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An analysis of sperm whale social structure: patterns of association and genetic relatedness

by

Jenny Christal

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

at

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "An analysis of sperm whale social structure: patterns of association and genetic relatedness"

by Jenny Christal

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This thesis is dedicated to my parents,
Phil and Norma Christal, with love.

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Abstract

The social structure of sperm whales (*Physeter macrocephalus*) in the eastern tropical Pacific Ocean was investigated by using photo-identification data (1985-1997) and molecular analysis of sloughed skin samples, to examine patterns of association and genetic relatedness between individuals. These analyses have revealed new levels of complexity and variability in sperm whale social structure.

Analysis of the temporal stability of associations between individuals confirmed the unstable nature of groups of female and juvenile whales. These groups were found to be temporary aggregations of separate, and more temporally-stable, social units. Social unit size was highly variable (3-24 members, mean 12.3). Instances of splitting and merging of units, and of transfers of individuals between units, indicated that unit membership was not necessarily entirely stable over periods of years. Molecular analyses (sexing, mitochondrial DNA sequencing, multi-locus microsatellite profiling) revealed the genetic structure of social units. In conjunction with simulation modeling, these results demonstrated that the units analysed were not strictly matrilineal, but included some unrelated individuals. Thus patterns of long-term association and genetic relatedness are indicative of some female dispersal from social units.

Analyses of association patterns within groups revealed that individuals were more likely to be in spatio-temporal proximity to members of their own unit, rather than to other group members. However, there were no clear indications of preferred companionships within units, and unit members did not appear to associate preferentially with respect to genetic relatedness.

Large male sperm whales have increased in abundance in the Galápagos Islands area in recent years. Aggregations of large males have been observed, within which individuals may associate closely. In conjunction with anecdotal indications of long-term or repeated associations between individuals, these findings indicate greater complexity in the social structure of large males than had been recognised previously.

List of Abbreviations and Symbols

α	alpha
A	adenine
bp	nucleotide base pair
χ^2	chi-square statistic
C	cytosine
°C	degrees Celsius
c.i.	confidence interval
Ci	Curie
d.f.	degrees of freedom
dATP	deoxyadenosine-5'-triphosphate
DNA	deoxyribonucleic acid
dNTP	deoxynucleoside-5'-triphosphate
f	female
γ	gamma
G	guanine
HCl	hydrochloric acid
hr	hour
h-s/g-g	half-sib/grandparent-grandchild
H_2O	water
IWC	International Whaling Commission
KCl	potassium chloride
km	kilometre

KW	Kruskal-Wallis one-way ANOVA
µCi	microCurie
µg	microgram
µl	microlitre
µM	micromolar
m	male
M	molar
$MgCl_2$	magnesium chloride
mm	millimetre
mmol	millimole
mM	millimolar
min	minute
mt	mitochondrial
N	number of constant companions
NF	non-fluke dive
n.s.	not significant
p	probability
P	phosphorus
PCR	polymerase chain reaction
Phe	phenylalanine
photo-ID	photo-identification
ppo	putative parent-offspring pair(s)
Q	quality

r	coefficient of relatedness
s	second
S	sulphur
SRY	sex-determining region Y gene
t	time period
T	thymine
Thr	threonine
TAE	tris-acetic acid-EDTA
tRNA	transfer ribonucleic acid
U	unit
UV	ultra-violet
V	volts
W	watts
WCI	Whale Conservation Institute
ZFX	zinc finger protein gene – X chromosome
ZFY	zinc finger protein gene – Y chromosome
°	degrees
'	minutes
#	number
♀	female
♂	male

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Photo-ID records from other researchers have contributed enormously to our long-term records of sperm whales in the Galápagos area. Godfrey Merlen plays a vital role in the continuation of sperm whale project. His independent trips have yielded many rolls of

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Publications

Much of the research presented in Chapter 3 also appears in:

Christal J., Whitehead H. and Lettevall E. (1998) Sperm whale social units: variation and change. Canadian Journal of Zoology 76: in press [Permission for the use of copyrighted material was obtained from the Canadian Journal of Zoology]

Some of the data presented in Chapter 4 also appeared in:

Christal J. & Whitehead H. (in press) A week in the life of a sperm whale group. *In*: Cetacean societies: field studies of dolphins and whales. Eds. Mann J., Connor R.C., Tyack, P. & Whitehead H. University of Chicago Press.

Chapter 6 provides an updated and expanded analysis of phenomena first reported in:

Christal J. and Whitehead H. (1997) Aggregations of mature male sperm whales on the Galápagos Islands breeding ground. Marine Mammal Science 13: 59-69

CHAPTER ONE

Introduction

WHY STUDY SPERM WHALE SOCIAL STRUCTURE?

Knowledge of the social structure of a species is fundamental to our understanding and interpretation of many aspects of that species' biology. The ways in which individuals interact, associate and hold relationships with conspecifics may reflect not only individual-specific characteristics such as age, sex, and physiological or reproductive status, but also aspects of a population's environment and ecology. Grouping characteristics and mating systems influence gene flow, and hence the genetic structure and diversity of populations (Sugg *et al*, 1996). The social structure of a population can also have important demographic consequences (Brault & Caswell 1993), particularly for long-lived, slowly-reproducing species.

Social structure appears to be an important correlate, and probable determinant, of communicative and cognitive behaviour (Byrne & Whiten 1988). Vocal communicative abilities seem to be particularly well-developed among marine mammals (Tyack 1986, Tyack & Sayigh 1997), and detailed studies of the social structure, and hence the social contexts, of such communication will be important in the analysis and interpretation of marine mammal communication.

Sperm whales (*Physeter macrocephalus*) have been the target of widespread and intensive whaling operations over the last few centuries (see below). A detailed study of sperm whale social structure may help to determine what impacts that whaling may have had (e.g. Kahn *et al.* 1993), and to predict and perhaps mitigate the impacts of future exploitation. Information from studies of social structure can be used to improve the accuracy of population parameter estimates, and thus to permit effective modeling of sperm whale populations - modeling which is essential for management and conservation purposes (Ohsumi 1983).

Analysis of the social structure of a population of sperm whales facilitates both intra- and inter-specific comparisons, and may aid in the search for ecological correlates of social behaviour. While comparisons within the cetacean order may illustrate the relative

importance of specific ecological factors in the marine environment, comparisons of cetaceans to terrestrial mammals can provide insights into the complexities of mammalian social structures, the similarities and differences between social evolution on land and in the sea, and the relative importance of different evolutionary forces (Weilgart *et al.* 1996, Connor *et al.* 1998).

FACTORS INFLUENCING SOCIALITY

The ultimate forces underlying the evolution of mammalian social systems have been the subject of a number of detailed reviews (e.g. Crook 1970, Eisenberg 1973, Crook *et al.* 1976, van Schaik & van Hooff 1983, Wrangham 1983b, Chesser *et al.* 1993), all of which deal with the subject in a far more detailed way than is possible, or appropriate, here. I propose simply to introduce some of the most widely-recognised factors, always bearing in mind two things: that the social systems of mammals are a result of the complex interactions of both internal constraints and external forces (van Schaik & van Hooff 1983), and that even in the most well-studied mammalian order, the primates, there is no general agreement about the ultimate factors for sociality, or even about how such factors can be recognised (van Schaik & van Hooff 1983, Wrangham 1983b).

Ecological factors are generally recognised as the most fundamental determinants of social systems. The social system exhibited by a particular species, or population, is best considered as the outcome of strategies that individuals employ to meet their three basic requirements: obtaining food, avoiding predators and finding mates (van Schaik & van Hooff 1983). Since ecological factors will influence the strategies employed in both foraging and predator avoidance, it is primarily these factors which will determine the distribution of individuals and hence the permanence and cohesion of social groups (Alexander 1974, Bradbury & Vehrencamp 1977, van Schaik & van Hooff 1983). Females and males differ in terms of which of the basic requirements is most limiting to their lifetime reproductive success. While food availability limits the female's ability to produce young, males are limited primarily by access to females (Trivers 1972, Bradbury & Vehrencamp 1977, Emlen & Oring 1977). Thus female distribution and sociality is expected to reflect the spatio-temporal distribution of resources (e.g. Wrangham &

Rubenstein 1986). Male distribution and sociality will be determined by female distribution and sociality, and the ability of a male or males to control females, or the resources necessary for females and young (Wrangham & Rubenstein 1986). Male strategies can, in turn, influence female associations (van Schaik & van Hooff 1983).

What aspects of the ecology of marine environments can be expected to shape cetacean (whale and dolphin) sociality? Cetaceans feed primarily on shoaling crustaceans (krill), squid and fish (although there are exceptions, such as the mammal-eating 'transient' killer whales). These prey types are mobile, and may be ephemerally and unpredictably distributed. In a fluid, three-dimensional environment, monopolisation of mobile prey may be difficult, and co-operative foraging strategies may be of value. Since a given area may not predictably contain prey, and resource defense would require expensive monitoring of large boundary surfaces, territoriality is not expected in cetaceans. Indeed, no cases have been documented, although this strategy has yet not been ruled out for the species where it is perhaps most feasible, the river dolphins, which live in relatively defined habitats. Female cetaceans are highly mobile and maneuverable, and the limitations which this may place on males' abilities to monopolise females may constrain mating system variability.

While it is not easy to quantify ecological variables in the marine habitat which cetaceans inhabit, comparisons of cetacean social systems with those of their terrestrial relatives may shed light on the selective forces which are likely to have shaped the social lives of mammals in these two very different environments.

DESCRIBING SOCIALITY

There are many different approaches to the description of sociality. Authors often describe a species' social system in terms of its mating system (Crook & Gartlan 1966), or group structure (e.g. Eisenberg *et al.* 1972). However, social systems are not necessarily equivalent to mating systems (Rowell 1988). For many species, mating is restricted to a limited breeding season, and as Waterman (1995) argues, classifying the

entire social system of a species according to interactions that take place during only one part of the year can be misleading. Group structure descriptions (often focusing on males, e.g. uni-male, multi-male) may seem appropriate for species with stable association patterns, but are problematic for species with fission-fusion patterns of association, such as many primates (Goodall 1986, Chapman *et al.* 1993) and most odontocetes (toothed cetaceans) (e.g. Smolker *et al.* 1992). Categorisation of sociality on the basis of group structure can result in apparent similarity between species which in reality have fundamental differences in their social behaviour (Lee 1994). There is enormous variation across studies in the temporal/spatial/interactive definition of a group and the determination of group membership, let alone the complication of differing terminology (clan, party, pride, school, band, pod etc.). This variability poses real problems for the comparison of social systems on the basis of group structure.

Clearly a more comprehensive approach is required. There are many aspects of animals' social behaviour that may be included in a description of their sociality. Categories of mating systems and group structure are discussed above, but what of group size and temporal stability, the nature of individual relationships, genetic relatedness, dominance, dispersal patterns and mating strategies? Should these and/or other factors be included in a description of sociality?

The search for an appropriate approach to the description of mammalian sociality is fraught by problems of terminology. A variety of terms have been used by different authors to describe the sociality of animals. Often these terms are neither defined, nor explained. There is an implicit assumption that the reader will have a clear understanding of what is meant by terms such as 'social organisation', 'social structure' or 'social system'. Yet where definitions are given, they vary in the aspects of sociality which are involved, and may even be contradictory, so that there is no consensus usage with which all readers will be familiar.

'Social system' is often used as all-encompassing term, sometimes in conjunction with 'social structure' and/or 'social organisation', but is rarely defined (e.g. Lott 1984). Some

authors use one of the two terms 'social structure' or 'social organisation' to describe some focal aspects of sociality such as group size and composition, ranging patterns, mating systems, and individuals' interactions and relationships (Wrangham 1983a, Frank 1986, Yeager 1991, Kappeler 1993). In general, no clear definition of the selected term is given, and the meanings of 'social structure' and 'social organisation' appear to be effectively equivalent. Other authors make this equivalency explicit, using 'social structure' and 'social organisation' interchangeably, either with or without a description of what aspects of sociality the synonymous terms include (Moss & Poole 1983, White 1992, Waterman 1995). I have found only two papers in which 'social structure' and/or 'social organisation' are explicitly defined. Each of the two approaches has been adopted by later authors, yet the two are incompatible, and can be interpreted as contradictory. Rowell (1972, 1979) adopts definitions which result in a distinct dichotomy between the terms:

social structure:	the composition of groups and the spatial distribution of individuals.
social organisation:	the pattern of interactions between individuals, a description of behaviour.

Following this approach, 'social structure' is restricted to numerical information about groups and dispersion, whereas 'social organisation' relates to the individual-specific nature of social behaviour. Van Schaik and van Hooff (1983) adopt Rowell's (1972, 1979) definitions, and conclude that social organisation can be regarded, in the ultimate sense, as the method used by individuals to achieve that social structure in which their primary interests (feeding, predator avoidance and reproduction) are best served. Hence the distinct constructions 'social structure' and 'social organisation' are seen to be related, although different kinds of social organisation can result in the same kind of social structure (van Schaik & van Hooff 1983).

While this clear determination of usage and meaning of terms is a distinct improvement over the variable usage and implicit meanings found in other papers, I would argue that 'social structure' and 'social organisation' as defined by Rowell (1972, 1979) are not

only related, but inter-related. The aspects of sociality which are divided into two domains by this approach in fact form a inter-dependent network, and separation of these aspects causes an artificial and restrictive division in descriptions of sociality.

Hinde (1976) developed a conceptual framework for the study and description of sociality. In his approach, social structure is considered to be determined by the nature and patterning of relationships between individuals, and these relationships are in turn determined by the nature and patterning of interactions between individuals. It is here that the conflict with Rowell's (1972, 1979) approach becomes obvious. According to Rowell (1972, 1979), interactions and relationships fall strictly into the domain of social organisation. However, Hinde (1976) does not divide aspects of sociality into two separate factions. While social structure is formally defined in terms of individuals' interactions and relationships, it comprises and is influenced by population dispersion and individual ranging patterns (Crook *et al.* 1976, Hinde 1976). Given these problems of unclear usage and conflicting definitions, it is important to avoid perpetuation of the inconsistent use of terminology, and to try to adopt exact definitions and usage.

'Social system' is a poorly-defined term which is nevertheless valuable as an all-encompassing descriptor. The topic of animal sociality is a complex one, and 'system' clearly infers the complexity and inter-relatedness of the many different factors which make up any given form of sociality. Hinde's (1976) conceptual framework is an important tool for studies of sociality (Whitehead 1997), and his model of a hierarchical system whereby relationships are made up of patternings of interactions, and social structure is determined by the patterning of relationships, provides a valuable formalisation of thought and terminology in this field. It also focuses attention on the appropriate level for consideration of the selective forces acting on sociality, the level of the individual (Hinde 1983). With the exception of Rowell's (1972, 1979) division of 'social organisation' and 'social structure', it is my feeling that the majority of authors are using the two terms synonymously. As a result, I intend to avoid use of the term 'social organisation', which I believe to be extraneous, and to adopt Hinde's (1976) terminology and approach to the description of 'social structure'.

INTERACTIONS AND ASSOCIATIONS AMONG CETACEANS

At the core of Hinde's (1976) approach are the patterns of interaction between individuals. Interactions among cetaceans, like those among terrestrial mammals, take a variety of forms, over a range of different temporal and spatial scales (Whitehead *et al.* in press). Interactive behaviours may include (but are not limited to) vocalisations (e.g. Tyack & Whitehead 1983), physical contact (including aggression, and sexual and socio-sexual behaviour, Connor *et al.* in press), and apparently altruistic or co-operative behaviours such as physical support of an injured conspecific, or the sharing of prey items (Caldwell & Caldwell 1966, Connor & Norris 1982, Baird & Dill 1996). Although it has been possible to study the nature and context of some forms of interaction in captive cetaceans, this has proved difficult for wild whales and dolphins. Cetaceans are fast moving, much of their behavioural interaction takes place below the surface of the water, and individuals may not be identifiable in real-time. This combination of factors may prevent the systematic recording of interactions between individuals. This problem is not unique to cetaceans, the interactive behaviours of many terrestrial species may also be unobservable, due to nocturnal habits, or to habitats which tend to obscure individuals.

So, how are we to examine relationships and social structure, if we can't fulfill the first requirement of Hinde's (1976) framework, the description and quantification of interactions? Whitehead (1997) explains how records of spatio-temporal proximity (pairs of individuals observed together), often described as 'associations', can be used as substitutes for records of actual interactions, provided that we define associations in relation to the circumstances in which interactions between individuals usually take place. Unfortunately, because of the difficulties of observing interactions, and of identifying the spatial and temporal scales over which cetaceans interact, we often do not know what those circumstances are. Thus many researchers studying social structure in cetaceans and other species make what Whitehead *et al.* (in press) describe as 'the gambit of the group'. They assume that individuals that are in spatial and/or temporal proximity are interacting, and therefore that such proximity can be used to define association. Although more information is clearly required in order to fully justify this assumption,

with a few exceptions, cetaceans in spatio-temporal proximity do seem to interact strongly with each other, and the 'gambit of the group' does seem to be at least roughly justified (Whitehead *et al.* in press). Thus associations may serve as appropriate indicators of interaction in cetaceans. Individuals which are in spatial (e.g. killer whales, *Orcinus orca* - Bigg *et al.* 1990) and/or temporal proximity (e.g. Hector's dolphins, *Cephalorhynchus hectori* - Slooten *et al.* 1993, and sperm whales - Whitehead *et al.* 1991) are considered to be associated, and the patterning of associations may be used to describe relationships, and hence social structure.

THE SPERM WHALE

The sperm whale is the largest of the toothed whales (odontocetes), and is distributed throughout all the world's oceans, from the equator to the polar ice caps (Rice 1989). Sperm whales show the greatest sexual dimorphism of all cetaceans. Mature males, at 15-18 m in length and 40-50 metric tons, are approximately 1.5 times as long and 3 times as heavy as mature females (Best 1979), and have the largest brains (Kojima 1951), and most extreme geographical segregation of the sexes, of any species. These remarkable characteristics suggest the potential for complex patterns of sociality.

LIFE HISTORY

At birth, the sex ratio is 1:1, and calves of both sexes are approximately 4 m in length, and 775 kg in weight (Best 1968). Growth rates are comparable for the first 9 years of life, after which males experience a sharp acceleration in growth, which eventually results in the marked sexual dimorphism of adults (Best 1970). Females reach sexual maturity at around 9 years of age, corresponding to a length of approximately 8.5-9 m (Best 1968). The gestation period is 14-16 months (Best 1968, Best *et al.* 1984), after which a single calf is born (multiple births are considered to be very rare, Gambell 1972). Lactation lasts for at least 24-25 months, and may increase in duration with the age of the mother. Weaning appears to be followed by a 'resting stage' in females, which may last for around 9 months, thus the minimum inter-calf interval is approximately 4 years (Best

1968). Puberty in males (defined as the age at which 50% of the population are producing spermatozoa) occurs at approximately 19 years of age (~12 m) and full sexual maturity (defined as the age at which 50% of the population have fully mature testes) at 25-27 years (~13.6 m, Best 1969, 1970). Physical maturity (fusion of the anterior thoracic epiphyses) occurs at an age of at least 35 years in males, and about 28 years in females (Best 1970). Reported estimates of adult mortality are 6.6%/year for males and 5.5%/year for females (International Whaling Commission 1982). However, these estimates come from whaling data and may be biased by the methods used (e.g. Best 1970), the falsification of catch statistics (Brownell *et al.* 1998, Kasuya 1998), and the fact that the populations being studied were heavily exploited.

ECOLOGY: DISTRIBUTION, DIET, PREDATORS

The worldwide distribution of sperm whales is reviewed thoroughly by Rice (1989). Female sperm whales and their juvenile offspring are found primarily in tropical waters, between the limits of 45° N and 40° S, which correspond approximately with the 15° C sea surface isotherm. This temperature-restricted distribution may reflect the limited thermal tolerance of calves. Mature male sperm whales, whose distributions overlap those of the females during the breeding season, are commonly found at higher latitudes, to the edges of the polar pack ice. Sperm whales are a deep water species, found primarily in waters greater than 1000 m in depth (Whitehead & Weilgart in press), although in some areas they may be found in shallower waters (Whitehead *et al.* 1992a, Scott & Sadove 1997, Hooker *et al.* in press). The distribution of sperm whales commonly correlates with regions of upwelling, which result in increased primary productivity, although there are a number of exceptions (Gulland 1974, Jaquet & Whitehead 1996).

Feeding primarily on meso-pelagic squid (Clarke 1980, Kawakami 1980), sperm whales are major predators of the oceanic ecosystem, removing around 100 million metric tons of biomass annually, an amount similar to that of all human fisheries combined (Kanwisher & Ridgway 1983).

There have been reports of harassment or attacks on sperm whales by large sharks (Best *et al.* 1984), short-finned pilot whales (*Globicephala macrorhynchus* - Weller *et al.* 1996), false killer whales (*Pseudorca crassidens* - Palacios & Mate 1996), and killer whales (*Orcinus orca* - Arnbom *et al.* 1987). None of these were thought to be serious predators of adult sperm whales (Berzin 1971, Jefferson *et al.* 1991), but recent observations of a fatal attack on adult sperm whales by killer whales (S. Mesnick pers. comm.) demonstrate that despite their large size and communal defense strategies, sperm whales are not immune to predation.

BEHAVIOUR: DIVING, FORAGING, VOCALISATIONS

Sperm whales are among the deepest diving marine mammals, with reported maximum dive depths of 1135-3195m (Heezen 1957, Norris & Harvey 1972, Clarke 1976, Watkins *et al.* 1993), although some of the higher values are based on rather tenuous evidence. Individual sperm whales in the Galápagos Islands area generally dive to depths of several hundred metres, for approximately 40 minutes, followed by a 10 minute surface interval (Papastavrou *et al.* 1989).

Sperm whales forage throughout the day and night, although groups of females often socialise during afternoon hours (Whitehead & Weilgart 1991). Feeding has never been observed, thus the methods used to find and capture prey at depth may only be inferred. Many squid species are luminescent (Clarke *et al.* 1993), which may facilitate detection, and luminescent mucus from previous captures, or the white colouration of the whales' jaws, may attract prey (Gaskin 1967). Most authors believe that sperm whales use echolocation for prey detection (Norris & Harvey 1972, Gordon 1987a, Goold & Jones 1995). It seems reasonable to suggest that various foraging techniques may be used, depending upon the luminousity, size and speed of prey items (Clarke *et al.* 1993).

It is the loud, regular broadband clicks produced by sperm whales throughout their dives (Backus & Schevill 1966, Mullins *et al.* 1988, Whitehead & Weilgart 1990, Goold & Jones 1995) that are thought to function in echolocation. Large male sperm whales may

emit very loud and distinctive 'slow clicks' (or 'clangs') on breeding grounds (Gordon 1987a, Weilgart & Whitehead 1988). Males may use these slow clicks to assess or avoid each other, or perhaps to indicate their presence to groups of females (Whitehead 1993). Codas (distinctive short patterned series of clicks, Watkins & Schevill 1977) are often heard when groups of females and juveniles are socialising. Codas are believed to function as communication signals (Weilgart & Whitehead 1993), and Watkins & Schevill (1977) suggested that some codas might be used for individual identification. Findings of group-specific coda repertoires indicate the existence of dialects in sperm whales (Weilgart & Whitehead 1997).

ABUNDANCE AND CONSERVATION STATUS

The sizes of sperm whale populations are poorly known. Although global abundance estimates of almost two million sperm whales have been reported (e.g. Rice 1989), these estimates cannot be considered reliable. The techniques and models used to calculate abundance have been criticised (Best *et al.* 1984, Cooke 1986), and evidence has recently come to light that many of the Japanese and Russian catch statistics used in population size estimation had been falsified (Brownell *et al.* 1998, Kasuya 1998). The sperm whale has been listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) since 1985, and is listed as 'vulnerable' by the International Union for Conservation of Nature and Natural Resources (IUCN 1996).

NOMENCLATURE AND PHYLOGENY

The sperm whale is referred to by two different scientific names, *Physeter macrocephalus* and *P. catodon*. The debate as to which is correct is complex (Husson & Holthuis 1974, Schevill 1986, 1987, Holthuis 1987, Rice 1989), and both continue to be widely used (e.g. Watkins *et al.* 1993, Palacios & Mate 1996, Clarke & Young 1998, Hooker 1998). Following the International Whaling Commission, the International Commission for Zoological Nomenclature, and Rice (in press), I will use *Physeter macrocephalus*.

The position of sperm whales within the cetacean phylogeny has been a question of intense debate in recent years. Molecular analyses of mitochondrial DNA (mtDNA) genes have suggested that the Physeteroidea (the sperm whale (Physeteridae: *Physeter macrocephalus*) and sister species the dwarf and pygmy sperm whales (Kogidae: *Kogia simus* and *K. breviceps* respectively)) are more closely related to the Mysticeti (baleen whales) than to the Odontoceti (toothed whales) (Milinkovitch *et al.* 1993, 1994, 1995, 1996). Support for this revised phylogeny is equivocal. Re-analysis of Milinkovitch *et al.*'s (1993, 1994, 1995) data (Cerchio & Tucker 1998), analyses of other mtDNA genes (Árnason & Gullberg 1994, 1996), and cladistic analyses of morphological data (Heyning 1997, Messenger & McGuire 1998) all strongly support the traditional positioning of the Physeteroidea within the Odontoceti. Pending confirmation of a definitive phylogeny, I intend to continue to use the traditional classification of the cetacean order, and to use the term 'odontocete' to refer to all toothed cetaceans, including sperm whales.

SPERM WHALE SOCIAL STRUCTURE

The sperm whale has held many different roles in the human imagination, from valued prey, to dreaded foe (Melville 1851), to a subject of fascination and academic interest. Although the complex nature of sperm whale society has been recognised since early whaling times (reviewed in Caldwell *et al.* 1966), approaches to studying social structure, and thus the types of information available, have changed considerably over time.

THE HISTORICAL PERSPECTIVE - INFORMATION FROM WHALING

The sperm whale derives its name from the spermaceti organ, a large lipid-filled structure in the head, which appears to function in the propagation of sound (Norris & Harvey 1972, Cranford *et al.* 1996). It was the possession of this prized spermaceti oil that led to the targeting of sperm whales for intensive and prolonged whaling. Primitive hand-harpoon and open-boat whaling, which began in the early eighteenth century and peaked in the 1840s, greatly reduced sperm whale populations in the Pacific, and probably worldwide (Best 1983, Whitehead 1995). Mechanized whaling increased in scale during

the twentieth century, with average annual catches of 25,000 animals during the 1960s (Best 1983). During this period, sperm whales were, both numerically and by weight, the most important component of the worldwide whaling catch (Best 1979). A ban on pelagic sperm whaling came into effect in 1980 (International Whaling Commission 1980), and commercial whaling was banned under the International Whaling Commission (IWC) moratorium in 1985.

Although early whaling records provide details of sperm whale distribution and anecdotal information on the biology of the species, it was only with the advent of modern whaling that scientific research began in earnest. Studies focused on anatomy, diet, growth and life-history parameters (e.g. Matthews 1938, Clarke 1956, Best 1968, 1969, 1970, Clarke & Paliza 1972, Clarke 1980, Kawakami 1980, Best *et al.* 1984), and are reviewed in Rice (1989).

Whaling research provided considerable insight into the social structure of sperm whales (reviewed by Caldwell *et al.* 1966 and Best 1979). It was recognised that adult males and females had very different geographic distributions, and were found in different types of groupings. Males were found to segregate from the females at or before puberty, and to migrate to higher latitudes (Ohsumi 1966). Younger males were found in 'bachelor schools', which consisted of animals of approximately the same age or length. These schools decreased in size with increasing age of the members, to the point where large mature animals were typically solitary (Best 1979). Sexually mature males returned to the tropical waters inhabited by females in order to breed. These males were traditionally viewed as 'harem masters', with each remaining with a single group of females throughout the breeding season (e.g. Berzin 1971). However, mark-recovery data, relative parasite loads, and indications of synchronous oestrus suggested that the duration of encounters between a mature male or males and a group of females might be considerably shorter than this (Best 1979, Best & Butterworth 1980).

Females of all ages and juvenile males were found in cohesive groups of 20-40 individuals, and were seen to exhibit epimeletic (care-giving) behaviour, with individuals

supporting and staying with harpooned, injured and even dead group members (Caldwell & Caldwell 1966). Mark-recapture tagging studies provided some evidence for long-term relationships between females (four pairs of females which were marked together were recaptured together 5-10 years later, Ohsumi 1971). Some authors, extrapolating from this limited evidence, concluded that all relationships between females were long-term (or permanent), and thus that groups were stable matrilineal entities (e.g. Fortom-Gouin & Holt 1980). However, the nature and stability of female groupings were far from clear. Groups consisting of immature animals of both sexes were reported, indicating that females, as well as males, dispersed from their natal groups (Clarke 1956, Gaskin 1970, Ohsumi 1971). While some authors reported segregation of females on the basis of reproductive status (Clarke 1956, Gaskin 1970), thus seeming to contradict the concept of permanent groupings, others found females of all reproductive states together in groups (Ohsumi 1971, Gambell 1972, Best 1979).

The data from whaling, even in the rare cases where whole schools were captured, could give very little information on inter- or intra-group relationships, or on undisturbed social behaviour (Best 1979, Rice 1989). Best's (1979) comprehensive summary of knowledge on social structure from invasive studies provides "only...an outline of the species' social organization, a skeleton in fact that needs 'fleshing-out' with direct field observations of social behavior" (Best 1979, p231).

THE CONTRIBUTION OF PHOTO-IDENTIFICATION STUDIES

Animals of many species have markings, colouration patterns or scars which allow individuals to be identified. In almost all species of cetaceans, some proportion of individuals have distinctive marks on their tail flukes, dorsal fin, head or back which allow them to be identified from photographs (Hammond *et al.* 1990). Whitehead & Gordon (1986) developed acoustic methods for detecting and tracking sperm whales, and proved the feasibility of photo-identification techniques for this species, with over 91% of animals being individually-identifiable (Arnbom 1987). These new non-invasive techniques enable researchers to find sperm whales, distinguish individuals, and to

recognise particular animals over time scales of years, facilitating the study of many aspects of social structure.

This new approach to studying sperm whales has been utilised in many areas (including: Sri Lanka (Gordon 1987b), Norway (Lindhard *et al.* 1988), the Azores (Gordon & Steiner 1992), eastern Canada (Whitehead *et al.* 1992a), New Zealand (Childerhouse *et al.* 1995), the South Pacific (Dufault & Whitehead 1995b) and the Carribean (Gordon *et al.* 1997)), however, the longest-running study is the one begun by Hal Whitehead and colleagues in the Galápagos Islands in 1985 (Whitehead & Arnbom 1987).

Photo-identification studies of sperm whales have provided a more detailed picture of social structure, particularly that of females and their juvenile offspring, than was previously possible. While the existence of long-term relationships between females was confirmed, investigation of the temporal duration of these relationships indicated that groups were not permanent entities (Whitehead *et al.* 1991). Instead, it appeared that groups of females and juveniles were temporary collections of smaller social units, and that these units formed the stable core of female society (Whitehead *et al.* 1991). The fundamental purpose of these social units is thought to be communal care of calves. This is indicated by observations of allo-suckling (Gordon 1987b), group defense of calves against predators (Arnbom *et al.* 1987), and baby-sitting (the serial accompaniment of a calf by different adults (Best *et al.* 1984, Gordon 1987b, Arnbom & Whitehead 1989), and reduction in diving synchrony among group members, leading to shorter intervals with no adult at the surface (Whitehead 1996a)).

Photo-identification studies of male sperm whales on the Galápagos Islands breeding ground have confirmed the roving nature of male mating strategies, with only hours to days being spent with a particular group of females (Whitehead 1993). Males are thought to avoid each other on breeding grounds (Whitehead 1993).

THE CONTRIBUTION OF MOLECULAR GENETIC STUDIES

Molecular genetic techniques are powerful tools in the study of social structure. A variety of genetic markers may be used to assess such crucial issues as identity, gender, maternal origins (thus dispersal/philopatry), paternity (thus mating system) and genetic relatedness (between individuals, and between groups). With the advent of techniques for obtaining and preserving skin samples from living whales, from which DNA may be extracted (Whitehead *et al.* 1990, Amos & Hoelzel 1991, Amos *et al.* 1992), it has been possible to apply molecular genetic techniques to the study of sperm whale social structure.

It is difficult, if not impossible, to distinguish between juvenile males and juvenile or adult females at sea. A sperm-whale-specific genetic marker has been developed to detect the male-specific SRY region of the Y chromosome, and thus to determine gender (Richard *et al.* 1994). Analysis of mitochondrial haplotypes and of microsatellite DNA markers has shown that groups include related individuals (Richard *et al.* 1996a). The data are consistent with groups consisting of two or more matrilines. Since groups generally consist of two or more social units, the obvious interpretation is that each unit is a single matriline. However, indications of paternal relatedness between maternally-unrelated members of groups suggest some long-term relationships between different matrilines (Richard *et al.* 1996a).

OUTSTANDING QUESTIONS: OBJECTIVES

The application of non-invasive techniques has clearly brought us far beyond Best's (1979) 'skeleton' of sperm whale social structure. Much of what has been learned has suggested considerable social complexity in this species, and has raised further questions concerning the details of social structure. The 'groups and units' model of the social structure of females and juveniles requires further examination and confirmation. The nature of social units remains unclear. How many members do units contain, how stable is unit membership, and what is the genetic structure of units? These questions have important consequences for interpretation of the functional basis of female sociality.

Questions relating to the behaviour of unit members within groups, and the correlation of social behaviour with genetic relatedness promise to deepen our understanding of the relationships between individuals, both within and between units. The social behaviour of large male sperm whales remains largely unknown.

These outstanding questions are the subject of this PhD thesis, questions which I will address by examining the social structure of sperm whales in the eastern tropical Pacific, using a combination of photo-identification and molecular genetic techniques.

CHAPTER TWO

Temporal analysis of the social structure of female and juvenile sperm whales

INTRODUCTION

The nature and duration of associations and relationships among females and their young are central aspects of social structure, since the sociality of males is shaped by the distribution and sociality of females (Wrangham & Rubenstein 1986). Although in certain cases, female sociality may be influenced by male strategies (e.g. infanticide, van Schaik 1996), patterns of association among females are generally thought to reflect the distribution of resources and predators (Emlen & Oring 1977, Bradbury & Vehrencamp 1997), and/or the need for co-operative infant rearing (Lee 1994).

Female sperm whales and juveniles of both sexes are encountered at sea in groups, generally of 20-40 animals, which exhibit co-ordinated behaviour and social cohesion (Caldwell *et al.* 1966, Best 1979). Male sperm whales disperse from these groups at or prior to puberty (Best 1979), and join groups only very briefly for mating, once sexually mature (Whitehead 1993). Whaling mark-recapture data provided the first evidence of the duration of female relationships. Ohsumi (1971) reported 4 cases of 2 females marked on the same day being captured together 5-10 years later. Photo-identification (photo-ID) studies provided further evidence of stable female relationships, with sets of females/juveniles being identified together in different years (Gordon 1987b, Whitehead & Waters 1990). These studies also indicated that group membership might not be completely stable (e.g. Whitehead & Waters 1990). Whitehead *et al.* (1991) fitted a model to the 1985-1989 sperm whale photo-ID data from the Galápagos study area, and suggested that groups were in fact short-term (mean 6.5 days) aggregations of smaller, stable social units. A primary goal of this chapter is to re-assess that model, using a much longer series of sperm whale photo-ID data (1985-1997) from the eastern tropical Pacific.

Traditionally, social structure has been analysed using techniques that fail to incorporate information on the temporal nature of relationships. While the calculation and display of association indices (e.g. Cairns & Schwager 1987) using cluster analyses, multi-dimensional scaling or maximum spanning trees (e.g. Morgan *et al.* 1976, Penzhorn 1984) may produce informative results, these analyses present a static picture of social

structure (Whitehead 1995). An additional drawback is that these techniques may either be impossible to implement on datasets involving large numbers of individuals, or may produce output that is difficult to assimilate and interpret effectively (Whitehead 1995). Whitehead (1995) attempted to overcome these problems by developing techniques for investigating the temporal scales and stabilities of relationships among identified individuals. I will apply these techniques (described below) to questions of social structure among female and juvenile sperm whales.

Studies on a wide variety of taxa have indicated that social structure may vary intra-specifically with population density (e.g. Lott 1984, Crockett & Eisenberg 1987, Branch *et al.* 1993). The numbers of sperm whales utilising the waters around the Galápagos Islands are known to have declined considerably (~20%/year) between 1985 and 1995 (Whitehead *et al.* 1997). I will assess whether the resulting reduction in population density is reflected in any differences in social structure among female and juvenile sperm whales, by comparing recent data with data collected earlier in the study.

METHODS

FIELD RESEARCH

Sperm whales were studied during a number of field projects between 1985 and 1997 in the eastern tropical Pacific (ETP) (Table 2.1). While the majority of research effort was focused on the Galápagos study area (1°30'S - 1°30'N, 89° - 92°30'W) (Figure 2.1), fieldwork was also performed off the western coast of Central and South America, from the Gulf of Panamá (7°N, 80°W) to Perú (19°S, 72°W), with most of this effort occurring off the coast of Ecuador (Figure 2.2). The research platforms were 10-20 m vessels (motor-sailing vessels with the exception of 'Ratty'), which spent 2-3 weeks at sea between port visits. Vessels were equipped with hydrophones for detecting and localising the distinctive broadband 'click' vocalisations of sperm whales (Backus & Schevill 1966). Once detected, sperm whales were approached, and tracked for as long as possible (day and night). Most encounters lasted from a few hours to a few days.

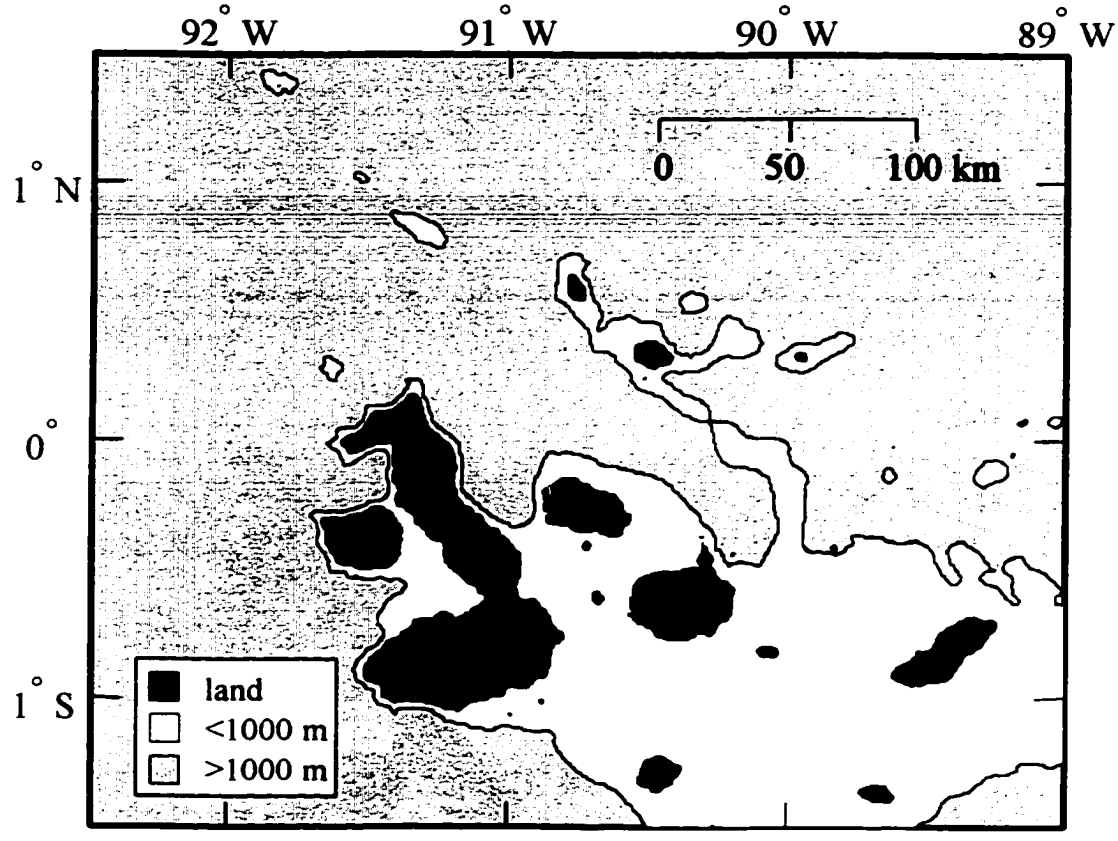

Figure 2.1. Map showing the Galápagos study area. Waters less than 1000 m in depth, where sperm whales are generally not found, are shown in white.

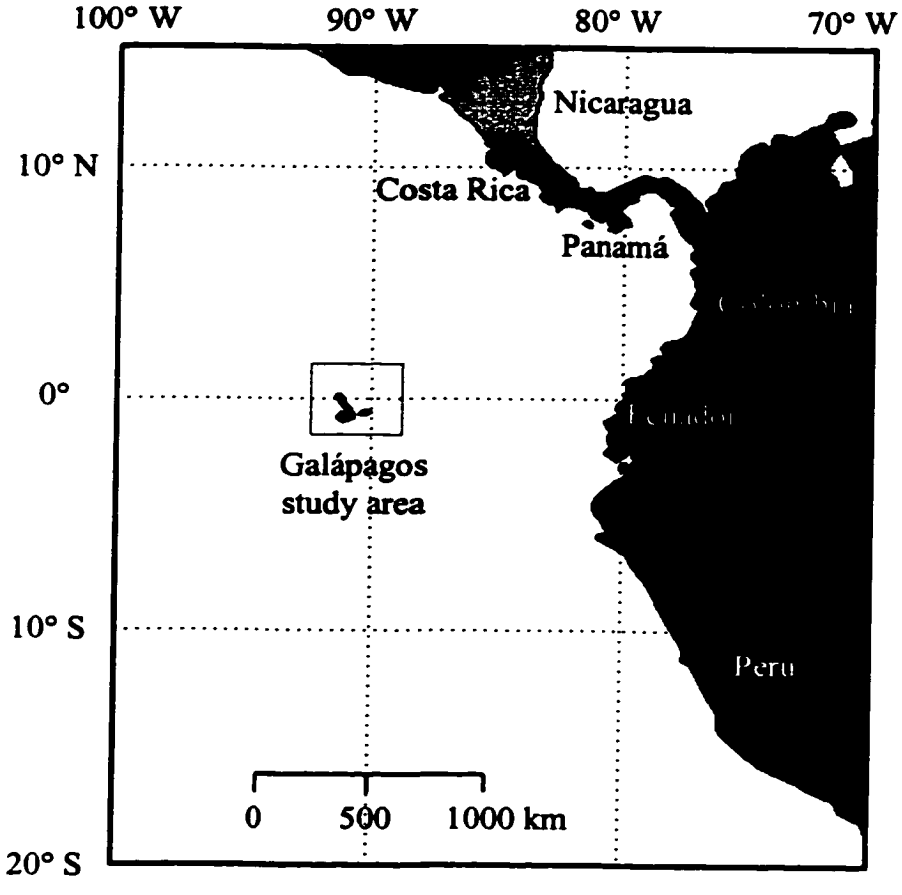

Figure 2.2. Map of the eastern tropical Pacific Ocean, encompassing research areas and indicating the Galápagos study area.

The decision to include data from outside the Galápagos study area in the analyses was made on the basis of a number of factors. Although earlier analyses suggested that sperm whales in the Galápagos study area and off mainland Ecuador/Perú might belong to distinct or slowly-mixing populations (Dufault & Whitehead 1993, 1995), more recent studies have found little geographically-based population structure within the South Pacific (Whitehead *et al.* 1998). Analyses of dialects, fluke-markings and genetics indicate that female and juvenile sperm whales show greater fidelity to their companions than to any particular geographic area (Whitehead *et al.* 1998). Animals are known to travel from the Galápagos area to the coasts of Panamá, Ecuador and Peru (whaling mark-recovery data - Ivashin 1978, Ramírez 1989; photo-ID data - Whitehead *et al.* 1997), and one social unit is known to have then returned to Galápagos waters (Christal *et al.* 1998). Excluding data collected outside the Galápagos study area therefore seems unnecessarily restrictive, since there is no evidence that there are distinct populations in the ETP region, and would result in some information on the long-term association patterns of individuals being omitted from analyses.

