INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

Bell & Howell Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

UMI®

Social organization and population structure of northern bottlenose whales in the Gully

by

Shannon Gowans

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

at

Dalhousie University
Halifax, Nova Scotia
Canada

May 1999

DALHOUSIE UNIVERSITY

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "Social organization and population structure of northern bottlenose whales"

by Shannon Gowans

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

Dated: June 28, 1999

External Examiner

Research Supervisor

Examining Committee

DALHOUSIE UNIVERSITY

July 19, 1999

AUTHOR: Shannon Gowans

TITLE: Social organization and population structure of northern bottlenose whales in the Gully.

DEPARTMENT: Biology

DEGREE: Ph.D. CONVOCATION: October YEAR: 1999

Permission is herewith granted to Dalhousie University to circulate and to have copied for non-commercial purposes, at its discretion, the above title upon the request of individuals or institutions.

[redacted]

Signature of Author

Dedication

This thesis is dedicated to those who made it possible for me to do this research: my parents Carol and Bruce Gowans and my husband Peter Simard. It is also dedicated to those who will continue this work, to discover more about the lives of northern bottlenose whales and to ensure that this population is protected.

Table of Contents

List of Tables

List of Figures

Abstract

The social organization and population structure of northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully was studied from 1988-1997 using photo-identification techniques. While all members of the population possess some natural marks on the dorsal fin and surrounding flank suitable for photo-identification, only 66 % (± 5%) of the individuals have marks which last for periods of years. Thus analyses which include matches over periods of years were restricted to those individuals with reliable marks, and the results scaled to account for the remainder of the population. Photographic techniques could also be used to reliably assign individuals to age/sex classes based on the development of secondary sexual characteristics in the melon profile.

Groups of northern bottlenose whales (individuals within five body lengths of each other and showing coordinated behaviour) were likely to contain interacting individuals, thus presence within the same group was used to define a social association. Groups of bottlenose whales were small (mean 3.04 ± SD 1.86, n = 1.281) and often composed of mixed age/sex classes. Most of the associations within the groups quickly dissociated, although sub-adult and mature males formed preferential associations with other members of their same age class and some of these associations lasted for periods of years. Female and immature males formed a loose network of associations with no preferential associations with other adult-sized animals.

Calves were born in June, July and August in the Gully, although births may have occurred outside these months. Probable mothers could be identified based on association patterns for several calves and juveniles, although not all young animals which were repeatedly observed could be assigned to a probable mother. Young bottlenose whales associated with individuals who could not be their mother (*e.g.*, males) even when no females were present, indicating that babysitting may occur although the costs, benefits, function and frequency of babysitting could not be determined.

The Gully population was small (130 individuals, 95% c.i. 104-170 from left side identifications; 122, 95% c.i. 100-157 from right side identifications) and may be largely distinct from other populations of bottlenose whales in the North Atlantic. Mortality, mark change and permanent emigration was estimated at 12% per year (95% c.i. 8-17) and there was no significant change in population size over the nine year study. Over the summer field season, individuals emigrated from, and re-immigrated into the Gully, spending on average 10 ± 5 days in the Gully. Estimates of the number of days spent outside of the Gully were imprecise and variable, however most individuals were resighted in the Gully in subsequent years. On average one-third of the population (43 ± 10 individuals) were present in the Gully at any given time.

Many aspects of the social organization and population structure of northern bottlenose whales in the Gully resembled those of bottlenose dolphins (*Tursiops truncatus*) in Monkey Mia, Australia and Sarasota, Florida. The similarities may result from similarities in the low variability of food resources in these study areas and horizontal spatial scale, although this hypothesis requires specific testing.

List of Abbreviations and Symbols

ANOVA	analysis of variance
B.C.	British Columbia
cm	centimetre
χ^2	chi-square statistic
CV	coefficient of variance
c.i.	confidence interval
CITES	Convention of the International Trade in Endangered Species
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
df	degrees of freedom
DNA	deoxyribonucleic acid
DMSO	dimethyl sulfoxide
F/I	female/immature male
G	G-test statistic
IUCN	International Union for the Conservation of Nature
IWC	International Whaling Commission
kHz	kilohertz
MM	mature male
MQ	quality of melon photograph
m	metre
mm	millimetre
mtDNA	mitochondrial DNA
P	probability
photo-id	photographic identification
lb.	pound
Q	quality of dorsal fin photograph
n	sample size
s	second
SRY	sex determining region – Y gene
SLR	single lens reflex
r_s	Spearman rank correlation

SD	standard deviation
SE	standard error
SM	sub-adult male
TDR	time depth recorder
U	unknown age/sex class
ZFY	zinc finger protein gene – Y chromosome

Acknowledgements

I would foremost like to thank my supervisor Hal Whitehead, who in 1993 agreed to take me on a two week trip to the Gully. At that time I had never been out on a boat for more than a few hours and had never sailed, nor could I promise Hal that I would not get seasick. After six field seasons in the Gully, I can now promise Hal I will not get seasick, unless it is very miserable or if he has shared the stomach flu with the entire crew. I did not know in 1993 when I first went to the Gully how much I would fall in love with the whales and the research, but I have spent many enjoyable hours with the whales, scrutinizing negatives, analysing data and writing. Hal is an inspirational supervisor, never asking more of anyone than he asks of himself – but if you know Hal, you know the high level of excellence he achieves. Thank you, Hal for pushing me to reach for that same level of achievement. Hal assisted in every aspect of this thesis, providing much appreciated mathematical and statistical help, as well as advice throughout the thesis. I especially appreciate the programs Hal wrote in Matlab to analyse social organization and population size and residency questions. Without those programs, this thesis would have either taken me much longer to complete, or would not have been able to explore as many of the fascinating aspects of social organization and population structure of bottlenose whales.

The next person I would like to thank is my husband Peter Simard, who had no idea what he was getting involved in when he started his honours thesis with Hal in 1994. His involvement in Gully research has lasted well beyond his own thesis, reading draft after draft of my thesis, listening to my thoughts and brainstorming about my results. I would like to thank Peter for all his help with making it possible for me to complete my thesis. My family (and Peter's) also provided much needed assistance throughout this thesis, from words of encouragement to the occasional loan and everything in between. Peter's honours work on the distribution of bottlenose whales in relation to physical oceanography gave the initial indication that bottlenoses whales in the Gully were probably benthic animals.

I would also like to thank Annick Faucher, who established the Gully bottlenose whale photographic catalogue and did much of the initial work on which this thesis is based. Unfortunately, health difficulties prevented Annick from receiving the doctorate she

deserved for this thesis. Sascha Hooker has also assisted throughout this thesis, from the many hours in the field, to many fruitful discussions about what 'this all means about bottlenose whale' and editing many drafts of chapters and publications. Sascha's own work on the diet, ranging and diving behaviour of northern bottlenose whales has provided a much broader context in which to interpret the results of my thesis. Merel Dalebout (University of Auckland, New Zealand) conducted the genetic analysis of biopsy samples, verifying my photographic sexing technique and giving an indication of reproductive isolation.

I would like to thank my supervisory committee members; Marty Leonard and Fred Harrington who have read many drafts of my thesis and provided many insightful comments, especially in keeping me from being too focused on cetaceans. Don Bowen also provided much useful assistance in earlier stages of my thesis by serving as external examiner for my Admission to Candidacy and Preliminary exam. Jakobina Arch, Robin Baird, Merel Dalebout, Nathalie Patenaude and several anonymous reviewers also provided helpful comments on several chapters. Ian McLaren kindly agreed to sit on my examining committee at the last minute when Fred (understandably) could not refuse the opportunity to conduct field work on Ellesmere Island at the same time as my defense. Bernd Würsig served as external examiner for my thesis exam and provided many constructive comments.

Funding for the Gully research has come from NSERC, World Wildlife Fund Canada, the Whale and Dolphin Conservation Society, National Geographic and the Canadian Humane Societies. I have been supported by several graduate scholarships; NSERC, Isaac Walton Killam Memorial Scholarship, Dalhousie Graduate Scholarship and funding from my supervisor.

Many people have participated in Gully research over the years, and I appreciate all their efforts. I would like to especially acknowledge the participation of Robin Baird, Brad Carter, Sascha Hooker, Sa'ad Al-Omari, Flip Nicklin, Peter Simard, Ryan Weatherbee, Lindy Weilgart, Ben Weilgart-Whitehead and Hal Whitehead who shared two or more trips to the Gully with me.

Chapter 1: Introduction

INTRODUCTION

The social organization and population structure of a species evolves through selective adaptations by individuals to optimally exploit their environment (*e.g.*, Wrangham and Rubenstein 1986, Caswell *et al.* 1997). This thesis describes the patterns of association between individual northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully, and assesses the size and structure of the Gully population. By comparing the results from this thesis with other cetacean studies, we gain insight into the selective pressures leading to the evolution of sociality and population structure in this species, and in cetaceans in general.

WHAT IS SOCIAL ORGANIZATION AND HOW DOES IT EVOLVE?

'Social organization'[1] is rarely defined although it is a commonly used term in behavioural ecology. One of the clearest, and probably most biologically relevant definitions is that of Hinde (1976), who states that the social organization of a species is based on interactions between individuals. The relationship between two individuals is described by the nature, quality and temporal patterning of the interactions between these individuals. The nature, quality and temporal patterning of these relationships describe the social organization. Therefore it is important not only to know which individuals are present together, but also to know 'who does what to whom, when and why' (Hinde 1976). While it is not always possible to observe and interpret the context of interactions, social organization can be studied by investigating and quantifying interactions, especially if it is possible to compare similarities and differences in the patterns of association between different classes of individuals (Whitehead 1997). In many species, because it is difficult to observe interactions (*e.g.*, interactions occur underwater or high in the tree canopy) analysis of social structure is often restricted to the level of association. In these instances associations are often defined by presence in the same group under the assumption that individuals within the same group are interacting (Whitehead and Dufault 1999).

---

[1] 'Social organization' in this thesis is synonymous with 'social structure'. However the term 'social organization' is used to avoid confusion with the term 'population structure'

The social organization of a species evolves through the influence of a number of different factors or selective pressures (see Figure 1.1). Many of these factors include feedback loops where a change in one element influences another element which in turn affects the original. For example, predation risk often lessens in large groups, but large groups may alter the tactics of predators that can change the predation risk. These feedback loops are especially important as the social behaviour of an individual can be influenced by social as well as ecological pressures. It is also important to remember that while social organization does evolve, selection acts on individuals rather than on the group or species. Therefore it is possible to have several different strategies within a species or group, which may be expressed at different times, by different individuals or under different conditions (Wrangham and Rubenstein 1986).

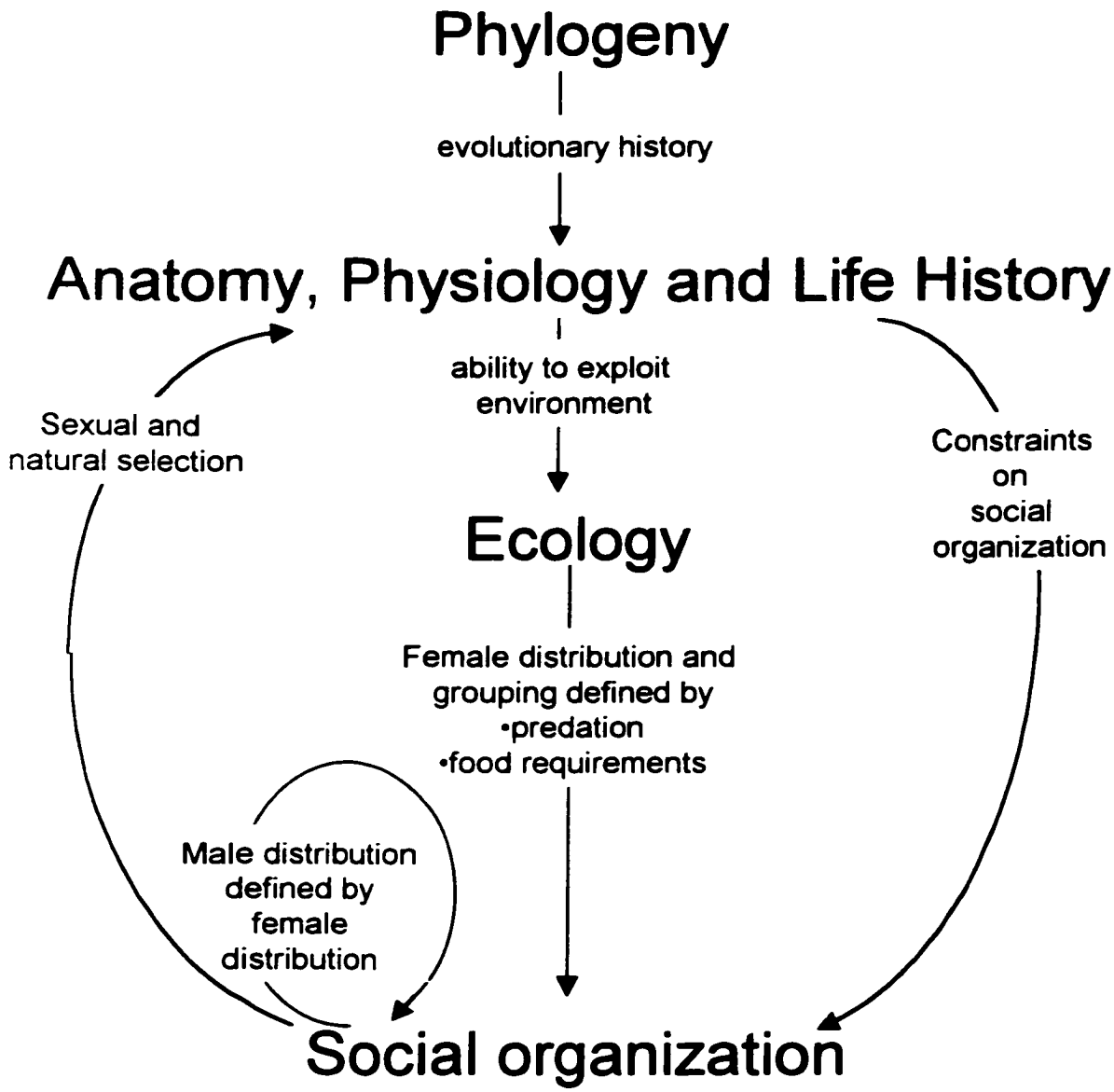
PRINCIPAL SELECTIVE PRESSURES INFLUENCING SOCIAL ORGANIZATION

The influence of ecology, anatomy, physiology and phylogeny on social organization in primates has been studied in detail (*e.g.*, Cheney *et al.* 1987) and the methods used to study primates are similar to those for studying cetaceans. There are parallels between the social organization of cetacean species and some primates, although most cetacean species have not been studied in detail (Connor *et al.* 1998). Therefore I will focus on primates to describe some of the principal pressures in the evolution of social organization (following Figure 1.1).

PAST HISTORY

Past evolutionary history can influence social organization through anatomical and physiological adaptations to the environment. For example, the digestive tract of mountain gorillas (*Gorilla gorilla beringei*) is suitable for hind gut fermentation which facilitates nutrient and energy extraction from herbaceous plants. Without this adaptation to their gut morphology, mountain gorillas would not be able to survive on a diet composed almost entirely of shoots and leaves. The diet of mountain gorillas has a strong influence on their social organization. Their food is widely and evenly dispersed, both spatially and temporally,

Figure 1.1: Principal selective pressures influencing social organization.



which reduces competition between individuals (and groups) for food (Watts 1996). Therefore, females do not have to group together to gain access to high quality food patches (Wrangham 1980; see below) nor can males defend a valuable food resource in order to gain access to mates (resource defense polygyny - Emlen and Oring 1977; see below).

Anatomical and physiological adaptations are often shared between related species. This may lead to similarities in social organization between closely related species, such as the similar life history traits between primate species in the same sub-family (Harvey *et al.* 1987). However, shared evolutionary history does not always result in similar social organization. For example, chimpanzees (*Pan troglodytes*) have different levels of bonding between males and females in three different study areas, even though two of these studies involve the same sub-species (Boesch 1996).

CURRENT PRESSURES

Influence of ecology on social structure

The influence of ecology on social organization is often different for males and females, especially during the breeding season or in species which maintain the same social organization throughout the year. The social organization of female mammals is usually more closely related to ecological parameters as female fitness (and reproductive success) is usually limited by ecological pressures (the ability to use resources to survive, produce and care for young), whereas the social organization of males is often related to access to reproductive females (Wrangham 1987). Various levels of predation, resource distribution and intraspecific competition favour different degrees of grouping among females and influence not only group size but also the structure within the group (Wrangham and Rubenstein 1986). In species that have different social organization during the breeding and non-breeding season, the social organization of males may be most related to ecology during the non-breeding season, and related to female access during the breeding season (*e.g.*, Ishibashi *et al.* 1998).

Primate species that experience high predation are generally found in groups, although some very small species rely on crypsis and being solitary to avoid predation. The exact size and structure of the group depends on the level of predation, types of predator defense, and constraints imposed by resource distribution and intraspecific competition. For example, when predation is reduced through cooperative defense, stable associations are favoured (Wrangham and Rubenstein 1986). High predation risk appears to favour small, multi-male groups in arboreal primates as several males are required to successfully defend infants from predation by other species (Van Schaik and Höstermann 1994).

Animals must not only avoid being eaten, but they must eat as well. Groups are favoured when resources are patchy, as individuals gather together to exploit the resource, while uniform resource distribution favours solitary individuals. Group size is often constrained by the distribution and density of resources. When resources are distributed in a way that is economically defensible by either an individual or a group, territoriality is expected (Wrangham and Rubenstein 1986).

Intraspecific competition, especially for food resources, can have a strong influence on social structure. Isbell (1991) argues that intraspecific competition over limited food resources is responsible for the evolution of female-bonded primate societies. In these groups, females cooperate to defend resources against others. If group members are related then the costs of sharing food resources are less, therefore kin-based groups and female philopatry are favoured (Wrangham 1980, Isbell 1991). Conversely, species that do not experience high levels of intraspecific competition for resources would not be expected to have strong female bonds as there would be no benefit to forming alliances against neighbours (Wrangham 1980). Additionally these species would not be expected to exhibit female philopatry. Data from a number of different primate species appear to fit these predictions (Wrangham 1980, Isbell 1991). A more recent investigation of philopatry in primates indicates that female philopatry may have evolved because the costs of female dispersal are higher than the costs of staying in the natal group (Isbell and Van Vuren 1996). However it is likely that both food competition and the costs of dispersal are involved in primate female philopatry.

Influence of the social organization of conspecifics on the social organization of individuals

Male mammals often attempt to increase their fitness by increasing mating opportunities. Therefore male distribution and social organization are defined, at least in part, by female distribution and social organization (Wrangham and Rubenstein 1986). When females are solitary and have synchronous estrus, males are unlikely to be able to mate with more than one female and monogamy generally occurs. Males in these situations may be able to increase their reproductive success by assisting in parental care (Emlen and Oring 1977). When females are grouped, the potential for polygyny exists. A single male or group of males may be able to increase their mating success by defending a group of females or a resource important to those females. Alternatively, females may choose a mate from a group based on dominance or a lek display (Emlen and Oring 1977).

Females may attempt to limit the number of males found within a group. In female-bonded groups that are territorial, each male that joins the group places an additional burden on the limited resources, which could otherwise be used by kin or alliance females. Therefore these females are predicted to try to limit the number of males to one, which they actually do by aggressively attacking incoming males (Wrangham 1980). Non-territorial female-bonded groups are predicted to show a different pattern of association with males. The addition of each male to these groups benefits females, as larger groups are more likely to win confrontations with interacting groups. Therefore having extra males is beneficial to females. This prediction is also supported in a number of different species of primates (Wrangham 1980).

The distribution and social organization of males may also have strong influences on the social organization of females. Infanticide by non-paternal males may be the driving force behind sociality in a number of primate species. Females maintain year round associations with one (or occasionally more) mature male, in order to prevent other males from committing infanticide to bring her back into estrus (Van Schaik and Kappler 1997). The social structure in mountain gorillas is likely tied to infanticide as females are not expected to live in groups based solely on diet or predation risk. However female mountain gorillas do live in groups, and associate with a dominant male. Females will sometimes switch groups,

shortly after weaning or losing a dependent offspring, but not while they have dependent young who would likely be killed by the new dominant male (Watts 1996).

Influence of social organization on anatomy and physiology

The social organization of a species may influence its anatomy and physiology through both natural and sexual selection. For example, if it is beneficial for an individual to be in a social group, and individuals within the group require signals to maintain their social bonds, then there would likely be natural selection for the anatomical features involved in communication (*e.g.*, Joffe and Dunbar 1997). Social organization has an obvious influence on anatomy via sexual selection. For example, polygynous species tend to be sexually dimorphic, with males being larger. If sperm competition exists then there may be selection for males with relatively large testes (Harcourt *et al.* 1981).

All of the principal selective pressures in the evolution of social organization described above and in Figure 1.1 are linked together through natural and sexual selection and it may not be possible, or even desirable, to try and tease out each link in the process. However by investigating the factors leading to the evolution of sociality and different patterns of social organization, we gain knowledge about the biology of the species and its interconnection to the environment.

WHAT IS POPULATION STRUCTURE AND HOW DOES IT EVOLVE?

POPULATION STRUCTURE

Populations[2] are rarely composed of a collection of identical individuals which are evenly spatially and temporally distributed. Instead, populations consist of groups of animals which share similar traits such as age, life-history stage, size, sex, genetics, geographic

---

[2] Population: a group of individuals sharing the same space and time, which are capable of reproducing. The scale of shared space and time is generally large and may be arbitrarily set to fit with a given study area. Subpopulation: a subset of individuals within a population which share similar traits. In the literature, subpopulations are most commonly defined by shared geography or genetics.

location, or behaviour (Caswell *et al.* 1997, Whitehead *et al.* 1998b). Many important elements of population dynamics can be missed if all individuals in the population are treated identically (see Table 1.1 for examples). Population structure describes the distribution of individuals with respect to these traits. The population structure of some species consists primarily of different subpopulations that are geographically isolated, while others show many levels of organization. It is important to identify which traits (or series of traits) best describe each population (Caswell *et al.* 1997).

Table 1.1: Examples of traits which can structure populations and their influence on population dynamics.

TRAIT	INFLUENCE ON POPULATION DYNAMICS	EXAMPLE STUDIES
Age	age-specific mortality and fecundity	Desharnais 1997
Life-history stage	stage-specific mortality (including cannibalism) and different habitat requirements for different stages	Desharnais 1997
Behaviour	behaviour modifications limit breeding between groups	Hewitt and Butlin 1997, Hoelzel *et al.* 1998b
Geography and behaviour	geographic isolation limits interbreeding, as do behaviour modifications	Dobson *et al.* 1998

Population structure can be influenced by social organization. When populations are divided into breeding groups, such as mated pairs or matrilineal groups, the distribution of genes throughout the population can differ from random mating as similar genotypes are concentrated within families (Sugg *et al.* 1996). Similarly, juvenile dispersal will influence genetic distribution and the distribution of individuals in various age and sex classes (*e.g.*, Dobson *et al.* 1998).

EVOLUTION OF POPULATION STRUCTURE

Past processes

The evolution of structure within populations, especially the evolution of subpopulations is often linked to past processes such as historical isolation between populations. In temperate terrestrial animals, historical periods of glaciation greatly influenced current population structures. During glaciation, populations of animals were restricted to a limited number of isolated refuges. Genetic drift and adaptations to the environment often led to genetic and behavioural differences between the populations. After glaciation, animals radiated out of the refuges and several populations came back into contact. Along the border of Spain and France there exist two races of meadow grasshopper (*Chorthippus parallelus*) which inhabit the same area but have different mating behaviours and gene distribution. One race can be traced back to a glacial refuge in Portugal while the other race evolved from a refuge near Greece. The differences in mating behaviour continues to limit interbreeding between these two races despite shared distribution (Hewitt and Butlin 1997).

Inheritance of cultural processes in matrilineal groups is believed to account for the largely non-geographical population structure in sperm whales (*Physeter macrocephalus*). In the South Pacific, individuals within matrilineal groups of female and immature sperm whales share similar mitochondrial haplotypes, vocalizations and fluke-markings. However pairs of groups with similar traits were not found in the same geographic locations. If cultural processes, such as predator defense tactics (which may lead to similarities in fluke-markings) and vocalizations are passed down and conserved within matrilineal groups along with mitochondrial haplotypes, and groups are able to range widely over long time scales (tens to hundreds of years), a non-geographical structure could evolve (Whitehead *et al.* 1998b). While group specific traits and large ranges could lead to a non-geographically based structure, cultural processes are likely required if the group specific traits persist for generations.

Population structure can also be influenced by genetic bottlenecks. Genetic and behavioural diversity decreases when populations are reduced. When the population size begins to

increase, there will still be limited genetic and behavioural diversity until there is sufficient time for adaptations and mutations to occur. If sufficient time has not passed, there will be limited diversity even if the population has become widely distributed. For example northern elephant seals (*Mirounga angustirostris*) were reduced to very low numbers (likely fewer than 30 individuals) at the turn of the century. The population size has increased dramatically to over 100 000 individuals, but it has very low genetic diversity and shows little population structure between the different breeding areas (Hoelzel *et al.* 1993).

Current pressures

Current pressures can also influence population structure. Patchy resources can lead to geographic isolation between subpopulations. Local adaptations can lead to genetic or behavioural differences (Hewitt and Butlin 1997). The existence of breeding groups can lead to clumped distribution of genetically similar individuals, and the age and sex structure of a population can be influenced by mating systems or a sex bias in parental investment (Dobson 1998)

There may also be breeding isolation within subpopulations, when individuals form breeding groups which do not freely exchange mates between groups. For example, colonies of black tailed prairie dogs (*Cynomys ludovicianus*) are patchily distributed in the short-grass prairie (Dobson *et al.* 1998). There is practically no mixing between the colonies which form subpopulations. Clumped within the colonies are wards, which have limited mixing with other wards. Within the wards, the prairie dogs live in breeding groups called coteries which consist of one to two males, several related philopatric females, yearlings and young of the year. Analysis of allozyme alleles, pedigrees and demography indicate that coteries consist of separate breeding groups and 15 to 20% of the total genetic variation of the colony occurs at the level of the coterie (Dobson *et al.* 1998).

Mating systems can influence the age and sex structure of populations. In polygamous systems males compete for access to females which can lead to increased male mortality, a population sex ratio biased towards females and an age skew towards younger males.

Increased male mortality may be directly linked to competition when males die from injuries sustained during fights, or from starvation during the mating season. Sub-adult male mortality may also be elevated due to the energetic demands of faster or longer periods of growth. Sexual dimorphism in body size may also increase male mortality if the large males are more susceptible to predation (Owen-Smith 1993).

The sex structure of a population can also be influenced by maternal condition. Following parental investment theory (Trivers and Willard 1973), female red deer (*Cervus elaphus*) are predicted to bias the sex ratio of offspring towards males when the mothers are in excellent condition, as high quality mature males tend to have higher reproductive success. This prediction was confirmed by field studies as dominant females, who have first access to food resources, tend to have more males (Clutton-Brock *et al.* 1984). This may mean that when environmental conditions are poor, fewer males are likely to be produced, skewing the sex ratio of that year class towards females.

Philopatry and intraspecific competition may also influence sex structure through biases in the sex ratio of offspring. Spotted hyenas (*Crocuta crocuta*) live in matrilineal clans of females with their dependent offspring and several immigrant males. Holekamp and Smale (1995) observed a change in the sex ratio from male biased before the fission of a clan to female biased after fission. They link the change to the cooperation between females to acquire resources. Before the clan split, competition between females for prey resources biased sex ratios toward male offspring which disperse at maturity. After the clan split, competition for resources was reduced as one clan moved to an unoccupied area. It was then beneficial to produce female offspring who would eventually cooperate with their mothers to acquire resources. Female offspring would also increase the growth rate of the clan, such that optimal clan size is reached faster (Holekamp and Smale 1995).

INFLUENCES ON CETACEAN SOCIAL ORGANIZATION

Most cetaceans are social animals. The size and stability of these groups vary among species (Connor *et al.* 1998). The ecological and social factors influencing cetacean social organization (predation, foraging, intraspecific competition and mate acquisition) are the

same as in terrestrial species, but the aquatic environment of cetaceans influences the costs and benefits of various behaviours and social organizations. One important difference between aquatic and terrestrial environments is that the costs of locomotion are much lower in the water (*e.g.*, Bose and Lien 1990, Williams *et al.* 1992). This permits cetaceans to range widely and has many influences on their social organization.

Cetaceans live in a predominantly three dimensional world with little cover from predators. Unlike terrestrial animals, cetaceans can rarely hide from predators and many species rely on group living to avoid predation. Group living often serves to decrease the number of attacks through increased vigilance, dilution and predatory avoidance of large groups (Norris and Schilt 1988). Sperm whales appear to reduce predation rates in two ways by living in groups. When attacked, groups of female sperm whales often engage in communal defense, placing any dependent young in the middle of a protective ring of adults (Arnbom *et al.* 1987, Weller *et al.* 1996). Even when no predator is present, female sperm whales in groups with calves alter their dive schedule, such that at least one adult is usually at the surface with young calves that are not capable of diving to foraging depths. This likely reduces predation on young calves and may be a form of reciprocal altruism or kin selection (Whitehead 1996a).

In the open ocean prey distribution tends to be patchy and unpredictable. Dense patches of food separated by large areas without food may encourage group living and cooperative foraging in oceanic dolphins and sperm whales. Large groups of dolphins and sperm whales are believed to spread out and forage over a large area and congregate together to feed when a dense patch of food is found (Würsig and Würsig 1980, Würsig 1986, Whitehead 1989). Dependence on mobile and difficult to catch prey may lead to the evolution of long term bonds between individuals in transient killer whales (*Orcinus orca*) that forage almost entirely on other marine mammals (Baird and Dill 1995, Baird In press).

Many dolphin species live in fission-fusion societies in which groups form and disassociate rapidly. When resources (such as prey or mates) are sometimes clumped and at other times evenly distributed, a fission-fusion lifestyle may be advantageous. To exploit clumped

resources, individuals and groups fuse together to form larger groups than when evenly distributed resources are being exploited (*e.g.*, Wells 1991b, Smolker *et al.* 1992, 1997, Slooten and Dawson 1994, Würsig *et al.* 1994b, Félix 1997).

In most mammals, individuals of one sex disperse before maturity, which limits inbreeding (Greenwood 1980). However, the relatively low travel costs in cetaceans may eliminate the need for dispersal in some species, if their natal group ranges widely and associates with other groups temporarily when mating occurs (Connor *et al.* 1998). In resident killer whale pods neither males nor females disperse from their natal pod (Bigg *et al.* 1990). Mating likely occurs during the frequent interactions between pods although mating has not been observed (Baird In press). Long finned pilot whales (*Globicephala melas*) also seem to fit this pattern (Amos *et al.* 1993), although only the apparent lack of dispersal has been studied in pilot whales.

The aquatic environment is a three dimensional environment, which makes territoriality or monopolizing a female or group of females difficult (Connor *et al.* 1998). Males may search for estrus females (Whitehead 1990c), mate promiscuously (suggested for many dolphin species *e.g.*, Slooten and Dawson 1994, Connor *et al.* 1996) or form coalitions to cooperatively herd females, as in bottlenose dolphins[3] (*Tursiops truncatus*) in Australia (Connor and Smolker 1996, Connor *et al.* 1996).

Many of the life history traits of cetaceans (such as long life spans, long lactation periods) lead to a long time period in which individuals can develop and maintain social bonds. Several species have strong bonds which last for periods of years (or the animals entire lifespan) and the social organization in these species is very complex. (*e.g.*, sperm whales, killer whales, and bottlenose dolphins; Connor *et al.* 1998).

---

[3] It has been suggested that bottlenose dolphins are not monophyletic. The Monkey Mia, Australia population may actually belong within the genus *Stenella*, and there may be other taxonomic differences between other populations (see Rice 1998). However following Rice (1998), I classify all of the populations discussed in this thesis as *Tursiops truncatus*.

INFLUENCES ON CETACEAN POPULATION STRUCTURE

The role that geographic isolation plays in creating structure within cetacean populations is likely linked to the temporal and spatial scale of variation in patchy resources. In the open ocean patches of resources tend to be labile and vary greatly in size as well as spatial and temporal location (*e.g.*, Haury *et al.* 1978, Horwood and Cushing 1978). As cetaceans have relatively low travel costs (*e.g.*, Bose and Lien 1990, Williams *et al.* 1992), they are able to move long distances to find resources. For example, El Niño events occur every few years and range in severity. These events dramatically change the distribution of prey throughout the South Pacific and sperm whales migrate long distances to find prey (Smith and Whitehead 1993, Jaquet and Whitehead 1996, Whitehead 1996b). These long range movements prevent geographic isolation and a geographically based population structure (Whitehead *et al.* 1998b).

While resources are still patchy in coastal environments, the spatial and temporal scale of the variability in location and size of patches is usually much smaller than in the open ocean (Haury *et al.* 1978, Horwood and Cushing 1978). Therefore cetacean species living in coastal environments often do not migrate long distances to find resources. Populations of coastal species may be broken up into geographically separate subpopulations which rarely interact (*e.g.*, Wells 1991b, Hoelzel 1998, Hoelzel *et al.* 1998b).

Humpback whales (*Megaptera novaeangliae*) spend the summers in a number of widely dispersed high latitude feeding grounds and then congregate in a small number of tropical breeding areas. As individuals tend to return to their mother's feeding ground throughout their lives, there is geographical structure to the mitochondrial gene distribution. However mixture on the breeding grounds leads to a reduced geographical structure in the nuclear gene distribution (Baker *et al.* 1998).

Some species of cetaceans have long term social bonds and large complex brains which may facilitate the evolution of cultural processes such as vocal traditions and foraging techniques. If these cultural processes are passed down through matrilineal groups, populations may be

structured through different cultural traits (Connor *et al.* 1998, Whitehead *et al.* 1998b). The population of killer whales off the coast of British Columbia, Canada and Washington state USA consists of mammal-eating transients and fish-eating residents which rarely interact, even though their geographic distributions are similar. If the foraging techniques are cultural traits which are passed down maternally, then these cultural processes are leading to a highly structured population (Hoelzel 1998).

Whaling history may have a strong influence on the age and sex structure in some cetacean populations. Sperm whales off the Galapagos Islands and mainland Equador have very low recruitment rates which is likely linked to extensive whaling of mature males in the 1960's and 1970's. This whaling removed almost every mature male and many sub-adult males from the population. As a result, there are currently few mature males on the breeding grounds, which leads to low calving rates and a population that is skewed towards older individuals and few mature males (Whitehead *et al.* 1997a).

WHY STUDY THE SOCIAL ORGANIZATION AND POPULATION STRUCTURE OF NORTHERN BOTTLENOSE WHALES?

The beaked whales (Family Ziphiidae), which include northern bottlenose whales, are some of the least understood large mammals. New species have been discovered within the past decade (Reyes *et al.* 1991) and genetic evidence suggests that there may still be more species to describe (Dalebout *et al.* 1998). Very little is known about most of the 19 described species, although there is limited information on three species which were the targets of commercial whaling (Baird's beaked whales – *Berardius bairdii*; Cuvier's beaked whales – *Ziphius cavirostris*; and northern bottlenose whales). By studying northern bottlenose whales we may begin to understand some of the factors influencing social organization and population structure in beaked whales, and broaden our knowledge of mammalian sociality.

Conservation and management decisions require as complete a knowledge base as possible about the social organization and population structure of a species, as well as its interactions with other species and its habitat. Northern bottlenose whales in the Gully, a submarine canyon off Nova Scotia (see Figure 1.2) are potentially threatened by industrial development

(Whitehead *et al.* 1997b). The Gully has recently been declared a pilot marine protected area by the Department of Fisheries and Oceans, Canada, in part to protect the northern bottlenose whale (Anonymous 1998) The boundaries and regulations of permitted and excluded activities in the protected area have not been finalized. Therefore, it is imperative that we understand as much as possible about these whales in order to make reasonable conservation decisions.

NORTHERN BOTTLENOSE WHALE

PHYSICAL DESCRIPTION

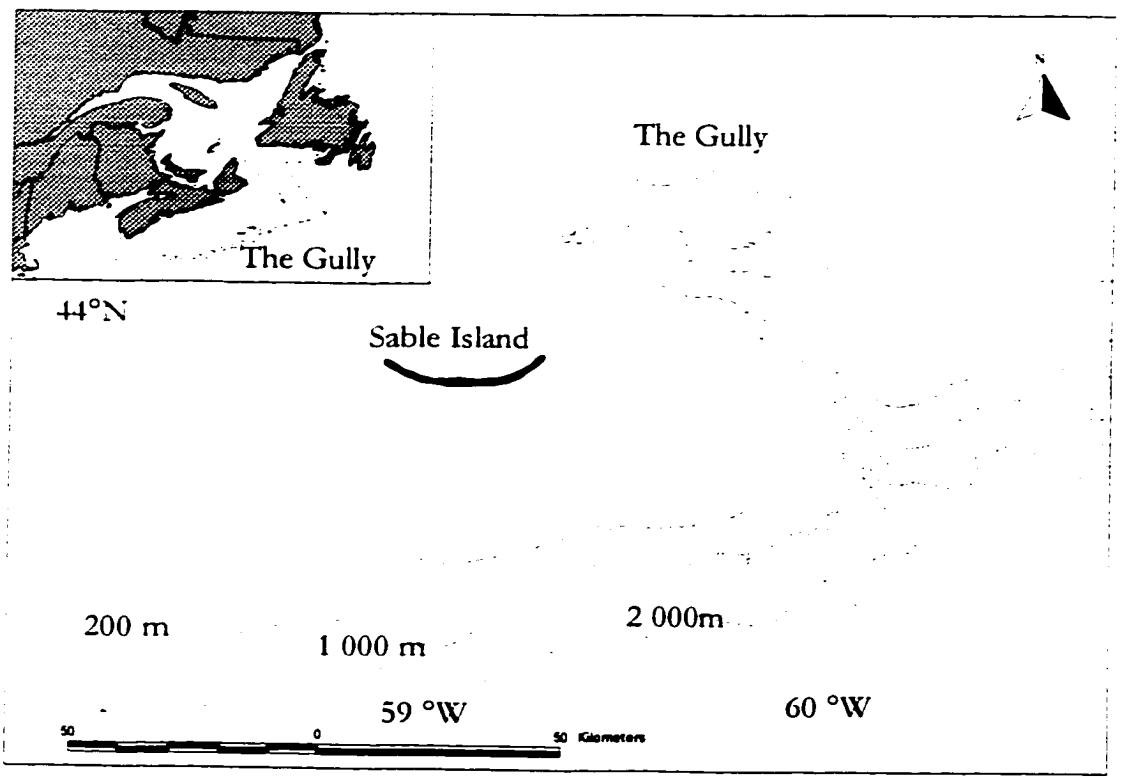
Northern bottlenose whales are medium-sized toothed whales ranging from six to nine meters long, with mature males approximately one meter longer than females (Benjaminsen 1972). Two conical teeth erupt only in mature males at the apex of the lower jaw, although occasionally a second set of teeth develop and erupt (Mead 1989b). The skull and melon profile of bottlenose whales is also sexually dimorphic (see Chapter 3), as the hyperdevelopment of the maxillary crests in males changes the melon profile from smooth and rounded to blunt and squared-off (Mead 1989b).

The colouration ranges from a deep chocolate brown on the dorsal area to grayish-white on the ventral surface. The melon area in newborns is whitish in colour and darkens with age, although the blunt area of the melon just above the beak becomes white in mature males. In older females a whitish band develops around the blowhole and encircles the girth of the whale (Mead 1989b).

PHYLOGENY

Traditionally cetaceans have been separated into the baleen whales (Mysticeti) and toothed whales (Odontoceti). Recently molecular genetic techniques have questioned the relationship between the sperm whale family (Physeteridae) and other odontocetes, and have not been able to determine the placement of the beaked whales family (Hasegawa *et al.* 1997). By combining molecular and morphological traits, Messenger and McGuire (1998)

Figure 1.2: Map showing the Gully study area.



concluded that both the sperm whale family and the beaked whales should be considered odontocetes. Additionally it appears that beaked whales are monophyletic and most closely related to the river dolphins (Messenger and McGuire 1998).

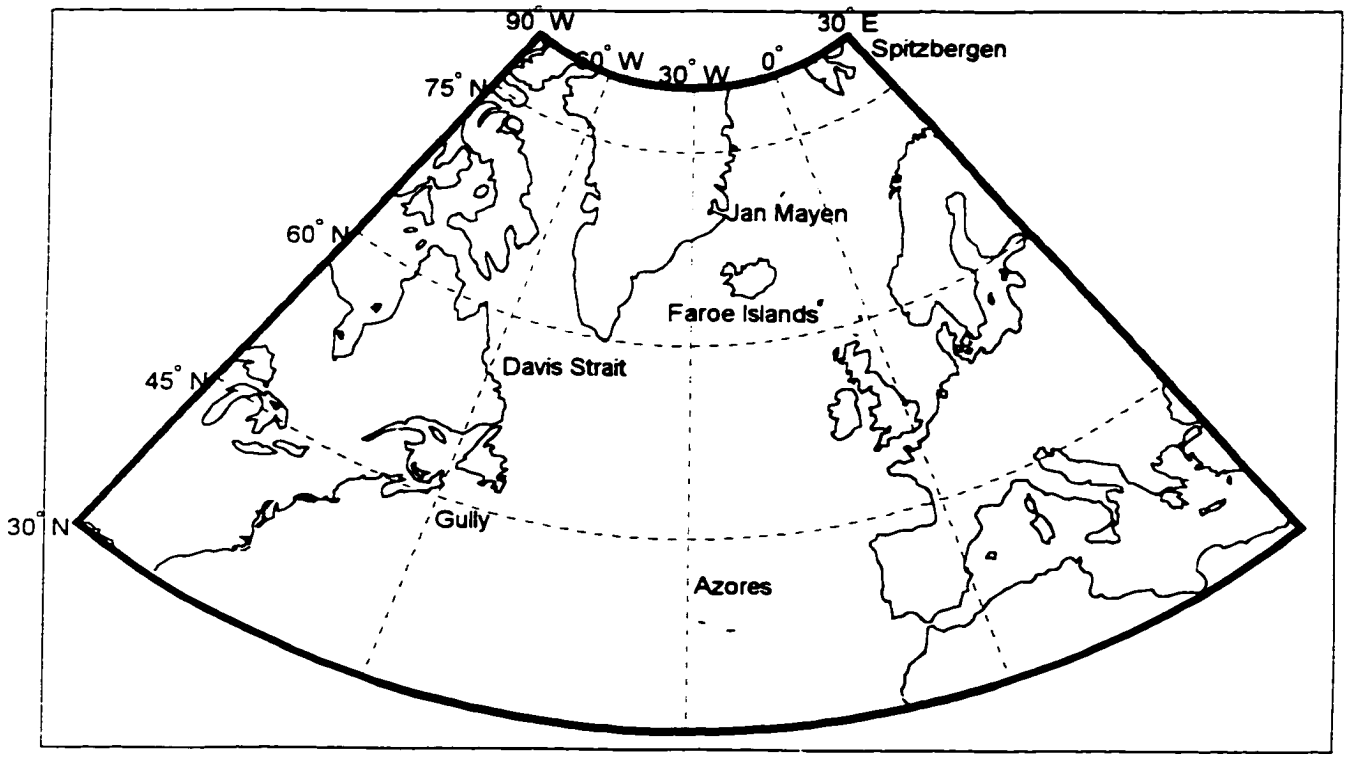
Within the beaked whale family, Hyperoodon is a separate genus with two recognized species (northern and southern bottlenose whales – *Hyperoodon planifrons*) that have geographically distinct ranges (Mead 1989b). A number of sightings of beaked whales in the tropical Pacific have been identified as a possible third Hyperoodon species but the exact species identification is not certain (Urbán *et al.* 1994, Pitman *et al.* 1999). Recent molecular work on southern bottlenose whales indicates that there may be more than one southern taxon (Dalebout *et al.* 1998).

ECOLOGY: DISTRIBUTION, DIET AND PREDATORS

Distribution

Northern bottlenose whales are found only in deep water in the North Atlantic (Figure 1.3) with the normal distribution stretching from Davis Strait to Nova Scotia in the western Atlantic and from Spitzbergen to the Azores in the east (Mead 1989b, Steiner *et al.* 1998). Known whaling grounds lie off Spitzbergen, Iceland, Jan Mayen and the Faroe Islands as well as Davis Strait and the Gully (see Figure 1.3 for whaling locations). There are a few sightings of bottlenose whales from the 1800's in the Mediterranean, although some of these may actually have been Cuvier's beaked whales (Mead 1989b). In the western north Atlantic there have been strandings as far south as Rhode Island and several strandings in the Gulf of St. Lawrence, but these areas are believed to be outside the normal range of the species (Mitchell and Kozicki 1975). Whales caught or photographically measured in various whaling grounds have different length distributions (Benjaminsen 1972, Bloch *et al.* 1996, Whitehead *et al.* 1997c) indicating there may be geographic isolation between the different whaling grounds.

Figure 1.3. Distribution of northern bottlenose whales, showing known areas of concentration (from whaling and whale watching observations).



Whaling catch data indicate a possible north-south annual migration from the Jan Mayen/Spitzbergen area to the Faroe Islands (Benjaminsen and Christensen 1979) but the evidence is weak and may represent a migration of whalers rather than whales. More recent data suggest that whales in the Gully and Davis Strait remain there year round (Reeves *et al.* 1993).

Diet

Stomach content analysis indicates that northern bottlenose whales feed primarily on squid, although other benthic organisms are sometimes consumed (Benjaminsen and Christensen 1979). Diving depths also indicate foraging at or near the ocean floor (Hooker and Baird 1999). The main prey species in the eastern North Atlantic appears to be *Gonatus fabricii*, a small squid usually found in deep water (Clarke and Kristensen 1980, Lick and Piatkowski 1998). In the western North Atlantic the congener species *Gonatus steenstrupi* is the most likely prey although this has not been confirmed (Kristensen 1981).

Predators

Reports of predation on northern bottlenose whales are rare. There are only two reports of killer whales attacking northern bottlenose whales, and in one case the bottlenose whales had already been harpooned by whalers (Jonsgard 1968a, b). Although killer whales have not been observed in the Gully in the past decade (Hooker *et al.* In press), whalers caught killer whales in the area in the 1960's (Mitchell and Reeves 1988). Pilot whales (*Globicephala* sp.) have been observed attacking sperm whales (Weller *et al.* 1996) and long finned pilot whales have been observed harassing bottlenose whales in the Gully (S.K. Hooker, Dalhousie University, pers. comm.).

LIFE HISTORY

Most of the information about the life history of bottlenose whales comes from whaling data. These data may not be representative of the whole population as whalers often selectively harvest larger animals (which would bias the samples toward older or faster growing individuals; Mitchell 1977). However, as these data came from populations that

had already been whaled for decades before the samples were collected, this may have biased the samples toward younger individuals in comparison to unharvested populations (*e.g.*, Horppila *et al.* 1996). If the life history characteristics for killer whales is compared between whaling and longitudinal photo-identification studies, the whaling data indicate females become sexually active much earlier, have shorter interbirth intervals and shorter lifespans than do the photo-identification data (Christensen 1984, Olesiuk *et al.* 1990). Counting layers of dentine in teeth to age cetaceans is problematic, as there are disagreements about how many layers of dentine are laid down per year, and aging older individuals can be difficult or impossible (*e.g.*, Bowen *et al.* 1983 and references therein) some of these discrepancies may be related to the tooth aging technique used by scientists working from whaling samples.

