	—	0	—	—	0	—	—	0	—	—	0
	1982	—	—	0	—	—	0	—	—	0	—	—	0
	1983	19.4	16.58	459	3.4	2.66	111	1.32	1.934	131	1.69	1.757	87
	1984	11.0	4.11	221	6.0	2.77	13	1.07	0.469	15	12.44	7.809	10
	1980-84	16.2	13.79	769	3.5	2.67	143	1.21	1.722	170	2.62	4.251	106

Table 1. Continued.

			Blow interval (s)			Number of blows per surfacing			Length of surfacing (min)			Length of dive (min)		
			mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Depth (m)	16–50	1980	12.3	7.23	750	5.9	2.97	40	1.37	0.578	60	4.28	4.567	11
		1981	13.2	9.48	649	3.9	2.58	132	1.01	0.731	138	4.05	5.224	58
		1982	12.0	2.56	21	6.3	2.31	3	1.46	0.384	3	15.52	2.923	2
		1983	14.0	7.71	392	3.0	2.07	114	0.75	0.568	112	1.83	2.456	49
		1984	11.6	4.41	1191	5.5	3.19	52	1.12	0.596	74	4.64	6.622	17
		1980–84	12.5	6.97	3003	4.1	2.77	341	1.01	0.667	387	3.52	4.877	137
	51–100	1980	—	—	0	—	—	0	—	—	0	—	—	0
		1981	13.4	5.34	126	4.9	3.26	18	1.20	0.809	18	6.57	4.232	8
		1982	18.1	6.97	14	1.3	0.58	3	0.26	0.207	3	0.33	0.073	3
		1983	—	—	0	—	—	0	—	—	0	—	—	0
		1984	14.5	7.80	42	4.7	2.36	7	0.99	0.465	7	1.68	1.313	8
		1980–84	14.0	6.21	182	4.5	3.04	28	1.05	0.741	28	3.52	3.869	19
	101–250	1980	—	—	0	—	—	0	—	—	0	—	—	0
		1981	13.3	6.74	74	4.5	2.66	11	1.14	0.537	11	0.50	0.349	3
		1982	13.7	6.67	355	7.7	4.95	25	1.98	0.982	32	13.94	8.143	17
		1983	21.0	14.13	8	1.7	0.58	3	0.34	0.275	3	1.36	0.389	2
		1984	13.5	12.88	14	5.3	1.16	3	0.88	0.113	3	7.75	1.532	2
		1980–84	13.8	7.16	451	6.3	4.47	42	1.63	0.982	49	10.69	8.713	24
	>250	1980	—	—	0	—	—	0	—	—	0	—	—	0
		1981	11.5	4.95	19	—	—	0	—	—	0	—	—	0
		1982	15.9	10.18	405	8.0	5.42	27	2.34	1.572	32	11.96	9.679	29
		1983	18.0	9.29	7	5.0	0	1	1.45	0.259	2	12.18	1.002	2
		1984	—	—	0	—	—	0	—	—	0	—	—	0
		1980–84	15.7	10.02	431	7.9	5.35	28	2.29	1.539	34	11.98	9.353	31

Table 1. Concluded.

		Blow interval (s)			Number of blows per surfacing			Length of surfacing (min)			Length of dive (min)		
		mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n
Whales with flukes raised at	1981	—	—	—	4.6	2.71	62	1.13	0.688	66	—	—	—
end of surfacing/start of	1982	—	—	—	7.8	5.85	19	2.09	1.254	25	—	—	—
dive	1983	14.0	8.43	144	3.4	2.16	47	0.80	0.492	40	1.48	1.820	28
	1984	11.6	4.43	701	6.2	2.96	39	1.22	0.530	51	7.06	7.895	18
	1981–84	12.0	5.40	845	5.0	3.42	167	1.22	0.810	182	3.66	5.756	46
Whales with flukes not raised	1981	—	—	—	3.9	2.58	85	1.02	0.742	85	—	—	—
at end of surfacing/start	1982	—	—	—	7.1	4.64	35	1.87	1.126	37	—	—	—
of dive	1983	18.0	14.80	614	3.2	2.44	178	1.11	1.614	204	1.86	2.233	105
	1984	11.7	4.89	549	4.9	2.76	35	0.98	0.561	47	5.74	6.712	18
	1981–84	15.0	11.69	1163	4.0	3.05	333	1.15	1.329	373	2.43	3.524	123
Whales with pre-dive flex	1981	11.0	5.84	85	6.5	2.42	11	1.30	0.499	11	0.44	0.312	3
	1982	14.3	9.82	280	12.5	3.62	11	3.09	1.038	14	19.00	7.877	13
	1983	17.2	13.52	177	5.1	2.77	32	1.55	1.262	26	1.81	2.327	19
	1984	11.5	4.47	229	6.5	2.03	16	1.28	0.454	19	10.79	6.367	10
	1981–84	13.8	9.57	771	6.8	3.69	70	1.74	1.159	70	8.68	9.215	45
Whales without pre-dive flex	1981	13.2	8.59	534	4.3	2.73	105	1.07	0.723	109	5.05	4.970	40
	1982	15.4	8.12	473	6.2	4.68	44	1.79	1.284	52	10.15	7.465	36
	1983	18.2	14.73	517	2.9	2.19	177	1.04	1.624	186	1.75	2.088	97
	1984	11.9	4.83	841	5.2	3.14	59	0.99	0.582	63	5.68	7.796	19
	1981–84	14.3	9.55	2365	4.0	3.09	385	1.13	1.285	410	4.40	5.765	192

1980 and 1984 the first blow interval averaged slightly longer than the mean of the subsequent ones.

Blows per Surfacing and Duration of Surfacing

In 1980-84 we measured the number of blows per surfacing and the duration of surfacing in presumably undisturbed non-calves 626 and 715 times, respectively. The overall mean values were 4.34 $\pm$ s.d. 3.254 blows per surfacing (range = 0-19 blows) and 1.19 $\pm$ s.d. 1.137 min at the surface (range = 0.03-13.17 min). Table 1 presents the values for each year of this study. These two variables showed a highly significant positive correlation with each other in each year (Table 2B). This positive correlation is a result of the relative stability of blow intervals. The frequency distributions for number of blows per surfacing and duration of surfacing (Figs. 3B, 3C) show considerably more variation from year to year than do the frequency distributions for blow intervals.

Duration of Dives

Our estimates of mean dive duration are biased downward to a degree that has varied somewhat from year to year. The reason for this bias is that it is more difficult to find and recognize a whale when it resurfaces after a long dive than after a short dive. In 1982, the conditions for measuring durations of long dives were better than in any other year because many of the whales were recognizable and we often circled over only one or two whales and could be certain that we had not missed any surfacings. Table 1 presents the mean duration of dive measured for each year. The substantially higher mean dive time for 1982 is only in part the result of the reduced bias against long dives, however, for in that year it was obvious that most whales were in fact making proportionally more long dives and fewer short dives than in any other year. In 1983, we obtained the lowest mean dive time for the study, but there was an especially strong sampling bias against long dives: most whales we circled in 1983 had few or no distinguishing marks and were in relatively large groups. The overall mean dive time for presumably undisturbed non-calves for all five years of this study was 4.42 $\pm$ s.d. 6.319 min (n = 333, range = 0.03-30.98 min).

Figure 3D presents the frequency distributions for duration of dive. In all years except 1982 there was marked skewing of the frequency distributions. For this reason, all statistical comparisons of dive times were done non-parametrically.

In 4 of 5 years there was a significant positive correlation between dive times before and after a surfacing; in 1980 the correlation was strong (0.659) but only marginally significant due to low sample size (Table 2A). Thus, a whale tends to make a series of dives of similar length rather than alternating short and long dives.

In most years, the duration of the dive preceding a surfacing was better correlated with both the duration of that surfacing and the number of blows in it than was the duration of the dive following the surfacing. The number of blows per surfacing showed a positive correlation with previous dive time that was significant in all five years and highly significant in most of them (Table 2D). The duration of surfacing similarly showed a highly significant positive correlation with the duration of the previous dive in all years

Table 2. Degree of correlation between all pairs of the following four
variables: number of blows per surfacing, duration of surfacing,
duration of previous dive, and duration of subsequent dive. Only
presumably undisturbed non-calves are included. r_s is the Spearman
rank correlation.

A. Previous dive vs. subsequent dive[a]

	r_s	n	sign. level
1980	0.659	8	(*)
1981	0.371	35	*
1982	0.695	29	***
1983	0.313	80	**
1984	0.682	11	*

B. Number of blows vs. surface time[a]

	r_s	n	sign. level
1980	0.801	65	***
1981	0.852	193	***
1982	0.936	56	***
1983	0.829	218	***
1984	0.875	75	***

C. Previous dive vs. surface time[a]

	r_s	n	sign. level
1980	0.757	15	**
1981	0.509	73	***
1982	0.734	35	***
1983	0.033	116	ns
1984	0.613	26	**

D. Previous dive vs. number of blows

	r_s	n	sign. level
1980	0.859	13	***
1981	0.550	70	***
1982	0.677	32	***
1983	0.225	98	*
1984	0.607	24	**

E. Subsequent dive vs. surface time[a]

	r_s	n	sign. level
1980	0.150	14	ns
1981	0.149	59	ns
1982	0.448	31	*
1983	0.101	110	ns
1984	0.460	21	*

F. Subsequent dive vs. number of blows

	r_s	n	sign. level
1980	0.415	13	ns
1981	0.205	58	ns
1982	0.591	26	**
1983	0.114	100	ns
1984	0.612	19	**

significance levels:

ns :		$p > 0.10$
(*):		$0.05 < p \leq 0.10$
* :		$0.01 < p \leq 0.05$
** :	$0.001 < p \leq 0.01$	
*** :		$p \leq 0.001$

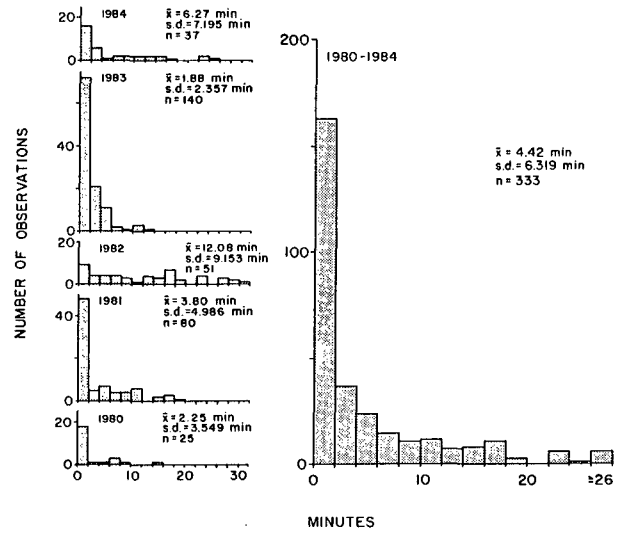[a] See Würsig et al. (1984a) for scatter diagrams.
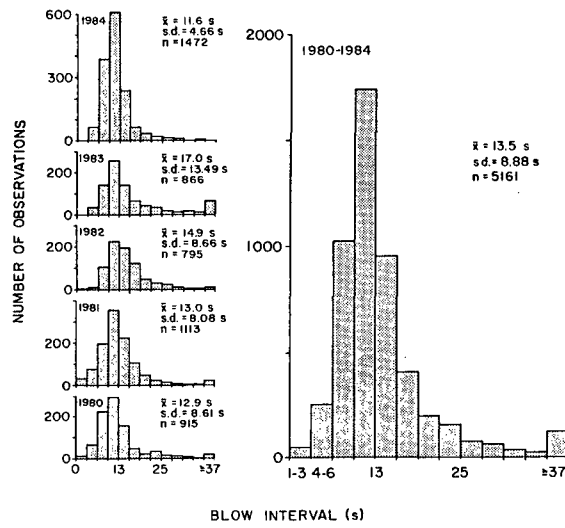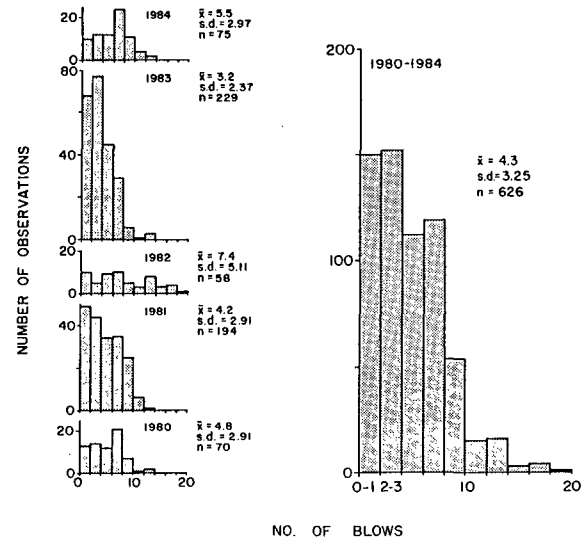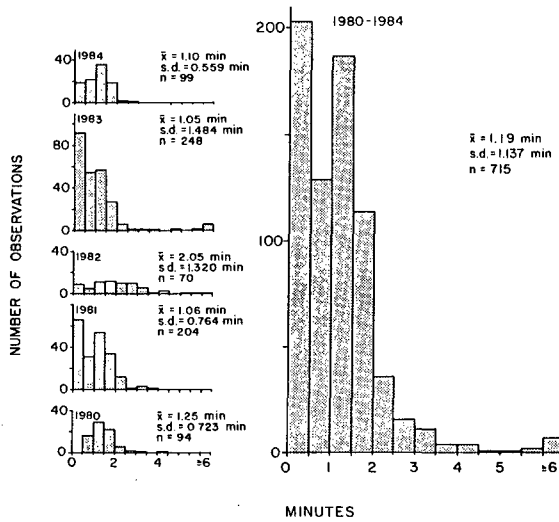
FIGURE 3. Frequency distribution of each of the four principal respiration, surfacing and dive characteristics for presumably undisturbed non-calves, 1980-84.

except 1983 (Table 2C).   In contrast, number of blows per surfacing and surface time were significantly correlated with the subsequent dive time only in 1982 and 1984 (Table 2E, F).   This suggests that the respiration and surfacing behavior of bowhead whales is determined more by the duration of the dive that has just ended than it is by the duration of the dive that is about to begin.

Blow Rate

The blow rate was calculated by dividing the number of blows during a complete surfacing by the sum of the durations of that surfacing and the subsequent dive (surface-dive cycles in which the dive was <30 s long were excluded from this analysis as too short to be meaningful).   The resulting number of blows per minute is a function of the surface time, dive time, and number of blows per surfacing, and describes the respiratory activity of the whale during a longer period of time than any of the constituent variables considered separately.   We measured the blow rate for presumably undisturbed non-calves 156 times in 1980-84 and obtained an overall mean value of 1.10 $\pm$ s.d. 0.873 blows per min (range = 0-4.36).   The frequency distributions for blow rates (Fig. 4A) show considerable variability from year to year; the mean value for 1982 was the lowest observed.

Proportion of Time at the Surface

The proportion of time that a whale was at the surface was calculated from all surfacings of known duration that were followed by dives of known duration.   As explained above, if a whale made shallow submergences between blows in the middle of a surfacing, it was considered to be at the surface the whole time.   We measured the proportion of time at the surface for 235 surface-dive cycles for presumably undisturbed non-calves in 1980-84 and obtained an overall mean value of 0.38 $\pm$ s.d. 0.284 (range = 0.01-0.98).   The frequency distributions for proportion of time at surface (Fig. 4B) vary considerably from year to year.   The mean values in 1982 and 1984 were lower than in other years.

The data in Figure 4B weight each surfacing/dive cycle equally, regardless of its total duration.   For purposes of evaluating sighting probability during aerial surveys, each cycle should be weighted proportional to its duration (Davis et al. 1982).   Based on this method, the overall mean proportion of time at the surface was 0.27; values for 1980-84 were 0.28, 0.25, 0.19, 0.43 and 0.11, respectively.

Calves and Mothers

Behavior of Mother-Calf Pairs

Calves of the year are light tan in color, distinct from the black or gray of non-calf bowhead whales.   An adult whale close to a calf was assumed to be its mother unless there was ambiguity due to the close proximity of a second adult.   In 1980, 1981 and 1982, calves were sighted 12, 16, and 16 times, respectively.   In 1983 they were only sighted 5 times, and in 1984 only 2 times, despite the fact that we spent more time circling over whales in these two years than in earlier years (Table 3).

A. BLOW RATE

BLOWS/MIN

B. PROPORTION OF TIME AT SURFACE
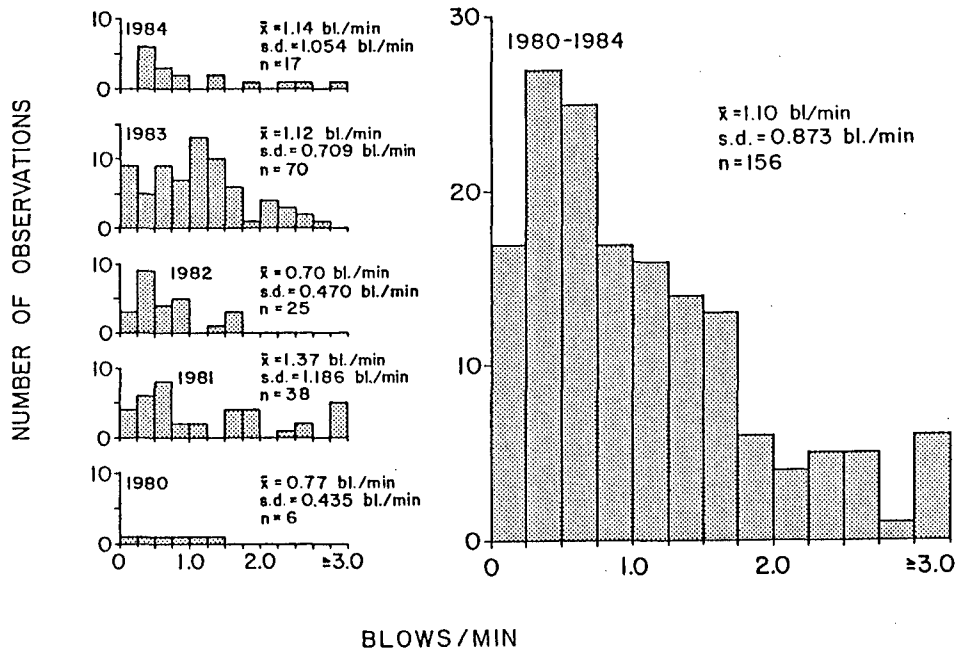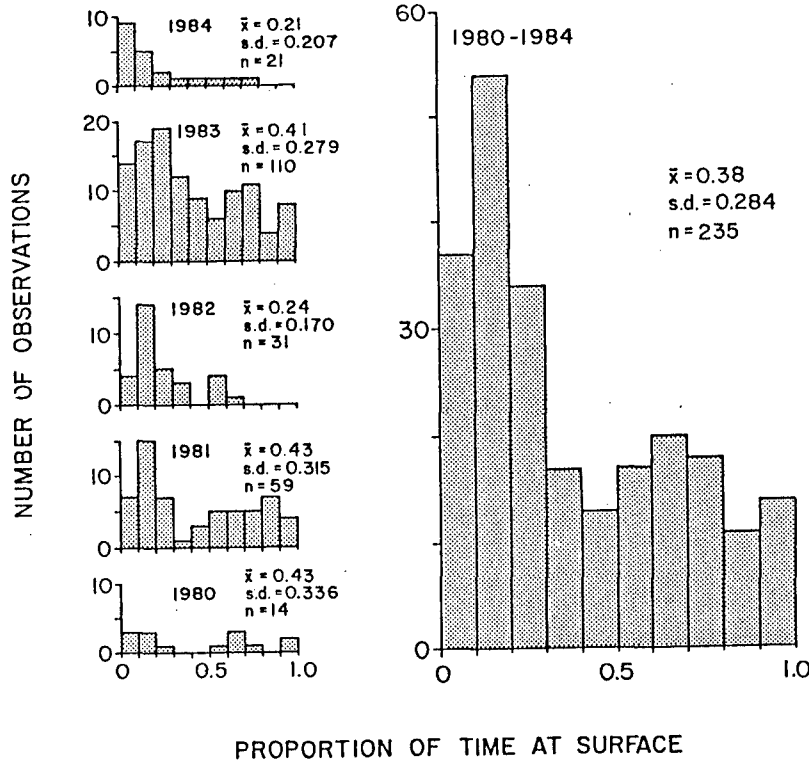

PROPORTION OF TIME AT SURFACE

FIGURE 4. Frequency distributions of (A) blow rate and (B) proportion of time at surface for presumably undisturbed non-calves, 1980-84. See text for definitions.