Table 2.1. Details of field projects.

field project dates	area	project leader	vessel
Feb 85	Ecuador	Hal Whitehead	Elendil
Feb 85 - Apr 85	Galápagos	Hal Whitehead	Elendil
Jan 87 - Jun 87	Galápagos	Hal Whitehead	Elendil
Apr 88	Galápagos	Susan Waters	Symbol
Oct 88 - Apr 89	Galápagos	Thomas Lyrholm	Siben
Apr 89 - Jun 89	Galápagos	Hal Whitehead	Elendil
Jan 91 - Mar 91	Ecuador	Hal Whitehead	Elendil
Mar 91 - Apr 91	Galápagos	Hal Whitehead	Elendil
Jun 92	Ecuador	Hal Whitehead	Balaena
Feb 93	Galápagos	Godfrey Merlen	Ratty
Mar 93 - Mar 94	Galápagos	Erland Lettevall (WCI)	Odyssey
Apr 93	Ecuador/Perú	Hal Whitehead	Balaena
Jan 94 - Jun 94	Galápagos	Godfrey Merlen	Ratty
Apr 95 - Jun 95	Galápagos	Hal Whitehead/Jenny Christal	Balaena
Jun 95	Panamá	Hal Whitehead/Jenny Christal	Balaena
Apr 96 - Jun 96	Galápagos	Godfrey Merlen	Ratty
Apr 97 - Jun 97	Galápagos	Jenny Christal	Ratty

PHOTO-IDENTIFICATION

Individual sperm whales can be identified by the distinctive patterns of marks along the trailing edge of the tail flukes (Arnbom 1987). Whales at the surface were approached from behind to a distance of 20-100 m, and a photograph taken of the tail flukes as they were raised at the start of a deep dive (fluke-up).

Mature males are readily distinguishable from juveniles and adult females on the basis of size, and all records for these individuals are excluded from these analyses. Records for first-year calves were also excluded, since they rarely fluke-up, and thus their probability of identification is not equivalent to that of older animals.

Fluke photograph analysis followed the methods devised by Arnbom (1987), with later refinements by Dufault and Whitehead (1993). Each black and white negative was assigned a quality (Q) grade from 1 (poor) to 5 (excellent) based on the focus and resolution of the image, the angle of the fluke relative to the negative plane, and the proportion of the fluke visible within the frame (Dufault & Whitehead 1993). Individuals were identified from negatives of $Q \geq 3$, and assigned identification numbers. A black and white print of the best negative available for each individual was digitized (using a *Calcomp*™ digitising tablet) into a computer catalogue which stores details of the locations and types of markings along the trailing edge of the fluke. Each new set of individuals was compared to the existing catalogue both visually, and using a computer matching program (Whitehead 1990b). Only identifications from photographs of quality $Q \geq 4$ were included in these analyses.

TEMPORAL ANALYSES

Temporal analysis techniques

Individuals were considered to be associated if they were identified on the same day. Since individuals are available for identification only roughly once per hour (when they

raise their tail flukes at the beginning of a dive), and are not photographed each time that they dive (since individuals may be spread over several kilometers), this association criterion minimises exclusion of associates which were present, but which were, by chance, not identified closely together in time. Light conditions in the study areas are suitable for photo-identification from 6am to 6pm, thus being identified on the same day is equivalent to being identified within 12 hours.

Lagged, intermediate, and null association rates were calculated, and models fitted (using maximum likelihood and binomial loss to the full data set), using SOCPROG 1.1 (H. Whitehead, programs available: http://is.dal.ca/~whitelab/index.htm), following the methodology of Whitehead (1995). The lagged association rate is simply an estimate of the probability of two individuals which were associated at some point (time zero), being associated after various time intervals (lags, *d*). The intermediate association rate is calculated in a similar way to the lagged association rate, except that only associations and potential associations (i.e. one of a dyad is seen) between the first and last recorded association of that dyad are considered. In the calculation of an intermediate association rate, the time lag *d* is the minimum of the time between a given sampling period and the first or last recorded association of the dyad. This rate is thus an estimate of the probability that associates remain associated between their first and last identifications together, and may be used to assess whether relationships are constant over time, or whether long-term associations often follow periods of separation. The null association rate is calculated on the basis of the size of the identified population, and estimates the expected lagged association rate for all time lags given completely random association among individuals in the population. All association rates were standardised (i.e. divided by the number of recorded associates on each occasion), to account for the fact that not all true associates of an individual are necessarily recorded during a sampling period in which that individual is identified (Whitehead 1995). Jackknifed estimates of precision for lagged association rates were calculated by jackknifing over periods of 30 days.

General description of social structure

The hypothesis to be tested is that standardised lagged association rate data from this longer time series will confirm the 'groups and units' model of sperm whale social structure developed by Whitehead *et al.* (1991) to fit the 1985-1989 (Galápagos only) data, with attrition (due to death, and the dispersal of juvenile males) being detectable over longer time scales.

Variation in social structure with population density?

The possibility of sperm whale social structure varying with population density was examined by dividing the total dataset into two periods: 1985-1990, when population densities were relatively high (Whitehead *et al.* 1997); and 1991-1997, when population densities were relatively low (Christal & Merlen 1997, Whitehead *et al.* 1997). To facilitate direct comparison of the data for these two time periods, standardised lagged association rates were re-scaled to a common y-axis intercept of 1, so that they approximated unstandardised lagged association rates (see Whitehead 1995).

Group size estimation

Since the members of a group of sperm whales are typically not all visible at one time, field estimation of group size is generally not possible, and alternative procedures, based on identifications and associations of individuals, must be used. Mean group size was estimated using the methods of Whitehead & Kahn (1992). If whales are found in groups of size M + 1, then M can be estimated by considering the number of an individual's associates (identified within a specified association interval) which are common to two intervals separated by a particular time lag (d) (Whitehead & Kahn 1992). The use of 'key' whales (the first 10 individuals identified on a given day that were also identified on another day), removes bias in this estimation procedure (Whitehead & Kahn 1992). Since the half-life for groups is estimated at approximately 6.5 days (Whitehead *et al.* 1991, and see later), only time lags over which it was likely that groups retained their membership (d = 1 day, 2 days, 3 days) were used to estimate M. Nonlinear estimation

was then used to estimate M + 1 (i.e. group size) and its standard error using results for all three values of *d*.

Estimates were calculated for association intervals of 2 and 12 hours (the first for comparison with earlier studies, and the latter since 12 hours has been shown to increase the probability of including all associates (Chapter 3)), for the whole dataset (1985-1997) and the two periods described above (1985-1990 and 1991-1997).

The differences between estimated group sizes calculated using the two different association criteria (2 hr versus 12 hr) were tested for each dataset separately, using Kruskal-Wallis non-parametric analysis of variance (KW) on estimates of M calculated for the three time lags (1 day, 2 days, 3 days). The same technique was used to test for differences between the estimates for the earlier and later years (for each of the association criteria separately).

RESULTS

PHOTO-IDENTIFICATION DATA

A total of 5129 Q≥4 photographs were taken during the study, from which 1809 individual female and juvenile sperm whales were identified, including 291 which were identified during multiple field projects (Table 2.2).

TEMPORAL ANALYSES

General description of social structure

The null association rate is extremely low (<0.001), reflecting the low probability of random re-association in this large population (Figure 2.3). The lagged association rate is clearly considerably greater than the null association rate, indicating that there are preferred associations between individuals over all time scales from 2 days to approximately 5.5 years.

Table 2.2. Summary of photo-identification data (females and juveniles only).

field project dates	location	# photos (Q≥4)	# individuals identified	# previously identified	# new	cumulative total (individuals)
Feb 85	Ecuador	7	3	0	3	3
Feb 85-Apr 85	Galápagos	633	284	0	284	287
Jan 87-Jun 87	Galápagos	1095	370	49	321	608
Apr 88	Galápagos	250	82	0	82	690
Oct 88-Apr 89[1]	Galápagos	613	348	69	279	969
Apr 89-Jun 89	Galápagos	843	293	70	223	1192
Jan 91-Mar 91	Ecuador	426	239	12	227	1419
Mar 91-Apr 91	Galápagos	113	72	33	39	1458
Jun 92	Ecuador	4	4	0	4	1462
Feb 93[2]	Galápagos	18	16	3	13	1475
Mar 93-Mar 94[3]	Galápagos	537	260	72	188	1663
Apr 93	Ecuador/Perú	182	91	20	71	1734
Jan 94-Jun 94[2]	Galápagos	32	22	8	14	1748
Apr 95-Jun 95	Galápagos	140	53	21	32	1780
Jun 95	Panamá	10	9	5	4	1784
Apr 96-Jun 96[2]	Galápagos	80	28	25	3	1787
Apr 97-Jun 97	Galápagos	146	24	2	22	1809

[1] courtesy of T. Lyrholm, [2] courtesy of G. Merlen, [3] courtesy of E. Lettevall, T. Lyrholm and the Whale Conservation Institute.

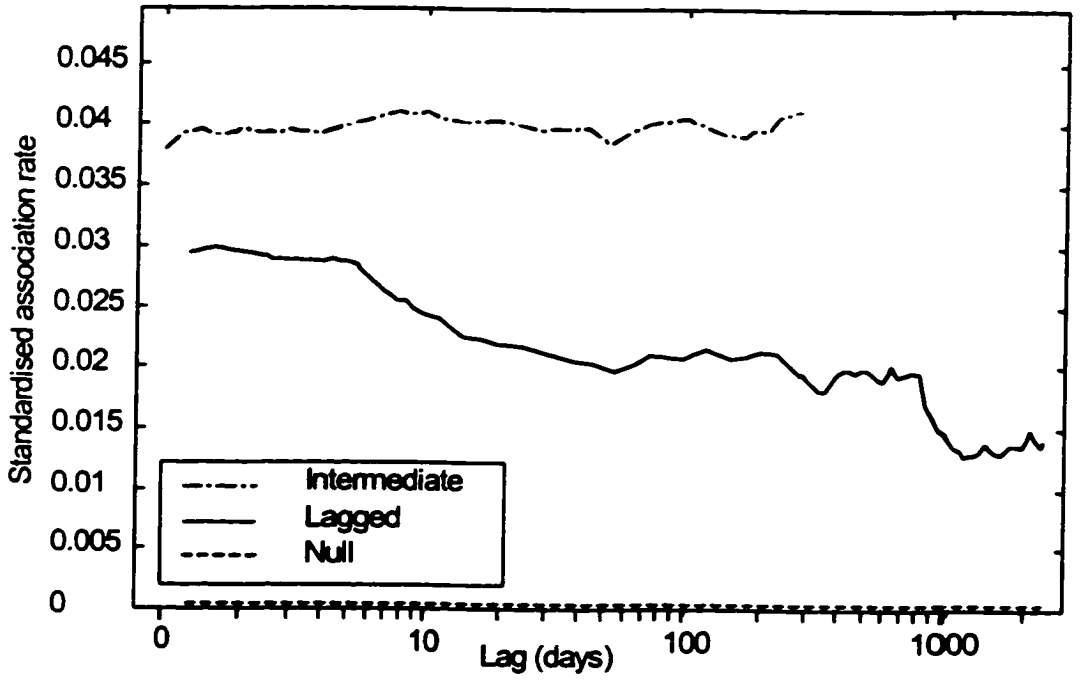

Figure 2.3. Standardised intermediate, lagged and null association rates for female and juvenile whales (1985-1997 dataset).

The lagged association rate shows two distinct declines. The first occurs over lags of one day to one month, and reflects the dissociation of groups into units. Over lags of one month to around 2½ years (~900 days) the lagged association rate is effectively constant, indicating that unit membership is reasonably stable over these time scales. The second distinct decline occurs over time lags of around 2¾ years (~1000 days), and indicates that there is some dissociation of unit members over these longer time scales. The intermediate association rate gives an indication of the constancy of associations (Whitehead 1995). The fact that the intermediate association rate in this case is effectively constant over all time lags is indicative of the fact that long-term associates do not dissociate between observed associations.

Various models were fitted to the lagged association rate data. The best fit was a model of the type: $g(d) = p_1 \cdot e^{-\mu_1 \cdot d} + p_2 \cdot e^{-\mu_2 \cdot d}$ (using the terminology of Whitehead (1995), where $g(d)$ is the lagged association rate over a time lag of d, p_k is a proportion of the total number of associates, and members of class p_k stay associated with an individual for a random length of time distributed according to the negative exponential distribution with parameter μ_k) (Figure 2.4).

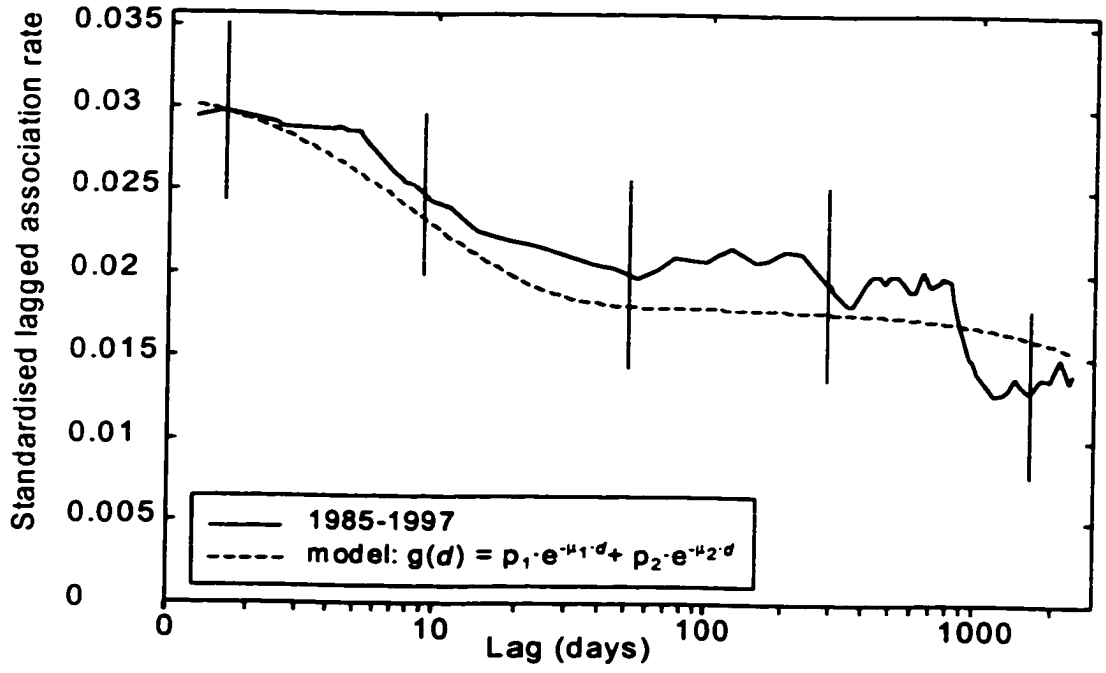

Figure 2.4. Standardised lagged association rate data (with jackknifed estimates of precision), showing the fitted model.

This model corresponds to a society in which each individual has some casual associates with which it associates for limited periods, and some long-term associates, which may eventually dissociate due to dispersal or death. Fitting this model to the standardised lagged association rate data, using a jackknife procedure (Figure 2.4), gave parameter estimates of:

$$\begin{aligned} p_1 &= 0.014 \quad \text{(s.e. 0.011)} \\ \mu_1 &= 1.082 \quad \text{(s.e. 0.897)} \\ p_2 &= 0.018 \quad \text{(s.e. 0.006)} \\ \mu_2 &= 0.025 \quad \text{(s.e. 0.133)} \end{aligned}$$

Fitted function: $g(d) = 0.014 \cdot e^{-1.082 \cdot d/10} + 0.018 \cdot e^{-0.025 \cdot d/365}$

The value μ_1 approximates the rate of dissociation of short-term associates over 10 day intervals, and indicates that the half-life of such associations is about 6.4 days (d = $10 \cdot (-\ln 0.5/1.082) = 6.4$). The value μ_2 approximates the annual rate of dissociation of long-term associates and indicates that this rate (which incorporates death and dispersal) is approximately 2.5% per year (s.e. 13.3%). The distinct nature of the drop in lagged association rates at 900-1000 days (Figure 2.4) is probably an artifact of the periodicity of data collection. Field seasons typically spanned several months, but tended to occur at the same time of year (Table 2.1), thus data are relatively sparse for longer lags that are not approximately annual. As a result, lagged association rates for the intervals just prior to the distinct drop (i.e. 800-900 days) may be based on relatively little data, and may perhaps artificially accentuate the nature of the decline.

Variation in social structure with population density?

Comparison of lagged association rates for the earlier versus later years of the study do suggest some differences in social structure (Figure 2.5). The standardised lagged association rate for 1991-1997 shows a less steep decline than that for 1985-1990 over time lags of 1-100 days, indicating less dissociation over short time intervals (although

the jackknifed estimates of precision suggest that this difference is not significant). The most noticeable difference between the curves is the divergence over time lags of >100 days. The dissociation indicated by the decrease in standardised lagged association rate for the 1985-1990 data is not present for 1991-1997.

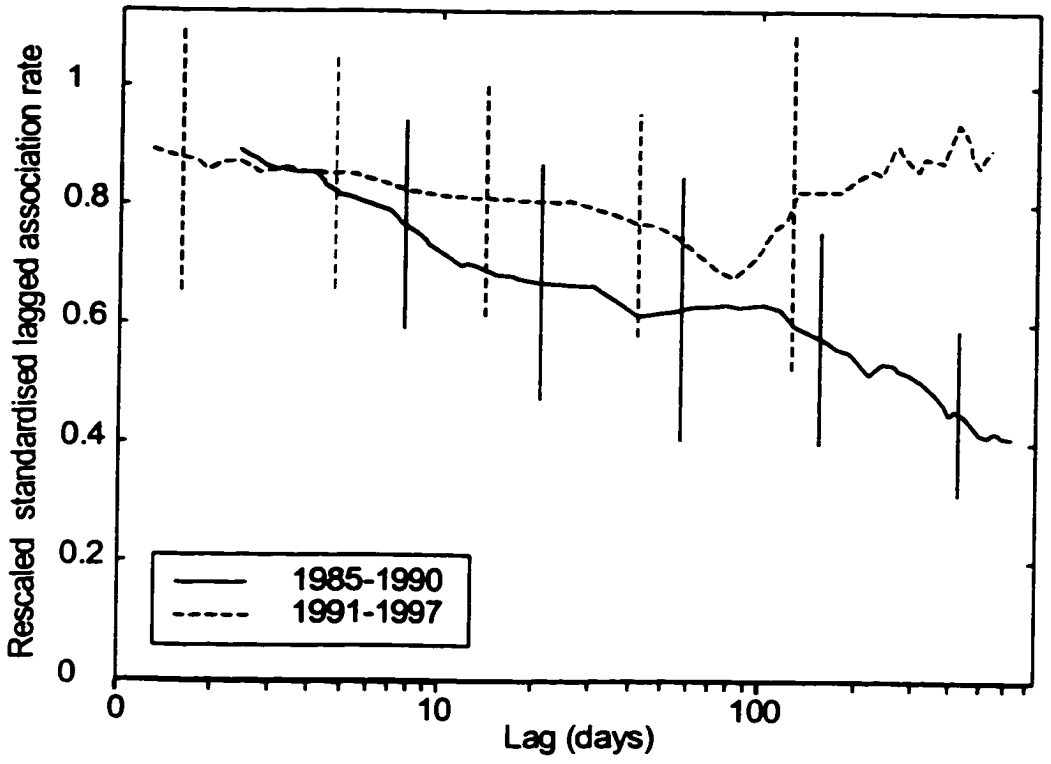

Figure 2.5. Lagged association rate data (with jackknifed estimates of precision), for 1985-1990 and 1991-1997.

Fitting of models to the two curves provides further indications of the nature of the difference in social structure. While the best fit to the 1985-1990 lagged association rate data is a model of the same type as that fit to the full data set, and corresponding to two levels of associates (Figure 2.6), the best fitting model to the 1991-1997 lagged association rate data indicates that the predominant class of associates are permanent companions (Figure 2.7).

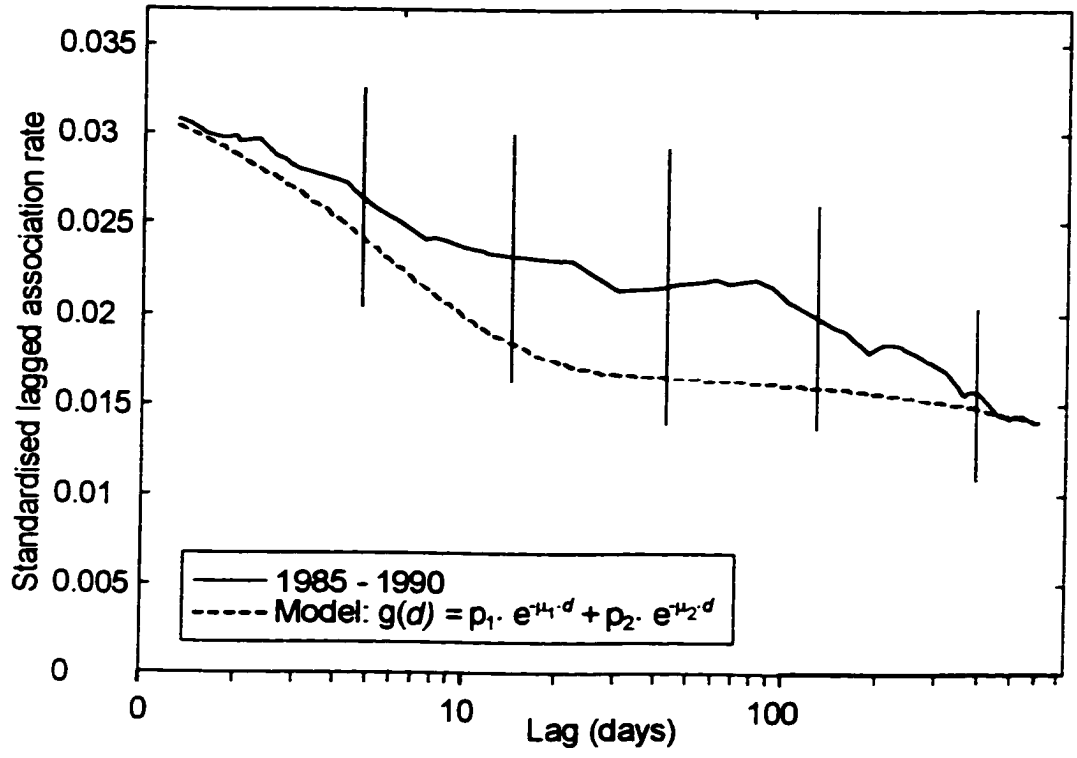

Figure 2.6. Standardised lagged association rate data for 1985-1990 (with jackknifed estimates of precision), showing the fitted model.

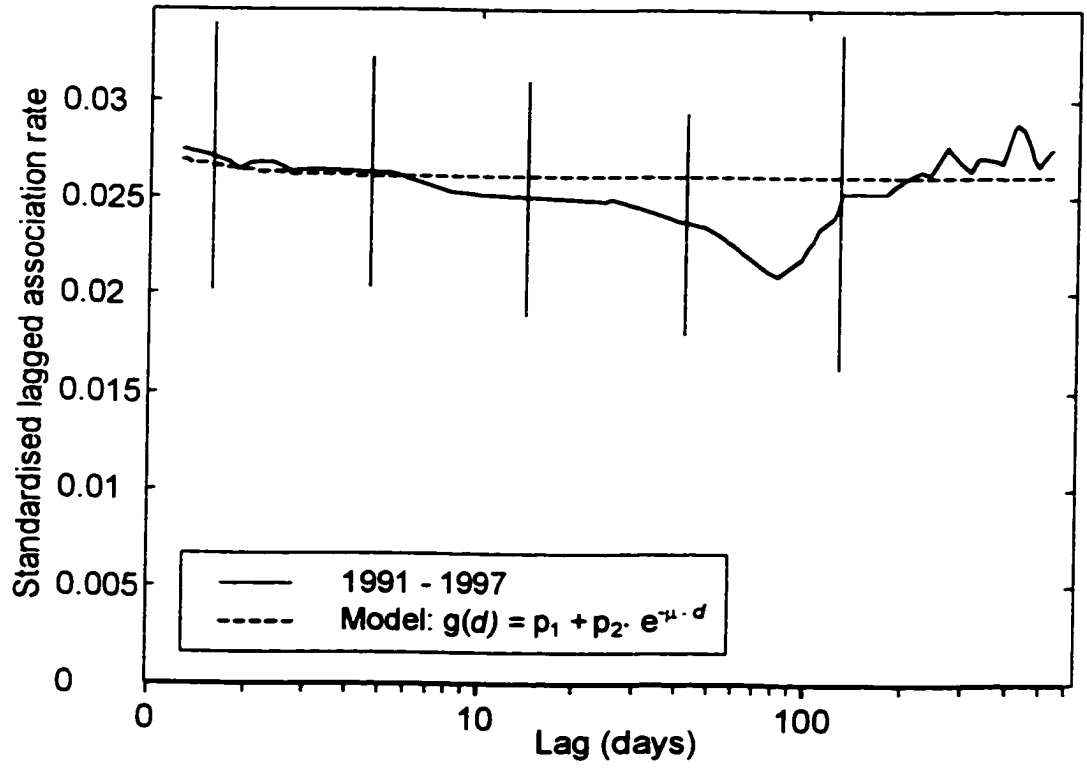

Figure 2.7. Standardised lagged association rate data for 1991-1997 (with jackknifed estimates of precision), showing the fitted model.

Mean group size

The estimates of M (group size – 1) for the 12 hr association criterion were significantly higher than those for the 2 hr association criterion for each dataset considered separately (KW, all $p = 0.05$). Estimates of M for the later period (1991-1997) were significantly higher than those for the earlier period (1985-1990), for both association criteria (KW, both $p = 0.05$). Estimated mean group sizes calculated using the different datasets and association criteria ranged from 21.83 to 40.61 individuals (Table 2.3).

Table 2.3. Mean group size estimates, using 2hr and 12 hr association criteria, for the whole dataset, early (high population density) and later (low population density) years. The standard error for each estimate is given in parentheses.

dataset	2 hr	12 hr
1985-1997	25.0 (*1.484*)	34.3 (*0.703*)
1985-1990	21.8 (*1.354*)	31.4 (*0.928*)
1991-1997	31.3 (*0.024*)	40.6 (*0.958*)

DISCUSSION

Temporal analysis of the social structure of female and juvenile sperm whales indicates that individuals have two classes of associates, differing in the periods of time over which relationships persist. 'Casual acquaintances' (*sensu* Whitehead *et al.* 1991) typically associate for less than 10 days, whereas 'constant companions' (*sensu* Whitehead *et al.* 1991) have relationships that last over periods of years (Figure 2.4). Intermediate association rates indicate that these long-term relationships are constant (i.e. associates do not separate and re-associate) (Figure 2.3), although long-term associates do dissociate at an average rate of 2.5%/year.

There is fairly good correspondence between these findings and those of Whitehead *et al.* (1991), which were based on a much shorter dataset (1985-1989). This analysis confirms the fission-fusion nature of sperm whale society, with groups being temporary entities, formed by the short-term association of smaller and more permanent social units. While

the analysis by Whitehead *et al.* (1991) gave no indication of dissociation of unit members, dissociation is apparent over the longer time scales considered in the current analysis.

Several factors may contribute to this dissociation of individuals. Dispersal of juvenile males and the death of individuals will terminate long-term relationships, as would movements of individuals between units or the splitting of units (possibilities examined in detail in Chapter 3). Analyses of rates and extents of changes in the identifying marks of sperm whales suggest that changes of sufficient magnitude that an individual will not be recognised are very rare (Dufault & Whitehead 1995a). Thus the 'loss' of identified individuals due to mark change probably constitutes a very small fraction of the observed dissociation rate. The value of 2.5%/year is considerably less than the standard estimate of natural mortality of females (5.5%/year, International Whaling Commission 1982), despite the fact that my estimate of dissociation rate incorporates factors beyond the mortality of adult females, suggesting that the IWC figure is a considerable overestimate.

Estimates of M (group size -1) for the whole dataset (1985-1997) differed significantly for the different association criteria (2 hr versus 12 hr). The '2 hr' estimate of mean group size (25.0) may be slightly biased downwards, towards the true mean unit size, since two members of the same unit are more likely to be identified closely together in time than are two members of the same group, but different units (see Chapter 5). However, it is also likely that the '12 hr' mean group size estimate (34.3) is inflated, by the identification, on at least some occasions, of members of more than one group during a single day. Although it is difficult to assess the relative weight of these two biases, and it is likely that the true mean group size lies between the two estimates, the bias associated with the '2 hr' criterion is thought likely to be less significant. Thus the value of 25.0 is considered to be the best estimate of mean group size for the 1985-1997 period. This value is consistent with those calculated from the Galápagos data in earlier years (Whitehead *et al.* 1991, Whitehead & Kahn 1992), and with a number of other estimates of mean group size for sperm whales in other parts of the world (Best 1979).

Comparison of lagged association rates for the earlier (high population density) and later (low population density) years of the study does indicate some differences in social structure (Figure 2.5). While the 1985-1990 data (Figure 2.6) are consistent with the 'groups and units' pattern apparent in the whole dataset (Figure 2.4), the data for 1991-1997 look very different. The 1991-1997 lagged association rate shows neither the initial marked decrease corresponding to the dissociation of groups into units, nor the later decrease corresponding to dissociation of unit members (Figure 2.7). The best-fitting model for the 1991-1997 data reflects this, indicating very few short-term associations, with the vast majority of associates being 'permanent' companions.

Focusing on the '2hr' estimates, mean group size for 1991-1997, 31.3 individuals, is 43.6% greater than the value of 21.8 estimated for 1985-1990 (Table 2.3). Mean group size is a function of three factors, mean unit size, the rate at which units join together to form groups, and the rate at which groups dissociate into their constituent units. Given the long inter-birth intervals of sperm whales (4-5 years, Best 1968), and the fact that fecundity of females in the Galápagos study area is reduced (Whitehead *et al.* 1997), it is unlikely that unit sizes would have increased markedly over the 12 years of this study. Thus it seems likely that this increase in mean group size relates primarily to changes in the aggregation of units. The lagged association rate data for 1991-1997 (Figure 2.7) indicate a reduced rate of dissociation of groups into units, when compared to the 1985-1990 data (Figure 2.6).

The increase in mean group size in sperm whales suggested by these analyses correlates with a reduction in population density in the Galápagos area over the same time period (Whitehead *et al.* 1997). Resource availability and dispersion is a primary determinant of group size in animals (Wrangham & Rubenstein 1986), and sperm whales have been found to aggregate more in areas and at times of greatest food abundance (Whitehead & Kahn 1992). Whitehead *et al.* (1997) concluded that the decrease in sperm whale abundance in the Galápagos area was due to consequences of past whaling, rather than to any decrease in food abundance. Hence if prey availability remained relatively constant during the study (given periodic fluctuations due to El Niño Southern Oscillation events),

then the relative prey abundance (i.e. prey abundance per whale) would have increased. Although it is difficult to assess relative prey abundance in any direct way, the relatively high feeding success of females and juveniles in recent years (see Table 6.9), compared to earlier years (Smith & Whitehead 1993), does seem consistent with this idea. Thus it is possible that the increases in mean size at the different levels of sperm whale society during the study may reflect increased aggregation permitted by increased relative prey abundance and reduced competition.

CONCLUSIONS

The temporal analyses of sperm whale social structure presented in this chapter add strength, but also complexity, to earlier findings. Lagged association rate data from a 12 year dataset confirm the fission-fusion, groups and units, nature of the sociality of female and juvenile sperm whales. An increase in mean group size, and in the apparent stability of groups, concurrent with a decrease in population density, indicate that there is some flexibility within this general pattern.

CHAPTER THREE

Sperm whale social units: variation and change

INTRODUCTION

One of the fundamental issues in any study of social species is the size and stability of social groupings. Among mammals, female grouping behaviour is thought to be related directly to resource acquisition and predation avoidance (Bradbury & Vehrencamp 1977, Emlen & Oring 1977, Wrangham 1980, Wrangham & Rubenstein 1986), so the pattern of social groups gives us insight into the ecology of the species. Female grouping behaviour is a strong determinant of male social behaviour (Emlen & Oring 1977, Wrangham & Rubenstein 1986), and therefore strongly constrains mating strategies and systems. The size and stability of social groups may vary with the types of interactions and strengths of relationships between individuals. Where group members are related, and/or are long-term associates, there is the potential for kin selection (Hamilton 1964) and for reciprocal altruism (Trivers 1971). Information on the nature and duration of bonds between individuals can aid in the assessment of the value of sociality for a species (Myers 1983).

Group size and membership may be recorded instantaneously for some species in some circumstances. However, in many situations this information is difficult to obtain, perhaps because not all members of a social group are visible together at one time, or some individuals, although present, are obscured from the observer's view. In cases where group membership cannot be determined visually, and instantaneously, measures of association must be developed to investigate the strength of relationships between individuals. Measures of association may be behavioural, spatial or temporal, but must always be selected with reference to the individual animal's experience, and at appropriate scales. It is then important to define rigorously what is meant by a group (Whitehead & Dufault in press). For any thorough analysis of social organisation or group dynamics, it is necessary to be able to identify animals individually.

The study of group membership and dynamics in cetaceans is complicated by the environment in which they live. Sperm whales dive in order to feed, hence foraging individuals are unavailable for surface counts of group size. Individual sperm whales are identifiable from photographs of their tail flukes (Arnbom 1987). Typically, the tail

flukes are raised only at the start of a foraging dive, and since the dive cycle time of sperm whales is approximately 50-60 minutes (Papastavrou *et al.* 1989), each individual is available for identification only roughly once every hour. Since individuals cannot usually be distinguished at the surface (except when the tail flukes are raised), behavioural or spatial measures of association cannot be collected routinely, and temporal measures, based on identification times, are the only readily available data for investigating social associations. Past research has used a 2 hour association criterion, so that 2 individuals are considered associates if they are photographically-identified within 2 hours of each other (e.g. Whitehead *et al.* 1991, 1992). I wished to test a range of temporal association criteria, to determine whether 2 hours is the most appropriate criterion for reflecting the association patterns of individuals.

Two other factors complicate the study of sperm whale sociality. Maximum longevity for female sperm whales exceeds 60 years (Gambell 1972), yet it is possible for research vessels to follow groups for a maximum of a few days at a time. Therefore the data collected can form only short-term 'snap-shots' in relation to an individual's lifetime experience of sociality. Sperm whales are not territorial, and females may have ranges in the order of 1000 km (Best 1979, Dufault & Whitehead 1995b, Whitehead *et al.* 1997). As a result, particular individuals are infrequently and unpredictably available for study.

Female sperm whales and their offspring live in a fission-fusion society, with observed groups representing temporary associations between permanent social units (Whitehead *et al.* 1991, Chapter 2). These units associate for periods of only hours to days (Whitehead *et al.* 1991, Chapter 2). Thus at any time a particular individual may have two sets of social associates: 'constant companions' and 'casual acquaintances' (Whitehead *et al.* 1991). Constant companions are members of an individual's own unit, and are 'permanent' associates. Casual acquaintances, however, are members of a separate, associating, unit.

Although female philopatry is thought to be the norm, there are suggestions of some female dispersal from stable units (Best 1979, Richard *et al.* 1996a), and of long-term

association between members of different matrilines (Richard *et al.* 1996a). Genetic studies have indicated that a group may consist of one or more matrilines (Richard *et al.* 1996a). The most obvious interpretation is that each constituent unit within a group comprises a single matriline. However, the study of genetic relationships within known units indicates that units may not all represent perfect matrilines, and that some may include individuals with different mitochondrial haplotypes (Chapter 4).

The nature and stability of social units have consequences for all aspects of sperm whale research, from behaviour, genetics and population modeling, to theories on the evolution of sociality. With a longer dataset available (1985-1997), it is now possible to begin to examine the structure of sperm whale social units. In this chapter, I consider the different temporal association measures which can be used in the analysis of sperm whale sociality, and determine which is the most appropriate. I estimate the numbers of constant companions of by known individuals, examine the possibility of preferred companionships within units, and calculate the frequency distribution of unit sizes, and overall mean unit size. I also investigate unit membership and consider evidence for the stability and dynamics of sperm whale social units.

METHODS

FIELD RESEARCH AND PHOTO-IDENTIFICATION

Details of field research and photo-identification methods are as described in detail in Chapter 2. Identification photographs of sperm whale tail flukes were collected in the Galápagos study area (Figure 2.1) and other regions of the ETP (Figure 2.2) between 1985 and 1997 (Table 2.1). Only photographs of Q≥4 (Dufault & Whitehead 1993), excluding first-year calves and mature males, were included in these analyses.

SELECTION OF KEY INDIVIDUALS

Sightings records for all individuals were searched in order to identify those animals which had been seen during at least three identification periods, with each period separated from all others by a gap of at least 30 days. This interval was selected so that any associates common to two separate identification periods were likely to be constant companions (as determined by Whitehead *et al.* 1991, and see Chapter 2). Any individual which had a sighting history conforming to these criteria was designated a key individual.

In order to identify the most appropriate temporal association criterion for use in this study, a number of different association intervals were analyzed. Past work has used a 2 hr association criterion (e.g. Whitehead *et al.* 1991, 1992). Clearly, the longer the time interval being considered, the greater the proportion of the total number of constant companions that will be identified. My aim was to find the association interval or range of association intervals which allow the most accurate estimation of individuals' true numbers of constant companions. The following association criteria were tested: 10 minutes, 30 minutes, 1 hr, 2 hr, 4 hr, 6 hr and 12 hr (since light conditions in the study area are suitable for photo-identification from almost exactly 6 am - 6 pm, an association criterion of 12 hr is equivalent to being identified on the same day).

The original photographs of the key individuals and all their associates (those identified using the 12 hr criterion) were scrutinised to check for incorrect or missed matches. Only two errors were found, both involving missed matches (i.e. a previously-identified whale was not recognised as such, and was given a new ID number on a second or subsequent sighting). Although it is impossible to rule out the possibility that errors remain, the use of only $Q \geq 4$ identifications, and the scrutinisation process, should mean that they are very few.

A QuickBasic™ program was used to investigate the associates of each of the key individuals. Once the association criterion is specified, the program outputs list (for each key individual) the first and last dates for each identification period, the number and

identities of all associates during each identification period, and the identification numbers of all individuals that were associates during at least two identification periods.

ESTIMATION OF NUMBER OF CONSTANT COMPANIONS

At any given time, the set of associates of a key individual will consist of a number (N) of companions who remain with it constantly, plus a variable number of casual acquaintances (Whitehead *et al.* 1991). The key individual and its constant companions together form a permanent unit of size N+1. As casual acquaintances remain with an individual for a few days at most (Whitehead *et al.* 1991, Chapter 2), and the population size is large (Whitehead *et al.* 1992b), I assumed that individuals associating with a whale during two or more periods separated by at least 30 days were constant companions.

For each whale I wished to estimate the number of constant companions, N. Suppose that a particular whale, I, was observed during three periods t_1, t_2 and t_3, then let:

n_{12} = number of associates common to t_1 and t_2
n_{13} = number of associates common to t_1 and t_3
n_{23} = number of associates common to t_2 and t_3
n_{123} = number of associates common to t_1, t_2 and t_3

So, if p_1, p_2 and p_3 are the probabilities that constant companions were identified in periods t_1, t_2 and t_3 respectively:

$$n_{12} \approx N \cdot p_1 \cdot p_2$$
$$n_{13} \approx N \cdot p_1 \cdot p_3$$
$$n_{23} \approx N \cdot p_2 \cdot p_3$$
$$n_{123} \approx N \cdot p_1 \cdot p_2 \cdot p_3$$

Therefore an estimator for N is:

$$N = \frac{n_{12} \cdot n_{13} \cdot n_{23}}{n_{123}^2}$$

This estimator is biased infinite if $n_{123} = 0$. Therefore, following Chapman's (1952) modification of the Petersen mark-recapture estimate, I used the following estimate of the number of constant companions of I:

$$[1] \quad N = \frac{(n_{12}+1) \cdot (n_{13}+1) \cdot (n_{23}+1)}{(n_{123}+1)^2} - 1$$

Simulations (performed by H. Whitehead) showed that this estimator is approximately unbiased with $n_{123}>2$, but has a negative bias with smaller n_{123}. N was estimated for all key individuals for each association criterion. For key individuals with four or more identification periods, N was calculated for each possible combination of three identification periods. The median value of the multiple estimates of N was then used as the estimate of N for that key individual.

Differences between mean estimates of N for the different association criteria were tested using Welch's approximate t tests (for comparison of two means with unequal variances, e.g. Davenport & Webster 1975)

UNIT DELINEATION

Units were delineated by identifying sets of individuals which had been associated during several identification periods. The working definition used to determine unit membership was: a set of individuals of which each was associated with at least two of the others during at least two identification periods. Where a unit was represented by only one key individual, all animals associated with that key individual during two identification periods were considered to be members of the key individual's unit.

PREFERRED COMPANIONSHIPS

If individuals within a unit have a subset of their constant companions with which they associate preferentially, and either these preferred companions show a greater degree of synchrony in their dive cycles, and/or, at least on some occasions, these sets of companions separate off as scattered sub-groups, then preferred companions would be likely to be identified closely together in time, but other unit members may not. Hence preferential associations of this type would result in artificially small constant companion number estimates using the shorter association intervals. To investigate this possibility the data were examined for indications of preferred companionships.

I considered the sets of associates of each key individual for each successive pair of identification periods, for both the 12 hr association criterion, and for shorter association criteria:

K = the set of associates (using the 12 hr criterion) common to t_1 and t_2
K_1 = of the total K, those associates (using a shorter criterion) present at t_1
K_2 = of the total K, those associates (using a shorter criterion) present at t_2
K_{12} = of the total K, those associates (using a shorter criterion) common to t_1 and t_2

If the set of constant companions which was identified within the shorter time interval of a key individual is simply a random assortment of the total number of constant companions present, then the expected value of K_{12}, $E(K_{12})$, can be calculated as:

$$[2] \quad E(K_{12}) = \frac{K_1 \cdot K_2}{K}$$

If preferred companionships do occur, then the extent to which the number of constant companions common to two periods (K_{12}) exceeds that expected by chance ($E(K_{12})$), will be greater for intervals closer to, rather than further from, identifications of a key individual. In order to test for evidence of preferred companionships, K_{12} and $E(K_{12})$

were calculated for each key individual, for each successive pair of identification periods, for two different shorter association criteria; 'less than 10 minutes', and 'more than 10 minutes but less than 20 minutes' from identifications of the key individuals. In order to reduce problems of non-independence of the data, only those values corresponding to the largest $E(K_{12})$ value for each individual were selected for analysis. The distributions of K_{12}-$E(K_{12})$ values (i.e. the extent to which numbers of associates differed from those expected by chance) for these two datasets were then compared using a Mann-Whitney U test.

UNIT STABILITY/DYNAMICS

The long-term association patterns of the key individuals were searched for any indications of unit membership change. Three forms of unit dynamics were investigated: splitting - defined as the division of a previously cohesive unit into two or more smaller units, merging - defined as the union of two previously distinct units, and transfers - the movement of one or more individuals from one unit to another. Estimates of rates of the three different types of unit membership change were calculated as the total number of changes for all individuals divided by total animal years (where total animal years equals the sum, for all individuals, of the number of years between first and last identification). For mergers and splits, each member of all affected units was considered to have undergone unit membership change, for transfers however, only those individuals directly involved were counted.