Females

While there may be biases and errors in the life history data from whaling studies, longitudinal studies on live bottlenose whales have not been carried out for sufficient time to yield life history data. From the whaling data, it is believed that females reach sexual maturity (defined as the presence of corpora lutea) between ages 8-13 years (Christensen 1973). Gestation is believed to last 12 months, with the peak of births occurring in April off Labrador (Benjaminsen 1972). Benjaminsen and Christensen (1979) report that the interbirth interval is two years and that lactation lasts one year. Ohlin (1893) found most mature females were lactating, which he believed indicated a prolonged lactation period. The oldest female aged by Christensen (1973) was 27 years old. Based on the comparisons between whaling and longitudinal studies in killer whales, the age of sexual maturity, interbirth interval and lifespan are likely underestimates.

Males

Male bottlenose whales reach sexual maturity (based on histological examination of testes) between ages 7-9 years, which coincides with the period of fastest growth of testes (Benjaminsen 1972, Benjaminsen and Christensen 1979). The oldest male aged by tooth

layers was 37 years old (Christensen 1973). These ages are also likely to be underestimates.

BEHAVIOUR: DIVING, VOCALIZATIONS AND SOCIAL ORGANIZATION

Diving

Bottlenose whales have long been believed to be deep divers. Whalers reported dives lasting 1-2 hours and whales taking out over 1,000 m of line after being harpooned (Benjaminsen and Christensen 1979). Recently, time depth recorders (TDR) were attached to two bottlenose whales in the Gully yielding approximately 30 hours of diving data. These whales were routinely diving to more than 800 m, making bottlenose whales one of the deepest diving marine mammals known to date (Hooker and Baird 1999).

Vocalizations

The predominant vocalizations of bottlenose whales are echolocation clicks. There appear to be two forms of echolocation clicks, regular click series and click trains (Hooker In prep.). Regular clicks tend to be heard when the whales are at depth, presumably foraging. The peak click frequency of regular clicks are 24 kHz. The optimal frequency for objects the size of their primary prey the *Gonatus* sp. squid (6 cm) is approximately 24 kHz (Hooker In prep.). Click trains tend to be heard when the whales are at the surface and are shorter and have more variation in the inter-click interval than regular clicks. These clicks may be used by the whales to echolocate the research vessel (Hooker In prep.). Early research indicated that bottlenose whales also make whistles and chirps (Winn *et al.* 1970) although Hooker (In prep.) did not record any whistles that were definitively made by bottlenose whales.

Social organization

Whalers quickly learned that the social organization of bottlenose whales assisted their catch efforts. Once a single individual in the group had been harpooned, the remaining group

members would not leave their dying companion and whalers would capture the entire group (Benjaminsen and Christensen 1979), a behaviour also exploited by killer whales attacking harpooned bottlenose whales (Jonsgard 1968a, b).

In Davis Strait and off Iceland the most common group size was 2-6 whales, although groups as large as 20 were observed (Benjaminsen and Christensen 1979). Groups of 2-3 whales tended to consist of individuals of the same sex and nearly the same age. Lactating females were sometimes found on their own with their calf, or two females and their calves were grouped together. Larger groups consisted of both males and females and were most common in April, the proposed mating season for bottlenose whales in Davis Strait (Benjaminsen and Christensen 1979). There is weak evidence that geographical segregation of the sexes may occur due to differences in the onset of migration (Benjaminsen and Christensen 1979).

Preliminary analysis of data from the Gully indicated that there were three main types of groups. Mature male groups consisted of 1-5 mature males, female groups consisted of 1-9 females and immature animals, and mixed groups consisted of 1-3 mature males and 2-8 females and immature animals. Smaller groups (1-4 animals) were most common. Several pairs of males formed associations that lasted at least two years whereas females only formed short term associations, lasting less than one field season (Faucher and Whitehead 1991).

ABUNDANCE AND CONSERVATION STATUS

Exploitation

The pre-exploitation population size of bottlenose whales in the North Atlantic is estimated at 40-50,000 individuals, although it is very difficult to accurately determine (Christensen 1976). One difficulty in estimating the pre-exploitation population size is accounting for the number of individuals which were harpooned but were not recovered by the whaling vessel (and presumably died). 'Loss and killed' estimates range from 10-25% of the captured animals (Reeves *et al.* 1993).

Bottlenose whales were valued for the high quality oil in the head as well as the value of the meat and blubber (Mitchell 1977). Commercial whaling began in 1850 by Scottish whalers. From 1877-1893, British and Scottish whalers captured 1,669 bottlenose whales, mostly from Greenland and Davis Strait. British whaling ended about 1892 when the price fell dramatically as the market was flooded with bottlenose whale products (Reeves *et al.* 1993). Norwegian whalers were active for the longest time and caught the most whales. The Norwegian fishery began in 1883, and 17,500 whales were caught before 1892. Unlike the British whaling industry, Norwegian whaling continued until 1926 when the fishery collapsed as there were no longer enough bottlenose whales to support a single species fishery. It is estimated that the Norwegians had caught approximately 57,500 whales between 1883 and 1926. From 1927-1973, Norwegian whaling of bottlenose whales continued as part of a multi-species fishery targeting minke (*Balaenoptera acutorostrata*), killer, pilot and bottlenose whales. During this period there were relatively few bottlenose whales caught, only 5,900 including 818 taken off Labrador from 1969-1971. There was also a small Canadian fishery for bottlenose whales. Whalers from Blanford, Nova Scotia captured 87 whales from the Gully and the Grand Banks of Newfoundland between 1962-1967. Commercial whaling for bottlenose whales ended in 1973 when Britain banned the import of whale meat for pet food, thus eliminating the commercial market (Reeves *et al.* 1993).

There is also a small traditional harvest of bottlenose whales that continues today in the Faroe Islands. The Faroe fishery is a drive fishery, similar to the pilot whale fishery, that mainly exploits whales that are close to shore and may be stranding. There are written catch records that date back to 1584 and record that only 811 whales have been caught since that time. Most years fewer than 10 individuals are taken and only 29 individuals were captured from 1970 to 1993 (Bloch *et al.* 1996).

Conservation status

The number of bottlenose whales in the North Atlantic was seriously reduced by 1926 when the single species fishery ended and a multi-species fishery began. The stock was considered seriously depleted by the mid 1970's when no catches were made and

commercial whaling ended (Mitchell 1977). There are no current population estimates of bottlenose whales for the North Atlantic, but it is unlikely that they have fully recovered from the intensive hunting (Reeves *et al.* 1993). Surveys in the late 1980's estimated there were 4,900 bottlenose whales off Iceland (CV = 0.16) and 900 bottlenose whales off the Faroe Islands (CV = 0.45) however these estimates were not corrected for the proportion of whales below the surface during the survey transect (Gunnlaugsson and Sigurjónsson 1990). Therefore these numbers should be viewed as minimum population estimates.

Northern bottlenose whales were listed as a protected species with the International Whaling Commission (IWC) in 1977 and placed in Appendix 1 of the Convention of the International Trade in Endangered Species (CITES) in 1984 (Reeves *et al.* 1993). They are listed by the International Union for the Conservation of Nature (IUCN) as Lower Risk – conservation dependent, which means that although the species is receiving protection, removal of that protection would likely lead to a more threatened listing within five years (Baillie and Goombridge 1996). Within Canada, the species has no designated status with the Committee on the Status of Endangered Wildlife in Canada (COSEWIC); however, the Gully population has been listed as Vulnerable since 1996 (Whitehead *et al.* 1997b).

THESIS OBJECTIVES

The objectives of my thesis were to assess the social organization and population structure of northern bottlenose whales in the Gully using photo-identification techniques. As photo-identification had not previously been used on bottlenose whales, my first objective was to assess the reliability of photo-identification to identify individuals based on natural marks (Chapter 2). I also assessed the reliability of categorizing individuals into age/sex classes based on photographs of the melon profile (Chapter 3). The next objective was to describe the general surface behaviour of bottlenose whales in the Gully, including time spent at the surface, group size and composition and visually observable behaviours (such as breaches and lobtails; Chapter 4). I described the social organization of bottlenose whales in the Gully, investigating differences in the patterns of associations between different age/sex classes (Chapter 5). Adult-calf interactions were investigated in detail in Chapter 6. The size of the Gully population and the residency of individuals within the Gully were investigated to describe the structure of the population (Chapter 7). Finally the results of analyses of social organization and population structure of northern bottlenose whales in the Gully were compared to those of other cetacean populations to explore the factors leading to the evolution of cetacean sociality and population structure (Chapter 8).

Chapter 2: Reliability of natural marks for individually identifying northern bottlenose whales: effects of photographic quality, mark type and location

INTRODUCTION

Photo-identification (photo-id) of individuals is a common and important technique in cetacean research (see Hammond *et al.* 1990 for a review). In studies of social organization and population structure it is usually assumed that individuals in the population are uniquely marked, have equal probability of "capture" and "recapture" and that marks do not change over time. However the use of natural marks can lead to violations of these assumptions (Hammond 1986). The assumption of uniquely marked individuals can be violated if two different individuals each possessing a few common marks are considered to be the same individual. Unequal capture probabilities can occur if individuals with obvious marks are identified by poor quality photographs, but individuals with more subtle marks are not. Mark change over time can also prevent recapture (Hammond 1986).

In analyses of social organization and population structure, it is important to select photographs and individuals to optimize the precision and accuracy of the results. If the criteria by which photographs and individuals were included in analyses are too lax, errors and biases may be introduced, while too strict criteria can lead to lack of precision and accuracy due to a smaller sample size (Friday 1997).

These problems have been considered in photo-id analyses (*e.g.*, Hammond 1986, 1990a), but few collections of photographs have been analyzed to assess quantitatively which photographs and individuals should be included in different types of analyses. Friday (1997) assessed the precision of population estimates of humpback whales when photographs of lower qualities were sequentially removed from the analysis and determined what quality of photographs should be included in these estimates. When estimating the population size of bottlenose dolphins using the Moray Firth of Scotland, Wilson *et al.* (1999) quantitatively assessed which individuals should be included in the mark-recapture analysis, but subjectively determined the quality of photographs to include. Dufault and Whitehead (1995) carried out an extensive analysis of mark change in a photo-id catalogue of sperm whales, although they did not specifically investigate photographic quality. The mark change analysis in this chapter is modeled after Dufault and Whitehead (1995). Complications

arising from using photographs of both left and right sides of a dorsal fin, as well as from the varying proportions of the flank visible in the photograph, are considered in this analysis.

This chapter describes the distribution of the observed mark types within the population to determine which mark types were useful in uniquely identifying individuals. The visibility of marks in photographs of different qualities were assessed to define what quality of photographs contained sufficient information to identify all individuals accurately. Quantitative analysis of mark change was used to assess the reliability of mark types for matching over various time scales. Matches of photographs of bottlenose whale melons (from beak to blowhole) were used to independently test the reliability of dorsal fin matches. Restricting the dataset would decrease the sample size, and reduce precision, thus the full and restricted (high quality photographs of reliably marked individuals) datasets were compared to determine whether using the restricted dataset lead to fewer violations in the assumptions.

METHODS

PHOTOGRAPHIC COLLECTION

Photographs of northern bottlenose whales were collected from the Gully, Nova Scotia (44° N, 59°W – see Figure 1.3) during the summers of 1988-1997 from sailing vessels with auxiliary engines (see Table 2.1 for details of field work). When conditions permitted, photographs were taken from both left and right sides of the dorsal fins and flanks of bottlenose whales which were within 30 m of the vessel. Photographs were taken irrespective of any obvious markings on the individual, and photographs were taken throughout the encounter, whether or not photographs had already been taken of a particular individual. Most photographs were taken with Canon AE1, AT1 (manual focus) or Elan IIE 35-mm (automatic focus) SLR cameras equipped with 300-mm f4 lenses, using either Kodak T-max or Ilford HP5 400 ASA black-and-white film. Melons were photographed in conjunction with dorsal fin photographs for use in sexing individuals (see Chapter 3 for details on sexing technique).

Table 2.1 Details of field work during dedicated field trips. Shorter opportunistic trips were made in October 1989, February 1990, July 1991 and 1992 and April 1997.

Year	Trip dates	Number of daylight hours spent in the Gully	Vessel
1988	July 8-21, July 25 – August 6	211	Elendil
1989	July 16-30, August 1-15	225	Elendil
1990	June 14-28, July 2-18, July 25 - August 12	401	Elendil
1993	July 10-23	143	Balaena
1994	July 31 – August 18	171	Balaena
1995	August 20 – September 2	76	Balaena
1996	June 7-25, July 4-21, July 27 – August 12, August 19 – September 2	659	Balaena
1997	June 7-23, July 1-19, July 24 – August 6, August 10-27	653	Balaena

Black-and-white negatives were examined on a light table with a 10x magnifying loupe. All negatives were assigned a qualitative quality rating (Q-value) from 1 to 6 based on focus, exposure, angle of the fin relative to the negative plane and the proportion of the frame filled by the fin (Arnbom 1987), with Q-6 being the highest quality photographs (see Figure 2.1 and Appendix 1 for details on the quality rating scheme). Q-1 photographs were extremely poor and were not included in the collection. The Q-value was independent of the markings on the individual. Sketches were made of the marks of each individual to assist in matching between negatives. The highest quality negative of each individual in each year was printed, and the photographs were compared with each other and to photographs from previous years. If a photograph matched an individual that was already known in the collection, the photograph and all other associated negatives were assigned to the whale's identification number. If not matched, the individual was given a new number and added to the catalogue. Photographic collections for left and right sides were maintained separately, although some identifications from different sides could be linked. The negative collection contained 8,751 negatives that were assigned an identification number and Q-value (see Table 2.2 for summary of photo-id data).

Table 2.2. Summary of photo-identification data (Q≥2).

Year	Number of frames	Left fin identifications	Right fin identifications
1988	123	18	19
1989	1202	109	96
1990	3116	171	167
1991	27	8	5
1993	549	46	53
1994	370	54	43
1995	82	14	17
1996	1751	94	86
1997	1531	99	90

ANALYSES

The analyses of marks in this study were similar to those used to establish the catalogue. All marks were sketched, and the marks were categorized into mark types (see Figure 2.2 for examples of mark types and Table 2.3 for descriptions). To assist in determining the sources of mark types, 115 colour slides (Kodachrome 200 ASA) were taken in July 1998. The slides were used to determine the colour of each mark type. I analyzed all negatives after having five years experience in photo-identification of bottlenose whales. All analyses were conducted at least six months after any new photographs were added to the catalogue, and I did not remember the previously assigned identifications photographic Q-values for most negatives.

Figure 2.1. Examples of photographs of different qualities (a Q-2, through e Q-6). All photographs are of individual 45 taken in 1997.

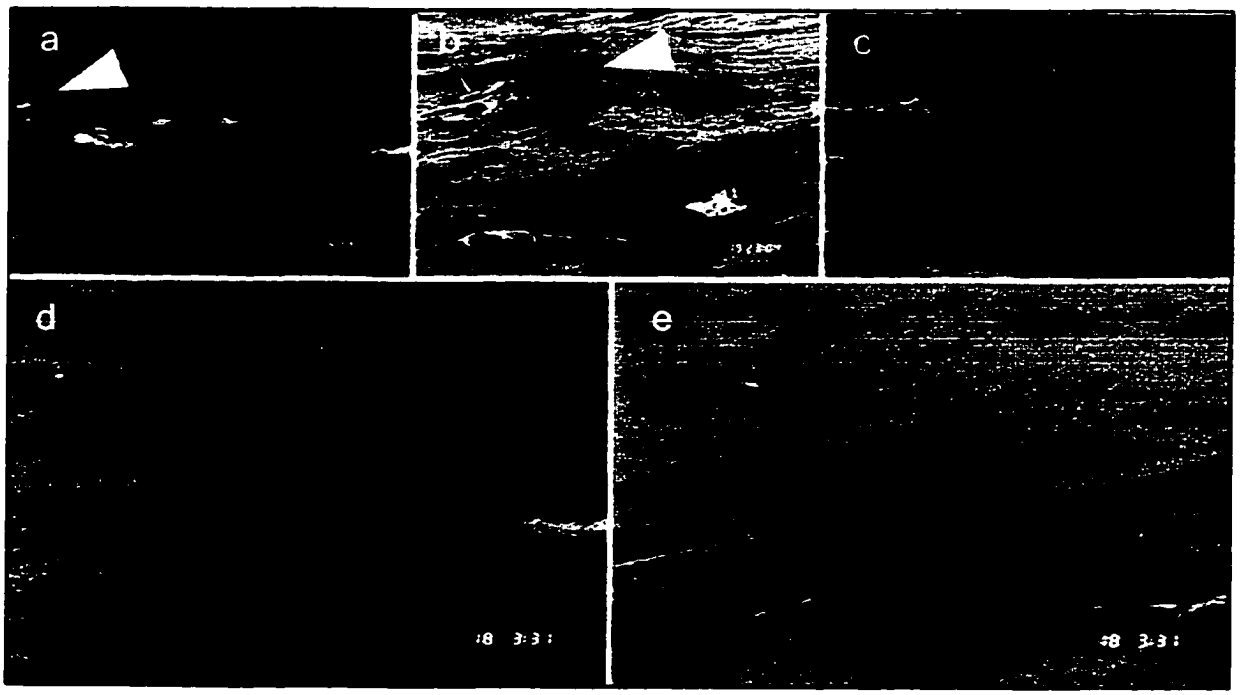


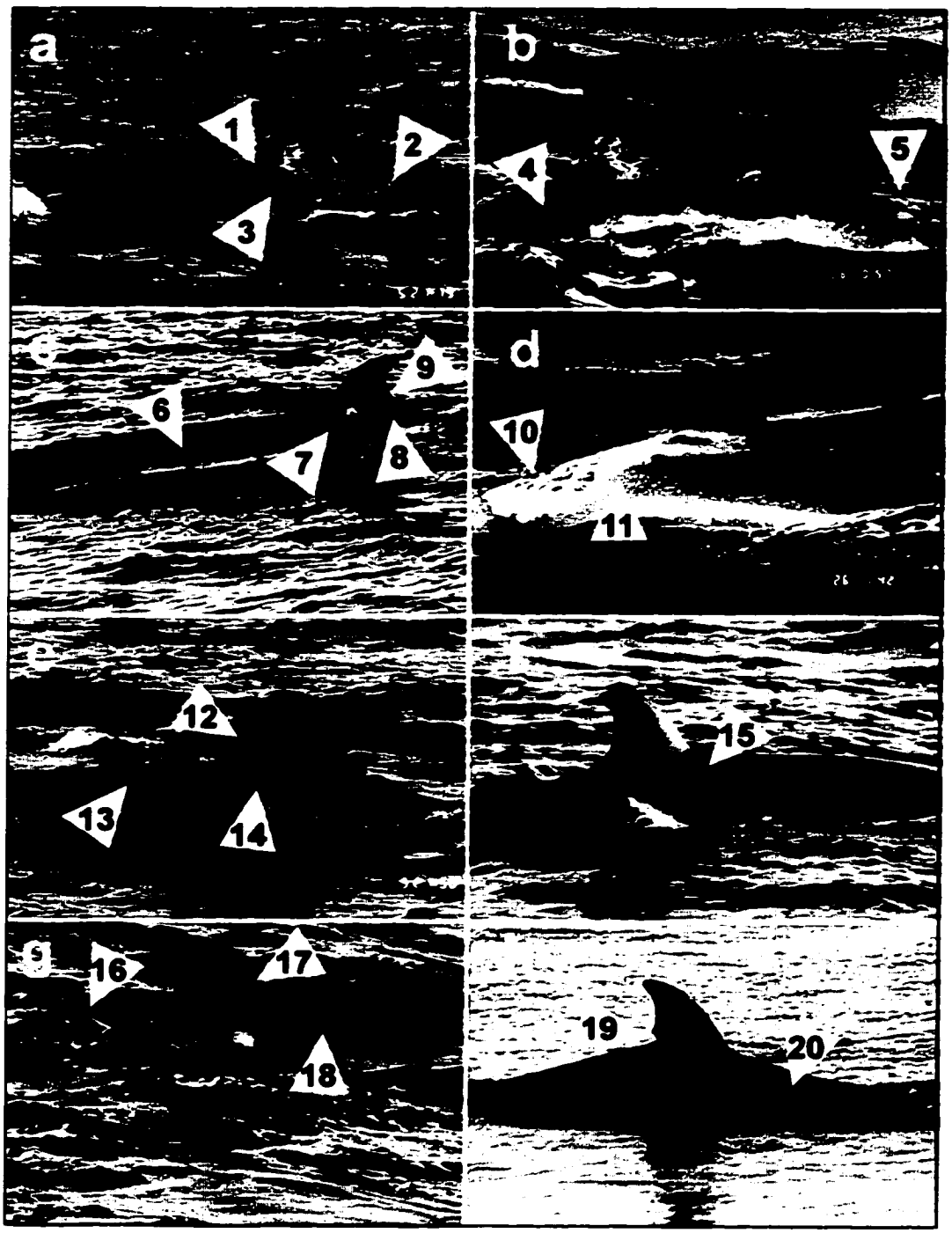
Table 2.3: Description of mark types.

MARK TYPE	COLOUR [1]	SIZE [2]	DESCRIPTION
Notch	May have white area surrounding missing tissue	Vary in size from less than 1 cm indentation to 10 cm	Located on dorsal fin
Back indentation	May have white area surrounding missing tissue	Less than 10 cm deep	Located posterior to dorsal fin
Large scar	White	Larger than 10 cm	Irregular shapes
LINEAR MARKS			
Short single linear scrape	white	Less than 5 cm	Single line
Long single linear scrape	white	Longer than 5 cm	Single line
Short parallel linear scrape	white	Less than 5 cm	Two parallel lines
Long parallel linear scrape	white	Longer than 5 cm	Two parallel lines, longer than five cm
Tooth rake	white	Usually less than 5 cm	Multiple parallel lines
Attachment	white	Disk less than 3 cm, trailing lines less than 10 cm	Circular disk 3-5 parallel lines trailing
Dark band	dark brown	5-10 cm long	Thin linear band – often appeared indented
Light band	cream	5-10 cm long	Thin linear band
PATCHES			
Small white dot	white	Less than 1 cm diameter	Circular in shape
Dark dot	dark brown	Less than 1 cm in diameter	Circular in shape
Dark circular patch	dark brown	Larger than 1 cm diameter	Circular in shape – often indented
Dark non-circular patch	dark brown	Larger than 1 cm	Irregular shape
Hatch	dark and light brown	Extended less than 10 cm from spine towards ventral surface, but extended at least 1 meter anterior from dorsal fin	Grid of dark brown colouration over normally pigmented skin
Light and dark patches	dark and light brown	Large – covering at least 50cm^2	Irregular shape, dark brown colouration over normal pigmentation
Dot in light patch	dark brown dot in light patch	Dot less than 1 cm diameter, light patch less than 3 cm diameter	Often appeared indented
Dark fringed circle	dark brown circle surrounding light brown	Less than 3 cm diameter	Often appeared indented
Circular light patch	cream	Larger than 5 cm diameter	Circular shape – not indented
Non-circular light patch	cream	Larger than 1 cm	Irregular shape
Mottled patches	white and cream over light brown	Large – covering at least 25 cm^2	Textured with light patches appearing raised

1) From colour slides taken in 1998

2) Size of mark estimated from width of dorsal fin (approximately 60 cm in adult female based on stranding measurements - Seargent *et al.* 1970, Mitchell and Kozicki 1975).

Figure 2.2. Examples of types of marks found on dorsal fins used to identify northern bottlenose whales. Mark types: 1) Dark dot, 2) Dot in light patch, 3) Dark non-circular patch, 4) Attachment, 5) Mottled patches, 6) Single long linear scrape, 7) Dark circular patch, 8) Dark fringed circle, 9) Short parallel linear scrape, 10) Back indent, 11) Large scar, 12) Dark band, 13) Light band, 14) Short single linear scrape, 15) Light and dark patches, 16) Large circular light patch 17) Small white dot, 18) Non-circular light patch, 19) Notch on dorsal, 20) Long parallel linear scrape.



Photograph quality and equal catchability

To investigate the effect of photograph quality on the visibility of the marks, individuals with at least one left fin negative of each quality (Q=2-6), taken within the same year, were selected. Only 36 individuals met these criteria. If an individual met these criteria in more than one year, only negatives from the first year it occurred were used in this analysis. If there was more than one negative of the same quality, the negative was randomly selected (using a random number table). Marks were sketched, categorized and counted as described above, without reference to the previously assigned fin identification number and quality. The presence or absence of each mark was compared between negatives of different qualities for each individual. This analysis was repeated on the same set of negatives, using reliable-marks (see below; mark types with no losses over the study period).

Mark distribution and the uniqueness of individuals

To assess whether individuals were uniquely marked, the distribution of marks within the population was analyzed. To observe as many mark types as possible only excellent quality photographs (Q≥5) were selected. I randomly selected 100 individuals from the 268 individuals with excellent quality photographs, and then randomly selected a single negative from each of the 100 individuals. Marks for each individual were sketched and counted as described above. Some of the individuals represented in the selected sample were sexed by photographs of their melons (Gray 1882). I used *t*-tests to determine whether males and females had different numbers of marks, as well as to compare the number of marks between older mature males and younger sub-adult males. I used G-tests to determine whether the proportion of individuals with reliable marks differed between different age and sex classes.

Mark change

This analysis used individuals that had negatives of Q≥4 in three or more years, and the highest quality negative of each individual in each year was selected. If there was more than

one negative of the same quality, the negative to be analyzed was selected randomly. Multiple comparisons were made for each individual. The number of animal years over which the comparisons were made was calculated from the total number of years between first and last photograph. For example, an individual photographed in 1989, 1990 and 1997 was examined twice, from 1989-1990 (1 animal-year) and 1990-1997 (7 animal-years) over a total of 8 animal-years (Dufault and Whitehead 1995). Pairs of negatives were compared on the light table at the same time, and both images were drawn on the same form. As there was no method other than photo-id to match individual bottlenose whales, individuals which were matched by photo-id were used to analyze the reliability of natural marks. To minimize the problems created by this lack of independence, each mark on each animal was assessed separately to determine if a mark had been gained or lost.

Gain and loss rates of each mark type per individual per year were calculated by dividing the total number of mark losses and mark gains by the number of animal years over which the comparisons were made. Gain and loss rates were compared for matches between photographs of different Q-values using G-tests. As G-tests are not appropriate for small samples (Sokal and Rohlf 1995), they were conducted only if there were more than 15 occurrences of gain or loss of that mark type. As different proportions of the flank were recorded on different negatives, only marks located in areas shown in both negatives were counted as a gain or loss.

Loss rates of individual marks were compared between negatives of different qualities by likelihood ratio methods, as some marks were lost very rapidly and the comparisons were made over years. If marks were lost at an instantaneous rate of μ/year, then the probability that a mark seen at time t_1 was also present at time t_2 was

$$e^{-\mu(t_2-t_1)}.$$

From the data, μ was estimated by maximum likelihood methods and the hypothesis that μ varies between photographic quality was tested using likelihood ratio tests (Sokal and Rohlf 1995).

Reliable mark types were defined as mark types with no losses over the 9-year study period. As some mark types were rare and present in only a few photographs selected for this analysis, I also used the criterion that a mark type had to occur more than five times in the 112 photographs that were analyzed for mark change to be considered reliable. Identification photographs in this study were centered on the dorsal fin and varying sections of the flank appeared in the photographs. Thus, marks located closer to the dorsal fin were more likely to be photographed than marks located further away. Marks, except for notches, can be located anywhere on the body, therefore it was important to determine what area of the body was routinely captured in photographs. All photographs ($Q \geq 4$) of individuals with reliable marks (other than notches, a mark found only on the dorsal fin) were examined for the presence or absence of the reliable mark and the proportion of photographs in which the mark was visible was calculated for each individual.

The proportion of the population that was reliably marked was calculated by comparing the number of photographs ($Q \geq 4$) containing individuals with reliable marks with the total number of photographs (Williams *et al.* 1993). This analysis was performed for each year when more than one month was spent in the field (1989, 1990, 1996 and 1997), and for left and right sides separately. The overall mean and SE in the proportions were calculated from the mean and SE of annual estimates.

All occurrences of an addition of a reliable mark were counted and the gain rate was calculated by dividing the number of occurrences by the number of animal-years compared. Gain of a reliable mark sometimes changed the status of the individual (from unreliable to reliable) and this rate of change was also calculated.

Melon matching

As the shape of bottlenose whale melons was sexually dimorphic (Gray 1882), a catalogue of melon photographs was also established (see Chapter 3 for more details). These photographs showed identifying marks and were used as an independent test of dorsal fin matches. If a photograph of a melon was linked in the field to a dorsal fin then the melon

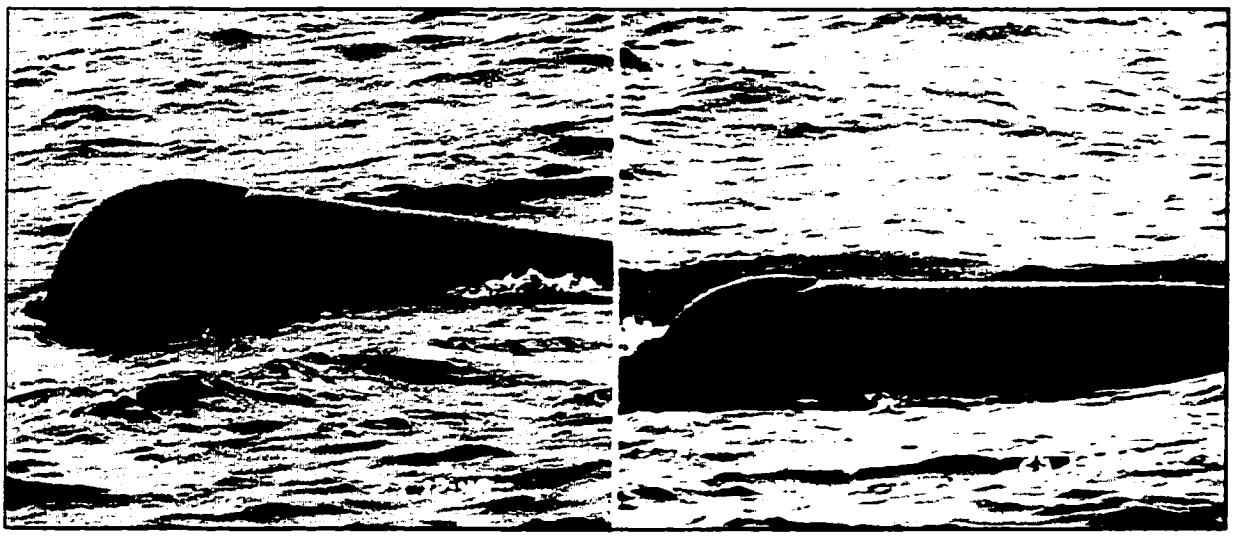
was assigned the same identification number. If a melon was not linked to a dorsal fin, and the melon negative contained marks useful for matching, it was assigned a separate melon identification number. Each year, the highest quality melon negative of each individual, including individuals with only a melon identification number, was printed. Each melon photograph was compared to every other melon photograph without reference to the melon or fin identification numbers. Individuals which were matched based on melon photographs were compared to matches based on dorsal fins to test the reliability of fin matches (See Figure 2.3 for an example of a match between melon photographs).

Violations of assumptions

Violations in the assumptions of mark-recapture (equal probability of capture and recapture, uniquely marked individuals, and no mark change) could arise if photographs of the same individual were not matched due to poor photographic quality, different individuals with a few common mark types were matched, or if mark change prohibited matching photographs of the same individual over time (Hammond 1986). To assess the possibility of two different individuals being matched as the same individual based on a few marks of common types, all photographs with a reliable mark from the mark distribution sample (see above) that had only one reliable mark visible in the frame were compared to determine likelihood of matching.

The proportion of photographs of an individual that were matched to photographs from different years were potentially influenced by photographic quality. Therefore, the resighting rate (proportion of individuals seen in any other year) was calculated for each quality category based on the maximum photograph quality assigned to an individual that year. As the matching process within a year was based upon a composite sketch of all the marks seen on all of the negatives taken in that year, drawings of individuals that were photographed many times were likely to have more marks. Therefore the resighting rates were calculated separately for individuals with differing numbers of photographs taken in a single year. Resighting rates were calculated only on left fin photographs and were calculated separately for all individuals and for individuals with reliable marks.

Figure 2.3. Examples of melon photographs that could be matched between a) 1996 and b) 1997.



The possibility that photographs of the same individual were not matched due to mark change was investigated by comparing the resighting rates for individuals between 1989-1990, 1996-1997 and 1990-1997 (long field seasons) for reliably and unreliably marked individuals. These time periods were selected to compare both short and long term resighting rates.

RESULTS

PHOTOGRAPH QUALITY AND EQUAL CATCHABILITY

While there was no clear quality cutoff point at which marks become visible, increasing the quality of the photograph increased the number of visible marks (see Table 2.4). On average less than 50 % of the marks visible on high quality photographs (Q≥4) were visible in Q-2 or 3 photographs (Table 2.4a). Reliable marks were more visible in lower quality photographs (Q<4) than unreliable marks (Table 2.4a and b). However there was a decline in the number of reliable marks when Q-2 or 3 photographs were included in the sample. When comparing reliable marks, Q-5 photographs did not have more marks than Q-4 photographs.

MARK DISTRIBUTION AND THE UNIQUENESS OF INDIVIDUALS

Bottlenose whales were well marked with many different mark types and possessed on average 17.1 different marks within an average photo-id frame (n=100, SD=15.8, range=1-106; Table 2.5 and Figure 2.2). Some mark types tended to be found on more whales and in greater numbers on each individual (Table 2.5). Common mark types (found on more than one third of the individuals) were *notch*, *short and long single linear scrapes*, *dark dot in light patch*, *large circular light patch* and *non-circular light patch*. However, even individuals with a few common marks were uniquely identified by the location, size and shape of each mark.

Table 2.4. Percentage of marks visible in first negative which were also visible in the second, for negatives of different photograph quality taken in the same year.

(a) All mark types (n=36, 5 negatives per individual)

	2nd negative					
1st	Q	2	3	4	5	6
	2	----	63	77	83	94
	3	55	----	83	86	95
	4	46	57	----	82	86
	5	40	47	65	----	84
	6	35	40	52	64	----

(b) Reliable mark types (n=26, 5 negatives per individual)

	2nd negative					
1st	Q	2	3	4	5	6
	2	----	71	100	100	100
	3	83	----	92	92	100
	4	78	61	----	89	94
	5	82	65	94	----	100
	6	64	55	77	77	----

Table 2.5. Distribution of mark types on 100 randomly selected individuals.

Mark type	Proportion of individuals with mark type	Mean number of marks per individual
Notch	0.37	0.48
Back indentation	0.04	0.05
Large scar	0.17	0.21
LINEAR MARKS		
Short single linear scrape	0.54	1.45
Long single linear scrape	0.37	0.83
Short parallel linear scrape	0.03	0.06
Long parallel linear scrape	0.06	0.05
Tooth rake	0.06	0.07
Attachment	0.02	0.03
Dark band	0.02	0.03
Light band	0.02	0.02
Small white dot	0.19	2.30
PATCHES		
Dark circular patch	0.26	0.81
Dark dot	0.16	1.12
Dark non-circular patch	0.02	0.04
Light and dark patches	0.20	0.20
Hatch	0.06	0.06
Dot in light patch	0.34	1.09
Dark fringed circle	0.13	0.14
Large circular light patch	0.88	6.17
Non-circular light patch	0.61	1.37
Mottled patches	0.13	0.24

Of the 100 individuals selected for analysis, 54 were assigned age or sex classes from melon photographs (33 female/immature male, 10 sub-adult male and 11 mature males.) There was no significant difference between the total number of marks found on female/immatures and on sub-adult and mature males (18.4 ± SE 20.9 marks per female/immature; 15.6 ± SE 11.3 per male; P=0.58), nor between sub-adult and mature males (17.7 ± SE 11.3 and 14.0 ± SE 11.5 respectively; P =0.46). There was no significant difference between the number of mature males and sub-adult males with reliable marks (55 % of mature males had reliable marks, 70 % of sub-adult males; G=0.02), nor were males more likely to be reliably marked than female/immatures (62 % males had reliable marks, 52

% female/immatures; $G = 0.76$). However the powers of these tests were low (*e.g.*, 27 % of females and 67 % of males would have to be reliably-marked to achieve a significant ($p<0.05$) result at this sample size). Thus the lack of power for the age and sex class comparisons indicates more data are needed before definitive conclusions can be reached.

MARK CHANGE

To examine mark change, I compared 112 pairs of negatives, involving 39 different individuals over 241 animal-years (Table 2.6). No losses were recorded for *notches*, *mottled patches*, *back indentation* and *tooth rakes*, although the number of comparisons containing *tooth rakes* was small ($n=2$; Table 2.6). With the exception of *long single linear scrapes*, *attachment* and *dark fringed circles*, gain rates were higher than loss rates.

Some mark types could not be compared across different photograph qualities as gain rates (G test, $P < 0.05$) and loss rates (likelihood ratio, $P < 0.05$) were significantly different between comparisons of different photograph qualities. These mark types were the marks with the highest gain or loss rates, and should not be considered reliable (Table 2.6). Reliable mark types, defined as ones with zero loss rates occurring in more than five samples, were *notches*, *back indentation* and *mottled patches*.

Seven individuals first identified in 1988 by *mottled patches*, *notches* or *back indentations* retained these marks through 1997. Although marks consisting of light coloured patches were observed 1,081 times in the mark change analysis, most were lost within one to three years and left no visible scars. The maximum duration a light patch mark lasted on a bottlenose whale was seven years and that was only for a single mark on one individual even though these mark types were counted 1,081 times in the mark change analysis. Most marks consisting of dark patches changed shape and location rapidly and left no permanent markings behind.

Table 2.6. Number of marks of each type gained and lost for comparisons of all quality types (Q≥4). Overall rates of gain and loss of marks per individual per year are shown as well as the estimated instantaneous loss rate(μ) of individual marks per year. Dashed lines represent mark types in which all marks were lost before resampling. Reliable marks are shaded. * Rates which were not comparable across different photograph qualities.

	Number of occurrences			Overall rates per animal year (marks/year)		Estimated loss (μ) per year
	Total	Gain	Loss	Gain	Loss	
Large scar	44	4	2	0.017	0.008	0.025
Short single linear scrape	164	80	55	0.332*	0.228*	0.519
Long single linear scrape	55	15	3	0.062	0.12	0.037
Shore parallel linear scrape	6	2	1	0.008	0.004	0.288
Long parallel linear scrape	8	1	1	0.004	0.004	0.074
Tooth rake	2	0	0	0	0	0
Attachment	1	0	1	0	0.004	----
Dark band	10	4	5	0.07	0.021	1.500
Light band	6	3	1	0.04	0.004	0.187
Small white dot	181	144	11	0.598*	0.046*	0.299
Dark circular patch	120	83	37	0.334*	0.154	----
Dark dot	16	11	5	0.046	0.021	----
Dark non-circular patch	25	15	9	0.062	0.037*	1.269
Light and dark patches	21	5	1	0.021	0.004	0.357
Hatch	5	3	1	0.012	0.004	0.182
Dot in light patch	146	62	38	0.257*	0.158*	0.477
Dark fringed circle	19	4	5	0.017	0.021	0.257
Large circular light patch	835	353	305	1.465*	1.266*	0.623
Non-circular light patch	240	87	74	0.361*	0.307*	0.344
Animal years		241	241			

Although marks on the back and flanks may persist over years they were not always photographed (Table 2.7). Reliable marks located less than one dorsal fin width (at the base) from the anterior and posterior insertion points of the dorsal fin, were routinely captured in photographs of the dorsal fin. Marks located further than one dorsal fin width were only included in approximately half of the photographs of an individual. Thus, I defined an individual as reliably-marked if it had at least one *notch*; or a *back indent* or *mottled patch* located within one dorsal fin base width of the dorsal fin.

Table 2.7: Proportion of photographs (Q≥4) in which indent on back or mottled patch is visible.

	Number of individuals	Negatives with mark	Total negatives	Proportion of negatives with mark
Indent on back				
All individuals	16	321	365	0.88
Mark closer than 1 dorsal fin	12	308	339	0.91
Mark further than 1 dorsal fin	4	13	26	0.50
Mottled patches pattern				
All individuals	84	689	917	0.75
Mark closer than 1 dorsal fin	70	603	763	0.79
Mark further than 1 dorsal fin	14	86	154	0.56

The mean proportion of individuals in the population that were reliably marked was 0.66 (± 0.05 SE) for all photographs (left side photographs 0.61 ± 0.06 SE; right side photographs 0.69 ± 0.03 SE). Addition of a reliable mark was relatively rare. Of 160 individuals with a reliable mark on their left side, only 13 individuals (8% of total; rate of gain = 3.3% per individual per year) gained a reliable mark within the nine-year study period. For five of these individuals (3% of total; rate of gain = 1.2% per individual per year), the gain of a reliable mark resulted in a change in status from unreliable to reliable. Of the 159 reliably marked right fins, 13 gained a reliable mark (8% of total, rate of gain = 3.2% per individual per year) and five changed status (3% of total; rate of gain = 1.2% per individual per year).

MELON MATCHING

There were 253 left and 225 right melon photographs, representing 173 and 149 individuals identified by dorsal fin identification and 31 and 34 individuals, with melon identifications alone, which were compared with all other melon photographs of the same side. Few melon photographs were matched to other melon photographs. Only 7.9 % of left melon photographs and 10.2 % of right melon photographs were matched to other melon photographs. Most of the matches were between melons where one of the pair of photographs was not linked to an identification number (48 % of matches) or between pairs of melons linked to the same identification number (33 % of matches). In 4 pairs the melon photographs matched but the corresponding fin identifications did not match (Table 2.8). In these cases, at least one photograph was poor quality (Q<4) or did not have a reliable mark.

Table 2.8: Summary of matches between melons linked to different fin identifications.

First whale identification (year of melon photograph)	Second whale identification (year of melon photograph)	Comparison of fins
#208 (1990)	#564 (1990)	#564 poor quality (Q-3) #208 no reliable marks
#413 (1990)	#1039 (1996-1997)	neither fin contains reliable marks
#271 (1990) left side	#651 (1993)	#271 no reliable marks #651 gained notch
#271 (1990) right side	#1289 (1996-1997)	#271 no reliable marks #1289 gained notch

VIOLATIONS OF ASSUMPTIONS

Of the 100 individuals sampled in the mark distribution section 42 had reliable marks. The number of reliable marks per individual ranged from one to five (mean = 1.64 ± 1.1 SE). Seventeen individuals possessed only one reliable mark, and all of these individuals were compared with each other to determine the possibility of matching to each other. Differences in mark shape, size and location differentiated all but one of the potential matches. However these two individuals could be differentiated by non-reliable marks as the photographs were taken in the same year.

Unequal probability of recapture also could occur if photographs of the same individual were not matched because of photographic quality. If more than two photographs were taken of an individual in a single year, the higher the maximum Q-value, the higher the probability that individual was matched to photographs taken in a different year (Table 2.9). When individuals with all mark types were considered, individuals with a maximum Q-value of 4 or lower were less likely to be matched in different years, except for Q-2 where all individuals matched, as marks visible at Q-2 were very obvious marks. When only individuals with reliable marks were considered, maximum Q-values of 3 or lower were unlikely to be matched in another year.

Table 2.9: Proportion of individuals which were matched to photographs taken in a different year.

a) all individuals

	Maximum Q-value in the year					
Total number of left fin photographs taken in a single year		2	3	4	5	6
	1-2	0.28	0.24	0.32	0.31	0.28
	3-4	1	0.46	0.45	0.31	0.70
	5-6	1	0	0.22	0.46	0.82
	7-8	-	-	0.48	0.50	0.60
			0.50	0.42	0.67	0.63
	11-19		-	0.76	0.59	0.64
	20+	-	-	0.50	0.65	0.77
	3+	1	0.42	0.44	0.69	0.70

b) individuals with reliable marks only

	Maximum Q-value in the year					
Total number of left fin photographs taken in a single year		2	3	4	5	6
	1-2	0.57	0.57	0.68	0.67	0.33
	3-4	1	0.55	0.76	1	1
	5-6	1	0	0.68	0.83	1
	7-8	-	-	0.77	0.71	1
	9-10	-	0.5	0.5	0.88	1
	11-19	-	-	0.85	0.76	0.76
	20+	-	-	0.6	0.71	0.88
	3+	1	0.5	0.73	0.78	0.89

Mark change hindered the ability of an observer to match photographs of the same individual and created unequal recapture rates. When comparing sets of photographs taken only one year apart, individuals with unreliable marks were still recaptured although at a lower rate than individuals with reliable marks (1989-1990 recaptured: 61% reliably marked individuals, 15% unreliable; 1996-1997: 48% reliable, 18% unreliable). Over a seven year period (from 1990-1997) no unreliably-marked individuals were recaptured, while 20% of the reliably marked individuals sighted in 1990 were resighted in 1997.

DISCUSSION

PHOTOGRAPH QUALITY

Poor quality negatives (Q≤3) did not contain sufficient information to consistently identify individual northern bottlenose whales. Some distinctive mark types, such as *notches* were visible in poor quality negatives and could be matched to a known individual, however other mark types were not visible in poor quality negatives. If poor quality negatives were included in analyses then notched individuals had a higher probability of capture and recapture. Mark type categorization also becomes more accurate in higher quality photographs. Accurate mark type categorization was found to be important when the matching process was computer-assisted and/or based on the presence or absence of mark types (*e.g.*, Whitehead 1990a). Agler (1992) investigated the effect of photographic quality and the distinctiveness of an individual fin whale (*Balaenoptera physalus*) on the reliability of photograph matches and she found that fewer mistakes were made in photograph matches if individuals were distinctive and/or the photographs were of high quality. Testing to see which quality photographs contain sufficient information to obtain accurate results optimizes the balance between reducing errors and maximizing data. In the case of bottlenose whales, omitting poor quality photographs (Q≤3) would reduce matching errors while maximizing sample size.

MARK DISTRIBUTION AND CAUSATION

The dorsal fin and flank of northern bottlenose whales were well marked and contained a variety of different mark types. While the major focus of this chapter was not to describe the cause of various mark types, some discussion is warranted, as the source of the mark can relate to its persistence. White markings appeared to be caused by wounds to the skin and underlying tissue. *Notches*, *back indentations* and *large scars* appeared to be caused by traumatic events that permanently damaged the skin and left long-term marks. *Back indentation* marks resembled rope or gear entanglement marks found on the tail and peduncle of right whales (*Balaena glacialis*) and bowhead whales (*Balaena mysticetus*), as well as bottlenose dolphins (Kraus 1990, Philo *et al.* 1992, Wells *et al.* 1998), although the marks on bottlenose whales were located much further forward. *Large scars*, such as the one found on individual #94 (Figure 2.2b), might also be caused by collisions with ships (Lockyer and Morris 1990). None of these individuals showed the track marks from collisions with propellers (as shown in Kraus 1990) although the dorsal fin of one individual was cleanly chopped off at the base, probably by a propeller, predator or entanglement in fishing line (Green *et al.* 1991).

Tooth rakes and other linear white marks appeared to be minor wounds in the dermal tissue (Bruce-Allen and Geraci 1985). Males in many species of beaked whales were heavily scarred with long linear marks, which were likely caused by teeth of other males in intraspecific competition (Heyning 1984). However bottlenose whales were not heavily scarred, and even mature males did not often exhibit long linear marks. Mature male bottlenose whales in the Gully were recently observed head-butting each other in an apparently aggressive manner (Gowans and Rendell In press). If head-butting was the predominant form of male-male competition, few scars from tooth rakes would be expected.

Linear marks including *tooth rakes* could have come from predators. Killer whales attack other cetaceans including bottlenose whales, and attacks were sometimes unsuccessful leaving individuals with marks (Jefferson *et al.* 1991). Pilot whales also attack cetaceans (*e.g.*, Weller *et al.* 1996), and long finned pilot whales were observed harassing bottlenose whales

in the Gully (the pilot whales engaged in high speed chases of the bottlenose whales and several pilot whales would encircle a single bottlenose whale; S.K. Hooker, Dalhousie University, pers. comm.). Sharks make deep wounds often leading to body deformity (Lockyer and Morris 1990, Long 1991), while short scrape marks could be caused by a variety of different sources, including unsuccessful predation attempts and abrasion with rocks or deep water corals (Lockyer and Morris 1990).

