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Variation in the Behavior of Humpback Whales: A study
of Individuals

by

Carole Anne Carlson

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
January, 1992

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FACULTY OF GRADUATE STUDIES

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by Carole Anne Carlson

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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ABSTRACT

Variation in the behavior of individuals within a seasonally returning population of humpback whales on Stellwagen Bank, Massachusetts, was studied using data collected between 1979 and 1985. The data presented were derived from observations aboard 30m commercial whalewatching vessels and dedicated cruises aboard a 12m research vessel. Possible relationships between behavioral measures and sex, age-class and reproductive status were examined.

Individual whales were photographically identified by natural markings on the ventral surface of the flukes as well as dorsal fin shape and prominent scarification. One hundred and twenty-seven individual humpback whales of known gender, that had been observed for more than one year, were chosen for the study.

Results of statistical analyses indicate that although there are few strong behavioral correlations between individuals, individual whales may be arranged in a rough continuum ranging from social to less social individuals.

The most significant differences in behavior between classes of whales were found between juveniles and adults. Juvenile whales generally approach boats, lobtail, breach, spyhop, flipper and rest more than adults, who are more social, feed more frequently and tend to be a greater distance from the centroid of whale distribution. There are significant relationships between age and sociality, mean group size and resting behaviors. Rates of resting were greater in younger whales while sociality generally increased with age.

Significant differences were found between gender and rates of feeding, sociality and arrival time with males generally feeding more frequently and arriving later than females. Females were generally more social. Pregnant and lactating females differed significantly in rates of arrival time, departure time, mean group size and sociality.

Statistical analyses indicate significant differences between individuals for near-boat, breaching and feeding events, time of residence, mean group size and sociality. Individual females tend to vary their behavior more than males, except for boat approaches and arrival time.

The behavioral events examined are reviewed and their possible function(s) discussed in the context of the new data presented.

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CHAPTER 1. INTRODUCTION

The purpose of this study is to examine the variation in behavior of individuals within a seasonally returning population of humpback whales that visited Stellwagen Bank, Massachusetts during 1979-1985 and to investigate possible relationships between behavior and sex, age-class and reproductive status.

1.1 The humpback whale: Natural history

Once I saw a whale
With "sentimental indian eyes"
And flippers as white as
snow
And barnacles all over his
belly
And his baleen thin as
hair
And his nose like a pickle

SEAN WONDER, AGE 7

The humpback whale, Megaptera novaeangliae (Figure 1.0), a member of the family Balaenopteridae, exists in all oceans of the world. Humpbacks are usually found in temperate, productive waters during the summer months and winter in



Figure 1.0. A breaching humpback whale.

tropical or sub-tropical waters (Matthews, 1937; Mackintosh, 1965). This migration relates to the life cycle of the species, as they feed during the summer and breed and calve during the winter months (Chittleborough, 1958; Matthews, 1937; Mackintosh, 1942). The gestation period is approximately twelve months and the most common breeding cycle results in one calf every two years, although successful post-partum ovulation in some females may result in two calves in two years (Chittleborough, 1958).

Like most baleen whales, humpback whales do not appear to group closely together. Most sightings are of single or two animals (Wolman and Jurasz, 1977; Mayo, 1982; Whitehead, 1983) and rarely exceed four or five (Evans, 1987) unless breeding or feeding aggregations are observed. Although little is known about the exact social structure of the humpback, group dynamics on low-latitude breeding grounds appear to be quite complex (Herman and Antinaja, 1977; Tyack and Whitehead, 1983; Mattila et al., 1985). Few long-term associations have been observed on high-latitude feeding grounds, except those noted by Baker et al. (1986) and Weinrich (1983) and the apparently strong bond existing between mother/calf pairs (Whitehead, 1983).

While wintering on low-latitude breeding grounds, single, male humpback whales produce a complex, highly-structured series of sounds called "songs" which continually evolve (Winn and Winn, 1978; Payne et al., 1983; Guinee et al.,

1983). The song may last from 6-30 minutes and is repeated without noticeable breaks between sequences (Payne, 1970). Humpback whales from the North Atlantic have a different song from that of humpback whales in the North Pacific, suggesting North Atlantic and North Pacific dialects (Winn et al., 1981), while songs recorded from two distinct breeding grounds in the South Pacific were found to be similar (Payne and Guinee, 1983).

While humpback whale "songs" have also been recorded on the high latitude feeding grounds (Mattila et al., 1987; McSweeney et al., 1989), most of the vocalizations recorded appear to be much less structured (Winn et al., 1979). These "social" vocalizations, related to group size (Silber, 1986), are generally variable in frequency and duration. Although attempts have been made to categorize these sounds (Thompson et al., 1986; Chabot, 1988), their relationship to the behavior and social structure of the humpback whale has not yet been determined.

Humpback whales display a series of spectacular surface behaviors including breaching, flippering, spyhopping and lobtailing which are discussed in detail in Chapter 4. Herman Melville (1851) said, "He is the most gamesome and lighthearted of all whales, making more gay foam and white water generally than any of them." Although observed and studied by many, the exact function(s) of these behaviors remains unclear (Whitehead, 1985a,b).

Individual humpback whales have been successfully identified through photographic documentation of natural markings; especially pigment patterns on the ventral surface of the flukes (Katona and Whitehead, 1981). These patterns, ranging in coloration from all-white to all-black, are not stable in some immature whales but appear to be generally stable in adults (Carlson et al., 1990). Acquired markings, such as parallel scars, believed to be caused primarily by the killer whale, Orcinus orca (Katona et. al, 1980; Whitehead and Glass, 1985), are useful for long-term identification of individual whales (Katona and Whitehead, 1981; Carlson, 1982). The ability to confirm identifications of individuals of this species is the key to detailed studies of population size and dynamics (Herman and Antinofa, 1977; Whitehead, 1982; Whitehead et al., 1983a,; Baker et al., 1985; Darling and Morowitz, 1986; Katona and Beard, 1990; Perry et al., 1990), seasonal return rate (Mayo, 1982; Glockner-Ferrari and Venus, 1983), temporal and spatial distribution (Whitehead et al., 1980; Herman et al., 1980; Baker and Herman, 1981; Mayo, 1982; Whitehead and Moore, 1982; Darling and Jurasz, 1983), social organization (Whitehead, 1983) and calving rate (Clapham and Mayo, 1990; Glockner-Ferrari and Ferrari, 1990).

1.1.1. Humpback whales of the western North Atlantic

Western North Atlantic humpback whales feed during spring, summer and fall in at least four, widely separated, high latitude areas; the Gulf of Maine (Mayo, 1982, 1983; Mayo et al, 1985), Newfoundland-Labrador (Whitehead et al., 1980, 1983b; Whitehead, 1983), Greenland (Whitehead et al., 1983a; Perkins et al., 1982, 1984), and Iceland (Brown, 1976; Martin et.al., 1984; Sigurjonsson and Gunnlaugsson, 1990). It has been found that the individual whales of these high-latitude areas constitute distinct subpopulations or "stocks", seldom mixing with whales of other areas during the feeding season (Katona et al., 1980; Katona and Beard, 1990).

Migration from the high-latitude feeding grounds to the West Indies generally occurs during late fall and early winter (Katona et al., 1980, Martin et al., 1984; Mattila et al., 1985). The largest known winter aggregation of western North Atlantic humpback whales is found on Silver Bank, off the coast of the Dominican Republic (Winn et al., 1975; Balcomb and Nichols, 1982; Whitehead, 1982; Whitehead and Moore, 1982; Mattila et al., 1985). Silver Bank, along with neighboring Navidad and Mouchoir Banks and Borinquen Bank off the coast of Puerto Rico (Mattila, 1983), appear to be areas where individual humpback whales from the high-latitude feeding grounds mix, possibly interbreed, and give birth to their young (Katona and Beard, 1990).

Generally during late winter and early spring, humpback whales of the western North Atlantic leave these low-latitude breeding and calving grounds, and return to their separate high latitude feeding areas.

1.2. Comparative studies

Comparative studies have been used extensively to answer questions about adaptation. Interspecific studies, intraspecific studies and studies of individuals attempt to examine how variation in behavior reflects differences in ecology. In this section I will review the three major groupings of comparative studies and discuss their applicability to detailed studies of animal behavior.

1.2.1. Interspecific comparisons

Interspecific comparisons may involve a few, or a pair of closely related species differing in an important aspect of their ecology. For example, Cullen (1957) examined the breeding behavior of the kittiwake, Rissa trydactyla, and compared it with that of the ground nesting gulls as a group. Her work indicates that the change to cliff nesting by the kittiwake affected many aspects of the life history of the species and led to morphological changes and behavioral alterations. While this type of study allows for the comparison of more detailed variables, it is not always possible to determine which ecological factor is responsible

for the evolution of a specific behavioral or morphological difference between two species (Clutton-Brock and Harvey, 1978).

Interspecific comparisons may also involve comparing a number of species categorized by ecological variables. Crook (1964), studied approximately 90 species of Weaver birds (Ploceinae) in an attempt to determine possible correlations between differences in social organization and ecology. Predation and food appeared to be the main selective pressures influencing the evolution of social organization. Detailed studies of social organization displayed by African antelope species (Jarman, 1974) demonstrated that they exhibit various types of social organization, each related to dispersion patterns of food items. Wiley's (1974) systematic study correlates social structure, life history patterns and ecology of 17 species of grouse (Tetraonidae) exhibiting a wide range of social structure and mating systems. Wiley's study exemplifies some general patterns in the evolution of mating systems among higher vertebrates. Clutton-Brock (1989) reviews and describes the distribution of mammalian mating systems. The diversity in mammalian mating systems is interpreted through a "simple framework of ecological relationships governing effects of male assistance of female breeding success and the defensibility of females by males". Such qualitative comparisons are useful for revealing broad trends in

evolution and general relationships between social organization and ecology. Generally, they have not helped us directly understand how differences between the behavior of individual animals of the same species relate to their ecology.

Quantitative comparisons testing qualitative hypotheses use formal statistics to test associations between behavioral and ecological traits (Clutton-Brock and Harvey, 1978). Harvey et al. (1978) examined sexual dimorphism in primate tooth size. Their results indicate that male tooth size is larger than expected in harem-forming species, supporting the sexual competition hypothesis for the evolution of larger teeth in males. Armitage (1981) examined the role of sociality as a life history tactic in 18 species of burrowing sciurids and concluded that reproductive effort is determined by body-size energetics. Patterns of association among body size, reproduction, physical and behavioral development and sociality in 17 closely related species of canids were studied by Bekoff et al. (1981). The analyses demonstrated a close relationship between life history tactics and behavioral patterns. These quantitative relationships between specific traits restricts the analysis to variables measured along an ordinal scale on a reasonable sample of species (Clutton-Brock and Harvey, 1978) and therefore, many questions remain unanswered because of a paucity of data. Furthermore, it may be

difficult to sort out the effects of different variables on the evolution of a trait. Questions about adaptive behavior may then be better examined by comparing differences in behavior between individuals of a single species.

1.2.2. Intraspecific or interindividual comparisons

Intraspecific or interindividual studies may involve comparing populations within a species in different parts of its range or individuals or groups within a population. This approach, complementary to the broad scale comparisons among species, looks at relationships between selection and behavior through studies of the behavior of individuals of the same species. Lack's (1966) studies on twenty-five species of birds, in various parts of their range, exhibiting a wide variety of feeding and breeding habitats, provide insight into how reproductive rates, density-dependent factors and dispersal relate to food supply and behavior in wild birds. Lack stresses the need for long-term studies of wild populations based on sound knowledge of the natural ecology of the species involved and the importance of well-designed field experiments to help expediate this otherwise slow process.

Bertram (1975) analyzed and compared long-term records of adjacent prides of wild lions, Panthera leo, living in presumably similar environmental conditions. By comparing the two groups, it was possible to show that some aspects of

their reproduction are caused by factors within each pride and not factors common to both. Betram's study demonstrates that there are a number of social factors, some unidentified, which are important in the reproduction of lions and affect the evolution of their social organization.

Rubenstein (1986) studied the ecology and sociality in a population of horses inhabiting Shackleford Banks, a barrier island off the east coast of North America. The horses exhibited a variety of adult association patterns in different regions of the island that had important ecological differences in habitat structure and the abundance and distribution of vegetation. His detailed observations of individuals examines a subset of social relationships; male-male, female-female, male-female and breeder-nonbreeder. These observations are the basis for his comparison and examination of equid (horses and zebras) social systems in general and the environmental and physical factors affecting their evolution.

1.2.3. Studies of individuals

Consistencies and variation in behavior should become apparent when detailed, long-term studies of known individuals in a population are conducted. Kummer (1968) documented the sociobiology of the hamadryas baboon, Papio hamadryas, over a 15 year period. This detailed study

highlights the social organization of the hamadryas; non-conventional by baboon standards. Long-term studies on the rhesus macaque, Macaca mulatta, population on Cay Santiago (Sade et. al., 1976; Drickamer, 1974), Japanese macaques, Macaca fuscata, at Arashiyama, (Koyama, et al., 1975), Takasakiyama (Masui et al., 1975) and Koshima (Kawai, 1965; Mori, 1975) in Japan and chimpanzees, Pan troglodytes, at Gombe Stream Park in Tanzania (Goodall, 1971; 1988) have provided much of the data on primate life history variables.

Goodall's study on the chimpanzees of Gombe now spans over 26 years and represents the longest continual field study of any mammalian species. This collaborative, cooperative, field research effort has shed new light on many aspects of chimpanzee behavior and contributed significantly to the understanding of the social structure, reproductive strategies and ranging and feeding behaviors of this species. The accumulation of series of detailed life histories of individuals with markedly different traits has added a dimension to the study of animal behavior and underlines the importance of longitudinal studies.

Moss' 14 year study of the African elephant, Loxodonta africana, in Amboseli National Park, Kenya has generated a series of papers on elephant social behavior, population dynamics and ecology. Moss (1983) and Moss and Poole (1983) describe the social organization of this population of approximately 680 individually identified elephants,

including 50 family units and 100 independent males. Moss (1981) examined the family units, composed of closely related females living in stable groups, and Poole and Moss (1981), Moss and Poole (1983) and Poole (1987) discuss the social behavior of adult males. The reproductive success of males and female choice are investigated in Poole (1989).

Long-term studies of killer whales, Orcinus orca (Bigg et al., 1990; Olesiuk et al., 1990;), and bottlenose dolphins, Tursiops truncatus (Wells and Scott, 1990), are clearly the most comprehensive studies on individually identified cetaceans to date. Olesiuk et al. studied the life history and population dynamics of resident killer whales in the coastal waters of British Columbia and Washington state, while Bigg et al. examined their social organization and genealogy. The long-term stability of 30 pods (discrete long-term breeding units composed of the same individuals), a total of 261 individual whales, allows for direct measurement of vital statistics. The absence of movement between pods permits an estimation of birth and mortality rates. Furthermore, these animals are non-migratory so that environmental controls acting on the dynamics of a pod occur locally. Detailed information on the growth, age, reproductive parameters, annual natural mortality rates for adult males, females and juveniles, pod characteristics, size and movements and associations of individual orcas, has given us a clear perspective on the complex social

structure and behavioral ecology of this species and insights into the sociality of toothed whales in general.

Wells and Scott's (1990) study of at least three adjacent populations of individually identified bottlenose dolphins along the central west coast of Florida has examined population structure and dynamics since 1970. The study focuses on one population of approximately 100 individuals, many of known gender and age. The long-term nature of this study and the high percentage of identifiable individuals has allowed for estimations of vital rates (e.g. fecundity rates, annual recruitment rate) and observations of social structure of this species.

Detailed, long-term studies of the southern right whale, Eubalaena australis (R. Payne et al., 1990), have generated invaluable data on reproductive parameters, migration, distribution, habitat use and group composition by area of a large, migratory species of baleen whale. Payne's study, initiated in 1970, continues to provide information on the life histories of over 900 individual whales, many of known sex.

Detailed studies such as these have the potential to, but have not yet, compared the behavior and strategies of individual cetaceans in different stages of their life history.

The work of Clutton-Brock et al. (1982) is a classic, long-term study of individuals within a population. The red

deer, Cervus elaphus, is ideal for this type of field research, because of its large body size, short life span and open, accessible habitat. This detailed study analyses and compares reproductive success and strategies of male and female red deer and examines the behavioral ecology of deer in the light of modern evolutionary theory.

It is clear that the most recent advances from research on behavioral and evolutionary ecology have come from a few detailed studies extending over several years of recognized individuals within a population. For many species of whales, particularly the baleen whales, studies of this nature are in their infancy. The work of Hoelzel et al. (1987) is an example of a study that begins to examine behavioral differences between individuals. They have shown that individually identifiable minke whales, Balaenoptera acutorostrata, have individual foraging specializations that are lasting and consistent. They suggest that these specializations are associated with particular feeding areas and represent learned strategies.

The fluctuating environment, long migrations and widespread distribution of many species of baleen whales would appear to make them inaccessible for detailed studies. However, comparative, long-term studies of local populations (Clapham and Mayo, 1990; Dorsey et al., 1990; Glockner-Ferrari and Ferrari, 1990; R. Payne et al., 1990; Perry et al., 1990; Sears et al., 1990) have begun to reveal answers

to basic biological questions on reproductive parameters, migration, seasonal return rate, distribution and habitat use. Genetic studies may soon give us insight into the reproductive strategies, sociality and dispersion of individuals. The work presented here examines and compares behavioral differences between individual humpback whales during different stages of their life history.

CHAPTER 2. METHODS

2.1. The study area

This study was primarily conducted in Massachusetts Bay (Fig. 2.1). The area of focus was Stellwagen Bank, a glacial deposit of gravel and sand approximately 30 km. long and as much as 10 km. wide. Depths along the axis of the bank vary from the shallowest location, 20 m. deep along the steep slope on the west side of the broad southern end to as much as 40 m. in the shallowest areas of the northwest end. The depths around the bank similarly vary, ranging from 50 m. along the gradual slope of the southeast side to 125 m. in the vicinity of the northeast edge. In contrast to Stellwagen Bank, the southern part of the study area, eastern Cape Cod Bay, is a relatively level-bottomed shallow basin, with depths ranging from 10 m. to approximately 50 m. The water is characterized by salinities above 32‰ and sea surface temperatures range from -1 C in midwinter to 26 C in midsummer (G. Giese, unpublished data).