RESULTS

IDENTIFICATIONS AND KEY INDIVIDUALS

Our database includes 5129 photographic identifications of $Q \geq 4$, representing 1809 individual sperm whales (excluding mature males and first-year calves) (see Table 2.2 for details). Of these, 91 individuals satisfied the requirements of having been photographically identified during at least three periods separated by at least thirty days,

and so were designated key individuals (Table 3.1). With the exception of eight individuals (members of a single unit) for which one identification period occurred off the coast of Ecuador, all identifications of the key individuals occurred within the Galápagos study area. In the vast majority of cases, because of the seasonal nature of the research, identification periods were separated by at least one year. These 91 key individuals and their associates formed the basis of this study of unit membership.

Table 3.1. Numbers of individual whales (key individuals) identified in three or more identification periods (Q≥4).

Number of identification periods	Number of individuals
3	57
4	24
5	10
total	91

ESTIMATION OF NUMBER OF CONSTANT COMPANIONS

The constant companion number analysis was performed for the 91 key individuals for each of the seven temporal association criteria. Estimated numbers of constant companions (N) ranged from 0-59. The mean estimates of key individuals' numbers of constant companions increased with increasing association interval (Figure 3.1). Clearly, the longer the time interval being considered, the greater the proportion of the total number of constant companions that will be identified, and thus the larger n_{123}. Therefore the trend in increasing estimate of mean number of constant companions associated with increasing association interval would be expected given the properties of my estimator, although some of the increase could be due to preferred associations within units (see below). The rate of increase slows as association interval increases and the mean estimates appear to be approaching an asymptote, which represents the true mean number of constant companions.

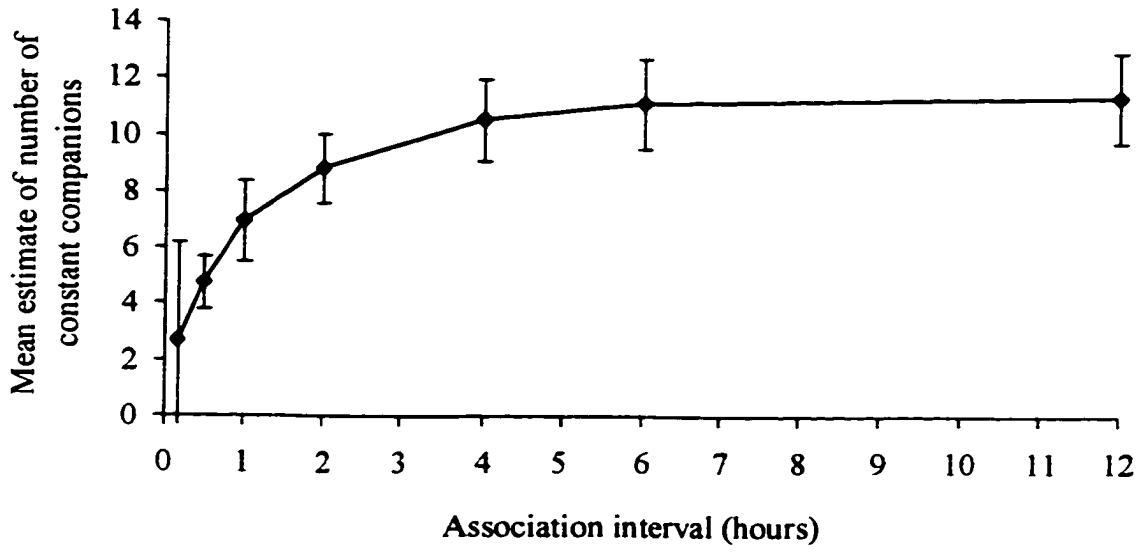

Figure 3.1. Comparison of mean estimates of the number of constant companions for all 91 key individuals, for the seven different temporal association intervals. Error bars depict one standard error about the mean.

There is no significant difference between the mean estimated number of constant companions for the 6 hr and 12 hr association intervals ($p>0.05$), but the estimate for the 12 hr association interval is significantly higher than those for the 4 hr and 2 hr association intervals (both $p<0.05$). Since the extent of bias in my estimator will be lowest for the longest association interval, the mean estimate of number of constant companions for the 12 hr association interval, 11.3, is my best estimate of the true value. Unit size is simply a key individual's number of constant companions, plus the key individual itself (i.e. N + 1), thus this analysis provides an estimate of mean unit size of 12.3.

UNIT DELINEATION

Units were delineated as described above. The number of units into which the key individuals and their associates were delineated decreased with increasing association interval (Table 3.2). This is a result of the artificial splitting of some larger units caused by the fact that fewer associates were identified during the shorter association intervals. Estimates of the number of constant companions for animals allocated to the same unit

were significantly less variable ($p<0.05$) than between units for all association criteria greater than 10 minutes (Table 3.2) as would be expected, since all members of the same unit have the same true number of constant companions.

Table 3.2. Unit delineation and statistical significance of within-unit correlation of estimated numbers of constant companions for the seven different association intervals.

	10 min	30 min	1 hr	2 hr	4 hr	6 hr	12 hr
# units[1]	46	37	31	28	24	21	19
n[2]	92	94	95	95	94	93	96
p	0.088	<0.001	0.008	0.013	0.021	0.045	0.029

[1] Number of units delineated using the working definition: a unit equals a set of individuals of which each was associated with at least two of the others during at least two identification periods.

[2] Number of key individuals (some key individuals, with four or more identification periods, were assigned to more than one unit on the basis of their sets of associates, for some association criteria. As a result, these individuals were included twice in ANOVAs to investigate the relationship between unit membership and constant companion number estimate (therefore n ranges from 92-96)).

When the frequency distribution of delineated units is examined (Figure 3.2, in this case using the 12 hr association criterion) it is clear that there is considerable variation in unit size. The estimated mean size of the delineated units (using this association criterion) is 10.4 (range 3-24, s.d. 6.23, c.v. 0.60). This value represents the mean size of units from the observer's perspective. A measure of unit size which is more relevant to the whales' experience of sociality is the size of unit in which the average individual found itself. This can be derived by summing the size of unit in which each individual found itself and dividing by the total number of individuals, to find the 'typical unit size' (Jarman 1974). Using the data shown in Figure 3.2, the typical unit size is 13.9.

Details of the size, membership and identification periods of the 19 units delineated using the 12 hr association criterion are provided in Appendix 1.

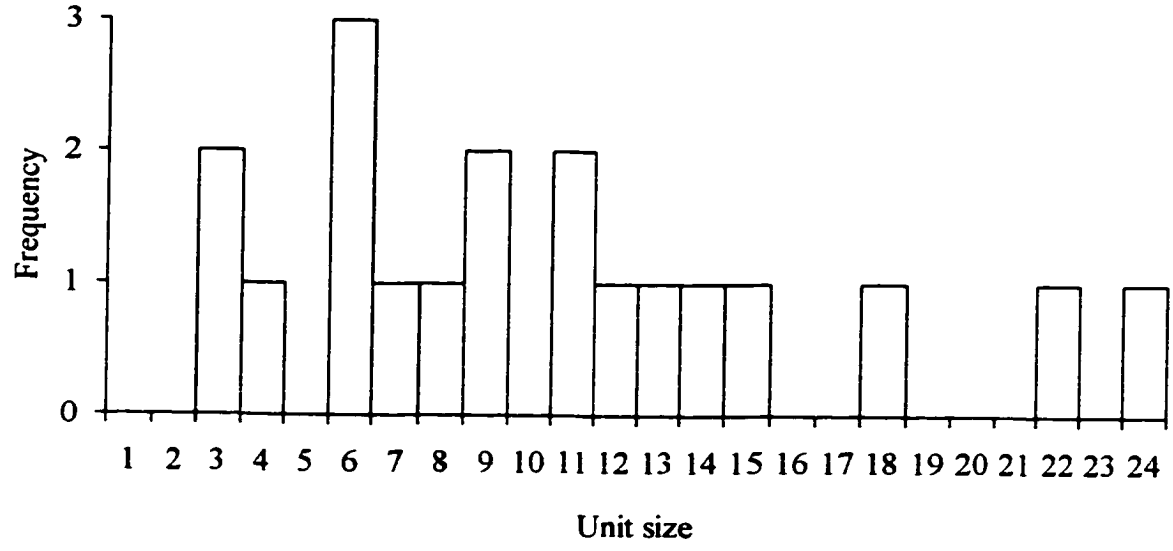

Figure 3.2. Frequency distribution of unit sizes delineated using the 12 hr association criterion.

PREFERRED COMPANIONSHIPS

The distributions of K_{12}-$E(K_{12})$ for the 10 minute association interval and the '>10 min but <20 min' association interval did not differ significantly (Mann-Whitney U test, $p = 0.142$), suggesting that there were no preferred companionships among unit members. For the 10 minute association interval, the observed number of associates common to two periods (K_{12}) exceeded that expected by random assortment ($E(K_{12})$) by a mean of only 0.10 companions. The fact that this value is double that for the '>10 min but <20 min' association interval (mean K_{12}-$E(K_{12}) = 0.05$), may indicate that there is in fact a very slight degree of preferred companionship occurring. The limited extent of any preferred companionship makes it unlikely to be a major contributor to the trend shown in Figure 3.1.

UNIT STABILITY/DYNAMICS

Although the delineated units generally appear to have closed membership (allowing for birth and death of unit members), an examination of the patterns of long-term association

does provide evidence for some variation about this norm. There are examples of splitting of units, merging of units and transfers of individuals between units.

The dataset provides some evidence for the splitting of a unit, although unfortunately the permanence of this split cannot be assessed. In 1995, a set of five individuals was identified together (in association with another unit). All of the animals had previously been identified as members of Unit A (Figure 3.3), the largest unit delineated in this study, with 24 members. The set of five animals seen in 1995 was followed continuously for seven days, yet none of the other 19 members of Unit A were seen during this week, or even during this field season. Because these 19 individuals have not been identified since 1991, and the set of five animals have not been seen since their identification in 1995, it is not possible to determine whether this separation represents a temporary dissociation or a permanent division of the unit.

In order to detect merging, which I define as the union of two previously distinct units, a considerable amount of information is required. Both of the original units must have been seen at least twice in order for delineation of those units to be possible (so that merging can be distinguished from transfers), and to ensure that the 'merged' unit is not simply a later sighting of all members of an original unit, not all of which were identified initially. In addition, the merged unit must have been sighted at least twice, so that merging of units can be distinguished from casual association. Given these requirements, and the small number of individuals that have been sighted in four or more periods (Table 3.1), it is perhaps not surprising that there is no clear cut example of merging in my dataset. There is, however, a case which exemplifies either merging or a transfer (Figure 3.4). In 1987 two whales (#793 and #795) were identified in association with thirteen other whales. Two months earlier a separate unit of approximately fifteen whales ('Unit B' in Figure 3.4) had been identified, and this pair was not seen. However, when Unit B was identified in 1988, 1994, 1995 and 1996, #793 and #795 were present. That these two whales had permanently joined a new unit is clear. What is not so clear is whether this is a case of merging or of transfer. If, at their initial identification in 1987, #793 and #795 were a unit of two individuals and their associates were simply casual acquaintances, then

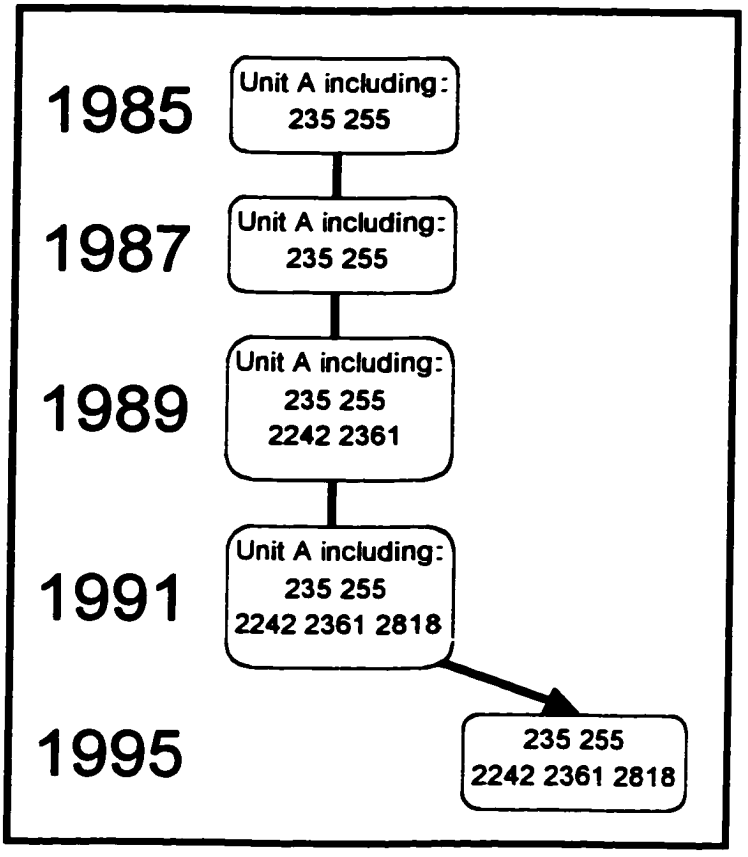

Figure 3.3. Splitting of Unit A.

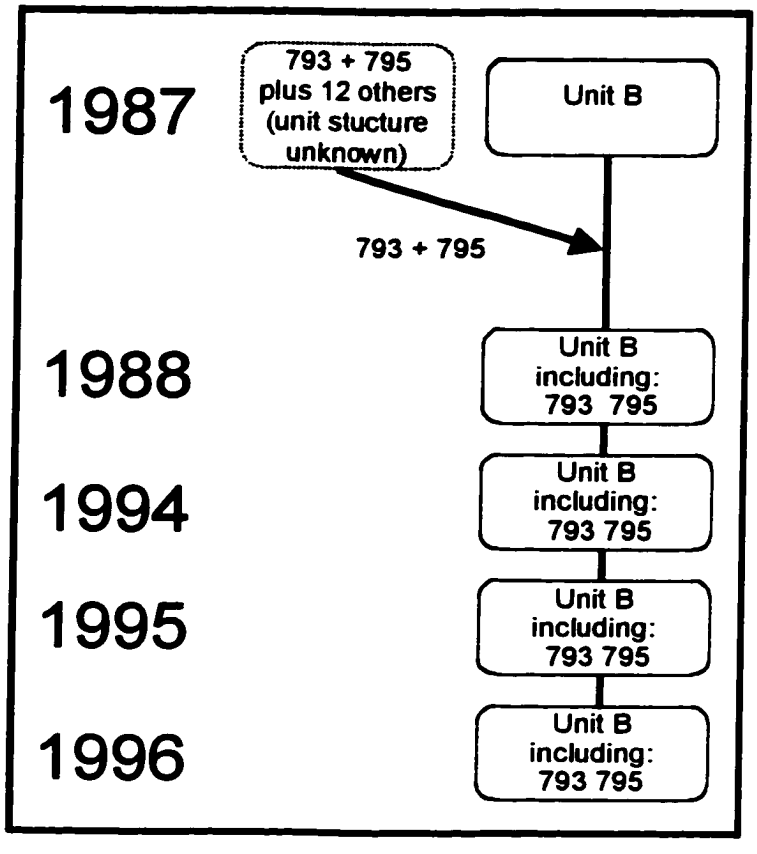

Figure 3.4. Transfer or merger of two individuals (#793 and #795) joining a larger unit.

the joining of this pair with Unit B represents merging of two units. Alternatively, if #793 and #795 were members of a larger unit in 1987, and then split from that unit to join Unit B, then this is a case of the transfer of two individuals between units.

The dataset also provides evidence for three definite transfers (without the complication of the possibility of merging). In each case a single individual transferred between units. Whale #236 was identified during four periods between 1985 and 1989 (Figure 3.5). It had approximately twenty associates during each of these periods. Only two associates were common to the first two identification periods, indicating that #236 was a member of a fairly small unit at this time. There were no associates in common between the second and third periods, but of the associates identified in the third period (all of which were new - i.e. none in common to the first or second period), fourteen were also identified in the fourth period. My interpretation is that #236 transferred from its original, small, unit to a completely separate, and larger unit, at some time between the second and third identification periods.

Whale #902 provides a second example of a transfer. Although its unit affiliation is unknown from its first sighting in 1987 (at which time it was associated with Unit F which was re-sighted in 1989 and 1996), #902 had no associates in common between 1987 and later sightings. In 1989 and 1993 it was identified as a member of Unit G (Figure 3.6).

Whale #2942 was first identified in 1994, with a previously-sighted unit (Unit E, Figure 3.7). When this individual was seen again, in 1995 and 1996, it was associated with a different unit (Unit B), and none of its associates from 1994 were identified.

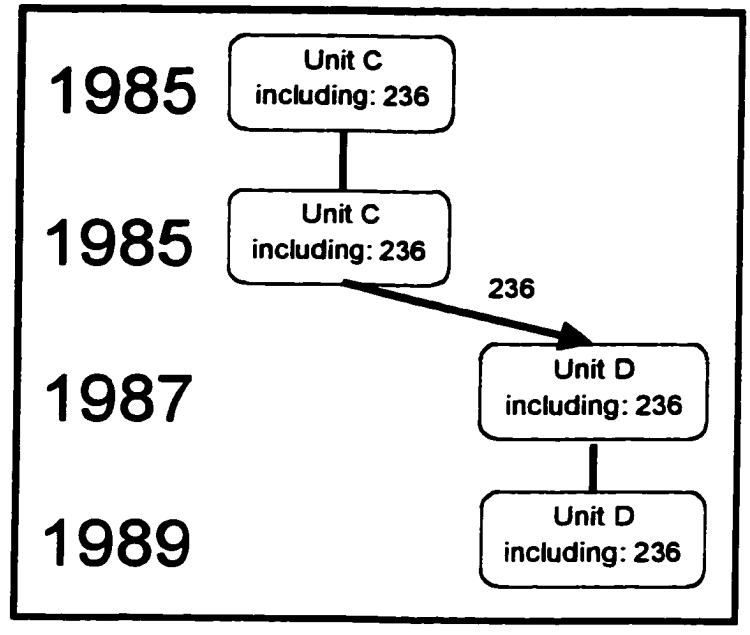

Figure 3.5. Transfer of individual #236 between two units.

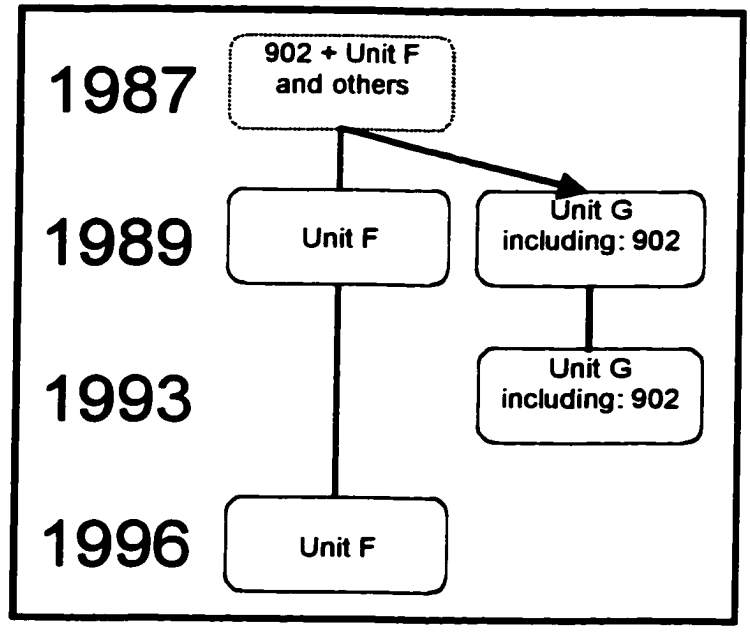

Figure 3.6. Transfer of individual #902, of unknown unit affiliation, into Unit G.

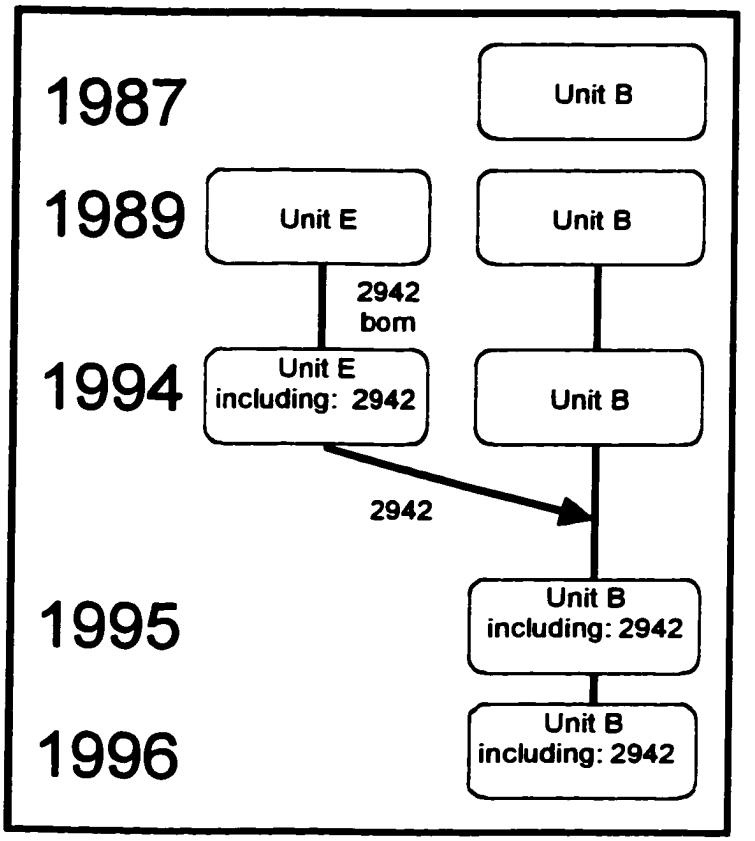

Figure 3.7. Transfer of a juvenile individual (#2942) between two units.

Who transfers? Of the three individuals which definitely transferred (Figures 3.5, 3.6, 3.7), and the two individuals which either merged or transferred (Figure 3.4), three animals are known or presumed to be female. Numbers 795 and 2942 were sexed using molecular techniques (see Chapter 4, Table 4.1). Number 793 was photographically measured (Gordon 1990, see Chapter 4 for further details of methodology) at a size which makes it unlikely to be male, given the number of years for which the animal has been known, and the expected age of male dispersal (Best 1979, Richard *et al.* 1996). No length measurement is available for #795, therefore its age is unknown, and age at transfer is also unknown. The measured length of #793 corresponded to an age of at least 30 years (Best 1970), therefore it was estimated to be at least 24 years of age, and thus sexually mature (Best 1968), at the time of unit membership change. Whale #2942 was also photographically measured in 1995, at which time its length corresponded to an age of 5-6 years. Thus at the time of transfer, it was an immature female of 4-6 years old. No information is available on the sex or age of whales #236 and #902. Hence of the animals which moved between units, three were females (one adult, one juvenile, and one of unknown age), and two were of unknown age and sex.

Rates of unit membership change were calculated separately for each type of change, over the 537 animal years encompassed by the data. It should be recognised that the following values are simply estimates, provided in order to indicate the order of magnitude of changes. The rates of unit membership change per individual per year were as follows: mergers 0.026, splits 0.028, transfers 0.009. These values indicate that there is roughly a 6.3% chance that any given individual will be involved in merging or splitting of a unit, or will transfer between units, within any given year. From the perspective of the unit, individuals transferred into units at a rate of 5%/unit/year (5 transfers in 100 unit years). Given the difficulties associated with detecting unit membership change (i.e. numbers of sightings required), these values should be considered to be minimum estimates.

DISCUSSION

UNIT SIZE

Use of the shorter association intervals (less than 2 hr) artificially reduced the estimated numbers of constant companions (Figure 3.1), and artificially increased the number of units delineated (Table 3.2). While preferred companionships among unit members might partially explain these results, the extent of any preference was too low to be detected statistically, and preferred companionships are unlikely to have had considerable effects on results. The asymptotic nature of the curve of mean number of constant companion estimates (Figure 3.1), with no significant differences between the values for the six hr and twelve hr association criteria, indicates that at these time intervals, the mean estimates approach the true mean numbers of constant companions.

Since analyses of potential biases in the estimates indicated that the extent of any bias would be least significant for the 12 hr association criterion, I consider the mean estimate of number of constant companions using this criterion, 11.3, to be my best estimate of the real mean number of constant companions. Since the mean estimates for the 2 hr and 12 hr association criteria are significantly different, past work using the 2 hr interval (e.g. Whitehead *et al.* 1991), may have slightly underestimated true numbers of associates.

Using 'number of constant companions plus 1' as unit size, mean unit size is estimated at 12.3. This agrees with the estimate of 'about 13' found by Whitehead *et al.* (1991), using lagged association rates calculated from data from 1985-1989. Although the mean size of the units delineated (using the 12 hr association criterion) is 10.4, the unit size experienced by the average individual (Jarman's (1974) 'typical unit size') is 13.9. There is considerable variation around these estimated mean unit sizes. Delineated unit sizes ranged from 3 to 24 individuals. De Vore and Hall (1965) suggest that a wide range of social group sizes in an apparently uniform environment indicate that social factors are more important than ecological factors in determining social group size. Unit size may be determined to some extent by demographic stochasticity, through factors such as

individual fecundity and sex ratios of offspring (c.f. Brault & Caswell 1993). Interpretation of variation in unit size is complicated by the social structure, which involves association of units into groups (Chapter 2). Although no data are available, it is possible that small units avoid some of the ecological costs of small group size by associating with other units more frequently than do larger units.

UNIT DYNAMICS

Cases of unit membership change can be documented reliably only for individuals which have been identified on a number of occasions (generally at least three), thus only the 91 key individuals in this study could provide evidence for unit dynamics. The fact that one split, one possible merger (or two individuals transferring together), and three separate transfers by single individuals were identified during the twelve years of the study indicates that unit membership change is not a particularly rare phenomenon. My rough estimates of unit membership change indicate that the average individual has a 6.3% probability per year of being involved in unit splitting, merging, or transfer. Since unit membership change could be detected only when the individuals involved were identified both prior to, and following, the change, it is likely that the number of changes is higher than that reported here. Maximum longevity for female sperm whales may exceed 60 years (Gambell 1972), thus there is clearly the potential for considerable non-demographic change in unit membership during an individual's life. The evidence for unit merging and transfers agrees with results from genetic studies of sperm whales which suggested long-term associations between different matrilines, and possible dispersal between groups (Richard *et al.* 1996a, and see Chapter 4)

Splitting

Splitting of social units, although rare, has been reported for several species which live in stable, female-bonded matrilineally-related groups (e.g. rhesus monkeys (*Macaca mulatta*) - Chepko-Sade & Sade 1979, baboons (*Papio sp.*) - De Vore 1965, African elephants (*Loxodonta africana*) - Moss 1988), including one other large odontocete

('resident' killer whales (*Orcinus orca*) - Ford *et al.* 1994). Fission of formerly cohesive social groups in these species was contingent on one or more of the following factors: above average group size, loss of the matriarchal female and therefore the bonds holding her daughters' sub-groups together, and disruption of the group due to the simultaneous death of several group members. Splitting of social groups was usually along lines of maternal relatedness (Chepko-Sade & Sade 1979, Moss 1988, Ford *et al.* 1994). Such patterns of matrilineal splitting can theoretically have profound micro- and macro-evolutionary consequences by accelerating genetic differentiation of social groups (Melnick & Kidd 1983).

The sperm whale social unit within which splitting has been documented in this study (Figure 3.3) was the largest of the 19 units delineated. Although there is no evidence to confirm the permanence of the split, lagged association rate analysis argues against re-association of individuals following dissociation (intermediate association rate data, Figure 2.3). I have no information on the pattern of maternal relatedness within the unit as a whole, so it is unclear whether this split followed matrilineal lines. However, the set of five individuals which separated from the larger unit form part of the analysis of genetic relatedness in Chapter 4, and appear not to be closely related (Figure 4.3). The proximate cause for the splitting of the unit is unknown. The ultimate cause presumably relates to group size effects. As Moss (1988) suggests for elephants, at a certain group size, a loss in feeding efficiency may outweigh the social benefits of large group membership.

Mergers

The evolutionary force for sociality in sperm whales remains uncertain. Although co-operative foraging may occur (Whitehead 1989), most authors suggest that alloparental care and protection of calves, with consequent inclusive fitness benefits, were important factors in the evolution of stable matrilineal units (Best 1979, Gordon 1987a, Arnbom & Whitehead 1989, Whitehead 1996a). My finding of a possible merging of two social units (Figure 3.4.) is unexpected in light of these theories. If sociality evolved because of

benefits to related individuals which stayed together, how do I explain the merging of two separate units?

One explanation which seems reasonable in this context is that of optimal group size. Membership of a small social group or unit may be costly for a variety of reasons, and if these costs are sufficiently high, members of these social groups may benefit through group fusion, even if they are unrelated to the members of the group that they join. The merging of social groups has previously been reported in a vervet monkey (*Cercopithecus aethiops*) population, as an apparent response by small groups to the costs of resource competition with larger groups (Isbell *et al.* 1991). A similar situation occurs among male lions, which engage in intense competition for breeding opportunities, and must defend the females they mate with for a prolonged period in order to avoid infanticide by incoming males (Packer *et al.* 1991). Male lions form coalitions in order to depose resident males, and to defend mated females. While these coalitions commonly consist of related males, individuals without close relatives may join together, since the costs of sharing mating opportunities with unrelated coalition partners are less than those of remaining alone and being unable to gain access to mates (Packer *et al.* 1991).

Whatever the ultimate cause of sociality among female sperm whales, whether it be protection from predation, communal calf-care, co-operative foraging etc., there is clearly some benefit to individuals from being a member of a unit. If the extent of this benefit increases as unit size increases, and is not entirely due to inclusive fitness benefits from association with related unit members, then individuals which are members of small units may gain by joining another unit, even if it is unrelated. If a small unit joins a larger unit (as in the case of #793 and #795 joining a unit of approximately 15 members, Figure 3.4), the benefits to the members of that larger unit, if any, are unclear. Perhaps the newcomers benefit their adopted unit by transmission of culturally-gained information such as the location of good feeding grounds?

It should be remembered that the unit membership change involving individuals #793 and #795 cannot be confirmed as an example of unit merging, since their original unit

affiliation is unknown. This change may actually have been a transfer of the two animals from one unit to another. The distinction between these two forms of unit membership dynamics has consequences for our understanding of sociality in sperm whales. The merging of units may make sense simply in terms of optimal group size (for whatever ultimate cause), especially where one unit is particularly small. The causes of transfers are less easy to imagine. Why should one or more whales elect to leave their set of (presumably closely-related) constant companions, to join another (presumably less closely-related) unit?

Transfers

Many cases of inter-group transfer are explained in terms of access to non-related mates. However, in species where males disperse from natal groups at or before puberty, female transfer between established groups is unusual (Greenwood 1980, Moss 1988, Clutton-Brock 1989).

Isbell & van Vuren (1996) suggest that transfer of females between established social units is most likely in situations where: 1. females face no inter-unit aggression from females; 2. relationships within units are undifferentiated (i.e. there is no dominance hierarchy); 3. the home ranges of units overlap. Sperm whales may fulfill all three criteria. The frequent associations of units to form larger groups (Chapter 2) are apparently harmonious, and since sperm whales are not territorial, and travel long distances (e.g. Whitehead *et al.* 1997), the range of a particular unit will overlap that of many others. The issue of intra-unit relationships is less clear-cut. While discussion of the existence of dominance hierarchies within sperm whale social units would be purely speculative, analyses in this chapter suggest that individual unit members do not have specific preferred companions.

Proximate causes for adult female inter-group transfer vary within and between species and may include infanticide avoidance, female-female aggression, oestrus, and reproductive failure (Moore 1984, Pusey & Packer 1987). Infanticide is not known to

occur in sperm whales, and seems unlikely given the short tenure of breeding males with social units. Aggression between females has never been reported, although Hooker (1998) reports scarring on female or juvenile male sperm whales which may be attributable to intra-specific interactions. Since female sperm whales in all reproductive states have been found in groups together (Best 1968), social unit membership generally seems to endure for far longer than the reproductive cycle, and access to males is unlikely to be affected by unit membership, the latter two factors (oestrus and reproductive failure) also seem unlikely to be important in this case. Adult female inter-group transfers in other species occur in a variety of contexts, and a variety of ultimate causes have been suggested. These are: access to superior mates, access to superior habitat and reduction of intra-group competition (Rutberg 1990). With the possible exception of the latter, again these causes seem to have little relevance to sperm whale sociality. One aspect of intra-group competition, the existence of which is difficult to test in this species, is reproductive suppression, whereby dominant females act to limit the reproduction of subordinate animals, leading to reproductive skew (e.g. Keller & Reeve 1994). This sort of system might be expected if reproductive females compete for the babysitting efforts of unit members, and might lead to dispersal by females which were being prevented from breeding.

The social and ecological costs of transferring between units are expected to limit its occurrence (Watts 1996). Individuals which move from their natal units will lose their affiliative relationships with familiar, related associates (Gouzoules & Gouzoules 1987), and any inclusive fitness benefits which they could have accrued in the future by helping relatives. These social costs will be ameliorated to some extent if animals transfer with members of their original unit. However, the three definite cases of transfers in this study involved lone individuals (Figures 3.5, 3.6, 3.7). Ecological costs, such as increased predation risk during transfer, will be low if, as is expected for sperm whales, direct transfer between units is possible (Watts 1996). Since sperm whales other than mature males are never found singly, or in very small groups (Whitehead & Weilgart 1991), I believe that transfers probably occur when two units are associated. Benefits to members of the new unit could relate to group size factors, or perhaps to transmission of cultural

information (as suggested for mergers). In each case of possible or definite transfer, the unit being transferred into was reasonably large (at least 11 members in each case) and group size benefits, or costs, conferred by one or two additional, unrelated unit members would seem unlikely to be great.

Given the presumed high social costs for transferring sperm whales, the lack of obvious proximate or ultimate causes, and the apparent lack of benefits to members of their new units in the cases documented, I am unable to provide a functional explanation for the occurrence of transfers.

CONCLUSIONS

The fact that merging of units and transfers of individuals between units occur has a number of consequences, both for the structure of the units concerned, and for our understanding of sperm whale sociality. Both these forms of unit membership dynamics result in units containing sets of unrelated individuals. Thus a unit may consist of two or more separate matrilines. These patterns of relatedness are unlikely to be affected by future reproduction, because all male genetic input is external to the unit. However, common paternity of calves of unrelated females would diminish genetic differentiation between matrilines over time (Dobson 1998, see Chapter 4). Although the observed variability of social unit sizes suggests that the benefits of remaining in a unit usually outweigh ecological benefits for optimal unit size, the occurrence of merging and transfers suggests that the ecological or social cost/benefit of leaving one's social unit may sometimes outweigh the cost/benefit of staying. These analyses demonstrate that there is considerable variability in the social structure of female and immature sperm whales.

CHAPTER FOUR

Genetic structure of sperm whale social units and groups

INTRODUCTION

Several earlier authors concluded, somewhat prematurely, that sperm whale groups were matrilineal in structure (e.g. Ohsumi 1971, Fortom-Gouin & Holt 1980). This conclusion was drawn on the basis of known long-term relationships between females (Ohsumi 1971), the presence of juveniles and females of all ages in groups (Best 1979), and the co-operative and helping behaviours observed within groups (Caldwell *et al.* 1966, Caldwell & Caldwell 1966).

Although the level of society at which we would now expect matrilineality is not the group, but the social unit (Whitehead *et al.* 1991, Christal *et al.* 1998, Chapters 2 and 3), this genetic structure is what we would predict on the basis of behavioural ecology theory. Female philopatry[1] is favoured in situations where available males are unlikely to be relatives, and where it does not otherwise limit access to mates (Greenwood 1980, Pusey 1987). The fact that all male sperm whales seem to disperse (Best 1979), and that mature males hold only very short-term breeding tenure within groups (Whitehead 1993), suggests that these criteria are met in sperm whale society. In situations where grouping of females is favoured, selection should usually favour grouping with relatives (e.g. Wrangham 1980, c.f. Giraldeau & Caraco 1993), and kin selection benefits are expected to promote co-operation within such groups (Hamilton 1964).

To date, there has been no direct evidence regarding the genetic structure of units. Morphological similarities within groups have been interpreted as evidence for genetic relatedness among group members (colour patterns - Yablokov 1974; shape of the fluke notch - Arnbom & Whitehead 1989, Dufault & Whitehead 1998). Since groups are only temporary entities (Whitehead *et al.* 1991, Chapter 2), these morphological similarities presumably reflect genetic relatedness at the unit level.

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1 Cetaceans appear to be aterritorial, thus I use the term philopatry in a strictly social sense (i.e. remaining with the mother), since the standard locational concept of philopatry/dispersal is not relevant (see Isbell & van Vuren 1996).

Past genetic analyses of sperm whale social structure have been restricted to the level of the group (Dillon 1996, Richard *et al.* 1996a), since the unit membership of sampled individuals has never previously been known. As such, these studies cannot provide direct evidence of the genetic structure of units, although inferences can be made. Groups were found to contain several different mitochondrial haplotypes, indicating the presence of members of several matrilines (Richard *et al.* 1996a, Whitehead *et al.* 1998). Since groups generally consist of two or more units (Whitehead *et al.* 1991, Chapter 2), the obvious interpretation is that each unit is represented by a single matriline. However, two findings indicated that unit structure might not be strictly matrilineal. Low numbers of parent-offspring pairs within groups, and the absence of mothers for several juvenile males, suggested the possibility of dispersal of adult females, or of juvenile males between groups (Richard *et al.* 1996a). Analysis of microsatellite markers revealed relatedness between group members which were not maternally-related (i.e. had different mitochondrial haplotypes), and this paternal relatedness was interpreted as evidence of long-term association between members of different matrilines (Richard *et al.* 1996a).

It is not only the genetic data that raise questions concerning the adherence of social units to the predicted matrilineal structure. Both Ohsumi (1971) and Best (1979) argue that some proportion of juvenile females disperse from the 'breeding groups' of adult females and their offspring. However, these conclusions are questionable, since in neither case were whole groups sampled, and Ohsumi's (1971) analysis is based on only three groups. Occasional sightings of mixed-sex groups of juveniles (Clarke 1956, Gaskin 1970), appear to support Best's (1979) and Ohsumi's (1971) arguments. However, such groups have not been seen since the end of whaling (J. Gordon, H. Whitehead, pers. comm.), and may have been artifacts of the whaling process – undersized individuals left after the killing of their adult companions. The transfers and possible merger documented in Christal *et al.* (1998) and Chapter 3 provide the first direct evidence for dispersal by female sperm whales, and strongly suggest that units may contain unrelated individuals.

Given the apparent conflict between the predicted strict matrilineal structure, and some of the evidence, the actual genetic structure of sperm whale social units is clearly of

considerable interest. The delineation of units (Christal *et al.* 1998, Chapter 3) has now made possible the examination of genetic relatedness at this fundamental level of sperm whale society.

MATERIALS & METHODS

GROUP AND UNIT MEMBERSHIP

Fieldwork was conducted around the Galápagos Islands (1°30'S - 1°30'N, 89° - 92°30'W) between April and June 1995, aboard a 12 m motor-sailing vessel. The samples discussed in this chapter were collected over a 7 day period (28 May - 3 June 1995) during which the research vessel tracked a single group of 22 individuals, and did not encounter any other whales (with the exception of a large male on two brief occasions). All 22 members of the group had been identified previously, or were identified subsequently, so that it was possible to determine unit membership for all individuals present in the group (see Chapter 3 for unit delineation methodology). Two units were present. Unit A2 was a set of 5 individuals which appeared to have split from their original unit, A (see Figure 3.3). Unit B had 17 members in 1995, including three animals which are believed to have transferred into this unit: a pair including one adult female (#795) and one probable adult female (#793), between 1987 and 1988 (Figure 3.4), and a single, juvenile female (#2942) between 1994 and 1995 (Figure 3.7).

SAMPLES: COLLECTION METHODS, PRESERVATION AND STORAGE

Pieces of sloughed skin were collected from the wake of a swimming whale, or from the 'slick' left on the surface after an individual fluked-up (tail flukes raised at the start of a deep dive), using a long-handled dip-net. A total of 46 sloughed skin samples were collected, plus one from the large male (#545), which is not considered here.

Care was taken to avoid the possibility of both cross- and human contamination. Nets were searched and cleaned thoroughly between samples, and forceps were used to handle

samples. While at sea, samples were preserved in a sodium chloride saturated 20% dimethyl sulphoxide solution (Amos & Hoelzel 1991) at ambient temperature (25-30°C). After three weeks, the samples were transferred to a -20°C freezer.

The Whitehead lab sperm whale skin sample database (including 697 samples from the Galápagos/Ecuador region, J. Christal, unpublished data) was searched for samples previously collected from the same individuals (in case any animals turned out to be unrepresented by samples from 1995). A single sample (GAL548) had been collected behind a cluster of two whales on 6 April 1991, one of which (#2242) was also present from 28 May - 3 June 1995. Since no sample collected in 1995 was known to have been collected from #2242, this sample from 1991 was included in analyses. If the genetic profile from this sample matched any of the samples collected in 1995, then both would have to have been from #2242, since the other whale from the cluster in 1991 was known not to be present in 1995.

PHOTOGRAPHIC LINKS TO INDIVIDUAL WHALES

Whenever possible, samples were collected from lone whales, and an identification photograph taken of the individual's tail flukes as it fluked-up (Arnbom 1987). In some cases, no identification was available, either because the whale did not fluke-up, or because the photograph taken was of poor quality. In other cases, skin was collected behind clusters of two or more whales, of which none, some, or all were identified. A sample was determined to be definitely linked to a particular individual if it was collected behind a single animal, and a good quality (Arnbom's (1987): $Q \geq 3$) photographic identification was taken at that time.

LENGTH MEASUREMENT AND AGE ESTIMATION

Standard growth curves (e.g. Best 1970) allow length measurements to be converted to age estimates. When conditions permitted, measurement photographs of individual sperm whales were taken from a known height above the sea surface (Gordon 1990). Whenever

possible, identification photographs were taken immediately following measurement photographs, so that measured lengths could be assigned to specific individuals. Length photograph analysis followed the methods of Gordon (1990) and Waters & Whitehead (1990). If multiple photographs of an individual were available, the mean value over all photographs was used as that individual's length estimate. Once sex was determined (see below), age was estimated by comparing each individual's length estimate to the standard male or female growth curve (Best 1970).

For those individuals for which no measured length estimate was available, minimum age was estimated using sighting histories. Sperm whales under five years of age are noticeably smaller than adult females, and thus if there was no record of an individual being small when first identified, it seemed reasonable to conclude that the animal was a minimum of five years of age at first sighting. Minimum age was therefore estimated as: 5 + the number of years between first sighting and 1995. Females estimated to be at least 9 years old were considered capable of being mothers (age at sexual maturity: 8-9 years, Best 1968).

A callus on the dorsal fin of sperm whales is a secondary sexual characteristic of females, although it may sometimes be present in juvenile males (Kasuya & Ohsumi 1966). Whenever possible, the presence or absence of a callus was recorded for individuals when identification photographs were taken. Although Gaskin (1970) describes methods of distinguishing juvenile males from females at sea using morphological criteria, in practice this is extremely difficult (Best 1979, pers. obs.), and gender was determined using molecular techniques (see below).

MOLECULAR TECHNIQUES

DNA extraction

DNA templates for polymerase chain reaction amplification (PCR, Mullis *et al.* 1986), for sexing and mitochondrial (mt) DNA sequencing analyses, were prepared by

thoroughly rinsing a small (4-20 mm^2) piece of skin in distilled water, then incubating the skin sample in 200 µl of a 5% chelating resin (Chelex 100, BioRad) at 56°C overnight. The samples were then vortexed for 10 s, boiled for 8 min, vortexed again for 10 s and centrifuged at 16,000 x g for 3 min. An aliquot of the supernatant was added directly to the PCR reaction (Walsh *et al.* 1991).