Cookie cutter sharks (*Isistius brasiliensis*) may have caused *white circular marks* (Jones 1971), although it was unlikely as the distribution of bottlenose whales and cookie cutter sharks does not overlap (Muñoz-Chápulli *et al.* 1988, Reeves *et al.* 1993). Lampreys (*Petromyzon marinus*) may also have made *circular marks* on whales (Pike 1951) and were a more likely source as lampreys inhabit the Gully (Halliday 1991). Lampreys were the most likely cause for the *attachment* marks described in this study, which were similar to those observed on fin whales (Agler *et al.* 1990).

Diatom layers have been observed on whales and dolphins (Nemato *et al.* 1980, Holmes *et al.* 1993), and may have caused the brown colouration in bottlenose whales (Mead 1989b). Skin biopsy samples from bottlenose whales in the Gully confirmed that diatoms were present on the skin (S.K. Hooker, Dalhousie University, pers. comm.). Dark patches (Figure 2.2 and Table 2.3) were likely patches of diatoms which routinely changed size and shape, but left no permanent marks. The dark patches observed on bottlenose whales were different in colour from the black lesions found in bottlenose dolphins in Scotland (Wilson *et al.* 1997). Bottlenose whale marks did not resemble light and dark patches found on bottlenose dolphins in Portugal which left scarring after the dark patches faded (Harzen and Brunnick 1997).

Wilson (1995) studied the progression of lesion types in bottlenose dolphins in Scotland, and suggested that the dark black lesions were active lesions which faded over time to white or cream lesions or healed skin. Similarities were observed between the light coloured patches (Figure 2.2 and Table 2.3) found on bottlenose whales and the cream lesions found in bottlenose dolphins (Wilson 1995), but there did not appear to be any "active" lesions on

the bottlenose whales. Lesions on cetacean skin can be caused by a variety of factors, including but not limited to infection, reactions to parasites and pollution (Wilson *et al.* 1997). Bottlenose dolphins in Scotland were coastal, and thus exposed to higher levels of pollution and variable temperatures and salinities, which may be linked to their high prevalence of lesions (Wilson *et al.* 1997, 1999).

Mottled patches did not appear to resemble any description of cetacean markings. In size and shape they were similar to the blue-grey cloudy lesions in bottlenose dolphins (Wilson *et al.* 1997), however *mottled patches* on bottlenose whales were cream and white. The persistence of the *mottled patches* indicates that they were unlikely to be an active infection, although they may have been the result of a previous infection.

MARK CHANGE

If the rate of change of marks was sufficiently low, individuals with all mark types could be included in all analyses. This is the case for marks on the trailing edge of sperm whale flukes (Dufault and Whitehead 1995, Childerhouse and Dawson 1996), but in bottlenose whales rates of mark change were highly variable. Some mark types (*i.e.*, linear marks and diatom patches) were gained and lost at rates that were unacceptable for use in individual identification for resights over periods of years. Reliable marks in bottlenose whales had similar gain and loss rates to sperm whale marks, which had near zero loss rates and approximate gain rates of 2 % per individual per year, (Dufault and Whitehead 1995, Childerhouse and Dawson 1996). Photographs of reliably marked bottlenose whales could be re-identified over years. In analyses that require the use of data spanning years, such as estimation of population size or long-term social organization, it is important to restrict the dataset to individuals that can be reliably re-identified. Wilson *et al.* (1999) investigated the duration over which marks were visible on bottlenose dolphins to determine which individuals should be included for estimates of population size. While calculating how long marks were visible gave some information about the reliability of mark types, gain and loss rates were less biased by the temporal arrangement of the field work, unless there were seasonal differences in mark loss or gain.

For most mark types, gain rates were higher than loss rates, indicating that marks accumulated over time. Marks which were suspected to be caused by diatoms tended to be lost rapidly. Minor wounds to the skin such as scrapes and *tooth rakes* were also lost rapidly. Minor wounds in bottlenose dolphins tended to heal and disappeared over 2.5 years although there was a wide range of healing periods from two months to four years (Wilson *et al.* 1999), which fit well with the rate of mark loss from this study. *Notches* and *back indentations* were caused by deep wounds and appeared to leave permanent scars. The light patches in this study (that resembled the cream lesions in bottlenose dolphins) had very high loss rates, and most were lost within one to three years. In bottlenose dolphins, some healed lesions lasted throughout a four-year study period although most lesions disappeared over approximately one year (Wilson *et al.* 1999).

As individuals accumulated marks over time, only including reliably marked individuals may in fact restrict analyses to older animals. In this study older mature males did not have a significantly higher proportion of reliable marks than sub-adult males, nor did females and immatures have a significantly lower proportion of reliable marks than mature and sub-adult males. However sample sizes for these tests were small, and the non-significant results may have been due to the low power of the test. As few immatures had been sexed, older individuals were likely to be over represented in the sample, which may also limit the power of the test to determine if older individuals possessed more reliable marks.

Changes in markings that altered the classification of bottlenose whales from unreliably to reliably marked were relatively rare, and were comparable with mark changes which altered the classification of individuals in other photo-id catalogues. Dufault and Whitehead (1995) categorized individual sperm whales in their catalogue based on the location of the largest mark on the trailing edge of the fluke. Changes in the categorization of flukes happened in 9.5 % of the comparisons in which mark change occurred; individuals had a 0.013 probability per year of undergoing a change in categorization (Dufault and Whitehead 1995). Humpback whales were categorized by the overall colouration of the fluke. Carlson *et al.*

(1990) found a change in the colouration categorization in 4.6 % of their comparisons, however they did not calculate the rate of change and most of the changes involved individuals less than two years of age.

Addition of a reliable mark occurs relatively rarely (3.3 % per individual per year) and was lower than the gain rate for notches (Table 2.6). This discrepancy arises because individuals with notches (and other reliable marks) were over-represented in the mark change sample, as individuals had to be identified in three or more years to be included in the mark change analysis. Therefore the estimated rate of gain, calculated by counting all occurrences of a gain of a reliable mark, was less biased than the rate of gain calculated from the mark change analysis. This bias did not affect the rate of gain of unreliable marks.

The calculated rate of change of status from unreliable to reliable (1.2 % per individual per year) must be viewed as a minimum rate as other individuals may have been photographed before the acquisition of a reliable mark, but it was not possible to match the reliably marked photograph to the earlier photograph.

MELON MATCHING

Relatively few of the melon photographs contained marks that were matched over years. The photographs which were matched were of individuals that had scarring or multiple linear scrapes on the melon. When melon photographs matched but fin identifications did not, at least one fin photograph of each pair either was of poor quality, or did not contain a reliable mark. While the sample size was small, the matches that were found supported the conclusion that analyses should only include individuals that possessed reliable marks, and high quality photographs.

VIOLATIONS OF ASSUMPTIONS

Violations of the assumptions of mark-recapture were minimized in northern bottlenose whales when the data were restricted to high quality photographs ($Q \geq 4$) of individuals that were reliably marked. One potential violation of the assumption was mistakenly matching two individuals that were actually different. However, individuals with high quality

photographs and reliable marks were unlikely to be mismatched and the matching protocol used throughout this study attempted to minimize the likelihood of this occurring by assigning new identification numbers to all individuals for which matching was uncertain.

CONCLUSION

While photo-id was an excellent technique for studying bottlenose whales, not all individuals were reliably identifiable, which can led to violations of the assumptions of mark-recapture. Sixty-six % (± 5%) of the population possessed marks that were reliable (*notches*, *back indentation* and *mottled patches* within one dorsal fin width of the dorsal fin) and had photographs of Q≥4. By restricting analyses to high quality photographs (Q≥4) and to reliably-marked individuals for analyses over a sample period of at least one year, errors could be minimized. Restricting analyses to reliably marked individuals and then scaling the results to account for the remainder of the population is a common technique (Williams *et al.* 1993, Wilson *et al.* 1999) and appropriate for photo-id studies of northern bottlenose whales. Quantitative assessment of photo-id catalogues to determine which quality photographs and which individuals should be included in analyses based on photo-id data will improve the precision of the results, minimize errors and reduce the probability of violating assumptions of mark-recapture analyses.

Chapter 3: Photographic technique for sexing northern bottlenose whales

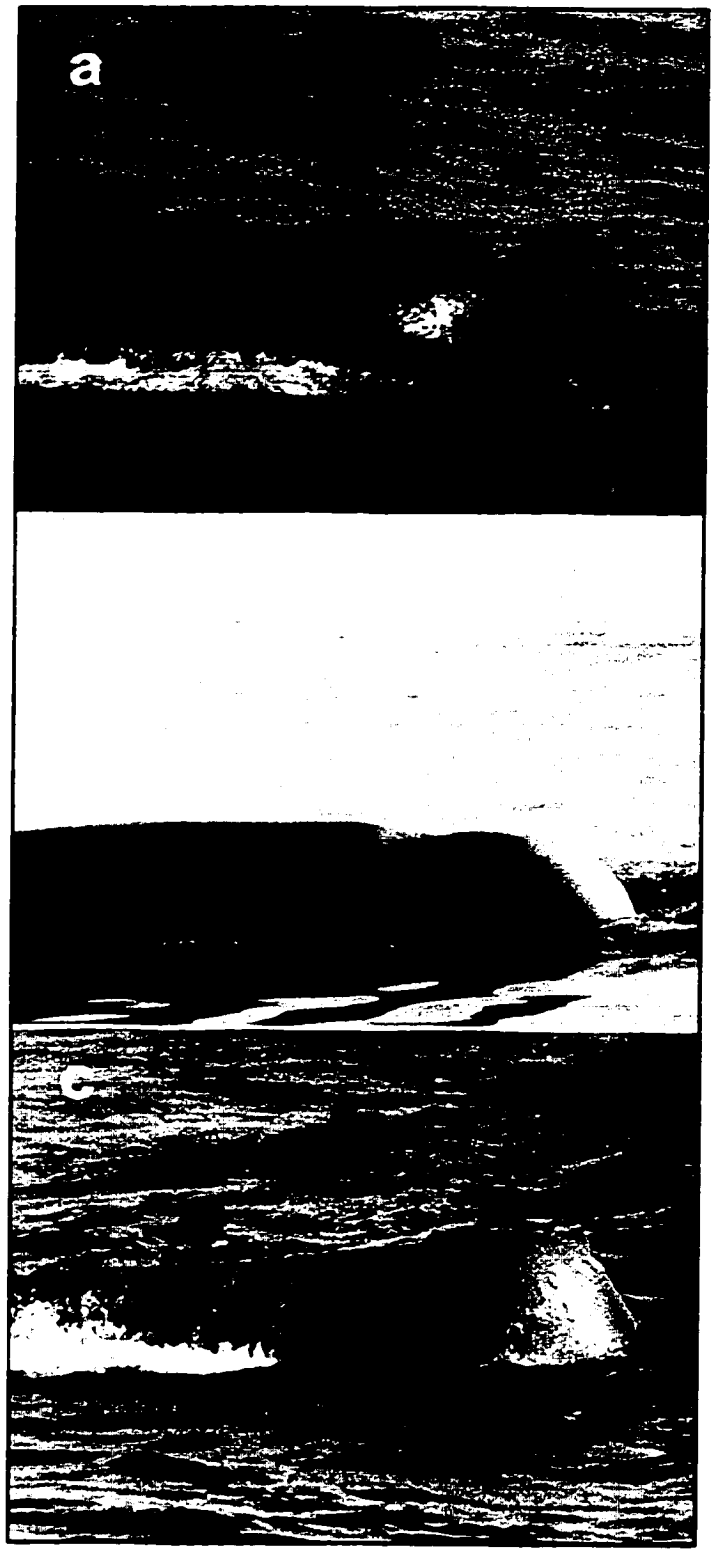
INTRODUCTION

The sex of an individual is an important variable to include in studies of population structure, social organization, distribution or behaviour. Although many species of cetaceans are sexually dimorphic, sex identification of animals observed at sea may be difficult. Individuals are often inferred to be female if they are observed in close proximity with young of the year (*e.g.*, Baker *et al.* 1987, Clapham and Mayo 1987, Slooten *et al.* 1993, Knowlton *et al.* 1994). However, this technique is problematic in deep diving species where "babysitting" (serial accompaniment of calves by alloparents) might occur (*e.g.*, sperm whales, Whitehead 1996a).

Northern bottlenose whales are sexually dimorphic and can be categorized as female/immature male, sub-adult male, or mature male based primarily on the melon profile. Mature males are on average one metre longer than mature females (Christensen 1973) and have a flattened white melon profile in comparison to the gray bulbous melon profile of females, while sub-adult males are intermediate between the two (Gray 1882; Figure 3.1).

This chapter investigates the reliability of melon photographs to consistently yield the same age and sex categorization, and compares sex classification based on melon photographs with genetic techniques. In addition, individual melon profiles taken over a number of years are used to investigate the onset of sexual maturity in this species based on the development of secondary sexual characteristics.

Figure 3.1: Sexual dimorphism in melon shape in bottlenose whales a) female/immature male; b) sub-adult male; c) mature male.



METHODS

FIELD TECHNIQUES

Field work was carried out during the summer months, between 1988-1997 in the Gully (44 °N, 59 °W) from a sailboat with an auxiliary diesel engine (see Whitehead *et al.* 1997c for details of field work and Chapter 2). When conditions permitted, bottlenose whales were approached to within approximately 30 m and melon and dorsal fin photographs were taken, although most of the melon photographs that could be used to categorize an individual were taken within 15 m of the vessel. Whenever possible, a suite of melon and dorsal photographs was taken of the same individual. Melon photographs were used to determine sex, while photographs of the dorsal fin were used for individual identification (see chapter 2 for more details on dorsal fin identification).

Genetic material was obtained from biopsy samples. In several other cetacean species, genetic samples have been non-invasively collected from skin found floating at the surface near whales (Amos *et al.* 1992). However bottlenose whales do not appear to shed skin at the surface. In 1996 and 1997 biopsy samples were collected using a 150 lb. draw crossbow (Barnett WildCat XL) at a range of 5 - 15 m (Hooker *et al.* submitted). The biopsy dart was composed of a cylindrical punch fitted with a dental broach (barbed filament to secure the skin sample), attached to the end of a standard crossbow bolt (Barrett-Lennard *et al.* 1996). A cylindrical stopper set 2.5 cm back from the tip of the punch allowed the bolt to rebound from the whale on impact. All samples were taken from the flank area near the dorsal fin. The dart was recovered from the water and the skin and blubber sample (2.0 cm long, 0.8 cm diameter) was removed. A small subsample of the biopsy was stored in salt-saturated dimethyl sulfoxide (DMSO) solution prior to genetic analysis.

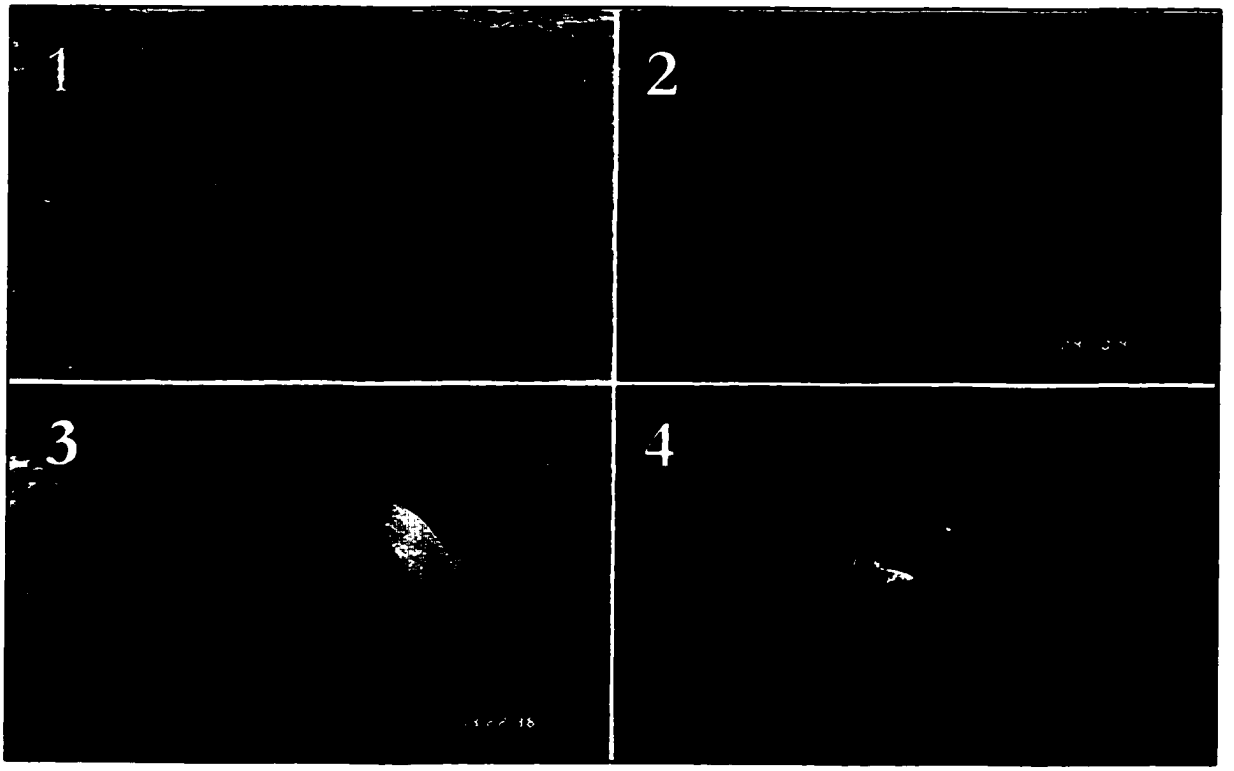
PHOTOGRAPHIC SEXING

Negatives were examined on a light table with a 10x magnifying loupe. Each melon photograph was assigned to a sex category: unknown (U); female/immature male (F/I); sub-adult male (SM); or mature male (MM) based on figures from Gray (1882; see Figure 3.1

for examples). Photographs were also assigned a melon photograph quality (MQ) which reflects the potential of the photograph to determine the sex of the individual (1 - unusable, 4 - excellent; See Figure 3.2 for examples). MQ was based on the exposure and focus of the photograph, the angle of the melon and the amount of melon visible above the surface (Arnbom 1987; and Appendix 1). In excellent quality photographs (MQ-4) the animal was perpendicular to the viewer, the beak was visible, and the photograph was in focus and well lit. Photographs of MQ-3 were lower in quality in one of these characteristics, however the quality designation was most sensitive to changes in the orientation of the whale and the amount of the melon which was visible. Low quality photographs (MQ-2) tended to show much less of the melon above the water or the whale was no longer perpendicular to the viewer. Unusable photographs were badly focused, showed little of the melon, or the whale had turned more than approximately 15° away from perpendicular. Melon photographs which were taken in the same suite as an identifiable dorsal fin photo were assigned the identification number of that individual. Photographs of well marked melons, which were not linked to a dorsal fin identification were assigned a melon identification code. The highest quality photograph of each individual in each year was printed and the photographs were compared to identify any matching individuals.

To assess whether melon photographs consistently and reliably allowed the sex of an individual to be determined as it passed through different developmental stages, sequential photographs taken of the same individual, and the sex category to which these photographs were assigned, were compared. Time between sequential photographs ranged from a few minutes to several years. All consecutive usable melon photographs (MQ≥2) of the same individual were compared. The rate at which individuals were mis-classified based on melon photographs was calculated by comparing all sets of three sequential melon photographs taken of the same individual on separate days, in which the categorization in the first and last photograph were the same. I then counted the number of times the middle photograph was classified differently than the earlier and later photographs. Three photographs were needed to differentiate between a mis-categorization and natural progression in melon shape as males matured.

Figure 3.2: Examples of melon photographs of varying quality (MQ 1 - unusable, 4 - excellent).



MOLECULAR SEXING

Molecular sexing analysis was conducted by Merel Dalebout (School of Biological Sciences, University of Auckland, New Zealand). The sex of the 20 animals from which skin biopsies were taken was identified using the ZFY (zinc finger protein gene – Y chromosome) method of Palsbøll *et al.* (1992) and the SRY (sex-determining region Y gene) method (Richard *et al.* 1994). DNA was extracted from all samples using a modification of the Chelex method (Walsh *et al.* 1991) developed by Neil Gemmell (unpublished) which allows long term storage of the genetic material obtained. Humpback whale samples of known sex were run as positive controls (1 male, 1 female) in ZFY digests. Samples from stranded southern bottlenose whales of known sex were run as controls (1 male, 1 female) in all SRY reactions. To determine whether the photographic technique accurately categorized the sex of the individual, a direct comparison was made with the results of genetic sexing for all individuals for which both melon photographs and biopsies were taken.

ONSET OF SEXUAL MATURITY

The minimum age of all individuals which had melon photographs taken in more than one year was estimated by assigning a minimum age of two years to each of these individuals when they were first sighted in the Gully based on age-length curves from whaling data (Christensen 1973), as all these individuals were "adult-size" when first sighted. In the field, the relative sizes of individuals were estimated, to determine if there were any juveniles present (see Chapter 6). Individuals which were approximately less than two thirds of the typical "adult-size" were called juveniles. According to age-length curves, individuals less than two thirds adult size were two years old or younger (Christensen 1973). From these estimates I estimated the minimum age when changes in melon shape began.

RESULTS

PHOTOGRAPHIC SEXING

During the study 1,059 melon photographs were taken, of which 356 could be assigned a sex category (MQ≥2), corresponding to 168 different fin identifications. There were 74

individuals that had multiple melon photographs (MQ≥2) over the study, and 191 comparisons were made between 1989 and 1997, the majority of which spanned only a single field season (n = 162). Comparisons between sequential melon photographs of the same individual taken several minutes to seven years apart showed that this technique allows consistent designation of sex, although one individual, #531 was mis-categorized as a sub-adult male in 1994, from a MQ-2 photograph (Table 3.1). The maximum time between comparisons was seven years for mature males and female/immatures, and three years for sub-adult males (Table 3.2).

There were 30 sets of three sequential melon photographs of the same individual, each taken on separate days. In only one set was the categorization from the middle photograph different from the earlier and later photograph (individual #531; see Table 3.2), therefore 3.3% of the categorizations were wrong. Thus, photographs of MQ-2 did include a mis-categorization, but the error rate was very low. In the catalogue, 356 photographs are of MQ≥2 (33.6% of the total melon catalogue), which represents 168 different fin identifications (110 female/immature males, 24 sub-adult males and 34 mature males).

Within a single field season, all photographs of the same individual yielded the same sex category (see Table 3.1). Four individuals were assigned to different sex categories in different years (see Table 3.2), changing from female/immature to sub-adult male. However one of these individuals (#531) was categorized as female/immature in 1990, sub-adult male in 1994, but was categorized again as female/immature in 1995 and 1996. Based on the high quality of the latter set of photographs, individual #531 should be considered a female/immature male, not a sub-adult male. The three other individuals that changed classification from female/immature to sub-adult male included at least one poor quality photograph (MQ-2) in the comparison series. Melon photographs taken three years apart were assigned different age/sex categories for individuals #102 and #267, while melon photographs seven years apart were assigned different age/sex categories for individual #28 (Table 3.2). Each of these individuals (#28, 102 and 267) were categorized as immature males when the photographic sexing was female/immature male and sub-adult male in later years.

Table 3.1: Consistency of the melon photograph technique for sexing individuals (number of comparisons shown).

a) all usable photographs (MQ≥2; 74 individuals, 191 comparisons)

Subsequent sexing	Time frame of comparisons	Initial sexing		
		Female / immature male	Sub-adult male	Mature male
Female / immature male	same year	99	1	
	different year	11		
Sub-adult male	same year		21	
	different year	4	3	
Mature male	same year			41
	different year			11

b) High quality photographs (MQ≥3; 35 individuals, 56 comparisons)

Subsequent sexing	Time frame of comparisons	Initial sexing		
		Female / immature male	Sub-adult male	Mature male
Female / immature male	same year	33		
	different year	3		
Sub-adult male	same year		4	
	different year			
Mature male	same year			11
	different year			5

Table 3.2: Individuals photographed in more than one year. Highest photograph quality (MQ) is shown in brackets (1 - unusable, 4 - excellent). Individuals for which the age/sex categorization changed over the study duration are shaded. (F/I = Female/immature male, SM = sub-adult male, MM= mature male).

Individual	Minimum age in 1997	Age/sex categorization based on melon photograph in:						
		1989	1990	1993	1994	1995	1996	1997
1	10		MM(4)		MM(2)		MM(3)	
26								
45	10		F/I (2)					F/I (3)
54	11		F/I (2)			F/I (2)		F/I (3)
71	10		MM(2)		MM(3)		MM(2)	MM(2)
102								
251	11		F/I (4)	F/I (2)	F/I (3)			
263								
355	11	MM(3)	MM(3)					
390	9		MM(2)		MM(2)			
480	9		MM(4)					MM(2)
507	9			F/I (3)				F/I (2)
531								
702	6			SM (2)			SM (3)	
824	5				MM(3)		MM(3)	MM(3)
1039	3						MM(3)	MM(3)
1046	3						F/I (3)	F/I (4)

MOLECULAR SEXING

Twenty individuals were successfully biopsied. Reactions of the whales to being biopsied were low to moderate (Hooker *et al.* submitted). ZFY amplification was successful for all biopsy samples (n=20), and identified 7 males and 13 females (ratio 1:1.86). The results from the SRY analyses were in complete agreement with those from the ZFY method (see Table 3.3). Ten of these individuals were also sexed from melon photographs (Table 3.3). The results from the melon photographs agreed with those from genetic analysis in nine out of the ten comparisons. The one individual for which the results may be contradictory (individual #143) was categorized as a female/immature male from the melon photographs, but determined to be a male by genetic analysis. This individual has been categorized as an immature male based on both genetic and photographic sexing.

Table 3.3: Comparison of the photographic sexing technique with results of molecular analysis for all individuals for which both techniques were used (F/I = female/immature male; MM = mature male).

Individual	Year individual first seen	Photographic sex category	Molecular sexing SRY	Molecular sexing ZFY
54	1988	F/I	Female	Female
619	1993	F/I	Female	Female
961	1995	F/I	Female	Female
1000	1996	F/I	Female	Female
1289	1990	F/I	Female	Female
1315	1997	F/I	Female	Female
1336	1997	F/I	Female	Female
143	1989	F/I	Male	Male
480	1990	MM	Male	Male
1039	1996	MM	Male	Male

ONSET OF SEXUAL MATURITY

The minimum age in 1997 was estimated for all individuals which were photographed in more than one year (Table 3.2). Individual # 28 was first sighted in 1989 when it already appeared to be adult size, and so would have been at least two years old (based on length growth curves from whaling data, Christensen 1973). Therefore this animal would have been at least three years old in 1990 when it was categorized as a female/immature male, and at least 10 years old in 1997 when it was categorized as a sub-adult male. Similarly, individual #102 was at least two years old when it was first sighted in 1988, at least seven years old in 1993 when it was categorized as female/immature male, and at least 10 and 11 years old in 1996 and 1997 respectively when it was categorized as a sub-adult male. Individual #267 was at least two years old when it was first seen in 1990, at least five years old in 1993 when it was categorized as female/immature male and at least eight and nine respectively when it was categorized as a sub-adult male in 1996 and 1997. The minimum age at which development of secondary sexual characteristics could occur is four years old (one year older than when individual #28 was last categorized as a female/immature). However the onset of sexual maturity more likely occurred after males reached age eight (one year after individual #102 was last categorized as female/immature).

DISCUSSION

Sexing northern bottlenose whales from photographs of the melon profile appears to be a reliable technique. Individuals can be consistently assigned to the same sex category from photographs taken up to seven years apart. However, by using melon photographs alone, it is impossible to distinguish between females and immature males.

Data from northern bottlenose whales hunted in the Faroe Islands indicated that melon shape begins to change when a male reaches 6.5 m in length, and individuals over 7 m exhibit the mature male melon shape (Bloch *et al.* 1996). Unfortunately these individuals were not aged nor were the testes examined, although length measurements were obtained. Whaling data from Iceland and Norway indicated that puberty in males appears to begin at age 5-7, sexual maturity occurs by age 12 and physical maturity by age 20, based on testes development and total length (Benjaminsen 1972, Benjaminsen and Christensen 1979). However, melon shape was not described for the different age or size classes. As mature whales from different parts of the North Atlantic differ in length (Benjaminsen 1972, Bloch *et al.* 1996, Whitehead *et al.* 1997c), it is difficult to compare the data available from the different areas.

Information obtained from this study may also help determine the age of onset of sexual maturity in males in the Gully. By collecting individual melon photographs over a sufficient period of time, males can be recognized as they develop the distinctive sub-adult and mature male melon shape. Three individuals (#28, #102 and #267) appear to be developing from immature males into sub-adult males (Table 3.2). Minimum age estimates indicate that the onset of sexual maturity in males occurred some time between age 3 and 10 for individual #28; 7-10 for #102 and 5-8 for #267. If these individuals were indeed approximately 2 years old when they were first seen, then these data fit well with whaling data regarding the onset of puberty. It has not been possible to verify the age-length growth-curve in detail, although there is some evidence that three or four year old animals in the Gully are still smaller than full grown adults (see Chapter 6), therefore the onset of sexual maturity may occur later. Additionally, as the initial categorizations were based only on low quality photographs (MQ-2), it is difficult to distinguish between the effect of

photograph quality and change in melon morphology in these cases. Size differences between animals in the Gully and off Labrador were unlikely to affect estimates of minimum age based on length-growth curves, as both adults and juveniles would be smaller in the Gully population (Christensen 1973, Whitehead *et al.* 1997c).

The individual (#143) for which the genetic results potentially contradicted those from the melon photographs (Table 3.3) also provided some insight into the age of onset of sexual maturity. Individual #143 was categorized as female/immature male from melon photographs but was determined to be a male by genetic analysis. This individual was first sighted in 1989 when he was at least two years old. No melon photographs were taken of this individual until 1996 when he was at least nine years old and was categorized as female/immature male (MQ-3). According to the whaling data he should have entered puberty by this age. There were several possible explanations for this discrepancy. First the biopsy sample could have been mis-labeled in the field and actually represents another individual. This was unlikely as we collected extensive video footage and field notes documenting this incident which indicate that the biopsy was taken from an individual with a notch in its dorsal fin, in a group of two whales. Analysis of dorsal fin photographs indicate only one notched individual (#143) was present during the encounter. Second, it was possible that the genetic results were wrong (false positive) and this individual was in fact female. Although the SRY results may be incorrect as SRY analysis (conducted by M. Dalebout, University of Auckland) incorrectly assigned the sex of 1 out of 19 samples (5% failure rate) of northern bottlenose whales of known sex, from whaling off Iceland and Norway (M. Dalebout, University of Auckland pers. comm.), it was unlikely that the results from both SRY and ZFY would be wrong for the same sample. Third, changes in melon shape may occur quite late in puberty, although a number of relatively small males (estimated age 4-6 years) in the Faroe Islands were developing sub-adult melon shape (Christensen 1973, Bloch *et al.* 1996). Fourth, it is possible that the age of sexual maturity, especially the onset of melon shape change, may be highly variable between individuals or populations. There is some evidence to support this hypothesis as other larger males (estimated age eight years) in the Faroe Islands had not yet started to develop sub-adult melon shape (Christensen 1973, Bloch *et al.* 1996).

The potential discrepancy between the melon photograph technique and genetic sexing indicates that nine year old individuals with a female/immature melon shape cannot be presumed to be female. A longer sighting history is required before an individual can be classified as a female based only on melon photographs.

CONCLUSION

While sexing animals from melon photographs cannot categorically be used to sex all individuals, it can provide some indication of age class for males. The second major advantage of this technique it that it is less invasive than collecting biopsies. Taking melon photographs to sex northern bottlenose whales is an efficient method, especially if a photo-identification study is already being conducted, since no extra personnel or equipment is required and a large number of individuals can be sampled in a single field season. Photographic techniques are also much cheaper than genetic techniques. However, biopsy samples can be used for a number of other complementary studies including pollutant and diet analysis, and genetic analysis of population structure (*e.g.*, Friday 1997, Palsbøll *et al.* 1997, Todd *et al.* 1997, Baker *et al.* 1998). In conclusion, I consider the melon photograph technique to be a very useful method for determining sex and age class (female/immature male, sub-adult male, and mature male) for northern bottlenose whales. This method could be adapted for other species which display gradual morphological changes during sexual maturity.

Chapter 4: Surface behaviour of northern bottlenose whales

INTRODUCTION

The social organization of a population can be defined as the set of relationships between individuals (and classes of individuals) where the relationship between two individuals is defined by their interactions (Hinde 1976). When interactions (such as individual A grooms individual B) are difficult to observe, then associations (presence in the same space and time) between individuals are sometimes used as a measure of interactions assuming that all individuals within a group are interacting (*e.g.*, the "gambit of the group" which assumes that presence in the same group is equivalent to a social interaction; Whitehead and Dufault 1999). In many species of cetaceans it is difficult to observe and document interactions and associations between individuals, even when they are at the surface. Therefore many analyses of social organization in cetaceans define association as presence in the same group (*e.g.*, Smolker *et al.* 1992, Slooten *et al.* 1993). Whenever this is done it is important to assess whether the 'group', as defined by the researcher, corresponds to a set of interacting individuals (Whitehead and Dufault 1999).

Northern bottlenose whales were typically found in relatively discrete groups of spatially clustered and behaviourally coordinated animals at the surface, ranging in size from one to ten individuals (Benjaminsen and Christensen 1979). Previous studies, mainly from whaling ships, did not indicate if individuals join or leave the group during a surface encounter, although they did note that group members often would not leave a dying companion (Benjaminsen and Christensen 1979).

The activity level of a group can sometimes be assessed by aerial behaviour such as breaches or lobtails. For example, Pryor and Kang Shallenberger (1991) used behaviours such as lobtailing and spyhops to assess the fear or stress level of spotted dolphins (*Stenella attenuata*) caught in tuna nets. In contrast, sperm and humpback whales appeared to use aerial behaviour in social situations, rather than when stressed (Whitehead 1985, Waters and Whitehead 1990a). Bottlenose whales may also display aerial activity when stressed as whalers report breaching and lobtailing after harpooning (Gray 1882, Ohlin 1893), and during tagging attempts a northern bottlenose whale in the Gully reacted with a lobtail when

a suction-cup tag stuck to its flank (Hooker *et al.* submitted). However, behaviours visible from above the water surface (breaches, spyhops, lobtails and sideflukes) have also been observed in groups of northern bottlenose whales when there was no obvious source of stress (pers. obs.).

This chapter investigates the size, stability and composition of groups of bottlenose whales while at the surface, as well as the patterns of behaviours such as lobtails and breaches which are visible from the surface.

METHODS

DEFINITIONS

Sighting: Continuous observation of whales at the surface. A sighting begins when whales are first observed and ends if whales have not been observed for at least 10 minutes. Sightings could involve one to several groups. A 10 minute cut-off was chosen based on visual examination of the data which indicated if no whales were visible for 10 minutes, whales were usually not re-sighted for long time periods.

Group: Whales observed within 5 body lengths of each other, within a single sighting, and showing coordinated behaviour (*e.g.*, similar heading, similar surfacing interval). A new group is identified and a new sighting begins if 10 minutes passes without whales at the surface.

Encounter interval: The time between the first observation of a group and the last observation of the same group (within the same sighting).

Photographic interval: The length of time between the first and last photograph taken of a single group, within a single encounter.

Surface interval: The length of time a group of whales spends at or near the surface, from the first surfacing of a whale, to the last dive of a whale in the same group. Surface interval differs from encounter length as whales can surface before or dive after our observations end.

Lobtail: The whale lifts its flukes above the surface and brings them back down flat against the water surface, usually creating a loud noise and splash. The flukes can be oriented

either dorsally or ventrally with respect to the water.

Breach: The whale brings at least 40% its body, head first out of the water. A loud noise and splash is often created when the whale lands back in the water.

Spyhop: The whale brings its head vertically out of the water. Bottlenose whales rarely bring their eyes out. This is often a slow behaviour with the whales remaining relatively motionless for a brief time (usually less than one second) when the whales are at the maximum height above the water.

Sidefluke: The whale swims on its side near the surface such that one fluke clears the water surface. This behaviour often occurs slowly, appearing almost leisurely, although the flukes sometimes thrash violently.

FIELD RECORDS AND STATISTICAL ANALYSIS

Sighting records consisted of the date, time and position whales were first and last seen within a sighting, and the range at which whales were first observed. Group records consisted of the date, time and position whales were first and last seen within the group, as well as the estimated number and age/sex classes of individuals within the group. Estimates of group size were made frequently in the field and the maximum estimate kept in an Access database.

The observations consisted of group follows (Mann 1999) usually of the group which was closest to the boat during a sighting. Incident sampling (Mann 1999) was used to record all occurrences of lobtails, breaches, spyhops and sideflukes. These behaviours were sufficiently obvious to the boat crew that all observations were likely recorded when collecting observations of lobtails, breaches, spyhops and sideflukes was a priority (see below). Counts of each behaviour in each group were stored in the Access database. Systat (Wilkinson 1997) was used for all statistical analysis in this chapter.

IDENTITY AND STABILITY OF GROUPS

From the data that were collected, there were two possible ways I could define sets of interacting individuals: 'groups' or 'sightings'. To investigate whether 'group' better described a collection of interacting individuals than 'sighting', groups that were found in

the same sighting were analyzed to see if they contained the same individuals. The identity of individuals within each group was determined from left-fin identification photographs[1] (see Chapter 2). I selected all sightings in which left-fin identification photographs were taken from two or more groups. The number of shared individuals was calculated between consecutively observed groups within the same sighting. I then counted the number of individuals identified in each of the two groups from the same sighting, and the number of individuals which were found in both groups. The proportion of individuals which were present in the smaller group which were also present in the larger group was calculated for each group size by the following formula:

$$\text{Proportion shared individuals} = \frac{\sum_i g_i i}{G \sum_i g_i}$$

where i = number of shared individuals

g_i = the number of groups in which i individuals were shared

G = estimated group size of the smaller group

To determine whether consecutively observed groups, which were not necessarily in the same sighting, contained the same individuals, I selected all groups with left-fin photographs. Group membership and the number and proportion of shared individuals was calculated as above for every consecutively observed group which was photographed on the same day.

Group size

The distribution and mean group size were calculated directly from field estimates, for all groups which had a field estimate. Typical group size (the size of group in which the average animal found itself) was calculated from field estimates following the methods of Jarman (1974) where:

---

[1] Analysis was restricted to left-fin photographs to avoid counting an individual twice (once from each side). All quality photographs were included in order to identify as many individuals in the group as possible. All individuals were included as marks were unlikely to change within a sighting. These restrictions were used throughout this chapter.

$$T = \frac{\sum_{j=1}^{n} x_j^2}{\sum_{j=1}^{n} x_j}$$

and T = typical group size

x_i = number of individuals in each of n groups

n = group size

To examine whether group size varied by month or year I calculated the frequency of each group size in June, July and August of 1990, 1996 and 1997 (all years with field work in all three months). A log linear model tested for interactions between year and month in the proportions of group sizes in the following categories: 1-2, 3-4, 5-6 and 7 or more individuals.

Did the membership of the group change throughout the encounter?

To investigate whether membership changed throughout the photographic interval I estimated the expected number of shared individuals between the start and end of the interval for each group size (assuming that there was no change in identity of individuals and that field estimates of group size were correct). For example, the probability of identifying the same two individuals at the start and end of the encounter in a group of four individuals is 1/6. Then for each group size, I used a one-sample student t-test to compare the expected number of shared individuals with the observed number.

Photographic interval should be roughly equivalent to the length of the encounter if whales were first photographed shortly after the encounter began and last photographed just before the encounter ended. As there were several occasions when the photographic interval was shorter than the encounter length, I used photographic interval rather than encounter length to investigate whether the identity of individuals changed throughout the observation of a group. I compared the identity of individuals within a group from the start of the photographic interval to the identity of individuals at the end of the observations of the same group. I selected all groups with an estimated group size of four

or larger that had at least four left-fin photographs taken during the encounter. To avoid resampling the same individuals, I selected only the first group on each day which met my criteria. To account for different probabilities of sharing individuals between the start and end of the encounter due to smaller or larger group sizes, I adjusted the number of comparisons with group size by the following method:

number of individuals to be compared = estimated group size/2

If the estimated group size was an odd number I rounded up to obtain the number of comparisons. I then counted the number of shared individuals between the start and end of the encounter. For example, if the estimated group size was five individuals and the first three identifications were #51, 59 and 124 and the last three identifications were #124, 131 and 54, there was one shared individual (#124). Spearman rank correlations and scatterplots were used to investigate whether groups with longer photographic intervals experience more change in group membership than shorter encounters.

GROUP COMPOSITION

Although attempts were made in the field to determine the age and sex classes of the individuals in the group, this was often difficult. To determine if the field notes on group composition were accurate I selected all groups in which the dorsal fin of a known male (as categorized by melon photographs – see Chapter 3) was photographed. I then compared how many of these groups indicated the presence of a male in the field notes.

Did the age/sex class composition of the group vary with group size or month?

As the field notes were not always accurate (see results), investigations of the age and sex class of individuals within a group were based on melon and fin photographs taken of individuals within the group. However, not all individuals were photographed in every group, nor has it been possible to determine the age/sex class of all individuals in the Gully. Therefore, I restricted the group composition analysis to groups in which the number of identified individuals was at least equal to the estimated number of individuals (as occasionally group sizes estimated in the field were lower than the number of identified

individuals), and at least half of the identified individuals had melon photographs of MQ≥2. To avoid resampling the individuals, I examined the identifications of all groups that met the above conditions and selected only the first group on each date.

From this restricted dataset, I determined the age and sex class composition for all groups of 1-6 animals (see Table 4.1 for the different group types). There were several ways the group composition could change over the field season. First, if the number of individuals of each age and sex class present in the Gully varied over the summer, the proportion of groups containing at least one individual of each age and sex class could vary by month. I used a G-test to determine whether the proportion of groups containing individuals of each age and sex class was different from random. Second, the frequency of each group type (see Table 4.1) could vary over the summer. I calculated the proportion of groups of each type and used a log linear model to test for interactions between the month and type of group.

Table 4.1: List of possible group types based on melon photographic categorization.

Group type	Minimum number of individuals in group
Female/immature (F/I) singleton	1
Sub-adult male (SM) singleton	1
Mature male (MM) singleton	1
F/I with other F/I	2
SM with other SM	2
MM with other MM	2
F/I - MM	2
F/I - SM	2
SM - MM	2
F/I - SM - MM	3

As there were no significant trends in group composition over the summer (see results) I calculated the overall proportion of each type of group by pooling different years of the study. The proportion of groups of each type an individual of each age/sex class finds themselves in may be different from the overall proportion of group types. For example, if all mature males were found in groups with female/immatures, then 100% of all the groups which contained mature males also contained female/immatures, although the overall

proportion of mature males with female/immature groups may be lower. I therefore calculated the proportion of groups which contain each age/sex class of an individual in the following way:

$$P_{ct} = \frac{A_{ct}}{A_c}$$

Where P_{ct}= proportion of groups that contain an individual of age/sex class (c) which are also of type (t)

A_{ct}= number of groups of type (t) containing individuals of class (c)

A_c= number of groups containing individuals of class (c)

SURFACE INTERVAL OF GROUPS

The surface interval of a group should be roughly equivalent to the encounter length. If the initial observation of a group of whales did not occur at the same time the whales surfaced (*i.e.*, the whales were at the surface for an unknown time period before they were noticed) then the surface interval was longer than the encounter length. As the initial surfacing of a group of whales was more likely to be missed if the whales were further from the boat, I compared the mean encounter length of groups that were initially sighted less than 500 m from the boat, with groups which were sighted further than 500 m using a 2 sample t-test. In this test, and all subsequent tests of surface interval I eliminated all groups in which the stop time was not recorded, or in which the encounter length was less than one minute (as encounter length was only recorded to the nearest minute). Similarly, I used a 2 sample t-test to determine whether groups containing young animals (see Chapter 6) spent longer at the surface than groups without young animals

Does surface interval vary with year or month or group size?

To determine whether the surface interval varied by month or year, I calculated the frequency of each surface interval (pooled in five minute intervals, for 1990, 1996 and 1997) in each year and month and tested for interactions using a log linear model. Spearman rank correlations were used to compare encounter length with estimated group size.

BEHAVIOURS VISIBLE ABOVE THE SURFACE

While occurrences of behaviour visible from above the water surface[2] were recorded throughout the study, accurate recording of all occurrences of these behaviours occurred only in 1989, 1993, 1994 and from July 28-August 10 1990. All analyses of behaviour rates were conducted based on these sampling periods. Restricting analyses of surface behaviours to 1989-1994 also eliminated years in which attempts were made to biopsy or suction-cup tag bottlenose whales in the Gully. This avoided complications of determining whether the surface behaviours were a reaction to the tagging or biopsy procedure, as breaches or lobtails were noted as reactions to these procedures in bottlenose whales or other species (Weinrich *et al.* 1991, Schneider *et al.* 1998, Hooker *et al.* submitted). Behaviour counts were converted to behaviour rates per individual animal per minute by the following formula:

$$\text{Behaviour rate} = \frac{\sum_i b_i}{\sum_i n_i t_i}$$

where b_i = number of occurrences of a behaviour in group *i*

n_i = number of individuals in group *i*

t_i = time interval group *i* was observed (in minutes)

Does the behaviour rate vary throughout the field season or by year?

I divided each field season when surface behaviours were accurately recorded into week long periods, where the first day in the field season was counted as day one of a week. I then calculated the rate of each of the four behaviours separately for each weekly period. In all cases when the week session included a change in calendar month, all observations of bottlenose whales actually occurred within a single calendar month, and therefore it was easy to assign each weekly period to a month and year. ANOVA was used to test for differences in behaviour rate with month and year and interactions between month and year.

---

[2] In this chapter the term 'surface behaviour' will refer only to lobtails, breaches, spyhops and sideflukes, although there are many other behaviours which whales engage in at the surface.

Does the behaviour rate vary with group size?

To test whether the behaviour rates varied with group size I calculated the behaviour rates separately for each behaviour and estimated group size. Spearman rank correlations tested for trends in the behaviour rate in relation to estimated group size and the correlations were displayed as a scatterplot.

RESULTS

IDENTITY AND STABILITY OF GROUPS

Out of 795 sightings, 544 contained only a single group (mean number of groups per sighting 1.94; SE = 0.077; range = 1-25). There were 75 sightings which contained two or more groups with left-fin photographs; a total of 216 different groups and 140 comparisons. Although there were numerous sightings in which the same individuals were observed in consecutive groups (see Table 4.2), the proportion of shared individuals was less than half for all group sizes, except for a group size of three animals.

Table 4.2: Number of shared individuals between consecutive groups in the same sighting. Counts represent number of groups.

# individuals in smaller group	Number of shared individuals					Proportion of individuals in the smaller group which are also in the larger group
	0	1	2	3	5	
1	47	22				0.32
2	23	18	4			0.29
3	3	1	1	4		0.56
4	2	2	3	3		0.43
5	1	3	1			0.20
6	1				1	0.42

If collections of interacting individuals were defined as 'groups' then the number of associates of an individual was smaller than if the 'sighting' definition was used, as fewer individuals were identified within a group. However the 'group' definition included only individuals which were acting in a unified manner. While 'sightings' may be relevant for determining larger scale aggregations of whales, potentially useful in looking at foraging

patterns, 'groups' appeared more likely to define a social aggregation.

Close examination of a long and complex sighting illustrated some of the different levels of interactions of individuals in groups within the same sighting. Sighting 44 began on August 10, 1989 (see Table 4.3 for details) at 10:37 and there was continuous observation of bottlenose whales until 16:52; 18 different groups were observed. Within this single sighting, several individuals were found within the same group multiple times, but were not observed to interact with others. For example, individuals #69, #97 and #98 were never found in the same group as individual #28. Individuals #1 and #2 were not observed until group 66 and were then frequently observed with many different individuals.

