To Sara,

This work is really half
yours. I couldn't have
done it without you. Thanks.

All my love,
Jim

Tenerife will always live on as
our great adventure. We accomplished
amazing things there! We proved our
strengths as a couple and as a family.
Con esperanza por la futura...

Te amo,
Jaime

SOCIAL ORGANISATION OF THE SHORT-FINNED PILOT WHALE, *Globicephala macrorhynchus*, WITH SPECIAL REFERENCE TO THE COMPARATIVE SOCIAL ECOLOGY OF DELPHINIDS

by

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Doctor of Philosophy

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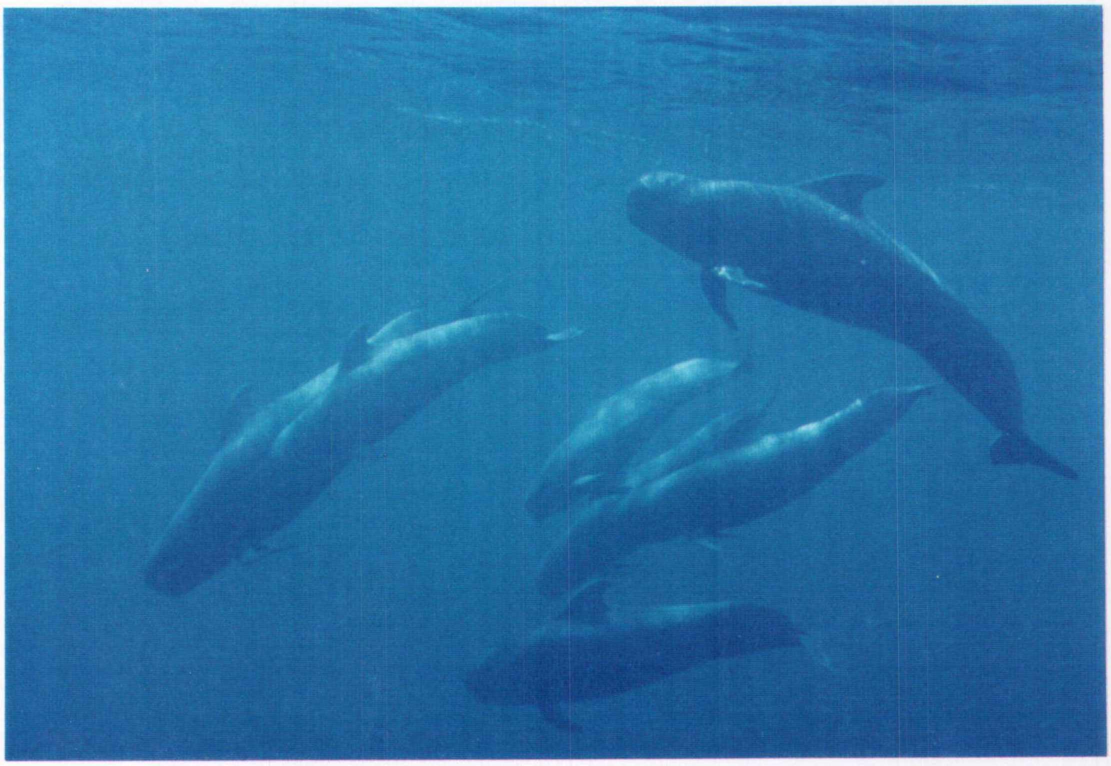
January 1993



Frontspiece. A family of short-finned pilot whales off Tenerife.

Dedicated to the memory of:

Robert J. Boran (1919 - 1982) and
Virginia R. Boran (1920 - 1990)

"Blackfish collect in schools, from ten or twenty, up to hundreds ... In low latitudes, during perfectly calm water, it is not unfrequent to find a herd of them lying quite still, huddled together promiscuously, making no spout and seemingly taking a rest."

Captain Charles M. Scammon, 1874

PREFACE

This thesis is the result of my own research, and contains no work done in collaboration, except where otherwise stated. The text does not exceed 80,000 words. No part of this thesis has been submitted to any other University in application for a higher degree.

ACKNOWLEDGEMENTS

This work was assisted by many people. First of all, I must thank my wife, Sara Heimlich-Boran, who helped throughout the project, both in the field and at home. Second, I thank my supervisor, Dr. John Harwood, for his contributions and patience. In Tenerife, I thank my friends and assistants, Sergio Escorza, Roberto Montero, Vidal Martin, and Robert Vonk. This project was supported by funding from Earthwatch, the American Museum of Natural History, the Whale and Dolphin Conservation Society, Cetacean Society International, and the American Cetacean Society. I also thank Dr. Tim Clutton-Brock and everyone from the Large Animal Research Group who gave me precious space in their lab and stimulating discussions over lunch.

SUMMARY

As a contribution to the understanding of comparative social trends within the cetacean family *Delphinidae*, a 22-month study was conducted on the short-finned pilot whale, *Globicephala macrorhynchus*, which has been suggested to have a unique social system in which males and females in the same group are related and mating occurs outside of the group. The individual identification of 495 pilot whales, analysed in daily group association patterns, allowed identification of 46 pods. They were classified as productive or non-productive based on the presence or absence of immature animals. Productive pods were significantly larger, although 12% of them lacked adult males. Two classes of whales (residents and visitors) were defined by patterns of occurrence, suggesting differential patterns of habitat use. Resident pods occasionally travelled together (41% of all groups) and associations between age and sex classes showed that in mixed-pod groups, the highest ranked associations of the reproductive females were with males from other pods, while within pods, adult males and females associated less. During summer, the proposed peak conception period, pilot whale groups were significantly larger and contained individuals from a significantly greater number of pods. These findings support the hypothesis that males and females mate when associating with individuals from other pods. A comparative analysis of sexual dimorphism, brain size, and testes size, habitat, prey and group size within the 17 delphinid genera identified a correlation between sexual dimorphism and body size, but relative measures of brain size and testes size did not correlate with broad ecological or social classifications. However, a comparison of three delphinid societies identified two distinct male mating systems: males of the small, mono-morphic *Tursiops truncatus* live in age/sex segregated groups and mate with a number of discrete female communities. Males in the large sexually dimorphic *Globicephala* spp. and *Orcinus orca* mate with associated female pods and yet remain with their female kin. This corresponds to the *avunculate* social system described in some human societies. It could evolve from a promiscuous mating system where there is little guarantee of paternity and where males that live with their kin increase their inclusive fitness.

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CHAPTER 1: INTRODUCTION

What are the benefits to group living? Societies, like physical characteristics, have evolved through adaptation to a variety of environmental selective pressures (Crook and Gartlan, 1966; Crook, 1970; Kummer, 1971; Alexander, 1974; Jarman, 1974; Wilson, 1975; Crook et al., 1976; Emlen and Oring, 1977; Jarman and Jarman, 1979; Eisenberg, 1981; Wrangham and Rubenstein, 1986). They are also dependent on the distribution and degree of interaction with close kin (Hamilton, 1964; West Eberhard, 1975; Kurland, 1977; Bertram, 1978; Michener, 1982; Packer and Pusey, 1982; Gouzoules, 1984; Sherman and Holmes, 1985; Trivers, 1985; Gouzoules and Gouzoules, 1987; Wade and Breden, 1987; Gittleman, 1989; Packer *et al.*, 1991). Indeed, kin selection, through the process of inclusive fitness (Hamilton, 1964), has been recognised as an important factor in the evolution of such basic societal elements as cooperation and altruism (Brown, 1978; Axelrod and Hamilton, 1981; Trivers, 1985; Moehlman, 1986; Moore, 1992), although certain forms of these elements also can occur with non-kin (Maynard Smith, 1979; Maynard Smith, 1982; Packer *et al.*, 1991; Mesterton-Gibbons and Dugatkin, 1992).

In most mammal species, however, it has been noted that one sex or the other disperses from their natal group, apparently to avoid inbreeding with close relatives and to find better feeding and mating opportunities elsewhere (Ralls *et al.*, 1979; Greenwood, 1980; Ralls *et al.*, 1980; Shields, 1982; Greenwood, 1983; Moore and Ali, 1983; Shields, 1983; Harvey and Ralls, 1986; Pusey and Packer, 1987a). In mammals, males are the most common sex to disperse (Greenwood, 1980). Species in which females are the emigrating sex have been shown to be those in which their age at first breeding exceeds the average male residence time (Clutton-Brock, 1989a); supporting the idea that dispersal is primarily a mechanism to avoid inbreeding.

The alternative to dispersal is natal philopatry, and it has been argued that the benefits of philopatry (even with certain degrees of inbreeding) and its occurrence in mammals has been underestimated (Bengtsson, 1978; Waser and Jones, 1983). In fact, there is some indication of the natal philopatry of both sexes in only a few species, for example, grey squirrels, blue duiker, brown hyenas and possibly Barbary macaques (Waser and Jones, 1983; Moore, 1992). Why is this so rare, and is there a direct, causal link between dispersal and the avoidance of inbreeding (Moore and Ali, 1983)?

I review evidence and present original observations on two mammals, the pilot whale, *Globicephala* sp., and the killer whale, *Orcinus orca*, both members of the order *Cetacea*, family *Delphinidae*, subfamily *Globicephalinae*, which appear to have very low (or possibly absent) levels of dispersal of either sex and resultant high degrees of relatedness between males and females within the same cohesive social group. A critical missing element in the understanding of cetacean societies is a description of the mating system. In order to develop hypotheses concerning delphinid mating systems, I also examine comparative trends in morphology, genetics and social behaviour within this diverse family.

Chapter 1 Introduction

1.1 THEORETICAL BACKGROUND

Ultimately, natural selection has operated on the costs and benefits to individuals of group living (Alexander, 1974). Social groupings occur when individual strategies of reproduction, resource acquisition and protection from predation are enhanced above and beyond the inevitable competition for mates and resources inherent in group living. The costs and benefits of these strategies are strongly affected by degrees of relatedness between individuals, resulting in kin selection through the process of inclusive fitness (Hamilton, 1964). In this light, much progress has been made in the study of social organisation by examining interactions between kin and non-kin utilising the methods of individual identification in long-term field studies of wild populations of ungulates (Clutton-Brock *et al.*, 1982), carnivores (Schaller, 1972; Packer, 1986; Packer *et al.*, 1988), elephants (Moss and Poole, 1983; Moss, 1988) and primates (Goodall, 1986; Stammbach, 1987). The strong social bonds in these groups are constantly tempered by competitive interactions for limited resources or mating opportunities. There are still many questions as to how these conflicts are mediated and what the resulting effects are on group stability.

A second fruitful method for understanding the diversity of social systems has been comparative studies, between related species in different environments or between different species in similar environments, in order to understand the selective pressures which are acting on the evolution of mammalian societies (Crook and Gartlan, 1966; Jarman, 1974; Clutton-Brock and Harvey, 1977; Harvey *et al.*, 1980; Harcourt *et al.*, 1981; Harvey and Bennett, 1983; MacDonald, 1983; Harvey and Harcourt, 1984; Schmitz and Lavigne, 1984; Harvey and Clutton-Brock, 1985; Gittleman, 1986; Packer, 1986; Wooton, 1987; Clutton-Brock, 1989b). These comparative studies have identified a variety of trends within and between mammalian orders, and have gone far towards explaining the evolution of life history and behaviour patterns. However, many groups of mammals are under-represented in these comparative analyses because of the difficulties involved in collecting long-term observations. This is true for many nocturnal, arboreal or burrowing mammals, but also for the order *Cetacea*, the whales and dolphins.

Cetaceans are the only permanently aquatic mammals, even pinnipeds (seals and sea lions) must come to land for breeding. The order contains species with the largest body size (the blue whale), the largest brain (the sperm whale), and the longest migration (the grey whale) of any mammal. They evolved from mesochinid condylarthan mammals in the middle Miocene, 60 million years ago (Gingerich *et al.*, 1983; Barnes, 1990) and colonised a completely different environment from that of terrestrial mammals. Although their closest terrestrial ancestors are the ungulates (Milinkovitch, 1991), they perhaps parallel the chiropterans in the degree of specialisation required for the colonisation of a three-dimensional medium (Norris and Schilt, 1988). Because they live in such a different environment, the study of cetaceans can provide a useful addition to an understanding of the ways in which habitat affects mammalian social systems (Würsig, 1989).

The cetacean family *Delphinidae* is especially suitable for comparative examination. The delphinid cetaceans exhibit a wide variability in body size, brain size, sexual dimorphism and social dynamics, from the 40 kg Hector's dolphin to the 4000 kg killer whale. Two recent long-term studies (each conducted for 20 years) have shown that dolphins exhibit a variety of group structures which offer opportunities for examining the determinants of fluctuations in group stability. Studies of the killer whale, *Orcinus orca*, the largest dolphin, have shown that this sexually-dimorphic animal travels in extremely stable, multi-male, female-biased groups for which no immigration or emigration has been documented (J.Heimlich-Boran, 1986a; 1986b; S. Heimlich-Boran, 1986; Hoelzel and Osborne, 1986; Osborne, 1986; Bigg *et al.*, 1987; J.Heimlich-Boran, 1988; S.Heimlich-Boran, 1988; Ford, 1989; Bigg *et al.*, 1990; Olesiuk *et al.*, 1990; Felleman *et al.*, 1991; Baird *et al.*, 1992). Males appear to grow to maturity and remain in their mother's social group throughout adulthood (S.Heimlich-Boran, 1986; 1988; Bigg *et al.*, 1990). In contrast, the smaller, relatively monomorphic bottlenose dolphin (*Tursiops truncatus*) lives in age and sex segregated groups and appears to have a more fluid social organisation, with frequent mixing between groups (Würsig and Würsig, 1977; Würsig, 1978; Würsig and Würsig, 1979; Shane *et al.*, 1986; Wells, 1986; Wells *et al.*, 1987; Ballance, 1990; Wells, 1991; Connor *et al.*, 1992a; 1992b). These variations in group structure and stability within a single mammalian family offer an excellent opportunity for comparative study to understand the causes of sociality.

Additional information on another large, sexually-dimorphic delphinid, the pilot whale (*Globicephala* sp.), has come from analyses of carcasses collected in conjunction with whaling operations. This whaling is done by driving entire social groups into restricted bays, and thus has provided some information on group composition. The primary anomalous feature of pilot whale social organisation is based on genetic research on long-finned pilot whales, *G. melas*, killed by Faeroese whalers, which has shown that group members, including the adult males, have a high degree of relatedness (Amos *et al.*, 1991a; 1991b; In press). This finding, similar to that described for *Orcinus*, implies a lack of dispersal and resultant strong degree of natal philopatry for both sexes. The prevalence of dispersal in most mammal and bird species has primaily been explained by the assumed necessary taboo on mating with close relatives in order to avoid inbreeding (Packer, 1979; Greenwood, 1980; Pusey, 1980; Shields, 1982; Greenwood, 1983; Moore and Ali, 1983; Shields, 1983; Pusey and Packer, 1987a; 1987b). Inbreeding is considered to have negative effects through an increase in homozygosity and the expression of deleterious, recessive genes (Ralls *et al.*, 1979; 1980). However, inbreeding can also be shown to have some positive effects (see also Shields, 1982; Moore and Ali, 1983; Shields, 1983). If a population has been inbred for many generations then the deleterious recessive genes should have been removed from the population through natural selection. The increased homozygosity may be an advantage in terms of kin selection because "inbred siblings are more closely related than outbred ones, and hence more able to benefit from kin selection" (p. 95: Moore and Ali 1983). Thus, inbreeding can promote sociality and altruism. Another positive effect of inbreeding could be "the establishment or maintenance of locality-specific co-adapted genomes" (Moore and Ali 1983; p. 96). Shields (1982, 1983) has even concluded that inbreeding may overcome the costs of sex (sensu: Williams, 1975; Maynard Smith, 1978) by reducing the rate of break-up of co-adapted parental genomes through meiosis. In light of the real costs of dispersal (e.g. increased mortality due to unknown resource distribution, predator concentrations, and conspecific inter- and intra-group competitive hierarchies), there may be a situation in which inbreeding is more beneficial than dispersing (Bengtsson, 1978). Shields (1982, 1983) developed the idea of "optimal inbreeding" in order to account for the necessity of balancing the costs of dispersing and the costs of inbreeding. Of course, there is no clear point at which a population becomes inbred; although definitions have been attempted such that "intense" inbreeding occurs when the breeding population is less than 100, or when partners are related closer than r=0.125, or full first cousins (Shields, 1982).

The occurrence of male natal philopatry, as suggested for killer whales and pilot whales, both sexually-dimorphic species living in multi-male groups, suggests a unique mating system (Greenwood, 1983; Shields, 1987). Delphinid mating systems are just beginning to be examined (Duffield and Wells, 1991). Paternity exclusion studies on long-finned pilot whales have shown that the adult males are not the fathers of the offspring in the groups (Amos *et al.*, 1991a; 1991b; In press), suggesting that mating is occurring between males and females from different social groups. This could be an indication of the concept of a "behavioural avoidance of inbreeding" proposed by Moore and Ali (1983), which appears to occur between close kin which come into contact with one another. The implication is that the social groups of these large delphinids are not mating groups, or at least that they have a highly cohesive nature for benefits other than immediate access to mating partners. Other benefits to group formation, such as improved avoidance from predation or improved resource acquisition through cooperation (Hamilton, 1971; Alexander, 1974; Bertram, 1978; Caro, 1987; Norris and Schilt, 1988; Packer and Ruttan, 1988; Packer *et al.*, 1990; Scheel and Packer, 1991), may be in effect. The possibility of this form of mating system appears to be unaccounted for in modelling of the evolution of mating systems (Clutton-Brock, 1989b). However, models such as these, based on elemental features of mammalian societies such as the distribution of mates and resources, have predictive value and throughout this thesis I will be reviewing the evidence provided by the current state of knowledge concerning the social ecology of dolphins and small whales in order to deduce elements of their mating systems.

Another anomalous feature of pilot whale society is that there is a relatively high percentage of post-reproductive females, who may live for 20-30 years beyond their last ovulation. Although an age-related decline in reproductive output is common for mammals (Clutton-Brock, 1984), a complete cessation with extended longevity is found only in a few primates (Hrdy and Whitten, 1987). The findings have come from shore fisheries for short-finned pilot whales (*G. macrorhynchus*) off Japan which have recorded males up to age 50 years and females up to age 70 (Kasuya and Marsh, 1984). One-quarter of the females greater than 36 years old showed no recent ovarian activity. Additionally, one-sixth of these post-reproductive females were still lactating (Kasuya and Marsh, 1984), probably due to the extended suckling of the last calf (Kasuya and Marsh, 1989). It has been hypothesised that a female near the end of her reproductive lifespan should increase her reproductive effort as her potential for future reproduction decreases (Fisher, 1930; Williams, 1966; Pianka, 1976; Clutton-Brock, 1984). By improving her calfs survival through a prolonged nursing period (as has been shown for red deer: Clutton-Brock *et al.*, 1982), the female may enhance her own lifetime reproductive success. The apparently inevitable decline in reproductive output through senescence results in selection for an increase in investment in the last offspring (Clutton-Brock, 1984). The continuation of life for 25 years after the last calf is born suggests that parental care is extremely important in these slowly-maturing mammals. These females may also provide additional benefits to the group such as assisting related females through the communal suckling of calves, a situation found in communal breeding mammals

(Gittleman, 1985), or perhaps serving as long-lived repositories of critical information about habitat and resources, as has been proposed for elephant matriarchs (Douglas-Hamilton and Douglas-Hamilton, 1975; Dublin, 1983; Moss and Poole, 1983; Moss, 1988). Observations of killer whales have confirmed a potentially similar situation: 24% of the adult females have never successfully given birth in 20 years and yet maintain close associations with other reproductive females who are assumed to be their daughters (Bigg *et al.*, 1990).

The observational studies of killer whales are just beginning to be confirmed through genetic analyses (Duffield, 1986; Stevens *et al.*, 1989; Hoelzel and Dover, 1990; Hoelzel, 1991a). However, there have been few detailed field studies of free-ranging pilot whales to examine the biological findings (although see Shane and McSweeney, 1990). For these reasons, a study of the social organisation of the pilot whale was undertaken to fill in gaps in the knowledge of social cetaceans.

1.2 AIMS OF THIS STUDY

I have examined the current state of knowledge of cetacean societies in the light of ecological and evolutionary theory, identified trends, and compared these findings with current theories of the evolution of society in terrestrial mammals.

Although there are useful large scale trends in mammalian evolution which could be identified from a study of all cetaceans, I focussed my attention on a comparative study of the social cetaceans. These are primarily the 37 species of the family *Delphinidae*, sub-order *Odontoceti*, the toothed whales (see Table 1.1 for a complete taxonomy). I examined trends in the characteristics of body size, brain size, sexual dimorphism and social dynamics for all delphinid species where data were available. I attempt to correlate the variability in these characteristics with broad environmental categories of favoured habitat and prey and compare these trends with terrestrial mammals in an attempt to isolate typical mammalian features of cetacean life from unique aquatic adaptations.

I also review a number of other long-term studies of delphinid social organisation to supplement the findings of evolutionary trends within *Delphinidae*. The primary sources of this information are from the studies of *Orcinus* and *Tursiops* mentioned above, but studies of other delphinid genera, although not as extensive, will also be reviewed in order to provide comparative results (Norris and Dohl, 1980a; Würsig and Würsig, 1980; Norris *et al.*, 1985; Kruse, 1989; Pryor and Shallenberger, 1991; Würsig *et al.*, 1989; 1991).

However, before analysing these trends, I describe an original study of the social organisation of the short-finned pilot whale, *Globicephala macrorhynchus*, conducted off the island of Tenerife, in the Canary Island archipelago. These islands, located just 200 km off the coast of northwest Africa, in an area of upwelling generated by the cold Canary current, had been reported to contain accessible populations of pilot whales and other smaller dolphins (Vonk and Martin, 1988; Herve-Gruyer, 1989; Herve-Gruyere, 1990). Utilising methods of individual identification (Würsig and Jefferson, 1990), a long-term study was initiated. This study is on-going and the results from almost two years presented here must be considered preliminary, as should any relatively short-term

Table 1.1. A list of the species, in taxonomic order, of the family *Delphinidae*, *Cetacea* (after Klinowska, 1991). References are selected studies concentrating on a given species and are not exhaustive

Scientific Name	Common Name	References
Order *Cetacea*		
Sub-Order *Odontoceti*	odontocetes	
Superfamily *Delphinoidea*		
Family *Delphinidae*	delphinids	
Subfamily *Steninae*:		
Steno bredanensis	rough toothed dolphin	
Sousa chinensis	Indo-Pacific humpbacked dolphin	28
Sousa teuszii	Atlantic hump-backed dolphin	3
Sotalia fluviatilis	tucuxi	12
Subfamily *Delphininae*:	delphinines	
Lagenorhynchus albirostris	white-beaked dolphin	
Lagenorhynchus acutus	Atlantic white-sided dolphin	
Lagenorhynchus obscurus	dusky dolphin	34,35
Lagenorhynchus obliquidens	Pacific white-sided dolphin	27,32
Lagenorhynchus cruciger	hourglass dolphin	
Lagenorhynchus australis	Peale's dolphin	
Grampus griseus	Risso's dolphin	23
Tursiops truncatus	bottlenose dolphin	see section 4.6.1.1
Stenella frontalis	Atlantic spotted dolphin	2
Stenella attenuata	pantropical spotted dolphin	2,13,15,21,25
Stenella longirostris	spinner dolphin	2,18,19,33,35
Stenella clymene	clymene dolphin	2
Stenella coeruleoalba	striped dolphin	2,16
Delphinus delphis	common dolphin	1,7,20,27
Lagenodelphis hosei	Fraser's dolphin	
Subfamily *Lissodelphinae*:		
Lissodelphis borealis	northern right whale dolphin	
Lissodelphis peronii	southern right whale dolphin	31
Subfamily *Cephalorhynchinae*:		
Cephalorhynchus commersonii	Commerson's dolphin	14
Cephalorhynchus eutropia	black dolphin	9
Cephalorhynchus heavisidii	Heaviside's dolphin	
Cephalorhynchus hectori	Hector's dolphin	11,29,30
Subfamily *Globicephalinae*:	globicephalines	
Peponocephala electra	melon-headed whale	5,10
Feresa attenuata	pygmy killer whale	24
Pseudorca crassidens	false killer whale	4,6,8,17,22,26
Orcinus orca	killer whale	see section 4.7.1.1
Globicephala melas	long-finned pilot whale	see Chapter 2
Globicephala macrorhynchus	short-finned pilot whales	see Chaps. 2, 3, & 4
Subfamily *Orcaellinae*:		
Orcaella brevirostris	Irawaddy dolphin	36

References: 1)Banks and Brownell, 1969; 2)Barlow, 1984; 3)Barros and Cockroft, 1991; 4)Brill *et al.*, 1992; 5)Bryden *et al.*, 1977; 6)Busnel and Dziedzic, 1968; 7)Collet and Saint Girons, 1984; 8)Comrie and Adam, 1938; 9)Crouetto and Medina, 1991; 10)Dawbin *et al.*, 1970; 11)Dawson and Thorpe, 1990; 12)Geise, 1991; 13)Hohn *et al.*, 1985; 14)Mermoz, 1980; 15)Myrick *et al.*, 1986; 16)Nishiwaki, 1975; 17)Nishiwaki and Tobayama, 1982; 18)Norris and Dohl, 1980; 19)Norris *et al.*, 1985; 20)Overholtz and Waring, 1991; 21)Perrin, 1969; 22)Pilleri, 1967; 23)Pilleri and Gihr, 1969; 24)Pryor *et al.*, 1965; 25)Pryor and Shallenberger, 1991; 26)Purves and Pilleri, 1978; 27)Ridgway and Green, 1967; 28)Saayman and Tayler, 1979; 29)Slooten and Dawson, 1992; 30)Thorpe *et al.*, 1991; 31)von Waerebeek, 1991; 32)Walker *et al.*, 1986; 33)Wells, 1984; 34)Würsig *et al.*, 1991; 35)Würsig and Würsig, 1980; 36)Gretarsdottir and Arnason, 1992 observational study on a long-lived, slow-maturing mammal. However, these results do contribute to an understanding of the family-wide trends in social behaviour analysed here.

This thesis begins with a review of the biological knowledge of pilot whales, and proceeds with results from my own field work on the distribution, behaviour and social structure of short-finned pilot whales are presented. Finally, I compare biological and behavioural trends within the delphinid cetaceans and attempt to integrate my findings with the current understanding of the evolution of mammalian social systems.

1.3 SUMMARY

Recent information on two delphinid cetaceans which live in highly cohesive social groups of mixed age and sex has suggested that both sexes remain in their natal groups into adulthood, resulting in high degrees of relatedness between males and females in the same social group. This questions the proposed relationship between dispersal and the avoidance of inbreeding. The benefits of living with kin are great and certain degrees of inbreeding have been shown to be important in the evolution of societies. The critical question relates to the nature of the mating system in these cetaceans. Comparative analyses of morphology, genetics and social behaviour of all delphinids, including original research on one of the aforementioned species, the short-finned pilot whale, is proposed. The study of the evolution of mammalian societies would benefit from a better understanding of delphinid cetaceans, who share common ancestry with terrestrial mammals and yet have adapted to life in an extremely different environment. Delphinid cetaceans are especially well-suited to examination because they exhibit a wide degree of variability in body size and social behaviour. Results from this study will be compared with trends in the evolution of terrestrial mammalian societies.

CHAPTER 2: REVIEW OF THE LIFE HISTORY AND BEHAVIOUR OF PILOT WHALES (*Globicephala* spp.)

2.1 INTRODUCTION

This chapter will provide an overview of the current knowledge of the morphology, physiology, behaviour and ecology of *Globicephala*. The scope of this review will be limited to those aspects which are used in later sections of this thesis; specifically: external appearance, taxonomy, genetics, sex differences in growth and body size, life history parameters of mortality and reproduction, ecological aspects of distribution and feeding ecology, and current knowledge on social organisation. These parameters are relevant to an understanding of the results of the field observations on *G. macrorhynchus* presented in Chapters 3 and 4, as well as contributing to knowledge of the comparative status of *Globicephala* within the family *Delphinidae* (Chapter 5).

Throughout this chapter, I will first present information for *G. macrorhynchus*, followed by a summary of any differences reported for *G. melas*. Most of the information comes from specimens collected in conjunction with whaling operations in Japan and the Faeroe islands, but information on world-wide distribution is primarily from strandings. Pilot whales are one of the most common cetacean species to strand, especially as a group in a mass stranding (Sergeant, 1982; Klinowska, 1986).

2.2 EXTERNAL APPEARANCE

The pilot whale (*Globicephala* spp.) is a medium to large delphinid, ranging in adult size from 3.6 to 6.3 m (see Section 2.5.1). There are two species recognised, the short-finned pilot whale, *G. macrorhynchus*, and the long-finned pilot whale, *G. melas* (see Section 2.3). As suggested by their names, they differ in the relative length of the pectoral flipper. In the short-finned species, the pectoral fin (measured from axilla to tip) is less than 15% of the body length (mean = 14.4%), while in the long-finned species it is greater than 16% (mean = 18.7%: Sergeant, 1962b). There are also other skeletal differences, chiefly in skull morphology (Fraser, 1950; van Bree, 1971).

Pigmentation is predominately black, hence the common name, "blackfish". There are three areas of lighter pigmentation which have been found to vary, both between species and between individuals of the same species (Yonekura *et al.*, 1980): the *throat patch*, the *post-dorsal saddle patch*, and the *post-ocular patch* (sensu Mitchell, 1970). The throat patch is a trident-shaped, light-grey patch located on the ventral surface which begins approximately below the angle of the gape of the mouth and the eye. The outer side prongs of this trident taper posteriorly to the axilla of the pectoral fins, while the central prong extends along the length of the body to the anus (the *mid-ventral streak* of Mitchell, 1970). This central stripe broadens into the *genital patch* around the genital slit in both species, extending outwards around the mammary slits in the female (Sergeant, 1962b; Mitchell, 1970; Yonekura *et al.*, 1980), and may help the young locate the mammaries during nursing (Mitchell, 1970). The throat patch is most distinct on the long-finned pilot whale (Sergeant, 1962b), appear-ing light grey to almost white, while it is faint to lacking in the short-finned pilot whale (Norris and Prescott, 1961; Yonekura *et al.*, 1980).

The post-dorsal saddle patch is just posterior to the dorsal fin. This patch covers the dorsal mid-line of the backbone, extending slightly forward to below the dorsal fin and down to the lateral mid-line of the body. The patch tapers posteriorly, extending to a point just anterior to the insertion of the tail flukes. The saddle patch appears slightly more distinct on short-finned pilots than on the long-finned species (Norris and Prescott, 1961). The whiteness of the patch also varies between two segregated forms of short-finned pilot whales off Japan, with the northern form having a whiter saddle than the southern form (Kasuya *et al.*, 1988a). Another distinction between these two forms is the distinctness of the posterior margin of the saddle. The northern form has a distinct posterior margin and the saddle does not extend posteriorly beyond the level of the anus, while on the southern form, the saddle gradually fades into the black body colour and extends almost to the tail flukes (Kasuya *et al.*, 1988a). These distinctions are most apparent on mature adults.

The post-ocular patch begins as a light grey spot dorso-posteriorly to the eye. It extends up towards the anterior insertion of the dorsal fin (Yonekura *et al.*, 1980). On short-finned pilot whales off the Canary Islands, this patch continues ventral to the dorsal fin, grading into the forward extension of the post-dorsal saddle.

It is interesting that the locations of these patches on pilot whales are similar to that of the more striking white marking of the killer whale (Davies, 1960). The eye spot, dorsal saddle patch and white ventral markings are broadly similar. Similarities in the pigmentation patterns of the smaller delphinids has also been noted by Mitchell (1970), who suggested they were adaptive responses for camouflage likely to represent evolutionary changes in pigmentation patterns from ancestral characteristics.

2.3 TAXONOMY

The genus *Globicephala*, meaning "round head", was first proposed by René Lesson in 1828. There are currently two accepted species: *Globicephala melas* Traill 1809 and *Globicephala macrorhynchus* Gray 1846 (Klinowska, 1991). The taxonomy of *Globicephala* has changed even recently and it is worth reviewing the history of the changes. I believe that there are important issues of variation within and between populations which can be addressed by an examination of taxonomy.

Specimens of the currently accepted genus *Globicephala* have been known under a variety of names: *Delphinus* Cuvier 1812, *Globicephalus* Lesson 1828, *Globiceps* Flower 1884, and *Sphaerocephalus* Gray 1864 (Hershkovitz, 1966). These were all clearly synonyms of *Globicephala*. There have been an even greater number of species names assigned to the two accepted species, but I will only review some of the more recent variations.

The short--finned pilot whale, *Globicephala macrorhynchus*, was named by Gray in 1846 (Gray, 1846) from a skull collected in the "South Seas". This is currently accepted as the only warm-water *Globicephala* species and is distributed throughout all tropical oceans (see Section 2.6.1). Other specific names were used for tropical *Globicephala*: *G. brachyptera* from the western Atlantic of America (Cope, 1876), *G. scammoni,* from the Pacific explorations of the whaler Charles Scammon (Scammon, 1869; Cope, 1876), and G. *seiboldii* (Gray, 1846). Gray later considered G. *seiboldii* to be a synonym of G. *macrorhynchus* (Gray, 1871), and the name fell out of use. Hershkovitz, in his Catalog of Living Whales, resurrected the name as a sub-species of *G. melaena*, applying to Pacific Ocean, tropical *Globicephala* (Hershkovitz, 1966). Van Bree reanalysed the type specimen of *G. seiboldii* and confirmed that it was a synonym for *G. macrorhynchus* (van Bree, 1971). *G. brachyptera* was reanalysed by Fraser and was also considered to be a synonym of *G. macrorhynchus* (Fraser, 1950). *G. scammoni* was used as the name for the Pacific short-finned pilot whale until recently (Norris and Prescott, 1961; Sergeant, 1962b), although it is now also considered to be a synonym for *G. macrorhynchus* (van Bree, 1971; Klinowska, 1991).

The long-finned pilot whale, *Globicephala melas* Traill 1809, has a less complicated history, although it has more recent controversy surrounding it. The earliest name given to the species was *Delphinus melas* by Traill in 1809. The genus was subsequently changed to *Globicephala* in 1828, as described above. In 1898, Thomas changed *melas* (from the Greek adjective, μελασ, meaning "black") to the latinized feminine form, *melaena*, in order to match the feminine generic name (Hershkovitz, 1966). Two species names had also been assigned to the southern hemisphere population of the long-finned pilot whale: *G. edwardii* Smith 1834 and *G. leucosagmaphora* (Rayner, 1939). Davies (1960) reviewed these and suggested they be given sub-specific status (*G. melaena edwardii*), distinguished from the northern form *(G.m.melaena)* on the basis of a greater amount of white pigmentation on the ventral, dorsal, and post-ocular patches (as defined in Section 2.2). Hershkovitz combined these two sub-species into the single sub-species *G. melaena melaena* and assigned the short-finned pilot whale to another sub-species, *G. m. sieboldi* (Hershkovitz, 1966). Finally, van Bree analysed the distinct features of the warm-water and cold-water pilot whales, and acknowledged the wide variation within these forms, and proposed each be given specific status as *G. macrorhynchus* and *G. melaena* (van Bree, 1971). *G. melaena* was the accepted species name for the long-finned pilot whale until 1989, when two eminent cetologists entered into a taxonomic debate. Dale Rice proposed reverting to the original masculine form, as this predated the feminine form (Rice, 1989), and the International Code of Zoological Nomenclature (1985 edition) recommends retention of original specific names, even though the generic name may not match it in gender, in the case of non-Latin (or non-Latinized) words (Rice, 1990)*. Schevill disagreed and pointed out that there was justification of the original changing of the specific name from *melas* to *melaena* because *melas* qualified as a latinized Greek word, and the Zoological Code allows the changing of specific names to match their new genus for latinized words (Schevill, 1990a). Thus, Schevill argued, the change from *melas* to *melaena* was justified and should be retained since it had come into such com-

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* The distinction between "transliteration" and "latinization" is at the core of the issue. The Zoological Code states: "When a Greek word in transliterated its letters are given their exact equivalents. When it is latinized it is given the form which is determined by the usage of classical Latin or, where that differs, of modern scientific Latin"; cited in Rice, 1990).

mon usage in the 20th century (Schevill, 1990a). Rice maintained that *melas* was clearly a Greek word that was transliterated (copied letter for letter) into Latin (as opposed to being "Latinized"), and thus was not eligible for change with a change in genus. He thus continued to recommend the name *Globicephala melas* (Rice, 1990). Schevill, in a response following Rice's most recent correspondence, contended that *melas* was the result for both a latinization and a transliteration of the Greek word for "black", and still maintained the usage of *melaena* (Schevill, 1990b). Thus, it is still possible to find both names today. I have followed Klinowska in her usage of *G. melas* (Klinowska, 1991).

The history of the naming of numerous species for the genus *Globicephala* illuminates a real phenomenon: geographic variation. There has been a trend towards a reduction in the number of species recognised in the classification of many genera of cetaceans. Much of this is due to an understanding of geographic variation in cetacean species (Perrin, 1984). Numerous characters, especially pigmentation, have been found to vary widely within an accepted species (Mitchell, 1970). This is also the case for *Globicephala*.

2.4 GENETICS

Recently, genetic methods for analysing the genetic diversity of populations and documenting paternities and relatedness (Burke, 1989) have been applied to populations of both pilot whale species. These results are interesting because they begin to provide an indication of the patterns of gene flow, and thus mating systems, in these whales. The techniques of DNA "fingerprinting" and the analysis of enzyme variability have both been used in these studies (Andersen, 1988; Wada, 1988; Amos *et al.*, 1991a; 1991b; In press). DNA "fingerprinting" allows the genetic variability of individuals to be identified from the electrophoretic analyses of allelic variation in hyper-variable fragments of DNA (Burke, 1989). It is most often used as a method to determine paternity. Electrophoretic enzyme analysis examines the allelic variability of polymorphic enzymes, but has a much lower resolution than DNA fingerprinting and can only be used to quantify population-wide variability (Andersen, 1988). All information reviewed here has been collected from whaling specimens.

The evidence for short-finned pilot whales suggests that they have a strong tendency to form discrete populations. For example, two forms of short-finned pilot whales hunted off the coast of Japan (Kasuya *et al.*, 1988a) have been shown to be genetically distinct (Wada, 1988). Wada (1988) studied electrophoretic enzyme differentiation on a sample of 204 northern-form and 167 southern-form pilot whales. A significant difference in gene frequencies was identified for the two forms, but the genetic distance between them was calculated to be at the inter-population level, indicating they were genetically isolated stocks (Wada, 1988). The two groups also had phenotypic differences in body size and pigmentation patterns (Kasuya *et al.*, 1988a). The northern form is larger (1.0 m for adult females and 2.0 m for adult males) than the southern form. There are also differences in body proportions: the head is rounder (when viewed from above), the dorsal fin of the male is slightly narrower and the flipper length is slightly longer in the northern form when compared to the southern form (Kasuya *et al.*, 1988a). The northern form also has a more prominent post-dorsal saddle patch.

The remainder of the genetic analyses I will review are on the long-finned pilot whales captured off the Faeroe Islands in the north Atlantic. The combination of the results from these studies show that pilot whales exhibit low levels of genetic variability within schools, while variability between some schools was found to be high, suggesting a degree of stock differentiation (Andersen, 1988; Amos *et al.*, 1991a; 1991b; In press).

The relatedness of individuals within pods was tested by comparing the observed to expected ratio of shared alleles for four age classes to determine whether individuals were accompanied by their mothers, their fathers or other more distantly related animals. The proportion of animals with their true mothers ranged from 80% for the youngest individuals to 25% for adults. However, the number of animals with their fathers was close to 0 for all age classes. This is evidence of a matrilineal social system (Amos *et al.*, In press). The shared proportion of alleles was also high among adult males, providing evidence that males remain in their natal pods (Amos *et al.*, In press).

For the DNA analyses, tissue samples (skin, kidney or muscle) were collected from 326 pilot whales from five pods (Amos *et al.*, 1991a; 1991b). The average band-sharing coefficient (the number of shared bands divided by the total number of bands) between randomly selected individuals from different pods was 0.56 (range: 0.37-0.78), a higher value than that reported for birds or humans (0.1 - 0.3), indicating low genetic variability (Amos *et al.*, 1991a).

Exclusion paternity analyses were conducted on five pods (34 mother/foetus pairs and 37 adult males) which had been completely sampled (Amos *et al.*, 1991a; 1991b). These analyses did not allow positive paternity assignments, only the exclusion or non-exclusion of specific males. Mature males from the same pod were excluded as fathers for 30 of the 34 mother/foetus pairs (88%) in paternity tests for 299 possible within-pod male/foetus pairs. In one case, a possible father from a different pod than the mother/foetus pair was identified out of 959 possible between-pod male/foetus pairs. In the four cases where possible fathers were identified from the foetal pod, the length of the foetus averaged 0.088 m and in all cases was less than 0.020 m in length, equivalent to a foetal age of less than five months. This suggested that breeding adult males and females are not maintaining a long-term association within the same pod (Amos *et al.*, 1991a).

A closer examination of the paternal alleles (i.e. those foetal alleles not found in the mother) in the foetuses of two cohorts from 30 mother/foetus pairs in the three largest pods was done to examine the relative paternal contribution to cohorts. This was to find out whether one male had fathered all of the calves in a cohort or whether there were indications of multiple fathers. It was found that the likelihood of all foetuses from the same pod and same cohort having a single male as father was 36 times greater than the likelihood that each foetus had a different father and five times greater than any specific combination of two fathers (Amos *et al.*, 1991a; 1991b). In any event, there were certainly fewer fathers than foetuses, indicating either that individual males were achieving multiple matings or possibly that groups of related males were breeding together (Amos *et al.*, 1991a; 1991b). Thus, pilot whales appear to fit the predicted variability in male reproductive success common to polygynous mammals (Clutton-Brock, 1986). On the other hand, the comparison of paternal genotypes between two foetal cohorts within the same pod indicated that the same male could not have been responsible for breeding in successive years (Amos *et al.*, 1991a). Thus, pilot whales do not appear to represent an extreme example of polygyny. This latter result also supports the hypothesis that males are not maintaining contact with (or exclusive access to) the same group of breeding females from year to year (Amos *et al.*, 1991a; 1991b).

Allele frequencies were also compared between adult females from the two largest pods and identified significant differences in allelic distribution ($X^2 = 43.5$, df = 9, P <<.001), indicating genetic divergence between the pods (Amos *et al.*, 1991b). This was surprising since the two pods were caught in nearby areas just two days apart. However, the ranking of the various alleles was similar for the two pods (Spearman r = 0.73, N = 16, P << .001), indicating a certain degree of relatedness due to “a shared genetic past or through genetic inputs from a common gene pool” (Amos *et al.*, 1991b, p.263).

There were also indications that adult males from the same pod were related. The method used to examine this was an examination of the frequencies of single locus alleles for heterozygotes, since heterozygotes should be more common in siblings (Amos *et al.*, 1991a). Males from both pods showed an excess of heterozygotes, although the excess was only significant in one of the pods and could have been due to the small sample sizes (Amos *et al.*, 1991a; 1991b).

Another finding was considered to be indicative of relatedness between two pods, perhaps in the form of "sister matrilines" (Amos *et al.*, 1991b). This was done by examining changes in the frequency of single alleles with the ages of the animals for two different pods. Parallel variation in the frequency of the “F” allele was identified for these two pods, especially for older animals. This was in spite of the fact that the overall frequency of the “F” allele varied by a factor of two between the pods. Correlated changes in allele frequency from age class to age class can provide some idea of the pattern of genetic input from males and females. However, female input would tend to dampen correlated variation, since females of different ages breed each year and the different allele frequencies between the two pods would be emphasised. If male genetic input was shared between the two pods for any given year, but varied from year to year, then the observed correlated changes in the allele frequency of similarly aged animals could be explained. Thus, a possible interpretation would be that the two pods represented “‘sister’ matrilines which have experienced similar male genetic input” (Amos *et al.*, 1991b, p.265) and the lower correlation for younger age classes would suggest that “although still spending time together, the pods have recently split, leading to divergent male inputs” (Amos *et al.*, 1991b, p.265).

The resulting picture of long-finned pilot whale social organisation is that pods represent groups of maternally-related females, i.e. that the social system is matrilineal (Amos *et al.*, 1991a). The mating system and specifically the reproductive success of males in these pods is not quite as clear. Since males did not appear to breed within their social group (perhaps deterred from mating with related pod females through behavioural inbreeding avoidance), they must be mating with females in other pods (Amos *et al.*, In press). Variance in male reproductive success was suggested, but the mechanism of how this operates is unknown. Perhaps there are elements of polygyny in this system, in that only a few external males are successful breeders (Amos *et al.*, 1991a), but there are only rare instances of all-male groups reported for pilot whales (Sergeant, 1962a;

Kasuya and Marsh, 1984; Chapter 4). The system still requires further examination.

2.5 LIFE HISTORY PARAMETERS

Knowledge of the life history parameters of *Globicephala* has primarily come from data collected in conjunction with whaling operations. Most of the methods used in these studies are standard, and thus suitable for comparison. The methods of age determination are the core of the results presented here and have been the subject of much analysis . Toothed cetaceans grow one set of teeth during their life. As the teeth grow, rings of dentine and cementum are laid down, much like the rings of a tree. This is likely to be due to within-year variation in net energy balance, perhaps relating to the diet. The controversy is over the rate at which these rings are deposited. Most evidence points to an annual rate of ring deposition, but there have been relatively few studies where it has been possible to document this with other sources of information (e.g. direct knowledge of the age of an animal born in captivity). There is also annual variation in the deposition of dentine which can result in thin rings which are difficult to recognise. The preparation of the materials (i.e. sectioning, staining, etc.) can also affect the readability of rings. However, some early studies (e.g. Sergeant, 1962a) have been reanalysed using more modern techniques (Kasuya *et al.*, 1988b), enhancing their comparability.

2.5.1 Body Size and Growth

An understanding of the patterns of growth in *Globicephala* was necessary for an estimation of the age and sex classes of whales identified photographically in the Canary Islands field study. The most complete data on body size and growth for short-finned pilot whales comes from the whaling operations off the Pacific coast of Japan (Yonekura *et al.*, 1980; Kasuya and Marsh, 1984; Kasuya and Matsui, 1984). Data were collected on 27 schools totalling 806 animals (565 females, 241 males and a few individuals of unknown sex) over a 16 yr period (Kasuya and Marsh, 1984). Dentinal layers were analysed and were determined to be deposited annually (Kasuya and Matsui, 1984).

Short-finned pilot whales are born at approximately 1.4 m and weighing 37 kg (Kasuya and Marsh, 1984; Kasuya and Matsui, 1984). The largest foetus of 36 specimens was 1.46 m and the smallest of 11 calves below 1.7 m was 1.36 m. The mean length at birth was calculated from the five smallest neonates (1.36 m - 1.42 m). Growth is rapid during the first 1.25 yrs, with both sexes averaging 2.30 m by the end of this period (Kasuya and Matsui, 1984). At this point, although growth rates slow for both sexes, males begin to grow faster than females. By 2.5 yrs of age, males are about 0.06 m larger than females (Kasuya and Matsui, 1984). Female growth continues at an annual rate of about 0.11 m/yr until a length of approximately 3.22 m is attained at the age of first ovulation of 9.0 yrs (Kasuya and Marsh, 1984). For males, this period lasts until about 10 yrs of age, with a slightly faster growth rate of 0.12 m/yr. At the end of this period, males are approximately 3.44 m in length, or around 0.2 m larger than females. The next phase of female growth is characterised by a slowing of the growth rate to about 0.03 m/yr until they reach their asymptotic length of 3.64 m at an age of 22 yrs (Kasuya and Matsui, 1984). In males, this next phase of growth continues until 27 yrs of age and an asymptotic length of 4.73 m. The growth rate is high (up to 0.13 m/yr) until the attainment of sexual maturity at lengths of 4.01 m to 4.22 m and ages of 14.6 yrs to 17 yrs (mean = 4.14 m and 15 yrs: Kasuya and Marsh, 1984). Then growth rate slows to about 0.03 m/yr until the asymptotic length is reached (Kasuya and Matsui, 1984). After the age of 22 for females and 27 for males, all individuals stop growing. Of course, there was variation in these growth patterns: the largest male recorded was 5.80 m and the largest female was 4.05 m.

Body weights were collected for 13 foetuses and 18 postnatal animals, up to the largest female of 3.55 m and 751.9 kg and the largest male of 2.91 m and 379.22 kg (Kasuya and Matsui, 1984). A length-weight relationship was calculated from these data:

$$\text{Weight (kg)} = 2.377 \times 10^{-5} * \text{Body Length(cm)}^{2.8873}$$

Although males were under-represented in the data used to generate this equation, the authors consider it valid for adults of both sexes (Kasuya and Matsui, 1984). Predicted weights for asymptotic adult body lengths were 1256 kg for males and 590 kg for females.

The resulting pattern of growth shows a high degree of sexual dimorphism for *G. macrorhynchus*, with adult males growing 1.3 times longer and 2.1 times heavier than females

Changes in body proportion with growth were also examined for 17 foetuses and 143 postnatal individuals from the same population (Yonekura *et al.*, 1980). The greatest variation was in the development of the melon. At birth, the melon is similar to that of other delphinids: a slight bump on the sloping forehead. The beak is well distinguished and projects approximately 0.02 m beyond the melon. However, by a length of 2.4 m (age = 2 yrs: Kasuya and Matsui, 1984), the melon begins to project beyond the snout (Yonekura *et al.*, 1980). After this, the degree of melon projection (MP: in cm) can be described by the equation:

$$\text{MP} = (1.257 \times 10^{-4} * \text{Body Length}^{2}) - (4.517 \times 10^{-2} * \text{Body Length}) + 3.64$$

This equation accurately described the rate of change in melon projection with body length for both males and females (Yonekura *et al.*, 1980). In other words, a male and female of the same length will have the same degree of melon projection, and thus melon projection is not a secondary sexual characteristic (Yonekura *et al.*, 1980). However, since male length at maturity (4.14 m) was greater than either the female asymptotic length (3.64 m) or the largest female recorded (4.05 m), all mature males have a greater degree of melon projection than mature females.

The growth parameters of long-finned pilot whales are broadly similar to those of short-finned pilot whales. The data available for long-finned pilot whales has come from measurements of 4641 whales, although only 437 of these animals were aged (Sergeant, 1962a). Kasuya *et al.*, (1988b) reanalysed the ages of all of the pilot whales from Sergeant's samples. Martin reported on the lengths of 116 pilot whales (52 of which were aged), that had stranded in Britain (Martin *et al.*, 1987). The main difference between the two species is that long-finned pilot whales are larger than short-finned pilot whales at all life stages. Length at birth is 0.37 m longer, length at female maturity is 0.49 m larger, and length for males at maturity is 0.76 m longer (Kasuya *et al.*, 1988b). The asymptotic length of female long-finned pilot whales is 1.25 m longer and for males is 0.84 m longer. Sergeant (1962a) also presented a length - weight curve for *G. melas* . The equation for this was:

$$\text{Weight (kg)} = 2.5 \times 10^{-5} * \text{Length(cm)}^{2.895}$$

Using this equation, an average adult male of 5.57 m would weigh 2224 kg and an average female of 4.89 m would weigh 1524 kg. These values were used for subsequent comparisons of sexual dimorphism in *Delphinidae* presented in Section 5.3.2.

2.5.2 Reproduction

Reproductive parameters in the short-finned pilot whale were studied on the same population of whales analysed for body size and growth parameters (see Section 2.5.1), but only about half of the whales were examined (14 of 21 schools and 493 of 806 individuals: Kasuya and Marsh, 1984). Reproductive status was studied by the macroscopic and histological examination of testes and epididymes for males and ovaries, uteri, mammary glands for females. Age was available from histological examination of rings in the teeth. Correlated information on school size and composition was also available because the entire school was driven and killed during the hunt (Kasuya and Marsh, 1984).

2.5.2.1 Male Sexual Maturity

Male sexual maturity was determined by examination of the 70 - 150 seminiferous tubules of the testes and was defined as the presence of spermatocytes, spermatids or spermatazoa (Kasuya and Marsh, 1984). Four stages of maturation were defined: 1) immature, with 100% of the tubules immature, 2) early -maturing, with less than 50% of the tubules mature, 3) late-maturing, with between 50% and 100% of the tubules mature, and 4) mature, with 100% of the tubules mature (Kasuya and Marsh, 1984). Testis weight was studied as the weight of a single testis since there was no significant difference in the weight of the left vs. the right testis (left testis = 49.4% ± 4.02% of the combined weight: Kasuya and Marsh, 1984). Testis weight was less than 100 g for immature males, between 100 and 400 g for maturing males and over 400 g for mature males. After the age of 25 yrs (corresponding to the cessation of growth), testis weights ceased to increase, but varied between 1700 and 3000 g for different individuals (Kasuya and Marsh, 1984). Most of the growth in testis weight was observed between the ages of 14 and 17 yrs.

Ages and lengths of males were plotted for each of the categories of maturation. Early-maturing males ranged from 3.24 m to 4.34 m in length (mean = 4.01 m) and 7.25 to 16.5 yrs of age (mean = 14.6 yrs). Late-maturing males ranged from 4.14 m to 4.55 m in length (mean = 4.14 m) and 14.5 to 29.5 yrs of age (mean = 15.8 yrs). Fully mature males ranged from 3.94 m to 5.25 m in length (mean = 4.22 m) and aged 15.5 to 45.5 yrs of age (mean = 17.0 yrs: Kasuya and Marsh, 1984). The mean values are those lengths and ages when

50% of the individuals were at (or beyond) each stage and represent the mean length and age of attainment of each of the maturation stages (Kasuya and Marsh, 1984). The distinctions between immature and early-maturing males and between late-maturing and mature males were not as clear as the distinctions between these two major groupings. Thus, males classified as late-maturing or mature were considered to be *functionally mature* and mean values of 4.14 m and 15.8 yrs were considered to represent length and age at functional maturity (Kasuya and Marsh, 1984). Also, the distinction between these two major groupings was closer for the relationship between length and maturity than it was for the relationship between age and maturity, indicating that males of large body size tended to mature at younger ages (Kasuya and Marsh, 1984). Finally, since both body weight (Kasuya and Matsui, 1984) and testis weight continued to increase until the age of 25, it is likely that *social maturity* (when males are successfully breeding within a social group), is attained at older ages than functional maturity (Kasuya and Marsh, 1984).

Long-finned pilot whale males had a much more rapid maturation than short-finned pilot whales, reaching functional maturity at 12 yrs as opposed to 17 yrs (Kasuya *et al.*, 1988b).

2.5.2.2 Female Reproductive Cycle

Female sexual maturity was defined as the age at first ovulation, detected by the presence of ovulation scars (*corpora lutea* and *corpora albicantia*) on the ovaries (Harrison, 1949; Kasuya and Marsh, 1984; Marsh and Kasuya, 1984). The youngest mature female was 8.25 yrs of age, while the oldest immature was 11.5 yrs old (Kasuya and Marsh, 1984). Body lengths varied from 3.00 m for the smallest mature female to 3.44 m for the largest immature female (Kasuya and Marsh, 1984). Age at maturity was also calculated from six pregnant females younger than t10 yrs old, using their age at death, the length of their foetuses and the known foetal growth curve, resulting in estimates of between 7.4 and 8.1 yrs for the age of first ovulation. The regression of body length on age showed that 50% of the females attained maturity by 8.5 to 9.5 yrs and at a length of 3.16 m, thus, 9.0 yrs and 3.16 m were estimated to be the mean age and body length at the onset of sexual maturity (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984).

One of the main findings of Kasuya and Marsh was that none of the female pilot whales past the age of 40 yrs had any signs of recent ovulation (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984). They noted that the oldest pregnant female in the sample (n=91 females) was 34.5 yrs and based on the size of her foetus, would have given birth at 35.5 yrs. One other female gave birth during the hunt and was subsequently aged at 35.5 yrs. The next youngest pregnant females were four 32.5 yr old animals (Kasuya and Marsh, 1984). The oldest females with recent ovulation scars on their ovaries were aged 39.5, 38.5 and 37.5 yrs. Since the oldest female in the sample was 62.5 yrs of age (Kasuya and Matsui, 1984), there appears to be an extended *post-reproductive period* in a female pilot whale's life (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986; 1991).

Before examining the characteristics used to define post-reproductive females, it is necessary to understand the cycles of actively reproducing females, the duration of the various stages of pregnancy, lactation and resting, and the life history parameters of ovulation rate, pregnancy rate and calving interval.

Ovulation rate was estimated by the rate of accumulation of ovulation scars. Error in the estimation of this rate will arise from: 1) variation in the age at attainment of sexual maturity; 2) change in ovulation rate during an individual's reproductive lifespan and 3) individual variation in the accumulation rate (Marsh and Kasuya, 1984). The age at first ovulation has been shown to vary from 7 to 12 yrs of age (Marsh and Kasuya, 1984). A plot of the number of corpora (lutea and albicantia combined) for females of various ages shows that there is an age-related decline in the rate of accumulation, suggesting error #2 is possible, but this has been summed for different individuals. This decline only holds for females less than 40 yrs old; the number of corpora in females older than this was independent of age ($r = 0.12$, $P > 0.2$: Marsh and Kasuya, 1984). The lack of individual histories due to the nature of the sampling also limits information on error #3. In spite of these difficulties, a single-phase exponential curve was fitted to the data ($r^2 = 0.66$). Predicted values suggest that ovulation rate slows throughout life, from 0.7 ovulations per year for a newly mature seven year old, to 0.14 ovulations per year for a 39 yr old (Marsh and Kasuya, 1984). Although the model does not account for the cessation of ovulation after age 40, it does suggest a slower ovulation rate of less than 0.13 ovulations per year above this age (Marsh and Kasuya, 1984).