Sexing

A male-specific 152 base pair (bp) fragment of the SRY gene was PCR-amplified from sloughed skin samples using sperm-whale-specific primers (SWSRY-1, SWSRY-2) designed by Richard *et al.* (1994). The SWSRY-1 primer was end-labeled with $\gamma^{32}P$, in a 10 µl reaction volume containing 4.5 µl H_2O, 10 mM Tris-acetate, 10 mM magnesium acetate, 50 mM potassium acetate, pH 7.5, 2 µM SWSRY-1, 3 µCi/µl $\gamma^{32}P$ ATP and 0.395 U/µl polynucleotide kinase. The labeling reaction was incubated at 37°C for 30 min, and terminated by incubation at 65°C for 15 min.

PCR amplifications were performed in a reaction volume of 10 µl containing 6.65 µl chelex supernatant, 2 mM $MgCl_2$, 50 mM KCl, 10 mM Tris-HCl, pH 8.3, 0.001% gelatin, 200 µM each dNTP, 1.0 µM each SWSRY-1 and SWSRY-2, 0.1 µM $\gamma^{32}P$-labeled SWSRY-1 and 0.625 units of Taq polymerase, overlaid with 20 µl mineral oil. PCR reactions involved 30 cycles, 7 with denaturation at 96°C for 1 min, annealing at 57°C for 1 min and extension at 72°C for 5 s, followed by 23 cycles with denaturation at 90°C for 1 min, annealing at 57°C for 1 min and extension at 72°C for 5 seconds. Six known-sex controls (4 males, 2 females) were included with each PCR run. Products were size fractionated in 6% glycerol tolerant polyacrylamide denaturing gels, using M13mp18 DNA as a size marker. The gels were dried and exposed to film for 24-48 hr. SRY amplification was performed twice for all samples, and a third time for any which showed ambiguous results in the first two reactions.

Since the SRY sexing technique provides a positive result for males, but no result for females, sexing results were confirmed by Joanna Bond (Molecular Ecology Group, Department of Zoology, Cambridge University, UK), and Sarah Mesnick (South West Fisheries Science Center, National Marine Fisheries Service, La Jolla, California) using ZFX/ZFY primers designed by Berubé & Palsbøll (1996), which provide positive results for both males and females.

Mitochondrial DNA sequencing

A 953 bp section of the mitochondrial control region (d-loop) was PCR-amplified using primers designed by Dillon and Wright (1993). One of these primers annealed to $tRNA^{Thr}$ while the other annealed to $tRNA^{Phe}$. PCR was carried out in a 25µl reaction volume containing 18 µl chelex extraction supernatant, 10 mM Tris-HCl (pH 8.3), 50 mM KCl, 2 mM $MgCl_2$, 200 µM each dNTP, 0.5 µM each primer and 2.5 units of *Taq* polymerase, overlaid with 20 µl mineral oil. The PCR runs involved thirty cycles of denaturation at 96°C for 30 s, annealing at 49-52°C for 30 s and extension at 72°C for 30 s. All PCR amplification experiments included controls in which no DNA was added.

The efficacy of PCR amplification was checked by size fractionation of products in 1% agarose gels (1 x TAE buffer) at 100V for approximately 2-3 hr, staining with ethidium bromide (0.5 µg/ml) and visualisation under UV light.

PCR products were purified in preparation for sequencing by incubation with exonuclease I (to remove excess PCR primers) and shrimp alkaline phosphatase (to remove unincorporated dNTPs) (Werle *et al.* 1994). Control region DNA was sequenced directly by the dideoxy method (Sanger *et al.* 1977), using α-^{35}S-dATP (1000 Ci/mmol) and T7 DNA polymerase (Pharmacia Biotech). The primers used were 'block A' and 'F rev' designed by Dillon (1996), and an additional primer 'NB' (5'-CCCAATTACATCTTTCCTAC-3') designed to permit sequencing in a central gap between the sequences produced using 'block A' and 'F Rev'.

Sequencing reactions were resolved on 8% polyacrylamide gels with 7.8 M urea, and 1x glycerol tolerant buffer. Gels were run at a constant power of 50 W for 2-5 hr, then fixed, dried, and exposed to film for 48-72 hr, or visualised using a BIO RAD GS-525 Molecular Imager System. Gels were read manually, twice, and data entered into GeneRunner software for verification and sequence alignment.

For each sample 450-500 bp of the control region was sequenced, including in each case the most variable region identified by Dillon (1996) and Lyrholm *et al.* (1996), 58-325 bp from the start of the control region.

Microsatellite analysis

Typing at 10 microsatellite loci (EV5, EV94, EV104 - Valsecchi & Amos 1996; FCB1, FCB17 - Buchanan *et al.* 1996; JB69, JB653 – J. Bond, unpublished primers; SW10, SW19 - Richard *et al.* 1996b; ACCC392 – Palsbøll *et al.* 1997a) was performed by Joanna Bond (Molecular Ecology Group, Department of Zoology, Cambridge University, UK). Statistical independence between loci had been tested using the GENEPOP program, and results were consistent with the assumption of unlinked markers (all $p>0.05$, J. Bond pers. comm.).

All samples were typed at at least 6 loci. Samples with identical microsatellite profiles at 6 or more loci were considered to be from the same individual. The rationale for this approach is that the probability of randomly sampling two sperm whales that each display the most common multi-locus microsatellite profile for the six least variable loci (using allele frequencies within the group) was 3.57×10^{-6} (i.e. 1 in 280,000). Whenever photo-identities were available for two genetic samples that matched at 6 or more loci, the photo-ID data confirmed that the samples were from the same individual. At least one sample for each individual was typed at all 10 loci.

ANALYSIS OF GENETIC RELATEDNESS

Relatedness

The strengths of genetic relationships between individuals were investigated using the program Relatedness 5.02 (Queller & Goodnight 1989, program available at http://www-bioc.rice.edu/~kFg/Gsoft.html). The coefficient of relatedness, r, was estimated for all pairs of individuals on the basis of microsatellite allele sharing and population allele frequencies (from ~130 additional samples typed by J. Bond). Average linkage cluster analysis of the resultant matrix of r values was used to depict the overall structure of the units, and of the group as a whole.

Kinship

The program Kinship 1.2 (Queller & Goodnight 1989, program available at http://www-bioc.rice.edu/~kFg/Gsoft.html) was used to test hypotheses of pedigree relationships between pairs of individuals. Given a particular hypothesis (e.g. parent-offspring), the program uses the r values, the population microsatellite allele frequencies, and the genotypes of the two individuals to calculate a likelihood ratio between that hypothesis and the null hypothesis (that the two individuals are unrelated). Significance levels are assigned to likelihood ratios by simulation using the hypothesis settings and the population allele frequencies. Three hypotheses were tested for all pairs of individuals in the dataset:

1. That they are parent and offspring.
2. That they are full siblings.

   This level of relatedness was not expected, given the mating system of sperm whales, but was tested for completeness.
3. That they are half-siblings or grandparent/grandchild.

   Since both involve pairs of individuals that have an r of 0.5 to a common relative, it is not possible to distinguish between these two types of

relationship without additional information on ages or other relationships of the individuals.

GENETIC STRUCTURE OF UNITS (AND GROUP)

The genetic structures of the units were compared to those of units generated using simulation models by Monte-Carlo significance-testing. Microsatellite profiles for 1000 sets of individuals (units), of the same size as each of the real units being considered, were generated on the basis of each of several unit structure models (see below) using programs written in Visual Basic. Since three individuals were known to have transferred into one of the units (Chapter 3), simulations were also run to investigate the underlying genetic structure of this unit when these individuals were omitted. Microsatellite profiles for founding individuals, and for fathers, were randomly generated on the basis of population allele frequencies. Microsatellite profiles for offspring were generated from those of their parents using standard rules of Mendelian inheritance. By comparing the real data to the distribution of the simulated data it was possible to test whether the real data were statistically-distinguishable from the unit structure models.

Demographic parameters used in simulations

Simulation models used a single set of demographic parameters: age-specific mortality, age-specific fecundity, and age of male dispersal.

Male dispersal was fixed at age 10. Estimates of mean age of males at dispersal vary considerably (4-5 years - Best 1979, 6 years (95% c.i.: 2.7-10.9 years) - Richard *et al.* 1996b, starting at 12 years of age - Ohsumi 1966, 15-21 years - Rice 1989) and there is little information on variation around the mean, thus a fixed value at approximately the mean of the estimates was selected.

Age-specific fecundity for females was determined using data from Best *et al.* (1984), with a minimum inter-calf interval of 4 years, single births, and a 1:1 birth sex ratio (Best

1968). Fecundity in the Galápagos study area between 1985 and 1995 was found to be considerably reduced (0.05 calves/female/year), probably due to heavy whaling for males off Peru in the 1960s and 1970s (Whitehead *et al.* 1997). This reduction in fecundity was incorporated into the simulations by fixing fecundity at 0.05 calves/female/year for all years after the unit reached a threshold size several animals below the number in the unit being modeled. Thresholds were fixed at values which prior testing had shown to result in reduced fecundity during the last 10-30 years of simulations.

Finding reliable mortality data for sperm whales proved problematic. The IWC 'sperm whale model' (International Whaling Commission 1982), uses a single value of 5.5%/year for natural adult female mortality. Analyses of long-term association patterns showed that this value may be an overestimation (Chapter 2), and preliminary modeling attempts indicated that the use of this value led to the extinction of the majority of matrilines. Independent modeling of population dynamics has shown that the use of the IWC 'sperm whale model' parameters leads to unsustainable populations (B. Taylor, pers. comm.). The IWC natural mortality estimate was calculated on the basis of age-distribution within heavily-exploited populations, using somewhat spurious techniques, and appears not to be reliable. Thus a suitable proxy for sperm whale mortality data was required. The killer whale (*Orcinus orca*) is a large odontocete with similar life history parameters to the sperm whale, and well-described age-specific mortality data (Olesiuk *et al.* 1990). Although it could be argued that predation on, and thus mortality of, sperm whales might be higher than for killer whales, direct evidence of fatal predation on adult sperm whales is scarce (reviewed in Rice 1989, Jefferson *et al.* 1991). Thus in the absence of reliable data for the sperm whale, the killer whale age-specific mortality values were adopted.

Since not all members of the real units were represented by genetic data, the simulated units were 'pruned' by randomly removing the requisite number of 'unrepresented' individuals, so that the data available mimicked that available for the real units.

Models:

1. Random

This is the 'null' model, with units constructed of randomly-selected individuals.

2. Unrelated females with offspring

This unit structure would be expected if, as suggested by Ohsumi (1971), all females disperse individually to juvenile schools, and the female members later join independent social units. It would also be expected if all females engaged in 'natal transfer' (i.e. transfer out of their natal unit into a different unit, Greenwood 1980). Although this is unexpected in societies with short-term male breeding tenure, like sperm whales, transfers between units have been documented (Chapter 3).

Units were formed by a random number of founding females (2-3 for the smaller unit, 7-10 for the larger) of random age (10-20), which reproduced according to the demographic parameters. All offspring dispersed at age 10.

3. Unrelated females with offspring – shared paternity of cohorts

If offspring of unrelated females are fathered by the same male, then relatedness within a unit will be increased. Common paternity of cohort members has been reported in another large odontocete, the long-finned pilot whale (*Globicephala melas*, Amos *et al.* 1991), and it certainly seems feasible among sperm whales. Synchrony of oestrus within sperm whale groups is indicated by pregnant females tending to be in similar states of pregnancy (Best & Butterworth 1980), and a report of two newborn calves in a group at one time (Weilgart & Whitehead 1986). Berzin (1971) and Yablokov (1974) suggest that skin colouration patterns provide strong evidence for a single father of several foetuses within a harem (*sic*).

Units were formed exactly as in 2 above, with the exception that any two or more offspring born in the same year had the same father.

4. Pure matriline

Prior to findings of transfers between units (Chapter 3), sperm whale social units were generally believed to be matrilineal in nature. Simulated matrilineal units were founded by a single female, of random age (10-20). Offspring born in the same year were fathered by different males.

5. Matriline with transfers

This model incorporates the transfer of females between units, within a general matrilineal structure. Matrilines were formed exactly as in 4 above, but with transfers of females out of and into units at rates estimated in Chapter 3. Thus females transferred out of their unit with a probability of 0.9%/individual/year, and a unit had a 5%/year probability of having an unrelated female (with randomly determined microsatellite profiles, and randomly selected age: 5-50) transfer into it.

Given the current state of knowledge regarding unit structure, this is the structure predicted to match the real data most closely.

Monte-Carlo significance testing

Two measures of the genetic structure of units were analysed. Firstly the number of putative parent offspring pairs (dyads sharing an allele at every microsatellite locus) was determined for all simulated units. Although the true number of parent-offspring pairs for each simulated unit was known, the valid comparison is with putative parent-offspring pairs (which may include some siblings or other pairs by chance), since this is the data available for the real units. Secondly, the average within-unit relatedness (r) of each simulated unit was estimated using Relatedness 5.02 (Queller & Goodnight 1989), as

above. Although these two measures of genetic structure are clearly related, and the two analyses cannot be considered to be independent, they do provide different insights into patterns of relatedness within units. Two units could theoretically have the same number of putative parent-offspring pairs, yet very different levels of average within-unit relatedness, if one consisted of unrelated females and their offspring and the other of closely-related females and their offspring. Conversely, a similar within-unit relatedness value could be obtained from a set of siblings and a pure matriline, yet the numbers of parent-offspring relationships would be very different.

In each case, the values of the two genetic structure measures for the real units were compared to the distributions of values for the simulated units for each model separately. All Monte-Carlo significance tests were two-tailed.

Group Structure

Given unexpected findings of relatively close genetic relatedness between members of the two units (see below), the possibility arose that two units shared a common ancestry. Thus the genetic structure of the group became of interest, despite the known separate recent histories of the units. Simulations were run for the group as a whole using each of the five models above.

RESULTS

IDENTITY OF SKIN SAMPLES

Of the 47 skin samples collected, 23 were linked to specific animals on the basis of photo-ID records, and represented 14 different individuals (2 of the 5 members of Unit A2, and 12 of the 17 members of Unit B). Microsatellite analysis of the single sample collected in 1991 from a pair of individuals, including one member of the current group (#2242, Unit A2), matched to an unidentified sample collected in 1995, thus both of these samples were determined to be from #2242 (since the other member of the pair from which the 1991 sample was collected was definitely not present in 1995). Genetic profiles

could therefore be matched to 15 identified individuals (3 members of Unit A2 and 12 of Unit B). Microsatellite analysis identified 3 additional unique genetic individuals. Thus of the total of 22 group members, 18 are represented by genetic data.

AGE AND SEX

Of 60 good quality measurement photographs taken, 40 could be linked to one or more individual whale(s) (in some cases, 2 or 3 whales could be measured from a single photograph, and the position of the relevant whale (left, middle, right) was recorded when identification photographs were taken). None of the measured lengths from unlinked photographs were outside the range of those that could be linked to individuals. Fourteen individuals were represented by one or more measurement photograph(s), and mean length estimates for these animals ranged from 8.2 to 11.0 m (Table 4.1). Age estimates (determined with reference to molecularly-determined sex, where available) for these individuals ranged from 6 to >30 years. For the remaining 8 individuals, minimum age estimates based on sighting histories ranged from 6 to 15 years.

Of the 14 identified individuals for which definite genetic sexing results were available (there was insufficient tissue for the sex of #3290 to be confirmed), only one was found to be male (Table 4.1). Two additional males were present among the 3 unidentified genetic individuals. Thus males constituted 17.7% of the 17 individuals for which sexing results were available, and at least 13.6% of the group as a whole.

Presence/absence data for calluses were not always consistent (i.e. for some individuals a callus was recorded as present and absent on different occasions). This clearly suggests that recognition of a callus at sea is not strictly reliable. As a result, an individual's status (callus absent or present) was determined only if the dataset included at least 3 records, with no inconsistency among these records. Ten individuals had a definite dorsal callus, while four did not (Table 4.2).

Table 4.1. Length, sex, and estimated age for members of the study group. For animals of unknown sex, age estimates based on length are given for both female (f) and male (m).

ID	unit	mean length estimate (m)	years since first sighting (in 1995)	sex	estimated age (years)
235	A2	-	10	-	≥15
255	A2	-	10	f	≥15
2242	A2	-	6	f	≥11
2361	A2	10.2	6	f	20
2818	A2	-	4	-	≥9
754	B	9.5	8	m	9
793	B	10.8	8	-	(f: >30, m: 14)
795	B	-	8	f	≥13
804	B	10.3	8	f	21
806	B	11.0	8	-	(f: >30, m: 15)
807	B	10.4	8	f	23
809	B	10.0	8	f	18
810	B	10.1	8	f	18
811	B	9.7	8	f	15
812	B	-	8	f	≥13
814	B	-	8	f	≥13
2935	B	-	1	-	≥6
2942	B	8.2	1	f	6
3287	B	8.6	-	f	8
3290	B	10.1	-	f?	(f: 19, m: 11)
3295	B	9.2	-	-	(f: 12, m: 8)
3303	B	9.4	-	-	(f: 13, m: 9)

Table 4.2. Presence/absence of dorsal callus with respect to age/sex.

ID	callus present?	age/sex (from Table 4.1)
2242	Y	adult f
2361	Y	adult f
2818	Y	?
754	Y	juvenile m
793	Y	?
795	N	adult f
804	Y	?
809	Y	adult f
810	Y	adult f
811	N	adult f
812	Y	adult f
2935	N	?
2942	N	juvenile f
3303	Y	?

Calluses were found to be present on some adult females and on the only juvenile male for which callus status was known. Calluses were absent on the single juvenile female, but also on two adult females. Given that calluses were not found universally on adult females, and that they are present on at least some juvenile males, callus data cannot be considered a valid method of age or sex determination for sperm whales, and was not used to infer sex for those individuals which were not sexed using molecular techniques.

Age/sex structure of units

Unit A2 consisted of 3 adult females, and 2 individuals of unknown sex which were at least 9 years of age. Unit B consisted of 8 adult females, 2 juvenile females (#2942 and #3287), 1 juvenile male (#754), and 7 other individuals for which sex, and thus age, could not be determined. All individuals were estimated to be at least 6 years old.

MITOCHONDRIAL DNA ANALYSIS

Mitochondrial DNA sequencing preceded the microsatellite analysis, hence genetic identities of samples were unknown. Sequencing was performed on 31 samples (since 10 samples were known to be duplicates on the basis of photo-ID data, and 6 samples failed to amplify after repeated attempts), which were later determined to represent all 18 genetic individuals.

Samples representing 17 of the 18 individuals produced identical sequences, corresponding to Dillon's (1996) and Lyrholm & Gyllensten's (1998) haplotype 1, the most common haplotype found in all oceans studied to date (North Atlantic, North Pacific, South Pacific, Indian - Dillon 1996, Lyrholm & Gyllensten 1998). The sample representing the 18th individual, #2361 (Unit A2), produced a sequence differing from haplotype 1 by 2 transition substitutions (Figure 4.1). This sequence matches Lyrholm & Gyllensten's (1998) haplotype 10, which has previously been found in a single sample from each of four locations: Galápagos and the western North Pacific (Lyrholm & Gyllensten 1998), Oregon and the Gulf of California (S. Mesnick, unpublished data).

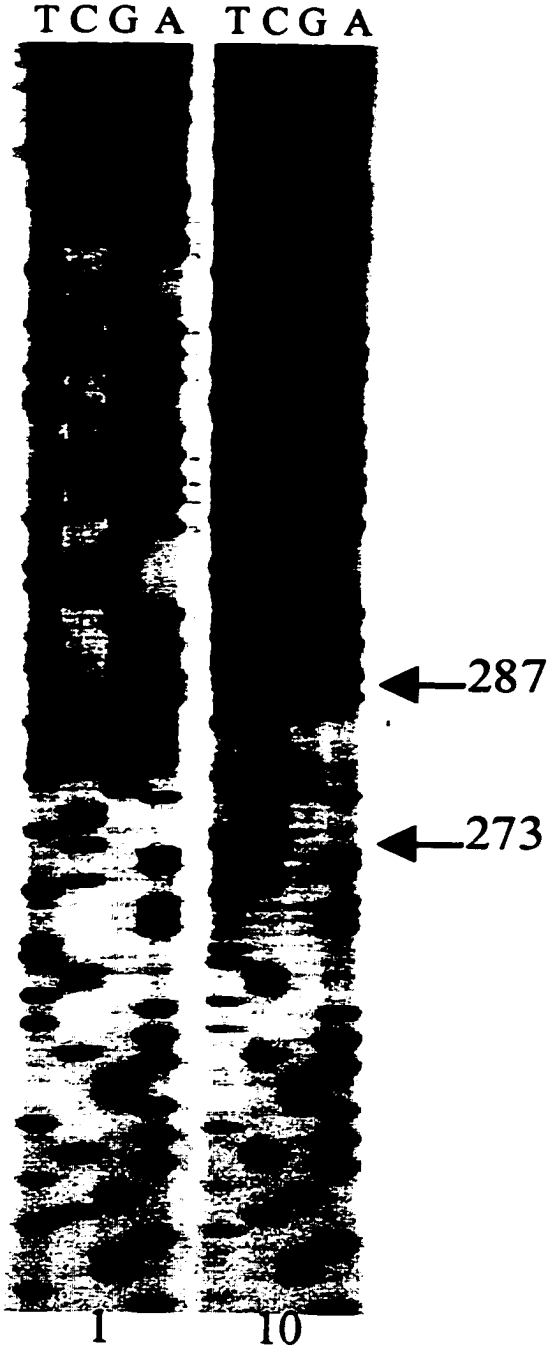

Figure 4.1. Part of the mitochondrial d-loop sequence for the two haplotypes present within the group, indicating the positions of the two transition substitutions. Haplotype numbers, and substitution sequence positions numbers are given relative to Lyrholm & Gyllensten (1998).

ANALYSIS OF GENETIC RELATEDNESS

Relatedness within units and group

The average linkage cluster analysis of pairwise estimates of genetic relatedness (r) for the 12 members of Unit B known to be represented by microsatellite data is shown in Figure 4.2. This analysis indicates that there are some close relatives among the unit members, but also that there are some individuals which are not closely related to any of the other members. Two individuals which are known to have transferred into the unit are seen to have no particularly close relationships with any other unit members (#795 and #2942, see Chapter 3 for details). Another animal, #754, is clustered alone, reflecting the fact that it has no relationships with other unit members that are closer than would be expected for any individual selected from the population at random (maximum pairwise r for #754 = -0.0335, average within population relatedness (using individuals simulated at random on the basis of population allele frequencies): 0.0006 (95% c.i.: 0.0034 to -0.0022)).

The three members of Unit A2 represented by microsatellite data are clearly not closely related (pairwise relatedness values: –0.011 to 0.032, Figure 4.3). Number 2361 is the individual with a haplotype different to that of all other group members.

When cluster analysis is performed on pairwise r values for all 18 group members represented by microsatellite data, the result is somewhat surprising (Figure 4.4). Rather than clustering separately, as was expected, the members of the two units are intermingled, and some close relationships between members of the different units are apparent (i.e. #2361 and #809/#810, #2242 and #812). It was not possible to assign the unidentified genetic individuals (samples not linked to specific identified animals) to units on the basis of relatedness estimates.

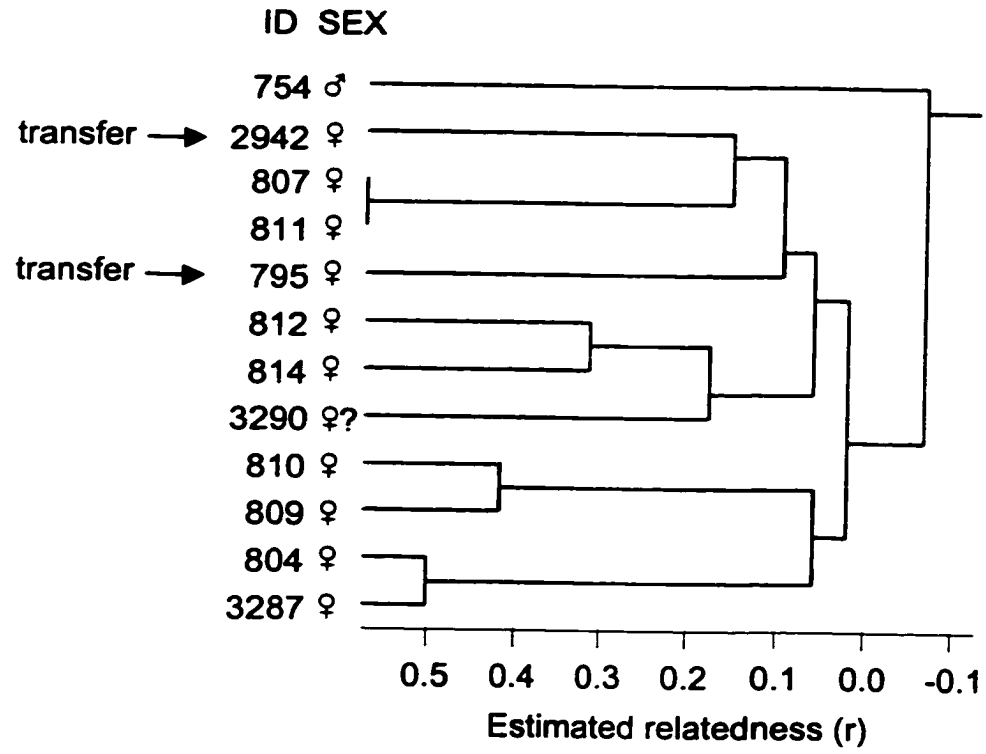

Figure 4.2. Average linkage cluster analysis of r values for Unit B. Animals known to have transferred into the unit are indicated (see Chapter 3 for details).

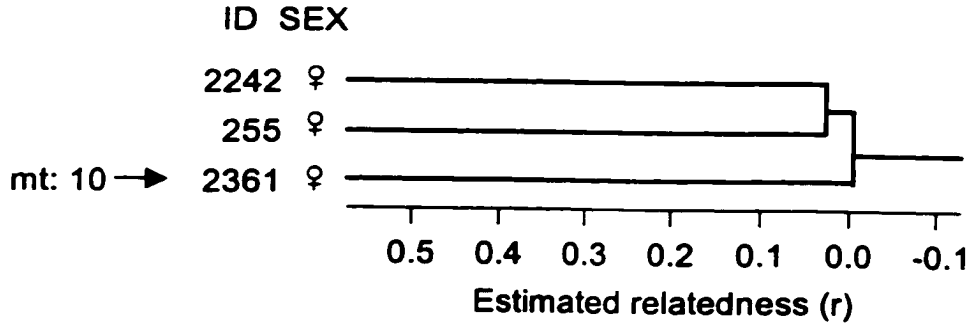

Figure 4.3. Average linkage cluster analysis of r values for Unit A2. This figure has been re-scaled to be directly comparable to the other cluster analyses. The individual which has a unique mitochondrial haplotype is indicated.

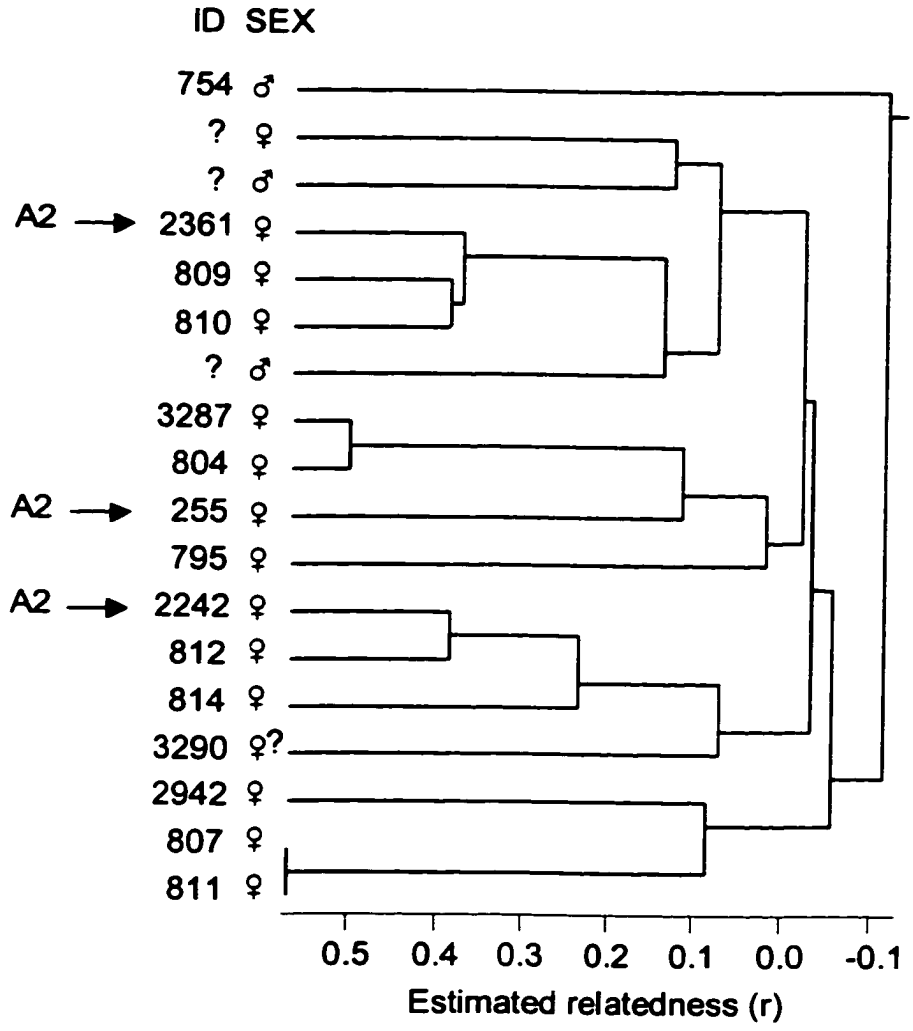

Figure 4.4. Average linkage cluster analysis of r values for the whole group. Samples which were not linked to specific individuals, but which contributed unique microsatellite profiles, are indicated as '?'. Members of the smaller unit, A2, are indicated by arrows.

Kinship

Two mother-offspring pairs were detected, both within Unit B. Both #804/#3287 and #807/#811 were found to be significantly likely to be mother-offspring pairs (versus the null hypothesis that each pair was unrelated, both $p<0.001$). The direction of these relationships can be determined by considering the age/sex data for these individuals (Table 4.1). Adult female #804 is the mother of the approximately 8 year old female #3287. Since adult female #807 is larger, and thus probably older than adult female #811, it is likely that #807 is the mother in this pair.

The test for full siblings detected only these same two pairs, indicating that there are no true full siblings in the dataset. Four pairwise relationships were determined to be half-sibships or grandparent/grandchild (h-s/g-g) (all $p<0.05$). Although two of these relationships were between members of the same unit (#809/#810, #812/#814, all Unit B), the other two were between members of different units (#255/#812, #2361/#809). The #255/#812 pairing is not obvious from Figure 4.4, but this appears to be an artifact of the clustering process. The #2242/#812 relationship, which appears close in Figure 4.4, was marginally statistically inconsistent with h-s/g-g relatedness. Five of the animals in the three h-s/g-g pairs are adult females, and the sixth (#255) is at least 15 years old, but of unknown sex, thus it is impossible to judge directly to which generations the individuals belong.

Each of the related pairs from different units includes one member which also has a within-unit h-s/g-g relative, and examination of the relatedness between the different-unit and same-unit relatives does allow some resolution of the pattern of relationships. Number 810 and #2361, both related at the h-s/g-g level to #809, also appear to be closely related to each other ($r = 0.369$, h-s/g-g likelihood ratio: 1.98 (ratio for pÈ0.05: 3.74)). Given a 0.347 type II error rate (rate of false rejection of the primary hypothesis) in this analysis, it seems quite possible that all three individuals are h-s/g-g. Since #2361 is the individual possessing a unique haplotype, these animals are unlikely to be related

though the maternal line. All three individuals are estimated to be of similar age (18-20 years, Table 4.1), thus it seems likely that they are all paternal half-sibs.

In the case of #812, its different-unit h-s/g-g (#255), is highly unlikely to share the same common relative as its same-unit h-s/g-g (#814) (for #255 vs #814, r = -0.232, h-s/g-g likelihood ratio = $1.54e^{-2}$). Given the minimum 9 year generation time, and female longevity of ~60 years, it seems unlikely that #812 is the grandmother of one and the grandchild of the other. The remaining alternatives are that #812 is the grandmother of both #255 and #814 through different offspring (unlikely given the low relatedness of #255 and #814), that either #814 or #255 is the grandmother of #812 whilst the other is a half-sib of #812 through the unrelated parent (most likely the father), or that #814 and #255 are half-sibs of #812 through different parents.

Therefore, although the issue cannot be resolved definitively, it is possible that both between-unit h-s/g-g relationships could be paternal half-sibships.

GENETIC STRUCTURE OF UNITS (AND GROUPS)

I will describe the genetic structure results for each unit separately, followed by those for the group as a whole.

Unit B

Since 12 of the members of the 17-member Unit B were known to be represented by microsatellite data, all simulated units were 'pruned' by random removal of five individuals. The number of putative parent-offspring pairs (ppo) found in Unit B, two, was significantly greater than for simulated units constructed of random individuals, but significantly less than that for all other simulated units structures (mean numbers of ppo >5 for all models, Table 4.3). Unit B has significantly lower average within-unit relatedness (r) than either pure matrilines or matrilines with transfers, although it could not be statistically-distinguished from unrelated females with offspring (different or

common paternity of cohorts), or from random individuals. Thus while the unit clearly does include some related individuals, the genetic structure is not compatible with models involving only, or predominantly, related members.

Table 4.3. Comparison of measures of unit genetic structure for Unit B with simulated units.

	Unit B		random	unrelated f + offspring	unrelated f + offspring (c.p.)[1]	pure matriline	matriline + transfers
ppo	2	mean (*s.d.*) significance[2]	0.043 (*0.208*) > **	5.213 (*1.542*) < **	5.164 (*1.411*) < ***	7.630 (*2.366*) < ***	6.868 (*2.209*) < **
r	0.0005	mean (*s.d.*) significance[2]	0.003 (*0.023*) n.s.	0.048 (*0.035*) n.s.	0.051 (*0.034*) n.s.	0.153 (*0.050*) < **	0.125 (*0.056*) < ***

Table 4.4. Comparison of measures of genetic structure for the 'core' of Unit B with simulated units.

	Unit B (14)		random	unrelated f + offspring	unrelated f + offspring (c.p.)[1]	pure matriline	matriline + transfers
ppo	2	mean (*s.d.*) significance[2]	0.034 (*0.187*) > **	4.651 (*1.208*) n.s.	4.626 (*1.296*) n.s.	6.290 (*2.124*) < *	5.094 (*1.816*) n.s.
r	-0.008	mean (*s.d.*) significance[2]	0.004 (*0.029*) n.s.	0.075 (*0.038*) < ***	0.075 (*0.041*) < **	0.171 (*0.057*) < ***	0.111 (*0.060*) < ***

[1] common paternity of cohorts

[2] significance results are presented as: '>' real unit data significantly greater than that for simulated units; '<' real unit data significantly less than that for simulated units; n.s.: not significantly different ($p \geq 0.025$), *: $p<0.025$, **: $p<0.01$, ***:$p<0.001$.

The genetic structure of the 'core' of Unit B (those 14 members which are not known to have transferred into the unit) suggests that even without these additions, the unit structure was not purely matrilineal. On the basis of numbers of putative parent-offspring pairs, the core of Unit B cannot be statistically-distinguished from either the matriline with transfers model, or the two models involving unrelated females and their offspring, although the actual number of ppo is considerably less than the means for these models (Table 4.4). However, the value of average within-unit r for this set of individuals is significantly lower than would be expected for any of the non-random unit membership models. This suggests that although there are some sets of relatives within the core of the unit, there are also some unrelated members in addition to those known to have transferred in.

Unit A2

Three of the five members of Unit A2 were known to be represented by microsatellite data, thus simulated units were 'pruned' of two individuals.

The genetic structure of Unit A2 cannot be distinguished statistically from any of the models on the basis of numbers of ppo (Table 4.5). The coefficient of relatedness (r) within the unit is significantly less than that for pure matrilines, although it is indistinguishable from the other four models.

Group

Group simulations were run to 22 members, then pruned of 4 individuals, to mimic the data available for the real group. The number of ppo for the group is significantly greater than for units of random individuals, but significantly less than for all other models (Table 4.6). Within group r is significantly less than for pure matrilines, or matrilines with transfers, but indistinguishable from either unrelated females and offspring (different or common paternity of cohorts) or random individuals.

Table 4.5. Comparison of measures of unit genetic structure for Unit A2 with simulated units.

	Unit A2		random	unrelated f + offspring	unrelated f + offspring (c.p.)[1]	pure matriline	matriline + transfers
ppo	0	Mean (*s.d.*) significance[2]	0 (*0*) n.s.	0.787 (*0.575*) n.s.	0.939 (*0.701*) n.s.	1.257 (*0.736*) n.s.	0.867 (*0.696*) n.s.
r	-0.0007	Mean (*s.d.*) significance[2]	0.012 (*0.081*) n.s.	0.151 (*0.135*) n.s.	0.144 (*0.126*) n.s.	0.327 (*0.117*) < **	0.178 (*0.147*) n.s.

Table 4.6. Comparison of measures of group genetic structure with simulated groups.

	Group (A2+B)		random	unrelated f + offspring	unrelated f + offspring (c.p.)[1]	pure matriline	matriline + transfers
ppo	2	Mean (*s.d.*) significance[2]	0.088 (*0.301*) > **	8.338 (*1.547*) < ***	8.463 (*1.667*) < ***	11.981 (*3.690*) < ***	12.801 (*2.950*) < ***
r	0.0092	Mean (*s.d.*) significance[2]	0.001 (*0.017*) n.s.	0.031 (*0.024*) n.s.	0.037 (*0.026*) n.s.	0.111 (*0.044*) < ***	0.104 (*0.042*) < ***

[1] common paternity of cohorts

[2] significance results are presented as: '>' real unit data significantly greater than that for simulated units; '<' real unit data significantly less than that for simulated units; n.s.: not significantly different ($p \geq 0.025$), *: $p < 0.025$, **: $p < 0.01$, ***:$p < 0.001$.

DISCUSSION

As Moore (1984) pointed out for primate research, premature assumptions of matrilineal group structure within species can lead to biases in the interpretation of observations. In order to be completely valid, interpretations of behaviour, and the development of theories concerning the evolution and benefits of sociality in a particular species, must be soundly based on an accurate knowledge of the genetic structure of social groupings. Although past analyses of genetic relatedness within sperm whale social groups have

suggested relatedness of group members (Richard *et al.* 1996a, Lyrholm & Gyllensten 1998), the current study represents the first empirical examination of the genetic relatedness of known long-term members of specific social units. Generalisation on the basis of information on only two units, both of which are known to have undergone membership change (Chapter 3), is perhaps inadvisable, yet the patterns of relatedness detected in this study show that at least some sperm whale units do not conform to the predicted pure matrilineal structure.

NATURE OF THE SOCIAL UNITS

Although the exact sex structure of the units is not known, the sex structure of the group conformed to previous reports (e.g. Ohsumi 1971, Richard *et al.* 1996a), with juvenile males making up approximately 15% of group members. The age structure of both units was biased towards older animals. There were no individuals under the age of six years in either unit, despite the presence of at least three adult females in Unit A2, and at least eight adult females in Unit B, suggesting that fecundity has been considerably depressed, at least in recent years.

Given the low mitochondrial DNA diversity of sperm whales (Lyrholm *et al.* 1996), and the fact that the haplotype of all but one of the sampled individuals is found in 30-40% of all individuals in the Galápagos/Ecuador/Peru area (Dillon 1996, Lyrholm & Gyllensten 1998), the sharing of this haplotype says very little about relatedness between, or even within the units. Despite the biased substitution patterns (and existence of mutational 'hot spots') in the sperm whale mtDNA control region (Lyrholm *et al.* 1996), it seems extremely unlikely that the two transition substitutions present in the haplotype of #2361 (Figure 4.1) both occurred as mutations within this particular individual, or its immediate ancestors. Thus the finding of different mitochondrial haplotypes within a single unit provides clear evidence for the presence of individuals with distinct maternal origins within a unit.

Patterns of relatedness within both units indicated the presence of unrelated members, although some close relationships were apparent in the larger unit, B (Figures 4.2, 4.3). Of the eighteen individuals sampled, only four were accompanied by a first-order genetic relative (parent or offspring), and no cases of grandmother-grandchild relationships could be confirmed. Despite the fact that an additional four individuals were not sampled, these findings are clearly not consistent with a pure matrilineal unit structure. However, the presence of two female offspring of approximately 8 and 15 years of age within the Unit B suggests that either not all females disperse from their natal units, or that dispersal may be delayed.

The lack of relatedness within Unit A2 indicates that the splitting of this set of individuals from Unit A (see Figure 3.3) did not occur along maternal lines, in contrast to reports for other species (e.g. Chepko-Sade & Sade 1979, Moss 1988, Ford *et al.* 1994). The unexpected finding of relationships between members of the different units (Figure 4.4) is most likely to be a result of common paternity, rather than reflecting matrilineal relatedness. An apparent paternal half-sib relationship between two unit members of similar age indicates that suggestions of common paternity of cohorts within a unit are reasonable.

Comparison of measures of unit genetic structure with simulated model data indicates that neither Unit A2, Unit B (all members, or only those not known to have transferred in) or the group as a whole are consistent with a pure matrilineal structure (Tables 4.3-4.6). The genetic structure of Unit A2 cannot be distinguished from any of the remaining four models, although it appears closest to that of random individuals (Table 4.5). The genetic structure of Unit B appears to be intermediate between that of random individuals, and the models involving unrelated females and their offspring (Tables 4.3), although the number of ppo is low. Although the number of ppo within the 'core' of Unit B is consistent with the model involving a matriline and transfers, within unit relatedness is significantly lower (Table 4.4). If we assume that the model parameters were reasonable (see below), then these results suggest that units include at least some

unrelated members, and that numbers are significantly higher than expected on the basis of the minimum estimates of transfer rates predicted in Chapter 3.

IMPLICATIONS

These two sperm whale social units are not matrilineal in nature – a fact that seems apparent even without considering the Monte Carlo simulation results. Although there are reasons why these results might not be representative of sperm whale social unit structure in general (see below), it is worthwhile to consider the implications of a non-matrilineal basis for sperm whale society. Sperm whale social units have typically been considered to exist primarily for communal care of calves, with 'nepotism' or kin selection benefits thought to promote cooperation among females (e.g. Whitehead 1996a). If units are not generally matrilineal, then kin selection benefits are unlikely to have played a major role in the evolution of social behaviour. Reciprocal altruism (Trivers 1971) has been suggested as a possible mechanism promoting cooperation among cetaceans (e.g. Connor & Norris 1982), and given the long lives and long-term associations (hence multiple opportunities for interaction), and apparent intelligence of female sperm whales, reciprocity seems a feasible alternative to kin selection benefits for the maintenance of social unit stability.

The fact that units seem not to be matrilineal appears to conflict with earlier findings of group-specific features (e.g. coda repertoires - Weilgart & Whitehead 1997, and fluke markings - Dufault & Whitehead 1998), which are correlated with mtDNA haplotypes (Whitehead *et al.* 1998). One possible (and admittedly speculative) explanation which resolves these disparate findings, is that there might be another level in sperm whale society, that of the community. Communities might consist of multiple units, with units within communities being more likely to associate together as groups than are units from different communities. If movements of animals between units occurred predominantly within rather than between communities, then one might expect relationships between members of different units, and cultural phenomena, such as dialects, might be broadly maintained within communities, rather than at the level of the unit. Such higher-level

structures are found among both elephants (Moss & Poole 1983) and killer whales (Bigg *et al.* 1990), species that have similarities to sperm whales in terms of both social structure and cultural phenomena (Ford 1991, Strager 1995, Weilgart *et al.* 1996). See Chapter 7 for further development of this, and other related ideas.