2.2. Whalewatching and research cruises

The observations presented in this study were made aboard the 30m. commercial whalewatching vessels DOLPHIN III, IV,

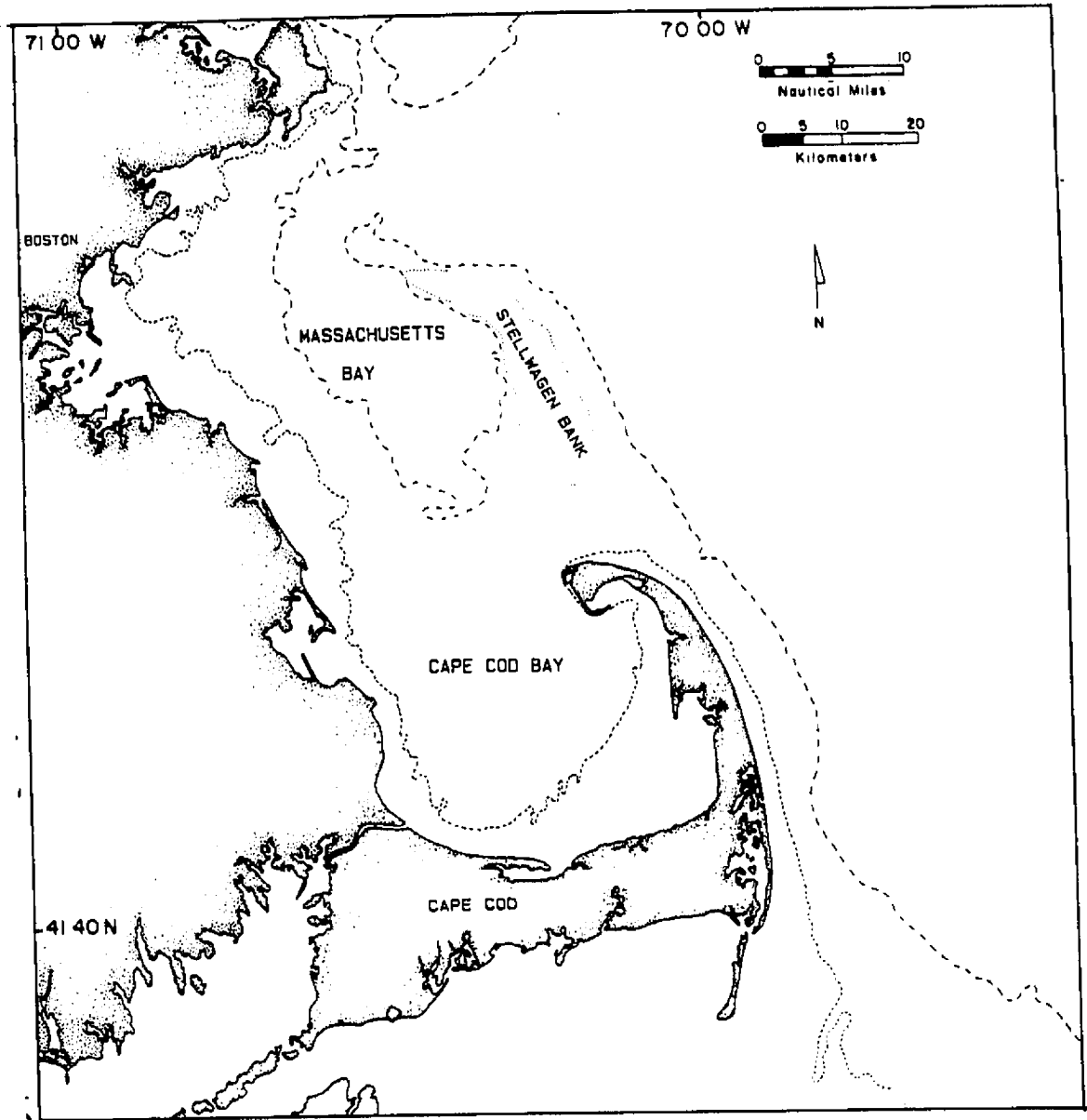


Figure 2.1. The study area.

V, and VI from 1979 to 1985 and the 12m. R/V HALOS from 1983 to 1985. The Dolphin Fleet ran four-hour cruises leaving Provincetown, Massachusetts one to three times a day during the period mid-April through October each year. The track of the vessels was dependent upon whale sightings and whale densities observed on previous trips. There was no predetermined pattern to the cruises. Dedicated cruises were initiated in the autumn of 1983 and were conducted throughout the year aboard the R/V HALOS. The number of cruises and the length of each field season are given in Table 2.1.

Approximately 80% of the cruises were made to the area on and around Stellwagen Bank. Most of the remaining cruises were made in Cape Cod Bay during the months of April and May, when concentrations of whales can be observed there.

2.3. Data collection

When whales were sighted, information on the species, number of whales, time, LORAN-C location, behavior and the identity of individuals (when possible) was recorded. The vessel attempted to maintain a position relative to the animal so that the bow of the boat directly faced either side of the individuals' dorsal fin or tail. This position allowed photographs useful for individual identification to be taken.

Table 2.1. Number of cruises, length of field season, and number of individual humpback whales observed between 1979 and 1985.

YEAR	NO OF CRUISES	FIELD SEASON	NO OF INDIVIDUALS OBSERVED
1979	164	04/17-10/29	47
1980	313	04/12-10/24	79
1981	525	04/11-11/04	89
1982	581	04/11-11/18	141
1983	685	04/07-11/20	121
1984	715	01/06-12/31	191
1985	805	01/06-11/11	221

2.4. Photographic equipment and film

Photographs were taken using Pentax ME and MX cameras and Pentax lenses ranging from 28 - to 400mm, with skylight filters. Each camera body was equipped with a Pentax 2 - 5 frame/second power winder for sequential photographs, and a recording data back for coding individual observations. Kodak Tri-X and Ilford HP5 black and white film rated at ASA 400 was used.

2.5. Identification of individual whales

The humpback whale has a number of morphological features which make it particularly easy to study individuals. The most significant of these is the difference in pigmentation patterns on the ventral surface of the flukes (Katona and Kraus, 1979; Katona et al., 1980). Individual whales were identified by this pattern, as well as dorsal fin shape (Mayo 1982; Mayo et al., 1985) and prominent scarification (Carlson 1982). All whales were given names based on prominent natural markings; this mnemonic device was initiated to facilitate field data collection.

2.6. Analysis of photographs

Contact sheets were made for each exposed roll of film. These were carefully analyzed and each frame was labeled with the name of a known individual humpback whale or numerically coded for unknown animals. A photographic

summary sheet was completed for each observation listing the date, file names of individuals in an association (whales were considered associated if they were within two body lengths of each other and generally synchronous in direction of movement and surfacing and diving behavior), data-back code (an alphanumeric code imprinted on negatives documenting film roll series, roll number, and observation) and field data sheet number (a numeric series issued to each field researcher to order data sheets by individual trips). Clear, well-focused photographs exhibiting field marks of each individual humpback whale were selected from each contact sheet to add to the established photographic catalog. All photographs used were printed using a 4 x 5 format on Kodak RC II Polycontrast paper.

2.7. Database

During the course of this study 348 individual humpback whales were photographed. Using a modification of Glockner-Ferrari's (1983) underwater photographic technique based on True's (1904) description of the genital region of humpback whales, and observations of known whales with calves (section 2.10), the gender of 168 individuals of this population has been determined (Seipt et al., 1984). A calf is defined as a whale whose length is judged to be half or less than that of the accompanying whale presumed to be its mother, and thus, less than one year old. A calf is

generally observed to be in close association and behavioral synchrony with its mother. An adult is defined as an individual whose age is greater than or equal to four years. Whales previously observed as a calf and whose age is less than four years are classified as juveniles. Forty-four reproductively mature females (known females whose age was 4 years or older) were observed with a total of 72 calves; calving intervals varied from one to four years. Of the 49 calves born prior to the 1985 field season, 39 have been observed in at least one of the years following birth (Clapham and Mayo, 1987).

2.7.1. Data entry and selection of individual whales

Data on the time of sightings, locations, movements, general behavior and associations of these individuals over an eight year period were entered into a D-base III+ data management system.

One hundred and twenty-seven individual humpback whales of known gender, that had been observed for more than one year, were chosen for the study. These individuals are listed by year in Appendix I and summarized by gender, age and reproductive status in Table 2.2.

2.8. Behavioral measures

The following behavioral measures were examined in this study for each whale in each year. Measures of feeding,

breaching, spyhopping, flippering and lobtailing, as well as low respiration and near-boat events, were derived from observation periods of 10 minutes or more. The measures indicate whether or not an individual whale displayed a given behavior during an observation and are not representative of the total number or percent of time spent displaying that behavior.

ARRIVAL TIME: The day of the first observed sighting within the study area (days from January 01).

DEPARTURE TIME: The day of the last observed sighting within the study area (days from January 01).

RESIDENCE TIME: The time period, in days, between arrival and departure.

LARGE SCALE RANGE: Log of the greatest observed distance an individual was identified from the centroid of its Stellwagen range during the summer months.

LOW LATITUDE OCCURRENCE: Observed presence or absence on the breeding grounds earlier that year.

MEAN GROUP SIZE: Mean group size of observed associations excluding calves.

LOW RESPIRATION EVENTS (Figure 2.2): The ratio of the number of observed periods of "rest" to the number of times observed.

BREACHING (Figure 2.2): The ratio of the number of observations in which a whale was breaching to the number of times observed.

NEAR-BOAT EVENTS (Figure 2.2): The ratio of the number of observations of an individual orienting towards vessels (within one body length) to the number of times observed.

FEEDING (Figure 2.3): The ratio of the number of times observed surface feeding to the number of times observed.

SOCIALITY: The ratio of the number of times observed associating with one or more other whales (not in feeding groups) to the number of time observed.

FLIPPERING (Figure 2.3): The ratio of the number of observations of flippering to the number of times observed.

LOBTAILING (Figure 2.4): The ratio of the number of observations of lobtailing to the number of times observed.

SPYHOPPING (Figure 2.4): The ratio of the number of observations of spyhopping to the number of time observed.

RELATIVE DISTANCE: The average distance of the individual from the centroid of the positions of all animals sighted that year. Relative distance was

calculated by converting LORAN-C locations of all humpback whales sighted from 1979 - 1985 to kilometers using a modification of an algorithm developed by Charles Mayo (unpublished). The new coordinates were averaged by year for all humpback whales as well as by year for the 127 individuals in the study. The following equation was used to determine the distance of each individual by year, from the centroid of humpback whale distribution:

$$\text{rel. dis.} = \sqrt{(x - \bar{x})^2 + (y - \bar{y})^2} \text{ where}$$

x and y = the average of all converted Loran-C co-ordinates of an individual whale in a given year, and

\bar{x} and \bar{y} = the average of all converted Loran-C co-ordinates of all humpback whales in a given year.

A data set of variables (by individual, by year) was created using the SYSTAT 4.0 data editor and is shown in Appendix II.

2.9. Statistical analyses

The data for most variables in this study are not normally distributed, even after square root, arcsine and log (+1) transformations. The majority of the test statistics used therefore, are non-parametric. Parametric test statistics were used when the variables tested showed a normal distribution, or when it was necessary to factor out between year differences in behavior and no non-parametric routines were available. Statistical analyses were generally performed using SYSTAT routines (Wilkinson, 1987).

The results of many statistical tests are given (with individual significance levels) in this thesis. There will undoubtedly be Type I errors (significant effects not reflecting real differences), but these should be few. In this thesis, I will concentrate more on patterns rather than "significant" results of individual tests.



BREACHING: A jump; the head breaks the surface of the water with the body at a 45 to 90 degree angle; in the air, the whale spins on its long axis or does not spin and re-enters the water, usually on its side or back.

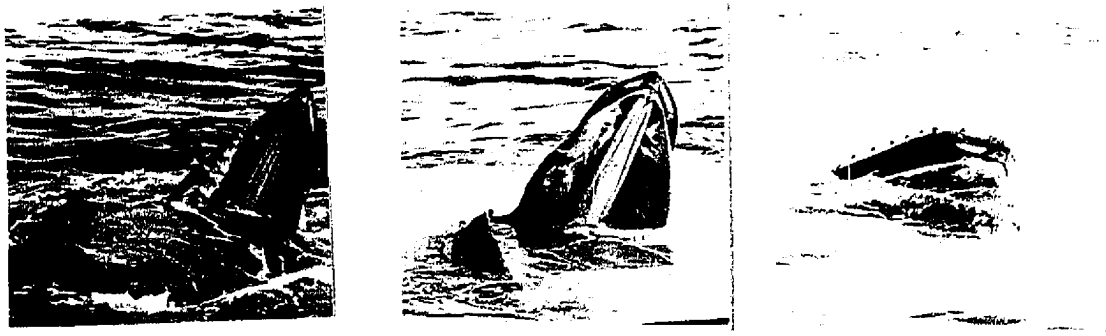


NEAR-BOAT: The whale, orienting to the vessel, displays a variety of activities including spyhopping, logging and flippering.

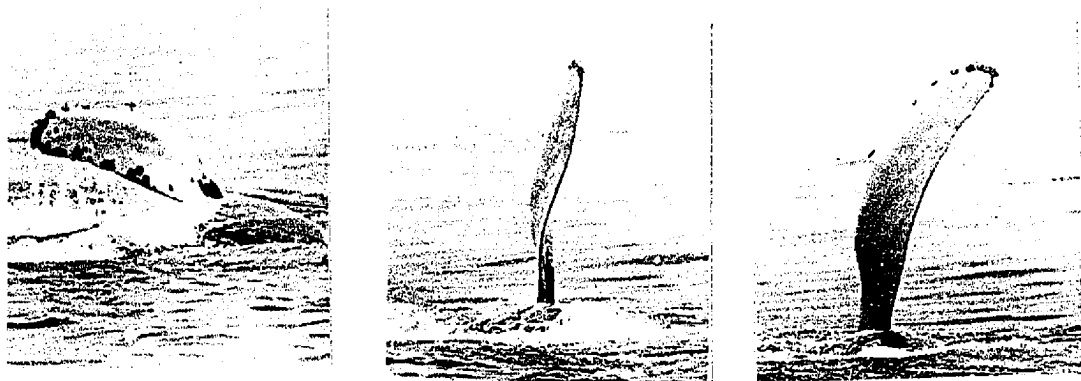


LOW RESPIRATION: The whale rests horizontally at the water surface without swimming, flippers extended from body, movement confined to drifting.

Figure 2.2. Descriptions and photographs of breaching behavior, near-boat behavior and low respiration events (resting) (Mayo et al., 1985).



LUNGE FEEDING: The whale rises forcefully with its mouth open through schools of fish or krill; this behavior usually associated with expulsion of bubbles. As water fills the mouth, the throat and belly of the whale expand, the ventral pleats unfold.



FLIPPERING: The whale rolls on its side or back, raises one or both flippers above water, and slaps the flipper(s) against the water surface.

Figure 2.3. Descriptions and photographs of lunge feeding behavior and flippering behavior (Mayo et al., 1985).



LOBTAILING: Head down, flukes are held above the surface and are forcefully slapped against the water.



SPYHOPPING: The whale slowly rises vertically in the water exposing the head, occasionally to the eyes and sinks back in the vertical position.

Figure 2.4. Descriptions and photographs of lobtailing behavior and spyhopping behavior (Mayo et al., 1985).

Table 2.2. Number of individual whales in study summarized by sex, reproductive status, and age. Occurrences=sighting of individual whale by year.

Number of individuals.....	127
Number of occurrences of individual whales.....	530
Number of females.....	78
Number of occurrences of females.....	346
Number of males.....	49
Number of occurrences of males.....	184
Number of females of known reproductive status.....	41
Number of occurrences of pregnant females.....	74
Number of occurrences of lactating females.....	64
Number of individuals of known age.....	32
Number of occurrences of individuals of age = 1 yr...	24
Number of occurrences of individuals of age = 2 yrs..	27
Number of occurrences of individuals of age = 3 yrs..	17
Number of occurrences of individuals of age = 4 yrs..	12
Number of occurrences of individuals of age \geq 5 yrs..	16
Number of occurrences of known juveniles.....	69
Number of occurrences of known adults.....	293



1



2



3



4



5

Figure 2.5. Categories of fluke coloration.

2.9.1. Relationship between gender and fluke coloration and scarification

The dependence of fluke coloration and parallel scarification on gender was examined using Chi Squared Contingency Table tests.

2.9.2. General behavioral correlations

Correlations between different behavioral variables (average of units for each individual whale, each year) and behavioral variables and sandlance, Ammodytes spp., abundance and whale abundance were examined using Spearman Correlation Coefficient statistics. The data on sandlance abundance used for this study was collected on Stellwagen Bank and adjacent waters by National Marine Fisheries Service, Northeast Fisheries Center biologists during standardized spring and fall bottom trawl surveys. The abundance of sandlance, expressed as the mean of the log-transformed number of sandlance per tow/year, was considered representative of Stellwagen Bank and is detailed in Payne et al. (1986). Whale abundance is expressed as number of whales/effort/year (Payne et al., 1990). Data on the occurrence of humpback whales was collected by naturalists working aboard commercial whalewatching vessels during the study period.

The behavioral correlations were further examined using principal components analysis to summarize relationships between variables in an attempt to provide summary variables

for use in later analysis. Varimax rotations did not substantially improve the interpretation of the factors and are therefore not presented.

2.9.3. Variation in behavior

The significance of differences in behavior with age, age-class (juvenile, adult), gender, reproductive status (lactating, pregnant) and year was examined using Kruskal-Wallis non-parametric one-way analysis of variance test. The Mann-Whitney U test was used for variables with 2 characters.

Two-way analysis of variance was used to compare differences between behaviors and age, age-class, gender and reproductive status by year. In no cases where significant effects were found was the interaction term also significant, with the exception of flippering and lobtailing in pregnant and lactating females. These behaviors are not discussed for this class of whales because of biases in the field data collection (section 3.6).

Consistencies in the year to year behavior of individuals was examined using the Friedman two-way analysis of variance statistic. Variation in behavior by individual male and female, by year, was further examined using two-way analysis of variance. A subset of the data, including 16 males and 16 females observed over a three year period (1983-1985), was used for these analyses. The reduced data set

eliminated individuals not observed in each of the three years selected, lactating females and juveniles, and enabled the tests to be more easily performed, using the computer packages available.

Wilkinson (1989) multi-way box plots were used to provide a simple graphic summary, using rank order statistics instead of means. They were originally presented by Tukey (1977) as schematic plots. Multi-way plots show the distribution of a single variable stratified across levels of a grouping variable and are useful for illustrating results of survey data on multiple groups. The notches implement simultaneous confidence intervals on the median of several groups. If the intervals do not overlap, one can be confident at approximately the 95% level that the group medians are different (McGill, Tukey and Larsen, 1978). The median is marked by the center horizontal line; lower and upper hinges are the upper and lower edges of the box, respectively. The ends of the whiskers are the adjacent (usually outermost) values. An * marks outside values and extreme outside values are marked with an O (Wilkinson, 1988).

CHAPTER 3. RESULTS

3.1. Fluke coloration and scarification

Initially, variables other than behavioral ones were also examined for this study. Due to a paucity of data many were excluded. Tests of fluke coloration and scarification however, indicate that there are some significant morphological differences between males and females and are therefore, briefly discussed.

Results of chi squared contingency test indicated a significant dependence of ventral surface fluke coloration pattern on gender (chi square=35.820 DF=6 $P < .001$) with females showing generally darker flukes (Table 3.1).

The dependence of the presence of parallel scars on gender was significant (chi square=4.595 DF=1 $P < .05$) with more males (24.5%) showing parallel scars than females (10.3%).

Table 3.1. Fluke coloration (as shown in Figure 2.5)
listed by gender.

<u>GENDER</u>	<u>COLORATION</u>				<u>TOTAL</u>
	1 and 2	3	4	5	
male	25	21	2	1	49
female	7	37	18	16	78

3.2. General behavioral correlations

Results of Principal Components analysis indicate that all the behavioral variables are fairly independent of each other (Table 3.2) with the exception of sociality and mean group size. The first five Eigenvalues are greater than one, accounting for only 59.31% of the total variance (15.81%, 12.72%, 11.71%, 10.29% and 8.78% respectively). The second principal component largely represents sociality and mean group size, and using it, individual whales may be arranged on a rough continuum, ranging from more social to less social individuals.

The matrix of Spearman Correlation coefficients (Table 3.3, 3.4, 3.5) generally mirrors the results of the Principal Components analysis and indicates the following important behavioral correlations by year:

- 1). Individuals that are more social arrive later and are a greater relative distance from the centroid of whale distribution, while less social individuals spyhop and flipper more, arrive earlier and stay longer.
- 2). Individuals that feed more, rest less.
- 3). During years when sandlance abundance was high, individuals flipped less, spyhopped less, arrived later, and were a greater distance from the centroid of whale distribution.

- 4). During years when whale abundance was high, individuals spyhopped more, flippered more, breached less, and stayed longer.

Table 3.2. Principal Component Analysis: Component loadings and Eigenvalues for those components with Eigenvalues greater than 1.0.