Table 3. Calf sightings and observation time in 1980-84. Both presumably
undisturbed and potentially disturbed periods are included. The
number of sightings of calves is approximate because multiple
counts of the same calf were possible where the calf and its mother
were not recognizable.

	1980	1981	1982	1983	1984
Number of calf sightings	12	16	16	5	2
Number of flights[a]	14	18	14	15	24
Calf sightings per flight	0.86	0.89	1.14	0.33	0.08
Hours in plane over whales	30.4	30.8	36.5	38.4	50.2
Calf sightings per hour	0.39	0.52	0.44	0.13	0.04
Total calf time at surface (min)	22.0	30.2	101.3	20.1	2.15
% of calf surface time unaccompanied by mother	7.3%	42.1%	37.7%	57.2%	100%

[a] Only flights with behavioral observations are considered.

In 1981, 1982, and 1983, calves spent about 40-60% of their time at the
surface unaccompanied by an adult, and during the two short observations of
1984, calves were alone 100% of the time. In 1980, however, they were seen
most of the time with the presumed mother. At times, mothers will dive--
presumably to feed in the water column--while the calf remains at the
surface; at other times the calf dives with the mother but surfaces before
the mother surfaces. We have seen lone calves and presumed mothers rejoin on
several occasions, once from as far apart as 1.6 km. Details of rejoining
are presented in Würsig et al. (in press).

We suspected that nursing was taking place when a calf dove toward the
teat region of the mother. During apparent nursing, the mother was usually
quite inactive at the surface. The longest nursing bout that we observed
occurred on 23 August 1982, and involved a calf that had been separated from
its mother (who was probably feeding nearby in the water column) for at least
71 min. The calf dove towards the mother's teat region six times, for
submergences lasting 18, 11, 27, 17, 12, and 10 s (mean = 15.8 $\pm$ s.d. 6.37
s). Brief surfacings between the nursing dives lasted 6, 6, 9, 11, 23, and
17 s (mean = 12.0 $\pm$ s.d. 6.75 s), and there was only one detectable blow in
each short surfacing. Although most bouts of nursing were shorter and
involved only one to two nursing dives, the number of blows per surfacing,
duration of surfacing, and duration of dive were all considerably reduced for
calves whenever they were nursing. The blow rates of calves while nursing
were higher than while with their mothers but not nursing (nursing blow rate:
2.8 $\pm$ s.d. 0.93 blows/min, n = 5; non-nursing blow rate: 0.5 $\pm$ s.d. 0.28

blows/min, n = 10; t' = 5.40, df = 4.5, p<0.01)[a]. We have detailed data on blow rates for one mother calf pair: during 1.7 h on 24 August 1982, while a pair was diving, travelling, and nursing, there was a significant positive correlation between the blow rates of the two animals (r = 0.87, n = 10, p = 0.001). Further details on mother and calf behaviors are in Würsig et al. (1984a, in press).

Segregation by Age Class

In all years, we noticed some clumping of mother-calf sightings, with usually more than one calf sighted in a particular area during a flight in which a calf was seen, interspersed with some flights or areas with no calves. We also had the impression that subadults, that is, non-calves that were not full grown, were often sighted together. Our ability to detect such segregation was weak, however, because we usually did not have length measurements for the specific whales that we observed. Davis et al. (1982, 1983, in prep.) and Cubbage et al. (1984) measured bowhead whales photogrammetrically in the eastern Beaufort Sea in the summers of 1981-84. In each year they found geographic variation in the distribution of length classes over several hundred kilometres. In 1982 they also had evidence that the distribution of length classes within a single area varied over time on a scale of days or weeks.

In 1983 we sighted calves with mothers only during the first two observation flights of the season, both on 7 August. These calf sightings occurred in deep water far offshore from our main area of observations in 1983, which was in shallow water in Mackenzie Bay, along the Yukon coast (Fig. 1). In the latter area most whales appeared smaller than full grown adults, and lacked the large white chin patches and pigmented tailstocks common in larger whales (cf. Davis et al. 1983). We obtained a few photogrammetric measurements using the techniques of Davis et al. (1983); these confirmed that, indeed, most whales in the Mackenzie Bay area were only 7-12 m long, i.e. shorter than the 13-m length at maturity:

Length category (m)	7-8	8-9	9-10	10-11	11-12	12-13
Number of whales	4	2	2	8	4	2

Thus, most of our 1983 data came from a major concentration of subadult whales that included few adults.

Simultaneous with our 1983 study, Cubbage et al. (1984) measured a larger sample of whales over a wider area. They found that bowheads west of Tuktoyaktuk tended to be <13 m long, a higher proportion of those off the Tuktoyaktuk Peninsula were >13 m long, and virtually all those whales farther east in Franklin Bay were >13 m.

In 1984 we observed only two calves, both on 17 August in Mackenzie Bay close to the Yukon shore. They were within an area where whales appeared to us to be mainly poorly-marked subadults, as in 1983. Extensive

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[a] t' is the t-statistic calculated assuming that the population variances are unequal.

photogrammetric data confirmed that most whales in Mackenzie Bay in August 1984 were again subadults (Davis et al. in prep.).

Mothers and Calves Compared to Other Bowheads

The respiration, surfacing and dive variables for calves, mothers, and all other non-calves are presented in Table 1 (all years) and in Figure 5 (overall 1980-84 values only). Due to the strong segregation by age class in 1983 and 1984, it is likely that many or most whales in the "all other non-calf" category were not fully mature animals, at least in those two years. Mothers with calves (labelled as 'adults with calves' in Fig. 5) were the only bowheads whose maturity we could ascertain. The overall mean blow intervals both of calves and of mothers were significantly longer than the mean for all other whales. For mothers, the mean blow interval was higher than that for other non-calves within every year as well as over all years, but for calves, the mean blow interval was higher than that for other non-calves only within two of the five years (Table 1). Since over half of the 1980-84 blow intervals for calves came from the year with the highest mean (1982), it is possible that our somewhat unexpected finding of longer blow intervals in calves than in other non-calves is not representative. The mean blow intervals of mothers and calves were not significantly different from each other.

For number of blows per surfacing, the overall mean for mothers was not significantly higher than that for other non-calves; but the mean for calves was significantly lower than that either for mothers or for other non-calves. For duration of surfacing, relative values of the three means were the same as for number of blows, with calves lowest and mothers highest. However, the difference between calves and other whales was not significant, whereas the mean surface time for mothers was significantly longer than the mean for either other category. Multivariate analysis, however, showed that the longer surface times for mothers may have been an artefact of depth or year effects (see below).

Mothers with calves showed the longest overall mean dive time of these three categories of whales; the mean dive time of mothers was significantly longer than that for other non-calves, but was not significantly longer than the mean for calves (Fig. 5). The calves' mean dive time was significantly longer than the mean for other non-calves. This latter difference may be an artefact of year-to-year differences in sample size and in mean dive time, however. Within any one year, calves had a shorter mean dive time than other whales, except in 1983 when the two means were quite close. But over 60% of the 1980-84 sample for calves came from 1982 when dives for all categories of whales were very long, whereas less than 10% of the 1980-84 sample for other whales came from 1982 and almost 50% came from 1983 when most measured dives were very short (Table 1).

There was no significant difference between the blow rates of mothers and calves, but the mean blow rates for both mothers and calves were significantly lower than for other non-calves. There was likewise no significant difference between the proportion of time at the surface for mothers and calves, but the mean value of each of these categories was lower than the mean for other non-calves.
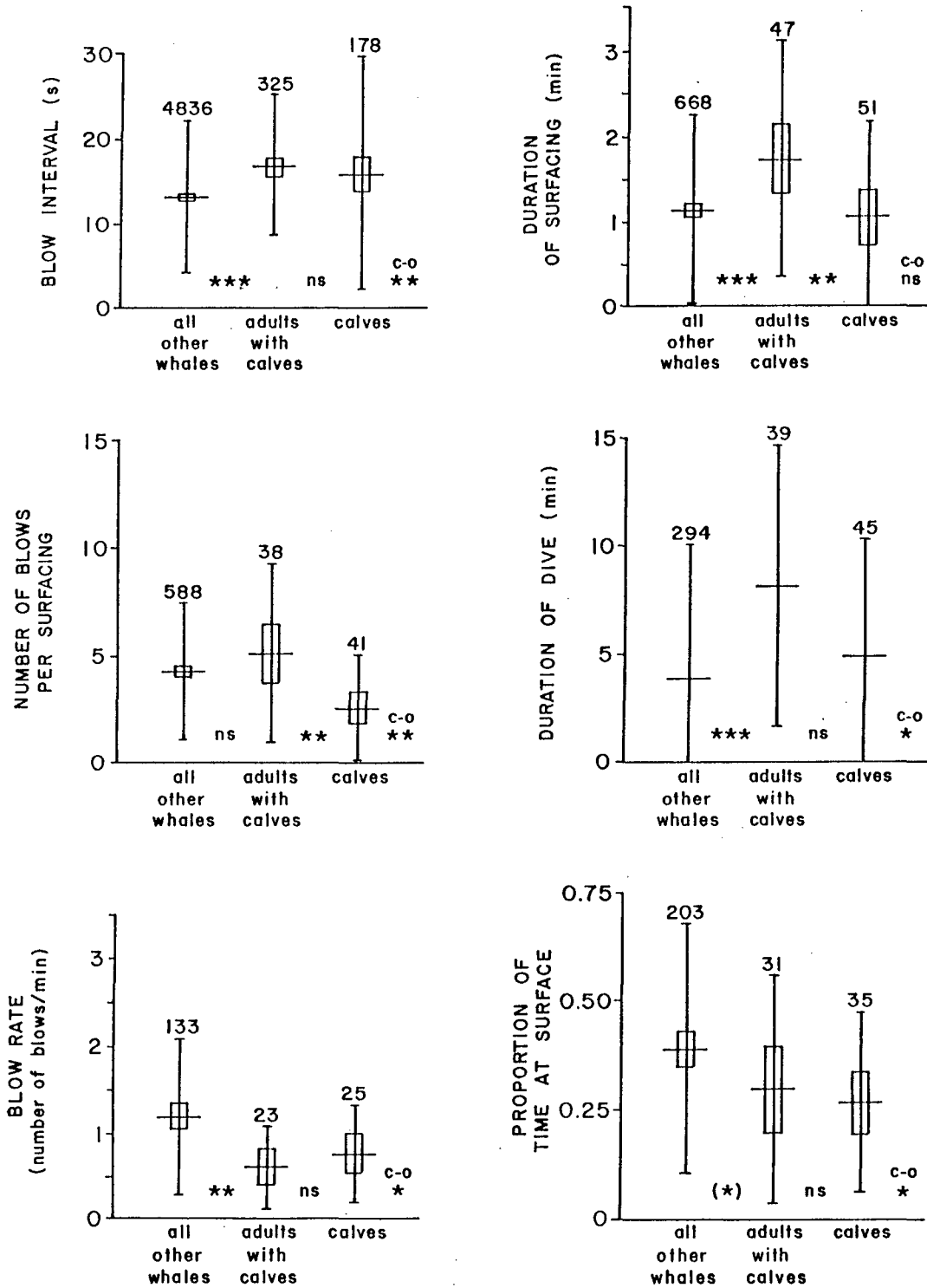
FIGURE 5.   Comparison of respiration, surfacing, and dive variables for calves, mothers and all other whales during presumably undisturbed periods, 1980-84.   Means $\pm$ s.d. (vertical line), $\pm$ 95% confidence intervals (rectangles), and sample sizes are shown.   Significance levels for 'Other-Mother', 'Mother-Calf' and 'Calf-Other' (C-O) comparisons are shown, coded as in Table 2 (p. 29).   The statistical tests used were Dunn's multiple comparison for duration of dive and Newman-Keul's test for all other variables.

Feeding Behavior

During the five years of this study we obtained data on several types of feeding by bowheads: feeding at or just below the surface, at or near the bottom, and probably in the water column (see Würsig et al. in press for more details).

Types of Feeding

Skim feeding occurred when whales moved forward with mouths open at or just under the surface. At times, whales skim fed alone; under such circumstances they were separated >75 m from other whales and were oriented in various directions. At other times, skim feeding occurred in coordinated echelons of up to 14 whales. Whales skim feeding in echelon were staggered to the side and behind the whale at the apex, with each whale separated by 5 to 50 m from the next whale. We suspect that echelon feeding increases the feeding efficiency of these whales, perhaps by helping them to catch prey that escape or spill from the mouth of an adjacent whale, or by reducing the ability of prey to escape to the side. We saw skim feeding only for several days in 1980, 1981, and 1983.

Bottom feeding had apparently occurred when whales surfaced with mud emanating from their mouths. We saw whales coming up with mud on two days in 1980, on one day in 1981, on three days in 1983, and on 12 days in 1984 (including observations near industrial activities). In 1984, when by far the greatest amount of probable bottom feeding was seen, we observed 96 incidents of whales with mud, from 13 August through 2 September, in water 6-24 m deep. Bottom feeding whales were usually >75 m from each other and did not appear to be cooperating while feeding. Interestingly, mud did not always emanate from the mouths of bottom feeding whales when they first surfaced. Of 14 complete surfacings when mud emanated directly from the mouth, it did so at the start of the surfacing only 5 times, and came from the mouth 10 to 83 s after surfacing during the remaining 9 surfacings (mean time after surfacing was $31 \pm$ s.d. 28.1 s). This indicates that the mouth may stay closed for a considerable period after surfacing.

The baleen whale that is best known for feeding on organisms in bottom sediment is the gray whale, Eschrichtius robustus (Nerini 1984). The relatively short and coarsely fringed baleen of that species probably is particularly adapted to bottom feeding. In contrast, bowhead whales have very long, finely fringed baleen well suited for skimming through clouds of prey and seemingly not well suited for bottom feeding. Nevertheless, the amounts of mud that we have occasionally seen pouring from the mouths of bowheads appeared too great to have been picked up incidentally while bowheads fed on water column organisms near the bottom. Therefore, bowheads at times take in considerable quantities of sediment or suspended particulates while feeding near the bottom.

Pebbles and bottom dwelling species have been found in bowhead stomachs (Johnson et al. 1966; Durham 1972; Lowry and Burns 1980; Hazard and Lowry 1984; Lowry and Frost 1984). Lowry and Burns (1980) found that most species in the stomachs of five bowhead whales killed off Kaktovik, Alaska, in fall were benthic amphipods. However, the benthic amphipods were an insignificant part of the overall volume of stomach contents; pelagic prey such as calanoid copepods and euphausiids were predominant. Lowry and Burns

suggested that a feeding dive probably involves swimming obliquely from surface to bottom and back, feeding the entire time. This is possible, but we suspect that bowheads usually concentrate their feeding at depths where prey is most abundant.

Stomachs of small, subadult bowheads have been found to contain some benthic prey, whereas stomachs of large adult bowheads contained only plankton (Lowry and Frost 1984). Interestingly, photogrammetric data showed that the area where we observed bottom feeding in 1983 and 1984 was occupied mainly by small, subadult bowheads (this study; Davis et al. in prep.). Thus, it is possible that bottom feeding is primarily or even exclusively an activity of young bowheads.

Water-column feeding probably occurs often in the Beaufort Sea in summer, but because it occurs below the surface and is not associated with mud, we have not been able to ascertain its frequency. We believe that water-column feeding occurred in most years and was the major feeding mode during 1982, when bowhead whales were generally encountered in deep water and dove for up to 0.5 h at a time. We suspect that feeding in the water column is generally not done cooperatively, unlike skim feeding in echelon. Whales believed to be water-column feeding were usually separated from each other by several hundred metres.

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

Respiration and Surfacing Characteristics of Feeding Bowheads

Figure 6 and Table 1 summarize the principal respiration, surfacing and dive variables for skim feeders, bottom feeders, and other bowheads. Many of the 'other' whales were probably feeding in the water column.

There were no significant differences in the respiration, surfacing and dive characteristics of bottom feeding whales compared to other whales. The sample sizes were low for bottom feeding whales, because all bottom feeders observed in 1980 and 1981 and most of those observed in 1983 were near industrial activities and were therefore excluded from this consideration. Skim-feeding whales, on the other hand, had a significantly longer overall mean blow interval than either bottom feeding whales or non-feeding whales. Skim-feeding whales also tended to remain at the surface significantly longer per surfacing than either other category of whale. The mean number of blows per surfacing for skim-feeding whales was not significantly different from the mean for either other category of whales, probably because of the long blow intervals for skim-feeders. The dives of skim-feeding whales were shorter than for either other category of whales, but the differences were not statistically significant.