THE VALIDITY OF MODEL ASSUMPTIONS

The validity of the Monte Carlo simulation results is contingent on the accuracy of the demographic parameters used in simulation models. Inaccuracies in the male dispersal, fecundity and mortality parameters might be expected to bias relatedness patterns within simulated units, and hence to influence the results, and interpretation, of this study.

The study group contains at least three males, all of which were estimated to be between 6 and 15 years of age, and one of which was individually measured and estimated to be 9 years of age (Table 4.1). This clearly suggests that estimates indicating male dispersal at ages of 4-6 years (Best 1979, Richard *et al.* 1996a), may be too low. The possibility remains that males disperse, on average, at ages above 10 years (the value used in the models). If this is the case, then both ppo and r may be slightly underestimated in the simulations, which would suggest that the real units are even more different from the predicted matrilineal/matrilineal + transfers structure than is shown in these analyses.

Estimates of age-specific fecundity based on whaling data are expected to be more accurate than estimates of mortality, since the exclusion of animals under the legal catch size would not be expected to introduce biases into the collection of females of various reproductive states, whereas mortality estimates were based on size/age distribution, and would be biased by the exclusion of small animals. Relatedness within units would be expected to be lower than that in the simulated datasets if the reduced fecundity observed in the Galápagos area has persisted for longer than the 10-30 years modeled. The supposed cause of this reduction in fecundity, the depletion of mature males, was first detected between 1976 and 1981 (Ramirez 1989), and no clear reduction in numbers of large males is apparent in catch statistics for 1947-1961 (Saetersdal *et al.* 1963). Thus it

seems reasonable to conclude that reduced female fecundity is a relatively recent occurrence, and that the simulations are likely to approximate reality reasonably well.

The assumption of the model which is most open to question is the suitability of killer whale age-specific mortality data as a proxy for sperm whales. If sperm whale mortality rates are actually higher than those for killer whales, then the relatedness measures calculated using the simulation models will be overestimated, since the death of unit members would be expected to reduce numbers of living parent-offspring pairs, and to reduce average relatedness within units. As discussed by Whitehead *et al.* (1997), sperm whales in the Galápagos region do not appear to be subject to current anthropogenic mortality (exploitation, incidental capture, pollution), or to poor nutrition or disease (although the latter cannot be ruled out). Thus the main possible cause of discrepancy between sperm whale and killer whale mortality rates seems likely to be predation. Killer whales appear to have no natural predators, whereas attacks on sperm whales by killer whales have been reported (e.g. Jefferson *et al.* 1991, S. Mesnick pers. comm.). It is difficult to assess the extent to which such attacks (many of which are unsuccessful) may increase sperm whale mortality rates. As a result I would argue that use of the killer whale mortality data was an appropriate proxy for sperm whale data, with the caveat that it is possible that the adoption of these values may have led to some overestimation of measures of genetic structure within simulated units.

Another assumption which is implicit in the models is that the sperm whales in the current study had not been subject to human fishing pressure. Yet there are two ways in which past whaling might have influenced the patterns of relatedness within the units. Whales are known to travel between the Galápagos area and Peruvian coastal waters (Ramirez 1989). If members of the two units being considered ranged into these waters during the whaling years (1941-1981) then it is possible that either particular individuals were removed, thus breaking up patterns of relatedness, or that these units actually represent the permanent association of remnants of other units, from which a large portion of the membership was cropped. In both cases, unit genetic structure would be expected to be less than purely matrilineal. It is difficult to determine, from the

information available, what proportion of legal-sized group members were typically taken. Although animals commonly escaped even those whaling efforts in which attempts were made to capture entire schools (e.g. Ohsumi 1971), the cohesive nature of sperm whale groups while under attack (Caldwell *et al.* 1966, Caldwell & Caldwell 1966) makes it likely that groups which experienced whaling lost multiple members.

CONCLUSIONS

In conclusion, while it is clear that there are some relatives within at least one of the social units, neither appears to conform to a matrilineal structure. If this pattern is representative of sperm whale society as a whole, then it places a new perspective on issues such as the forces for the evolution of sociality in sperm whales, and thus has considerable implications for our understanding of sperm whale social structure. However, there are various factors which might suggest that the genetic structure of these units may not be representative of 'normal' social structure in an unexploited population. Both of these units are known to have experienced unit membership change within the last 10 years (Chapter 3). It might be argued that such changes are not very frequent, and that these units are anomalous. However, the two units involved, A2 and B, are among the most frequently identified (see Appendix 1), and as such there was a far greater potential for the detection of membership change within these units than among many of the others.

Even in the absence of the direct removal of individuals, past whaling may have disrupted normal patterns of genetic relatedness by causing a reduction in fecundity leading to increased generation times, and decreased unit growth or unit size stability. These anthropogenic impacts on unit structure may perhaps have increased pressure for amalgamation of units (on the basis of optimal size considerations). Thus, while the results for the two specific units analysed are intriguing, and somewhat surprising, their generality for contemporary units, and for the structure of units in an unexploited population, is unclear. In order for these issues to be resolved, further studies focusing on the genetic structure of sperm whale populations at the level of the unit are

recommended. While studies on a truly unexploited population may not be possible, further investigation of movement patterns of units within the eastern tropical Pacific may indicate the likelihood of units known from the Galápagos area having been impacted directly by Peruvian whaling.

CHAPTER FIVE

Patterns of association within sperm whale groups: reflections of long-term relationships and genetic relatedness?

INTRODUCTION

Grouping behaviour entails a variety of costs and benefits to individuals (as reviewed extensively elsewhere, e.g. Krebs & Davies 1987, Lee 1994). While some of these costs and benefits (e.g. predator- and food-related factors) relate to all forms of groups, from temporary aggregations to long-term stable social units, others (e.g. access to helpers for rearing of offspring) relate primarily to membership of long-term groups. Costs of intra-group competition may be mitigated by the evolution of a variety of forms of mutualism (Connor 1995): by-product mutualism, kin selection (Hamilton 1964), reciprocity (Trivers 1971) or pseudo-reciprocity (Connor 1986). While kin selection benefits require the presence of relatives, many of the other forms of mutualism are contingent on multiple interactions between a given pair of individuals. As such, mutualistic, cooperative relationships are likely to occur predominantly between long-term associates.

In many species with social structures based around long-term social units, inter-unit encounters are commonly avoided, or characterised by aggression. This lack of affiliation between social units is generally attributed to resource or reproductive competition (e.g. Cheney 1987). However, inter-unit animosity is not universal. Among, for example, sperm whales (Whitehead et al. 1991, Chapter 2), killer whales (Heimlich-Boran 1986, Bigg et al. 1990, Baird & Dill 1995), and elephants (Moss & Poole 1983), permanent social units commonly associate together. These species are all characterised by a lack of both territoriality and within-unit mating activity (although the latter has not been ruled out for killer whales - Hoelzel *et al.* 1998), thus factors which might otherwise lead to intense inter-unit competition appear to be reduced. When social units associate, there will be two distinct classes of relationship within the resultant groups. While relationships between members of the same unit are likely to be based on long-term affiliation and cooperation, and frequently genetic relatedness, these aspects of relationships between members of different units will be less strong (with the exact nature of inter-unit relationships contingent on the frequency of associations between the units). As a result, if there is intra-group competition, it is likely to be distributed unevenly, being greater between, rather than within units.

Whitehead (1989) suggests that within groups of sperm whales, individuals which forage in proximity to others may benefit by catching prey that elude their neighbours, or by gaining information about prey presence through the echolocation of nearby animals (by-product mutualism). Although Watkins & Schevill (1977) report that male sperm whales scatter as they dive, little is known of the underwater spatial organisation of foraging groups of females and juveniles. However, recent underwater footage (using a CRITTERCAM - a video camera attached to a whale) indicates that animals may remain in close proximity during dives (G. Marshall, pers. comm.). This might suggest the possibility of cooperative foraging by associating sperm whales (but see Whitehead 1989 for counter-arguments on the basis of prey mobility).

Given that groups of sperm whales contain social units within which individuals hold long-term relationships (Chapter 3), and may be genetically-related (Chapter 4), and that there appears to be the potential for cooperative or by-product benefits to accrue between animals in proximity to each other, we might predict that within groups, members of the same unit should associate preferentially.

In this chapter I address questions of relationships between individuals, and consider whether patterns of short-term association (spatio-temporal co-ordination) reflect both longer-term relationships and genetic relatedness. I will consider whether members of a unit associate more closely with each other than with other individuals present within groups. I will also present a case study (involving the two units, A2 and B, introduced in Chapter 4), that illustrates the patterns of association within a group, and address the issue of whether individuals which are more closely related show greater affiliation in the short-term.

METHODS

IDENTIFICATIONS

Photo-identification field techniques and analysis were as described in Chapter 2. All photographs assigned Arnbom's (1987) Q°3 were included in the association analyses.

RELATIONSHIP MEASURES

Long-term relationships: unit membership

The units considered in this analysis are those delineated using the techniques described in Chapter 3: individuals were determined to be members of the same unit if they were identified within 12 hr of each other on at least two occasions, with those occasions being separated by a gap of at least 30 days (unit membership and identification dates are listed in Appendix 1). Thus unit membership was determined on the basis of long-term association, and beyond the requirement that individuals be sighted on the same day, short-term association patterns were not considered.

Short-term associations

Two different measures of short-term association were considered:

1. in cluster together

    Groups of sperm whales around the Galápagos Islands typically forage in rank formation, with individuals spread out over hundreds of metres or a few kilometres, aligned perpendicular to the direction of travel (Whitehead 1989, pers. obs.). During their surface intervals between foraging dives, individual sperm whales are found in 'clusters' - defined as animals which are within 100 m of each other, showing co-ordinated behaviour (Whitehead & Arnbom 1987). In practice, animals within a cluster generally swim parallel to and within 1-2 body lengths of each other. Although individuals very occasionally join or leave clusters, membership is typically fixed throughout the 6-10 min surface interval, and cluster members generally fluke synchronously, or within a few seconds of each other (J. Christal, unpublished data). A cluster may contain a single individual, and at most includes the entire group (although this occurs almost exclusively in social contexts, when identifications are rarely obtained).

Only those clusters involving 2-6 individuals were considered in these analyses. In some cases, not all members of a cluster were identified - due to highly synchronous fluking, or poor quality photographs. All clusters from which at least two individuals were identified were included in analyses. Data on cluster membership were not available for all sightings of all units, therefore this measure is considered only for the case study of Units A2 and B.

2. identified within 10 min

For two animals to be identified within a 10 min interval, not only must their dive cycles be reasonably well-synchronised, but they must also be in fairly close spatial proximity ($< \sim 1000$ m), in order for the research vessel to approach both animals and obtain identification photographs. Thus identification within 10 min indicates close temporal and spatial coordination. In practice, many of the associates identified within this time interval would have been clustered.

For both association measures, the sampling period of two hours was selected, as a compromise between two opposing factors. The longer the sampling period, the greater the probability of artificial lumping of separate groups seen on the same day. However, short sampling periods increase the potential for autocorrelation between samples due to sequential associations between individuals (i.e. if surface intervals remain synchronous over several dive cycles). Two individuals identified in association (according to either of the association measures), on a single occasion within a two hour sample, were considered to be associated within that sample, but no weighting was given to multiple instances of association within a sample.

Association indices

The commonly-used association indices (e.g. half-weight, twice-weight, simple ratio - Cairns & Schwager 1987) were determined to be unsuitable for the broader analysis of associations within units versus between unit members and other whales. The

denominators of these indices all include the number of samples in which either animal of a pair was identified – regardless of whether the other animal was also identified. In order to be recognised as a member of a unit, an individual must have been identified in at least two identification periods, separated by at least 30 days (Chapter 3) – yet by definition, non-unit members must not have been identified during more than one of the identification periods for that unit (otherwise they would have considered to be members of that unit). Thus use of these standard indices introduces a bias, since the probability of a particular unit member being identified in the absence of a given non-unit member is greater than that of that unit member being identified in the absence of another member of its unit. In order to avoid this bias, a custom association index was used for this analysis. Using the notation of Cairns & Schwager (1987), where:

x = number of samples in which A and B were associated

y_{ab} = number of samples in which A and B were both identified, but were not associated

this index is: $$\frac{x}{x + y_{ab}}$$

Thus this association index measures the frequency of association between two individuals, over only those samples during which both individuals were identified.

The simple ratio association index (Cairns & Schwager 1987) was selected for use in the case study, following Ginsberg & Young (1992). The problems described above are not present here, since, with only minor exceptions, all individuals were known to be present on all days.

Symmetric association matrices were produced using SOCPROG 1.1, a series of programs developed in MATLAB 5.1 by Hal Whitehead (programs available at http://is.dal.ca/~whitelab/index.htm).

For the broader analysis, all identifications of all members of a specific unit, and of animals identified on the same day as any unit member(s) were considered. For the case study, the identifications considered were those collected during a 7 day period in 1995 (28 May - 3 June) when Units A2 and B were observed continuously, in the absence of any other females/juveniles.

Genetic relatedness

The analysis of genetic relatedness within and between Units A2 and B is described in detail in Chapter 4. Genetic data were available for 3 of the 5 members of Unit A2, and 12 of the 17 members of Unit B. Pairwise estimates of the coefficient of relatedness, r, were calculated on the basis of microsatellite genotypes at 10 variable loci, using Relatedness 5.02 (Queller & Goodnight 1989, program available at http://www-bioc.rice.edu/~kFg/Gsoft.html). Average linkage cluster analyses of the pairwise estimates of r for the whole group and for Units A2 and B separately are shown in Figures 4.4, 4.3 and 4.2 respectively.

ANALYSIS OF CORRELATIONS BETWEEN RELATIONSHIP MEASURES

For the broad analysis, the general direction of differences between mean pairwise association indices for 'within unit' pairs versus 'between unit and other' pairs (i.e. between a unit member and any non-unit group member) was tested, over all units, using a sign test. This test considers the relative numbers of positive and negative differences between the two means, using units as cases. Given no association preference in either direction, the numbers of positive and negative differences should be equal. A sign test indicates the significance of any deviations from equality.

For the case study, matrices of relationship measures were compared using Mantel tests (Mantel 1967). The significance of the Mantel statistic was tested by means of a Monte Carlo test, using 1000 random permutations, as recommended by Schnell et al. (1985).

Two specific questions were addressed: Do individuals associate preferentially with members of their own unit? Do the association rates of pairs of individuals correlate with genetic relatedness?

RESULTS

SHORT-TERM ASSOCIATIONS VERSUS UNIT MEMBERSHIP

All units

For 16 of the 19 units, the mean pairwise 'within unit' association index was greater than that for 'between unit and other' pairs (Table 5.1), indicating an association preference for members of one's own unit (the magnitude of which varied between units). The three exceptions share no obvious features that distinguish them from the other units, and in two of these cases (F and M), the negative difference is small. The direction of the association preference was significant over all units (sign test, $n = 19$, $p = 0.004$).

Table 5.1. Comparison of mean pairwise association (10 min) within units versus between members of specific units and other individuals. 'Direction of difference': mean 'within unit' index minus mean 'between unit and other' index.

unit	mean pairwise association index		% difference	direction of difference
	within unit	between unit and 'other'		
A	0.342	0.219	56.16	+
B	0.386	0.190	103.16	+
C	0.500	0.183	173.22	+
D	0.248	0.190	30.53	+
E	0.439	0.406	8.13	+
F	0.350	0.362	-3.31	-
G	0.191	0.137	39.42	+
H	0.667	0.325	105.23	+
I	0.417	0.330	26.36	+
J	0.323	0.201	60.70	+
K	0.292	0.220	32.73	+
L	0.381	0.171	122.81	+
M	0.500	0.518	-3.47	-
N	0.578	0.115	402.61	+
O	0.130	0.231	-43.72	-
P	0.676	0.360	87.78	+
Q	0.491	0.198	147.98	+
R	0.331	0.226	46.46	+
S	0.340	0.299	13.71	+

Case study: A2+B

A total of 79 clusters (size 2-6, mean = 3.05) were included in the analysis. Each of the 22 group members was identified in 3 to 15 of these clusters (mean = 9.182). Members of the group showed a significant preference for clustering with members of their own unit (Table 5.2, Figure 5.1). This preference was also significant for the < 10 min association measure.

Table 5.2. Comparison of short-term association indices within and between units: matrix correlation (*r*) and significance of Mantel tests (p). Numbers of pairwise relationships within each category are given in parentheses.

association measure	mean pairwise association index			*r*	p
	within A2 (10)	within B (135)	between A2 and B (85)		
clustered	0.254	0.066	0.014	0.376	<0.001
< 10 min	0.197	0.078	0.052	0.209	0.003

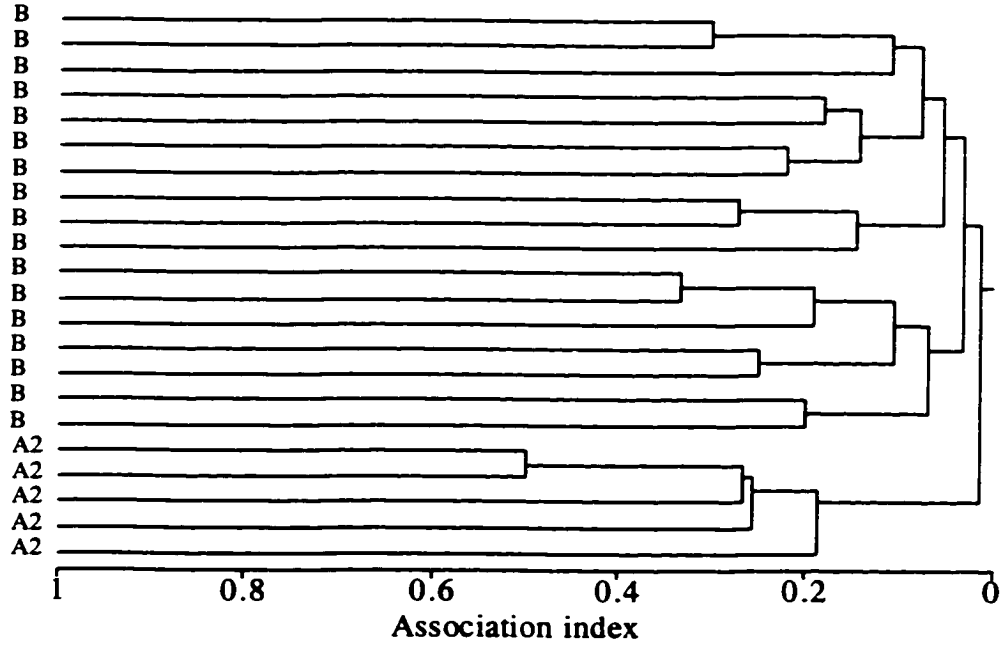

Figure 5.1. Average linkage cluster analysis of the association matrix for the 'in cluster together' association measure, for members of units A2 and B.

SHORT-TERM ASSOCIATIONS VERSUS GENETIC RELATEDNESS

There was no significant correlation between genetic relatedness and unit membership (r = -0.185, p=0.063), reflecting the existence of probable paternal half-sib relationships between members of the different units (see Figure 4.4). Mantel tests were performed for both the whole group (for the 15 members for which genetic data were available), and Unit B only (for the 12 members for which genetic data were available). Given the limited amount of data available for Unit A2 (genetic data for 3 of 5 members), a Mantel test was not appropriate. There was no apparent correlation between patterns of short-term association and genetic relatedness within the group as a whole (Table 5.3), or within Unit B alone (Table 5.4), although in the latter case the observed correlation did approach significance.

Table 5.3. Matrix comparisons of short-term measures of association with genetic relatedness (whole group): matrix correlation (r) and significance of Mantel tests (p).

association measure	r	p
clustered	0.082	0.185
< 10 min	0.029	0.398

Table 5.4. Matrix comparisons of short-term measures of association with genetic relatedness (Unit B only): matrix correlation (r) and significance of Mantel tests (p).

association measure	r	p
clustered	0.190	0.063
< 10 min	0.137	0.151

DISCUSSION

PATTERNS OF ASSOCIATION WITHIN GROUPS

The results of these analyses indicate that individual sperm whales within groups associate preferentially with members of their own unit. This preference is apparent not only in terms of cluster membership (Table 5.2, Figure 5.1), but also in the looser

(< 10 min) measure of spatio-temporal proximity (Tables 5.1 and 5.2). These findings indicate that the spatio-temporal distribution of individuals within a group of sperm whales is not random – those individuals that hold long-term relationships (i.e. are members of the same unit) are more likely to be close together, and to exhibit synchronised diving behaviour.

The apparent segregation of social units within groups of sperm whales contrasts with reports for other species. Within groups of elephants and killer whales, individuals from associating social units (family groups and pods respectively) are described as mixing freely (Moss & Poole 1983, Osborne 1986, R. W. Baird pers. comm.). However, I am not aware of any studies in which the extent of segregation or inter-mixing of social units has been explicitly examined, as it has in this study. The inter-mingling of social units (family groups) among elephants may reflect the fact that particular family groups show association preferences for other family groups which are known or presumed to share a common ancestry (Moss & Poole 1983). Thus when family groups aggregate, even those individuals which are members of different families have relationships based on repeated associations, and are more closely related than would be members of two randomly-selected family groups. However, within killer whale communities, inter-pod associations appear to be more random (Bigg et al. 1990), and do not seem to reflect recent common ancestry (where common ancestry is indicated by similarity of vocal dialects - Ford 1991). Evidence for between-unit association preferences among sperm whales is equivocal. Given the methods used for delineation of units (Chapter 3), if there are strong and consistent association preferences, then two or more units might have been lumped and considered a single unit. However, some of the units reported in this study have been identified in association with as many as seven other known units (J. Christal, unpublished data), suggesting that if preferences do exist, they may be diffuse or non-exclusive. Further arguments relating to the existence of between-unit association preferences, in the context of group-specific characteristics found in previous studies (vocal dialects - Weilgart & Whitehead 1997, fluke-markings - Dufault & Whitehead 1998, genetics - Dillon 1996, Richard et al. 1996a), are raised in Chapters 4 & 7.

PATTERNS OF ASSOCIATION WITHIN UNITS

No correlation was found between short-term patterns of association and genetic relatedness within a unit (Table 5.4), suggesting that close relatives do not affiliate preferentially (the same result was found at the level of the group, Table 5.3). Such an association preference might be expected on the basis of inclusive fitness, if short-term spatio-temporal association confers mutualistic benefits, and has been reported for several primate species (Yamada 1963, Rosenblum et al. 1966, Pusey 1983). The fact that no significant correlation was found between short-term affiliation and genetic relatedness may reflect a number of factors. Firstly, this analysis was based on behavioural data over a single week, within a single unit, and not all unit members were represented. Hence, such a correlation might have been present, but was not detectable using the available data. Secondly, sperm whales are long-lived, thus genetic relatives may hold relationships over decades. Therefore details of affiliation patterns over periods of a few days may be irrelevant in relation to lifetime relationships. As such, this was not a particularly powerful test for affiliative relationships among relatives, although it does represent the first time that such an analysis has been possible for sperm whales.

POTENTIAL BIASES

In the broad analysis of association patterns, there is one main factor which had the potential to introduce biases. This is the problem of multiple groups. If members of two separate groups (one of which contains a known unit) are identified within a given sampling period, then members of the group which does not include the unit of interest will be considered to be 'others' (i.e. potential associates of the unit members), and included in analyses. Since groups are by definition separate entities, the probability of association between members of the unit and members of the other group, using a short-term measure (i.e. identified within 10 min), is effectively zero. Thus false inclusion of members of other groups would bias the mean pairwise 'between unit and other' index downwards, hence artificially increasing the difference between 'within unit' and 'between unit and other'. While the selection of a two hour sampling period would seem

likely to have minimised this problem, it is possible that residual effects remain. While such effects may have introduced a slight bias in particular cases, it does not seem likely that this bias would have been of sufficient frequency and magnitude to explain the widespread lower values for mean 'between unit and other' indices. This bias is not an factor in the results presented for the case study, since no other groups were seen during the week-long encounter with the group considered.

CONCLUSIONS

These findings suggest that patterns of association within groups, and particularly patterns of clustering, reflect long-term relationships within units, although correlations with genetic relatedness are not apparent. The delineation of units is a complex procedure, requiring multiple sightings of individuals over periods of months or years (Chapter 3), and the questions raised by the results in this thesis clearly indicate that the unit is the level of sperm whale society on which future research should focus (Chapters 3 and 4). The analyses in this chapter suggest that patterns of short-term association over periods of days may be used to infer unit membership, and perhaps to increase sample sizes for future behavioural or genetic analyses, by facilitating the delineation of putative social units.

CHAPTER SIX

The abundance and behaviour of large male sperm whales around the Galápagos Islands

INTRODUCTION

Historical and modern whaling records provide a wealth of information on distribution, morphology, physiology and reproductive status of male sperm whales (e.g. Best 1969, 1970), but it is only since the advent of non-invasive research (Whitehead & Gordon 1986) that it has been possible to study the behaviour and associations of individuals in detail. Research has focused primarily on groups of females and juveniles (e.g. Gordon 1987b, Whitehead *et al.* 1991), and the social structure of males remains among the least understood aspects of sperm whale biology. Studies are currently underway in Norway (Lindhard & Strager 1989, Erland Lettevall pers. comm.), New Zealand (Childerhouse *et al.* 1995) and Canada (Whitehead *et al.* 1992a), but information on the behaviour and sociality of male sperm whales on breeding grounds is limited (Whitehead 1993).

Males disperse from their natal social units before attaining sexual maturity. Estimates of the age of dispersal are highly variable (4-5 years - Best 1979, 6 years (95% confidence interval: 2.7-10.9 years) - Richard *et al.* 1996a, starting at 12 years of age - Ohsumi 1966, 15-21 years - Rice 1989), but most authors agree that dispersal occurs prior to puberty (defined as the age at which 50% of individuals have spermatozoa in the testes), which occurs at approximately 19 years of age (Best 1970). Males attain sexual maturity (defined as the age at which 50% of individuals have fully mature testes) at an average age of 26 years (Best 1969), although physical maturity does not occur until at least the age of 35 years (Best 1970). Dispersing males form 'bachelor schools', and are found in increasingly smaller groups and at higher latitudes as they grow larger (Best 1979). The largest males tend to be solitary and can be found in polar waters (Clarke 1956). Sexually mature males migrate back to warmer waters to breed (Best 1979). There is little information on the durations of, or intervals between, these migrations.

In contrast to the long-term, highly social units of female sperm whales and their juvenile offspring (Whitehead *et al.* 1991 and Chapters 3-5), relationships between males seem much less strong and durable. While loose associations (Caldwell *et al.* 1966) and relatively frequent 'grouping' of males (within 200 m of each other) (Childerhouse *et al.*

1995) have been reported from higher latitudes, no repeat associations between identified males over more than a few hours have been found previously in temperate waters (Whitehead *et al.* 1992a), or on the Galápagos breeding ground (Whitehead 1993).

On the breeding grounds, mature males rove between groups of females, spending only hours or days with each (Whitehead 1993). The nature of relationships between males on the breeding ground is unclear. Although more than one mature male may be seen with a particular group of females at the same time (Best 1979, Rice 1989, Whitehead 1993), evidence suggests that male sperm whales may avoid each other when around groups of females, perhaps by listening for the distinctive 'slow clicks' that mature males characteristically make (Weilgart & Whitehead 1988, Whitehead 1993). Watkins *et al.* (1993) suggest the existence of dominance interactions between large males.

Although previous research and observations suggest little in the way of affiliative relationships between maturing or mature male sperm whales, mass strandings of two or more large males have been recorded (Bryant 1979, Lucas & Hooker 1997, Reeves & Whitehead 1997, Jauniaux *et al.* 1998). This suggests some form of cohesive social structure among males which has yet to be detected by boat-based studies focusing on spatial scales of tens of metres.

In this chapter I discuss the numbers, associations and aggregative behaviours of mature males on the Galápagos Islands breeding ground, focusing in particular on the behaviour of males identified in 1995 and 1997.

METHODS

FIELD RESEARCH

All research and identifications occurred in the Galápagos study area (1°30' S - 1°30' N, 89° - 92°30' W, Figure 2.1). Although this chapter refers back to the earlier research seasons (see Table 2.1 for dates and details), the aggregative and associative behaviours

described occurred exclusively during two research seasons: 6 April - 4 June 1995 (39 days of effort, large males (see definition below) sighted on 10 days) and 1 April - 25 May 1997 (44 days of effort, large males sighted on 13 days). Anecdotal data is included from 1993 (WCI Odyssey expedition), but since data collection methods were not analogous, these data were not incorporated in analyses. Additional identifications were obtained in both 1996, and 1998 (April/May – not included in Table 2.1) by Godfrey Merlen, but behavioural records were not collected at these times.

Searching and tracking methodology, photographic techniques and photo-identification analysis are described in Chapter 2. Only identification photographs of Q≥4 (Arnbom 1987) are considered to be of sufficient quality to ensure certainty of identification of individuals between years. However, identifications of Q≥3 are considered adequate for the re-identification of an individual within a research season. Thus Q≥3 identifications and the data relating to them are used throughout this chapter, with the exception of matching of individual identifications between years. In our database, large males are given identification numbers in the range #500 - #599.

DEFINITIONS

The following definitions are used throughout this chapter:

I define 'large male' as any distinctively large (>12m) sperm whale. Since female sperm whales in the Galápagos study area rarely reach 11m in length (Waters & Whitehead 1990a), any animal estimated to be 12m or more in length can reliably be considered to be male.

A 'sighting' is a visual observation of a single large male at the surface (thus an observation of two large males together at the surface constitutes two sightings), and is considered to terminate when that individual submerges or dives.

An 'aggregation' is defined as a number of large males (at least 2) being present in the same general area (within a few km of each other) on the same day. The minimum number of mature males present in any given aggregation was estimated from the maximum value for any of the following criteria: (1) total number of large males individually identified ($Q \geq 3$) on that day. (2) Number of fluke-ups observed within a 30 minute period. Since dive cycle times of sperm whales are generally greater than 40 min (Papastavrou *et al.* 1989, and Figure 6.4, any two or more fluke-ups within this time period can be attributed to different individuals. (3) The sum of the number of large males visible at the surface and the number of individuals known or believed to be male heard on the directional hydrophone at the same time. In many cases, the expected distance (and therefore click 'volume') and direction of all the large males recently seen at the surface were known, so that specific vocalisations could be attributed to specific large males with a reasonable degree of confidence. When small numbers of individuals are present, the exact number can be estimated from the patterning of clicks. Off the Galápagos, female and juvenile sperm whales are never found alone or in small groups of 2 to 3 (Whitehead & Weilgart 1991), therefore individuals heard clicking alone or in pairs could justifiably be considered male.

'Cluster' and 'clustering' are used in exactly the same sense as for female and juvenile animals (Chapter 5). Two or more whales swimming at approximately the same speed and in the same direction, within 100 m of each other, are considered to be a cluster, or to be clustered (Whitehead & Arnbom 1987).

A variety of surface active behaviours were recorded. A 'breach' is a leap from the water, with at least half of the body visible above the surface (Waters & Whitehead 1990b). A 'spy-hop' is the slow raising of the whale's head above the water surface (Whitehead & Weilgart 1991). A 'lob-tail' involves the flukes being raised above the water and then thrashed down onto the water surface (Waters & Whitehead 1990b). 'Side-fluking' occurs when one fluke is seen oriented vertically but moving horizontally above the water surface (Whitehead & Weilgart 1991).

LENGTH MEASUREMENT AND AGE ESTIMATION

Body length can be converted to an approximate age estimate using age-length keys (e.g. Rice 1989), and thus gives an indication of the maturity of an individual. In 1995, the body lengths of large males were estimated visually whenever possible, and measurement photographs were taken from a known height above the sea surface, allowing total length to be estimated using the methods of Gordon (1990) and Waters & Whitehead (1990b). Estimates of length from different photographs of the same whale were averaged. In 1997, photographic measurement was not possible because of the nature of the research vessel, and visual estimates for individual animals were not made.

BEHAVIOUR AND LOCATION RECORDING

In both 1995 and 1997 the behaviour and locations of large males in relation to each other were studied. During sightings with whales, the exact times (to the second) of surfacings, surface active behaviours and fluke-ups were recorded whenever possible. In addition, the estimated distance and compass bearing from the boat, and direction of heading (in degrees) were recorded. In 1995 these data were recorded each minute, using a Toshiba 2000 Sxe laptop computer and a specially-written QuickBasic program, for a focal whale or cluster of whales, and for all other clusters within 1000 m of the focal whale(s). In 1997, efforts were made to record this information for all visible whales (visual range was approximately 5000 m, given the height of the observer above the sea surface), and data were therefore recorded less frequently for particular individuals. In both years, direction of heading at fluke-up was recorded on all occasions when it could be ascertained, and when there had been no submergences or sudden changes of direction (which could represent avoidance of the research vessel and result in altered heading). Recording sessions terminated when the last individual fluked-up, or when no whales were observed at the surface for 2-3 min (i.e. an animal submerged without fluking up, and a resurfacing could not reliably be assigned to the same individual).

ASSOCIATIONS

Associations between individual large males were examined at a variety of temporal and spatial scales. Individuals identified on the same day were considered to be members of the same aggregation. Individuals identified within 2 hours of each other were considered to be reasonably closely spatially associated, since the distance which the research vessel moved during 2 hour periods while actively engaged in photo-identification work was small, on the order of ~2-8 km. Individuals identified within 10 min of each other were considered to be closely associated. In order to be identified within this interval, two animals must not only be fairly synchronised in their diving patterns, but also be within approximately 1 km of each other in order for the research vessel to be able to approach and photograph the second, having photographed the first. Clustering of two males represented the closest level of association.

DIVE DURATIONS

The frequency and duration of dives give some indication of the general behaviour (e.g. socialising or foraging) of sperm whales. Three aspects of the diving pattern of large males were examined. Surface interval is the exact time spent at the surface, from initial surfacing to fluke-up (surface intervals involving shallow dives (submersion for periods exceeding 30 s) and/or avoidance behaviour (apparent disturbance by the research vessel) were excluded). Dive cycle duration is the interval between two subsequent fluke-ups by the same large male (photographically-identified at both fluke-ups). Dive duration is the period between a fluke-up and surfacing by the same identified large male. For both dive cycle duration and dive duration, any intervals in which there was an intervening fluke-up by an unidentified whale (which could therefore have been the 'target' male) were excluded. Since fluke-up times can be collected more systematically than surfacing times, the majority of diving pattern data will concern dive cycle durations.

FEEDING SUCCESS

As whales fluked-up, the presence or absence of faeces was recorded whenever possible. These data are used to provide an indication of feeding success (for detailed methodology and justification see Whitehead (1996) and Smith and Whitehead (1993)).

RESULTS

SIGHTINGS, IDENTIFICATIONS AND ABUNDANCE

Sightings

Large males were sighted on 56 days during major field studies. The sighting rate (days large males sighted per day of effort) was comparable between years when large males were observed exclusively in association with females/juveniles (1985-1991), and years when large males were observed in aggregations (1995, 1997), although numbers of sightings were considerably higher both overall, and per day in the latter years (Table 6.1).

Table 6.1. Sightings of large males (major field studies only).

year(s)	# days effort	# days large males sighted	sighting rate[1]	# sightings	mean # sightings per day[2]	mean # identified (Q≥3)/day[3]
1985	31	10	0.32	26	2.60	1.30
1987	61	10	0.16	39	3.90	1.40
1989	22	11	0.50	30	2.72	1.00
1991	17	2	0.12	4	2.00	1.00
1995	39	10	0.26	62	6.20	2.17
1997	44	13	0.30	223	17.15	2.92
1985-1991	131	33	0.25	99	3.00	1.21
1995-1997	83	23	0.28	285	12.39	3.00

[1] number of days large males sighted per day of effort.
[2] calculated for those days on which large males were sighted.
[3] calculated for those days on which at least one large male was identified (Q≥3).

Identifications

Fifty-four large males were identified in the Galápagos study area with Q≥4 between 1985 and 1997 (170 identification photographs). The number of large males identified in 1997, 25, was remarkably high, being equivalent to the total number of large males identified during the preceding 9 research seasons (Figure 6.1).

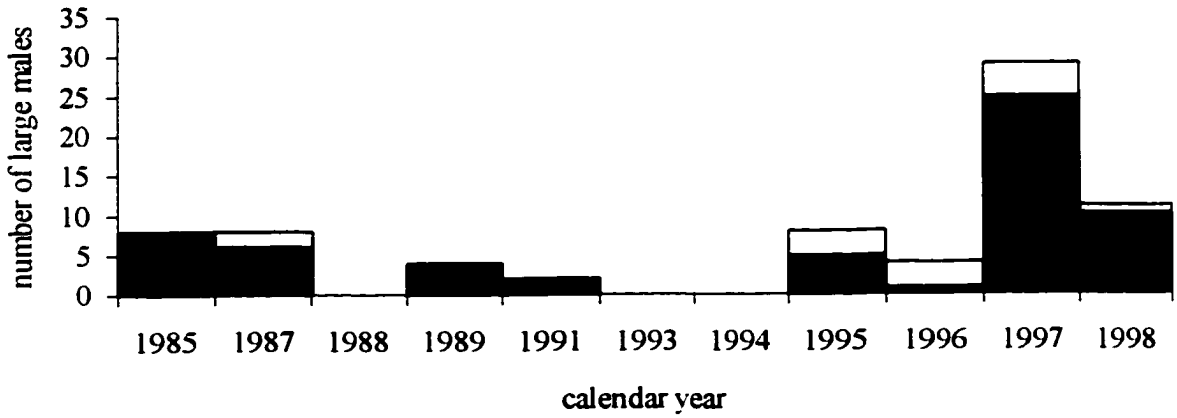

Figure 6.1. Number of large males identified in the Galápagos study area for each calendar year in which research occurred. The black bars represent the number of large males identified from high quality (Q≥4) photographs, the white sections represent those large males for which only good quality (Q3) identifications were made.

Re-identifications

Six of the 54 large males were identified in two or more different years (Table 6.2). Prior to 1995, there had been only one male identified in multiple years (#507 – over an interval of 6 years – Whitehead 1993). However, since 1995, five other large males have been identified in multiple years, over intervals of one to two years. There were no re-sightings of males between the earlier years of the study (1985-1991) and more recent years (1993-1998). Discussion of the issue of seasonality of re-sightings is limited by the seasonality of the research. However, of the four sightings of #538, three were in April/May, but the other (1993) was in October, suggesting that presence in the area may not follow strictly annual cycles, at least in some cases.

Table 6.2. Multi-year re-sightings of individual large males.

ID	1985	1987	1988	1989	1991	1993	1994	1995	1996	1997	1998
507	✓				✓						
538						✓		✓		✓	✓
540								✓		✓	✓
546									✓	✓	✓
548									✓	✓	
555										✓	✓

Thus 11.1% of males ever identified (Q≥4) were identified in two or more years. In comparison, 16.7% of the 1333 females/juveniles identified (Galápagos study area only, Q≥4) were identified in two or more years (Chapter 2). There was no significant difference in the proportion of animals re-sighted between years when males are compared to females/juveniles ($\chi^2 = 2.639$, 4 d.f., $0.75 < p < 0.5$), suggesting that large males are no less likely than females/juveniles to return to the Galápagos study area over periods of years.

No identification photographs of mature males have matched to juvenile animals previously identified in Galápagos, or elsewhere. This was not unexpected, since males appear to spend a number of years at higher latitudes following dispersal from their natal units, before attaining socio-sexual maturity (at age ~25-27, Best 1969) and returning to the breeding grounds. The duration of this interval is unclear, since estimates of age at dispersal vary greatly between authors (from 4 years up to 21 years, e.g. Best 1979, Richard *et al.* 1996a, Rice 1989), but it seems quite possible that the average interval between dispersal and return to the breeding grounds may exceed the 13 year span of our data.

No large males identified in the Galápagos study area have matched to males identified in other regions of the South Pacific. Numbers of males identified in several other regions are very small (two off the mainland of Ecuador (1000 km to the east), two near the Christmas Islands (7300 km to the west), one near the Phoenix Islands (9000 km to the

west) and two near Tonga (9200 km to the west south west) (S. Dufault and H. Whitehead, unpublished data), and the lack of matches is therefore unsurprising. There were also no matches (J. Christal, unpublished data) between males identified in the Galápagos area and the 136 males identified at Kaikoura, New Zealand (12000 km to the south west) by Steve Dawson and colleagues (Childerhouse *et al.* 1995, N. Jaquet unpublished data).

Abundance

Prior to 1997, large males represented 1.87% of the identified (Q≥4) population of sperm whales using the Galápagos study area (25 large males, 1309 females/juveniles). With the addition of the 1997 and 1998 data this percentage increased considerably, to 4.03% (54 large males, 1341 females/juveniles), although large males still formed a very small fraction of the population. The relative abundance of large males, as a percentage of the total number of individuals identified (Q≥4) per calendar year, increased from <3% prior to 1995 to a high of 51% in 1997 (Figure 6.2). The absolute abundance of large males clearly increased dramatically in 1997.

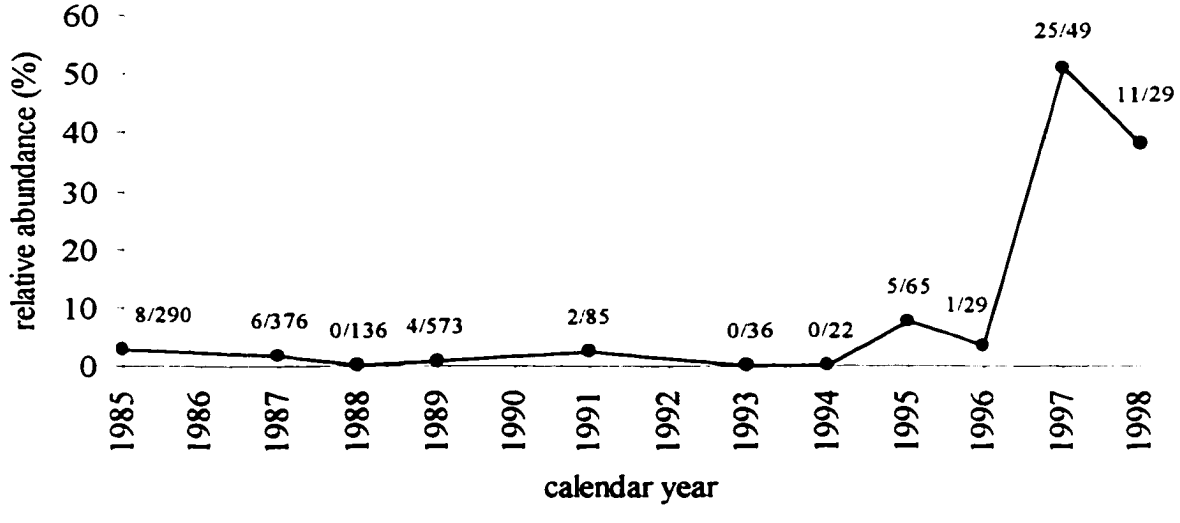

Figure 6.2. Relative abundance of large males, as a percentage of the total number of individuals identified (Q≥4) in the Galápagos study area in each calendar year. Figures over the data points represent 'number of large males / total number of individuals'.

Numbers of individuals, and of re-sightings between years, were insufficient for any meaningful estimation of large male 'population size' (i.e. the total number of males visiting the Galápagos study area).

LENGTH MEASUREMENT AND AGE ESTIMATION

In 1995, good quality measurement photographs were obtained for only two males, #538 and #540 (both of which were also identified in 1997). Number 538 was measured to be 12.33 m (n = 4) in length, indicating an age in the early twenties (estimated from growth curves in Rice 1989), and suggesting that this animal might not have attained sexual maturity (Best 1969). Number 540 was measured to be 16.27 m (n = 2) in length, a size which indicates that the animal was probably at least 30 years old and both sexually and physically mature (Best 1969, 1970, Rice 1989). Visual estimates for these two individuals were 13.5 m and 15 m respectively. All visual estimates of the lengths for three of the other identified individuals were in the range 13-15 m, indicating that these were probably mature animals. Although neither length measurements nor individual length estimates are available for 1997, three experienced observers agreed that all animals were at least 12 m in length, indicating that these animals were probably sexually, if not necessarily physically, mature.