The duration of the calving interval was estimated by examining the proportion of females in each of the stages of pregnancy, lactation and resting (Kasuya and Marsh, 1984). This assumes a uniform distribution of females of various reproductive stages in the overall sample (i.e. there is no seasonal bias in catch samples) and that individual schools are also representative of the proportion of females of the reproductive stages in the population as a whole.

The gestation period was estimated at 14.9 months by Kasuya and Marsh (1984), using an examination of the frequency distribution of foetal body lengths (Kasuya and Marsh, 1984). However, recent information for long-finned pilot whales suggests that gestation only lasts for 11.8 months (A.R.Martin, pers.comm.). Since it is unlikely that these congeneric species have such different gestation periods, this discrepancy will have to be resolved. I will continue to present Kasuya and Marsh's estimate because it was an inherent part of some of their calculations, such as of pregnancy rate.

The annual pregnancy rate (calculated as the proportion of pregnant females times 12 /14.9, to account for the fact that gestation was calculated to last longer than one year) was calculated as 0.25, meaning that 25% of the adult females were pregnant over any given year.

The mean length of lactation, estimated from the proportion of lactating females relative to the number of pregnant females times a correction factor for the long gestation period, was 3.48 yrs (Kasuya and Marsh, 1984). This was slightly shorter than the estimated weaning age of calves (4.0 yrs) described in Section 2.5.3, but this could be explained by the fact that the length of lactation includes nursing terminated by calf mortality, while weaning age does not (Kasuya and Marsh, 1984).

All females who were neither pregnant or lactating were classified as resting. The resting period was calculated in a similar fashion to that of the lactation period, and was estimated at 5.46 yrs.

Some females classified as lactating or resting were post-reproductive (see below), and thus these calculations would give an overestimate of the lactating and resting periods of females still reproducing. If the proportion of post-reproductive females (15.5% of lactating females, 49% of resting females) is excluded from the calculations, the new estimates are lactation period: 2.90 yrs and resting period: 2.78 yrs. These estimates of gestation, lactation and resting can be summed to give the overall calving interval of 10.18 yrs including post-reproductive females, and 6.92 yrs excluding post-reproductive females (Kasuya and Marsh, 1984).

This estimate of calving interval assumes constant rates of pregnancy, lactation and resting for females of all ages. However, all of these stages appear to vary with the age of the female, culminating with the onset of the post-reproductive period at around 35 to 40 yrs of age. Females were grouped into age classes to examine this variation. Annual pregnancy rate was shown to drop from 30.9% of females at 10 yrs old to 4.7% at 36 yrs old. The mean duration of lactation rose from 1.8 yrs for 15 yr old females to 3.2 yrs for 24 yr old females to 9.4 yrs for 36 yr old females. The resting period also increased with age. It appeared to be constant for all females younger than 24 yrs at 1.5 years, then increasing to 7.4 years for females aged 36 yrs.

The cessation of ovulation and the occurrence of post-reproductive females was confirmed through a variety of methods. In addition to pregnancy, female reproductive status was determined by the forms of *corpora*, or scars of ovulation, on the surface of the ovary. After ovulation, a *corpus luteum* is formed. The absence of *corpora lutea* was an indication of a lack of recent ovulation and was a prerequisite condition for the definition of post-reproductive females. The *corpus luteum* regresses into a *corpus albicans* in as little as two years in young females, but appears to regress at a much slower rate in older females (Marsh and Kasuya, 1984). *Corpora albicantia* were classified into young, medium, and old on the basis of external features such as colour, texture and size. The change of a *corpus albicans* from "young" to "old" was a continual process, so these categories are somewhat arbitrary, but the rate of this process appears to slow during pregnancy. Also, since there was no evidence of ovulation past age 40 yrs, the presence of a medium *corpus albicans* in a 55.5 yr old female suggests the process may be quite slow in old females (Marsh and Kasuya, 1984). The absence of young *corpora albicantia* was also a prerequisite for the definition of post-reproductive females. The *corpora albicantia* appear to remain throughout life, based on the lack of a negative skew in size distribution for older *corpora* and the lack of a decrease in modal *corpus* size with increasing age of the female, and thus provided a permanent record of reproductive history (Marsh and Kasuya, 1984). The presence of large (>8 mm) Graafian follicles within the ovaries was also used as an indication of reproductive activity, with a decline in large follicle abundance observed in animals of increasing age (Marsh and Kasuya, 1984). Also, large follicles which did not ovulate (atretic follicles) were found to be more common with increasing female age (Marsh and Kasuya, 1984). Using these characteristics, 60 females (24% of the sample of 245) were classified as post-reproductive; the number classified into each of the categories is given in brackets below, along with the reproductive stage. The three types of post-reproductive females were: 1) females with medium *corpora albicantia* but lacking large follicles {2 lactating, 10 resting}, 2) females with old *corpora albicantia* and only atretic follicles {3 lactating, 3 resting}, and 3) females with only old *corpora albicantia* and no follicles {6 lactating, 36 resting} (Marsh and Kasuya, 1984; Figure 8).

Based on the definition of post-reproductive females outlined above, the youngest post-reproductive female was aged 29.5 yrs, and the proportion increased in older females (8.5% for females aged 28 to 32 yrs, 19.6% for ages 32 to 36, 33.3% at ages 36 to 40, and 100% for all females older than 40 yrs: Kasuya and Marsh, 1984). Thus, the post-reproductive period appeared to begin as early as 30 yrs, but more commonly after the age of 40 yrs (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984).

Kasuya *et al.* (1988b) re-examined the data on long-finned pilot whales in light of these findings, and found that the females do not appear to have an extended post reproductive period. Female long-finned pilot whales also matured at an earlier age (6 yrs vs. 9 yrs) and had no apparent age-dependent decline in pregnancy rate (Kasuya *et al.*, 1988b).

2.5.2.3 Seasonality of Reproduction

There was only limited evidence suggesting a seasonal variation in male reproductive activity (Kasuya and Marsh, 1984). This was tested by examining variation in three indications of reproductive activity (threshold testis weights for sperm production, overall testis weight, and seminiferous tubule diameter) for animals killed in three different "seasons" (determined by available sample sizes): February, May/June/July, and December (Kasuya and Marsh, 1984). The greatest changes were noted in the threshold weights of maturing testis producing spermatozoa. Spermatozoa were detected in smaller testis during May -July than during December, indicating increased reproductive activity in May through July (Kasuya and Marsh, 1984). Secondly, seasonal changes in seminiferous tubule diameters for mature males were found to vary significantly on a seasonal basis, being slightly larger in males of 4.80 m to 4.99 m during May to July (Kasuya and Marsh, 1984). There were no significant seasonal differences in testis weights between seasons. However, since the testis weights of mature males showed a wide range of values, it is possible that at least some males exhibit variation in mating activity. Since seasonal sample sizes were small and the results were inconclusive, Kasuya and Marsh (1984) "consider that a substantial proportion of the adult male population of *G. macrorhynchus* is probably capable of successful reproduction throughout the year".

Analysis of the length frequency distribution of foetuses and calves less than 1.55 m was used to determine the seasonality of births (Kasuya and Marsh, 1984). Body lengths were plotted by month of capture and the mean date at which all individuals attained the mean birth length of 1.40 m (using the foetal growth curve developed by Kasuya and Matsui, 1984) was estimated. The mean date of birth varied from 25 July to 12 August, depending on the applicability of the linear foetal growth curve to different length classes of animals used in the calculations. The inclusion of all animals resulted in an estimate of the mean birth date of 2 August with a standard deviation of 73.3 days. Using a gestation period of 14.9 months, the mean date of conception would be in May (Kasuya and Marsh, 1984). The overall frequency of parturition date estimates for individual animals ranged throughout all months of the year, with the bulk of births occurring between May and November and with a mode in July/August. This indicates that pilot whale reproductive activity is only "diffusely seasonal" (Kasuya and Marsh, 1984).

Ovarian activity in female pilot whales showed a similar pattern. There was a seasonal cycle in the growth of ovarian follicles in lactating and immature females, with the peak from May to July (Marsh and Kasuya, 1984). Follicle growth was considered to be an indication of impending ovulation (Marsh and Kasuya, 1984), and the peak season corresponds to the mean conception date of May (Kasuya and Marsh, 1984).

2.5.3 Duration of Lactation and Weaning

Lactation is considered separately because it has relevance to the mother-calf relationship observed in Canary Island pilot whales. Lactation was determined by the presence of milk in the mammary glands. Seventy-four females were classified as lactating in the Japanese whaling sample (Kasuya and Marsh, 1984). Pilot whale milk had a "texture like cow's milk and colour varying from creamy white to a distinct green" (Kasuya and Marsh, 1984).* The duration of lactation was estimated from four sets of data. Stomach contents showed that the youngest calf with solid food was 0.5 yrs and the oldest calf with milk (along with squid beaks) was 2.75 yrs old. Milk was also recorded in two unidentified stomach contents collected from a school in which the two youngest members were 2.5 and 3.0 yrs old. Thus, the estimate of the duration of lactation from this method ranged from 0.5 to 3.0 yrs. The first occurrence of solid food corresponds to the age at which the teeth erupt (Kasuya and Marsh, 1984).

The second method to estimate the duration of lactation was the comparison of the number of lactating females with the age and number of juveniles caught in the same school. This method assumed that each female was nursing only one calf at the time of death, that no suckling calf was older than any weaned calf, that sexually-mature animals were completely weaned and that both mother and calf were caught in the same school. The oldest presumed suckling individuals were a 15.5 yr old, histologically-immature male and two 13.5 yr old immature males (Kasuya and Marsh, 1984). The youngest, fully weaned calf was 2.0 yrs, but there were many presumed suckling calves up to 6 yrs of age. The conclusions were "that some precocious calves complete weaning by the age of 2.0 yrs, but that a few calves continue to suckle until the age of 10 yrs" (Kasuya and Marsh, 1984). The mean age at weaning was estimated at 3.5 to 5.5 yrs, with a median of 4 yrs (Kasuya and Marsh, 1984).

The presence of three suckling males greater than 13 yrs of age could be explained by the loss of younger calves during the drives of the schools in question, but all drives occurred in calm conditions and this possibility was considered highly unlikely by all observers, including the whalers themselves (Kasuya and Marsh, 1984). The presence of old, suckling calves was correlated with the

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* The presence of green milk appeared to be a real phenomenon, not dependent on either the quantity of milk in the mammaries or the time since death, and showed a seasonal variation suggesting it was related to seasonal changes in diet (Kasuya and Marsh, 1984).

presence of old, lactating females and suggests that older females nurse their calves longer than young females (Kasuya and Marsh, 1984; 1989). The implications of this possibility in relation to the occurrence of post-reproductive females will be discussed below.

The third method of estimating lactation period was by examining the difference between female age of last parturition and the age of the oldest lactating females (Kasuya and Marsh, 1984). The oldest pregnant female in the sample was 35.5 yrs old and the oldest female with signs of recent ovulation was 39.5 yrs old (Marsh and Kasuya, 1984). However, many females between the ages of 29.5 and 39.5 showed no recent signs of ovulation (Marsh and Kasuya, 1984). The age of the oldest pregnant female (35.5 yrs) was used as the estimate of age of last parturition (Kasuya and Marsh, 1984). A sample of 12 females older than 35.5 yrs were still lactating (range: 36.5 to 50.5 yrs; mean = 43.4 yrs). Only one female had a recent ovulation scar, or *corpus luteum* (age: 36.5 yrs), while the rest had only scars of past ovulations, or *corpus albicans* (Kasuya and Marsh, 1984). The mean length of lactation after the estimated age of last parturition was 7.83 yrs (Kasuya and Marsh, 1984). This estimate was compared with the estimate using the age of the calves caught in the same school (described above), and in most cases there was a close agreement with the two estimates. The two anomalous estimates were in cases when old, lactating females (aged 50.5 and 47.5 yrs) were caught in the same school with young calves (four and 4.5 yrs old, respectively). Since one of the assumptions of the calf age method was that no suckling calf was older than any weaned calf, the two calves were assumed to be nursing from the lactating females, and the females' age of last parturition would have been 46.5 and 43 yrs old, respectively. Both of the females were classified as having only "old" *corpus albicans* in their ovaries, which, although observed to form from *corpus luteum* as quickly as two years in young females, were considered to form at a much slower rate in old females (Marsh and Kasuya, 1984). However, if these calves were assumed to be the offspring of other, young pregnant females caught in the same schools, and were already weaned, the next oldest calves in the schools were 10.5 and 14.5 yr old histologically-immature males. This corresponded to the situation with two other old, lactating females who were predicted to be nursing adolescent male calves (Kasuya and Marsh, 1984). Thus, the assumption that all suckling calves were younger than all weaned calves may not always be valid (Kasuya and Marsh, 1984). It could also have been possible that the old females were nursing young, fostered calves, but there was no information relevant to this possibility (Kasuya and Marsh, 1984). When the age of the presumed suckling calf (including the revised estimates of the anomalous examples) was subtracted from the lactating females' age, the mean age of last parturition was 34.3 yrs, close to the 35.5 yrs of the oldest pregnant female in the sample (Kasuya and Marsh, 1984).

In summary, the nursing period of short-finned pilot whales appears to be long, varying from 2-14 yrs. Long periods of nursing are considered to be related to the extended period of learning required for social cetaceans (Brodie, 1969). The evidence shows that pilot whale calves begin to take solid food as early as the first year, after the teeth erupt in the jaw, and may be weaned as early as 2 yrs. However, many continue to nurse up to 6 yrs and the oldest presumed nursing calves were 14 yr old immature males. In all cases, there was a relationship between the duration of lactation and the age of the female. Females who had no recent signs of ovulation (and were assumed to be post-reproductive) were often still lactating and were presumed to be nursing their last calf. The extended duration of lactation in these post-reproductive females represents an increased parental investment when the female's potential for future reproduction has ceased. This is in accordance with evolutionary parental investment theory and the partitioning of reproductive effort (Trivers, 1972; Clutton-Brock, 1984). In two of 12 cases there was a possibility that females were nursing fostered calves, as has been observed in other social mammals (e.g. lions: Schaller {1972}; elephants: Dublin {1983}).

2.5.4 Longevity, Mortality and the Sex Ratio

The maximum longevity for Japanese short-finned pilot whales differed between sexes. The oldest male in the catch was 45 yrs old, while the oldest female was 62 yrs (Kasuya and Matsui, 1984). There are no reports of all-male groups which would indicate any older males were segregated from the female and calf groups, so this finding was considered to be an indication of differential mortality (Sergeant, 1962a; Kasuya and Marsh, 1984).

The sex of 155 foetuses and calves less than 2.2 m (about 0.5 yrs old) was 48% female, giving a male:female sex ratio of 1:0.92, which was not considered significantly different from a one-to-one sex ratio (Kasuya and Marsh, 1984). The catch statistics from the drive whaling, where all animals in a school were killed, showed that 67.3% of 483 postnatal individuals were female (sex ratio = 1:2.05), significantly different from a one-to-one sex ratio (X^2 $P < .001$: Kasuya and Marsh, {1984}). However, when this catch is segregated into 10 year age classes, the sex ratio becomes increasingly female-biased for older animals. For animals younger than 20 yrs old the sex ratio does not differ significantly from a one-to-one sex ratio (0-10 yrs: 1:1.5, N=115, P >0.2; 10-20 yrs: 1:1.45, N=120, P >0.2). However, by the age of 20-30 yrs, the sex ratio of 1:1.85 was different from one-to-one (N=114, P<0.02) and was significantly female-biased for all older age classes (30-40 yrs: 1:3.17, N=71, P<.05; 40-46 yrs: 1:5.17, N=37, P<.001). Finally, after the age of 46 yrs, females represented 100% of the population (N=26, P< .001: (Kasuya and Marsh, 1984). The overall adult sex ratio was 77% female, or 1:3.35. This could have been biased towards an overestimation of the number of males by the whalers' preference for schools with the most males. Separate analysis of the sex ratio of schools caught alone (i.e. when the whalers had no chance to select one school over another: see Section 2.7) found a female ratio of 87%, or 6.7 females for every adult male (Kasuya and Marsh, 1984).

The age distribution of 150 males and 318 females, pooled into three-year age classes, was used to calculate mortality rates (Kasuya and Marsh, 1984). The assumptions for this method of determining mortality rates are that the population is stable or has a known rate of increase. The lack of evidence supporting these assumptions makes the following mortality rate estimates speculative (Kasuya and Marsh, 1984). The best fit for the data was to calculate separate least-squares linear regressions for the two oldest of three age groups for each sex. Mortality rates for the youngest age group was estimated by extrapolation and corrected observed frequencies because there was an apparent bias against females with young calves in the catch (Kasuya and Marsh, 1984). Mortality rates for males from birth to nine yrs (age at sexual maturity) was 11.02%, from ages nine to 30 yrs was 4.01% and for males 27 to 46 yrs was 11.25%. Mortality for females from zero to 6.5 yrs was 7.34%, for females from 6.5 to 48 yrs was 2.54% and for females from 45 to 63 yrs was 14.45% (Kasuya and Marsh, 1984). These are typical "U"-shaped mammalian mortality patterns. Males had higher mortality than similarly-aged females for nearly all ages. The period of high juvenile mortality showed the greatest difference between males and females. Also, the increase in adult mortality occurred around 18 years earlier in males than females (27 yrs vs. 45 yrs).

Life tables were constructed from these data, using parameters of single births, a neonatal sex ratio of one-to-one, and the previously estimated rates of maturity and pregnancy (Kasuya and Marsh, 1984). The resultant predictions closely agreed with the observed data. The mean life expectancy of newborn calves was 12 years in males and 22 years in females. The adult sex ratio was 3.7 females: 1 male, slightly higher than the observed sex ratio of 3.3:1. The annual pregnancy rate was 12.85% of the female population. The gross annual reproductive rate (rate of calves of both sexes produced annually by the female population) was around 5.8%. The average calf production per female living to reproductive age was 4.39 calves. The mean proportion of post-reproductive females was predicted at 24% of the adult female population, close to the 25% observed.

Long-finned pilot whales had a different pattern of mortality than short-finned pilot whales (Kasuya *et al.*, 1988b). Although long-finned pilot whales also exhibited differential mortality between the sexes, with adult males having higher mortality than similarly aged females, mortality in both sexes increased around ages 21-25 yrs. Also, longevity in the long-finned pilot whale appeared to be as much as 20 years shorter than for short-finned pilot whales in females and 10 years in males, suggesting an overall higher mortality rate for this species (Kasuya *et al.*, 1988b).

2.5.5 Summary of Short-Finned Pilot Whale Life History

The reproductive lives of the southern form of Japanese short-finned pilot whales can be divided into three phases (Kasuya and Marsh, 1984). Males have a long (15.9 yr) period of sexual maturation, throughout which they may continue to nurse if they are the last offspring of an old mother. After reaching sexual maturity, they continue to grow in body size, eventually growing to twice the mass of a female (1200 kg vs. 570 kg). From the ages of 16 to 25, males continue to grow at a relatively high rate, including growth in the testes, suggesting a continuation of the process of maturation. Growth slows during the latter part of this period, but continues until 27 yrs when asymptotic body size is reached and they are fully adult. They undergo only minor seasonal variation in reproductive potential and are probably capable of fathering offspring for most of the year. This would be expected since births were predicted for all months (from the length frequencies of foetuses), in spite of a unimodal peak of conception in May and birth in August. They have higher mortality rates than females throughout their lives, resulting in a female-biased sex ratio of up to 3.7 adult females for every male. A few males may live until the age of 45, 22 years less than the female lifespan of 62.

Female pilot whales have a relatively shorter period of maturation compared to males, although it is still long by mammalian standards. Until sexual maturity, at ages between 8 and 11 yrs, female growth rates are only slightly less than those of males. However, female growth slows after first ovulation, and there is no adolescent growth spurt as there is for males. Female growth ceases by 22 yrs of age, with an asymptotic body size equivalent to the body size of an 11 yr old adolescent male. The first pregnancy occurs at 8-9 yrs, with a 15 (or 12) month gestation, and a minimum one year period of nursing. The calving interval for primiparous females was three years. Calving interval increases with age, due to longer periods of lactation and resting between pregnancies. A highly productive female may have had four calves by the age of 21, when the calving interval may have increased to 5-6 yrs. After this period, pregnancy rate drops, along with an increase in the calving interval. By the age of 35, the female may have had 2-3 additional calves, but after this age, nearly all females have ceased to give birth. The highly reproductive female may have had six or seven calves, but the average lifetime calf production was 4.4 calves. Some (about 15%) may continue to lactate and nurse their last calf, especially if it is a male with a long maturation period. By the age of 52, all females have ceased lactating. Life may continue for another ten years. Thus, the three phases of a female pilot whale's life are 9 yrs of maturation, 26 yrs of producing calves, and 36 yrs of post-reproductive life.

2.6 ECOLOGY

2.6.1 Distribution

Water temperature appears to be the primary factor in determining the differences between the distribution of the two species of *Globicephala*. *G. melas* has an antitropical distribution, with two separate populations occurring in the cold, temperate waters of the northern and southern hemispheres (Davies, 1963), while *G. macrorhynchus* has a circum-equatorial distribution, favouring waters above 15°-16°C. I will first describe the distributions of the two species separately and then examine the areas of overlap.

The short-finned pilot whale is distributed in all warm-water oceans. In the Atlantic Ocean, these whales are found north to 39°N along the coast of America (Sergeant, 1982) and range across the north Atlantic to Madeira at 30°N (Maul and Sergeant, 1977), the Azores (Clarke, 1981) and France (Duguy, 1968). The species does not appear to enter the Mediterranean (Brown, 1961; McBrearty *et al.*, 1986). There have been sightings throughout western Atlantic, including the Bahamas and the Virgin Islands (Taruski and Winn, 1976), the eastern Gulf of Mexico (Fehring and Wells, 1976), the Caribbean islands of St. Vincent and St. Lucia (Caldwell *et al.*, 1971; Caldwell and Caldwell, 1975) and Venezuela at 10°N (Casinos and Bou, 1980). Reports from the eastern Atlantic have come from Senegal (Cadenat, 1957), the Canary Islands (Vonk and Martin, 1988) and the Cape Verde Islands (Fraser, 1950). The southern-most reports are from São Paulo, Brazil at 25°S (Schmiegelow and Filho, 1989) and off the Indian Ocean coast of South Africa at 34°S (van Bree *et al.*, 1978; Ross, 1984).

In the Pacific, the short-finned pilot is commonly found as far north as 42° N along the Japanese coast (Kasuya, 1975; Kasuya *et al.*, 1988a) and to about 35° N along the California coast (Norris and Prescott, 1961; Seagars and Henderson, 1985), although reports exist from as far north as 51°N off the coast of British Columbia (Baird and Stacey, 1989). Short-finned pilots are seen off Mexico (Norris and Prescott, 1961) and in the vicinity of the Pacific Islands, such as Hawaii (Shane and McSweeney, 1990) and Tahiti (M.Poole, pers.comm.) In the western south Pacific, the short-finned pilot has been reported from Java at 5°S (Dammerman, 1924), and as far south as 41°S off Tasmania (Baker, 1983). However, the most southerly mass stranding has been in north Australia, while all other sightings from further south (including reports from New Zealand) have been of single animals (Baker, 1983; Nicol and Croome, 1988). There are only a few reports of short-finned pilot whales in the Indian Ocean, although there has not been much research effort there (Leatherwood and Reeves, 1989). They have been sighted off Sri Lanka at 10°N (Alling, 1986) and there have been strandings from as far north as Calcutta at 22°N (Silva, 1987) and off south-east India (Alagarswami *et al.*, 1973).

The distribution of short-finned pilot whales off the coasts of Japan has been shown to vary seasonally (Kasuya, 1975; Kasuya *et al.*, 1988a). The two genetically-distinct populations off the Japanese coast (Wada, 1988) are at least partially segregated by water temperature (Kasuya *et al.*, 1988a). The southern form occurs primarily south of 30°N in the winter and south of 37°N in the summer (Kasuya *et al.*, 1988a). This corresponds to the northward movement of the boundary region of the 18°C surface isotherm of the Kuroshio current (Uda, 1954; Kasuya, 1975). The lower limit of thermal tolerance for this southern form appears to be just under 20° C (Kasuya *et al.*, 1988a). The northern form occurs between 36°N and 43°N in the summer and between 35°N and 36°N in the winter corresponding to temperature preferences between 12°C and 24°C (Kasuya *et al.*, 1988a). This lower thermal tolerance corresponds to the 10°C-15°C front of the cold water Oyashio Current (Kasuya *et al.*, 1988a).

Although long-finned pilot whales are found in both hemispheres of the Atlantic Ocean, there are no current records of a northern population in the Pacific Ocean. However, skulls have been found in Japan (45°N) from the 10th century, showing that the species used to exist there (Kasuya, 1975). The population in the north Atlantic appears to extend north towards Greenland with sightings at 62°N (Brown, 1961) and reports along the western Atlantic from Canada (Needler, 1931; Mathewson, 1935; Sergeant and Fisher, 1957; Geraci and St. Aubin, 1977) and the United States south to 36° N (Paradiso, 1958; Sergeant, 1982). Long-finned pilot whales are commonly sighted across the central Atlantic at 50°N (Brown, 1961). Sightings from the eastern Atlantic are common in the Faeroe Islands (Brown, 1961), off Britain (Ritchie, 1924; de Kock, 1956; Fraser, 1974; Evans, 1980; Martin *et al.*, 1987), Spain (Casinos and Vericad, 1976) and in the Mediterranean (McBrearty *et al.*, 1986). The southernmost sightings of this northern population are from one stranding in the Canary Islands at 28°N (Vonk and Martin, 1988) and from 25°N off the coast of Mauritania, northwest Africa (Nores and Perez, 1988).

The southern population of the long-finned pilot whale appears to have a continuous distribution around the southern hemisphere (Davies, 1960; Brownell, 1974). In the south Atlantic, long-finned pilot whales are commonly found off the eastern and southern South African coast at 35°S (van Bree *et al.*, 1978; Ross, 1984), while in the southern Indian Ocean there are reports from Kerguelen Is., at 48°S (Brownell, 1974). Along the Atlantic coast of South America their distribution is probably limited by the Falkland (=Malvinas) current (Casinos, 1981). The most southerly report is at 68° S, off Antarctica (Brownell, 1974). In the south Pacific, long-finned pilot whales have been recorded from Chile (Torres *et al.*, 1975), Tasmania at 42°S (Gales *et al.*, 1992), southeastern Australia (Davies, 1960) and New Zealand (Oliver, 1924; Gaskin, 1968a).

Distribution of the long-finned pilot whale in the western north Atlantic has been shown to be seasonal (Sergeant and Fisher, 1957; Sergeant, 1962a; Mercer, 1967; Waring *et al.*, 1990; Overholtz and Waring, 1991). Along the Newfoundland coast, the animals first occur in the coastal bays in mid-July and remain until October (Sergeant and Fisher, 1957; Sergeant, 1962a; Mercer, 1967). This pattern of occurrence closely parallels the movements of squid in this region (see Section 2.6.2). The offshore distribution during this period is the most northerly of the year (Brown, 1961; Waring *et al.*, 1990), although pilot whales may be found in deep water areas of the north Atlantic during all seasons (Brown, 1961). During the winter and spring, the animals appear to move south to warmer, Gulf Stream waters, primarily along Grand Bank (Sergeant and Fisher, 1957; Sergeant, 1962a; Waring *et al.*, 1990; Overholtz and Waring, 1991). Over 80% of the pilot whales caught in offshore fishing nets (along the continental shelf) were caught between March and July (Waring *et al.*, 1990). However, pilot whales are also occasionally reported from inshore waters of Newfoundland during the winter (Mercer, 1967).

There are a number of areas of overlap between the two species of *Globicephala* (van Bree *et al.*, 1978; Nores and Perez, 1988). In the northern hemisphere, the species only overlap in the Atlantic Ocean. As described above, *G. melas* extends south to 25°N latitude, while *G. macrorhynchus* has been found as far north as 45°N (Nores and Perez, 1988). The situation along the northwest African coast is most interesting. *G.melas* occurs off Morocco and Mauritania, while *G. macrorhynchus* is only reported from Senegal. However, the majority of sightings offshore of the mainland coast, in the Cape Verde, Canary, and Madeira Islands, have been of *G. macrorhynchus*. This appears to be related to prevailing ocean temperatures. The cold-water species, *G. melas*, travels south with the influence of the Canary Current, which lowers water temperatures off northwest Africa through an upwelling of deep cold water (Nores and Perez, 1988). Offshore, the water is warmer, so the warm-water species, *G. macrorhynchus*, is able to penetrate north to Madeira and the Azores (Maul and Sergeant, 1977; Clarke, 1981). It would be expected that observations of *G. macrorhynchus* in the Bay of Biscay would be correlated with warm water intrusions during the fall, but they appear to occur throughout the year (Nores and Perez, 1988). Along the western Atlantic, the two species overlap between 36° and 38°N (Sergeant and Fisher, 1957; Paradiso, 1958; Sergeant, 1982). The reports from the western Atlantic are all of stranded animals, so there is little information on variations in distribution relative to oceanographic features. However, the warm-water Gulf Stream would be expected to allow *G. macrorhynchus* to penetrate north. Correspondingly, when the Gulf Stream shifts to more offshore flow, it would be expected that *G. melas* could penetrate further south with the influence of the cold Labrador current. In any event, current information suggests a wider zone of overlap along the eastern Atlantic compared to the western Atlantic.

In the southern hemisphere, a zone of overlap distinguished by varying temperature regimes has been noted along the southern coast of South Africa at 34°S (van Bree *et al.*, 1978; Ross, 1984). The Atlantic coast of South Africa is characterised by the cold-water Benguela Current, while the warm-water Aghulhas Current flows along the Indian Ocean coast, causing an area of mixing along the southern coast. Accordingly, the bulk of the *G. macrorhynchus* strandings are reported from the eastern section of this coast, while the bulk of the *G. melas* strandings were found to the west, with an area of overlap between (van Bree *et al.*, 1978). There was no differential seasonality for the occurrences of the two species, suggesting both may be resident (van Bree *et al.*, 1978). Around Australia, both species have been reported to strand on Tasmania at 41°S (Nicol and Croome, 1988), but the short-finned pilot observations were only of a single animal. The most southerly mass stranding for the short-finned species was off northern Australia, out of the reported range for long-finned pilot whale (Baker, 1983). There is currently insufficient information about the distribution of the two species to determine the extent of overlap off South America in the south Pacific.

2.6.2 Feeding Habits

Pilot whales are primarily considered to be squid feeders, although they will occasionally feed on fish (Sergeant, 1962a; Mercer, 1975; Seagars and Henderson, 1985; Overholtz and Waring, 1991; Gales *et al.*, 1992). This information comes from stomach contents as well as from correlated distributions of populations with the distribution of squid. I will first review the reported stomach contents for *Globicephala* and then examine the few distribution studies. Finally, I will consider some of the implications of squid feeding for an understanding of the behavioural ecology of pilot whales.

Pilot whales are commonly found stranded on beaches throughout the world (Sergeant, 1982; Klinowska, 1986). This has provided an opportunity to collect stomach contents to examine the animals' feeding habits. There are problems with potential bias arising in this sort of analysis because the representativeness of the sampling methods in unknown. Animals that strand alone are often diseased and may not have fed for a long period of time (Klinowska, 1986). Information on feeding habits collected from these animals may be biased. However, it can be argued that in the case of mass stranding (Klinowska, 1986), many of the animals are perfectly healthy who can provide accurate information on food habits, although the possibility of group-wide disease cannot be ruled out. Some additional information on feeding habits has come from the incidental capture of pilot whales* in offshore fishing operations along the continental slope of the western north Atlantic between 35°N and 43°N (Waring *et al.*, 1990; Overholtz and Waring, 1991). Pilot whales represented 55% of the marine mammal incidental catch (N = 297 animals) from 1977 to 1988 (Waring *et al.*, 1990). This potentially provides a more representative sample of dietary habits.

Long-finned pilot whales captured off the coast of Newfoundland were found to feed predominantly on the short-finned squid *Illex illecebrosus* (Sergeant, 1962a). During the first five years of the study, only squid were found

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* Although the most common pilot whale of this area is the long-finned pilot whale, this area of capture is an area of potential overlap between *G. melas* and *G. macrorhynchus* (see Section 2.6.1). Thus, unless examined by skilled observers, the possibility exists that some reports were of the short-finned pilot whale.

in pilot whale stomachs. In the following year, squid fishermen reported a disappearance of squid from inshore waters where the whales were captured. Pilot whale catches dropped, and the few whales that were caught were found with cod (*Gadus morhua*) or Greenland turbot (*Reinhardtius hippoglossoides*) in their stomachs (Sergeant, 1962a; Mercer, 1975). This trend continued for two years, until squid began to reappear in the whales' stomachs as well as in the fishermen's catches (Sergeant, 1962a). More recently, the offshore distribution of pilot whales along the continental slope of the northeastern United States (39° N latitude) has been shown to coincide with the distributions of Atlantic mackerel (*Scomber scombrus*) and butterfish (*Peprilus triacanthus*), as well as with the distribution of both long-finned (*Loligo peali*) and short-finned squid (Smith *et al.*, 1990; Waring *et al.*, 1990; Overholtz and Waring, 1991). Mackerel dominated the diets of four pilot whales caught in fishing trawl nets during a 30-day period in March and April, comprising an average of 71% of the wet weight of stomach contents (Overholtz and Waring, 1991). Long-finned squid comprised the remaining 29% of the four animals and 100% of a fifth animal (Overholtz and Waring, 1991). However, the quantities of prey observed in the stomachs were estimated to supply only 1.8 - 28% (mean = 9.2%) of the daily food requirements of the animals (Overholtz and Waring, 1991). Pilot whales also tended to be caught more by mackerel fishing boats (85% of the total pilot whale catch of 297 animals) than by long- and short-finned squid fishing boats (13.8% of the catch: Waring *et al.*, 1990), although this may not necessarily relate to dietary preferences because the wide opening of pelagic mackerel nets could "corral larger delphinid species such as pilot whales" (Waring, 1990, p.357).

Feeding rates for captive short-finned pilot whales are limited, but a 5.26 m male ate 45 kg of squid and mackerel per day, a > 4.0 m female ate 36 kg/day and a 3.7 m female ate 18 kg/day (Norris in Sergeant, 1962a). This is an average daily feeding rate of 3% of the body weight. This suggests that large animals may need to feed two to three times per day to obtain similar quantities of food to those of captive animals. Of course, rates of feeding in captivity may not represent feeding rates in the wild, where food is not available ad libitum.

There did not appear to be any diurnal pattern in feeding for long-finned pilot whales caught off Newfoundland. Observations were limited, but animals were observed feeding prior to capture and were documented to have fresh stomach contents during daylight hours. Whales could be heard close to shore during the night, implying they were feeding then as well. This is different from the pattern of predominate night-time feeding reported for *G. macrorhynchus* in captivity (Kritzler, 1952).

2.7 SOCIAL ORGANISATION

Kasuya and Marsh examined the school structure of 27 short-finned pilot whale schools caught in a drive whaling operation off the southern coast of Japan (Kasuya and Marsh, 1984). Data on body length, age, and reproductive status were examined from the carcasses after the hunt. Pre-hunt sighting information on the numbers of distinct groups within these schools was available for 16 of the schools. Some of the schools had been isolated from larger aggregations by the whalers before driving, while other schools were sighted and driven as a single school. Thus, there was information on the structure of individual schools as well as the patterns of school aggregation (Kasuya and Marsh, 1984).

School size for all schools ranged from 14 to 52 (mean = 30.9 whales). The eight schools located alone ranged in size from 14 to 38 whales (mean = 24.6 whales), while the seven schools selected from aggregations were larger (range: 20 to 52 whales, mean = 35.1). This could have been because the whalers selected the largest schools from aggregations (Kasuya and Marsh, 1984).

The number of mature males in all 27 schools ranged from zero (one school) to 18 (one school). When these two schools were removed from the analyses as outliers, the number of adult males ranged from one to eight. In the solitary schools, the number of males ranged from one to three. In contrast, the selected schools had from one to eight adult males, with four of seven selected schools having four or more adult males. This is further evidence of selection by whalers, in this case selecting for adult males who were prized for their larger size (Kasuya and Marsh, 1984). The overall ratio of mature females (excluding post-reproductive females) to mature males for 11 schools with complete data ranged from 1.1 to 21.0 females per male. All of these schools had pregnant and lactating females, indicating they were breeding schools. The one school with 18 mature males had five pregnant females, and one in oestrus. In attempting to explain the large number of males, Kasuya and Marsh (1984) discount the possibility that males congregate around oestrus females by pointing out that other schools had greater numbers of females in oestrus. There were no significant correlations with the proportions of other school members which could satisfactorily explain the observed distribution of adult males in the schools (Kasuya and Marsh, 1984). Kasuya and Marsh conclude: "...either mature males stay in the same breeding schools for a period exceeding one female breeding cycle, or that their movement between breeding schools is controlled by (unknown) factors other than the female reproductive cycle" (Kasuya and Marsh, 1984).

The occurrence of maturing males also varied widely between schools: one school had five of the 12 maturing males. Kasuya and Marsh suggest this uneven distribution could be because of immature males aggregating at puberty; leaving their natal school and associating with similar aged males (Kasuya and Marsh, 1984). However, there were no observations of all-male adolescent groups, indicating that even if adolescent males were joining together, they were still members of a mixed age and sex school. Since the sample size was small, it seems that local variation in the age and sex composition of schools could also be explained by only a few females having a slight preponderance of sons. However, there were no variations in the proportions of adolescent females in the schools.

There did not appear to be any school-based synchronisation of oestrus: seasonal samples found females at a variety of stages in the reproductive cycle (Kasuya and Marsh, 1984). Along with the lack of strong seasonality to male testicular activity, this suggests that mating could be occurring over a wide time period. There was also variation in the numbers of post-reproductive females, suggesting they were not essential members of a school.

Off Newfoundland, the majority of long-finned pilot whale schools were of mixed age and sex. Only two schools were found to have a majority of males and no school contained only males (Sergeant, 1962a).

2.8 DISCUSSION

There are both similarities and differences between the biology and behaviour of the two species of *Globicephala*. The two species appear to be adapted to different temperature regimes. This could be related to the ancient cooling of much of the worlds' oceans. The development of antitropical distributions is a widespread phenomenon of cetacean speciation (Davies, 1963). The cold-water long-finned pilot whales probably adapted to these changing temperatures, while the warm-water species found refuge in the warm-water core area of the Indo-Pacific region. This distinction persists today, even with the potential for sympatry.

In spite of these distributional differences, the anatomical differences between the two species are very slight. There are no clear explanations for the observed variation in flipper length and skull morphology. In fact, the variation in flipper length is counter-intuitive, since cetacean appendages are known to be sites of thermoregulation (Hampton and Whittow, 1976). It would be expected that animals living in warmer waters would have longer appendages than those living in cold waters. The opposite is the case. It is possible that the differences between the two species may simply be the result of genetic drift (Wilson, 1975). Pigmentation patterns are similar (Sergeant, 1962b; Yonekura *et al.*, 1980), and differences fall within the range of variation reported between two populations of the same species (Kasuya *et al.*, 1988a).

Most important to the present study is whether there is evidence for significant differences between the social systems of the two species. For the short-finned pilot whale, there is convincing evidence for the presence of post-reproductive females (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984) and little genetic information to document the mating system. Genetic data from long-finned pilot whales suggests a unique mating system and pattern of dispersal (Amos *et al.*, 1991a; 1991b), while analysis of the life history parameters from the same population is still underway (A.R.Martin, pers. comm.). It will be important to understand how applicable the findings from one species are to the other species.

A comparison of the life history parameters from both species was limited to some extent by different histories of exploitation, which could have resulted in differing mortality rates (Kasuya *et al.*, 1988b). Both species do exhibit differential mortality between the sexes, with adult males having higher mortality than similarly aged females (Kasuya *et al.*, 1988b). However, the pattern of mortality was different for the two species: both sexes of long-finned pilot whales exhibited an increase in adult mortality around ages 21-25, while short-finned males showed this increase in mortality much earlier than females (28 yrs vs. 46 yrs). This resulted in different sex ratios between the species, with less female bias in long-finned pilot whales. Longevity appears to be much shorter in long-finned pilot whales, indicating an overall higher mortality rate for this species (Kasuya *et al.*, 1988b). The difference in longevity was matched by an earlier age of sexual maturity for long-finned pilot whales (females: 6 yrs vs. 9 yrs, males: 12 yrs vs. 17 yrs). There was no apparent age-dependent decline in pregnancy rate for long-finned pilot whales, indicating a lack of post-reproductive females (Kasuya *et al.*, 1988b), compared to the situation with short-finned pilot whales where females were rarely pregnant past 36 yrs and rarely lactating past 51 yrs, although they lived for an average of 63 years (Kasuya and Marsh, 1984;

Marsh and Kasuya, 1984). All of these results suggest that the long-finned pilot whale has a "less-specialised" life history than the short-finned pilot whale, with less differential mortality between the sexes, a sex ratio closer to unity, and less specialisation in female reproductive patterns in the form of a post-reproductive senescence (Kasuya *et al.*, 1988b).

Comparisons with other cetaceans will be reviewed more completely in Chapter 5, however, a few points can be made. In the sperm whale, the sex ratio in the breeding schools is also female-biased (Best, 1979; Gordon, 1987; Whitehead and Arnbolm, 1987). However, there does not appear to be any significant differences in mortality between the sexes and longevity appears to be equivalent between males and females. The biased sex ratio arises from the geographical segregation of a proportion of males from the breeding schools (Ohsumi, 1966). This is very different from the situation with pilot whales, where male mortality is higher than female mortality, resulting in a shorter male longevity (Kasuya and Marsh, 1984). Also, the observations of segregated groups of males for either short-finned or long-finned pilot whales are rare (Sergeant, 1962a; Kasuya and Marsh, 1984), and are certainly less than would be necessary to explain the female-biased sex ratios assuming equal mortalities for the sexes. The only indications of male immigration were a few schools which had more males than predicted from the average sex ratio, possibly indicating switching of schools. The conclusion on social organisation is that pilot whales live in groups of female-related kin, potentially including males as well.

2.9 SUMMARY

This review of pilot whale biology and behaviour has examined six main features which are referred to in later sections of this thesis. First, aspects of external appearance are used in the identification of individual animals (Chapter 4). Second, an understanding of pilot whale taxonomy allows comparisons to be made between the two species (Chapter 5). Third, genetic studies are critical in a consideration of mating system hypotheses (Chapter 5). Fourth, sex differences in growth and body size are used to classify free-ranging animals into age and sex categories (Chapter 4). Fifth, life history parameters, specifically the differential longevity and patterning of reproductive effort in females are used to place *Globicephala* in a comparative context with the rest of *Delphinidae* (Chapter 5). Sixth, ecological elements of distribution and feeding behaviour are considered in the analysis of pilot whale distribution around the Canary Islands (Chapter 3).

CHAPTER 3: DISTRIBUTION OF SHORT-FINNED PILOT WHALES OFF TENERIFE, CANARY ISLANDS, SPAIN

3.1 INTRODUCTION

The geographical and seasonal distribution of delphinids has been related to prey distribution (Nishiwaki and Handa, 1958; Mercer, 1975; Condy *et al.*, 1978; Würsig and Würsig, 1980; Irvine *et al.*, 1981; Lopez and Lopez, 1985; Heimlich-Boran, 1986), tidal currents (Felleman *et al.*, 1991), underwater topography (Evans, 1971; Hui, 1979; Heimlich-Boran, 1988; Würsig *et al.*, 1991), water depth (Saayman and Tayler, 1979; Würsig and Würsig, 1979; Wells, 1986; Ballance, 1990) and ocean temperature (Uda, 1954; Mercer, 1967; Gaskin, 1968b; Nishiwaki, 1975; Perrin, 1984; Kasuya *et al.*, 1988a; Mate, 1989). The correlation between delphinid distribution and these environmental characteristics indicates that these animals monitor their environment closely and are able to respond to fine-grained changes.

Pilot whales are characteristically found in deep water, where they are considered to feed on their favoured prey, squid (Leatherwood and Reeves, 1983; Seagars and Henderson, 1985; Klinowska, 1991; Overholtz and Waring, 1991; Gales *et al.*, 1992). Observations have been limited due to the pelagic nature of these whales, but some regularly-occurring populations have been identified (Sergeant and Fisher, 1957; Norris and Prescott, 1961; Mercer, 1967; Taruski and Winn, 1976; Shane and McSweeney, 1990). Many of these have been exploited by whaling operations and thus have been unavailable for consistent observations (Sergeant, 1962a; Caldwell *et al.*, 1971; Mitchell, 1975; Kasuya and Marsh, 1984; Price, 1985; Gibson-Lonsdale, 1990). A few reports have documented regular movements within a confined area (Shane and McSweeney, 1990) but, in one case, along the channel islands of California, the whales distribution shifted abruptly during a year of warm-water intrusion (Shane, 1985).

I conducted a 22 month study on the geographical distribution and seasonal occurrence of short-finned pilot whales off Tenerife in the Canary Island archipelago.

3.2 METHODS

3.2.1 Survey Methods

Field operations were based in the town of Los Cristianos, on the southwest coast of Tenerife. Two vessels were used. The permanent research vessel was a 4.7 m Zodiac inflatable. This was best-suited for close approaches to whales, photographic identification and under-water observations. From 16 June to 2 September 1990 and from 31 March to 26 June 1991, a 13.1 m ketch was chartered for 60 days. It was best suited to long-term observations and rougher sea conditions. At times, these two vessels worked together, covering a greater number of pilot whale groups over a wider area.

3.2.2 Seasonal Occurrence

The seasonal occurrence of whale and dolphin sightings was compared to sighting effort in order to quantify relative presence in the study area. Sighting effort was quantified in two ways: shore effort and boat effort. Both were dependent on observer availability, sea state, sighting conditions, and equipment function. Calculations of the proportion of sighting days per effort day (sightings per unit effort, or *SPUE*) were used to compare occurrence between months and between seasons.

3.2.3 Mapping

The geographical distribution of whales and dolphins in the study area was quantified by accurately plotting all travel routes. From the boat, locations were determined by compass triangulation on shore markers. These bearings were plotted on a map overlaid with 2 km square quadrats by computer using trigonometric calculations based on the locations of the shore markers. In order to categorise the steepness, or slope, of each quadrat a *Contour Index* (Hui, 1979), which is the percent change in depth within the quadrat, was used. This was calculated as:

$$CI = 100\frac{M - m}{M}$$

where m = the minimum depth and M = the maximum depth within each quadrat. Depths were estimated to the nearest 50 m from nautical charts. The average of the minimum and maximum depth was also used to categorise the quadrat. Whale usage of each quadrat was classified into three categories based on the number of tracks: heavy use, moderate use and light use. Light usage was defined as a quadrat with five or fewer tracks through it, moderate usage was 6 to 10 tracks and heavy usage was defined as having more than 10 whale tracks.

3.2.4 Description of the study area

The archipelago of the Canary Islands extends over 500 km between 27° 37' and 29° 23' N, and 13° 20' and 18° 16' W. At their closest point, the islands are within 100 km of the coast of Morocco. There are seven main islands: Lanzarote, Fuerteventura, Gran Canaria, Tenerife, La Palma, Gomera, and El Hierro. The total area of the islands is approximately 7,273 km^2 (Schmincke, 1976). The Canary Islands are one of the major volcanic island chains in the Atlantic Ocean; there are a few active volcanoes, with the most recent eruption in 1971 on La Palma (Schmincke, 1976). The climate is dominated by oceanic influences of the north-east trade winds (Fernandopullé, 1976). About 80% of the rainfall occurs between October and March and about 60% in December and January (Fernandopullé, 1976). Figure 3.1 shows the generalised wind patterns off the west coast of Tenerife and Gomera. The calm waters on the southwest lee side of the islands are relatively consistent, although occasional shifts in the winds to the north create rough water conditions throughout the strait between Tenerife and Gomera. Temperatures vary between 18°C and 28°C, much cooler than would be expected by the latitudinal position of the islands. This cooling is

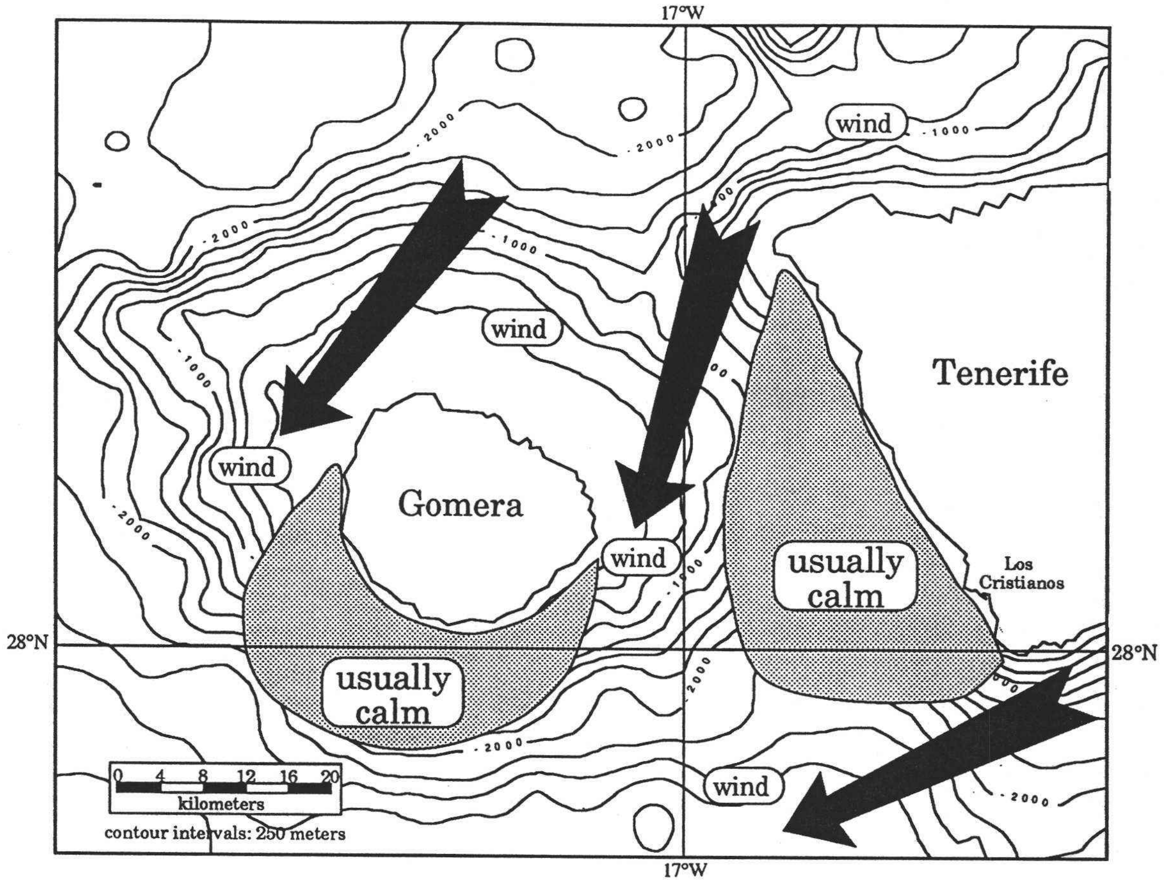

Figure 3.1. Generalised characteristics of trade wind patterns, indicated by arrows. Calm areas were in the lee of the islands of Tenerife and Gomera. Wind was a limiting factor in the distribution of search effort.

caused by the cold-water Canary current which flows out of the north and generates upwelling off the African coast. The bulk of the upwelling occurs to the west of the islands (Boje and Tomczack, 1978), but some effect is still felt within the archipelago.

Figure 3.2 shows a contour map of the study area off Tenerife and Gomera. The contour profile is steep, dropping from the peak of Mt. Teide, at 3718 m elevation, to ocean depths of over 2000 m. The main bathymetric feature is the canyon between the two islands. Tenerife and Gomera are the two closest Canary Islands (about 27 km apart) and the sea bed is just over 1000 m deep in the channel between them. The depths increase to over 2000 m deep to the north and the south, forming a "saddle" in the channel. The slopes on either end of this saddle are steepest to the south and a 1000 m deep canyon is formed. The southward flow of the Canary current between the islands is constrained by the channel and eddies and gyres have been noted.

Stranding reports of cetaceans in the Canaries between 1980 and 1987 recorded six species of dolphins: the common dolphin *Delphinus delphis*, the bottlenose dolphin *Tursiops truncatus*, the striped dolphin *Stenella coeruleoalba*, the rough-toothed dolphin *Steno bredanensis*, Risso's dolphin *Grampus griseus*, and the short-finned pilot whale *Globicephala macrorhynchus* (Vonk and Martin, 1988). Sperm whales, pygmy sperm whales and unusually high numbers of four species of beaked whales were also recorded. Since most of the animals stranded alive, it appears that these species are found in the vicinity of the Canaries, and were not simply carcasses carried by oceanic currents from distant areas. *Globicephala*, *Tursiops* and *Delphinus* are regularly seen nearshore and there have also been observations of killer whales, *Orcinus orca*, in the same region (Herve-Gruyer, 1989; 1990).

3.3 RESULTS

3.3.1 Seasonal Occurrence

Field work was conducted from October 1989 through July 1991. Vessel effort totalled 1134.3 hrs over 200 vessel days (Figure 3.3). Vessel surveys were conducted at an average interval of 3.30 ± 0.29 days (all values mean ± S.E., n = 199 intervals), with a maximum gap between surveys of 29 days. Weather conditions occasionally prevented surveys, especially during December through February, when winter storms could occur for up to two weeks. Effort increased during two intensive periods: June-August 1990 and April-June 1991. These were also the periods when the large sailboat was chartered, allowing extended days at sea during rougher weather.

Whales were located on 155 days and observed for 542.8 hrs of the 200 vessel survey days (78%) and 1131.3 hrs of vessel effort (48%). The intervals between whale encounters ranged from one to 29 days, and averaged 4.26 ± 0.41 days (n = 154). Summaries of the observation data relative to effort are presented for both hours and days in Figure 3.3. The data on observation hours represent the total hours of each boat, whether they were together or not, and thus tended to overestimate both effort and observations. Also, since hours included time returning to port from offshore whale observations, effort hours

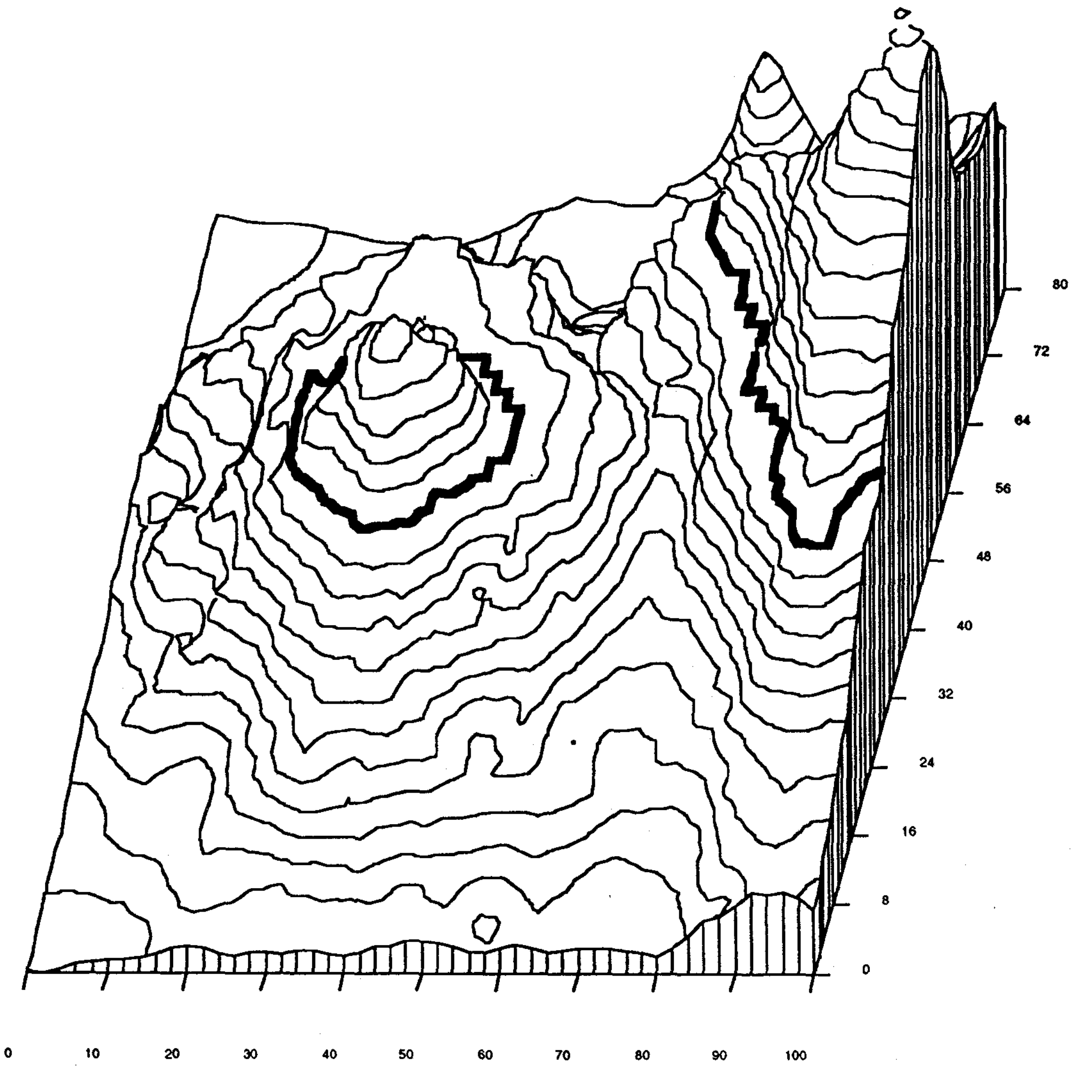

Figure 3.2. Three dimensional contour map of the bathymetry in a 100 km x 80 km area around Tenerife and Gomera. Contour intervals are 250 m and sea level is indicated in bold. Elevations range from +3718 m (Mt. Teide on the right) to a maximum sea depth of -3200 m (lower left). The minimum depth of the saddle between Tenerife and Gomera of 1120 m forms a south-facing, closed canyon below this depth.