Social Behavior

Behavior was termed social when whales appeared to be nudging or pushing one another, orienting toward each other when <1/2 whale length apart, or chasing each other. We observed apparent mating--consisting of two whales rolling ventrum to ventrum and stroking each other with their flippers--on
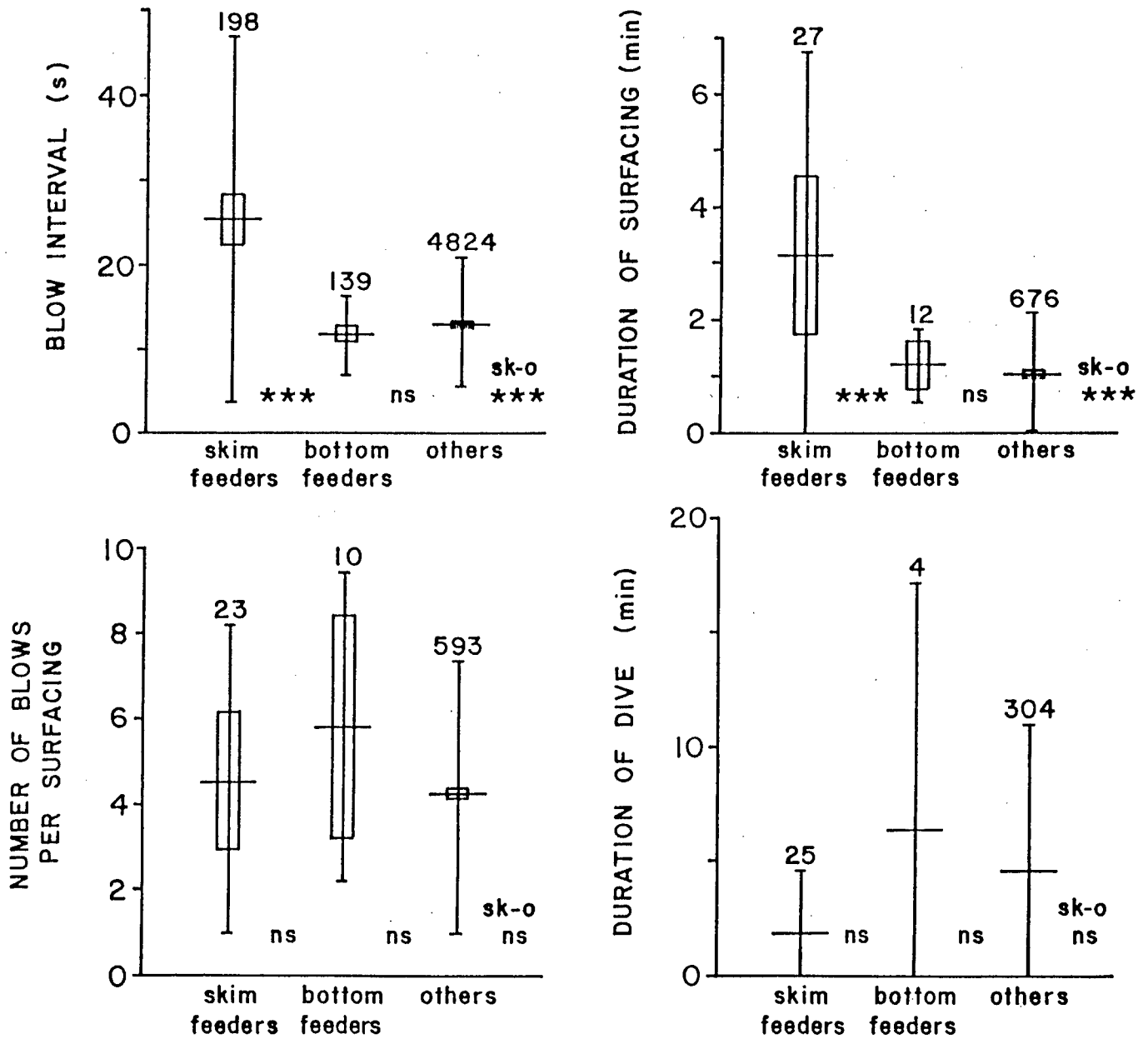
·FIGURE 6.   Comparison of respiration, surfacing and dive variables for
skim feeding, bottom feeding, and other bowheads, 1980-84.   Only presumably
undisturbed non-calves are included.   *** means p<0.001; ns means p>0.1.   The
statistical tests used were Dunn's multiple comparison for duration of dive
and Newman-Keul's test for all other variables.

only two occasions, both in 1981. Würsig et al. (in press) provide further descriptions of social interactions. Interactions between mothers and calves, between whales skim feeding in close proximity, and between whales lying close together but not actively interacting were not included as social interactions in this analysis. Whales may, of course, communicate by sound and thus may socialize over far greater distances than those described here. Because groups of whales usually could not be reidentified positively from one dive to the next, we treated observations of social behavior at intervals >5 min as independent for the purpose of counting numbers of interactions. Conversely, we did not score social behavior in the same area more than once in 5 min when counting its frequency unless separate groups were identifiable. We observed socializing that involved calves on only one occasion, on 7 August 1983, when two calves interacted quite boisterously for about 5 min. This case occurred in the presence of seismic noise, so it is not included in the analysis below.

Social behavior occurred with rather low frequency in all years. We calculated rates of socializing by dividing the number of instances of socializing by the number of whale-hours at the surface (the sum of the durations of all observed surfacings including those of calves). In 1980, there were approximately 30 social incidents, but data on them were too incomplete to allow calculation of a precise socializing rate. In 1981-84, the socializing rate varied from year to year by as much as a factor of five. The highest and lowest rates were observed in 1981 and 1982, respectively (Table 4).

Table 4. Rate of active socializing among presumably undisturbed bowhead whales, 1981-1984.

Year	1981	1982	1983	1984
Number of instances of socializing	36	7	20	14
Whale-hours of observation	6.7	6.3	7.9	7.6
Socializing rate (instances/wh.-h.)	5.4	1.1	2.5	1.8

More socializing took place in early August than at the end of August and beginning of September (Fig. 7A, chi-square = 19.42, df = 3, p<0.001). This trend was evident every year. There seemed to be more social activity in water 16-50 m deep than in other depths (Fig. 7B), but the socializing data in the 16-50 m category come mainly from several days in 1981, and may not be representative. There was no consistent trend in the rate of socializing with respect to time of day (Fig. 7C), contrary to our earlier suggestion based on fewer data (Würsig et al. in press).

Socializing Whales Compared to Non-Socializing Whales

The mean blow interval for socializing whales was slightly but significantly longer than for non-socializing whales (Fig. 8 and Table 1). Duration of surfacing and number of blows per surfacing were similar for socializing and non-socializing whales, but multivariate analysis (below) revealed a tendency for surfacings to be longer in socializing whales, after
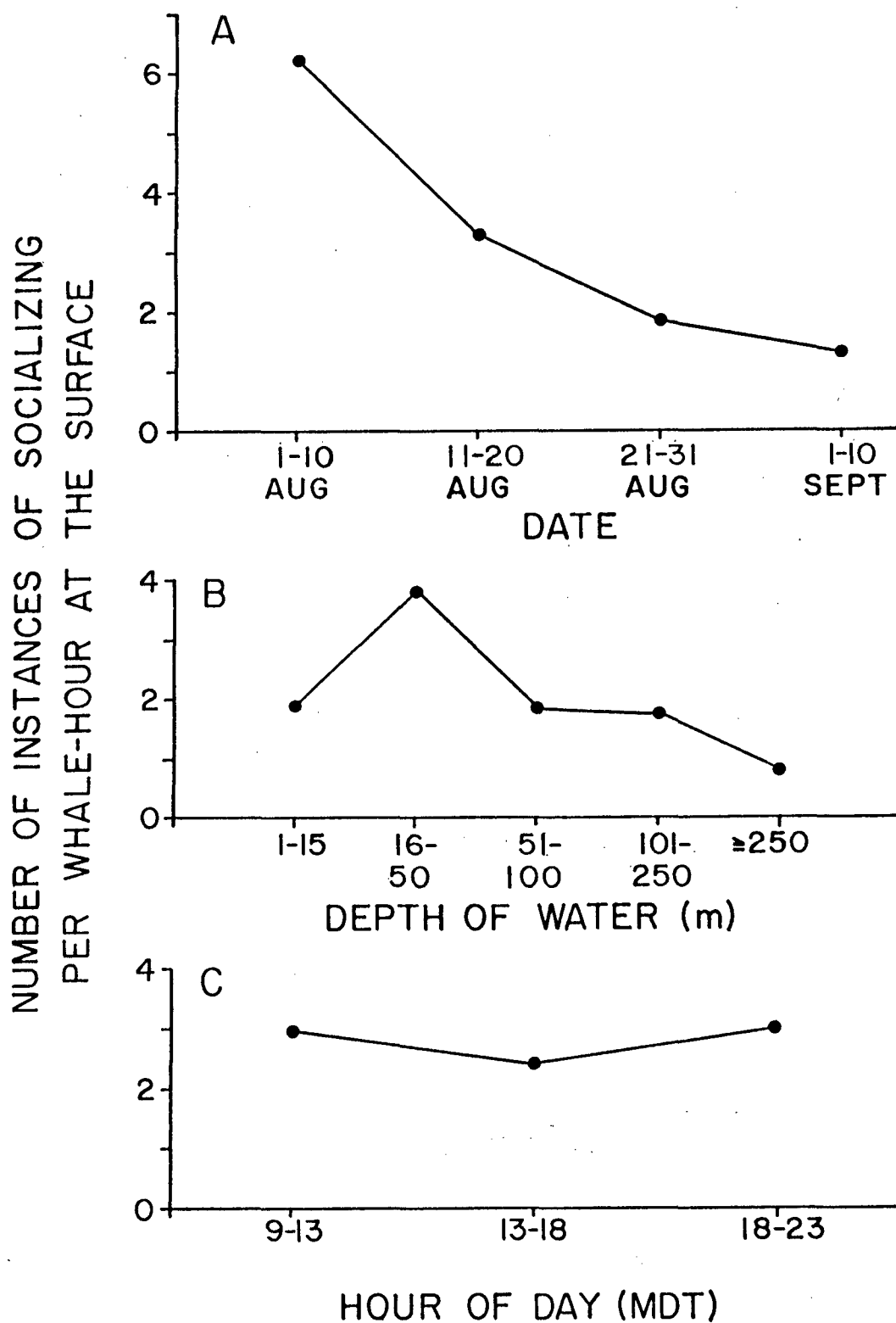
FIGURE 7.   Rate of socializing by presumably undisturbed bowheads in relation to (A) date, (B) depth of water, and (C) time of day, 1981-84.
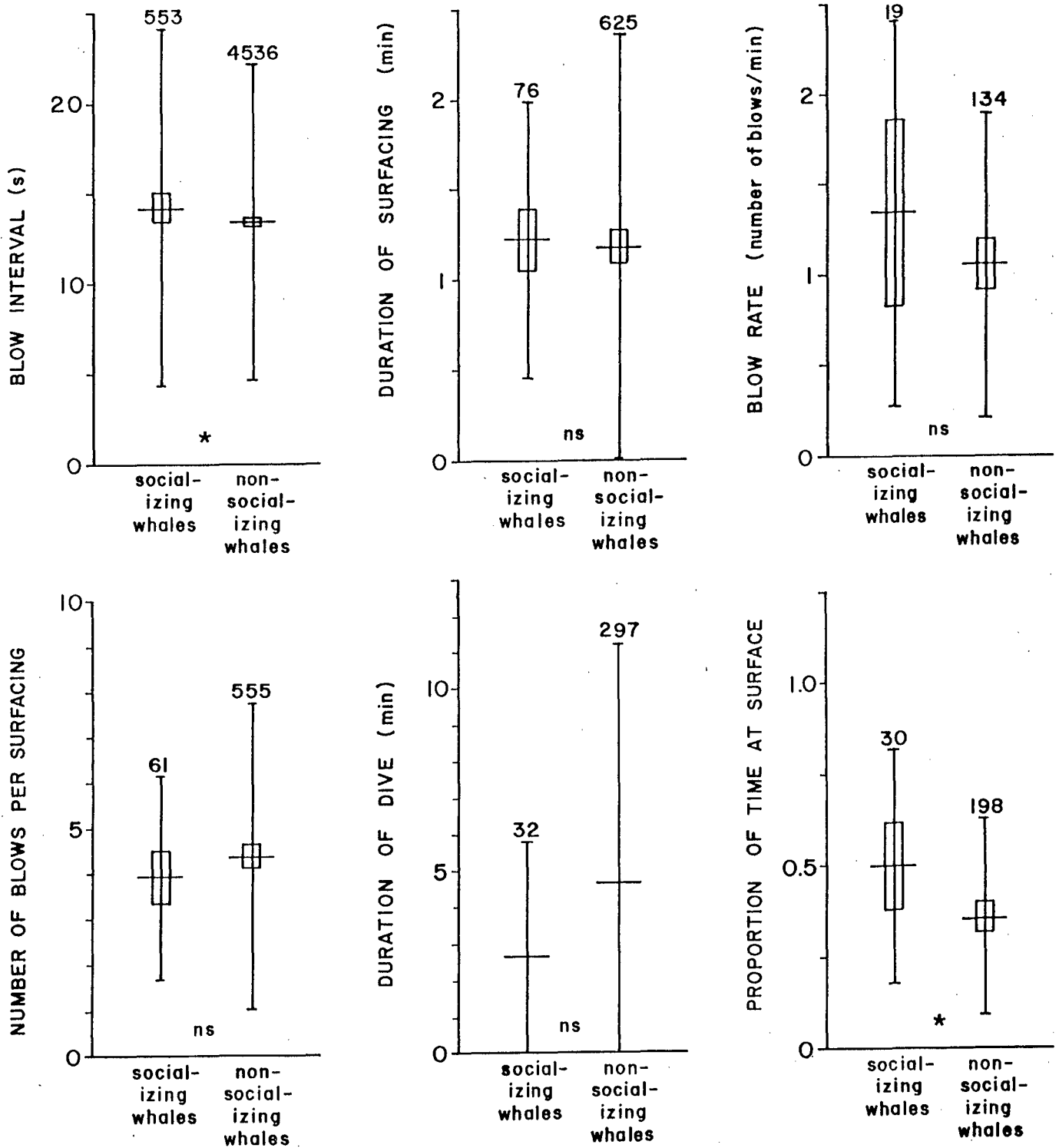
FIGURE 8. Comparison of respiration, surfacing and dive characteristics for socializing and non-socializing bowheads, 1980–84. Only presumably undisturbed non-calves are included. * means 0.05>p>0.01; ns means p>0.1. The statistical tests used were Mann-Whitney U test for duration of dive and t-test for all other variables.

allowing for other factors. Dives by socializing whales tended to be shorter than dives by whales that were not socializing, but not significantly shorter. Both the mean blow rate and the mean proportion of time at the surface were higher in socializing whales, but the difference was significant only for the latter variable.

In the process of interacting with nearby whales, socializing whales often make turns while at the surface. In contrast, non-socializing whales often come to the surface and dive again without changing direction. The difference in frequency of turns between these categories of whales was very highly significant (chi-square = 21.68, df = 1, p<<0.001; see Table 5).

Table 5. Frequency of turns during complete surfacings of actively socializing and non-socializing bowheads, 1980-1984. Only presumably undisturbed non-calves are included.

	Socializing Whales	Non-socializing Whales
Surfacings with turns	35	171
Surfacings without turns	30	477
Total surfacings	65	648
% surfacings with turns	53.8%	26.4%

Whales in Groups vs. Lone Whales

We also analyzed the effect of group size on the main surfacing, respiration, and dive variables by comparing lone whales to whales in groups of two or more. A group was defined as all whales within five body lengths of each other. Whales in a group are not necessarily interacting socially in the way that we have defined for socializing above. However, the proximity required for whales to be classified as being in a group normally must represent at least a minimum level of social interaction. For this analysis of lone whales vs. whales in groups, we excluded skim-feeding whales from both categories in order not to confuse the effect of skim-feeding, which often occurred in groups, with any effect of group size.

Trends in respiration, surfacing and dive variables for lone whales vs. whales in groups were, for the most part, consistent with trends for non-socializing vs. socializing whales (Table 1; Fig. 9 vs. 8). The overall mean blow interval for whales in groups was significantly higher than that for lone whales, and the overall mean number of blows per surfacing for whales in groups was significantly lower. There was no significant difference in the mean surface time or mean dive time. The overall mean blow rates were not significantly different, but the whales in groups spent a significantly higher mean proportion of their time at the surface than did the lone whales.
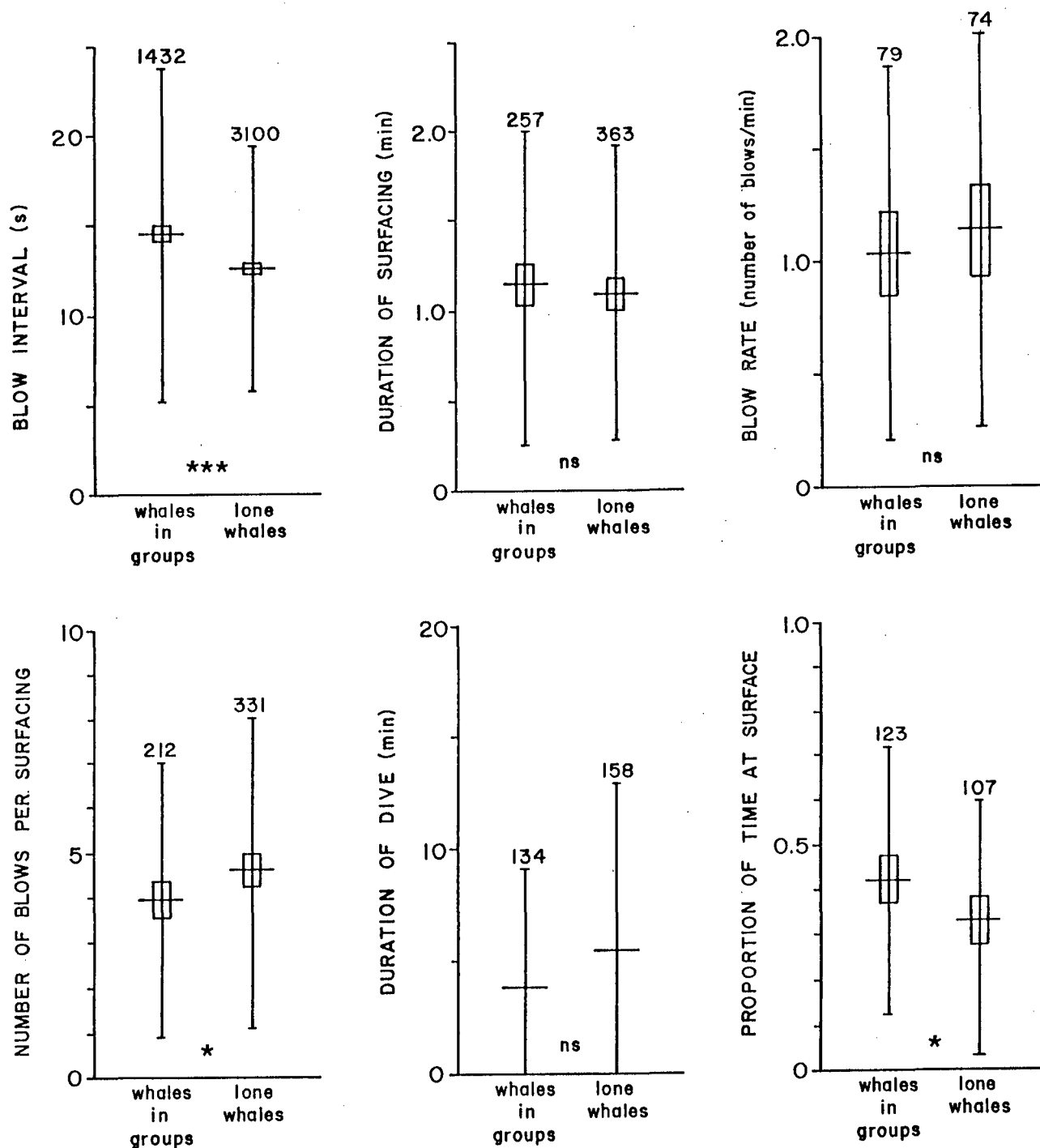
FIGURE 9.   Comparison of respiration, surfacing and dive characteristics for lone whales and whales in groups, 1980-84.   Calves and skim feeding whales are excluded from both categories, and only presumably undisturbed periods are considered.   Significance levels coded as in Table 2 (p. 29).   The statistical tests used were Mann-Whitney U test for duration of dive and t-test for all other variables.