RESIDENCY

Prior to 1995, mean known residency of large males (span from first day of identification to last day of identification) over all years was 14.5 days (n = 22). When individuals identified on only one day are excluded, mean known residency was 25.8 days (n = 11). In 1995 and 1997, when large males were observed in aggregations, mean known residency was 5.0 days (n = 22), with mean known residency of 11.9 days (n = 8) for large males identified on more than one day. These differences may reflect the relative duration of fieldwork effort in different years. Maximum known residency was similar both pre-1995 (36 days) and in 1995/1997 (40 days).

LARGE MALES AND GROUPS OF FEMALES/JUVENILES

The increase in numbers of sightings of large males (Table 6.1) was concurrent with a decrease in encounters with groups of females/juveniles (in this context, encounter rate is defined as the number of groups encountered per hour of acoustic searching) (Figure 6.3). This indicates that as groups of females/juveniles became more scarce, large males not only became more abundant (Figure 6.2), they also became more aggregated.

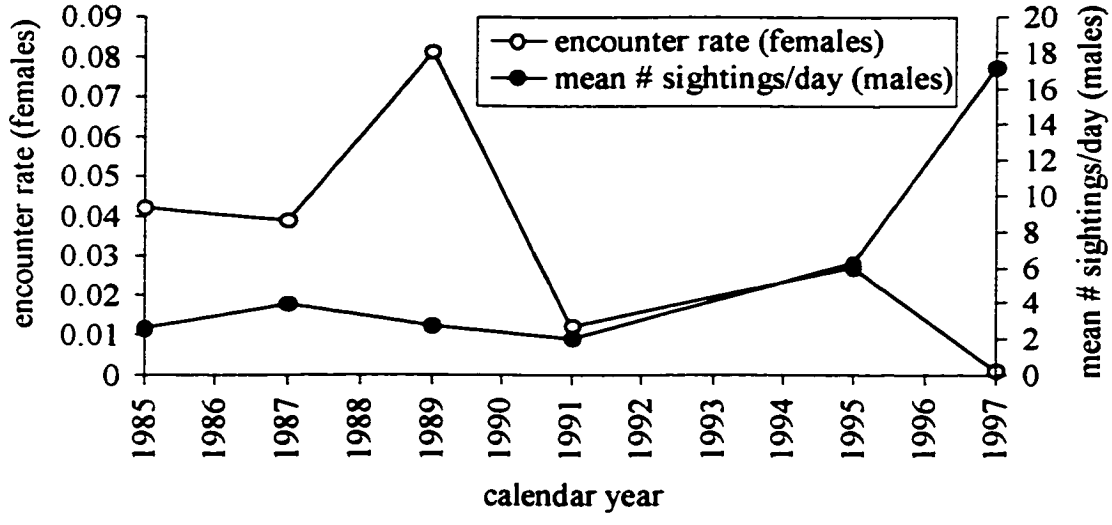

Figure 6.3. Contrasting trends in encounter rate for females (number of groups encountered per hour of acoustic searching), and in mean number of sightings per day of large males (calculated for only those days when at least one large male was identified (Q≥3)) for major field studies only.

Identification:

The proportion of days on which a large male or males were identified (Q≥3) on which females/juveniles were also identified changes dramatically over the sequence of years in which large males were identified (Table 6.3). Prior to 1995, on every day on which a large male (or males) was identified, females/juveniles were also identified, and large males were never sighted more than 2000 m or 1 hr from a sighting of females/juveniles (Whitehead 1993). In 1995, females/juveniles were identified on only one of the six days

on which large males were identified. In subsequent years, females/juveniles were never sighted on days on which large males were identified.

Table 6.3. Presence of females/juveniles on days on which large males were identified (Q≥3).

year	# days Q≥3 IDs (all)	# days Q≥3 IDs (males)	# days Q≥3 IDs (females/juveniles)	proportion of days with male(s) identified with f/j also identified
1985	31	10	31	1
1987	54	10	54	1
1989	56	11	56	1
1991	9	2	9	1
1995	21	6	16	0.167
1996	8	3	5	0
1997	16	12	4	0
1998	7	5	2	0

Association - 1995:

Although no large males were identified (Q≥3) while in association with females/juveniles in 1995, one large male was seen in association with a group of females/juveniles on two occasions. Identification photographs were of poor quality (Q2) due to film processing problems, but this animal (#545) was definitively identified in the field as being different to all other large males identified that year, and was not identified on any other occasions. Number 545 was seen in association with a group for short periods on two consecutive days. On 31 May, #545 was first seen at one end of a rank of approximately 20 females/juveniles. The large male remained at the surface for 20 min after all members of the group dived, then he dived, and was not seen again that day. On the following day (1 June), the same male was observed 400 m away from the group, but was not seen to cluster with any of the group members, and appeared to leave the area 15 min later. The remainder of the large males identified in 1995 were sighted at closest intervals of 1 hour to 5 days before or after an encounter with a group of females/juveniles

Association - 1997:

Only one group of females/juveniles was encountered in 1997. This encounter occurred at the very beginning of the research season, and no large males were sighted until 5 days after the group was lost. With the exception of this lone male (#540), all other large males identified in 1997 were identified 24 to 45 days from the encounter with the group.

AGGREGATIONS

Of the 23 days on which males were sighted in 1995 and 1997, there were only four days on which the minimum number of large males present was one (Table 6.4). Two of these days (31/5/95, 1/6/95) are the days on which a lone male was observed in association with a group of females/juveniles (see above). Aggregations of large males were observed on 19 days, with minimum sizes of aggregations ranging from 2 to 7 individuals (Table 6.4).

Aggregations were not stationary, but moved over time (e.g. Figure 2 in Christal & Whitehead 1997), and on some occasions, aggregations involving entirely, or primarily, different individuals were found in the same area on consecutive days (e.g. off Cabo Rosa, Isabela 4/5/97 - 5/5/97 and 11/5/97 - 12/5/97; Banks Bay 14/5/97 - 15/5/97) (Table 6.4, Figure 6.4). Aggregations showed little consistency of membership over periods greater than one day. This finding may be due in part to the fact that it was rare for the minimum number of males present to be identified, and in part to the relatively low numbers of large males identified on more than one day, especially in 1997 (4 individuals/year, Table 6.4).

Aggregations were generally characterised by consistency of heading. The distribution of fluke-up headings on days when at least 2 males were present, and when at least 5 fluke-up headings were recorded (Figure 6.5), clearly shows that on the majority of days, the large males were co-ordinated in their direction of travel. The trend appears to be clearer in 1995, and in the first two days in 1997, with less co-ordination in heading on the 14th,

15th and 21st of May 1997. One possible explanation for the increased variability in heading on the 14th and 15th of May 1997 is that on these days, the large males were within an enclosed bay, and thus travel in a consistent direction was not possible.

Table 6.4. Minimum numbers of males present per day, 1995 & 1997. See Figure 6.4 for locations.

date	minimum # males present	# males identified (Q≥3)	males identified	location
23/4/95	3	2	536 537	SE of Marchena
24/4/95	3	1	538	E of Marchena
25/4/95	5	5	536 538 539 540 541	S of Pinta
27/4/95	3	1	540	SE of Pinta
5/5/95	3	0		NNE of Pinta
6/5/95	3	2	538 541	NE of Pinta
15/5/95	2	0		60km WSW Roca Redonda
16/5/95	3	2	533 534	W of Banks Bay
31/5/95	1	0	(group of females/juveniles)	SW of Marchena
1/6/95	1	0	(group of females/juveniles)	S of Marchena
11/4/97	2	1	540	SE of Marchena
28/4/97	3	1	540	NE of Marchena
1/5/97	2	1	550	W of Pinta
2/5/97	1	1	550	Punta Albemarle, Isabela
4/5/97	4	2	551 552	off Cabo Rosa, Isabela
5/5/97	6	6	546 553 554 555 557 558	off Cabo Rosa, Isabela
6/5/97	3	0		off Cabo Rosa, Isabela
11/5/97	4	3	559 560 561	off Cabo Rosa, Isabela
12/5/97	3	2	548 562	off Cabo Rosa, Isabela
13/5/97	1	1	563	60km W of Elizabeth Bay
14/5/97	7	7	546 555 564 565 566 567 568	Banks Bay
15/5/97	6	5	546 569 570 571 572	Banks Bay
21/5/97	5	5	538 540 573 574 575	off Cabo Marshall, Isabela

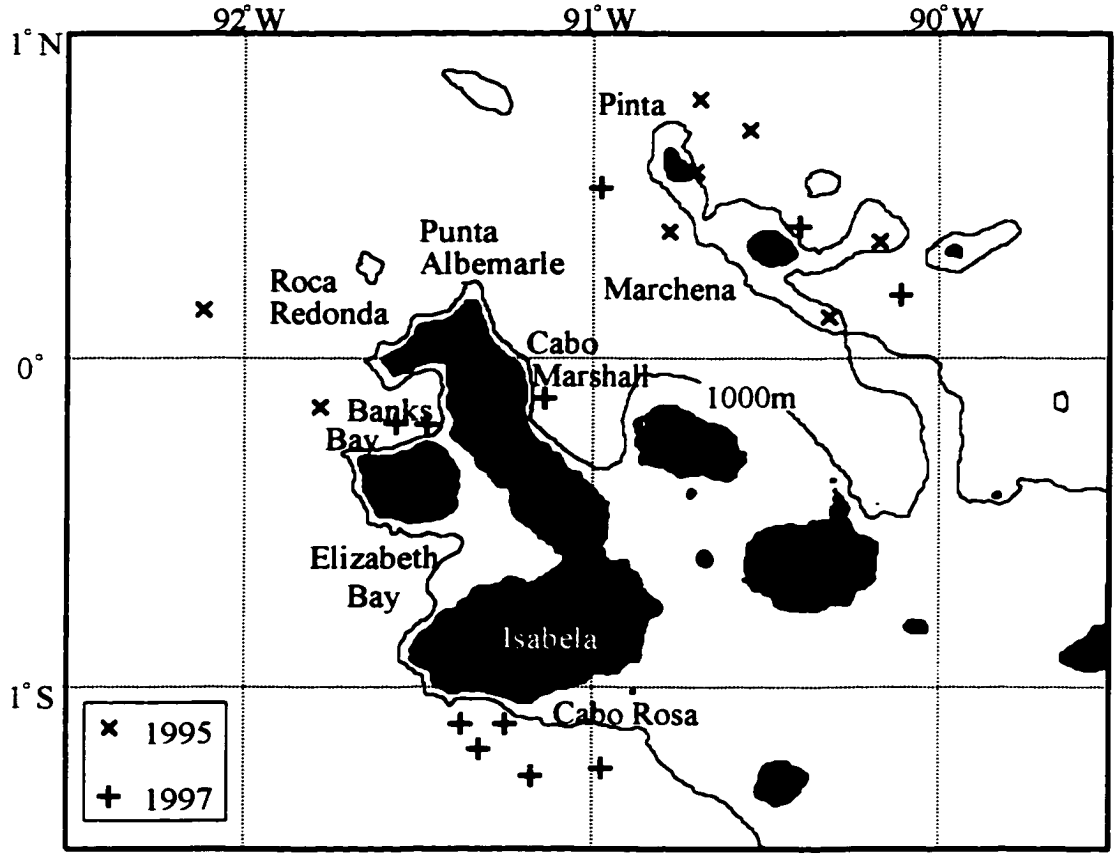

Figure 6.4. Positions of aggregations of large males in 1995 and 1997.

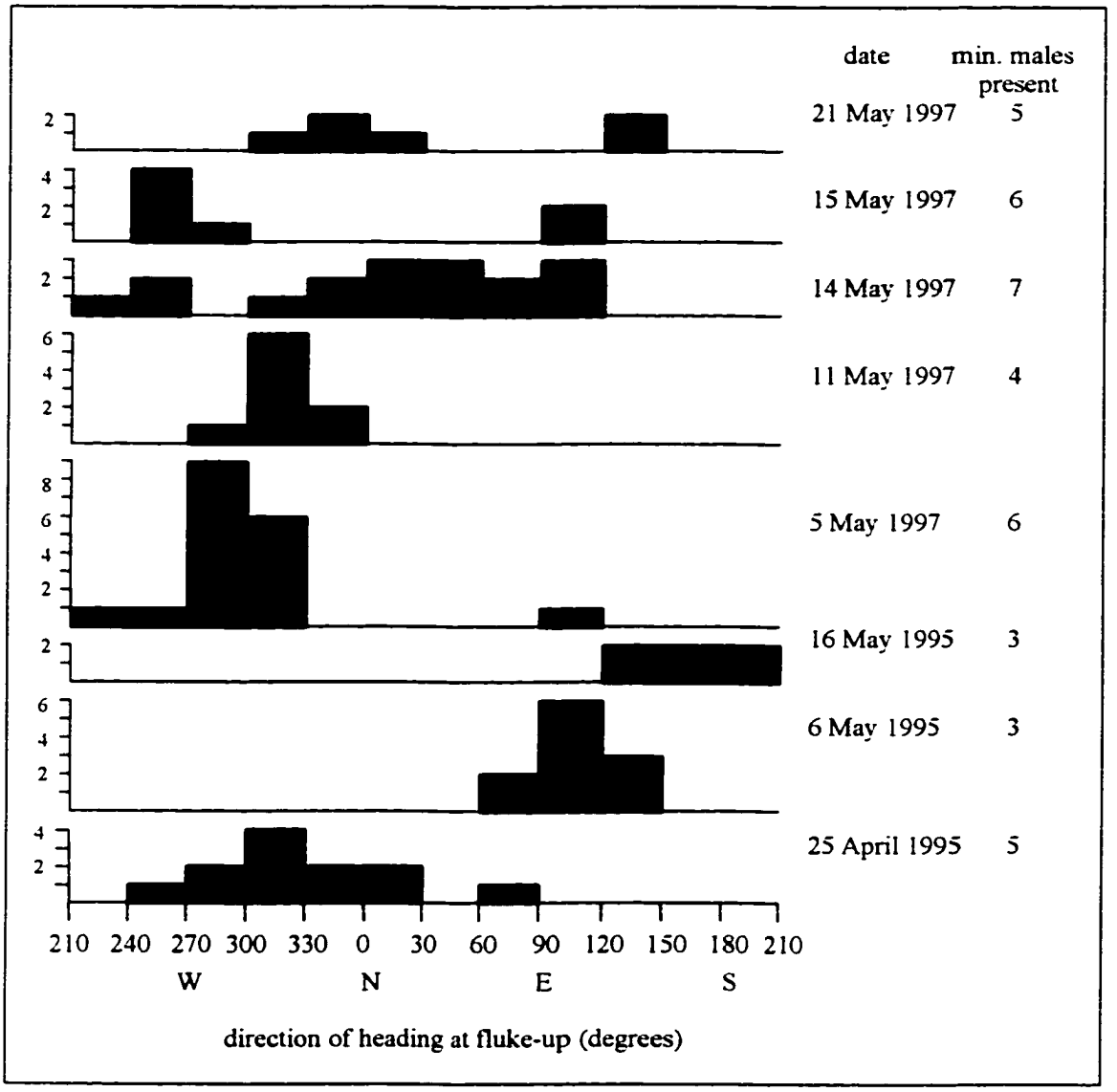

Figure 6.5. Consistency of heading of large males at fluke-up. All recorded headings are shown on those days on which at least 2 males were present, and heading at fluke-up was recorded on at least 5 occasions. Headings were excluded if the animal submerged during the surface interval, or if it showed distinct changes in heading, since either of these behaviours could relate to avoidance of the research vessel.

ASSOCIATIONS AND BEHAVIOUR WITHIN AGGREGATIONS

Associations between individual large males

Large males identified in 1995, and particularly in 1997, clearly had the potential to associate with a greater number of large males both per day (Table 6.1, mean # identified per day), and within a field season (Figure 6.1), than did those large males identified earlier in the study. This is reflected in the mean number of associates (<2hr) per individual per day and per year (Table 6.5). Large males identified in 1995 and 1997 were significantly more likely to have at least one large male associate (identified within 2 hours) than were those large males identified in earlier years (1985-1991: 18 loners vs. 4 with associates, 1995 + 1997: 6 loners vs. 31 with associates, $\chi^2 = 24.60$ 1df, $p < 0.001$).

Table 6.5. Mean numbers of associates (identified within 2 hours) of large males identified on the Galápagos Islands breeding ground.

year(s)	mean # associates per large male per day	mean # associates per large male per year
1985-1991	0.152	0.272
1995	1.229	1.750
1997	1.523	1.862

Despite the fact that in 1997 (when animals at greater distances were recorded) 43% of all recorded fluke-ups were within 10 min of a fluke-up by another male, large males were identified within 10 min of each other on only 6 occasions, four of which involved clustered males. This finding probably reflects a number of factors, but does give some indication that although males may appear to be temporally-synchronised, they are rarely close together in space. Only two large males (#570 and #572) were identified within 10 min of each other on more than one occasion. These two individuals were identified as members of a clustered pair at two consecutive surfacings 45 min apart.

Only four males in each year were identified on more than one day (Table 6.6), thus the scope for an examination of the temporal duration of associations is somewhat limited. Of those males, one was the only individual identified on both days that it was identified (#550), and two others were the only individuals identified on all but one of the days that they were identified (#540, 1995 & 1997). Thus only five males were identified with same-day associates on two or more days, and only those males could provide evidence for the temporal duration (>1 day) of associations between large males. Number 536 had no associates (same-day) in common between the two days on which it was identified. Number 538 and #541 were identified 46 min apart on 25/4/95 and 43 min apart on 6/5/95, 11 days later. Number 546 and #555 were identified 59 min apart on 5/5/97, and 2 hr 54 min apart on 14/5/97, 9 days later. In each case, one of the large males was identified on an additional day when the other was not. Although these data are somewhat anecdotal, and the two associations could simply be random re-associations after intervals of several days, it is also possible that they illustrate some form of short-term relationship between specific large males.

One further piece of evidence suggests that such relationships could persist over much longer time scales. Number 538 and #540 were identified 1 hr 7 min apart on 25/4/95, 41 min apart on 21/5/97, 25 months later, and on the same day (9/5/98) 12 months after that. Although #538 had been previously identified on the same day as three presumed males in 1993, #540 was not identified at that time.

Clusters

Prior to 1995, clusters containing two males had been observed on only 8 occasions, with one brief observation of three males in a cluster (Whitehead 1993). However, on every one of these occasions, males were not the only members of clusters. In each case at least 7 females/juveniles were also present. Large males had never been observed to cluster in the absence of females/juveniles.

Table 6.6. Associates of large males, 1995 and 1997. Associates common to 2 days within the same year are shown in **bold**. Associates common to two days in different years are shown in ***bold italic***.

male	dates identified	other males identified same day	other males <2hr	other males <10 min	other males clustered
536	23/4/95	537	537	537	537
	25/4/95	538 539 540 541	541	-	-
537	23/4/95	536	536	536	536
538	24/4/95	-	-	-	-
	25/4/95	536 539 ***540*** **541**	539 ***540*** **541**	-	-
	6/5/95	**541**	**541**	-	-
	21/5/97	***540*** 573 574 575	***540***	-	?(1)[1]
539	25/4/95	536 538 540 541	538 540	-	-
540	25/4/95	536 ***538*** 539 541	***538*** 539	-	-
	27/4/95	-	-	-	-
	11/4/97	-	-	-	-
	28/4/97	-	-	-	-
	21/5/97	***538*** 573 574 575	***538*** 573 574	-	-
541	25/4/95	536 **538** 539 540	536 **538**	-	-
	6/5/95	**538**	**538**	-	-
543	16/5/95	544	544	544	-
544	16/5/95	543	543	543	-
546	28/3/96	-	-	-	-
	5/5/97	553 554 **555** 557 558	554 **555** 557	-	-
	14/5/97	**555** 564 565 566 567 568	565 567 568	568	568
	15/5/97	569 570 571 572	570 572	-	?(3)[1]
547	22/4/96	-	-	-	-
548	23/4/96	549	-	-	-
	12/5/97	562	-	-	-
549	23/4/96	548	-	-	-
550	1/5/97	-	-	-	-
	2/5/97	-	-	-	-
551	4/5/97	552	552	-	-
552	4/5/97	551	551	-	-
553	5/5/97	546 554 555 557 558	554 555	-	-
554	5/5/97	546 553 555 557 558	546 553 555	-	-
555	5/5/97	**546** 553 554 557 558	**546** 553 554	-	-
	14/5/97	**546** 564 565 566 567 568	565 566	566	-
557	5/5/97	546 553 554 555 558	546 558	-	-
558	5/5/97	546 553 554 555 557	557	-	-
559	11/5/97	560 561	560 561	-	-
560	11/5/97	559 561	559 561	561	561

Table 6.6 continued

561	11/5/97	559 560	559 560	560	560
562	12/5/97	548	-	-	-
563	13/5/97	-	-	-	-
564	14/5/97	546 555 565 566 567 568	-	-	-
565	14/5/97	546 555 564 566 567 568	546 555 566	-	-
566	14/5/97	546 555 564 565 567 568	555 565	555	-
567	14/5/97	546 555 564 565 566 568	546 568	-	?(1)[1]
568	14/5/97	546 555 564 565 566 567	546 567	546	546
569	15/5/97	546 570 571 572	-	-	-
570	15/5/97	546 569 571 572	546 571 572	572 (x2)[2]	572 (x2)[2]
571	15/5/97	546 569 570 572	570 572	-	-
572	15/5/97	546 569 570 571	546 570 571	570 (x2)[2]	570 (x2)[2]
573	21/5/97	538 540 574 575	540	-	-
574	21/5/97	538 540 573 575	540 575	-	-
575	21/5/97	538 540 573 574	574	-	-

[1] '?' indicates that the large male was identified as a member of a cluster, but that the other member(s) were not identified. Numbers in parentheses indicate the number of additional, unidentified males in the cluster.

[2] '(x2)' indicates that this pair of individuals were observed as a clustered pair on two separate occasions, which were separated by a dive of 45 min duration.

In 1995, clustering of large males in the absence of females/juveniles was observed on two occasions, both during the same 1 hr period. Both occasions involved the same two large males (#536, #537), plus in one case a third, unidentified large male. In 1997, clustering of large males was observed on 18 occasions. The majority (13) of these clusters involved pairs of large males, although clusters of 4 males together were observed on 4 occasions, and a single cluster of 5 males was also recorded. Clustering was observed on 4 of the 13 days on which large males were sighted, and in three different locations. Eight different males were identified as members of clusters. It is likely that more individuals were involved in clustering behaviour, since not all clustered males were identified on each occasion.

Given that there was only one case where two large males were both identified on the same two days in 1997 (#546 and #555), it is perhaps unsurprising that no pair of males was identified as clustered together on more than one day. [#546 was identified as a member of a cluster on 2 of the 3 days on which it was identified in 1997, on 14/5/97 (one of the days in common with #555) it was identified in a clustered pair with #568, on 15/5/97 (when #555 was not identified), #546 was the only identified member of a cluster of 4]. One pair of large males was identified clustered together on two consecutive surfacings on 15/5/97. Number 570 and #572 surfaced 22 s and 400 m apart, and converged to form a cluster within a minute of #572 surfacing. They remained clustered at the surface, traveling slowly, parallel and <10 m apart for slightly more than 7 min, before fluking-up 6 s apart (14:01:40, 14:01:46). At 14:32, #572 resurfaced, followed by #570 at 14:37:40. Again the two males converged and formed a cluster within 1 min of #570 surfacing. Eight min later, the two males fluked-up within 1 s of each other (14:46:30, 14:46:31). There were a number of subsequent sightings of clusters during that afternoon. Clusters of 2, 2, 4, 2, 4, 5 and 4 were recorded between 15:30 and 17:30. Given that #570 and #572 were present, and that the estimated number of males present was only 6, it seems likely that these two males were involved in at least some of this clustering activity, and quite possibly remained clustered with each other throughout this time.

Clustering occurred exclusively after noon. On the three days in 1997 when most of the recorded clusters were seen (14/5/97, 15/5/97 and 21/5/97), the aggregations were observed from dawn until dusk (6am - 6pm). In each case, during the morning hours, individual males were solitary, surfaced asynchronously and were spread out over several kilometers. In the afternoon, surfacing times became more synchronous and clustered pairs began to be seen. On both 14/5/97 and 15/5/97 larger clusters were observed later in the afternoon and tended to form from the joining of pairs.

Behaviour in clusters

Clustered large males behaved much as clustered females/juveniles do. The animals swam slowly at the surface, parallel, and generally within 10-20 m of each other. Males involved in clusters in 1997 were significantly more likely to submerge without fluking-up (non-fluke dive: NF) than those observed alone (clusters: 31 NF in 47 sightings, solitary: 13 NF in 171 sightings, $\chi^2 = 77.88$, 1 d.f., $p < 0.001$). Sample sizes were smaller in 1995, and there was no detectable difference in frequency of non-fluking dives between males in clusters and those alone (clusters: 2 NF in 5 sightings, solitary: 9 NF in 57 sightings, $\chi^2 = 1.83$, 1 d.f., $0.25 < p < 0.1$).

There have been no observations of clearly aggressive behaviour between large males during this study (1985 - 1997). Prior to 1995, there had been only one recorded incident of possible aggression between large males. In 1987, two large males were observed side by side a few metres apart within a cluster which included nine females/juveniles, and these males engaged in much thrashing of flukes at or beneath the water surface (Whitehead 1993). Only two instances of possible agonistic behaviour among large males were observed during the years in which aggregations were recorded (1995, 1997). On 14/5/97, a large male surfaced 1000 m away from, and directly ahead of a clustered pair. It then headed directly for the pair, a behaviour which was not observed on any other occasion. As this third animal approached to a distance of 50 m from the pair, all three individuals submerged without fluking-up. Big upwellings of water were visible in the area, and both a spy-hop and a side-fluke were observed. Clearly some form of energetic

interaction was occurring below the surface. No other animals were visible at the surface at this time. Eleven min later, approximately 500 m from the previous location, a cluster of four individuals surfaced. This cluster was thought very likely to be the three large males plus one additional animal. If this is the case, and if the behaviour described did represent an agonistic interaction, then it did not result in either avoidance or further agonistic behaviour. On 21/5/97, one large male thrashed its tail flukes at another large male with which it was clustered. This behaviour did not elicit any clear response, the two animals remained clustered and fluked-up synchronously several min later.

Fluking synchrony of males in clusters

Of the twenty clusters observed in 1995 and 1997, there were only six in which both animals fluked-up, all of which involved pairs of large males. These clusters involved at least seven different males on three different days. Fluking was extremely synchronous on five of the six occasions. The time between fluke-ups was 1 s in two cases, 6 s in two cases, 11 s, and 3 min 9 s. Mean time between fluke-ups of clustered males was thus 35.7 s, (5 s excluding the long interval). Fluking synchrony for males in pairs is directly comparable to that of females/juveniles in clusters of two. Of the 44 female/juvenile pairs for which both fluke times were recorded in 1997, 41 intervals were <10 s, 2 others were 11 s and 21 s, and there was 1 extended interval of 3 min 18 s. Mean time between fluke-ups for females/juveniles in pairs was 8.25 s (3.83 s excluding the extended interval).

Surface active behaviour

Rates of surface active behaviours were compared between large males in Galápagos (1995 & 1997), large males in the temperate waters of the Scotian Shelf (Canada) and groups of females in Galápagos (Table 6.7). Surface active behaviours were performed less frequently by large males in both regions than by groups of females and juveniles. The low rates observed for large males preclude meaningful comparison between the two regions.

Table 6.7. Comparison of rates of surface active behaviours of large males off the Galápagos Islands and the Scotian Shelf, and of groups of females/juveniles off the Galápagos Islands.

	large males		females/juveniles
	Galápagos Islands[1]	Scotian Shelf[2]	Galápagos Islands[3]
# breaches per fluke-up	0.018	0.027	0.177
# lob-tails per fluke-up	0.063	0.000	0.220
# spy-hops per fluke-up	0.027	0.068	0.100
# side-flukes per fluke-up	0.103	0.068	0.167

[1] data for 1995 and 1997 in the absence of females/juveniles.
[2] data from Whitehead *et al.* (1992).
[3] data from Whitehead and Weilgart (1991).

Surface active behaviours (breaching, spy-hopping, lob-tailing, side-fluking) were infrequent during observations of large males in the Galápagos area in 1995 and 1997, occurring in only 20 of 125 hours of observation. Rates of occurrence differed with respect to the maximum number of large males seen at the surface at one time in any given hour. Overall, surface active behaviours were more frequent, per individual, during hours when two or more males were seen at the surface at the same time than during hours when only one male was observed, although this higher frequency was apparent only for breaches and side-fluking (Table 6.8).

Table 6.8. Frequency of surface active behaviours by large males (1995 and 1997).

			proportion of total male hours[1] during which specific surface active behaviours were observed				
max. # males at surface	hours	male hours[1]	breach	spy-hop	lob-tail	side-fluke	any
1	76	76	0.000	0.026	0.026	0.039	0.066
2+	49	126	0.016	0.024	0.024	0.095	0.119

[1] Where 'male hours' = number of hours during which males were observed, multiplied by the maximum number of males present at the surface during each hour, so that rates of surface active behaviour are essentially 'per capita'.

Breaching was recorded on only two occasions, once in 1995 and once in 1997. In each case a large male performed two consecutive breaches. In 1995 no other large male had

been seen for 15 min prior to the breaches, or for 35 min afterward. These two breaches were followed by a series of 4 lob-tails. In 1997, a second large male was present 600 m from the breacher, and a third animal surfaced 300 m from the breacher within 2 min of the second breach. In 1995 the two spy-hops recorded were performed by lone males, but of the four seen in 1997, three occurred within a cluster of at least three males, and one followed the two breaches described above. Lob-tailing was recorded on a total of 6 occasions. One case involved a lob-tail by one member of a 5-male cluster, and the remainder involved lone males. Side-fluking was the most frequently recorded surface active behaviour, being observed on 15 occasions, and occurred in a variety of contexts in both years.

Diving behaviour

Males were observed to fluke-up in the majority of sightings (1995: 82.2%, 1997: 77.7%), indicating that the animals were initiating deep dives, presumably in order to feed. Exact dive cycle times (timing of both initial and final fluke-up recorded to the second) were recorded on 2 occasions in 1995, and 12 occasions in 1997. Mean dive cycle duration was 52 min 48.6 s (standard deviation: 1 min 42.7 s), with a range from 43 min 59 s to 67 min 30s (Figure 6.6).

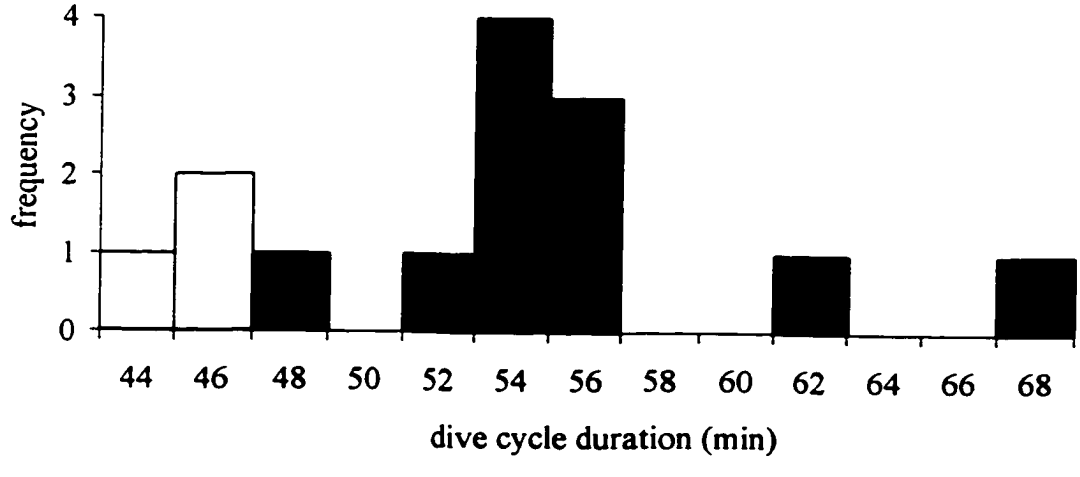

Figure 6.6. Frequency distribution of dive cycle times for large males in 1995 and 1997. Clustered males shown in white, lone males in black.

Although the data are limited, it appears that there may be some connection between social behaviour and diving pattern. The three shortest dive cycle durations recorded all related to males which were clustered, either at the end of the dive cycle (n = 1) or both at the beginning and end of the dive cycle (n = 2). Exact surface intervals (surfacing time to fluke-up) ranged from 6 min 40 s to 13 min 17 s, with a mean of 9 min 40 s (n = 22, s.e.: 20.6 s) (Figure 6.7).

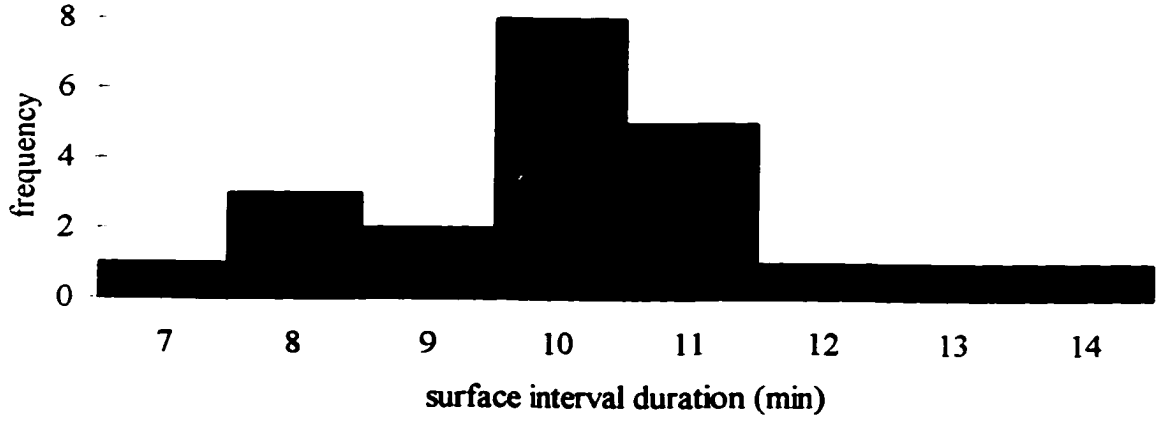

Figure 6.7. Frequency distribution of surface interval durations for large males in 1995 and 1997.

Exact dive duration (fluke-up to surfacing time) was recorded on only four occasions: 31 min 39 s, 36 min 0 s, 43 min 31 s and 47 min 12 s (mean: 39 min 35.5 s). All recorded surface intervals and dive durations were for non-clustered large males.

FEEDING SUCCESS

Feeding success for large males (defecations per fluke-up) in 1995 and 1997 was comparable to rates observed for females/juveniles in the region in previous years (Smith & Whitehead 1993). However, in both years, male feeding success was significantly lower than that of females/juveniles in the same general areas (1995: $\chi^2 = 4.15$, 1df, $0.05 < p < 0.025$; 1997: $\chi^2 = 19.97$, 1df, $p < 0.001$, Table 6.9).

Table 6.9. Feeding success (defecations per fluke-up) of large males versus females and juveniles.

	large males	females/juveniles
1995	0.042	0.213
1997	0.098	0.418

DISCUSSION

There are two main results from this study of large males on the Galápagos Islands breeding ground. Firstly, large males constitute a very small proportion of the identified population, but numbers increased considerably in 1997 (Figure 6.1). Secondly, as the abundance of groups of females/juveniles has decreased, previously unreported aggregative and social behaviours among large males have been observed.

ABUNDANCE

Large males constituted only 4.03% of the identified population in the Galápagos study area (1985-1998) (1.87% prior to 1997), in comparison with 15% in catches between 1830 and 1850 (Hope & Whitehead 1991), and 16% predicted by the models of the Scientific Committee of the International Whaling Commission (Whitehead 1990a). Sperm whales were hunted heavily in the waters off Perú between 1947 and 1981, and large males were virtually eliminated (Saetersdal *et al.* 1963, Ramirez 1989).

There are several possible explanations for the increase in large male abundance, none of which are mutually-exclusive. The recent increase in numbers of males in the Galápagos region may reflect a recovery following the decimation due to whaling. With the cessation of whaling in 1981, numbers of large males may have begun to increase slowly. The number of male sperm whales in Antarctic waters appears to have increased during the 1980s (Butterworth *et al.* 1995), and newly mature animals are now able to migrate back to the tropical waters without encountering whalers. Past whaling is expected to

affect aspects of the population biology of ETP sperm whales for a considerable number of years (Whitehead *et al.* 1997).

The population of females and juveniles utilising the Galápagos waters decreased dramatically, by 20% per year, between 1985 and 1995 (Whitehead *et al.* 1997), and in 1997 only a single group of females and juveniles was encountered during two months of searching. Concurrently, the relative, as well as the absolute, abundance of males increased (Figure 6.2). One possible explanation for the apparent increase in numbers of large males is that they were always there in larger numbers, but the greater detectability (both visually and acoustically) of groups of females and juveniles, and the larger numbers of groups present, meant that large males were less likely to be detected during earlier years of the study. However, the fact that the sighting rate for large males (days sighted/days of effort) remained effectively constant across all years (Table 6.1) suggests that males were not more likely to be detected in years when females were scarce.

Another possibility for the increase in numbers of males is that the enormous reduction in female/juvenile use of the Galápagos area might now permit large males to successfully utilise these waters for foraging. One of the predominant theories for the segregation of males to higher latitudes is that sexual selection favours large size in males, and that males are better able to obtain the requisite quantities of food in colder waters where they are not competing with females for resources (Best 1979). The extent of such foraging competition in the Galápagos would be expected to have declined with the reduction in female population density, perhaps making this a more profitable feeding ground for males. Certainly the feeding success of large males in the Galápagos study area was comparable with that of females/juveniles in previous years (although it was significantly lower than that of females/juveniles in the same year). This was despite the fact that an 'El Niño Southern Oscillation' event occurred in 1997, and foraging success is generally negatively correlated with the occurrence of this phenomenon (Smith & Whitehead 1993, Whitehead 1996b).

AGGREGATIVE AND SOCIAL BEHAVIOURS

The behaviour of large males in 1995 and 1997 contrasts with that of earlier years in a number of ways. Prior to 1995, large males on the Galápagos breeding ground had never been sighted more than 2000 m or 1 hr from an observation of females and juveniles (Whitehead 1993). By contrast, the vast majority of the sightings of large males between 1995 and 1998 were on days when no females and juveniles were identified (Table 6.3), and were separated by many days, or weeks, from a sighting of females/juveniles. This difference is presumably closely connected to the reduction in numbers of females and juveniles present in the Galápagos region (Whitehead *et al.* 1997). In other tropical regions, observations of males independent of groups of females and juveniles have been more frequent (Ecuador - Dufault and Whitehead, unpublished data; central tropical Pacific - Whitehead, unpublished data; Seychelles - Kahn 1991), and may be attributable to the less-aggregated distributions and lower densities of females in these areas when compared to earlier observations in the Galápagos area (Kahn *et al.* 1993).

Although males are thought to avoid each other on the Galápagos breeding ground when females/juveniles are present (Whitehead 1993), in the absence of females/juveniles a number of aggregative and social behaviours were observed. Larger numbers of males were identified per day in 1995 and 1997 than in previous years (Table 6.1). There were also more sightings per day, indicating that males were not only more abundant but also more aggregated (Figure 6.3). Aggregations consisting of a minimum of 2-7 large males were recorded on 19 of the 23 days on which large males were identified in 1995 and 1997 (Table 6.4). Although some form of social cohesion is suggested by the consistency of heading of individuals in these aggregations (Figure 6.5), there is little data available on stability of aggregation membership. Consistency of heading could in fact reflect individuals' independent responses to factors such as prevailing current conditions.

However, a number of factors do suggest that large males within these aggregations exhibit some form of sociality. Large males in years when aggregations occurred had more associates (other large males identified within 2 hours) on average than did large

males in earlier years (Table 6.5), and were significantly less likely to have no associates. Despite the limited data available for the examination of the duration of associations, there were two instances of association of two individuals over a span of 9-11 days, and one pair were associated in three different years. These cases could reflect random re-association of individuals, but they might also reflect stable short- or long-term relationships between at least some individual large males.

Temporal and spatial co-ordination are generally considered to reflect social relationships between individuals, and clustering of large male sperm whales indicates a degree of social affiliation. Clustering of large males was rarely observed prior to 1995. Clusters involving large males only were first seen in 1995 (Christal & Whitehead 1997), and were observed with greater frequency in 1997. These clusters are indicative of social behaviour in a number of ways. Although there is little direct evidence for the duration of associations between clustered individuals, in one case it is possible that two large males were clustered together at most if not all surfacings over several hours. Large males in clusters were more likely to submerge without fluking, and when they did fluke, dive times were shorter than for non-clustered animals (Figure 6.6). Both of these facts suggest that clustered large males were involved in less foraging activity than were non-clustered individuals. The fact that clustering among large males occurred exclusively in the afternoon is reminiscent of the pattern seen among females/juveniles, whose socialising periods are more likely to occur after noon than in the morning, although clustering activity occurs throughout the day (Whitehead & Weilgart 1991). Surface active behaviours are thought to have a social function (Waters & Whitehead 1990b, Whitehead & Weilgart 1991), and were observed more frequently among females and juveniles than among large males in 1995 and 1997 (Table 6.7), reflecting the higher degree of sociality among females and juveniles than among large males. However, overall rates of surface active behaviours by large males in the Galápagos area, in the absence of females/juveniles, were higher when two or more males were observed during an hour, than when only one male was present (Table 6.8), suggesting that aggregated males were engaging in social interaction.

Why should large males form aggregations and engage in social interaction on a breeding ground? I have two main theories, neither of which is entirely supported or refuted by the available data. The first concerns the absence of females, and the second relates to mating strategies.

In the absence of females, it may be that large males revert to their 'normal' bachelor behaviour. Although the forces underlying the formation of bachelor groups are unknown, it may be that these forces support the aggregation of large males at lower latitudes, if mating opportunities, and associated competition, are not present. The aggregation of large male sperm whales could simply reflect local prey aggregation, although this would not explain the reported social behaviours, and feeding success was not high. Large males might also benefit from proximity to each other in terms of predator defense. Although adult sperm whales were thought to be effectively immune to predation because of their large size (Rice 1989), several large animals (adult females or large juvenile males) were recently attacked and killed by killer whales (S. Mesnick, pers. comm.), and a large male identified in the Galápagos region in 1997 had fresh bite marks with trailing flesh on its flukes (pers. obs.).

An alternative possibility, which seems less likely, given the absence of females, is that aggregation and social interaction of large males relates to mating strategies. Males might form groups in order to develop dominance hierarchies, or coalitions. Watkins *et al.* (1993) propose the former, but their suggestion is based on single instance of 'agonistic vocalisations' and occasional chases when two large males were associated with a group of females. No such behaviour has been reported by other researchers on the same breeding ground (Dominica, Gordon *et al.* 1997) or among large males interacting with females on the Galápagos Islands breeding ground (Whitehead 1993). Although there have been several reports of fighting between large male sperm whales (reviewed by Caldwell *et al.* 1966), and of scarring and broken teeth (Best 1979, Kato 1984, Clarke & Paliza 1988), suggesting that fights are not rare occurrences, there have been no observations of overt aggression on the Galápagos breeding ground in either the presence (Whitehead 1993) or absence of females (this chapter).

Coalitions among adult male cetaceans have been reported (Connor *et al.* 1992a, b), and more than one large male sperm whale may be present with a group of females at a given time (Best 1979). However, there is no evidence concerning the duration of associations between these males (Whitehead 1993). Given the relative indefensibility of mating access to females in the three-dimensional oceanic environment, and the low reproductive rate of those females (Best 1968), coalitions would seem to be a costly, rather than beneficial strategy in this species.