There were 436 groups for which the next group was also observed on the same day. When the number of individuals in the smaller group was small (1-2 individuals) the subsequent group often did not contain the same individuals (see Table 4.4 for details). However, when the smaller group was relatively large ($\geq$3), the same individuals were often found in the subsequent groups, although the effect was not large (for groups of less than five animals the proportion of shared individuals was 0.24, for groups over five the proportion of shared individuals was 0.34).

Table 4.3: Identifications within the 18 different groups that were observed during sighting 44 on Aug 10, 1989. Brackets indicate groups in which an individual was identified by right fin photographs only.

Group	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72
Time start	10:37	12:05	12:10	12:17	12:25	12:45	13:10	13:25	13:30	14:01	14:25	14:45	15:25	15:30	15:40	16:00	16:20	16:45
Time end	11:55	12:06	12:13		12:35	13:05	13:20		13:55	14:20	14:35	15:20		15:35	16:00	16:15	16:40	16:52
Estimated number individuals	5	1	1	2	2	4	3	1	2	5	2	7	1	3	5	6	4	2
Individuals present	69 97 98	(28)	98			54 101 102			(104) 105 106	5 28 45 (104) 106 113		1 2 28 106 115 116			(1) 15 17 28 118 120	(15) 17 18 28 (115)	1 2 (17) (18)	1 2 120

Table 4.4: Number and proportion of shared individuals between consecutive groups which occurred on the same day.

Group size	Number of shared individuals						Proportion of individuals which were also seen in previous group
	0	1	2	3	4	5	
1	185	57					0.24
2	75	30	13				0.24
3	19	5	7	8			0.37
4	6	5	5	4	2		0.40
5	2	5	1				0.18
6	1			1	2	1	0.53
10					1		0.40
13						1	0.39

Group size

Field estimates of group size were made for 1,281 groups. The mode was three animals which closely corresponded to the mean (mean = 3.04; SD = 1.86, range = 1-14; see Figure 4.1). The typical group size (Jarman 1974) was 4.17. The three-way interactions between year, month and the frequency of observed group sizes (pooled as groups of 1-2, 3-4, 5-6 and 7 or more animals) was non-significant (log linear model $P = 0.61$). When the three-way interaction was removed from the model, the interaction terms between the frequency of group size and year, as well as group size and month were also non-significant ($P = 0.61$ and 0.10 respectively). Therefore, there were no significant differences among the observed frequencies of different group sizes in different years or months, although there may have been a slight trend towards larger groups later in the summer (see Figure 4.2).

Did the membership of the group change throughout the encounter?

To test if the membership within a group changed within a single encounter, the expected mean number of shared individuals (assuming no change in group membership) was compared to the observed mean for each group size from 4-7 animals, by a one-sample t-test (see Table 4.5). The observed means were significantly lower than the expected mean for groups of five individuals, indicating that group membership changed throughout the encounter. However, there were no significant differences for group sizes of four, six or seven, indicating no change in membership.

Table 4.5: Test of mean number of observed shared individuals against predicted number for group size 4-7. Significant results are shaded.

Group size	Number observed groups	Observed mean ±SD	Expected mean	*P*
4	43	1.04 ± 0.65	1	0.643
6	10	1.60 ± 0.70	1.5	0.662
7	9	1.55 ± 1.23	2.27	0.121

There were 82 groups which had an estimated group size of 4-7 individuals and which had at least four left-fin photographs taken during the encounter (only the first group observed each day was included). Scatterplots of the number of shared individuals showed some tendency for fewer shared individuals over longer photographic intervals (see Figure 4.3), although the trends were slight for most group sizes. There were insufficient data to test for change in group membership for groups larger than seven individuals. Spearman rank correlations between the number of shared individuals and photographic interval were non significant for all group sizes (group size 4: r_s =-0.017; 5: r_s =-0.202, 6: r_s =-0.169, 7: r_s =-0.542), although the correlation was quite large for groups of seven individuals. This indicated that group membership did not change significantly more during longer photographic intervals.

GROUP COMPOSITION

Of the 496 groups in which a known male (categorized by melon photographs) was photographed, the field notes of only 200 groups indicated that a male was present. Thus the field notes did not accurately describe group composition. There were 181 groups in which all members were likely photographed and at least half of the identified individuals were sexed, although relatively few groups were completely sexed (see Table 4.6). Of the 181 groups which met the above criteria, 176 were photographed on separate days and all analyses of group composition were based on these 176 groups.

Did the age/sex class composition of the group vary with group size or month?

The limited data made it difficult to make any strong conclusions about how age/sex class composition varied with group size (see Table 4.6), although a few general comments can be made. Solitary individuals were equally likely to be any of the three age/sex classes. Groups which contained both age classes of males, but no females/immatures were rare. While larger groups tended to have all three age and sex classes, if only one class was present then it was usually female/immature.

Figure 4.1: Distribution of observed and typical group sizes of bottlenose whales in the Gully. Typical group size (Jarman 1974) is the group size as experienced by a typical individual whale.

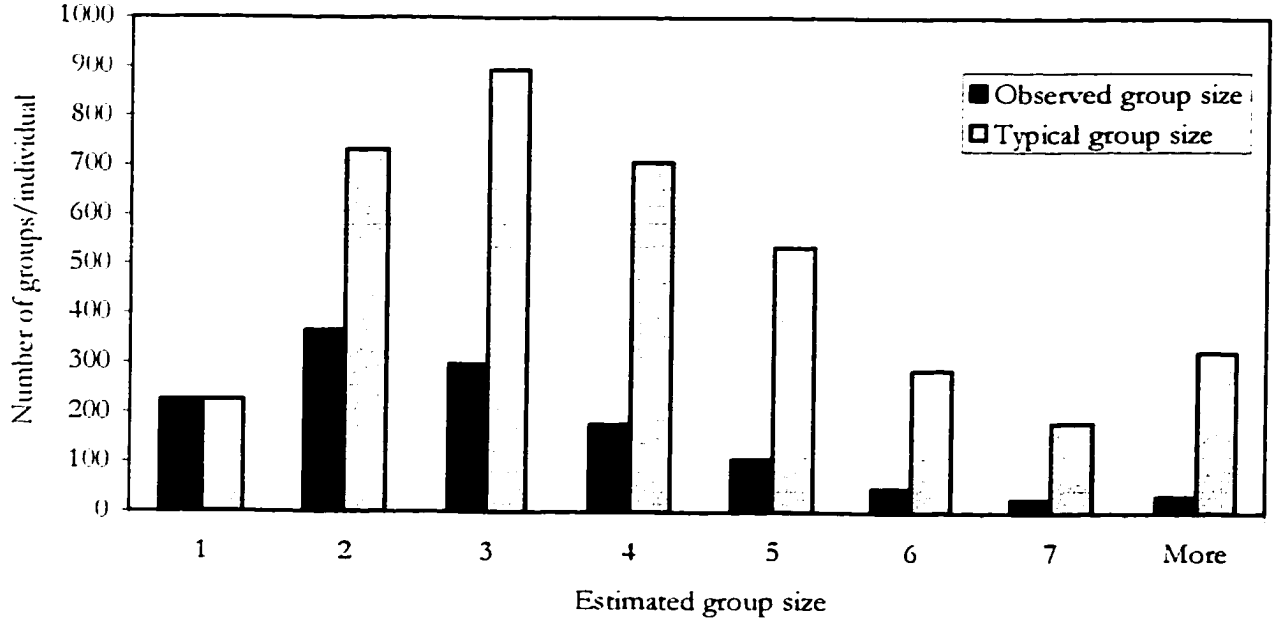


Figure 4.2: Distribution of observed group sizes of bottlenose whales by month.

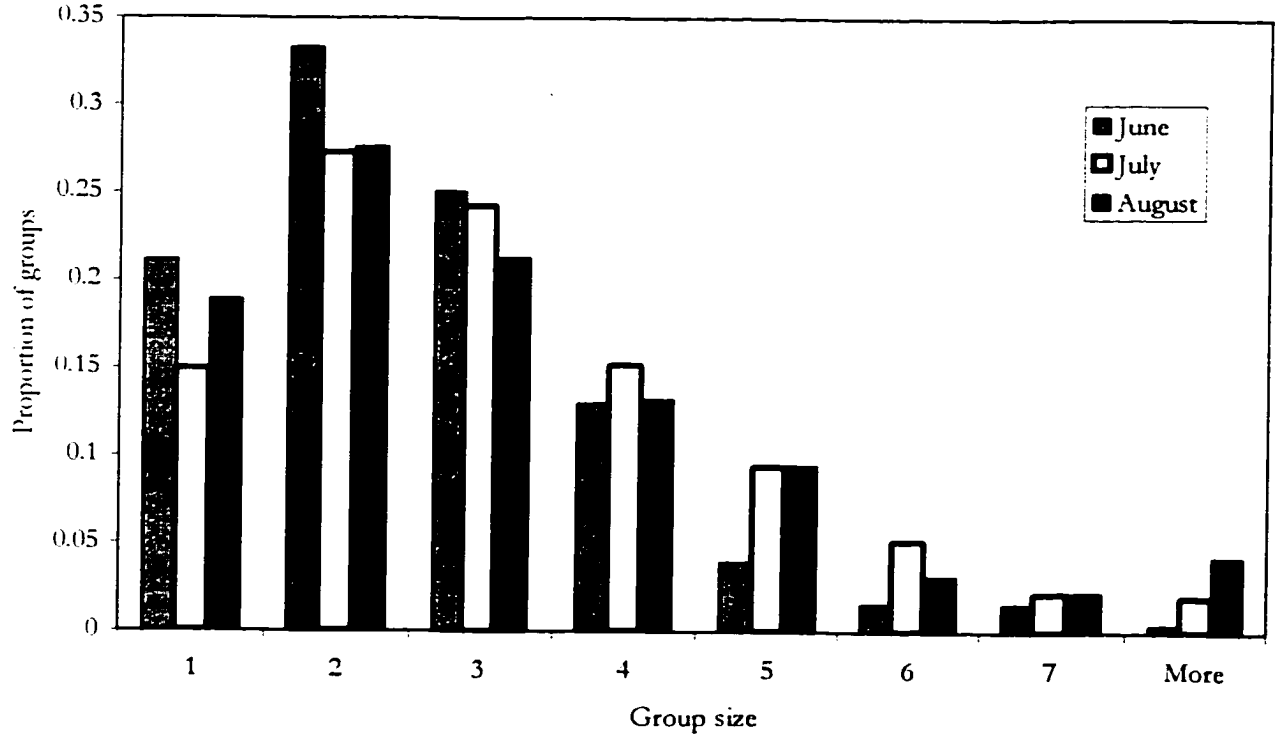


Figure 4.3 The number of shared individuals between the beginning and end of the group in relation to the interval between the first and last photograph.

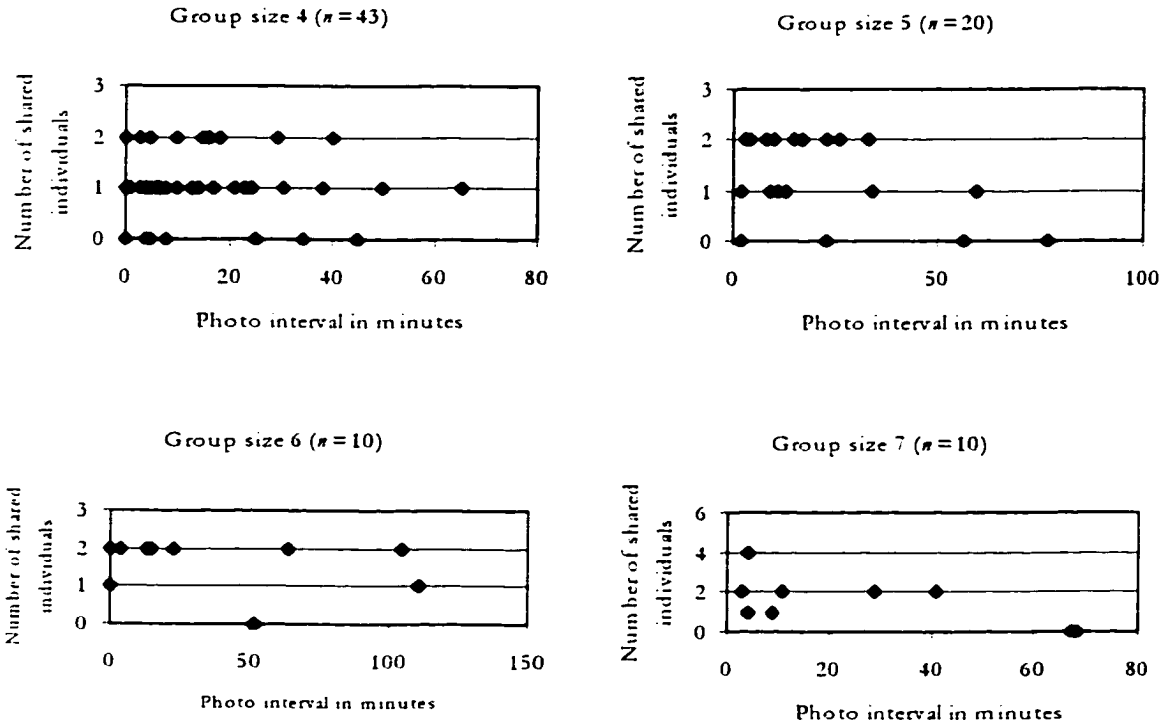


Table 4.6: Known and unknown age and sex composition of groups of sizes 1-6. (F/I = Female/immature male; SM = Sub-adult male; MM = mature male).

Group size	Composition	composition	all individuals sexed	at least half sexed but not all
1	Single age/sex class	F/I	11	
		SM	9	
		MM	8	
2	Single age/sex class	F/I	12	15
		SM	0	2
		MM	3	4
	2 age/sex classes	F/I-SM	9	
		F/I-MM	3	
		SM-MM	0	
3	Single age/sex class	F/I	3	5
		SM	1	0
		MM	0	0
	2 age/sex classes	F/I-SM	2	3
		F/I-MM	3	3
		SM-MM	0	2
	3 age sex classes	F/I-SM-MM	0	
4	Single age/sex class	F/I	1	2
		SM	0	1
		MM	0	1
	2 age/sex classes	F/I-SM	1	7
		F/I-MM	1	5
		SM-MM	0	4
	3 age sex classes	F/I-SM-MM	1	1
5	Single age/sex class	F/I	0	2
		SM	0	0
		MM	0	0
	2 age/sex classes	F/I-SM	1	6
		F/I-MM	1	1
		SM-MM	0	0
	3 age sex classes	F/I-SM-MM	0	2
6	Single age/sex class	F/I	1	4
		SM	0	1
		MM	0	0
	2 age/sex classes	F/I-SM	0	2
		F/I-MM	0	2
		SM-MM	0	3
	3 age sex classes	F/I-SM-MM	0	6

There were no differences between the observed sex composition of groups consisting of two or three individuals from a random distribution (Table 4.7), although the sample sizes were small (27 groups of two individuals; and 9 groups of three individuals).

Table 4.7: Observed and expected distribution (if distribution is random) of the sexes of individuals within groups of a) two individuals and b) three individuals (F/I = female/immature).

a)

	2 F/I	2 Male (either age)	Male and F/I
Observed distribution	12	3	12
Expected distribution	12	3	12

b)

	3 F	2 F/1 male	1 F/2 male	3 Male
Observed	3	3	2	1
Expected	3	3	2	1

While G-tests did not indicate any significant differences among the proportion of groups in each month which contained at least one mature male, sub-adult male or female/immature (see Table 4.8), the presence of mature males may have peaked in August, female/immatures in July and the presence of sub-adult males seemed nearly constant over the summer.

Table 4.8: Proportion of groups in each month which contain at least one individual of known age/sex class.

	Number of groups	Female/immature	Sub-adult male	Mature male
June	38	.79	.45	.37
July	77	.91	.47	.34
August	66	.71	.44	.50
χ^2 - 2 df		0.28	0.062	2.2

The frequency of each type of group also did not change over the summer (log linear model, interaction term P =0.815); therefore groups of each type from separate months can be pooled together. The two most common group types were female/immature – female/immature and female/immature – sub-adult male (see Table 4.9), while most of the

other group types were relatively rare. The most common group type for mature males included female/immatures or groups with all three age/sex classes. Similarly, most sub-adult males were found in groups containing female/immatures or groups with all three classes. However, female/immatures were most commonly found in groups with other female/immatures and relatively rarely found in groups with all three age/sex classes.

Table 4.9: The distribution of group types. Group types other than singleton also contain individuals of unknown age/sex class (F/I = female/immature; SM = sub-adult male; MM = mature male).

Group type	# of groups	Proportion of groups	Typical group composition of individuals of a given age/sex class		
			F/I	SM	MM
F/I singleton	11	0.06	0.08		
SM singleton	9	0.05		0.12	
MM singleton	8	0.05			0.11
F/I - F/I	46	0.26	0.34		
SM - SM	5	0.03		0.06	
MM - MM	8	0.05			0.11
F/I-SM	35	0.20	0.26	0.44	
F/I-MM	24	0.14	0.18		0.34
SM-MM	11	0.06		0.14	0.15
F/I-SM-MM	20	0.11	0.15	0.25	0.28
number of groups containing each class			136	80	71

SURFACE INTERVAL OF GROUPS

Although the encounter length of groups initially observed within 500 m of the vessel was slightly longer (mean =16.9 minutes SD=31.5, n=303 groups) than for groups initially observed farther than 500 m (mean =15.4, SD=19.1, n=244 groups), the difference was not significant (t=-0.681, P=0.496). Therefore it was a reasonable assumption that the encounter length was approximately equivalent to surface interval. Thus all groups with a recorded stop time and surface interval over one minute were used for further analyses of surface interval. The mean surface interval was 15.6 minutes (SD=20, n=1152 groups – see Figure 4.4) and ranged from one minute to four hours and 35 minutes. Surface intervals of 10 minutes or less accounted for more than half of the groups observed. Groups

containing young animals spent significantly longer at the surface (mean=24.3 minutes, SD=24.0, n=128) than groups without young animals (mean=14.8, SD=19.3, n=1007; t=5.083, P=0.000).

Does surface interval vary with month and year or group size?

Log linear models indicated that there was no difference in surface interval in relation to month or year of observation (P=0.435). There was a significant correlation between surface interval and group size (r_s = 0.404, P>0.01) such that the surface interval increased with increasing group sizes. However, small groups occasionally had long surface intervals; on one occasion a singleton was observed at the surface alone for 70 minutes.

BEHAVIOURS VISIBLE ABOVE THE SURFACE

Bottlenose whales were observed for 8,270 minutes during the field trips when accurate records of surface behaviour were kept. While each surface behaviour was observed more than 100 times, the behaviour rates (per individual per minute of observation) were still relatively low (see Table 4.10). Lobtails and spyhops were the most common behaviours, while breaches were observed least often.

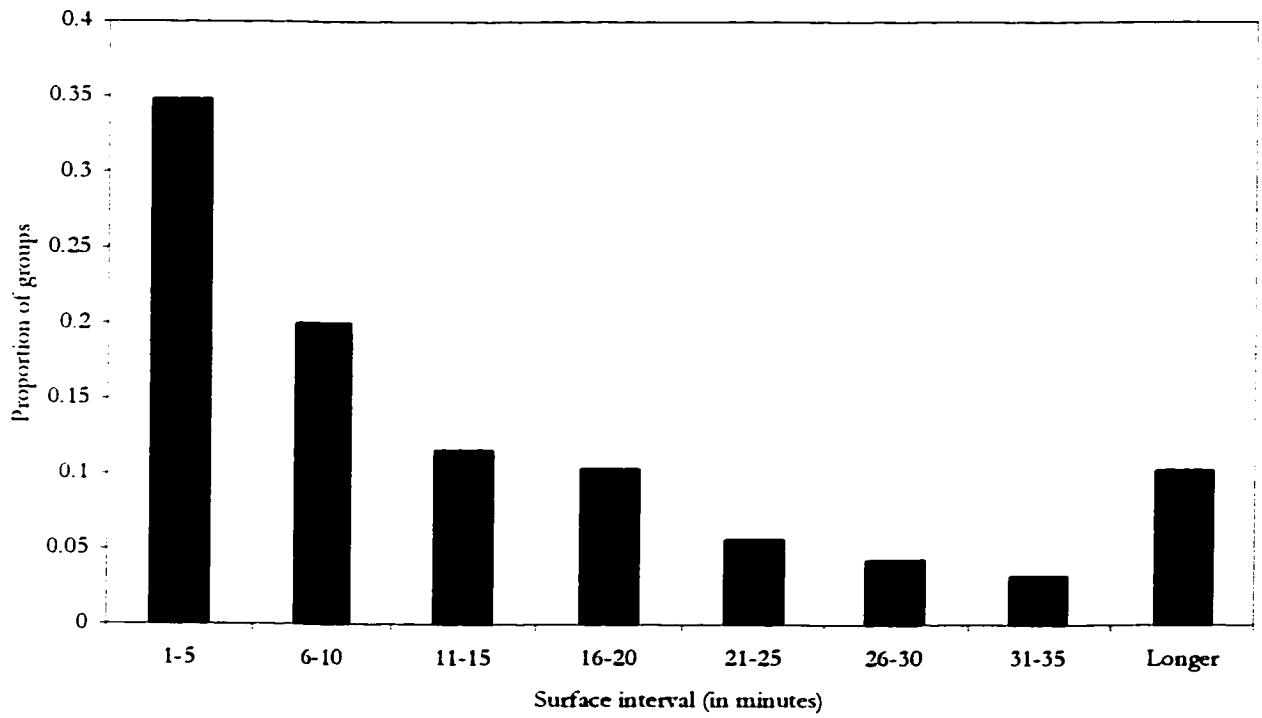
Table 4.10: Rates of surface behaviours.

Behaviour	# occurrences	Rate / individual / minute observation
Lobtail	574	0.0142
Breach	151	0.0037
Spyhop	566	0.0140
Sidefluke	295	0.0073

Did behaviour rates vary by year or month or group size?

The behaviour rates did not vary significantly by month, year or by an interaction between month and year (ANOVA: all P values <0.01), nor was there a significant correlation between behaviour rates and estimated group size. The behaviour rate of spyhops peaked in medium sized groups, although the sample size for these data set was limited. None of the other behaviour rates showed any trend with group size.

Figure 4.4: Surface intervals of groups of northern bottlenose whales.



DISCUSSION

IDENTITY AND STABILITY OF GROUPS

Individuals are likely to interact with each other if they are found within the same clustering of individuals. However, there is no standard definition of group and many terms (*e.g.*, party, school, pod, unit, sub-group) are used to define differing levels of clustering, each with no set definition. If interactions are assumed to be roughly equivalent to associations and associations are defined as presence in the same group, then it is essential that the group definition relates to interacting individuals (Whitehead and Dufault 1999). As no single definition of a group can be relevant to all species, it is important that group definitions are relevant to the species and population being studied (Chapman *et al.* 1993). Simply sharing the same area at the same time is not necessarily equivalent to a social interaction. 'Groups' of bottlenose whales in the Gully, however, appeared to contain interacting individuals, and so 'the gambit of the group' (assumption that presence in the same group is equivalent to a social interaction, Whitehead and Dufault 1999) was probably justified.

Group size

The estimated group size from this study was similar to those of other studies of bottlenose whales (see Table 4.11). The small differences in estimated group size may be methodological (differing sampling methods, different time of year sampled), or there may be population differences.

Many cetaceans found in the open ocean tend to form groups of 20 to 1000 individuals. However, bottlenose whales are found in groups of comparable size to many coastal dolphins (see Table 4.12). The similarities in group size between dolphins found in large coastal bays and bottlenose whales in the Gully may be related to the spatial and temporal variability of food resources (see Chapter 8 for a detailed discussion of the similarities

between northern bottlenose whales in the Gully and bottlenose dolphins[3] in large coastal bays). For example, Defran and Weller (1999) argue that larger group sizes found in bottlenose dolphins in the Southern California Bight, in comparison to groups of bottlenose dolphins in large coastal bays, is likely related to the much higher variability of food resources off California.

Table 4.11: Estimates of group size in various populations of northern bottlenose whales. When "group" was defined, it was similar to the definition in this study (usually a small spatial cluster).

Location	Year of survey	Months of survey	Survey method	Mean	Range	Reference
Faroe Islands	1584-1993	Year round – most data August to October	Drive fishery	2.1	1-7	Bloch *et al.* 1996
Iceland	1960-70	April to June	Whaling	3.9	1-20	Benjaminsen and Christensen 1979
Iceland	1989	July	Ship survey	3.1		Sigurjónsson *et al.* 1989
Labrador	1960-70	April to June	Whaling	3.1	1-20	Benjaminsen and Christensen 1979
Iceland and Faroe Islands	1987	June to July	Ship survey	2.6	1-10	Sigurjónsson *et al.* 1989
Gully	1988-1997	June-August	Focal group follows	3.0	1-14	this study

[3] It has been suggested that bottlenose dolphins are not monophyletic. The Monkey Mia, Australia population may actually belong within the genus *Stenella*, and there may be other taxonomic differences between other populations (see (Rice 1998). However following Rice (1998), I classify all of the populations discussed in this thesis as *Tursiops truncatus*.

Table 4.12: Group sizes of coastal and oceanic species[1]. 'Group' definitions were roughly equivalent to this study's definition.

SPECIES	LOCATION OF STUDY	SURVEY METHOD	GROUP SIZE	REFERENCE
PREDOMINANTLY COASTAL SPECIES OR POPULATIONS				
Bottlenose dolphin	Bahamas	Group follow	7.5 (SD = 3.72)	Herzing and Johnson 1997
	Monkey Mia, Australia	Group follow	4.8 (SD = 2.7)	Smolker *et al.* 1992
	Sarasota, Florida	Group follow	4.84 (SD = 4.31)	Wells *et al.* 1980
	Moray Firth, Scotland	Group follow	6.45	Wilson 1995
	Southern California Bight	Group follow	19.8 ± 18.4	Defran and Weller 1999
	ETP[2]	Ship survey	22.7	Wade and Gerrodette 1993
Spotted dolphin	Bahamas	Group follow	7.7 (SD = 1.35)	Herzing and Johnson 1997
	ETP[2]	Ship surveys	ranges from 75 to 149 in different areas	Wade and Gerrodette 1993
Humpback dolphin (*Sousa chinensis*)	South Africa	Group follow	6 (SD = 2.72)	Karczmarski 1996
Hector's dolphin (*Cephalorhyncus hectori*)	New Zealand	Group follow	usual range 2-8	Slooten and Dawson 1994
Transient killer whale	Vancouver Island, B.C.	Group follow	4.21	Baird and Dill 1996
COASTAL AND OCEANIC				
Dusky dolphin (*Lagenorhyncus obscurus*)	Argentina	Group follow	usually 6-15 range 6-300	Würsig and Würsig 1980
Spinner dolphin (*Stenella longirostris*)	Hawaii	Group follow	range 6-250	Norris and Dohl 1980
	ETP[2]	Ship surveys	ranges from 111 to 134 in different areas	Wade and Gerrodette 1993
PREDOMINANTLY OCEANIC				
Most mesoplodons		Incidental sightings and strandings	small groups (2-6)	Mead 1989a
Baird's beaked whale	Japan	Whaling reports	7.4 (range up to 50)	Balcomb 1989
Pilot whales		Whaling reports and ship surveys	mean ranges from 25 to 85 in different areas	Bernard and Reilly 1999
Sperm whales	Galapagos	Group follows	20	Arnbom and Whitehead 1989
Striped dolphin (*Stenella coeruleoalba*)	ETP	Ship surveys	70 (CV = 0.05)	Wade and Gerrodette 1993
Common dolphin (*Delphinus delphis*)	ETP	Ship surveys	ranges from 254 to 472 in different areas	Wade and Gerrodette 1993
Fraser's dolphin (*Lagenodelphis hosei*)	ETP	Ship surveys	394 (CV = 0.20)	Wade and Gerrodette 1993
Risso's dolphin (*Grampus griseus*)	ETP	Ship surveys	12 (CV = 0.08)	Wade and Gerrodette 1993
Rough toothed dolphin (*Steno bredanensis*)	ETP	Ship surveys	15 (CV = 0.18)	Wade and Gerrodette 1993

1) I have included most cetacean species and populations which have been studied in a similar manner.
2) ETP = Eastern Tropical Pacific. Populations of dolphins found in the Eastern Tropical Pacific are predominantly oceanic, but they are included with other populations of the same species.

Does the membership of the group change throughout the encounter?

Although bottlenose whales in the Gully did not live in permanent associations (see Chapter 5), it was not clear from this analysis if changes in group membership routinely occurred during a photographic interval (see Table 4.5). The significantly lower than expected number of shared individuals for groups of five animals, but not for other group sizes groups (4, 6 or 7 individuals) was unexpected. Individuals would be expected to leave groups if the costs to staying in the group outweigh the benefits of staying in the group. Similarly, individuals would be expected to join groups when the benefits are higher than the costs of remaining solitary (or in the group in which they are currently– Alexander 1974). Sampling difficulties were the most likely explanation for this result. Only 10 groups of size six and seven met the criteria needed to examine changes in group membership, and the sample size for groups of five individuals was half that of groups of four individuals (see Table 4.5). However, there is no obvious biologically relevant reason why group membership is likely to change over the photographic interval only in groups of five animals. Optimal group size theory predicts that group membership would be more likely to change when groups are far from optimal size (Alexander 1974). However, if a broad range of group sizes were optimal (especially over long time periods) there would be few costs and little benefit to changes in group size. However the results did indicate that group membership can change over the photographic interval, and although the correlation was not significant, group membership may be more likely to change when the photographic interval is longer.

GROUP COMPOSITION

As the field notes on age and sex class composition of a group were unreliable, and relatively few individuals in the Gully have been categorized by melon photographs, my data on group composition were sparse and less reliable than those from whaling studies on bottlenose whales in which the sex of every group member was determined from the carcasses. Although proportions of male only, female only, and mixed sex groups captured off the Faroe Islands (Bloch *et al.* 1996) were similar to those found in the Gully, Benjaminsen and Christensen (1979) found that small groups (1-5 individuals) off Labrador

were usually composed of a single sex, whereas in the Gully many small groups consisted of both males and females (see Table 4.6).

Species with long term bonds between mature individuals of both sexes (such as killer whales - Baird In press) are unlikely to show seasonality in group composition. However, species with distinct breeding seasons and more fluid group structure (such as humpback whales or bottlenose dolphins) do show seasonal differences in group composition, although mixed sex groups may be found outside the breeding season (Clapham *et al.* 1992, Clapham 1993, Connor *et al.* 1996). Bottlenose whales off Labrador have a peak calving season in April and it is speculated that mating also occurs in April (Benjaminsen 1972). In the Gully, calving may occur in the summer (see Chapter 6), which coincided with the presence of mature males in the groups.

SURFACE INTERVALS OF GROUPS

The length of time a group of bottlenose whales spent at the surface is highly variable (see Figure 4.4), ranging from less than a minute to over four hours, although groups with young animals were at the surface significantly longer than groups without young animals. Dive times and dive depths were also variable, even between consecutive dives by the same individual (Hooker and Baird 1999), which may lead to the variation in surface interval. In comparison, individual sperm whales showed a fairly stereotyped pattern of an approximately 40 minute dive followed by a ten minute surface interval, while they were foraging (Papastavrou *et al.* 1989). However, sperm whales in many areas were likely routinely diving to approximately the same depth (the deep scattering layer; Papastavrou *et al.* 1989), while bottlenose whales appeared to be diving to the sea floor, which in the Gully, dramatically varied in depth over short spatial scales (Hooker and Baird 1999).

This variability in surface intervals makes it difficult to define associations between individuals temporally (*i.e.*, photographed within X minutes). As more than half of the groups had a surface interval of ten minutes or less, defining an association between two individuals as having been photographed within ten minutes of each other could result in associations between individuals which were in separate groups, especially if the group

which was closest to the boat submerged and we began photographing a different group. Analysis of the identity of groups indicates that consecutive groups (even those within the same sighting) often were composed of different individuals (see Table 4.2 and 4.3). Therefore, defining associations temporally (even using a short time period such as 10 minutes), will likely create associations between individuals that were not actually interacting.

BEHAVIOURS VISIBLE ABOVE THE SURFACE

Incident sampling, which was used to record surface behaviours, should only be used when observers are likely to record all occurrences of the behaviour (Mann 1999). Aerial behaviours such as breaching and lobtailing were very easily observed and likely recorded every time they occurred as observers had both visual and audible cues. Spyhops and sideflukes were less likely to be observed, as there was no audible cue. However during the time periods when recording such behaviour was a priority, it was unlikely that many occurrences would be missed as the visual cue was still obvious.

As animals must bring at least 40% of their body out of the water during breaches, they were the most energetically expensive behaviour described in this paper (see Whitehead 1985, for calculated energy expenditure by humpbacks breaching), and they occurred at the lowest rate in bottlenose whales (see Table 4.10). Breaches may be too expensive to perform routinely and lobtails (the other percussive behaviour) occurred at higher rates. Therefore lobtails may be a 'cheaper' way of creating sound.

There are numerous proposed explanations for aerial behaviour in cetaceans (see Whitehead 1985, for a comprehensive list). Some of the explanations are: to observe above the water surface, fight with predators or conspecifics, obtain food or communicate with conspecifics. However, it was unlikely that bottlenose whales were breaching or spyhopping to make above water observations as they often breached relatively far (several hundred meters) from the boat, and they do not usually bring their eyes out of the water when they spyhop (pers. obs.). I have often observed bottlenose whales close to the boat (less than five

meters), swimming on their sides at the same speed and direction as the boat, with one eye appearing to be oriented towards the boat. Additionally, Hooker (In prep.) indicated that bottlenose whales in the Gully sometimes make non-foraging echolocation vocalizations which she believes may be used to investigate the research vessel.

Aerial behaviours could also represent a form of aggression. Competitive groups of humpback whales on the breeding grounds often engage in aggressive behaviour which can include sideflukes and lobtails (Tyack and Whitehead 1983, Pack *et al.* 1998). However, there is no evidence to suggest that any of these behaviours represent aggression in bottlenose whales. The only obviously aggressive behaviour by bottlenose whales in the Gully was recorded in 1998 and involved two mature males circling each other and ramming heads below the water surface (Gowans and Rendell In press).

Cetaceans which feed near the surface may use lobtailing or breaching when feeding to stun prey or prevent fish schools from dispersing (Würsig and Würsig 1980, Baird and Dill 1995). However, it is unlikely that bottlenose whales, which feed at great depth, would use aerial behaviours in feeding.

Aerial behaviours may serve as a form of communication or social interaction with conspecifics. When dusky dolphins encounter a large school of prey, many individuals perform percussive aerial behaviours similar to breaches. Würsig and Würsig (1980) suggest that these loud leaps are a form of communication to other dusky dolphins about the presence of a dense patch of food. For these dolphins, it is beneficial to recruit other dolphins to the prey school as large numbers of dolphins are required to cooperatively herd the fish in a tight school, from which the dolphins can efficiently feed (Würsig and Würsig 1980). Similarly, Whitehead (1985) concluded that humpback whale breaching is most likely a form of communication perhaps similar to an exclamation mark, emphasizing other, perhaps vocal, communications in social situations. Sperm whale breaching and lobtailing most often occurs during social interactions when different groups of whales merge or split up (Waters and Whitehead 1990a). Social interactions or communication were the most likely explanation for aerial behaviours, especially percussive behaviours, in cetaceans

generally, as well as for bottlenose whales. However, the support for this hypothesis is mostly circumstantial and requires rigorous testing, which is beyond the realm of the data usually available.

CONCLUSION

'Groups' of bottlenose whales (individuals within five body lengths of each other and showing coordinated behaviour) were more likely to contain interacting individuals than 'sightings' (continuous observation of whales at the surface). While consecutive groups sometimes contained some of the same individuals, and membership within a group sometimes changed during the surface interval, the spatial and behavioural definition of 'group' in this study seems the best way to define a social association at present. Bottlenose whale groups were relatively small (mean 3.04 ± SD 1.86, n = 1,281) and similar in size to some species of coastal dolphins and mesoplodons. Groups rarely contained both mature and sub-adult males unless female/immatures were also present, and larger groups tended to contain individuals of all three age and sex classes. Female/immatures were most often found in groups containing other female/immatures, while mature and sub-adult males were typically found in groups containing female/immatures or all three age/sex classes. Lobtails and spyhops were the most common behaviours visible above the surface, while sideflukes and breaches were rarer and these behaviours most likely represent a form of communication used in social situations.

Chapter 5: Social organization

INTRODUCTION

The social organization of a population is based upon the nature and quality of interactions between individuals (Hinde 1976). In most cetacean species (and many terrestrial species) it is not possible to observe interactions, such as grooming or physical contact and therefore, individuals are assumed to be interacting if they are members of the same group (Whitehead and Dufault 1999). Relationships between pairs of individuals can be described by the characteristics and temporal patterning of their associations. By summarizing the pattern of relationships between individuals, the general social organization can be described (Hinde 1976).

The social organization of female mammals is usually closely related to their ecology, as female fitness is largely determined by their ability to give birth, nurse and wean offspring. The fitness of male mammals is largely determined by their ability to find and inseminate females and the social organization of males is related to the distribution and social organization of females (Wrangham 1987). Therefore, the social organization of individuals of each sex is often different, even within the same species. Patterns of associations also change with age, as reproductively mature individuals often act differently from immature animals.

Deep water foraging by female sperm whales is believed to be an important factor leading to the evolution of sociality in these whales (Best 1979, Whitehead 1996a) . Young sperm whales do not appear to be capable of diving to foraging depths and are vulnerable to predators at the surface (Best 1979). When calves are present, female and immature sperm whales alter their dive schedules, such that at least one adult-size animal is at the surface with the calf. It has been suggested that this communal babysitting (while the mother forages at depth) is responsible for the formation of long-term bonds between female sperm whales (Whitehead 1996a). Male sperm whales show a very different pattern of association from that of females, as sub-adult males disperse from the female units and migrate to temperate waters where they form "bachelor herds". As they mature, the males become more solitary and migrate towards the poles. Socially mature males migrate to the

tropics during the breeding season to mate with females, who remain year round in tropical waters (Best 1979).

The nature and temporal patterning of associations of northern bottlenose whales is examined in this chapter, focussing on age and sex class differences. Models that consider time lags between associations are appropriate for this study as it spans nine years and group membership was not constant even within a single encounter (Chapter 4). Therefore, association patterns were not expected to be static, and pooling all associations over several years potentially masks many important details of this species' social organization. As northern bottlenose whales are also deep diving (Hooker and Baird 1999), it was initially expected that their social organization would resemble the pattern found in sperm whales.

METHODS

ASSOCIATION DEFINITION AND INDEX

Two individuals were considered to be associated if they were photographed within the same group (see Chapter 4 for justification of this definition of association). Most analysis was restricted to high quality photographs ($Q \geq 4$) of reliably marked individuals (see section on preferred companionship for exceptions). To maximize the ability to sample associations, I only included individuals that were known from both left and right side photographs. If I restricted analyses to only left or right identifications, I would have missed counting an association when individual A was photographed by a left fin and individual B by a right fin within the same group, which would bias the association indices downwards (see Table 5.1). If I included all left and right photographs I would have identified associations between the left and right side of the same individual, when each side was assigned a different identification, which would bias the association indices upwards. Relatively few reliably marked individuals were excluded from the analysis by this restriction as the types of marks which were reliable (notches, back indents and mottled patterns; see Chapter 2) tended to permit matching between left and right sides (see Table 5.2).

An overall index of association for all potential diads was created using the simple ratio method (using notation from Cairns and Schwager 1987) which estimates the proportion of time individuals A and B were in the same group.

$$\frac{x}{x + y_{AB} + y_A + y_B}$$

where x = number of days in which both animals were identified in the same group

y_{AB} = number of days in which both animal A and B were identified, but were not grouped

y_A = number of days in which only animal A was identified

y_B = number of samples in which only animal B was identified

For all analyses except preferred companionship, the sampling period was set at one day to avoid replicate associations within the same day, which would not be independent. The simple ratio index was chosen as it is the least biased of the standard association indices (Ginsberg and Young 1992). In each group not all individuals were photographed, nor were all individuals were identifiable (Chapter 2). Therefore there were occasions when pairs of individuals were associated but the associations were not detected by my sampling technique. Thus the association indices were biased downwards. All association indices were calculated and analyzed using SOCPROG 1.2 (H. Whitehead, programs available: http://is.dal.ca/~whitelab/index.htm). While hierarchical cluster displays, sociograms and principal components analysis are often used to describe social organization (Whitehead and Dufault 1999), they were not appropriate for bottlenose whales as they do not consider time lags between associations, and thus may mask many of the important details of social organization in bottlenose whales.

Table 5.1: Associations between individuals # 1 and #3 when identifications from only left fins, right fins or both left and right fins were considered.

	# groups associated	# days associated	Simple ratio association index
Left fins only	4	4	0.31
Right fins only	4	3	0.23
Both left and right fins	10[1]	7	0.44

1) This value was greater than 4+4 as there were 2 groups in which one individual was identified only by the left fin, and the other only by the right fin. Using only left or right fins would not have detected these associations.

Table 5.2: Reliably marked and sexed individuals.

	Number of reliably marked individuals		
	Identified by left fin only	Identified by right fin only	Identified by both left and right fin
All individuals	47	45	113
Female/immature	9	7	31
Sub-adult male	0	3	15
Mature male	1	1	18

GENERAL PATTERN OF ASSOCIATIONS

To determine if there were differences in the patterns of association between and within age and sex classes, a Mantel test was used to test the null hypothesis that association rates (*i.e.*, probability of being in the same group) between and within classes were similar (*e.g.*, Schnell *et al.* 1985). For each age and sex class the mean association index (and standard deviation) was calculated. The 'best buddy' of each individual (the associate which shared the highest association rate) was identified and the association indices between 'best buddies' within the age and sex classes were averaged and standard deviations calculated. 'Best buddy' association indices were termed maximum associates. Individuals included in this analysis were reliably marked, had left and right side identifications, and were sexed either by melon photograph or biopsy sample (see Chapter 3 for details), although one male which was only sexed by biopsy was excluded as he could not be assigned to an age class.

PREFERED COMPANIONSHIP

To determine if the patterns of associations between individuals were different from random, 1:0 association matrices were calculated for each 5 day period, such that diads were assigned a value of 1 if they were photographed within the same group and 0 if they were not. The association matrix was then permuted following the procedure described by Bejder *et al.* (1998), in which pairs of rows and columns were randomly chosen from the association matrix. The 1:0 association values were then inverted between rows. This preserved the row and column totals (keeping constant the number of identified individuals in each group, and the number of groups in which each individual was observed). As successive association matrices were not independent, the number of permutations required to obtain an accurate *P*-value testing whether the real data differentiated from random, was determined by conducting increasingly larger numbers of permutations until the p-value stabilized (Bejder *et al.* 1998).

To increase the sample size of associated pairs which could be permuted, all quality photographs were included in the permutations. If photographs of two different individuals were incorrectly matched due to poor quality photographs, then individuals which were not truly associated could be considered associates. This would bias the tests towards lower indices of associations, and the results of the permutation tests would be less likely to be significant, than if only high quality photographs were considered. However, if few individuals were incorrectly matched, then the increased sample size would result in a more powerful test. To test whether the inclusion of low quality photographs was biasing the results, the permutation tests were conducted on all quality photographs and on photographs of $Q \geq 4$ only. All permutations were first conducted on all reliably marked individuals with left and right side identifications, and then on each age and sex class separately.

Short term companionship

As individuals do move in and out of the Gully over the summer field season (see Chapter 7), associations may appear significantly different from random simply due to this effect (*i.e.*,

individuals associate randomly with all animals present in the Gully, and do not associate with those who were not present). By constraining the permutations of the association matrix to short time intervals, these effects can be removed (see Whitehead In press). The sampling period was set at five days, as single day sampling periods were too brief to contain many associations. As bottlenose whales spend on average 10 days in the Gully (SE = 5; see chapter 7), individuals were unlikely to have moved in or out of the Gully during the five day sampling period.

By randomly permuting the group to which individuals were assigned (while keeping the number of groups in which animals were observed constant) within the five day sample period, I could test the null hypothesis that there were no preferred companions within the five day period. Preferred associations within five-day periods will reduce the number of pairs of associated individuals, and so decrease the mean group size. Therefore, if the mean association index for the observed data was significantly lower than the randomly permuted data, then the null hypothesis was rejected at $p<0.05$ (Whitehead 1999). These permutations were first conducted on all reliably marked individuals with left and right side identifications, and then on each age and sex class separately.

Long term companionship

To test for long term companionship, the associations of each individual within a sampling period were permuted, while keeping the number of associations of each individual the same. If some pairs of animals were associated in different sampling periods more often than by chance, this would increase the standard deviations of the association indices. Thus, if the standard deviation of the observed association indices was significantly higher than that of the randomly permuted data, then the null hypothesis (preferential companionship between sampling periods) was rejected (Whitehead 1999).

TEMPORAL PATTERN

Standardized lagged and null association rates were calculated for associations between all

reliably marked individuals with left and right fin identifications (Whitehead 1995). Lagged association rates estimate the probability that two animals sighted together at a given time will still be associated at some time lag later. The null association rate indicated random association. Lagged and null association rates were standardized (by dividing the rate by the number of recorded associates on each occasion) as not all individuals in the group were identified. Jackknife techniques, in which data from each date were sequentially omitted from the dataset and the analysis rerun, were used to determine the precision of the estimated lagged association rates (Sokal and Rohlf 1995).

I then fitted models describing temporal patterns of association to the full dataset using maximum likelihood and binomial loss techniques to determine which model fit best. Jackknife techniques were used to calculate the standard error of the model terms, and gave a conservative estimate of the precision of the terms (Sokal and Rohlf 1995). The models included the following types as described by Whitehead (1995):

constant companions: stable associations over time, changed only by birth or death
rapid disassociation: very short term associations (much less than one day)
casual acquaintances: longer term associations which dissociate over time (greater than several days)

I also included models with a combination of different levels of association (models tested: constant companions; casual acquaintances; rapid disassociation and constant companions; rapid disassociation and casual acquaintances; constant companions and casual acquaintances; rapid disassociation, constant companions and casual acquaintances). I then plotted the standardized lagged and null association rates and best fit models (using maximum likelihood to fit models) for each age and sex class separately.

CASE STUDIES OF SAMPLE INDIVIDUALS

I selected one individual of each age and sex class which was photographed many times over several years and identified all of its associates that had been sexed to illustrate how

individuals fit with the general pattern described by the quantitative analysis. To increase the chance of showing a true association, I considered individuals to be associated if they were photographed in the same group based on all quality photographs

RESULTS

GENERAL PATTERN OF ASSOCIATION

Association patterns between and within classes were not similar (Mantel test t=2.12; P=0.983): associations within the age and sex classes were higher than the associations between classes. Given this difference, I excluded associations between the different classes in the remaining analyses, focussing on the association patterns of the population as a whole, and within each age and sex class.

The mean association index for each age and sex class indicated that both sub-adult and mature males had significantly higher association indices with other males, and had significantly higher association indices than females (Table 5.3). Maximum association indices (highest association index of all pairs) were variable (Table 5.4), indicating that some individuals had high association indices with their 'best buddy', while others had much lower indices. The high values for mature males associated with other mature males, indicated that the 'best buddy' of a mature male was most often another mature male. Similarly sub-adult males were 'best buddies' with other sub-adult males, while female/immature did not show an age or sex class preference for their 'best buddy' (see Case studies section below for examples of how individuals interact with each other).

Table 5.3: Mean association index (SD) of the different age/sex classes.

	FEMALE/IMMATURE	SUB-ADULT MALE	MATURE MALE
Female/immature	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)
Sub-adult male	0.01 (0.01)	0.04 (0.05)	0.02 (0.02)
Mature male	0.01 (0.01)	0.02 (0.02)	0.02 (0.02)

Table 5.4: Maximum association index (SD) of the different age/sex classes.

