FEMALE REPRODUCTIVE STRATEGIES AND MOTHER-CALF RELATIONSHIPS OF COMMON DOLPHINS (*Delphinus delphis*) IN THE HAURAKI GULF, NEW ZEALAND.

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ABSTRACT

This study reviewed the habitat use, social organisation and behaviour of common dolphin groups categorised by their youngest member, as well as the behaviour of common dolphin calves of different age classes.

Most newborn calves were sighted over late spring and early summer, and in water temperatures warmer than for other groups. The water depths at which common dolphin groups were found did not vary according to the age class of their youngest member. However, only groups containing newborns or infants were sighted under 20 metres of water depth. A high percentage of groups encountered contained calves (82.5%), suggesting the importance of the Hauraki Gulf for common dolphins' reproduction.

Groups of common dolphins containing calves were found to be of larger size than any other group type. All groups proved to be similarly involved in different behavioural states and showed comparable patterns of association with other species, although groups including newborns were significantly less likely to be seen associated with whales and birds. Groups of common dolphins as a whole did not show a differential reaction to the boat according to the age class of their youngest member. However, mothers and their young calves kept greater distances to the boat than mothers and older calves did, suggesting that the boat may be perceived as a threat during the newborn period.

Most of the behaviours that characterise mother-calf relationships varied according to calf age class. The occurrence, frequency, duration and distance of separations increased with older aged calves. A similar increase was found in the time spent without the mother, in the occurrence of association with non-mother dolphins, in the time spent in 'echelon position', and in both mothers' and calves' dive time. Mothers also had longer dive times than calves. Older aged calves tend to present the lowest proportion of synchronous breaths. These changes are likely to represent a gradual increase in calves' independence.

Results from this study have extended our knowledge of common dolphins' reproductive ecology, demonstrated that studies of mother-calf relationships in pelagic species of dolphins can be achieved, and allowed future research needs to be identified and management recommendations to be made.

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EXPLANATION OF TERMS

Calf age classes

Common dolphin calves were categorised according to their size relative to that of their mothers.

Infant: individual around half the size of the mother.

Juvenile: individual around two-thirds the size of the mother.

Newborn: individual noticeably less than half the size of the mother.

Group and individual identification

Adult: all individuals that are neither newborns, nor infants or juveniles.

Calf: general term designating non-adult dolphins and including newborns, infants and juveniles.

Group: dolphins observed in close proximity, within 200 metres of each other, and in apparent association, moving in the same direction or engaged in the same behaviour.

Mother: adult individual consistently associated with a smaller animal.

Group type

Each group of common dolphins was categorised according to the age class of its youngest member.

Group type 1: the youngest member of the group was a newborn calf.

Group type 2: the youngest member of the group was an infant.

Group type 3: the youngest member of the group was a juvenile.

Group type 4: group composed only of adults.

Activity state (definitions derived from Shane *et al.*, 1986; and Shane, 1990a)

Feeding: dolphins are involved in an effort to capture and consume prey. They are observed herding and chasing fish.

Milling: dolphins remain within a given area, not moving in any definite direction, and continuously changing their heading.

Resting: dolphins are grouped in a tight formation and are moving slowly at the surface in a co-ordinated manner, and in one particular direction.

Socialising: dolphins are essentially involved in social behaviours, such as mating, rubbing and playing. Much physical interaction and surface displays can be observed.

Travelling: dolphins are all moving at a sustained speed in a persistent direction.

Mother-calf relationships

Allomaternal behaviour: association of a calf with a non-mother dolphin.

Calf solitary surfacing: calf breaks the surface of the water for a breath on its own.

Echelon position: calf is swimming alongside its mother, paralleling her course less than 30cm from her side.

Infant position: calf is swimming underneath its mother.

Nursing position: the calf's rostrum is in contact with the mother's mammary slit area for over two seconds.

Overlapping surfacing: mother and calf break the surface of the water one immediately after the other, resulting in a breathing overlap.

Separation: observable increase (>1 metre) in the distance between a calf and its mother.

Synchronous surfacing: mother and calf break the surface of the water in perfect unison.

Reaction to the boat

Attraction: the dolphins are coming towards the boat, swimming at the bow for extended periods of time and staying around the boat even if stopped.

Avoidance: dolphins are continuously changing their heading away from the boat.

Neutral: no observable reaction or change in the behaviour of the dolphins can be noticed, they are not attracted to the boat and neither avoiding it.

Mating behaviours

Mating behaviours with genital contact: genital-to-genital presentation, beak-to-genital contact.

Mating behaviours without genital contact: non-genital contact including rubbing, chase, leap, head slap.

Oceanographic seasons

Summer: January to March.

Autumn: April to June.

Winter: July to September.

Spring: October to December.

Chapter 1: INTRODUCTION

Common dolphins (*Delphinus delphis*) represent one of the most abundant and most widely distributed species of cetaceans (Evans, 1987). They can be found in all oceans and all seas of the world, and their abundance has been estimated to a few million (Gaskin, 1992). Paradoxically, common dolphins also represent one of the least studied species to date, and our knowledge on many aspects of their life history and behaviours appears to be rather limited.

For many years, post-mortem data from stranding events and fisheries by-catch have represented the only source of information available on common dolphins. Scientific investigations of wild populations of common dolphins have indeed been restricted by several of the factors that characterise the species. Common dolphins usually inhabit deep offshore waters that can prove difficult to access on a regular basis for researchers (Evans, 1987). Therefore, many of the observations made on wild common dolphins have remained of anecdotic status. Common dolphins are also mostly found in relatively large and fast moving groups (Dawson, 1985; Evans, 1994), limiting the range of data that can be collected, as well as the possibility of studying individual animals. As a result, most of the information found in the literature regarding common dolphins relates to their anatomy, genetics, and biology, and many of the questions regarding social organisation that have been answered for other cetacean species have not yet been addressed for common dolphins.

In order to enhance our knowledge of common dolphins, a few recent studies have focused on documenting the behaviour and ecology of the species. The identification of common dolphin populations located closer to shore, and the use of consistent surveys, have enabled these studies to gather relevant information on the distribution and abundance of the species in different locations (Bearzi *et al*., 2003; Neumann, 2001; Cañadas *et al*., 2002; Dohl *et al*., 1986; Goold, 1998; Selzer and Payne, 1988), as well as on seasonal movements (Dohl *et al*., 1986; Forney and Barlow, 1998; Yukhov *et al*., 1986; Bearzi *et al*., 2003; Würsig *et al*., 1997; Neumann, 2001; Goold, 1998; Selzer and Payne, 1988), and feeding strategies and activity budgets (Neumann, 2001). Some insights into common dolphins' social organisation were also provided by the study conducted by Neumann (2001). Although these findings provide basic data on common dolphins and constitute the foundation for further research to take place, several other aspects of common dolphins' behaviour need to be investigated in order to reach a better understanding of the population dynamics of the species. The main goal of this study is to redress the lack of information in certain areas of our knowledge of common dolphins, and more specifically to contribute to an increased understanding of their reproductive ecology.