CONCLUSIONS

Numbers of large sperm whales present on the Galápagos breeding ground are low, but appear to have increased considerably in recent years. This seems a positive sign for the recovery of a population which appears to have been affected considerably by the virtual elimination of sexually-mature males (Whitehead *et al.* 1997). It is also possible that the reduced numbers of females and juveniles (Whitehead *et al.* 1997) may have reduced resource competition to the point where the area became a profitable feeding ground for males. Aggregative and social behaviours of large males on a breeding ground have not been documented previously, and interpretation is complicated by the concurrent decrease in abundance of groups of females and juveniles. Sociality among large males may reflect a combination of factors relating to prey availability, predator defense and/or mating strategies. The duration and stability of associations between individuals are unclear, but the data presented here suggest that the social structure of large male sperm whales, while far from the cohesive pattern observed among females and their offspring, is more complex than was previously recognised.

CHAPTER SEVEN

General discussion

In this thesis I have addressed questions of sperm whale social structure using a combination of photo-identification and molecular genetic techniques. The long-term nature of the photo-ID study (1985-1997) facilitated both the examination of general association patterns among a large number of identified animals (Chapter 2), and the detailed description of the structure and stability of social groupings (Christal *et al.* 1998, Chapter 3). The combination of several genetic techniques has provided a detailed picture of the relatedness of individuals, and of the genetic structure of social groupings (Chapter 4). Information on the membership of social units (Chapter 3), and the genetic relationships within units (Chapter 4), allowed patterns of short-term association to be discussed in the context of known social and genetic relationships (Chapter 5). Finally, I have provided the first account of aggregative and associative behaviour among large male sperm whales on a breeding ground (Christal & Whitehead 1997, Chapter 6).

FRAMEWORK FOR DISCUSSION

At the very beginning of this thesis, I raised four general reasons for studying the social structure of sperm whales:

1. To examine how grouping characteristics and mating systems influence gene flow, and hence the genetic structure of a population.

2. To establish the social context of cognitive and communicative behaviour.

3. To consider the impacts of past exploitation, and, by gaining more detailed knowledge of population parameters, to make suggestions regarding the mitigation of future exploitation.

4. To provide the potential for intra- and inter-specific comparisons, facilitating discussion of the similarities and differences between mammalian social structures.

At this point, it is pertinent to ask how the results reported in this study may contribute to each of these four goals. I will begin with a brief overview of my findings, and then discuss them in the context of each of these four topics separately. The first three sections will focus predominantly on the implications of my results for our understanding of sperm whale biology, and the final section will put these findings into the broader context of mammalian social structures and social evolution.

A REVIEW OF RESULTS

GROUPS AND UNITS

Temporal analyses of associations among individual sperm whales (Chapter 2) confirm previous suggestions of the temporary nature of groups of female and juvenile sperm whales (Whitehead *et al.* 1991). Groups were shown to consist of smaller, and more temporally-stable social units, associating together for periods of days. Although groups usually appear cohesive, and group members are co-ordinated in their behaviour, individuals within groups associate preferentially with members of their own unit (Chapter 5).

THE NATURE OF SOCIAL UNITS

Sperm whale social units, as described in this study, do not fit the stable, strictly matrilineal model (i.e. complete female social philopatry, with new units forming only by fission of existing units) which has been explicitly or implicitly assumed by previous researchers (e.g. Ohsumi 1971, Best 1979, Fortom-Gouin & Holt 1980, Whitehead *et al.* 1991, Richard *et al.* 1996a, Weilgart *et al.* 1996, Whitehead 1996, Weilgart & Whitehead 1997). While there are some relatives within units, numbers of parent-offspring pairs are too low to be consistent with pure matrilines, and the general pattern of relatedness within units is indicative of the presence of unrelated individuals (Chapter 4). These findings reflect reports of social dynamics – the merger of social units, and the transfer of individuals between units (Chapter 3). Individuals within units showed no apparent

preference for particular companions (Chapter 3), and did not appear to associate differentially on the basis of genetic relatedness (Chapter 5).

MALE SOCIALITY

The sociality of large males reported in Chapter 6 (and Christal & Whitehead 1997) differs markedly from previous descriptions of solitary, avoidance, or aggressive behaviour in tropical waters (i.e. traditional breeding grounds, Best 1979, Clarke & Paliza 1988, Whitehead 1993). Males were not only found in aggregations, which might be reflections of local prey concentration or prevailing current conditions, but were observed to engage in close social affiliation – the type of affiliation (clustering, synchronous diving etc.) which is indicative of unit membership of females/juveniles within groups (Chapter 5). Although there is little evidence concerning the duration of associations between individual males, what evidence there is suggests the possibility of long-term relationships between males, a novel and intriguing finding.

VARIABILITY IN SOCIAL STRUCTURE

Females/juveniles

Unit size was found to vary considerably, from 3 to 24 individuals (Chapter 3). If units were strictly matrilineal, then this range of unit sizes might simply reflect unit-specific demography, in terms of individual fecundity and the sex-ratio of offspring (c.f. Brault & Caswell 1993). If, however, units are formed partly by the aggregation of unrelated individuals (Chapter 4), then such variation in size is indicative of little or no selection for some optimal unit size, suggesting that ecological factors are not primary determinants of unit size (De Vore & Hall 1965).

Group size varied over the 12 years of the study, increasing in the latter years, when overall sperm whale abundance in the Galápagos region was reduced (Chapter 2). This finding seems to support the argument that the aggregation of units to form groups relates

primarily to resource availability, since it appears that larger groups form at times of greater relative prey availability.

Males

The apparent increase in the social behaviour of males, reported in Chapter 6, occurred in conjunction with a marked decrease in the abundance of females, thus it is difficult to tease out the relative influences of various factors (increased number of males present, reduced reproductive opportunities, alteration in primary use of the area (i.e. foraging vs breeding)). What is clear is that the social structure of male sperm whales is more plastic than previously believed, and may vary in response to their ecological and social environment.

A CAVEAT

Many of the results reported in this study are somewhat surprising in light of prevailing assumptions regarding sperm whale social structure. One possible explanation for these discrepancies is that this study is the most detailed so far completed, and that this detailed approach has revealed genuine levels of complexity beyond those detectable in previous studies. In the past, detailed studies of sperm whale behaviour have overthrown widely-held but erroneous views based on less-detailed observation (e.g. the concept of 'harem masters', Best 1979, Whitehead 1993). However, there is another factor that must be considered: human exploitation.

The results of this study cannot necessarily be considered to be representative of the social structure of a 'natural' unexploited population. Peruvian whaling in the decades prior to the study (Saetersdal *et al.* 1963, Ramirez 1989) appears to have impacted sperm whale society in a number of direct and indirect ways. The removal of large numbers of adult males (Ramirez 1989) has clearly had major impacts on the reproduction of females, apparently reducing fecundity (Whitehead *et al.* 1997, Chapter 4) and potentially influencing the size and stability of social units. The reduction in numbers of animals off

the coast of South America seems to have led to the influx of animals previously found around the Galápagos Islands, with consequent reduction of numbers in that area (Whitehead *et al.* 1997), and apparent changes in the social structure of the remaining animals (Chapter 2). The extent to which the social units described in this study may have been impacted directly by whaling is unknown. The removal of individual females and juveniles may have broken up patterns of relatedness within units and/or led to the permanent merger of unrelated 'remnant' units. Thus the extent to which the social structure reported in this thesis reflects the 'typical' social structure of the species is unclear.

SOCIAL STRUCTURE AND GENETICS

Social structure may have significant influences on the genetic properties of populations (Mathews & Porter 1993, Sugg *et al.* 1996), and differences between the sexes in breeding and dispersal patterns have major consequences for genetic subdivision and kin structure of populations (Pope 1998). For example, female philopatry promotes genetic differentiation between mammalian social groups (Emlen & Oring 1977, Chesser 1991, Pope 1998). As a result, examination of genetic structure within and between social groupings can be highly informative about social structure (e.g. Amos *et al.* 1993).

HOW MATRILINEAL ARE SPERM WHALE GROUPS?

Several previous research projects have investigated the genetic structure of sperm whale groups. Lyrholm & Gyllensten (1998) found greater homogeneity of mtDNA haplotypes (which are maternally-inherited) within versus between groups, indicating that members of groups were matrilineally-related. On the basis of combined mtDNA and microsatellite DNA data, Richard *et al.* (1996a) concluded that groups contained genetically-related individuals, but that not all grouped animals were genetic relatives. While group structure was generally matrilineal, the three groups considered in Richard *et al.*'s (1996a) study all contained members of more than one matriline. Some groups have been found to consist of a single mtDNA haplotype, and groups tend to have one predominant

haplotype (representing on average 79% of sampled individuals) indicating a matrilineal basis to group structure, however, up to five different haplotypes have been found within a single group (Dillon 1996, Whitehead *et al.* 1998).

At first sight, the results reported in the current study appear to conflict somewhat with these reports of genetic structure within groups. My analyses (Chapter 2) confirm the findings of Whitehead *et al.* (1991), and show that groups are not necessarily permanent entities, but typically consist of separate 'stable' social units, which associate together for periods of days. I have documented transfers of individuals between social units (Christal *et al.* 1998, Chapter 3), and have found that the genetic structure of two specific social units is not strictly matrilineal (Chapter 4).

Thus previous research has indicated a matrilineal basis to groups, yet I report that groups comprise separate units, and that even these constituent units are not strictly matrilineal in structure. How can these disparate findings be reconciled? There appear to be three scenarios which might explain the apparent conflict between my findings and those of previous researchers. Here, I present a brief outline of these scenarios, before considering each in greater detail.

I. Whaling has impacted both the specific units within which I investigated genetic structure, and the general social structure in the ETP. Thus the patterns of genetic relatedness and the association of separate units within groups that I report are abnormal, whereas the matrilineal group structures reported by other researchers (some of which were found in other regions) are the 'normal' condition.
II. Patterns of relatedness within groups reflect the preferential association of particular units (those related through common ancestry) – i.e. there is a higher, 'community' level within sperm whale society.
III. Indications of matrilineal genetic structure at the level of the group are a reflection of predominantly matrilineal structure at the level of the unit.

Scenario I: impacts of whaling

Under scenario I, groups within unexploited populations are stable matrilineal entities, whereas the direct or indirect effects of whaling have resulted in the pattern of units and temporary groups reported for an exploited population in the ETP (Whitehead *et al.* 1991, Chapter 2), and have broken up patterns of relatedness within the units (Chapter 4). If this were the case, we might expect greater haplotypic homogeneity within groups in relatively unexploited regions, versus those in the ETP. Although data are limited, there is no apparent difference in within-group homogeneity between the western south Pacific (5 groups), where recent whaling seems to have been much less intense, and the ETP (15 groups) (Whitehead *et al.* 1998). Data are not available on a group-by-group basis for Lyrholm & Gyllensten's (1998) analysis. However, many of their groups are from regions where whaling has been intense (the northern North Pacific, and the ETP), and their findings of within-group homogeneity were significant in each region.

Thus much of the data which is indicative of within-group matrilineal structure comes either from the ETP, or from other regions where whaling might be expected to have influenced social and genetic structure to a similar extent. Therefore it seems that scenario I does not provide a convincing explanation for the disparate findings of this, and previous, studies. Research on other populations might allow the generality and normality of the social structure reported here (Chapters 2 and 3) to be investigated. Unfortunately, although sperm whaling ceased over a decade ago, its effects are long-lasting (Whitehead *et al.* 1997), and no truly unexploited population is known to exist.

Scenario II: communities

Scenario II – the existence of a higher hierarchical level of social structure (communities) within sperm whale society – was discussed briefly in Chapter 4. According to this scenario, units are seen as separate, 'normal', matrilineal entities, not as artifacts of whaling, and the existence of haplotypic homogeneity at the group level is explained on the basis of preferential association between units which share a common ancestry.

Communities might consist of multiple units, with units within communities being more likely to associate together as groups than are units from different communities. This would be expected to lead to population genetic structure at the level of the community, with greater homogeneity within rather than between communities. The population structure of sperm whales in the South Pacific has no clear geographic basis (Dillon 1996, Whitehead *et al.* 1998), suggesting that if such communities do exist, they are not segregated geographically.

Preferential association of units is fundamental to this scenario. Some of the evidence for and against such preferences was discussed in Chapter 5. In some species where stable social units associate on a regular basis, pronounced preferences for association with particular units are apparent (Moss & Poole 1983, Yeager 1991, Baird & Dill 1995), although this phenomenon is not universal (Bigg *et al.* 1990). Given the methods used for unit delineation (Chapter 3), units which showed consistent association preferences could have been lumped as single entities (i.e. if they were identified together on two or more separate occasions), thus masking the true extent of preferential association. However, some of the units delineated in this study have been identified in association with many other units, indicating that preferences, if they exist, are likely to be diffuse, or non-exclusive. Findings of group-specific vocal dialects (Weilgart & Whitehead 1997) are indicative of association preferences between closely-related units, although there are other possible explanations (see below for further discussion).

My findings that female philopatry is not universal (Chapter 3) and that unit structure may not be strictly matrilineal (Chapter 4), are not necessarily inconsistent with this scenario. If animals transferring between units did so predominantly within, rather than between, communities, then within-group homogeneity (at least at the haplotypic level) would still be largely retained. Rates of transfer are relatively low (Chapter 3), and the impacts on group genetic structure would be minimised if those animals that transfer have low reproductive success (i.e. do not contribute largely to the genetic constitution of the unit which they join). This suggestion is consistent with findings that in 'female-bonded' (*sensu* Wrangham 1980) primates, transfers of females between groups

commonly occurred as a result of the expulsion of subordinate members from their natal group (reviewed by Moore 1984). Individuals which were subordinate within a group of relatives seem unlikely to be particularly successful in intra-group resource or reproductive competition within a group consisting of non-relatives, and would thus be expected to have low reproductive success.

Scenario III: matrilineal units

Within scenario III, the existence of matrilineal structure within groups is considered to be due purely to the matrilineal structure of units, and is therefore contingent on units being largely matrilineal. The occurrence of transfers between units need not conflict with this argument, provided that they are rare and/or that transferring individuals have low reproductive success (as discussed above). Findings of multiple haplotypes within groups (Dillon 1996, Richard *et al.* 1996a, Whitehead *et al.* 1998), are strongly suggestive of the presence of multiple matrilines, each of which might be equivalent to one constituent unit. Haplotypic diversity among sperm whales is low (Lyrholm *et al.* 1996), and it seems more likely that the presence of multiple haplotypes is indicative of the presence of animals of disparate origins, than that they represent recent evolution within a single matrilineal lineage. However, Dillon (1996) reported some groups comprising a single haplotype, and the predominance of a single haplotype within other groups. How can such a finding be reconciled with the concept of separate units within groups?

If units are largely matrilineal, then there would seem to be a variety of factors which might result in one haplotype predominating within groups. I do not wish to suggest that any of these alone provides a complete resolution of the apparent conflict between my results and those of previous authors, or that by proposing these ideas I am attempting to explain away the results reported by my predecessors. However, the overall pattern of apparent matrilineal structure within groups described by Dillon (1996) and colleagues (Whitehead *et al.* 1998), and Lyrholm & Gyllensten (1998) is consistent with findings of unit structure within groups if some or all of the following phenomena occur, even at

fairly low rates. Although the typical group in the ETP appears to consist of more than one unit (Whitehead *et al.* 1991, Chapter 2), there have been sightings of groups which contain only one unit (pers. obs.). Thus findings of matrilineal structure within groups may, on some occasions, be due to groups being single matrilineal units. Another possibility relates to the low diversity of sperm whale mitochondrial haplotypes (Lyrholm *et al.* 1996). Even if groups are a result of the random association of units (i.e. there is no preferential association between closely-related units, as discussed above), it is likely that associating units may share a haplotype on at least some occasions, particularly if that haplotype is one of the three which have been found in 60-100% of all individuals sampled in each of a number of different oceanic areas (Dillon 1996, Lyrholm & Gyllensten 1998). There is considerable variation in the size of units delineated in the current study (Chapter 3, Appendix 1). If groups consist of units of disparate sizes, and the different units have different haplotypes, then the haplotype of the largest unit will predominate. One final, and admittedly speculative, explanation relates to the evenness of sampling within groups. Many of the groups which were considered in previous analyses were somewhat poorly sampled, relative to a typical group size of 20-40 individuals (e.g. Best 1979, Chapter 2): 4-7 samples/group (mean: 5, Lyrholm & Gyllensten 1998), 2-19 samples/group (mean: 7, Dillon 1996). Members of units have been shown to associate preferentially within groups, thus units may be both temporally- and spatially-segregated (Chapter 5). If sampling within a particular group occurred over a fairly short period of time, or from a particular region within the group, then it is possible that units would have been differentially sampled, and the predominance of a single haplotype might thus reflect the predominance of members of one unit among the set of sampled individuals.

Conclusions

Overall, it would seem that scenario I (impacts of whaling) provides the least convincing argument, although further studies of social structure in less depleted populations are required before it can be ruled out. However, both scenarios II (communities) and III (matrilineal units) do seem to introduce feasible explanations that would make my findings consistent with those of previous studies. Confirmation of either will require

further research – research that must be focused at the level of the unit. Confirmation of association preferences between related units will require a considerable amount of additional data on the association patterns of known units, as well as on their haplotypic structure, and would be aided by the delineation of further units. Confirmation of scenario III requires further study of the detailed genetic structure of units, as well as investigation of those processes by which predominant haplotypes may be found within groups. At the present time, no genetic samples are available for any of the members of the 17 delineated units not considered in Chapter 4 (Whitehead lab sperm whale skin database, J. Christal unpublished data), thus further examination of genetic structure at the level of the unit is not possible. Skin samples, photographically-linked to specific individuals, should therefore be collected whenever possible, in the hopes that members of further delineated units may be sampled.

Although the process of unit delineation is complex, and requires at least three separate identification periods (>30 days apart) of some members, there are good prospects for further units to be recognised. There are a large number of individuals in the photo-ID catalogue which have been identified in two separate identification periods, thus as photo-ID work continues, we may hope that some of these animals will be seen again. In addition, as shown in Chapter 5, patterns of short-term association over periods of days may be indicative of unit membership, allowing putative units to be delineated, and genetic structure to be examined.

SOCIAL CONTEXT OF COMMUNICATION

An animal's social environment is an important factor in the learning and development of vocal communication (Snowdon & Hausberger 1997). Members of stable social groups may share vocal characteristics or repertoires (e.g. Ford 1991, Brown & Farabaugh 1997), and where such repertoires are group-specific, and there is the potential for interbreeding between groups, they may be considered to be dialects (Connor 1982). The stable, bisexually-philopatric, matrilineal pods of 'resident' killer whales possess distinct

dialects, which can be used to construct a genealogy of pods based on vocal traditions (Ford 1991).

Weilgart & Whitehead (1997) reported the existence of group-specific dialects (coda repertoires) in sperm whales. Again we have essentially the same apparent paradox as that discussed in the context of population genetic structure: a group-specific characteristic in a system where groups are not permanent entities, and where even the constituent units may not be purely matrilineal. Members of groups appear to show common vocal characteristics, yet groups contain individuals from different origins. The arguments associated with scenarios I and III (above) seem unlikely to be relevant here (although group-specific dialects might be consistent with scenario III if groups commonly comprise a single unit, or tend to include one larger unit, the dialect of which predominates by simple weight of numbers). Scenario II, the existence of communities within sperm whale society, appears most consistent with the existence of group-specific dialects. Thus groups with similar dialects would associate preferentially. Since coda repertoire is correlated with dominant mtDNA haplotypes within groups (Whitehead *et al.* 1998), such preferential association would account both for haplotypic homogeneity within groups, and the group-specific nature of dialects. It is pertinent to note at this point that this pattern is not apparent within the only other cetacean species which is known to posses vocal dialects. Inter-pod associations among 'resident' killer whales do not correlate with possession of similar vocal dialects (Ford 1991). However, given the differing social structures of 'resident' killer whales and sperm whales, and different contexts in which pods and units interact, this should not be extrapolated to infer that the same occurs in sperm whales.

Vocal learning is known to occur in young sperm whale calves (Watkins *et al.* 1988), hence coda repertoires seem most likely to be learned from the mother or other members of an individual's social unit. Thus findings that units may not be strictly matrilineal (Chapter 4), since individuals transfer between units (Chapter 3), would seem to conflict with findings of distinct dialects in social groups, since the presence of unrelated individuals, which learned their vocal repertoires elsewhere, would be expected to lead to

homogenisation of dialects. This suggests that either rates of transfer, or the reproductive success of transferring animals, must be low. An alternative is that transferring animals modify their vocal repertoire on joining a new social unit, through vocal convergence. Bottlenose dolphins are capable of learning vocalisations from new social companions (Tyack & Sayigh 1997), and it seems possible that the same may be true for sperm whales. Learning of new vocalisations would have to occur predominantly on the part of the newcomer, rather than of established members of the unit, otherwise homogenisation of dialects would be expected.

IMPACTS AND MITIGATION OF EXPLOITATION

Exploitation may affect the social structure of a population in a variety of ways, contingent on the degree of depletion and the age/sex categories exploited (e.g. International Whaling Commission 1986).

As described above, whaling has had a number of direct and indirect effects on sperm whales in the eastern tropical Pacific, and some of my findings could be interpreted as artifacts of this past exploitation. Although exploited populations of some other whale species appear to have recovered relatively quickly following the end of whaling (e.g. gray whales – Reilly 1987, humpback whales - Paterson *et al.* 1994), the same does not appear to be true of sperm whales (Whitehead *et al.* 1997). Given the long-distance movements of sperm whales, their longevity and slow reproductive rates, exploitation may be expected to affect sperm whale populations over large areas, and for considerable time after the cessation of whaling effort.

There are rumours of a possible resumption of whaling for sperm whales by the Japanese in the North Pacific. Whatever the ethical, conservation, and international legal implications of such action, the findings of this study allow me to predict some ways in which impacts could be mitigated. Firstly, the take of large males should be strictly limited. Findings of apparent common paternity within and between social units (Chapter 4), and the known roving mate-searching strategy of males (Whitehead 1993), suggest

that relatively few males are needed to fertilise all receptive females. However, this does not appear to be the case, either in theory (e.g. Beddington & May 1980) or in practice (Whitehead *et al.* 1997), and the consequences of over-exploitation of males appear to be severe and long-lasting. Fecundity may decrease dramatically (Whitehead *et al.* 1997), and this reduced rate of reproduction will limit the ability of the population to rebound from depleted levels.

Fortom-Gouin & Holt (1980) recommend zero catch quotas for females, and such a precautionary approach certainly seems appropriate, particularly since it is not possible to determine the true extent to which populations were depleted by past whaling (Cooke 1986). If however, females are to be taken, there are two separate and somewhat conflicting factors that should be taken into account in the determination of how quotas should be filled: the potential for population growth, and genetic (and cultural) diversity. While the former relates primarily to sustainable harvesting, the latter is an important aspect of the long-term conservation and management of species.

Given the long-term cooperative relationships held within social units, and the apparent importance of such cooperation in the rearing of offspring (Pervushin 1966, Gambell et al. 1973, Best 1979, Weilgart & Whitehead 1986, Gordon 1987, Whitehead 1996), removal of individuals from units seems likely to be more damaging to population growth than would be the cropping of entire units, since it is probable that the removal of unit members will impact negatively on the survival and fitness of some of the remaining animals (as in elephants – Poole & Thomsen 1989). If units were strictly matrilineal, then the harvesting of whole groups (and therefore whole units) would be likely to reduce genetic and cultural diversity. The fact that units do not seem to be strictly matrilineal suggests that this reduction might not be quite so great. However, if scenario II (above) is correct, and closely-related units tend to associate as groups, then the harvesting of whole groups may have major impacts on diversity. Clearly, further research is required before the relative importance of these factors, and therefore the least damaging whaling strategy, can be determined.

Any attempt to restart sperm whaling should be preceded by a complete review of the parameters used in modeling population size and maximum sustainable yield. Much of the data on which the current model (International Whaling Commission 1982) is based has been shown to have been falsified (Brownell *et al.* 1998, Kasuya 1998). Findings of this study (Chapter 2) indicate that 'natural' female mortality was greatly overestimated, which would have led to an underestimation of the extent of whaling mortality, and thus inflated population size estimates. Further detailed research is required in order to determine accurate sperm whale population parameters.

POTENTIAL FOR INTRA-SPECIFIC COMPARISONS

No other population of sperm whales has been studied in comparable detail, or over a comparable time span, to the one described in this study. Understanding of sperm whale social structure in the ETP has increased considerably as data accumulated over the 13-year project (e.g. Whitehead & Arnbom 1987, Whitehead & Waters 1990, Whitehead *et al.* 1991, Christal *et al.* 1998, and this study), a demonstration of the value of long-term research for uncovering the details of complex social structures. Sperm whales have a global distribution (Rice 1989), and within this range it seems likely that different environmental and ecological conditions or cultural drift may have resulted in differences in social structure (Gordon 1987). Intraspecific variation in social structure has been illustrated in a wide range of taxa (Lott 1984, Baird in press), and is apparent within the single population considered in this study, even over relatively small time scales (Whitehead & Kahn 1992, Chapters 2 & 6). In addition, the varying extent of exploitation within populations seems likely to lead to differences in the observed social structure. While findings in other regions (e.g. Gordon 1987, Gordon *et al.* 1997) seem generally consistent with the earlier results of Whitehead & colleagues (Whitehead & Arnbom 1987, Whitehead & Waters 1990), with some minor differences (Whitehead & Kahn 1992), the more detailed results presented in this study should not be extrapolated to other populations without further research in other areas.

SPERM WHALE SOCIAL STRUCTURE IN THE BROADER CONTEXT

Having considered the implications of my research for our understanding of sperm whale society, it is important to consider a broader context. How does the social structure of sperm whales as described in this thesis compare and contrast with patterns in other mammalian species, both marine and terrestrial? Can such comparisons provide insights into the complexities of mammalian social structures, and social evolution?

The social structures and social evolution of cetaceans have recently been reviewed in considerable detail, and compared and contrasted to those of terrestrial mammals (Connor *et al.* 1998, Mann *et al.* in press). There has also been a thorough discussion of the high degree of convergence between the social structure of sperm whales and that of elephants (Weilgart *et al.* 1996). These reviews deal with these issues in far more breadth and detail than is possible, or appropriate, here. Rather than reiterating arguments made elsewhere, I intend to focus my discussion on two specific issues raised by this thesis: the evolution of matrilineal group structures, and the frequency and implications of deviations from strict matrilineality.

THE EVOLUTION OF MATRILINEALITY

The evolution of female sociality has been a topic of considerable debate and research in recent years, particularly among primatologists. Much discussion was stimulated by Wrangham's (1980) 'female bonding' model, with stable cooperative relationships among females evolving as a response to strong between-group competition for patchy resources, and an intrinsic prediction of matrilineality, yet it has been shown to have little empirical support (e.g. van Schaik 1983, 1989, Terborgh & Janson 1986). Instead, it appears that group living by females is more likely to have evolved because grouping led to reduced predation risks (van Schaik 1983, Terborgh & Janson 1986, Dunbar 1988, Mitchell *et al.* 1991, Janson 1992). Gregariousness leads to resource competition, both within and between groups. The exact form of resource competition is determined by the distribution of food resources relative to group size, and it is this that determines the

nature of female social relationships (van Schaik 1989). Where resources are not defensible, or not worth defending, leading to 'scramble' competition (*sensu* van Schaik & van Noordwijk 1988), variations in individual power cannot be translated into variation in access to food, so social phenomena such as dominance and alliance formation are of no benefit to individuals, relationships between individuals are undifferentiated, and individuals may frequently move between groups (van Schaik 1989). By contrast, if the limiting resource is monopolisable, 'contest' competition (*sensu* van Schaik & van Noordwijk 1988) results, and differences in power lead to differential access to resources, and thus differential fitness. In such a society, dominance hierarchies and alliances are favoured, since coalitionary aggression is necessary for individuals to gain access to resources (e.g. Mitchell *et al.* 1991). Thus contest competition leads to the formation of stable female groups, and consequently female philopatry and matrilineal group structure, since alliances with kin will be promoted by inclusive fitness benefits (van Schaik 1989).

Factors other than competition over resources may also lead to matrilineality. Lee (1994) suggests that when food is dispersed or evenly distributed, resource competition may be low, and in these circumstances, the need for cooperative infant rearing may become the critical influence on female associations. Persisting sociality of females, and thus matrilineality, is promoted by circumstances in which the presence or actions of non-mothers can improve infant survival (Gittleman 1985). These circumstances are most common when infant mortality is due primarily to specific threats such as disturbance or predation, rather than to random environmental stochasticity (Lee 1994).

Matrilineality in terrestrial mammals

The matrilineal group is seen as the basis of many mammalian social structures (e.g. Eisenberg 1977), reflecting the retention of female young within their natal groups, and the maintenance of group stability on the basis of inclusive fitness benefits. Matrilineal social structures predominate among group-living primates (Lee 1994). The food resources of the numerous Cercopithecine species (vervets, baboons and macaques) and

other frugivores tend to occur in relatively large, defensible patches, thus promoting within-group competition, dominance, alliances, and female philopatry (e.g. van Schaik 1989, Sterck *et al.* 1997). However, where food patches are typically small, and within-group resource competition is consequently low, non-matrilineal structures may occur (e.g. Mitchell *et al.* 1991). Species which feed on lower quality, more evenly-distributed foods, such as leaves, have more variable social structures, but among these are some species where matrilineality appears to have been promoted by the need for high levels of cooperative infant care (Lee 1994). Ape societies are not matrilineal. In these species, females are either essentially solitary (orangutans - van Schaik & van Hooff 1996), or tend to be found with unrelated females, their patterns of sociality determined to a large extent by male reproductive strategies (e.g. White 1992, Tutin 1996).

Matrilineal structures are relatively rare among other mammalian genera. Stable groupings of any form are infrequent among ungulate species, where group composition tends to be flexible in response to variable food distribution over large areas, and resources are generally not defensible (Jarman 1974). In the few species of carnivores where matrilineality occurs, it reflects a requirement for cooperative hunting and defense of carcasses, and also communal infant care (e.g. lions - Packer & Pusey 1983, Packer *et al.* 1991, hyaenas - Frank 1986). Elephants provide an example of a hierarchical matriarchal society, with progressively higher levels based on the preferential association of matrilineally-related groups (Moss & Poole 1983). This is the species with a social structure most closely comparable to that of sperm whales (Weilgart *et al.* 1996), although the existence of preferential association among sperm whale social units has yet to be investigated fully. As in sperm whales (Best 1979, Whitehead 1993), males disperse from their natal groups, form loose bachelor herds or are solitary, and rove between female groups when in reproductive condition (Barnes 1982).

Matrilineal cetaceans

Although the majority of cetaceans are gregarious to some extent (true solitariness presumably being selected against by high predation risks - Norris & Dohl 1980), stable

groupings are relatively rare. Association patterns of mysticetes and some of the smaller odontocetes vary, and appear to be flexible with respect to the variable distribution of food resources (e.g. Whitehead & Carlson 1988, Perry *et al.* 1990, Weinrich 1991, Slooten *et al.* 1993). Matrilineality has been reported for only four species of odontocetes ('resident' killer whales - Bigg *et al.* 1990, Olesiuk *et al.* 1990; short-finned pilot whales – Kasuya & Marsh 1984; long-finned pilot whales – Amos *et al.* 1991, 1993, Amos *et al.* 1991; sperm whales - Dillon 1996, Richard *et al.* 1996a). There are also indications of some degree of matrilineality within bands of female bottlenose dolphins (Duffield & Wells 1991). Groups of narwhals have been reported to be 'matrifocal' (Hay & Mansfield 1989, Palsbøll *et al.* 1997b), but there appear to be no genetic or long-term behavioural data to confirm whether groups are truly matrilineal in this species.

What forces appear to have led to matrilineality in cetacean social structures? The variation in size of stable social units among sperm whales and 'resident' killer whales suggests a low degree of selection pressure on unit size (Christal *et al.* 1998, Baird in press, Chapter 3), indicating that resource-related factors are unlikely to be major contributors to the evolution of matrilineality in these species. For sperm whales, this argument is strengthened by the fact that units typically forage in association with other units, and it seems that it is group size, rather than unit size, that may vary with respect to resource availability (see Chapter 2). Females of these species invest highly in their singly-born offspring, lactating for several years, and producing calves at a minimum of 4-5 year intervals (Best *et al.* 1984, Olesiuk *et al.* 1990). Thus individual calves represent a major proportion of their mother's lifetime direct fitness. Although predation on adult female sperm whales appears to be limited (Berzin 1971, Jefferson *et al.* 1991), calves are thought to be more vulnerable to predators. During predatory attacks, sperm whale calves tend to be placed in the centre of the group (e.g. Arnbom *et al.* 1987), and appear to be protected by group members. During normal foraging activities, females or juveniles in groups containing calves may act to reduce the overall synchrony of dive cycles within the group, resulting in decreased periods of time when calves are alone at the surface (Whitehead 1996). Although 'resident' killer whales have no confirmed natural enemies (Jefferson *et al.* 1991), an agonistic encounter between 'residents', and

mammal-eating 'transients' has been observed, indicating a possible requirement for calf protection in both forms of this species (Baird & Dill 1996, Baird in press). Thus it seems likely that in both sperm whales and killer whales, inclusive fitness benefits derived through communal care and defense of calves have been the selective force behind the evolution of matrilineality (Gordon 1987, Baird in press, Whitehead & Weilgart in press). While matrilineality in terrestrial mammals may reflect either within-group contest competition or cooperative care requirements, or a combination of these two factors, matrilineality among cetaceans appears to relate primarily to the need for help with infant rearing.

DEVIATIONS FROM STRICT MATRILINEALITY

Given the apparent benefits of matrilineality, the finding that some female sperm whales are not socially philopatric (Chapter 3) and thus that sperm whale social units may not be strictly matrilineal (Chapter 4), is somewhat surprising, and difficult to reconcile with social evolution theory (as discussed in Chapter 3). How widespread are such deviations from strict matrilineality, and what explanations for this phenomenon have been proposed?

There is conclusive evidence for the lack of dispersal by females (or males) from 'resident' killer whale pods (Bigg *et al.* 1990). Thus it appears that strict matrilineality is maintained. Although this pattern has been assumed for many mammalian species in which matrilineality is indicated (e.g. elephants - Moss & Poole 1983), there seem to be relatively few cases where the strict matrilineality of social groups has been confirmed, either through long-term observations (over the lifetimes of individuals), or genetic analyses.

Although the social structures of bottlenose dolphin (*Tursiops spp.*) communities are not characterised by the long-term distinct social units seen in sperm whales and 'resident' killer whales, observations did suggest the existence of matrilineal structures within bottlenose dolphin society. Females have a wide network of associates, and interact with

most other females within their community, but within this structure, there are subsets of females (bands) which associate together more strongly (Wells *et al.* 1987, Wells 1991, Smolker *et al.* 1992). Juvenile females leave their natal bands to join subadult groups, and later leave these groups to join bands upon the birth of their first calf (Wells *et al.* 1987, Wells 1991). Several females have been observed to rejoin their natal band, and multiple generations of a single lineage were known to be present within bands, indicating that band structure was matrilineal. However, genetic analyses have shown that the stable bands of females may include members from different maternal lineages, and that some females may disperse between communities (Duffield & Wells 1991), indicating that, as in sperm whales, the long-term association patterns of bottlenose dolphins are not entirely consistent with strict matrilineality.

Evidence for deviations from strict matrilineality is not restricted to cetaceans. Moore (1984) presents evidence of substantial female transfer between groups in a number of 'female-bonded' primates, demonstrating that stable groups of females are not always matrilineal. He interprets the lack of clear behavioural differences between groups in species with strict matrilineality, and in those with frequent female transfer, as evidence that kin selection may have been somewhat overemphasized as an evolutionary force for the maintenance of social group stability (Moore 1984).

Transfers between matrilines will result in the presence of unrelated individuals within social groups. Such movements would appear to be costly to transferring individuals, which will lose both their affiliative relationships with familiar, related companions, and any inclusive benefits that might have been gained in future by helping those relatives (Gouzoules & Gouzoules 1987). However, it seems that in many circumstances, such transfers may reflect individuals making what is essentially 'the best of a bad job'. Many cases of transfer between matrilineal groups in primates seem to be a result of competition among females, of the costs of subordinate status within dominance hierarchies and/or to direct expulsion (typically by same-sex group members, Jones 1980, Moore 1984). Dominant individuals may exert reproductive suppression, limiting or preventing the reproduction of subordinates, and leading to reproductive skew

(Vehrencamp 1983). While skew theory predicts that subordinates should be reluctant to disperse if their chances of surviving and breeding outside the natal group are low (since they may gain inclusive fitness benefits through helping in the care of dominants' offspring, e.g. Keller & Reeve 1994), dispersal may be favoured if subordinates may gain direct fitness by breeding elsewhere. It is unclear whether transfers of female sperm whales and bottlenose dolphins are the result of these factors. Dominance hierarchies have been detected among bottlenose dolphins in a captive environment (Samuels & Gifford 1997), but it is unknown whether they exist among wild cetaceans. While information on reproductive suppression among cetaceans is unavailable, this phenomenon is closely associated with the occurrence of helping behaviours (Keller & Reeve 1994), such as the babysitting observed in sperm whales (Whitehead 1996). Reproductive suppression also most likely in species where females form long-term cooperative groups (Snowdon 1996). However, it typically occurs in circumstances where there is selection for some optimal group size, and as shown in Chapter 2, this does not appear to be the case for sperm whale social units. As yet, the deviations from strict matrilineality reported in this study cannot be fully explained, and further investigation of this issue is clearly warranted.

APPENDIX ONE

Details of delineated units

Table A1.1. Details of the 19 units delineated using the methodology outlined in Chapter 3 (12 hr association criterion). 'Key individuals' (animals identified during at least three identification periods, where each period is separated from the others by an interval of at least 30 days) are indicated in **bold**.

unit name	unit size	members	identification periods[1]
A[2]	24	**117** **234**[2] **235**[3] **253** **254** **255**[3] 257 **448** **449** **487** **488** **489** 490 **499** **600** 605 751 **800** 802 2204 **2242**[3] 2314 **2361**[3] 2818[3]	*1*: 24/2/85, 7/3/85, 8/3/85 *2*: 5/1/87, 6/1/87, 7/1/87, 8/1/87, 9/1/87, 18/1/87 *3*: 9/3/87 *4*: 29/10/88 *5*: 11/3/89 *6*: 5/4/91, 6/4/91
A2	5	**235**[3] **255**[3] **2242**[3] **2361**[3] 2818[3]	*7*[4]: 28/5/95, 29/5/95, 30/5/95, 31/5/95, 1/6/95, 2/6/95, 3/6/95
B[5]	22	**754** **793**[6] **795**[6] **804** 805 **806** **807** **808** **809** **810** **811** **812** 813 **814** 815 2333 **2935** **2942**[8] 3287 3290 3295 3303	*1*: 20/1/87, 22/1/87, 23/1/87 (*2*[7]: 22/3/87) *3*: 29/12/88 *4*: 15/2/94, 16/2/94, 19/2/94, 18/3/94 *5*: 28/5/95, 29/5/95, 30/5/95, 31/5/95, 1/6/95, 2/6/95, 3/6/95 *6*: 22/6/96
C	3	**236**[9] 101 220	*1*: 24/2/85 *2*: 30/3/85
D	15	**236**[9] 1010 1014 1016 1017 1020 1021 1022 1115 1119 1121 1123 1124 1127 1130	*1*: 2/6/87, 3/6/87 *2*: 18/5/89
E	18	**759** **761** 762 **803** **852** **854** 1721 **1723** 1724 1729 **1735** **1935** 1936 1993 2041 2048 2080 2158	*1*: 11/3/87 *2*: 20/4/88 *3*: 26/4/89, 27/4/89, 29/4/89, 1/5/89, 2/5/89, 4/5/89, 14/5/89, 17/5/89 *4*: 30/3/91 *5*: 1/6/93 *6*: 18/6/94

Table A1.1 continued

F	12	**728 732** 731 **733 745 748 798** 921 923 **940 960** 962	*1*: 3/1/87 *2*: 16/4/87, 18/4/87, 19/4/87 *3*: 5/3/89 *4*: 28/4/96, 29/4/96
G	11	**902**[10] 1817 1821 1822 1823 1824 1826 1831 1833 1835 1837	*1*: 15/4/89, 16/4/89 *2*: 26/4/93, 27/4/93
H[2]	4	**234**[2] 620 **621** 760	*1*: 25/2/85 *2*: 5/1/87, 7/1/87, 8/1/87, 18/1/87 *3*: 9/3/87, 21/3/87
I[2]	7	**234**[2] **424** 426 **427 429** 468 469	*1*: 25/2/85, 10/3/85 *2*: 12/3/87 *3*: 13/5/87 *4*: 11/3/89 *5*: 5/4/91
J	9	**282 283** 284 285 286 287 **305** 316 475	*1*: 9/3/85, 10/3/85 *2*: 12/4/85 *3*: 13/3/87
K	13	**125 126 127 329** 335 392 **409 410 412 413** 416 857 858	*1*: 27/3/85, 31/3/85 *2*: 22/3/87 *3*: 6/4/91 *4*: 24/6/93 *5*: 4/2/94, 5/2/94, 20/2/94, 21/2/94
L	14	**827 828 830 831 832 834 836** 839 **840 841 845** 3128 3131 3134	*1*: 7/2/87, 8/2/87, 9/2/87, 11/2/87, 12/2/87 *2*: 12/5/87, 13/5/87 *3*: 3/4/89 *4*: 27/4/93 *5*: 23/6/93 *6*: 6/2/94, 7/2/94, 17/2/94, 18/2/94, 20/2/94
M	3	**2236** 2326 2327	*1*: 11/11/88 *2*: 13/1/89 *3*: 13/2/89
N	6	**1009** 1025 **1026** 1094 1111 1902	*1*: 30/5/87, 4/6/87 *2*: 18/4/89 *3*: 6/3/94, 7/3/94, 9/3/94
O	8	931 932 **997** 1001 1002 1004 1152 1988	*1*: 11/5/87, 12/5/87 *2*: 27/4/89, 28/4/89, 2/5/89, 3/5/89, 6/5/89, 7/5/89 *3*: 14/5/93
P	9	**145 149 199 263** 277 278 **345 617** 618	*1*: 6/3/85, 30/3/85, 14/4/85, 15/4/85 *2*: 30/4/89, 5/5/89, 20/5/89 *3*: 24/6/93

Table A1.1 continued

Q	6	**1029** 1106 1951 1970 1971 1977	*1*: 4/6/87 *2*: 13/1/89 *3*: 21/5/89
R	11	**2964** 2965 2973 3040 **3053 3054** 3081 3087 3103 3420 3668	*1*: 28/3/93 *2*: 1/6/93, 3/6/93 *3*: 29/12/93 *4*: 27/3/94
S	6	716 718 721 848 **843** 851	*1*: 13/2/87 *2*: 2/5/87 *3*: 20/2/94

[1] Only those dates when at least two members of the unit were sighted are listed.

[2] #234 is considered to be a member of three separate units (A, H, I), due to the complex nature of its association history. It is possible the separation of these units is an artifact of the unit delineation process.

[3] This set of five individuals separated from the rest of Unit A between 1989 and 1991 (see Figure 3.3), and are designated Unit A2 (with the rest of the original unit being A1). Unit A2 is the focus of detailed genetic and behavioural analysis in Chapters 4 and 5.

[4] Sighting of Unit A2 (see footnote 3) only.

[5] Unit B is the focus of detailed genetic and behavioural analysis in Chapters 4 and 5.

[6] #793 and #795 either transferred into or merged with Unit B between 1987 and 1989 (see Figure 3.4).

[7] #793 and #795 only, prior to transfer/merge.

[8] #2942 transferred into Unit B between 1994 and 1995 (see Figure 3.7).

[9] #236 transferred between Units C and D between 1985 and 1987 (see Figure 3.5).