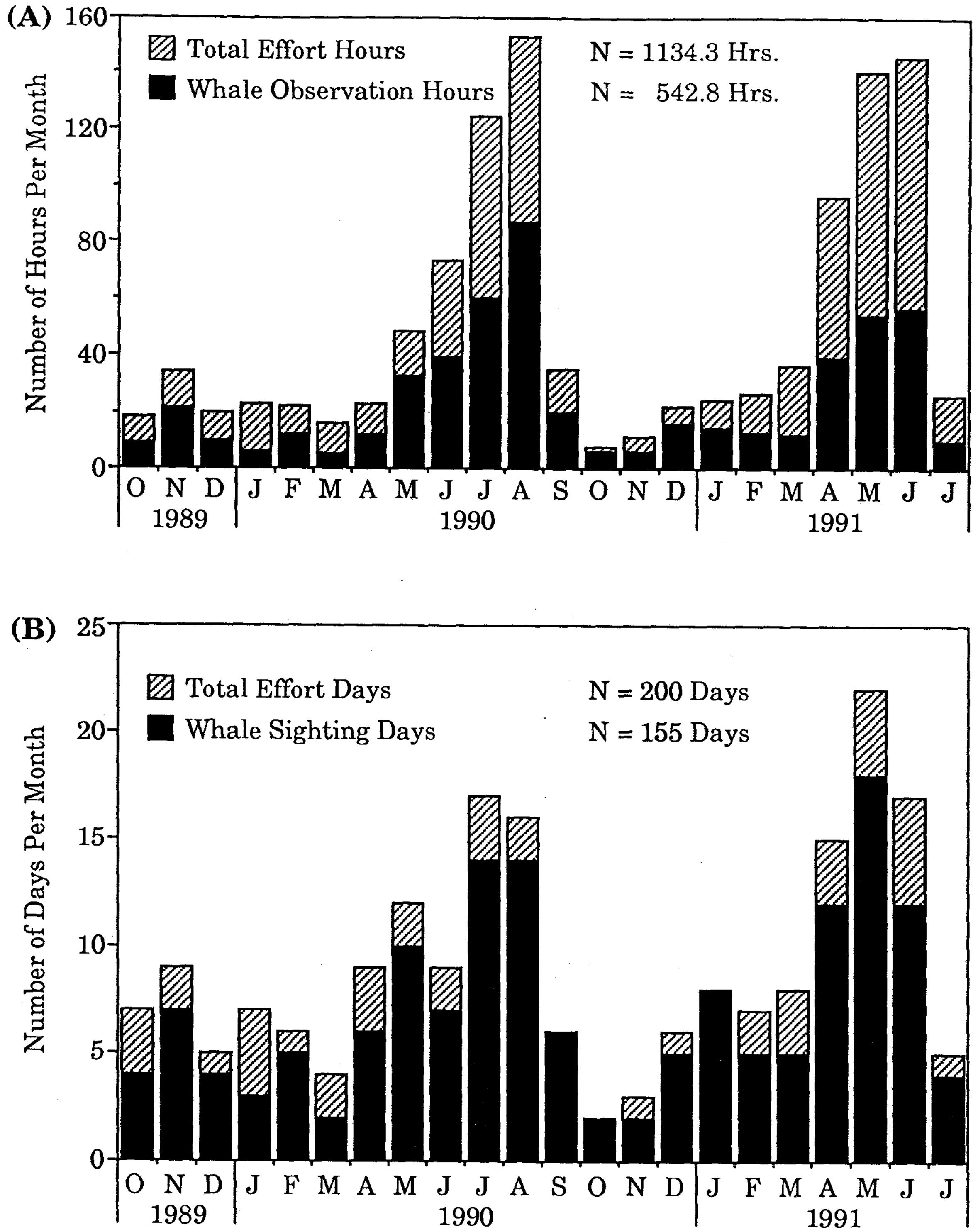

Figure 3.3. Summary of effort and observations in hours per month (A) and days per month (B). The seasonal increase in effort was when two vessels were used. Both vessels were used to calculate number of hours per month, while days were counted with both vessels combined.

tended to be overestimated. The hourly data were not analysed further for seasonal occurrence, but they give some indication of the seasonal distribution of the whale observations. The primary effort was to collect photographs of all individuals and to maximise the time spent with whales. The amount of time spent with a group (before moving on to locate other groups) was dependent on the behaviour of the whales (e.g. respiration patterns, consistent direction of travel, avoidance behaviour). Because of this potential bias, data on relative seasonal occurrence in the study area was only tabulated for complete sampling days.

The occurrence of pilot whale groups was examined for trends in seasonal occurrence. Whales were located in all 22 months of the study. However, monthly SPUE ranged from 0.43 to 1.00 observation days per effort day, with an average of 0.77 ± 0.03 (Figure 3.4). Monthly SPUE values were pooled by month, three-month seasons, and for all seasons combined. None of these combinations showed significant seasonal differences (Kruskal Wallis; month: $H = 10.05$, $df = 11$; season/year: $H = 6.56$, $df = 7$; pooled season: $H = 3.72$, $df = 3$, $P > .05$). Sample size, however, had a highly significant effect on the variation, illustrated by a plot of the SPUE as a function of the total number of effort days (Figure 3.5). Months with samples of fewer than 10 days showed a significantly greater variation in SPUE values, suggesting that 10 days was a minimum sample size necessary to quantify relative occurrence. Unfortunately, only months in the spring and summer had sufficient sample sizes (Figure 3.5), thus annual variation in occurrence could not be properly tested. However, the similarity between values for the spring and for months with sufficient sample sizes suggests that whale occurrence during this period is constant.

3.3.2 Geographic Distribution

A total of 252 quadrats (1008 km^2) were covered while searching for pilot whales (Figure 3.6). The majority of the search effort was conducted within 10 km of the southwest coast of Tenerife (Figure 3.6). Additionally, eight transects were conducted to the southern coast of Gomera Island and five transects were conducted to the northwestern tip of Tenerife at 28° 20' N. However, whales were only located in 54, or 21%, of the quadrats covered (Figure 3.7). Pilot whales were never documented in any of the surveys to northwest Tenerife and Gomera, although other species, such as bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), rough-toothed dolphins (*Steno bredanensis*) and Atlantic spotted dolphins (*Stenella frontalis*) were all located in these areas. This indicates a preference by pilot whales for the waters off southwestern Tenerife

Thus, the total area of observation for these whales was 216 km^2, between 27°58'N and 28°08'N, and 16°41'W and 16°52'W. The average depth of the 54 quadrats was 1386 ± 70 m and the average Contour Index was 34.0 ± 3.0. However, the whales were not observed equally in all of the quadrats. Categorisation of quadrats by the relative whale usage showed that only 13 of the quadrats (25% of all quadrats where whales were observed) were heavily used, 14 (27%) were moderately used and 25 (48%) were only lightly used. Heavily used quadrats had significantly shallower average depth (1151 ± 74 m, Kruskal Wallis $H = 6.00$, $df = 2$, $P < .05$) than moderately used (1365 ± 128 m) or lightly used (1520 ± 117 m) quadrats (Figure 3.8). Areas of heavy usage also had

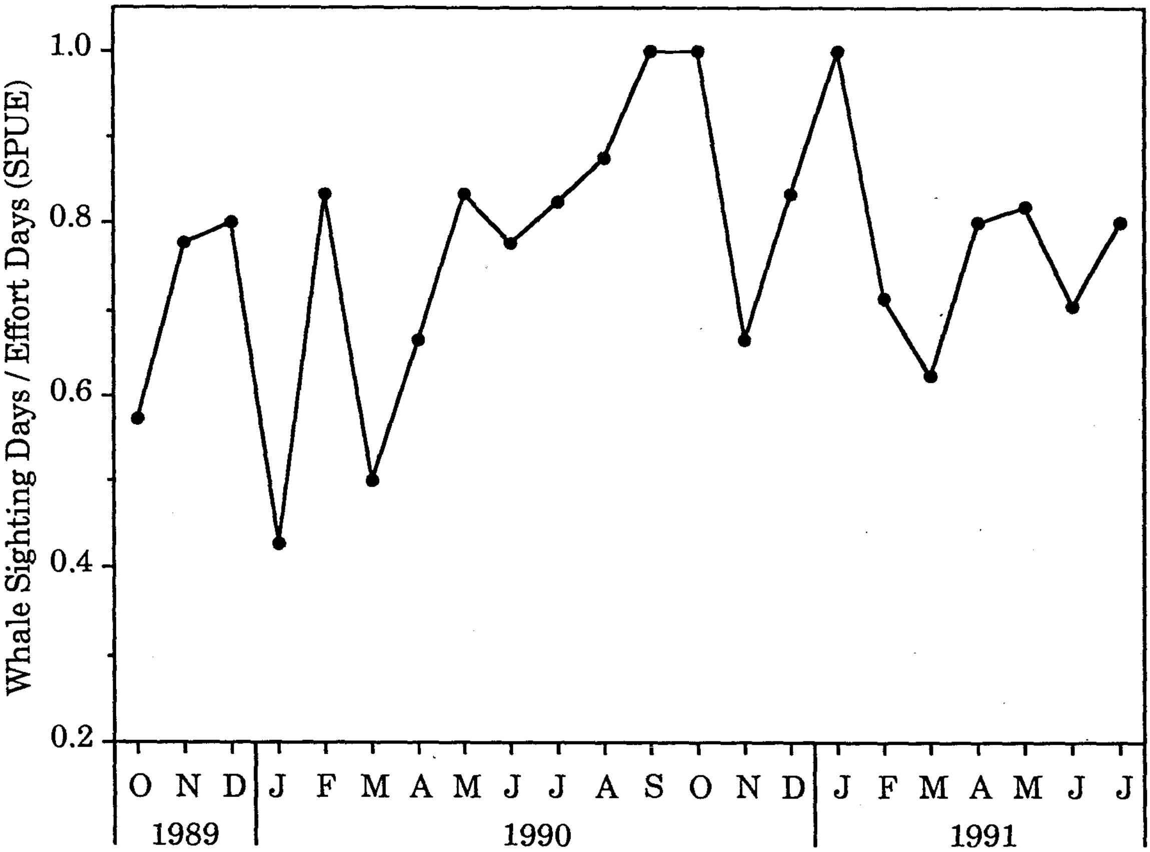

Figure 3.4. Plot of Sighting Per Unit Effort (SPUE) for the 22 months of the study. SPUE averaged 0.77 ± 0.03 (mean ± S.E.). There were no significant seasonal differences for pooled months or seasons.

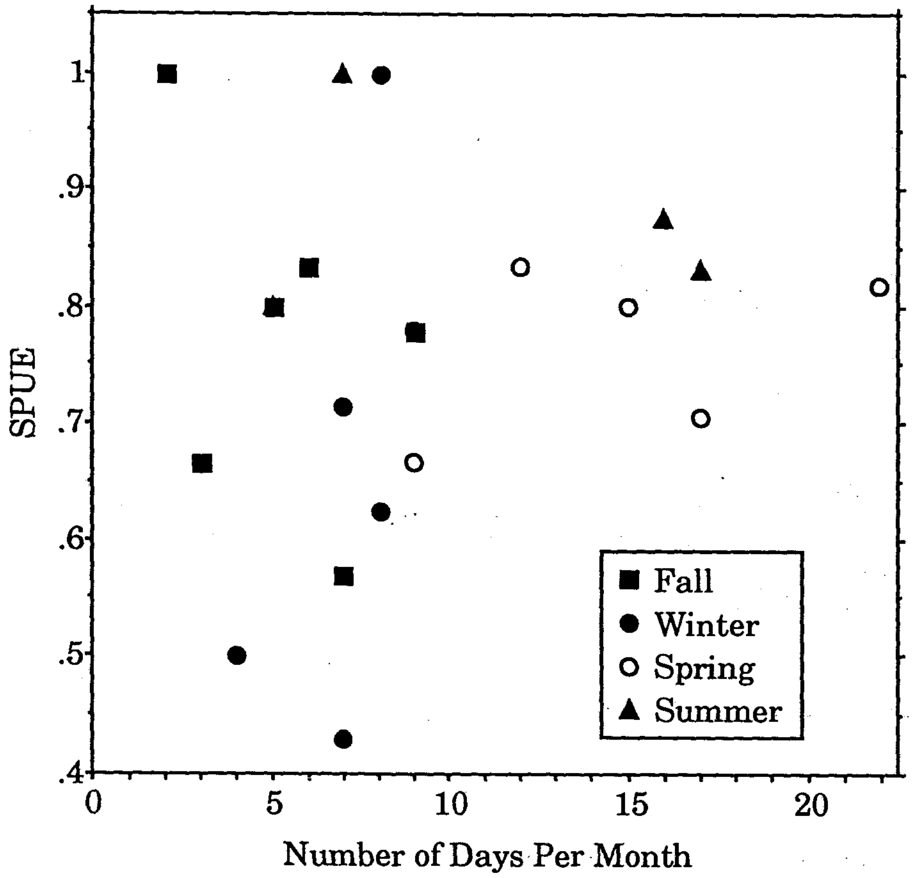

Figure 3.5. Plot of the Sighting Per Unit Effort (SPUE: whale sighting days/effort days) as a function of the number of effort days for each of the 22 months of the study. Months are displayed for each of the pooled seasons: fall (Oct-Dec), winter (Jan-Mar), spring (Apr-Jun) and summer (Jul-Sep). Months with fewer than 10 effort days showed the greatest variation in SPUE.

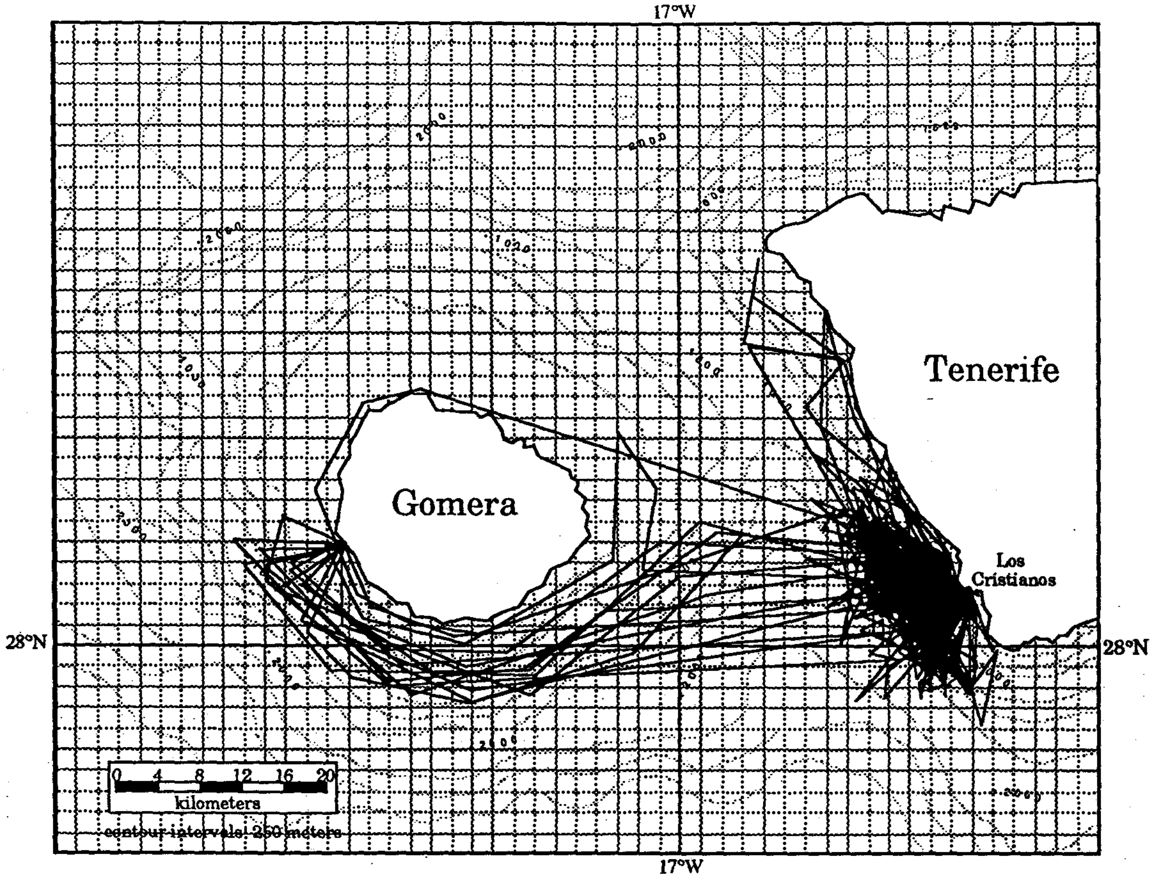

Figure 3.6. A summary plot of all vessel effort tracks. Most of the effort was concentrated off Tenerife, but eight transects were conducted off south Gomera and five were conducted to the northwest tip of Tenerife.

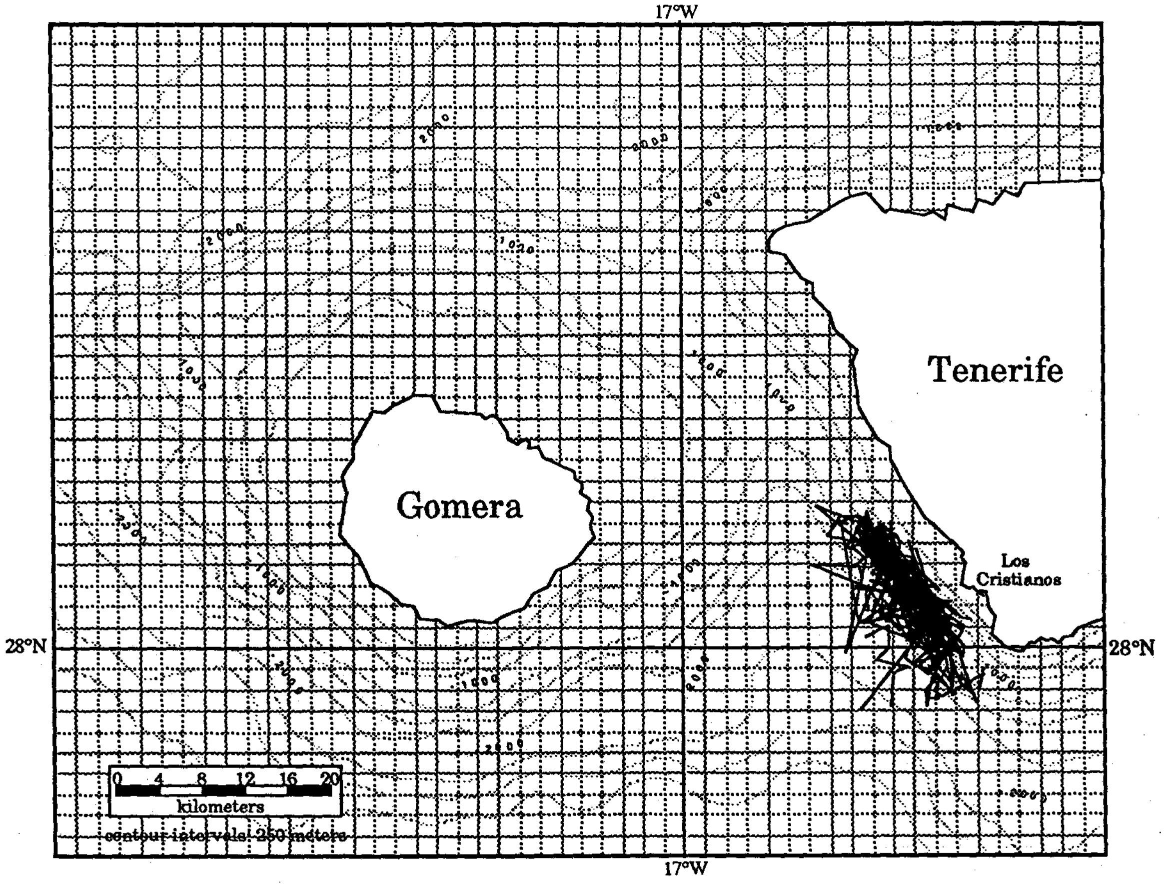

Figure 3.7. A summary plot of all vessel tracks while following whales. The majority of whale sightings were centered over the steep slopes along the 1000 m. depth contour.

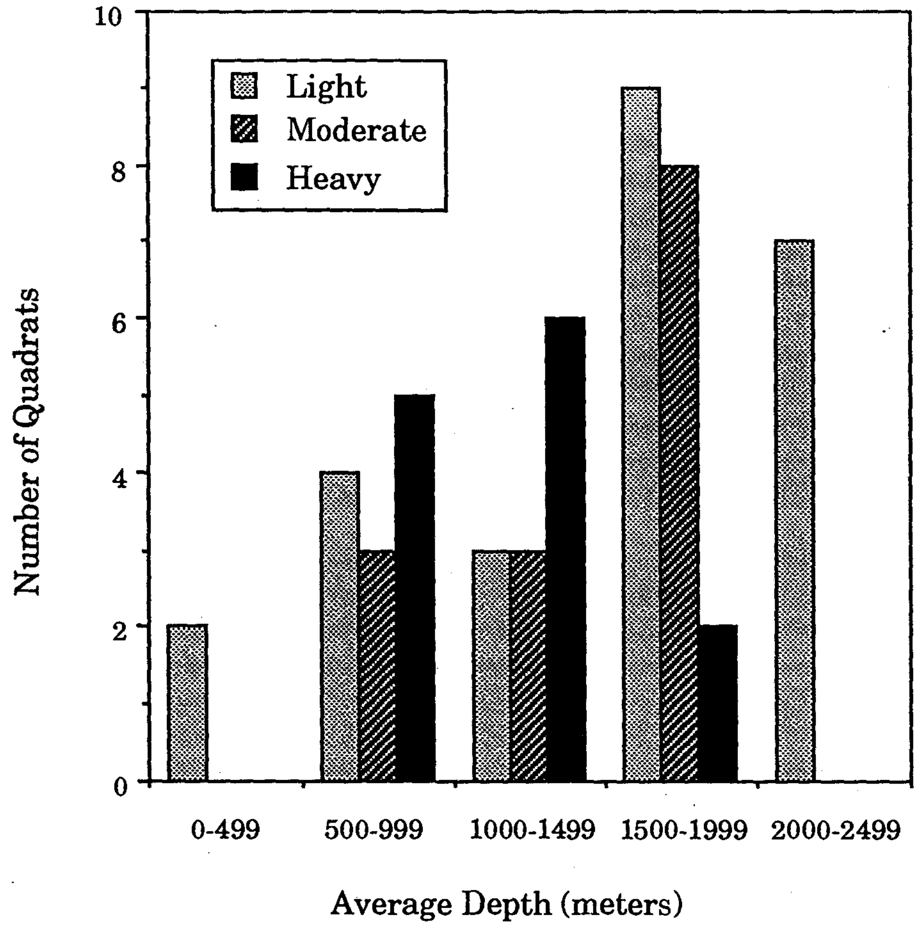

Figure 3.8. The average depth of quadrats plotted by frequency of whale usage. The three categories were significantly different ($H = 6.0$, $df = 2$, $P < .05$) with heavily used quadrats shallower (1151 ± 74 m) than either moderate (1365 ± 128 m) or light (1520 ± 117 m) usage quadrats.

significantly larger Contour Indices (heavy: 43.2 ± 3.2, moderate: 34.6 ± 6.4, light: 28.9 ± 4.7; Kruskal Wallis H = 7.40, df = 2, P < .02), indicating that the whales preferred areas of steeper slope. These data suggest that the whales are using specific portions of the Tenerife offshore habitat.

3.4 DISCUSSION

Numerous studies have documented an association between delphinids and underwater topography. My own studies found that killer whales commonly foraged over area of high relief (J.Heimlich-Boran, 1988). It appeared that they were using underwater seamounts (which were necessarily also areas of high slope) as a barrier against which to herd fish. Salmon also tended to collect in these areas during ebb tides to avoid losing ground on migrations to their natal rivers (Felleman *et al.*, 1991). Common dolphins have been well studied off the southern California coast (Evans, 1971; Hui, 1979), where there are a series of underwater escarpments. Dolphins collect over these areas, which are known to be areas of upwelling and nutrient mixing that support the anchovy food chain (Hui, 1979). Thus, distribution can provide some indication of feeding ecology.

Pilot whales appear to be similarly localised in areas of high relief along the 1000 m depth contour off southwest Tenerife. This is also known for upwelling. Drift buoy studies have mapped out the main current flows of this area (Molina, 1979). The predominant current through the area, the Canary Current, enters the strait between Tenerife and Gomera, forms a counter clockwise gyre current which starts mid-strait at the midpoint of Tenerife, flows southeast, and then circles north and offshore again at the midpoint of the island. The area of this current flow corresponds to the main area where pilot whales were observed. Unfortunately, the missing element in this picture is how this current affects local prey resources. It is likely to generate upwelling and mixing as it turns away from the coast, but there are no fisheries in the area which can provide any indication of the affects on prey resources. Thus, until further data become available, it can only be said that pilot whale distribution was correlated with the steep slopes along the 1000 meter depth contour where a gyre current is potentially generating upwelling.

Behavioural evidence of the importance of this specific area comes from observations of the whales at the boundaries of the area. During six such observations, the whales slowed their travel and spread out, eventually rejoin and moving off in the opposite direction. These "turn-arounds" have also been observed in killer whales and were correlated with the occurrence of slack tides, when the tidal current changed direction (Felleman *et al.*, 1991). It could be that similar current processes are affecting the pilot whales. The implication is not that the whales are somehow limited by currents, but that currents affect prey distribution and the whales may pay attention to them, perhaps even use them to locate or predict prey concentrations. Recent telemetry studies of squid, which are pilot whales' preferred prey (Mercer, 1975; Seagars and Henderson, 1985; Clarke, 1986; Overholtz and Waring, 1991), have shown they use upwelling currents to reduce the energetic costs of locomotion, in a similar way that raptors use updrafts for soaring (M.Wells, pers.comm.).

The strong bias in the distribution of effort does not allow any firm conclusions on pilot whale distribution in other areas. Although surveys outside of this area were often limited by the trade winds, many other species of delphinid, but not pilot whales, were located in the 800 km^2 which were surveyed off Gomera and northwest Tenerife. Anecdotal reports from daily dolphin-watching boats along the northwest coast of Tenerife, which have run trips two times a day for the last two years, have never reported pilot whales. Sailing clubs, which run regular 7-day trips from Tenerife to La Gomera, La Palma, El Hierro and Gran Canaria, have never reported sightings of pilot whales.

3.5 SUMMARY

The distribution of short-finned pilot whales in the Canary Islands was studied over a 22 month period. Whales were located on 155 days during all months and there were no significant seasonal differences in the sighting per unit effort (SPUE), although months with sample sizes less than 10 days have large variance in SPUE. All pilot whale observations occurred within a 200 km^2 area, with an area of heavy usage of 50 km^2. The whales preferred areas of steep slope along the 1000 m depth contour. Pilot whales were never documented in any of the outlying surveys to northwest Tenerife and Gomera. The area of whale use was characterised by a deep canyon and current patterns which could be generating upwelling. Further studies should focus on gathering information on prey distribution in this area.

CHAPTER 4: SOCIAL ORGANISATION OF SHORT-FINNED PILOT WHALES (*Globicephala macrorhynchus*)

4.1 INTRODUCTION

Field studies of free-ranging mammals, utilising methods of individual identification, have greatly enhanced our understanding of their social systems. Research into the social lives of primates (Goodall, 1986; Stammbach, 1987), carnivores (Schaller, 1972; Packer, 1986; Packer *et al.*, 1988), ungulates (Clutton-Brock *et al.*, 1982) and elephants (Moss and Poole, 1983; Moss, 1988) have shown that individuals vary widely in their behaviour. All individuals ultimately attempt to maximise their reproductive success through individual strategies of resource and mate acquisition, but there are differing costs and benefits for the various age and sex classes of a population (Clutton-Brock, 1986). For example, in most polygynous mammals, males disperse from their natal group at maturity and search for mating opportunities elsewhere as a means of avoiding inbreeding, while females remain with their group and breed in association with their female relatives (Greenwood, 1980; Pusey, 1980; Shields, 1982; Greenwood, 1983; Moore and Ali, 1983; Shields, 1983; Pusey and Packer, 1987b). Thus, males in such groups can be expected to have very different social associations from females. An understanding of the social networks of associations and relationships is essential in defining social structure and mating system.

Recent studies of large members of the cetacean family *Delphinidae* have demonstrated unique patterns of dispersal and association. Long-term observational studies of killer whales, *Orcinus orca* have revealed a total lack of dispersal of either sex from natal groups, with males remaining in the social group of their mothers, sisters and related offspring into adulthood (S.Heimlich-Boran, 1986; S.Heimlich-Boran, 1988; Bigg *et al.*, 1990; Olesiuk *et al.*, 1990). The role of males in these groups is still not well understood. Adult males have a lower degree of association with members of their pod than females and immatures (S.Heimlich-Boran, 1986; 1988). There is a multi-level social organisation, with groups of pods forming isolated communities (Bigg *et al.*, 1990). Genetic studies on the same populations show relatively high degrees of inbreeding at the community level, while finding indications of reproductive isolation between communities (Stevens *et al.*, 1989; Hoelzel and Dover, 1990; Hoelzel, 1991a). Long-finned pilot whales (*Globicephala melas*) appear to have some similar elements in their social system: genetic analyses have found that males were not the fathers of the foetuses in their own pods, some pods were found to be closely related, and there is also some degree of reproductive isolation between groups, implying well-defined patterns of genetic interchange (Andersen, 1988; Amos *et al.*, 1991a; 1991b; In press). These studies all raise questions as to the nature of the mating system of these large, sexually-dimorphic delphinids.

In the following section, I report the results from a 22-month study of the social organisation of free-ranging, short-finned pilot whales (*Globicephala macrorhynchus*) off the western coast of Tenerife in the Canary Island archipelago from October 1989 through July 1991. The primary goals of this study were to identify individual pilot whales, examine the patterns of associations between individuals, determine the levels of social organisation defined by these associations and finally to use this evidence to examine the hypothesis that mating may occur outside of the core social groups.

4.2 METHODS

4.2.1 Photographic Sampling Methods

The photographic identification of individual pilot whales was the primary initial goal of this study and formed the basis for all other analyses. The majority of the field effort consisted of trying to photograph as many pilot whales as possible. The aim was to photograph all individuals in a group and then move on to photograph another group. Logbooks were used to maintain an ad libitum record of events (Altmann, 1974). Information recorded included start and end times of vessel trips, course information such as heading and periodic compass triangulation on landmarks (as described in Chapter 3), start and end times of each pilot whale group observation, comments on all other pilot whale groups observed from the vessel out to the horizon (within a 2 km radius with binoculars), and general notes on behaviour. Once a group was located, the vessel slowly approached from the side and slightly to the rear. A constant throttle was maintained because it was found that sudden changes in engine noise could startle a group, causing it to dive. The best conditions for photography were when the vessel approached to within 20 m, but it was often possible to approach individuals to within 1 m.

Black-and-white photographs and colour slides were taken using a 35 mm Nikon FE-2 camera equipped with a 70-210mm zoom lens and a Nikon F4 camera equipped with a 80-300mm auto focus zoom lens. Both cameras were equipped with motor drives to take photographs at three to five frames per second and data backs for imprinting date and time on each frame of film. Underwater photographs were taken with a Nikonos V camera using a f2.8 35mm lens and an f1.4 28mm lens.

4.2.2 Photographic Analysis

All negatives were examined visually for identifiable whales. Negatives from the first nine months of the study were examined under a 20x compound microscope for initial identifications at the end of each field day. After returning to Cambridge, all films were examined using a Photovix II Film Video Processor, which allows negative or positive images to be relayed to a video screen for magnification and viewing. This viewing of negative materials was the most efficient for the initial location of identification photos. When high quality images were located of an individual, black-and-white prints were made for an identification catalogue.

Initially, it was necessary to determine what constituted a "usable" identification photograph. This *photographic quality* must be determined independently of the *recognisability* (defined below) of the identification characteristics of the animal being photographed in order to quantify the proportion of usable photographs versus the proportion of re-identifiable whales (Hammond, 1986; Mizroch *et al.*, 1990). The photographs were classified into three quality categories: 1) excellent, 2) good, and 3) poor. Six basic elements of photographic quality were evaluated: 1) proper exposure with good contrast, 2) focus, 3) lighting conditions, such as glare and backlit silhouettes, 4) proportion of the frame filled by the whale's image (i.e. the distance of the whale from the camera), 5) angle of the longitudinal axis of the whale to the film plane of the camera, and 6) the amount of the whale's body visible above the water line. Obviously, as focus decreased and the distance between the camera and the whale increased, the ability to see identifying characteristics decreased. Lighting conditions were important considerations for the visibility of faint scratches and pigmentation marks. The angle between the whale and the film plane of the camera was more difficult to evaluate and could introduce error in identification due to apparent changes in the relative location and spacing of identifying characteristics. These elements were evaluated visually. Cues for whales not travelling parallel to the film plane were the angle of the water line relative to the horizon and the ratio of dorsal fin height to width. Photographs of these whales could be identified by sloped water lines (relative to the horizon) and narrowed dorsal fins. Excellent photos were those with proper exposure, sharp focus and direct lighting from a sun at 45° declination behind the photographer on full frame images of a whale high out of the water with the transverse axis of the whale parallel to the film plane. All types of identifying characteristics could be recognised in these quality of photographs. Good photographs were slightly lacking in some element of photographic quality, but were still potentially usable as an identification photograph. Poor photographs were blurry images of distant whales and were not used.

4.2.3 ID Characteristics

Whales were identified on the basis of naturally occurring marks and scars on the dorsal fin and back. Some of these marks were pigmentation patterns. Short-fin pilot whales in the eastern tropical Atlantic do not have distinct "saddle patches", or areas of light grey located along the backbone just posterior to the dorsal fin, as has been shown for pilot whales in other parts of the world (Yonekura *et al.*, 1980). However, they do have distinct post-orbital blazes which rise up from the eye to the anterior edge of the dorsal fin. These marks blend into a fainter saddle patch which tapers down along the backbone to the caudal peduncle. In excellent lighting conditions, it was possible to use irregularities in the pattern of these pigmentation marks to distinguish individuals. However, the most common characters used for identification were nicks in the trailing edge of the dorsal fin and scratches along the side of the body just below the dorsal fin. The most likely cause of these nicks and scratches was the teeth of conspecifics. It is unknown in what behavioural context these scars were received, whether in play or aggression. They were found on all age/sex classes. Additional scars were caused by encounters with larger objects, probably small boat propellers, resulting in large chunks removed from the back and caudal peduncle. One juvenile appeared to have been bitten by a large predator, such as a shark or killer whale.

Identification characteristics were classified into 24 categories based on dorsal fin shape (especially hooked or with a hump on the leading edge), number and location of nicks (cuts in the trailing edge of the dorsal fin) classified by location by dividing the dorsal fin into thirds, dings (dents in the leading edge of the fin), and tabs (projections from the trailing edge of the fin) and the presence of barnacles. The categories (and their three letter abbreviations were: 1) Cleanfin: CLF, 2) Cleanfin w/ Scallops: CLS, 3) Cleanfin w/ Barnacles: CLB, 4) Unique Individuals: IND, 5) Dolphin-Like Fin: DLF, 6) Hooks: HOO, 7) Serrated Hooks: HOS, 8) Front Dings or Humps: FDH, 9) Raggedy w/ Fingers or Tabs: RFT, 10) Small Multiple Nicks: SMN, 11) Two Small Nicks: TSN, 12) Large Double Nicks: LDN, 13) Small Base Nicks: SBN, 14) Large Base Nicks: LBN, 15) Small Nicks Middle Third: SNM, 16) Large Nicks Middle Third: LNM, 17) Small Nicks Top Third: SNT, 18) Large Nicks Top Third: LNT, 19) Nicks Near Tip: NNT, 20) Square-Tips: SQT, 21) Flap Finger Tips: FFT, 22) Small Round Tips: SRT, 23) Large Round Tips: LRT, and 24) Handles: HND.

Each individual which could be classified into one of these categories had varying degrees of *recognisability*. This was defined as the ability to repeatedly identify the same individual in photographs of different quality. For example, an animal with the upper half of its dorsal fin missing would have a high recognisability, even in a poor quality photograph. On the other hand, a clean-fin animal, with a faint pigmentation mark could only be identified in the highest quality photo. Also, the more identifying marks an animal had, the greater was its recognisability. An animal with a single nick could be confused with another animal with a nick in the exact same location. With increasing numbers of marks, the probability of two animals sharing the same marks becomes infinitesimally small. Thus, the two elements of photographic quality and recognisability are interrelated and together contribute to the confidence in identifications.

The initial identification of an individual, regardless of recognisability, required an excellent quality photograph which clearly indicated some set of identifying characteristics. This photograph was printed in 12 cm by 17 cm format and stored as a Master ID in a card catalogue file under the ID Type category. Subsequent negatives of that individual were all compared to this master photo. Identifications from all frames of film were entered onto computer to aid in cross-referencing multiple sightings of the same individuals.

4.2.4 Unidentifiable Individuals

The whales identified in this study represent only a portion of the whales observed. Some individuals had no identifying marks and even the highest quality photograph would not provide any guarantee of repeat identification. In order to provide an estimate of these "clean-finned" animals, field count estimates of the total number of animals present in a group under observation were compared to the number of clearly identifiable animals recorded in the photographs of that same group. Differences between these two counts provided an estimate of unidentifiable animals in the group. This was expressed as a percentage of the total group count and averaged for all groups which had field count estimates made after a minimum 30 min observation (to assure sufficient time to make an accurate count).

4.2.5 Age/Sex Classification

Whales were classified into five age/sex categories: 1) adult males, 2) mothers, or females with calf, 3) other adults, 4) juveniles, and 5) calves, using relative photogrammetric methods (J.Heimlich-Boran, 1986b) and visual cues. Physical characteristics of pilot whale age and sex classes were derived from published measurement data (Yonekura *et al.*, 1980; Kasuya and Marsh, 1984; see Chapter 2 for review) and were used to calculate expected relative measurements. The physical characteristics utilised in this study were relative body size, relative location of the dorsal fin along the body, and relative dorsal fin shape. Multiple photographs of identified individuals were examined for suitable relative photogrammetric features. The relative physical characteristics could be quantified for some individuals with measured photos, while for others the characteristics were determined qualitatively. Additionally, visual estimates of relative size were recorded in the field, especially for very large or very small animals. Other information was collected from the degree of association with different-sized animals over repeated observations.

Adult males were identified by their large size relative to all other whales (see review in Chapter 2). The differences in growth and maturation are such that even young, newly-matured adolescent males are 14% larger than a fully adult female which has attained her asymptotic length (4.14 m vs. 3.64 m). Males also differ from females in other body proportions, such as the relative position of the dorsal fin on the body, dorsal fin width and the shape of the melon. Dorsal fin position was quantified from measurements available from 56 mature animals (10 males and 46 females) published by Yonekura *et al.* (1980): 1) total body length, 3) tip of snout to blowhole, and 8) bottom of notch of flukes to the apex of the dorsal fin (numbers refer to Yonekura's measurement numbers). The distance from the blowhole to the apex of the dorsal fin (B-DF) was calculated by: B-DF = (1–8) – 3; . The width of the dorsal fin at the base (measurement no. 16) was then expressed as a proportion of the calculated measurement, and termed the "blowhole/dorsal fin ratio" (BDFR). Males had significantly higher BDFRs than females (0.65 ± 0.04 vs. 0.58 ± 0.02; mean ± 95% C.I.; $t = 4.15$, $P < .0001$), indicating that their wide dorsal fins occupied a greater proportion of their backs. BDFRs greater than 0.60 calculated from photographs of Canary Island pilot whales were considered to be an identifying characteristic of adult males. The dorsal fins of male Japanese pilot whales were significantly wider and taller than the dorsal fins of females, and the change was associated with male maturation (Yonekura *et al.*, 1980). Three categories of dorsal fin shape were scored into three qualitative categories for each animal. The width of the dorsal fin at the base was scored relative to the distance from the blowhole to the leading edge of the dorsal fin. The height of the dorsal fin was scored in relation to the width of the fin. Finally, the presence of a hump along the leading edge of the dorsal fin just above the back was scored according to it's development. In order to be classified as an adult male, an animal must have scored in the highest category for at least two of the three characteristics. The melon of an adult male is characterised by a flattened anterior surface and square corners at the top and sides. The projection of the melon beyond the tip of the lower jaw differs between adult males and females. Melon projection for 28 mature females (lengths from 3.2 to 3.8 m) ranged from 0 cm to 8.0 cm and averaged 3.6 ± 1.6, while melon projection for 5 mature males (4.2 to 4.7 m) ranged from 6 to 13 cm and averaged 9.3 ± 2.7 cm (Yonekura *et al.*, 1980, Fig.3). These features were often visible, especially in underwater photographs.

Mothers were defined as all full-sized animals with a repeated association with a small calf or juvenile. The calf had to be present on all observations of the mother. Occasionally, a calf had associations with more than one adult; in this case, the animal with which it associated for a majority of the time was assumed to be the mother.

The category of unknowns was defined as all full-sized animals who did not have characteristics of adult males and who did not have a consistent association with a specific immature animal. This category was potentially composed of a combination of adult females and adolescent males. Comparisons of body length growth data for male and female short-finned pilot whales in Japan allowed the possible age range of the adolescent males to be estimated. Females mature at 3.22 m and ceased to grow after 3.64 m (Kasuya and Matsui, 1984). Males of similar size to newly mature females would be approximately 8 yrs old, while males similar to fully-grown females would be approximately 12 yrs old. If the midpoint between these lengths (3.43 m) was considered to be the size at which a full-size animal was distinguished from a juvenile, then males of this size would be approximately 10 yrs old (Yonekura *et al.*, 1980). This was within the lower range of body lengths and ages at which males were found to be capable of sperm production (early-maturing category of Kasuya and Marsh, 1984, see review in Section 2.5.2.1), although still less than the mean length and age at full maturity (4.14 m and 15 yrs). It has also been shown that males and females of similar body size do not differ in any of the characteristics used to identify adult males (Yonekura *et al.*, 1980). These characters are only larger on adult males because of their continued growth after females cease to grow. Thus, there was no way to distinguish these adolescent males from adult females without calves. Underwater photographs of the genital region were attempted, but were never successful.

Immature animals were identified by their small size relative to all other whales. There were two categories of immature animals: juveniles and calves. Calves were the smallest class of immatures. Newborn calves (up to one month old) could be identified by an undeveloped melon, which resulted in a lumpy appearance of the head in front of the blowhole due to the visibility of the dorsal ridge of the skull. Calves of less than a year of age could be identified by the presence of foetal folds. These are the result of a lateral folding of the foetus in the womb and remain visible as creases which fade to lightly pigmented stripes during the first year of life. Older calves were defined in two ways: first, as those animals with a consistent association with a mother, which probably continues up to a minimum age of three years, the nursing period (Kasuya and Marsh, 1984), and second, as those animals which were less than two-thirds the size of the mother. Size and age correlations indicate a maximum of four years of age for an animal of this relative size (Yonekura *et al.*, 1980). Juveniles were defined as immatures larger than two-thirds the size of the mother and smaller than adults. The ages of the apparent juveniles would have been different for males and females, because of the faster male growth rates. Female juveniles were estimated to be between 4-9 yrs of age, male juveniles would have been less than 8 yrs (Yonekura *et al.*, 1980; Kasuya and Marsh, 1984). While it was usually possible to determine the mother of all calves, juveniles often had a wider variety of associates and the identification of their mothers was more difficult.

4.2.6 Group Definition

The primary aim in defining pilot whale groups was to examine long-term patterns of association between identified individuals. The hypothesis was that pilot whales have a multi-level society, with inseparable core groups of mothers and their offspring associating with other core groups to form relatively stable pods, which in turn associated on a less regular basis with other pods to form a clan. The key element in the definition of a group was its long-term stability. In this respect, no attempt was made to record subtle changes in individual associations.

A pilot whale group was defined as all whales within 250 m of each other exhibiting similar behavioural characteristics, such as direction and speed of travel, timing of surfacing, and general activity level. This definition covered all situations. The majority of groups were more cohesive than this, consisting of animals travelling parallel to one another with a maximum of five body lengths (20 m) between adjacent individuals.

The data set of photographs used for the identification of groups was restricted to those observations when times were recorded for each photograph (i.e. when the camera data backs were operating) and when log entries clearly described group formations in terms of inter-individual distances. At times, individuals were spread across wide areas, and it was not possible to define groups.

Ultimately, groups were characterised by the identity of the individuals photographed. Although five separate groups may have been observed in the field, it was often the case that the same individuals were identified in more than one group. Groups with any common members were considered to be repeat sightings of the same group, and were recorded as a single group. For example, if whale 1 was seen with whales 2, 3, and 4 in the morning, and later in the same day with whales 2, 5, and 6, then the one group recorded for that day consisted of whales 1, 2, 3, 4, 5, and 6. This helped to assure complete sampling of the groups, although it also introduced a bias: changes of group membership by individuals during a day were disregarded. It was also necessary to assign an individual to only one group each day in order to fulfil one of the underlying assumptions of the association analyses described below.

A unique number was assigned to each group, composed of the sighting day number and a sequential group number for that day.

4.2.7 Pair Associations

The quantification of associations within a social group is an important aspect of the study of social behaviour. A variety of field studies have used measures of association to describe various elements of animal society (Schaller, 1972; Guinness *et al.*, 1979; Clutton-Brock *et al.*, 1982; Lott and Minta, 1983; S.Heimlich-Boran, 1986, 1988; Bigg *et al.*, 1990). The original approaches to quantifying associations were in studies of community ecology (Dice, 1945; Cole, 1949), which needed to describe the degree of association between species located together in a geographical area in order to define a "community". The application of association indices to the study of social organisation is more recent, and the original intention of the equations should always be considered in the newer application to animal societies. The common goal of any association analysis is to quantify the co-occurrences of some unit of interest . The degree of co-occurrence is then used to define population-wide patterns of association.

There are two main problems to be considered when quantifying associations; one is common to associations between species and individuals, while the second arises when applying the methods developed for species associations to the quantification of associations between individual animals.

The shared problem for associations between species and individuals is the problem of the reciprocity of associations. An association between A and B actually has two components: A's association with B, and B's association with A. For an example, Ginsburg and Young (1992) consider the case of an association between a species of tree and a species of grass sampled from an equal number of woodland and plains habitats. Assume that the tree species was found in all woodland samples, while the grass species was found in both woodlands and plains. The association between grass and tree from the tree's perspective would be 100%, since they were only located together in the woodland samples. The association from the perspective of the grass would be only 50%, since the grass was found without the tree in all of the plains samples. Dice (1945) dealt with this problem by presenting two types of indices: one type to present the non-reciprocal values described in the example above, termed "association" indices, and another type, termed "coincidence" indices, which presented association as an average for both A and B. However, this use of multiple indices was too unwieldy for most analyses and the emphasis has since been to generate a single index of association which fairly reflects the true association between two units of interest.

The specific ways in which different indices deal with the problem of reciprocity will be discussed shortly, but first it is necessary to understand the problems which arise when applying species association indices to individual associations. The problem is essentially one of defining the unit of sampling. When sampling for the co-occurrence of species on a plot of land, each plot (if randomly chosen) is a separate and independent sample. Two species found together in a sample are always considered to be co-occurring. However, when sampling the social groupings of free-ranging animals, the unit of sampling must be defined (e.g. 15 min scan samples: (Altmann, 1974), but what ever the unit is, it would often be possible to locate more than one grouping of animals during this time period. Thus, a pair of animals may be located together in the same sample, and yet also occur in separate groups. A solution would be to treat each group as an independent sample. But if the groups are located closely together in time, the composition of the groups may be interrelated and dependent. In other words, it may be possible to predict the presence of one group from the initial location of some other group, but the samples would no longer be independent. Alternatively, the time period of sampling, although not instantaneous, must be short enough that changes in group memberships are unlikely during the course of sampling.

There are three primary indices which are currently in use. One of these is Dice's "coincidence" index, termed the Half-Weight Association Index by Cairns and Schwager (1987). In order to understand the various approaches of these indices, it is necessary to use the common terminology (Table 4.1), presented in recent reviews of association indices (Cairns and Schwager, 1987; Ginsburg and Young, 1992). The equations for these indices are presented in Table 4.2.

The need for unbiased indices of association is increased by another unique feature of sampling associations between free-ranging animals. It is not always possible to locate all known members of a study population in every sample. This could be an indication of differential probabilities of locating individuals and could introduce bias into the calculations. For example, conspicuously marked individuals or individuals which favour larger groups may be easier to

Table 4.1. Summary of association index notation (Cairns and Schwager, 1987).

Types of samples

N{E} denotes the number of samples in which event E occurs
x = N{A and B are located together in one group}
y = N{A and B are located in separate groups}
y_a = N{only A is located}
y_b = N{only B is located}
y_{ab} = N{both A and B are located separately}
$y = y_a + y_b + y_{ab}$
z = D* =N{neither A nor B is located}
$n = N^* = x + y + z$ (* terminology of Ginsburg and Young, 1992)

Total sightings

Of A: $n_a = x + y_a + y_{ab}$
Of B: $n_b = x + y_b + y_{ab}$
Of A without B: $T_a = y_a + y_{ab}$
Of B without A: $T_b = y_b + y_{ab}$
Of A and B together: $T_t = x$

Table 4.2. Three common association indices.

$$\text{Half Weight Association Index} = \frac{x}{\frac{1}{2}(n_a + n_b)} \quad \text{or} \quad \frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$$

$$\text{Twice Weight Association Index} = \frac{x}{x + T_a + T_b} \quad \text{or} \quad \frac{x}{x + 2y_{ab} + y_a + y_b}$$

$$\text{Ratio Association Index} = \frac{x}{x + y} \quad \text{or} \quad \frac{x}{x + y_{ab} + y_a + y_b}$$

locate. This is the reason for isolating the different types of "y" sightings, when the pair is not located together. The most important term in these equations (which is unique to studies of individual associations due to the unit of sampling problem mentioned earlier) is y_{ab}. This is the count of the times a pair was located in the same sample, but not in association. Obviously, the greater this number, the weaker the association between the pair. The Twice Weight Association Index emphasises this term the most.

Ginsburg and Young (1992) compared these three measures of association and considered the Ratio Association Index to be the least biased. The Half Weight Index tends to overestimate levels of association since it averages the counts of y_a and y_b, thus reducing the denominator. On the other hand, the Twice Weight Index tends to underestimate association since it double counts the samples in which members of the pair are located separately (y_{ab}). The Ratio Association Index quantifies association as a simple proportion of the number of times a pair was seen together compared to the total number of samples in which either member of a pair was sighted. Cairns and Schwager (1987) found this index to be least biased when sampling was random in relation to the probability of locating a pair together versus when separate.

The Ratio Index of Association was used for this study. Ginsburg and Young (1992) presented a simplified version of the Ratio Association Index equation presented in Table 4.2:

$$\text{Ratio Association Index} = \frac{X}{N - D}$$

The denominator of this equation is the total number of viewing period minus the number of viewing periods in which neither A nor B were seen. This is equivalent to the total number of days in which either A or B were seen. This equation was modified slightly to fit the data format of this study, as described below.

Pilot whale groups were recorded as described in Section 4.2.6. All pair-wise associations between whales identified in the same groups were tallied once per day using a Microsoft QuickBasic© program. These were termed "group counts". Simultaneously, a tally of the total number of groups in which each individual occurred was recorded as "ID Sums". Pair-wise association counts were also made on a daily basis, disregarding whether the pair was seen in the same group on that day or not. These were termed "day counts". The difference between day counts and group counts equalled the y_{ab} term (Table 4.1), or the number of days in which both members of a pair were observed in separate groups. The denominator of the Ratio Association Index equation was calculated as the number of days in which either member of the pair was seen. This was equivalent to the sum of the number of total days each member was seen (whether alone or together) minus the number of days they were seen together. The calculation of all terms used in the association equations is summarised in Table 4.3.

Table 4.3. Summary of terms and calculation methods used in pilot whale Ratio Association Index analysis.

Computed Values:

Group xab = number of group counts for each pair of whales
Day xab = number of day counts for each pair of whales
ID $\text{Sum}_a = n_a = \text{Day } x_{ab} + y_a + y_{ab}$ = total number of days whale a was seen
ID $\text{Sum}_b = n_b = \text{Day } x_{ab} + y_b + y_{ab}$ = total number of days whale b was seen

$$\text{Ratio Association Index} = \frac{\text{Group } x_{ab}}{(\text{ID Sum}_a + \text{ID Sum}_b) - \text{Day } x_{ab}}$$

4.2.8 Age/Sex Class Associations

Associations between individuals were summarised by the age and sex class designations of the animals involved. Pair association indices for the various class combinations were pooled and compared for significant differences using the Kruskal-Wallis rank ANOVA test. Dunn's non-parametric multiple comparisons were used to identify the primary sources of the differences (Zar, 1984).

4.2.9 Cluster Analysis

In order to define higher order levels of associations for these whales, such as long-term social groups, a symmetrical matrix of association indices between all possible pair combinations was analysed for naturally occurring clusters using the Cluster Analysis module of the Statistical Package for the Social Sciences (SPSS) program. A variety of hierarchical, agglomerative clustering methods are available in SPSS. The result of this clustering is a tree-like hierarchy showing the structure of clustering from all individuals as separate clusters to all individuals as members of one large cluster. Second, the methods conduct the clustering in the direction from separate clusters to a single cluster, as opposed to divisive methods which begin with the individuals all clumped and divide them into clusters. Hierarchical agglomerative methods are best suited to these data because social structure is also hierarchical in nature and the null hypothesis for the structure of this society is that each individual forms its own cluster with no stable outside associations.

The methods chosen for these data compute squared Euclidean distances for the pair association indices and cluster them using the Unweighted Pair-Group Average Method (UPGMA), also called the "average linkage between groups" method. The measure of squared Euclidean distance is used to quantify the distance between two association indices as plotted on x,y coordinates. The fact that these are squared distances serves to give more weight to larger distances. UPGMA has also been chosen by other statisticians as the most robust form of clustering which meets three simple conditions (Kaufman and Rousseeuw, 1990). The first condition is that the dissimilarity between merging clusters are monotone decreasing. Second, the dissimilarities between clusters must be unambiguous. In some methods (e.g. the weighted average method), the selection of one of two equivalent choices in cluster formation result in very different dissimilarities between subsequent clusters. Third, dissimilarities between clusters should be statistically consistent, with larger samples resulting in more meaningful clusters.

4.2.10 Pod Definition

The resultant dendogram from the cluster analysis was used to identify distinct groupings of individuals. These grouping were defined as "pods", using the terminology from killer whale social groupings (Bigg *et al.*, 1990). There are no universally accepted methods for determining the statistical significance of these clusters (Sokal and Sneath, 1963). Dendograms attempt to represent multi-dimensional relationships in two dimensions. The process of hierarchical, agglomerative cluster analysis generates a continuum of clusters. The dendogram is useful in visually displaying the associations between individuals and can make "natural" clusters apparent. In addition to this, the cluster distance coefficients calculated by UPGMA can also be used for guidance in deciding how many clusters are needed to represent the data (SPSS, 1990). As more and more distant clusters are joined, the interval from one distance coefficient to the next increases. A plot of these intervals versus the coefficients themselves was used to identify the appropriate limit to cluster distance. A pod was defined as any cluster of animals which had a distance coefficient of less than 3.0. This was not exactly equivalent to pair association indices because the clustering method used averages of these indices when joining clusters. Pods were given letter names according to the order in which at least one of the individuals was seen in the course of the study (i.e. the first pod seen was "A" pod, the second was "B" pod, etc.). Pods which were linked by cluster distances between 3.0 and 4.0 were termed *linked* pods. These pods were named with a matching letter followed by sequential numbers (e.g. "A1" pod, "A2" pod, etc.). Pods linked at cluster distances greater than 4.0 were given letter-only names.

A number of young animals and animals seen only once had to be removed from the bulk of the association analyses due to computer memory limitations. In order to determine pod assignments for these animals, a frame-by-frame analysis of available photographs was undertaken to determine the identity of all members of the immediate group or groups in which these animals were associated. These animals were assigned to the pod which they most commonly accompanied.