BEHAVIOR	COMPONENT LOADINGS				
	1	2	3	4	5
Near-boat	-0.200	0.143	-0.517	0.307	0.410
Lobtail	0.216	0.222	0.168	0.646	0.094
Breach	0.083	0.330	0.473	0.517	-0.179
Feeding	0.254	0.014	0.299	-0.317	-0.400
Spyhop	-0.159	0.158	-0.426	0.212	0.143
Social	0.350	0.771	-0.140	-0.245	0.060
Flipper	-0.258	0.415	0.180	0.312	-0.412
Resting	-0.381	0.170	0.069	0.080	0.258
Arrive	0.513	-0.101	0.479	0.010	0.522
Depart	-0.345	0.260	0.596	-0.290	0.481
Reside	-0.797	0.268	0.078	-0.276	-0.030
Mean group	0.407	0.702	-0.253	-0.286	-0.016
Rel distance	0.576	-0.110	-0.145	-0.084	0.085

EIGENVALUES				
1	2	3	4	5
2.055	1.654	1.522	1.337	1.141

Table 3.3. Matrix of Spearman correlation coefficients of mean values of behavioral variables for each year including spring/summer sandlance abundance (SL), average sandlance abundance (ASL), and whale abundance (MNABUND). Significant values (<.05) are highlighted.

	Near-boat	Lobtail	Breach	Feeding	Spyhop
Near-boat	1.000				
Lobtail	0.432	1.000			
Breach	0.036	0.523	1.000		
Feeding	-0.429	-0.252	-0.321	1.000	
Spyhop	-0.252	-0.455	-0.577	-0.090	1.000
Social	0.214	-0.090	0.429	-0.143	-0.721
Flipper	-0.018	-0.427	-0.613	-0.342	0.927
Resting	0.214	-0.108	0.179	-0.857	0.450
Arrive	0.500	0.018	0.464	-0.179	-0.703
Depart	0.321	-0.324	0.250	-0.286	-0.108
Reside	-0.429	-0.847	-0.464	-0.000	0.811
Mean group	0.393	-0.072	-0.357	0.250	0.414
Rel distance	0.464	-0.126	0.286	-0.000	-0.649
SL	0.468	0.200	0.378	0.252	-0.800
ASL	0.036	0.091	0.414	0.577	-0.564
MNABUND	-0.357	-0.667	-0.750	0.071	0.883
	Social	Flipper	Resting	Arrive	Depart
Social	1.000				
Flipper	-0.577	1.000			
Resting	-0.071	0.595	1.000		
Arrive	0.893	-0.559	0.036	1.000	
Depart	0.679	-0.036	0.357	0.714	1.000
Reside	-0.250	0.739	0.429	-0.321	0.286
Mean group	-0.321	0.306	-0.036	-0.071	0.286
Rel distance	0.821	-0.523	-0.071	0.964	0.643
SL	0.667	-0.773	-0.396	0.847	0.396
ASL	0.342	-0.755	-0.505	0.523	0.216
MNABUND	-0.464	0.847	0.241	-0.607	-0.000
	Reside	Mean grp	Rel dist	SL	ASL
Reside	1.000				
Mean group	0.250	1.000			
Rel distance	-0.250	0.000	1.000		
SL	-0.559	0.108	0.883	1.000	
ASL	-0.342	0.216	0.595	0.818	1.000
MNABUND	0.857	0.321	-0.536	-0.739	-0.595

Table 3.4. Matrix of Spearman correlation coefficients of mean values of behavioral variables, for each year, for juveniles, including spring/summer sandlance abundance (SL), average sandlance abundance (ASL), and whale abundance (MNABUND). Significant values (< .05) are highlighted.

	Near-boat	Lobtail	Breach	Feeding	Spyhop
Near-boat	1.000				
Lobtail	0.214	1.000			
Breach	0.179	0.357	1.000		
Feeding	-0.393	-0.107	-0.107	1.000	
Spyhop	0.143	-0.357	-0.750	-0.036	1.000
Social	0.464	0.357	0.036	0.107	-0.179
Flipper	0.321	-0.643	-0.179	-0.214	0.679
Resting	0.250	-0.071	0.286	-0.679	0.179
Arrive	0.179	0.357	0.464	0.393	-0.750
Depart	0.143	-0.571	0.321	0.321	-0.286
Reside	-0.071	-0.857	-0.393	-0.143	0.643
Rel distance	0.321	0.357	0.357	0.429	-0.464
SL	0.180	0.378	0.288	0.541	-0.541
ASL	-0.180	0.342	0.180	0.865	-0.324
Mean group	0.286	0.321	-0.286	0.179	0.286
MNABUND	-0.071	-0.857	-0.393	-0.143	0.643
	Social	Flipper	Resting	Arrive	Depart
Social	1.000				
Flipper	-0.357	1.000			
Resting	-0.643	0.571	1.000		
Arrive	0.571	-0.643	-0.571	1.000	
Depart	-0.071	0.286	-0.036	0.429	1.000
Reside	-0.357	0.857	0.321	-0.714	0.214
Rel distance	0.250	-0.393	-0.286	0.821	0.464
SL	0.414	-0.577	-0.541	0.919	0.396
ASL	0.234	-0.505	-0.613	0.887	0.216
Mean group	0.821	-0.143	-0.571	0.107	-0.429
MNABUND	-0.357	0.857	0.321	-0.714	0.214
	Reside	Rel dist	SL	ASL	Mean grp
Reside	1.000				
Rel distance	-0.679	1.000			
SL	-0.739	0.955	1.000		
ASL	-0.595	0.739	0.818	1.000	
Mean group	-0.107	-0.107	0.054	0.162	1.000
MNABUND	1.000	-0.679			-0.107

Table 3.5. Matrix of Spearman correlation coefficients of mean values of behavioral variables, by year, for adults, including spring/summer sandlance abundance (SL), average sandlance abundance (ASL), and whale abundance (MNABUND). Significant values (< .05) are highlighted.

	Near-boat	Lobtail	Breach	Feeding	Spyhop
Near-boat	1.000				
Lobtail	0.299	1.000			
Breach	0.090	0.679	1.000		
Feeding	-0.198	-0.393	-0.321	1.000	
Spyhop	-0.282	-0.450	-0.505	0.288	1.000
Social	0.144	-0.714	-0.286	0.606	0.288
Flipper	-0.252	-0.321	-0.643	-0.357	0.559
Resting	0.288	0.321	0.357	-0.964	-0.162
Arrive	0.703	-0.036	0.357	-0.107	-0.414
Depart	0.360	-0.179	0.429	-0.179	-0.018
Reside	-0.559	-0.786	-0.536	0.071	0.739
Rel distance	0.432	-0.321	0.214	0.071	-0.342
SL	0.627	0.090	0.378	0.252	-0.555
ASL	0.264	0.054	0.414	0.577	-0.209
Mean group	0.306	0.179	-0.000	0.536	0.487
MNABUND	-0.396	-0.643	-0.750	0.071	0.847
	Social	Flipper	Resting	Arrive	Depart
Social	1.000				
Flipper	-0.214	1.000			
Resting	-0.429	0.321	1.000		
Arrive	0.464	-0.571	0.250	1.000	
Depart	0.500	-0.357	0.393	0.821	1.000
Reside	0.321	0.643	-0.000	-0.321	0.107
SL	0.505	-0.811	-0.162	0.847	0.523
ASL	0.613	-0.811	-0.450	0.523	0.414
Mean group	0.321	-0.214	-0.393	-0.000	0.036
MNABUND	0.143	0.821	-0.036	-0.500	-0.179
	Reside	Rel dist	SL	ASL	Mean grp
Reside	1.000				
Rel distance	-0.107	1.000			
SL	-0.595	0.811	1.000		
ASL	-0.414	0.613	0.818	1.000	
Mean group	-0.179	-0.071	0.198	0.523	1.000
MNABUND	0.893	-0.393			-0.000

3.3. Variation in behavior with age-class

Mann-Whitney U test statistics indicated highly significant differences between age-classes in rates of near-boat behavior, lobtailing behavior, breaching behavior, spyhopping behavior, sociality, resting behavior, residence time, departure time and mean group size and significant relationships between age-class and rates of surface feeding behavior, flippering behavior and relative distance (Table 3.6). Juveniles generally appeared to approach boats, lobtail, breach, spyhop, flipper and rest more frequently than adults, while analyses indicated that adults surface fed more frequently and were more social. Juveniles appeared to leave the study area later and had a longer residence time than adults.

Box plots of age-class and rates of near-boat behavior, breaching behavior, lobtailing behavior and spyhopping behavior are shown in Figure 3.1; box plots of age-class and rates of resting behavior, surface feeding behavior, sociality and mean group size are shown in Figure 3.2; box plots of age-class and departure, residency, flippering behavior and relative distance are shown in Figure 3.3.

Table 3.6. Natural logs of mean scores for behavior by age-class with Mann-Whitney U Test statistics.

BEHAVIOR	JUVENILE	ADULT	MANN-WHITNEY STATISTIC
Near boat	.146	.079	MW=10089 P=<.001
Lobtail	.053	.042	MW=8963 P=.002
Breach	.121	.096	MW=9056 P=.003
Feeding	.127	.187	MW=6036 P=.010
Spyhop	.032	.020	MW=9119 P=<.001
Social	.467	.593	MW=4768 P=<.001
Flipper	.071	.063	MW=8411 P=.054
Resting	.083	.048	MW=9846 P=<.001
Arrive	5.028	4.910	MW=9066 P=.417
Depart	5.629	5.388	MW=11844 P=.004
Reside	4.640	4.023	MW=12199 P=.001
Mean group	1.058	1.147	MW=4792 P=<.001
Rel distance	1.303	1.594	MW=7943 P=.051

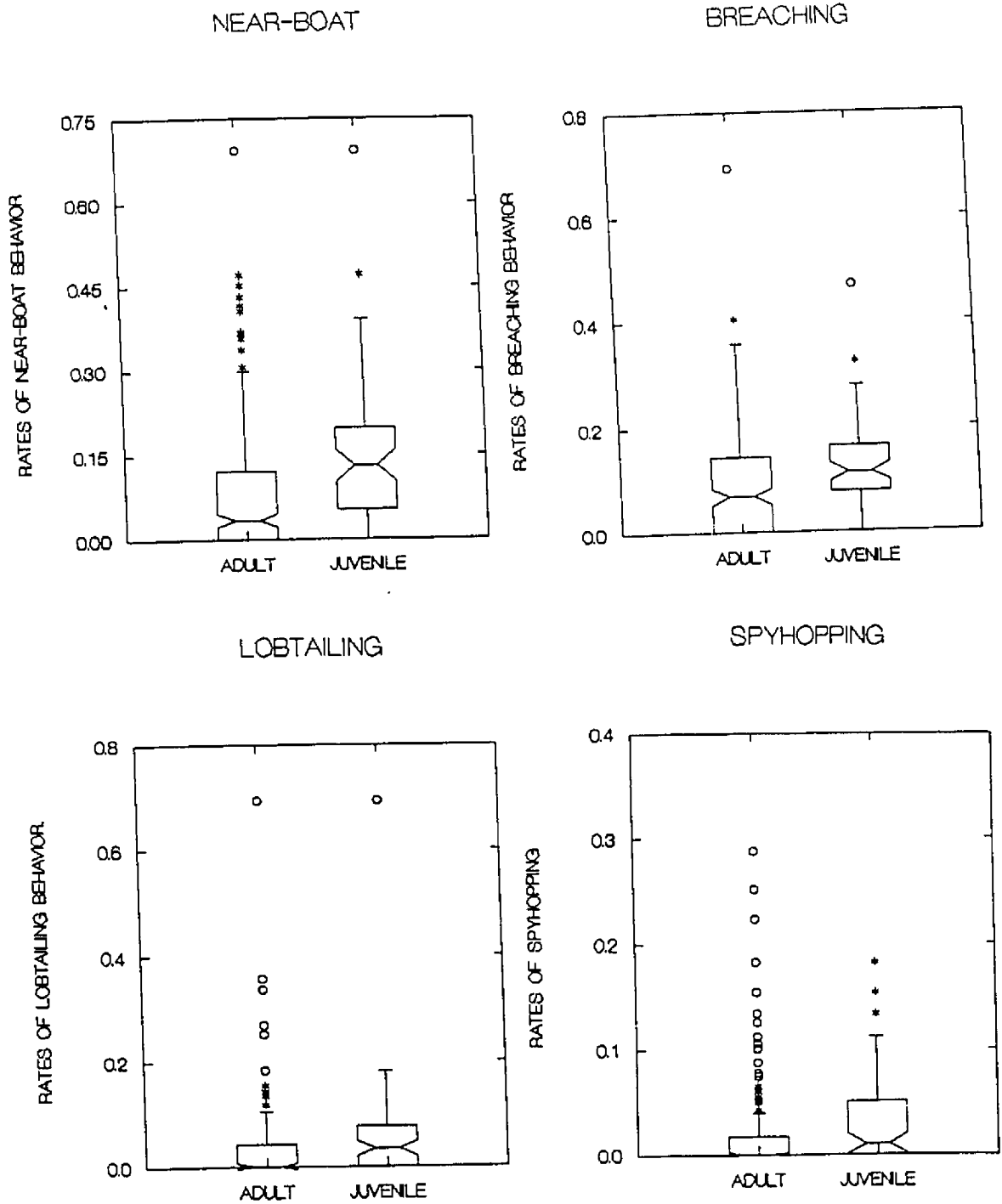


Figure 3.1. Box plots of rates of near boat behavior, breaching behavior, lobtailing behavior and spyhopping behavior by age-class. N=357.

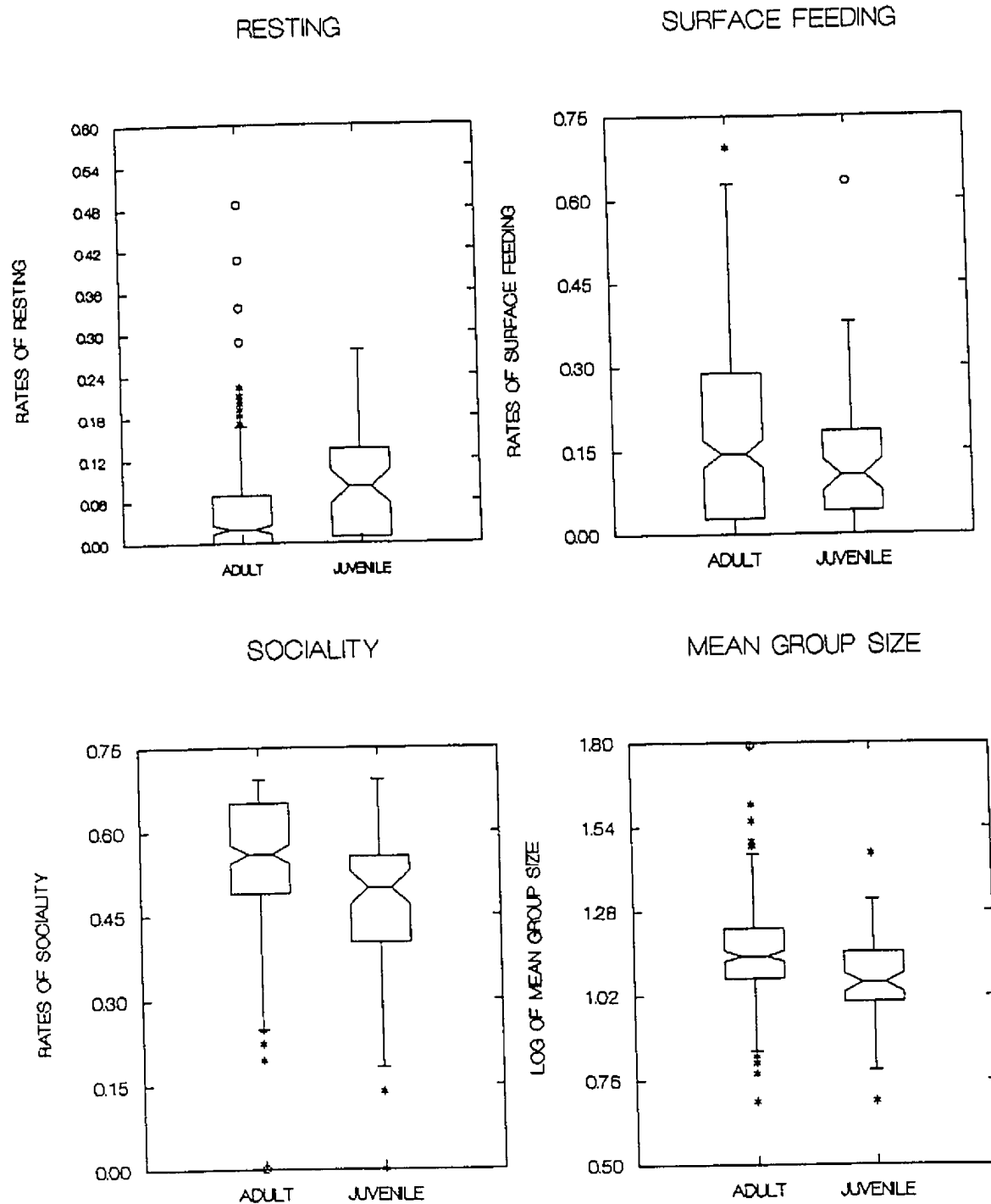


Figure 3.2. Box plots of rates of resting behavior, surface feeding behavior, sociality and mean group size by age-class. N=357.

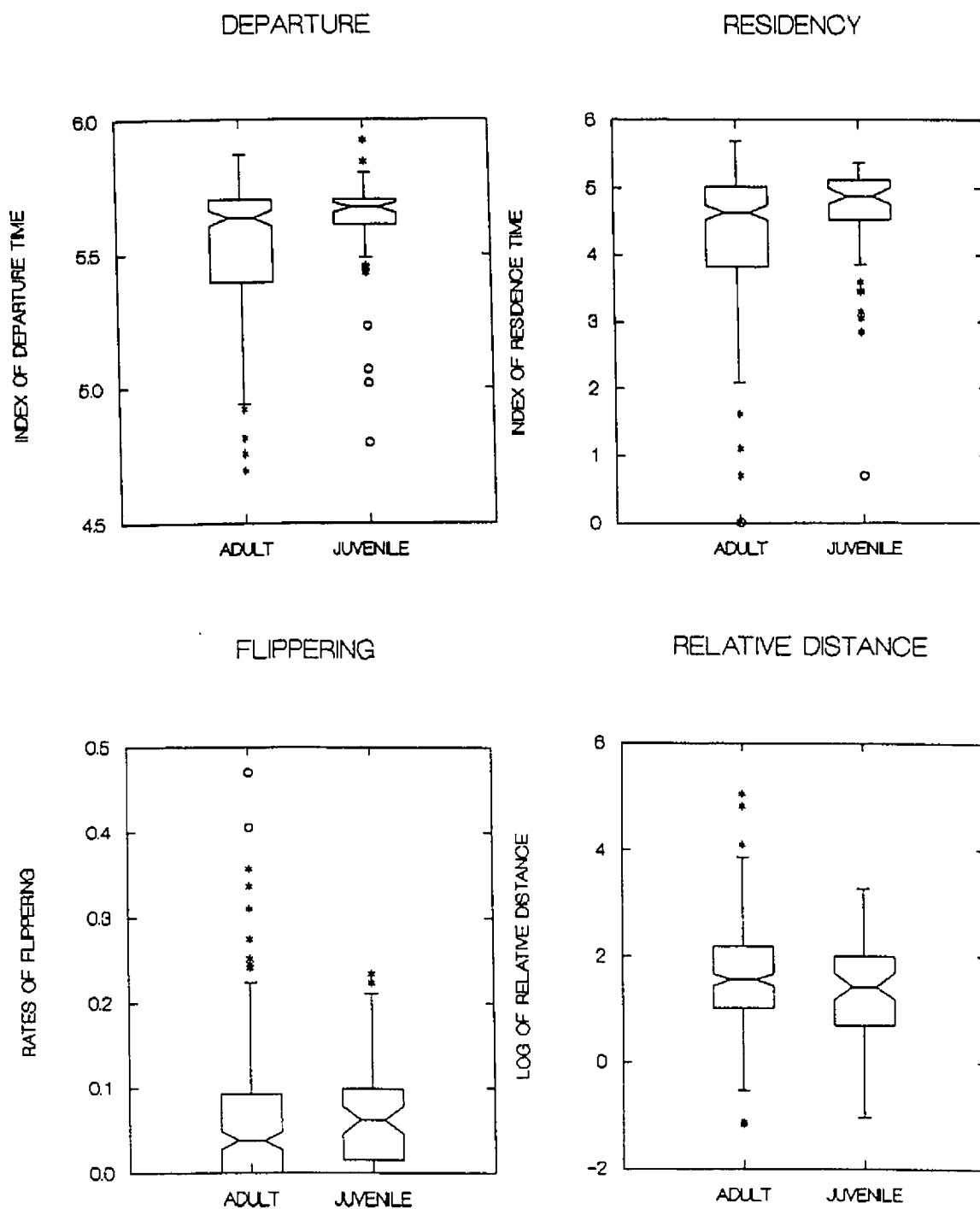


Figure 3.3. Box plots of rates of departure, residency, flipping, and relative distance by age-class.
N=357

The above analyses may be confounded by between year effects. In order to reduce these effects, two-way analysis of variance test statistics for behavior by age-class, by year were performed. The results of these analyses (Table 3.7) indicate highly significant differences between juveniles and adults for near-boat events, feeding events, sociality, resting, time of residence, time of departure, and relative distance from the centroid of whale distribution and significant differences between juveniles and adults for breaching events and mean group size.