	FEMALE/IMMATURE	SUB-ADULT MALE	MATURE MALE
Female/immature	0.14 (0.08)	0.06(0.07)	0.10 (0.10)
Sub-adult male	0.11 (0.08)	0.23 (0.27)	0.13 (0.14)
Mature male	0.14 (0.10)	0.12 (0.13)	0.19 (0.17)

PREFERED COMPANIONSHIP

When photographs were restricted to Q≥4, few of the results of the permutation tests were significant (see Appendix 2). However the tests were often significant when all quality photographs were included (see below). The inclusion of potentially mis-matched individuals (due to low quality photographs) should bias the results towards lower significance in the permutation tests. As many of the tests were significant only when all quality photographs were included, few mis-matched individuals were likely included. It seemed that the increased probability of identifying individuals using poor quality photographs outweighed the problems of misidentification for this analysis.

The mean association index for the observed data were significantly lower than that of the randomly permuted data (permuting the group to which individuals were assigned) in all cases except female/immature associations with other female/immatures (Table 5.5). Thus, females /immatures do not form preferential companionships with other female/immatures over short time periods (five days). However individual mature or sub-adult males, do preferentially associate with other mature or sub-adult males, respectively. Similarly, the standard deviation of the mean association index of the observed data were significantly higher than that of the randomly permuted data (randomly permuting the associations of each individuals) for all cases except female/immatures (Table 5.6). Therefore there was long term preferential companionship among mature and sub-adult males. I did not expect to find long-term preferential companionship among female/immatures as they did not show evidence of short term preferential companionships.

Table 5.5: Mean association indices for observed and randomly permuted data constrained within five day samples. Individuals considered were reliably marked, had both left and right fin identifications, and photographs of all qualities. Lower mean association indices for the observed data indicates preferred companionship. ** significant at $P<0.05$.

Dataset	Number of permutations	Mean association index		P-value
		Observed data	Random data	
All individuals (n=113)	10,000	0.0139	0.0152	0.0002**
Female-female associations (n=31)	160,000	0.0180	0.0191	0.0748
Sub-adult male – sub-adult male associations (n=15)	10,000	0.0575	0.0684	0.0078**
Mature male – mature male associations (n=18)	20,000	0.0269	0.0329	0.0001**

Table 5.6: Standard deviation of mean association indices for observed and randomly permuted data, constrained within five day samples. Individuals considered were reliably marked, had both left and right fin identifications, and photographs of all qualities. Higher SD of the mean association indices for the observed data indicates preferred companionship. ** significant at $P<0.05$.

Dataset	Number of permutations	SD of mean association index		P-value
		Observed data	Random data	
All individuals (n=113)	20,000	0.0524	0.0508	0.9853**
Female-female associations (n=31)	20,000	0.0441	0.0446	0.2134
Sub-adult male – sub-adult male associations (n=15)	10,000	0.1341	0.1308	0.9785**
Mature male – mature male associations (n=18)	10,000	0.0718	0.0648	0.9903**

TEMPORAL PATTERN

The standardized lagged association rate was higher than the null (or random) association rate for all individuals for time lags less than approximately 1100 days (roughly three years; see Figure 5.1). Therefore, associations were not random for time periods less than three years in length. Lagged association rates were highest for short time lags, and decreased after approximately 100 days (roughly one field season), indicating that many associations between individuals did not last more than one field season. The model which best described the pattern of associations was:

$g(d) = Ae^{-B*d}$

where g(d) = lagged association rate at lag (d)

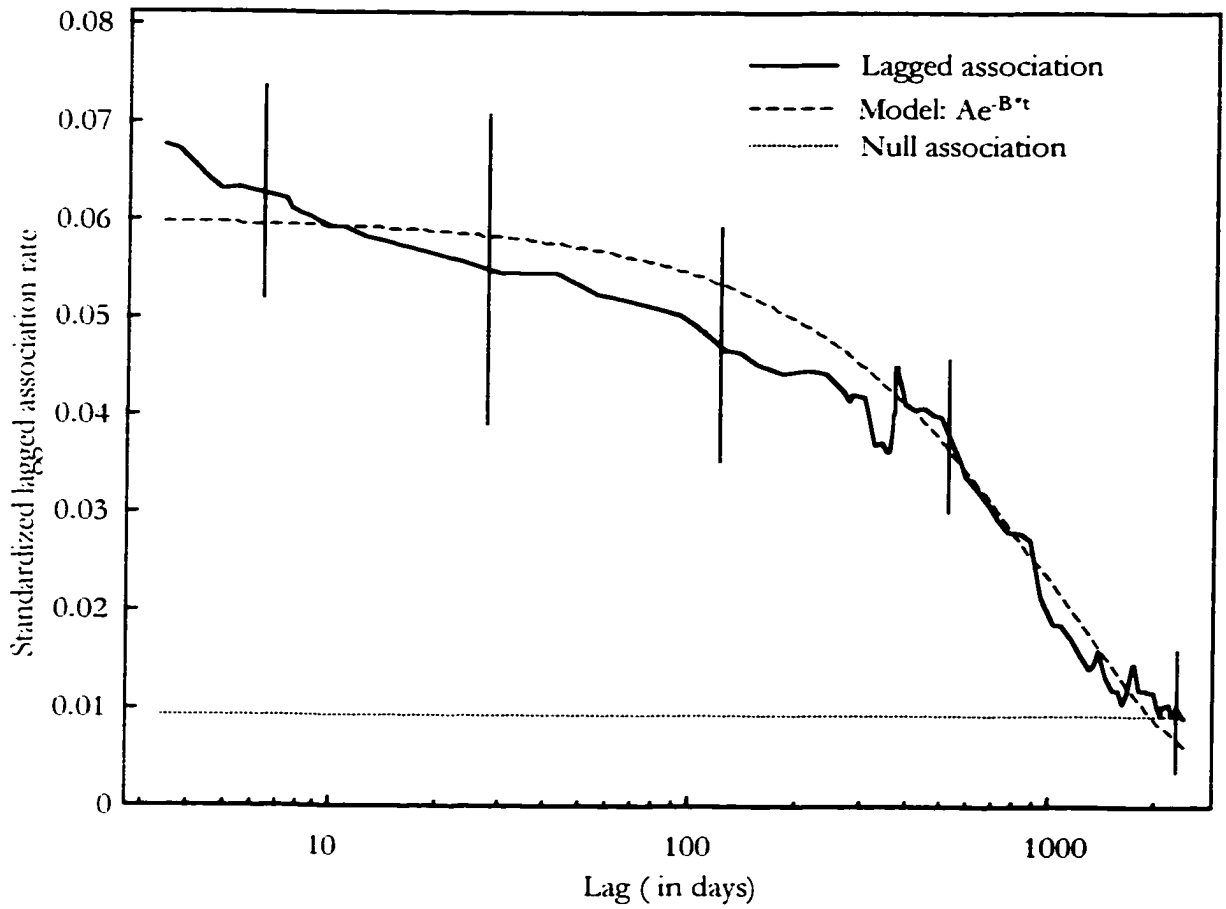
A=0.059862 (*SE* 0.0109)

B= 0.000949 (*SE* 0.000257)

d= time lag.

This model represents casual acquaintances. The error bars were quite large, indicated a lack of precision in estimating the pattern. However, the model fit the observed pattern well and remained within all of the error bars. There was a gradual decline in the lagged association rate from time zero to approximately 100 days, the end of a field season. After approximately 350 days there was a steeper decline in association rates until the association rates were roughly random after lags of about three years. No data were collected over lags from 100 days to lags of slightly less than one year, when field work was not conducted. There were also relatively few data collected over one year lags, as many individuals were not sighted in successive years.

Figure 5.1 Standardized lagged association rates of all reliably marked individuals (with jackknifed estimates of precision) showing fitted model and null associations.



By age and sex class

There were insufficient data to accurately estimate standardized lagged association rates for sub-adult males. However, the best fit model for both female/immatures and mature males was the same model which fit the full dataset (Ae^{-B*t}; see Figure 5.2), although small sample sizes may have prevented differentiation of each age/sex class. The model terms were:

Female/immature males:

A= 0.15038 (*SE* 0.09157)

B= 0.00213 (SE 0.01216)

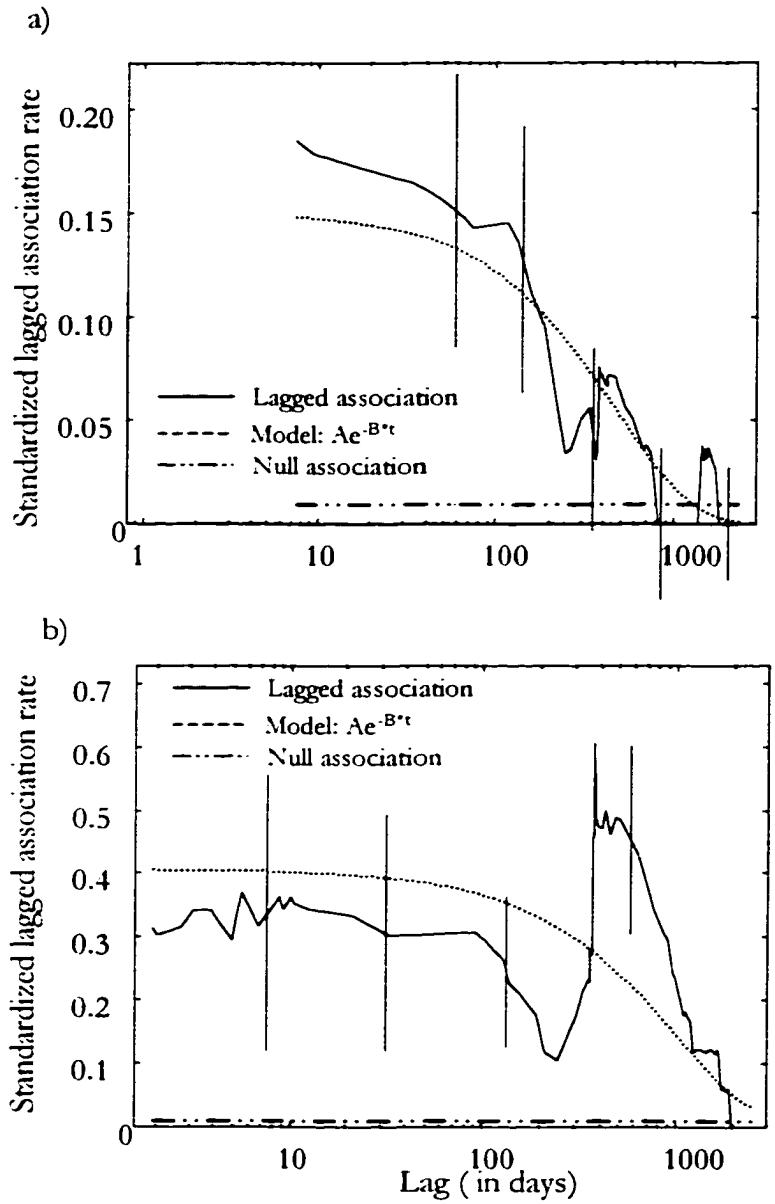
Mature males:

A=0.40501 (SE 0.15568)

B = 0.00103 (SE 0.00030).

For female/immature males and mature males, the associations dropped below random for lags longer than 1000 days; however, the precision of the estimates was much lower for the separate age and sex classes, due to the smaller sample sizes. The peak in associations between mature males at approximately two years (700 days) was likely due to sampling effort, as associations were repeatedly sampled at lags of approximately yearly intervals, due to nature of field work. Therefore, this peak likely does not represent a real elevation in the associations between mature males, but instead a peak in resampling associations. After lags of approximately 100 days, the lagged association rate of both female/immatures and mature males declined steeply, indicating many disassociations over the winter.

Figure 5.2: Standardized lagged association rates (with jackknifed estimates of precision) for a) female/immatures and b) mature males, showing fitted models and null association rates.



CASE STUDIES

The three individuals selected for the case studied typified the patterns of association for each age and sex class, although there were some variations. Much of the variability in association pattern may be due to individual differences, although incomplete identification of all group members, and an inability to simultaneously sample more than one group, will inflate the variability.

Individual #1 was a mature male that was often observed between 1989 and 1997 (see Table 5.7). He was repeatedly associated with many different individuals, and repeatedly associated with the same individual over a few days but rarely over more than one year. He appeared to form a preferential companionship with #3, another mature male, in 1989, 1990, and 1994, although the two individuals were not always seen in the same group in 1989. In 1996 and 1997, these two individual were not sighted together, although both animals were observed in 1997. In 1998, #1 and #3 were observed in the same group, aggressively head-butting each other (see Gowans and Rendell In press). Examination of the association indices indicated that individuals #1 and #3 were maximum associates ('best buddies') of each other (simple ratio association index = 0.44).

Individual #13 was a sub-adult male when he was photographed in 1988-1990. He was most often associated with other sub-adult males (see Table 5.8), and was repeatedly associated with #32, another sub-adult male in July 1989, July 1990 and August 1990. Neither #13 nor #32 have been sighted since 1990, so it is not known how long this association lasted. There were two 'best buddies' of #13; individuals #32 and #59 (simple ratio association index 0.43)

Individual #45 associated with many different individuals (see Table 5.9) from every age and sex class, as would be expected for a female bottlenose whale. She did not appear to preferentially associate with any class of individuals, although she did repeatedly associate with #1 and #3 (both mature males) in 1990. She also repeatedly associated with #56 and #961 (both female/immatures) in 1997, although all of these repeat associations were over short time scales. The 'best buddy' of #45 was a mature male (#3 – simple ratio association index 0.17).

Table 5.7 All sexed associates of individual #1, a mature male, from 1989-1997 (* indicates identifications based on photographs of Q<4). Other sexed individuals may have been present but not photographed and most groups also included unsexed associates. Blank columns indicate a day in which #1 was observed with no identified sexed associates.

Year	89							90				94	96			97
Month	7			8				7			8	8	7	8		8
Date	23	24	25	3	10	11	13*	27	28	29	5	13	29	1	4	24
ID																
Mature male associates																
3	◆	◆	◆*	◆				◆	◆	◆	◆	◆				
15					◆*											
37						◆		◆								
71														◆*		
120					◆											
225													◆*	◆		
290										◆						
407								◆	◆							
508												◆				
824															◆	
Sub-adult male associates																
13		◆							◆	◆						
21		◆														
28		◆		◆	◆											
32		◆		◆					◆	◆						
51				◆					◆	◆						
59									◆	◆						
102											◆					
152									◆							
406								◆	◆	◆						
Female/immatures associates																
45				◆					◆	◆	◆	◆				
47				◆												
54				◆												
76							◆		◆							
61							◆									
89						◆										
322												◆				
390												◆				
409									◆			◆				
418									◆							
440										◆						
531												◆				
633												◆				

Table 5.8: All sexed associates of individuals #13, a sub-adult male, from 1988-1990 (* indicates identifications based on photographs of Q<4). Other sexed individuals may have been present but not photographed and most groups also included unsexed associates. Blank columns indicate a day in which #13 was observed with no identified sexed associates.

Year	88	89		90			90	
Month	7	7	8	7			8	
Date	28*	24	4	27	28	29	8*	9*
ID								
Mature male associates								
1		◆			◆	◆		
3					◆	◆		
37				◆		◆		
290						◆		
101							◆	
Sub-adult male associates								
21		◆*						
102	◆*			◆				
28		◆						
32		◆		◆*	◆	◆		◆
59				◆*	◆	◆		◆
51					◆	◆	◆*	◆*
406					◆			
152					◆			
Female/immature associates								
76					◆			
399				◆*				
409				◆*	◆			
418					◆			
440								◆

Table 5.9: All sexed associates of individuals #45, a female, from 1989-1997 (* indicates identifications based on photographs of Q<4). Other sexed individuals may have been present but not photographed and most groups also included unsexed associates.

Year	89		90				93		94		95	96	97					
Month	8		7			8	7		8		8	6	8					
Date	3	10	6	28	29	5	15	20	12	13	29	22	4	12	14	16	18	25
ID																		
Mature male associates																		
1	◆			◆	◆	◆				◆								
3	◆			◆	◆	◆												
71																	◆	
290					◆													
480															◆	◆*		
508									◆	◆								
824																	◆	
1039																◆		◆
1292																	◆	
Sub-adult male associates																		
28	◆	◆															◆	
32	◆																	
51	◆																	
102						◆												
120												◆						
124															◆			
152				◆*														
406					◆													
Female/immature associates																		
47	◆		◆*															
54	◆												◆*					
56															◆	◆		◆
251										◆								
390										◆								
409							◆			◆								
418				◆														
440					◆													
531									◆	◆								
633							◆			◆	◆							
653									◆	◆								
712								◆*										
804																		◆
961													◆*	◆	◆			
1239													◆					

DISCUSSION

The initial expectation of this study was that the social organization of bottlenose whales would resemble that of sperm whales, given the similarities in their ecology. Both sperm and bottlenose whales are deep divers which live offshore and eat squid (Benjaminsen and Christensen 1979, Papastavrou *et al.* 1989, Hooker and Baird 1999). However, the observed patterns of associations of bottlenose whales were very different from the associations found in sperm whales. Female sperm whales form strong bonds with other members of their unit, most of whom are kin, although there are some changes in unit membership over time (Christal 1998, Christal *et al.* 1998). Mature male sperm whales are usually solitary, especially on the breeding grounds (Whitehead *et al.* 1992, Whitehead 1993), although aggregations of mature males sometimes form (Childerhouse *et al.* 1995, Christal 1998). Relatively few mature male sperm whales have been observed on multiple occasions in association with other mature males, although two pairs of males have been observed together over periods of days, and there have been repeat associations involving one pair of mature males over several years. Despite these associations, mature male sperm whales are much less social than females (Christal 1998).

The social organization of northern bottlenose whales appeared to be very different from that of sperm whales. Bottlenose whales live in a fission-fusion society in which group membership frequently changes, although some individuals form long term (1-2 year) bonds (Figure 5.1). Female and immature bottlenose whales formed weaker bonds than sub-adult and mature males (Table 5.3 and 5.4). Unlike males, females and immature animals did not preferentially associate with members of their own age and sex class, nor did their associations with other individuals differ significantly from random (Table 5.5 and 5.6). Mature and sub-adult males preferentially associated with members of their own class and individuals formed preferential associations with other males, some of which lasted for periods of years (Table 5.5 and 5.6 and Figure 5.2).

This pattern of associations is similar to that found in bottlenose dolphins[1] off Florida and Australia. In both of these locations, females form loose networks of associations, associating with many different individuals, and most do not preferentially associate with any particular individual. However, some females form weak bonds with other females while most of the mature male bottlenose dolphins in these populations form long term bonds with one or two other mature males, that have lasted up to 20 years. Stable relationships between males likely form in order to cooperatively monopolize a female during the breeding season. However, the consortships rarely last for the entire breeding season, and individual females may consort with many different males in a single season; therefore, the mating system is likely promiscuous (Wells 1991b, Smolker *et al.* 1992, Connor *et al.* 1996, 1999).

Off Monkey Mia, Australia, there are two orders of alliances among male bottlenose dolphins, which appear to form to increase the chances that a group of males will successfully sequester a female. Stable associations of pairs and triplets of males form the first-order and individuals within these alliances cooperate to aggressively herd females. Occasionally, two groups of these stable alliances cooperate together (second-order alliance) to steal a female away from a third alliance (Connor *et al.* 1992). Recently, a third form of alliance has been described for male bottlenose dolphins in Monkey Mia. Some males do not form stable associations with other males, but instead a large number (14) of males loosely associate with each other, and individuals routinely change associates among the 14 animals. This large 'superalliance' functions as a second-order alliance, in which many males cooperate together during conflicts with males of stable first-order alliances (Connor *et al.* 1999). Bottlenose dolphins in Moray Firth, Scotland are an interesting comparison, as no male alliances have been found (Wilson 1995). Coastal bottlenose dolphins in the Southern California Bight show more fluid association patterns than Monkey Mia, Sarasota or Moray Firth study areas, with individuals associating with a large number of different associates and few long term associations were identified. Unfortunately the sex of the few individuals in

---

[1] It has been suggested that bottlenose dolphins are not monophyletic. The Monkey Mia population may actually belong within the genus *Stenella*, and there may be other taxonomic differences between other populations (see Rice 1998). However following Rice (1998), I classify all of the populations discussed in this chapter, and throughout the thesis, as *Tursiops truncatus*.

long term associations was not known and therefore, it is difficult to assess if these were male alliances (Weller 1991).

Chimpanzees also live in a fission-fusion society similar to bottlenose dolphins. Strongly bonded philopatric males form the core of stable groups while females have looser relationships. Males often form alliances with each other to gain access to valuable resources or to increase their dominance status (Nishida and Hosaka 1996). Recently, male alliances have been observed cooperating to sequester estrus females and prevent other males from mating with them, but permitted the mating behaviour of alliance partners (Watts 1998).

While male bottlenose whales do form stable associations which last for years, similar to bottlenose dolphins and chimpanzees, they have not been observed cooperating together to gain access to females, or any other resource. The only aggressive interaction observed between bottlenose whales occurred in 1998 when two mature males (#1 and #3) were observed repeatedly head-butting each other. These two males had been previously associated with each other (in 1989, 1990, 1994; see Table 5.7) and then were observed separately in 1996 and 1997 (Gowans and Rendell In press). Interactions between individual bottlenose whales are difficult to record as only very rarely can the directionality of interactions (who does what to whom) be observed. Therefore, it is possible that male bottlenose whales form stable bonds to cooperate to increase mating opportunities, although the function of these potential alliances is not clear.

Similarities between the social organization of bottlenose whales and bottlenose dolphins may be related to the benthic ecology of the Gully and to the long term residency of individual bottlenose whales (see Chapter 8 for more details). Northern bottlenose whales appear to be primarily benthic foragers (Hooker In prep.) and there may be a benthic influx of nutrients into the Gully which may lead to a relatively constant and reliable food resource (Gardner 1989, Harding 1998). Bottlenose dolphins in Monkey Mia and Sarasota do not migrate and also appear to have constant and reliable food resources (Wells 1991b, Smolker *et al.* 1992), while bottlenose dolphins off the Southern California Bight depend on more

variable and labile food resources, and have a different pattern of association (Weller 1991, Defran and Weller 1999, Defran *et al.* 1999).

CONCLUSION

Bottlenose whales live in fission-fusion groups, with most associations quickly dissociating. Female and immature bottlenose whales form a loose network of associations, with no preferential association between individuals, or with a specific age or sex class. Sub-adult and mature male bottlenose whales form preferential associations with other members of their same age class, and these associations can last for periods of years. The function of these stable associations is unclear, although they may be related to access to females. as in bottlenose dolphins. The social organization of bottlenose whales is similar to that of some populations of bottlenose dolphins (off Monkey Mia Australia and Sarasota Florida), and very different to the pattern of associations in sperm whales.

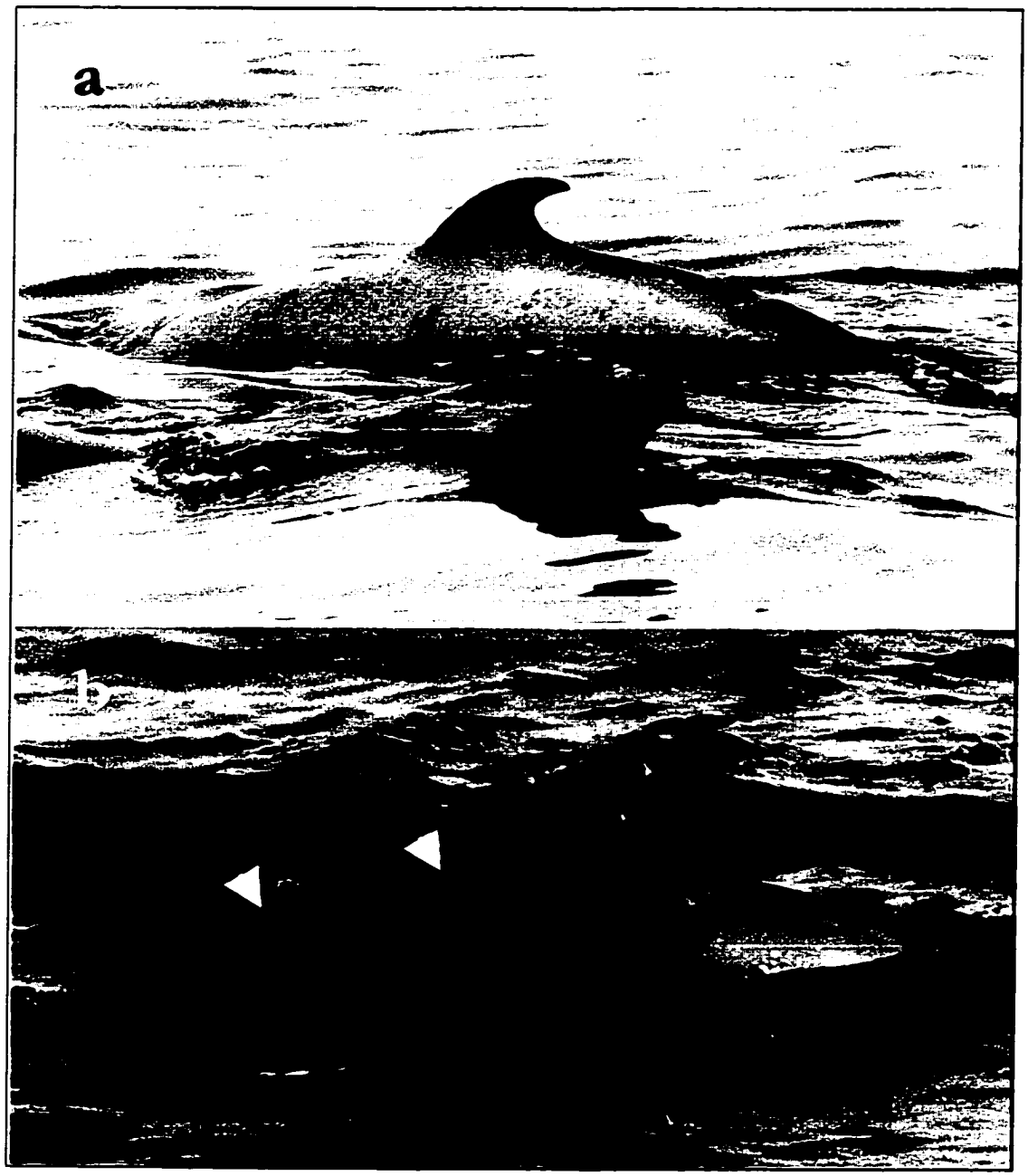
Chapter 6: Bottlenose whale calves and juveniles

INTRODUCTION

Very little is known about the behaviour of northern bottlenose whale calves and juveniles. Seasonal differences in the length of fetuses, from whaling records off Labrador, indicate that most calves were born off Labrador in April through June (Benjaminsen 1972), although some calves were likely born outside of this period. No studies have investigated the length of lactation in this species, although it is likely similar to that of other large odontocetes (sperm whale – at least two years; Best 1968; killer whale – one to two years; Haenel 1986). Nor are there any data on the length of time young animals remain associated with their mothers.

Very young cetacean calves have morphological features such as fetal folds (transverse bands of light coloured skin) and bent-over dorsal fins which are related to the folded position of the calf while in utero (see Figure 6.1; Tavolga and Essapian 1957, Kastelein *et al.* 1990). The presence of fetal folds in young animals has been used to identify the peak calving season in a number of different species (*e.g.*, Jefferson 1989, Fernandez and Hohn 1998) although few studies have been conducted on the longevity of fetal folds or bent-over dorsal fins. The dorsal fins of killer whale calves appear to straighten within hours of birth (R.W. Baird, Pacific Whale Foundation, pers. comm.; D. Odell, SeaWorld Inc., pers. comm.; J. McBain, SeaWorld Inc., pers. comm.). Observations of bottlenose dolphin births in captivity also indicate that the dorsal fins straighten within several hours of birth, while fetal folds last for approximately six weeks (Tavolga and Essapian 1957, Kastelein *et al.* 1990). The dorsal fins of a few bottlenose dolphins calves never straightened, and it is believed that these represent congenital deformities (J. McBain, SeaWorld Inc., pers. comm.). Observations of other wild cetacean calves indicate fetal folds are short lived. In southern right whales they lasted less than two weeks (S. Burnell, Australian Marine Mammal Research Centre, Sydney University, pers. comm.), while in Sowerby's beaked whales (*Mesoplodon bidens*) they likely lasted less than four months (J. Nichols, Woods Hole Oceanographic Institute, pers. comm.). However one year old bottlenose dolphins in the Moray Firth of Scotland still possessed fetal folds (Wilson 1995). Given the extremely short duration of bent-over dorsal fins and the relatively short duration of fetal folds,

Figure 6.1: Photographs of calves showing a) bent-over dorsal fin and b) fetal folds.



observations of individuals with these features may be useful in determining calving seasonality of northern bottlenose whales in the Gully.

In some cetacean species, calves and their mothers are preferentially found in larger groups. Transient killer whale groups with calves tend to be larger than groups without calves and larger than optimal group size for foraging. Baird and Dill (1996) suggest that these large groups function to protect transient killer whale calves from attacks by resident killer whales.

Association patterns between cetacean mothers and offspring range from almost constant physical contact in southern right whales (Taber and Thomas 1982), to serial accompaniment of sperm whale calves by different members of their social group (Whitehead 1996a), to frequent separations between mother and calf bottlenose dolphins in which the calf may or may not associate with other animals (Mann and Smuts 1998). In the deep diving sperm whale, other group members babysit calves while the mother forages at depth. This prevents the calf, that presumably cannot dive as deep or as long as its mother, from being left alone at the surface vulnerable to predators. Adults in social groups with calves alter their diving schedule, such that at least one adult usually remains at the surface and associates with the calf (Whitehead 1996a). Communal care of calves may be the driving force of sperm whale sociality (Best 1979, Whitehead 1996a).

Mother-offspring bonds in most odontocete species last for periods of years. Pilot and killer whales show the longest bonds as neither males nor females disperse even after sexual maturity (Bigg *et al.* 1990, Amos *et al.* 1991). In sperm whales, male offspring begin to disperse from their natal group at age six, while females may reside with their mothers for many years or even their entire life (Richard *et al.* 1996, Christal 1998). In bottlenose dolphins mothers may remain associated with their offspring for long time periods although close association patterns only last until about age four (Wells 1991b). Therefore it is reasonable to assume that bonds between bottlenose whale mothers and their offspring should last for several years.

Several different possible patterns of associations between adults and young bottlenose whales can be examined. These patterns are not necessarily mutually exclusive, nor do all individuals within the population necessarily have to behave in a similar manner.

1. Calves are able to dive to their mothers' foraging depths and remain associated with their mother throughout dives and surface intervals. If this occurs, calves should not be observed at the surface alone and should always be associated with their mothers. This situation has been observed in bottlenose dolphins off Monkey Mia, Australia during the first week of life, when mothers remain constantly associated with their calves, and the calves forage with their mothers (Mann and Smuts 1998). Foraging dives in this study are much shallower than in bottlenose whales (~15 m; Smolker *et al.* 1992).

2. Calves are left at the surface while their mothers forage at depth. If this occurs, calves should be observed alone at the surface frequently, and their most frequent associate should be their mother. Calves of bowhead whales are left alone at the surface for more than ten minutes while mothers dive to feed below the water surface (Würsig *et al.* 1986).

3. Mothers may not dive as deep (or for as long) while they have a dependent calf. In this situation, calves would be observed alone at the surface for relatively short periods of time, but remain most closely associated with their mothers. Lactating spotted dolphins tended to feed on surface dwelling fish, rather than on mid-water squid, upon which most non-lactating animals feed (Bernard and Hohn 1989). If bottlenose whale mothers change their diving behaviour during lactation, there may be greater variability in the diet of females than males, and calves and their mothers should rarely be separated.
4. Mothers continue to dive at depth throughout lactation, and leave their calves at the surface with other members of a tightly bonded group, as observed in sperm whales (Whitehead 1996a). For this situation to arise, females with young should form tight bonds with other animals, and the calves associate with other members of their tightly

bonded group while their mothers are absent. Calves should not be left on their own and should repeatedly associate with a small number of different individuals.

5. Calves are left at the surface, associated with other adults who are not part of a tightly bonded group. Calves would rarely be left alone at the surface and would associate with a large number of different individuals.

The initial expectation of this study was that northern bottlenose whales would provide communal care for calves within a tightly bonded group, while mothers forage at depth, similar to sperm whales, the only well studied, deep-diving cetacean (Whitehead 1996a).

Alloparental care (care of young animals by non-parents) can benefit the young animal (*e.g.*, protection from predators while the mother was absent), the mother (*e.g.*, increased foraging efficiency) or the alloparent (*e.g.*, gaining parenting experience). Additionally alloparental care may be costly to the young, mother or alloparent and it is important to investigate both the costs and benefits of alloparental care to determine its function (Hrdy 1976). Alloparents in bottlenose dolphins were most often young females, who had not yet given birth. As mothers did not increase foraging when their infants were being alloparented, the main benefit of alloparental care was to the alloparent who gained experience in parenting (Mann and Smuts 1998). In contrast, alloparental behaviour in sperm whales appears to benefit the calf, who otherwise would be left alone at the surface, vulnerable to predators, and the mother who is able to forage at depth. As adult sperm whales altered their dive schedule when calves were present, they appear to be actively participating in the alloparenting, although the alteration in dive schedule may have minimal costs. Alloparents were adult females and sub-adults of both sexes (Whitehead 1996a).

This chapter explores the seasonality of observations of calves and juveniles in the Gully, and investigates the pattern of association between calves or juveniles and their accompanying adults.

METHODS

DEFINITIONS

Calf: young of the year, characterized by fetal folds and or bent-over dorsal fin; calves with bent-over dorsal likely younger than calves with only fetal folds (see Figure 6.1).

Juvenile: young individuals; less than two-thirds adult size; likely older than one year and less than five years.

Young animals: individuals identified as either calves or juveniles.

Immature: approximately adult sized individuals; have female/immature male melon shape; known to be immature male if genetically sexed as male while having female/immature melon shape, or if initially sexed by melons as female/immature then later sexed by melon as sub-adult male (see Chapter 3 for details on melon sexing).

Associate: individual photographed in the same group as an identified young animal (same definition as in Chapter 5)[1].

SEASONALITY OF SIGHTINGS OF YOUNG ANIMALS

Previous to 1994, field records did not indicate whether young animals were calves or juveniles. Therefore I used data from 1994-1997 to investigate the seasonality of calf sightings, to try to determine the calving period. Calves with bent-over dorsal fins are likely only several days old, as they straightened within hours in bottlenose dolphins and killer whales (Tavolga and Essapian 1957, Kastelein *et al.* 1990; R.W. Baird, Pacific Whale Foundation, pers. comm.; D. Odell, SeaWorld Inc., pers. comm.; J., McBain, SeaWorld Inc., pers. comm.); therefore the date of the sighting was used as an approximate birth date. To determine if there were any significant differences in yearly or monthly rates of calf sightings, I counted the number of occurrences of groups with calves and used a log linear model to test for interactions between year and month. Similarly, a log linear model was used to test for seasonality in the sighting rate of young animals in 1990, 1996 and 1997 (all years with three months field work).

---

[1] Analysis was restricted to individuals who have been identified by a left-fin photograph to avoid counting an individual twice (once from each side). All quality photographs were included to identify as many associates as possible.

SIZE OF GROUPS CONTAINING YOUNG ANIMALS

To determine whether calves and juveniles are found preferentially in larger groups, I calculated the total number of young animals found in each group size (from field estimates of group size) as well as the total number of animals which were found in each group size (number of groups of each size multiplied by the group size). I then calculated the proportion of animals in each group size that were young animals. A Spearman rank correlation was used to test for a significant trend in the proportion with increasing group size.

COMPOSITION OF GROUPS CONTAINING YOUNG ANIMALS

I analyzed the age and sex composition of associates of young animals following the methodology in Chapter 4. Analysis of groups with young animals was restricted to groups in which all members were likely identified, and at least half of the identified individuals had been sexed.

INDIVIDUALS ASSOCIATED WITH CALVES AND JUVENILES

The photo-identification history of calves and juveniles can be used to investigate the possibility of babysitting[2] in this species and the general pattern of adult-young interactions. Not all young animals possessed marks suitable for photo-identification, and photographs were not taken of every young animal in the field, as some groups with young animals appeared to avoid the boat and were not pursued. I therefore examined the sighting history of all young animals identified, and selected all calves or juveniles which were observed in more than one group throughout the study. Photo-identification records from July and August 1998 (which were analyzed by J. Arch, Dalhousie University) were also examined for re-sightings of young animals observed in 1988-1997. I tested three hypotheses which, if true, would help me to identify mothers for each young animal.

Hypothesis 1: Young animals associate with their mothers whenever the young animals are at the surface. If babysitting does not occur, then the mother should always be

---

[2] Babysitting in this and similar studies is defined as the accompaniment of young animals in the absence of the mother. It is considered a form of alloparental care if the adults alter their behaviour to provide care to the calves (Kleiman and Malcolm 1981, Whitehead 1996a)

present in the same group, unless the young animal was solitary. If babysitting does occur, then the young animal may associate with other individuals, but it should still often associate with its mother. To test this hypothesis I identified all of the individuals which were observed in the same group as each young animal and looked for repeat associates, for each year that the young animal was observed. The individual which associated most often with the young animal was the potential mother.

Hypothesis 2: Mothers associate with their offspring whenever the mothers are at the surface, although the young animal may associate with other individuals (especially if babysitting does occur). For each year that the young animal was observed, I calculated the proportion of time the potential mother was observed in the same group as a calf or juvenile. I used the presence or absence of young animals for this test rather than the presence of an identified offspring as not all calves or juveniles were identified in each group.

Hypothesis 3: If the young animal survives the winter, it continues to associate with its mother in the next summer, assuming that mother-offspring associations last for periods of years. To test this hypothesis I examined the photo-identification record of each potential mother in the following year to determine the proportion of time each potential mother spent with a juvenile in the year following its identification as a potential mother.

Additionally, the age and sex classification of all associates were examined to eliminate the identification of males as mothers. For young animals identified in more than one year (including observations in 1998), the sighting history was examined for associates common to more than one year. Probable mothers met the requirements of hypotheses 1 and 2, and either met the requirement of hypothesis 3 or were not observed in the following year.

Length measurements of identified calves

Lengths of individual bottlenose whales can be estimated from photographs taken from a known height (10 m up the mast of the boat) which include the horizon and a whale approximately parallel to the horizon (Gordon 1990). From these photographs the range between the boat and various parts of the whale (such as fluke notch, posterior emargination of the dorsal fin, blowhole, snout and tip of the beak could be calculated based on the following formula (after Waters and Whitehead 1990b):

$$d = \frac{RH}{(R+H)\sin\alpha} + \frac{(RH)^2}{[(R+H)\sin\alpha)]^3}$$

where d = distance to the point on the whale from the boat

R= radius of the earth

H = height of the camera (10 m)

α = angle subtended by the whale and the horizon at the camera [=arctan(distance between the point and the horizon/focal length of the lens)]

If two or more points were visible on the whale, then the distance between the two points could be estimated by (after Waters and Whitehead 1990b):

$$L = \sqrt{d(1)^2 + d(2)^2 - 2d(1)d(2)\cos\beta}$$

where L= distance between two points

d(1)= distance between the boat and point 1 on the whale

d(2)= distance between the boat and point 2 on the whale

β= arctan(size of the photographic image from point 1 to 2/focal length of the lens.

If points 1 and 2 were beak tip and fluke notch, then the distance between the two points was equal to the length of the whale. If the points visible on the whale were not the tip of the beak or the fluke notch then the total length of the whale was estimated from partial lengths. All lengths were estimated by Brad Carter (Dalhousie University; Carter 1997).

RESULTS

SEASONALITY OF CALF SIGHTINGS

Analysis of the seasonality of calf sightings was restricted to 1994-1997 when calves and juveniles were differentiated in the field. Log linear models indicated calf sightings were not associated with particular months (P =0.682) or years (P =0.979) and there was no interaction between months and years (P =0.192; Figure 6.2). In 1996 and 1997 field work was conducted in June, July and August, but there was no consistent trend to the sighting of calves in the Gully over the summer. The presence of very young calves (individuals with bent-over dorsal fins) indicates that calving occurred in or near the Gully in June, July and August (see Table 6.1 and Figure 6.2).

Table 6.1: Sightings of calves with bent-over dorsal fins or fetal folds over the summer study period. It is unknown how many calves are involved in these sightings as only a few calves were photographed and had identifying marks.

	# groups	# days
Bent dorsal	15	10
Fetal folds	35	16

SEASONALITY OF SIGHTINGS OF YOUNG ANIMALS

Log linear models indicated that there were no significant trends in the proportion of groups containing young animals (both calves and juveniles) by year or month (three way interaction term P =0.299; two way interaction: presence or absence of young animals by year P =0.805; by month P =0.904). There were also no obvious trends in the data (see Figure 6.3). In June 1990 the proportion of groups containing young animals was high, much lower in June 1996 and no young animals were observed in June 1997. Similarly July and August observations of young animals were high in 1996 and 1997 but low in 1990.

Figure 6.2: Proportion of groups containing calves by month and year.

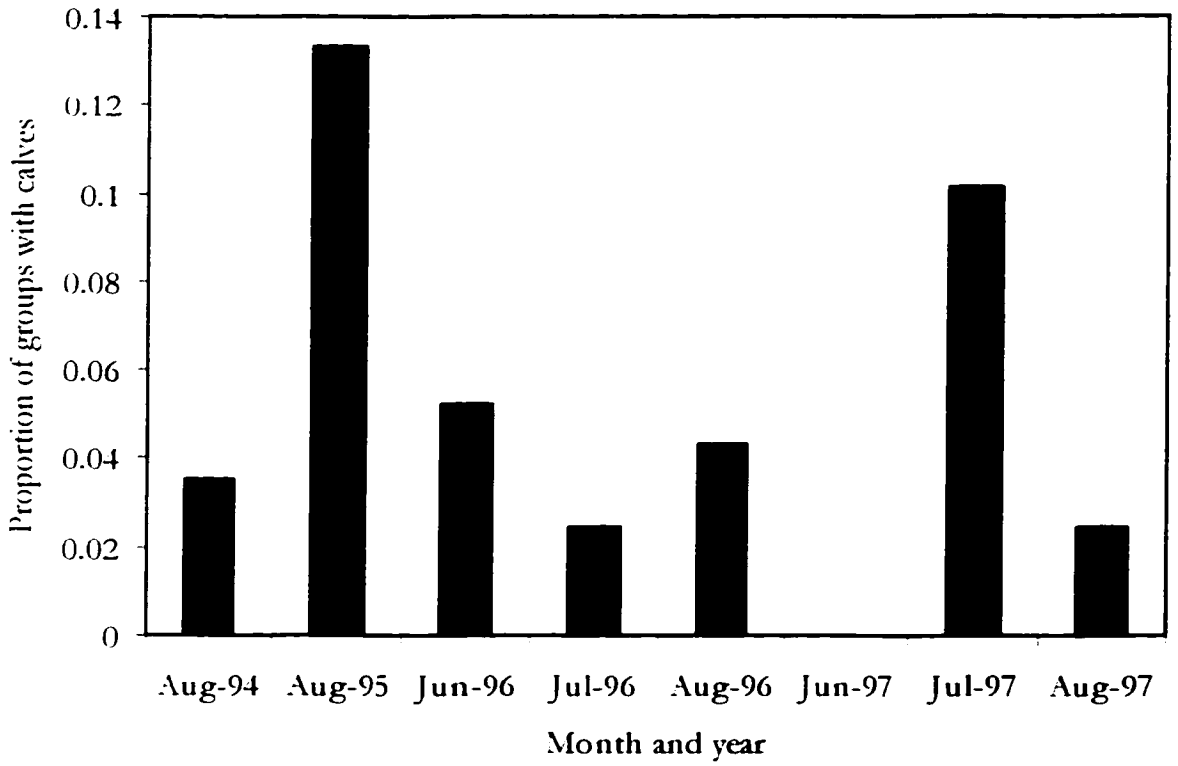
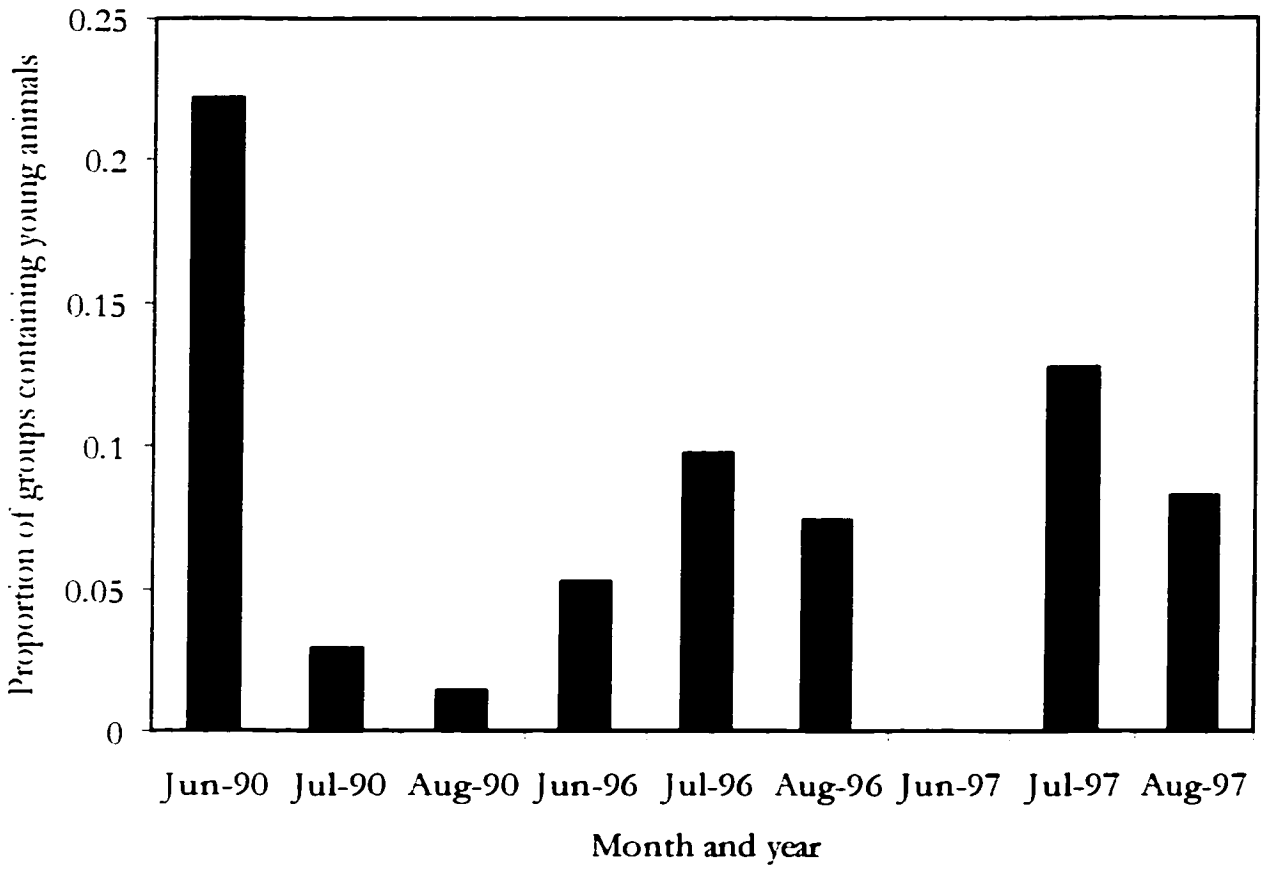


Figure 6.3: Proportion of groups containing young animals in 1990, 1996 and 1997.