4.2.11 Pod Associations

Following the identification of pods, a final analysis was done to examine higher-level associations between those pods. These associations between pods were termed "clans", again following the nomenclature of Bigg *et al.* (1990). In order to calculate this, the individual identities in the data on groups were changed to the pod identities of those individuals. Then, groups were pooled by day, and pair associations for all pods seen on the same day were counted. The result of this data manipulation was that two pods were counted as co-occurring whenever at least one member from each pod was identified on the same day. There was no attempt to weight the presence of a pod by the total number of its members observed, as this was likely to be partially due to the variable recognisability of different pod members. Associations between pods were quantified using the same Ratio Association Index used for individual association.

4.3 RESULTS

4.3.1 Identification and Classification of Individual Whales

Pilot whales were photographed on 147 days. Over 26,000 frames of film were taken and 10,190 frames (39% of the total images) met the criteria of a usable identification photograph (see Section 4.2.2). Information on group composition to examine patterns of association was collected on 128 days, when detailed information was also collected on the time of each photograph and the spatial structure of individual groups.

A total of 495 individual pilot whales were catalogued. A summary of identifications by the 24 ID characteristics is presented in Table 4.4. There was

Table 4.4. Summary of pilot whale identifications and average recognisabilities for the 24 fin types.

Fin Type	Description	No. of whales	Recogognisability
CLF	Cleanfin	22	3
CLS	Cleanfin with Scallops	11	2-3
CLB	Cleanfin with Barnacles	10	2-3
IND	Unique Individual	10	1
DLF	Dolphin-Like Fin	8	1-2
HOO	Hook	21	1-2
HOS	Hook with Scallops	14	1
FDH	Front Dings or Humps	11	1-2
RFT	Raggedy Fins with Tabs	36	1
SMN	Small Multiple Nicks	51	2
TSN	Two Small Nicks	23	1-2
LDN	Large Double Nicks	17	1
SBN	Small Base Nick (lower third)	8	2-3
LBN	Large Base Nick (lower third)	20	1-2
SNM	Small Nick Middle third	14	2-3
LNM	Large Nick Middle third	27	1-2
SNT	Small Nick Top third	28	2-3
LNT	Large Nick Top third	25	1-2
NNT	Nick Near Tip	50	1-2
SQT	Square Tip	19	1-2
FFT	Flap Fin Tip	17	1-2
SRT	Small Round Tip	18	1-2
LRT	Large Round Tip	15	1
HND	Handle	20	1

wide variation in the degree of recognisability of these whales. The animals in the "Individual" category were the most distinctive. All had either major dorsal fin injuries or uniquely shaped fins. For example, whale #21 ("Splitfin") had a large flap partially cut more than halfway through the fin which remained constant throughout the study. Whale #40 had very few nicks or scars, but was placed in the Individual category because of its squat, triangular fin which was different from all others. Alternatively, whales in the cleanfin category all had a very low recognisability. The summary of the recognisability of all animals is presented in Figure 4.1.

The age and sex classification of the 495 identified whales resulted in 104 adult males, 109 adult females with calves, 218 unknown animals, 33 juveniles and 31 calves. An additional 17 juveniles and 60 calves were recognised by consistent associations with identified mothers, but did not have sufficient identifying characteristics to be included in the identification catalogue. This brought the total number of animals to 572. The proportion of animals was 18.2% males, 19.1% mothers, 38.1% unknowns, 8.7% juveniles and 15.9% calves. The ratio of mature males to mature females with calves was 1:1.05, not significantly different from unity. If all of the unknowns were assumed to be adult females without calves (an unlikely assumption: see Section 4.2.5), the adult male: adult female sex ratio would be 1:3.14. This is a maximum estimate of the socionomic sex ratio (sensu Clutton-Brock *et al.*, 1977).

Mother-calf relationships were determined for 85 (93%) of the calves and 35 (70%) of the juveniles. For the remaining immatures it was not possible to identify a consistent relationship with a specific female. The number of calves per female ranged from 1 to 3, and averaged 1.26 ± .05, all values: mean ± SE, n = 109. Ten newborn calves were identified during the study. Three were estimated to be less than one month of age, while seven were observed at around six months of age (criteria for ageing described in Section 4.2.5). An additional two calves were observed as stillborns: dead foetuses which were carried by an adult female. Table 4.5 presents the dates of these observations and suggests that most births occur from May through June, although births may occur at other times as well. Birth periods in other populations of pilot whales have also been shown to be diffusely seasonal, having a single mode with births occurring in all months (Sergeant, 1962a; Kasuya and Marsh, 1984; Martin *et al.*, 1987, pers.comm.)

The proportion of unidentifiable animals was calculated for 35 groups and ranged from 0% to 34% (14.8 ± 0.7). An average proportion of 15% unidentifiable animals was used to revise analyses of group size which utilised only identified whales. Assuming that unidentifiable animals were distributed equally in all groups, comparisons of differences in group size between seasons or classes of animals should still be valid.

The recognisability of the five age/sex classes is presented in Figure 4.2. Males were the most recognisable, while immatures were very difficult to recognise.

4.3.2 Patterns of Occurrence: Residents and Visitors

The 495 pilot whales were identified in 2610 daily sightings (equal to the identification of one individual on one day) over 147 days of photographic sam-

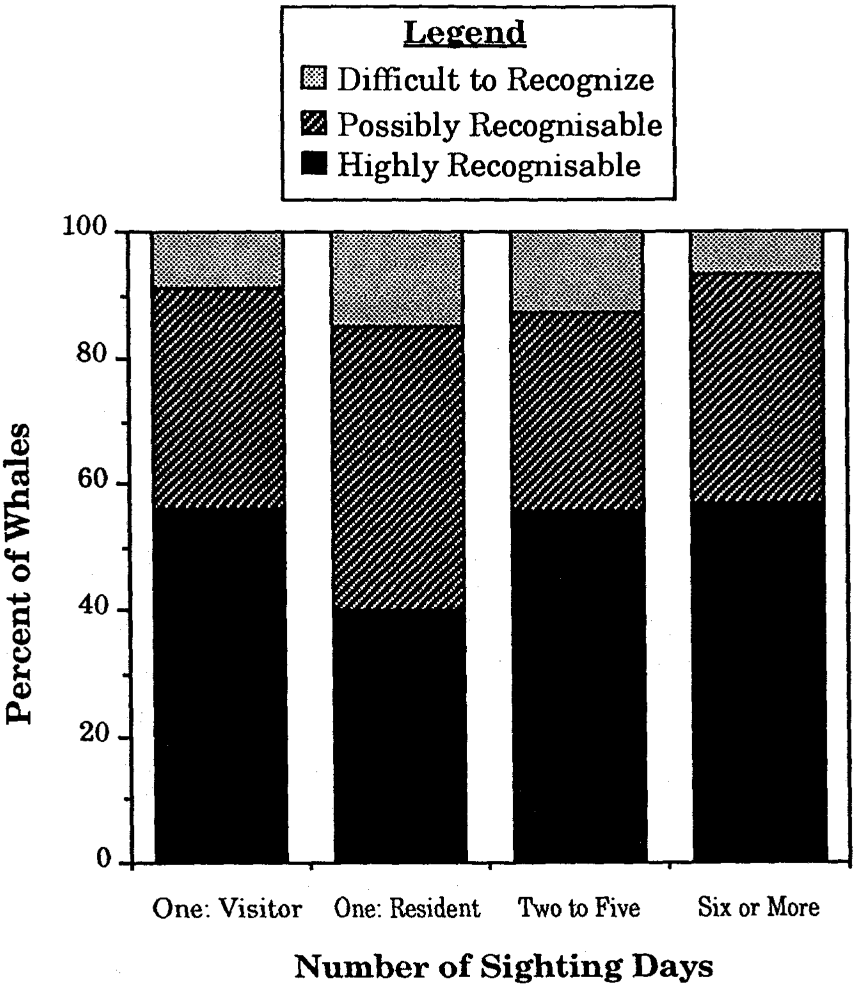

Figure 4.1. Recognisability of adult whales with different sighting histories. Whales were categorised by their number of sighting days throughout the course of the study. Residents seen on one day only had significantly lower recognisabilities than other residents ($P < .02$).

Table 4.5. Summary of information used to identify calving period.

TYPE OF OBSERVATION (with age estimate)	OBSERVATION DATE	ESTIMATED BIRTH MONTH
Stillborn calf (≤ 0 months):	28 April 1990 5 May 1991	April - May May
Newborn calf (≤ one month):	20 June 1990 5 December 1990 5 June 1991	May - June November May
Presence of foetal folds (≤ six months) n = 7:	August - November	February - May

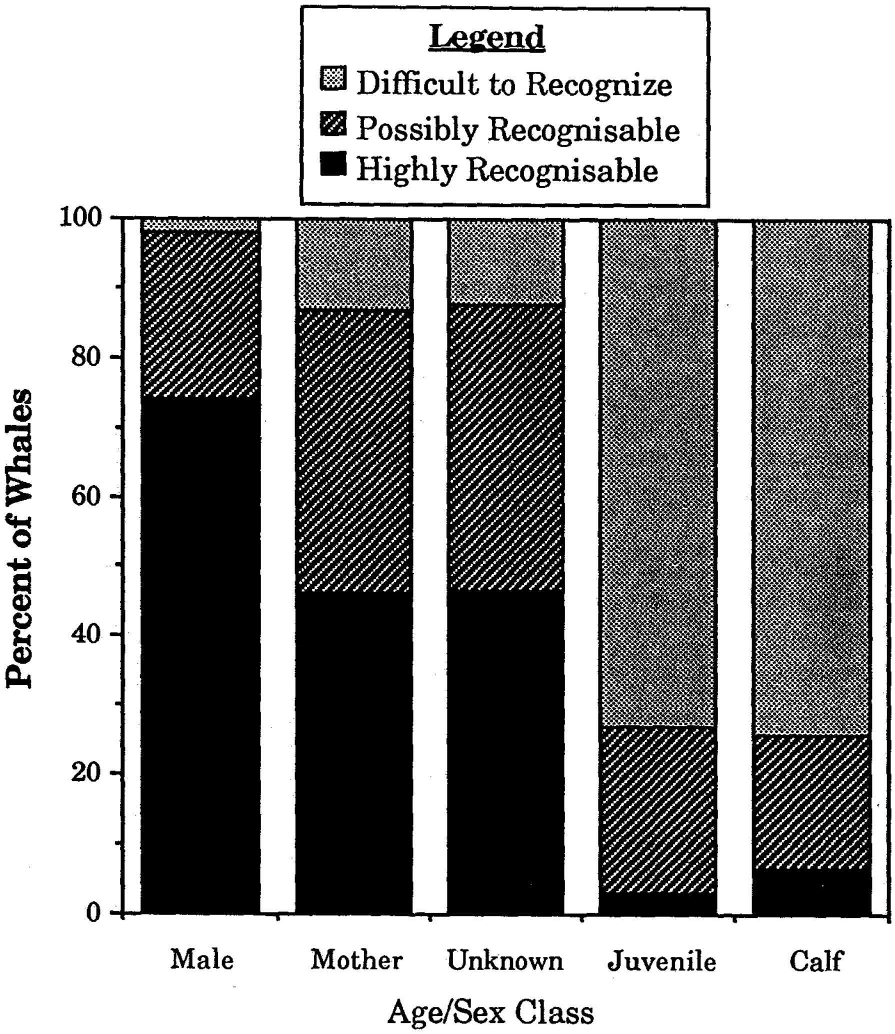

Figure 4.2. Recognisability for five age and sex classes. Adult males had significantly higher recognisabilities than immature whales.

pling. The number of daily sightings per animal varied from one (n = 186 animals) to 28 (n = one animal: #40) and averaged 5.27 ± 0.27 (Figure 4.3). A number of the animals seen only once were documented in discrete groups and not in the company of any animals seen more than once. There were 15 such groups, totalling 107 animals, and these animals were termed *visitors*. The remaining animals were considered as *residents*. A number of analyses were conducted in order to document the validity of this terminology. Variability in sighting frequency could be due either to a real difference in patterns of occurrence, or to a sampling bias resulting from factors such as recognisability of individuals and the timing of sightings. For example, if an animal was difficult to recognise or was not identified until the latter part of the study, it would have a lower probability of being sighted again. In order to attempt to isolate these factors, I examined the recognisability and timing of sightings for animals seen only once.

The timing of the initial sightings of all adults is presented in Figure 4.4. Individuals are plotted according to the quarter of the study period in which they were first sighted. These sightings were significantly different from that expected by chance ($X^2 = 150.46$, df = 9, $P < .001$), primarily due to the fact that 82% of the animals seen on six or more days were initially sighted in the first quarter and 84% of the animals seen on two to five days were seen in the first half of the study. (This could be partially due to the decreasing probability of being seen on multiple days as the study drew to a close.) There were no significant quarterly differences between the occurrences of the two classes of visitors and residents seen on one day ($X^2 = 2.751$, df = 3, $P > .05$). Sixty-one percent of the visitors were seen in the first half of the study, showing they had ample opportunity to be resighted. Additionally, the recognisability of visitors was not significantly different between quarters (Figure 4.5), with 54% of the visitors sighted in the first half of the study having a high degree of recognisability. Comparisons of recognisabilities for all whales (Figure 4.1) showed that there were no significant differences between the recognisability of visitors and residents seen more than once (56% vs. 52% highly recognisable; $X^2 = 0.486$, df = 2, $P > .05$). This indicates that visitors had an equal probability of resighting due to their recognisability and suggests that the category of visitor animals is a valid one.

The situation is different for residents seen on only one day. The recognisability of all animals presented in Figure 4.1 shows that the recognisability of residents seen on only one day was significantly less than that for the more frequently seen residents (40% vs. 57% highly recognisable; $X^2 = 7.967$, df = 2, $P < .02$), indicating that sighting bias may account for the lack of multiple sightings for these animals. The 86 resident adults seen only once may include some animals which could be classified as transient visitors to the area, but since they were observed in association with other animals seen more than once, I have included them in the resident category. They were not included in the analysis of association patterns because of computer memory limitations. However, they were included in the analysis of the final composition of social groups presented later.

Comparisons were also made between the sighting histories and recognisabilities of adults (age/sex classes: male, mother and unknown) and immatures (age/sex classes: juveniles and calves). Adults were seen from once (186 whales) to 28 times (one whale), while young animals were seen from once (31 whales) to 16 times (two whales). There were no significant differences (two-tailed t=

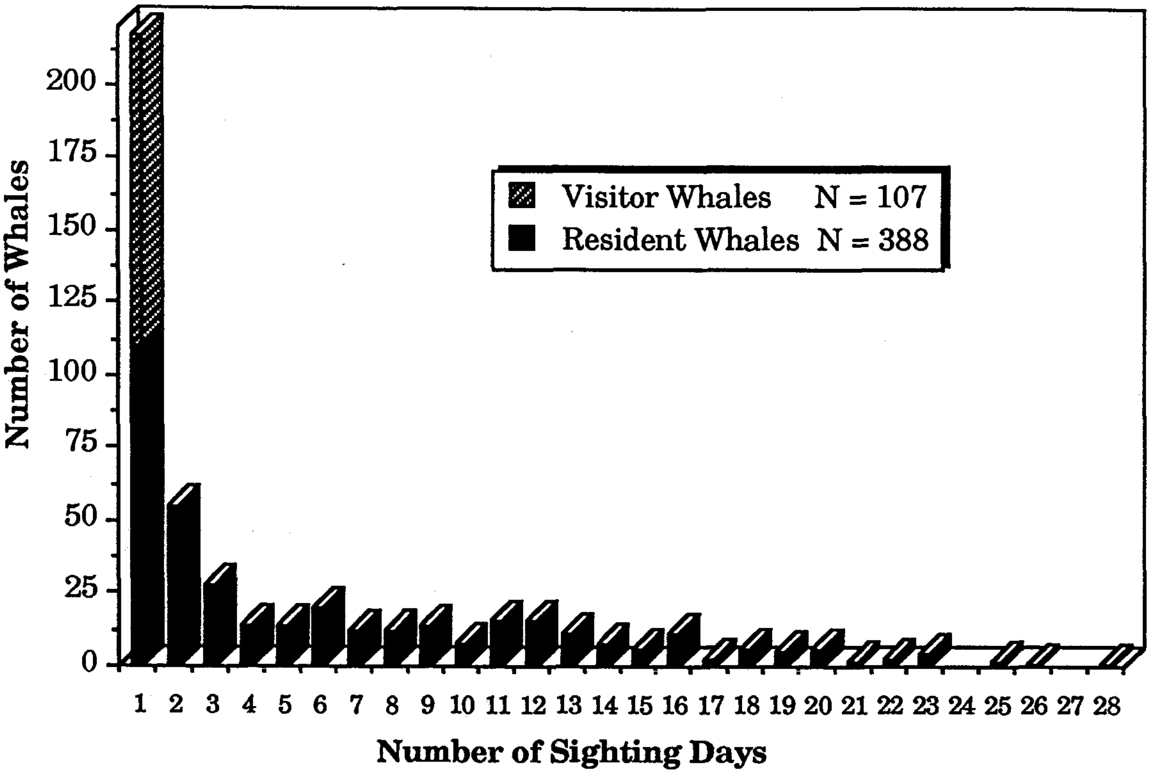

Figure 4.3. Sighting frequencies for all identified whales. See text for definition of "residents" and "visitors". The average number of sighting days for all whales was 5.27 ± 0.27.

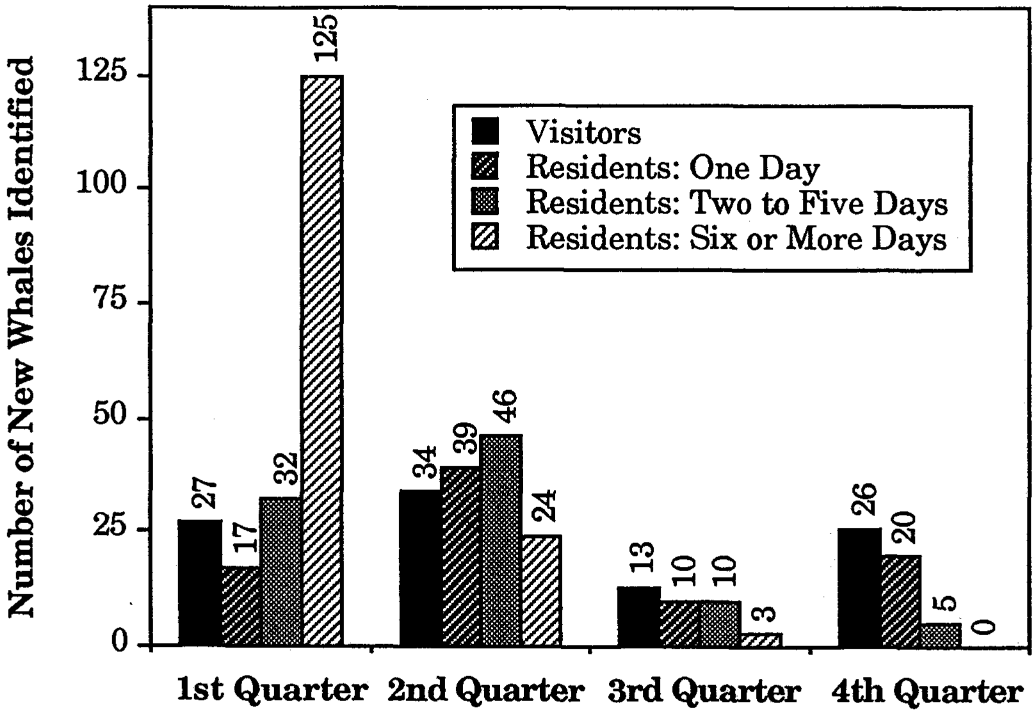

Figure 4.4. The quarterly timings of the initial identifications of whales with similar sighting histories. Whales were categorised by their number of sighting days throughout the course of the study.

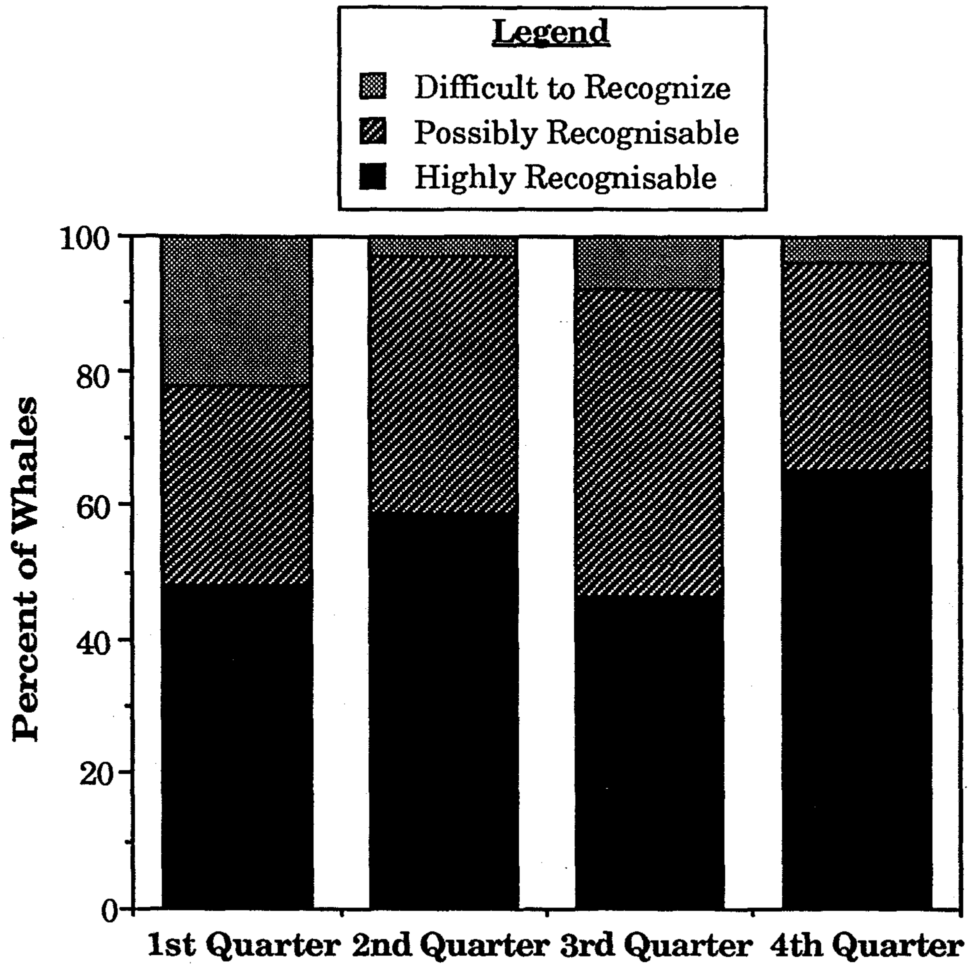

Figure 4.5. Recognisability of all adult visitor whales grouped by the quarter of the study when they were sighted.

0.442, v = 493, p > .50) between the sighting frequencies for adults (5.51 ± 0.30 sightings per adult, n = 431) and immature animals (3.70 ± 0.51 sightings per immature, n = 64). However, the recognisabilities of immatures were markedly different from those of adults (Figure 4.2), making their recognition in subsequent sighting difficult. Indeed, there were 77 clean-finned immatures who were only recognised because of their consistent relationships with identified adults. Immature animals were removed from further analysis on patterns of occurrence and association, but were included in later summaries of pod composition.

The cumulative sighting curve for all identified adults is presented in Figure 4.6. This curve continued to increase for both residents and visitors, suggesting that continued sampling will still be required before all animals using the Tenerife area are identifed. The individual sighting histories for all resident adults are plotted in Figure 4.7. This shows the high degree of repeat occurrence for many of these individuals which will be analysed in more detail by the examination of patterns of individual associations within groups.

4.3.3 Group Size

The basis of the analysis of associations was the documentation of pilot whale groups. Using the sampling criteria for well-defined groups outlined in Section 4.2.6, 277 groups of pilot whales were recorded over 123 encounter days. Group size ranged from two to 34 identifiable individuals (7.9 ± 0.4, N = 277). This is an underestimate of actual group size due to the estimated 15% of the population which is unidentifiable.

Group size was examined for seasonal variation. It was hypothesised that group size might vary according to variation in food availability or to mating opportunities. Group sizes were pooled for both years by month, by four three-month "seasons"(beginning in January) and by two "half-years" (summer: April-September, winter: October-March). Groups of identifiable whales were significantly larger during the half-year summer months than during the winter months (8.47 ± 0.48 vs. 6.89 ± 0.48 whales per group, Mann-Whitney U = 10375.5, n(summer) = 171 groups, n(winter) = 106 groups, Z = 2.03, P < .05). There were no significant differences in the number of identifiable whales per group pooled by month (Kruskal-Wallis rank ANOVA H = 16.03, df = 11, P > .05) or by season (H = 4.93, df = 3, P > .05).

Another way of examining seasonal variation in grouping patterns was to examine the number of groups located on any given day. The number of groups ranged from one to nine (2.25 ± 0.12 groups per day, N = 123). There were no significant seasonal variations found for any of the temporal combinations (month: Kruskal-Wallis H = 13.52, df = 11, P > .05; season: H = 6.83, df = 3, P > .05; half-year Mann-Whitney U = 2006, n(summer) = 78, n(winter) = 45, Z = 1.39, .20 > P > .15). The fact that whales were found in larger groups during the summer, and yet there were no significant seasonal variations in the number of groups located, could indicate either that there was a seasonal influx of whales that joined existing groups or that a reduced number of whales were travelling in larger groups. The question of seasonal variation will be brought up again in the analysis of associations between pods in Section 4.3.7.

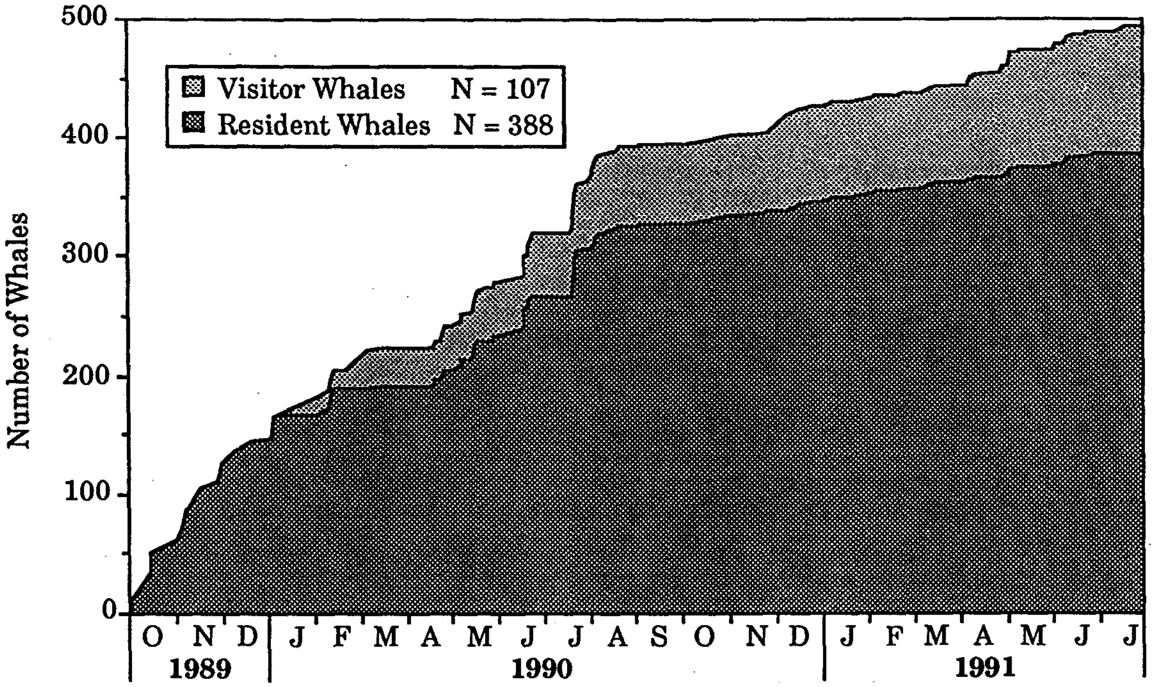

Figure 4.6. Cumulative sighting curve for all identified pilot whales. See text for definition of "resident" and "visitor" whales.

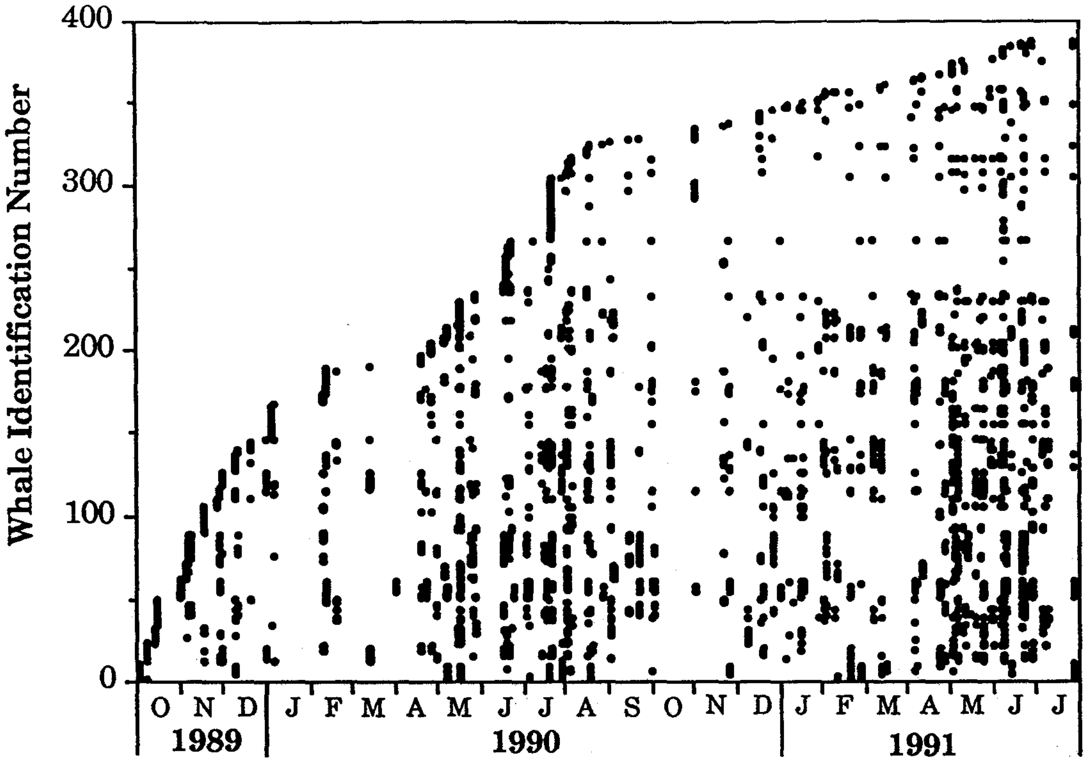

Figure 4.7. Sighting histories for all resident pilot whales. Each dot (•) represents one or more identification photographs of an individual whale on one day.

4.3.4 Association Patterns and the Definition of Pods

The overall distribution of association coefficients is presented in Figure 4.8. The average association value was 0.178 ± 0.003 (N = 3971). There were a total of 29,890 possible pair combinations for the group of 245 whales. Only 3971 (13%) of these pairs were ever observed. Almost half of the observed pairs had association coefficients of less than 0.10, while 64 pairs had coefficients of 1.0 (i.e. they were always observed together). This shows a high degree of selection in association patterns and suggests that whales do not associate at random.

The final group association patterns for the 245 resident adults seen on more than one day are presented in the cluster dendograms in Figures 4.9a-f. These figures are plotted according to Cluster Distance Coefficients (CDC's) calculated by SPSS to form clusters. The increasing variability in the distance at which clusters were formed is presented in Figure 4.10. Clusters formed at a distance of less than 3.0 are shown to be closely linked. Clusters formed above 3.0 show increasing variability in CDC. This is the reason that all clusters linked below 3.0 were defined as *within-pod* clusters, while clusters formed above 3.0 were defined as *between-pod* links. Clusters formed between pods at CDCs of 3.0-4.0 were defined as linked pods and given shared-letter, alpha-numeric pod names emphasise the links between them. I chose a CDC of 4.0 as a limit somewhat arbitrarily, however, selection of higher CDCs (e.g. 5.0 or 5.5) only linked one additional pair of pods.

A total of 31 "pods" were identified from this analysis. As a means of verifying the validity of the pod definitions, the individual pair association indices were classified as to whether they were between two members of the same pod, between two members of associated pods, or between two whales from different pods. Over 96% of the possible "within-pod" associations and 80% of the "between-linked-pod" associations were observed, compared to only 8% of the "between-pod" associations (Table 4.6). The association indices for each of these pair combinations were found to be significantly different (Kruskal-Wallis H = 2419.48, df = 2, P < .0001), with association indices for within pod pairs over twice as high as associations between animals from linked pods (.391 ± .007 vs. .072 ± .001), and over five times higher than associations for pairs from different pods (.072 ± .001; see Figure 4.11). This indicates that the pod definitions are valid and identify distinct grouping patterns in these pilot whales.

Since these 31 pods were defined only on the basis of associations between 245 adult animals seen more than once, it was necessary to assign pod membership to the additional 250 identified whales which had been removed from the analyses (see Section 4.2.9). The 15 groups of 107 visitors were each defined as a separate pod. For the remaining 143 resident animals, pod assignment was possible for 130 using the method described in Section 4.2.10; the thirteen animals without a pod assignment were all seen only once, either alone or associated with animals from more than one pod. Additionally, the 77 clean-finned immatures described in Section 4.3.1 were assigned the pod identity of the animal with whom they associated. This brought the total number of animals used in the pod analyses to 559 (495 identified individuals - 13 individuals without pod assignments + 77 clean-finned immatures added by association).

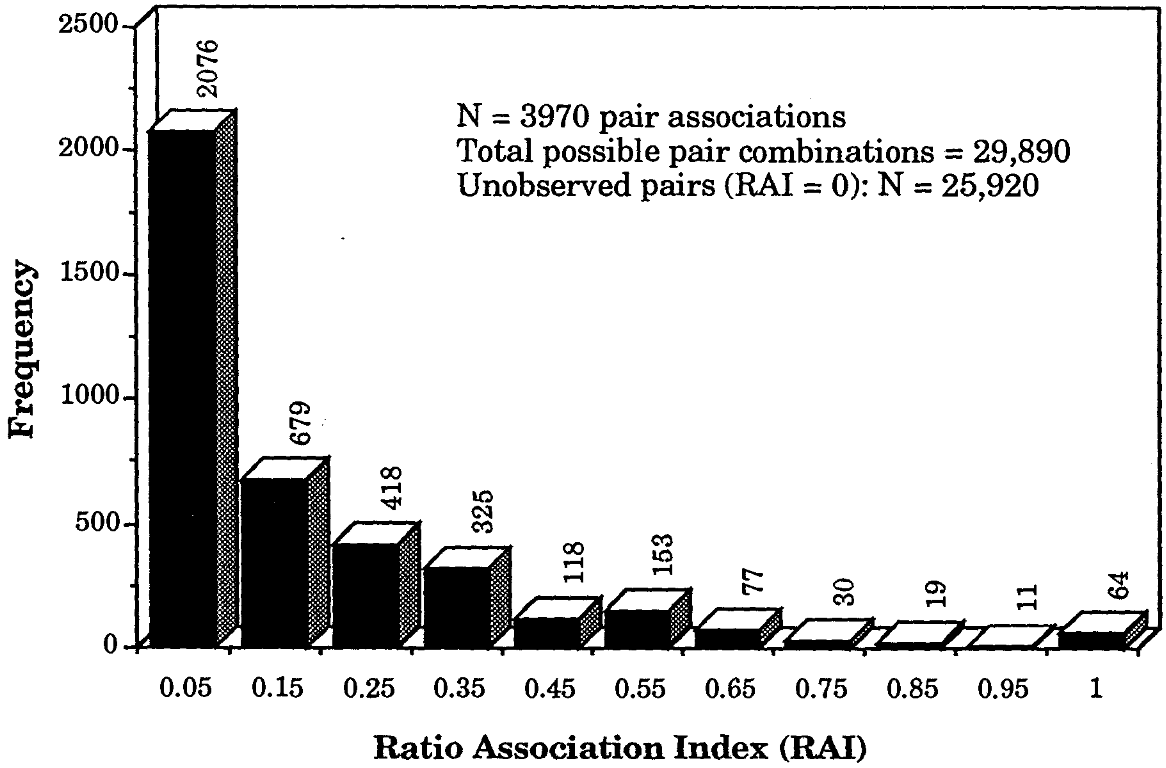

Figure 4.8. Frequency distribution of ratio association indices for 245 adult whales seen on more than one day. Category labels indicate the upper limit of the category. 87% of the pair combinations were never observed.

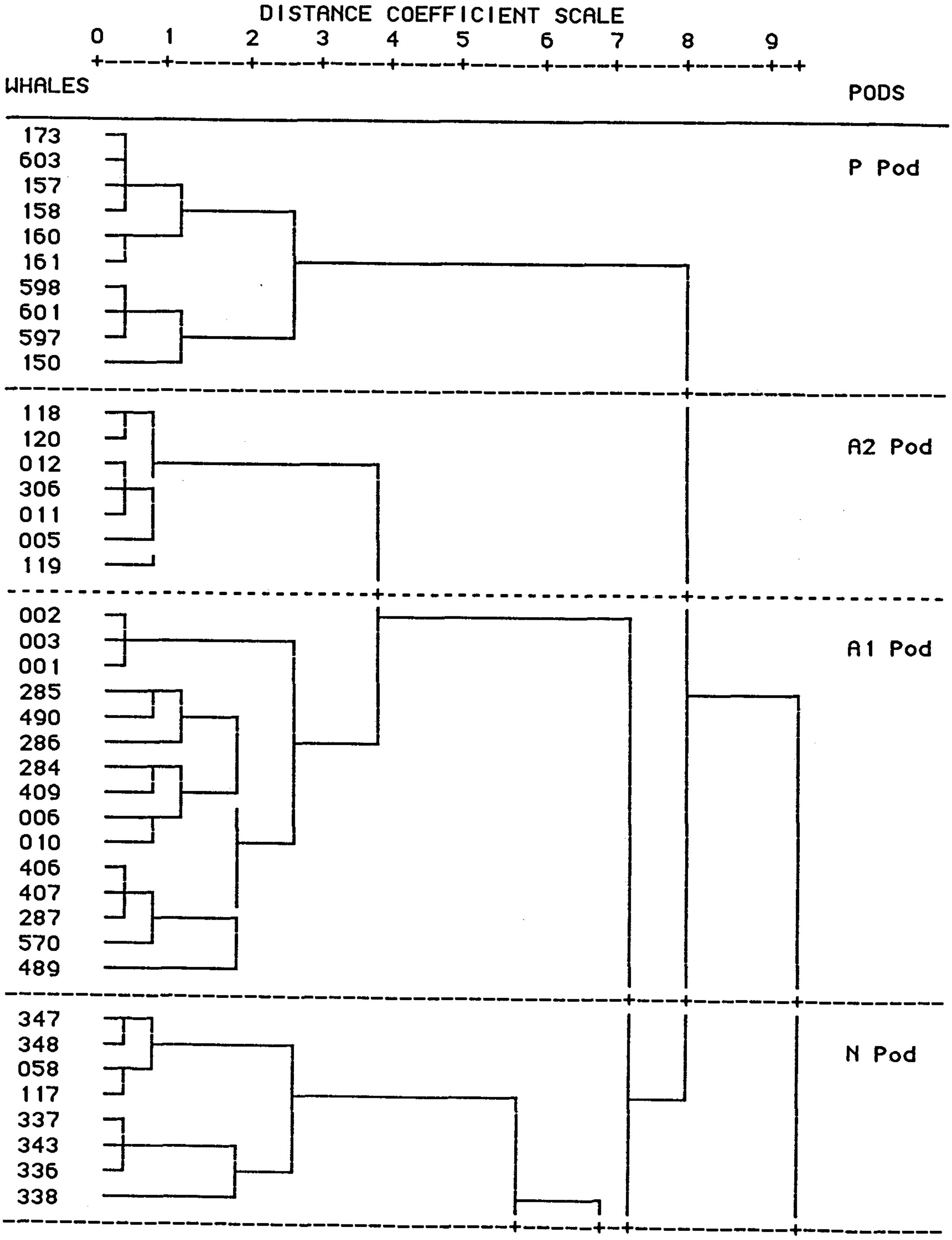

Figure 4.9a. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

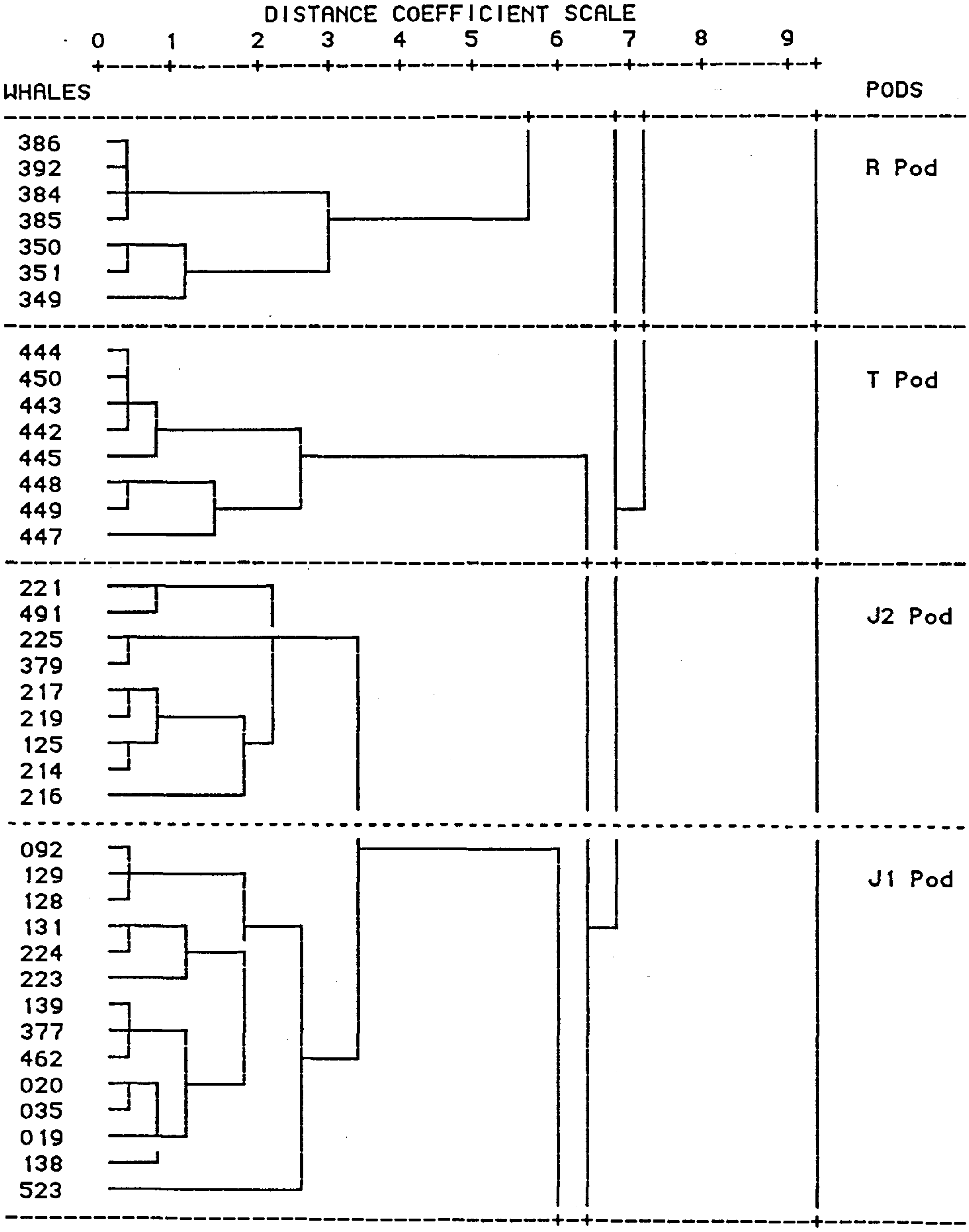

Figure 4.9b. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

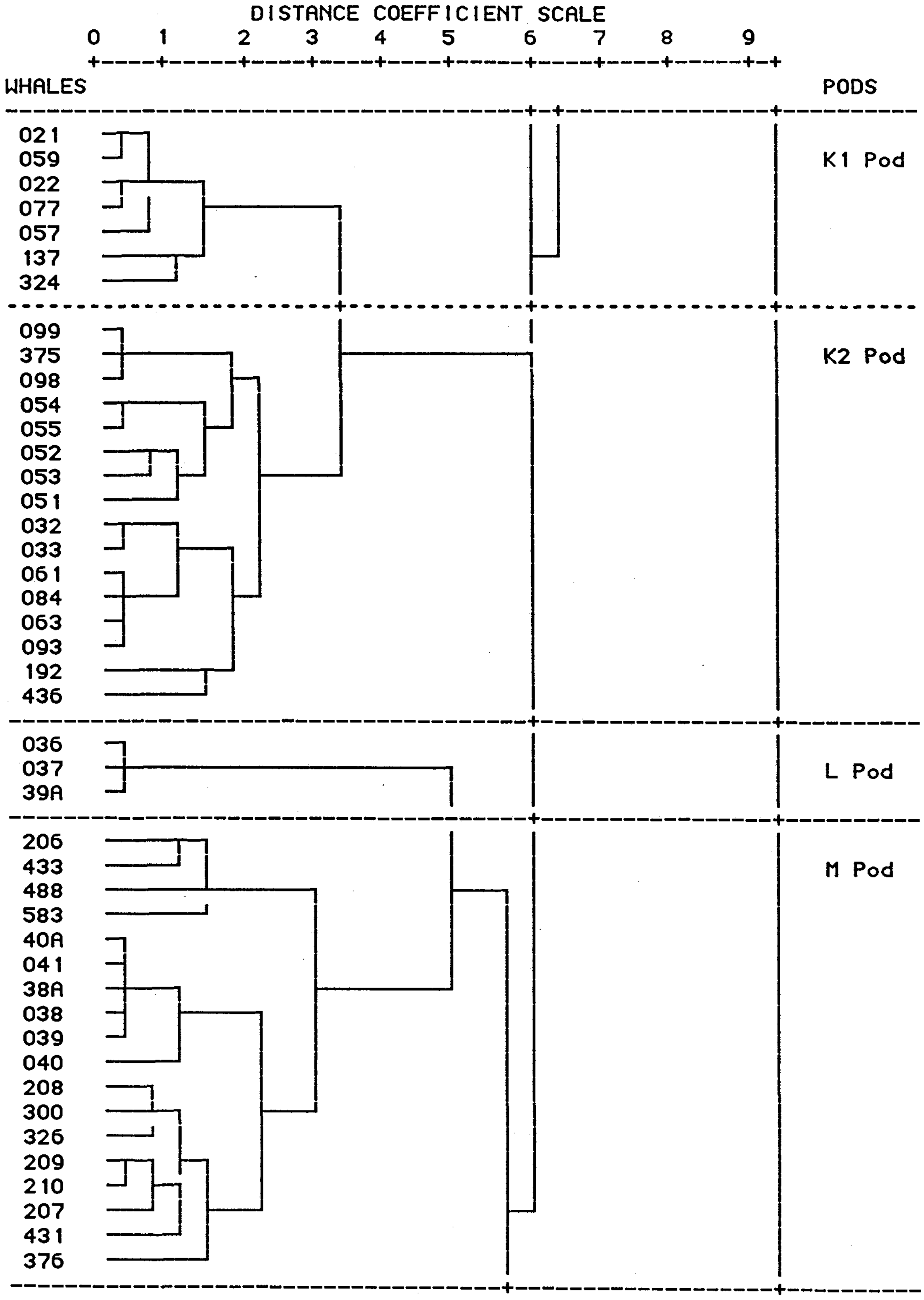

Figure 4.9c. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

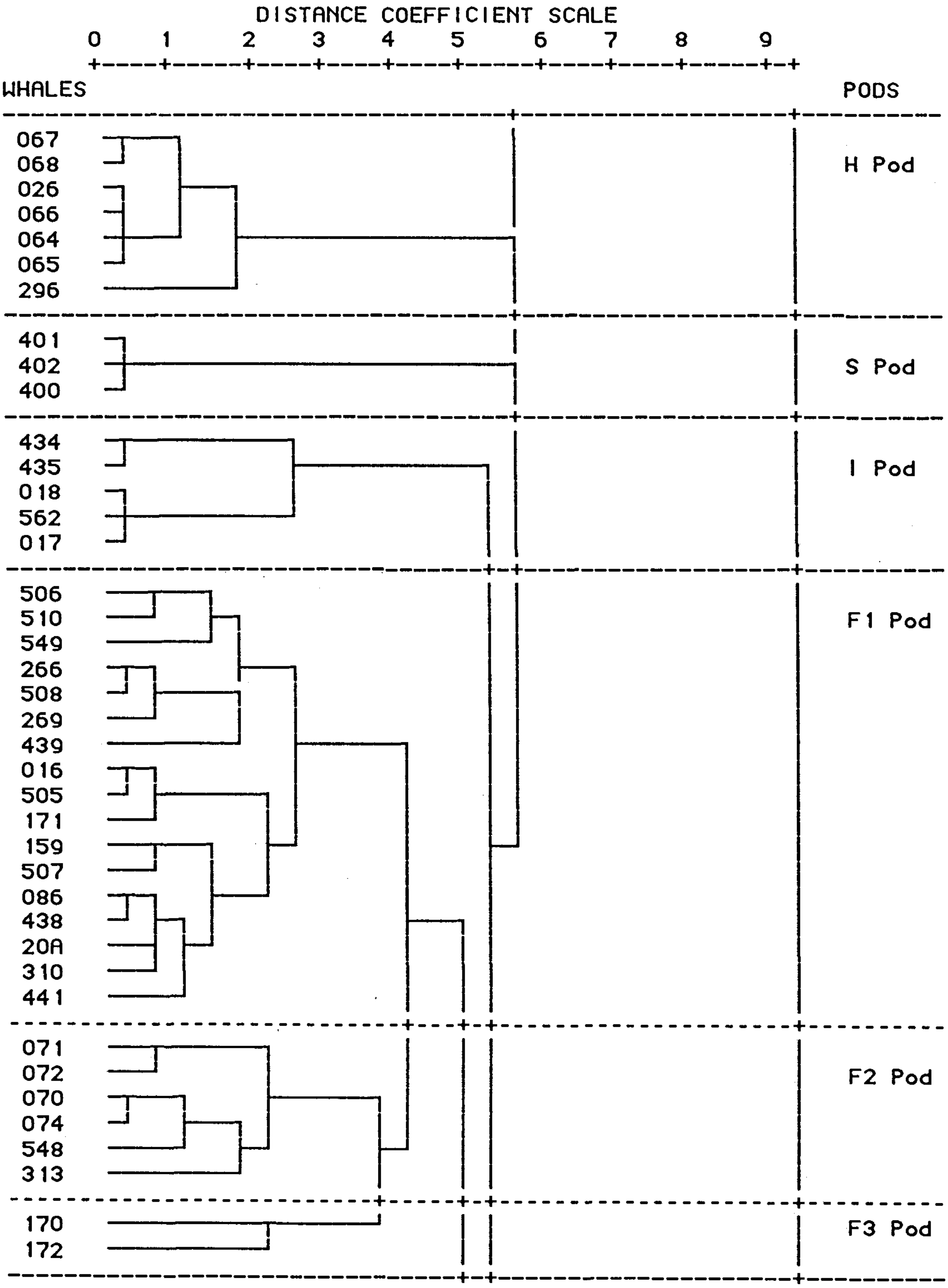

Figure 4.9d. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

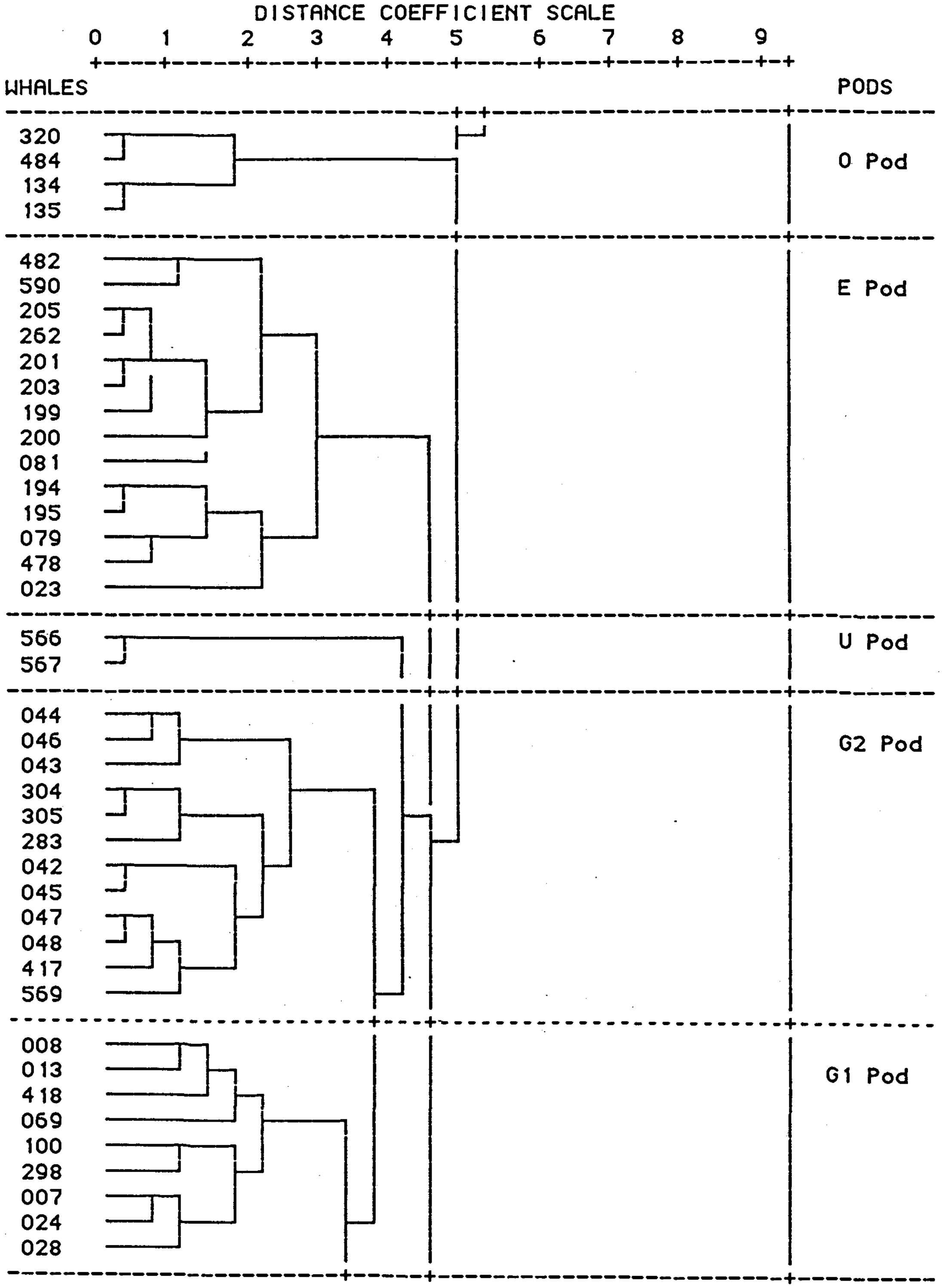

Figure 4.9e. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

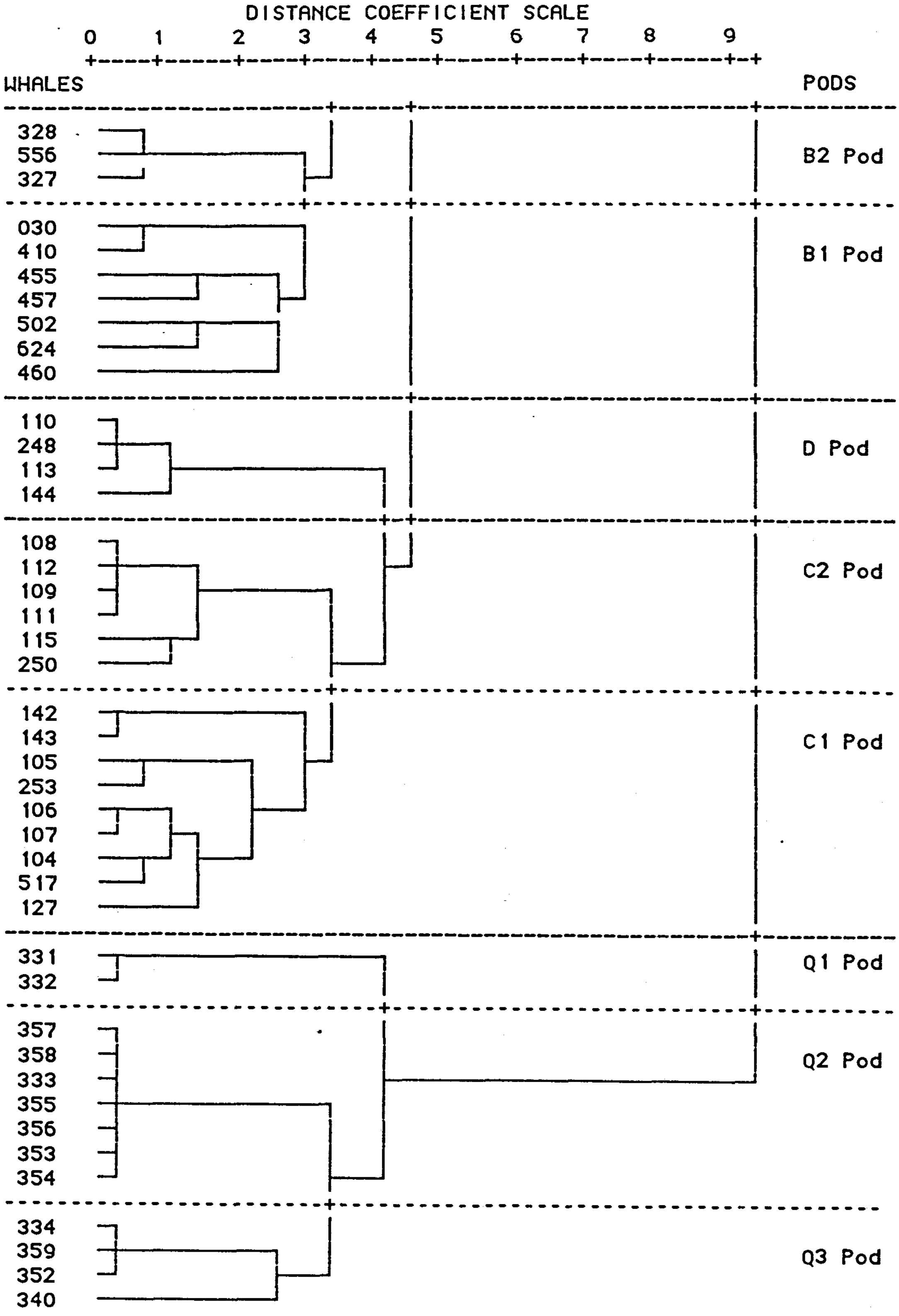

Figure 4.9f. Dendogram of associations between individual pilot whales. Pods were defined as clusters linked by distance coefficients of less than 3.0 and are separated by heavy dashed lines. Pods linked by clusters at distances between 3.0 and 4.0 were designated "linked pods", given shared-letter number names and are separated by heavy dashed lines. Source: SPSS Cluster Analysis.