Although between year effects will be discussed in section 4.3, it is of interest to note here that no significant differences in within-year sighting data was found for the occurrence of juvenile males, juvenile females, adult males or adult females during the study period (Clapham et al., in review).

Table 3.7. Two-way analysis of variance test statistics for behavior by age-class by year.

BEHAVIOR	JUVENILE/ADULT		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	18.093	<.001	3.483	.002
Lobtail	.585	.445	1.037	.401
Breach	6.145	.014	19.996	<.001
Feeding	6.892	.009	2.332	.032
Spyhop	2.327	.128	1.356	.232
Social	1.382	<.001	14.653	.222
Flipper	.867	.353	1.622	.141
Rest	7.927	.005	1.037	.401
Arrive	1.463	.227	1.550	.161
Depart	5.111	.001	.909	.489
Reside	10.204	.002	5.110	<.001
Mean group	5.178	.025	2.302	.039
Rel distance	6.862	.009	9.340	<.001

3.4. Variation in behavior with age

Mean scores for behaviors by age as well as Kruskal-Wallis statistics are shown in Table 3.8. Analyses indicate that the relationships between age and sociality and age and mean group size were highly significant with sociality generally increasing with age. The relationship between resting and age was significant; rates of resting were greater for younger whales than mature ones.

Sociality, mean group size, rates of resting behavior and surface feeding behavior were plotted against age in Figure 3.4. Although not highly significant (Table 3.8), rates of surface feeding behavior were plotted against age to determine if general trends exist.

Two-way analysis of variance test statistics for behavior by age, by year (Table 3.9), indicate highly significant differences by age for sociality and mean group size and a significant difference by age for resting events.

Table 3.8. Natural logs of mean scores for behavior by age with Kruskal-Wallis test statistics.

BEHAVIOR	AGE					KRUSKAL-WALLIS STATISTIC
	1	2	3	4	5+	
Near-boat	.161	.136	.140	.142	.155	KW=.920 P=.90
Lobtail	.034	.078	.040	.034	.037	KW=6.09 P=.193
Breach	.125	.131	.102	.104	.093	KW=2.73 P=.604
Feeding	.084	.132	.181	.132	.153	KW=8.95 P=.062
Spyhop	.032	.026	.042	.051	.031	KW=3.75 P=.442
Social	.411	.473	.537	.538	.533	KW=14.3 P=.006
Flipper	.061	.080	.072	.094	.083	KW=.386 P=.818
Resting	.107	.075	.060	.056	.034	KW=9.42 P=.051
Arrive	5.092	4.986	5.004	5.042	4.991	KW=2.93 P=.570
Depart	5.636	5.627	5.620	5.623	5.445	KW=7.74 P=.102
Reside	4.507	4.714	4.716	4.678	4.127	KW=1.47 P=.322
Mean group	.988	1.067	1.143	1.141	1.148	KW=18.0 P=.001
Rel dis	1.523	1.156	1.222	1.894	1.54	KW=4.53 P=.339

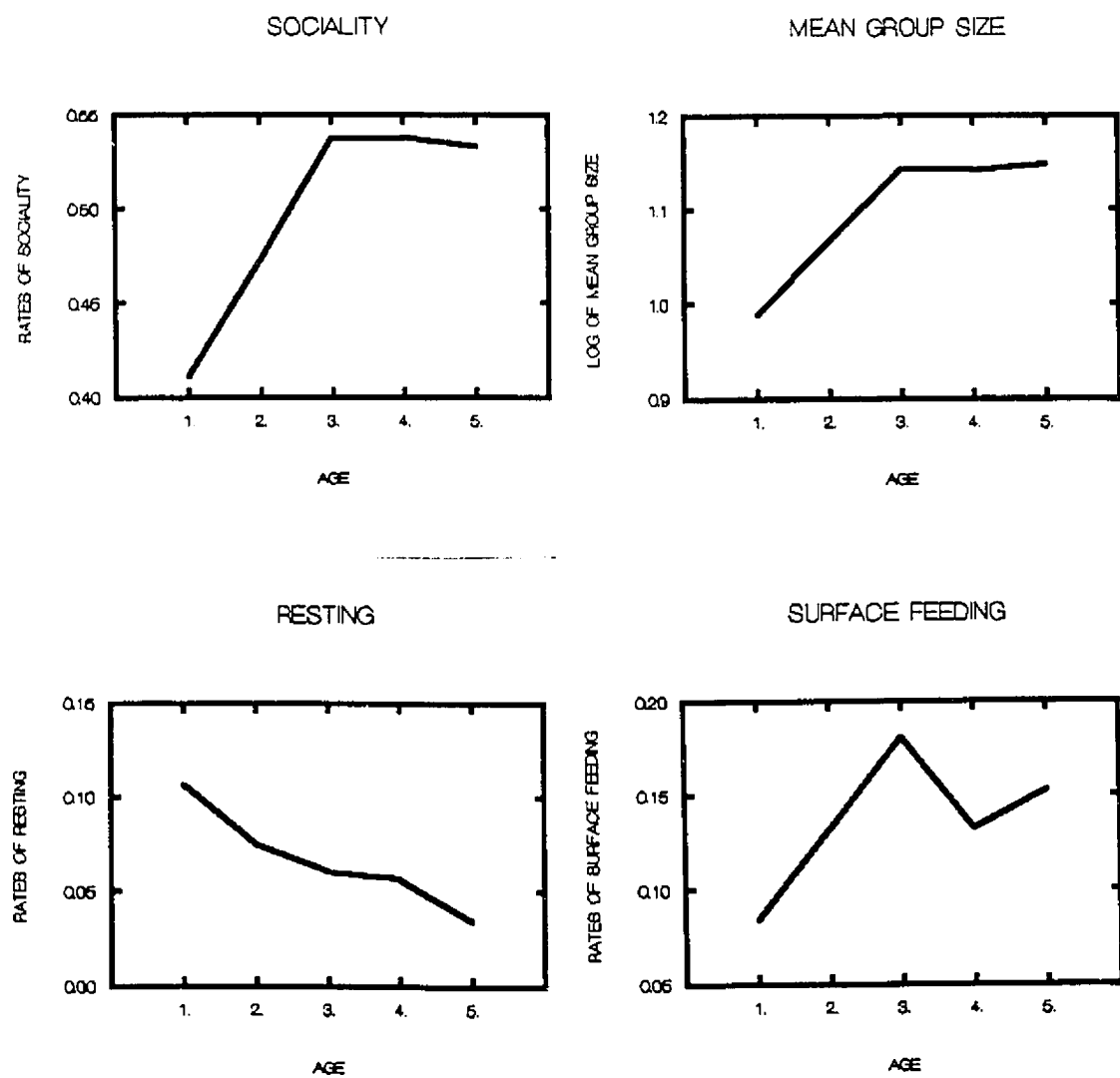


Figure 3.4. Sociality, mean group size, rates of resting behavior and surface feeding behavior plotted by age.

Table 3.9. Two-way analysis of variance test statistics for behavior by age, by year.

BEHAVIOR	AGE		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	.289	.884	.920	.485
Lobtail	.583	.676	1.316	.259
Breach	.778	.542	1.612	.154
Feeding	1.932	.113	1.409	.221
Spyhop	.764	.552	2.845	.014
Social	4.069	.005	.555	.765
Flipper	.545	.703	1.105	.366
Resting	2.851	.029	1.031	.411
Arrive	.379	.823	4.581	<.001
Depart	1.815	.134	2.289	.043
Reside	1.614	.178	1.027	.414
Mean group	5.217	.001	1.819	.105

3.5. Variation in behavior with gender

Mann-Whitney U test statistics and mean scores for behavior by gender are shown in Table 3.10. Results indicate a significant relationship between gender and rates of surface feeding, sociality and arrival time; males generally fed more and arrived later than females; females generally were more social than males.

Box plots of rates of surface feeding behavior, sociality, arrival and relative distance, by gender, are shown in Figure 3.5.

Two-way Analysis of Variance Test statistics for behavior by gender, by year (Table 3.11), indicate highly significant differences between males and females for time of arrival and departure and a significant difference for feeding events. Parametric statistics indicate significant differences between gender and rates of feeding, arrival time and departure time. The relationship between gender and sociality suggested by the non-parametric analysis may be confounded by between year effects.

Table 3.10. Natural logs of mean scores for behavior by gender with Mann-Whitney U test statistics.

BEHAVIOR	MALE	FEMALE	MANN-WHITNEY STATISTICS
Near-boat	.092	.103	MW=25090 P=.987
Lobtail	.045	.057	MW=25414 P=.785
Breach	.105	.113	MW=24869 P=.834
Feeding	.197	.169	MW=27431 P=.033
Spyhop	.026	.020	MW=23041 P=.072
Social	.509	.525	MW=28324 P=.018
Flipper	.067	.055	MW=22930 P=.108
Resting	.052	.061	MW=26366 P=.320
Arrive	5.101	4.895	MW=28122 P=.027
Depart	5.579	5.393	MW=29750 P=.217
Reside	4.184	4.019	MW=30926 P=.594
Mean group	1.113	1.120	MW=26246 P=.394
Rel distance	1.530	1.633	MW=33240 P=.099

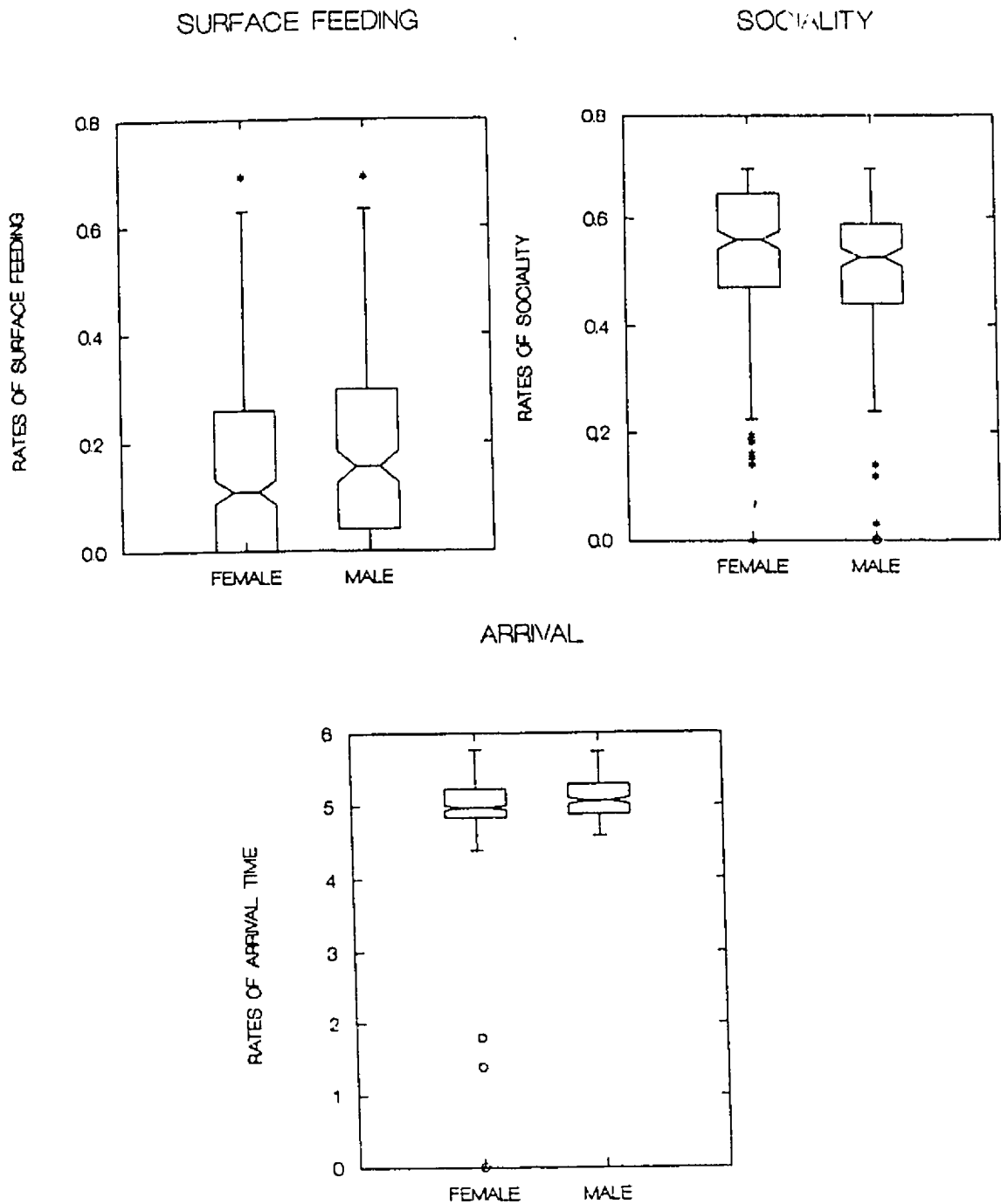


Figure 3.5. Box plots of rates of surface feeding behavior, sociality and arrival by gender. N=463

Table 3.11. Two-way analysis of variance test statistics for behavior by gender, by year.

BEHAVIOR	GENDER		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	.341	.559	4.033	.001
Lobtail	.307	.580	7.471	<.001
Breach	.609	.435	17.079	<.001
Feeding	4.640	.032	6.363	<.001
Spyhop	.632	.422	1.452	.193
Social	1.351	.246	1.889	.081
Flipper	1.413	.235	4.350	<.001
Resting	.875	.350	2.633	.016
Arrive	7.735	.006	5.986	<.001
Depart	7.183	.008	1.834	.091
Reside	.339	.561	10.250	<.001
Mean group	.268	.605	5.099	<.001
Rel distance	.668	.414	19.890	<.001

3.6. Variation in behavior with reproductive status

Mother-calf pairs breached and lobtailed more frequently than pregnant females, and arrived and departed from the study area later in the season while pregnant females were generally observed in larger groups and were more social (Table 3.12). Rates of breaching and lobtailing however, are confounded by the inclusion of calf behavior with that of the mother during field data collection. Since, in my data sets, it is impossible to separate the two, these relationships will not be considered in the discussion.

Box plots of rates of sociality ,mean group size, arrival and departure, by reproductive status, are shown in Figure 3.6.

Two-way analysis of variance test statistics for behavior by female reproductive status, by year (Table 3.13) indicate highly significant differences between pregnant and lactating females for breaching events, sociality, time of arrival and departure and a significant difference in mean group size.

Table 3.12. Natural logs of mean scores for behavior by reproductive status with Mann-Whitney U test statistics.

BEHAVIOR	LACTATING	PREGNANT	MANN-WHITNEY STATISTIC
Near-boat	.095	.071	MW=2309 P=.085
Lobtail	.052	.050	MW=2371 P=.034
Breach	.192	.118	MW=2688 P< .001
Feeding	.149	.192	MW=1835 P=.486
Spyhop	.014	.012	MW=2201 P=.175
Social	.307	.530	MW=3021 P< .001
Flipper	.048	.058	MW=2027 P=.797
Resting	.057	.059	MW=2035 P=.766
Arrive	4.828	4.609	MW=2876 P=.012
Depart	5.276	5.040	MW=3006 P=.002
Reside	3.819	3.620	MW=2618 P=.164
Mean group	.935	1.145	MW=2445 P< .001
Rel distance	1.498	1.712	MW=1681 P=.148

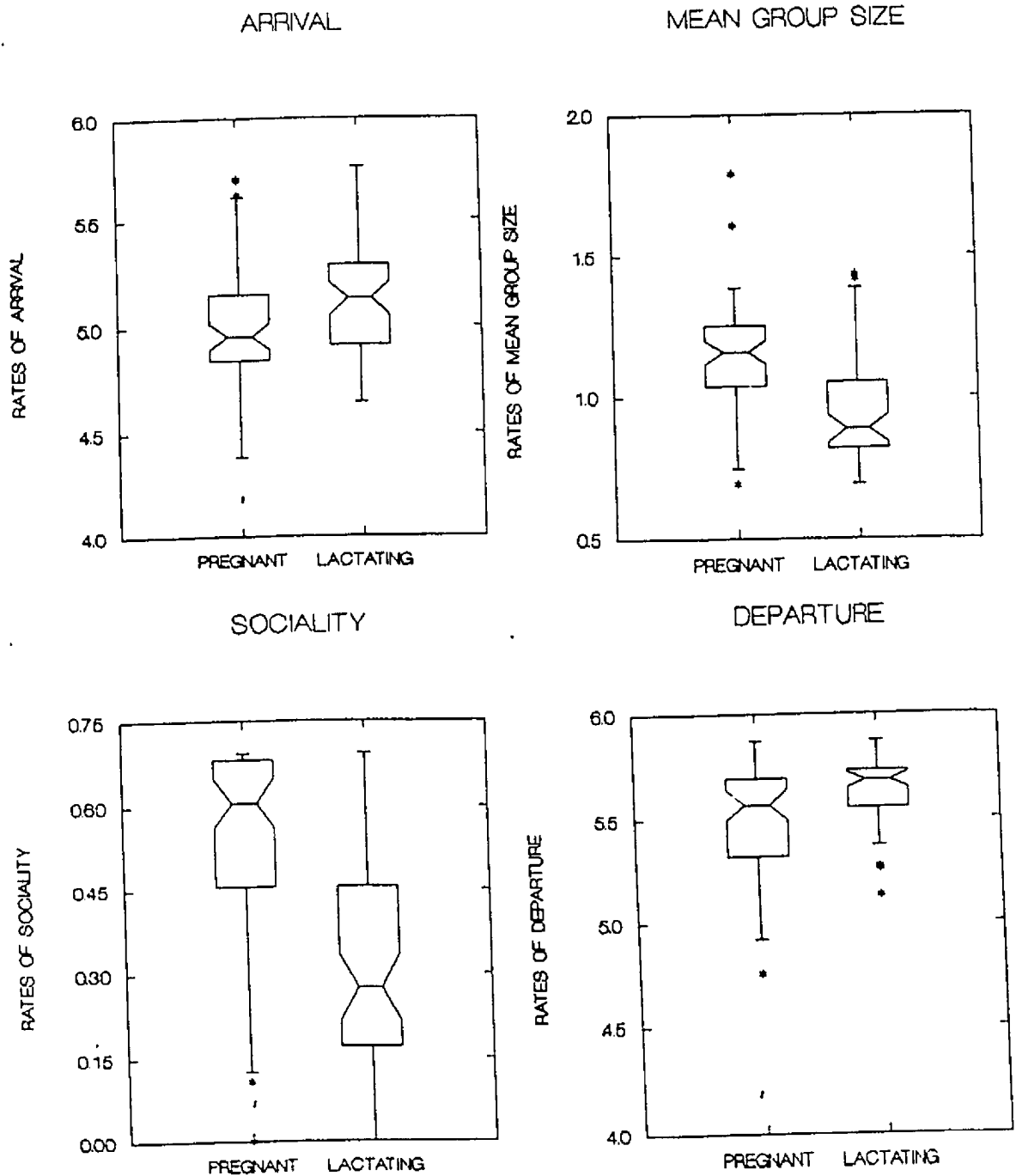


Figure 3.6. Box plots of rates sociality, mean group size, arrival and departure by reproductive status. N=136.