SIZE OF GROUPS CONTAINING YOUNG ANIMALS

The relative proportion of young animals in each group increased with increasing group size (r_s=0.991; 6 df; Figure 6.4). On three occasions, solitary individuals were observed to be juveniles. Calves were never observed on their own for a complete encounter, although there were three occasions when the adult associates of the calf were no longer visible at the surface, and the calf remained at the surface for up to 10 minutes unaccompanied.

COMPOSITION OF GROUPS WITH YOUNG ANIMALS

There were 16 groups that contained young animals and met the restrictions required to analyze the age and sex composition of the group (all members likely identified and at least half the identified individuals sexed; see Table 6.2). Five groups contained only a calf or juvenile and an "adult sized" animal, usually a female (or possibly another immature animal as melon photographs cannot distinguish between females and immature animals), but on one occasion, the associate was an immature male. On that occasion individual #1023 (a very young calf with a bent dorsal fin and fetal folds) was observed alone with an immature male, #143 (see Chapter 3 for more details on the sexing of #143). Mature males were not observed in groups with young animals, until the groups became relatively large (five animals). Sub-adult males were associated with young animals in groups as small as three individuals.

Figure 6.4: Proportion of individuals in each group size which were young animals.

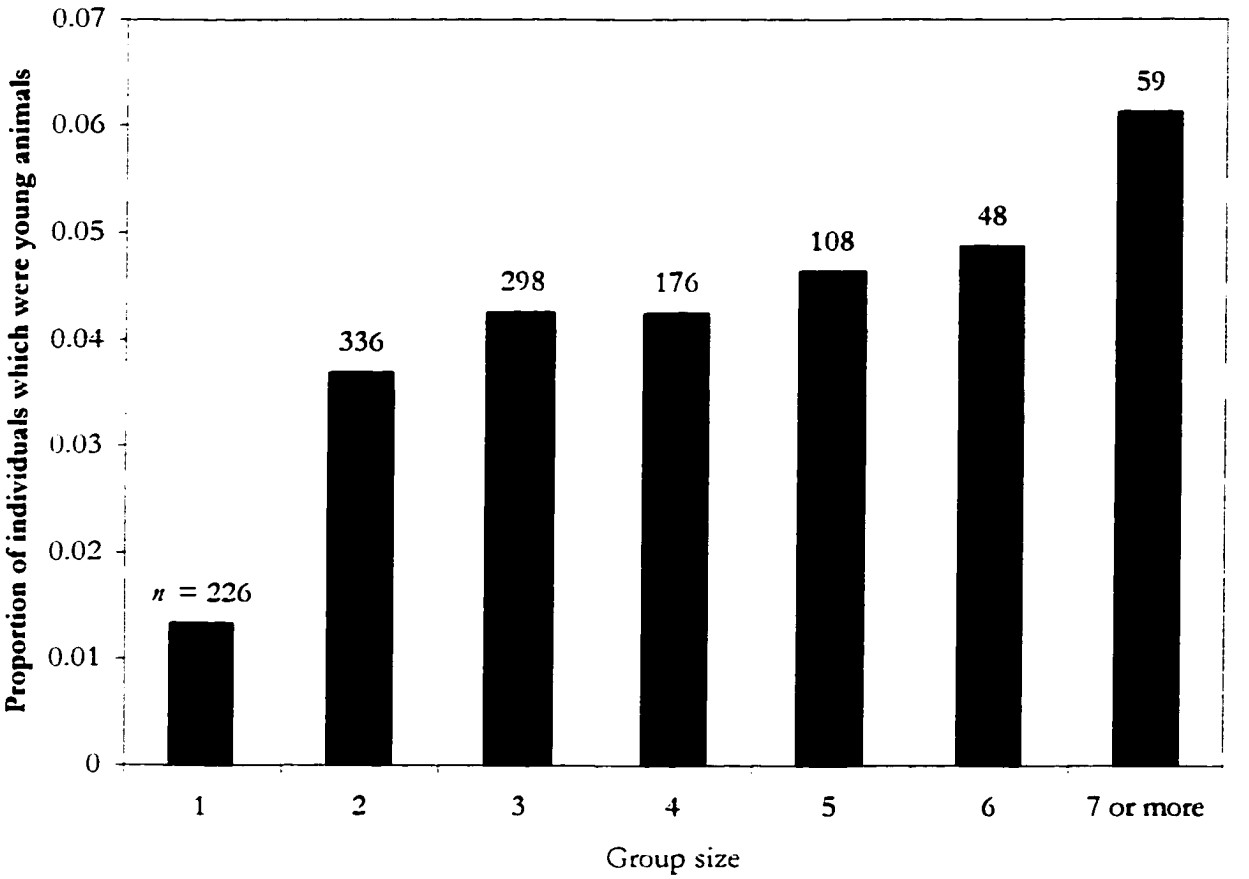


Table 6.2: Age and sex composition of groups which contained young animals.

Group size	Group composition	All sexed	At least half the individuals sexed
2	1 Female/immature with 1 young animal	4	
	1 Immature male with 1 young animal	1	
3	2 Female/immature with 1 young animal	1	
	1 Female/immature and 1 sub-adult male with young animal	2	
4	3 Female/immature with 1 young animal	1	
5	4 Female/immature with 1 young animal		1
	4 Female/immature and mature males with 1 young animal		1
6	5 Female/immature and immature males with 1 young animal		1
	5 Female/immature and mature males with 1 young animal		1
	All three classes present with young animal		1
7	All three classes present with 1 young animal		1
9	8 Female/immature and mature males with 1 young animal		1

INDIVIDUALS ASSOCIATED WITH CALVES AND JUVENILES

Between 1988 and 1997, 16 calves and juveniles were photographically identified (see Table 6.3). Few young animals were identified prior to 1994, as this was not a research priority then. Three calves were observed on multiple days within the same field season and one of those (#1272) was also observed as a juvenile. Five juveniles were observed on multiple days within the same year, and two of the three (#1146 and #1239) were observed in more than one year. Individual #1146 was identified as a juvenile in 1998, but it was also observed in 1996 and 1997. Although no size estimates were made during the earlier sightings, it would have presumably been at least one year old when first observed in 1996, as no fetal folds were observed (although it may have been born much earlier in the year). If it was one year old in 1996 then, it was at least three years old when identified in 1998 as a juvenile, indicating that young animals are not adult sized until at least age four. However if it was born earlier in 1996, then it would have been two when observed in 1998, and may not reach adult size until at least age three. Another juvenile (#1334) observed in more than one year may have been adult size in 1998 and therefore no longer a juvenile.

Table 6.3: Photographically identified calves and juveniles.

ID	Year	Age class	Age features used to determine class	Estimated length (m)	# days observed
301	1990	Juvenile	Size	3.4	3
642	1993	Juvenile	Size	4.2	4
682	1993	Juvenile	Size	5.3	3
830	1994	Juvenile	Size		1
882	1994	Juvenile	Size		1
888	1994	Calf	Fetal folds	2.5	1
902	1994	Juvenile	Size		1
1023	1996	Calf	Bent dorsal and fetal folds	2.9	2
1136	1996	Calf	Bent dorsal and fetal folds		1
1146	1996	Juvenile[1]			1
	1997	Juvenile			2
	1998	Juvenile	Size		10
1239	1997	Juvenile	Size		3
	1998	Juvenile	Size		5
1272	1997	Calf	Fetal folds		3
	1998	Juvenile[2]			1
1274	1997	Calf	Fetal folds		2
1276	1997	Juvenile	Size		1
1285	1997	Calf	Fetal folds		1
1334	1997	Juvenile	Size		1
	1998	[3]			3

1) No age class was identified for 1146 until 1998 when it was determined to be a juvenile; photographs from 1996 and 1997 do not show fetal folds or bent dorsal therefore assigned juvenile status for these years
2) No age class was identified for #1272 in 1998, however it would presumably be juvenile; no fetal folds were observed in 1998
3) No age class was identified for 1334 in 1998, it may have been still juvenile, or it may have matured

Lengths of five young animals were estimated for photographically (Table 6.3). The two measured calves were both less than three metres long, while each of the juveniles were more than three metres in length. As the measurements for the juveniles were quite different from each other, they may represent individuals of different ages. Of the three measured juveniles individual #682 may have been the oldest and #301 the youngest.

Identification of mothers

No associate met all of the criteria of the three hypotheses supporting its motherhood (observed in most or all of the groups with the young animal, observed with a young animal in most sightings, and observed in the following year associated with a juvenile; see Table 6.4: details of the sighting histories of all young animals observed on more than one group and their associates are listed in Appendix 3). However it was possible to identify several probable mother-offspring pairs (Table 6.4).

Probable mother-offspring pairs

There was strong support for the identification of three probable mothers (#507, 54 and 1332; Table 6.4). Individual #507 was likely the mother of juvenile #642 as #507 was present all the time that #642 was observed at the surface, and a juvenile was present whenever #507 was sighted. Melon sexing indicated #507 was a female/immature. After 1993, #507 was not sighted until 1996 when juvenile #642 would have been at least four. However #642 was never sighted after 1993. By 1996, #642 may have been weaned and dissociated from its mother. Alternatively #642 may have died as in 1993 it was observed with deformities along its spine that may have been congenital. Individual #54 was identified as the probable mother of juvenile #1239 as they were often associated in 1997 and 1998. Genetic and melon sexing also indicated #54 was female. Juvenile #1239 spent less time with #54 in 1998 than in 1997. Both #54 and #1239 were observed without the other in 1997 and 1998 indicating that probable mothers do not spend all their time at the surface with their offspring. The third probable mother #1332, was almost always associated with juvenile #1334 in 1997 and 1998 and has been identified as a female/immature by photographic techniques.

Based solely on association patterns, I could have identified #131 was the probable mother of #1146, as both animals were almost always associated in 1997 and 1998 (Table 6.4). However, melon photographs taken in 1998 (analyzed by J. Arch, Dalhousie University) indicated that #131 was a sub-adult male (MQ-2). Individual #45 was also repeatedly associated with #1146 in 1997 and 1998 and was female/immature based on melon

photographs and may have been the mother. However #1146 was more often associated with #131 than #45 in 1997 and 1998. Neither #45 nor #131 were associated with #1146 in 1996.

Table 6.4: Identification of probable mothers (highest associate) based on repeat associations with offspring. (** strong support for mother-offspring pair; * moderate support , ?? contradictory support).

ID	Age class	Year	Highest associate	Percentage of time spent by		
				Young with highest associate[1]	Highest associate with calf or juvenile[2]	Highest associate with juvenile following year[3]
642	Juvenile	1993	507 *	100	100	Not observed until 1996
682	Juvenile	1993	54	58	73	Not observed until 1995
			690	48	100	Not observed again
1023	Calf	1996	143	35	17	0
1146	Juvenile	1996	none			
	Juvenile	1997	131 ??	100	100	99
			45 *	25	61	70
	Juvenile	1998	131 ??	99	99	--
			45 *	75	70	--
1239	Juvenile	1997	54 **	100	90	90
		1998	54 **	75	90	--
1272	Calf	1997	159 *	91	42	54
1334	Juvenile	1997	1332 **	100	100	99
	Juvenile?	1998	1332 **	99	99	--

1) Tests hypothesis that the mother was likely to be associated with her offspring on several occasions (percent of time young at surface that mother present as well).
2) Mother likely to be associated with her offspring whenever she was at the surface (percent of time mother at surface that she was associated with the appropriate age young animal).
3) Mother likely to be associated with a juvenile the following year (percent of time mother at the surface that she was associated with a juvenile).

There was moderate support of #159 to be the mother of calf #1272 as they were often associated in 1997, however #159 was observed in many groups in 1997 without a calf present. Most of the observations of #159 without a calf occurred after #1272 was sighted, therefore these cannot represent observations of #159 before the birth of calf #1272. No sexing information was available on individual #159.

Repeatedly sighted young animals that could not be assigned a potential mother

Several young animals were observed on multiple occasions but no potential mother could be assigned. Juvenile #301 was observed on three different days in 1990 (Table 6.3) but never resighted with any associate. On one occasion, juvenile #301 was observed on its own with no associates (Appendix 3). Juvenile #682 was repeatedly observed with both #54 and #690 in 1993, however juvenile #682 spent much less time with either of these associates, than did offspring with strong links to a probable mother (Table 6.4). Calf #1023 was also observed on two days in 1996 and its only repeat associate was an immature male #143, and this pair of animals spent relatively little time together (Table 6.4).

DISCUSSION

SEASONALITY OF SIGHTINGS

As there were no significant trends in the monthly observations of calves or juveniles (Figure 6.2 and 6.3), little can be inferred about when and if peak calving occurs. However, the presence of very young calves in the Gully during all three study months indicates that calving likely occurs in or near the Gully during these months, although the calving period may extend outside of these months. It was not possible to estimate the birth date of young calves as nothing is known about the duration of fetal folds in northern bottlenose whales, although one individual observed with fetal folds in 1997 did not possess these folds in 1998, indicating that the folds may last less than one year (Table 6.3). One calf with a bent dorsal fin was photographed on two different dates, nine days apart (Table 6.3). The dorsal fin was still bent when it was last observed, indicating that bent dorsal fins in

bottlenose whales may persist longer than bent dorsal fins in bottlenose dolphins or killer whales (Tavolga and Essapian 1957; R.W. Baird, Pacific Whale Foundation, pers. comm.; D. Odell, SeaWorld Inc., pers. comm.; J. McBain, SeaWorld Inc., pers. comm.). Alternatively, individual #1023 may have had congenital deformities to the dorsal fin which prevented straightening, as observed occasionally in bottlenose dolphins (J. McBain, SeaWorld Inc., pers. comm.). Although one bottlenose whale maintained a bent-over dorsal fin for at least nine days, it is still reasonable to presume that calves with these features were very young, likely born within a few weeks of the sightings. The lengths of individuals identified as calves based on fetal folds or bent dorsal fins were also smaller than those of juveniles (Table 6.3), indicating that these were very young animals.

GROUP SIZE AND COMPOSITION

As young bottlenose whales were more often found in larger groups (Figure 6.4), females and their young may benefit from larger groups. Female transient killer whales and their young were disproportionately found in larger groups than those of optimal size for foraging. These larger groups may function to protect young animals from attacks from resident killer whales, the only possible predator identified to date (Baird and Dill 1996). To date there have been no observed predatory attacks on bottlenose whales of any age in the Gully, nor any observations of dead animals. However several adult whales show tooth rakes that may have been inflicted by killer or pilot whales (see Chapter2).

Individuals of all age and sex classes were found in groups with young animals, however mature males were associated with young animals only in relatively large groups (Table 6.2), even though mature males were observed in smaller groups as well (Chapter 4). In almost all groups with young animals, at least one individual that was sexed as a female/immature animal. However one group consisted of an immature male and a young calf, clearly indicating that even young calves sometimes associate with individuals that cannot be their mother.

INDIVIDUALS ASSOCIATED WITH CALVES AND JUVENILES

Identification of probable mothers

Based on repeat associations between photographically identified calves and juveniles and other members of the Gully population, three mother-offspring pairs were identified with reasonable confidence (Table 6.4). Each of the probable mothers had been photographically categorized as female/immature, and one was confirmed to be female by genetic techniques. These pairs were repeatedly associated over several days within a single field season, and two pairs were associated over two different years. During the first year of observation of these mother-juvenile pairs, the juvenile was associated with the mother almost all of the time the juvenile was observed, although the mother was sometimes observed in groups in which the juvenile was not photographed, and even in groups in which no juvenile was present (Table 6.4). By the second year of observation, juveniles spent less time associated with their probable mother (Table 6.6). There was also moderate evidence to support one potential mother-calf pair (#159-#1272), although the sex of the potential mother was unknown. However, the association pattern between mother and calf was similar to patterns of mothers and juveniles (Table 6.4).

Using association patterns to define mother-offspring relationships may, however, be problematic in bottlenose whales. Based solely on association patterns, individual #131 would have been identified as the probable mother of juvenile #1146 (Table 6.4), but melon photographs in 1998 indicated that individual #131 was a sub-adult male. It is possible that the sex categorization of this individual was incorrect and this individual was actually female. The highest quality melon photograph taken for #131 was MQ-2, and photographs of this quality have an estimated 3.3% error rate in categorization (Chapter 3). If individual #131 was actually a female, then it was probably the mother.

Alternatively, the age of juvenile #1146 may explain this association pattern. The juvenile #1146 was most likely at least one year old in 1996 when it was first observed as no fetal folds were visible. Therefore it was at least two or three when it was associated with #131 and it may have been even older. Sub-adult bottlenose dolphins preferentially associate with

other sub-adults, and early associations between males may lead to long term stable bonds as adults (Wells 1991b). As the adult social organization of bottlenose whales and bottlenose dolphins were similar and mature males of both species formed long term stable bonds (Chapter 5), juvenile #1146 may be a male beginning to form a long term bond with #131. The difficulty in determining a probable mother for juvenile #1146 despite its long sighting history indicates that all other identifications of probable mothers should be considered tentative.

Evidence of babysitting

Solitary bottlenose whale juveniles have been observed as well as in groups likely associated with their mother, and in groups without their mother (Figure 6.4 and Table 6.2). A calf has never been observed in a group entirely on its own, but calves have been left alone at the surface by their associates for up to 10 minutes. Young calves also associated with individuals who could not be their mothers in the absence of their mothers (Table 6.2).

Individual #1023 provides the clearest example of babysitting in this study. It was not possible to identify a probable mother for this calf as the only repeat associate was an immature male (Table A3.4). Sighting histories of the associates of calf #1023 also did not identify a probable mother as none of the associates were repeatedly observed in groups with calves (Table A3.12). During one sighting of calf #1023, it was definitely not associating with its mother as its only associate was an immature male(#143). The sighting history of #143 in 1996 indicates that the only calf he was associated with that year was #1023 and only on one day. This suggests that the male may not have altered his behaviour to associate with the calf, but instead the calf may have simply associated with any individual that remained at the surface, thus not constituting alloparental care.

Patterns of association between adult and calves

Five different patterns of adult calf interactions could be examined based on the association data. The first pattern predicted that calves were able to dive with their mother to foraging

depths and therefore should not be left alone at the surface, and should always associate with their mother. There were only three sighting of calves left alone at the surface. Juveniles were only slightly more often left alone at the surface (Figure 6.4). Additionally, calves and juveniles were not always associated with the same individual (their probable mother, Table 6.4), and this hypothesis is unlikely to describe the pattern of association between adults and calves, although nothing is known about the diving abilities of young bottlenose whales. Similarly, the second pattern, in which mothers leave their calves alone at the surface while foraging, can also be rejected as calves and juveniles were rarely alone at the surface (Figure 6.4).

There was little evidence to support or reject the third pattern, in which lactating females alter their diet to feed on prey located nearer the water surface. Fatty acid analysis of biopsy samples indicated all biopsied individuals were most likely feeding on benthic squid (Hooker In prep.), but it is not known if any of the biopsied animals were lactating at the time they were biopsied. One sample was taken from individual #54 in 1997 when she was associated with juvenile #1239 and was identified as the probable mother (Table 6.4). As #1239 has not been aged, and the lactation period of bottlenose whales is unknown, it is uncertain if #54 was lactating when the biopsy sample was taken. There was no indication that her diet was significantly different from the other biopsied whales, including males (Hooker In prep.).

There was no evidence to suggest that female bottlenose whales and their young formed tightly bonded groups to communally care for their offspring (Table 6.4 and Chapter 5), as found in sperm whales (Whitehead 1996a). While calves were not often left alone, they did not repeatedly associate with a number of different animals within a tightly bonded group. Nor do females form tightly bonded groups (Chapter 5).

The pattern that best fit with the observations of associations between adults and young bottlenose whales was one in which calves were occasionally left alone at the surface, but most often associated with either their mother, or other nearby adults (Appendix 3). This may indicate that young animals can dive to foraging depths, or mothers may not often be

diving to foraging depths during the periods we observed the whales (daylight hours during the summer, although other adults were diving to the seafloor during these periods; Hooker and Baird 1999). Young animals rarely had more than one repeat associate, although older juveniles such as #1146 in 1998 had several (Appendix 3). Some young animals were associated more often than others, with the individual identified as their probable mother, and it was not possible to identify a probable mother for all young animals (Table 6.4). This mixed pattern could be explained in several different ways. Young animals that were frequently observed, but could not be assigned a probable mother may have been orphans, although this was unlikely. Alternatively, differences in maternal condition may alter the amount of time a mother spends with her offspring. Mothers in poor condition may have to feed more to survive and lactate, and therefore must leave their offspring at the surface more often. The sex of the offspring may also alter maternal care. As male bottlenose whales are larger than females, mothers of male offspring may have to feed more often to raise a large healthy male. The available data do not permit exploration of these hypotheses.

Sighting histories of individuals identified as probable mothers indicated that maternal (or alloparental) care in this species may be complicated. Although individual juveniles were often observed with their probable mother at the surface, probable mothers were observed in the same year without any juveniles present. During these occasions, the juveniles may be associating with other animals or be solitary, or were missed in the field notes.

Babysitting by bottlenose dolphins and sperm whales seems different from that found in bottlenose whales. In bottlenose dolphins, most babysitters were young females who gained parenting experience (Mann and Smuts 1998). The only confirmed babysitter in bottlenose whales was an immature male, who would be unlikely to benefit through gaining parenting experience. Finally females that repeatedly associated with a young animal tended to be categorized as potential mothers so female babysitters may be more common than this study indicates.

Sperm whale females and their young form stable units that persist for years and generally consist of related individuals (Christal 1998, Christal *et al.* 1998). Alloparents may be related

individuals and/or individuals who repeatedly associate with calves for years. Therefore, babysitting may be a form of reciprocal altruism or kin selection (Whitehead 1996a). Bottlenose whale females do not seem to form stable associations with other females even for short time periods (Chapter 5). However, bottlenose whale females associate with most members of the Gully population over time, given the large number of associates of females and the small population size (Chapter 5 and Chapter 7). Therefore it is possible that the entire Gully population functions as a single unit that routinely breaks up into small clusters. If this situation is true, then reciprocal altruism might explain babysitting in bottlenose whales.

While there is some evidence for babysitting in bottlenose whales, further studies of costs and benefits to participants are required before the function and nature of alloparental care in bottlenose whales begins to be understood. Genetic confirmation of motherhood as well as relationships to alloparents would greatly increase our understanding of this system. Focal follows of young animals and their mothers (Mann and Smuts 1998) would also be very useful. Information on the diving ability of young bottlenose whales would also help determine if bottlenose whale calves must separate from their mother while she forages at depth.

CONCLUSION

Bottlenose whale calves were born in or near the Gully in June, July and August, although births also may occur outside these months. Calves and juveniles were preferentially found in larger groups, and with female/immature animals present. Probable mothers could be identified from association patterns for several calves and juveniles, although not all young animals observed on multiple occasions could be assigned a probable mother. The most likely individual to be the mother based on association patterns for one of the juveniles was categorized as a sub-adult male, indicating some repeat associates of juveniles may not be the mother. There was some evidence of babysitting in bottlenose whales, although the costs, benefits and function of this behaviour cannot yet be determined.

Chapter 7: Population size and structure

INTRODUCTION

In the past, human activity has affected bottlenose whales in the Gully. Whalers took 87 bottlenose whales from the Gully and surrounding waters from 1962 to 1967 (Reeves *et al.* 1993). Current activities, such as natural gas exploration and exploitation, could potentially affect the whales through noise or chemical pollution, or ship strikes (Whitehead *et al.* 1997b, Hooker *et al.* In press). The recent decision to create a marine protected area in the Gully gives hope that in the future, human effects on the whales will be minimal (Anonymous 1998). Accurate estimates of population size and growth (or decline) are essential parameters for conservation decisions such as boundaries and regulations for marine protected areas. While the size of the Gully population has been previously estimated (Whitehead *et al.* 1997c), this estimate was based on a smaller dataset, and violations of the assumptions of mark-recapture analysis were not as rigorously tested as was done in Chapter 2.

Information about the size of a population also gives indications about the geographic structure of that population. A population which is closed (having no immigration or emigration) is likely geographically isolated from other populations of the same species, although there are examples, such as killer whales off B.C., where two populations are reproductively isolated, but share the same geographic area (Hoelzel *et al.* 1998a). Population sizes can also indicate geographic structure if only a few individuals reside in the study area, and they are separated from other conspecifics by large sections of poor quality habitat. However, even very low migration rates between populations may prevent inbreeding (Stacey *et al.* 1997).

The age and sex structure of a population can have implications for population dynamics. For example, the low reproductive rate of Galapagos sperm whales may be due to the virtual elimination of all mature males 20-30 years ago through intensive whaling off Peru. Currently, there may be insufficient numbers of mature males to find estrous females and

inseminate them (Whitehead *et al.* 1997a). The current age and sex structure of the Gully population of bottlenose whales may give indications about the affects of past whaling on the population, and its future viability.

Small population sizes and high mortality rates are implicated in the decline and potential extinction of several cetacean species. North Atlantic right whales were hunted to very low numbers by the 1900's and population recovery has been very slow, with an estimated population size of 300 individuals. Recent increases in mortality (from 1% per year in 1980 to 6% per year in 1994) and increases in the interbirth interval (from 3 years to 5 years) has led to the prediction of extinction of the species within 200 years (Caswell *et al.* 1999). The vaquita (*Phocoena sinus*) is represented by a single population with high mortality rates and declining abundance. It has a very limited range, only in the northern reaches of the Gulf of California. Estimates of the population size are imprecise, ranging from 224-855, and declining at 18% per year, likely due to fishing by-catch mortality (Barlow *et al.* 1997). As the Gully population of bottlenose whales is known to be small (230 animals from previous estimates: Whitehead *et al.* 1997c), it is important to assess mortality levels and trends in population size to assess its viability.

Individual bottlenose whales are sometimes found in the Gully canyon itself and spend the rest of the time outside the canyon, presumably foraging along the shelf edge (Whitehead *et al.* 1997c). The potential effects of development and protection through a marine protected area may depend on whether individuals spend most of the time in the Gully (resident) or are only briefly found there (transient). Age and sex classes may use the Gully differently. For example, if mature males rove between female groups (Whitehead 1990c), they may spend less time in the Gully than other classes. Residency in the Gully may also vary seasonally or yearly in response to ecological factors or human activity.

This chapter estimates the size and growth of the Gully population and its age and sex structure. The residency of individuals within the Gully is also examined for different age and sex classes and in different years. This information will give a clearer picture of how bottlenose whales use the Gully and of the importance of the Gully to this population.

METHODS

FIELD RESEARCH

Descriptions of the fieldwork are given in Chapter 2. Analyses based on dorsal fin photographs were restricted to Q≥4 to eliminate poor quality photographs (see Chapter 2 for details).

POPULATION SIZE AND TRENDS

To determine if the population was open or closed (to immigration, emigration, mortality or birth), a discovery curve was plotted. Populations of long lived animals may appear to have little or no mortality if sampled over a short proportion of their lifespan. The cumulative number of individuals identified (by left fin photographs) was plotted against the cumulative number of high-quality left fin photographs. The cumulative number of individuals was also plotted for reliably marked individuals (see Chapter 2 for a definition of reliably marked individuals).

Population size and trends were estimated separately for left and right side identifications based on all Q≥4 photographs of reliably marked individuals using the POPAN module of SOCPROG 1.2 (Whitehead 1999) with calendar years as units. Three models were fitted to the population estimates using log-likelihood methods to determine which model best described the population. Maximum likelihood methods, conditioned on the first capture, were used to estimate population parameters of each model. The three models were:

Closed (Schnabel): population has no mortality, birth, immigration or emigration

Mortality: population remains the same with mortality balanced by birth; mortality is equivalent to permanent emigration or mark change which prevents recapture; similarly birth is equivalent to permanent immigration or mark change which causes a previously identified animal to be identified as a new animal

Mortality + trend: population grows or declines at a constant rate

Likelihood support functions were used to estimate 95% likelihood confidence intervals for

each parameter (Edwards 1992). The likelihood method of calculating confidence intervals is valid as the capture of individuals is independent because there were no permanent associations (see Chapter 5; Edwards 1992). Jolly-Seber methods of calculating the population size, mortality/emigration and birth/immigration separately for each year were inappropriate for this dataset, as this method estimates many different parameters resulting in inaccurate estimates (see Table 2.2; Jolly 1965).

To investigate the potential growth or decline in population size, the population size after 20 years of constant change, was determined from the estimated rate of change as well as maximum and minimum rate of change (from 95% c.i.).

AGE AND SEX STRUCTURE

The population size of each age and sex class was estimated and modeled as described above for the entire population. To calculate the proportions of the population that were sexed and reliably marked, the number of melon photographs (MQ≥2) which were linked to a reliably marked fin identification in each class was divided by the total number of melon photographs linked to a fin identification. The proportion was calculated separately for each year and then averaged (see Chapter 2 for calculating the proportion of reliably marked individuals in the entire population). The estimated number of reliably marked sexed individuals was then scaled to calculate the estimated number of sexed individuals in the population.

RESIDENCY IN THE GULLY

The residency of individuals in the Gully was investigated by plotting the lagged identification rate within a single field season (similar to the lagged association rates described in Chapter 5). All photographs used in this study were taken in the Gully (as defined by the 500 m contour and by 43.5°N). Lagged identification rate was defined by the following formula:

$$R(\tau) = \frac{P(\tau)}{N}$$

where $R(\tau)$ = lagged identification rate for time lag (τ)

$P(\tau)$ = probability individual is still in the Gully after time lag (τ)

N = number of individuals in the Gully

τ = time lag

Lagged identification rates were estimated by

$$R(\tau) = \frac{\sum_{i} \sum_{j\, t_j = t_i + \tau} m_{ij}}{\sum_{i} n_i \sum_{j\, t_j = t_i + \tau} n_j}$$

where n_i = individual identified at time i

m_{ij} = number of individuals identified in both times *i* and *j*

The maximum lag (τ) between photographs that I considered was 100 days, which was greater than the number of days in a single field season. Individuals did not have to be reliably marked to be included in the analyses as marks were unlikely to have experienced sufficient change to preclude re-identification within 100 days (see Chapter 2). Mortality and birth rates were considered to be zero in these analyses as few births or deaths were likely over the 100 day sampling period. Three models of residency were fitted to the residency rate plot using log-likelihood methods to determine the best model. Jackknife techniques (in which data from each date were sequentially eliminated from the dataset) were used to calculate error bars and standard errors for each model parameter. The three models were:

Closed (no changes in the individuals present in the Gully)

$$= \frac{1}{N}$$

Emigration (individuals could leave the Gully, but never return)

$$= \left(\frac{1}{N}\right)^{\frac{-\tau}{O}}$$

Emigration and re-immigration (individuals could enter and leave the Gully, then re-enter the Gully, Whitehead 1990b)

$$= \left(\frac{1}{N}\right) + \frac{\frac{1}{I} + \left(\frac{1}{O}\right)^{-\tau\left(\frac{1}{I}+\frac{1}{O}\right)}}{\frac{1}{I}+\frac{1}{O}}$$

where N = number of individuals in the Gully

I = time spent inside the Gully

O = time spent outside the Gully

τ = time lag

Residency rates were calculated and models fitted for each age and sex class separately and for each year with more than one month spent in the field. The proportion of individuals in the Gully at any given time was calculated by dividing the estimated number of whales in the Gully by the total population size.

SITE FIDELITY[1] BETWEEN YEARS

To examine whether individuals in the population showed fidelity to the Gully, I calculated the number of years in which each reliably marked individual was photographed (Q≥4; individuals with a left fin identification). To determine whether there were any differences in resightings over periods of years amongst the age/sex classes, I selected all reliably marked individuals photographed in 1990 (Q≥4; left fin identification) and then calculated the proportion which were also observed in years both before and after 1990 for each age/sex class. I repeated this analysis for all reliably marked individuals photographed in

[1] Site fidelity = constant presence or routine sightings (*i.e.*, several times a year) in study area.

1996. These were the only two years which had sufficient data in that year as well as subsequent and previous years.

RESULTS

POPULATION SIZE AND TRENDS

The discovery curve indicated that the population was not closed throughout the study period, even if unreliably marked individuals were excluded (Figure 7.1). Therefore the population was experiencing births or immigration, which was not surprising in a nine year study period. Within a single year the population was not closed, as new individuals were continually identified throughout each field season, even in the long field seasons (Figure 7.1).

Of the three models tested to describe the population (closed, mortality, mortality + trend), the mortality model fitted best (see Table 7.1). The mortality + trend model fitted the data no better than the simpler mortality model. Based on the model, the population estimate of reliably marked individuals was 86 or 81 individuals, from left or right side identifications. The estimated mortality, emigration and mark change rate was 12% per year (left side) and 15% per year (right side) per year. The support surface for the 95% c.i. of the estimations of population size and mortality rate are shown in Figure 7.2. The population estimate of reliably marked individuals (95% c.i.) ranged from 74-104 individuals (left side) and 71-96 individuals (right side; Table 7.1). As 66 ± 5% of the individuals in the total population were reliably marked (see Chapter 2), the total number of individuals in the population was estimated to be 130 (104-170) and 122 (100-157) for left and right side identifications.

Figure 7.1: Discovery curve showing the number of new individuals identified each day. An open population would be indicated by the failure of the curves to reach an asymptote even within a single field season.

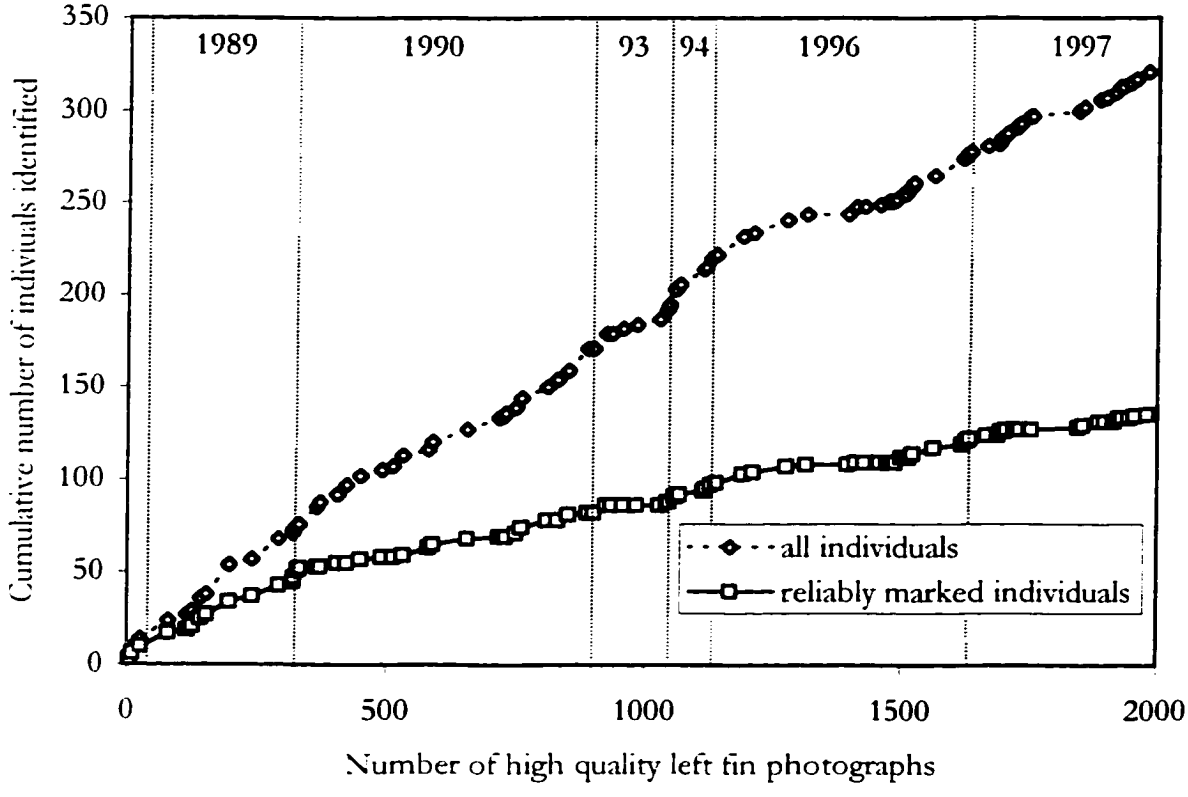


Table 7.1: Population estimates for all reliably marked individuals (95 % likelihood confidence intervals in brackets). Best-fit models are shaded.

Data set	Model	Population estimate	Mortality (% per year)	Trend (% per year)	Log likelihood
Left side (n=130)	Closed	138 (119-163)	-	-	-236.37
	Mortality + trend	87 (74-105)	12 (6.4-17)	0.84 (-4.3- + 6.4)	-219.14
Right side (n=133)	Closed	145 (125-170)	-	-	-251.83
	Mortality + trend	81 (71-96)	15 (11-21)	-1.3 (-5.9- + 3.1)	-223.79

When using mark-recapture analysis to estimate population size, the capture probabilities must not be heterogeneous, which could lead to negative bias in the population estimate (*e.g.*, Hammond 1990b). To test for heterogeneity, the residual differences between the observed identification histories and the expected histories (from the fitted model) were plotted. A U-shaped curve would indicate heterogeneity, which did not occur when the mortality model was fitted (see Figure 7.3; Cormack 1985). This indicated that individuals were not more or less likely to be in the Gully in any year.

Although the mortality model fitted the data better than the mortality + trend model, some indication of possible trends in the population growth could be investigated using the estimates from this model. The direction of the trend (growth or decline) were opposite for left and right side identifications; therefore, it was impossible to determine whether the population is decreasing or increasing. However, these results did not necessarily indicate that the population was stable. A larger dataset will be required to determine if there are any significant trends in the population growth. Potential growth or decline can be estimated by calculating the population size after 20 years of constant increase or decrease. If we assume that the current population size is 130 individuals (maximum likelihood estimate of total population based on left fin identifications) and impose a constant growth

Figure 7.2: Support surface contours for estimates of population size and mortality rate of reliably marked individuals, based on mortality model. Support function values less than 2 approximate the 95% c.i. region. * indicates maximum likelihood estimate.

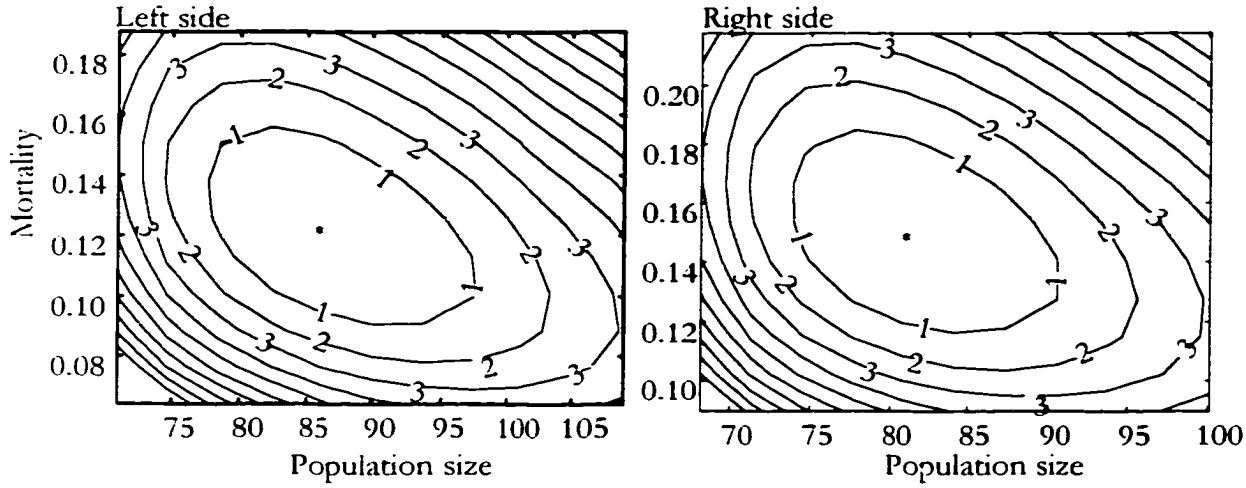
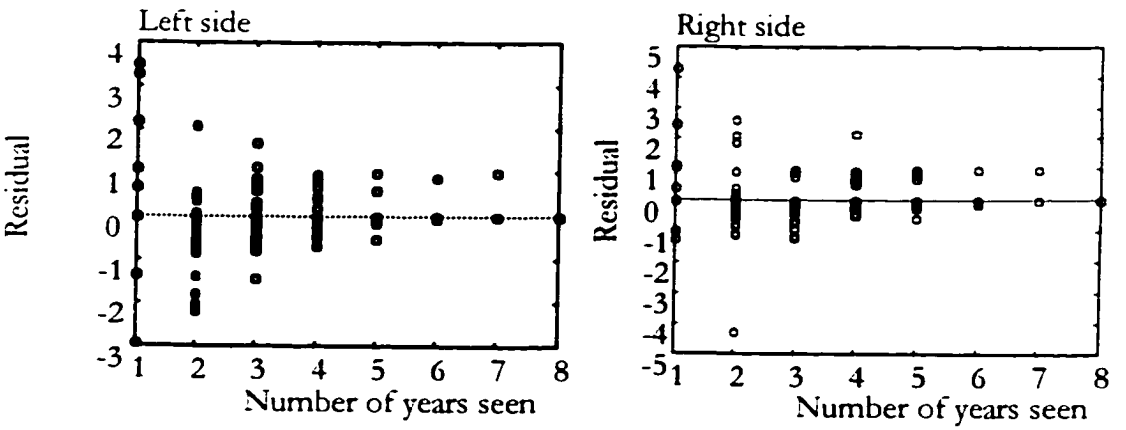


Figure 7.3: Residual difference between the expected and observed number of individuals (based on mortality model) with each identification history plotted against the number of years identified for that identification history.



rate of 0.84% per year (maximum likelihood estimate; see Table 7.1) then the population will be 154 individuals after 20 years. However, the population will shrink to 54 individuals if we impose a constant trend of –4.3% per year (lower limit of 95% c.i.), or will grow to 450 individuals if a constant trend of 6.4% per year is imposed (upper limit of 95%c.i.).

AGE/SEX STRUCTURE

The results of modeling the population size and mortality rates for each age/sex class separately are shown in Table 7.2. There were insufficient data to test the mortality + trend model on these datasets. The best-fit model for both female/immatures and mature males was the mortality model, while a closed model best described the sub-adult male class. However, sub-adult males had the smallest sample size. Mortality rates were lower for the female/immature class, than for either the sub-adult or mature male class although these differences were not significant. Some heterogeneity was observed in the residual plots (not shown), indicating that the population estimates may be negatively biased.

The proportion of each age/sex class that was reliably marked is shown in Table 7.3 along with the estimated population size for each age and sex class. The combined estimated number of individuals in each age and sex class was lower than the estimated total population size as there were some individuals in the population that had not been sexed. The ratio of female/immatures to males (sub-adult and mature combined) was close to parity (1.11:1) for the total estimated population, indicating that there were slightly more female/immatures than maturing or mature males, which was not surprising as some immature males were included in the female/immature class. The ratio of sub-adult males to mature males was also close to parity (1.16:1) and indicated that there were slightly more sub-adult than mature males.

Table 7.2: Population estimates of reliably marked individuals within each age and sex class (95% c.i.). Results were for right side identifications, however, the left side results were similar. Best fit models are shaded.

DATASET	MODEL	POPULATION ESTIMATE	MORTALITY (PER CENT)	LOG LIKELIHOOD
Female/immature male (n=47)	Closed	35 (29-43)		-82.01
Sub-adult male (n=18)				
	Mortality	15 (13-23)	11 (-0.93 - + 29)	-22.98
Mature male (n=19)	Closed	19 (15-27)		-38.63

Table 7.3: Population size estimates of sexed individuals and the proportion of each age and sex class which were reliably marked.

Age/sex class	Proportion of population which is sexed and reliably marked (±SE)	Total population size of sexed individuals (95% c.i.)
Female/immature male	54.8±5.3	47 (37-87)
Sub-adult male	67.2±13.7	22 (16-43)
Mature male	67.4±9.8	19 (14-30)

RESIDENCY

The fit of the three models of residency to left side identifications is shown in Table 7.4. The emigration and re-immigration model best described the data, indicating that within a summer, individuals may enter, leave and re-enter the Gully. On average, there were 43 individuals in the Gully at any given time (33.1 % of the population). Individuals resided in the Gully for approximately 10 days. The standard error of the estimate of the residency period outside of the Gully was large in comparison to the actual estimate, which could indicate that individuals spend variable time periods outside the Gully, and/or that the summer field seasons have not been able to sample a large number of exits and re-entries to the Gully.

Table 7.4: Estimated residency parameters (±SE) for all individuals based on left fin identifications in all years (Q≥4). Best-fit model shaded.

Model	Estimated number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	Log likelihood
Closed	103±13			-2474
Emigration	63±11	37±15		-2428
[redacted]				

Age/sex class differences

The lagged identification rate for each age/sex class are shown in Figure 7.4, as well as the predicted rate for each of the three models (closed, emigration, and emigration and re-immigration). The emigration and re-immigration models fit all three datasets, although the log likelihood ratio indicated that the best-fit model for sub-adult males was the closed model, and for mature males the best model was the emigration model (see Table 7.5). However the smaller sample size (therefore larger jackknife error bars; Figure 7.4) of the sub-adult and mature male datasets, likely precluded the more complex emigration and re-immigration model from being selected. Based on the emigration and re-immigration model, individuals of all age/sex classes, resided in the Gully for approximately 13 days before leaving (Table 7.5).

Figure 7.4: Time lag between photographs of the same individual in each age/sex class. Vertical lines are jackknife error bars.

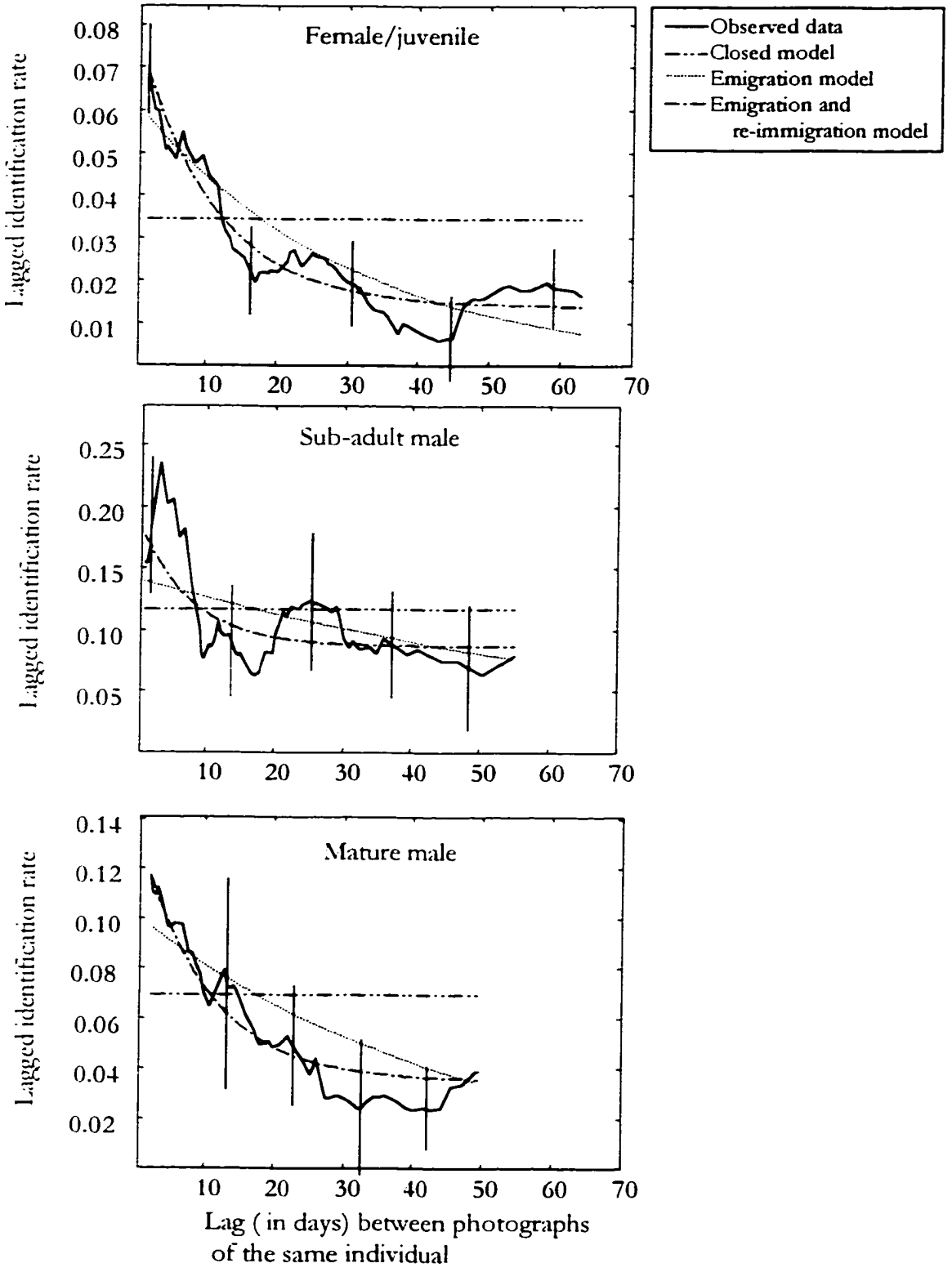


Table 7.5: Estimated residency parameters (±SE) for each age/sex class based on left fin identifications in all years (Q≥4). Best-fit model shaded.