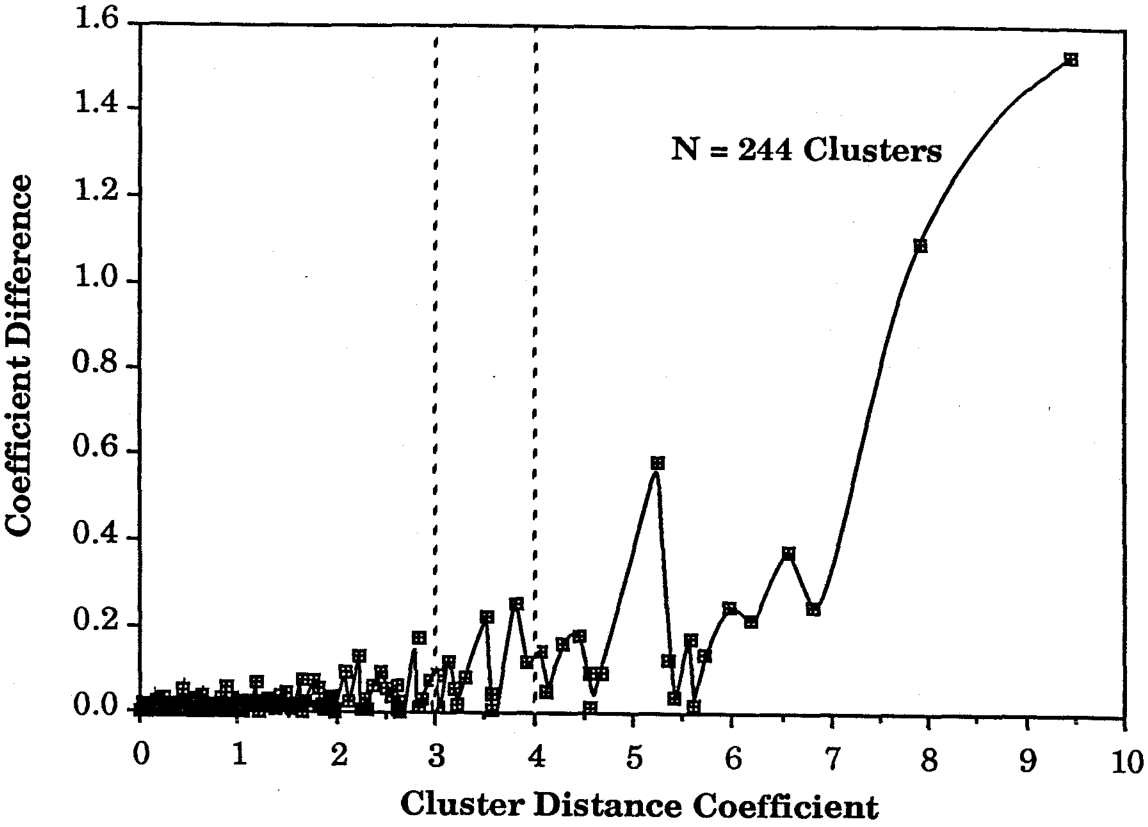

Figure 4.10. Cluster Distance Coeffiecients (CDC: calculated by the unweighted pairs group averaging method of hierarchical cluster analysis on the ratio association indices of 245 pilot whales) are plotted as a function of the difference between sequential coefficients (e.g. coefficient 2 - coefficient 1). The increasing distance at which clusters were formed was used as an indicator of pod divisions. Clusters formed at CDC < 3.0 were defined as pods. Pods joined at 3.0 < CDC < 4.0 were defined as *linked* pods.

Table 4.6. Comparison of three types of individual associations based upon the pod membership of individuals.

Association Type	Possible Pairs	Observed Pairs	Percent
Within Pod	1167	1129	96.7
Between Linked Pods	724	583	80.5
Between Pods	27999	2258	8.1
TOTAL	29890	3970	13.3

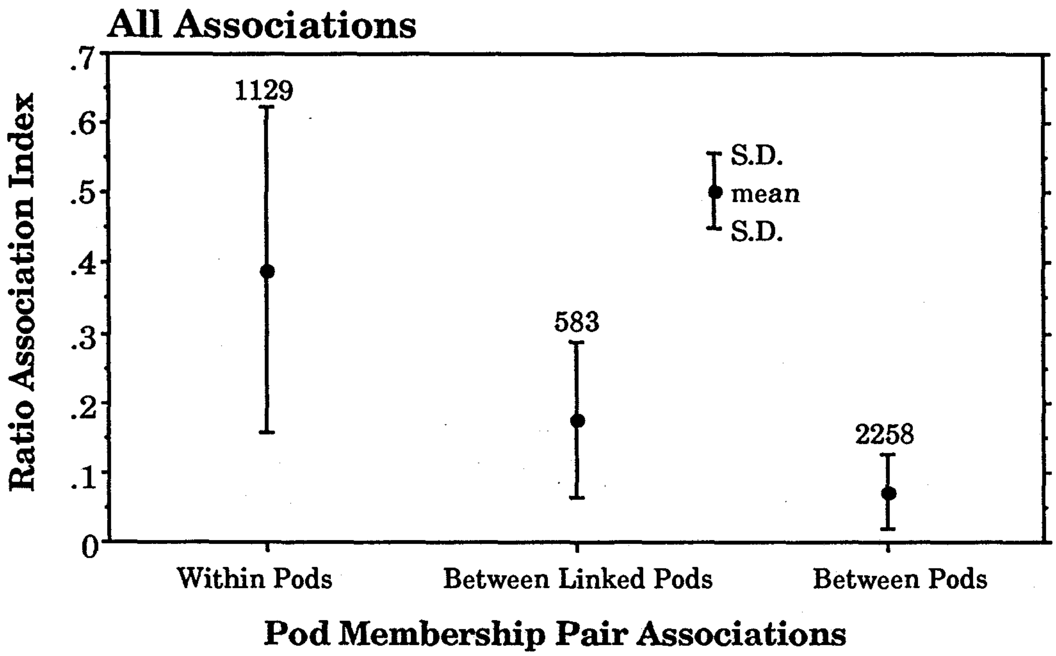

Figure 4.11 Average ratio association indices for all pair associations based on the pod membership. Sample sizes for each bar indicate the total number of pairs for each association type. See text for definition of "linked" pods.

4.3.5 Pod Composition

Pod size for the total sample of 46 pods ranged from two to 33 and averaged 12.2 ± 1.3 (Table 4.7). The distribution of pod sizes showed a slight bimodality due to five pods with 25-27 whales (Figure 4.12). In addition to the classification of resident and visitor pods, pods were classified as productive (32 of 46: 70%) or non-productive (14 pods or 30%) based on the presence of mothers and immature animals (Table 4.7, Figure 4.13). Variation in pod size was tested for the relative effects of residency and productivity in a two factor rank ANOVA; both factors had significant effects on pod size (productivity: $H = 22.12$, $df = 1$, $P < .001$; residency: $H = 4.96$, $df = 1$, $P < .05$), but the interaction factor was not significant ($H = 2.93$, $df = 1$, $P > .05$) indicating the two factors acted independently on pod size. Thus, resident pods were significantly larger than visitor pods (14.1 ± 1.6 vs. 8.2 ± 1.5) and productive pods were significantly larger than non-productive pods (15.5 ± 1.4 vs. 4.6 ± 0.6). Comparisons of resident and visitor pods showed there were no significant differences in the numbers of productive and non-productive pods (residents: 24 productive, 7 non-productive vs. visitors: 8 productive, 7 non-productive; $X^2 = 2.77$, $df = 1$, $P > .05$).

The age and sex composition of all pods is presented in Figure 4.13. Four of the productive pods (12%) had no adult males in association with them and could be considered "nursery" pods. Two of the non-productive pods were composed solely of adult males (both visitor pods totalling two and six), one was composed of three unknown animals and the remaining seven non-productive pods were composed of a mixture of adult males and unknowns.

The number of males per pod ranged from zero (five pods) to six (one pod) and averaged 2.5 ± 1.4 males per pod. Overall, the percentage of males per pod was 25.7 ± 3.6%, but resident pods had significantly lower percentages of males than did visitor pods (19.4 ± 3.1% vs. 38.6 ± 8.0%, $U = 334.5$, $Z = 2.39$, $P < .02$), and productive pods had significantly lower percentages of males when compared to non-productive pods (16.4 ± 2.2% vs. 46.9 ± 8.2%, $U = 370$, $Z = 3.49$, $P < .001$).

The number of mothers per productive pod ranged from one (11 pods) to twelve (one pod) and averaged 3.2 ± 0.4 mothers per pod. Mothers comprised 19.9 ± 1.5% of all productive pods and there were no significant differences in the percentages of mothers in resident vs. visitor pods (Mann-Whitney $U = 132.5$, $Z = 1.632$, $P > .10$).

The numbers of unknown animals per pod ranged from zero (two all-male pods) to 14 (one pod), with an average of 4.7 ± 0.5 unknowns per pod. One pod was composed solely of three unknowns. Overall, the percentage of unknowns averaged 41.2 ± 3.3%. There were no significant differences in the percentages of unknowns in visitor pods compared to resident pods ($U = 235.0$, $Z = 0.59$, $P >> .05$), but there were higher percentages of unknowns in non-productive pods than in productive pods (36.0 ± 2.8% vs. 53.1 ± 8.2%, $U = 317.5$, $Z = 2.23$, $P <.05$).

The number of immatures (juveniles and calves combined) in productive pods ranged from one (14 pods) to 12 (one pod), with an average of 4.3 ± 0.6 immatures per pod. Immatures comprised 27.7 ± 2.2% of all productive pods. There were no significant differences in the percentages of immatures between resident and visitor pods ($U = 115.0$, $Z = 0.83$, $P >> .05$). There were also no significant differences between the resident pod vs. visitor pod percentages of either

Table 4.7. Summary of pod sizes (mean ± S.E.) for resident, visitor, productive and non-productive pilot whale pods (see text for defintions). Sample sizes of the number of pods in each category are given in parentheses.

	Resident	Visitor	Total
Productive	16.9 ± 1.6 (24)	11.2 ± 2.1 (8)	15.5 ± 1.4 (32)
Non-productive	4.6 ± 0.9 (7)	4.7 ± 0.9 (7)	4.6 ± 0.6 (14)
Total	14.1 ± 1.6 (31)	8.2 ± 1.5 (15)	12.2 ± 1.3 (46)

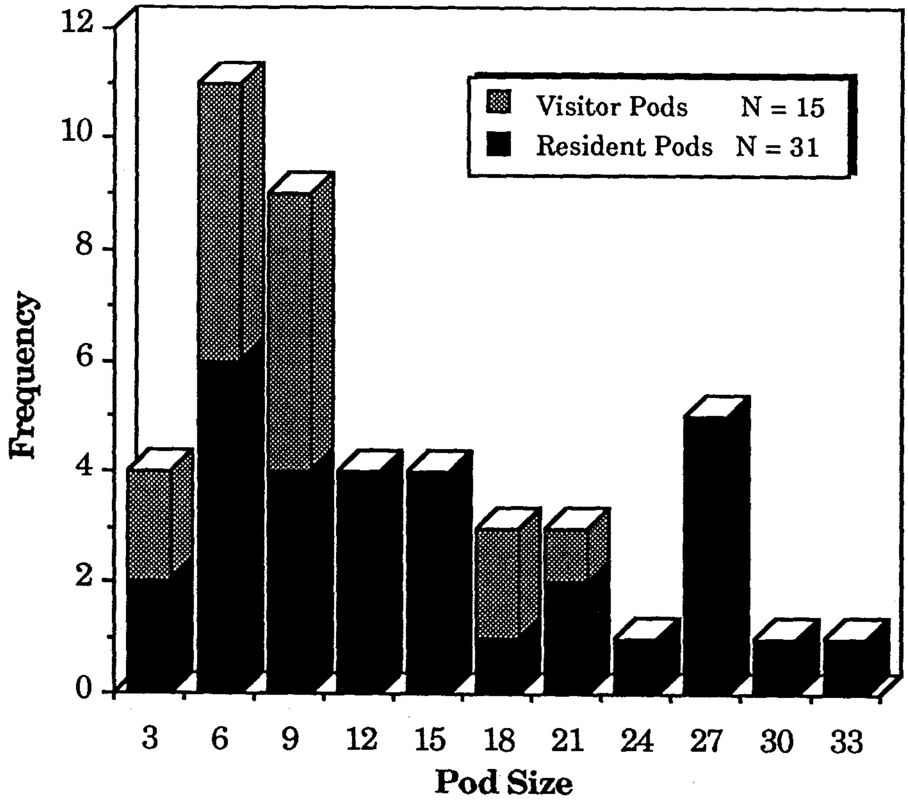

Figure 4.12. Frequency histogram of pod sizes (including clean-finned immatures). Size categories indicate the upper limit of the interval.

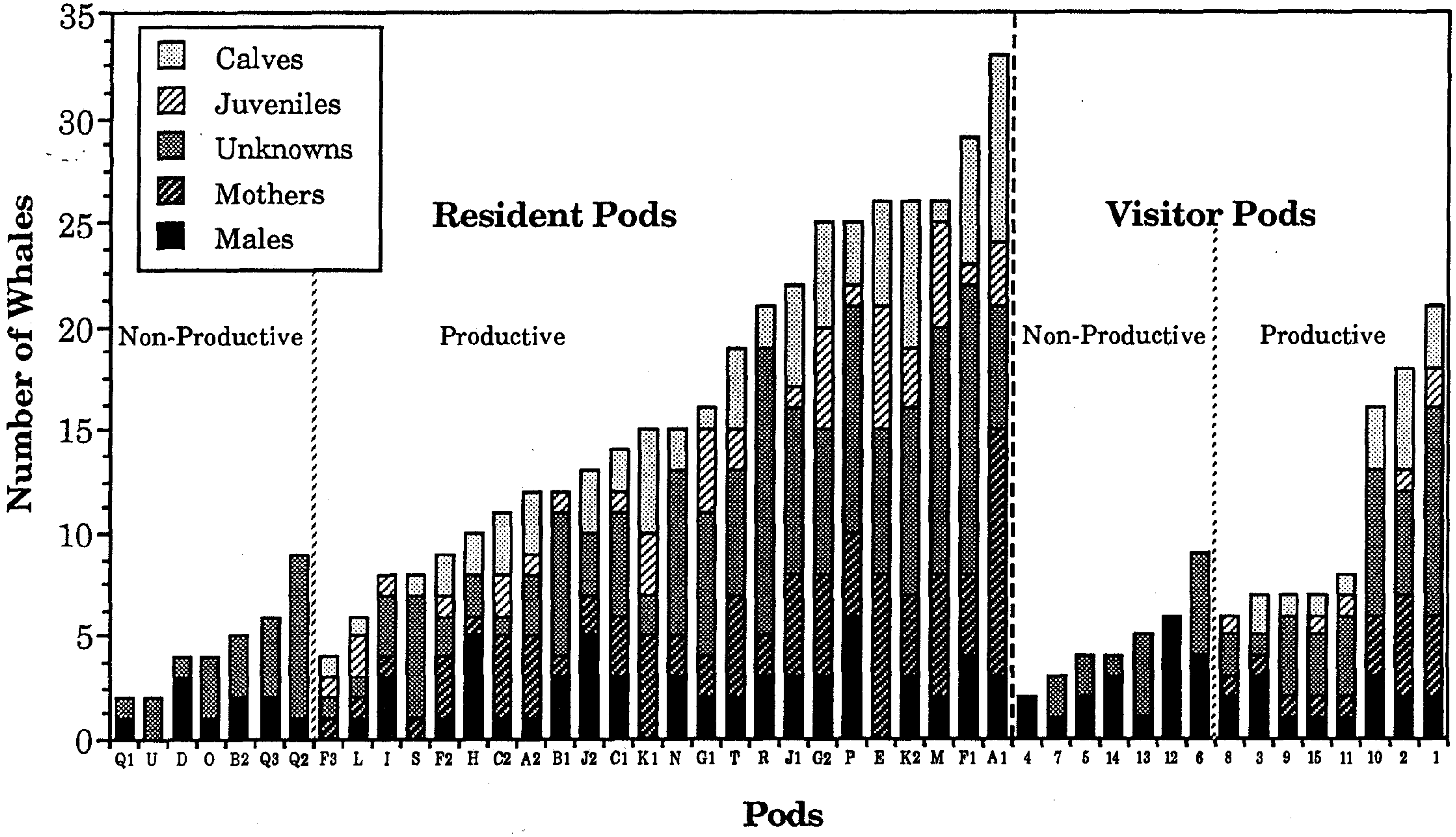

Figure 4.13. Pod size and age/sex composition (including clean-finned immatures) for 46 pods. Pods were defined as "productive" or "non-productive" based on the presence of immatures. See text for definition of "resident" and "visitor" pods. Resident pods were significantly larger than visitor pods and productive pods were significantly larger than non-productive pods.

of the immature subsets of juveniles (U = 117.0, Z = 0.92, P > .05) or calves (U = 103.0, Z = 0.30, P > .05).

4.3.6 Variability in Associations with Age/Sex and Pod Membership

Pod membership and age/sex class had a significant effect on the variability in associations between all non-immature whales. The removal of immatures, who by definition had highest associations with their presumed mothers, removed all suspected kin relationships from this analysis. The combination of the factors of pod membership and age/sex class were compared for effects on the ranks of association indices in a two-way rank ANOVA (Zar, 1984). The pod and class factors were both significant (pod factor H = 2418.300, df = 2, P < .001; class factor H = 19.561, df = 5, P < .005), but the interaction factor was not (H = 4.437, df = 10, P > .05). This shows that the two factors of pod membership and age/sex class acted independently on the level of association, and that pod membership had a relatively greater effect than age and sex class. The comparison of association indices depending on pod membership and independent of age and sex class was already described in Section 4.3.4 (see Figure 4.11) as a verification of the definition of the pods.

Variability in associations, depending upon the age/sex class of the pair members, was analysed in more detail in order to examine the bases of the relationships between males, females, unknowns and immatures within and between pods. Overall (i.e. independent of the pod memberships of the associating whales), associations between unknown whales were the highest ranked, while those between males and unknowns ranked second (Figure 4.14). Multiple comparisons showed that these two types of associations were significantly different from all associations involving mothers, which were not significantly different from each other.

For within-pod associations, there were significant differences between age and sex class association indices (Kruskal-Wallis rank ANOVA, H = 21.38, P < .001), with all associations within and between males and unknowns (e.g. male:male, male:unknown and unknown:unknown pairs) significantly higher than all associations in which mothers were members (Dunn's multiple comparisons, P < .05; Figure 4.15). The highest ranked associations were between adult males, indicating that male:male pairs had the most consistent relationships. Of all associations involving mothers, associations between mothers and other mothers ranked the highest , while associations between mothers and adult males ranked the lowest (Figure 4.15).

When linked pods associated (Figure 4.16), associations were still significantly different from each other (H = 23.29, P < .001), but the significantly higher ranked association indices were no longer just for male:male, male:unknown and unknown:unknown pairs. Associations between males and mothers from linked pods were also significantly higher than all other mother associations and not significantly different from male:male associations (male:mother = 0.189 ± .011 vs. male:male = 0.198 ± .021, P > .05).

Associations between whales from unlinked pods showed the same overall pattern of significantly higher associations within and between the classes of males and unknowns (Kruskal-Wallis H = 22.99, P < .001; Figure 4.17). However, mothers' associations with other mothers were ranked significantly

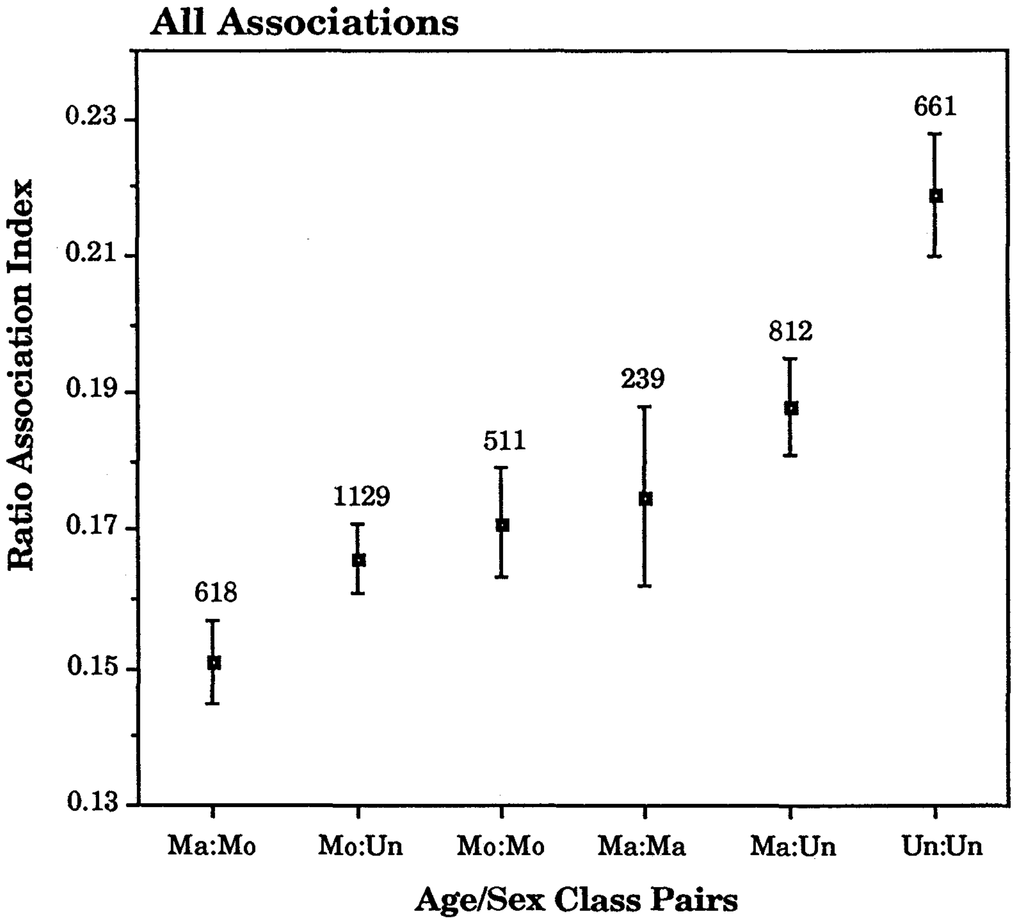

Figure 4.14. Average association indices (mean ± S.E.) for all pair associations (excluding immatures), grouped by age and sex class. Age and sex class abbreviations are for adult males (Ma), mothers (Mo), and unknowns (Un). Sample sizes for each bar indicate the total number of pairs for each age/sex class combination.

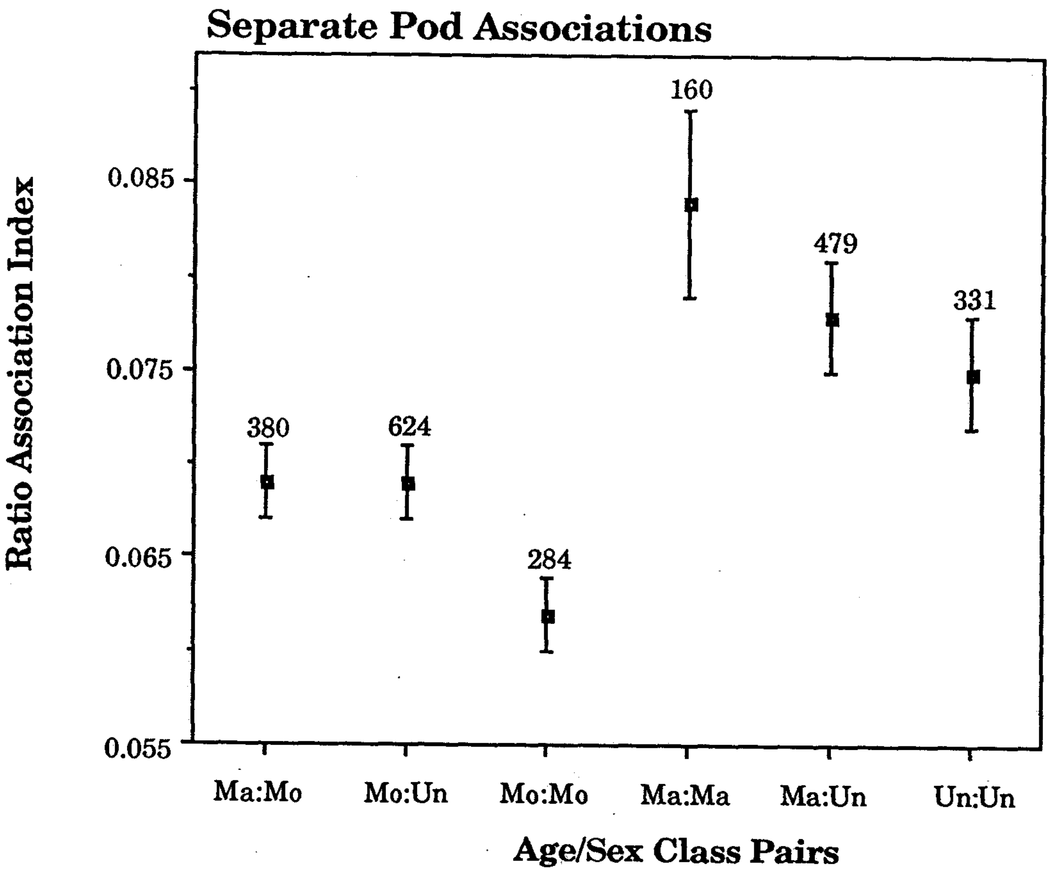

Figure 4.17. Average association indices (mean ± S.E.) for pair associations (excluding immatures) between members of different pods grouped by the age and sex class of each of the members of the pair. Age and sex class abbreviations are for adult males (Ma), mothers (Mo), and unknowns (Un). Sample sizes for each bar indicate the total number of pairs for each age/sex class combination.

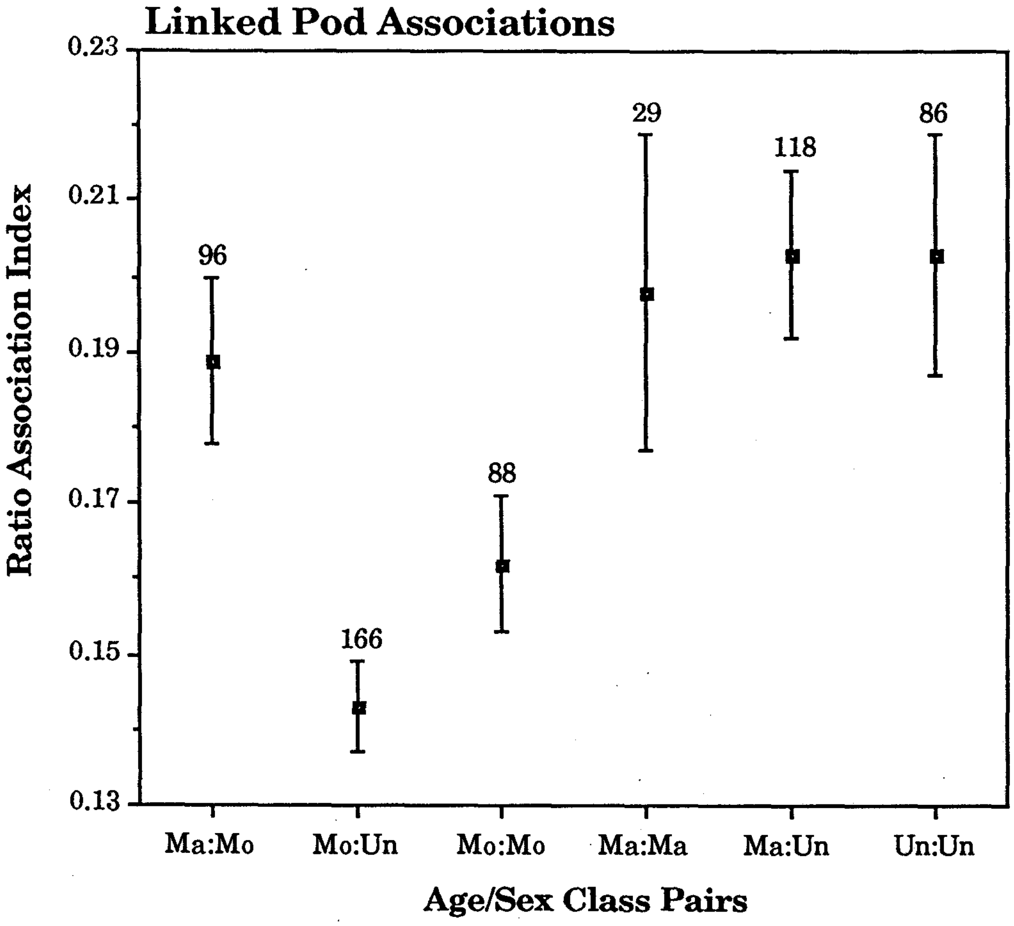

Figure 4.16. Average association indices (mean ± S.E.) for pair associations (excluding immatures) between members of linked pods grouped by the age and sex class of each of the members of the pair. Age and sex class abbreviations are for adult males (Ma), mothers (Mo), and unknowns (Un). Sample sizes for each bar indicate the total number of pairs for each age/sex class combination.

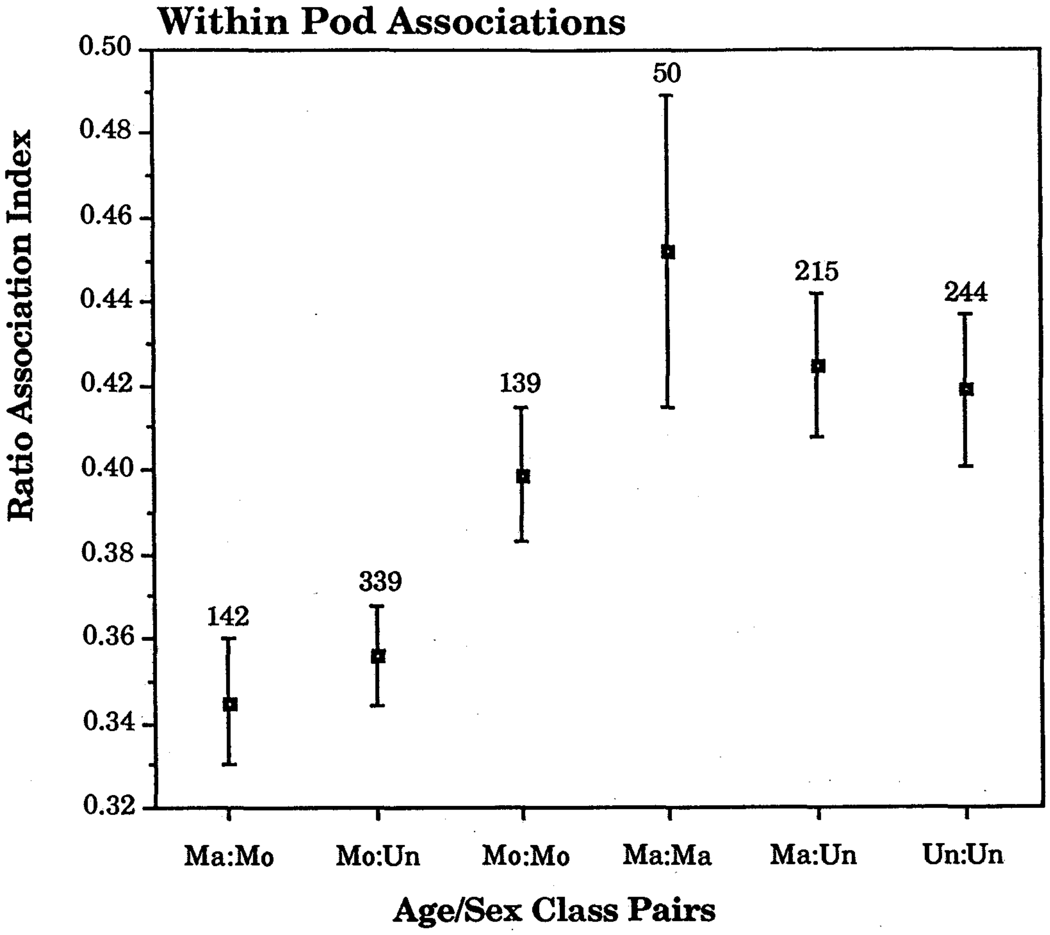

Figure 4.15. Average association indices (mean ± S.E.) for pair associations (excluding immatures) between members of the same pod grouped by the age and sex class of each of the members of the pair. Age and sex class abbreviations are for adult males (Ma), mothers (Mo), and unknowns (Un). Sample sizes for each bar indicate the total number of pairs for each age/sex class combination.

lower than male:male and male:unknown associations ($P < .05$), and were the lowest ranked of all the mothers associations.

4.3.7 Associations Between Pods

My definition of a pilot whale pod was based on the most common pair-wise associations. As described in Section 4.3.4, the association indices for pairs of whales from the same pod were significantly higher than indices for pairs of whales from different pods. I would like to focus on associations between members of different pods in order to attempt to identify levels of social organisation above the pod level, other than associations between *linked* pods, as defined in Section 4.2.10.

Table 4.6 showed that only 8.1% of the 27999 possible between-pod pairs were recorded between the 245 resident adults seen on more than one day. However, this still represented 57% of all pairs observed (2258 of 3970). Many of these pairs were, however, seen infrequently. The average number of sightings for all 3970 pairs was 2.31 sightings per pair. Whales from the same pod were seen together 4.62 times, while pair of whales from different pods were seen together only 1.15 times.

Another way to look at this is to examine the pod composition of the 277 groups identified in the field. The mean number of pods identified in the groups was 1.66 ± 0.06. The majority of groups (59%) contained only one pod. Twenty-five pods were represented in these lone pod groups and I compared the number of individuals identified in these groups to the total number of individuals defined for that pod. The average was that 37.8 ± 2.0% of the individuals in the pods were identified in the groups. Six of the groups were made up of all pod members, but these were for small pods. However, when the maximum percentages were extracted for each of the 25 pods, the average rose to 66.4 ± 26.0%. There were few instances when all pod members were identified together in one group.

There were 86 groups which contained whales from more than one unlinked pod. The number of pods represented by one or more members in these group ranged from 2 to 10, and averaged 2.78 ± 0.13, indicating a certain degree of fluidity in the social groupings of these pilot whales. There were 453 possible pair combinations between pods (excluding the 12 associated pod combinations) and 144 (32%) were observed. However, there did not appear to be any consistent patterns in which pods travelled together. An analysis of the associations between pods found no distinct clusters of pods (Figure 4.18). Table 4.8 shows the specific ratio association indices for the various pod combinations. There does not appear to be any higher level social structure which is clearly defined beyond the pod level.

The seasonality of the occurrence of groups with more than one pod was examined in a similar fashion to the analyses done on group size (Section 4.3.3). Significantly more pods were observed together during the six-month summer (April-September: 1.77 ± 0.09 pods/group) compared to the winter (1.48 ± 0.08; Mann-Whitney $U = 10182.5$, $n(\text{summer}) = 171$, $n(\text{winter}) = 106$, $Z = 1.96$, $P < .05$). The number of pods identified per group was significantly correlated with group size for both summer and winter (common $r_W = 0.637$, $P < .001$; Figure 4.19). It can be seen that nearly all of the large groups, and the group with the

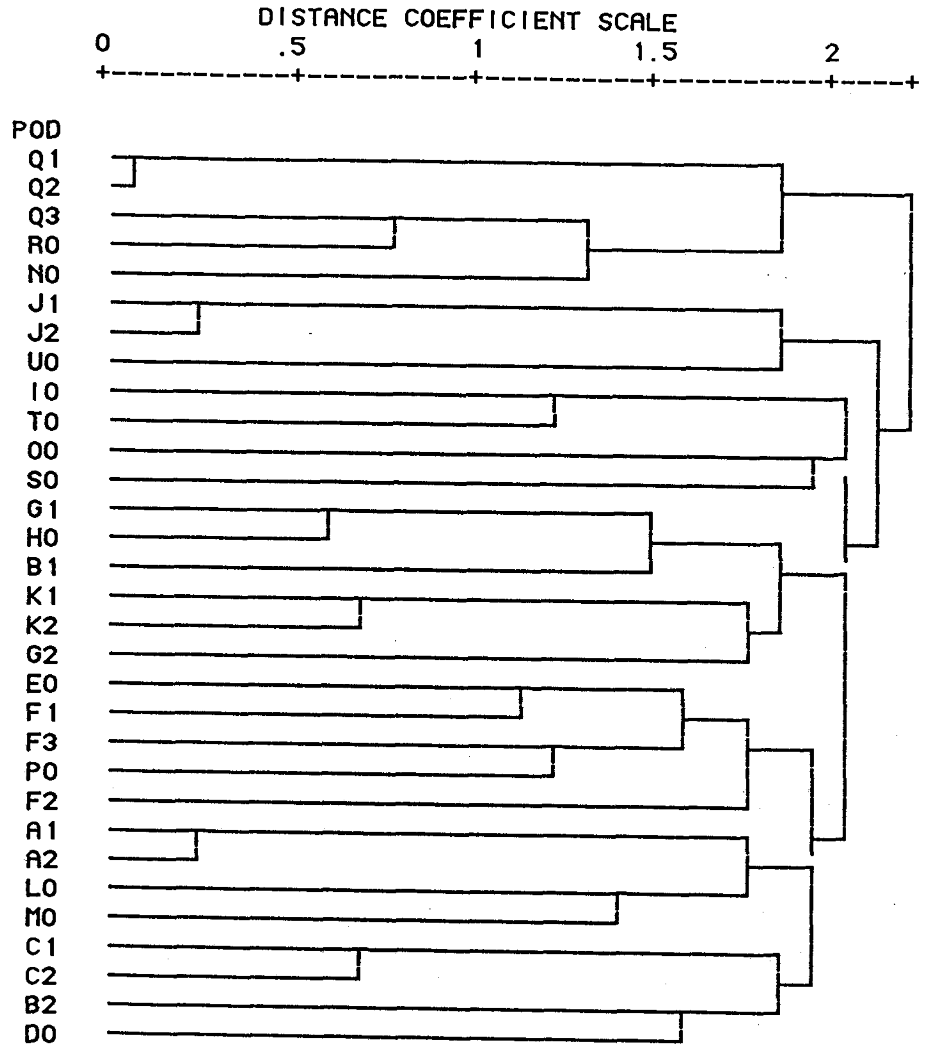

Figure 4.18. Dendogram for associations between pilot whale pods. Pod associations were tallied using a Ratio Association Index. Counts were totalled independently for each group observed (e.g. no association was tallied for pods seen in separate groups on the same day). Source: SPSS Hierarchical Cluster Analysis, Average Linkage Between Groups method.

Table 4.8. Ratio association indices for pods. Shading indicates below the mean and +1, +2 and +3 SD above the mean.

	Q1	Q2	Q3	R	N	J1	J2	U	I	T	O	S	G1	H	B1	K1	K2	G2	E	F1	F3	P	F2	A1	A2	L	M	C1	C2	B2	D
Q1	1	█	▒															░		▒	▓		▒						░		
Q2	.400	1	█																												
Q3	.167	.333	1	▓	▓								░	░																	
R			.250	1	▓								░	░																	
N			.143	.125	1		░						▒	▒		░	░	░				▒						░			
J1						1	█						░	░		░		░	░	▒		░		░	░		░	░	░		
J2					.036	.326	1	░					░			░	░	░	░	░		░		░	░		░	▒			
U							.087	1																							
I									1	▓										░											
T									.125	1			░		▒	░				▒							░				
O											1						░														
S												1															░				
G1			.048	.045	.083	.019	.024			.042			1	█	░		░	░	░	░					░	░	▒	▒	░		
H			.050	.048	.087	.019							.258	1	▓	░	▒	▒	░	░		░		░	░		░	░	░		
B1										.063			.032	.148	1	░	░			░			▒		▒			░			
K1					.043	.020	.025			.045				.057	.034	1	▓	░		░							░				░
K2					.021		.016				.044		.016	.070	.019	.224	1	░	░	░						░	░	░	░		░
G2	.043				.042	.019	.024						.026	.086		.057	.034	1	░	░		░		░	░		░	░	░		
E						.040	.025						.027	.028			.017	.028	1	▓	░	░		░	░	░	░	░	▒	░	▒
F1	.094					.067	.039		.030	.061			.042	.043	.050	.021	.014	.043	.143	1	▓	▒	▒	░	░		░	░	▒		
F3	.125																		.048	.133	1	▓	▓						░		
P					.111	.027	.038							.045				.045	.048	.063	.143	1		░	▒		░		░		
F2	.111														.063					.061	.125		1	░					░		
A1						.019	.024							.027				.056	.028	.043		.045	.043	1	█	░	▒	░	░		
A2						.044	.029						.031	.032	.087			.032	.033	.024		.063		.333	1	░	░	▒	▒		
L													.026				.016		.027					.026	.031	1	▒	░	░		▒
M						.025	.014			.019		.020	.079	.047		.031	.034	.031	.031	.040		.020		.098	.052	.097	1	░	░	░	░
C1					.048	.059	.070						.115	.036	.020		.026	.018	.018	.015				.018	.085	.018	.024	1	▓		░
C2	.040					.038							.025	.026			.016	.026	.083	.063	.042	.042	.040	.053	.063	.025	.030	.229	1		▒
B2																			.045								.019			1	░
D																.036	.019		.074							.069	.017	.043	.103	.067	1

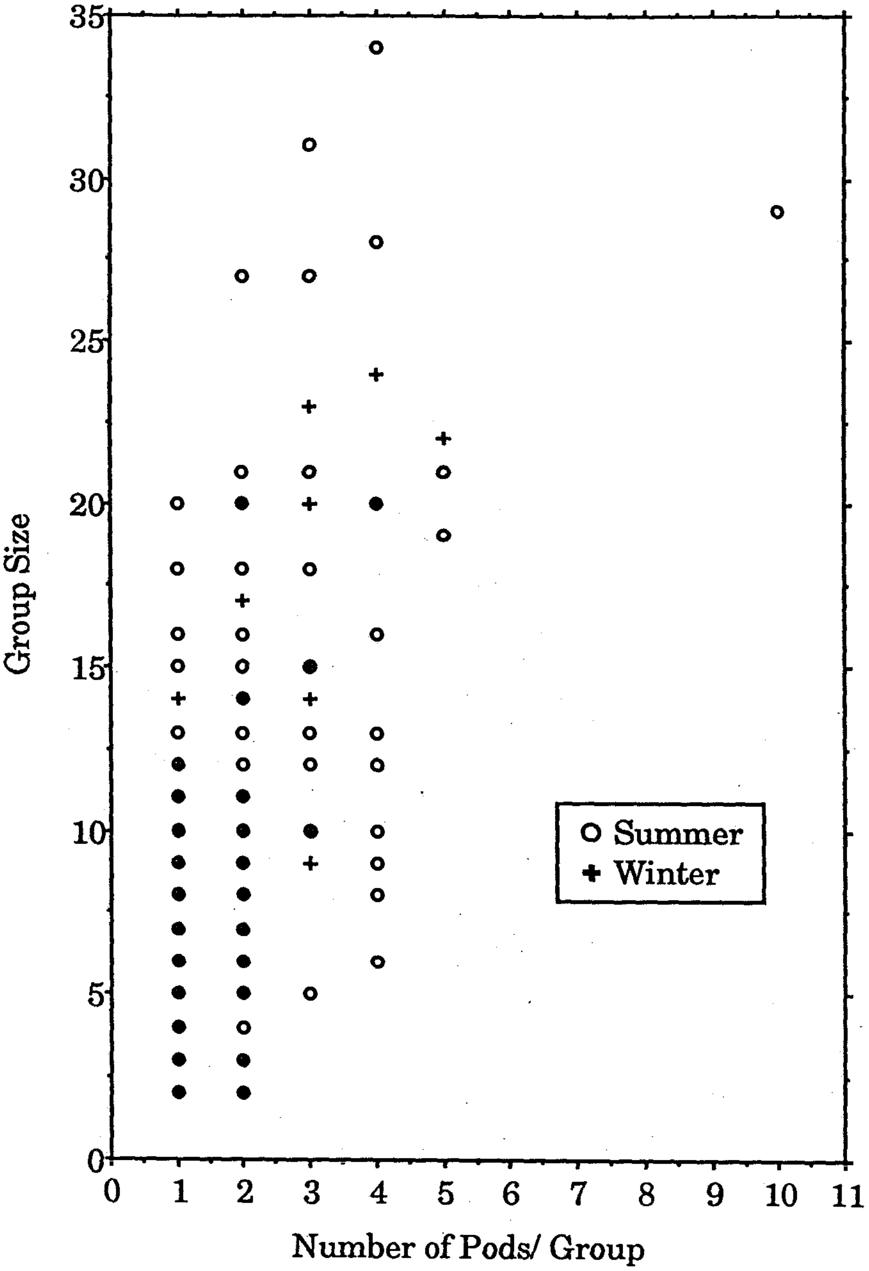

Figure 4.19. The relationship between group size and the number of pods identified per group. Both group size and the number of pods/group were significantly larger during summer (April-September) compared to winter.

greatest number of pods were identified during the summer. Thus, the summer months from April through September appears to be when pods are more likely to group up and travel together.

4.4 DISCUSSION

The original goals of this study were to identify individuals and define the patterns of social groupings. I will review these goals and then discuss the contribution of my findings to an understanding of pilot whale social organisation and mating system.

4.4.1 Pilot Whale Identification and Classification

I have shown that individual pilot whales could be identified from high quality photographs. However, there was a wide degree of variability in the recognisability of these whales and an estimated 15% of the whales were unrecognisable. This was primarily due the high dependence of recognisability upon the presence of scars. Scars were stable throughout the course of the study (apart from the minor healing of fresh scars), but an animal without scars needed to have a distinctive fin shape to be recognisable. This dependence on chance events (e.g. obtaining a scar) limited the possibility of recognising all individual pilot whales. Some groups may have had a lower probability of being scarred (and thus a higher probability of being unidentifiable), perhaps related to dominance status, but since the context of scarring was never observed this cannot be confirmed or denied. Identification is certainly aided when there are permanent features of pigmentation which can be found on all animals (as is the case with the "saddle patches" of killer whales: Bigg *et al.*, 1987). However, the technique is still applicable to less distinctively marked species.

The definition of the age and sex classes for this study was based on the age, growth and reproductive maturity data from Japanese pilot whales, with the implicit assumption that these two populations had similar life history and growth patterns. The most likely differences would be in absolute body size, as was found between two distinct stocks of short-finned pilot whales off Japan (Kasuya *et al.*, 1988a). The fact that long-finned pilot whales have very similar patterns of growth and dimorphism to the smaller short-finned pilot whales (Sergeant, 1962a, 1962b; Kasuya *et al.*, 1988b), suggests that these are generic traits and should be comparable between populations.

The best-defined age and sex classes of the present study are the adult males and the mothers. Adult males should be unequivocally identified because mean size at sexual maturity was greater than the largest female in the entire Japanese sample of 565 females (Kasuya and Matsui, 1984); the continued development of the characters of relative dorsal fin position, and the size and shape of the dorsal fin and melon were distinctly linked to this larger body size (Yonekura *et al.*, 1980; Kasuya and Matsui, 1984). "Mothers" were distinct full-sized animals, smaller than males, and in continued association with specific immature animals. Although this relationship was assumed to be between a female and her offspring, it was impossible to distinguish a foster relationship. The long maturation period of pilot whales (9 yrs for females and 15 yrs for males [Kasuya and Marsh, 1984]), combined with the minimum calving interval of 3 yrs for primiparous females (Kasuya and Marsh, 1984), indicate that females will have a number of offspring with them at any given time. Even older females, which apparently extend the nursing period of the last calf, should have young up to the age of 8 yrs in attendance (Kasuya and Marsh, 1984). This should guarantee that all recently reproductive females would have been classified as mothers in the present study. Immature animals were less distinct. The smallest animals were undoubtedly immatures. However, the transitions from calf to juvenile and juvenile to adult were not always clear. Variability in individual growth rates would cause different aged animals to be placed in the same class. The behavioural distinctions of relative time spent away from the company of adults gives some indication of relative independence, but since weaning has been shown to vary widely, depending on the age of the mother (Kasuya and Marsh, 1984; Section 2.5.3), even this may vary for similarly-aged animals. Finally, the greatest problems in defining the age and sex structure of pilot whale pods were due to the class of "unknowns", which comprised 38% of the whales. This class could have been composed of adult females without calves or adolescent males aged 8-12 yrs. The adult females could have been from the class of newly mature animals who had not yet had their first calf or alternatively they could have been post-reproductive females whose calves had all reached maturity. The young males potentially classified as unknowns were within the lower size range of "early-maturing" males in the Japanese sample (Kasuya and Marsh, 1984). The proportion of adolescent males should be small since this size range only applied to males for four years of their lives, compared to the much longer duration for which females maintained this body size. The proportion of early maturing males to resting females in solitary pods off Japan (considered to be a better representation of the age and sex structure of these whales than pods caught from aggregations) was 1:18, or 5.3% of all females without calves (Kasuya and Marsh, 1984; Table 35). This further suggests that the bulk of the unknowns were females.

The development and application of methods of stereo-photogrammetry to obtain actual body length measurements, as has been done for underwater photographs of sharks (Klimley and Brown, 1983), surface photographs of sperm whales (Gordon, 1987), and aerial photographs of spinner dolphins (Scott and Perryman, 1991), could reduce some of the limitations of relative size estimation.

4.4.2 Residents and Visitors

A large degree of variability was found in the patterns of occurrence of pilot whales. Some animals were seen on a regular basis, while others were seen only infrequently. In order to examine the implications of this result, two simple definitions are proposed. Members of a group of animals seen only once without any associations with animals seen more than once were defined as visitors. Animals seen more than once, or animals seen once but in association with animals seen more than once, were defined as residents. I have shown that these differences in sighting histories were not due to sampling bias. Over half of the visitors observed were seen in the first half of the study and a significant proportion of them were highly recognisable. These two factors gave them a high probability of being seen again. The fact that they were not strengthens the case for this definition of visitors.

The range of distribution of these visitors is unknown. The visitors off Tenerife could be resident in other areas of the Canary Islands, although there have been no confirmed reports of other concentrations. It is also unlikely that whales would venture into an area such as Tenerife, which seems to be highly favoured by at least some pilot whales, and never return. Visitors may be sighted again in the Tenerife area as the study continues. Perhaps they simply return at intervals greater than the length of this study.

However, it is not uncommon for there to be varying patterns of residency in cetacean populations. Although these animals do not appear to be territorial, using the conventional definition for terrestrial mammals (Norris and Dohl, 1980b), they often have favoured home ranges (Wells, 1978; Wells *et al.*, 1987; Ballance, 1990). Killer whales in Puget Sound have distinct patterns of residency, with residents and transients differing in social structure and feeding ecology (Felleman *et al.*, 1991). Although there are no detailed studies of free-ranging pilot whales which have demonstrated the presence of a transient class of animals, there are some anecdotal sources of information.

In the harpoon whaling for short-finned pilot whales off the Antillean islands of St. Vincent and St., Lucia in the Caribbean Sea (Caldwell and Caldwell, 1975), whalers report that pilot whales respond in two different ways to being hunted by a small boat equipped with a hand-held gun harpoon (Caldwell, pers. comm.). Some groups are very easy to approach and one or two animals can be easily killed. Other groups are impossible to get anywhere near, and actively avoid the whaling boats. The implication is that some groups know the intention of the whaling boat, while others do not. Since this fishery only kills one or two animals from a group at a time, the survivors have an opportunity to learn about the intentions of the whalers. Any groups which were resident to the area would have the opportunity for multiple encounters with the whalers, allowing them to learn the whalers' intentions. The animals which do not avoid the whalers could be transient animals, unfamiliar with the area and with no previous experience of whaling on which to base a flight response.

In summary, it is quite possible that the visitor groups of pilot whales described in this study represent a distinct community of whales. At the very least, I have shown that they do not occur in the Tenerife region with any great frequency. Further conclusions will have to await long range radio-tracking of the Tenerife pilot whales in order to better understand their ranging patterns.

4.4.3 Reliability of Pod Definitions

The term "pod" has been used to define consistent pilot whale groups identified in this study. The term was originally used by 19th century American whalers for any group or herd of whales. The definition of pods for stable groups of killer whales was based on the largest group of whales that travelled together for at least 50% of the time (Bigg *et al.*, 1990). I feel that the term also applies to pilot whale groups, although the groups of pilot whales may not be as stable as killer whale groups. "Pod" is used in this sense to mean any group of whales with consistent associations between individuals. The duration of existence for a pod should be measured in months and years, not in hours and days.

Perhaps one of the strongest verifications for the pod divisions is in Table 4.6. This shows that although only 13% of all possible pair combinations were observed overall, 96% of the possible within-pod pair associations defined by the cluster analysis were observed. Also, the level of these within-pod associations were found to be significantly higher than those between animals from linked or un-linked pods (Figure 4.11). These two analyses also lend support to the idea of "linked" pods. The percent of the possible pair combinations between linked pods was high (80%), but the level of the associations was closer to that between completely different pods than it was to within-pod associations. However, the cluster analysis of pod associations was inconclusive (Figure 4.18). There was no evidence of discrete "clans", as has been described for killer whales (Bigg *et al.*, 1987; Ford, 1989; Bigg *et al.*, 1990). This suggests that it is the relationships between specific individuals which form the links between linked pods. The linked nature of pods has been documented for long-finned pilot whales by parallel genetic variation in allele frequencies between separate pods (Amos *et al.*, 1991b). These parallels were closer for older animals, suggesting that linked pods shared common ancestors, but that the pods did split and younger animals were more distantly related (Amos *et al.*, 1991b).

4.4.4 Seasonality of Occurrence and Association

The pattern of a seasonal variation in group size described here for pilot whales, with larger groups composed of more pods occurring during the summer months, is similar to the pattern described for killer whales (S.Heimlich-Boran, 1988; Felleman *et al.*, 1991). For killer whales, this has been related to the seasonal influx of migrating salmon (J.Heimlich-Boran, 1986a). I do not have sufficient information about prey resources in the Canary Islands to make a similar association for pilot whales. However, the season of larger group size does correspond to the proposed conception period, based on back-calculations assuming a 12-month gestation (recently identified for long-finned pilot whales: A.R.Martin, pers. comm.) and a peak in births during the summer (June: this study, Section 4.3.1; July: Kasuya and Marsh, 1984). If these assumptions defining summer as the peak conception period apply to Canary Island pilot whales, then the increased association of whales from different pods during this season could be for mating. This would support the hypothesis that mating occurs between pods. Unfortunately, I never observed any sexual interactions in over 500 hours of observation.

However, there is no indication of a strict seasonality to pilot whale births. Births of all populations have been shown to have a wide dispersion, albeit with a single summer peak (Sergeant, 1962a; Kasuya and Marsh, 1984; Martin, pers. comm.; present study). There also did not appear to be any significant synchrony of ovulation in Japanese pilot whale pods (Kasuya and Marsh, 1984). This diffuse seasonality may be why multi-pod groups were observed throughout the year. In any event, the lack of a fixed breeding season is likely to have profound effects on the mating system (Clutton-Brock, 1989b).

It is not clear whether specific individuals have seasonal patterns of occurrence. There were no apparent seasonal patterns to the occurrence of visitor whales (Figure 4.4), and sample sizes were too small to test the occurrence of individual resident whales for seasonal variation in occurrence. It would also be difficult to look for seasonal variation in the identification of new whales, since the rate of new identifications changed throughout the course of the study (see Figure 4.6).