The importance of studying the reproductive patterns of a species in order to comprehend its social organisation has been emphasised by several authors (Townsend, 1935; Sverdrup *et al*., 1942; Whitehead and Mann, 2000; Thayer *et al*., 2003). In fact, reproduction is one of the main drivers of animals' social behaviour, and as such, it has been identified as being the source of most of the behavioural biology that characterise a species (Townsend, 1935; Sverdrup *et al*., 1942). In cetaceans, only females actively parent and therefore, their role as a mother represents a fundamental element of any whale or dolphin population and is likely to influence its social structure (Whitehead and Mann, 2000). For these reasons, investigating the reproductive strategies used by female cetaceans appears to be of primary importance in order to appreciate the dynamics of a population (Whitehead and Mann, 2000; Thayer *et al*., 2003).

The only delphinid species for which female reproductive strategies and mother-calf relationships have been extensively studied is the bottlenose dolphin (*Tursiops truncatus*) (Evans, 1987; Whitehead and Mann, 2000). These studies have emphasised the conditions favoured by females in the production and care of their young, and this has lead to an enhanced understanding of the behavioural ecology of the species (Mann and Smuts, 1998, 1999; Mann *et al*., 2000). In the field of reproductive ecology, breeding seasonality represents the only variable ever investigated for common dolphins. However, many studies have relied on the analysis of postmortem specimens, which may not always provide reliable conclusions (Fernandez and Hohn, 1998). Observations of wild populations have lead to some interesting results, but the significance of breeding seasonality for the species has never been discussed.

In an attempt to obtain an insight into female reproductive strategies and mother-calf relationships in common dolphins, a 14-month study was conducted in the Hauraki

Gulf, New Zealand. The waters of the Hauraki Gulf provide a great opportunity to further our knowledge of common dolphins. Compared to other locations worldwide, common dolphins can be found in relatively shallow waters and in smaller groups (O'Callaghan and Baker, 2002), allowing observations to take place on a daily basis and providing suitable conditions to monitor their behaviour. Common dolphins are also found year-round in the Hauraki Gulf, which enables the investigation of temporal patterns such as breeding seasonality. The objectives for this study are represented by the following general research questions:

1) Do the common dolphins in the Hauraki Gulf display reproductive seasonality?
2) What are the specific characteristics of common dolphin groups containing calves?
3) What is the role of the Hauraki Gulf for female common dolphins?
4) What are the behavioural patterns that describe the relationships between calves of different age and their mothers?

Answering these questions will have different beneficial outcomes. Firstly, it will enable us to increase our knowledge of common dolphins in a field never investigated before for the species. Secondly, due to the important role of mother-calf relationships within cetacean populations, a better understanding of females' reproductive strategies will lead to a better appreciation of the potential effects of different growing threats on the dolphins. Thirdly, the results of this study will provide baseline data on different characteristics of common dolphin groups, as well as on mother-calf relationships. The importance of baseline observations has been emphasised by different authors, especially in investigating the impact of tourism on the dolphins (Bejder and Dawson, 1999; Constantine, 1999), as they enable the identification of subsequent changes in the behaviour of the animals, and allow researchers to consider them relative to changes in their environment.

The content of this thesis is set as follows (Figure 1):
Chapter 2 presents a review of the current literature available on common dolphins, as well as on mother-calf relationships in other delphinid species. Based on this knowledge, specific hypotheses are developed in order to investigate the general research questions outlined above. The methods used to collect data during field observations are described in chapter 3. In chapter 4, the results of the statistical

analysis conducted on the empirical data are presented for each of the hypotheses investigated in this study. In chapter 5, results on common dolphins' breeding seasonality, on the characteristics of common dolphin groups containing calves, and on common dolphin calves' development are discussed in light of other studies conducted on similar topics. The significance of each of these results is also reviewed. Finally, chapter 6 summarises the main findings of this study, outlines their implications for the common dolphins of the Hauraki Gulf, and includes suggestions for future research and recommendations for the conservation of the species.