Table 3.13. Two-way analysis of variance test statistics for behavior by reproductive status by year.

BEHAVIOR	PREGNANT/LACTATING		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	1.220	.272	1.323	.253
Lobtail	.028	.868	2.320	.037
Breach	8.672	.004	15.928	<.001
Feeding	1.111	.294	1.611	.150
Spyhop	.086	.770	1.710	.326
Social	11.274	<.001	4.154	<.001
Flipper	.080	.350	1.330	.249
Resting	.069	.793	.605	.726
Arrive	9.979	.002	5.277	<.001
Depart	18.168	<.001	3.712	<.001
Reside	1.274	.261	4.137	.001
Mean group	3.565	.061	6.685	<.001
Rel distance	1.391	.241	7.100	<.001

3.7. Variation by year

The relationships between all behavioral measures and year were significantly different (Table 3.14). The year 1979 was characterized by higher rates of near boat and breaching behavior, whales were generally more social, arrived later and were a greater distance from the centroid of whale distribution. Rates of surface feeding behavior were highest during 1980 and 1981; during 1981, whales were generally further from the centroid of distribution. During 1982 flippering, resting, generally long residence times and greater distances from the centroid of distribution were higher. During 1983, rates of flippering and resting were high; whales generally departed earlier and were closer to the centroid of distribution. Long residency periods were characteristic of 1984 and 1985. Rates of spyhopping and flippering were high during 1985; whales generally stayed longer, were in larger groups and were closer to the centroid of distribution than they were in any other year tested.

Plots of rates of spyhopping behavior, breaching behavior, lobtailing behavior, flippering behavior, resting behavior and surface feeding behavior, by year, are shown in Figure 3.7; plots of rates of near-boat behavior, sociality, arrival, departure, residency and relative distance, by year, are shown in Figure 3.8.

Table 3.14. Natural logs of mean scores for behavior by year with Kruskal Wallis statistics (KW STAT).

BEHAVIOR	YEAR							KW STAT
	1979	1980	1981	1982	1983	1984	1985	
Near-boat	.157	.076	.121	.107	.078	.069	.112	KW=19.994 P=.003
Lobtail	.208	.071	.045	.038	.046	.026	.046	KW=23.255 P=.001
Breach	.356	.157	.086	.152	.109	.095	.077	KW=50.921 P<.001
Feeding	.127	.271	.255	.165	.128	.184	.159	KW=29.084 P<.001
Spyhop	.004	.016	.016	.027	.021	.017	.032	KW=38.468 P<.001
Social	.579	.537	.564	.544	.523	.525	.494	KW=22.794 P=.001
Flipper	.028	.014	.038	.070	.070	.059	.076	KW=71.556 P<.001
Resting	.070	.030	.038	.075	.071	.054	.055	KW=29.419 P<.001
Arrive	5.380	4.977	5.099	5.021	4.837	5.013	4.795	KW=76.320 P<.001
Depart	5.566	5.364	5.490	5.594	5.299	5.561	5.370	KW=65.721 P<.001
Reside	2.711	3.356	3.739	4.410	4.098	4.358	4.357	KW=45.986 P<.001
Mean grp	1.130	1.140	1.146	1.152	1.063	1.101	1.174	KW=34.812 P<.001
Rel dist	1.946	1.725	2.125	1.907	1.180	1.809	1.031	KW=110.43 P<.001

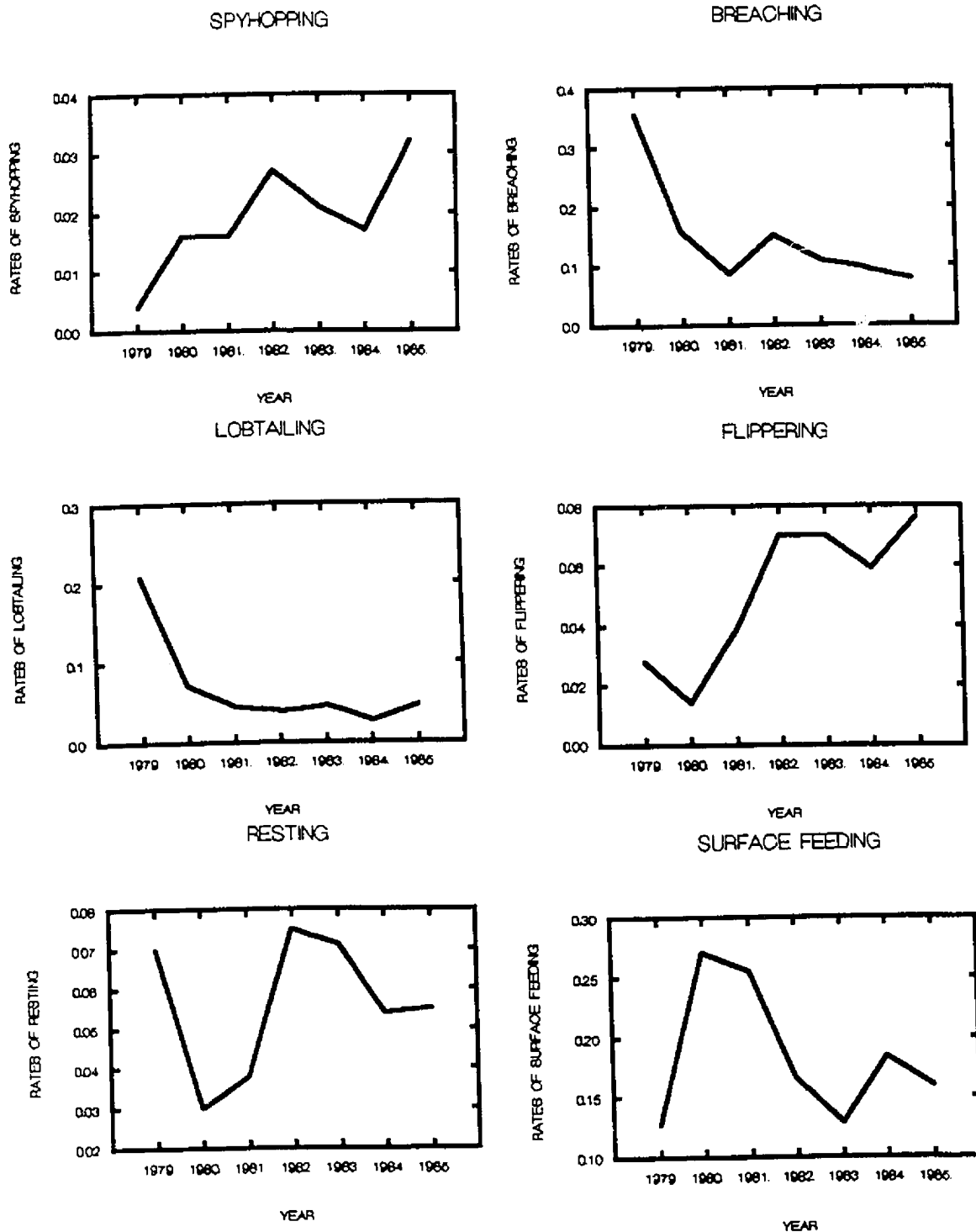


Figure 3.7. Rates of spyhopping behavior, breaching behavior, lobtailing behavior, flipping behavior, resting behavior and surface feeding behavior plotted by year.

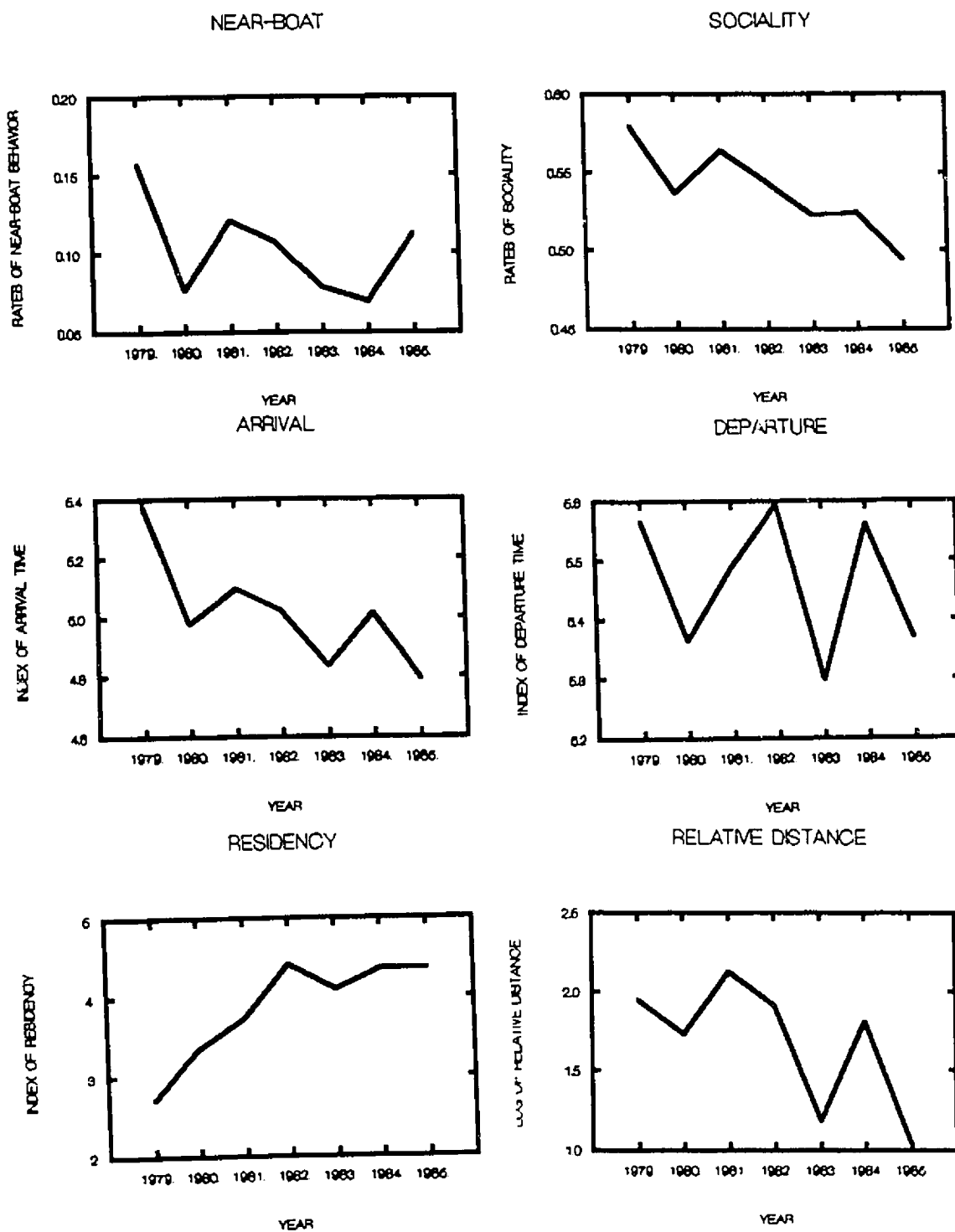


Figure 3.8. Rates of near boat behavior, sociality, arrival, departure, residency and relative distance plotted by year.

3.8. Variation in behavior by individual

Friedman two-way analysis of variance test statistics for behavior by individual whale, by year (Table 3.15), indicate significant differences between individuals for near-boat, breaching and feeding events, time of residence, mean group size and sociality. Individual females tend to vary their behavior more than males except for boat approaches and arrival time.

Results for behavior by individual females (Table 3.16) indicate significant differences between individuals for feeding events, sociality, time of residence and mean group size. Results for males (Table 3.17) indicate significant differences between individuals for near-boat events and time of residence.

Two-way analysis of Variance Test statistics for behavior by individual females by year (Table 3.16), indicate highly significant differences between females for near-boat events, sociality, time of departure and mean group size and significant differences for breaching and feeding events. Results for males (Table 3.17) indicate a highly significant difference for near-boat events and significant differences for feeding events, time of arrival and time of residence.

Table 3.15. Friedman two-way analysis of variance test statistics (FTS) for behavior by individual by year.

BEHAVIOR		MALES	FEMALES	ALL WHALES
Near-boat	FTS=	26.425	20.529	48.663
	P=	.023	.197	.023
Lobtail	FTS=	12.917	11.287	32.443
	P=	.533	.792	.396
Breach	FTS=	19.792	23.961	46.799
	P=	.137	.090	.034
Feeding	FTS=	16.483	27.562	51.165
	P=	.285	.036	.013
Spyhop	FTS=	11.775	17.327	29.347
	P=	.624	.365	.551
Social	FTS=	20.817	28.268	52.400
	P=	.106	.029	.010
Flipper	FTS=	19.722	21.000	42.295
	P=	.137	.179	.085
Resting	FTS=	18.333	22.078	41.867
	P=	.192	.141	.092
Arrive	FTS=	22.447	21.255	46.356
	P=	.070	.169	.038
Depart	FTS=	17.392	20.842	35.697
	P=	.236	.210	.257
Reside	FTS=	23.792	27.824	48.244
	P=	.049	.033	.025
Mean group	FTS=	18.733	26.268	47.286
	P=	.175	.050	.031
Rel distance	FTS=	17.333	24.680	41.212
	P=	.239	.076	.104

Table 3.16. Two-way analysis of variance test statistics for behavior by individual female, by year.

BEHAVIOR	FEMALE		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	3.321	.002	3.554	.041
Lobtail	.893	.549	4.884	.015
Breach	2.378	.021	1.440	.253
Feeding	2.374	.021	1.293	.289
Spyhop	.777	.691	1.995	.154
Social	2.758	.009	6.153	.006
Flipper	2.387	.020	2.411	.107
Resting	.919	.554	3.243	.053
Arrive	1.785	.086	2.432	.105
Depart	2.805	.008	4.259	.024
Reside	1.304	.260	.062	.940
Mean group	3.780	.001	30.326	<.001
Rel distance	1.896	.066	9.078	.001

Table 3.17. Two-way analysis of variance test statistics for behavior by individual male, by year.

BEHAVIOR	MALE		YEAR	
	F-RATIO	PROBABILITY	F-RATIO	PROBABILITY
Near-boat	3.447	.002	2.029	.149
Lobtail	.973	.504	.734	.489
Breach	1.827	.078	3.269	.052
Feeding	2.260	.028	1.725	.195
Spyhop	1.333	.244	.444	.645
Social	3.367	.331	.331	.721
Flipper	1.315	.254	1.078	.353
Resting	1.285	.271	.726	.492
Arrive	2.338	.023	7.952	.002
Depart	1.134	.371	20.460	<.001
Reside	2.173	.034	5.208	.011
Mean group	1.849	.074	3.107	.059
Rel distance	1.649	.119	1.873	.171

3.9. General highlights of results

- 1). Parametric (including year effects) and non-parametric (without year effects) tests generally agree in significance of effects.
- 2). Female humpback whales have generally darker flukes than males, while males show more parallel scars than females.
- 3). There appears to be little correlation between behavioral variables, except that individual humpback whales may be arranged on a continuum based on sociality that is interlaced with related behavioral variables (especially relative distance, spyhopping, flippering and residence patterns).
- 4). During years when sandlance abundance was high, individuals flippered and spyhopped less, arrived later and were a greater distance from the centroid of whale distribution.
- 5). During years when whale abundance was high, individuals spyhopped more, flippered more, breached less and stayed longer.
- 6). Rates of resting are generally lower as individuals approach maturity, while rates of sociality generally increase.
- 7). All behavioral variables showed significant differences between the years of the study.

- 8). There is more variation in rates of behavior between juveniles and adults than is found between any other classes of whales tested (male/female, pregnant/lactating, age-class).
- 9). There is more consistent variability in sociality, group size and feeding rates between classes of whales (juvenile/adult, male/female, age-class and lactating/pregnant) than was found for any of the other variables tested.
- 10). There are significant, consistent (over years) individual differences in behavior, particularly among females.

CHAPTER 4. DISCUSSION

4.1. Humpback whale behavior

Our understanding of whale behavior has greatly increased due to long-term field studies and the collection of quantitative, observational data. By examining the context of behaviors, various authors have discussed possible functions for specific activities (e.g. Tyack, 1982; Clark, 1983; Whitehead, 1985a,b; Waters and Whitehead, 1990). In this section, I will review the behavioral events examined in this study, compare them with similar activities in other species (when possible), and discuss their function in the context of the new data presented. Lastly, I will generally discuss between year differences in behavior.

4.1.1. Near-boat behavior

Near-boat approaches (Figure 2.2) have been observed in several species of cetaceans. Swartz (1986) reports that with light boat traffic in Laguna San Ignacio most gray whales, Eschrichtius robustus, are not disturbed and approximately 5% follow boats. Dalheim (1986) reports that the whales are primarily 'attracted' to small boats with idling engines. Norris et al. (1983) describe two encounters of gray whales approaching the 49m barkentine Regina Maris while she lay at anchor. The first encounter,

lasting approximately one hour, involved a juvenile of unknown sex, circling around the vessel and rubbing lightly against her hull. One to three additional animals, also juveniles, approached Regina from time to time, always staying outside the primary animal. Payne et al. (1983) report that in southern right whales, Eubalaena australis, near-boat approaches only follow slow advances by boats; approaches to almost stationary vessels was reported by Leatherwood et al. (1982) in Southern Hemisphere minke whales and Donovan (1982 ms) for Bryde's whales in Peruvian waters. Watkins (1986) described the reactions to boats of four species of baleen whales in Cape Cod bay; right whales Eubalaena glacialis, fin whales, Balaenoptera physalus, minke whales, Balaenoptera acutorostrata, and humpback whales. Over a period of years, gradual changes in reaction of the whales, varying with increased experience and levels of habituation, were recorded. Minke whales changed from 'frequent positive interest' to a relative lack of interest; fin whales changed from 'generally negative' to uninterested reactions, humpback whales dramatically changed from 'relative disinterest' to often 'strongly positive reactions'.

Humpback whales that feed off of Cape Cod have often been observed approaching vessels, particularly commercial whale watching vessels and small motor vessels that are idling or drifting. Near-boat approaches to commercial whalewatching

vessels have lasted for periods of over one hour. The duration of the approach is not always determined by the whale(s); on many occasions the vessels attempt to back away from the whale(s) in order to return to port or allow another vessel to approach.

Examining the possible costs and benefits of near-boat approaches is beyond the scope of this paper. However, on some occasions, the approaches appeared to serve a specific function. During the summer of 1989, a mature female (SA-1, Salt) and her calf, approached commercial whalewatching vessels. Salt would swim away from the vessel and dive for periods of time exceeding 15 minutes while the calf remained within a few meters of the hull. The behavior of the calf ranged from resting to surface active behaviors (e.g. breaching, lobtailing) to rolling-over or spyhopping. Salt would surface and orient to the calf, only to swim away after a few minutes, thus repeating the cycle. This general behavior was observed on more than one occasion and with other mother-calf pairs. It is possible that the idling vessel served as an acoustical indication of the calf's location. Near-boat approaches may involve active surface feeding by one or more individual whales as they feed upon thick shoal schools of bait fish that occasionally surface around and directly under drifting whalewatching vessels. Finally, in areas of moderate to heavy small-boat traffic, individual whales have been observed to orient close to the

hull of drifting whalewatching vessels, away from fast moving boat(s), especially if the boats are actively pursuing the whale.