Environmental Factors

Depth of Water

Blow intervals did not show any consistent trend with depth (Fig. 10; Table 1). Therefore, although there were statistically significant differences between means for various depth categories, we suspect that these differences were due to factors other than depth. The other three variables--number of blows per surfacing, surface time, and dive time--all showed more or less clear tendencies to increase with increasing depth.

Number of blows per surfacing showed the increasing trend most clearly (Fig. 10). The means for the shallowest three categories (≤ 100 m) were not significantly different from each other, but the means for each of the two deepest categories were significantly different from the means for each of the three shallower depths ($p < 0.05$ in each case, Newman-Keuls tests). Subsequent multivariate analysis, however, showed that this apparent effect of water depth may be an artefact of year-to-year effects (see below).

For duration of surfacing, as for number of blows per surfacing, the means for the three shallowest depth categories did not differ significantly. The mean for the deepest category, >250 m, was significantly higher than any of the other means ($p < 0.001$ in each case, Newman-Keuls tests). The mean for 101-250 m was significantly higher than the means for <16 m and for 16-50 m ($p < 0.025$ in each case).

For duration of dive, means for the two deepest categories were significantly greater than means for the three shallowest categories (Dunn's multiple comparisons, $p < 0.05$ in each case). Means for the two deepest categories were similar, as were means for the three shallowest categories.

In general, number of blows per surfacing, duration of surfacing and duration of dive tended to be greater in deep (>100 m) water than in shallow (≤ 100 m) water. These trends were largely attributable to the high values of these variables in 1982, a year when most observations were in deep water (Figs. 1,2). There was only very limited evidence that the trends existed within single years (see Würsig et al. 1984a and Table 1). Thus, it is difficult to determine whether the trends were attributable to depth or year effects (see 'Multivariate Analysis' section below).

Time of Day and Date in Season

For each of the four principal surfacing, respiration, and dive variables, we looked at the mean value for presumably undisturbed non-calves by hour of day. We failed to find any apparent trend by hour of day for any of the variables in any of the five years or in all five years combined. The only exception was for blow intervals in 1983 when mean values were considerably longer in the hours 16:00 to 18:00 MDT. These were hours when much skim feeding was observed; skim feeding whales in 1983 had particularly long blow intervals, and the long mean blow intervals at this time probably were due to the activity of the whales rather than the time of day. We conclude that time of day had no consistent effect on any of the four principal variables.
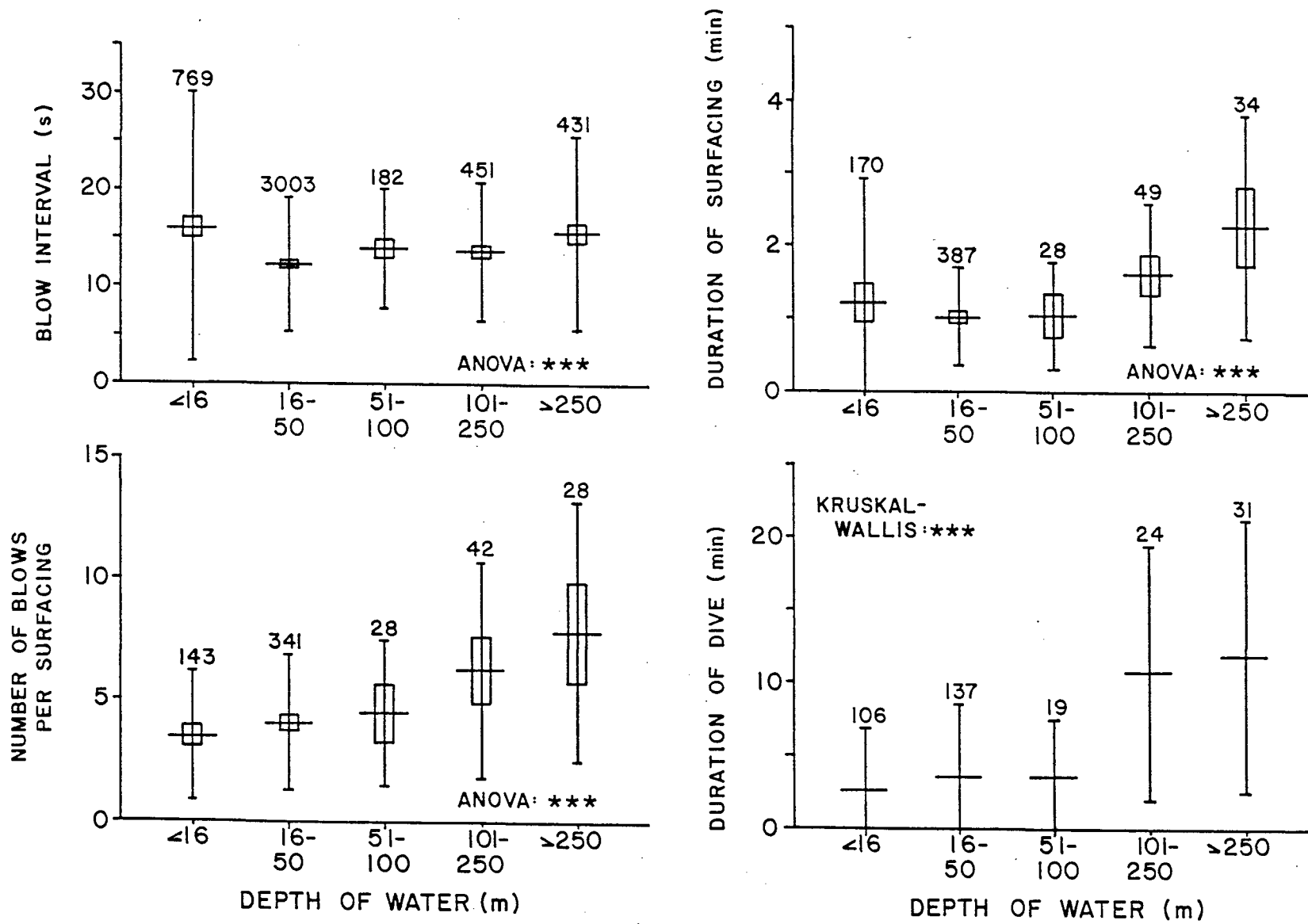
FIGURE 10. Comparison of respiration, surfacing and dive characteristics for bowheads in five categories of water depth, 1980-84. Only presumably undisturbed non-calves are included. *** means $p \leq 0.001$.

We also looked for seasonal trends in the four principal surfacing, respiration, and dive variables over the period of our study, from 1 August to 10 September. We divided this period into four 10- or 11-day periods (1-10 Aug, 11-20 Aug, 21-31 Aug, and 1-10 Sep); in the last period we collected data only in 1981 and 1984 (Fig. 2A). Blow interval, number of blows per surfacing, duration of surfacing and duration of dive all showed no consistent trend across these 10-day periods. As previously noted, frequency of active socializing did decline over the period (Fig. 7A).

Multivariate Analysis

Introduction

In preceding sections, we analyzed relationships of the principal surfacing, respiration and dive variables (for presumably undisturbed bowhead whales) to environmental factors and whale activities. Factors that appeared to have a statistically significant effect on at least one of the variables were the following: status of whale (mother, calf or other), behavior of whale (skim feeding or not feeding; socializing or not), group size, depth of water, and year of observation. We found no evidence that surfacing, respiration and dive variables were affected by occurrence of bottom feeding, time of day, or date within our short field season. In some cases we partitioned the data by year, activity of whale, etc., in an attempt to allow for the multiplicity of factors that might simultaneously affect the variable in question. In all cases we separated calves from older whales. With these exceptions, however, all preceding analyses examined one factor at a time. We knew that some factors were interrelated, like year and depth of water, and suspected that others might be. Hence we used multiple regression analysis to try to sort out the relative importance of each factor.

Three dependent variables were considered in separate multiple regression analyses: number of blows per surfacing, duration of surfacing, and mean blow interval. The last of the variables was the sum of all blow intervals in a surfacing divided by the number of blow intervals. Thus, each surfacing was represented by one case in each multiple regression analysis. Data from 1980 were excluded because too many of the necessary predictor variables were unknown. Data from calves were excluded because of the considerably different behavior of calves. Because of rightward skew in the distributions of all three dependent variables (Fig. 3A-C), logarithmic transformations were used:

$$LOGNBL = \log_{10}(NBLOWS + 1), \text{ where } NBLOWS = 0 \text{ to } 19;$$
$$LOGSFC = \log_{10}(LENSFC), \text{ where } LENSFC \text{ is in seconds};$$
$$LOGMBI = \log_{10}(MEANBI), \text{ where } MEANBI \text{ is in seconds}.$$

Test runs with the dependent variable not transformed gave very similar results as those on the transformed data, showing that the results were not sensitive to the type of transformation chosen.

Seventeen variables were considered as potential predictors of the three dependent variables:

YEAR.82	1 if year = 1982; 0 if not.
YEAR.83	1 if year = 1983; 0 if not.
YEAR.84	1 if year = 1984; 0 if not.

(Note: No 'dummy variable' for 1981 was needed; 1981 was treated as the standard year against which others were compared.)

DATE & DATE.SQ	– Date, in days after 31 July, and its square (to test for non-linear relationship).
TIME & TIME.SQ	– Hour + Min/60 (0-24 scale) and its square (to test for non-linear relationship).
LOG.DEPTH	– log (Water depth in metres); transformed because of extreme skewness.
SEA.STATE	– Sea state, 0-5 scale.
ICE.%	– Percent ice cover.
GT.5%.ICE	– Greater than 5% ice cover = 1; otherwise 0.
ALT.AIRCR	– Aircraft altitude, in hundreds of feet (cases with ALT<15 excluded because they were considered potentially disturbed).
MOTHER	– 1 if recognized as mother because of presence of calf; 0 if not.
BOTTOM.FEED	– 1 if whale brought mud to surface during this surfacing, indicative of bottom feeding; 0 if not.
SKIM.FEED	– 1 if skim feeding during this surfacing; 0 if not.
ACT.SOCIAL	– 1 if active socializing; 0 if not.
GT.ONE	– 1 if group size>1 (i.e., if another whale within 5 whale lengths); 0 if not.

Only those cases for which all 17 predictors were known were used in the analyses. The resulting sample sizes were 479 for NBLOWS, 538 for LENSFC, and 966 for MEANBI. The ratio of variables to cases was low in each analysis, so the results are comparatively reliable.

Several multiple regression equations were calculated for each of the three dependent variables. These included equations containing

- all 17 predictor variables,
- all 14 predictors exclusive of year variables,
- the 3 year variables only, and
- the 'backwards elimination' equation, including all variables that were of significant value as predictors (nominal $p \leq 0.05$).

Equations including various other combinations of variables were also examined to assess the effects of intercorrelations among predictors on the results. We used an interactive stepwise multiple regression program, ELF version 5 (Winchendon Group 1983), with enhancements by LGL. The accuracy of this microcomputer program was confirmed by duplicating similar analyses previously done with BMDP (Dixon and Brown 1977).

Because of the large sample sizes, simple and partial correlations were statistically significant even when the degree of correlation was very low. Most of the 'highly significant' correlations noted below ($p < 0.001$) involved correlation coefficients in the 0.15 to 0.25 (or −0.15 to −0.25) range. Most correlations significant at the 1% ($0.01 \geq p > 0.001$) level were in the ± 0.10 to ± 0.15 range. We have not placed much emphasis on variables significant only at the 5% level.

Number of Blows per Surfacing (LOGNBL)

The univariate analyses described in earlier sections showed that number of blows per surfacing tended to be high in 1982 (Fig. 3), marginally higher for single whales than for whales in groups (Fig. 9), and higher for whales in deep water (Fig. 10). There was nothing unusual about the number of blows per surfacing by mothers, socializers, or skim- or bottom feeders; and there was no obvious relationship to date or time of day (see Table 6A, univariate column). The simple correlations of the variables used in the multiple regression analyses showed that LOGNBL tended to be high in 1982 and 1984, and low in 1983, relative to other years (Table 6A, simple correlation column). The only other strong simple correlations were with water depth (r = 0.226) and aircraft altitude (r = -0.153, all altitudes at least 457 m). There were also significant intercorrelations between many predictor variables. For example, water depth and aircraft altitude were strongly correlated with year.

When all 17 predictor variables were included in a multiple regression equation (Table 6A), the only variables significant at the nominal 1% level were the years 1982 and 1984, in both of which LOGNBL tended to be high. Water depth and aircraft altitude were no longer significant as predictors of LOGNBL after year effects were taken into account. If year variables were excluded, depth was positively related to LOGNBL ($r_{partial}$ = 0.190). The backwards elimination procedure resulted in an equation including only three predictor variables, all of which were year variables (Table 6A, 'optimum' column).

In summary, year to year variation was the most conspicuous contributor to variation in number of blows per surfacing. Once year effects were taken into account, there was no clear evidence that any other variable affected LOGNBL. However, water depth and (to a lesser degree) group size, average aircraft altitude and average ice cover at observation sites differed among years. It is possible, but unprovable, that depth or perhaps some of these other variables affected LOGNBL. The most important conclusion is that the apparent effect of water depth on number of blows per surfacing, as suggested by Fig. 10, cannot be distinguished from a generalized year effect.

Duration of Surfacing (LOGSFC)

The earlier univariate analyses showed that duration of surfacing tended to be high in 1982 (Fig. 3), higher for mothers and skim-feeders than for others (Figs. 5,6), and higher for whales in deep water (Fig. 10). There was nothing unusual about durations of surfacing by bottom feeders, socializers or whales in groups, and there was no obvious relationship to time or date (Table 6B, univariate column). The simple correlations of the variables used in the multiple regression analyses provided very similar results (Table 6B, simple correl. column).

When all 17 predictors were considered together, five predictors were positively related (at p<0.01) to LOGSFC: 1982, 1984, aircraft altitude, skim feeding, and socializing. The backwards elimination procedure resulted in an equation that included these same five variables at similar significance levels, plus three additional variables that were also positively related to LOGSFC—date, water depth and sea state (Table 6B, 'optimum' column). Note that the multiple regression analysis revealed apparent relationships between

Table 6. Summary of univariate and multiple regression analyses of relationships between (a) environmental and activity variables and (b) surfacing and respiration variables.

Predictor Variable	A. No. Blows per Surfacing					B. Duration of Surfacing					C. Blow Intervals				
	Uni-variate[a]	Simple Correl.	All 17 Variables	Year Excluded	'Optimum'	Uni-variate[a]	Simple Correl.	All 17 Variables	Year Excluded	'Optimum'	Uni-variate[a]	Simple Correl.	All 17 Variables	Year Excluded	'Optimum'
YEAR.81	Fewer					Shorter					Intermed.				
YEAR.82	High	+++[c]	++		+++	Long	+++	+++		+++	Intermed.	+++	++		+++
YEAR.83	Fewest	---	ns		-	Shorter	---	ns			Long	+++	+++		+++
YEAR.84	Fewer	+++	+++		+++	Shorter	ns	++		+++	Shortest	---	ns		
DATE	No trend	(+)	ns	ns		No trend	+	ns	ns	+	No trend	ns	ns	ns	++
DATE.SQ	[b]	+	ns	ns			+	ns	ns			ns	ns	ns	
TIME	No trend	ns	ns	ns		No trend	ns	ns	+		No trend	ns	ns	ns	-
TIME.SQ		ns	ns	ns			ns	ns	-			ns	ns	ns	
LOG.DEPTH	+++	+++	(+)	+++		+++	+++	+	+++	++	No trend	+	ns	+	
SEA.STATE		ns	ns	ns			ns	+	ns	+		--	ns	ns	
ICE.%		ns	-	--			ns	ns	-			ns	ns	ns	
GT.5%.ICE		+	+	++			ns	ns	(+)			ns	ns	ns	
ALT.AIRCR		---	ns	ns			ns	+++	(+)	+++		(+)	ns	ns	
MOTHER	ns	+	ns	ns		+++	+++	(+)	+		+++	+++	ns	ns	
BOTTOM.FEED	ns	ns	ns	ns		ns	ns	ns	ns		ns	ns	ns	ns	
SKIM.FEED	ns	ns	+	ns		+++	++	+++	+++	+++	+++	+++	+++	+++	+++
ACT.SOCIAL	ns	ns	(+)	ns		ns	(+)	+++	+++	+++	+	(+)	ns	ns	
GT.ONE	-	ns	ns	-		ns	ns	ns	ns		+++	+++	++	+++	+++
% Var. Expl.		16.8	11.4	13.3			17.6	14.1	16.2			12.7	9.3	12.1	
# Cases			479					538					966		

[a] Summary of univariate results is based on Figure 3 (year effects), Figure 5 (mother vs. other), Figure 6 (skim- and bottom-feeders vs. other), Figure 8 (active socializers vs. other), Figure 9 (whales in groups vs. singles), Figure 10 (depth), and the text (time and date).

[b] Blanks in the table denote variables that were not analyzed, or not included in the multiple regression equation.

[c] Pluses indicate positive and significant correlations or partial correlations; minuses indicate negative relationships;
  +++ or --- means $p \leq 0.001$
  ++ or -- means $0.01 \geq p > 0.001$
  + or - means $0.05 \geq p > 0.01$
  (+) or (-) means $0.1 \geq p > 0.05$
  ns means $p > 0.1$

LOGSFC and both socializing and aircraft altitude even though there was no significant simple correlation with either variable. Conversely, there was no evidence that mothers had longer surface times after other factors were taken into account. Skim feeding and socializing remained significant as predictors of LOGSFC regardless what other variables were dropped from the equation. This indicates that the higher surface times for these two groups of whales were real and not spurious indirect effects. However, the removal of any one of depth, altitude and year from the equation affected the apparent significance of one or more of the others. Hence their effects on LOGSFC could not be separated.

In summary, skim-feeding and socializing bowheads tended to remain at the surface for unusually prolonged periods. The latter effect was not recognizable from univariate analyses. In contrast, the relatively long surface times displayed by mothers and by whales in deep water might be spurious results of intercorrelated factors, most notably the fact that many sightings of mothers and most sightings in deep water occurred in 1982, a year with long surface times. The depth effect did not disappear entirely when year and other variables were taken into account (Table 6B), and it is possible that much of the apparent year effect was actually a depth effect.