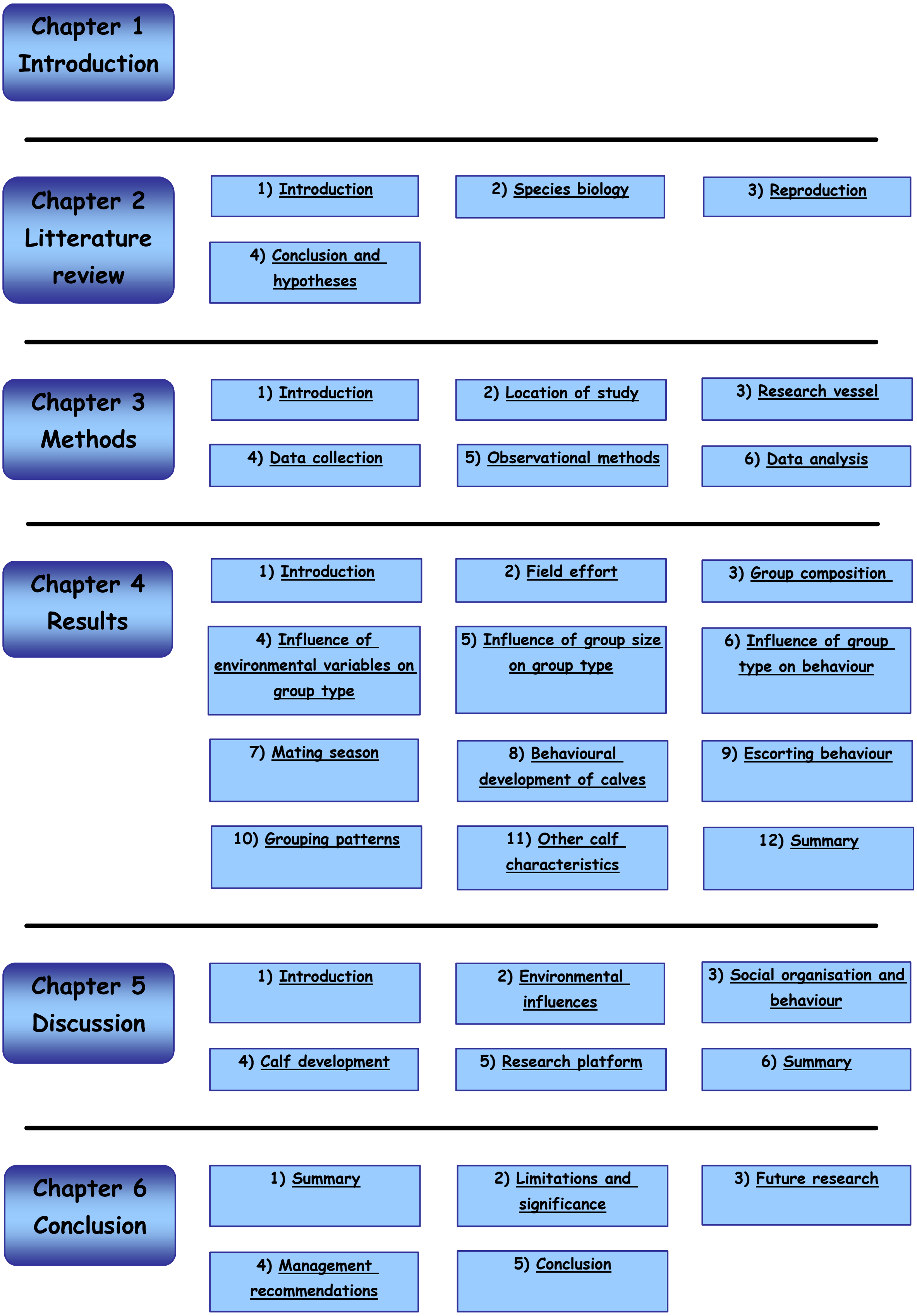


Figure1. Thesis structure diagram

Chapter 2: LITERATURE REVIEW

1) Introduction

The purpose of this chapter is to review the current state of knowledge on the biology and reproduction of common dolphins. The different topics addressed are summarised in figure 2. The first part concentrates on a general presentation of the species; and topics related to its taxonomic status, biology, distribution and abundance, and ecology are discussed. Description of common dolphins' habitat, social organisation, feeding strategies, vocalisation, and conservation are included within the ecology subsection. This review provides insights into common dolphins' society, which are necessary in order to understand their reproductive patterns.

Life history parameters related to reproduction, along with the reproductive ecology of common dolphins are presented in the second part of this chapter. The areas of common dolphins' reproduction still to be investigated are identified in this section. Firstly, the reproductive biology of common dolphins is described, using published data on the gestation period, pregnancy rate, interbirth interval, parturition process, physical characteristics of calves and their growth, lactation and weaning, and sexual maturity. Secondly, the behavioural aspects of reproduction are reviewed, providing information on mating and calving, as well as on calf behavioural development, mother-calf relationships and allomaternal behaviour. When specific data on common dolphins is lacking, relevant information available for other cetacean species is presented.

Finally, in the last section of this chapter, the status of knowledge on common dolphins' reproduction is summarised. Emphasis is made on those areas where little or no empirical data are available, and leads to the presentation of hypotheses designed to address some of these deficiencies, thus providing the rationale for the study reported in subsequent chapters.

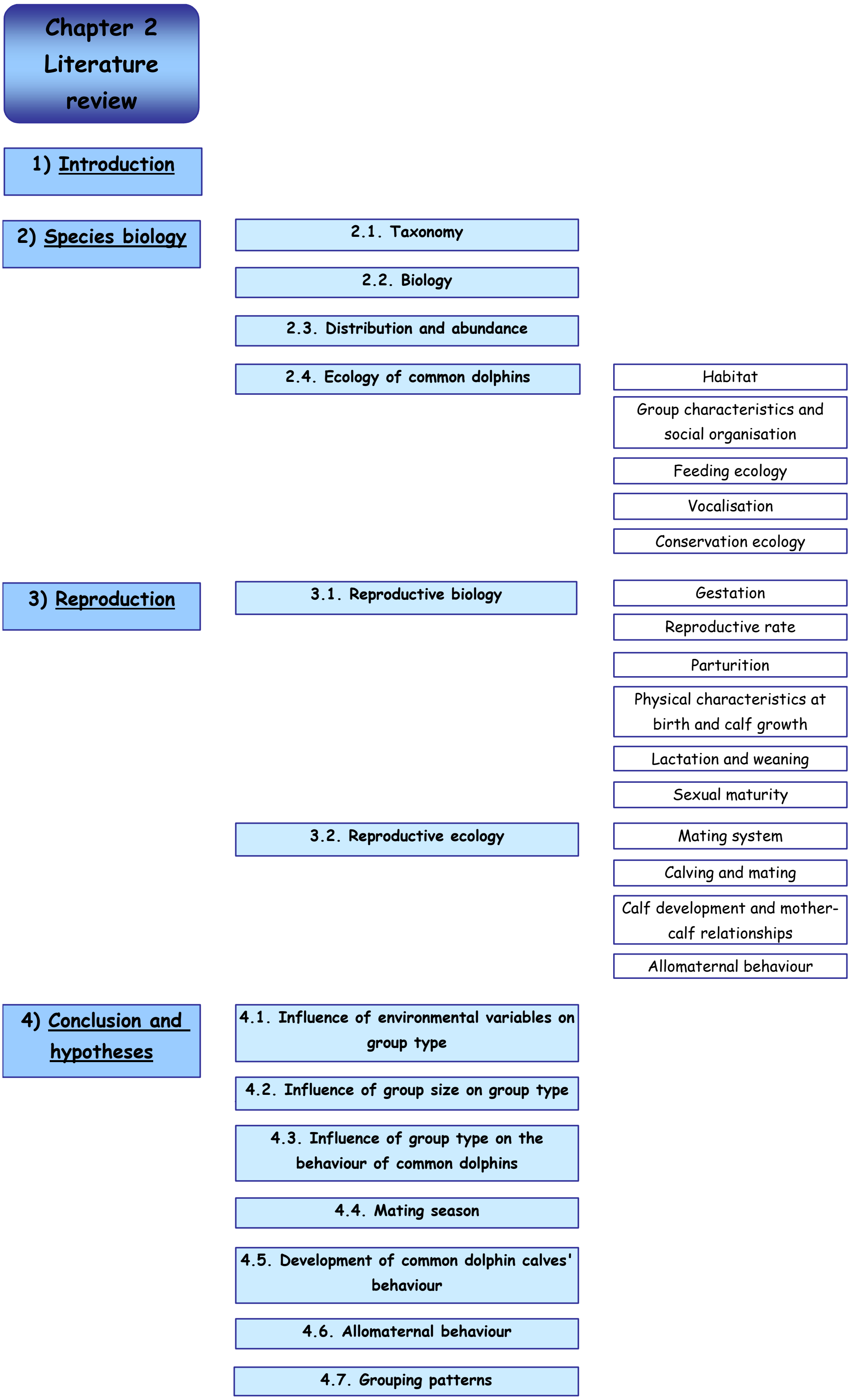


Figure2. Structure diagram of the 'Literature review chapter'.