Generally however, during near-boat approaches, one or more whales will circle around, or under the boat and various behaviors (e.g. flippering, breaching, lobtailing, spyhopping), which may at other times serve different functions, may be observed (Evans, 1987; Watkins, 1986). During this study, juveniles and mother/calf pairs approached boats significantly more than males, females, adults and pregnant females. It is of interest to note that both juvenile animals and mother-calf pairs are generally less social than other classes of whales. Watkins (1986) reported that 'young whales' would tend to investigate his vessel, even in the 'early period' of his study, when whales could be approached only occasionally. Similarities exist between Norris et al.'s (1983) description of two instances of near-boat approaches by juvenile gray whales and the majority of the approaches I have observed by juvenile humpback whales. Firstly, the object of the approach appears to be the hull of the vessel, especially below the waterline and towards the stern. They suggest the approaches could have had a sexual context, or the approaches of a juvenile to a mother whale. Secondly, in approaches involving two or more individual whales, one whale will oftentimes maintain an orientation closer to the

boat than the others; occasionally, this involves light aggression towards the other whale(s). Many of the near-boat encounters with whales during this study have involved light contact with the vessel; both dorsal and ventral orientations to the hull have been observed. Although there is no evidence to interpret this behavior as sexual, it is a possibility. C. Haycock (personal communication) described a 'sickly', abandoned, humpback calf that continually approached commercial fishing and whalewatching vessels with its mouth open and tongue visible. The calf appeared to be attempting to suckle on the hull of the vessel, lending some support to Norris et al.'s speculation of juveniles approaching a 'mother whale'.

It is important to note that near-boat behavior is not characteristic of whale populations in all areas. For example, Swartz (1986) reports that during the southerly migration, in areas of heavy small boat traffic, gray whales rarely follow boats and more often avoid them. Baker et al. (1982) studied the effect of vessel traffic on the behavior of humpback whales in Southeastern Alaska during the summer of 1981 and reported no vessel approaches. F. Cawthorn (unpublished data) reported that Tongan humpback whales instantly fled upon an approach closer than 25 yds., attributing this behavior to the use of dynamite by Tongan natives while hunting the whales.

Why whales approach and orient to boats is not clear. It appears that near-boat approaches serve various functions to different classes of whales in different areas during various aspects of their life cycle (feeding, breeding, migration).

4.1.2. Breaching, flipping and lobtailing

Breaching, flipping and lobtailing, shown in Figures 2.2, 2.3 and 2.4, respectively, constitute the surface active behaviors examined in this study (with the exception of feeding which is discussed separately in section 4.1.3). Scammon (1874) first described these behaviors as characteristic of the humpback whale, however, they have been reported in other species of cetaceans including southern right whales (Clark, 1983; Payne, 1990), bowhead whales (Wursig et al., 1986), gray whales (Norris et al., 1983), sperm whales (Waters and Whitehead, 1990), minke whales (Eds and MacFarlane, 1987) and killer whales (Balcomb et al., 1980). Although much speculation exists, the function(s) of these behaviors remain unclear.

Whitehead's (1985a,b) reviews of humpback whale breaching, flipping and lobtailing discusses many of the theories of aerial behavior and analyses their nature, context and hydrodynamics. Interpretations of the function of these behaviors are numerous. For example, it has been suggested that breaching may aid in the removal of parasites

(Beale, 1893), signify a reaction to excitation (Madsen and Herman, 1980), serve a social or communicatory role (Norris et al., 1983; Clark, 1983; Baker and Herman, 1984; R. Payne, 1990), be related to feeding (Mitchell, 1974; Pryor, 1986) or amusement and play (Beale, 1893; Pryor, 1986). Whitehead's analysis indicates that these surface active behaviors may have multiple functions; there appear to be strong correlations, both intra and interspecifically, with sociality in general.

Results of this study indicate that breaching and lobtailing behaviors are generally performed more by juveniles and mother-calf pairs than adults and that flippering is generally more common in juveniles. If breaching, flippering and lobtailing are correlated with sociality (e.g. aggression, signalling, courtship), they would be expected to occur in classes of animals that are generally more social, yet juveniles and mother/calf pairs are less social than the other classes of whales examined. Waters and Whitehead (1990) found that breaches and lobtails by sperm whales were often made singly and often in circumstances which appeared to be nonsocial and Wursig et al. (1986) report that breaches, lobtails and flipper slaps by bowhead whales were usually carried out by lone whales. As with sperm whales (Waters and Whitehead, 1990) and southern right whales (R. Payne, 1990), breaches and lobtails, particularly by juvenile animals, may be play. It

appears that the transition to adulthood is a time when individuals acquire skills that may be of intermediate and long-term benefit (Walters, 1987). Gentry (1974) observed adult-like behavior in 2 week-old sealions and concluded that play experience was a vehicle by which behavioral patterns present in the young are changed over time, manifesting themselves in the adult with extremely new functions.

Whitehead (1985a) reports on the seasonality of breaching behavior in humpback whales. He found that breaching is performed significantly more often in the winter than in the summer, and at times of important social interactions. Since mating and calving take place during the winter, social interactions then would be more important. The observations of juveniles performing these activities on the feeding grounds more commonly than adults may reflect the development of social patterns in the young as play and may indirectly support the general correlation with sociality.

4.1.3. Feeding

The feeding behavior of the humpback whale (Figure 2.3) has been described by many authors (eg. Jurasz and Jurasz, 1979; Hain et al., 1982; Weinrich et al.; 1985; Hays et al., 1985; Dolphin, 1987).

During this study, adults were observed surface feeding significantly more than juveniles, with males generally

feeding more than female whales. There was no significant difference in feeding rates between pregnant and lactating females.

Weinrich et al. (1985) examined habitat use patterns as a function of age and reproductive status in humpback whales. Juvenile whales generally appeared to be outside of the feeding groups in areas that probably were 'suboptimal' for feeding, however the rates of feeding were not discussed. The lower rate of feeding by juveniles may best be explained by the different energetic needs of juveniles and adult whales. Adults primarily invest in reproductive success while juveniles invest in the building of muscle tissue and general growth. The latter requires a much lower caloric input (Weinrich et al., 1985; Brodie, 1968).

It is more difficult to interpret the differences in feeding between male and female humpback whales; published, quantitative data on intersexual differences in prey size and prey preference are generally lacking. However Mizue (1949) observed no noticeable difference in food type between male and female right whales, blue whales and humpback whales; Oshumi (1979) suggested that female minke whales fed more actively than males. Kawamura (1970) concluded that the stomach contents of male sei whales were greater in weight and volume than females, but that females fed more often.

A major problem in interpretation is that the feeding events examined in this thesis are all surface feeding events. It is difficult to say what proportion of total feeding time, or its efficiency, that this behavior represents. It is also possible, as suggested by Weinrich et al. (1985), that certain classes of whales may feed in sub-optimal areas or in different depth stratas of the water column. This may represent less of a problem when comparing juvenile and adult feeding rates as there is a high negative correlation between feeding and resting. The feeding differences may reflect the fact that juveniles spend more time resting than adults. Finally, intersexual differences in feeding may also reflect the migratory nature of males and females, particularly pregnant females. It is possible that pregnant females have a greater feeding range and 'search' more than other classes of whales. Wursig et al. (1986) found that pregnant bowhead whales generally fed alone and Bogoslovskaya et al. (1981; 1982) report that pregnant female gray whales are the most common individual feeders. In other words, feeding is not all it appears to be on the surface.

4.1.4. Spyhopping

Spyhopping (Figure 2.4) has been observed in gray whales, bowhead whales, humpback whales, right whales, sperm whales (Pryor, 1986) and killer whales (Balcomb et al., 1980).

Unlike most whale behavior, few theories concerning the nature or function of spyhopping exist. In a review on non acoustical communication behavior of the great whales, Pryor (1986) reported that spyhopping is generally associated with visual inspection. L. H. Weilgart and H. Whitehead (personal communication) found a correlation between spyhopping and resting in sperm whales.

This study indicates that juveniles generally spyhop more than adults and that there is a slight tendency for males to spyhop more than females. Spyhopping is often observed, but is not correlated with near-boat approaches. This is most likely due to the fact the approaches are more characteristic of juvenile whales.

Although visual inspection of the air environment seems to be the most common interpretation of spyhopping, the whales' eyes are not always visible (C. Carlson, personal observation). Spyhopping therefore, may serve several functions. Whales resting in a vertical position, being slightly buoyant, may end up with part of their rostrum (snouts) above the surface of the water, or spyhopping may be the result of the maneuvering of a whale in an active social group or to a vessel. Quantitative observations for comparisons of spyhopping and group size in humpback whales are not yet available. Such data are necessary to further examine the nature of this activity, especially in a social context.

4.1.5. Low respiration or resting

Low respiration events or resting (Figure 2.2) in cetaceans has been described by many authors. McCormick (1969) described two types of resting behavior in bottlenose dolphins, Tursiops truncatus, and the Pacific white-sided dolphin, Lagenorhynchus obliquidens, the light and deep sleep phases. The deep sleep phase, by description, is similar to that observed in large baleen whales. Ljungblad et al. (1986) report on resting rates of bowhead whales in the northern Bering Sea, southern and coastal Chukchi Sea and the Beaufort Sea, Clark (1983) describes resting behavior of the southern right whale in Peninsula Valdes, Argentina, and Condy et al. (1978) describe the resting behavior of groups of killer whales, Orcinus orca at Marion Island (Prince Edward Island group). Norris et al.'s (1983) description of the resting behavior of gray whale mother-calf pairs in the breeding lagoons of Baja, California is similar to the reports of mother-calf humpback whales in Hawaii waters by Glockner-Ferrari and Venus (1983). The mother/calf pairs were observed to 'float', remaining 'quiet' for long periods of time. These accounts of resting behavior are, for the most part, descriptive and do not allow for interspecific or intraspecific comparisons.

This study indicates that juveniles rest significantly more frequently than adult whales, lactating females and pregnant females. Interpretation of these results is

difficult as there is a paucity of published, quantitative data on resting behavior.

Interspecific comparisons have been conducted on the sleep patterns of 69 species of mammals (Elgar et al., 1988). Their study shows consistent patterns of associations between sleep variables and aspects of a species morphology, metabolic rate and development. The time spent in 'quiet sleep' was negatively correlated with body size and basal metabolic rate. They suggest that the duration of quiet sleep may reflect foraging requirements of the species.

Juveniles and adult humpback whales differ, among other ways, in their energetic needs. As mentioned in section 4.1.3, adults primarily need energy for reproduction and the building of fat while younger whales need energy for the building of muscle tissue and growth. According to Brodie (1968), the development of muscle tissue requires a much lower caloric input. This may help to explain the negative correlation between feeding and resting and may lend support to the speculation by Elgar et al. (1988) that sleep may reflect foraging requirements.

The function of rest in juvenile whales is not clear and probably serves many functions. While one of the functions may be to facilitate growth and development, it is possible that the comparatively low caloric input needed by juveniles

and aspects of their sociality may have helped to maintain the resting behavior observed.

4.1.6. Sociality/ Mean group size

Alexander (1974) stated that ecological factors forming the evolution of social groups may fall in two main classes: predator pressure and resource distribution. Wrangham and Rubenstein (1987) added that it is important to recognize intraspecific competition as a third class.

Results of this study on sociality and group size indicate that there are distinct differences in the rates of sociality between different classes of humpback whales. Adults are generally more social than juveniles, females more than males and pregnant females more than lactating ones. With the exception of a few observations of long-term associations on feeding grounds (Baker et al., 1985; Weinrich et al., 1985) and the strong bond between mother-calf pairs (Whitehead, 1983; Clapham and Mayo, 1987), the nature of the associations appear to be casual. This type of association has been reported in other species. For example, Jarman and Southwell (1986) examined the sociality of eastern Grey Kangaroos, Macropus giganteus, and reported that group size is not limited by tight and closed associations of individuals (other than mothers and their young). Frequencies of associations varied between

individuals and even the most frequently associating individuals were not always found together.

What are the possible factors influencing sociality in humpback whales? Although predation risks have been reported as a possible factor influencing the formation of groups in some species of whales (e.g. Best, 1979; Arnborn and Whitehead, 1989), this does not appear to be a causal factor in the population of humpback whales in this study. There have been no reports of predator attacks (such as Orcinus orca) on humpback whales in the southern Gulf of Maine. Furthermore, although tooth scars have been observed on individual whales in this population, only two incidents of known whales observed with 'new' tooth marks have been recorded. In both cases, the individuals were lactating females returning with calves and had clearly been attacked by a predator (C. Carlson, personal observation). The scars on the females were healed, indicating that the attack may have occurred on the breeding grounds or during the migration north.

More probable is the influence of resource distribution and prey patch size. This has been demonstrated in a number of species (e.g. Kummer, 1971; Jarman, 1974; Vehara, 1986; Wrangham, 1986) including whales. Wursig et al. (1986) report that bowhead whales occur in aggregations and are not randomly distributed on the feeding grounds. The size and distribution of these aggregations changes dramatically from

year to year and appears to be related to the general productivity of the area. Whitehead (1983) reported that the group size of humpback whales off Newfoundland was correlated with the size of the prey schools they were feeding on. This 'casual' sociality during feeding has also been observed in chimpanzees (Reynolds, 1965) where groups of variable sizes break-up and re-form, apparently in direct response to the availability of food.

Examining the factors that may affect sociality in humpback whales may be related to, but is not the same as examining why there are differences in sociality between various classes of whales. In this study, sociality is generally correlated with age. As an individual humpback whale approaches sexual maturity, its rate of social interactions and feeding generally increases while rates of resting decrease.

The sociality of pregnant and lactating humpback whales on low-latitude breeding grounds is markedly different from that observed on high-latitude feeding grounds. Mobley and Herman (1985) report that groups of whales with calves were generally characterized by a triad of mother, calf and 'escort', generally a male (Glockner-Ferrari and Ferrari, 1985; Mobley and Herman, 1985). When no calf was observed, singletons and pairs were most frequently seen. Furthermore, groups with a calf would tend to take on new members far more readily than to lose them. Herman and

Antinoja (1977) and Glockner-Ferrari and Ferrari (1985) also report a high incidence of accompaniment of mother-calf pairs on the Hawaiian breeding grounds. Tyack and Whitehead (1983) proposed that the 'escorts' in breeding areas may be mature males seeking access to estrus females. This has generally been supported by recent data (e.g. Glockner-Ferrari, 1985; Mobley and Herman, 1985). By contrast, there is a low incidence of accompaniment of mother-calf humpback whales in feeding areas (Nemoto, 1964; Weinrich et al., 1985; Clapham and Mayo, 1987). This may be partly explained by the fact that opportunities for a mature male to mate with a female are presumably generally restricted to winter breeding areas. It is also possible that the low incidence of associations by mother-calf pairs on the feeding grounds may help to reduce feeding competition. Segregation of mother/calf pairs on summer feeding grounds has been reported by Wursig et al. (1986) in bowhead whales, Ljungblad et al. (1985) in gray whales and Kasamatsu and Ohsumi (1981) in minke whales. It is more difficult to explain why pregnant females are significantly more social than mother-calf pairs. One advantage of an associate might be to enhance acoustical vigilance for feeding whales. Using this information may direct attention to the area where a group of whales are successfully foraging and may therefore enhance feeding efficiency. It seems unlikely that forming an association would greatly increase feeding

competition, as humpback whales are often observed in pairs. Whitehead (1983) and Clapham and Mayo (1987) report that the majority of observations, excluding feeding groups, of humpback whales on the feeding grounds were of single animals or pairs.

Results of this study further show that females are generally more social than males. It is possible, that in females, an associate may help to increase feeding efficiency while the feeding strategy of males may be to actively search for productive areas within their feeding range. As female reproductive success is generally related to absolute food intake, and male reproductive success to relative (to the other males) food intake, it may pay males to adopt the risky strategy of searching in more unusual places for large prey concentrations which would not be discovered by other males. It is also possible that males may be more efficient at feeding than females as reported by Kawamura (1970) in sei whales.

4.1.7. Arrival, departure and residency

Age and sex-related segregation during the migration of baleen whales from summer feeding grounds to winter breeding grounds has been described by many authors. Rice and Wolman (1971) and Swartz (1986) report on temporal segregation of gray whales on migrations to and from the lagoons at Baja, California. Late pregnant females lead the southward

migration followed by resting females, immature females, adult males and lastly immature males. The northward migration is led by newly pregnant females, followed by adult males, anoestrus females, immature males and finally, mother-calf pairs. Clark (1983) reports that the succession of arrival for southern right whales in Golfo San Jose, Peninsula Valdes, Argentina, is similar to that described for gray whales. Immature and female sei whales are observed early on the breeding grounds (Gambell, 1968) with a predomination of mature whales and males later. Pregnant females are the first to leave for the polar feeding grounds. In blue whales and fin whales (Mackintosh, 1942; Laws, 1961), male and pregnant females are the first to arrive in the Antarctic, followed by resting females and finally, mother-calf pairs. The order of the return migration is the same with post-lactation females joining the resting class. Best (1982) noted that minke whales show a segregation by sex during their winter migration with mature males outnumbering the females by more than 2 to 1, and a segregation by size in females with mature females arriving later than immature ones. Chittleborough (1958) and Dawbin (1966) describe known migratory routes of Southern Hemisphere humpback whales. They report that lactating females with their weaning calves led the migration to the breeding grounds followed by immature whales, mature males and resting females and finally,

females in late pregnancy. The return migration is led by females in early pregnancy, followed by immature whales, resting females and mature males, and lastly, mother/calf pairs.

The results of this study generally indicate that females arrive earlier than males, adults arrive earlier than juveniles and pregnant females arrive earlier than mother-calf pairs. Results further indicate that pregnant females are the first to arrive on the feeding grounds and suggest that adults generally leave earlier than juveniles, females generally leave earlier than males, and pregnant females generally leave earlier than mother-calf pairs. My analysis of residency time indicates that juveniles generally remain longer than adults, males remain slightly longer than females, and mother-calf pairs remain longer than pregnant females.

It is difficult to discuss the succession of arrival, departure and residency time in the context of these results considering the nature of the observations. Recorded observations of arrival and departure indicate the dates that an individual whale was first and last photographed. They do not necessarily indicate the actual date that the individuals arrived from or left for the breeding grounds. Coverage of the study area before April and after October in most of the years of this study was minimal and it is also

possible that other humpback whales were present in areas that we were not able to survey.

It may be of interest however, to examine the general trends of a specific class, pregnant and lactating females, in the context of the data presented and existing knowledge of the feeding range and distribution of this population of humpback whales. The early sightings of pregnant females in the study area is in agreement with Dawbin's (1966) account of the early arrival of females on the feeding grounds. Yet, contrary to Dawbin's finding, pregnant females generally leave the study area earlier than mother/calf pairs. Considering the energetic needs of pregnant females this appears to be counter-intuitive, less the nature of the study area and movements of individuals are examined. Clapham and Mayo (1987) report that mature females were observed significantly more frequently (on a greater number of days) in years when they had a calf than in years when they did not. Furthermore, pregnant females, observed off Brier Island, Nova Scotia, are often observed on Stellwagen Bank in years when they have calves (C. Haycock, unpublished data). It is possible that the apparent early departure of pregnant females from the study area actually reflects their greater feeding range and search activities than those shown by mother-calf pairs. Learning the broad range of traditional feeding grounds may make them more adaptive to prey changes. For example, Bi-2 (Binoc) was observed on a

number of occasions feeding on northern Stellwagen Bank during the summers of 1980, 1981 and 1982. Her distribution pattern and residency time changed dramatically during 1983 when she was observed feeding on both northern and southern Stellwagen Bank during spring summer and fall. Binoc returned in 1984 to southern Stellwagen with her first observed calf. Finally, Stellwagen Bank may be an optimum area for mother-calf pairs as it provides them with shallow waters, an adequate food supply, and general freedom from predators (e.g. Orcinus orca) while the adjacent near-shore waters may provide some protection from rough weather (Clapham and Mayo, 1987).