4.4.5 Age and Sex Structure of Pilot Whale Pods

There are still many unknown elements of pilot whale social organisation, primarily due to the incomplete data on age and sex structure. In spite of these difficulties, some evidence suggests that the adult sex ratio of Canary Island pilot whales was similar to the sex ratio of Japanese pilot whales. Kasuya and Marsh (1984) found that 22.6% of the adult population were males, giving an adult sex ratio of 1 male for every 3.4 females (Kasuya and Marsh, 1984). Their life history model, which accounted for fishing bias for pods containing large males, estimated 21.15% males and a sex ratio of 1:3.7. The highest female-biased adult sex ratio for Canary Island pilot whales would result from the assumption that all unknowns and all clean-finned animals were adult females. This would give a total adult female population of 376 females (109 mothers + 218 unknowns + 15% clean-finned animals), and would result in a sex ratio of 21.7% males or 1 male:3.6 females. This is probably a overestimate, but even if the unknowns were composed of 10% newly mature males, the sex ratio would still be equal to 1:3.4 (104 males:109 mothers + (218 unknowns - 10%) + 15% clean-fins). The sex ratio for long-finned pilot whales caught off Newfoundland was 1:3.7 (Sergeant, 1962a), equal to that for the Japanese life history model.

There appeared to be fewer reproductive females in the Canary Islands than there were off Japan. Reproductive females composed 58.3% of all adult females from the actual whaling data and 52.4% for the life history model estimates (Kasuya and Marsh, 1984). Combined with the two corresponding adult sex ratios, the ratio of adult males to reproductive females was 1:2.00 and 1:1.95, for the original data and life history model, respectively. The age and sex classifications for the present study found the percent of the adult female population classified as reproductive (i.e. mothers) would be only 35.7% (assuming 90% of unknowns to be non-reproductive adult females). The calculated male:mother ratio was 1:1.05. This lower proportion of reproductive females could be due to improper assumptions concerning the unknown class of animals, or it could indicate real differences in reproductive rates between these two populations. For example, the whales off Japan have a history of exploitation, which could affect population density and local carrying capacity (see Fowler, 1984).

Pods of Canary Island pilot whales were classified as productive and nonproductive on the basis of the presence of immature animals. Two of the 14 nonproductive pods were composed of only males, one was composed of three unknowns, while the rest were mixed males and unknowns. This could be an indication of male segregation into separate pods, especially if these unknowns were adolescent males. Other studies of pilot whales have reported pods with an apparent abundance of males, but there are no previous reports of all-male pods (Sergeant, 1962a; Kasuya and Marsh, 1984). However, the two all male pods were visitors pods and thus seen only once. Additional animals in these pods could have remained unidentified.

The association patterns of Canary Island pilot whales provided some insight into the nature of the relationships between the age and sex classes. The associations between adult males and the unknown class of whales were consistently higher than all associations involving mothers except when linked pods travelled together. Mothers' associations with adult males from linked pods were significantly higher than mothers' associations with each other and with the unknowns, and were not significantly different from the other male associations. If mothers are considered to be the reproductive females in the population, then their frequent associations with adult males from linked pods could support the hypothesis that mating is occurring outside of the pods. If mating was occurring within pods, higher association might be expected between adult males and females with calves from the same pods. Genetic studies of long-finned pilot whales indicate that males are not breeding within their own pods (Amos *et al.*, 1991a; 1991b).

The high association levels between adult males within the same pods may also correspond to the findings from genetic studies in Faeroese long-finned pilot whales. Adult males in the same pods had high degrees of relatedness, based on an excess of heterozygotes on single locus alleles, which are more common in siblings (Amos *et al.*, 1991a; 1991b). Males within the same pod could be brothers maintaining associations into adulthood, as has been shown for chimpanzees (Goodall, 1986) and lions (Packer and Pusey, 1982; Packer *et al.*, 1991). In any event, male pilot whales appear to be stable members of the pods outlined in this study.

4.4.6 Conclusions

The conclusions about pilot whale social organisation in the Canary Islands must still be considered tentative since observational studies utilising the identification of individuals require long-term effort to understand slowly-maturing, long-lived animals such as pilot whales. However, the findings from this study do not contradict the previously available biological data on pilot whales. Pilot whale pods exhibited stable group membership in groups of mixed age and sex throughout the two years of observation. Males were lacking from some of the productive pods, suggesting that there may not be a long-term bond between males and breeding females. Males exhibited high levels of association with each other (supported by genetic studies of relatedness in long-finned pilot whales) and with reproductive females from other pods. They had low levels of association with the reproductive females in their own pod, suggesting that mating might not occur within the pods (supported by DNA-fingerprinting and paternity exclusion studies in long-finned pilot whales). If mating was occurring within pods, higher associations would be expected between adult males and mothers. Groups tended to be larger and to consist of animals from different pods during the season when conception is likely to occur, suggesting that mating could occur when pods join together. The implications of a breeding system where mating occurs primarily between separate social groups suggest that the cohesive nature of pilot whale pods is based on non-reproductive benefits. Resource utilisation and predator defence have been proposed as benefits to group living. Although young pilot whales may be subject to low levels of shark and killer whale predation, it is likely that the ability to locate and capture patchy, clumped food resources may be a significant advantage of group formation in a three-dimensional, featureless environment. Squid, the pilot whales' favoured prey, is an obligate schooling animal (Hurley, 1978; Clarke, 1986) and it is likely that cooperation is required in it's capture (Norris and Schilt, 1988). It would be beneficial to maintain long-term associations with the same individuals (preferably kin) to foster that cooperation (Axelrod and Hamilton, 1981).

4.5 SUMMARY

A 22-month field study on short-finned pilot whales was conducted off Tenerife in the Canary Islands off north-west Africa. Four-hundred-ninety-five individual pilot whales were identifed from photographs of naturally-occurring marks and scars on the dorsal fin and back. Individuals were classified into five age and sex categories: 107 adult males, 109 females with calves (or mothers), 219 unknowns (either adult females without calves or adolescent males), 33 juveniles (greater than two-thirds the size of the mother) and 31 calves (less than two-thirds the mother's size). Two classes of whales were defined by patterns of occurrence: residents and visitors. Residents were all animals seen more than once or seen once, but in the company of animals seen more than once. Visitors were defined as animals seen only once but not in the company of animals seen more than once. There were 15 distinct visitor groups, totalling 107 identifed animals and 16 clean-finned immatures.

Two-hundred-seventy-seven groups of resident pilot whales were identified over 147 days. Associations between pairs of individuals were tallied to calculate a ratio association index and hierarchical, agglomerative clustering methods were applied to the matrix of association values to determine clusters of individuals, termed *pods*. Pod structure was analysed for age and sex composition, and pods were defined as productive or non-productive based on the presence of immature animals. Productive pods were significantly larger, although 12% of them were lacking adult males. Whales from different pods occasionally travelled together, and associations between age and sex classes showed significant differences depending on the pod membership of the individuals. Overall, associations involving adult males were higher than associations involving mothers. However, the highest ranked associations between mothers and members from their own pod were with other mothers, while the mothers' highest associations with other pods were with adult males. During summer (April-September), pilot whale groups were significantly larger and contained individuals from a significantly greater number of pods, suggesting that pods were more likely to group up during the summer.

These data support the hypothesis that male pilot whales remain in their natal pod and mate with females in associated pods. Further studies on wild populations are needed, especially utilising DNA fingerprinting, in order to verify this hypothesis.

CHAPTER 5: COMPARATIVE SOCIAL ECOLOGY OF DELPHINIDS: TOWARDS AN UNDERSTANDING OF MATING SYSTEMS

5.1 INTRODUCTION

Mammalian mating systems show correlation with a variety of biological, social and ecological factors: the degree of sexual dimorphism (Ralls, 1977), relative brain size (Humphrey, 1976; Dunbar, 1992; Sawaguchi, 1992), relative testes size (Harcourt *et al.*, 1981; Harvey and Harcourt, 1984; Parker, 1984), patterns of dispersal (Shields, 1987; Clutton-Brock, 1989a), habitat complexity (Verner and Willson, 1966), distribution of resources (Orians, 1969; Emlen and Oring, 1977), genetic heterogeneity (Chepko-Sade *et al.*, 1987), parental care (Trivers, 1972; Clutton-Brock, 1989b) and the distribution of potential mates (Orians, 1969; Emlen and Oring, 1977; Andelman, 1986). The relative importance of each of these factors is variable across mammalian species, but general trends have demonstrated predictive value (see review in Clutton-Brock, 1989b).

The study of delphinid mating systems and social ecology is still underdeveloped compared to the relatively large body of equivalent work on many terrestrial mammals (see reviews in Norris and Dohl, 1980b; Wells *et al.*, 1980; Gaskin, 1982; Evans, 1987; Würsig, 1989). However, long-term studies on some dolphin species are beginning to provide sufficient information on distribution, dispersal patterns, social relationships and ecology to allow comparable examination. Additionally, the newly available techniques of genetic analysis (Burke, 1989) being applied to cetaceans (Hoelzel, 1991b; Amos *et al.*, 1992) are beginning to suggest unique patterns of mating (Amos *et al.*, 1991a; 1991b; In press). This chapter reviews the information currently available for delphinids utilising a comparative approach and proposes hypotheses about their mating systems.

The comparative approach has become a widely used tool in the attempts to understand the adaptive significance of species differences in morphology and behaviour within mammalian orders (Harvey and Pagel, 1991). These methods have been applied to primates (Clutton-Brock and Harvey, 1977; Clutton-Brock *et al.*, 1977; Harvey *et al.*, 1978; Clutton-Brock, 1980; Harvey *et al.*, 1980; Harcourt *et al.*, 1981; Harvey and Bennett, 1983; Harvey and Harcourt, 1984; Harvey and Clutton-Brock, 1985), carnivores (MacDonald, 1983; Gittleman, 1986), bats (Eisenberg and Wilson, 1978), ungulates (Jarman, 1974) and other small mammals (Mace *et al.*, 1981). Most work has examined variation in social organisation relative to ecology (Crook, 1970; Wrangham and Rubenstein, 1986).

The first part of this chapter will be a broad examination of the cetacean family *Delphinidae* through a comparison of morphological and behavioural traits, specifically the relationships within and between six characters: body size, brain size, testes size, group size, diet and habitat preference. Trends are then compared to those used in current theories of mating systems. Three main questions will be addressed. First, what is the extent of sexual dimorphism within the family and can sexual dimorphism be related to group size? Second, what are the trends of relative brain size in relation to group size, diet, and habitat preference? Third, what are the trends in relative testes size related to group size and what are the implications for mating systems this suggests in terms of the importance of sperm competition (Parker, 1984)?

Following this general examination is a more detailed review of the delphinid genera for which there is comprehensive information. Detailed field studies examining group stability and group-specific habitat use patterns have been possible with the development of methods for the individual identification of cetaceans (Würsig and Würsig, 1977; Würsig and Jefferson, 1990). The most thorough studies have been conducted on *Tursiops truncatus* (Würsig and Würsig, 1977; Würsig, 1978; Würsig and Würsig, 1979; Shane *et al.*, 1986; Wells, 1986; Wells *et al.*, 1987; Ballance, 1990; Wells, 1991; Connor *et al.*, 1992a; 1992b) and *Orcinus orca* (Balcomb *et al.*, 1982; Bigg, 1982; Ford, 1984; Balcomb and Bigg, 1986; J.Heimlich-Boran, 1986a; 1986b; S.Heimlich-Boran, 1986; Hoelzel and Osborne, 1986; Osborne, 1986; Bigg *et al.*, 1987; J.Heimlich-Boran, 1988; S.Heimlich-Boran, 1988; Ford, 1989; Bigg *et al.*, 1990; Olesiuk *et al.*, 1990; Felleman *et al.*, 1991; Baird *et al.*, 1992). There is also some information on *Stenella* spp. (Norris and Dohl, 1980a; Norris *et al.*, 1985; Würsig *et al.*, 1989; Pryor and Shallenberger, 1991; Würsig *et al.*, 1991), *Lagenorhynchus* spp. (Würsig and Würsig, 1980; Würsig *et al.*, 1989; 1991) and *Grampus* (Kruse, 1989). An examination of the details of habitat use and social organisation for these genera can be used to test family-wide trends and to propose hypotheses for delphinid mating systems.

To properly introduce trends in *Delphinidae*, it is instructive to first review mammalian trends in sexual dimorphism, relative brain size, and relative testes size. In addition to the classifications of group size, diet, and habitat I will present for delphinids, additional classification categories have been compiled for terrestrial mammals. These are mating system (Alexander *et al.*, 1979), socionomic sex ratio (Clutton-Brock, *et al.*, 1977), metabolic rate (Armstrong, 1983; Schmitz and Lavigne, 1984), trophic level (Wooton, 1987), and a variety of life history parameters such as length of gestation (Pagel and Harvey, 1988), age at first reproduction (Wooton, 1987), and lifespan (Pagel and Harvey, 1988).

Relationships have been clearly demonstrated between body size, group size and diet for both primates (Clutton-Brock *et al.*, 1977) and ungulates (Jarman, 1974; Jarman and Jarman, 1979). For example, smaller antelope have more selective diets and disperse widely in less-open habitats, while larger antelopes show less diet selectivity and occur in larger groups (promoted by predator defence) in open grassland habitat (Jarman 1974; Jarman and Jarman, 1979). For primates as well, larger species tend to occur in larger groups (Clutton-Brock and Harvey, 1977). This trend is not exclusive, though: bears are one of the largest of carnivores and live solitarily (Caro, 1989; Gittleman, 1989).

Sexual dimorphism in body size varies widely within the mammalian orders (Ralls, 1977). In the majority of sexually-dimorphic species, the male is larger than the female (although see Ralls, 1976). Darwin (1871) proposed that bigger males were better equipped to compete with other males for access to females (intra-sexual selection), and in turn, that females could choose to mate with larger males (epigamic selection). The result of this sexual selection is that males show greater variation in reproductive success than do females (Bateman, 1948; Clutton-Brock, 1986). This has been shown to be the case for a wide variety of mammals: sexual dimorphism and variance in reproductive success is greater in species where a small number of males can deny other males access to a group of breeding females (Clutton-Brock and Harvey, 1977; Clutton-Brock *et al.*, 1977; Alexander *et al.*, 1979). Other explanations for sexual dimorphism have been based on ecological and energetic factors which will be presented in more detail in Section 5.4.1.

Jerison (1973) reviewed the evolution of brain size and proposed that larger brains conferred enhanced abilities to collect, process and integrate complex environmental information. Wherever this conferred a selective advantage, larger brains evolved. The best documented trends in brain size are related to the distribution of food resources and home range size (Mace *et al.*, 1980). For example, frugivorous bats have larger brains than insectivorous bats (Eisenberg and Wilson, 1978). The proposed reason is because larger brains provide the increased ability to process the complex spatial and temporal information required to exploit a patchy, clumped resource such as fruit (Eisenberg and Wilson, 1978). For similar reasons, frugivorous primates have relatively larger brains than folivorous species (Clutton-Brock, 1980). The correlation between larger brain size and a larger home range is considered to be an indication of the fact that larger brains may be required to accommodate mental maps for larger areas (Clutton-Brock and Harvey, 1980; Mace *et al.*, 1980).

Another hypothesis which links larger brain size to group structure has been termed the *social complexity* hypothesis (Humphrey, 1976; Dunbar, 1992; Sawaguchi, 1992). This proposes that a complex social life requires a complex intellect to process the information of multiple, overlapping relationships. Recent evidence for this comes from a comparison of neocortex volume and group size. Neocortical volume was found to be a function of group size; group size explained more of the variation in neocortical volume than did the ecological variables of percent fruit in the diet or day journey length (Dunbar, 1992). Dunbar (1992) proposed that, while the initial impetus towards larger brains in primates may have been due to ecological factors, brain evolution may have been accelerated by the potential for increasing social complexity and the resulting benefits of social coalitions and the ability to exploit knowledge of the behaviour of other individuals. In fact, Dunbar (1992) proposed that brain size may actually put an upper limit on group size.

The cetacean brain has always attracted much attention due its large size and convoluted appearance (Breathnach, 1960; Lilly, 1964; Ridgway *et al.*, 1966; Elias and Schwartz, 1969; Jansen and Jansen, 1969; Pilleri and Gihr, 1969; Pilleri and Gihr, 1971; Morgane and Jacobs, 1972; Jerison, 1973; Ridgway and Brownson, 1984; Morgane *et al.*, 1986a; Morgane *et al.*, 1986b; Ridgway, 1986a; 1986b; Ridgway and Wood, 1988; Ridgway, 1990). Worthy and Hickie (1986) reviewed relative brain size in marine mammals and found that cetacean brains fit the general allometric relationship with body size for all mammals. Jerison (1986) has noted that large delphinid brains are apparently not essential in a three-dimensional environment (e.g. bird brains), in reduced gravity (e.g. human adaptability to life in space), in the aquatic environment (e.g. fish brains) or to acoustic processing (e.g. bat brains). It is more likely to be the ways in which they process external information in terms of environment and society which has resulted in the evolution of large brains (Jerison, 1986). It has also been noted that cetaceans of similar body size have very different sized brains (e.g. the delphinids *Grampus*, *Orcinus*, *Lagenorhynchus* and *Cephalorhynchus* have brains two to three times larger than the physeterids, ziphids and platanistids *Kogia*, *Ziphius*, *Platanista* and *Pontoporia*, respectively: Ridgway, 1986b). I examine relative brain size within the family *Delphinidae* in order to help identify ways in which larger brains may be used by these animals.

The relative size of a male's testes has been shown to vary with mating system, and has been related to the potential for sperm competition where larger sperm volumes are able to out-compete other male's sperm for fertilisation (Parker, 1984). In primates, species in which multiple reproductive males occur in the same group and in which females are likely to copulate with more than one partner per oestrus have larger testes for their body weight than those where groups have a single breeding male and females invariably mate with only that male (Harcourt *et al.*, 1981; Harvey and Harcourt, 1984). This often translates into the occurrence of increased male-male competition and increased sexual dimorphism in species with larger testes (Harcourt *et al.*, 1981; Harvey and Harcourt, 1984; Kenagy and Trombulak, 1986). Kenagy and Trombulak (1986) found odontocete cetaceans to have the largest relative testes size of all mammals and predicted extreme multi-male breeding systems for these animals. They suggest that there are indications of high degrees of social interactions (referencing Gaskin, 1982), but they also speculate that aquatic copulation presents different selective pressures for a "high level of sperm delivery" perhaps related to the complex vaginal folds in female odontocetes (Kenagy and Trombulak, 1986).

The comparison of social trends within *Cetacea* has been limited by available information. Würsig (1989) reviewed the state of knowledge on a variety of aspects of the behaviour and ecology of all cetaceans. Wells *et al.*, (1980) presented an overview of trends in social ecology within odontocetes, but primarily focussed on Wells' own work on *Tursiops* (see Section 5.3.5.1). One of the predominant relationships is between group size and habitat: river and coastal dolphins live in much smaller groups than most pelagic dolphins. Another trend was the variability in the occurrence of age and sex segregation (reported in *Tursiops* and *Stenella*, apparently absent in other species). There is a clearly a need for a complete review of delphinid social ecology.

5.2 METHODS

The comparative analysis of variation in morphological trends is best examined by establishing relationships at one taxonomic level and examining the deviances from these relationships at the taxonomic level immediately below this (Clutton-Brock and Harvey, 1979; Harvey and Mace, 1982; Harvey and Pagel, 1991). Species are often not valid for comparison because of the lack of independence between species characters within the same genera (Harvey and Pagel, 1991), I will be examining trends within the family *Delphinidae* and variation in these trends for the 17 delphinid genera. This has not substantially limited the data set since 11 of the 17 genera are mono-specific. All data for the six multi-species genera (*Sousa, Lagenorhynchus, Stenella, Lissodelphis, Cephalorhynchus* and *Globicephala*) were calculated from means of the species values (presented in Table 5.1).

The data used in this review were collected from a wide variety of sources. Body size and length and age at maturity was collected from field studies when possible, but additional information was collected from reviews of mammals in general (Poole, 1985) and cetaceans in particular (Bryden, 1972; Leatherwood

Table 5.1. Summary of morphology, group size and ecology for the 32 species of delphinid cetaceans. Lengths in italics are maximum lengths, all others are means. See text for sources.

		Adult Length (m)		Length	Adult Weight (kg)		Weight	BRAIN DATA			Testes (g)	Group Size		Ecological Type	
Subfamily	Species	male	female	Dimorphism	male	female	Dimorphism	Brain (g)	Body (kg)	N	(comb.wt.)	min.	max.	Diet	Habitat
STENINAE	*Steno bredanensis*	2.50	2.45	1.020	107	91	1.176				2300	10	50	1	4
	Sousa chinensis	*2.80*	*2.44*	1.148	285	260	1.096					4	30	1	1
	Sousa teuszii	2.00	1.95	1.026								3	25	1	1
	Sotalia fluviatilis	1.87	1.82	1.027	43	40	1.075	688	42	1	2120	2	30	1	1
DELPHININAE	*Lagenorhynchus albirostris*	2.60	2.59	1.004	267	266	1.004					3	100	1	3
	Lagenorhynchus acutus	2.50	2.24	1.116	160	160	1.000	1200	120	1	740	7	700	1	3
	Lagenorhynchus obscurus	1.88	1.91	0.984							1600	10	200	1	3
	Lagenorhynchus obliquidens	1.75	1.60	1.094	90	90	1.000	1102	85	6	1118	50	1000	1	3
	Lagenorhynchus cruciger	*1.83*	*1.83*	1.000	150	150	1.000					200	1000	1	3
	Lagenorhynchus australis	*2.16*	*2.16*	1.000										2	3
	Grampus griseus	3.70	3.42	1.082	385	335	1.149	2411	317	2	12520	15	300	2	4
	Tursiops truncatus	2.70	2.54	1.063	275	220	1.250	1680	151	12	1966	15	500	1	3
	Stenella frontalis	2.20	2.20	1.000							1956	8	50	1	4
	Stenella attenuata	2.05	1.95	1.051	91	62	1.468				700	10	3000	1	4
	Stenella longirostris	1.79	1.76	1.017	60	60	1.000				900	15	1000	1	4
	Stenella clymene	*1.85*	*1.85*	1.000	60	60	1.000					100	500	1	4
	Stenella coeruleoalba	2.39	2.26	1.058	158	136	1.162	835	62	9	450	25	3000	1	4
	Delphinus delphis	2.40	2.10	1.143	115	85	1.353	836	68	10	3344	100	1000	1	3
	Lagenodelphis hosei	2.36	2.35	1.004	163	163	1.000				2490	100	800	1	4
LISSODELPHININAE	*Lissodelphis borealis*	2.63	2.17	1.212								100	300	1	3
	Lissodelphis peronii	*2.30*	*2.36*	0.975								75	1000	1	3
CEPHALORHYNCHINAE	*Cephalorhynchus commersonii*	1.36	1.39	0.978	60	60	1.000					9	100	2	2
	Cephalorhynchus eutropia	1.53	1.51	1.013	62	62	1.000					11	40	2	2
	Cephalorhynchus heavisidii	1.30	1.30	1.000								5	20	2	2
	Cephalorhynchus hectori	1.25	1.37	0.912	36.8	45	0.818					5	20	2	2
GLOBICEPHALINAE	*Peponocephala electra*	2.68	2.68	1.000	125	125	1.000				2200	150	1500	2	4
	Feresa attenuata	*2.64*	*2.43*	1.086							754	30	300	2	4
	Pseudorca crassidens	5.32	4.47	1.190	1727	1270	1.360				14800	30	50	3	3
	Orcinus orca	6.70	5.80	1.155	4000	2750	1.455	5618	2049	3	46200	15	100	3	3
	Globicephala melas	5.57	4.89	1.139	2224	1524	1.459	2511	1000	3	14400	30	1000	2	4
	Globicephala macrorhynchus	4.73	3.64	1.299	1260	563	2.238				6940	15	500	2	4
ORCAELLINAE	*Orcaella brevirostris*	*2.35*	*2.32*	1.013	97	96	1.010					6	20	1	1

NOTES: Diet: 1) fish, 2) squid, 3) meat; Habitat: 1) estuarine, 2) coastal, 3) shelf, 4) pelagic and Reeves, 1983; Perrin and Reilly, 1984; Rice, 1984; Klinowska, 1991). Mean values for body size were used when available, but in a few cases only maximum body size was reported. This should not affect the sexual dimorphism estimates since these were simply ratios of male and female values. Although body weight is usually the best variable to examine sexual dimorphism (Clutton-Brock *et al.*, 1977), this was not available for eight species from six genera and the use of weight variables would have meant the loss of two genera (*Lissodelphis* and *Feresa*). There was a significant correlation between dimorphism in body weight and dimorphism in body length (Figure 5.1: Spearman Rank Correlation r_S = 0.888, t = 6.96, df = 13, P << .001), therefore sexual dimorphism in body length was used for all analyses. Brain size data was derived entirely from reviews (Breathnach, 1960; Lilly, 1964; Ridgway *et al.*, 1966; Pilleri and Gihr, 1969; Pilleri and Gihr, 1971; Morgane and Jacobs, 1972; von Bonin, 1973; Ridgway and Brownson, 1984; Morgane *et al.*, 1986b; Ridgway, 1986b). Data on individual brain and body weights were available for 46 specimens from nine species (Table 5.1); median values were used when more than one individual was available from any given species. For comparative analyses, the two *Lagenorhynchus* species were pooled to create a generic mean value. Testes weights were extracted from field reports and general reviews (Harrison, 1969; Perrin and Reilly, 1984). Additional sources are listed in the footnotes of Table 1.1.

Body size has been shown to have a confounding effect on the comparison of morphological characters due to allometric growth (Harvey and Mace, 1982; Harvey and Pagel, 1991). However, residuals from the straight line relationship of log transformed characters regressed on log body size will accurately describe character variation with the effects of body size removed (Harvey and Pagel, 1991). For this study, all measurements (body size, brain size and testes size) were log-transformed and the line of best fit was calculated by reduced major axis analysis (Imbrie, 1956). Reduced major axis analysis is recommended because it calculates a line of best fit without assuming a dependent-independent relationship between the two variables, as is the case for linear regression analysis (Harvey and Mace, 1982). In other words, it allows for the potential of error in the measurement of both of the variables, as is likely to be the case with the measurements presented here. Although Harvey and Pagel (1991) have recommend the use of major axis analyses over reduced major axis analyses, the latter has been shown to be more robust when errors are unknown (Rayner, 1985).

Social and ecological categories of delphinids were assigned from general descriptions of distribution, behaviour and diet (Fitch and Brownell, 1965; Wells *et al.*, 1980; Gaskin, 1982; Leatherwood and Reeves, 1983; Clarke, 1986; Evans, 1987; Klinowska, 1991). Minimum and maximum group sizes were derived from field studies where available; in many cases, group sizes were only available from small samples of chance encounters at sea. The two categories may be considered similar to the distinction between core groups and population groups which share a home range (Gittleman, 1989). When detailed field studies were available, minimum group sizes were derived from reported mean group sizes. In many cases, group sizes were only available from chance encounters at sea. Ecological parameters were classified into combinations of two categories: diet and habitat. Diet was classified into three categories: 1) feeding on fish (*icthyophagous*), 2) feeding on squid (*teuthophagous*), and 3) feeding on other marine mammals (*sarcophagous*: Gaskin, 1982). These diet categories were not exclusive, many of the species classified as fish-eaters were also reported to occasionally take squid and vice versa. The assignment of a species to these diet cat-

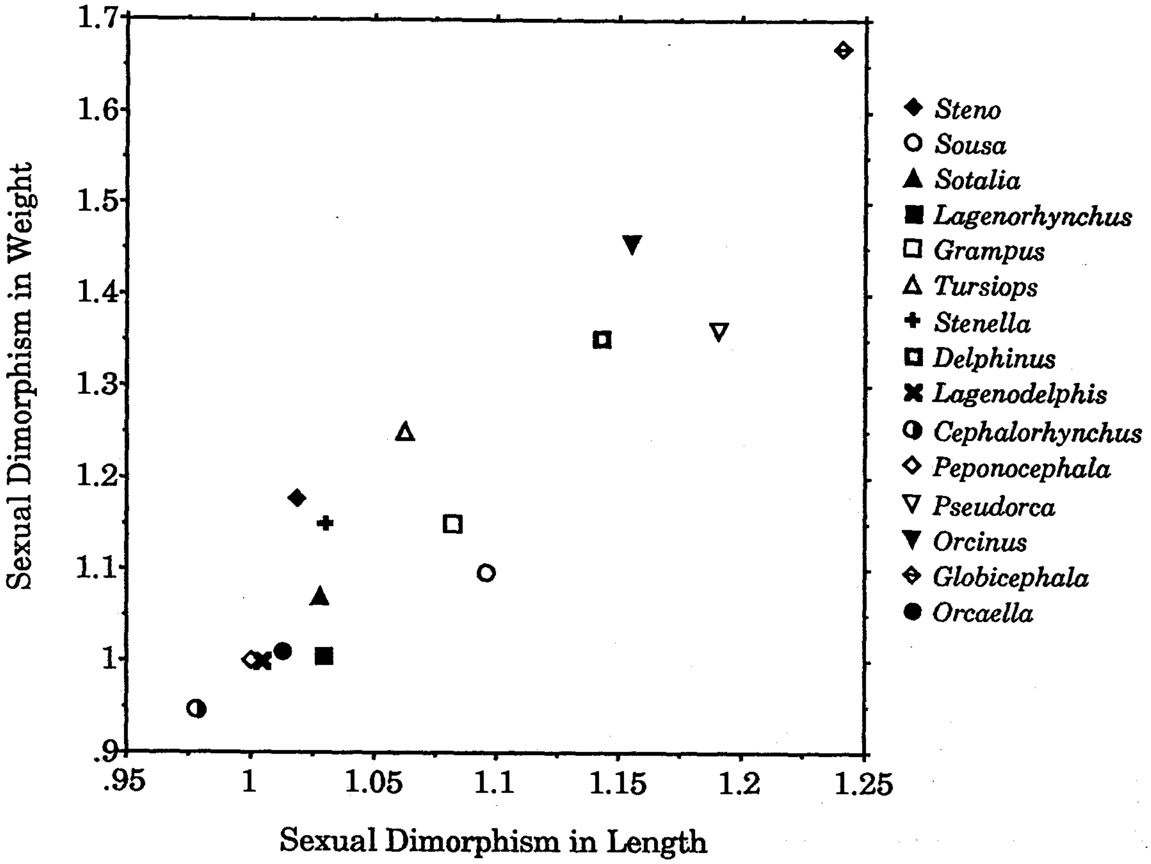

Figure 5.1 Comparison of sexual dimorphism in length with sexual dimorphism in weight for 15 genera. Points for multi-specific genera are averages of species values. The two measures were significantly correlated (Spearman r = 0.888, t = 6.96, df = 13, P < .001).

egories was based on predominant prey, and thus the categories are broad generalisations. On the other hand, the classification of meat-eaters was based on the presence of even limited cases of hunting other marine mammals. This was especially true for *Pseudorca*: there have been no detailed studies of diet for this species, only stomach contents from strandings (mostly fish) and occasional reports of them hunting marine mammals (Perryman and Foster, 1980). Additionally, in *Orcinus*, which is noted for its predation on other marine mammals, some populations feed primarily on fish (Jefferson *et al.*, 1991). Therefore, as even rare occurrences of hunting warm-blooded prey might reflect on brain size, I included the diet category of meat eaters. Habitat zone was classified into four categories: 1) estuarine, or occasionally entering fresh water, 2) coastal, 3) shelf, or ranging from nearshore to the continental shelf, and 4) pelagic, or always offshore.

Detailed data on social systems were only available for the subfamilies *Delphininae* and *Globicephalinae*, and were compiled from existing accounts and my own observations on *Globicephala* (from Chapters 3 and 4) and *Orcinus* (Heimlich-Boran and Heimlich-Boran, ms.).

5.3 RESULTS

5.3.1 Ecological Classification

The classification of diet and habitat for all delphinid species is presented in Table 5.1. There were twelve possible combinations of the three diet and four habitat categories, but only eight were observed. Fish feeders were found in all habitats, but there were no squid feeders which were predominately coastal or estuarine, simply because of the primary shelf and pelagic distribution of squid (Clarke, 1986). The genera which hunted other marine mammals were found only along the continental shelf and in the pelagic zone.

5.3.2 Sexual Dimorphism

Sexual dimorphism in body length in relation to mean body length of males and females for the 17 genera in the family *Delphinidae* is presented in Figure 5.2. Sexual dimorphism was significantly correlated with average adult body length ($r_S = 0.51$, $t = 2.296$, $df = 15$, $P < .05$). The genus *Cephalorhynchus*, the smallest delphinids, was the only genera in which females were larger than males (mean body sizes of 1.39 m vs. 1.36 m; male: female length ratio = 0.978). This situation was most pronounced for *C. hectori* with females almost 10% longer than males (Table 5.1). Males were larger than females in all other genera. Although the degree of sexual dimorphism was significantly correlated with body size, the genera with the greatest sexual dimorphism, *Globicephala* (mean body sizes of 5.11 m for males vs. 4.12 m for females; male: female length ratio = 1.24), ranked only third largest in size. The medium-sized dolphins ranged between these two extremes (Figure 5.2).

Comparisons were made between the two best-represented subfamilies: *Delphininae* (six genera) and *Globicephalinae* (five genera). When all genera were included, there were no significant differences in sexual dimorphism

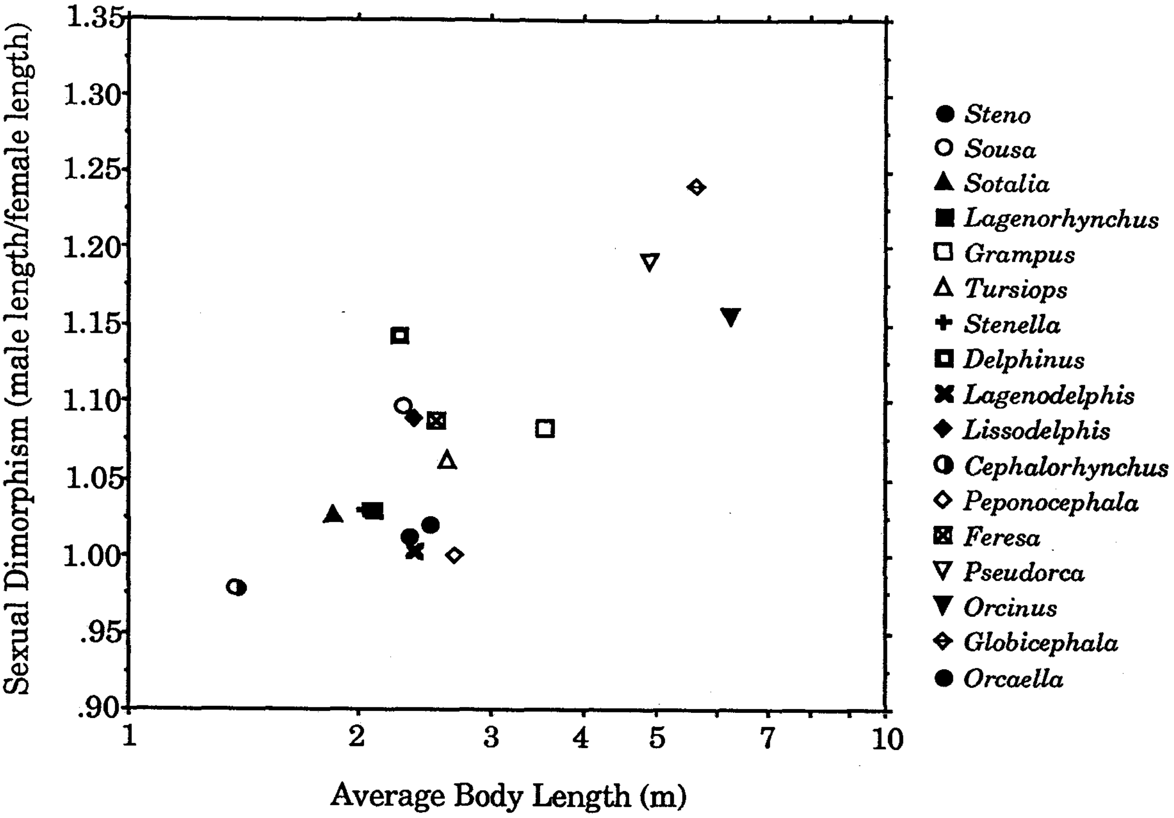

Figure 5.2. Sexual dimorphism in body length plotted against average of adult male and adult female body length for 17 genera of *Delphinidae*. All data were calculated from generic averages of species values.

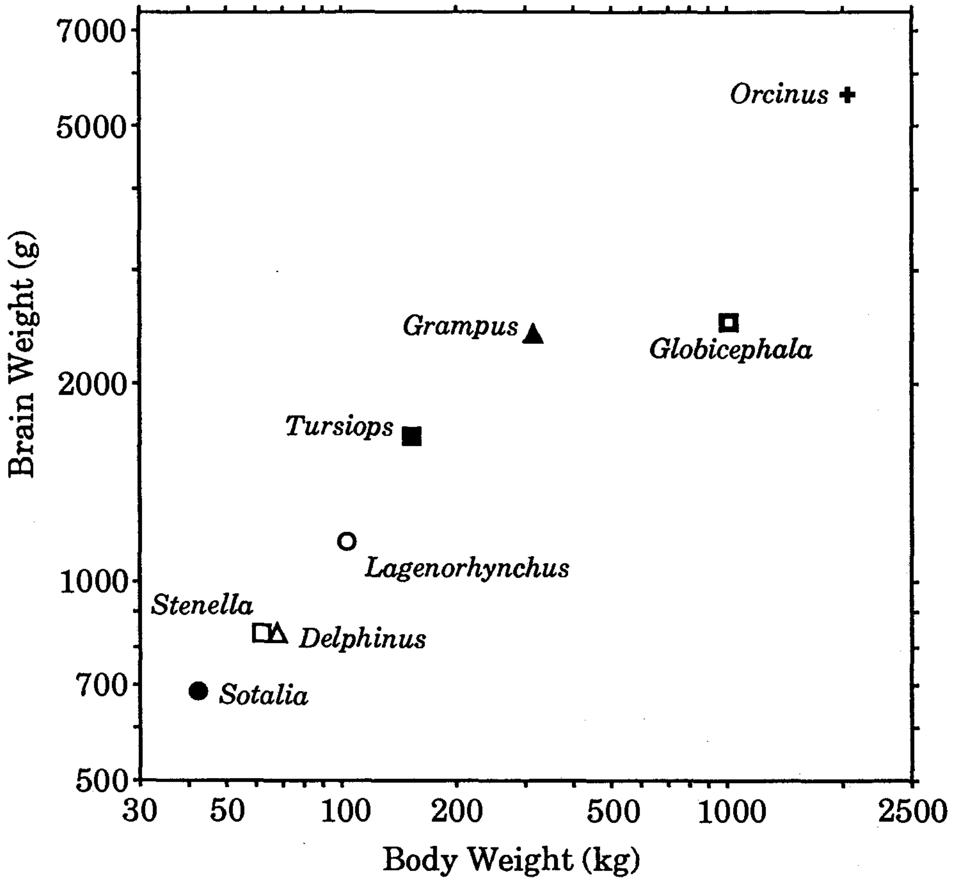

Figure 5.5. Brain weight plotted against body weight for eight genera of *Delphinidae*. The data were significantly correlated ($r = 0.97$, $t = 9.59$, $df = 7$, $P << .001$).

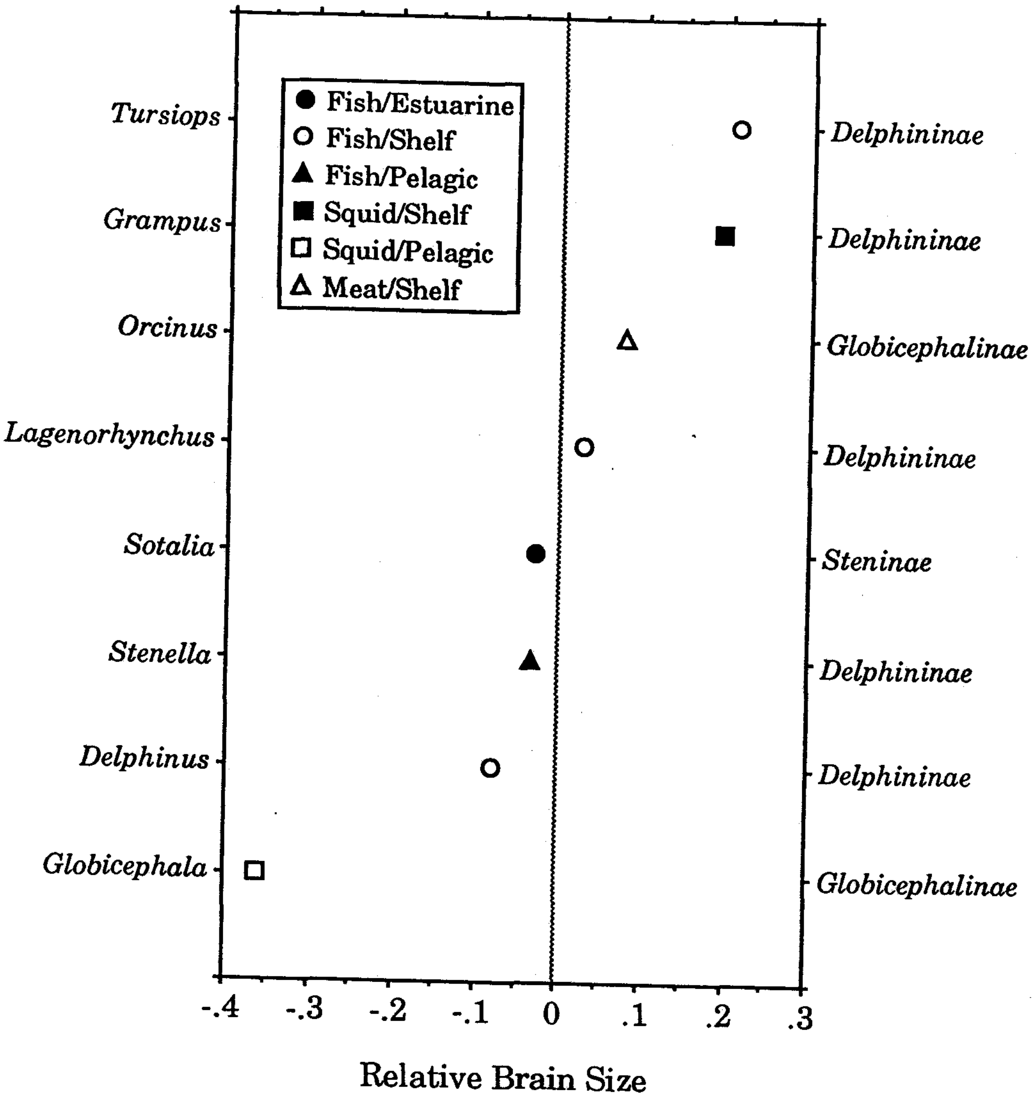

Figure 5.6. Relative Brain Size plotted by ecological classification for eight genera of *Delphinidae*.

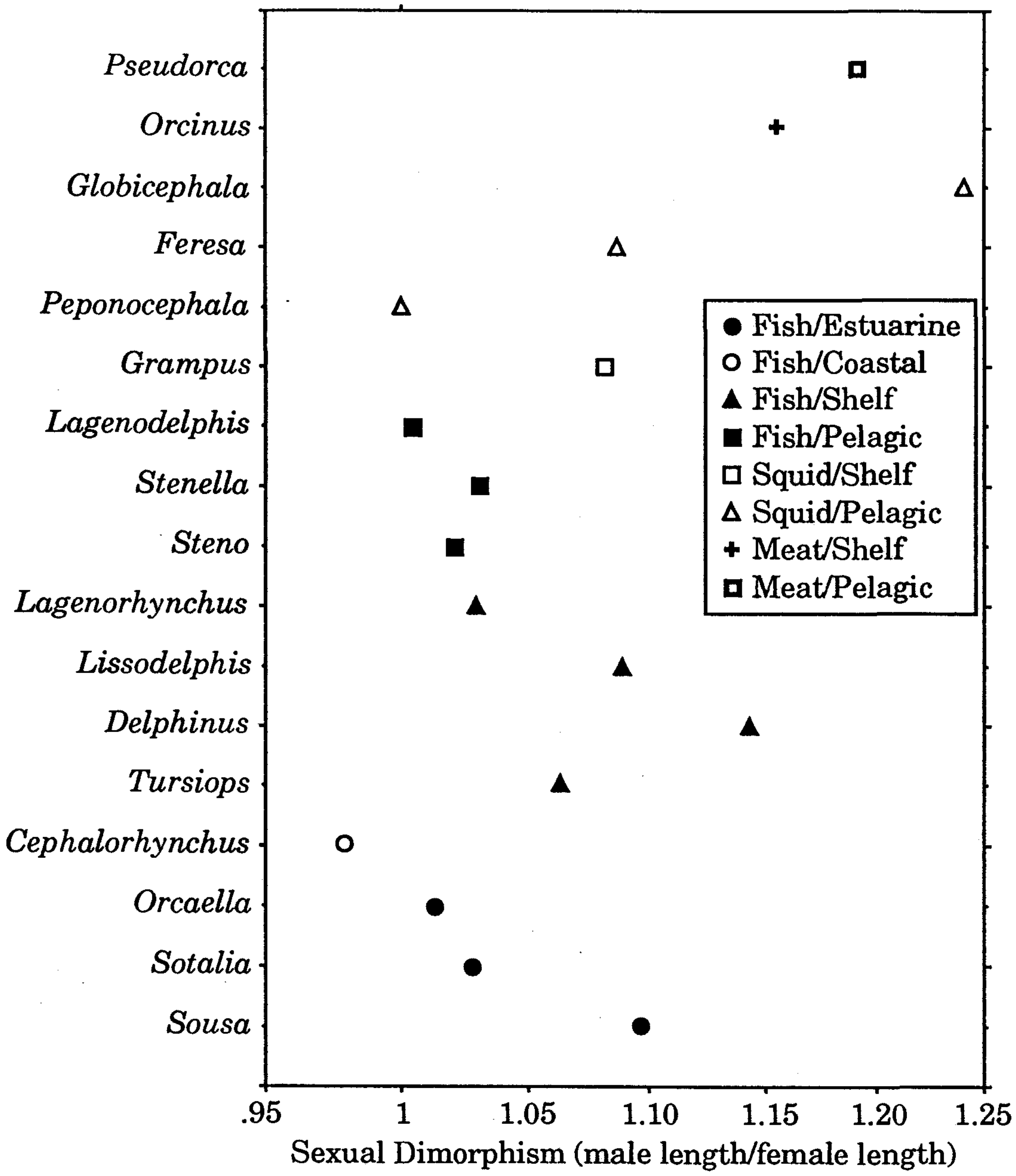

Figure 5.3. Sexual Dimorphism plotted according to ecological classification for 17 genera of *Delphinidae*.

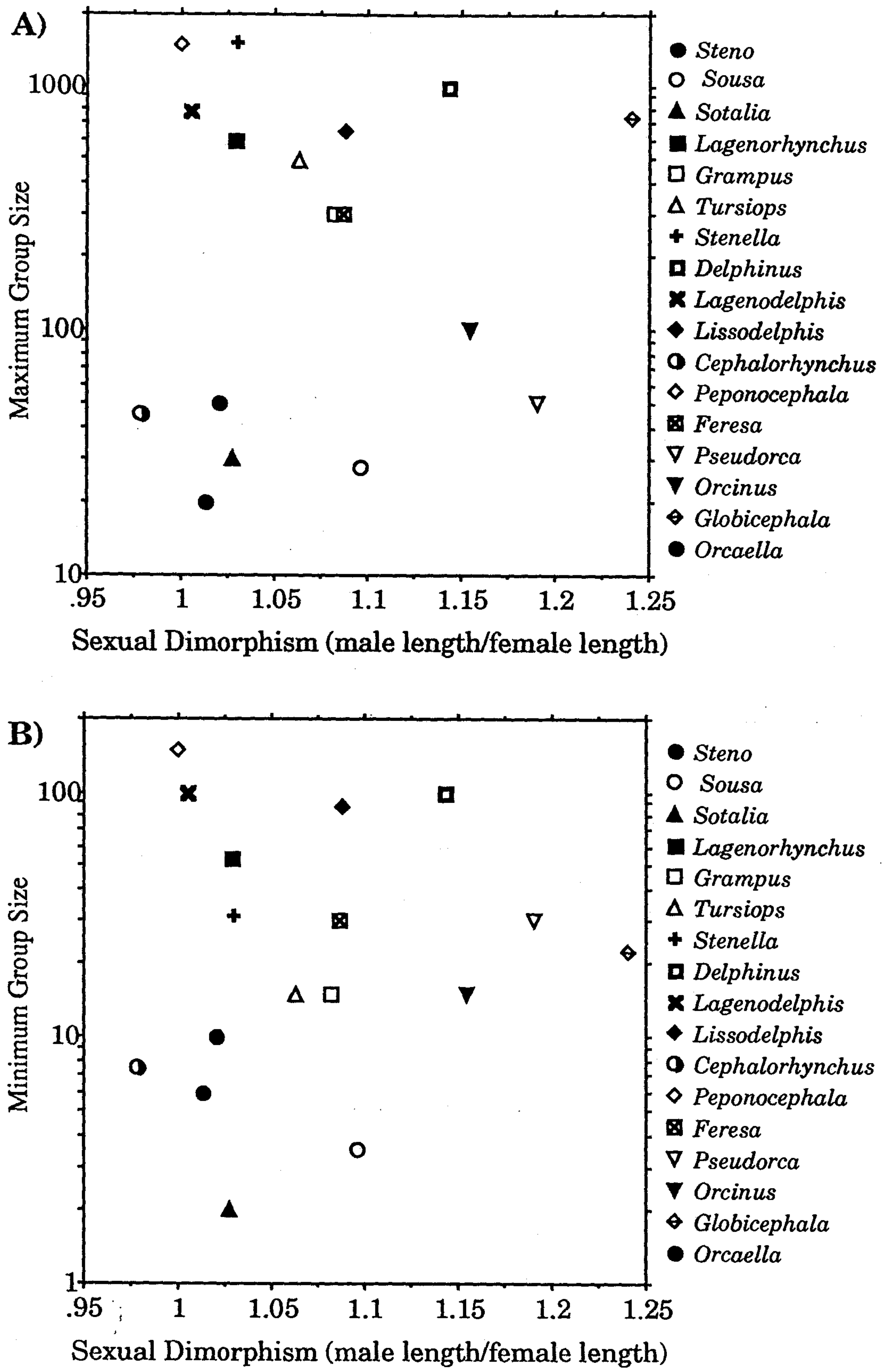

Figure 5.4. Sexual dimorphism in body length plotted against A) maximum and B) minimum mean generic group size.

(*Delphininae* vs. *Globicephalinae*: length ratio: 1.06 ± 0.020 vs. 1.13 ± 0.042, Mann-Whitney $U = 23$, $Z = 1.46$, $P > 0.05$; weight ratio: 1.15 ± 0.056 vs. 1.37 ± 0.139, $U = 18.5$, $Z = 1.39$, $P > 0.05$). However, data for *Peponocephala*, one of the least known *Globicephalinae* genera (Nishiwaki and Norris, 1966) were published as exactly the same lengths for males and females. This was suspected to be due to incomplete data, so the genus was removed. After this removal, there were significant differences in sexual dimorphism between the two subfamilies (recalculated *Globicephalinae*: length ratio: 1.17 ± 0.032, $U = 23$, $Z = 2.34$, $P < 0.02$; weight ratio: 1.5 ± .091, $U = 18$, $Z = 2.32$, $P < 0.05$).

Sexual dimorphism was compared for the ecological classifications of the genera (Figure 5.3). There were no significant differences which could be related to the eight ecological categories of diet and habitat (Kruskal-Wallis $H = 8.144$, $df = 7$, $P > 0.05$). Diet and habitat were also tested separately, but there were still no significant differences (diet: $H = 3.757$, $df = 2$, $P > 0.05$; habitat: $H = 5.378$, $df = 3$, $P > 0.05$).. There were also no significant correlations for sexual dimorphism and group size (Figure 5.4: minimum group size $r_S = 0.057$, $t = 0.221$, $df = 7$, $P > 0.05$; maximum group size $r_S = 0.064$, $t = 0.248$, $df = 7$, $P > 0.05$).

5.3.3 Relative Brain Size

Brain size is known to vary allometrically with body size (Gould, 1966; Jerison, 1973). Brain weight was significantly correlated with body weights for eight genera of *Delphinidae* (Figure 5.5: $r = 0.97$, $t = 9.59$, $df = 7$, $P << .001$. Reduced major axis analysis resulted in a linear equation for the natural log-transformed data:

$$\ln \text{Brain Weight (g)} = .51 \ln \text{Body Weight (kg)} + 4.64$$

The slope of this line (0.51 ± 0.04) was equivalent to estimates made using all odontocete cetaceans (0.55 ± 0.17, principle components analysis, $n = 24$ species: Worthy and Hickie, 1986). The slope for all mammals has been shown to be approximately 0.75 and is scaled with metabolic rate, but a decrease in slope is common when comparing lower taxonomic levels (a process known as the *taxonomic scaling effect*: Pagel and Harvey, 1989).

Residuals calculated from the reduced major axis were termed Relative Brain Sizes (RBS) and show the degree to which the different genera deviated from family-wide trends, independent of body size (Harvey and Pagel, 1991). Relative Brain Sizes are plotted for all genera in relation to ecological classification in Figure 5.6. *Tursiops* had the largest RBS, with a brain 21% larger than that predicted by the reduced major axis fit. *Grampus* and *Orcinus* also had brain sizes larger than expected (19% and 8%, respectively). *Globicephala* had the smallest RBS (36% less than expected), while *Delphinus* was also less than expected (8%). The other genera were all within 5% of the predicted values. None of this variability could be explained by the combined ecological classifications (Figure 5.6: Kruskal-Wallis $H = 4.0$, $df = 5$, $P >> 0.05$). Separate tests were run on diet alone and habitat alone, but there were no significant trends (diet: $H = 0.5$, $P >> .05$; habitat: $H = 3.1$, $P > 0.05$). Comparisons of RBS for minimum and maximum group sizes are presented in Figure 5.7. There were no significant correlations for either of the group size estimates (minimum group size $r_S =$

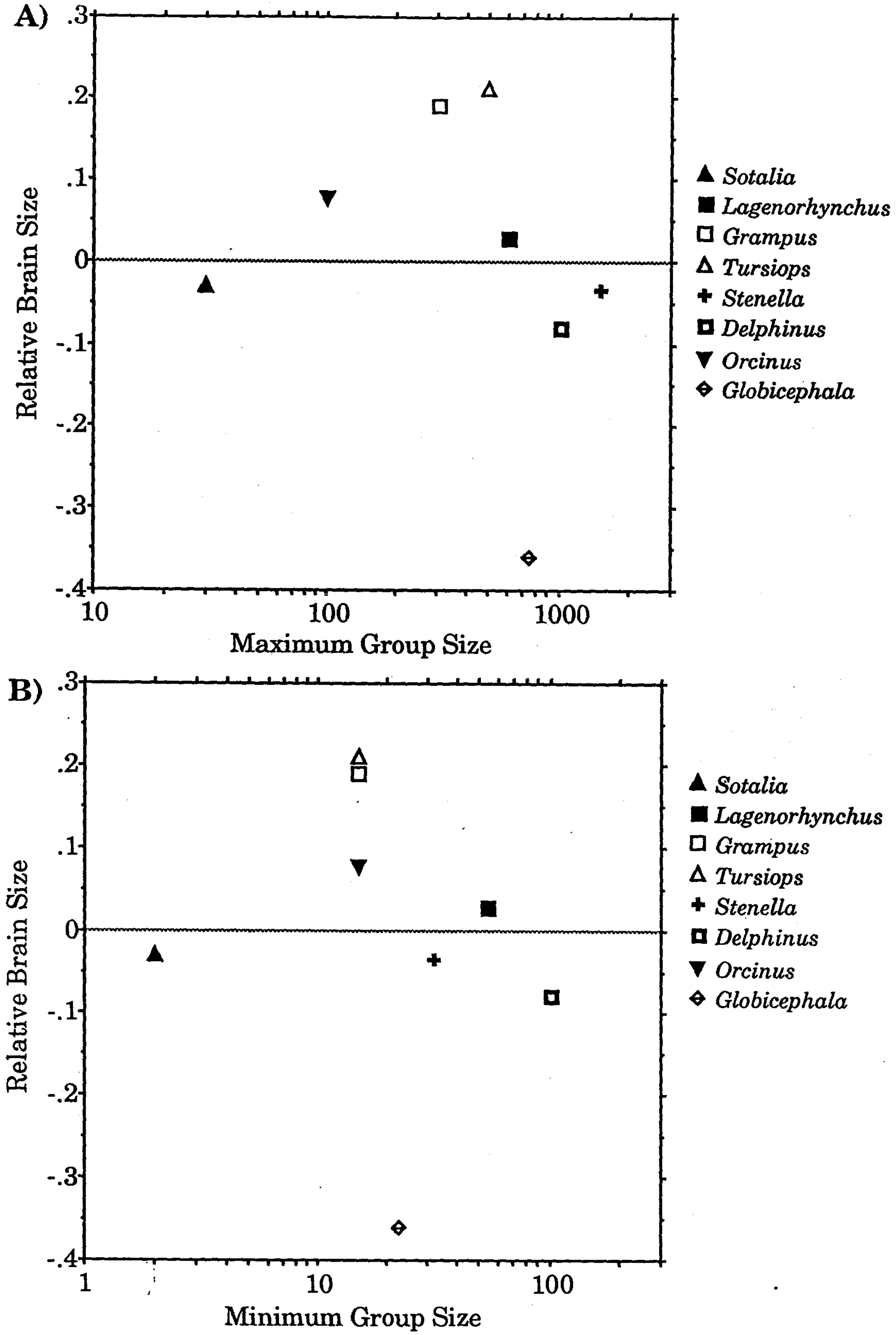

Figure 5.7. Relative Brain Size plotted for A) maximum and B) minimum group size.