2) Species biology

2.1. Taxonomy

Since the description of the genus *Delphinus delphis* by Linnaeus in 1758, the taxonomy of the common dolphin species has been a well-discussed topic within the scientific community, and at least 24 nominal species have been proposed (Hershkovitz, 1966; Hall, 1981; Gaskin, 1992; Perryman and Lynn, 1993; Heyning and Perrin, 1994; Carwardine, 1995). Until recently, most authorities agreed on the existence of one species worldwide: *Delphinus delphis*, while the differentiation into subspecies remained a matter of opinion. The several differences between the short-beaked common dolphin, *Delphinus delphis*, and the long-beaked common dolphin, *Delphinus capensis*, were acknowledged by most authors; but while some claimed that these differences resulted from two distinct evolutionary lines (Dall, 1873; Banks and Brownell, 1969), others believed that the two morphotypes represented the extremes of a single species that do not interbreed (Hershkovitz, 1966; Van Bree and Purves, 1972; Mitchell, 1975).

The analysis of 320 specimens of common dolphins from the Northeast Pacific Ocean by Heyning and Perrin (1994) based on colour pattern, body length and cranial morphology, strongly suggested that the short-beaked and long-beaked forms should be considered as two different species, at least for that particular stock. They also provided strong evidence against the hypothesis of a continuum between these two forms (Heyning and Perrin, 1994). Their work was further confirmed through genetic studies by Rosel *et al*. (1994), who proved that the two Northeast Pacific populations do not share any mitochondrial DNA haplotypes, and therefore are reproductively isolated from one another.

The status of three other potential subspecies has remained controversial throughout the years and is still being investigated today: *Delphinus bairdii* Dall, a neretic form which has a range limited to Baja California in the Northeast Pacific Ocean (Banks and Brownell, 1969), *Delphinus tropicalis*, a very long-beaked form in the Northern Indian Ocean (Van Bree, 1971; Honacki *et al*., 1982; Rice, 1998; Jefferson and Van

Waerebeek, 2002), and *Delphinus delphis ponticus* Barabash, an endemic subspecies in the Black Sea (Barabash, 1935; Tomilin, 1957; Heptner *et al*., 1996).

The species of common dolphins inhabiting New Zealand waters has not been genetically investigated, thus limiting knowledge of its taxonomic status to assumptions. Based on anatomical observations, it has been suggested that the common dolphins found around the coast of both the North and the South Islands, including the Hauraki Gulf, correspond to the short-beaked form (Gaskin, 1972). Even though no definite conclusion can be drawn until further research is completed, it is assumed that the short-beaked common dolphin, *Delphinus delphis*, was investigated in the present research project and will therefore be referred to as such throughout the study.

2.2. Biology

Upon sighting of a common dolphin, one of the most striking external features is its colouration (Plate 1). Its criss-cross colour pattern has been described as one of the most complex of any cetacean (Mitchell, 1970), and it constitutes a prime criterion to visually distinguish common dolphins from any other delphinid species (Evans, 1994). The interaction of the dorsal overlay and cape forms the common dolphin four-part hourglass colour pattern of dark grey to black dorsally, buff to pale yellow anterior thoracic patch, light to medium grey on the flank, and a white abdominal field (Mitchell, 1970; Nishiwaki, 1972; Perrin, 2002). This unique colouration has evoked alternative names for common dolphins around the world; such as whitebelly dolphin in the Eastern Tropical Pacific, or saddleback dolphin on the Atlantic coast (Evans, 1994). Although a general pattern of external appearance can be described, common dolphin colouration is probably the most variable and unstable characteristic of the species (Evans, 1994). Such variation, not only between but also within each subspecies (Heyning and Perrin, 1994; Carwardine, 1995), excluded its use as a taxonomic criterion (True, 1889).

Evans (1994) claimed that sexual dimorphism can be observed in the colouration near the genital area, with male common dolphins presenting a black blaze just above the genital region, while females have a narrow band of black with grey countershading in the same area. However, this pattern varies between and within stocks (Evans, 1994).


Courtesy of Dirk Neumann

Plate 1. Common dolphins are characterised by a unique colour pattern.

While working with short-beaked common dolphins in the Northwestern Bay of Plenty, New Zealand, Neumann (2001) did not manage to distinguish males and females on this criterion, as the genital blaze was only apparent on a small number of individuals. However, he proved that common dolphins are sexually dimorphic in the morphology of their peduncle, with only sexually mature males presenting a postanal hump (Neumann, 2001). At sea, differential identification of male and female common dolphins can prove difficult as sexual differences, such as size and colouration, are subtle and hard to distinguish (Carwardine, 1995). In some cases, the sex of the animals can be inferred from behavioural clues. In fact, as male dolphins do not tend to provide parental care to their young (Caldwell and Caldwell, 1972; Wells *et al.*, 1987; Whitehead and Mann, 2000), those individuals consistently accompanied by a calf can be sexed as females with reasonable certainty (Wells *et al.*, 1987).

Other external anatomical characteristics of short-beaked common dolphins include a prominent beak demarcated from the melon, an erected recurved dorsal fin, and pointed pectoral fins (Nishiwaki, 1972; Gaskin, 1992; Evans, 1994). The pectoral and dorsal fins of adult individuals usually present light grey to white patches with diffused edges (Heyning and Perrin, 1994). Dorsal fin colouration, along with its shape, has been successfully used for photo-identification of common dolphins in previous studies (Neumann, 2001; Neumann *et al.*, 2002). The dorsal fin also tends to be sexually dimorphic, being larger in adult males than females (Heyning and Perrin, 1994).

If we only consider *Delphinus delphis*, the mean adult body length usually ranges between 1.80m and 2.30m (Gaskin, 1992; Evans, 1994), but larger individuals of length up to 2.6m (Katona *et al.*, 1993; Evans, 1994), as well as smaller specimens (Heyning and Perrin, 1994; Perrin, 2002; Silva and Sequeira, 2003) have been recorded. Mean adult weight ranges from 80kg to 136kg (Evans, 1994). Male common dolphins are on average 5% larger than females, but it should be noted that these measures also vary geographically (Nishiwaki, 1972; Evans, 1994; Heyning and Perrin, 1994; Silva and Sequeira, 2003).

Until today, the life span of common dolphins has only been estimated. Data from the Black Sea suggest that males can live up to 22 years and females up to 20 years (Klinowska, 1991).

2.3. Distribution and abundance

Delphinus delphis represents the most abundant and the most widely distributed dolphin species throughout the world's oceans (Dohl *et al*., 1986; Evans, 1994; Perrin, 2002), hence its name: the common dolphin. It is recognised that despite its vast range, its population is organised in a series of geographically distinct subpopulations (Gaskin, 1992; Carwardine, 1995; Heyning and Perrin, 1994; Perrin and Brownell, 1994; Jefferson and Van Waerebeek, 2002), which probably have a relatively low rate of genetic interchange (Gaskin, 1992; Natoli *et al*., in press).