Age/sex class	Model	Number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	Log likelihood
Female/immature male (n=67)	Closed	29±4			-744.35
	Emigration	16±3	30±10		-719.51
Sub-adult male (n=17)					
	Emigration	7±3	89±131		-276.19
	Emigration and re-immigration	5±2	13±7	16±23	-274.26
Mature male (n=27)	Closed	14±3			-203.35
	Emigration and re-immigration	7±3	13±12	38±118	-197.05

Year differences

As individuals in all age and sex classes had similar lagged identification rates (see above), all individuals were pooled together to look at yearly differences, which are shown in Figure 7.5 for 1990, 1996 and 1997 (all years with more than one month in the field). The lagged identification rates for 1990 and 1997 were similar and best fit the emigration model (see Table 7.6), although the data were not inconsistent with the more complex emigration and re-immigration model. The field season in 1990 was shorter than in 1996 and 1997, which may account for the reduced maximum lag values. In 1990 and 1997, individuals spent on average 12 days in the Gully. In 1996 however, individuals spent fewer days in the Gully (mean 5 days) and the best fit model was emigration and re-immigration. There were fewer individuals in the Gully in 1996 and 1997 than in 1990. If we assume that the total population was 130 animals (see above), then the proportion of the total population which was present in the Gully at a given time (based on estimates from the emigration and re-immigration model) declined from 0.41 in 1990 to 0.21 and 0.25 in 1996 and 1997 respectively.

Figure 7.5: Time lag between photographs of the same individual in long field seasons. Vertical lines are jackknife error bars.

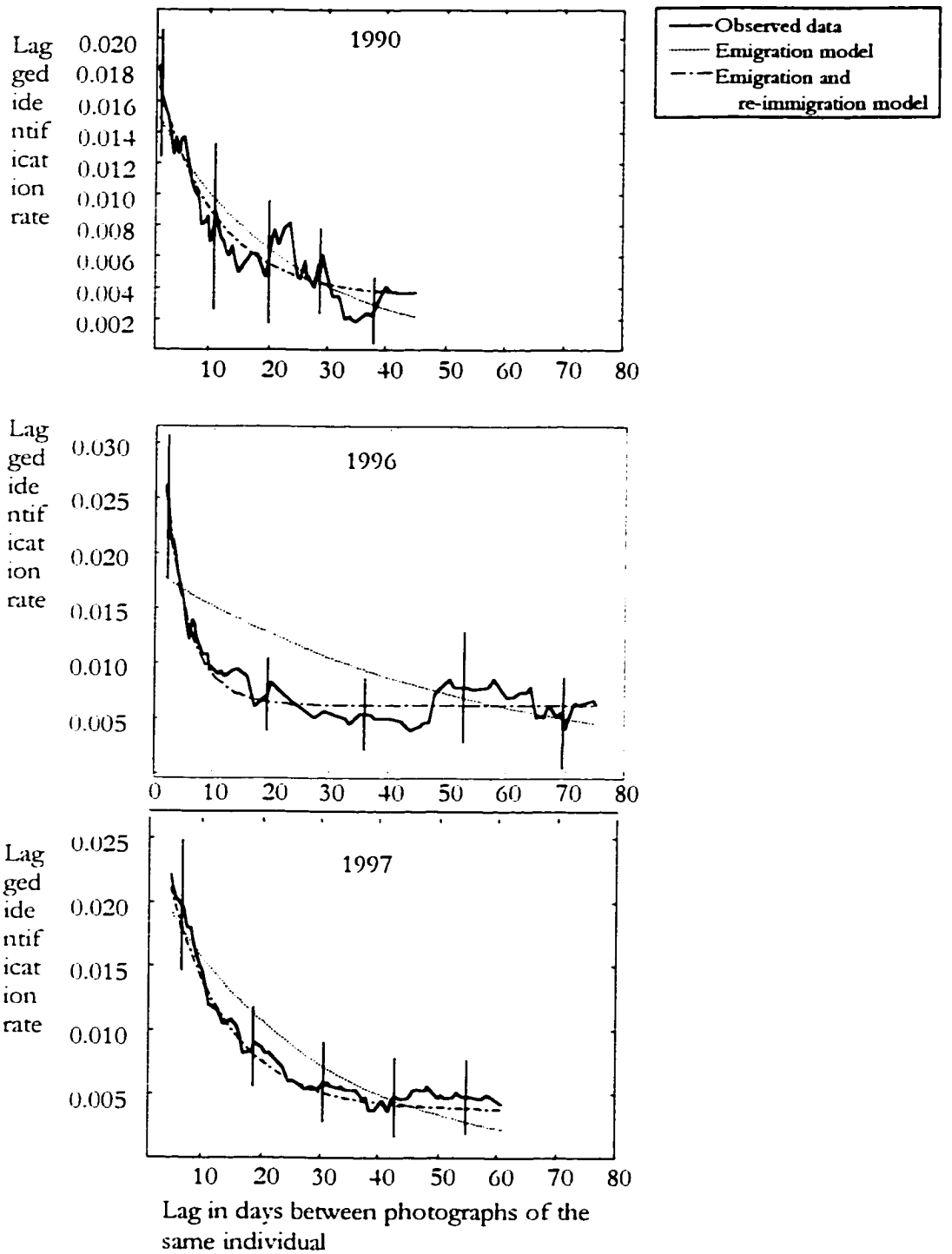


Table 7.6: Estimated residency model parameters (±SE) for individuals based on left fin identifications in each of the years with long field seasons (Q≥4). Best-fit model shaded.

Year	Model	Estimated number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	Log likelihood
1990 (n=119)	Closed	124±21			-1006
	Emigration and re-immigration	53±19	12±12	55 *	-982
1996 (n=81)	Closed	95±20			-560
	Emigration	54±16	53±30		-547
1997 (n=79)	Closed	103±21			-428
	Emigration and re-immigration	32±16	12±10	84±136	-408

* SE very large (over 1 million)

SITE FIDELITY BETWEEN YEARS

Most reliably marked individuals were photographed in the Gully in more than one year, although 38.4% of individuals had not been observed in more than one year by 1997 (see Table 7.7). Approximately half of the reliably marked individuals (50.4%) were photographed in three or more years, indicating at least some individuals repeatedly return to the Gully. As residency analysis indicated individuals spend roughly one to five months outside the Gully (Table 7.4), most individuals probably would be found in the Gully several times a year. There were no obvious differences between the resightings of different age/sex classes (Table 7.8), indicating all classes showed similar site fidelity.

Table 7.7: Number of individuals resighted in the Gully in different years (based on left fin identifications reliably marked individuals Q≥4).

Year first observed	Number of different years photographed						
	1 year	2 years	3 years	4 years	5 years	6 years	7 years
1988 (n=8)	0	0	3	2	1	1	1
1989 (n=44)	7	23	4	4	4	1	1
1990 (n=33)	18	7	3	4	1		
1993 (n=6)	2	3	1				
1994 (n=10)	7	1	1	1			
1995 (n=4)	0	2	2				
1996 (n=20)	14	6					
Percent of individuals (n=125)	38.4	33.6	11.2	8.8	4.8	1.6	1.6

Table 7.8: Proportion of reliably marked individuals of each age/sex class observed in 1990 or 1996 which were also resighted in previous and subsequent years.

AGE/SEX CLASS	OBSERVED IN 1990	OBSERVED IN 1996
All individuals (including unsexed)	0.667	0.694
Female/immature male	1.000	0.667
Sub-adult males	0.667	1.000
Mature males	0.667	0.889

DISCUSSION

POPULATION SIZE AND TRENDS

The estimated population size (130 animals) was smaller than a previous estimate based on 1988-1995 data (230 animals; Whitehead *et al.* 1997c). However the change was not due to a declining population, but instead to a difference in the estimated proportion of the population which was reliably marked. In the earlier estimate, only individuals with notches on the dorsal fin were included in the population estimate analysis, and it was estimated that 29% of the population was notched. Based on the analysis from Chapter 2, more individuals (66% of the population) can be considered reliable marked. The analysis of reliable markings in Chapter 2 was more rigorous than that of Whitehead *et al.* (1997c), and therefore this population estimate was probably more accurate.

The Gully population is small and is largely distinct from other populations of bottlenose whales in the North Atlantic. Preliminary results of mtDNA haplotypes indicates that there is a statistically significant difference between the distribution of haplotypes between the Gully and Labrador, although the test is not strictly valid due to small sample sizes (M.L. Dalebout, University of Auckland, pers. comm.). Bottlenose whales in the Gully are also smaller than bottlenose whales found elsewhere in the North Atlantic (Whitehead *et al.* 1997c) giving further indication of reproductive isolation. The small population size also indicates that the Gully population is isolated from the rest of the North Atlantic; for if whales from the Gully were freely mixing with all other bottlenose whales in the North Atlantic, the entire population of the North Atlantic would be only 130 animals. Recent sightings of bottlenose whales off Labrador, Iceland and the Faroe Islands indicate that the North Atlantic population is much larger than 130 animals (Gunnlaugsson and Sigurjónsson 1990, Reeves *et al.* 1993). The Gully population has likely always been small, although, it may still be recovering from the whaling catch of up to 87 individuals between 1962 and 1967 (Reeves *et al.* 1993). Unfortunately, there was not sufficient power in the dataset to determine the trend of population change.

Estimated mortality rates (which also included mark change and permanent immigration) were imprecise (see 95 % c.i. in Table 7.1) and higher than expected mortality for a long-lived marine mammal (*e.g.*, Small and DeMaster 1995). Analysis from Chapter 2 indicates that reliable marks were gained at a rate of 3.3% per individual per year and were not lost over time, although some marks may be obscured by the gain of new ones. If mark change is estimated at 3% per individual per year, then the mortality + permanent emigration rate can be estimated at 9 or 12 % per year for left and right identifications respectively, which was still higher than expected. While the rate of mortality + permanent emigration + mark change rates for female/immatures was slightly lower than that of sub-adult and mature males, and the precision of these estimates was poor, the estimate may indicate the possiblity that may males have higher mortality rates than females, as found in killer whales (Olesiuk *et al.* 1990). However, small sample sizes limit the precision of the mortality estimates, especially for each age/sex class.

Although the Gully population size was smaller than either the North Atlantic right whale or vaquita (Barlow *et al.* 1997, Caswell *et al.* 1999), and had higher estimated mortality rates (+ permanent emigration), bottlenose whales are less likely to become extinct as the Gully population does not represent the entire species. Recent surveys off Iceland and the Faroe Islands, as well as sightings from Davis Strait indicate that bottlenose whales are routinely sighted further north than the Gully (Sigurjónsson *et al.* 1989, Gunnlaugsson and Sigurjónsson 1990, Reeves *et al.* 1993). While there is some evidence for reproductive isolation between bottlenose whales in the Gully and other areas of the North Atlantic (see above), low levels of migration (on the order of one or two individuals per generation) can prevent inbreeding (Stacey *et al.* 1997) and may be occurring. However the small population size in the Gully does indicate that the population could easily be threatened by human activity.

The number of bottlenose whales in the Gully also resembled the estimated population size of several cetacean species which live in estuarine or coastal environments, especially those which were not isolated from neighbouring populations and show site fidelity (see Table 7.9; and Chapter 8 for further discussion). Coastal environments, especially estuaries, may not be able to support large populations of marine mammals, especially populations with strong site fidelity. Similarly, the Gully ecosystem may only support a small number of resident bottlenose whales, unlike open ocean habitats in which species such as female sperm whales can range widely for dispersed food (Whitehead 1996b, Whitehead *et al.* 1997a). Off New Zealand, an aggregation of male sperm whales inhabits a submarine canyon and also has an estimated size similar to bottlenose whales in the Gully (Childerhouse *et al.* 1995).

Table 7.9: Population sizes and site fidelity of some coastal and offshore populations of cetaceans (* indicates populations which are not isolated from neighbouring populations).

Species	Study location	Population estimate	Site fidelity	References
Bottlenose dolphin	Moray Firth, Scotland (coastal)	129	Yes	Wilson *et al.* 1999
	Monkey Mia (coastal)	300+*	Yes	Smolker *et al.* 1992
	Sarasota Florida (coastal)	100*	Yes	Wells and Scott 1990
	Southern California Bight (coastal)	~250*	No	Defran and Weller 1999, Defran *et al.* 1999
Humpback dolphins	South Africa (coastal)	200-400 *	No	Karczmarski 1996
Sperm whales	Galapagos Islands (oceanic)	1 245 *	No	Whitehead *et al.* 1997a
	Kaikoura, New Zealand (coastal submarine canyon)*	60-108	Some	Childerhouse *et al.* 1995

* This aggregation does not represent an entire population as only immature males are present.

RESIDENCY RATE

Throughout the summer field season, individuals enter the Gully, spend on average 10 days there and then leave, to re-enter at some time later. It is not possible to precisely estimate the time period individuals are spending outside the Gully as the field seasons are not long enough to sample many re-entry events. However most reliably marked individuals have been photographed in more than one year (Table 7.8) and residency rates indicate individuals do return to the Gully. All age/sex classes spent similar time periods in the Gully (see Table 7.5), but there were yearly differences in residency period and the proportion of individuals in the Gully at a given time (see Table 7.6). In 1990, a relatively large proportion of the total population (0.41) was present in the Gully at any given time, which corresponded to the high sighting rate that year. In 1996 and 1997 a smaller proportion of the total population were in the Gully at a given time (0.21 and 0.25 respectively), which corresponded to a lower sighting rate (Hooker In prep.). During 1996, individuals also remained in the Gully for shorter time periods than in other years, which may indicate that conditions were less favourable for bottlenose whales that year within the

canyon itself, in comparison with outside areas. The temporal variability in the use of the Gully (both proportion of individuals found in the Gully and in the residency period) could be linked to either ecological factors or human activity. While changes in ecological factors (such as prey density or distributions) between 1990 and 1996/1997 have not been studied (*e.g.*, Harrison and Fenton 1998 and references therein), there have been marked differences in human activity near the Gully over this time period. In 1990, there was an active fishery for groundfish along the edges of the Gully and little activity related to natural gas exploration or exploitation. However, in 1996 and 1997 there was no ground fishery in the area (due to a moratorium on cod fishing imposed in 1993) but there was an increase in activities related to gas exploration and exploitation.

Lagged identification rates have not previously been applied to any photo-identification data, although resightings of the same individual over time have been occasionally described in some detail. Wilson *et. al* (1999) plotted the sightings of individual bottlenose dolphins in the Moray Firth for sequential surveys. Some individuals appeared to follow an emigration and re-immigration pattern of sightings although this question was not examined directly (Wilson *et al.* 1999; Figure 4). In comparison, bottlenose dolphins in Sarasota Florida appeared to be mainly resident, rarely interacting with individuals from nearby populations and emigration and immigration rates were low (Wells 1991b).

CONCLUSION

The Gully population of bottlenose whales was small (130 individuals) and may be distinct from the rest of the North Atlantic population. The population was not closed within the Gully, with the combined mortality, mark change and emigration rate estimated at 12% per year (95% c.i. 8-17). There was no significant increase or decrease in the population size between 1988-1997, although the trends estimated from left and right side data were in opposite directions (left fin: 0.84% per year, 95 % c.i. –4.3-6.4; right fin: -1.3 % per year, 95% c.i. –5.9-3.1). The sex ratio was roughly 1:1, with approximately equal numbers of sub-adult and mature males. Over the summer field season, individuals emigrated from, and re-immigrated into, the Gully, and spent on average 10 days before leaving. The residency patterns were similar between the age and sex classes, but there were annual differences with a higher proportion of the population present in the Gully in 1990 than in 1996 and 1997; and individuals spent less time in the Gully in 1996 than in 1990 and 1997. Most reliably marked individuals showed some site fidelity between years to the Gully.

Chapter 8: General discussion

The overall purpose of this thesis has been to describe the social organization and population structure of northern bottlenose whales in the Gully and relate these features to their foraging ecology. In all animal species, social organization and population structure are related to ecology as all individuals must find food and most seek protection from predators. Additionally, individuals who survive to sexual maturity need to find mates and the distribution of mates is usually governed by ecological variables. Therefore ecology has driven much of the evolution of social organization and population structure (Wrangham and Rubenstein 1986, Hewitt and Butlin 1997).

SUMMARY OF RESULTS

Groups of bottlenose whales (individuals within five body lengths and coordinating behaviour) probably consisted of interacting individuals (Chapter 4) and most of the associations within the groups were brief (on the order of hours to days; Chapter 5). The social organization of bottlenose whales in the Gully consisted primarily of strong long term bonds between males, which could last for periods of years and a loose network of female associations (Chapter 5). Most young animals associated predominately with their probable mother although babysitting did occur. It is not known however if babysitting in bottlenose whales provided benefits to the mother or young animal, or if the adult companion altered its behaviour to provide babysitting, therefore constituting alloparental care (Chapter 6). The Gully population was small (130 individuals) and individuals routinely left and re-entered the Gully. Bottlenose whales spent on average 10 days in the Gully before leaving, and approximately one-third of the population was present in the Gully at any given time (Chapter 7).

The foraging ecology of bottlenose whales appears to be primarily benthic in focus (Hooker In prep.), although they must return to the surface to breathe. Characteristics of their benthic ecology may lead to similarities in social organization and population structure

with other cetaceans, including some populations of bottlenose dolphins[1] found in much shallower waters.

SOCIAL ORGANIZATION IS RELATED TO ECOLOGY

The social organization of female mammals depends on ecology (predominately foraging ecology) as fitness is related to the production and survival of young, which is related to the females' ability to obtain necessary resources for producing, feeding and protecting offspring. Therefore, female grouping and association patterns should be influenced by the distribution of resources as well as the ability of individuals and groups to exploit these resources (Wrangham and Rubenstein 1986). Male social organization is related in part to ecology, as males must also find food and avoid predation. In most mammals however, males provide little to no parental care, so the reproductive success of a male is related to his ability to find and mate with as many females as possible. Therefore, the social organization of male mammals will be influenced strongly by the distribution and grouping patterns of females, at least during the breeding season. The ability of a male to mate with a female is often constrained by the behaviour and distribution of other males, as males often deter other males from joining "their" group (Wrangham and Rubenstein 1986).

Several populations of bottlenose dolphins in large coastal bays (such as off Shark Bay off Monkey Mia, Australia and Sarasota Bay off Sarasota, Florida) clearly show sex differences in social organization. Within these large bays there are relatively few ecological factors which would cause individuals to form strong permanent bonds with each other. Foraging tends to be solitary and individuals rarely cooperate to feed as food resources are dispersed and individuals differ in preferred foraging techniques (Shane 1990, Smolker *et al.* 1997). Shark attacks, especially on juveniles, do occur and are occasionally fatal; however, dolphins do not band together for protection or to protect calves. Bottlenose dolphins tend to flee when large sharks are observed and individual females may be able to defend their calves

---

[1] It has been suggested that bottlenose dolphins are not monophyletic. The Monkey Mia population may actually belong within the genus *Stenella*, and there may be other taxonomic differences between other populations (see Rice 1998). However following Rice (1998), I classify all of the populations discussed in this chapter as *Tursiops truncatus*.

from attacks by relatively small sharks (Wells 1991a, Connor and Heithaus 1996, Mann and Barnett 1999). Therefore, there may be few benefits to forming permanent bonds and high foraging costs, and females form only loose networks of associations (Wells 1991b, Smolker *et al.* 1992) However, mature males form strong bonds with each other; in order to cooperatively herd females (Wells 1991b, Connor *et al.* 1992, 1999).

Differences in reproductive strategies between males and females can also lead to ecological differences between the sexes. Sperm whales clearly exhibit this phenomenon as females and their young remain year round in the relatively unproductive but warm tropical waters. Males disperse from their natal groups and migrate towards the more productive polar waters, where they grow much larger than the females. Large, reproductively active males migrate back to tropical waters to mate (Best 1979).

POPULATION SIZE AND STRUCTURE IS ALSO RELATED TO ECOLOGY

The ecology of an individual influences the size and structure of the population it inhabits. Population size is constrained by the carrying capacity of the environment, while the population structure can be influenced by the temporal and spatial variability of resources (Whitehead *et al.* 1998b, Defran *et al.* 1999). For example, ephemeral and or labile food resources lead to long range movements and migrations in sperm whales and bottlenose dolphins in the Southern California Bight (Whitehead *et al.* 1998b, Defran *et al.* 1999), while more constant food resources may lead to long term residency, as is observed in bottlenose dolphins found in Monkey Mia, Sarasota and the Moray Firth (Wells 1991b, Smolker *et al.* 1992, Wilson 1995). If individuals must move over long distances to find and exploit variable resources, the distribution of individuals also becomes variable. This may shape the evolution of the social organization of the species as the distribution and social organization of females influences the social organization of males (Wrangham and Rubenstein 1986).

SOCIAL ORGANIZATION AND POPULATION STRUCTURE OF BOTTLENOSE WHALES IN RELATION TO ECOLOGY

Best (1979) and Whitehead (1996a) suggest that the social organization of sperm whales has evolved because of deep diving and the need to communally care for young while mothers forage at depth. Therefore, I initially set out to test the hypothesis that the social organization and population structure of northern bottlenose whales would resemble that of sperm whales as both species are deep divers and feed on squid (Best 1979, Hooker and Baird 1999, Hooker In prep.). However, there were few similarities between the social organization and population structure of sperm whales and northern bottlenose whales (Table 8.1). Therefore, it appears unlikely that the deep diving teuthivorous ecology was the primary influence driving the evolution of social organization and population structure in northern bottlenose whales. This does not necessarily mean the social organization of sperm whales was not driven by deep diving, although it does indicate that not all deep diving cetaceans require strong female bonds to provide communal care of young. Further studies on other deep diving cetaceans may help resolve this issue.

As there were few similarities between bottlenose and sperm whales, I then compared my results to the social organization and population structure of other well-studied cetaceans. As Table 8.2 suggests, the social organization of northern bottlenose whales was most similar to that of some populations of bottlenose dolphins (such as Sarasota Bay off Florida and Shark Bay off Monkey Mia Australia), in which most males form strongly bonded coalitions of two to 14 animals and females form loose networks of associations (Wells 1991b, Smolker *et al.* 1992). There were also some similarities between the population structure of bottlenose dolphins and northern bottlenose whales in the Gully, although differences did occur (Table 8.1 and Table 8.2).

Table 8.1: Social organization and population structure of sperm whales, northern bottlenose whale.

	SPERM WHALE	NORTHERN BOTTLENOSE WHALE
STUDY AREAS	Eastern Tropical Pacific	The Gully
SOCIAL ORGANIZATION		
Group size	20	3.04±1.86
Female-female bonds	Strong	Weak
Male-male bonds	Weak to non-existent	Strong
Length of associations between strongly bonded individuals	Mostly life long (Females)	Some pairs associated at least several years (Males)
Babysitting benefit mother or calf	Yes	Unknown
POPULATION SIZE AND STRUCTURE		
Size	1245	130
Span of movements[1]	~1,000 km	~10 km within Gully ~ 200 km outside[2]
Isolated from neighbouring populations	Unlikely, but difficult to define population	Likely
Site fidelity[3]	No	Likely
References	Whitehead 1996a, Whitehead *et al.* 1997a, Christal 1998, Christal *et al.* 1998	This study

1) Over periods of months – however this measurement not well studied
2) Span of movements outside the Gully not well studied.
3) Site fidelity = constant presence or routine sightings (*i.e.*, several times a year) in study area.

Table 8.2: Social organization and population structure of well-studied cetaceans (see Table 8.1 for sperm and bottlenose whales).

	Resident killer whale	Pilot whale	Spinner dolphin	Hector's Dolphin	Bottlenose dolphin
Study areas	B.C./ Washington	World	Hawaii	Banks Peninsula, New Zealand	Sarasota and Monkey Mia
SOCIAL ORGANIZATION					
Group size	mean 12; range 3-59	mean 25-85 different areas	20; range 6-250	2-8	4.8
Female-female bonds	Strong	Likely strong	Weak	Weak	Weak
Male-male bonds	Strong	Likely strong	Weak	Weak	Strong
Length of associations between strongly bonded individuals	Lifelong	Likely lifelong	Mostly short term; but some long term associations	Short term	Likely lifelong
Babysitting benefit mother or calf	Unknown	N/A	N/A	N/A	No
POPULATION SIZE AND STRUCTURE					
Size	less than 300	~10,000 – 100,000	~1,000	~500-1,000	~ 100 Sarasota; ~ 300 Monkey Mia
Span of movements[1]	~250 km	Unknown but likely large	~100 km	~10 km	~10 km
Isolated from neighbouring populations	No	No	No	Yes	No
Site fidelity[2]	Yes	Unknown	Some	Yes	Yes
References	Bigg *et al.* 1990, Baird In press	Amos *et al.* 1991, Bernard and Reilly 1999	Würsig *et al.* 1994a, Marten and Psarako In press	Slooten *et al.* 1993, Bejder *et al.* 1998	Wells 1991b, Smolker *et al.* 1992

1) Over periods of months – however this measurement not well studied
2) Site fidelity = constant presence or routine sightings (*i.e.*, several times a year) in study area.

While there were similarities between the social organization of northern bottlenose whales and some populations of bottlenose dolphins, other populations of bottlenose dolphins showed different patterns of associations (Table 8.3). Of the four long-term studies on bottlenose dolphins focusing on social organization, only populations found in Monkey Mia and Sarasota show long-term bonds between males. These two populations have long term site fidelity, with individuals rarely leaving the study area (Wells 1991b, Smolker *et al.* 1992). Bottlenose dolphins in the Moray Firth do leave the study area at times, while bottlenose dolphins in the South California Bight range widely rarely staying long in one area (Wilson 1995, Defran *et al.* 1999). The differences in the range and movements of individuals are likely linked to differences in the distribution and variability of prey. Bottlenose dolphins in the South California Bight likely experience the greatest variability in prey availability and distribution due to the strong but episodic influence of El Niño. This population also showed the largest group sizes, most fluid association patterns and the greatest span of movements (Table 8.3). Thus the spatial range and movements of individuals may be leading to differences in social organization amongst bottlenose dolphins and in cetaceans in general.

Table 8.3: Social organization and population structure of several different populations of bottlenose dolphins[1].

	Sarasota	Monkey Mia	Moray Firth	Southern California Bight
STUDY AREA				
Large coastal bay	yes	yes	mostly, but open to ocean	no
SOCIAL ORGANIZATION				
Group size ± SD	4.8 ± 4.3	4.8 ±2.7	6.45	19.8 ± 18.4
Female –female associations	Loose network	Loose network	Loose network	No individuals sexed, but few strong associations and most were weak and fluid
Male – male associations	Long term bonds between some individuals, some singletons	Long term bonds between some individuals, one large group of associated individuals	No detected long term bonds	
POPULATION STRUCTURE				
Isolated from neighbouring populations	No	No	Yes	No
Span of movements[2]	~50 km	~50 km	~70 km	600+ km
Repeat yearly sightings[3]	Most individuals resighted over years	Most individuals resighted over years	Most individuals resighted over years	Few repeat sightings within small study areas
References	Wells 1991b	Smolker *et al.* 1992, Connor *et al.* 1999	Wilson 1995	Weller 1991, Defran and Weller 1999, Defran *et al.* 1999

1) Other populations have been studied, but only over short time periods or did not focus on social organization. Many studies on bottlenose dolphins are currently in progress and will likely elucidate many of the ecological factors driving sociality in bottlenose dolphins.
2) Over periods of months – however this measurement not well studied
3) Site fidelity = constant presence or routine sightings (*i.e.*, several times a year) in study area.

WHY DO NORTHERN BOTTLENOSE WHALE SOCIAL ORGANIZATION AND POPULATION STRUCTURE RESEMBLE BOTTLENOSE DOLPHINS FOUND IN LARGE COASTAL BAYS?

The ecologies of northern bottlenose whales and bottlenose dolphins from large coastal bays appear very different. The average depth of the study areas off Sarasota and Monkey Mia is less than 10 m (Wells 1991b, Smolker *et al.* 1992). While Moray Firth off Scotland is deeper (less than 235 m, Wilson 1995), bottlenose whales in the Gully are usually found in waters deeper than 1,000 m (Hooker *et al.* In press). All these bottlenose dolphin study areas are in large bays, although the Monkey Mia study area covers only a small portion Shark Bay (Wells 1991b, Smolker *et al.* 1992, Wilson 1995), while the Gully is located approximately 200 km off shore (Hooker *et al.* In press). Additionally both Monkey Mia and Sarasota study areas are in tropical waters with much higher water temperatures than either the Gully or Moray Firth (Wells 1991b, Smolker *et al.* 1992, Wilson 1995, Hooker *et al.* In press). However, the similarities in population structure and social organization do exist (Table 8.1). As ecological features are likely driving the evolution of social organization and population structure, there should be some ecological similarities between the Gully and the large coastal bays where these populations of bottlenose dolphins are found.

Northern bottlenose whales are benthic foragers

All evidence suggests that northern bottlenose whales in the Gully are probably primarily benthic foragers (Hooker In prep.). Analysis of their diving behaviour indicated that they are routinely dive deeply, to or at least very near, the sea floor (Hooker and Baird 1999). Diet analysis conducted on biopsy samples indicated that bottlenose whales in the Gully mainly feed on adults of the squid genus *Gonatus*, which is believed to live near the sea floor (Hooker In prep.). The distribution of bottlenose whales in the Gully also showed no significant correlation with concentrations of biomass in the upper water column but did show some correlation with mid water biomass (Hooker In prep.). Additionally, whalers off Labrador found mud on the beaks and benthic animals, including starfish and sea cucumbers in the stomachs of bottlenose whales (Benjaminsen and Christensen 1979).

Gully may resemble a "benthic-estuary" for benthic animals

Plankton concentrations within and outside the Gully were not much different, nor was there any evidence to support the hypothesis that surface and mid water concentrations of biomass were higher inside the Gully than outside (Head and Harrison 1998). Therefore it is unlikely that the concentration of bottlenose whales in the Gully is supported directly by surface or mid-water biomass. Although there have been no direct studies of benthic currents in the Gully (Harding 1998), it has been suggested that there is an inflow of nutrients into the Gully along the sea floor. Submarine canyons are believed to funnel nutrients from the shelf edge to the deep ocean (Gardner 1989), and benthic biodiversity is greatly increased in slope waters at depths from 40 to 1,290 m (Haedrich *et al.* 1980).

If there is a benthic influx of nutrients, then the Gully may resemble an estuarine ecosystem for benthic animals. As the ecosystem of the main prey of bottlenose whales (*Gonatus* sp.) appears to be mainly benthic in nature with little direct input from surface phytoplankton, bottlenose whales should be considered predominantly benthic animals, that happen to travel to the surface to breath, rather than surface animals that dive to feed. The benthic environment of the Gully may be less variable than the surface and mid-water environments as the influx of nutrients may be more constant and predictable, as found in Baltimore Canyon (Gardner 1989). The constant and predictable nature of food resources for bottlenose whales within the restricted area of the Gully may be driving the similarities in population structure and social organization between bottlenose whales and bottlenose dolphins in large coastal bays.

Gully unique on east coast North America

Cetacean abundance along the shelf break of the United States was not generally elevated in submarine canyons (Kenney and Winn 1987), in contrast to the high abundance found in the Gully (Whitehead *et al.* 1998a). However, the Gully represents a unique bathymetric feature along the east coast of North America, as it is much larger in size in comparison to other canyons on the shelf, and cuts much deeper into the shelf edge (Whitehead *et al.* 1998a). The shape of other canyons may not support a similar deep water influx of nutrients, or the other canyons may be too small to support a resident population of

cetaceans. While several other submarine canyons throughout the world have abundant populations of cetaceans (*e.g.*, Kaikoura New Zealand, Trincomalee Sri Lanka, and Monterey California), all of these canyons are located close to shore and likely have different physical oceanography than an offshore canyon (Whitehead *et al.* 1998a), and so may not resemble a "benthic-estuary".

IMPLICATIONS FOR UNDERSTANDING NORTHERN BOTTLENOSE WHALES IN OTHER AREAS

If the benthic influx of nutrients into the Gully drives the pattern of social organization and population structure of northern bottlenose whales, then it may be problematic to assume that other populations of bottlenose whales behave similarly. The Gully may be a unique habitat for bottlenose whales, as no other populations are known to reside in a canyon. As all other populations do appear to live near the shelf break and feed benthically (Benjaminsen and Christensen 1979), there may still be some similarities. However other cetacean species (*e.g.*, bottlenose dolphins; Table 8.3) show differences between populations.

Additionally it may be problematic to assume that all bottlenose whales behave like bottlenose whales in the Gully, as the Gully population is likely a disturbed population. Although all populations of northern bottlenose whales in the North Atlantic were affected by whaling (Reeves *et al.* 1993), the degree of depletion and recovery may vary between populations. Whaling between 1962 and 1967 not only removed a large proportion of the population (87 bottlenose whales from the Gully and surrounding area; Reeves *et al.* 1993) but also a pod of killer whales in the area was removed, which may have been the main predator of bottlenose whales (Mitchell and Reeves 1988). Current activities, including fishing and oil and gas development in the area may also be altering the behaviour of the whales.

IMPLICATIONS FOR UNDERSTANDING CETACEAN SOCIALITY

The horizontal range and movements of individuals may be a very important factor in determining the social organization of cetaceans, although vertical movements may also be important, at least in some species. For example, much of sperm whale sociality appears to

be driven by communal babysitting while the mother forages (Best 1979, Whitehead 1996a). Bottlenose whales appear to have a more flexible system of care for young animals in which offspring are sometimes left alone at the surface, sometimes strongly associated with a probable mother, and sometimes associated with non-mothers (Chapter 6). Several factors may be involved in the lack of structured babysitting in bottlenose whales: young animals may be able to dive with their mothers so that babysitting is not required; predation risk may be lower in bottlenose whales; and the density of whales in the Gully may be high enough that there are often other animals at the surface with which a young animal may associate. Therefore, the deep diving behaviour of bottlenose whales has not led to a similar social organization as found in sperm whales.

The similarities in horizontal ranging and movements of bottlenose whales and some populations of bottlenose dolphins probably lead to the similarities in social organization and population structure despite differences in diving ranges (Hooker and Baird 1999; Table 8.1 and 8.2). Comparisons of different populations of bottlenose dolphins indicates that differing horizontal range and movements, which are likely related to food distribution, may lead to differences in sociality and population structure even within a species (see Table 8.3). Many of these differences may be related to the distribution and variability of prey, which led to differences in horizontal movements and ranging behaviour. When food resources are labile, cetaceans may live in larger groups and range over large areas (*e.g.*, sperm whales in the Eastern Tropical Pacific; Arnbom and Whitehead 1989, Smith and Whitehead 1993 and bottlenose dolphins in the Southern California Bight; Defran and Weller 1999, Defran *et al.* 1999).

If the social organization and population structure of northern bottlenose whales in the Gully is being driven by the benthic influx of nutrients in the Gully, then one would expect that other beaked whales which reside in submarine canyons may show a similar pattern of social organization and population structure. However, there is little known about most populations of beaked whales. Observed groups of Cuvier's beaked whale and most mesoplodons are fairly small (usually in 2-6 animals) which may indicate similar social organization to northern bottlenose whales (Heyning 1989, Mead 1989a). In contrast,

Baird's and Arnoux's beaked whales (*Berardius arnouxii*) are often found in larger groups (six or more individuals) and may have a different social organization (Balcomb 1989). Preliminary results from studies on dense beaked whales (*Mesoplodon densirostis*) off the Bahamas (from 1992-1998) indicates that while individuals appear to routinely return to the same general area, the social organization is very different from northern bottlenose whales. In dense beaked whales, there have been no observations of groups containing more than one adult male, and individual adult males sometimes associate with the same female group for months (D. Claridge, Bahamas Marine Mammal Survey, pers. comm.).

The differences in social organization and population structure between sperm and northern bottlenose whales may also represent niche separation between deep diving squid eaters. Sperm whales range widely and feed on a wide variety of different species of squid (Kawakami 1980, Smith 1992, Whitehead *et al.* 1997a) whereas bottlenose whales, at least in the Gully, appear to be mainly resident (Chapter 7), and appear to feed primarily on one species of squid (Hooker In prep.). Similar niche separation occurs in African antelope. Reedbucks (*Redunca* sp.) and similar species are highly selective foragers, preferring only a few food types, live in relatively small groups and have small home ranges. Buffaloes (*Syncerus caffer*) and elands (*Taroutragus derbianus*), on the other hand do not feed selectively, foraging on a wide range of vegetation, live in large groups and have large home ranges (Jarman 1974).

OVERALL CONCLUSIONS

The social organization and population structure of northern bottlenose whales appear to be related to their ecology, but not to the aspects of ecology that they share with sperm whales (deep diving, squid eating). Instead, the social organization and population structure may be related to the benthic nature of the ecosystem on which bottlenose whales depend. Within the deep waters of the Gully, there appears to be a profitable food source with relatively little temporal or spatial variation (compared to most oceanic areas). Therefore it is very important to investigate the appropriate ecological variables that drive the evolution of social organization and population structure. In cetaceans, the variability and predictability of resources, which may be indicated by the spatial range and movements of individuals, appears to be a important in the evolution of social organization and population structure. Further studies on social organization, population structure and ranging behaviour will help elucidate the selective pressures leading to sociality in northern bottlenose whales and other cetaceans.

Appendix 1: Photographic quality ratings

Table A1.1: Factors involved in defining photographic quality ratings (Arnbom 1987).

Factor	Description	Comments
Focus	Clarity of the image	photographic quality was very sensitive to focus, any blurryness degraded the image noticeably
Size	Proportion of the fin located in the frame	Photographic quality was less sensitive to size, however subtle marks were not detectable if the whale was distant
Exposure	Relative darkness or lightness of the photo	Photographic quality relatively insensitive to exposure although very dark or very light photographs were assigned lower quality
Orientation	angle between the anterior-posterior axis of the whale and plane of the camera lens	Photographic quality less sensitive to orientation, however angles greater than 30° reduced the quality rating
Percent visible	Area of the fin and flank visible	Photographic quality relatively insensitive to percent visible, if the entire fin was exposed.

Table A1.2: Photographic quality.

Q-value	Comments
6	Exceptional quality photograph: everything perfect. In focus, whale close to the boat and parallel when photographed, well exposed, and the entire fin and flank approximately one dorsal fin width anterior and posterior to the fin exposed
5	Excellent quality photograph: most factors perfect. In focus, , whale close to the boat and parallel when photographed, however may have slightly poorer exposure or less of the whale visible
4	High quality photograph: most factors good. Photograph still in focus but, whale may be further from boat when photographed or less parallel orientation. Alternately the exposure may be poor or only the dorsal fin visible.
3	Low quality photograph: most factors OK but one factor very poor: Photograph out of focus, whale distant, or orientation poor. Exposure may be very bad, or dorsal fin partially obscured by water
2	Very poor photographs: most factors very bad: Photograph out of focus, whale distant, and orientation poor. Exposure may be very bad, and dorsal fin partially obscured by water
1	Unusable photograph: all factors very bad: Practically impossible to distinguish features of dorsal fin

Appendix 2: Testing permutation results for photographs of Q≥4

Testing for preferred companionship against randomly permuted data using photographs of Q≥4 indicated few significant results (Table A2.1 and A2.2; see Chapter 5 for full details on using randomized permutations to test for preferred companionship). As significant results were obtained when all quality photographs were included (Table 5.5 and 5.6) the potential problems created by misidentification of individuals was outweighed by the benefits of increasing the power of the test.

Table A2.1: Mean association indices for observed and randomly permuted data constrained within five day samples. Individuals considered were reliably marked, had both left and right fin identifications, and photographs of all qualities. Lower mean association indices for the real data indicates preferred companionship. ** significant at $P<0.05$.

Dataset	Number of permutations	Mean association index		*P*-value
		Observed data	Random data	
All individuals (n=107)	40,000	0.01035	0.01138	0.00005**
Female-female associations (n=31)	40,000	0.01382	0.01405	0.38795
Sub-adult male – sub-adult male associations (n=15)	20,000	0.04795	0.05001	0.26295
Mature male – mature male associations (n=18)	10,000	0.02223	0.02388	0.15950

Table A2.2: Standard deviation of mean association indices for observed and randomly permuted data, constrained within five day samples. Individuals considered were reliably marked, had both left and right fin identifications, and photographs of all qualities. Higher SD of the mean association indices for the real data indicates preferred companionship. ** significant at $P<0.05$.

Dataset	Number of permutations	SD of mean association index		P-value
		Observed data	Random data	
All individuals (n=107)	40,000	0.04779	0.04603	0.88528
Female-female associations (n=31)	20,000	0.04206	0.04191	0.64310
Sub-adult male – sub-adult male associations (n=15)	10,000	0.13474	0.13495	0.44590
Mature male – mature male associations (n=18)	10,000	0.07946	0.06696	0.81250

Appendix 3: Assumptions about associations between adults and calves or juveniles

Testing hypothesis 1: Young animals and their mothers associate at the surface. If babysitting does not occur, then the mother should always be present in the same group. If babysitting does occur, then the young animal may associate with other individual, but it should still be associated with its mother frequently.

Table A3.1: Associates of juvenile 301 in 1990.

Date	Time	Associates	Age/sex class
26/06/90	8:46-9:06	302	Female/immature
05/07/90	19:09-19:15	None	
08/07/90	10:25-10:48	352	

Table A3.2: Associates of juvenile 642 in 1993.

Date	Time	Associates	Age/sex class
12/07/93	17:41-17:48	507	Female/immature
15/07/93	17:12-17:25	507	Female/immature
		2 unidentified associates	
15/07/93	17:34-18:20	507	Female/immature
15/07/93	19:13-19:30	54	Female
		507	Female/immature
		667	
		682	Juvenile
16/07/93	9:05-9:30	507	Female/immature
		2 unidentified associates	
17/07/93	9:05-9:35	507	Female/immature

Table A3.3: Associates of juvenile 682 in 1993.

Date	Time	Associates	Age/sex class
15/07/93	19:13-19:30	54	Female
		507	Female/immature
		642	Juvenile
		667	
17/07/93	10:16-10:26	629	Female/immature
		690	Female/immature
17/07/93	12:13-12:38	54	Female
		690	Female/immature
19/07/93	16:51-17:12	102	Immature male
		701	Female/immature

Table A3.4: Associates of calf 1023 in 1996.

Date	Time	Associates	Age sex class
10/06/96	9:09-9:42	1024	
		2 unidentified associates	
10/06/96	9:45-10:41	1025	Female/immature
		1 unidentified associate	
19/06/96	11:56-12:33	143	Immature male
		1062	
		1063	
19/06/96	12:56-13:06	143	Immature male

Table A3.5: Associates of juvenile 1146 in 1996, 1997 and 1998.

Date	Time	Associates	Age/sex class
25/08/96	16:55-17:16	37	Mature male
		124	Sub-adult male
		1039	Mature male
		1142	
		1143	Mature male
		1144	
		1 unidentified associate	
24/08/97	14:21-14:58	131	Sub-adult male
		649	
		1337	
		1357	Sub-adult male
		1358	Female/immature
		7 unidentified associates	
25/08/97	9:45-9:57	45	Female/immature
		56	Female/immature
		131	Sub-adult male
		1039	Mature male
		1 unidentified associate	
19/07/98	11:51-12:08	45	Female/immature
		131	Sub-adult male
		1414	
		1 unidentified associate	
	13:13-13:38	89	Female/immature
		131	Sub-adult male
		1417	
		2 unidentified associates	
20/08/98	15:05-17:11	10	
		33	Mature male
		56	Female/immature

		131	Sub-adult male
		824	Mature male
		907	
		1414	
		1422	
		1452	
		1454	
		1458	
26/07/98	16:28-16:35	45	Female/immature
		1019	
		1332	Female/immature
	17:43-18:11	37	Mature male
		45	Female/immature
		131	Sub-adult male
		1332	Female/immature
		1334	Juvenile
		1472	
27/08/98	16:00-16:12	3	Mature male
		131	Sub-adult male
		2 unidentified associates	
28/07/98	10:08-10:25	131	Sub-adult male
		1472	
	12:59-14:07	45	Female/immature
		131	Sub-adult male
		824	Mature male
		907	
		1019	
		1424	
	15:05-15:36	45	Female/immature
		131	Sub-adult male
		1019	
		1470	
	17:45-18:47	45	Female/immature
		131	Sub-adult male
		1019	
		1 unidentified associate	
09/08/98	15:50-16:39	45	Female/immature
		131	Sub-adult male
		1019	
		1 unidentified associate	
10/08/98	15:51-15:59	45	Female/immature
		131	Sub-adult male
		1019	
11/08/98	8:55-9:27	45	Female/immature

		94	Sub-adult male
		131	Sub-adult male
		1019	
		1501	
		1 unidentified associate	
	9:39-10:42	45	Female/immature
		131	Sub-adult male
		1019	
		1501	
		2 unidentified associates	
15/08/98	8:29-10:09	3	Mature male
		45	Female/immature
		94	Sub-adult male
		131	Sub-adult male
		1019	
		1336	Female/immature
		1404	
	15:52-16:18	3	Mature male
		131	Sub-adult male
		804	Female/immature
16/08/98	8:48-9:28	45	Female/immature
		131	Sub-adult male
		1019	
		1404	

Table A3.6: Associates of juvenile 1239 in 1997 and 1998.

Date	Time	Associates	Age/sex class
02/07/97	11:43-12:12	54	Female
		409	Female/immature
		4 unidentified associates	
02/07/97	12:40-12:42	54	Female
		409	Female/immature
		3 unidentified associates	
02/07/97	13:37-13:42	54	Female
		409	Female/immature
		3 unidentified associates	
31/07/97		54	Female
		102	Sub-adult male
		950	Mature male
		1292	Mature male
		1293	
04/08/97		45	Female/immature
		54	Female
		961	Female
20/08/98	15:23-15:55	54	Female
		1313	Female/immature
26/08/98	18:45-19:14	1470	Juvenile
28/08/98	06:39-06:56	1469	
		4 unidentified associates	
	14:16-14:55	1	Mature male
		10	
		33	Mature male
		54	Female
		1454	
		1 unidentified associate	
08/08/98	12:07-12:37	54	Female
09/08/98	10:06-10:41	54	Female
		102	Sub-adult male
		1500	

Table A3.7: Associates of calf 1272 in 1997 and as a juvenile in 1998.

Date	Time	Associates	Age sex class
07/07/97	10:58-11:06	54	Female
		159	
		1270	
		1 unidentified associate	
07/07/97	11:38-11:46	159	
		952	Female
08/07/97	18:26-18:41	159	
09/07/97	16:32-16:35	2 unidentified associates	
14/07/98	10:43-10:56	2 unidentified associates	

Table A3.8: Associates of calf 1274 in 1997.