-0.51, t = 1.46, df = 7, $P > 0.05$; maximum group size $r_S = -0.57$, t = 1.71, df = 7, $P > 0.05$).

5.3.4 Relative Testes Size

The combined weight of both testes was examined in relation to male body weight for 13 delphinid genera (Figure 5.8). The relationship between testes weight and body weight was described by the reduced major axis line of best fit:

$$\ln \text{Testes Weight (g)} = 0.95 \ln \text{Body Weight (kg)} + 2.79$$

This relationship was significant (r = 0.86, t = 5.64, df = 12, $P < 0.001$). The slope of the line (0.95 ± 0.17) was higher than the common slope for all primates of 0.66 (Harvey and Harcourt, 1984) or the value of 0.72 reported for all mammals (Kenagy and Trombulak, 1986), but since error values were not available for these other slopes, the significance of the difference is unknown. Following Harvey and Harcourt (1984), Relative Testes Sizes (RTS) were calculated as observed/expected ratios from the line of best fit and are presented in Figure 5.9. There were no clear patterns in the taxonomic distribution of RTS values: members of all subfamilies had representatives with larger than expected testes size. There were also no significant correlations between testes size and group size (Figure 5.10; minimum group size r = 0.19, t = 0.20, df = 12, $P \gg 0.05$; maximum group size r = -0.01, t = 0.01, df = 12, $P \gg 0.05$).

An inverse relationship has been proposed between sexual dimorphism and relative testes size in light of the fact that males in single male breeding systems are highly dimorphic (due to increased male-male competition) and have relatively small testes (because they can control access to the female(s) in their group (Harvey and Harcourt, 1984; Fig. 2). I compared the sexual dimorphism (male/female length ratios) and Relative Testes Size values and found no significant correlation (Figure 5.11; $r_S = -0.36$, t = 1.27, df = 12, $P > 0.05$).

5.3.5 *Delphininae* Social Systems

5.3.5.1 *Tursiops*

The bottlenose dolphin, *Tursiops truncatus*, is probably the best-known delphinid. The species is found in coastal waters around the world and has been shown to adapt to a wide variety of environmental conditions (Shane *et al.*, 1986). The diet of bottlenose dolphins shows a wide degree of variability (Barros and Odell, 1990), and they are considered to be one of the most generalised dolphins (Barnes, 1990). Life history, hormonal and observational studies of bottlenose dolphins have indicated that males and females have different rates of maturation, with males maturing at around 10 years of age and females maturing around six or seven years of age (Sergeant *et al.*, 1973; Hohn, 1980; Wells, 1986). Lifespan estimates of 44 years for females and 33 years for males are based on the oldest known individuals aged by dentinal tooth rings (Hohn *et al.*, 1989), indicating that males have higher mortality rates than females. Recent studies have provided no evidence for sexual dimorphism (Hersh *et al.*, 1990). Births appear to be diffusely seasonal; they occur during all months, but with a

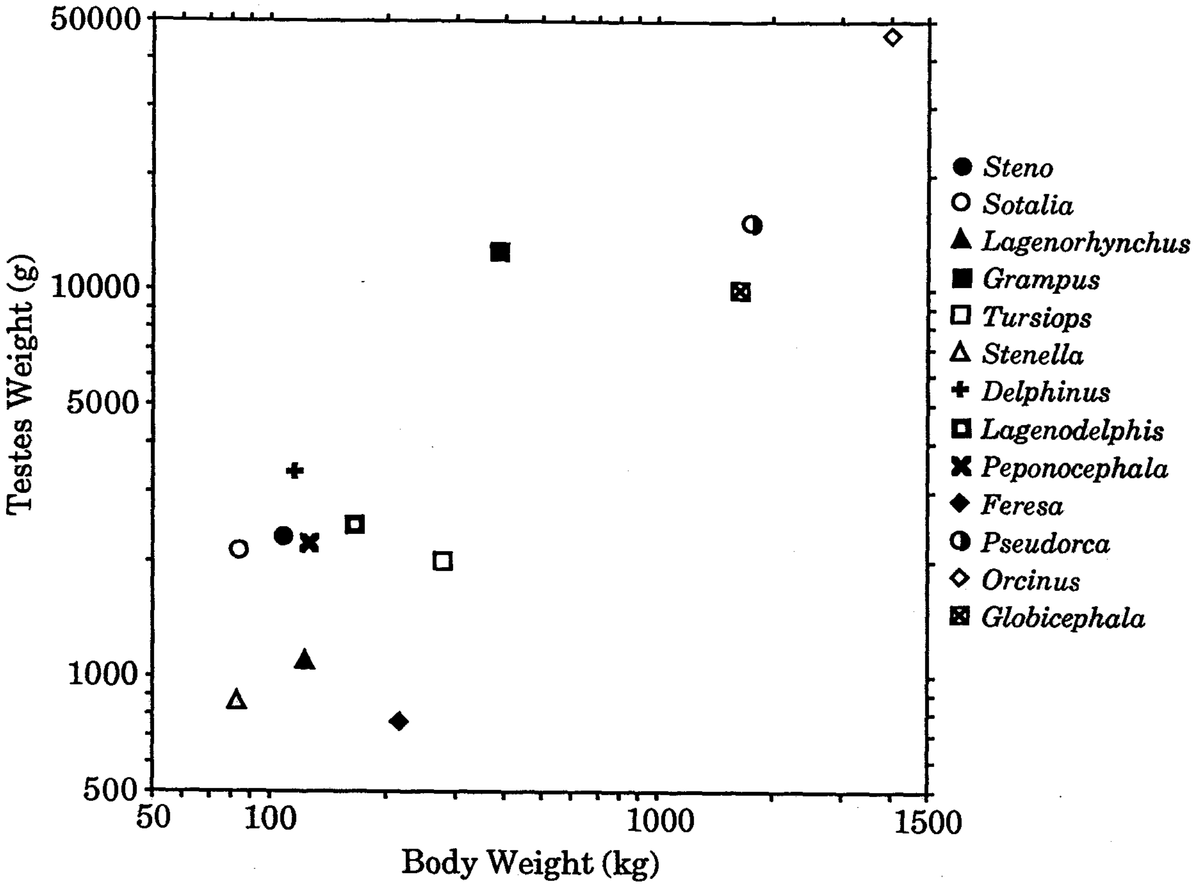

Figure 5.8. Combined testes weight (g) plotted against body weight (kg) on a logarithmic scale for 13 genera of *Delphinidae.*

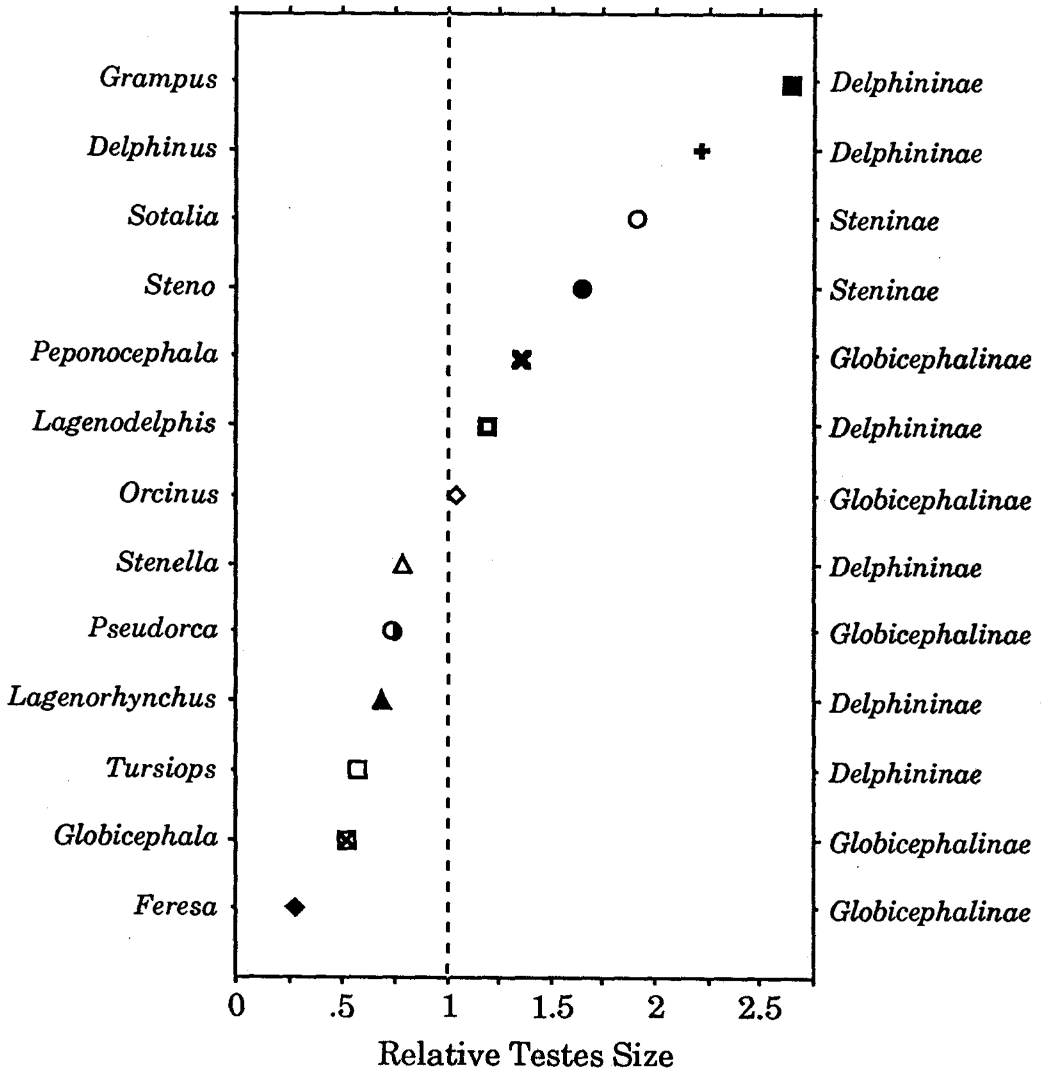

Figure 5.9. Relative Testes Size plotted for 13 genera and three subfamilies of *Delphinidae*.

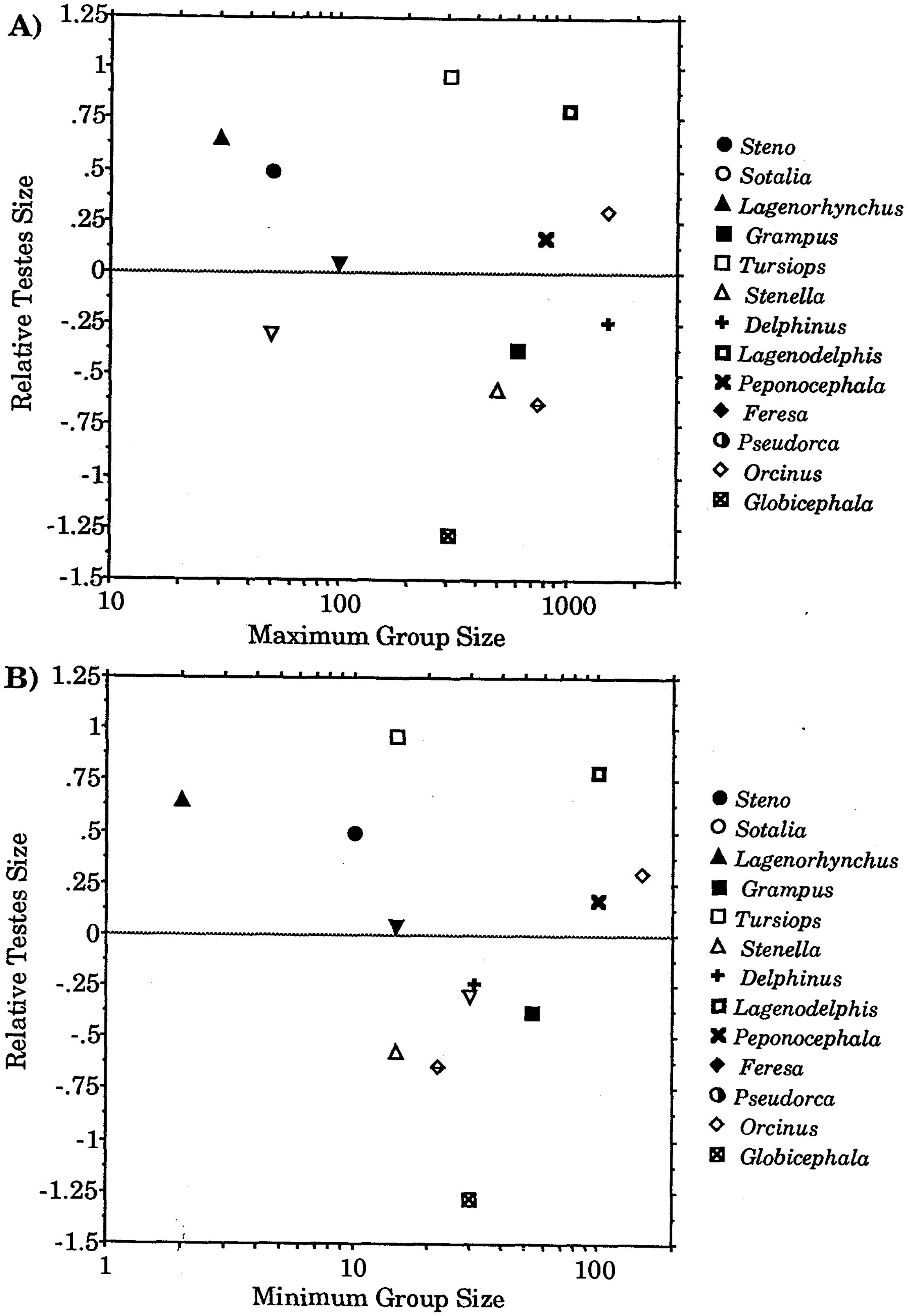

Figure 5.10. Relative Testes Size (RTS) compared to A) maximum and B) minimum group size for 13 genera of *Delphinidae*.

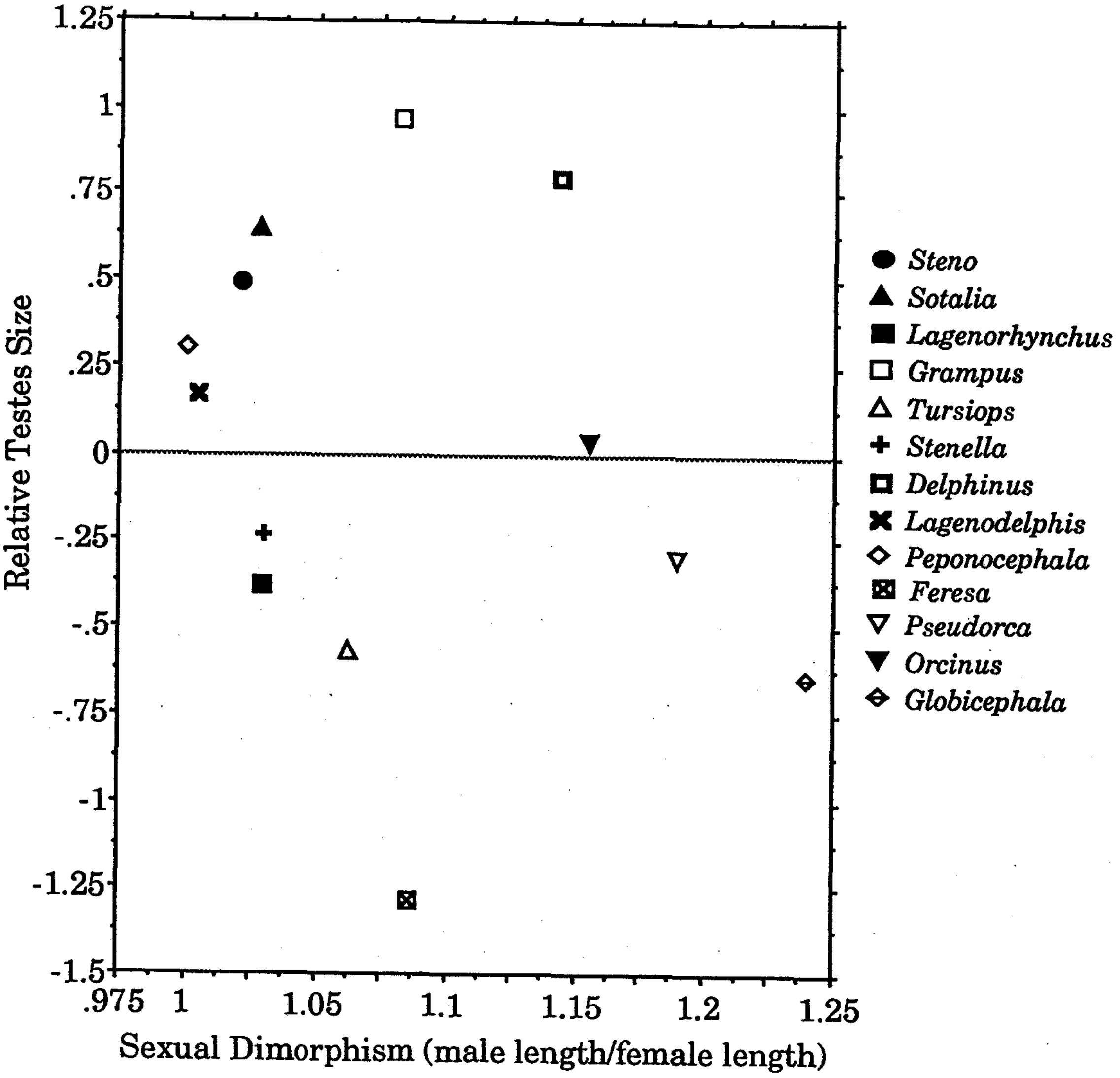

Figure 5.11 Relative Testes Size plotted against sexual dimorphism.

peak of births off Florida in June and July, corresponding to the period of highest water temperature (Wells *et al.*, 1987).

The most complete studies of the social organisation of bottlenose dolphins have been conducted since 1970 along 160 km of the west coast of Florida (Irvine and Wells, 1972; Wells, 1978; Wells *et al.*, 1980; Irvine *et al.*, 1981; Irvine *et al.*, 1982; Wells, 1986; Wells *et al.*, 1987; Hohn *et al.*, 1989; Scott *et al.*, 1990; Wells and Scott, 1990; Duffield and Wells, 1991; Wells, 1991), but observations of habituated *Tursiops* off western Australia have also contributed some well-documented short-term observations (Connor and Smolker, 1985; Connor *et al.*, 1992a; 1992b). The Florida study has used a diverse array of techniques, including radio-tracking, the identification of animals from naturally occurring marks and periodic capture/release programs (Wells, 1991). Known animals were captured to measure, sex and to collect teeth samples for ageing, blood samples for hormonal analyses and DNA for genetic analyses (Wells and Scott, 1990).

Three communities of dolphins, with mutually exclusive home ranges, have been identified off Florida (Wells, 1986; Wells *et al.*, 1987). Data from the central community, termed the Sarasota community, generated the bulk of the conclusions on *Tursiops* social organisation. This community was comprised of 84 dolphins, with an adult sex ratio of 26 females (70%) to 11 males (30%), or 2.4 females per male (Wells *et al.*, 1987). Different patterns of habitat use indicated a high degree of age and sex segregation. Only 31% of 536 completely sampled groups were composed of mixed age and sex (Wells *et al.*, 1987). Four *bands* of females were identified within the Sarasota community and occasionally mixed with each other (Scott *et al.*, 1990). The most common group composition was of dolphins of similar age, sex and reproductive status, resulting in the formation of female/calf groups, juvenile groups and all male groups (Wells *et al.*, 1987). Highly related females (indicated by a sharing of a specific marker chromosome: Duffield and Wells, 1991) demonstrated high degrees of association, showing that familial relationships formed the basis of at least some female bands (Wells *et al.*, 1987). However, these groups exhibited a wide range of associations and it was rare to observe all members of a band together at any given time (Wells *et al.*, 1987). Male:male associations were highly specific, with some males forming consistent pairs or trios, others never interacted. Male:male bonds were formed between male calves of the same cohort and these bonds persisted into adulthood. In fact, the two mothers of one pair had a strong association and travelled in the same band, suggesting they may be related (Wells *et al.*, 1987). These were similar to the male alliances described below for Australian *Tursiops*.

The *Tursiops* mating system appeared to consist of males moving between groups of females. Males from adjacent communities were observed associating with the Sarasota females during the breeding season. Sarasota community males were absent from the range of Sarasota females for up to several months, during which time they probably came in contact with dolphins from the adjacent communities. Genetic evidence for interchange between communities came from shared polymorphic enzyme profiles and mitochondrial DNA haplotypes between communities, the latter also indicated a low rate of female exchange (Duffield and Wells, 1991). The patterns of differential distribution between the sexes within communities and occasional mixing between females and males from different communities, indicated that males were the most likely vectors for the genetic interchange implied by the genetic heterozygosity (Wells *et al.*, 1987).

Genetic evidence for a certain degree of reproductive isolation between communities came from observations of allelic differences in polymorphic blood enzymes and the discovery of a unique, bi-satellited chromosome limited to three generations of Sarasota dolphins (Duffield and Wells, 1991). This suggested that some mating was occurring within the community as well. Although male:female interactions were relatively uncommon, when males did interact with adult females, it tended to be with receptive females, who were females known to have given birth and their period of receptivity back-calculated utilising the mean gestation period of 12 months (Wells *et al.*, 1987). No animals were ever documented to permanently change communities, further indicating the discreteness of the communities. The disappearance of animals which could not be accounted for through mortality indicated the maximum emigration rate out of the Sarasota community was less than 2-3% year^{-1} (Wells *et al.*, 1987).

Within the Sarasota community there were two different patterns of male associations with adult females: the resident male and the roving male patterns, distinguished by the relative duration of the association. The resident male pattern involved a single adult male repeatedly associating with a female or group of females within the range of the female activities, and only occasionally leaving to visit other female bands. Roving males, on the other hand, tended to be pairs, or occasionally trios, of males which moved between female groups and extended their movements beyond the range of the Sarasota community females (Wells *et al.*, 1987). On a few occasions, these groups of roving males were observed to interact aggressively with adult males from adjacent communities resulting in bloodied scars (Wells, 1991). Only resident males were observed to form associations with receptive females, although this may not necessarily indicate mating success (Wells *et al.*, 1987). Both single males and groups of males occasionally disappeared from the female range for weeks or months (Wells, 1991). In summary, the classification of males as members of the Sarasota community was complicated by their wider distribution and occasional disappearance for several months, but they still interacted with Sarasota females more than they did with females from other communities (Wells, 1986).

Evidence that *Tursiops* males may attempt to control access to receptive females comes from research on *Tursiops* off western Australia (Connor and Smolker, 1985; Connor *et al.*, 1992a, 1992b). Pairs and triplets of adult males with consistently high levels of association in a variety of behavioural contexts, termed an *alliance* (Connor *et al.*, 1992a), have been observed in cooperative herding of females. This behaviour was also observed on a few occasions in Florida (Wells *et al*, 1987). The herding bouts off Australia involved chasing, displays (acrobatic leaps and underwater turns), acoustic emissions termed *popping* and aggression (hitting with the tail and biting or ramming) by the males towards the female (Connor *et al.*, 1992a; 1992b). Often the female would try to escape by swimming away rapidly, but the males would work cooperatively to herd her again. The longest duration of association between a herded female and a male alliance was 28 days (Connor *et al.*, 1992a). Occasionally, two or more of these alliances would form second-order alliances and cooperate to take a female from another alliance (Connor *et al.*, 1992a). Comparisons of the herding frequency for females based on their reproductive status indicated that pregnant (and thus not receptive) females were significantly less likely to be herded than were potentially-receptive, non-pregnant females (Connor *et al.*, 1992a). The frequency of partner changes within triadic alliances increased just prior to the mating season, when male *Tursiops* exhibit a surge in serum testosterone levels (Connor *et al.*, 1992a). Males with erections were observed attempting to mount herded females, but it was not possible to observe intromission. Taken together, this evidence suggests that the male alliances cooperate to control access to receptive females. However, females appear to be able to mate with multiple males; some females were herded by up to 13 males during the season in which they conceived (Connor *et al.*, 1992a). Coalition alliances of males have also been reported for lions (Bygott *et al.*, 1979) and baboons (Smuts and Watanabe, 1990).

In summary, *Tursiops* social structure appears to be composed of four "structural units": mother-calf pairs; subadult groups of both mixed and single sex; female bands with associated female-calf pairs and females with older offspring; and adult male groups. Although these units interact to varying degrees within a community, consistent patterns of segregation in the forms of habitat use and social association have been seen in over 20 years of observation (Wells, 1991). Even for the relatively stable female bands, there is a high degree of fluidity in group interactions, with many observations of the group split into subunits. Group formation occurred as calves matured and became independent from their mother, forming groups of subadult animals. Accurate ageing and surveys of reproductive status indicated these subadult groups contained adolescent animals who were sexually mature, but not yet socially mature (Wells, 1991). Maturing males gradually grew isolated from these groups while maturing females began to join female bands; in a number of cases females rejoined their natal band (Wells, 1991). Upon reaching full adulthood, males associated more regularly with female bands, but were always found more frequently in pair or trios with other males and ranged over a wider area than the female groups (Wells, 1991).

A promiscuous mating system appears to be the best explanation for the data on bottlenose dolphins off Florida (Wells, 1986; Wells *et al.*, 1987). This is based on the short-term interactions between males and females (indicated by the high degree of age/sex segregation within communities and the lack of permanent exchange of roving males between communities) and that males appear to interact with multiple female bands within their own community as well as with females from different communities. Additional evidence comes from the lack of sexual dimorphism (Hersh *et al.*, 1990) and the potential for sperm competition (Parker, 1984): indicated by large testes size (Kenagy and Trombulak, 1986; Wells, *et al.*, 1987) and a high concentration of sperm in the ejaculate (Schroeder, 1990; Schroeder and Keller, 1990). However, there is also evidence for a polygynous mating system because male alliances compete to maintain access to receptive females (Connor *et al.*, 1992a, 1992b), males are heavily scarred, males from different communities interact aggressively, and resident males appear to have a higher degree of interaction with receptive females than do roving males (Scott *et al.*, 1990; Wells, 1991). But the most convincing evidence for promiscuity was the preliminary paternity exclusion studies using DNA fingerprinting which have excluded Sarasota males in 13 of 14 cases as fathers of the Sarasota calves (Duffield and Wells, 1991).

5.3.5.2 *Stenella*

The six species of the genus Stenella are all pelagic and are usually only sighted far from land (Perrin, 1975). However, a few situations have allowed regular observations on two *Stenella* species: *Stenella longirostris*, the spinner dolphin, along the west coast of Hawaii (Norris and Dohl, 1980a; Norris *et al.*, 1985; Würsig *et al.*, 1989; 1991) and the spotted dolphin, *Stenella attenuata*, restrained in tuna purse seine nets in the eastern tropical Pacific (Pryor and Shallenberger, 1991). The picture which has emerged from these studies is of extremely fluid societies with frequently shifting patterns of association between individuals and groups. However, there are also indications of a high degree of behavioural coordination, suggesting repeated interactions between cooperating groups, which is usually characteristic of kin-related groups. Unfortunately, there have been no genetic studies of *Stenella* social groups to confirm or deny relatedness in these animals.

Although spinner dolphins are usually found in deep water, the steep slope of the Hawaiian sea floor creates deep water close to shore and probably accounts for the species' nearshore occurrence. During the course of a two year study, 224 individual dolphins were identified and sighted from one time (98 dolphins) to 69 times, with an average of 6.4 sightings per animal (Norris and Dohl, 1980a; Norris *et al.*, 1985; Würsig *et al.*, 1991). Thirty-six dolphins were seen 10 or more times throughout the study, indicating a certain degree of residency, but there appeared to be individual differences in distribution. Eight dolphins were seen primarily in the southern part of the study area, ten were seen primarily in the northern part of the study area and six were seen in all areas. However, even for these repeatedly sighted dolphins, only small numbers were regularly seen together. The conclusions were that spinner dolphins lived in continually changing groups except for a few core associations (Norris and Dohl, 1980a; Norris *et al.*, 1985). Detailed underwater observations of groups identifed the presence of age and sex subgroups within schools. Adult males commonly travelled as a unit and often maintained position between the observers and the rest of the school. Other subgroups noted were female - calf groups and apparent juvenile groups (Norris and Dohl, 1980b; Norris *et al.*, 1985).

Spinner dolphins had a strict diurnal regime and were found in nearshore shallow waters (usually protected bays) during the day and moved offshore to deep, pelagic waters at night. This pattern of movement has been related to predation and food supply. The dolphins fed at night on prey associated with the deep, scattering layer which rises to the surface at night and drops down to approximately 500 m during the day (Norris and Dohl, 1980a; Gabriel and Thomas, 1988). Daytime presence in protected coastal bays may also serve to avoid pelagic shark predation (Norris and Dohl, 1980a; Norris *et al.*, 1985; Würsig *et al.*, 1991). Following rapid movement into the bays during the morning, the small groups of dolphins spent most of the day resting and socialising (Würsig *et al.*, 1991). Group size remained relatively constant in the bays, suggesting an optimal number of resting dolphins for each bay. This, in conjunction with the observation that different individual dolphins occurred in a bay from day to day, further emphasises the fluid nature of spinner dolphin society. At dusk, the animals grew more active, eventually forming "rallying" groups which coalesced and moved offshore (Norris and Dohl, 1980a; Norris *et al.*, 1985). Radio tracking of dolphins allowed them to be followed at night, when they were found to occur in large, widely dispersed groups, considered to be feeding assemblages of groups from each of the bays and along the coast. Since group composition remained stable in nearshore groups during the day, it was deduced that changes in group composition took place as large groups broke up and moved inshore at dawn. The changing membership of nearshore groups resulted in an eventual socialising between all or most members of the entire community of over 500 dolphins (Norris *et al*., 1985). It has been hypothesised that this high degree of group fluidity is an important means to maintain social bonds in a large number of animals which may need those bonds in order to cooperate effectively while feeding (Norris and Dohl, 1980b; Würsig, 1986; Norris and Schilt, 1988).

Spotted dolphins, *Stenella attenuata*, are regularly caught by tuna purse seine fishing operations in the eastern tropical Pacific (Perrin, 1975), because tuna are known to accompany dolphin schools (Pryor and Schallenberger, 1991). As part of attempts to reduce dolphin mortality in these nets, an observational study of the behaviour of dolphins while restrained in the nets was conducted (Pryor and Schallenberger, 1991). Although occasionally both spinner and spotted dolphins were present in the nets, the two species always maintained separate groups. Underwater observations were collected on eleven sets of the net in which over 4000 dolphins were encircled; focal animal observations were made on 97 spotted dolphins (Pryor and Schallenberger, 1991). Dolphins were aged on the basis of changes in colour pattern and adults were sexed by dimorphic features such as the post-anal keel. The behaviours of the various age and sex classes provided some insight into social relationships for this species.

Although school size of spotted dolphins in the net sets varied from 23 to 1000, subgroups were apparent and were composed of less than 20 dolphins which maintained an inter-animal distance of less than 2 m and surfaced to breathe synchronously (Pryor and Schallenberger, 1991). Females with calves maintained close proximity to one another, often on the perimeter of the school, and often interacted with each other, unlike adult pairs which remained side-by-side. The female-calf pairs were occasionally observed in groups, associating with other female-calf pairs. The composition of these groups changed, but the groups were always comprised of adult females and young immature animals. All-juvenile subgroups were also observed. These were composed of 3-6 animals and remained stable in composition, always travelling side by side. Adult male subgroups were the most conspicuous; composed of 3-8 dolphins which moved in unison. Pryor and Schallenberger (1991) state: "They cruised slowly through the school without swerving or altering speed, while a path opened up before them". This freedom of movement through the school and avoidance by other school members suggested that these animals were dominant (Pryor and Schallenberger, 1991). Social aggression was common within these schools (usually indicated by gaping and head nodding) and occurred within adult male subgroups, although apparently less frequently than within juvenile subgroups and between mothers and their calves. On two occasions, aggressive interactions were observed between two male subgroups. The large degree of synchrony and affiliative behaviour within spotted dolphin schools suggests they are familiar with each other and represent a relatively stable unit (Pryor and Schallenberger, 1991). The presence of discrete colour patterns within schools (Perrin, 1969), suggests some degree of relatedness between these animals. Other observations in the tropical Pacific suggests a certain degree of age segregation, with some schools composed entirely of juveniles and others (such as those reported on here) composed of reproductive animals and young calves (Hohn *et al*., 1985; Myrick *et al*., 1986). The resulting picture of spotted dolphin social organisation is one of age and sex segregation within and between schools, with dispersal of the juvenile segment of the population.

5.3.5.3 *Lagenorhynchus*

Lagenorhynchus is a multi-species genus (see Table 5.1), but only *L. obscurus,* the dusky dolphin, has been studied (Würsig and Würsig, 1980; Würsig *et al*., 1989, 1991). While these studies have primarily been concerned with patterns of habitat use, they have also provided insight into *Lagenorhynchus* social structure.

Dusky dolphins were studied in two locations: off Golfo San Jose, Argentina in the south Atlantic (Würsig and Würsig, 1980; Würsig *et al*., 1989, 1991) and off Kaikoura, New Zealand in the south Pacific (Würsig *et al*., 1989, 1991). In Argentina, the dolphins were primarily found in depths less than 100 m, foraging for schools of southern anchovy (*Engraulis anchoita*). The majority of feeding occurred during the day, when anchovy tend to school, and dolphins generally rested close to shore at night, probably to avoid killer whale predation. During the day, stable group units of usually less than ten dolphins were observed searching the bay, with up to 30 of these groups spread from 1-8 km apart. Once food was located, other groups apparently located prey through acoustic and visual cues such as associated flocks of feeding birds, and the several groups converged to herd and capture prey cooperatively. After feeding, the dolphins remained in large schools and engaged in a high activity level of socialising. Although photo-identification studies have been limited, the fission and fusion of dusky dolphin groups appears to result in continual changes in group membership. Similar to Hawaiian spinner dolphins, the widespread social interactions provided by a fluid social structure probably enhance the bonding mechanisms required for the maintenance of a large number of cooperating school members (Würsig and Würsig, 1980; Würsig, 1986; Würsig *et al*., 1989, 1991).

Off New Zealand, dusky dolphins live in a very different habitat and feed over deep water on prey associated with the deep scattering layer (Würsig *et al*., 1989, 1991). Group sizes are consistently large and do not exhibit the patterns of fission and fusion found in the Argentine dolphins. However, there are still distinct subgroups within these large schools. It is unknown whether the composition of these subgroups remains stable. The lack of clear patterns of fission and fusion may be related to the fish prey of New Zealand dusky dolphins, which is not a schooling species, and cooperative herding on the part of the dolphins does not seem to be required for its capture. This exemplifies that ecological parameters affect aspects of dolphin society (Würsig *et al*., 1989, 1991).

5.3.5.4 *Grampus*

The taxonomic status of *Grampus griseus*, Risso's dolphin, has long been debated (Nishiwaki, 1963; Nishiwaki, 1964; Fraser, 1966; Mead, 1975). It is the only delphinid lacking teeth in the upper jaw and some authors have proposed a placing it in a mono-specific family *Grampidae* (Nishiwaki, 1972). Its' external appearance resembles the globicephalines, with a blunt nose and prominent melon (Mead, 1975). It has occasionally been placed in the *Globicephalinae.* However, in terms of skull morphology and anatomy of the air sacs (Fraser and Purves, 1960), it appears to be most closely related to *Tursiops*. This is the current basis for placing *Grampus* in the *Delphininae* (Klinowska, 1991), with the similarities in facial anatomy between *Grampus* and globicephalines being seen as convergent evolution, as it is with monodontid whales (Fraser, 1966; Mead, 1975).

There has been only one complete study of *Grampus* using photo-identification of individuals (Kruse, 1989). This two-year study was conducted along the central west coast of California from October 1985 to November 1987. Fifty-nine schools were located and group size ranged from 3 to over 500 (mean ± S.D.: 63 ± 87.9; median: 30). A total of 800 individuals were identified and it was estimated that only two-thirds of the animals observed in the field were identifiable. The number of sightings per individual ranged from one (588 dolphins) or two (161 dolphins) up to eight times (two dolphins). The rate of identification of new animals continued to increase throughout the study, indicating that only a small percentage of the *Grampus* visiting the region were identified (Kruse, 1989). There was some seasonal variation in *Grampus* occurrence, with more animals seen during the fall (September-November) than during all other seasons. Groups of fewer than 30 dolphins travelled and behaved in unison, but larger groups exhibited a distinct sub-group structure. Age and sex segregated subgroups were noted in groups of over 60 dolphins and were composed of females with calves (nursery groups), juveniles or large, calfless animals. Some associations within the large, calfless animal subgroups were observed repeatedly over 10 months. However, beyond these stable subgroups, fluctuations in the group size indicated that groups were "dynamic aggregations" (Kruse, 1989). Although the age and sex of the large, calfless individuals was not known, evidence from strandings has shown similar groups to be composed of animals of the same age and sex. Thus, the limited observations suggest that *Grampus* occurs in stable, age and sex segregated groups which interact fluidly with a larger population (Kruse, 1989).

5.3.5.5 Summary of *Delphininae* Social Systems

These reviews of social organisation in four genera of the sub-family *Delphininae* have shown a variety of broad similarities which I suggest are characteristic of the group. One characteristic is the clearly defined age and sex segregation of *Tursiops* and *Stenella*, exemplified by the dispersal of adolescent age classes from the breeding groups (Wells *et al.*, 1987; Norris *et al.*, 1985). Age and sex segregation was also suggested in observations of large *Grampus* schools (Kruse, 1989), but there is still not enough information on the age and sex of identified populations of *Lagenorhynchus* to know the degree of segregation in these animals (Würsig and Würsig, 1980). The only available information on sex ratio was from the observational studies of *Tursiops*, where there were 2.4 adult females for every 1 adult male (Wells *et al.*, 1987). This was presumed to be due to the more rapid maturation in females and higher male mortality. Group fluidity also takes different forms in these dolphins. In *Tursiops*, bands of females have only statistical tendencies to associate and they are not exclusively observed together as an indivisible unit (Scott *et al.*, 1990; Wells, 1991). Males exhibit the greatest fluidity, moving beyond the community ranges of the females (Wells *et al.*, 1987). It may be that age and sex segregation enhances this fluidity by the isolation of adolescents from their natal groups, thus increasing their exposure to other segments of the community. In Argentine dusky dolphins, group fluidity occurs between stable units which interact in large after-feeding assemblages (Würsig and Würsig, 1980; Würsig *et al.*, 1989, 1991) and this was similar to *Grampus* observations of fluid interactions between stable subgroups

(Kruse, 1989). In Hawaiian spinner dolphins fluidity appears to occur at the individual level, and there appear to be no stable sub-units (Norris *et al.*, 1985; Würsig *et al.*, 1991).

5.3.6 *Globicephalinae* Social Systems

The five genera in the subfamily *Globicephalinae* have significantly different trends in sexual dimorphism than other delphinids. This suggests that it will be instructive to consider the social systems of these genera separately from those of the *Delphininae* reviewed above. Unfortunately, detailed studies in social organisation are only available for two of these genera: *Orcinus*, the killer whale, and *Globicephala*, the pilot whales.

5.3.6.1 *Orcinus*

The killer whale (*Orcinus orca*) social system which has been studied to date is characterised by long-term stability of associations between all age and sex classes within populations and a high degree of variation in social structure between reproductively (and sometimes, though not always, geographically) isolated populations. This provides a clear indication of the inbred nature of killer whale communities, giving the species a strong potential to form populations with distinct social and behavioural characteristics (Hoelzel and Dover, 1990; Hoelzel, 1991a).

Killer whale social organisation has primarily been studied in the inland marine waters off Washington State, USA and British Columbia, Canada since 1973 (Balcomb *et al.*, 1982; Bigg, 1982; Ford and Fisher, 1983; Ford, 1984; Hoyt, 1984; Balcomb and Bigg, 1986; Haenel, 1986; J.Heimlich-Boran, 1986b; J.Heimlich-Boran, 1986a; S.Heimlich-Boran, 1986; Hoelzel and Osborne, 1986; Osborne, 1986; Bigg *et al.*, 1987; Baird and Stacey, 1988; J.Heimlich-Boran, 1988; S.Heimlich-Boran, 1988; Ford, 1989; Bigg *et al.*, 1990; Hoelzel and Dover, 1990; Morton, 1990; Olesiuk *et al.*, 1990; Felleman *et al.*, 1991; Baird *et al.*, 1992). Individuals are identified by distinctive pigmentation patterns just posterior to the dorsal fin, termed *saddle patches*, and photographic surveys have been conducted every year since 1973 (Bigg *et al.*, 1987; 1990).

Two forms of killer whales have been defined in this region: *residents* and *transients* (Bigg *et al.* 1987; 1990). These two forms differ in a wide variety of behavioural aspects of distribution, seasonal occurrence, acoustic dialects, and prey choice (Ford and Fisher, 1983; Ford, 1984; Hoelzel and Osborne, 1986; Heimlich-Boran, 1988; Ford, 1989; Felleman *et al.*, 1991; Baird *et al.*, 1992) Morton, 1990; J.Heimlich-Boran, 1986), as well as genetic aspects of pigmentation patterns, dorsal fin morphology and mitochondrial DNA, which indicate they probably represent distinct races of killer whales (Duffield, 1986; Baird and Stacey, 1988; Stevens *et al.*, 1989; Hoelzel and Dover, 1990; Hoelzel, 1991a). The two forms have probably evolved from distinct foraging specialisations, forming an Evolutionary Stable State (ESSt) due to disruptive selection against generalists (Baird *et al.*, 1992). Genetic evidence from the analysis of mtDNA have identified significant differences in restriction fragment patterns between residents and transients, which indicates that the two forms have distinct maternal lineages (Stevens *et al.*, 1989; Hoelzel and Dover, 1990; Hoelzel, 1991a). DNA fingerprinting of nuclear genomes found that band-sharing coefficients were 2-3 times lower between populations than they were within populations and supports the hypothesis of significant reproductive isolation (Hoelzel and Dover, 1990). In fact, the two forms appear to be as genetically distinct as North Pacific populations were from a south Atlantic population, probably resulting from a high degree of inbreeding within small regional populations (Hoelzel and Dover, 1990). Assuming a standard divergence of 5×10^{-9} base pairs/year, this degree of difference implies a two million year period since the two forms shared a common ancestor (Hoelzel, 1991a). This degree of reproductive isolation of sympatric populations is rare, especially when the primary isolating mechanisms appear to be behavioural (Hoelzel and Dover, 1990).

Resident killer whales live in two reproductively isolated communities (Bigg *et al.*, 1990). The communities have core areas and the boundary between communities corresponds to an area of limited tidal mixing, which could also limit salmon migrations (Felleman *et al.*, 1991). There have been no reports of permanent interchange of individuals between these communities (Bigg *et al.*, 1990), and the two communities have distinct vocal dialects (Ford and Fisher, 1983; Ford, 1989). Genetic studies comparing mtDNA D-loop base pair sequences between whales from the two resident communities identified a difference of two base pairs out of a total of 591 (0.2%: Hoelzel, 1991a). Although sample sizes were two small to compare the significance of this variation, the most likely explanation involved a colonisation of the separate community home ranges by more than one matriline following the retreat of the ice shelf 40,000 years ago (Hoelzel and Dover, 1990). This supports the hypothesis of the current reproductive isolation of the two resident communities (Hoelzel, 1991a).

The primary social unit of resident whales is the pod (Bigg *et al.*, 1990). A pod was defined as "the largest cohesive group of individuals within a community that travelled together ...for at least 50% of the time" (Bigg *et al.*, 1990: p.388). Pod membership was determined over a number of years and has been based on a cluster analysis of surfacing associations (Bigg *et al.*, 1990). Pod membership did not change in the 20 years of observations and some pod members were observed in photographs taken during capture operations in the 1960's. There were a number of levels to pod structure. Some pods occasionally (between 5% and 50% of the time) split into smaller units termed *subpods*, which were usually never separated from each other for more than one month (Bigg *et al.*, 1990). Pods were composed of an average of 1.7 subpods (range: 1-3). Although members of the same subpod were found to travel together 95% of the time, distinct association patterns within the subpods have been demonstrated (S.Heimlich-Boran, 1986; 1988). These groupings are termed *intra-pod* groups (Bigg *et al.*, 1990). Subpods contained an average of 1.9 intra-pod groups (range: 1-11) and intra-pod groups contained an average of 3.6 whales (range: 2-9).

Pods were found to consist of overlapping generations of females and their offspring. Genealogies were defined with three levels of certainty: positive, highly probable and probable. *Positive genealogies* were defined as those between adults and calves born during the course of the study. *Highly probable genealogies* were determined for animals which were immature at the start of the study and mothers were deduced from a ranking of associations coefficients with all adult females. *Probable genealogies* were those determined for animals that were adult at the start of the study. The determination of probable genealogies was based on consistent association patterns, scaled relative to the high degree of association between known mother-offspring pairs.

There appeared to be a class of females who were post-reproductive, similar to the situation for short-finned pilot whales (Marsh and Kasuya, 1984). Some females were never observed to give birth during the course of the study and were considered to be the oldest females. Other females were considered to have recently become post-reproductive if they gave birth to calves at the beginning of the study and then had no more calves for at least the last ten years of the study (Olesiuk *et al.*, 1990). It was possible that some of the post-reproductive females may have been infertile, young females, but the documented occurrence of such females was rare (all but one of the females who matured during the study gave birth).

Associations continued between mothers and known male and female offspring into adulthood (Bigg *et al.*, 1990). Positive mother-offspring relationships have been determined for 133 offspring which ranged in age from 0.5 to 14.5 years (mean age = 5.7 years) at the end of the study. Highly probable mother-offspring relationships were determined for 80 juveniles, which were aged 13.5 to 34.5 years (mean = 19.7 years) by the end of the study (Bigg *et al.*, 1990). Probable mothers were determined for 34 of the 102 animals that were adults at the start of the study. Changes in associations between mothers and their offspring were found to vary with the age and sex of the offspring (Bigg *et al.*, 1990). Young female calves had slightly stronger associations with their mother than did male calves, indicating a greater degree of independence for male calves. However, by the age of 10, male calves began to have higher average associations with their mothers than female calves. As young females matured and gave birth to their own calves, their association with their mothers continued to drop until the young female's early 20's, when the association index levelled out at around 25%. In contrast, associations between mothers and their sons levelled out at around 10 years of age at an association index of around 40%. Thus, adult sons maintained stronger association with their mothers than did females, probably because the young females spent more time with their own calves (Bigg *et al.*, 1990). Another side of this strong male-mother relationship was shown by the fact that the presence of adult males made intra-pod groups more independent. This was indicated by a weakening of the bond between a female and the other members of her pod when her son matured. As females reached post-reproductive age, they often had strong associations with actively reproducing females, who were probably their daughters of younger sisters (S.Heimlich-Boran, 1986; 1988). Often, these older females also spent time with immature animals, suggesting a form of allo-parental care (S.Heimlich-Boran, 1986; Haenel, 1986).

The picture of killer whale social organisation which has emerged from these genealogies is one of matrilineally based relationships forming the structure of intra-pod groupings (S.Heimlich-Boran, 1986; 1988; Bigg *et al.*, 1990). The generalised matrilineal group was composed of a grandmother, her adult son and adult daughter, and the offspring of the daughter. Intra-pod groups were composed of an average of 2.3 generations (range: 1-4). Adult sons tended to travel closest to their mothers, while daughters were slightly farther away with their own offspring. Adult males with no living mother continued to travel with their adult sister's group, but often travelled on the periphery. In some cases, the association between two sisters decreased after their mother died. Some matrilineal groups were linked by a common mother, with one of the daughters being in a separate intra-pod group. The fission between two sisters such as this was likely to be the basis of new subpod formation. There were no observations of the dispersion of entire matrilineal groups into new pods. Thus, matrilineal groups within a subpod were likely to be closely related. The time frame in which new pods form is likely to be similar, but to occur over a much longer period (Bigg *et al.*, 1990). If fission of intra-pod groups took one generation (2-3 decades), then the formation of new pods could take many decades, if not centuries. Associations between pods were assumed to be based on shared genealogies, but in a number of cases the patterns of travelling associations did not correspond to the acoustic clans documented by Ford (1989). Since acoustic dialects are more likely to reflect shared ancestry accurately than travelling associations, it appeared that associations between pods were not based on relatedness. This would support the hypothesis that mating occurs between pods, which would likely associate with unrelated pods in order to reduce inbreeding. A system of travelling in kinship groups which form the basis of higher levels of social organisation has been described for a wide variety of terrestrial mammals, including primates (Kummer, 1968; Kurland, 1977; Gouzoules and Gouzoules, 1987; Stammbach, 1987), lions (Bertram, 1976), elephants (Douglas-Hamilton and Douglas-Hamilton, 1975; Dublin, 1983; Moss and Poole, 1983) and ground squirrels (Michener, 1982; Sherman and Morton, 1984; Sherman and Holmes, 1985). Bigg and co-workers conclude that the killer whale social system, with its lack of dispersal of either sex, could result "from a particularly strong requirement that reliable and familiar associates be available for hunting or maintaining territorial boundaries,...or from a unique breeding strategy" (Bigg *et al.*, 1990: p. 397).

The main element missing from the detailed long-term observations outlined above has been information on the reproductive success of males. I have summarised all observations of socio-sexual behaviour (defined by the observation of an erect penis) in the southern community of resident *Orcinus* from six years of observations (Heimlich-Boran and Heimlich-Boran, ms.). Although the sample size was small, I believe the data have valid implications for an understanding of the mating system of *Orcinus*. Sexual behaviour was observed between adult whales on 30 separate bouts. Eighteen of the 30 bouts (60%) involved males and females together, while the remaining 12 bouts (40%) were of male only groups. Although not directly indicative of mating patterns, the male-only bouts will be discussed because they serve to clarify male-male relationships between pods. The male only groups were almost always composed of males from more than one pod (11 of 12 bouts). The single observation of males from the same pod involved two adult and one adolescent male (17 yrs old). All males were identified in 8 of the 11 multi-pod bouts; adult males were present in all cases, and at least one adolescent male (8-15 yrs old) was present in half of the cases. These multi-pod observations involved males travelling together in tight subgroups for up to 3.5 hrs. Sometimes the male groups were separate from all other whales, but on two occasions, females were observed hovering nearby and oriented towards the males. Males were usually in tight body contact with each other, actively pushing one another. Usually just one male would surface with an erection, but on one occasion, two males did so simultaneously. There were never any observations of overt aggressive interactions between the males in these groups, although most males had old scars.

The sexual interactions between males and females were most relevant to an understanding of the *Orcinus* mating system. Fourteen of the 18 bouts involved members from different pods. Only one male was observed in all but one case, when three were identified (but only one surfaced with an erection. Three adolescent males (ages 10 - 15 yrs) were involved in seven (44%) of the observations and three adult males were involved in the remaining nine cases. Thus, only six of the 16 adolescent and adult males in the three resident pods were ever observed in heterosexual encounters. The number of females involved in these heterosexual encounters varied from one (five cases) to two or three (seven cases). Twelve females were identified in 11 cases; six of the females were *post-reproductive* adult females (defined by Bigg *et al.*, 1990) and the other six were females with calves. The behaviour during these male-female sexual encounters usually consisted of the male swimming with the female or group of females for a period of time and then rolling sideways with an erection. On three of the cases, the female rolled belly-up, apparently attempting to avoid intromission. Two of the three avoiding females were previous mothers. On one occasion, the male actively pursued the female while she tried to swim away. Once, the male swam upside down underneath the female. Other whales occasionally showed some interest in these groups. In two cases, immature animals remained nearby, probably associates of the female. On three occasions, other adult males were nearby, always from the same pod as the female and once, the male was the female's probable son (Bigg *et al.*, 1990). During one case, adult male J3 charged adult male L19, who had just surfaced with an erection around two J pod females. The males both dove when approximately 3 m apart, and nothing further was observed.

There were no documented births which corresponded to these mating attempts and since the majority of females involved were post-reproductive, the matings did not appear to be for procreation. Little is known of the patterning of sexual activity in male delphinids (Ridgway and Green, 1967; Perrin and Reilly, 1984), but in general male killer whales show a broadly diffuse seasonal pattern to sperm production (Christensen, 1984), suggesting they would have been reproductively active. The seasonal pattern of the observations indicates that the peak of the interactions between males and females coincided with the proposed period of peak conception determined by the seasonality of births (Bigg *et al.*, 1990) as well as corresponding to the salmon season when pods travel in large, multi-pod assemblages (J.Heimlich-Boran, 1986a; 1988). In any event, copulation frequency is known to be a poor indicator of paternity (Stern and Smith, 1984). The value of these observations lies in the indication that sexual interactions occur less frequently with close kin (i.e. members from the same pod) than they do with other whales.

The resulting picture of killer whale social organisation is of a multi-level society with a high degree of stability on all levels. The long-term consistencies of intra-pod groups, subpods, pods, clans and communities all contribute to this stability. This has been verified in the genetic analyses by the relatively high degrees of inbreeding (Hoelzel, 1991a). The lack of male dispersal suggests that males must benefit from group membership.

5.3.6.2 *Globicephala*

Information and original data have been presented for the two *Globicephala* species in Chapters 2-4. In summary, although the two species differ in some morphological and life history traits (Kasuya *et al.*, 1988b), there appear to be general similarities in social structure, indicated by similar age and sex composition (Kasuya and Marsh, 1984) and shared indications of genetic segregation between adjacent groups (Andersen, 1988; Wada, 1988). *Globicephala* groups are highly cohesive, making them susceptible to drive whaling (Gibson-Lonsdale, 1990) and mass stranding (Sergeant, 1982; Klinowska, 1986). Genetic information of *G.melas* has shown all group members to be related, including adult males and adult females within the same pod (Amos *et al.*, 1991a; 1991b). In all studies, pods have been primarily composed of mixed age and sex. The few rare observations of all male groups indicate only limited segregation of the sexes (Sergeant, 1962a; Kasuya and Marsh, 1984; Chapter 4). There was a high degree of differential mortality between the sexes: female longevity of *G.macrorhynchus* was over 20 years longer than male longevity, resulting in a female-biased adult sex ratio (Kasuya and Marsh, 1984). Females ceased ovulating by the age of 40 and lived for an average of 23 years in an extended post-reproductive period (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986; 1991). Some of these females continued to nurse their last calf for up to 15 years (Kasuya and Marsh, 1984; 1989).

Genetic evidence relating to the mating system came from paternity studies of *G.melas* which found that males were not the fathers of the offspring in the pods (Amos, 1991a; 1991b). It was also found that only one or a few related males were fathering the young, indicating a certain level of male variance in reproductive success and suggesting polygyny. However, it was also found that the male genetic contribution to cohorts changed from year to year (Amos, 1991a; 1991b), indicating a certain degree of promiscuity. Wilson (1975) has suggested that even promiscuous matings need not be random. Analyses of associations for *G.macrorhynchus* indicated that male:female interactions were most common when *linked* pods (separate pods with regular patterns of association) travelled together. Although mating was never observed, these associations could indicate a possible time when out-group breeding could occur. The season when members of more than one pod were observed together corresponded to the supposed peak season of conception.

5.3.6.3 Summary of *Globicephalinae* Social Systems

There are a number of similarities between the social systems of *Orcinus* and *Globicephala* which suggest they may be common globicephaline traits and which are in contrast to the open nature of delphinine communities described above. A comparison of life history traits and pod sizes for *Orcinus* and *G. macrorhynchus* is presented in Table 5.2. Killer whales have a slightly longer longevity for both sexes, but the maturation period for male pilot whales is essentially the same as for male killer whales. This is because the maturation periods are equivalent for male and female killer whales, while female pilot whales mature much sooner than pilot whale males. Differences in reproductive parameters are indicated by the longer calving interval in pilot whales. Pilot whale calving intervals increased from three years for primiparous females to 10 years for females older than 30 (Kasuya and Marsh, 1984). Killer whale calving intervals ranged from two to 12 years, but the regression of calving interval on age of the female had a low rate of increase (slope = 0.086) and only accounted for 7.7% of the observed variation in calving interval (Olesiuk *et al.*, 1990). Female in both species had a long post-reproductive period which represented a similar proportion of the total lifespan (about 37%).

Table 5.2. Comparison of life history parameters for *Orcinus orca* and *Globicephala macrorhynchus*. *Orcinus* data were compiled from a horizontal study of life history using observational data and *Globicephala* data were from a vertical analysis of a complete sampling of carcasses.