Short-beaked common dolphins are generally found in the Northwest Atlantic from Newfoundland to Florida; in the Northeast Atlantic from the North Sea to Gabon, including closed seas such as the Mediterranean, the Red Sea and the Black Sea; in the Southwest Pacific around New Caledonia, New Zealand and Tasmania; in the Northwest Pacific from Honshu to Taiwan; and in the Northeast Pacific from Northern California to Central Chile (Evans, 1994; Heyning and Perrin, 1994) (Figure 3). Although this represents the general distribution of common dolphins around the world, there have been sightings both North and South of these points (for example, in Northern British Columbia, Western Canada: Leatherwood *et al*., 1982; Evans, 1994; and in Norway: Haug *et al*., 1981).

Short-beaked common dolphins are found around most coasts of New Zealand but their exact distribution varies seasonally (Gaskin, 1968; Bräger and Schneider, 1998). Their distribution has been described as meso-pelagic and it was suggested that their occurrence southward is more restricted in winter than in summer (Gaskin, 1972). Most sightings occur off the East coast of both the North and the South Islands, especially in the Eastern Cook Strait, in the Hauraki Gulf, around Eastern Northland (Gaskin, 1972), and in the Bay of Plenty (Neumann, 2001) (Figure 4). Common dolphins are seen less often on the West Coast, and sightings have been reported predominantly during the summer season (Gaskin, 1972; Bräger and Schneider, 1998).

Although no exact number appears to be available, most authors believe that the worldwide abundance of short-beaked common dolphins reaches a few million, which makes them by far the most abundant dolphin species (Gaskin, 1992). Nonetheless,

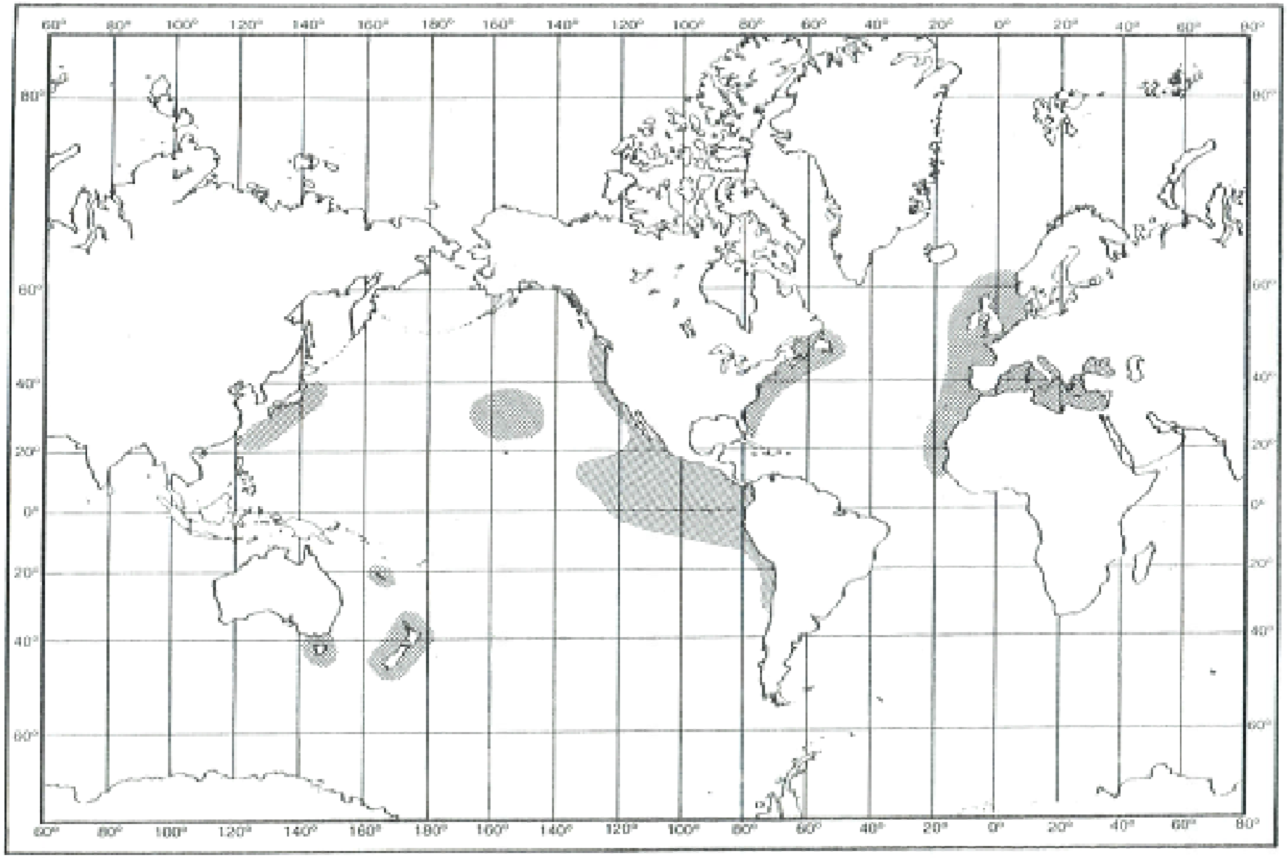


Figure 3. Distribution of common dolphins worldwide. The grey areas represent the known range of the species. (Source: Heyning and Perrin, 1994)