Blow Interval (LOGMBI)

Univariate analyses showed that blow intervals tended to be shortest in 1984 and longest in 1983 (Fig. 3). Blow intervals averaged longer for mothers (Fig. 5), skim feeders (Fig. 6), socializers (Fig. 8) and whales in groups (Fig. 9) than for other whales. There was nothing unusual about blow intervals of bottom feeders, and no clear trends with respect to water depth, time or date. The simple correlations of the variables used in the multiple regression analyses provided very similar results, and also showed a negative correlation between LOGMBI and sea state (Table 6C).

A multiple regression equation including all 17 predictors explained only 12.7% of the variance in LOGMBI, lower than for either of the other two dependent variables (Table 6). Four of the 17 predictors were significantly and positively related to LOGMBI: 1982, 1983, skim feeding and group size>1 (Table 6C). With years removed from the equation, the partial correlations with skim feeding and group size remained about as before, and only one additional variable--depth--acquired marginal significance (Table 6C). This suggests that, for blow intervals, the effects of years and other variables are less seriously confounded than was true in the analyses of LOGNBL and LOGSFC. The backwards elimination procedure produced an equation with six predictor variables, including 1982, 1983, date, time, skim feeding, and group size. All partial correlations, except the marginal one with time, were positive. The negative relationship to time suggests that LOGMBI had a slight tendency to decrease late in the day after effects of other variables were taken into account.

These results confirm the univariate evidence that blow intervals tended to be long in 1983, for skim feeders, and for whales in groups. The partial correlations do not confirm the univariate trends for longer blow intervals in the cases of mothers or socializers. However, the relationships of LOGMBI to group size, mothers, and socializing were confounded. Socializing, by our definition, occurs only in groups, and mothers are almost always identified by close proximity of a calf. When group size was excluded from the

regression equations, positive partial correlations (p<0.05 or better) with mothers and socializing became evident.

Synchrony of Behaviors

Bowheads within groups often surfaced and dove in rough synchrony. At times we also had the strong impression that whales of different groups, greater than five whale lengths from each other, had partially synchronized surfacing-dive patterns. However, because we usually did not know exactly how many whales were in an area, and we could not identify all whales, our analysis of potential synchrony is incomplete. We investigated the possibility of synchronized surfacing-dive patterns during five observation sessions for which we believed we had nearly complete records of the surfacings of whales in our observation circle. We compared the observed number of 3-min intervals with 0, 1, 2, etc. single whales or groups at the surface against the expected number if there were no synchrony, i.e., assuming a Poisson distribution.

During 4 of 5 tests, we found no significant deviation in surfacing pattern from that of a Poisson distribution, although the data were suggestive of possible synchrony during two tests. On 2 September 1984, however, synchrony was strongly indicated. The session involved approximately three lone whales within a 3 km diameter circle, each whale about 250-1000 m from the others. Surfacings and dives were monitored for 42 3-min intervals. There were fewer intervals with one whale and more intervals with two whales than expected (Table 7), indicating that two of the separated whales tended to surface together (chi-square = 7.83, df = 2, p<0.025); however, we do not know whether these were always the same two whales.

Table 7. Data for analysis of surfacing synchrony in three lone whales on 2 September 1984. Expected values were derived from the observed mean of 1.2 whales at the surface per 3-min interval (± s.d. 0.98, n = 42). See text for discussion.

Maximum number of whales at surface during 3-min interval	Observed number of intervals	Expected number of intervals[a]
0	13	12.7
1	10	15.2
2	16	9.1
>3	3	5.1

[a] Assuming a Poisson distribution with mean 1.2

Potential synchrony in surfacings and dives is especially difficult to analyze because number of whales involved is not known, whales may move into or out of the area while under observation, and whales may move into or out of groups. The apparent synchrony on 2 September 1984 occurred while lone whales were possibly feeding in the water column; during other times when

synchrony has been suspected (but has remained unsubstantiated by analysis), subsurface feeding has also usually been indicated. We do not know why whales some distance apart from each other would wish to be at or below the surface at the same time, but it is possible that in this manner they remain in better acoustic contact. Donald Ljungblad (Naval Ocean Systems Center, San Diego, pers. comm.) believes that bowheads sometimes make more sounds just before they surface, and they may stay in contact and synchronize surfacings in this manner. We attempted to correlate sounds and surface-dive behavior in this study, but our limited data do not substantiate the suggestion that sounds are more frequent at any particular part of the dive cycle.

<div align="center">Miscellaneous Behaviors</div>

Play

Although whales may engage in play during various social interactions, we could not separate play from possible mating activity or aggression. Therefore, we considered whales to be playing only when they associated with an object other than another whale. We saw such associations in 1981, 1982, and 1984. Play behavior during 1981 and 1982 is summarized in Würsig et al. (in press), and we present only a brief overview here.

Log Play.--We observed whales playing with logs up to about 10 m long on two occasions in 1981, and once each in 1982 and 1984, for 5 s, 10 min, at least 1.5 h, and 5 min, respectively. Most contact with the log consisted of the whale nudging or pushing the log with the head or body. Sometimes the log was clasped by the flippers while the whale was belly-up underneath the log, or was lifted up by the back or tailstock.

Association with objects other than conspecifics has been described for at least four other species of large whales (a humpback whale, Couch 1930; a sperm whale, Nishiwaki 1962; right whales, Payne 1972; and gray whales, Swartz 1977). Some specific elements of log play in bowheads were strikingly similar to play with seaweed observed in southern right whales (Payne 1972); both involved lifting the object with the head, moving the object along the back, and patting it with the flippers. Attempts to submerge the log with the head are also reminiscent of a motion made by male right whales when attempting to mate with uncooperative females (Payne, in review).

Calf Play.--Calves were seen alone at the surface on about ten occasions, apparently 'waiting' for their mothers to come up from a dive. Usually calves were rather inactive at those times; however, on two occasions in 1982 they interacted with debris in the water. On 19 August 1982, a calf swam in a meandering line of surface debris approximately 2 m wide and probably composed mainly of invertebrates. The calf associated with the line for 12.3 min, with rapid and often jerky movements, reminiscent of any uncoordinated young mammal. We do not believe that the calf was feeding on the debris in a concerted manner, although its mouth was open slightly for brief periods. It is possible that the calf was practicing skills required for skim feeding.

The second incident, on 23 August 1982, involved a calf moving within an area about 40 m wide and 100 m long marked by dispersed fluorescein dye from one of our dye markers. The calf actively rolled and twisted within the dye,

reorienting itself at the edge of the dye in order to stay within the dyed area for 22.3 min. The association with this area ended when the calf left the dye and oriented toward its mother, which was approaching the calf at 120 m distance. When the two joined, the calf began nursing. It is possible that, as in the previous account, the calf may have oriented toward suspended matter while practicing skills used to feed on clouds of invertebrate prey. If so, some play may be of functional value.

Aerial Activity

Aerial activity, consisting mainly of breaches, tailslaps, and flipper slaps, occurred sporadically throughout our five field seasons. General descriptions of these activities are presented in Würsig et al. (in press), and the frequency of aerial activity each summer is shown in Table 8.

Table 8. Frequency of aerial activity, 1980-84, based on whale-hours of observation at the surface. Both presumably undisturbed and potentially disturbed periods are included. Rates are probably overestimated because we occasionally observed bowheads specifically to document aerial behavior.

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

Breaches were usually performed by whales that were >100 m from other whales, and occurred both as single breaches and in series of up to 19 breaches with no interruptions by other surface activity. The mean interval between breaches within a series was $0.53 \pm$ s.d. 0.154 min (n = 66). Tailslaps onto the surface of the water included single slaps and uninterrupted series of up to 148 slaps. The mean of 266 measured intervals between successive tailslaps was 4.9 s ($\pm$ s.d. 1.94 s). Flipper slaps onto the surface of the water also included single slaps and up to 10 slaps in an uninterrupted series, with the mean of 43 measured intervals within a series being 2.9 s ($\pm$ s.d. 1.62 s). Thus, breach intervals are longest, tailslap intervals are much shorter, and flipper slap intervals are the shortest. This ordering corresponds roughly to the amount of body mass the whale lifts above the surface of the water.

The longest bouts of aerial behavior that we observed were by lone whales and usually consisted of alternating series of tailslaps, flipper slaps, and breaches. A particularly dramatic series involving two whales occurred on 22 Aug 1983. A lone whale that was aerially active before we began circling it interspersed 49 tailslaps with 6 breaches during 11.8 min of observation. Its blow rate was 1.61 blows/min if it did not blow during the breaches or 2.12 blows/min if it blew during every breach. A second whale began breaching 300 m away as the first whale surfaced after its last

breach series. The second whale made 64 breaches, 36 tailslaps and 48 flipper slaps during the 75 min that we observed it. During that time, its blow rate was between 1.19 and 2.04 blows/min, depending on whether or not it blew during the breaches. The first whale moved away from the second as the second began breaching, and we soon lost sight of it. We left the area about 9 min after we last saw the second whale submerge, and we do not know whether it resumed aerial activity on its next surfacing.

Some tailslaps and flipper slaps occurred in groups of whales, either as single slaps or in short series of up to 10 slaps, sometimes while the whales were actively socializing. On one occasion in 1981, the socializing appeared to include copulation between two animals, in addition to numerous tailslaps and flipper slaps by both animals. On three occasions we have seen a bowhead whale strike another with its tail flukes or a flipper in an apparently aggressive manner: once each in 1980 and 1981, one whale slapped its tail onto the head of another, and in 1983, a whale slapped a flipper three times onto the back of another whale, which responded by hitting the first whale on the back with its flukes six times.

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

We observed calves aerially active on only two occasions in five field seasons. One involved a single tail slap and the second, seen from shore on Herschel Island, was of a calf aerially active for 29 min during which it made 37 breaches or partial breaches, with up to three-quarters of the body remaining in the water. The calf breached back and forth, changing direction often, and therefore stayed within 1 km of the presumed mother, although it covered a distance of at least 3 km in its meandering course. This kind of meandering is similar to right whale calves breaching in 'circles' near their mothers (Thomas and Taber 1984). When the calf stopped breaching, it rapidly headed back toward the adult. Further detail on the breaching of this calf is supplied in Thomas (1982).

Aerial activity probably has several functions. Single tailslaps or flipper slaps may indicate disturbance or aggression, as when possibly precipitated by the approach of an airplane (see Richardson et al. 1985c) or when directed against a conspecific. Bouts of aerial activity may signal 'arousal' of some type, and may also serve to communicate to nearby conspecifics. Our sonobuoy recordings showed that many breaches and tailslaps produce pulses of low-frequency underwater noise (see 'Bowhead Sounds' below). Breaches, tailslaps and flipper slaps may also represent play behavior and may not always have a function beyond play.

In other species of large whales, the function of breaching and other aerial behavior remains uncertain. Whitehead (1985), in reviewing current hypotheses about functions of breaching, noted that breaching is most common in species that have many close-range social interactions. In humpback whales, _Megaptera novaeangliae_, breaching is more common on winter mating and calving grounds than on summer feeding grounds. Whitehead suggested that a breach might be a display of strength in male humpbacks (directed at receptive females and/or competing males) and that play might be the main

function of breaching in calves. Payne (in review) argued that breaching by southern right whales in winter functions at times as an acoustic signal to maintain contact between animals. Both authors reported that tail slaps and flipper slaps are often associated with breaching, and both felt that breaching likely has more than one function. However, breach sounds may not be especially suitable as long-distance contact signals; they are created at the surface and, at a distance, are no stronger than calls.

Behaviors Associated with Dive

Several seconds before some (but not all) dives, bowhead whales make a pre-dive flex--a distinctive concave bending of the back, with the back about 0.5 to 1 m below the level of the tail and rostrum. Rostrum and tail usually lift slightly out of the water during the flex, and considerable white water may be created near these two points. The whale then straightens its back and lies momentarily still before arching the back convexly as it pitches forward and down. During 25 timed observations in 1983, pre-dive flexes occurred a mean of 15.4 $\pm$ s.d. 12.00 s before the dive. On rare occasions we saw two or even three flexes before a dive.

We collected consistent data on occurrence of pre-dive flexes in 1981-84. Within specific years, the proportion of dives preceded by flexes ranged from about 1/10 to 1/4 (Table 9). Dives preceded by a flex were longer than those not preceded by a flex (Table 1; for 1981-84, Mann-Whitney U = 3302, $0.01 < p < 0.02$). Surfacings with flexes were longer and had more blows than surfacings without flexes (see Table 1; $p < 0.001$ for both variables in 1981-84). There was no significant difference in the mean blow interval for surfacings with and without a pre-dive flex.

Table 9. Percent of dives preceded by a pre-dive flex or by raised flukes in presumably undisturbed non-calves.

	1981	1982	1983	1984
% of dives preceded by pre-dive flex	10.1%	24.4%	15.5%	20.4%
Number of dives scored for pre-dive flex	178	131	277	269
% of dives preceded by raised flukes	46.7%	48.8%	19.5%	51.3%
Number of dives scored for raised flukes	214	125	390	448

During the dive, the whale arches (makes its back convex) and pitches forward and down. During 51 timed arches in 1983, the arch began a mean of 5.1 $\pm$ s.d. 8.36 s before the final disappearance of the whale's body. If the angle of the dive is steep, the tail is usually raised above the surface; if not, the tail may remain below or just touch the surface. Data on the presence or absence of raised flukes during dives were tabulated for 1981-84. Flukes were raised out of the water on about half of the dives in every year, except in 1983, when only about one fifth of the dives were preceded by raised flukes (Table 9). We had information on the presence or absence of both raised flukes and pre-dive flexes for 803 surfacings in

1981-84. A flex occurred during 137 of these surfacings, and flukes were raised at the end of 321 of the surfacings. These two pre-dive behaviors occurred together during 84 surfacings, much more frequently than the 55 times expected by chance (chi-square = 31.3, df = 1, p<<0.001).

In 1981-84, the mean duration of dives that started with raised flukes was longer than that for dives that started with flukes not raised, but the difference was not statistically significant (Table 1). There was no significant difference in the durations of surfacings that ended with and without raised flukes. The mean number of blows per surfacing was, however, significantly higher for surfacings that ended with flukes raised (t = 5.21, df = 498, p<0.001). In addition, the mean blow interval was significantly lower for surfacings that ended with flukes raised (t = 7.79, df = 2006, p<0.001).

Underwater Blows

The number of underwater blows that we observed varied widely from year to year. Considering both disturbed and undisturbed periods, the number of underwater blows seen per year was as follows:

1980	1981	1982	1983	1984
158	66	6	347	5

We have been uncertain how to interpret underwater blows ever since we first observed them in 1980. We tentatively classified them as a potential type of feeding behavior in that first year, because of their similarity to some bursts of bubbles associated with feeding in humpback whales (Hain et al. 1982). We did not see any direct evidence of feeding in connection with underwater blowing in 1980, but in that year the incidence of underwater blows seemed correlated with the incidence of various feeding behaviors. In 1981, there were again some indications that high numbers of underwater blows occurred on occasions with much feeding behavior, but we again failed to see any specific feeding behavior associated with any underwater blow. In 1983 we observed a very high number of underwater blows, and many of them occurred near socializing whales.

We observed the whales that made (or probably made) 43 of the 131 underwater blows seen during presumably undisturbed periods in 1983. Those 43 underwater blows were produced as or just after the whale dove out of sight. Of those 43 blows, 14 were produced by whales that were actively interacting with another whale just before the underwater blow, and 23 blows (including the 14) were produced by whales within five body lengths of one or more other whales. In at least one case it appeared that the interaction continued underwater after the whales dove. Of the 88 underwater blows produced by unseen whales in 1983, 23 blows were within five body lengths of one or more whales at the surface. The remaining 65 underwater blows appeared at the surface with no whales visible nearby.

To quantify the relationship between underwater blowing and socializing, we calculated underwater blow rates by dividing the number of underwater blows seen by the total whale-hours of observation, including periods both at the surface and underwater. (The resulting rates somewhat underestimate the actual underwater blow rate because underwater blows cannot occur while whales are at the surface. We felt that our estimates of whale-hours of

observation while whales were underwater were too imprecise to be useful, however, especially when large numbers of whales were under observation.) For 1982 and 1984, the underwater blow rate was too low for meaningful analysis, and for 1980, adequate data were not available often enough for reliable quantification. Based on behavioral observation sessions in 1981 and 1983, there was a positive correlation between rate of underwater blows and rate of socializing (for 1981, Spearman r_s = 0.53, n = 17 sessions, 0.02<p<0.05; for 1983, r_s = 0.92, n = 15, p<0.001).

The correlation of underwater blows with socializing, plus observations of underwater blows within actively socializing groups in 1983, indicates that underwater blows sometimes were part of the repertoire of behaviors involved in social interactions. Clark (1983) reported frequent underwater blow sounds in interacting groups of southern right whales. One of us (RP) has noted that forceful underwater blows in these right whales often occur during aggressive social interactions. For humpback whales in apparently aggressive social contexts, both forceful underwater blows and curtains of bubbles (produced by whales exhaling underwater while moving forward) have been reported (Darling et al. 1983; Tyack and Whitehead 1983; Baker and Herman 1984). We do not know whether the underwater blows by socializing bowheads in 1983 were likewise of an aggressive nature, or whether at times underwater blows in bowheads have functions unrelated to socializing.

Bowhead Sounds

There is now considerable information about the acoustic behavior of the bowhead whale (Ljungblad et al. 1980, 1982, 1983, 1984a; Clark and Johnson 1984; this study). Most of these efforts have concentrated on describing the calls of the bowhead and their associations with various observed behaviors. Interpretation of the biological significance of calls has relied heavily on a comparison between bowhead and southern right whale calls. The two species show remarkable similarities in their call repertoires, and more is known about the functions of calls of the southern right whale (Clark 1982, 1983). In general, the majority of bowhead vocalizations are low (<400 Hz) frequency-modulated (FM) calls. Bowheads also produce a variety of other sound types that are acoustically more complex, sometimes with energy up to 3-4 kHz, but less common than the simple FM sounds.

In this section we first summarize the methods used to obtain, analyze and categorize our field recordings of bowhead sounds. This is followed by descriptions of the different sound types and the contexts, both social and environmental, in which they were heard. To clarify factors that affect bowhead acoustic behavior under presumably undisturbed conditions, we searched for associations between these acoustic data and other relevant conditions. These associations are important for the proper interpretation of results obtained during potentially disturbed conditions.

Methods

All sound recordings were obtained via 68 sonobuoys (AN/SSQ-57A or AN/SSQ-41B) deployed near bowheads in the eastern Beaufort Sea (128° to 140°W longitude, Fig. 1) during the 1 August to 8 September periods in 1980-1984. Most sonobuoys were dropped 0.5-1.0 km from bowheads that were under observation from the aircraft circling at 457-610 m altitude. Later in the recording sessions, whales could either be closer or farther away. The

hydrophone was deployed to 18 m below the surface (occasionally 9 m in 1981) in water depths ranging from 11 m to 950 m. In a few cases water depth was so shallow that the hydrophone was on the bottom. Sonobuoy signals were recorded with calibrated equipment aboard the observation aircraft (Greene 1985).