[10] #902 transferred into Unit G between 1987 and 1989 (see Figure 3.6)

Literature Cited

Alexander R.D. (1974) The evolution of social behavior. Annual Review of Ecology and Systematics 5, 325-383

Amos B. and Hoelzel A.R. (1991) Long-term preservation of whale skin for DNA analysis. Reports of the International Whaling Commission, Special Issue 13, 99-103

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

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

Amos W., Barrett J. and Dover G.A. (1991) Breeding system and social structure in the Faeroese pilot whale as revealed by DNA fingerprinting. In: Genetic Ecology of Whales and Dolphins. Reports of the International Whaling Commission, Special Issue 13. (Ed.: Hoelzel A.R.) International Whaling Commission, Cambridge, 255-268

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

Árnason U. and Gullberg A. (1994) Relationship of baleen whales established by cytochrome b gene sequence comparison. Nature 367, 726-728

Árnason U. and Gullberg A. (1996) Cytochrome *b* nucleotide sequences and the identification of five primary lineages of extant cetaceans. Molecular Biology and Evolution 13, 407-417

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

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

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

Backus R.H. and Schevill W.E. (1966) *Physeter* clicks. In: Whales, dolphins and porpoises. (Ed.: Norris K.S.) University of California Press, Berkeley, CA, 510-527

Baird R.W. (in press) The killer whale - foraging specializations and group hunting. In: Cetacean societies: field studies of dolphins and whales. (Eds.: Mann J., Connor R.C., Tyack P. and Whitehead H.) University of Chicago Press, Chicago

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

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

Barnes R.F.W. (1982) Mate searching behaviour of elephant bulls in a semi-arid environment. Animal Behaviour 30, 1217-1223

Beddington J.R. and May R.M. (1980) A possible model for the effect of adult sex ratio and density on the fecundity of sperm whales. Reports of the International Whaling Commission, Special Issue 2, 75-76

Berubé M. and Palsbøll P. (1996) Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5, 283-287

Berzin A.A. (1971) The sperm whale. Pischevaya Promyshlenmost, Moscow (Translated by the Israel Program for Scientific Translations, ed. Yablokov, AV).

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

Best P.B. (1969) The sperm whale (*Physeter catodon*) off the west coast of South Africa. 3. Reproduction in the male. Investigational Report of the Division of Sea Fisheries, South Africa 72, 1-19

Best P.B. (1970) The sperm whale (*Physeter catodon*) off the west coast of South Africa. 5. Age, growth and mortality. Investigational Report of the Division of Sea Fisheries, South Africa 79, 1-27

Best P.B. (1979) Social organization in sperm whales, *Physeter macrocephalus*. In: Behavior of marine animals. Vol. 3. (Eds.: Winn H.E. and Olla B.L.) Plenum, New York, 227-289.

Best P.B. (1983) Sperm whale stock assessments and the relevance of historical whaling records. Reports of the International Whaling Commission, Special Issue 5, 41-55

Best P.B. and Butterworth D.S. (1980) Timing of oestrus within sperm whale schools. Reports of the International Whaling Commission, Special Issue 2, 137-140

Best P.B., Canham P.A.S. and Macleod N. (1984) Patterns of reproduction in sperm whales *Physeter macrocephalus*. Reports of the International Whaling Commission, Special Issue 6, 51-80

Bigg M.A., Olesiuk P.F., Ellis G.M., Ford J.K.B. and Balcomb K.C.I.I.I. (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, 383-399

Bradbury J.W. and Vehrencamp (1977) Social organization and foraging in emballonurid bats. III. Mating systems. Behavioral Ecology and Sociobiology 2, 1-17

Branch L.C., Villarreal D. and Fowler G.S. (1993) Recruitment, dispersal, and group fusion in a declining population of the plains vizcacha (*Lagostomus maximus*; Chinchillidae). Journal of Mammalogy 74, 9-20

Brault S. and Caswell H. (1993) Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74(5), 1444-1454

Brown E.D. and Farabaugh S.M. (1997) What birds with complex social relationships can tell us about vocal learning: vocal sharing in avian groups. In: Social influences on vocal development. (Eds.: Snowdon C.T. and Hausberger M.) University Press, Cambridge, UK, 98-127.

Brownell R.L.J., Yablokov A.V. and Zemsky V.A. (1998) USSR pelagic catches of North Pacific sperm whales, 1949-1979: conservation implications. IWC SC/50/CAWS27

Bryant P. (1979) The Baja sperm whale mass-stranding. Whalewatcher 13(2), 10

Buchanan F.C., Friesen M.K., Littlejohn R.P. and Clayton J.W. (1996) Microsatellites from the beluga whale *Delphinapterus leucas*. Molecular Ecology 5, 571-575

Butterworth D.S., Borchers D.L., Chalis S., De Decker J.B. and Kasamatsu F. (1995) Estimates of abundance for southern hemisphere blue, fin, sei, humpback, sperm, killer and pilot whales from the 1978/79 to 1990/91 IWC/IDCR sighting survey cruises, with extrapolations to the area south of 30 degrees for the first five species based on Japanese scouting vessel data. Reports of the International Whaling Commission 45, 444

Byrne R. and Whiten A. (1988) Machiavellian intelligence. Clarendon Press, Oxford.

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

Caldwell D.K., Caldwell M.C. and Rice D.W. (1966) Behavior of the sperm whale *Physeter catodon* L. In: Whales, dolphins and porpoises. (Ed.: Norris K.S.) University of California Press, Berkeley, 677-717.

Caldwell M.C. and Caldwell D.K. (1966) Epimeletic (care-giving) behavior in Cetacea. In: Whales, dolphins and porpoises. (Ed.: Norris K.S.) University of California Press, Berkeley, 755-789

Cerchio S. and Tucker P. (1998) Influence of alignment on the mtDNA phylogeny of cetacea: questionable support for a Mysticeti/Physeteroidea clade. Systematic Biology 47, 336-344

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

Chapman D.G. (1952) Inverse, multiple and sequential sample censuses. Biometrics 8, 286-306

Cheney D.L. (1987) Interactions and relationships between groups. In: Primate societies. (Eds.: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T.) University of Chicago Press, Chicago, 267-281.

Chepko-Sade B.D. and Sade D.S. (1979) Patterns of group splitting within matrilineal kinship groups. Behavioral Ecology and Sociobiology 5, 67-86

Chesser R.K. (1991) Gene diversity and female philopatry. Genetics 127, 437-447

Chesser R.K., Sugg D.W., Rhodes O.E., Novak J.M. and Smith M.H. (1993) Evolution of mammalian social structure. Acta Theriologica 38 S2, 163-174

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

Christal J. and Merlen G. (1997): Galapagos sperm whale research 1997. Final report to the Galapagos National Park Service, November 1997.

Christal J. and Whitehead H. (1997) Aggregations of mature male sperm whales on the Galapagos Islands breeding ground. Marine Mammal Science 13, 59-69

Christal J., Whitehead H. and Lettevall E. (1998) Sperm whale social units: variation and change. Canadian Journal of Zoology 76 in press

Clarke M.R. (1976) Observation on sperm whale diving. Journal of the Marine Biological Association of the United Kingdom 56, 809-810

Clarke M.R. (1980) Cephalopoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Report 37, 1-324

Clarke M. and Young R. (1998) Description and analysis of cephalopod beaks from stomachs of six species of odontocete cetaceans stranded on Hawaiian shores. Journal of the Marine Biological Association of the United Kingdom 78, 623-641

Clarke M.R., Martins H.R. and Pascoe P. (1993) The diet of sperm whales (*Physeter macrocephalus* Linnaeus 1758) off the Azores. Philosophical Transactions of the Royal Society of London, Series B 339, 67-82

Clarke R. (1956) Sperm whales of the Azores. Discovery Report 28, 237-298

Clarke R. and Paliza O. (1972) Sperm whales of the Southeast Pacific. Part III: Morphometry. Hvalradets Skrifter 53, 1-106

Clarke R. and Paliza O. (1988) Intraspecific fighting in sperm whales. Reports of the International Whaling Commission 38, 235-241

Clutton-Brock T.H. (1989) Female transfer and inbreeding avoidance in social mammals. Nature 337, 70-72

Connor D.A. (1982) Dialects versus geographic variation in mammalian vocalizations. Animal Behaviour 30, 297-298

Connor R.C. (1986) Pseudo-reciprocity: investing in mutualism. Animal Behaviour 34, 1562-1566

Connor R.C. (1995) The benefits of mutualism: a conceptual framework. Biological Reviews 70, 427-457

Connor R.C. and Norris K.S. (1982) Are dolphins reciprocal altruists? The American Naturalist 119, 358-374

Connor R.C., Smolker R.A. and Richards A.F. (1992a) Dolphin alliances and coalitions. In: Coalitions and alliances in humans and other animals. (Eds.: Harcourt A.H. and de Waal F.B.M.) Oxford University Press, Oxford, 415-442.

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

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

Connor R.C., Wells R.S., Mann J. and Read A.J. (in press) The bottlenose dolphin, *Tursiops spp*: Social relationships in a fission-fusion society. In: Cetacean societies: field studies of dolphins and whales. (Eds.: Mann J., Connor R.C., Tyack P. and Whitehead H.) University of Chicago Press,, .

Cooke J.G. (1986) A review of some problems relating to the assessment of sperm whale stocks, with reference to the Western North Pacific. Reports of the International Whaling Commission 36, 187-190

Cranford T.W., Amundin M. and Norris K.S. (1996) Functional morphology and homology in the odontocete nasal complex: implications for sound generation. Journal of Morphology 228, 223-285

Crockett C.M. and Eisenberg J.F. (1987) Howlers: variations in group size and demography. In: Primate Societies. (Eds.: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T.) University of Chicago Press, Chicago, 54-68.

Crook J.H. (1970) Social organization and the environment: aspects of contemporary social ethology. Animal Behaviour 18, 197-209

Crook J.H. and Gartlan J.S. (1966) Evolution of primate societies. Nature 21, 1200-1203

Crook J.H., Ellis J.E. and Goss-Custard J.D. (1976) Mammalian social systems: structure and function. Animal Behaviour 24, 261-274

Davenport J.M. and Webster J.T. (1975) The Behrens-Fisher problem, and old solution revisited. Metrika 22, 47-54

De Vore I. (1965) Changes in population structure of Nairobi Park baboons 1959-1963. In: The baboon in medical research. Vol. 1. (Ed.: Vagtborg H.) University of Texas, Austin, 17-28.

De Vore I. and Hall K.R.L. (1965) Baboon ecology. In: Primate behavior: field studies of monkeys and apes. (Ed.: De Vore I.) Holt, Rinehart and Winston, New York, 20-52.

Dillon M.C. (1996): Genetic structure of sperm whale populations assessed by mitochondrial DNA sequence variation. Ph.D. Dissertation, Dalhousie University, Halifax, Nova Scotia, Canada.

Dillon M.C. and Wright J.M. (1993) Nucleotide sequence of the d-loop region of the sperm whale (*Physeter macrocephalus*) mitochondrial genome. Molecular Biology and Evolution 10, 296-305

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

Dufault S. and Whitehead H. (1993) Assessing the stock identity of sperm whales in the Eastern Equatorial Pacific. Reports of the International Whaling Commission 43, 469-475

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

Dufault S. and Whitehead H. (1995b) The geographic stock structure of female and immature sperm whales in the South Pacific. Reports of the International Whaling Commission 45, 401-405

Dufault S. and Whitehead H. (1998) Regional and group-level differences in fluke markings and notches of sperm whales. Journal of Mammalogy 79, 514-520

Duffield D.A. and Wells R.S. (1991) The combined application of chromosome protein and molecular data for the investigation of social unit structure and dynamics in *Tursiops truncatus*. In: Genetic Ecology of Whales and Dolphins. Vol. Reports of the International Whaling Commission, Special Issue 13. (Ed.: Hoelzel A.R.) International Whaling Commission, Cambridge, 155-169.

Eisenberg J.F. (1973) Mammalian social systems: are primate social systems unique? In: Proceedings from the symposia of the fourth congress of the International Primatological Society. Vol. 1. (Ed.: Menzei E.W.) Karger, Basel, 232-249.

Eisenberg J.F. (1977) The evolution of the reproductive unit in the class mammalia. In: Reproductive behaviour and evolution. (Eds.: Rosenblatt J.S. and Komisanik B.R.) Plenum Press, New York, 39-71.

Eisenberg J.F., Muckenhirn N.A. and Rudran R. (1972) The relation between ecology and social structure in primates. Science 176, 863-874

Emlen S.T. and Oring L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197, 215-223

Ford J.K.B. (1991) Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology 69, 1454-1483

Ford J.K.B., Ellis G.M. and Balcomb K.C. (1994) Killer whales: the natural history and genealogy of *Orcinus orca* in British Columbia and Washington State. UBC Press, Vancouver.

Fortom-Gouin J.-P. and Holt S.J. (1980) Reasons for recommending zero female catch limits for sperm whales. Reports of the International Whaling Commission, Special Issue 2, 261-262

Frank L.G. (1986) Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. Animal Behaviour 34, 1500-1509

Gambell R. (1972) Sperm whales off Durban. Discovery Report 35, 199-358

Gambell R., Lockyer C. and Ross G.J.B. (1973) Observations on the birth of a sperm whale calf. Southern African Journal of Science 69, 147-148

Gaskin D.E. (1967) Luminescence in a squid *Moroteuthis* sp. (probably *ingens* Smith), and a possible feeding mechanism in the sperm whale *Physeter catodon* L. Tuatara 15, 86-88

Gaskin D.E. (1970) Composition of schools of sperm whales *Physeter catodon* Linn. east of New Zealand. New Zealand Journal of Marine and Freshwater Research 4, 456-471

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

Giraldeau L.-A. and Caraco T. (1993) Genetic relatedness and group size in an aggregation economy. Evolutionary Ecology 7, 429-438

Gittleman J.L. (1985) Functions of communal care in mammals. In: Evolution: essays in honour of John Maynard Smith. (Eds.: Greenwood P.J., Harvey P.H. and Slatkin M.) Cambridge University Press, Cambridge, 187-205.

Goodall J. (1986) The chimpanzees of Gombe: patterns of behavior. Harvard University Press, Cambridge, Mass.

Goold J.C. and Jones S.E. (1995) Time and frequency domain characteristics of sperm whale clicks. Journal of the Acoustical Society of America 98, 1279-1291

Gordon J.C.D. (1987a): Behaviour and ecology of sperm whales off Sri Lanka. Ph.D. Dissertation, University of Cambridge, Cambridge.

Gordon J.C.D. (1987b) Sperm whale groups and social behaviour observed off Sri Lanka. Reports of the International Whaling Commission 37, 205-217

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

Gordon J.C.D. and Steiner L. (1992) Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Reports of the International Whaling Commission 42, 1992

Gordon J.C.D., Moscrop A., Carlson C., Ingram S., Leaper R., Matthews J. and Young K. (1997): Distribution, movements and residency of sperm whales off the commonwealth of Dominica, Eastern Carribean: implications for the development and regulation of the local

whale watching industry. Paper SC/49/O27 presented to the Scientific Committee of the International Whaling Commission, September 1997.

Gouzoules S. and Gouzoules H. (1987) Kinship. In: Primate societies. (Eds.: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T.) University of Chicago Press, Ltd., London, 299-305.

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

Gulland J.A. (1974) Distribution and abundance of whales in relation to basic productivity. In: The whale problem. (Ed.: Schevill W.E.) Harvard University Press, Cambrige, MA, 27-52.

Hamilton W.D. (1964) The genetical evolution of social behaviour I, II. Journal of Theoretical Biology 7, 1-52

Hammond P.S., Mizroch S.A. and Donovan G.P. (Eds.) (1990) Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission, Special Issue 12. The International Whaling Commission, Cambridge. 440 pages.

Hay K.A. and Mansfield A.W. (1989) Narwhal *Monodon monoceros* Linnaeus, 1758. In: River dolphins and the larger toothed whales. Handbook of marine mammals. Vol. 4. (Eds.: Ridgeway H. and Harrison R.) Academic Press, London, 145-176.

Heezen B.C. (1957) Whales entangled in deep sea cables. Deep-Sea Research 4, 105-115

Heimlich-Boran S.L. (1986) Cohesive relationships among Puget Sound killer whales. In: Behavioral Biology of Killer Whales. (Eds.: Kirkevold B.C. and Lockard J.S., Series Ed.: Maple T.L.) Zoo Biology Monographs, Volume 1. Alan R. Liss Inc., New York, 251-284.

Heyning J.E. (1997) Sperm whale phylogeny revisited: analysis of the morphological evidence. Marine Mammal Science 13, 596-613

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

Hinde R.A. (1983) Ultimate factors determining individual strategies, relationships and social structure. In: Primate social relationships, an integrated approach. (Ed.: Hinde R.A.) Sinauer Associates Inc., Sunderland, Massachusetts, 250-255.

Hoelzel A. R., Dalheim M. and Stern S. J. (1998) 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

Holthuis L.B. (1987) The scientific name of the sperm whale. Marine Mammal Science 3, 87-89

Hooker S.K. (1998) Extensive scarring observed on female or juvenile male sperm whales off the Galápagos Islands. Mammalia 62, 134-139

Hooker S.K., Whitehead H. and Gowans S. (in press) Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. Conservation Biology

Hope P.L. and Whitehead H. (1991) Sperm whales off the Galápagos Islands from 1830-50 and comparisons with modern studies. Reports of the International Whaling Commission 41, 273-283

Husson A.M. and Holthuis L.B. (1974) *Physeter macrocephalus* Linnaeus, 1758, the valid name for the sperm whale. Zoologische Mededelingen, Rijksmuseum van Natuurlijke Historie te Leiden 48 (19), 205-217

International Whaling Commission (1980) Chairman's report of the 30th meeting. Reports of the International Whaling Commission 30, 26-27

International Whaling Commission (1982) Report of the sub-committee on sperm whales. Reports of the International Whaling Commission 32, 68-86

International Whaling Commission (1986) Report of the workshop on the behaviour of whales in relation to management. Seattle, Washington, 19-23 April 1982. Reports of the International Whaling Commission, Special Issue 8, 1-56

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

Isbell L.A., Cheney D.L. and Seyfarth R.M. (1991) Group fusions and minimum group sizes in vervet monkeys (*Cercopithecus aethiops*). American Journal of Primatology 25, 57-65

IUCN (1996) 1996 IUCN red list of threatened animals. IUCN, Gland, Switzerland.

Ivashin M.V. (1978) Soviet investigations of Cetacea June 1976 to May 1977. Reports of the International Whaling Commission 28, 119-122

Janson, C.H. (1992) Evolutionary ecology of primate social structure. In: Evolutionary ecology and human behavior. (Eds.: Smith E.A. and Winterhalder B.). Aldine de Gruyter, New York, 95-130

Jaquet N. and Whitehead H. (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 organisation of antelope in relation to their ecology. Behaviour 48, 215-267

Jauniaux T., Brosens L., Jacquinet E., Lambrigts D., Addink M., Smeenk C. and Coignoul F. (1998) Postmortem investigations on winter stranded sperm whales form the coasts of Belgium and the Netherlands. Journal of Wildlife Diseases 34, 99-109

Jefferson T.A., Stacey P.J. and Baird R.W. (1991) A review of killer whale interactions with other marine mammals: predation to co-existence. Mammal Review 21, 151-180

Jones C.B. (1980) The functions of status in the mantled howler monkey, *Alouatta palliata* Gray: intraspecific competition for group membership in a folivorous neotropical primate. Primates 21, 389-405

Kahn B. (1991): The population biology and social organization of sperm whales (*Physeter macrocephalus*) off the Seychelles: Indications of recent exploitation. MSc Thesis, Dalhousie University, Halifax, Nova Scotia, Canada.

Kahn B., Whitehead H. and Dillon M. (1993) Indications of density-dependent effects from comparisons of sperm whale populations. Marine Ecology Progress Series 93, 1-7

Kanwisher J.W. and Ridgway S.H. (1983) The physiological ecology of whales and porpoises. Scientific American 248 (6), 199-218

Kappeler P.M. (1993) Variation in social structure: the effects of sex and kinship on social interactions in three lemur species. Ethology 93, 125-145

Kasuya T. (1998) Evidence of statistical manipulations in Japanese coastal sperm whale fishery. IWC document SC/50/CAWS10,

Kasuya T. and Marsh H. (1984) Life history and reproductive biology of the short-finned pilot whale *Globicephala macrorhynchus* off the Pacific coast of Japan. Report of the International Whaling Commission, Special Issue 6, 259-310

Kasuya T. and Ohsumi S. (1966) A secondary sexual character of the sperm whale. Scientific Report of the Whales Research Institute, Tokyo 20, 89-94

Kato H. (1984) Observation of tooth scars on the head of male sperm whale, as an indication of intra-sexual fightings. Scientific Report of the Whales Research Institute, Tokyo 35, 39-46

Kawakami T. (1980) A review of sperm whale food. Scientific Report of the Whales Research Institute, Tokyo 32, 199-218

Keller L. and Reeve H.K. (1994) Partitioning of reproduction in animal societies. Trends in Ecology and Evolution 9, 98-103

Kojima T. (1951) On the brain of the sperm whale (*Physeter catodon* L.). Scientific Report of the Whales Research Institute, Tokyo 6, 49-72

Krebs J.R. and Davies N.B. (1987) An introduction to behavioural ecology. 2nd edition. Blackwell Scientific Publications, Oxford,England.

Lee P.C. (1994) Social structure and evolution. In: Behaviour and evolution. (Eds.: Slater P.J.B. and Halliday T.R.) Cambridge University Press, Cambridge, 266-303.

Lindhard M. and Strager H. (1989): Andenes whale safari & sperm whale research. 1989 Progress Report.

Lindhard M., Knutsen L.O. and Strager H. (1988): The Norwegian Whale Safari Project 1988.

Lott D. (1984) Intraspecific variation in the social systems of wild vertebrates. Behaviour 88, 266-325

Lucas Z.N. and Hooker S.K. (1997): Cetacean strandings on Sable Island, Nova Scotia, 1990-1996. International Whaling Commission, Scientific Committee Document SC/49/06.

Lyrholm T. and Gyllensten U. (1998) Global matrilineal population structure in sperm whales as indicated by mitochondrial DNA sequences. Proceedings of the Royal Society of London. Series B. 265, 1679-1684

Lyrholm T., Leimar O. and Gyllensten U. (1996) Low diversity and biased substitution patterns in the mitochondrial DNA control region of sperm whales: implications for estimates of time since common ancestry. Molecular Biology and Evolution 13, 1318-1326

Mann J., Connor R.C., Tyack P. and Whitehead H. (Eds.) (in press) Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago.

Mantel N. (1967) The detection of disease clustering and a generalised regression approach. Cancer Research 27, 209-220

Matthews L.H. (1938) The sperm whale, *Physeter catodon*. Discovery Report 17, 93-168

Matthews N.E. and Porter W.F. (1993) Effect of social structure on genetic structure of free-ranging white-tailed deer in the Adirondack Mountains. Journal of Mammalogy 74, 33-43

Melnick D.J. and Kidd K.K. (1983) The genetic consequences of social group fission in a wild population of rhesus monkeys (*Macaca mulatta*). Behavioral Ecology and Sociobiology 12, 229-236

Melville H. (1851) Moby Dick or the whale. Northwestern University Press, Evanston (1988).

Messenger S.L. and McGuire J.A. (1998) Morphology, molecules, and the phylogenetics of cetaceans. Systematic Biology 47, 90-124

Milinkovitch M.C., Orti G. and Meyer A. (1993) Revised phylogeny of whales suggested by mitochondrial ribosomal DNA sequences. Nature 361, 346-348

Milinkovitch M.C., MeyerA and Powell J.R. (1994) Phylogeny of all major groups of cetaceans based on DNA sequences from three mitochondrial genes. Molecular Biology and Evolution 11, 939-948

Milinkovitch M.C., Orti G. and Meyer A. (1995) Novel phylogeny of whales revisited but not revised. Molecular Biology and Evolution 12, 518-520

Milinkovitch M.C., Leduc R.G., Adachi J., Farnir F., Georges M. and Hasegawa M. (1996) Effects of character weighting and species sampling on phylogeny reconstruction: a case study based on DNA sequence data in cetaceans. Genetics 144, 1817-1833

Mitchell C.L., Boinski S. and van Schaik C.P. (1991) Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). Behavioural Ecology and Sociobiology 28, 55-60

Moore J. (1984) Female transfer in primates. International Journal of Primatology 5, 537-589

Morgan B.J.T., Simpson M.J.A., Hanby J.P. and Hall-Craggs J. (1976) Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56, 1-43

Moss C. (1988) Elephant memories: thirteen years of life in an elephant family. William Morrow and Company, Inc., New York.

Moss C.J. and Poole J.H. (1983) Relationships and social structure of African elephants. In: Primate social relationships. (Ed.: Hinde R.A.) Sinauer Associates, Inc., Sunderland, Massachusetts, 315-325.

Mullins J., Whitehead H. and Weilgart L.S. (1988) Behaviour and vocalizations of two single sperm whales, *Physeter macrocephalus*, off Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences 45, 1736-1743

Mullis K., Faloona F., Scharf S., Saiki R., Horn G. and Erlich H. (1986) Specific enzymatic amplification of DNA in vitro: The polymerase chain reacion. Cold Springs Harbor Symposia on Quantitative Biology LI, 263-273

Myers J.P. (1983) Space, time and the pattern of individual associations in a group-living species: sanderlings have no friends. Behavioral Ecology and Sociobiology 12, 129-134

Norris K.S. and Dohl T.P. (1980) The structure and functions of cetacean schools. In: Cetacean behavior: mechanisms and functions (Ed.: Herman L.M.) Wiley-Interscience, New York

Norris K.S. and Harvey G.W. (1972) A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). In: Animal orientation and navigation. (Eds.: Galler S.R., Schmidt-Koenig K., Jacobs G.J. and Belleville R.E.) NASA Special Publications, Washington DC, 397-417.

Ohsumi S. (1966) Sexual segregation of the sperm whale in the North Pacific. Scientific Report of the Whales Research Institute, Tokyo 20, 1-16

Ohsumi S. (1971) Some investigations on the school structure of sperm whale. Scientific Report of the Whales Research Institute, Tokyo 23, 1-25

Ohsumi S. (1983) Parameters in sperm whale population models, needed from historical whaling record, and their sensitivity. Reports of the International Whaling Commission, Special Issue 5, 23-28

Olesiuk P.F., Bigg M.A. and Ellis G.M. (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

Osborne R. W. (1986) A behavioral budget of Puget Sound killer whales. In: Behavioral biology of killer whales. (Eds. Kirkevold B. and Lockard J. S.) Alan R. Liss Inc., New York, 211-249

Packer C. and Pusey A.E. (1983) Adaptations of female lions to infanticide by incoming males. The American Naturalist 121, 716-728

Packer C., Gilbert D.A., Pusey A.E. and O'Brien S.J. (1991) A molecular genetic analysis of kinship and cooperation in African lions. Nature 351, 562-565

Palacios D.M. and Mate B.M. (1996) Attack by false killer whales (*Pseudorca crassidens*) on sperm whales (*Physeter macrocephalus*) in the Galápagos Islands. Marine Mammal Science 12, 582-587

Palsbøll P.J., Berubé M., Larsen A.H. and Jørgensen H. (1997a) Primers for the amplification of tri- and tetramer microsatellite loci in baleen whales. Molecular Ecology 6, 893-895

Palsbøll P.J., Heide-Jorgensen M.P. and Dietz R. (1997b) Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from mtDNA analysis. Heredity 78, 284-292

Papastavrou V., Smith S.C. and Whitehead H. (1989) Diving behaviour of the sperm whale, *Physeter macrocephalus*, off the Galapagos Islands. Canadian Journal of Zoology 67, 839-846

Paterson R., Paterson P. and Cato D.H. (1994) The status of humpback whales (*Megaptera noveangliae*) in East Australia thirty years after whaling. Biological Conservation 70, 135-142

Penzhorn B.L. (1984) A long-term study of social organization and behaviour of Cape Mountain zebras, *Equus zebra zebra*. Zeitschrift fur Tierpsychologie 64, 97-116

Perry A., Baker C.S. and Herman L.M. (1990) Population characteristics of individually identified humpback whales in the Central and Eastern North Pacific: a summary and critique. Reports of the International Whaling Commission, Special Issue 12, 307-317

Pervushin A.S. (1966) Nabliudeniia za rodami u kasholotov. Zool. Zh. 45, 1892-1893

Poole J.H. and Thomsen J. (1989) Elephants are not beetles: implications of the ivory trade for the survival of the African elephant. Oryx 23, 188-198

Pope T.R. (1998) Effects of demographic change on group kin structure and gene dynamics of populations of red howling monkeys. Journal of Mammalogy 79, 692-712

Pusey A.E. (1983) Mother-offspring relationships in chimpanzees after weaning. Animal Behaviour 31, 363-377

Pusey A.E. (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution 2, 295-299

Pusey A.E. and Packer C. (1987) Dispersal and philopatry. In: Primate societies. (Eds.: Smuts B.B., Cheney D.L., Seyfarth R.M., Wrangham R.W. and Struhsaker T.T.) University of Chicago Press, Chicago, 250-266.

Queller D.C. and Goodnight K.F. (1989) Estimating relatedness using genetic markers. Evolution 43, 258-275

Ramírez P. (1989) Captura de cachalotes en Paita: 1976-1981. Boletin de Lima 63, 81-88

Reeves R.R. and Whitehead H. (1997) Status of the sperm whale, *Physeter macrocephalus*, in Canada. Canadian Field-Naturalist 111, 293-307

Reilly S. B. (1987) Reanalysis of rate of change in the California-Chukotka gray whale stock, 1967/68 – 1979/80. Reports of the International Whaling Commission 37: 347-349

Rice D.W. (1989) Sperm whale. *Physeter macrocephalus* Linnaeus, 1758. In: Handbook of marine animals. Vol. 4. (Eds.: Ridgway S.H. and Harrison R.) Academic Press, London, 177-233.

Rice D.W. (in press) Marine mammals of the world: systematics and distribution. Society for Marine Mammalogy, Special Publication 4.

Richard K.R., McCarrey S.W. and Wright J.M. (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., Dillon M.C., Whitehead H. and Wright J.M. (1996a) Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular analyses. Proceedings of the National Academy of Sciences 93, 8792-8795

Richard K.R., Whitehead H. and Wright J.M. (1996b) Polymorphic microsatellites from sperm whales and their use in the genetic identification of individuals from naturally sloughed pieces of skin. Molecular Ecology 5, 313-315

Rosenblum L.A., Kaufman I.C. and Stynes A.J. (1966) Some characteristics of adult social and autogrooming patterns in two species of macaque. Folia Primatologica 4, 438-451

Rowell T.E. (1972) Social behaviour of monkeys. Penguin, London.

Rowell T.E. (1979) How would we know if social organization were not adaptive? In: Primate ecology and human origins. (Eds.: Bernstein I.S. and Smith E.O.) Gartland STPM Press, New York and London, 1-22.

Rowell T.E. (1988) Beyond the one-male group. Behaviour 104, 189-201

Rutberg A.T. (1990) Inter-group transfer in Assateague pony mares. Animal Behaviour 40, 945-952

Saetersdal G., Mejia J. and Ramírez P. (1963) La caza de cachalotes en el Peru. Estadisticas de captura para los anos 1947-1961 y un intento de analizar las condiciones de la poblacion en el periodo 1954-1961. Instituto de Investigacion de los Recursos Marinos. Boletin 1(3), 45-84

Samuels A. and Gifford T. (1997) A quantitative assessment of dominance relations among bottlenose dolphins. Marine Mammal Science 13, 70-99

Sanger F., Nicklen S. and Coulson A.R. (1977) DNA sequencing with chain terminating inhibitors. Proceedings of the National Academy of Sciences 74, 5463-5467

Schevill W.E. (1986) The international code of zoological nomenclature and a paradigm: the name *Physeter catodon* Linnaeus 1758. Marine Mammal Science 2, 153-157

Schevill W.E. (1987) Reply to Holthius 1987. Marine Mammal Science 3, 89-90

Schnell G.D., Watt D.J. and Douglas M.E. (1985) Statistical comparison of proximity matrices: applications in animal behaviour. Animal Behaviour 33, 239-253

Scott T.M. and Sadove S.S. (1997) Sperm whale (*Physeter macrocephalus*) sightings in the shallow shelf waters off Long Island, New York. Marine Mammal Science 13, 317-321

Slooten E., Dawson S.M. and Whitehead H. (1993) Associations among photographically identified Hector's dolphins. Canadian Journal of Zoology 71, 2311-2318

Smith S.C. and Whitehead H. (1993) Variations in the feeding success and behavior of Galápagos sperm whales (*Physeter macrocephalus*) as they relate to oceanographic conditions. Canadian Journal of Zoology 71, 1991-1996

Smolker R.A., Richards A.F., Connor R.C. and Pepper J.W. (1992) Sex differences in patterns of association among Indian Ocean bottlenose dolphins. Behaviour 123, 38-69

Snowdon C.T. (1996) Infant care in cooperatively breeding species. In: Parental care: evolution, mechanisms and adaptive significance. (Eds.: Rosenblatt J.S. and Snowdon C.T.) Academic Press, San Diego, California

Snowdon C.T. and Hausberger M. (Eds.) (1997) Social influences on vocal development. University Press, Cambridge, UK. 352 pages.

Sterck E.H.M., Watts D.P. and van Schaik C.P. (1997) The evolution of female social relationships in nonhuman primates. Behavioural Ecology and Sociobiology 41, 291-309

Strager H. (1995) Pod-specific call repertoires and compound calls of killer whales (*Orcinus orca* Linnaeus 1758), in the waters of northern Norway. Canadian Journal of Zoology 73, 1037-1047

Sugg D.W., Chesser R.K., Dobson F.S. and Hoogland J.L. (1996) Population genetics meets behavioural ecology. Trends in Ecology and Evolution 11, 338-342

Terborgh J. and Janson C.H. (1986) The socioecology of primate groups. Annual Review of Ecology and Systematics 17, 111-135

Trivers R.L. (1971) The evolution of reciprocal altruism. Quarterly Review of Biology 46, 35-57

Trivers R.L. (1972) Parental investment and sexual selection. In: Sexual selection and the descent of man, 1871-1971. (Ed.: Campbell B.) Aldine, Chicago

Tutin C. (1996) Ranging and social structure of lowland gorillas in the Lope Reserve, Gabon. In: Great ape societies. (Eds.: McGrew W.C., Marchant L.F. and Nishida T.) Cambridge University Press, Cambridge, 58-70.

Tyack P. (1986) Population biology, social behavior and communication in whales and dolphins. Trends in Ecology and Evolution 1, 144-150

Tyack P.L. and Sayigh L.S. (1997) Vocal learning in cetaceans. In: Social influences on vocal development. (Eds.: Snowdon C.T. and Hausberger M.) Cambridge University Press, Cambridge, 208-233

Tyack P. and Whitehead H. (1983) Male competition in large groups of wintering humpback whales. Behaviour 83, 132-154

Valsecchi E. and Amos W. (1996) Microsatellite markers for the study of cetacean populations. Molecular Ecology 5, 151-156

van Schaik C.P. (1983) Why are diurnal primates living in groups? Behaviour 87, 120-144

van Schaik C.P. (1989) The ecology of social relationships amongst female primates. In: Comparative socioecology. The behavioural ecology of humans and other mammals (Eds.: Standen V. and Foley R.A.) Blackwell, Oxford, 195-218

van Schaik C.P. (1996) Social evolution in primates: the role of ecological factors and male behaviour. Proceedings of the British Academy 88, 9-31

van Schaik C.P. and van Hooff J.A.R.A.M. (1983) On the ultimate causes of primate social systems. Behaviour 85, 91-117

van Schaik C.P. and van Hooff J.A.R.A.M. (1996) Towards an understanding of the orangutan's social system. In: Great ape societies. (Eds.: McGrew W.C., Marchant L.F. and Nishida T.) Cambridge University Press, Cambridge, 3-15.

van Schaik C.P. and van Noordwijk M.A. (1988) Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). Behaviour 105, 77-98

Vehrencamp S.L. (1983) Optimal degree of skew in cooperative societies. Animal Behaviour 31, 667-682

Walsh P.S., Metzger D.A. and Higuchi R. (1991) Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. Bio-Techniques 10, 506-513

Waterman J.M. (1995) The social organization of the cape ground squirrel (Xerus inauris; Rodentia: Sciuridae). Ethology 101, 130-147

Waters S. and Whitehead H. (1990a) Population and growth parameters of Galapagos sperm whales estimated from length distributions. Reports of the International Whaling Commission 40, 225-235

Waters S. and Whitehead H. (1990b) Aerial behaviour in sperm whales. Canadian Journal of Zoology 68, 2076-2082

Watkins W.A. and Schevill W.E. (1977a) Spatial distribution of *Physeter catodon* (sperm whales) underwater. Deep-Sea Research 24, 693-699

Watkins W.A. and Schevill W.E. (1977b) Sperm whale codas. Journal of the Acoustical Society of America 62, 1486-1490

Watkins W.A., Moore K.E., Clark C.W. and Dahlheim M.E. (1988) The sounds of sperm whale calves. In: Animal sonar. (Eds.: Nachtigall P.E. and Moore P.W.B.) Plenum, New York, 99-107.

Watkins W.A., Daher M.A., Fristrup K.M., Howald T.J. and Notorbartolo di Sciaria G. (1993) Sperm whales tagged with transponders and tracked underwater by sonar. Marine Mammal Science 9, 55-67

Watts D.P. (1996) Comparative socio-ecology of gorillas. In: Great ape societies. (Eds.: McGrew W.C., Marchant L.F. and Nishida T.) Cambridge University Press, Cambridge, 16-28.

Weilgart L.S. and Whitehead H. (1986) Observations of a sperm whale (*Physeter catodon*) birth. Journal of Mammalogy 67, 399-401

Weilgart L.S. and Whitehead H. (1988) Distinctive vocalizations from mature male sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 66, 1931-1937

Weilgart L. and Whitehead H. (1993) Coda communication by sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. Canadian Journal of Zoology 71, 744-752

Weilgart L. and Whitehead H. (1997) Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behavioral Ecology and Sociobiology 40, 277-285

Weilgart L., Whitehead H. and Payne K. (1996) A colossal convergence. American Scientist 84, 278-287

Weinrich M.T. (1991) Stable social associations among humpback whales (*Megaptera novaengliae*) in the southern Gulf of Maine. Canadian Journal of Zoology 69, 3012-3018

Weller D.W., Wursig B., Whitehead H., Norris J.C., Lynn S.K., Davis R.W., Clauss N. and Brown P. (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. (1991) The role of long-term study in understanding the social structure of a bottlenose dolphin community. In: Dolphin societies: discoveries and puzzles. (Eds.: Pryor K. and Norris K.S.) University of California Press, Berkeley and Los Angeles, California, 199-225

Wells R.S., Scott M.D. and Irvine A.B. (1987) The social structure of free-ranging bottlenose dolphins. In: Current Mammalogy, Vol. 1 (Ed.: H. H. Genoways) Plenum Press, New York, 247-305

Werle E., Schneider C., Renner M., Volker M. and Fiehn W. (1994) Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Research 22, 4354-4355

White F.J. (1992) Pygmy chimpanzee social organization: variation with party size and between study sites. American Journal of Primatology 26, 203-214

Whitehead (1995) Investigating structure and temporal scale in social organizations using identified individuals. Behavioral Ecology 6, 199-208

Whitehead H. (1989) Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galápagos Islands. Canadian Journal of Zoology 67, 2131-2139

Whitehead H. (1990a) Assessing sperm whale populations using natural markings: a progress report. Reports of the International Whaling Commission, Special Issue 12, 377-382

Whitehead H. (1990b) Computer assisted individual identification of sperm whale flukes. Reports of the International Whaling Commission, Special Issue 12, 71-77

Whitehead H. (1993) The behaviour of mature male sperm whales on the Galápagos Islands breeding grounds. Canadian Journal of Zoology 71, 689-699

Whitehead H. (1995) Status of Pacific whale stocks before modern whaling. Reports of the International Whaling Commission 45, 407-412

Whitehead H. (1996a) Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral 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) Analysing animal social structure. Animal Behaviour 53, 1053-1067

Whitehead H. and Arnbom T. (1987) Social organization of sperm whales off the Galapágos Islands, February-April 1985. Canadian Journal of Zoology 65, 913-919

Whitehead H. and Carlson C. (1988) Social behaviour of feeding finback whales off Newfoundland: comparisons with the sympatric humpback whale. Canadian Journal of Zoology 66, 217-221

Whitehead H. and Dufault S. (in press) Techniques for analyzing vertebrate social structure using identified individuals: review and recommendations. Advances in the Study of Behavior

Whitehead H. and Gordon J. (1986) Methods of obtaining data for assessing and modeling sperm whale populations which do not depend on catches. Reports of the International Whaling Commission, Special Issue 8, 149-166

Whitehead H. and Kahn B. (1992) Temporal and geographic variation in the social structure of female sperm whales. Canadian Journal of Zoology 70, 2145-2149

Whitehead H. and Waters S. (1990) Social organisation and population structure of sperm whales off the Galápagos Islands, Ecuador (1985 and 1987). Reports of the International Whaling Commission, Special Issue 12, 249-257

Whitehead H. and Weilgart L. (1990) Click rates from sperm whales. Journal of the Acoustical Society of America 87, 1798-1806

Whitehead H. and Weilgart L. (1991) Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour 118, 275-296

Whitehead H. and Weilgart L. (in press) The sperm whale: social females and roving males. In: Cetacean societies: field studies of dolphins and whales. (Eds.: Mann J., Connor R.C., Tyack P. and Whitehead H.) University of Chicago Press, Chicago

Whitehead H., Gordon J., Mathews E.A. and Richard K.R. (1990) Obtaining skin samples from living sperm whales. Marine Mammal Science 6, 316-326

Whitehead H., Waters S. and Lyrholm T. (1991) Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behavioral Ecology and Sociobiology 29, 385-389

Whitehead H., Brennan S. and Grover D. (1992a) Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. Canadian Journal of Zoology 70, 912-918

Whitehead H., Waters S. and Lyrholm T. (1992b) Population structure of female and immature sperm whales (*Physeter macrocephalus*) off the Galapagos Islands. Canadian Journal of Fisheries and Aquatic Sciences 49, 78-84

Whitehead H., Christal J. and Dufault S. (1997) Past and distant whaling and the rapid decline of sperm whales off the Galapagos Islands. Conservation Biology 11, 1387-1396

Whitehead H., Dillon M., Dufault S., Weilgart L. and Wright J. (1998) Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. Journal of Animal Ecology 67, 253-262

Whitehead H., Christal J. and Tyack P. (in press) Studying cetacean social structure in space and time: innovative techniques. In: Cetacean societies: field studies of dolphins and whales. (Eds.: Mann J., Connor R.C., Tyack P. and Whitehead H.) University of Chicago Press, Chicago

Wrangham R.W. (1980) An ecological model of female-bonded primate groups. Behaviour 75, 262-300

Wrangham R.W. (1983a) Social relationships in comparative perspective. In: Primate social relationships: an integrated approach. (Ed.: Hinde R.A.) Blackwell, Oxford, 325-334.

Wrangham R.W. (1983b) Ultimate factors determining social structure. In: Primate social relationships, and integrated approach. (Ed.: Hinde R.A.) Sinauer Associates Inc., Sunderland, Massachusetts, 255-262.

Wrangham R.W. and Rubenstein D.I. (1986) Social evolution in birds and mammals. In: Ecological aspects of social evolution. (Eds.: Rubenstein D.I. and Wrangham R.W.) Princeton University Press, Princeton, New Jersey, 452-470.

Yablokov A.V. (1974): Proposal for agenda item 6.8.3. IWC document SC/SP74/Doc38, report prepared for a special meeting of the scientific committee of the International Whaling Commission, La Jolla, California. December 3-13 1974.

Yamada M. (1963) A study of blood-relationship in the natural society of the Japanese macaque: an analysis of co-feeding, grooming, and playmate relationships in Minoo-B troop. Primates 4, 43-65

Yeager C.P. (1991) Proboscis monkey (*Nasalis larvatus*) social organization: intergroup patterns of association. American Journal of Primatology 23, 73-86