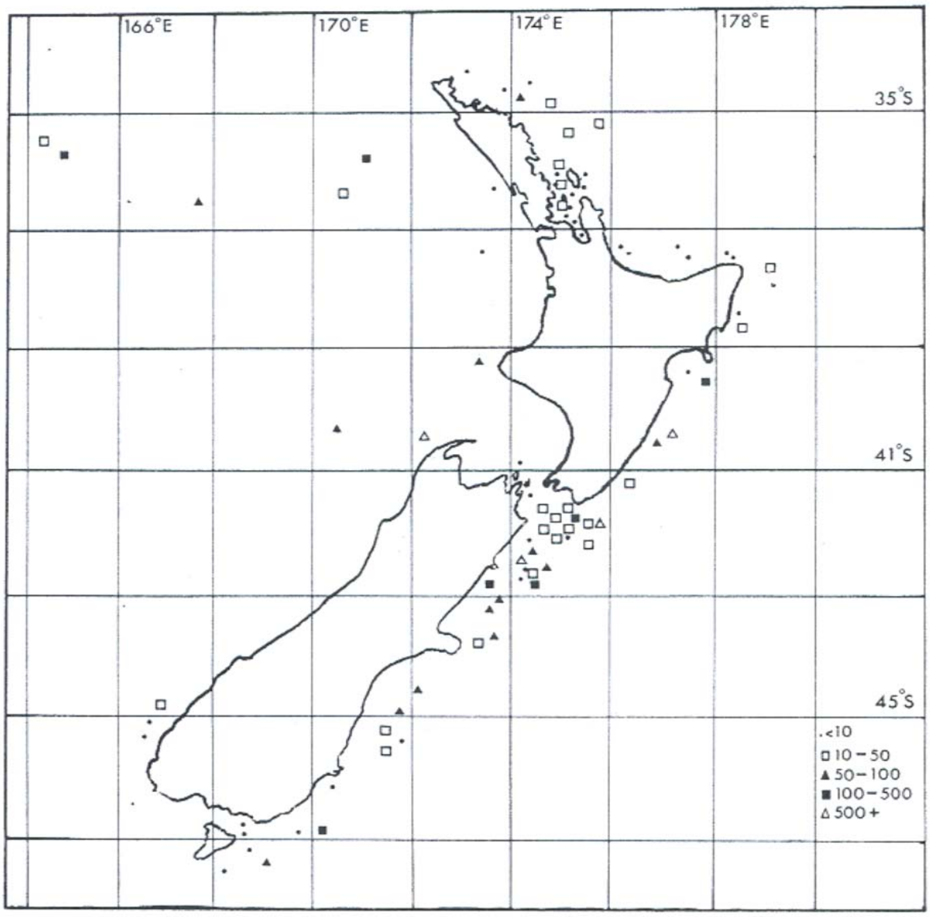


Figure 4. Summer distribution of common dolphins around New Zealand. The legend refers to the number of dolphins sighted.
(Source: Gaskin, 1968)

there have been a number of population abundance investigations for specific areas and an estimate of 3,112,300 was made for the entire Tropical Eastern Pacific (Holt and Sexton, 1990), and a conservative estimate of more than 30,000 common dolphins are believed to inhabit the North Atlantic (Nishiwaki, 1972; Winn, 1982). For the Black Sea, two different surveys have been conducted: aerial surveys yielded an estimate of 50,000 common dolphins (Yukhov *et al*., 1986), while ship-based line-transects estimated a total of 96,000 animals (Sokolov *et al*., 1997). In New Zealand waters, it is reported that common dolphins are the most abundant cetacean; however no estimate of population size has been made (Dawson, 1985). Until recent years, the worldwide population of common dolphins was believed to be relatively stable, but declines have been identified both in the Mediterranean and in the Black Sea (Viale, 1994; Carwardine, 1995; Gannier, 1995; Stanev, 1996). Common dolphins used to be abundant in many parts of the Mediterranean; areas from where they are now absent or extremely rare (Bearzi *et al*., 2003). Bearzi and colleagues (2003) propose that this decline could be the result of different factors including pollution, overfishing of food resources, indirect catches and unregulated direct exploitation.

2.4. Ecology of common dolphins

- Habitat

Dolphin species have been classified into two generic categories according to their habitat: pelagic species, which inhabit offshore oceanic waters, and coastal species, found inshore and along shorelines (Wells *et al*., 1980; Evans, 1987). *Delphinus delphis* is recognised as a pelagic dolphin, primarily distributed along the edge of the continental shelf and only venturing occasionally into shallow inshore waters (Selzer and Payne, 1988; Gaskin, 1992; Evans, 1994). Common dolphins have been recorded in depths between 26 and 5121m (Winn, 1982), but are more often found between 100 and 1000m depth contours (Selzner and Payne, 1988; Cañadas *et al*., 2002). Although common dolphins appear to be resident in some part of their range (Carwardine, 1995; Politi, 1998), seasonal movements have been reported for many populations (Southern California: Dohl *et al*., 1986; Northeastern Pacific: Forney and Barlow, 1998; Black Sea: Yukhov *et al*., 1986; Mediterranean: Bearzi *et al*., 2003; New Zealand: Würsig *et al*., 1997; Neumann, 2001; Northeast Atlantic: Goold, 1998; North West Atlantic:

Selzer and Payne, 1988). These movements, as well as common dolphins' distribution, are influenced by a great number of variables including: sea surface temperature (Gaskin, 1968; Banks and Brownell, 1969; Selzer and Payne, 1988; Goold, 1998; Neumann, 2001), salinity (Selzer and Payne, 1988), prey availability (Evans, 1980; Haug *et al.*, 1985; Cockcroft and Peddemors, 1990; Evans, 1994; Young and Cockcroft, 1994), thermocline (Reilly, 1990), oxygen minimum layer (Polachek, 1987), and sea floor profile (Hui, 1979a, 1985; Dohl *et al.*, 1986; Selzer and Payne, 1988; Gaskin, 1992).

Common dolphins favour tropical, subtropical and warm temperate waters (Selzer and Payne, 1988; Gaskin, 1992; Evans, 1994; Goold, 1998). In their study, Selzer and Payne (1988) recorded common dolphins in waters ranging from five to 22.5°C with a mean of 11°C. Winn (1982) found similar results with temperatures comprised between one and 24°C, and 90% of the sightings being between seven and 22.4°C. On the East Coast of New Zealand, *Delphinus delphis* are associated with a minimum sea surface temperature of about 14°C (Gaskin, 1968; Webb, 1973a, 1973b; Bräger and Schneider, 1998). Many authors recognise that the influence of sea temperature on the dolphins might only be secondary. The distribution of common dolphins is more likely to reflect that of their favoured prey species, which are in turn influenced by water temperature (Banks and Brownell, 1969; Selzer and Payne, 1988; Bräger and Schneider, 1998; Goold, 1998; Neumann, 2001).

One of the most specific characteristics of common dolphin habitat is probably its tendency to be located in areas of steep sea floor relief, above conspicuous features such as sea mounts or escarpments (Hui, 1985; Dohl *et al.*, 1986; Selzer and Payne, 1988). Yet again, bottom topography is more likely to have a primary influence on food availability, rather than a direct effect on the dolphins' distribution (Hui, 1985). As a result of topographically induced upwelling, areas of high sea floor relief often offer nutrient-rich waters carried upward towards the surface (Sverdrup *et al.*, 1942) and may provide greater feeding opportunities for species such as the common dolphin (Evans, 1974; Au and Perryman, 1985).

- Group characteristics and social organisation

Common dolphins are usually found in large active herds, in which members can often be seen leaping in synchrony (Dawson, 1985; Jefferson *et al.*, 1993; Evans, 1994; Carwardine, 1995). A wide range of group sizes have been recorded for this species, with as few as about 10 individuals and up to schools of over 10,000 animals (Heyning and Perrin, 1994). Mean group size varies significantly from one population to another but also within populations (illustrated by results in Hui, 1979a; Evans, 1980; Dohl *et al.*, 1986; Notarbartolo di Sciara *et al.*, 1993; Cañadas *et al.*, 2002; Mussi *et al.*, in press; Vella, in press; Politi and Bearzi, in press), and can partially depend on assessment methods and the group definition used in different studies. Group size can also vary according to water depth (Cañadas *et al.*, 2002), season (Hui, 1979a; Evans, 1980; Dohl *et al.*, 1986) and time of the day (Carwardine, 1995). These factors could be related to feeding efficiency and the need for smaller or larger groups depending on the type of prey available in a particular environment (Würsig, 1986).