The procedure for analyzing tape recordings was slightly different in 1980-81 than in 1982-84. For 1980-81, tapes were listened to at normal speed and a general description of each sound and its time of occurrence were noted. Sounds judged to be of sufficient intensity were converted into hard copy spectrograms using a Spectral Dynamics SD 301C real-time analyzer or a Kay 6019A spectrograph. From each spectrogram, CWC measured the sound's initial, final, lowest and highest frequencies ($\pm$ 10 Hz) and its duration ($\pm$ 0.1 s). From these analyses and ongoing analyses of bowhead calls recorded during the spring migrations of 1979 and 1980 (Clark and Johnson 1984), eight general categories of sound types were recognized (see Table 11, below). In later analyses the number of categories was reduced to seven, with any occurrences of the rare double call type pooled with the inflected call type.

All 1982-84 recordings were listened to at normal speed while a continuous spectrographic output was displayed on a memory oscilloscope. This spectrographic visual image was obtained by playing the taped analog signal into the Spectral Dynamics SD 301C real-time analyzer, which was coupled to a Tektronix 5111 memory oscilloscope. By this procedure the analyst (CWC) could simultaneously hear the sounds and see their spectrographic image. This procedure greatly facilitated both the detection of faint signals and the categorization of the sounds as one of the seven call type categories. In 1982-84 the analyst also judged the relative intensity of each call, subjectively, as either loud or faint. Loud calls represented whales near the sonobuoy; these whales were the ones being observed visually, counted, and sometimes subjected to simulated industrial disturbance.

In all years, sounds associated with respiration, referred to as blow sounds, and sounds associated with aerial displays (breaching, tail slapping, flipper slapping), referred to as slap sounds, were noted. All call data were tabulated by the aforementioned seven call types and, in 1982-84, by relative intensity. All data were also categorized according to presence and type of potential disturbance. In this section, we present results obtained under presumably undisturbed conditions. The results obtained during potentially disturbed conditions are presented in the disturbance section (Richardson et al. 1985c).

Over all five summers, there were 129.2 h of recordings during 64 different recording sessions on 49 days, considering both presumably undisturbed and potentially disturbed conditions. Under the presumably undisturbed conditions there were 56.5 h of recordings during 42 different recording sessions on 34 days. These 56.5 h of data from presumably undisturbed conditions are the basis of all further discussion in this section. In some cases, however, we deal with <56.5 h of data since there were periods of acoustic recording when either the number of whales in the observation area and/or their behavior was unknown.

To standardize for observation periods of varying duration and with different numbers of animals, call counts were expressed as calls per whale-hour (calls/wh-h). This call rate was computed by dividing the number of sounds by the duration of the recording session and by the estimated number of whales within about 5 km of the sonobuoy. To compare acoustic behavior under various conditions, we often determined the proportions of calls that were complex. The complex call proportion was the sum of the high, pulsed tone and pulsive calls divided by the total number of calls.

Blow and Slap Sounds

A total of 396 blow sounds were recorded in 1980-84 during presumably undisturbed periods. There were dramatic year-to-year variations in the number of blow sounds recorded, and in the rate per whale-hour (Table 10). Especially large numbers of blows were heard in 1983. Figure 11a,b illustrates a normal above-water blow sound and an underwater blow sound.

Changes in number of blow sounds appeared to be associated with the amount of feeding or socializing. On average there were a third more blow sounds during feeding or socializing (1.2 blow sounds/wh-h) than during other behaviors (0.8 blow sounds/wh-h). This general association was possibly a result of a higher level of physical exertion, which may have caused the whales to respire more deeply or forcefully during feeding or socializing than during other behaviors. However, blow sounds were not always associated with feeding and socializing. In 1980-81, 36 blow sounds were heard during 17.8 wh-h of feeding, while in 1984 no blow sounds were heard in 28.5 wh-h of feeding. In 1982, 22 blow sounds were heard in 53.3 wh-h of socializing, while in 1983 there were 161 blow sounds in only 48.3 wh-h of socializing. Many of the social blow sounds in 1983 were coincident with visible underwater blows, which were probably heard at greater distances than surface blows due to better energy coupling with the water. Another factor confounding the general association between blow sounds and feeding or socializing is that the number of blow sounds recorded was strongly affected by the proximity of the hydrophones to the animals. For example, 35 blow sounds were heard on 17 August 1984 between 15:24 and 17:04 h when several different whales (not feeding or socializing) were within several hundred metres of the hydrophones. Their blow sounds were extremely clear in their aural detail, and we were able to hear an unusually large number of these animals' respirations.

Bowhead slap sounds, which are best described as short (<0.2 s) broadband signals with sharp onsets, were difficult to identify because of their similarity to certain ship noises. Therefore slap sounds were noted only if they were loud and relatively undistorted and occurred when ships were absent or quiet. Figure 11c,d illustrates breach and tailslap sounds. Of the 64 slap sounds recorded, 21 were during a flight on 22 August 1983, when a whale was engaged in a prolonged bout of breaching, tail slapping and pectoral flipper slapping. These were our clearest examples of bowhead slap sounds associated with specific visual aerial behaviors that were observed. At a range of several hundred metres, peak received levels of slap sounds from these breaches and tail slaps were 115-118 dB and 107-118 dB//1 μPa, respectively (Greene 1984). Interestingly, not all aerial behaviors produced audible slap sounds. For example, during one 2.4 min period on 22 August 1983, we saw six breaches by one whale; only the first three breaches were clearly audible. Similar results were found for tail slaps and pectoral

Table 10. Number and rates of blow sounds recorded in different years, subdivided by activity of nearby bowheads.

	No. of Recording Periods	No. Blow Sounds Recorded	Hours of Recording	Whale-h of Recording	Rate, Blows per Whale-h
1980-81					
Feeding	2	36	2.2	17.8	2.0
Soc. & Feed.	1	43	1.5	36.7	1.2
Socializing	5	13	6.5	54.7	0.2
Other Behav.	2	18	0.7	4.2	4.3
Sub-Total	10	110	10.9	113.4	1.0
1982					
Feeding	0	0	0.0	0.0	0.0
Socializing	3	22	5.3	53.3	0.4
Other Behav.	8	7	9.0	48.2	0.1
Sub-Total	11	29	14.3	101.5	0.3
1983					
Feeding	2	35	1.5	9.1	3.8
Socializing	5	161	4.2	48.3	3.3
Other Behav.	3	6	1.2	9.5	0.6
Sub-Total	10	202	6.9	66.9	3.0
1984					
Feeding	4	0	5.1	28.5	0.0
Socializing	3	2	2.6	16.9	0.1
Other Behav.	10	39	5.1	29.5	1.3
Sub-Total	17	41	12.8	74.9	0.5
1980-84					
Feeding	8	71	8.8	55.4	1.3
Soc. & Feed.	1	43	1.5	36.7	1.2
Socializing	16	198	18.6	173.2	1.1
Other Behav.	23	70	16.0	91.4	0.8
Total	48	382	44.9	356.7	1.1

Time in sec.
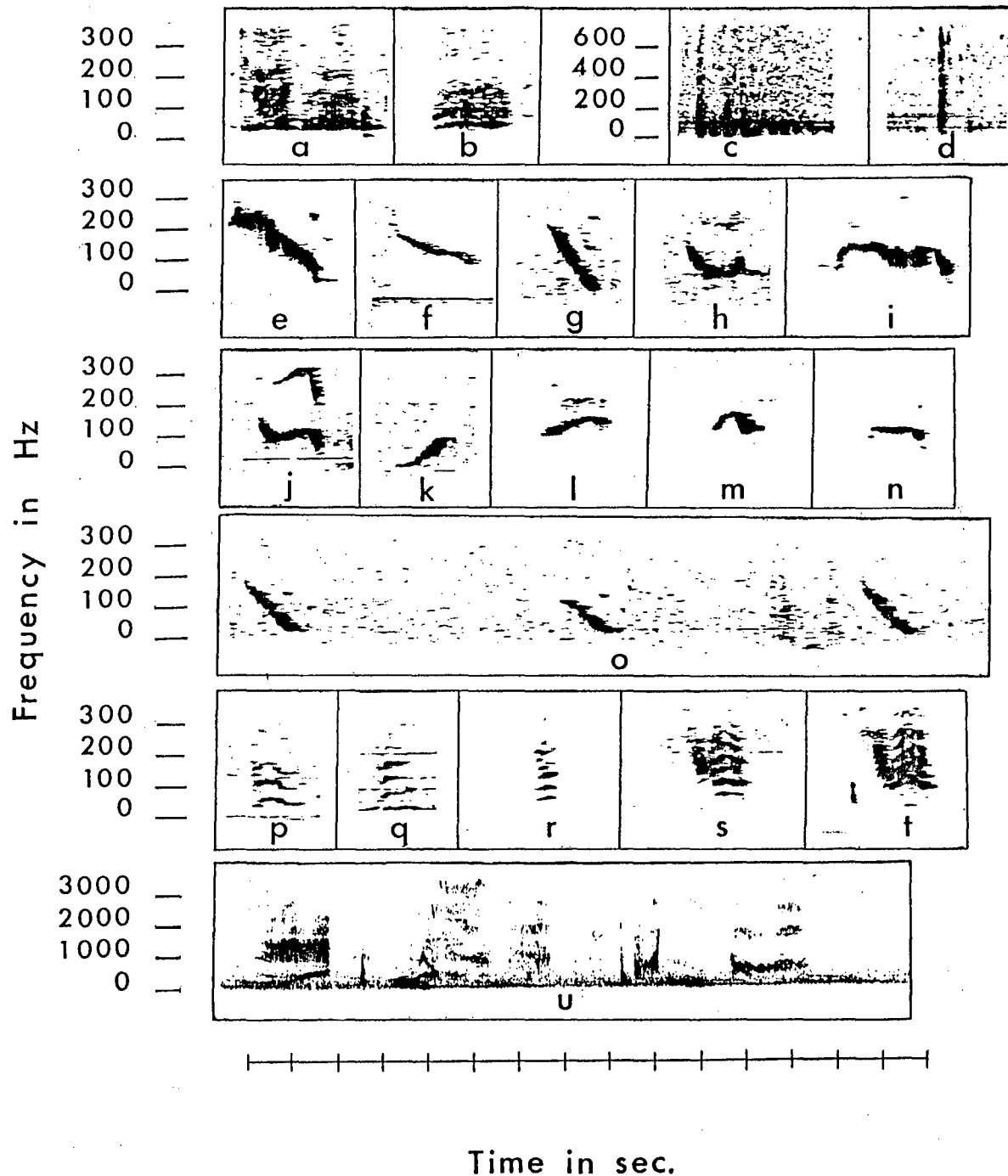
FIGURE 11. Sounds produced by bowhead whales: (a) normal blow sound; the first half is the expiration and the second half is the inhalation; (b) underwater blow sound; (c) breach slap sound with several echoes; (d) tailslap sound with single echo; (e-n) examples of simple FM calls; (o) three calls from a series containing a total of 26 nearly identical FM downsweeps; (p-t) examples of pulsed tonal calls; and (u) series of pulsive screams. See Würsig et al. (1982, p. 117) for additional examples.

flipper slaps. Apparently, there is considerable variation in the acoustic level of different breaches, tail slaps and flipper slaps. Breach sounds were concentrated at lower frequencies than were tailslap sounds (Fig. 11c vs. 11 d; Greene 1984).

Call Types and Their Characteristics

Not including blow and slap sounds, the majority (86%) of sounds recorded in 1980-84 were tonal, frequency-modulated calls lasting 1-2 s. All of the types of calls previously reported for migrating bowheads (Ljungblad et al. 1982; Clark and Johnson 1984) were also recorded here. Figure 11 illustrates a variety of the common, low tonal FM calls as well as the rarer pulsed tonal and pulsive scream calls. The pulsed tone call was called a harmonic call in our earlier reports. Table 11 is a summary of some of the acoustic characteristics for these call types in 1980-81. Although no quantitative comparisons were made between seasons, visual inspection of spectrograms and aural judgements indicated that there were no differences between the general characteristics of sounds in the summers of 1980-84.

Variations in Acoustic Behavior

In 1980-81, calls were not coded as either loud or faint, and therefore call rates were computed using the total number of sounds heard. In 1982-84 when the loud/faint distinction was made, call rates were computed using either the total number of calls or the total number of loud calls. Because of the subjective nature of the loud vs. faint distinction, and the fact that the number of whales within audible range of the sonobuoy was only estimated, the calculated call rates are only estimates.

Call production may be influenced by environmental factors such as water depth, sea state and percent ice cover, all of which affect detectability of calls and may also affect the whales' acoustic behavior. Other factors that may affect rates of vocalization include the density, ages and activities of the whales, abundance of food, etc.

Effects of Environmental Conditions.--Recorded call rates in 1982 were much higher than in other years:

	1980-81	1982	1983	1984
Total call rate (calls/wh-h)	2.2	45.3	2.8	2.6
Loud call rate (calls/wh-h)	-	8.3	0.9	0.9
Whale-h	114.1	108.8	91.6	82.0
Average depth (m)	29	260	24	31

The high apparent call rates in 1982 were probably related to a greater range of detectability in deep water. In 1982 most sonobuoys were in deep water (260 m on average); in all other years most were in shallow water (28 m average). The calculated call rates per whale-hour consider only the whales within about 5 km. In 1982 we probably underestimated the number of whales whose calls were detected, thereby resulting in inflated call rates. In fact, there was a significant correlation ($n = 50$, $r = 0.31$, $0.01 < p < 0.05$)

Table 11. Acoustic parameters of bowhead call types during presumably undisturbed conditions, 1980–81. Mean ± s.d. are shown.

	Call Type							
Acoustic Parameter	Up	Down	Constant	Inflected	Double	High	Pulsed Tone	Pulsive
Initial frequency (Hz)	146 ± 62	200 ± 53	230 ± 24	249 ± 41	210 ± 45	720 ± 295	68 ± 16	–
Final frequency (Hz)	174 ± 80	133 ± 40	229 ± 23	255 ± 25	250 ± 115	666 ± 216	65 ± 16	–
Lowest frequency (Hz)	146 ± 62	200 ± 53	230 ± 24	156 ± 29	146 ± 50	590 ± 160	–	1006 ± 387
Highest frequency (Hz)	174 ± 80	133 ± 40	230 ± 24	254 ± 40	256 ± 82	793 ± 182	–	1470 ± 405
Duration (s)	1.5 ± 0.4	1.3 ± 0.4	1.2 ± 0.4	1.2 ± 0.6	2.1 ± 0.2	0.7 ± 0.3	1.5 ± 0.4	1.3 ± 0.5
Sample size	75	26	14	11	9	15	47	57

between water depth and total call rate when all five years were considered. There were no significant correlations between call rates and sea state or ice conditions.

Effects of Social and Behavioral Context.--In the following discussion we compare the call types recorded near socializing and non-socializing whales, feeding and non-feeding whales, whales with and without calves, and situations when most whales were subadults (1983, 1984 Yukon Coast) or adults (1982 Herschel Island). The variable compared was the proportion of calls that were complex. Proportions rather than actual rates were used since 1982 rates were extremely high regardless of whale activity; this year effect might mask any possible relationship between social context and acoustic behavior if call rates were considered. The Mann-Whitney U test was used to test for the significance of differences between call proportions under these various conditions.

Socializing vs. Non-socializing -- Types and rates of bowhead calls may be related to the social context according to preliminary analysis of (a) our 1980-81 summer data, and (b) spring and fall data from Alaska (Ljungblad et al. 1983, 1984a). In both of these studies, there were several cases when high proportions of complex calls clearly were associated with high levels of social activity. These analyses suggested that swimming and resting bowheads produce mostly low FM tonal calls, whereas bowheads in active social groups produce a variety of complex sounds. To test this hypothesis, we compared the proportion of calls that were complex during periods when at least some of the whales near the sonobuoy were socializing vs. periods when no socializing was observed. We found a higher proportion of complex calls during periods with socializing, but the difference was not statistically significant. This was true both for all calls in 1980-84 ($U = 252$,; $n = 17$ social periods vs. $n = 23$ non-social periods) and for loud calls in 1982-84 ($U = 105$; $n = 11$ vs. 16). The lack of a significant association between socializing and complex calls is similar to results reported by Ljungblad et al. (1984a). Our failure to observe a significant association between socializing and complex calls may be the result of our inability to isolate the sounds of socializing whales. During periods with socializing, there were almost always other whales in the area that were not socializing but may have been vocalizing. In addition, we could not tell whether socializing continued underwater after we observed it occurring at the surface. We scored a whole recording session as "social" if any socializing was seen; however, socializing may not have lasted for the entire session, further diluting the sounds of socializing whales with sounds of non-socializers.

Feeding vs. Non-feeding -- There was no significant difference between the proportions of loud calls that were complex on occasions with and without skim- or bottom feeding ($U = 33$; $n = 2$ feeding vs. 25 other occasions). There was a tendency for loud tonal call rates to be lower for skim- or bottom feeding whales as compared with other whales (1983-84 data only, 0.58 vs. 0.95 tonal calls/wh-h).

Calves Present vs. Absent -- When a calf was present, the presumed mother was sometimes very near the calf, but at other times they were separated either horizontally or vertically. We suspected that calls were involved in the process of rejoining. To compare calls in the presence and absence of calves, we analyzed the proportions of loud calls that were complex. There was no significant difference ($U = 81$; $n = 9$ occasions with

calves vs. 18 without). Altogether, loud tonal call rates were higher for periods with calves than for periods without calves but this result is a consequence of the fact that 8 of 9 'with-calf' periods were in 1982 when call rates were exceptionally high.

Subadults vs. Adults -- In 1982 not only were most observations made over deep water but the majority of animals were estimated to be adults (large, well-marked animals, cf. Davis et al. 1983). This contrasts with the 1983 and 1984 data taken in shallow water when most of the animals were subadults (small, poorly-marked animals, cf. Davis et al. in prep.). To compare calls in 1982 with 1983-84, the proportions of loud calls that were complex were examined. There was no significant difference between results from 1982 and 1983-84 (U = 90.5; n = 12 occasions in 1982 vs. 15 in 1983-84).

Comparison with Acoustic Behavior During Migration

The types of sounds recorded during the summers of 1980-84 in the eastern Beaufort Sea are qualitatively very similar to those reported during the spring and fall migrations (Ljungblad et al. 1980, 1982; Clark and Johnson 1984). Comparisons can be made, in terms of proportions and rates (calls/h), between our summer data and the data from the 1984 spring migration past Barrow (Clark et al. 1985) since the two data sets have been analyzed similarly.