Date	Time	Associates	Age/sex class
07/07/97	14:02-14:11	54	Female
		952	
		1 unidentified associate	
13/07/97	12:58-13:02	2 unidentified associates	

Table A3.9: Associates of juvenile 1334 in 1997 and 1998.

Date	Time	Associates	Age sex class
16/08/97	9:52-10:28	124	Sub-adult male
		1332	Female/immature
22/07/98	09:28-10:13	1469	
		1470	Juvenile
26/07/98	16:37-16:58	1	Mature male
		1332	Female/immature
	17:48-18:11	37	Mature male
		45	Female/immature
		131	Sub-adult male
		1146	Juvenile
		1332	Female/immature
		1472	
27/07/98	08:34-08:53	1332	Female/immature

Testing Hypothesis 2: Mothers associate with their offspring whenever they are at the surface. Although the young animal may associate with other individuals (especially if babysitting does occur), the mother should associate with her offspring whenever she is at the surface. Juvenile 301: This juvenile was associated with two individuals, each of which were only observed once during the summer; in association with 301. Neither associate nor the juvenile were observed in previous or subsequent years

Table A3.10: Sighting history of associates of juvenile 642 in 1993. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 642 was present. * individual is another juvenile.

ID	July 12	14	15				16	17				19
54		o				•					•	
507	•			•	•	•	•	•	•			
667			•			•						
682*						•				•	•	•

Table A3.11: Sighting history of associates of juvenile 682 in 1993. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 682 was present. * individual is another juvenile.

ID	July 12			14	15					16						19		20
54				o					•						•			
107	o															•	o	
507			•				•	•	•	•	•	•						
629		o				o							o		•			•
642*			•				•	•	•	•		•						
667					•				•									
690															•	•		
701																•	o	

Table A3.12: Sighting history of associates of calf 1023 in 1996. Each box represents a group and • indicates a calf was present; o no calf present. The shaded columns indicate groups in which calf 1023 was present.

ID	June 10			17				18				19			20			Aug 25	27	
143				o	o	o	o					•	•		o	o		o	o	o
1024	•																			
1025		•	o																	
1062						o			o	o	o	•		o		o	o			
1063						o	o		o		o	•		o						

Table A3.13: Sighting history of associates of juvenile 1146 in 1996. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1146 was present.

ID	June 9		10		July 30	Aug 1		Aug 25		Aug 27	
37	o	o	o					•			o
124		o		o	o	o	o	•	o		
1039				o				•			
1142								•		o	o
1144								•			

Table A3.14: Sighting history of associates of juvenile 1146 in 1997. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1146 was present.

ID	June 21			July 31			Aug 4	12		14	16					18	20			24	25				
45				o	o	o	•	o	•	o		o	o			o					•				
56										o	o	o	o	o							•				
131																				•	•				
649																				•					
804	o	o	o															o			•				
1039										o	o	o	o								•				
1337														o	o		o			•		o	o	o	
1357																			o	•					
1358																			o	•			o		

Table A3.15: Sighting history of repeat associates of juvenile 1146 in 1998. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1146 was present. Individuals which associated with 1146 in only one group are not shown.

ID	July 14				19			20	21	26		27			28					Aug 9		10	11		15			16	17
45		o	o	o	•			o	o	•	•	o				•	•	o	•	o	•	•	•	•	•			•	•
131					•	•	•				•		•		•	•	•		•		•	•	•	•	•	o	•	•	
1019	o									•				o		•	•		•		•	o	•	•	•	o		•	•

Table A3.16: Sighting history of repeat associates of juvenile 1239 in 1997. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1239 was present. Individuals which associated with 1146 in only one group are not shown.

ID	July 2			3	6	7			9		13							16	31	Aug4
54	•	•	•			•	•	o										o	•	•
409	•	•	•	o	o				o	o	o	o	o	o	o	o	o			

Table A3.17: Sighting history of associates of juvenile 1239 in 1998. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1239 was present.

ID	July 14	20			21		22	23	26							27			28						29	Aug 8		9		15			19		21	
1	o		o	o	o		o								•		o		o					•												
10		•					o		o	o			o	o					o					•		o				o						
33		•					o		o				o	o					o					•		o							o	o		
54						•										•					•			•			•	•								
102																																				
1313						•				o	•					•												•			o					
1454		•					o												o					•											o	o
1469								•			•							•		•		•			•											
1470								•							•					•	•		•	•		•										
1500																												•								

Table A3.18: Sighting history of associates of calf 1272 in 1997. Each box represents a group and • indicates a calf was present; o no calf present. The shaded columns indicate groups in which calf 1272 was present.

ID	July 2			7				8	9			13					16	31	Aug 4	25
54	o	•	•	•	•		•										o	o	o	
159				•	•	•		o	•	•	o									o
1270					•															
952						•	•					o	•	•	o	•	o			

Table A3.19: Sighting history of associates of calf 1274 in 1997. Each box represents a group and • indicates a calf was present; o no calf present. The shaded columns indicate groups in which calf 1274 was present.

ID	July 2			7				11	13				31		
54	o	•	•	•	•		•						o	o	o
952						•	•	•	•	o	•	o			

Table A3.20: Sighting history of repeat associates of juvenile 1334 in 1998. Each box represents a group and • indicates a juvenile was present; o no juvenile present. The shaded columns indicate groups in which juvenile 1334 was present. Individuals which associated with 1334 in only one group are not shown.

ID	July 22		26					27
1332		o	•	o	•	•	•	•

Literature cited

Agler, B. A. 1992. Testing the reliability of photographic identification of individual fin whales (*Balaenoptera physalus*). Reports of the International Whaling Commission 42:731-737.

Agler, B. A., J. A. Beard, R. S. Bowman, H. D. Corbett, S. W. Frohock, M. P. Hawvermale, S. K. Katona, S. S. Sadove and I. E. Seipt. 1990. Fin whale (*Balaenoptera physalus*) photographic identification: methodology and preliminary results from the western North Atlantic. Reports of the International Whaling Commission (special issue) 12:349-356.

Alexander, R. D. 1974. The evolution of social behaviour. Annual Review of Ecology and Systematics 5:325-383.

Amos, B., J. Barrett and G. A. Dover. 1991. Breeding behaviour of pilot whales revealed by DNA fingerprinting. Heredity 67:49-55.

Amos, B., C. Schlötterer and D. Tautz. 1993. Social structure of pilot whales revealed by analytical DNA profiling. Science 260:670-672.

Amos, W., H. Whitehead, M. J. Ferrari, D. A. Glockner-Ferrari, R. Payne and J. Gordon. 1992. Restrictable DNA from sloughed cetacean skin; its potential for use in population analysis. Marine Mammal Science 8:275-283.

Anonymous. 1998. Thank you for saving the Gully. Working for wildlife: A quarterly action. World Wildlife Fund Canada 1.

Arnbom, T. 1987. Individual identification of sperm whales. Reports of the International Whaling Commission 37:201-204.

Arnbom, T., and H. Whitehead. 1989. Observations on the composition and behaviour of groups of female sperm whales near the Galápagos Islands. Canadian Journal of Zoology 67:1-7.

Arnbom, T., V. Papastavrou, L. S. Weilgart and H. Whitehead. 1987. Sperm whales react to an attack by killer whales. Journal of Mammalogy 68:450-453.

Baillie, J., and B. Goombridge, eds. 1996. The 1996 IUCN red list of threatened animals. IUCN Species Survival Commission, Gland, Switzerland.

Baird, R. W. In press. The killer whale - foraging specializations and group hunting. *in* J. Mann, R. C. Connor, P. Tyack and H. Whitehead, eds. Cetacean Societies. University of Chicago Press, Chicago.

Baird, R. W., and L. M. Dill. 1995. Occurrence and behavior of transient killer whales: seasonal and pod-specific variability, foraging behavior and prey handling. Canadian Journal of Zoology 73:1300-1311.

Baird, R. W., and L. M. Dill. 1996. Ecological and social determinants of group size in *transient* killer whales. Behavioral Ecology 7:408-416.

Baker, C. S., A. Perry and L. M. Herman. 1987. Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. Marine Ecology Progress Series 41:103-114.

Baker, C. S., L. Medrano-Gonzales, J. Calambokidis, A. Perry, F. Pichler, H. C. Rosenbaum, M. Straley, J. R. Urbán, M. Yamafuchi and O. von Ziegesar. 1998. Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. Molecular Ecology 7:695-707.

Balcomb, K. C. 1989. Baird's beaked whale (*Berardius bairdii* Stejneger, 1883) and Arnoux's beaked whale (*Berardius arnuxii* Duvernoy, 1851). Pages 261-288 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 4. River dolphins and the larger toothed whales. Academic Press, London.

Barlow, J., T. Gerrodette and G. Silber. 1997. First estimates of vaquita abundance. Marine Mammal Science 13:44-58.

Barrett-Lennard, L., T. G. Smith and G. M. Ellis. 1996. A cetacean biopsy system using lightweight pneumatic darts, and its effect on the behavior of killer whales. Marine Mammal Science 12:14-27.

Bejder, L., D. Fletcher and S. Bräger. 1998. A method for testing association patterns of social animals. Animal Behaviour 56:719-725.

Benjaminsen, T. 1972. On the biology of the bottlenose whale, *Hyperoodon ampullatus* (Forster). Norwegian Journal of Zoology 20:233-241.

Benjaminsen, T., and I. Christensen. 1979. The natural history of the bottlenose whale, *Hyperoodon ampullatus* (Forster). Pages 143-164 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine animals. Volume 3. Plenum, New York.

Bernard, H. J., and A. A. Hohn. 1989. Differences in feeding habits between pregnant and lactating spotted dolphins (*Stenella attenuata*). Journal of Mammalogy 70:211-215.

Bernard, H. J., and S. B. Reilly. 1999. Pilot whales *Globicephala* Lesson, 1828. Pages 245-279 *in* S. H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals. Volume 6. Academic Press, London.

Best, P. B. 1968. The sperm whale (*Physeter catodon*) off the west coast of South Africa. 2. Reproduction in the female. Investigational Report. Division of Sea Fisheries 66:1-32.

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. Pages 227-289 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine animals. Volume 3. Plenum, New York.

Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford and K. C. Balcomb. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports of the International Whaling Commission (special issue) 12:383-405.

Bloch, D., M. Desportes, M. Zachariassen and I. Christensen. 1996. The northern bottlenose whale in the Faroe Islands, 1584-1993. Journal of Zoology (London) 239:123-140.

Boesch, C. 1996. Social groupings in chimpanzees. Pages 101-113 *in* W. C. McGrew, L. F. Marchant and T. Nishida, eds. Great ape societies. Cambridge University Press, Cambridge.

Bose, N., and J. Lien. 1990. Energy absorption from ocean waves: A free ride for cetaceans. Proceedings of the Royal Society of London, B 240:591-605.

Bowen, W. D., D. E. Sergeant and T. Øritsland. 1983. Validation of age estimation in the harp seal *Phoca groenlandica*, using dental annuli. Canadian Journal of Fisheries and Aquatic Sciences 40-:1430-1441.

Bruce-Allen, L. J., and J. R. Geraci. 1985. Wound healing in the bottlenose dolphin(*Tursiops truncatus*). Canadian Journal of Fisheries and Aquatic Sciences 42:216-228.

Cairns, S. J., and S. J. Schwager. 1987. A comparison of association indices. Animal Behaviour 35:1454-1469.

Carlson, C. A., C. A. Mayo and H. Whitehead. 1990. Changes in the ventral fluke pattern of the humpback whale *(Megaptera novaeangliae)*, and its effects on matching; evaluation of its significance to photo-identification research. Reports of the International Whaling Commission (special issue) 12:105-111.

Carter, B. 1997. Length distribution of northern bottlenose whales (*Hyperoodon ampullatus*) in the Gully with a comparison between this population and another residing in the Labrador Sea. B.Sc. Honours Thesis. Dalhousie University, Halifax, Nova Scotia.

Caswell, H., R. M. Nisbet, A. M. de Roos and S. Tuljapurkar. 1997. Structured-population models: Many methods, a few basic concepts. Pages 3-17 *in* S. Tuljapurkar and H. Caswell, eds. Structured-population models in marine, terrestrial and freshwater systems. Chapman and Hall, New York.

Caswell, H., M. Fuijiwara and S. Brault. 1999. Declining survival probability threatens the North Atlantic right whale. Proceedings of the National Academy of Sciences of the United States of America 96:3308-3313.

Chapman, C. A., F. J. White and R. W. Wrangham. 1993. Defining subgroup size in fission-fusion societies. Folia Primatologica 61:31-34.

Cheney, D. L., R. M. Seyfarth, B. B. Smuts and R. W. Wrangham. 1987. The study of primate societies. Pages 1-8 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker, eds. Primate societies. Chicago University Press, Chicago.

Childerhouse, S. J., and S. M. Dawson. 1996. Stability of fluke marks used in individual photoidentification of sperm whales at Kaikoura, New Zealand. Marine Mammal Science 12:447-451.

Childerhouse, S. J., S. M. Dawson and E. Slooten. 1995. Abundance and seasonal residence of sperm whales at Kaikoura, New Zealand. Canadian Journal of Zoology 73:723-731.

Christal, J. 1998. An analysis of sperm whale social structure: patterns of association and genetic relatedness. Ph.D. Dissertation. Dalhousie University, Halifax, Nova Scotia.

Christal, J., H. Whitehead and E. Lettevall. 1998. Sperm whale social units: variation and change. Canadian Journal of Zoology 76:1431-1440.

Christensen, I. 1973. Age determination, age distribution and growth of bottlenose whales, *Hyperoodon ampullatus* (Forster), in the Labrador Sea. Norwegian Journal of Zoology 21:331-340.

Christensen, I. 1976. The history of exploitation and the initial status of the Northeast Atlantic bottlenose whale (*Hyperoodon ampullatus*). . (Food and Agriculture Organization of the United Nations, Advisory Committee on Marine Resources Research, Scientific Consultation on Marine Mammals, Bergen Norway, 31 August - 9 September [unpublished])

Christensen, I. 1984. Growth and reproduction of killer whales, *Orcinus orca*, in Norwegian coastal waters. Reports of the International Whaling Commission (special issue) 6:253-258.

Clapham, P. J. 1993. Social organization of humpback whales on a North Atlantic feeding ground. Symposia of the Zoological Society, London 66:131-145.

Clapham, P. J., and C. A. Mayo. 1987. Reproduction and recruitment of individually identified humpback whales, *Megaptera novaeangliae*, observed in Massachusetts Bay, 1979-1985. Canadian Journal of Zoology 65:2853-2863.

Clapham, P. J., P. J. Palsboll, D. K. Matilla and O. Vasquez. 1992. Composition and dynamics of humpback whale competitive groups in the West Indies. Behaviour 122:182-194.

Clarke, M. R., and T. K. Kristensen. 1980. Cephalopod beaks from the stomachs of two northern bottlenosed whales (*Hyperoodon ampullatus*). Journal of the Marine Biological Association of the United Kingdom 60:151-156.

Clutton-Brock, T. H., S. D. Albon and F. E. Guinness. 1984. Maternal dominance, breeding success and birth sex ratios in red deer. Nature 308:358-360.

Connor, R. C., and M. R. Heithaus. 1996. Approach by great white shark elicits flight response in bottlenose dolphins. Marine Mammal Science 12:602-606.

Connor, R. C., and R. A. Smolker. 1996. 'Pop' goes the dolphin: a vocalization male bottlenose dolphins produce during consortships. Behaviour 133:643-662.

Connor, R. C., R. A. Smolker and A. F. Richards. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops sp.*). Proceedings of the National Academy of Sciences of the United States of America 89:987-990.

Connor, R. C., A. F. Richards, R. A. Smolker and J. Mann. 1996. Patterns of female attractiveness in Indian Ocean bottlenose dolphins. Behaviour 133:37-69.

Connor, R. C., J. Mann, P. L. Tyack and H. Whitehead. 1998. Social evolution in toothed whales. Trends in Ecology and Evolution 13:228-232.

Connor, R. C., M. R. Heithaus and L. M. Barre. 1999. Superalliance of bottlenose dolphins. Nature 397:571-572.

Cormack, R. M. 1985. Examples of the use of GLIM to analyse capture-recapture studies. Pages 243-273 *in* B. J. T. Morgan and P. M. North, eds. Statistics in ornithology. Springer-Verlag, Berlin.

Dalebout, M., A. van Heldon, K. van Waerebeek and C. S. Baker. 1998. Molecular genetic identification of southern hemisphere beaked whales (Cetacea: Ziphiidae). Molecular Ecology 6:687-692.

Defran, R. H., and D. W. Weller. 1999. Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. Marine Mammal Science 15:366-380.

Defran, R. H., D. W. Weller, D. L. Kelly and M. A. Espinosa. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. Marine Mammal Science 15:381-393.

Desharnais, R. A. 1997. Population dynamic of *Tribolium*. Pages 303-328 *in* S. Tuljapurkar and H. Caswell, eds. Structured-population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York.

Dobson, F. S. 1998. Social structure and gene dynamics in mammals. Journal of Mammalogy 79:667-670.

Dobson, F. S., R. K. Chesser, J. L. Hoogland, D. W. Sugg and D. W. Foltz. 1998. Breeding groups and gene dynamics in a socially structured population of prairie dogs. Journal of the Mammal Society of Japan 79:671-680.

Dufault, S., and H. Whitehead. 1995. An assessment of changes with time in the marking patterns used for photo-identification of individual sperm whales, *Physeter macrocephalus*. Marine Mammal Science 11:335-343.

Edwards, A. W. F. 1992. Likelihood. John Hopkins University Press, Baltimore.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-222.

Faucher, A., and H. Whitehead. 1991. The bottlenose whales of "the Gully.". Final report for 1988-1990 project to WWF-Canada. World Wildlife Fund Canada, Toronto.

Félix, F. 1997. Organization and social structure of the coastal bottlenose dolphin *Tursiops truncatus* in the Gulf of Guayaquil, Equador. Aquatic Mammals 23:1-16.

Fernandez, S., and A. A. Hohn. 1998. Age, growth and calving season of bottlenose dolphins (*Tursiops truncatus*) off coastal Texas. Fishery Bulletin US 96:357-365.

Friday, N. 1997. Evaluating photographic capture-recapture estimates of abundance of North Atlantic humpback whales. Ph.D. Dissertation. University of Rhode Island.

Gardner, W. D. 1989. Baltimore Canyon as a modern conduit of sediment to the deep sea. Deep-Sea Research 36:323-358.

Ginsberg, J. R., and T. P. Young. 1992. Measuring association between individuals or groups in behavioural studies. Animal Behaviour 44,2:377-379.

Gordon, J. C. D. 1990. A simple photographic technique for measuring the length of whales from boats at sea. Reports of the International Whaling Commission 40:581-588.

Gowans, S., and L. Rendell. In press. Head-butting in northern bottlenose whales (*Hyperoodon ampullatus*): A possible function for big heads. Marine Mammal Science.

Gray, D. 1882. Notes on the characters and habits of the bottlenose whale (*Hyperoodon rostratus*). Proceedings of the Zoological Society of London 1882:726-731.

Green, H. C., J. Östman and A. D. Driscoll. 1991. A case of dolphin entanglement leading to a portion of the fin being cut off - how "round nick" became "butch". Abstract in Ninth biennial conference on the biology of marine mammals, Chicago. p. 29.

Greenwood P.J. 1980 Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140-1162.

Gunnlaugsson, T., and J. Sigurjónsson. 1990. NASS-87: Estimation of whale abundance based on observations made onboard Icelandic and Faroese survey vessels. Reports of the International Whaling Commission 40:571-580.

Haedrich, R. L., G. T. Rowe and P. T. Polloni. 1980. The megabenthic fauna in the deep sea south of New England USA. Marine Biology 57:165-179.

Haenel, N. J. 1986. General notes on the behavioral ontogeny of Puget Sound killer whales and the occurrence of allomaternal behavior. Pages 285-300 *in* B. C. Kirkevold and J. S. Lockard, eds. Behavioral biology of killer whales. Alan R. Liss, New York.

Halliday, R. G. 1991. Marine distribution of the sea lamprey (*Petromyzon marinus*) in the northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 48:832-842.

Hammond, P. S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. Reports of the International Whaling Commission (special issue) 8:253-282.

Hammond, P. S. 1990a. Capturing whales on film - estimating cetacean population parameters from individual recognition data. Mammal Review 20:17-22.

Hammond, P. S. 1990b. Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. Reports of the International Whaling Commission (special issue) 12:135-139.

Hammond, P. S., S. A. Mizroch and G. P. Donovan, eds. 1990. Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters. Volume Special Issue 12. International Whaling Commission, Cambridge.

Harcourt, A. H., P. H. Harvey, S. G. Larson and R. V. Short. 1981. Testis weight, body weight and breeding system in primates. Nature 293:55-57.

Harding, G. C. 1998. Submarine canyons: deposition centres for detrital organic matter. Pages 105-106 *in* W. G. Harrison and D. G. Fenton, eds. The Gully: A scientific review of its environment and ecosystem. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 98/83, Ottawa.

Harrison, G., and D. Fenton, eds. 1998. The Gully: a scientific review of its environment and ecosystem. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 98/83, .

Harvey, P. H., R. D. Martin and T. H. Clutton-Brock. 1987. Life histories in comparative perspective. Pages 181-196 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker, eds. Primate societies. University of Chicago Press, Chicago.

Harzen, S., and B. J. Brunnick. 1997. Skin disorder in bottlenose dolphins (*Tursiops truncatus*), resident in the Sado estuary, Portugal. Aquatic Mammals 23:59-68.

Hasegawa, M., J. Adachi and M. C. Milinkovitch. 1997. Novel phylogeny of whales supported by total molecular evidence. Journal of Molecular Evolution 44(Supplement 1):S117-S120.

Haury, L. R., J. A. McGowan and P. H. Wiebe. 1978. Patterns and processes in the space-time scales of plankton distributions. Pages 277-327 *in* J. H. Steel, ed. Spatial pattern in plankton communities. Plenum, New York.

Head, E. J. H., and W. G. Harrison. 1998. Biological Oceanography - Plankton. Pages 71-104 *in* W. G. Harrison and D. G. Fenton, eds. The Gully:: A scientific review of its environment and ecosystem. Canadian Stock Assessment Secretariat Research Document 98/83, Ottawa.

Herzing, D. L., and C. M. Johnson. 1997. Interspecific interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas, 1985-1995. Aquatic Mammals 23:85-99.

Hewitt, G. M., and R. K. Butlin. 1997. Causes and consequences of population structure. Pages 350-372 *in* R. J. Krebs and N. B. Davis, eds. Behavioural ecology: An evolutionary approach, 4th Edition. Blackwell Scientific, Oxford.

Heyning, J. E. 1984. Functional morphology involved in the intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi*. Canadian Journal of Zoology 62:1645-1654.

Heyning, J. E. 1989. Cuvier's beaked whale - *Ziphius cavirostris*. Pages 289-308 *in* S. H. Ridgway and R. Harrison, eds. Handbook of marine mammals. Volume 4. Academic Press, London.

Hinde, R. A. 1976. Interactions, relationships and social structure. Man 11:1-17.

Hoelzel, A. R. 1998. Genetic structure of cetacean populations in sympatry, parapatry, and mixed assemblages: Implications for conservation policy. Journal Of Heredity 89:451-458.

Hoelzel, A. R., J. Halley, S. J. O'Brien, C. Campagna, T. Arnbom, B. J. Le Boeuf, K. Ralls and G. A. Dover. 1993. Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. Journal Of Heredity 84:443-449.

Hoelzel, A. R., M. Dahlheim and S. J. Stern. 1998a. Low genetic variation among killer whales (Orcinus orca) in the eastern North Pacific and genetic differentiation between foraging specialists. Journal Of Heredity 89:121-128.

Hoelzel, A. R., C. W. Potter and P. B. Best. 1998b. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of bottlenose dolphins. Proceedings of the Royal Society of London B, Biological Sciences 265:1177-1183.

Holekamp, K. E., and L. Smale. 1995. Rapid change in offspring sex ratio after clan fission in the spotted hyena. American Naturalist 145:261-278.

Holmes, R. W., S. Nagasawa and H. Takano. 1993. The morphology and geographic distribution of epidermal diatoms on the Dall's porpoise (*Phocoenides dalli* True) in the northern Pacific ocean. Bulletin of the National Science Museum, Tokyo, Series B 19:1-18.

Hooker, S. K. In prep. Resource and habitat use of northern bottlenose whales in the Gully: Ecology, diving, and ranging behaviour. Ph.D. Dissertation. Dalhousie University, Halifax.

Hooker, S. K., and R. W. Baird. 1999. Deep-diving behaviour of the northern bottlenose whale *Hyperoodon ampullatus* (Cetacea: Ziphiidae). Proceedings of the Royal Society of London, B 266:671-676.

Hooker, S. K., H. Whitehead and S. Gowans. In press. Spatial, temporal and environmental correlates of cetacean distribution in a submarine canyon--implications for the design of a marine protected area. Conservation Biology.

Hooker, S. K., R. W. Baird, S. Al-Omari, S. Gowans and H. Whitehead. submitted. Behavioral reactions of northern bottlenose whales to biopsy and tagging procedures. Journal of Wildlife Management.

Horppila, J., K. Nyberg, H. Peltonen and T. Turunen. 1996. Effects of five years of intensive trawling on a previously unexploited smelt stock. Journal of Fish Biology 49:329-340.

Horwood, J. R., and D. H. Cushing. 1978. Spatial distribution and ecology of pelagic fish. Pages 355-385 *in* J. H. Steele, ed. Spatial pattern in plankton communities. Plenum Press, New York.

Hrdy, S. B. 1976. Care and exploitation of non-human primate infants by conspecifics other than the mother. *in* J. S. Rosenblatt, R. A. Hinde, E. Shaw and C. Beer, eds. Advances in the Study of Behaviour 6. Academic Press, London.

Isbell, L. A. 1991. Contest and scrabble competition: Patterns of female aggression and ranging behavior among primates. Behavioral Ecology 2:143-155.

Isbell, L. A., and D. Van Vuren. 1996. Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour 133:1-36.

Ishibashi, Y., T. Saitoh and M. Kawata. 1998. Social organization of the vole *Clethiromomys rufocanus* and its demographic and genetic consequences: A review. Research on Population Ecology 40:39-50.

Jaquet, N., and H. Whitehead. 1996. Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135:1-9.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behaviour 48:215-267.

Jefferson, T. A. 1989. Calving seasonality in Dall's porpoise in the Eastern North Pacific. Marine Mammal Science 5:196-200.

Jefferson, T. A., P. J. Stacey and R. W. Baird. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Review 4:151-180.

Joffe, T. H., and R. I. M. Dunbar. 1997. Visual and socio-cognitive information processing in primate brain evolution. Proceedings of the Royal Society of London, B 264:1303-1307.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and dilution--stochastic model. Biometrika 52:225-247.

Jones, E. C. 1971. *Isistius brasiliensis*, a squaloid shark, the probable cause of crater wounds on fishes and cetaceans. Fish. Bull 69:791-798.

Jonsgard, A. 1968a. Another note on the attacking behaviour of killer whale (Orcinus orca). Norsk Hvalfangst-Tidende 57(6):175-176.

Jonsgard, A. 1968b. A note on the attacking behaviour of killer whale (Orcinus orca). Norsk Hvalfangst-Tidende 57(4):84.

Karczmarski, L. 1996. Ecological studies of humpback dolphins *Sousa chinensis* in the Algoa Bay region, Eastern Cape, South Africa. Ph.D. Dissertation. University of Port Elizabeth, South Africa.

Kastelein, R. A., T. Dokter and P. Zwart. 1990. The suckling of a bottlenose dolphin calf (*Tursiops truncatus*) by a foster mother, and information of transverse birth bands. Aquatic Mammals 16:134-138.

Kawakami, T. 1980. A review of sperm whale food. Scientific Reports of the Whales Research Institute 32:199-218.

Kenney, R. D., and H. E. Winn. 1987. Cetacean biomass densities near submarine canyons compared to adjacent shelf/slope areas. Continental Shelf Research 7:107-114.

Kleiman, D. G., and J. R. Malcolm. 1981. The evolution of male parental investment in mammals. Pages 347-387 *in* D. J. Gubernick and P. H. Klopfer, eds. Parental care in mammals. Plenum, New York.

Knowlton, A. R., S. D. Kraus and R. D. Kenney. 1994. Reproduction in North Atlantic right whales (*Eubalaena glacialis*). Canadian Journal of Zoology 72:1297-1305.

Kraus, S. D. 1990. Rates and potential causes of mortality in north Atlantic right whales (*Eubalaena glacialis*). Marine Mammal Science 6:278-291.

Kristensen, T. K. 1981. The genus *Gonatus* Gray, 1849 (Mollusca: Cephalopoda) in the North Atlantic. A revision of the North Atlantic species and description of *Gonatus steenstrupii* n.sp. Steenstrupia 7:61-99.

Lick, R., and U. Piatkowski. 1998. Stomach contents of a northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. Journal of the Marine Biological Association of the United Kingdom 1998:643-650.

Lockyer, C. H., and R. J. Morris. 1990. Some observations on wound healing and persistence of scars in *(Tursiops truncatus)*. Reports of the International Whaling Commission (special issue) 12:113-118.

Long, D. J. 1991. Apparent predation by a white shark *Cachardoon carcharias*) on a pygmy sperm whale *Kogia breviceps*. Fishery Bulletin US 89:538.

Mann, J. 1999. Behavioural sampling methods for cetaceans: A review and critique. Marine Mammal Science 15:102-122.

Mann, J., and H. Barnett. 1999. Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops* sp.) calf: Defense and reactions by the mother. Marine Mammal Science 15:568-575.

Mann, J., and B. B. Smuts. 1998. Natal attraction: Allomaternal care and mother-infant separations in wild bottlenose dolphins. Animal Behaviour 55:1-17.

Marten, K., and S. Psarako. In press. Long-term site fidelity and possible long term associations in spinner dolphins (*Stenella longirostris*) seen in 1978-79 and again in 1995-98 off Oahu, Hawaii. Marine Mammal Science.

Mead, J. G. 1989a. Beaked whales of the genus *Mesoplodon*. Pages 349-430 *in* S. H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals. Volume 4. Academic Press, London.

Mead, J. G. 1989b. Bottlenose whales *Hyperoodon ampullatus* (Forster, 1770) and *Hyperoodon planifrons* Flower, 1882. Pages 321-348 *in* S. H. Ridgway and R. Harrison, eds. Handbook of Marine Mammals. Volume 4. Academic Press, London.

Messenger, S. L., and J. A. McGuire. 1998. Morphology, molecules, and the phylogenetics of cetaceans. Systematic Biology 47:90-124.

Mitchell, E. 1977. Evidence that the northern bottlenose whale is depleted. Reports of the International Whaling Commission 27:195-203.

Mitchell, E., and V. M. Kozicki. 1975. Autumn stranding of a northern bottlenose whale (*Hyperoodon ampullatus*) in the Bay of Fundy, Nova Scotia. Journal of the Fisheries Research Board of Canada 32:1019-1040.

Mitchell, E., and R. R. Reeves. 1988. Records of killer whales in the western North Atlantic, with emphasis on eastern Canadian waters. Rit Fiskideildar 11:170-183.

Muñoz-Chápulli, R. J., C. R. Salgado and J. M. De La Serna. 1988. Biogeography of *Isistius brasiliensis* in the north-eastern Atlantic, inferred from crater wounds on swordfish (*Xiphias gladius*). Journal of the Marine Biological Association of the United Kingdom 68:315-321.

Nemato, T., P. B. Best, K. Ishimaru and H. Takano. 1980. Diatom films on whales in South African waters. Scientific Reports of the Whales Research Institute 32:97-103.

Nishida, T., and K. Hosaka. 1996. Coalitions strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. Pages 114-134 *in* W. C. McGrew, L. F. Marchant and T. Nishida, eds. Great ape societies. University of Cambridge Press, Cambridge.

Norris, K. S., and T. P. Dohl. 1980. The structure and functions of cetacean schools. *in* L. M. Herman, ed. Cetacean Behavior: Mechanisms and Functions. Wiley-Interscience, New York.

Norris, K. S., and C. R. Schilt. 1988. Cooperative societies in three dimensional space: On the origins of aggregations, flocks, and schools with special reference to dolphins and fish. Ethology and Sociobiology 9:149-179.

Ohlin, A. 1893. Some remarks on the bottlenose-whale (Hyperoodon). Acta. Univ. Lund. 29:1-13.

Olesiuk, P., M. A. Bigg and G. M. Ellis. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Reports of the International Whaling Commission (special issue) 12:209-243.

Owen-Smith, N. 1993. Comparative mortality rates of male and female kudus: The costs of sexual dimorphism. Journal of Animal Ecology 62:428-440.

Pack, A. A., D. R. Salden, M. J. Ferrari, D. A. Glockner-Ferrari, L. M. Herman, H. A. Stubbs and J. M. Straley. 1998. Male humpback whale dies in a competitive group. Marine Mammal Science 14:861-873.

Palsboll, P. J., A. Vader, I. Bakke and M. Raafat El-Gewely. 1992. Determination of gender in cetaceans by the polymerase chain reaction. Canadian Journal of Zoology 70:2166-2170.

Palsboll, P. J., J. Allen, M. Bérubé, P. J. Clapham, T. P. Feddersen, P. S. Hammond, R. R. Hudson, H. Jørgensen, S. Katona, A. H. Larsen, F. Larsen, J. Lien, D. K. Matilla, J. Sigurjónsson, R. Sears, T. Smith, R. Sponer, P. Stevick and N. Oien. 1997. Genetic tagging of humpback whales. Nature 388:767.

Papastavrou, V., S. C. Smith and H. Whitehead. 1989. Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galápagos Islands. Canadian Journal of Zoology 67:839-846.

Philo, L. M., J. C. George and T. F. Albert. 1992. Rope entanglement of Bowhead whales (*Balaena mysticetus*). Marine Mammal Science 8:306-311.

Pike, G. C. 1951. Lamprey marks on whales. Journal of the Fisheries Research Board of Canada 8:275-281.

Pitman, R. L., D. M. Palacios, P. L. Brennan, B. J. Brennan, K. C. Balcomb and T. Miyashita. 1999. Sightings and possible identity of a bottlenose whale in the tropical Indo-Pacific: *Indopacetus pacificus*? Marine Mammal Science 15:531-549.

Pryor, K., and I. Kang Shallenberger. 1991. Social structure in spotted dolphins (*Stenella attenuata*) in the tuna purse seine fishery in the Eastern Tropical Pacific. Pages 160-196 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Discoveries and puzzles. University of California Press, Berkley.

Reeves, R. R., E. Mitchell and H. Whitehead. 1993. Status of the northern bottlenose whale, *Hyperoodon ampullatus*. Canadian Field-Naturalist 107:490-508.

Reyes, J. C., J. G. Mead and K. Van Waerebeek. 1991. A new species of beaked whale *Mesoplodon peruvianus* sp. n. (Cetacea: Ziphiidae) from Peru. Marine Mammal Science 7:1-24.

Rice, D. W. 1998. Marine mammals of the world: Systematics and distribution. The Society for Marine Mammalogy, Lawrence Kansas.

Richard, K. R., S. W. McCarrey and J. M. Wright. 1994. DNA sequence from the SRY gene of the sperm whale (*Physeter macrocephalus*) for use in molecular sexing. Canadian Journal of Zoology 72:873-877.

Richard, K. R., M. C. Dillon, H. Whitehead and J. M. Wright. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences of the United States of America 93:8792-8795.

Schneider, K., R. W. Baird, S. Dawson, I. Visser and S. Childerhouse. 1998. Reactions of bottlenose dolphins to tagging attempts using a remotely-deployed suction-cup tag. Marine Mammal Science 14:316-324.

Schnell, G. D., D. J. Watt and M. E. Douglas. 1985. Statistical comparison of proximity matrices: applications in animal behaviour. Animal Behaviour 33:239-253.

Sergent, D. E., A. W. Mansfield and B. Beck. 1970. Inshore records of Cetacea for eastern Canada, 1949-1968. Journal of the Fisheries Research Board of Canada 27:1903-1915.

Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pages 241-265 *in* S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego.

Sigurjónsson, J., T. Gunnlaugsson and M. Payne. 1989. NASS-87: Shipboard sightings surveys in Icelandic and adjacent waters June-July 1987. Reports of the International Whaling Commission 39:395-409.

Slooten, E., and S. M. Dawson. 1994. Hectors dolphin - *Cephalorhynchus hectori* (van Benden, 1881). Pages 311-333 *in* S. H. Ridgeway and R. Harrison, eds. Handbook of Marine Mammals. Volume 5. Academic Press, London.

Slooten, E., S. M. Dawson and H. Whitehead. 1993. Associations among photographically identified Hector's dolphins. Canadian Journal of Zoology 71:2311-2318.

Small, R. J., and D. P. DeMaster. 1995. Survival of five species of captive marine mammals. Marine Mammal Science 11:209-226.

Smith, S. C. 1992. Sperm whales and mesopelagic cephalopods in the waters off the Galápagos Islands. M.Sc. Thesis. Dalhousie University, Nova Scotia, Canada.

Smith, S. C., and H. Whitehead. 1993. Variations in the feeding success and behaviour of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Canadian Journal of Zoology 71:1991-1996.

Smolker, R. A., A. F. Richards, R. C. Connor and J. W. Pepper. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123:38-69.

Smolker, R. A., A. F. Richards, R. C. Connor, J. Mann and P. Berggren. 1997. Sponge-carrying by Indian Ocean bottlenose dolphins: possible tool-use by a delphinid. Ethology 103:454-465.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. 3rd Edition. W.H. Freeman and Company, New York.

Stacey, P. B., V. A. Johnson and M. L. Taper. 1997. Migration within metapopulations: The impact upon local population dynamics. Pages 267-291 *in* I. Hanski and M. E. Gilpin, eds. Metapopulation biology: Ecology, genetics and evolution. Academic Press, San Diego.

Steiner, L., J. Gordon and C. J. Beer. 1998. Marine mammals of the Azores. Abstract. 1st World Marine Mammals Science Conference, Monaco, January 1998. p128.

Sugg, D. W., R. K. Chesser, F. S. Dobson and J. L. Hoogland. 1996. Population genetics meets behavioural ecology. Trends in Ecology and Evolution 11:338-342.

Taber, S., and P. Thomas. 1982. Calf development and mother-calf spatial relationships in southern right whales. Animal Behaviour 30:1072-1083.

Tavolga, M. C., and F. S. Essapian. 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zoologica 42:11-31.

Todd, S., P. Ostrom, J. Lien and J. Abrajano. 1997. Use of biopsy samples of humpback whale *Megaptera novaeangliae* skin for stable isotope (d13c) determination. Journal of Northwest Atlantic Fisheries Science 22:71-76.

Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90-92.

Tyack, P., and H. Whitehead. 1983. Male competition in large groups of wintering humpback whales. Behaviour 83:132-154.

Urbán, J. R., S. S. Ramirez and J. C. Salinas. 1994. First record of bottlenose whales, *Hyperoodon* sp. in the Gulf of California. Marine Mammal Science 10:471-473.

Van Schaik, C. P., and M. Höstermann. 1994. Predation risk and the number of adult males in a primate group: A comparative test. Behavioural Ecology and Sociobiology 35:261-272.

Van Schaik, C. P., and P. M. Kappler. 1997. Infanticide risk and the evolution of male-female associations in primates. Proceedings of the Royal Society of London, B 264:1687-1694.

Wade, P. R., and T. Gerrodette. 1993. Estimates of cetacean abundance and distribution in the eastern tropical Pacific. Reports of the International Whaling Commission 43:477-493.

Walsh, P. S., D. A. Metzger and R. Higuchi. 1991. Chelex-100 as a medium for simple extraction of DNA for PCR-based typing of forensic material. Biotechniques 10:506-513.

Waters, S., and H. Whitehead. 1990a. Aerial behaviour in sperm whales, *Physeter macrocephalus*. Canadian Journal of Zoology 68:2076-2082.

Waters, S., and H. Whitehead. 1990b. Population and growth parameters of Galápagos sperm whales estimated from length distributions. Reports of the International Whaling Commission 40:225-235.

Watts, D. P. 1996. Comparative socio-ecology of gorillas. Pages 16-28 *in* W. C. McGrew, L. F. Marchant and T. Nishida, eds. Great ape societies. Cambridge University Press, Cambridge.

Watts, D. P. 1998. Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. Behavioural Ecology and Sociobiology 44:43-55.

Weinrich, M. T., R. H. Lambertsen, C. S. Baker, M. R. Schilling and C. R. Belt. 1991. Behavioural responses of humpback whales (*Megaptera novaeangliae*) in the Southern Gulf of Maine to biopsy sampling. Reports of the International Whaling Commission (special issue) 13:91-97.

Weller, D. W. 1991. The social ecology of Pacific Coast bottlenose dolphins. MA Thesis. San Diego State University.

Weller, D. W., B. Würsig, H. Whitehead, J. C. Norris, S. K. Lynn, R. W. Davis, N. Clauss and P. Brown. 1996. Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. Marine Mammal Science 12:588-594.

Wells, R. S. 1991a. Bringing up baby. Natural History 100:56-62.

Wells, R. S. 1991b. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-225 *in* K. Pryor and K. S. Norris, eds. Dolphin societies: Discoveries and puzzles. University of California Press, Berkley.

Wells, R. S., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. Reports of the International Whaling Commission (special issue) 12:407-415.

Wells, R. S., A. B. Irvine and M. D. Scott. 1980. The social ecology of inshore odontocetes. Pages 263-317 *in* L. M. Herman, ed. Cetacean Behaviour: Mechanisms and Functions. John Wiley & Sons, Toronto.

Wells, R. S., S. Hofmann and T. L. Moors. 1998. Entanglement and mortality of bottlenose dolphins, *Tursiops truncatus*, in recreational fishing gear in Florida. Fishery Bulletin US 96:647-650.

Whitehead, H. 1985. Humpback whale breaching. Investigations on Cetacea 17:117-155.

Whitehead, H. 1989. Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. Canadian Journal of Zoology 67:2131-2139.

Whitehead, H. 1990a. Computer assisted individual identification of sperm whale flukes. Reports of the International Whaling Commission (special issue) 12:71-77.

Whitehead, H. 1990b. Mark-recapture estimates with emigration and re-immigration. Biometrics 46:473-479.

Whitehead, H. 1990c. Rules for roving males. Journal of Theoretical Biology 145:355-368.

Whitehead, H. 1993. The behaviour of mature male sperm whales on the Galapagos breeding grounds. Canadian Journal of Zoology 71:689-699.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. Behavioral Ecology 6:199-208.

Whitehead, H. 1996a. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioural Ecology and Sociobiology 38:237-244.

Whitehead, H. 1996b. Variation in the feeding success of sperm whales: temporal scale, spatial scale and relationship to migrations. Journal of Animal Ecology 65:429-438.

Whitehead, H. 1997. Analyzing animal social structure. Animal Behaviour 53:1053-1067.

Whitehead, H. 1999. Programs for analysing social structure. SOCPROG 1.2; http://is.dal.ca/~whitelab/index.htm.

Whitehead, H. In press. Testing association patterns of social animals. Animal Behaviour.

Whitehead, H., and S. Dufault. 1999. Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Advances in the Study of Behavior 28:33-74.

Whitehead, H., S. Brennan and D. Grover. 1992. Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70:912-918.

Whitehead, H., J. Christal and S. Dufault. 1997a. Past and distant whaling and the rapid decline of sperm whales off the Galápagos Islands. Conservation Biology 11:1387-1396.

Whitehead, H., A. Faucher, S. Gowans and S. McCarrey. 1997b. Status of the northern bottlenose whale, *Hyperoodon ampullatus*, in the Gully, Nova Scotia. Canadian Field Naturalist 111:287-292.

Whitehead, H., S. Gowans, A. Faucher and S. McCarrey. 1997c. Population of northern bottlenose whales in the Gully, Nova Scotia. Marine Mammal Science 13:173-185.

Whitehead, H., D. Bowen, S. Hooker and S. Gowans. 1998a. Marine mammals of the Gully region. Pages 186-221 *in* W. G. Harrison and D. G. Fenton, eds. The Gully: a scientific review of its environment and ecosystem. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 98/83, Ottawa.

Whitehead, H., M. Dillon, S. Dufault, L. Weilgart and J. Wright. 1998b. Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. Journal of Animal Ecology 67:253-262.

Wilkinson, L. 1997. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL.

Wilkinson, L., G. Blank and C. Gruber. 1996. Desktop data analysis with SYSTAT. Prentice Hall, Upper Saddle River, New Jersey.

Williams, J. A., S. M. Dawson and E. Slooten. 1993. The abundance and distribution of bottlenose dolphins *Tursiops truncatus* in Doubtful Sound, New Zealand. Canadian Journal of Zoology 71:2080-2088.

Williams, T. M., W. A. Friedl, M. L. Fong, R. M. Yamada, P. Dedivy and J. E. Haun. 1992. Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. Nature 355:821-823.

Wilson, B., P. M. Thompson and P. S. Hammond. 1997. Skin lesions and physical deformities on bottlenose dolphins in the Moray Firth: Population prevalence and age-sex differences. Ambio 26:243-247.

Wilson, B., H. Arnold, G. Bearzi, C. Fortuna, R. Gaspar, S. Ingram, C. Liret, S. Pribanic, A. J. Read, V. Ridous, K. Schneider, K. W. Urian, R. S. Wells, C. Wood, P. M. Thompson and P. S. Hammond. 1999. Epidermal diseases in bottlenose dolphins: Impacts of natural and anthropogenic factors. Proceedings of the Royal Society of London, B 266:1077-1085.

Wilson, B., P. S. Hammond and P. M. Thompson. 1999. Estimating size and assessing trends in a coastal bottlenose dolphin population. Ecological Applications 9:288-300.

Wilson, D. R. B. 1995. The ecology of bottlenose dolphins in the Moray Firth, Scotland: a population at the northern extreme of the species' range. Ph.D. Dissertation. Aberdeen University, Aberdeen, Scotland.

Winn, H. E., P. J. Perkins and L. Winn. 1970. Sounds and behavior of the northern bottlenose whale. 7th Annual Conference on Biological Sonar and Diving Mammals, Stanford Research Institute, Menlo Park, California. Pages 53-59.

Wrangham, R. W. 1980. An ecological model of female-bonded primate groups. Behaviour 75:262-300.

Wrangham, R. W. 1987. Evolution of social structure. Pages 578 *in* B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker, eds. Primate societies. University of Chicago Press, Chicago.

Wrangham, R. W., and D. I. Rubenstein. 1986. Social evolution in birds and mammals. Pages 452-470 *in* D. I. Rubenstein and R. W. Wrangham, eds. Ecological aspects of social evolution. Princeton University Press, Princeton, New Jersey.

Würsig, B. 1986. Delphinid foraging strategies. Pages 347-359 *in* R. J. Schusterman, J. A. Thomas and F. G. Wood, eds. Dolphin cognition and behavior: A comparative approach. Lawrence Erlbaum Associates, Hillwood,NJ.

Würsig, B., and M. Würsig. 1980. Behaviour and ecology of the dusky dolphin, *Lagenorhynchus obscurus* in the south Atlantic. Fishery Bulletin US 77:871-890.

Würsig, B., E. M. Dorsey, M. A. Fraker, R. S. Payne and W. J. Richardson. 1986. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea. Reports of the International Whaling Commission (special issue) 8:167-175.

Würsig, B., R. S. Wells, M. Würsig and K. S. Norris. 1994a. Population structure. Pages 122-140 *in* K. S. Norris, B. Würsig, R. S. Wells and M. Würsig, eds. The Hawaiian Spinner Dolphin. University of California Press, Berkeley.

Würsig, B., R. S. Wells, M. Würsig and K. S. Norris. 1994b. A spinner dolphin's day. Pages 65-102 *in* K. S. Norris, B. Würsig, R. S. Wells and M. Würsig, eds. The Hawaiian spinner dolphin. University of California Press, Berkley.