Common dolphins are known to sometimes associate with other cetacean species. In the Mediterranean, mixed groups of *Delphinus delphis* and striped dolphins (*Stenella coeruleoalba*) are often encountered (Cañadas *et al.*, 2002; Frantzis and Herzing, 2002). In these waters, they have also been sighted with Risso's dolphins (*Grampus griseus*) (Cañadas *et al.*, 2002; Frantzis and Herzing, 2002) and bottlenose dolphins (Politi *et al.*, 1994; Bearzi and Notarbartolo di Sciara, 1995). Association with Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (Brown and Norris, 1956; Evans, 1994), pilot whales (*Globicephala* spp.) (Evans, 1994; Cañadas *et al.*, 2002; Perrin, 2002), dusky dolphins (*Lagenorhynchus obscurus*) (Würsig *et al.*, 1997), and various species of Mysticete whales (Evans, 1994; Sei whale *Balaenoptera borealis*, Bryde's whale *Balaenoptera edeni* and Minke whale *Balaenoptera acutorostrata*: Neumann, 2001) have also been reported.

Large schools of common dolphins are thought to be composed of smaller units of about 20 to 30, perhaps closely related, individuals (Evans, 1980, 1994). Like most species of oceanic dolphins, it is probable that common dolphins live in a fission-fusion society, in which the composition of large schools change from day to day but still include some long-term associations and functional subgroups (Norris and Dohl, 1980a; Wells *et al.*, 1999; Neumann, 2001). Functional division and sex and/or age segregation appears to occur in many different dolphin species and populations (Sergeant *et al.*, 1980; Perrin and Reilly, 1984; Wells *et al.*, 1987; Perryman and Lynn, 1994; Rogan *et al.*, 1997; Cox *et al.*, 1998). Evidence for such segregation in common dolphins has been provided by the analysis of by-catch data (Ferrero and Walker, 1995; Silva and Sequeira, 2003) and by active observations of wild populations (Neumann, 2001). Both types of studies suggested the existence of three types of groups within common dolphin society:

- nursery groups containing only females, including pregnant and lactating females with their calves,
- mixed groups of both sexes and all ages, and
- male bachelor groups composed either exclusively of immature males or males of all ages.

The segregation of females in order to form nursery groups has been reported for a number of dolphin species (bottlenose dolphins: Shane *et al.*, 1986; Wells *et al.*, 1987; Scott *et al.*, 1990; Bel'kovitch, 1991; Mann and Smuts, 1999; Dall's porpoises *Phocoenoides dalli* and harbour porpoises *Phocoena phoconea*: Read and Hohn, 1995; dusky dolphins: Würsig and Würsig, 1980; Hawaiian spinner dolphins *Stenella longirostris*: Johnson and Norris, 1994). When the bond with the mother is broken, the young leave these groups to form juvenile pods of similar aged individuals, either of the same sex (usually males) or of mixed sex (Tyack, 1986; Wells *et al.*, 1987; Evans, 1987).

- Feeding ecology

Common dolphins prey on a wide variety of fish and squid species and their diet is known to go through annual and seasonal fluctuations due to changes in prey availability and abundance (Young and Cockcroft, 1994). Their diet also varies with location but generally depends on small, mesopelagic shoaling fish species (like sardines, anchovies, mackerel and pilchard) and squid from the deep scattering layer (Pascoe, 1986; Evans, 1987; Overholtz and Waring, 1991). Young and Cockcroft (1994) analysed the stomach contents of 297 common dolphins and found 36 different fish species in their samples. However, 86.9% by weight of their diet was made up of only five prey species (dominated by pilchard), which strongly suggest that common dolphins are opportunistic feeders (Young and Cockcroft, 1994). They also showed a clear difference in the contribution of particular prey species to the diet of males and females: mature females tend to have a more diverse diet, which suggest that females feed actively on prey species other than the more abundant pilchard, or that they feed as opportunistically as possible (Young and Cockcroft, 1994). This trend towards a more diverse diet appears to be related to the higher energy demands faced by females (Young and Cockcroft, 1994). Females' reproductive state has also proved to have an influence on diet in many different dolphin species (examples include bottlenose dolphins: Cockcroft and Ross, 1990; spinner dolphins and spotted dolphins *Stenella attenuata*: Bernard and Hohn, 1989), including common dolphins (Young and Cockcroft, 1994).

Research conducted in Southern California showed that common dolphins tend to start feeding at dusk and continue throughout the night (Evans, 1994). Until the study by Neumann in 2001, feeding strategies of common dolphins had not been described in detail. The only information available beforehand consisted of diving depths involved in foraging, which were reported to occur between nine and 50 metres (Evans, 1994). Neumann (2001) described different methods used by this species in the context of feeding; most of them involving cooperation between individuals. Carouseling, which consist of dolphins cooperatively surrounding a school of fish, was most frequently observed, suggesting that it might represent the most efficient strategy for preying on small schooling fish in the open ocean (Neumann, 2001).

- Vocalisation

Common dolphins' vocalisations have not been studied as extensively as those of bottlenose dolphins. However, common dolphins are known to produce the entire acoustic repertoire common to most delphinids; including whistles, echolocation clicks and burst-pulse sounds (Moore and Ridgway, 1995). Recordings made from large schools show that common dolphins are very vocal and tend to synchronise their whistling with the other members of the group (Evans, 1994). The predominant sounds produced by common dolphins vary with the time of the day, and could be due to a differential activity budget during day and night (Evans, 1994). Their high-pitched squeals can be heard above the surface as the dolphins ride the bow of boats (Dawson, 1985; Jefferson *et al*., 1993).

- Conservation ecology

The conservation status of the world population of common dolphins is considered as being at lower risk by the 1996 IUCN Red List of Threatened Animals (Baillie and Groombridge, 1996). The recent decline observed in the Mediterranean subpopulation was considered by the IUCN in 2003, and the status of common dolphins was reclassified as endangered for that particular area (Bearzi, 2003). Although the worldwide population is not under threat, the factors that are causing problems in the Mediterranean could also potentially be affecting other subpopulations.