The relative proportions of tonal and complex calls were very similar at the two times of year; 85% of springtime calls were tonal as compared to 83% in summer. Correspondingly, 15% of the springtime calls were complex as compared to 17% in summer. However, considering the seven recognized types of calls, there were differences in the proportions of the different call types depending on the season:

				Percent of Calls of Each Type			
	Up	Down	Con-stant	Infl-ected	High	Pulsed Tone	Pul-sive
Spring 1984	37.3	19.3	11.7	16.9	0.1	11.7	3.0
(n = 15876 calls, 321.5 h)							
Summer 1980-84	34.9	21.5	18.7	8.2	4.1	6.2	6.3
(n = 6537 calls, 56.6 h)							

There were proportionately twice as many inflected and pulsed tone calls in spring as in summer. There were, proportionally, only one-fortieth as many high calls and half as many pulsive calls in the spring as in the summer. The results concerning high and pulsive calls must be qualified by the consideration that these two call types are often very difficult to identify in the spring because of their similarity to some sounds produced by white whales (Delphinapterus leucas), which were sometimes numerous near the

hydrophones. However, this problem did not exist for either the inflected or pulsed tone call types, which were certainly more prevalent in the spring than in the summer. The reason for this seasonal difference is not clear.

Overall, apparent calling rates in calls/h were greater in the summer (115.5 calls/h) than in the spring (49.4 calls/h). However, the importance of these rate differences is not clear since we do not know the number of whales nearby during each period of observation in spring, and therefore the spring rates cannot be standardized in terms of calls per whale-hour. Also, depths at recording sites in spring were shallower (20-25 m) than the average depth in summer (113 m). Spring recording sessions lasted for many days, including periods when few or no whales were nearby, whereas summer sessions were for several hours and were always near whales.

Ljungblad et al. (1983, 1984a) report relative proportions of tonal and complex calls for spring and fall that are quite different from those reported here (in spring, 57% complex in 1982 and 41% complex in 1983; in fall 28% complex in 1982 and 37% complex in 1983). These higher proportions of complex calls are probably a result of sonobuoys being dropped more often near socializing groups. The difference is not a result of discrepancies in procedures for call categorization since the different analysts have conferred and agreed on this method.

Associations of Bowheads with Other Species

During the 5 years of this study, we occasionally observed a few other animal species near bowheads: glaucous gulls (Larus hyperboreus), arctic terns (Sterna paradisaea), phalaropes (probably red-necked phalaropes, Phalaropus lobatus), gray whales (Eschrichtius robustus), ringed seals (Phoca hispida), and white whales (Delphinapterus leucas).

During this study, birds were seen near bowheads on at least 30 occasions. Flocks of up to 50 phalaropes were often present near skim-feeding bowheads. At times, phalaropes appeared to follow the whales, alighting on water disturbed by the whales. The birds probably fed on some of the same plankton species that the bowheads were eating. MacIver (1984) reported red-necked phalaropes associating with feeding humpback whales. Whalers often used the presence of phalaropes to indicate presence of 'whale feed' and, therefore, where whales were likely to be found (Bockstoce in press). Glaucous gulls and arctic terns were also seen circling and passing over skim-feeding bowheads on a few occasions, presumably foraging on the plankton brought to the surface or perhaps bowhead feces. The number of gulls and terns in any one incident ranged from 1 to 8. In Baffin Bay, northern fulmars (Fulmarus glacialis) have been seen feeding on bowhead feces (C.R. Evans, LGL, pers. comm.).

White whales were observed in the same general area as bowheads on at least 15 occasions in 1980-84. The closest approach seen was on 17 August 1983 when two white whales were 45 m from a bowhead and oriented toward it. On 22 August 1983 we observed a white whale within 100 m of a bowhead whale. In neither case did we see any obvious interaction between the two species. The sounds made by white whales underwater are at higher frequencies than most bowhead sounds, but are often intense (e.g., Ford 1977; Wood and Evans 1980). It is likely, therefore, that bowhead whales and white whales knew of

each other's presence on several occasions, but we do not know what effects their sounds may have had on each other.

Ringed seals were seen near bowheads on at least five occasions, once within 15 m (24 Aug 1981). No obvious interactions were noted. However, the seals may have been feeding on some of the same organisms as the whales, or on other organisms (e.g., fish) that were feeding on the same species as the bowheads. Lowry et al. (1978) found large zooplankton—euphausiids and amphipods—in the stomachs of both ringed seals and bowhead whales that had been taken in Alaskan waters.

Lone gray whales were seen in the general vicinity of bowheads on two occasions. On 29 August 1980, a gray whale was seen very briefly at 70°42'N, 128°58'W; it was about 800 m from a bowhead whale. On 18 August 1982, a gray whale was seen with muddy water streaming from its mouth, indicative of bottom feeding. The whale was at 69°37'N, 138°30'W in an area with approximately six bowheads, none of which appeared to be bottom feeding. The gray whale was about 500 m from the closest bowhead, and there was no apparent interaction between them. Rugh and Fraker (1981) reviewed earlier sightings of gray whales in the Canadian Beaufort Sea.

DISCUSSION

Year-to-Year Variations in Behavior of Bowheads

Of the year-to-year variations in behavior that we observed during the five years of this study, one of the more dramatic has been the considerable differences in the locations where we encountered bowhead whales each year (Richardson et al. 1985a). In 1980, many bowheads came close to shore off the Mackenzie Delta and Tuktoyaktuk Peninsula. From 1980 to 1982 there was a progressive increase in the depth of water in which bowheads were observed. In 1983 and 1984 we again found bowheads in very shallow water close to shore, but in a different part of the study area. In 1983 and 1984, the nearshore whales were along the Yukon coast in a region from which they were absent in 1980 and 1981, west of the area where they were so common in 1980.

Another difference between 1983-84 and 1980 was the age composition of nearshore whales. In 1980 these whales included calves and mothers and other presumably mature whales, as indicated by large white chin patches and white areas on the tailstock and flukes. In 1983, mothers with calves were encountered only in deep water >100 km north of the immature group (this study) and in offshore areas much farther east (McLaren and Davis 1985; J. Cubbage pers. comm.). In 1984, calves were sighted near shore during only one flight. Most whales near shore in 1983 and 1984 were subadults, based on length measurements and the rarity of white markings on the tail. Because of age-class segregation and because we rarely flew far offshore in 1983 and 1984, our calf sighting rate was lower in 1983-84 than in 1980-82 (Table 3).

Feeding is presumed to be the predominant activity of bowheads summering in the Beaufort Sea. Observed frequencies of various types of feeding varied from year to year; in 1980 we saw indications of bottom feeding, skim-feeding, and water-column feeding; in 1981 we saw skim-feeding and water-column feeding; and in 1982 we presumed that most whales were water-column feeding but had little direct evidence for this aside from observations of long dives. Feeding activity in 1983 was probably most like that in 1980, as

the feeding behavior observed near shore was bottom feeding and skim-feeding. In contrast to 1980 and 1981, none of the skim-feeding observed in 1983 was by whales in echelon formation. In 1984, bottom feeding but no skim feeding was observed; water column feeding probably also occurred.

We saw variable amounts of social behavior over the years, with the rate of socializing lowest in 1982, when whales were in the deepest water, and highest in 1981 (Table 4). In all years the rate of socializing was lower in late August and early September than in early August. We presume that this seasonal decrease is part of a longer term seasonal decline in frequency of socializing from spring migration, when mating and boisterous interactions appear to occur (cf. Rugh and Cubbage 1980), to fall migration, when there is little social behavior.

There was considerable variation in the number of underwater blows, with by far the highest number in 1983. In 1981 and 1983, there was a positive correlation between rates of underwater blowing and of socializing, and in 1983 we observed many underwater blows near actively socializing whales.

The rate of aerial activity has not varied very much from year to year. It is interesting that the rate of aerial activity should have been so stable over five years when so many other activities have varied to a much greater extent.

The types of sounds recorded underwater in the presence of bowheads have been the same in all five years of this study. Measured call rates, however, varied considerably among years. There were indications that changes in depth of water and social context were related to the variations in apparent call rates. For example, in 1982, when there was a six-fold increase in average water depth during recording sessions compared to 1980-81, total number of calls recorded was much higher. Calls from whales far away are more likely to be detected in deep than in shallow water. In 1982, the majority of the calls were low, frequency-modulated calls and the rate of socializing was less than in 1980-81. Associated with this drop in socializing was a decrease in the proportion of complex harmonic or pulsive sounds from 56% in 1980-81 to 10% in 1982. In 1983, this value increased to 15%, concurrent with an increase in socializing. Complex pulsive sounds are believed to be associated with socializing in southern right whales as well as bowheads (Clark 1982, 1983).

We wondered whether there might be some cyclicity to the year-to-year changes in behavior of bowhead whales. In the southern right whale, most mature females bear calves every third year and are absent from the calving grounds in Argentina during the two years between calves (except for a brief stay early in the winter by some females the year after giving birth to a calf--Taber and Thomas 1982). There is, therefore, a different population of mature females on the calving grounds each year for three years, after which the pattern is repeated. It is possible that the breeding cycle in bowhead whales is similar to that of southern right whales (Davis et al. 1983; Nerini et al. 1984), but, after five years of study, we have no consistent evidence that the considerable year-to-year variation in behavior of bowheads forms a repeating pattern.

Year-to-Year Variations in Behavior of Other Cetaceans

In our study, two of the main attributes that varied from year to year were (a) bowhead distribution within the eastern Beaufort Sea, and (b) the frequency and type of feeding. Both might reflect changes in prey distribution, abundance, or species composition. We do not have sufficient data on the prey of these bowheads to test such a relationship. Stomach contents of bowheads from the eastern (i.e. Canadian) Beaufort Sea have not been collected, and factors affecting zooplankton dynamics in that area have not been studied in any detail. There are indications, however, that some of the variability in bowhead distribution is related to variability in water mass characteristics, which are presumed to reflect differences in prey availability (Borstad 1984; LGL, ESL and ESSA 1984). In addition, the most impressive case of near-surface skim feeding that we observed (18 Aug 1981) was at a location where copepod abundance in near-surface waters was unusually high (Griffiths and Buchanan 1982).

Studies of other baleen whales provide quite direct evidence for changes in geographic distribution in response to changes in their prey. Humpback whales are a good example of this because they feed on different kinds of prey in different areas and they have been studied intensively in recent years. On Stellwagen Bank near Cape Cod, where sand lance (Ammodytes americanus) were present in large concentrations, individual humpback whales returned in consecutive years (Mayo 1982, 1983). Their movements within each summer were quite predictable even to the extent of which points on the bank (separated by only 25 km) they occupied early and late in the season. In contrast, humpback whales that feed farther north near Newfoundland utilize mainly capelin (Mallotus villosus). Sighting rates for humpbacks in one small nearshore area roughly quadrupled over three years, while humpbacks disappeared from a second area farther offshore (Whitehead 1981). Capelin stocks offshore collapsed at the same time that humpbacks and spawning schools of capelin became plentiful inshore. Whitehead concluded that summer distribution of humpbacks changed in direct response to the failure of offshore capelin stocks. Similarly, Bryant et al. (1981) found evidence that the disappearance of humpbacks from Glacier Bay, Alaska, in 1980 was attributable to a low krill population in that year. Thus, when the prey species remained in the same place in high abundance, humpback whales returned each year to the same area. When the prey moved dramatically, the whales also moved.

The above examples are from humpback whales that summer and feed nearshore, but the same kinds of conclusions have been drawn from studies of whales feeding farther from shore, in open ocean areas in the Antarctic and in the North Pacific. Data obtained from the 'Discovery' expeditions showed that changing distributions of rorquals in the Antarctic Ocean were related to the variable distribution of their principal prey, the krill Euphausia superba (Mackintosh 1965). Mauchline and Fisher (1969) demonstrated that major concentrations of krill in the Antarctic may occur in different places in different years, appearing unpredictably in any given year at new locations often hundreds of kilometres away from the concentration centers of a previous year. Meteorological factors, specifically the tracks of major storms, may be partly responsible for the variable distribution of krill and, hence, whales (Beklemishev 1960).

In rorquals feeding in the open North Pacific ocean, there is great year-to-year variability in food availability, whale diet, whale distribution, and time of occurrence on the feeding grounds (Nemoto 1959). Over 6 years, the principal prey of fin whales alternated each year between euphausiids and Calanus copepods. Plankton tows demonstrated that this reflected alternating abundance of these prey items in the area (Nemoto 1957). Nemoto also noted that blue whales do not migrate to an area southeast of the Kamchatka Peninsula when euphausiids are not abundant. However, when euphausiids are abundant, blue whales arrive there early in summer. The entire migration route of blue whales in the North Pacific may be determined by annual fluctuations in the distribution of the main centers of euphausiid concentration (Nemoto 1957).

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

Changes in prey availability probably affect other aspects of behavior, such as social and aerial behavior. Gray whales on the north side of the Alaska Peninsula in spring apparently feed on both inbenthic and epibenthic prey (Gill and Hall 1983). While feeding on the bottom, gray whales are usually solitary, but while feeding on patchily distributed prey in the water column, they tend to aggregate. This aggregation gives a greater chance for social interactions (BW, pers. observ.). As well, low-intensity aerial behavior, consisting of flippers and fluke tips raised above the water surface, often occurs while gray whales feed on epibenthic prey in shallow water, but does not occur during bottom feeding. This variation in behaviors exists on a regional basis and a day to day temporal basis, and probably is related to different relative abundances of food types. Humpback whales in the Frederick Sound area of southeast Alaska also feed near the surface and below it, and the relative frequencies of different feeding modes change between years (C.S. Baker, Univ. Hawaii, pers. comm.). Surface feeding involves lunges through the prey, often resulting in half-breaches and other forms of aerial activity. Feeding in the water column involves little surface activity. Surface lunge feeding often occurs in concert with other whales; non-surface feeding is more often solitary (Jurasz and Jurasz 1979).

Given the above, we suspect that the observed annual variation in bowhead behavior is also in large part a reflection of varying horizontal and vertical distribution of their prey. For example, we saw little socializing in 1982, when bowheads appeared to feed mainly in the water column, and more social activity while many whales fed close to the surface near shore. To understand for any given year where bowheads are likely to concentrate and how they are likely to feed, it will be necessary to understand factors affecting prey distribution. It is not known to what extent the distribution of the prey of bowheads in the eastern Beaufort Sea is affected by factors like (1) timing and amount of spring run off from the Mackenzie River, (2) distribution of ice during spring and summer, (3) wind patterns and paths of major storms, and (4) the variable distribution of the plume of turbid brackish water from the Mackenzie River. Any or all of these interrelated

factors could affect prey distribution and therefore the distribution and behavior of bowheads (Borstad 1984; LGL Ltd. in prep.).

A further uncertainty is the degree to which the present Western Arctic bowhead stock is food-limited. The total size of this stock is clearly lower than before commercial exploitation, so the present stock might not be food-limited. If so, details of summer distribution of bowheads might not be predictable even with a detailed understanding of prey distribution. However, the number of bowheads now summering in the eastern Beaufort Sea may be a high proportion of the number that summered there before commercial exploitation (Fraker 1983). Also, populations of potential food competitors (e.g., arctic cod, Boreogadus saida; Lowry and Frost 1981; Frost and Lowry 1984) may have increased since the beginning of commercial whaling. Thus, bowheads summering in the eastern Beaufort Sea may be food-limited at present. Also, the important limitation is probably not the total amount of food available. Bowheads apparently must concentrate their feeding in areas with dense patches of zooplankton (Brodie 1981; Griffiths and Buchanan 1982). If patch locations vary, as is likely, then bowhead distribution is also likely to vary. Thus, an understanding of prey variability would be especially important in understanding the variable activities and distributions of bowhead whales.

Comparisons with Bowhead Whales in the Alaskan Beaufort Sea

During both spring and fall migration into and out of the Beaufort Sea, bowhead whales engage in all of the major behaviors observed on the summering grounds, but with different relative frequencies. Thus, while travelling is the predominant activity during migration, socializing and mating also occur, more often in spring than in summer or fall. Feeding has been reported in fall, and (rarely) in spring, as well as summer. Aerial activity occurs in spring, summer and fall, and young-of-the-year are closely associated with their mothers, probably nursing, in all three seasons. We will review the evidence for each of these types of activity in turn.

During spring migration, bowhead whales appear to do little feeding before they reach the Canadian Beaufort Sea. Bowheads taken in Alaskan waters in spring usually have nearly empty stomachs (see Marquette et al. 1982 for review). Some, however, do contain food (e.g., Hazard and Lowry 1984).

Bowheads seen off northern Alaska in September as well as October are often described as migrating, but it is clear that many are feeding, loitering, and exhibiting behavior very similar to that in the Canadian Beaufort Sea in summer. Bowheads may loiter for considerable periods in the eastern portion of the Alaskan Beaufort Sea during late August through early October, and considerable feeding occurs at these times between Kaktovik, Alaska, and the Alaska-Yukon border (Ljungblad et al. 1980, 1983, 1984a; Lowry and Burns 1980; Ljungblad 1981; Lowry and Frost 1984). Bowheads seen in this area in late August and September typically dive repeatedly in the same locations, and do not begin to travel rapidly westward until later in September or early October when freeze-up accelerates. Nine bowheads killed and examined near Kaktovik in autumn had been feeding recently, mainly on copepods or euphausiids (Lowry and Frost 1984). The eastern part of the Alaskan Beaufort apparently is a part of the main summer feeding range.

Later in autumn, bowheads tend to travel more consistently and rapidly toward the west. However, feeding has also been reported just east of Point Barrow during several autumns, and also off the Soviet coast (e.g., Braham and Krogman 1977; Braham et al. 1977; Lowry et al. 1978; Johnson et al. 1981; Marquette et al. 1982). The rate and consistency of feeding during fall migration probably are lower than in summer, but quantitative data are lacking.

The primary mating period of bowhead whales is in early spring and includes the spring migration (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Johnson et al. 1981; Ljungblad 1981). Everitt and Krogman (1979) described a particularly active mating group of six whales seen on 8 May 1976 near Point Barrow, Alaska. We saw some evidence for mating in the Canadian Beaufort Sea in August of both 1980 and 1981, but not in later years. Even the active rolling at the surface that we observed in 1981, however, was not as boisterously active as the large mating group described by Everitt and Krogman. Mating probably is more common during spring migration than during summer in the Beaufort Sea. Non-mating social activity also appears to be more common during the spring migration, but quantitative data for spring are lacking. There is a waning of social activity during the summer, and by late fall it does not occur often (Ljungblad et al. 1984a,b).

Aerial activity similar to what we observed in the eastern Beaufort Sea—breaches, tail slaps, flipper slaps, spy hops and rolls—has been observed in bowheads during spring migration (Carroll and Smithhisler 1980; Rugh and Cubbage 1980). Rugh and Cubbage recorded breaches by 23% of 280 bowheads observed in 1978 from Cape Lisburne, Alaska, a rate far above what we observed, but also higher than the reports from other spring observation sites (Pt. Barrow and Pt. Hope, Alaska). Although quantitative comparisons are not possible among the various observation sites, our impression is that aerial behavior is more frequent during spring migration than on the summer feeding grounds. This is consistent with the fact that Rugh and Cubbage (1980) observed the rate of breaching to decline through the spring season. Aerial activity in fall appears to occur at about the same frequency as in summer (B. Würsig, pers. obs.).