Parameter	***O.orca*** [1, 3]	***G.macrorhynchus*** [2]
Age at sexual maturity: male	15.0 yrs [f]	15.8 yrs [h]
Age at physical maturity: male	21.0 yrs [g]	25.0 yrs [i]
Age at sexual maturity: female	11.7 [d] - 14.9 yrs [j]	9.0 yrs [e]
Reproductive lifespan	25.5 yrs	24.0 yrs
Lifetime calf production	5.47 calves	4.39 calves
Mean calving interval	5.32 yrs [m]	6.92 yrs [m]
Age at post-reproductive	39.1 yrs [k]	39.5 yrs [l]
Mortality rate: male (age)	0.039 (15.5-30.5+)	0.0393 (9-30)
Mortality rate: female (age)	0.0114 (15.5-65.5+)	0.0251 (18-47)
Longevity: male	36.5 [a,c] - 60 yrs [b]	46 yrs [a]
Longevity: female	77.5 [a] - 90 yrs [b]	63 yrs [a]
Life expectancy at birth: male	16.6 yrs [b]	12.11 yrs [b]
Life expectancy at birth: female	28.9 yrs [b]	22.26 yrs [b]
Adult sex ratio (all females)	1 male:1.7 females [b]	1 male:3.7 females [b]
Adult sex ratio (reprod. only)	1 male:1.15 females [b]	1 male:1.95 females [b]
Mean pod size	15.7	12.2 ± 1.3
Calving peak	1 January	25 July

References: 1)Olesiuk *et al*., 1990); 2) Kasuya and Marsh, 1984; 3) Bigg *et al*., 1990; 4) Present study; Notes: a) oldest aged animal; b) life table estimation; c) males that were adult when observations began had only minimum age estimates based on assumption of attainment of physical maturity in year prior to study; d) age at first conception; e) age at first ovulation; f) based on 50% males beginning allometric growth of the dorsal fin; g) based on 50% males completing allometric growth of the dorsal fin; h) based on 50% animals with mature testes; i) based on 50% males completing testes weight growth; j) age at first birth; (k) mean age at birth of last calf; l) mean age at last ovulation; m) excluding post-reproductive females

While male dispersal rates are not well known in *Globicephala*, the infrequent occurrence of all male groups and the high degrees of relatedness of males within groups, suggests that there is a similar pattern of natal philopatry to *Orcinus*. While there have been no paternity studies of *Orcinus*, behavioural observations suggest the males are not the fathers of the young in their pod. Rather, the *Orcinus* males appeared to be the brothers or uncles of the young in their pod.

5.4 DISCUSSION

Mammalian mating systems are based on individual male and female strategies of reproductive success (Darwin, 1871; Trivers, 1972). The strategies of the two sexes may be very different. Males, in their attempt to maximise the number of offspring sired (Bateman, 1948), appear to adapt their strategies to the distribution of receptive females. Where possible, males do all they can to control access to their mates (mate guarding), often through competition with other males, in order to guarantee their successful production of offspring (Emlen and Oring, 1977). Females, because of their relatively larger contribution to the production of offspring (in terms of egg production, gestation and lactation), are best served by maximising their ability to provide adequate food and protection for the successful survival of offspring to reproductive maturity (Trivers, 1972; Wrangham, 1980; Gaulin and Sailer, 1985; Clutton-Brock, 1986). Since female distribution is based on ecological factors to a much greater degree than that of males (Wrangham, 1980; Gaulin and Sailer, 1985), the order of causation in determining a mating system appears to be that resources determine female dispersion, which in turn, determines male dispersion (Davies, 1991). Interwoven with this basic framework are a myriad of other factors such as the distribution of predators and resource competitors, male parental care and phylogenetic constraints on life history and reproduction. Variation in the relative importance of these factors demonstrates predictive value in the definition of mating systems (Clutton-Brock, 1989b; Davies, 1991).

Four generalised types of mating system have been described, based on the number of mates for any given breeding season and the duration of the mating bond: 1) monogamy, where one male and one female maintain an exclusive mating bond, 2) polygyny, where one male mates with multiple females, maintains a prolonged mating bond with that group of females and excludes other males from access, 3) polyandry, where one female mates with multiple males, and 4) promiscuity, where males mate with any receptive females and there is no prolonged mating bond (Orians, 1969; Wilson, 1975; Emlen and Oring, 1977; Clutton-Brock, 1989b; Stirling, 1983). Monogamy, although common in birds, occurs in only about 5% of mammalian species (Kleiman, 1977): primarily in canids (Moehlman, 1986) but also in primates (Rutberg, 1983). Monogamy appears to be favoured where male paternal care is required in some way for the survival of offspring (Clutton-Brock, 1989b). Monogamy has also been viewed as means by which the male guarantees paternity (Trivers, 1972). Polyandry is also rare in mammals, which Orians (1969) predicted on the basis of the relatively greater investment females have in the production of young. Polyandry is most common in birds where a female can lay her eggs and then desert the male while he is brooding the eggs (Lack, 1968; Trivers, 1972). The female is thus able to lay multiple clutches with different males through the course of one breeding season. The remaining two mating systems: polygyny and promiscuity, are the two most common forms of polygamy in mammals. These systems are primarily differentiated by the duration of the bond between males and females and by the relative number of multiple matings that each sex obtains. Unfortunately, some discussions of mating systems incorporate promiscuity as a form of polygyny, using a classification system based on gamete contributions to zygotes (Wiley, 1974; Ralls, 1977). Since these systems are characterised by social groups of multiple males and females, they will be the most likely candidates for delphinid mating systems and will be the focus of the rest of the discussion.

I will now address the elements of sexual dimorphism, brain size, testes size, and the form and frequency of social relationships predicted for these mating systems, and examine the data on delphinid morphology and social structure to postulate hypotheses for specific delphinid mating systems. I primarily consider *Tursiops* (*Delphininae*), and *Orcinus* and *Globicephala* (*Globicephalinae*). These were the only genera which had sufficient comparable observations on social systems. I have already argued that there are similarities between *Tursiops* and the other delphinine genera based on the limited data available, but I cannot make any further conclusions. Thus, although I may refer to entire subfamilies in the subsequent discussion, I can really only make conclusions about the three well-studied genera.

5.4.1 Patterns of Body Size and Sexual Dimorphism

The central tenet of the relationship between sexual dimorphism and mating system is that sexual dimorphism is indicative of male-male competition for access to females resulting in polygyny (Bartholomew, 1970; Crook, 1972; Clutton-Brock *et al.*, 1977; Ralls, 1977; Alexander *et al.*, 1979; Stirling, 1983; Clutton-Brock, 1989b). There were clear trends in the occurrence of delphinid sexual dimorphism which were correlated with body size, ranging from the smallest genus (*Cephalorhynchus*), in which females were larger than males, to one of the largest genera (*Globicephala*) in which males were 1.2 times longer and 1.7 times heavier than females. How does this compare to reported degrees of sexual dimorphism in other mammals? Ralls (1977) defined *extreme* sexual dimorphism as a ratio of male weight to female weight greater than 1.6 and documented this in 8 of 20 mammalian orders. The maximum reported weight dimorphism in primates was around 2.3 for the baboon, *Papio hamadryas* (Clutton-Brock *et al.*, 1977: Fig. 1). Thus, the degree of sexual dimorphism in delphinid cetaceans is not extreme.

There were significant differences in both weight and length sexual dimorphism between the two delphinid subfamilies of *Globicephalinae* and *Delphininae* (Section 5.3.2). The difference in dimorphism between the subfamilies corresponds to some of the observed differences in social structure, specifically the female biased sex ratio in the species with the greater sexual dimorphism. This is the same relationship described for primates, although primates exhibited a wider variation in sex ratio (ranging as high as 13.5 females per male: Clutton-Brock *et al.*, 1977: Fig.1) than the highest ratio of 3.7 female per male in *Globicephala macrorhynchus* schools off Japan (Kasuya and Marsh, 1984). The implication is that *Globicephala* and *Orcinus* could have been selected for large size through intra-sexual selection via male-male competition.

What is the evidence for male-male competition in delphinids? The role of aggression in cetacean societies in general is not well understood (Norris, 1967).

The bulk of reports on aggressive interaction and dominance hierarchies come from observations of captive animals (McBride and Hebb, 1948; McBride and Kritzler, 1951; Kritzler, 1952; Brown and Norris, 1956; Tavolga and Essapian, 1957; Brown, 1960; Pryor *et al.*, 1965; Tavolga, 1966; Saayman *et al.*, 1973; Bateson, 1974; Defran and Pryor, 1980; Östman, 1991). These observations suggest aggressive interactions are relatively common between all ages and sexes. However, the degree to which this is the result of confined conditions is unknown. Pryor and Schallenberger (1991), who were experienced dolphin trainers, reported similar aggressive behaviours to those in captivity during their observations of spinner dolphins temporarily captured in tuna seine nets, but, again, the animals were confined. However, they did note a prevalence of aggression within subgroups of adult males, suggesting an element of male-male competition. There is no quantitative information on the frequency of aggression in wild dolphin societies, although occasional observations of aggressive interactions between individuals and groups are worth examining. Wells (1991) has reported on observations of aggressive interactions between *Tursiops* males from different communities: "The interactions have included such behaviours as tail slaps and violent leaps onto each other, resulting in bloodied fin edges and rostra" (p.220). Connor *et al.* (1992a; 1992b) have provided the most detailed accounts of aggression in the wild, both between male alliances and the females they aggressively herd, and between two or more male alliances as they attempted to steal herded females from one another. One observation of a presumed aggressive response (blowing bubbles and head-shaking) was noted in Tenerife pilot whales in response to a SCUBA diver in the water. In general, aggression has been noted by the occurrence of tooth scars inflicted by conspecifics (McCann, 1974; Wells, 1991). However, even very young calves are scarred and mouthing and scratching with the teeth is undoubtedly an element in play behaviour. As more underwater observations are conducted, it is likely that observations of aggression will increase.

The behaviours of *Turisops* males within the male alliances described above indicate reduced male:male competition (Connor *et al.*, 1992a; 1992b) and may be considered to be similar to male coalitions of lions (Bertram, 1976; Bygott *et al.*, 1979) or grey langurs (Hrdy, 1977). Kin selection predicts that the males in these coalitions would be related, but this does not necessarily have to be so: the predictions of the benefits of this behaviour are very similar whether it is driven by kin selection or game theory (Packer and Pusey, 1982). In fact, genetic analyses of lions has shown that many of these males are unrelated (Packer *et al.*, 1991). This could also be the case with dolphin coalitions. Since dolphin litter size is one, there is no chance for brothers to be the same age as there would be for larger lion litters. Associations between similarly-aged male *Tursiops* appear to be between male calves from the same cohort. Although *Tursiops* parturition is only broadly seasonal, there are still seasonal peaks in births and a tendency for females of similar reproductive condition to associate (Wells *et al.*, 1987; Scott *et al.*, 1990). This facilitates the formation of such cohorts. Male *Tursiops* coalitions (Connor *et al.*, 1992a; 1992b) may represent such cohorts.

A ritualised form of male-male competition in *Orcinus* may occur in the form of socio-sexual interactions between adult males (Heimlich-Boran and Heimlich-Boran, ms.). Sexual behaviour among interacting males has been observed in captive *Tursiops* (Östman, 1991) and has parallels with mounting behaviour and penile display in terrestrial mammals such as ungulates (Coe, 1967; Geist, 1971; Hall, 1983; Klemm *et al.*, 1983), macropods (Kaufmann, 1974) and primates (Ploog and McClean, 1963; Kawamura, 1967; Ploog, 1967; Hanby, 1974; Hanby and Brown, 1974; Hanby, 1976; de Waal, 1982; Smuts and Watanabe, 1990). These behaviours appear to function primarily as dominance displays (in that the individual mounting or displaying an erect penis has been documented to be dominant via other methods), but have also been interpreted as warnings to foreign conspecifics or even appeasement greetings (Wickler, 1966). For *Orcinus*, these interactions occurred just prior to the period of predominance of male-female interactions, as might be expected if these penile displays had a role in establishing a hierarchy which could be used to determine access to receptive females. The common occurrence of maturing adolescent males in these groups is also suggestive of competitive dominance interactions, since these males are likely to be in the process of forming relationships with the adult males in their own pod and in the community at large. Males in these groups were usually in body contact with each other; this could represent a form of the pushing and shoving contests for which large body size would be selected, as has been suggested for red deer (Clutton-Brock *et al.*, 1979; Clutton-Brock, 1972). These are similar to the "necking" contests between groups of male giraffes, which are also accompanied by erections (Coe, 1967). Their occurrence in male groups of *Orcinus* could be an indication of male-male competition, which is suggested by the sexual dimorphism of these whales. But the ritualised form of the behaviour makes it difficult to distinguish from affiliative behaviour, which would be encouraged by the relatedness of the males within the community (Bigg *et al.*, 1990).

For *Tursiops*, males in coalitions cooperate to compete with other coalitions (Connor *et al.*, 1992a; 1992b) and Sarasota males have aggressive interactions with non-Sarasota males (Wells *et al.*, 1987; Wells, 1991), *Orcinus* appears to have a lack of inter-group aggression, and males from different communities have been observed to actively avoid each other (Morton, 1990). When two *Orcinus* pods from the same community meet, a ritualised greeting occurs (Osborne, 1986); in contrast to aggressive interactions, these were the times when sexual interactions were observed (Heimlich-Boran and Heimlich-Boran, ms). The initial meeting of two pods is stereotyped. Each pod forms a line (side-by-side) and the two pods approach face to face. After less than one minute the pods submerge and subsequently surface in a tight group with individuals from the two pods completely mixed and in body contact (Osborne, 1986). The initial phase of this *intermingling* behaviour is similar to observations of interactions between neighbouring bands of female langurs, but, in the case of the langurs, the result of such a stand-off is often fighting (Hrdy, 1977). The intermingling aspect of the behaviour is more like the ritualised greetings of wild dogs (Estes and Godard, 1967; Frame *et al.*, 1979), hyenas (Kruuk, 1972; Mills, 1990), baboons (Smuts and Watanabe, 1990) and elephants (Moss, 1988). The lack of aggression may be related to the high degrees of relatedness described for this population of *Orcinus* (Hoelzel and Dover, 1990).

In summary, the evidence for male-male competition in delphinids is still unclear. However, the lack of observations of aggressive male:male interactions in *Orcinus* over 20 years of study, suggests it does not play a major role. The lack of observations can not be attributed to the difficulty of observing male:male aggression in cetaceans: there are well documented observations of aggression between male humpback whales on their breeding grounds (Tyack, 1981; Tyack and Whitehead, 1983; Baker and Herman, 1984).

There is a problem in relating the observed sexual dimorphism and potential male-male competition with the presence of a polygynous mating system for delphinids. Polygyny appears to be ruled out for the sexually dimorphic subfamily (*Globicephalinae*). This is also the group with low or absent rates of male dispersal, resulting in high degrees of relatedness between males and females in the same social group. Additionally, this group demonstrates lower degrees of genetic heterogeneity with indications of a more closed population structure (Duffield, 1986; Stevens *et al.*, 1989; Hoelzel and Dover 1990; Duffield and Wells, 1991; Hoelzel, 1991a). In general, polygyny is correlated with greater rates of male dispersal, due to increased intra-sexual competition forcing males to disperse and find better mating opportunities elsewhere (Greenwood, 1983; Shields, 1987). This dispersal, in turn, serves to increase genetic heterogeneity by enlarging the effective population size (Chepko-Sade *et al.*, 1987). Effective population sizes have not been calculated for the two well-studied groups of *Orcinus* and *Tursiops*, and this is difficult even with the best data sets (Chepko-Sade *et al.*, 1987). The positive relationship between increased genetic heterogeneity and male dispersal rates in the relatively monomorphic delphinine *Tursiops* will be discussed below.

Variability in delphinid sexual dimorphism does not appear to be completely explained by hypotheses of sexual selection leading to polygyny. Ralls (1977) found the relationship between sexual dimorphism and polygyny to be highly predictable in extreme cases. However, the lack of extreme dimorphism in the globicephalines may indicate that other explanations are appropriate. There have been two general categories of explanations for sexual dimorphism other than sexual selection: ecological and energetic.

The primary ecological explanation has been the concept of *niche differentiation,* which was originally noted in birds with dimorphic variation in characters such as bill length, indicating that males and females are feeding in different ways (Selander, 1966; Selander, 1972). This serves to reduce inter-sexual feeding competition and allows a more efficient utilisation of resources. This has been shown to be the case for sexually-dimorphic weasels which do not breed polygynously: hunting is done in burrows and the male is able to capture larger prey while the smaller female is able to go into narrower burrows and exploit different areas (Brown and Lasiewski, 1972). It is not clear how important this process is in other mammals, although differences in diet have been reported for male and female *Turisops* (Barros and Odell, 1990). A widely-dispersed resource may also favour larger body size to increase the ranging distance (via increased muscle mass) from a fixed site to locate food and result in selection acting on the sex which is primarily responsible for feeding the young (Bertram, 1979), although this is not applicable for cetaceans. This may be especially common in predators whose searching and pursuit costs are high (Schoener, 1969). Habitat may also affect sexual dimorphism. Terrestrial primates may be more dimorphic than arboreal primates because the latter are limited in their ranging by the smallest branch which will support their weight (Clutton-Brock *et al.*, 1977). Aquatic species should be even less limited by gravitational forces and thus relatively free from constraints on increasing body size (Economos, 1983). Sexual dimorphism has been shown to be distributed differently in three-dimensional, aquatic environments (Alexander *et al.*, 1979). Male pinnipeds may be selected for small body size (e.g. male Weddell seals are smaller than females) through intra-sexual competition because the improved agility associated with small body size may be beneficial in competition (Alexander *et al.*, 1979). Another hypothesis relating sexual dimorphism to habitat involves selection for small female body size. In fluctuating environments, females may be selected for early maturation which would result in a smaller body size (Wiley, 1974). Male body size may be free from this constraint.

Other hypotheses explaining sexual dimorphism have centred around differential energetic constraints on the two sexes. Sandell (1989) developed the concept of a process of energetic optimisation leading to sexual dimorphism. He modelled the energy requirements of breeding and non-breeding times and identified which sex was living closest to the optimum. This often corresponded to the sex which experienced the greatest mortality. Females may also be selected for small body size because larger body size presents dangers of hyperthermy to the developing embryo because a decrease in the surface to volume ratio will serve to reduce heat loss (Greenwood and Wheeler, 1985). In cool, aquatic environments, these limits on female body size may be released and could explain why female baleen whales are larger than males (Ralls, 1976; Greenwood and Wheeler, 1985). Although hyperthermy can also kill sperm, many male mammals have external testes (a scrotum) to free them from this limitation and can evolve larger body sizes (Greenwood and Wheeler, 1985). Male cetaceans have internal testes, but they have been shown to have complex counter-current heat exchange systems in order to keep the sperm cool (Rommel *et al.*, 1992).

It is apparent that, apart from sexual selection, there are abundant theories to explain the occurrence of sexual dimorphism, suggesting that the presence and form of dimorphism is the result of complex processes, and multiple factors may be in effect for different species. It is difficult to evaluate the various ecological or energetic theories (as opposed to the sexual selection theories) for the occurrence of sexual dimorphism in delphinids. There is a critical lack of information about the distribution of resources in the oceans and the ways in which delphinids may exploit them. A number of theories suggest that in the aquatic environment selective pressures on body size are likely to be very different compared to on land. The lack of any clear correlation between dimorphism and ecological variables in delphinids may be a result of my classification of ecology. Factors other than preferred distance from shore and the taxonomic classification of prey may be important. There is also insufficient information about the energetics of delphinids to understand the importance of the surface to volume ratio in cold, aquatic environments (Kleiber, 1961; Brodie, 1975; Hampton and Whittow, 1976; Schmitz and Lavigne, 1984). The critical importance of the energetics of locomotion in water is just beginning to be understood. Recent studies suggest that delphinids do all they can to maximise energy efficiency (Blake, 1983; Whitehead, 1985; Fish and Hui, 1991; William *et al.*, 1992).

In summary, I conclude that the discrepancy between the greater degree of sexual dimorphism (indicating polygyny) and the low rates of sex-biased dispersal (arguing against polygyny) indicate that the delphinid sexual dimorphism is not clearly related to the mating system. The significant increase in dimorphism in the larger species is probably an indication of the effect of factors other than sexual selection. The detailed patterns of delphinid mating systems (reviewed below) must be explained in terms of reproductive success before the role of sexual dimorphism can be understood.

5.4.2 Brain size, Ecology, and Social Behaviour

Analyses of Relative Brain Sizes (RBS) for nine genera of *Delphinidae* identified that variability in brain size was independent of body size. However, none of the social and ecological classifications identified any significant trends. Larger RBSs may provide the improved neural processing needed to locate patchy food resources for frugivorous primates (Clutton-Brock, 1980), carnivorous-omnivorous carnivores (Gittleman, 1986) and frugivorous bats (Eisenberg and Wilson, 1978). This diet hypothesis did not apply to these delphinids; for example, the two squid-feeding species (*Globicephala* and *Grampus*) were found to have very different RBSs. However, the categorisation of diet on the basis of taxonomic classification (e.g. fish vs. squid) is overly simplistic. If the selective advantage of large brains is the additional neural processing required to locate ephemeral yet rich patches of food which are evenly and widely distributed (Jerison, 1973; Mace *et al.*, 1980), variation in RBS should be related to the behaviour and distribution of the prey. The degree of schooling behaviour of the prey could also affect RBS: schools are effective predator avoidance systems (Hamilton, 1971) and animals preying on active schooling prey would (in theory) require greater neural processing capabilities than those which capture solitary or sedentary fish (Norris and Schilt, 1988). Both squid and fish have schooling and non-schooling representatives, so the classification of diet based on these categories would miss the behavioural aspect of the prey. Detailed prey data are not available for most delphinids. In cases where they are, the dolphins appear to prey on a wide variety of types (Fitch and Brownell, 1965; Clarke, 1986; Barros and Odell, 1990; Barros and Cockroft, 1991; Overholtz and Waring, 1991; Gales *et al.*, 1992). It could also be argued that all resources which delphinids exploit (except for the bottom-dwelling crustacean used by *Cephalorhynchus*) are patchily distributed and thus there would be selection for larger brains across the taxa.

Another hypothesis to explain relatively larger brains in comparative studies has been the *social complexity* hypothesis, and this may have some relevance to social structure and mating system. For the present study, the only social variable which could be used to test this hypothesis was group size. No significant trends were found, but perhaps other elements of society (such as socionomic sex ratio) may explain the variability in brain size better. The two genera for which we possess the most information on social structure, *Tursiops* and *Orcinus*, both have relatively larger brains than other delphinids. This is consistent with a social complexity hypothesis. However, *Globicephala*, which appears to share many elements of complex social structure with *Orcinus*, had a relatively much smaller brain. Although relative brain sizes of all delphinids are significantly above the regression of brain and body size for all mammals (Worthy and Hickie, 1986), and this may have relevance to an understanding of their social organisation.

Although cetacean brains are generally larger than the brains of terrestrial mammals (Jerison, 1973), they have a less complex structure (Morgane *et al.*, 1986b; Morgane *et al.*, 1986a; Ridgway, 1986b). The dolphin brain has a greater degree of cortical folding than the human brain (index of 4.47 vs. 2.86: Elias and Schwartz, 1969), but the average volume of the cortex is 80% of the human's because dolphin cortex is so thin (Ridgway, 1986b). Also, there is reduced cortical differentiation indicated by the *agranularity* of the cortex, which is characteristic of the primitive mammalian brain (Morgane *et al.*, 1986b). It has been proposed that this reduced granularity is because the primitive cetacean ancestors split off from the rest of mammals before the more advanced granularity of the modern terrestrial mammalian brain evolved (Morgane *et al.*, 1986a). They have apparently compensated for this primitive cellular condition by an enormous enlargement of the surface area of the cortex (Morgane *et al.*, 1986a). It may be that these essential differences of cetacean brains make them incomparable with the brains of terrestrial mammals. However, simplified brain structures need not necessarily imply limited processing abilities (Jerison, 1986). For example, the visual cortex of birds is significantly simpler in structure than the mammalian visual cortex, but birds have vision equivalent to primates (Jerison, 1986). Jerison (1986) suggests "..at present, it may be heuristic to continue to accept simple quantitative measures {of brain size} and to disregard differences in organisation".

It is likely that the large brain of delphinids is specialised for acoustic signal processing, especially echolocation (Evans and Bastian, 1969; Herman and Tavolga, 1980; Wood and Evans, 1980; Jerison, 1986; Worthy and Hickie, 1986; Moore, 1991). Although bats echolocate and have much smaller brains (Eisenberg and Wilson, 1978), the frequency spectrum of signals which they project and the cochlear adaptations they use to receive these signals covers a much narrower band than that of delphinids (Worthy and Hickie, 1986). The use of broad band clicks, rapid click repetition rates (up to 1000/sec.) and the fine-grained resolution of delphinids (Popper, 1980) likely requires a great deal of neural processing (Wood and Evans, 1980). This could explain the large relative brain sizes compared to other mammals (Worthy and Hickie, 1986).

5.4.3 Relative Testes Size and the Potential for Sperm Competition in Delphinids

Models for the evolution of sperm competition (Parker, 1984) are based on two strategies of male mating behaviour which centre around the concept of paternity assurance (Alexander, 1974). First, a male may guard the female (or a group of females) to prevent second matings by other males through male-male conflict, thus guaranteeing his paternity. Alternatively, if the female (or group of females) is not defensible, thus reducing the male's paternity assurance, then the male can only compete with other males through increasing his volume of sperm to out-compete other male's sperm in the fertilisation of the ovum. The selection for either of these strategies depends on the costs to the female of the male's behaviour. If mate guarding or multiple matings are costly to the female there will be male-female conflict and the system will be destabilised. However, if mate guarding is not costly (or is even beneficial) to the female, then mate guarding will evolve. An example of this is found in the behaviour of female fallow deer mating on leks: it is beneficial to them to mate with a single male on his lek because his presence reduces the usual harassment she receives from multiple males attempting to mate (Clutton-Brock, 1989b). If multiple matings are not costly (or are beneficial) to the female (as in the case of lions: Davies and Boersma, 1984), then sperm competition will evolve.

Kenagy and Trombulak (1986) were first to suggest that odontocete cetaceans have exceptionally large testes compared to other mammals. Observations from captive *Tursiops* suggest that mating occurs promiscuously (McBride and Hebb, 1948; Brown and Norris, 1956; Tavolga and Essapian, 1957; Tavolga, 1966; Tayler and Saayman, 1972; Saayman *et al.*, 1973). However, *Tursiops* had relatively small testes for a delphinid (Figure 5.9). This would appear to indicate that other delphinid species (previously unstudied) have even greater potential for sperm competition.

5.4.4 Patterns of Dispersal and Genetic Diversity

Patterns of dispersal in mammals are also likely to be important in determining the form of social relationships (Harcourt and Stewart, 1983; Wrangham, 1983; Smuts, 1987), the degree of genetic variation due to levels of inbreeding (Melnick and Hoelzer, 1992), the prevalence of nepotism and other altruistic acts present through kin selection (Moore, 1992) and the form of mating systems (Shields, 1987). In most mammal and bird species, one sex or the other disperses from their natal group, apparently to avoid inbreeding with close relatives, but perhaps also to find better feeding and mating opportunities elsewhere (Packer, 1979; Greenwood, 1980; Pusey, 1980; Shields, 1982; Greenwood, 1983; Moore and Ali, 1983; Shields, 1983; Pusey and Packer, 1987a; 1987b). Alternatively, natal philopatry has been shown to have benefits to group living (Bengtsson, 1978; Shields, 1983); in fact the entire principle of kin selection is based on natal philopatry (Moore, 1992). It is beneficial for kin to remain together because altruism is favoured and animals can cooperate in resource acquisition with reduced benefits to cheaters who exploit the system. Thus, there is ultimately a cost-benefit trade-off related to resource and mate acquisition and avoidance of predation involved with the decision to disperse or remain in a natal group. Documented dispersal patterns in *Tursiops* suggest that mixing between communities occurs through the movement of males (and to a lesser extent females: Duffield and Wells, 1991). There is genetic evidence of reproductive isolation between killer whale communities (Hoelzel and Dover, 1990; Hoelzel, 1991a) and strong observational evidence of a complete lack of male dispersal from natal groups (Bigg *et al.*, 1990). These differences are apparent in comparisons of mtDNA variation between *Tursiops* and *Orcinus* (Duffield and Wells, 1991). These differences in dispersal patterns and degree of genetic heterogeneity provide the strongest available evidence that the two species have different mating systems.

5.4.5 Hypothetical Delphinid Mating Systems

I propose that the well-studied members of the two delphinid subfamilies, *Delphininae* and *Globicephalinae* have different social systems. The lack of a long-term bond between reproductive males and females in both groups indicates mating must primarily be occurring promiscuously. Females remain in association with kin in both groups, but the stable units of *Orcinus* society (pods) encompass three levels (intra-pod, subpod and pod) whereas the stable *Tursiops* female bands which interact fluidly appear to be equivalent to only the smallest *Orcinus* unit. The behaviour of the males in these two species is different.

In *Tursiops*, males remain (in the long-term) on their natal home ranges, but disappear for weeks or months at a time, suggesting they are adopting a *roving male* strategy (Clutton-Brock, 1989b; Whitehead, 1990). In one sense, this is a *resource defence* system, where the range of a male (or group of males) encompasses the ranges of more than one female community (Clutton-Brock, 1989b; Davies, 1991). However, the males apparently only defend their natal community, as indicated by aggressive interactions with males from adjacent communities primarily along the periphery of the range. Roving may be an alternate to mating with non-kin female bands within the male's own community. The strategy of roving has been hypothesised to be most beneficial if females are unpredictably distributed or clumped into small units(Clutton-Brock, 1989b), as bands of *Tursiops* females are. Other males appeared to remain longer in a female community's home range and move from female group to female group, perhaps sampling for receptive females. Models of the trade-off between these two strategies of roving and residency indicate that males should stay resident when the travel time between female groups is greater than the oestrus period of a single female (Whitehead, 1990). Indications that female *Tursiops* have spontaneous, multiple ovulations (Kirby and Ridgway, 1984) over a wide seasonal range (Wells *et al.*, 1987) suggest that it would be difficult for males to predict when there is a maximum likelihood of encountering receptive females. Ovulation may be detectable at close range through the chemo-reception of hormonal cues in small quantities of urine (Nachtigall, 1986; Schroeder, 1990). However, the range of detection of such clues is limited in water due to dilution

Males will also form alliances to control access to receptive females (Wells *et al.*, 1987; Wells, 1991; Connor *et al.*, 1992a; 1992b). These alliances may be based on kinship, but are likely to be also due to the formation of cohorts of more distantly related males; a similar situation of alliance formation as described for lions (Packer *et al.*, 1991). Such alliances may be aided by the comparative ease in defending female groups in shallow water, the primary habitat of this species. Nevertheless, field observations indicate that two or three males are required to herd a female. Thus female behaviour appears to be promiscuous unless males actively intervene. Even with herding, there can be no certainty of paternity. Males do not maintain long-term contact with the females and return to the common pattern of age and sex segregation within their natal community. Males appear to provide no parental care as they are segregated from the young for most of the time. The variability in the reproductive success of males is still unknown and ongoing paternity studies may undermine this view of *Tursiops* society.

There is also strong evidence of a promiscuous mating system in *Orcinus* , defined by the lack of a mating bond between breeding males and females. While observations of mating are limited, sexual interactions appear to be occur between members of different pods. However, the males involved in these interactions returned to their natal pod. Given that males appear to remain closely bonded to their natal group, mating between pods would be a clear example of inbreeding avoidance (defined as the avoidance of mating with immediate kin: Shields, 1987). A similar situation was noted in interactions between kin in the black-tailed prairie dog (Hoogland, 1982). Occasionally, a female came to maturity in the coterie of her adult male kin. One of the mechanisms involved in avoiding inbreeding was apparently based on the rejection of potential mates who were recognised as kin (Hoogland, 1982). However, all indications are that genetic exchange occurs entirely within the confines of the local *Orcinus* community (Stevens *et al.*, 1989; Bigg *et al.*, 1990; Hoelzel and Dover, 1990; Hoelzel, 1991a). Males within a community appear to have ritualised interactions, which could either represent dominance or affiliative behaviour. This would fit with Moore's (1992) suggestion that there should be a lack of overt aggression and a prevalence of ritualised behaviours between closely related animals.

Globicephala, although not yet studied in a long-term observational study, appears to share a number of social system features with *Orcinus*. The genetic information from *G. melas* indicates that males and females from the same pod are related (Amos *et al.*, 1991a; 1991b). Although the overall community structure is unknown, there are indications of genetic differentiation between pods, suggesting a restricted mating population (Andersen, 1988). My observations of *G. macrorhynchus* confirmed the existence of two, apparently non-interacting, segments of the population (resident and visitors), as well as patterns of association between pods which could provide the basis for the observed genetic differentiation. The resident community showed no indication of age and sex segregation. The pods often split into smaller groups, making them basically equivalent to *Orcinus* subpods. Associations of the reproductive females were found to be predominantly with males when the linked pods travelled together, further supporting the idea of an inbreeding avoidance mechanism.

However, the main question to be asked about these groups is: Why do the males remain in their natal group? I propose that they do so because of a promiscuous system of mating with a low confidence of paternity. While *Tursiops* males appear to be able to control access to females through herding, there have never been any similar observations in *Orcinus*. This could be because of the females large body size and the reduced mobility of the even larger males. Guarding of females in an aquatic three-dimensional habitat must be extremely difficult. An indication of this comes from a comparison of mating systems of pinnipeds which copulate on land or in water (Stirling, 1983). Species which copulate on land are highly polygynous and sexually dimorphic with one male controlling access to a large number of females (Le Boeuf, 1974). Species with aquatic copulation show low degrees of polygyny and sexual dimorphism (Stirling, 1983) probably due to the males inability to control access to the female because of her increased mobility underwater and the difficulty of maintaining aquatic territories (Ralls, 1977). In the face of this inability to guarantee paternity, sperm competition (Parker, 1984) should be important. While *Orcinus* falls exactly on the predicted line relating testes size to body size within *Delphinidae*, this family-wide degree of testes development has been shown to be significantly greater than expected for mammals in general (Kenagy and Trombulak, 1986).

Why should a male return to his natal group after mating? Why not rove and search out other receptive females? I think there are four answers: 1) the low densities of large predators, such as *Orcinus* and *Globicephala* (Bonner, 1988), may make the roving model's travel time between receptive females greater than the duration of a female's oestrus (Whitehead, 1990), 2) the costs of moving to an unfamiliar area and facing a potentially unwelcome reception, may be too high (Bengtsson, 1978); 3) the benefits of cooperatively hunting with known pod mates may increase feeding efficiency (Packer and Ruttan, 1988) and 4) increased inclusive fitness within a pod (Hamilton, 1964).

Inclusive fitness is a measure of an individual's fitness which includes not only its own reproductive success, but also the reproductive success of its relatives, devalued by the appropriate degree of relatedness (Wilson, 1975; Trivers, 1985). In promiscuous mating systems, males have little guarantee of paternity (Alexander, 1974), thus, they are unlikely to form a bond with a female and provide any parental investment to her offspring, because these may have been sired by another male (Trivers, 1972). This risk of cuckoldry or desertion (Trivers, 1972) is likely to be great for golobicephalines because of the apparent lack of mate guarding. Hamilton (1964) reasoned that an animal should base any altruistic behaviour (e.g. any behaviour which may be detrimental to individual fitness but apparently beneficial to a neighbour's individual fitness) on the *degree of relatedness* (r), or the proportion of shared genes between it and its neighbour. Specifically, the ratio of gain to loss (K) of any altruistic behaviour should be greater than the reciprocal of the degree of relatedness ($K > 1/r$: Hamilton, 1964). For example, parents are related to their offspring by 0.5 because, on average, each parent contributes one-half of the offspring's genome. Thus, any social act between parents and offspring should be favoured by natural selection if the ratio of benefit to cost is greater than two. Even if the parent dies, it could have increased it's inclusive fitness through kin selection (Maynard Smith, 1964).

Promiscuous mating systems have considerable effects on the certainty of male paternity, or the degree to which a male can judge his degree of relatedness to his offspring (Alexander, 1974). A male mating in such a system may have a degree of relatedness to his mate's offspring of 0.5 (if he is the father) to 0 (if another male is the father). However, he is sure of his degree of relatedness to his mother and his siblings, through what has been termed *uterine kinship* (Flinn, 1981). Thus, paternity uncertainty only reduces relatedness through putative patrilineal kinship links, and has no effect on relatedness through matrilineal kinship links. Alexander (1974) noted that in promiscuous mating systems, a male may be more sure of his relatedness to his sister's offspring ($r = 0.25$ or 0.125, depending on whether the brother and sister are full or half siblings) than he would be to the offspring of his mate, with r varying between 0-0.5 depending on his confidence of paternity. Alexander (1974; 1977) modified Hamilton's altruistic equation to $K > (1/r) * p$, where p equals paternity certainty. With no confidence of paternity, any offspring of his sister would be his closest relatives in the next generation (Alexander, 1974). The model predicts there should be a *paternity threshold*, p_t, or a degree of paternity certainty below which altruistic behaviour towards his sister's offspring will increase his inclusive fitness more than caring for his putative offspring with unrelated females. Various assumptions provide estimates of a critical value of p_t between 0.268 (Kurland, 1979) and 0.33 (Flinn, 1981).

This rationale has been used to explain the evolution of human societies in which the mother's brother or uncle has a greater responsibility for the young in a group than he does for his own offspring (Alexander, 1977; Kurland, 1979; Flinn, 1981; Flinn and Low, 1986; Borgerhoff Mulder, 1991). These societies are characterised by a large degree of promiscuity, occasionally with the man and wife living in completely separate houses. A quantitative survey of 150 randomly chosen societies found a significant correlation between the importance of this avuncular relationship and degree of paternity confidence (Flinn, 1981). These societies have been termed *avunculate* societies (Alexander, 1977).

I propose that *Orcinus* and *Globicephala* live in avunculate societies. In relation to other forms of human society, Alexander (1974) suggested that avunculate societies could share elements of both matriarchal- and patriarchal-based cultures. In relation to mammalian societies, I would suggest that an avunculate society be considered as a matriarchy (since differential mortality will always result in females being the oldest members) with adult male sons and brothers attached.

Kurland (1979) compared primate societies with avunculate human societies and concluded that the behaviours of females of many primate species were similar to human females in terms of the formation of matrifocal groups with a permanent association of uterine kin (Kurland, 1977), but there were no cases where males preferentially associated with female uterine kin, and he concluded the avunculate social system was uniquely human. Questions have been raised about the validity of Flinn's (1981) survey and the evidence for high promiscuity levels in humans. It has been suggested the critical element in the explanation of avunculate societies are whether they are based on sex-specific differences in dispersal costs or in differential benefits from cooperating with kin (Borgerhoff Mulder, 1991).

Moore (1992), in his review of the relationship between dispersal and nepotism in primates, outlined an argument which contributes to an explanation of the benefits of such societies. Dispersal and nepotism are linked by the simple fact that nepotism, defined as the direction of beneficial or altruistic acts toward kin, can not develop if kin have dispersed (Moore, 1992). In other words, contacts between kin need to be sufficiently frequent to allow nepotism to develop. The link between these two processes has been enhanced by an attempt to explain the prevalence of male dispersal in most mammals, using theories of the evolution of nepotism through kin selection (Hamilton, 1964) and the evolution of matrilineally-related female primate groups based on the defendability of food resources (Wrangham, 1980). Coupled with documentation of inbreeding depression (Ralls *et al.*, 1979; 1980), a common scenario of male dispersal has been proposed. Moore (1992) states this scenario as:

> "In all but a few exceptional species, primate troops are formed of matrilineally related females which cooperatively defend their feeding range and/or guard each other against predators. Since inbreeding depression is a potentially serious problem, inbreeding must be avoided. The easiest way to do this is by differential dispersal from the natal group. Since females are staying, males have to go. Accordingly, male-biased dispersal, placing limits on possibilities for male nepotism, is the predicted consequence of female nepotism plus inbreeding depression." p.362

Why should there be a causal link between dispersal and nepotism? I believe that avunculate societies suggest there need not be. Four conditions should be required for the formation of an avunculate society: 1) high benefits to remaining with kin (e.g. from nepotism), 2) low rates of dispersal of both sexes, 3) a mechanism for extreme inbreeding avoidance through out-group mating and 4) low degrees of paternity certainty. The benefits of remaining with kin have evolved through kin selection (Hamilton, 1964). In the traditional female philopatry/male dispersal system, kin-selected benefits for females accrue within the social group while kin selection for males is beneficial through kin-biased dispersal of brothers (Bertram, 1976; Bygott *et al.*, 1979; Packer and Pusey, 1982; Cheney and Seyfarth, 1983; Packer *et al.*, 1988; Packer *et al.*, 1991). In the less common male philopatry/female dispersal system, males receive the within-group benefits, while females transfer and then build up their own kin in a different group (Pusey, 1980; Goodall, 1986). Avunculate societies allow both sexes to benefit from within-group kin selection. Since all group members are related, the potential for inclusive fitness gains are greatly increased, whereas with one sex dispersing, inclusive fitness gains through interactions between adults are limited to one sex. The second condition appears to entail the costs of inbreeding depression which are presumed to necessitate dispersal, but the third condition solves this dilemma.

The process of a male mating outside of his social group does not appear to have any clear precedence in other mammalian societies. There is some evidence of very low or zero rates of male dispersal in Barbary macaques, with males leaving periodically to mate with females in adjacent groups (Mehlman, 1986), but the field studies are still relatively short-term. Some male brown hyenas remain within their natal groups, but this appears to result from delayed dispersal due to unfavourable conditions; males eventually disperse when there is another female group to join (Mills, 1990). However, the social groups of *Orcinus* represent *feeding* groups of related kin and the seasonal multi-pod aggregations of all community members are the true *breeding* groups, as defined by Gittleman (1989). Moore (1992) has pointed out that the presumed obligatory causality between dispersal and inbreeding avoidance can be reconsidered through carefully defining dispersal as the dispersal of gametes (Shields, 1987), not requiring a dispersal of individuals. If a low degree of paternity confidence is overlaid on top of these other considerations, an avunculate social system may be optimal.

The final question is: why are the groups of *Globicephala* and *Orcinus* so stable? If I am correct in hypothesising an avunculate social system for these whales, it has to be primarily based on either: 1) the benefits accrued to adult males by living in a group with closely related females, or 2) the excessively high costs of dispersal into adjacent groups of females. There is no way to evaluate these costs with the present data, except to explore the benefits of staying in a group and then assume that dispersal cost would involve the loss of those benefits. It would seem that the benefits would have to be non-reproductive, because living with your kin with whom you avoid inbreeding would reduce your immediate access to potential mates; although membership of a dominant matriline could improve access to females in other matrilines. The primary non-reproductive benefits to group living are improved resource acquisition and protection from predators (Alexander, 1974; West Eberhard, 1975; Bertram, 1978; Wrangham and Rubenstein, 1986).

Improved resource acquisition could come about through cooperative hunting, which can only evolve when the per capita rate of food intake within a group exceeds that of a solitary individual (Packer and Ruttan, 1988). Comparisons of group sizes in resident and transient *Orcinus* have suggested that the larger resident group sizes may be related to improved benefits from cooperative hunting on an abundant, schooling prey such as salmon (J.Heimlich-Boran, 1987; Felleman *et al.*, 1991; Baird *et al.*, 1992), while small transient group sizes are optimal for the individual capture of single, large prey such as pinnipeds. However, it is likely that *Orcinus* hunting pinniped prey also cooperate (Lopez and Lopez, 1985; Hoelzel, 1991c; Jefferson *et al.*, 1991), and that the differences in group size are simply foraging specialisations (Baird *et al.*, 1992).

Norris and co-authors (Norris and Dohl, 1980b; Norris and Schilt, 1989) have proposed that one of the main benefits to group living in delphinids comes from the *sensory integration system*, which involves "the receipt of environmental information by any member of a group, and passage of a reaction to it through the group in all directions within the school" (Norris and Schilt, 1988, p.156). This system could be used for the group detection of prey and improve the feeding success of all individuals. In fact, observations of *Orcinus* feeding on salmon schools suggested that it was primarily prey detection (by flank formation swimming) and prey herding (by splashing and vocalising while progressing towards shorelines or underwater seamounts) which were cooperative. Once feeding commenced the whales broke ranks and fed individually (J.Heimlich-Boran, 1988).

Resource distribution has been shown to be one of the prime determinants of group formation and mating systems (Orians, 1969; Alexander, 1974; Emlen and Oring, 1977; Clutton-Brock, 1989b; Davies, 1991). Even in terrestrial environments, where ecological research has been conducted for many years, the dispersion of resources is difficult to categorise. Terms such as *clumped* and *patchy* are widely used, but have no standard, quantitative definitions. The distribution of resources in the marine environment is even less well understood. Correlations between delphinid occurrence and the known distribution of their preferred prey has been applied on a broad seasonal basis (Würsig and Würsig, 1979; 1980; J.Heimlich-Boran, 1986), but the long-term variability of the majority of marine resources is unknown. The ocean is often a highly stratified environment with thermoclines and density boundaries which will affect the distribution of prey. The three dimensional distribution of prey could also place unknown constraints on resource utilisation. However, it has been suggested that the predictability and abundance of seasonal migrations of salmon returning to their natal rivers is likely to be the reason resident *Orcinus* populations have been established in the inland marine waters off British Columbia (J.Heimlich-Boran, 1986; J.Heimlich-Boran, 1988; Felleman *et al.*, 1991; Baird *et al.*, 1992). The season when salmon are most abundant is also the season when pods travel together in large aggregations, when most sexual interactions were observed between males and females, and the peak season of conception (Olesiuk *et al.*, 1990; Felleman *et al.*, 1991; Heimlich-Boran and Heimlich-Boran, ms.). One of the primary implications of an avunculate social system with inbreeding avoidance is that cohesive social groups must periodically make contact for out-group mating. This can only be done in an area with sufficient resources to support the nutritional requirements of more than one social group. The apparent narrow range of distribution of pilot whales off Tenerife (Chapter 3), also suggests that this is an area where resources are locally abundant and contact between pilot whale pods could be maintained.

The second major benefit to group living is protection from predation, and this has been discussed as a primary factor in the evolution of delphinid schools (Norris and Dohl, 1980b; Wells *et al.*, 1980; Norris and Schilt, 1988). Any organism living in an open habitat is susceptible to predation (Hamilton, 1971). The sensory integration system discussed above is probably a key adaptation to occupying such habitats, and is used by both fish and dolphin schools (Norris and Schilt, 1988). However, the development of echolocation has given delphinids and inherent advantage over sharks and has probably allowed them to maintain a high degree of social complexity (Norris and Schilt, 1988). Although predation is likely to be less important for large-bodied delphinids compared to smaller species, it cannot be ruled out. I observed a young pilot whale with large scars which was probably from a shark attack. Larger body size could confer an advantage for male globicephalines in terms of potentially defending the pod from shark attack. Males often travelled on the periphery of the pod and when approached underwater by divers, always came close for an inspection. Dolphins have been known to attack sharks, probably as a form of group defence (Wood *et al.*, 1970; Corkeron *et al.*, 1987).

These indications of a role in group defence for male delphinids could be considered as a form of parental care. Other anecdotal indications of a parental role for *Orcinus* males comes from observations of allo-parental care, involving males "baby-sitting" young calves while their mothers were away (Haenel, 1986). Also, a male *Globicephala* off Tenerife was observed in close association with a newborn calf, less than one week old, while its mother presumably dove to feed. Male *Orcinus* have also been considered to have a teaching role in hunting (Lopez and Lopez, 1985; Guinet, 1991; Caro and Hauser, 1992). Males were observed to catch sea lions on the beach and then bring them offshore to waiting juveniles. Although the degrees of relatedness of these animals was unknown, the allo-parental role of the whales off British Columbia could be explained through the inclusive fitness gained via an avunculate social system.

Total natal philopatry allows for a build-up of cultural knowledge through the maintenance of inter-generational bonds (Bonner, 1980; Nishida, 1987). Older members, especially the longer lived females, have the experience and memory of previous feeding success (Würsig, 1986). This is similar to the role ascribed to matriarch elephants: as repositories of critical information about the surrounding habitat in terms of the temporal and spatial distribution of resources (Douglas-Hamilton and Douglas-Hamilton, 1975; Dublin, 1983; Moss and Poole, 1983; Moss, 1988). This may be of more importance for marine mammals than terrestrial mammals, given the patchy distribution of resources in the three-dimensional marine environment (Würsig, 1986; Norris and Schilt, 1988; Norris and Pryor, 1991). All animals in the pod would benefit from enhanced success which must surely come from working within a culturally co-adapted group.

The complexity of globicephaline life is also suggested by the long maturation period, which indicates that a considerable amount of learning is necessary for survival (Brodie, 1969). This long maturation also requires large amounts of parental investment, and the presence of a long period of reproductive senescence with an extended lifespan (Kasuya and Marsh, 1984; Marsh and Kasuya, 1984; 1986; Bigg *et al.*, 1990; Olesiuk *et al.*, 1990; Marsh and Kasuya, 1991) may be a form of *terminal investment* (Trivers, 1974; Clutton-Brock, 1984). Parental investment theory predicts that as a female reaches the end of her lifespan the costs of parental investment, in terms of delayed future reproduction, will decrease (Trivers, 1972). This will select for a longer period of terminal investment, and result in a reduction in parent-offspring conflict (Trivers, 1974). An overall increase in reproductive effort towards the end of the lifespan has been predicted for species in which reproductive value declines with age, but has been difficult to document (Clutton-Brock, 1984). In red deer, although fecundity declines with age, maternal investment increases for older females. Offspring survival has been shown to increase with an increase in suckling bouts for the young of older females (Clutton-Brock *et al.*, 1982). In a related finding, survival in calves whose mothers failed to raise a subsequent calf was also enhanced through delayed weaning and the attainment of higher social rank (Clutton-Brock, 1984). Combined, these two factors provide a mechanism for the evolution of the post-reproductive period in globicephalines.

The confirmation of the existence of an avunculate social system in globicephalines will require measurement of degrees of relatedness within and between pods. However, I believe that the existence of such a system is the best explanation of the current data set available for these whales. Also, the system's existence is predictable within the current theories of natural and kin selection, given the occurrence of low male dispersal, low confidence of paternity, and large benefits to living with kin.

These broad generalisations on the social organisation and mating systems of delphinids are undoubtedly overly simplified. I am quite sure that further research will show subtle variations in these trends, especially as more populations are studied. Most of the research presented here is based on single populations of each species, so there is little information on the effects different environments may have on social systems, nor on how widespread such systems are.

5.5 SUMMARY

The cetacean family *Delphinidae* was examined in a two part comparative study: 1) the morphological, ecological and behavioural characteristics of sexual dimorphism, brain size, testes size, group size, diet and habitat preference were examined relative to current theories of mating systems and 2) a detailed comparison of genetic and observational studies on the social structure of three genera (*Tursiops* {subfamily *Delphininae*}, *Orcinus* and *Globicephala* {*Globicephalinae*}) was used to develop hypotheses concerning mating systems. Sexual dimorphism was significantly correlated with absolute body size, ranging from the smallest genus, *Cephalorhynchus*, in which females were larger than males, to the large globicephaline whales, with males up to 1.7 times larger than females. Brain size also varied significantly with body size, but measures of relative brain size did not correlate with diet, habitat or group size. In fact, species with similar diets or group structures had very different relative brain sizes. Relative testes size also showed variation independent of body size, but again was uncorrelated with group size as might have been predicted from the theory of sperm competition. The lack of correlation between these morphological characteristics and the ecological and social classifications could have been due to the choice of inappropriate categories of diet and habitat because of a lack of ecological data for delphinids.

Tursiops (and a few other delphinine genera) were shown to live in age and sex segregated groups in which all individuals primarily interacted with other individuals of similar age and reproductive status. Fluidly-interacting bands of females and calves formed relatively discrete communities which showed some signs of genetic differentiation. Males primarily remained within specific areas of their natal home range, but appeared to leave to interact with adjacent communities. Males were considered to be the vectors of genetic interchange between communities and aggressive interactions were observed between males from different communities. Males occasionally formed coalition to herd females, presumably to control mating access. *Orcinus* lived in highly stable pods of mixed age and sex from which no dispersal of either sex was observed in 20 years of observation. Community structure consisted of a number of pods which freely interacted on a seasonal basis. Genetic studies indicated high degrees of inbreeding within communities and differentiation from adjacent communities. A sympatric form with highly different group structure and foraging specialisations was reproductively isolated, further emphasising the closed population structure. Limited observations of sexual interactions suggested mating was taking place between pods within the same community. Although not documented through long-term observations, genetic and short term observations of *Globicephala* suggested they may also live in pods of mixed age and sex in which adult males and females are related and the males are not the fathers of the offspring in the group. Seasonal association between males and females from different pods was suggested as the time when out-group mating could occur. The pattern of age and sex associations was similar to *Orcinus*. The shared life history features such as differential mortality for males and females and the presence of a long post-reproductive period during the last one-third of the females' life, suggests that these two globicephaline whales shared the same social system.

A promiscuous mating system was proposed for both of these groups, based on the short-term contact between mating males and females. Delphinine males appeared to adopt a roving male strategy, occasionally forming coalitions to control access to receptive females, and ranging into adjacent female communities. A social system, previously only documented for humans, was hypothesised to account for the globicephaline observations. This is termed an *avunculate* social system which consists of a matriarchy with adult male sons and brothers attached. This can arise when paternity certainty is so low that a male will be more closely related to his sister's offspring than he will be to the offspring of his mate. Males appear to perform functions of group defence from predators, offer occasional allo-parental care and could aid in food detection and capture, which could result in benefits through inclusive fitness. The benefits of living with kin could result in a build-up of cultural knowledge through the maintenance of inter-generational bonds. Confirmation of this unique social system will have to await further studies on paternity and the variance in male reproductive success.

CHAPTER 6: CONCLUDING DISCUSSION

The aim of this thesis has been to examine the social ecology of the cetacean family *Delphinidae* in light of current theories of the organisation and evolution of terrestrial mammalian societies. In order to expand the information available for this examination, I conducted a study on the social organisation of the short-finned pilot whale, for which there was much biological information collected from carcasses, but which had been relatively unstudied in the wild. A population of almost 500 pilot whales was located off the Canary Island of Tenerife and were found to frequent an area of steep bathymetric slopes along the 1000 m depth contour. The social organisation of these whales, which travelled in 31 pods, supports hypotheses for a system in which related males and females live together in a social group and mate with associated groups.

Comparative studies of the *Delphinidae* tested for family-wide trends in sexual dimorphism, relative brain size and relative size of the testes in order to further examine delphinid mating systems. While these dolphins and small whales fit into some of the predicted mammalian trends, especially relating to allometric growth and an inherent variability with absolute body size, there was a general lack of correlation of these morphological trends with ecological and social classifications. The classification system suffered from a general lack of information on the specifics of feeding ecology and social systems of these animals, and the variables of group size, habitat and taxonomic classification of prey were likely too general. However, the findings do support the view that delphinids have relatively large brains (Jerison, 1973; 1986) and testes (Kenagy and Trombulak, 1986) when compared to other mammals. The implications of these views are that delphinids: 1) have complex requirements for neural information processing relating to food-finding in a patchy, three-dimensional environment or to the maintenance of diverse social relationships, and 2) have promiscuous mating systems in which paternity can not be assured and thus have developed mechanisms for sperm competition (Parker, 1984).

A review of long-term studies on social organisations of the bottlenose dolphin and the killer whale identified two broadly different patterns of social interactions. While the small, monomorphic dolphins live in age and sex segregated groups which interact fluidly, in a form of fission-fusion society, the large sexually-dimorphic killer whales and pilot whales live in stable groups of mixed age and sex. Bottlenose dolphins maintain genetic heterogeneity through a temporary interchange of males between female communities. However, there has been no dispersal of juvenile animals or adult males from the killer whale groups in 20 years of observation and this population has been described as "inbred" (Hoelzel and Dover, 1990; Hoelzel, 1991a). I presented some original observations of these whales which provided the suggestion that mating was occurring between associated groups.

Thus, while the small dolphins fit into the general theories of mammalian mating systems, following a "roving male" strategy (Clutton-Brock, 1989b; Whitehead, 1990) between adjacent female communities, the larger dolphins, like the killer whale and pilot whale, do not clearly match any previously described system for non-human mammals. However, a human social system, in which males maintain associations with their female kin while mating outside of this group, termed an *avunculate* (Alexander, 1977; Kurland, 1979; Flinn, 1981; Flinn and Low, 1986), could provide a possible explanation.

The development of hypotheses concerning delphinid mating systems has necessarily been based on limited data and must be considered a first step in establishing underlying principles involved in the social evolution of this diverse family. The main hypothesis has been that apparent differences in social organisation should be correlated with differences in morphology. In most studies of this sort on terrestrial mammals, the mating system is used as a categorising variable to examine morphological trends in sexual dimorphism, brains and testes. I was working at the problem from the other direction: I have examined morphological trends and used predictions, based on theories of the evolution of mating systems, to compare with the available observations of delphinid social organisation. As in any comparative study, the common correlation of two sets of variables does not imply causation; the possibility exists that a third variable is affecting both in a similar way. In this case, the third variable (broadly speaking) is likely to be ecological. Unfortunately, the classification of marine habitats is extremely difficult and there is much need for the synthesis of current knowledge of physical and biological oceanography with studies of these large marine predators.

Additionally, there is need for an expansion of the application of genetic methods for cetaceans. The current impetus for the utilisation of genetic techniques for describing the mating and resultant reproductive success of terrestrial mammals is even more critical for marine mammals, given the difficulties of observation. The few analyses of delphinid genetic heterogeneity have provided many of the suggestive results for the hypotheses of mating systems presented here. It is likely that the revolution started by the implementation of these methods will continue and the results will undoubtedly contribute still more to our understanding of all mammalian societies.

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