4.1.8. Relative distance

Relative distance (in the context of this study), defined as the average distance of the individual from the centroid of the positions of all animals sighted that year, is described in detail in section 2.9.

Some of the literature on the distribution of baleen whales generally examines segregation by age, sex or reproductive status. Norris et al. (1983) and Swartz (1986) discuss the marked segregation of mother/calf gray whales in the breeding lagoons and Swartz (1986) details segregation on the feeding grounds. Mother-calf gray whales in Laguna San Ignacio differ in their distribution, swimming patterns, group size and residency from other classes of animals.

Although they routinely travel the length of the lagoon, they tend to concentrate in areas away from those frequented by other whales. Norris et al. (1983) states that the activity of the sexually active groups may be disruptive to mother-calf pairs and may even cause separation. Segregation also exists in the Arctic feeding grounds. Ljungblad et al. (1985) reported mother calf/pairs distributed in specific near-shore areas of the northern Bering and eastern Chukchi Seas; Yablokov and Bogoslovskaya (1984) describe age differentiation of a stock, with young animals congregated near the Koyak coastline while groups of adults were found in more northerly waters; Bogoslovskaya et al. (1982) report that Soviet whaling records indicate that small animals predominated the catches from specific coastal waters, mother-calf pairs were distributed in shallow coastal waters and larger animals were found offshore. The segregation of gray whales appears to be a behavioral characteristic that prevails throughout the species range (Swartz, 1986). Wursig et al. (1986) report that bowhead whales, in the Canadian Beaufort Sea, occur in aggregations with a tendency for mother-calf pairs to be segregated from other whales. Clark (1983) found that mother/calf southern right whales reside in shallow water and are segregated from other groups which generally remain offshore; Kraus and Prescott (1985) report a spatial segregation in North Atlantic right whale mother-calf pairs from the more active

groups offshore. Kasamatsu and Oshumi (1981) conclude that Southern Hemisphere minke whales show temporal and spatial intersexual segregation on high latitude feeding grounds. Males are more abundant in lower latitudes while females are observed more frequently in higher latitudes, near the ice edge. Also, mother/calf pairs are only observed in temperate waters at lower latitudes during this season. Tarasevich (1967) reports that North Pacific fin whales form a variety of groupings on the feeding grounds, with males generally forming larger groups than females. Larger, older, mature fin whales occur alone or in groups of their own sex, while smaller and younger, mature animals generally occur in mixed groups. Jurasz and Jurasz (1979) and Baker et al. (1985) report that segregation by size, age, sex or reproductive condition in humpback whales on Alaskan feeding grounds was not observed. Goodale (1981) examined latitudinal and longitudinal distribution between humpback whale mother-calf pairs and animals without calves between Cape Hatteras, North Carolina and Nova Scotia. Significant differences between the two classes was found in the water depth, with mother/calf pairs found significantly more in shallow water. Weinrich et al. (1985) conclude that the humpback whale population of Stellwagen Bank and Jeffreys Ledge (Massachusetts) is comprised of three components: surface feeding groups, juveniles and mother-calf pairs.

They report that the groups are often present in different temporal and spacial patterns.

Results of this study indicate that adult whales are significantly further from the centroid of whale distribution than juvenile animals and that (although not highly significant) females are on average further than males.

The segregation of juveniles from adult animals generally support the findings of Weinrich et al. (1985), unless the centroid of whale distribution is coincident with areas of heavy surface feeding activity. These data indicate that this is probably not the case as adult whales were observed surface feeding significantly more than juvenile animals. It may better be explained by the general use of the study area during the duration of this study. Although Stellwagen Bank is an important area for humpback whales (Mayo, 1982), distribution and habitat use vary from year to year. On many occasions, juvenile whales were observed in the area for a number of consecutive days when no known adult whales were observed (C. Carlson, personal observation) while large, surface feeding aggregations were reported to the north and/or southeast of the study area. It is possible that juvenile animals generally roam less and establish more defined seasonal ranges than do mature animals whose energetic needs may require searching for productive areas

in a patchy environment. Some evidence for seasonal 'site tenacity' by juvenile animals is reported by Mayo (1982).

The fact that mother-calf pairs do not generally appear to segregate from other classes of whales is in agreement with the observations of Jurasz and Jurasz (1979) and Baker et al. (1985), but does not necessarily disagree with the findings of Goodale (1981). This may reflect the fact that Stellwagen Bank, a generally heavy use area for whales, also provides mother-calf pairs with a number of advantages, including shallow water. This is detailed in section 4.1.7.

There appears to be a slight tendency for females to be further from the centroid of whale distribution than males. This may reflect, in part, the possibility that pregnant females roam more (section 4.1.7) or that the behavior of individual females generally varies more than that of males (section 4.2). Wursig et al. (1986) observed that pregnant bowhead whales generally fed alone, which would, in part, explain this finding. Unfortunately, for my study, quantitative data on feeding group size and composition are lacking. Furthermore, the centroid of whale distribution as defined in this study, is the centroid of distribution as found by the whalewatching vessels.

4.2. Individual differences in behavior

Differences in the behavior of individuals have been reported in a variety of species (e.g. Lopez, 1978; Clutton-

Brock et al., 1982; Armitage, 1986; Goodall, 1988). Studies of this nature, particularly in baleen whales, are generally lacking. However, a few studies have begun to examine behavioral differences between individual whales. D'Vincent et al. (1989) studied cooperative lunge feeding among groups of humpback whales off southeast Alaska. They report that the groups were characterized by tightly clumped individuals that appeared to follow the cues of 1 or 2 lead individuals, rather than relying on combined sensory integration of all members during lunge feeding events. Hoeltzel et al. (1989) collected data on 23 individually identifiable minke whales around the San Juan Islands. Most individuals specialized on one of two feeding strategies that were consistent over a period of 5 years. Each strategy was associated with a particular feeding area. They suggest that the individual specializations represent learned strategies and are adapted to variations in the distribution of the same prey species. Hays et al. (1985) report on a unique feeding strategy of an individual humpback whale in the presence of other 'normally feeding' whales, suggesting that individual whales may utilize several techniques in an effort to concentrate prey. The whale, a female named Cats Paw, has been observed off Cape Cod, Massachusetts since 1982 and can be readily identified by her distinct, consistent style of feeding. Schilling et al. (1991), reported on the spread of a novel feeding behavior, lobtailing before feeding (LTA), from 1980

to 1989. 12.5% of the whales first photographed before 1982 were observed LTA feeding as opposed to 56.2% first photographed after 1982.

Results of my study indicate that there are significant differences between individuals for rates of near-boat, breaching and feeding events, time of residence, mean group size and sociality and that females tend to vary their behavior more than males.

Although it is beyond the scope of this study to analyze the behavior of individual humpback whales in terms of costs, benefits or individual life strategies, data on individual differences in behavior may have more than academic applications.

Individual behavioral differences may have profound importance for the management of marine mammals threatened by pollution and/or commercial fisheries (Harwood, 1990). Harwood states that management policies will have to recognize the variability between individuals and not focus on "a mythical average seal or whale". Variable levels of bioaccumulating environmental contaminants in individuals of the same sex and age group from a particular area may be the result of individual foraging strategies. Harwood further states that the development of modern techniques such as biopsy sampling and telemetry may lead to the identification of "pollutant hot-spots".

Finally, culling marine mammals that may be accused of competing for fish resources with commercial fisherman may not solve the perceived problem, particularly if individuals are developing different feeding strategies and the cull does not target the "offenders".

4.3. Between-year differences in behavior

The behavioral variables examined showed significant differences between all years of this study. This is hardly surprising considering the variable and unpredictable environment of humpback whales. To examine these differences fully, it would be necessary to construct a matrix which would include a vast number of physical, biological and behavioral variables. Clearly, it is beyond the scope of this thesis to attempt such a task. It is possible however, to begin to address these differences by examining possible relationships between all behavioral variables and sandlance abundance and whale abundance.

4.3.1. Sandlance abundance

Although the humpback whale has been described as a generalist in feeding habits (Mitchell, 1974), recent observations of feeding humpbacks in the Gulf of Maine indicate that sandlance have become an increasingly important prey species (Hain et al., 1982; Mayo, 1982) and the only prey species significantly correlated with humpback

whale distribution in the Gulf of Maine between 1978 and 1982 (Payne et al., 1986; 1990). Strong correlations between the distribution of humpback whales and density and distribution of particular prey has also been reported in other areas (eg. Lien and Merdsoy, 1979; Whitehead and Carscadden, 1985).

Results of this study indicate that during years of high sandlance abundance, individual whales flippered and spyhopped less, arrived later and were a greater distance from the centroid of whale distribution.

The distance of whales from the centroid of whale distribution may well reflect the distribution of prey, as Payne et al. (1986; 1990) have concluded from their analysis. Late arrival may suggest that individuals from the Gulf of Maine stock spend time feeding in offshore or more southerly waters before arriving in the Stellwagen area. This would support Kenney et al.'s (1981) suggestion that, for the Gulf of Maine stock, the Great South Channel is the major exit/entry between the Gulf of Maine feeding area and the deeper, offshore migration route. Correlations with prey abundance and flippering and spyhopping are more difficult to speculate on as the function(s) of these behaviors remain unclear. It is possible however, that flippering, if used as a "signal", is more functional when there is less distance between individual whales, particularly adults (Table 3.5).

Additionally, juveniles surface fed significantly more during years when prey abundance was high (Table 3.4). This may indirectly support the findings by Weinrich et al. (1985) that juveniles generally appear to be in "sub-optimal" areas or feed in different areas of the water column.

4.3.2. Whale abundance

Whale abundance was negatively correlated with breaching and positively correlated with spyhopping, flippering and long residency time. There is a significant negative correlation with breaching and whale abundance and a significant positive correlation with spyhopping and whale abundance in adults, while there is a significant negative correlation between lobtailing and whale abundance in juveniles. Interpretation of these data is difficult; as mentioned earlier, the function of these surface behaviors remains unclear.

Furthermore, interpretation of these data in general are complicated by the complexity of the relationships of the numerous variables that may affect between-year differences in behavior.

CONCLUSIONS

Information on the differences in behavior of classes of whales, as presented in this thesis, should be of importance to future behavioral studies examining the function(s) of behaviors which remain unclear. Furthermore, this work may serve as a model of how to compare various classes of individuals in other whale studies.

Lastly, individual behavioral differences may have important management implications. Management policies should begin to recognize the variability between individuals and not focus on an "average whale". For it is clear that sound management policies are necessary for the survival of species, particularly one as endangered as the humpback whale.

APPENDIX I

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
ABRAXUS	AB1	1980	F	U	U	U
ABRAXUS	AB1	1981	F	U	U	U
ABRAXUS	AB1	1982	F	U	U	U
ABRAXUS	AB1	1983	F	P	U	A
ABRAXUS	AB1	1984	F	L	U	A
ABRAXUS	AB1	1985	F	U	U	A
AGASSIZ	AG1	1979	M	U	U	U
AGASSIZ	AG1	1980	M	U	U	U
AGASSIZ	AG1	1981	M	U	U	U
AGASSIZ	AG1	1982	M	U	U	A
AGASSIZ	AG1	1983	M	U	U	A
AGASSIZ	AG1	1984	M	U	U	A
AGASSIZ	AG1	1985	M	U	U	A
ALPHORN	AL3	1984	M	U	1	J
ALPHORN	AL3	1985	M	U	2	J
ALTIPLANA	AL1	1979	F	U	U	U
ALTIPLANA	AL1	1980	F	U	U	U
ALTIPLANA	AL1	1981	F	U	U	A
ALTIPLANA	AL1	1982	F	U	U	A
ALTIPLANA	AL1	1983	F	U	U	A
ALTIPLANA	AL1	1984	F	P	U	A
ALTIPLANA	AL1	1985	F	L	U	A
ANCHOR	AN1	1984	F	U	1	J
ANCHOR	AN1	1985	F	U	2	J
APALOOSA	AP2	1983	F	U	U	U
APALOOSA	AP2	1984	F	U	U	U
APALOOSA	AP2	1985	F	U	U	U
APEX	AP1	1982	F	P	U	A
APEX	AP1	1983	F	L	U	A
APEX	AP1	1984	F	U	U	A
APEX	AP1	1985	F	U	U	A
ARC	AR5	1984	F	U	U	U
ARC	AR5	1985	F	U	U	U
ARROW	AR2	1981	F	U	U	U
ARROW	AR2	1982	F	U	U	U
ARROW	AR2	1984	F	P	U	A
ARROW	AR2	1985	F	L	U	A
ASE	AS1	1983	F	U	U	U
ASE	AS1	1984	F	U	U	U
ASE	AS1	1985	F	U	U	U
AURORA	AU1	1983	F	U	1	J
BAJA	BA4	1983	F	U	U	U
BAJA	BA4	1984	F	U	U	U
BAJA	BA4	1985	F	U	U	U
BATIK	BA3	1984	F	U	1	J

WHALE	CODE	YEAR	GENDER	RGPRO STATUS	AGE	JUV/ ADULT
BATIK	BA3	1985	F	U	2	J
BELTANE	BE1	1981	F	U	1	J
BELTANE	BE1	1982	F	U	2	J
BELTANE	BE1	1983	F	U	3	J
BELTANE	BE1	1984	F	P	4	A
BELTANE	BE1	1985	F	L	5	A
BINOC	BI2	1980	F	U	U	U
BINOC	BI2	1981	F	U	U	U
BINOC	BI2	1982	F	U	U	U
BINOC	BI2	1983	F	P	U	A
BINOC	BI2	1984	F	L	U	A
BINOC	BI2	1985	F	U	U	A
BISLASH	BI1	1979	F	U	U	U
BISLASH	BI1	1980	F	U	U	U
BISLASH	BI1	1981	F	U	U	A
BISLASH	BI1	1982	F	U	U	A
BISLASH	BI1	1983	F	U	U	A
BISLASH	BI1	1984	F	U	U	A
BISLASH	BI1	1985	F	U	U	A
BUCKSHOT	BU2	1979	F	U	U	U
BUCKSHOT	BU2	1981	F	U	U	U
BUCKSHOT	BU2	1982	F	U	U	A
BUCKSHOT	BU2	1984	F	U	U	A
BUCKSHOT	BU2	1985	F	P	U	A
CARDHU	CA4	1981	F	P	U	A
CARDHU	CA4	1982	F	L	U	A
CARDHU	CA4	1983	F	U	U	A
CARDHU	CA4	1984	F	P	U	A
CARDHU	CA4	1985	F	L	U	A
CATSPAW	CA5	1982	F	L	U	A
CATSPAW	CA5	1983	F	P	U	A
CATSPAW	CA5	1984	F	L	U	A
CATSPAW	CA5	1985	F	U	U	A
CHECK	CH2	1984	M	U	U	U
CHECK	CH2	1985	M	U	U	U
CHIMES	CH3	1984	F	U	U	U
CHIMES	CH3	1985	F	U	U	U
CHURCHILL	CH1	1979	M	U	U	U
CHURCHILL	CH1	1980	M	U	U	U
CHURCHILL	CH1	1981	M	U	U	U
CHURCHILL	CH1	1982	M	U	U	A
CHURCHILL	CH1	1983	M	U	U	A
CHURCHILL	CH1	1984	M	U	U	A
CHURCHILL	CH1	1985	M	U	U	A
CLIPPER	CL5	1983	F	U	U	U
CLIPPER	CL5	1984	F	U	U	U
CLIPPER	CL5	1985	F	U	U	U

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
CLOUD	CL2	1980	M	U	3	J
CLOUD	CL2	1981	M	U	4	A
CLOUD	CL2	1982	M	U	5	A
CLOUD	CL2	1983	M	U	6	A
CLOUD	CL2	1984	M	U	7	A
CLOUD	CL2	1985	M	U	8	A
CODA	CO7	1984	F	U	1	J
CODA	CO7	1985	F	U	2	J
COLT	CO5	1982	M	U	1	J
COLT	CO5	1983	M	U	2	J
COLT	CO5	1984	M	U	3	J
COLT	CO5	1985	M	U	4	A
COLUMBIA	CO3	1980	F	U	U	U
COLUMBIA	CO3	1981	F	U	U	U
COLUMBIA	CO3	1982	F	U	U	U
COLUMBIA	CO3	1983	F	P	U	A
COLUMEIA	CO3	1984	F	L	U	A
COLUMBIA	CO3	1985	F	U	U	A
COMET	CO4	1981	M	U	U	A
COMET	CO4	1982	M	U	U	A
COMET	CO4	1983	M	U	U	A
COMET	CO4	1984	M	U	U	A
COMET	CO4	1985	M	U	U	A
COMPASS	C10	1984	F	U	U	U
COMPASS	C10	1985	F	U	U	U
COUGAR	CO9	1983	F	U	U	U
COUGAR	CO9	1984	F	U	U	U
COUGAR	CO9	1985	F	U	U	U
COVE	CO6	1982	M	U	U	U
COVE	CO6	1983	M	U	U	U
COVE	CO6	1984	M	U	U	U
COVE	CO6	1985	M	U	U	A
CROWN	CR3	1983	F	U	U	U
CROWN	CR3	1984	F	U	U	U
CROWN	CR3	1985	F	U	U	U
CRYSTAL	CR1	1982	M	U	2	J
CRYSTAL	CR1	1983	M	U	3	J
CRYSTAL	CR1	1984	M	U	4	J
CRYSTAL	CR1	1985	M	U	5	A
CYGNUS	CY1	1980	M	U	U	U
CYGNUS	CY1	1981	M	U	U	U
CYGNUS	CY1	1982	M	U	U	A
CYGNUS	CY1	1983	M	U	U	A
CYGNUS	CY1	1984	M	U	U	A
CYGNUS	CY1	1985	M	U	U	A
DIAMOND	DI3	1984	M	U	U	U
DIAMOND	DI3	1985	M	U	U	U

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
DIGIT	DI1	1980	M	U	U	U
DIGIT	DI1	1981	M	U	U	U
DIGIT	DI1	1982	M	U	U	U
DIGIT	DI1	1983	M	U	U	A
DIGIT	DI1	1984	M	U	U	A
DIGIT	DI1	1985	M	U	U	A
EBONY	EB1	1981	F	U	U	U
EBONY	EB1	1982	F	P	U	A
EBONY	EB1	1983	F	L	U	A
EBONY	EB1	1984	F	L?	U	A
EBONY	EB1	1985	F	P	U	A
EIDER	EI1	1983	F	P	U	A
EIDER	EI1	1984	F	L	U	A
EMBER	EM1	1983	M	U	1	J
EMBER	EM1	1984	M	U	2	J
EMBER	EM1	1985	M	U	3	J
EPAULET	EP1	1981	F	U	1	J
EPAULET	EP1	1982	F	U	2	J
EQUUS	EQ1	1979	F	L	U	A
EQUUS	EQ1	1980	F	P	U	A
EQUUS	EQ1	1981	F	L	U	A
EQUUS	EQ1	1982	F	U	U	A
EQUUS	EQ1	1983	F	P	U	A
EQUUS	EQ1	1984	F	L	U	A
EQUUS	EQ1	1985	F	P	U	A
FALCO	FA1	1979	F	P	U	A
FALCO	FA1	1980	F	L	U	A
FALCO	FA1	1981	F	U	U	A
FALCO	FA1	1982	F	U	U	A
FALCO	FA1	1983	F	P	U	A
FALCO	FA1	1984	F	L	U	A
FALCO	FA1	1985	F	P	U	A
FEATHER	FE1	1979	F	L	U	A
FEATHER	FE1	1980	F	P	U	A
FEATHER	FE1	1981	F	L	U	A
FEATHER	FE1	1982	F	U	U	A
FERN	FE3	1983	F	U	U	U
FERN	FE3	1984	F	U	U	U
FERN	FE3	1985	F	U	U	U
FLAG	FL1	1981	F	P	U	A
FLAG	FL1	1982	F	L	U	A
FLAG	FL1	1984	F	P	U	A
FLAG	FL1	1985	F	L	U	A
FLAME	FL2	1982	M	U	U	U
FLAME	FL2	1983	M	U	U	A
FLAME	FL2	1984	M	U	U	A
FLAME	FL2	1985	M	U	U	A