Travelling is clearly more pronounced in spring and late autumn than in summer but bowheads sometimes move long distances within the July-early September period. Carroll and Smithhisler (1980) estimated that 95% of the time that bowheads were observed migrating past Point Barrow and Point Hope in the spring, from 1975 through 1978, animals 'exhibited the normally expected migratory surfacing patterns', i.e. were travelling. Similarly, Davis and Koski (1980) and Koski and Davis (1980) found that eastern arctic bowheads migrating along the coast of Baffin Island in fall travelled consistently to the southeast. Ljungblad et al. (1984a) have found that, after a certain year-specific date in late September, most bowheads seen in the Alaskan Beaufort Sea are travelling strongly westward, whereas before that date most are feeding and loitering. We have no estimate for the percent of time that bowheads summering in the eastern Beaufort Sea were actively travelling; it was low but not zero. Although direct observations of rapid travel during summer were infrequent, changes in distribution from week to week and month to month provided proof that large numbers of whales often travel long distances within the eastern Beaufort Sea and Amundsen Gulf during summer (Renaud and Davis 1981; Davis et al. 1982; Richardson et al.

1985a). Within-season resightings of individually-recognizable bowheads also show considerable movement within the summer (Davis et al. 1983, in prep.). One identifiable whale was photographed near Herschel Island on 18 August 1982, 154 km to the northeast on 23 August 1982, and again near Herschel Island on 5 September 1982 (Davis et al. 1983).

Because the predominant activity of bowheads during spring and late fall is travelling, their surfacing pattern is slightly different from that usually seen in summer. During the intervals between blows within a surfacing sequence, migrating bowheads usually make brief shallow dives called 'series' dives (Rugh and Cubbage 1980). Series dives may occur because of the hydrodynamic advantage to a moving whale of avoiding wave generation at the air-water interface. Summering bowheads, on the other hand, often remain at the surface between blows, probably because it is easier to breathe if the whale remains at the surface and because submerging provides no hydrodynamic advantage if the whale is not trying to make forward progress.

The behavior of bowhead calves during autumn migration is very similar to behavior seen in summer. It includes nursing and 'waiting at the surface' while mothers are diving (B. Würsig, pers. obs.). Most calves are apparently born in late winter or spring; nursing presumably occurs during spring migration as well as summer and autumn. Many bowhead calves remain with their mothers for at least the first part of the fall migration (Davis and Koski 1980; Ljungblad et al. 1984a). The age of weaning of bowhead calves is not known, but some southern right whale calves remain with their mothers for one year and ultimately separate from their mothers after returning to the wintering area (Taber and Thomas 1982).

In comparing the quantitative data on surfacing, respiration and dives that we have gathered for summering bowheads with similar data for migrating bowheads, we must use caution. Different investigators have gathered their information and defined their variables in somewhat different ways, because of differences in vantage point and in surfacing behavior of the whales. The comparisons that seem valid are presented here.

In comparison with our results, Koski and Davis (1980) found longer blow intervals for eastern arctic bowheads migrating along the coast of Baffin Island in the autumn of 1979 (our data for non-calves 1980-84: $13.5 \pm$ s.d. 8.88 s, n = 5161; Koski and Davis: $16.1 \pm$ s.d. 8.29 s, n = 399; t = 5.66, p<0.001).

The overall mean number of blows per surfacing that we recorded for non-calves in the eastern Beaufort Sea from 1980 through 1984 was $4.3 \pm$ s.d. 3.25 (n = 626), less than the values reported for bowheads on their spring migration off Alaska by Carroll and Smithhisler (1980; mean = $6.5 \pm$ s.d. 2.84 blows per surfacing, n = 41; t = 4.23 p<0.001) and by Rugh and Cubbage (1980; a mean of approximately 6.4 blows per surfacing). The overall mean duration of surfacing that we observed in non-calves during 1980-84 was $1.2 \pm$ s.d. 1.14 min (n = 715). This was slightly shorter than the approximate mean of 1.52 min that we derived from data collected by Carroll and Smithhisler (1980) from bowheads during spring migration. Our value was also shorter than the mean reported for bowheads during fall migration in the eastern

arctic by Koski and Davis (1980): 1.69 $\pm$ 1.01 min, n = 93; in comparison with our data, t = 4.03, df = 806, p<0.001.

During summer, durations of dives by undisturbed non-calf bowheads varied more from year to year than did the aforementioned variables. The overall mean dive duration for 1980-84 was 4.4 $\pm$ s.d. 6.32 min (n = 333, range = 0.03 to 31.0 min). Braham et al. (1979) reported that dives of whales migrating past Cape Lisburne, Alaska, in spring ranged from 1.7 to 28 min, but those authors did not give a mean. Carroll and Smithhisler (1980) found long dives, 15.6 $\pm$ s.d. 5.0 min (n = 63), during spring migration; and Koski and Davis (1980) found somewhat shorter dives of duration 8.65 $\pm$ s.d. 2.73 min (n = 88) during autumn migration in the eastern arctic. Both of these mean dive times for migrating bowheads exceed our overall 1980-84 mean for summering whales. However, our results from the summer of 1982 (12.08 $\pm$ s.d. 9.15 min, n = 51) are more similar to observations during migration.

On 6-30 September 1983, behavior of bowheads was studied in the Alaskan Beaufort Sea, between Prudhoe Bay and the Alaska-Yukon border (Ljungblad et al. 1984b). These data were gathered from a circling Twin Otter aircraft; techniques were similar to those during our study. Blow intervals, number of blows per surfacing, duration of surfacing and duration of dives for non-calves all averaged somewhat higher in the Alaskan study than in our five-year study. However, there was a great deal of overlap, and for each variable, some of our annual means were higher than the mean value in Alaska in 1983. In the autumn of 1983, Ljungblad et al. (1984b) found more travelling and less socializing than we found one month earlier in the Canadian Beaufort Sea. They found no skim- or bottom feeding in Alaskan waters in 1983, although both have been observed there in other autumns.

Calls recorded in spring and fall were similar to those recorded in summer but occurred in different proportions. The most common call types in all seasons were tonal FM sounds. The proportions of complex calls were greater in summer than in spring recordings from ice camps (Clark et al. 1985, Clark pers. obs.) but less than in spring or fall recordings via sonobuoys dropped from aircraft (Ljungblad et al. 1983, 1984a). This difference resulted from the different sampling methods, perhaps including a tendency to drop sonobuoys near interacting groups of whales during spring and fall. The higher proportion of complex calls in spring relative to fall (Ljungblad et al. 1984a) appears to reflect the greater amount of social activity in spring.

Bowhead whales on their summering grounds, including the eastern part of the Alaskan Beaufort Sea up to mid or late September, appear to have the same basic repertoire of behaviors as do migrating bowheads. However, summering and migrating bowheads differ in the relative amounts of time spent in different activities--feeding, socializing, breaching and other aerial behavior, and travelling. At least some of the differences appear to occur as a continuum between seasons rather than an abrupt change. Travelling is the predominant activity during spring and fall migrations, while feeding is the predominant activity during summer. The average length of stay in any one area is therefore longer in summer, but considerable travelling occurs in summer and some feeding occurs during migration, especially in fall. Although quantitative comparisons of surfacing, respiration, dive and acoustic characteristics are not always possible and need to be treated with

caution, there appear to be some significant quantitative differences between the seasons, but few qualitative differences.

Comparisons with Other Baleen Whales

Bowhead whales spend their entire lives in arctic and near-arctic waters, apparently never moving far from the ice edge. This habit separates them from all other baleen whales, which may move into temperate or subtropical waters (see, for example, review by Lockyer and Brown 1981). This may be the reason that parturition occurs mainly in spring in bowheads, but in early winter for other species (Nerini et al. 1984). But behavior is in large part determined by feeding mode and related ecological factors, and here similarities between bowhead whales and several other species are evident.

Gray, bowhead, and right whales are often found in shallow water, and all of these species feed on small invertebrates. While gray whales usually feed near the bottom (e.g., Bogoslovskaya et al. 1981; Nerini 1984), both right and bowhead whales may skim their food at or near the surface (Watkins and Schevill 1976, 1979; Payne in review, for right whales; Würsig et al. in press for bowheads). But all three species are also adaptable in feeding behavior. Gray whales will feed on mysids associated with kelp (Darling 1977) for example, and apparently feed on _Pleuroncodes_ sp. in the water column (Norris et al. 1983). Right whales also feed below the surface, probably straining swarms of copepods and other small invertebrates in the water column (Pivorunas 1979; Payne in review). While it has long been known that bowhead whales feed at the surface and in the water column (Scoresby 1820), it was recently established from stomach content analyses (Durham 1972; Lowry and Burns 1980; Hazard and Lowry 1984), and from our observations of bowhead whales surfacing with muddy water streaming from their mouths, that bowheads sometimes feed near or at the bottom. It is not surprising that we found many similarities in the behavior of these species. Bowhead and right whales, in particular, are morphologically and taxonomically quite similar, and appear to obtain their food in very much the same ways. In fact, Rice (1977), mainly relying on a detailed comparison of morphology of bowhead and right whales, suggested that the two species be put in the same genus, _Balaena_.

The sleeker rorquals (Balaenopterid whales) generally gather their food more actively by lunging through concentrations of prey, and at least in the case of humpback whales, have developed complicated behavioral strategies for confining and concentrating their prey (Jurasz and Jurasz 1979; Hain et al. 1982). In general, the behavior of bowhead whales is more similar to that of gray and right whales than it is to the behavior of rorquals.

Gray whales spend part of the winter in warm water, near the shores of Baja California, and most of the summer feed in the northern Bering and southern Chukchi seas. Western Arctic bowheads make much shorter migrations, spending their winters in the pack ice of the Bering Sea and their summers predominantly in the Beaufort Sea. The two species thus use the Bering Sea at different seasons--gray whales to feed in summer and bowhead whales apparently to mate and calve in winter. However, the summer and autumn habitats overlap in part. Both gray and bowhead whales feed in the southern Chukchi Sea in autumn, and in the 19th century bowheads as well as gray whales occurred there in summer (Townsend 1935; Dahlheim et al. 1980). We

have seen single gray whales in the Canadian Beaufort Sea during four of our five years of bowhead whale work, but this represents the outer fringe of the gray whale's summer range (Rugh and Fraker 1981).

Like bowhead whales summering in the Beaufort Sea, gray whales summering in the Bering Sea spend most of their time feeding. However, both bowheads and gray whales (Sauer 1963; Fay 1963) occasionally socialize during the summer. The blow rate of gray whales feeding near St. Lawrence Island in July 1982 was similar to that of non-calf bowhead whales in 1980-84 (gray whale mean = 0.93 $\pm$ s.d. 0.229 blows/min, n = 67 whales; bowhead whale mean = 1.10 $\pm$ s.d. 0.873 blows/min, n = 156 blow rates; gray whale data from Würsig et al. 1984b). The basic pattern of diving for several minutes and then surfacing, generally for 2-10 respirations, is also similar for the two species on their summer feeding grounds.

Right whales, like bowhead whales, often appear to feed in the water column and to stay in the same general area for days. Right whales, like bowheads, also skim feed at the surface (Watkins and Schevill 1976, 1979), and they at times aggregate into echelons while skim feeding (Payne in review). In right whales, these echelons usually consist of only 3 to 6 whales, while we saw up to 14 bowhead whales skim feeding in echelon. However, Payne's observations of right whales have been obtained during the late winter and early spring, which is not the period of maximum feeding intensity for right whales. Bowhead and right whales have both been observed making the same kinds of nudges and pushes during socializing, but the winter-spring social activity of right whales is much more boisterous than the summer social activity of bowheads. Observations of bowhead whales in spring indicate that their social-sexual activity at that season can be every bit as boisterous as is seen in mating groups of right whales (Everitt and Krogman 1979; Carroll and Smithhisler 1980; Rugh and Cubbage 1980; Johnson et al. 1981; Ljungblad 1981). The belly-up position of a female bowhead photographed in spring in the Alaskan Beaufort (Everitt and Krogman 1979) indicates that females may attempt to evade potential mates who pursue them in large mating aggregations in the same way that female right whales evade males in Argentine waters (Payne in review). A photograph showing a remarkably similar mating group of right whales is shown in Payne (1976). The fact that similar-looking social aggregations are seen in both species argues for a similar social system, although it does not show that the social systems are similar in all details.

The acoustic behavior of right whales and bowheads is remarkably similar. Their low tonal FM calls are essentially identical, and the up call is their most common call type. In right whales, Clark (1982, 1983) has shown that up calls are contact calls, and that complex calls are associated with highly active social groups, many of which were sexually active. For the two cases in 1981 when bowheads were highly active, the proportions of complex calls were unusually high (72 and 85%). Ljungblad et al. (1983, 1984a) also observed highly active, often mating, whales that were apparently producing complex calls at high rates. In this study, we were not able to show an overall correlation between proportions of complex calls and social activity. Our definition of socializing included groups that were only mildly active. We were also not able to determine which specific whales were responsible for the sounds being recorded. Thus, our results are consistent with the idea that socializing bowheads tend to produce many complex calls, although our data do not specifically show this.

Relevance to Studies of Disturbance Responses

This study was planned primarily to assist the interpretation of the simultaneous study of responses of bowheads to potential disturbance. The results confirm that data on normal behavior are essential as a basis for recognizing and evaluating reactions to disturbance. We found that undisturbed behavior of summering bowheads varies considerably from day to day and from year to year, both in terms of general activities and distribution and in terms of surfacing, respiration and dive characteristics. Consequently, no observed variations in bowhead behavior that appear to be caused by disturbance can be properly attributed to the disturbance until natural variability has been taken into account.

Data on surfacing, respiration and dive characteristics are useful for assessing disturbance responses because these characteristics can be measured repeatedly with relative ease and because it is clear that they change in the situation where immediate disturbance reactions are most dramatically obvious, i.e. when a boat travels through a group of whales (Richardson et al. 1985c). Among the obvious reactions of bowheads to this situation are shortened surfacings with fewer blows per surfacing. It is reasonable to expect that milder forms of disturbance might cause similar but less dramatic changes in surfacing and respiration patterns, and the disturbance portion of this overall study has found suggestions of such changes in the presence of several different forms of industrial activity. Throughout the analysis for the presence or absence of disturbance responses, however, comparisons with the behavior of presumably undisturbed bowheads were made, as the only method to identify potentially disturbed behavior.

An example of the use of normal behavior data in the analysis of disturbance responses is the selection of undisturbed whales to serve as partial controls for the opportunistic observations of whales in the presence of seismic noise (Richardson et al. 1985c). Because we found considerable differences in surfacing, respiration and dive characteristics between calves and other bowheads, the few data from calves were excluded. Because we found suggestions of differences with depth of water, only whales in comparable water depths were compared. Because we found variations in behavior at different times during the summer, only whales observed during the same day or on adjacent days were compared, insofar as possible.

In some cases, data from several seasons of study were necessary in order to detect an important relationship. For example, in all five years of this study, the rate of socializing decreased progressively from early August to early September. If industrial activity were initiated in the middle of this period in a region frequented by bowheads, and if a lower rate of socializing were observed after the potential disturbance started, that change could be discounted as a reaction to the industrial activity as long as the decrease were comparable to the normal seasonal decrease in socializing identified during this study.

In addition to providing control observations against which to assess observations in the presence of specific kinds of potential disturbance, an understanding of the normal behavior of bowhead whales is necessary to make informed judgements on a more general level about the likelihood that industrial activity will have deleterious effects. For example, we observed that mothers and calves at times become separated while the mothers are

presumably feeding, and that they apparently reunite by calling to each other. This indicates that prolonged masking of those calls by loud industrial noises might cause premature separation of calves from their mothers. Another example derives from our discovery that some bowheads feed at the bottom. This result shows that the availability of prey at or near the bottom should be taken into account in evaluating the importance of an area to bowheads.

Recommendations for Further Research

After five seasons of research, we have a solid base of information on the short term normal behavior of bowhead whales during summer. However, we know virtually nothing about affiliations between whales, lengths of times individual whales are engaged in specific behaviors before changing activity, and the relationship of feeding and other behaviors to distribution and availability of prey. Many avenues of research are possible, but we mention several major ones which would build directly on our foundation.

Bowhead whales are at times recognizable by natural markings peculiar to an individual. However, our usual aerial vantage point, which generally has us >1 km from whales as we circle around them, is not optimal for getting detailed information on the identifying features of individuals. In addition, whales can travel underwater for several km, and we often lose sight of them as they move unobserved out of our circle of observation.

A radio tag on the back of one or more whales would solve many of these observational difficulties: we would be able to observe an electronically identified whale throughout an observation session, locate it even when it travels away from the aircraft, monitor its affiliations with other whales not only during an observation session but also on subsequent days, obtain dive time and surface time information during multiple observation sessions, possibly including periods of bad weather and darkness, and monitor longer range movements than the ones we have been able to obtain. Because radio tagging would enhance our knowledge of the surfacing-dive pattern and allow us to stay with a whale for long times, this technique would also be extremely valuable for the monitoring of potential disturbance reactions during industrial activities. Several types of radio tags have been successful on gray, fin, humpback and bryde's whales (Ray et al. 1978; Watkins et al. 1981; Goodyear 1983; Mate and Harvey 1984). By whatever technique of attachment, the radio could be monitored directly from an airplane, a boat, or the shore, as opportunity permits. A more sophisticated radio tag could probably give heart rate information, which has proven useful in assessing harassment in free ranging bighorn sheep (MacArthur et al. 1979).

Davis et al. (1982, 1983) and Cubbage et al. (1984) recently showed that high-resolution photogrammetry can distinguish many individual bowheads by natural marks and pigmentation patterns. We recommend that such high resolution photography be continued and expanded, because it can give valuable information on site tenacity, large scale movement patterns of individuals, and whale-whale affiliations over time (including, perhaps, between years). The photogrammetric technique, which gives accurate data on sizes of whales, can also assess age segregation over the entire range of

bowhead whales, and can therefore help us to determine the social structure of bowhead whales.

We have described several different feeding modes and feeding areas in our five-year study, and we have speculated that variations in feeding behavior and location are largely due to variations in prey distribution. We have no direct evidence for this assertion, however. To assess the importance of particular areas to bowhead whales, we need to confirm the link between distribution of prey and location and feeding mode of the whales. Trained behavioral observers should work in conjunction with any program to sample prey availability and factors controlling it. In this way, distribution of prey can be linked with distribution and feeding behavior of bowhead whales.

We know very little about the distribution and behavior of bowhead whales in winter or early spring. Although there are logistic difficulties, we recommend systematic observations, especially from the air, of bowhead whales during late winter and spring. Many calves may be born then, but we do not know what social affiliations occur in early spring, and how much feeding, if any, occurs at that time. A behavior study in early spring would not just fill a major gap in understanding of the normal behavior of bowhead whales, but would also allow us to assess the possibility of different reactions to potential disturbance during the time when bowhead whales are in the northern Bering Sea, with many engaged in mating and calving.

ACKNOWLEDGMENTS

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