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
FRINGE	FR1	1979	F	L	U	A
FRINGE	FR1	1980	F	L?	U	A
FRINGE	FR1	1981	F	P	U	A
FRINGE	FR1	1982	F	L	U	A
FRINGE	FR1	1983	F	P	U	A
FRINGE	FR1	1984	F	L	U	A
FRINGE	FR1	1985	F	P	U	A
GLO	GL2	1984	F	U	U	U
GLO	GL2	1985	F	U	U	U
HACHE	HA5	1983	F	U	U	U
HACHE	HA5	1984	F	U	U	U
HACHE	HA5	1985	F	U	U	U
HALOS	HA4	1984	M	U	1	J
HALOS	HA4	1985	M	U	2	J
HELIX	HE2	1984	M	U	U	U
HELIX	HE2	1985	M	U	U	U
IBIS	IB1	1980	F	U	1	J
IBIS	IB1	1981	F	U	2	J
IBIS	IB1	1982	F	U	3	J
IBIS	IB1	1983	F	U	4	A
IBIS	IB1	1984	F	U	5	A
IBIS	IB1	1985	F	P	6	A
IRIS	IR1	1984	M	U	1	J
IRIS	IR1	1985	M	U	2	J
ISTAR	IS1	1979	F	L	U	A
ISTAR	IS1	1980	F	P	U	A
ISTAR	IS1	1981	F	L	U	A
ISTAR	IS1	1982	F	U	U	A
ISTAR	IS1	1983	F	P	U	A
ISTAR	IS1	1984	F	L	U	A
ISTAR	IS1	1985	F	P	U	A
IVEE	IV2	1984	F	U	U	U
IVEE	IV2	1985	F	U	U	U
IVORY	IV1	1979	F	U	U	U
IVORY	IV1	1980	F	U	U	U
IVORY	IV1	1981	F	U	U	U
IVORY	IV1	1982	F	P	U	A
IVORY	IV1	1983	F	L	U	A
IVORY	IV1	1984	F	P	U	A
IVORY	IV1	1985	F	L	U	A
JANUS	JA1	1981	F	P	U	A
JANUS	JA1	1982	F	L	U	A
JANUS	JA1	1983	F	P	U	A
JANUS	JA1	1984	F	L	U	A
JANUS	JA1	1985	F	P	U	A
KOHOUTEK	KO1	1983	M	U	U	U
KOHOUTEK	KO1	1984	M	U	U	A

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
KOHOUTEK	KO1	1985	M	U	U	A
LACE	LA2	1980	F	U	U	U
LACE	LA2	1982	F	U	U	U
LACE	LA2	1983	F	U	U	A
LACE	LA2	1984	F	U	U	A
LACE	LA2	1985	F	U	U	A
LAMBDA	LA3	1982	M	U	U	U
LAMBDA	LA3	1984	M	U	U	A
LAMBDA	LA3	1985	M	U	U	A
LANCE	LA4	1983	M	U	1	J
LANCE	LA4	1985	M	U	3	J
LEUKOS	LE1	1983	F	U	U	U
LEUKOS	LE1	1984	F	U	U	U
LEUKOS	LE1	1985	F	U	U	A
LIGHTNING	LI1	1979	F	U	U	U
LIGHTNING	LI1	1980	F	U	U	A
LIGHTNING	LI1	1981	F	U	U	A
LIGHTNING	LI1	1982	F	U	U	A
LIGHTNING	LI1	1984	F	P	U	A
LIGHTNING	LI1	1985	F	L	U	A
LINER	LI3	1981	F	U	U	U
INER	LI3	1982	F	U	U	U
LINER	LI3	1983	F	U	U	U
LINER	LI3	1984	F	U	U	A
LINER	LI3	1985	F	P	U	A
LITTLE SPOT	LI2	1981	M	U	2	J
LITTLE SPOT	LI2	1982	M	U	3	J
LITTLE SPOT	LI2	1983	M	U	4	A
LITTLE SPOT	LI2	1984	M	U	5	A
LITTLE SPOT	LI2	1985	M	U	6	A
MARS	MA1	1979	F	U	U	U
MARS	MA1	1980	F	U	U	U
MARS	MA1	1981	F	P	U	A
MARS	MA1	1982	F	L	U	A
MARS	MA1	1983	F	P	U	A
MARS	MA1	1984	F	LP	U	A
MARS	MA1	1985	F	L	U	A
METEOR	ME1	1981	M	U	U	U
METEOR	ME1	1982	M	U	U	U
METEOR	ME1	1983	M	U	U	A
METEOR	ME1	1984	M	U	U	A
METEOR	ME1	1985	M	U	U	A
MIDNIGHT	MI2	1979	F	U	U	U
MIDNIGHT	MI2	1980	F	U	U	U
MIDNIGHT	MI2	1981	F	U	U	U
MIDNIGHT	MI2	1982	F	U	U	A
MIDNIGHT	MI2	1983	F	U	U	A

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
MIDNIGHT	MI2	1984	F	U	U	A
MIDNIGHT	MI2	1985	F	P	U	A
MIRROR	MI1	1980	M	U	U	U
MIRROR	MI1	1981	M	U	U	U
MIRROR	MI1	1982	M	U	U	U
MIRROR	MI1	1983	M	U	U	A
MIRROR	MI1	1984	M	U	U	A
MIRROR	MI1	1985	M	U	U	A
MURAL	MU1	1980	F	U	U	U
MURAL	MU1	1982	F	U	U	U
MURAL	MU1	1984	F	U	U	A
NEW MOON	NE1	1982	M	U	U	U
NEW MOON	NE1	1983	M	U	U	U
NEW MOON	NE1	1984	M	U	U	U
NEW MOON	NE1	1985	M	U	U	A
NOTCH	NO1	1981	M	U	U	U
NOTCH	NO1	1982	M	U	U	A
NOTCH	NO1	1983	M	U	U	A
NOTCH	NO1	1984	M	U	U	A
NURSE	NU1	1979	F	P	U	A
NURSE	NU1	1980	F	L	U	A
NURSE	NU1	1981	F	L?	U	A
NURSE	NU1	1982	F	P	U	A
NURSE	NU1	1983	F	L	U	A
NURSE	NU1	1984	F	P	U	A
NURSE	NU1	1985	F	L	U	A
OLYMPIA	OL1	1979	F	U	U	U
OLYMPIA	OL1	1980	F	U	U	U
OLYMPIA	OL1	1981	F	U	U	U
OLYMPIA	OL1	1982	F	P	U	A
OLYMPIA	OL1	1983	F	L	U	A
OLYMPIA	OL1	1984	F	P	U	A
OLYMPIA	OL1	1985	F	L	U	A
ONYX	ON1	1980	F	U	U	U
ONYX	ON1	1981	F	U	U	U
ONYX	ON1	1982	F	U	U	U
ONYX	ON1	1984	F	U	U	A
ONYX	ON1	1985	F	U	U	A
CRBIT	OR1	1979	F	U	U	A
ORBIT	OR1	1980	F	U	U	U
ORBIT	OR1	1981	F	U	U	U
ORBIT	OR1	1982	F	U	U	A
ORBIT	OR1	1983	F	P	U	A
ORBIT	OR1	1984	F	L	U	A
ORBIT	OR1	1985	F	P	U	A
ORION	OR2	1979	M	U	U	U
ORION	OR2	1980	M	U	U	U

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
ORION	OR2	1981	M	U	U	U
ORION	OR2	1982	M	U	U	A
ORION	OR2	1983	M	U	U	A
ORION	OR2	1984	M	U	U	A
ORION	OR2	1984	M	U	U	A
OTHELLO	OT1	1979	M	U	U	U
OTHELLO	OT1	1980	M	U	U	U
OTHELLO	OT1	1981	M	U	U	A
OTHELLO	OT1	1982	M	U	U	A
OTHELLO	OT1	1983	M	U	U	A
OTHELLO	OT1	1984	M	U	U	A
OTHELLO	OT1	1985	M	U	U	A
PATCHES	PA2	1980	M	U	U	U
PATCHES	PA2	1981	M	U	U	U
PATCHES	PA2	1982	M	U	U	U
PATCHES	PA2	1983	M	U	U	A
PATCHES	PA2	1984	M	U	U	A
PATCHES	PA2	1985	M	U	U	A
PEGASUS	PE2	1979	F	L	U	A
PEGASUS	PE2	1981	F	P	U	A
PEGASUS	PE2	1982	F	L	U	A
PEGASUS	PE2	1983	F	U	U	A
PEGASUS	PE2	1984	F	P	U	A
PEGASUS	PE2	1985	F	L	U	A
PEPPER	PE1	1980	F	U	U	U
PEPPER	PE1	1981	F	P	U	A
PEPPER	PE1	1982	F	L	U	A
PEPPER	PE1	1983	F	U	U	A
PEPPER	PE1	1984	F	U	U	A
PEPPER	PE1	1985	F	P	U	A
PETRA	PE3	1979	F	U	U	U
PETRA	PE3	1982	F	U	U	A
PETRA	PE3	1984	F	U	U	A
PI	PI2	1984	F	U	U	U
PI	PI2	1985	F	U	U	U
POINT	PO2	1979	F	U	U	U
POINT	PO2	1980	F	U	U	U
POINT	PO2	1981	F	U	U	U
POINT	PO2	1982	F	U	U	A
POINT	PO2	1983	F	U	U	A
POINT	PO2	1984	F	P	U	A
POINT	PO2	1985	F	L	U	A
POLARIS	PO4	1984	F	U	U	U
POLARIS	PC4	1985	F	U	U	U
QUOTE	QU3	1984	M	U	U	U
QUOTE	QU3	1985	M	U	U	U
RAVEN	RA3	1985	M	U	U	U

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
RAVEN	RA3	1984	F	U	U	A
RAVEN	RA3	1985	F	U	U	A
REGULUS	RE1	1984	M	U	1	J
REGULUS	RE1	1985	M	U	2	J
ROPE	RO1	1981	M	U	U	U
ROPE	RO1	1982	M	U	U	U
ROPE	RO1	1983	M	U	U	U
ROPE	RO1	1984	M	U	U	A
ROPE	RO1	1985	M	U	U	A
RUNE	RU1	1980	F	U	U	U
RUNE	RU1	1981	F	U	U	U
RUNE	RU1	1982	F	P	U	A
RUNE	RU1	1983	F	L	U	A
RUNE	RU1	1984	F	P	U	A
RUNE	RU1	1985	F	L	U	A
SALT	SA1	1979	F	P	U	A
SALT	SA1	1980	F	L	U	A
SALT	SA1	1981	F	U	U	A
SALT	SA1	1982	F	P	U	A
SALT	SA1	1983	F	L	U	A
SALT	SA1	1984	F	P	U	A
SALT	SA1	1985	F	L	U	A
SCISSORS	SC4	1983	F	U	U	U
SCISSORS	SC4	1984	F	U	U	U
SCISSORS	SC4	1985	F	U	U	U
SCRATCH	SC1	1979	F	U	U	U
SCRATCH	SC1	1980	F	U	U	U
SCRATCH	SC1	1981	F	U	U	U
SCRATCH	SC1	1982	F	U	U	A
SCRATCH	SC1	1983	F	U	U	A
SCRATCH	SC1	1984	F	P	U	A
SCRATCH	SC1	1985	F	L	U	A
SCYLLA	SC2	1982	F	U	1	J
SCYLLA	SC2	1983	F	U	2	J
SCYLLA	SC2	1984	F	U	3	J
SCYLLA	SC2	1985	F	U	4	J
SCYTHER	SC3	1982	M	U	3	J
SCYTHER	SC3	1983	M	U	4	A
SCYTHER	SC3	1984	M	U	5	A
SCYTHER	SC3	1984	M	U	6	A
SEAL	SE3	1984	M	U	1	J
SEAL	SE3	1985	M	U	2	J
SHARK	SH2	1984	F	U	U	U
SHARK	SH2	1985	F	U	U	U
SICKLE	SI1	1979	F	U	U	U
SICKLE	SI1	1981	F	U	U	U
SICKLE	SI1	1982	F	U	U	A

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
SICKLE	SI1	1983	F	U	U	A
SICKLE	SI1	1984	F	U	U	A
SICKLE	SI1	1985	F	P	U	A
SILVER	SI2	1979	F	P	U	A
SILVER	SI2	1980	F	L	U	A
SILVER	SI2	1981	F	U	U	A
SILVER	SI2	1982	F	P	U	A
SILVER	SI2	1983	F	L	U	A
SILVER	SI2	1984	F	P	U	A
SILVER	SI2	1985	F	L	U	A
SINESTRA	SI3	1979	F	U	U	U
SINESTRA	SI3	1980	F	P	U	A
SINESTRA	SI3	1981	F	L	U	A
SINESTRA	SI3	1982	F	P	U	A
SINESTRA	SI3	1983	F	L	U	U
SINESTRA	SI3	1984	F	U	U	A
SINESTRA	SI3	1985	F	P	U	A
SIRIUS	SI4	1983	M	U	1	J
SIRIUS	SI4	1984	M	U	2	J
SIRIUS	SI4	1985	M	U	3	J
SLINGSHOT	SL2	1983	M	U	1	J
SLINGSHOT	SL2	1984	M	U	2	J
SLINGSHOT	SL2	1985	M	U	3	J
SOCKEYE	SO3	1984	M	U	U	U
SOCKEYE	SO3	1985	M	U	U	U
SOD	SO1	1979	F	U	U	U
SOD	SO1	1980	F	U	U	U
SOD	SO1	1981	F	U	U	U
SOD	SO1	1982	F	U	U	A
SOD	SO1	1983	F	U	U	A
SOD	SO1	1984	F	P	U	A
SOD	SO1	1985	F	L	U	A
SPEAR	S2P	1985	M	U	1	J
SPECKLES	SP3	1981	M	U	U	U
SPECKLES	SP3	1982	M	U	U	U
SPECKLES	SP3	1983	M	U	U	U
SPECKLES	SP3	1984	M	U	U	A
SPECKLES	SP3	1985	M	U	U	A
SPLINTER	SIP	1985	F	U	1	J
SPOON	SP1	1979	F	U	U	U
SPOON	SP1	1980	F	U	U	U
SPOON	SP1	1981	F	U	U	A
SPOON	SP1	1982	F	P	U	A
SPOON	SP1	1983	F	L	U	A
SPOON	SP1	1984	F	U	U	A
SPOON	SP1	1985	F	U	U	A
STRIPES	ST7	1984	M	U	U	U

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
STRIPE	ST7	1985	M	U	U	U
STUB	ST1	1979	M	U	U	U
STUB	ST1	1980	M	U	U	U
STUB	ST1	1981	M	U	U	U
STUB	ST1	1982	M	U	U	A
STUB	ST1	1983	M	U	U	A
STUB	ST1	1984	M	U	U	A
STUB	ST1	1985	M	U	U	A
SWORD	SW1	1985	M	U	1	J
TALON	TA2	1982	F	U	1	J
TALON	TA2	1983	F	U	2	J
TALON	TA2	1984	F	U	3	J
TALON	TA2	1985	F	U	4	A
TANITH	TA3	1982	F	U	2	J
TANITH	TA3	1983	F	U	3	J
TANITH	TA3	1984	F	U	4	A
TANITH	TA3	1985	F	U	5	A
TASSLE	TA1	1981	M	U	2	J
TASSLE	TA1	1982	M	U	3	J
TASSLE	TA1	1983	M	U	4	A
TASSLE	TA1	1984	M	U	5	A
TASSLE	TA1	1985	M	U	6	A
THORN	TH3	1985	M	U	2	J
TIARA	TI2	1984	M	U	1	J
TIARA	TI2	1985	M	U	2	J
TRIDENT	TR4	1983	F	U	1	J
TRIDENT	TR4	1984	F	U	2	J
TRIDENT	TR4	1985	F	U	3	J
TRINE	TR5	1981	F	P	U	A
TRINE	TR5	1982	F	L	U	A
TRINE	TR5	1983	F	P	U	A
TRINE	TR5	1984	F	L	U	A
TRINE	TR5	1985	F	P	U	A
TRITON	TR3	1981	M	U	U	U
TRITON	TR3	1982	M	U	U	U
TRITON	TR3	1983	M	U	U	U
TRITON	TR3	1984	M	U	U	A
TRITON	TR3	1985	M	U	U	A
TRUNK	TR2	1979	M	U	U	A
TRUNK	TR2	1980	M	U	U	A
TRUNK	TR2	1981	M	U	U	A
TRUNK	TR2	1982	M	U	U	A
TRUNK	TR2	1983	M	U	U	A
TRUNK	TR2	1984	M	U	U	A
TRUNK	TR2	1985	M	U	U	A
TUSK	TU1	1980	M	U	1	J
TUSK	TUI	1981	M	U	2	J

WHALE	CODE	YEAR	GENDER	REPRO STATUS	AGE	JUV/ ADULT
TUSK	TU1	1982	M	U	3	J
TUSK	TU1	1983	M	U	4	A
TUSK	TU1	1984	M	U	5	A
TUSK	TU1	1985	M	U	6	A
VEIL	VE3	1982	F	P	U	A
VEIL	VE3	1983	F	L	U	A
VEIL	VE3	1984	F	P	U	A
VEIL	VE3	1985	F	L	U	A
WALRUS	WA3	1984	M	U	U	U
WALRUS	WA1	1985	M	U	U	A
WARRIOR	WA1	1982	F	U	U	A
WARRIOR	WA1	1983	F	P	U	A
WARRIOR	WA1	1984	F	L	U	A
WARRIOR	WA1	1985	F	P	U	A
ZEBRA	ZE1	1984	F	U	U	U
ZEBRA	ZE1	1985	F	U	U	U

APPENDIX II

Data set

INDCODE: Computer code for each individual humpback whale.

GENDER: Male or female.

REPSTAT: Reproductive status of females, pregnant or lactating, when known.

FLUCOL: Fluke coloration ranging from 1 - 5 (Figure 2.5).

FARSCAR: Presence or absence of parallel scars on flukes.

ARRIVE: Day of first observed sighting in study area.

DEPART: Day of last observed sighting in study area.

RESIDE: Number of days between arrival and departure.

SOUTH: Observed presence on the breeding grounds earlier that year.

LOGDIS: Log of the greatest observed distance an individual was identified from the centroid of its Stellwagen range.

AGE: Age in years of all individuals observed as calves in previous years.

CJA: Calf, juvenile or adult.

RELDIS: The average distance of the individual from the centroid of positions of all animals sighted that year.

MEANGRP: The mean group size of all associations.

NBDAV: Near-boat/numobs(number of observations)
LTAILAV: Lobtail/numobs
SURFEDAV: Feeding/numobs
SPYHOPAV: Spyhoping/numobs
BREACHAV: Breaching/numobs
LOGAV: Resting/numobs
FLIPAV: Flipping/numobs
SOCIOAV: Social/sociobs
LRELDIS: Log reldis
LMEANGRP: Log meangrp
LNBDATAV: Log nbdatav
LLTAILAV: Log ltailav
LSURFEDAV: Log surfedav
LSPYHOPAV: Log spyhopav
LBREACHAV: Log breachav
LLOGAV: Log logav
LFLIPAV: Log flipav
LSOCIALAV: Log socialav
LARRIVE: Log arrive
LDEPART:Log depart
LRESIDE: Log reside

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