Incidental catches by commercial fisheries is an extended problem and the common dolphin represents the most prominent by-caught species every year for both the pelagic purse-seine and drift net fisheries (Evans, 1994). For example, in 1988, an estimate of 16,189 (± 1300) common dolphins were killed in the purse-seine tuna fishery in the Eastern Tropical Pacific (Hall and Boyer, 1990). Common dolphins have also been considered as competitors by a number of fishing communities. As a consequence, direct kills of the species were common practice in the 1950s. Common dolphin meat was also used for human consumption in the Black Sea (Gaskin, 1992) and still is in some areas (Kemper *et al.*, 2001; Bearzi *et al.*, 2003). Other potential threats include overfishing of common dolphins' food resources, as well as habitat degradation (Bearzi *et al.*, 2003; Bearzi, 2003). Global warming, which in some areas induces a rise in water temperatures and therefore modifies prey distribution, is affecting the marine ecosystem dynamics, including all cetacean species that inhabit this ecosystem (Viale, 1994; Bearzi *et al.*, 2003). It has been suggested that increases and decreases in the relative abundance and distribution of small cetaceans off the Northeast coast of the United States (Katona *et al.*, 1993; Kenney *et al.*, 1996) could to be due to this phenomenon (Palka *et al.*, 1997). Finally, high contamination rates of organochlorines such as PCBs (polychlorinated biphenyl) have been reported in different areas (Mediterranean: Vicente and Charbert, 1978; Viale, 1994; Bearzi *et al.*, 2003; Atlantic and Pacific coasts of the United Stated: O'Shea *et al.*, 1980; Eastern Atlantic: Alzieu *et al.*, 1982). These increases in pollution levels can induce changes in distribution of the species, and can result in immunosuppression and reproductive impairment (Viale, 1994; Bearzi *et al.*, 2003).

3) Reproduction

3.1. Reproductive biology

- Gestation

Pregnancy is rather difficult to assess in wild populations of cetaceans, but some observations have proved successful. Using underwater visual inspection of increased girth and swollen abdomens in Atlantic spotted dolphins (*Stenella frontalis*), Herzing (1997) was able to identify mid-term pregnancies. Connor *et al.* (1992a) also reported that swelling is visible two or three months prior to parturition in Indian Ocean bottlenose dolphins. In captive bottlenose dolphins, movements of the foetus in the mother's belly can sometimes be observed (McBride and Kritzler, 1951). However, the classification of a female dolphin as having been pregnant still relies on the later observation of a calf (Wells *et al.*, 1987; Herzing, 1997).

Like many of dolphins' life history parameters, the gestation period varies between species, among populations of the same species, and depends on the assessment methods used within studies. In odontocetes, the length of gestation tends to increase with the size of the animals (Whitehead and Mann, 2000) and ranges from nine months for the harbour porpoise and the pygmy sperm whale (*Kogia breviceps*) (Harrison, 1969; Whitehead and Mann, 2000) to 15 or 16 months for the sperm whale (*Physeter macrocephalus*), pilot whale and killer whale (*Orcinus orca*) (Harrison, 1969; Perrin and Reilly, 1984; Whitehead and Mann, 2000). Gestation periods reported for common dolphins range between 9.2 (Asdell, 1964) and 11.3 months (Danil and Chivers, 2003), with most values between 10 and 11 months (Harrison, 1969; Harrison *et al.*, 1969; Gaskin, 1972, 1992; Perrin and Reilly, 1984; Ferrero and Walker, 1995). This pattern fits with records for other species of same approximate size (10-12 months for *Stenella* and *Lagenorhynchus* spp.: Perrin and Reilly, 1984).

- Reproductive rate

The reproductive rate of a species can be described at the population level with the annual pregnancy rate, but also at the individual level with the mean interbirth interval. These two parameters are logically correlated, as more births are expected within a year if intervals between births are rather small. Both parameters are known to vary between species and between populations of the same species (Whitehead and Mann, 2000). The annual pregnancy rate recorded for common dolphins in the Black Sea is the highest of all delphinids, with 75% of females being pregnant on any given year (Perrin and Reilly, 1984). However, other values reported for the Black Sea and the Eastern Tropical Pacific stocks average around the 43% mark (Perrin and Reilly, 1984; Danil and Chivers, 2003). For spinner dolphins in the Eastern Tropical Pacific, which inhabit a similar niche, share similar schooling characteristics and are about the same size as common dolphins (Whitehead and Mann, 2000), Perrin and Reilly (1984) reported an annual pregnancy rate of between 26.5 and 30.8%.

The time interval between each birth is strongly influenced by gestational time and duration of lactation of the species considered (Whitehead and Mann, 2000). For common dolphins, interbirth interval varies between 1.3 years in the Black Sea, which corresponds to the high reproductive rate described above, to 2.6 years in the North and Eastern Tropical Pacific (Perrin and Reilly, 1984). Some authors have reported an infertile resting period occurring every three pregnancies (Harrison *et al.*, 1969; Gaskin, 1972). Perrin and Reilly (1984) report that spinner dolphins have calves every 2.9 to 3.3 years, spotted dolphins every 2.5 to 3.9 years, and striped dolphins every 1.4 to 4.2 years; which is, on average, less often than common dolphins do.

- Parturition

While cetacean births are only rarely observed in the wild, captivity offers the opportunity to describe such events in detail (Evans, 1994). From captive observations and post-mortem inspections of pregnant females, it appears that female dolphins tend to produce a single calf, with twin births only occurring occasionally and usually resulting in non-viable calves (Harrison, 1969; Evans, 1987; Van Waerebeek and Read, 1994; Wells and Norris, 1994; Whitehead and Mann, 2000). Singleton births are likely to be favoured by the need for large neonates and the importance of fast growth of calves in an aquatic environment (Whitehead and Mann, 2000). The calf is born tail first (Harrison, 1969; McBride and Kritzler, 1951; Wells and Norris, 1994). Harrison (1969) suggested that, due to the unique body shape and physiology of foetal odontocetes, caudal presentation is more likely to produce successful births. Even though some births are known to have taken up to two hours, parturition is usually rapid and calves are born within half an hour after start of labour (McBride and Kritzler, 1951; Schroeder, 1990). When the foetus falls free, the mother typically whirls about face, which induces the umbilical cord to break (McBride and Kritzler, 1951). Schroeder (1990) noticed that six of the seven births observed at the Naval Ocean Systems Centre occurred at night. This could explain why observations of parturition in the wild are so rare, but this hypothesis remains to be tested as females might also isolate themselves from human contact during such events.

- Physical characteristics at birth and calf growth

At birth, dolphin calves present a number of specific characteristics that differentiate them from older individuals. The most striking one is obviously size (Plate 2). In fact, body length, from the birth of the calf onwards, can be used to obtain an estimation of its age, although accuracy is likely to decrease as the calf grows (Jonsgård, 1969). Many cetacean studies have used body length of the animals in order to classify them as neonates, or as calf versus non-calf (common dolphins: Würsig, 1986; Perryman and Lynn, 1993; Heyning and Perrin, 1994; Silva and Sequeira, 2003; bottlenose dolphins: Cockroft and Ross, 1990; Hansen, 1990; Mead and Potter, 1990; Urian *et al.*, 1996; Bearzi *et al.*, 1997; Grellier *et al.*, 2003; Thayer *et al.*, 2003; spinner dolphins: Norris *et al.*, 1994; spotted dolphins: Herzing, 1997). In common dolphins, adult length varies between and among populations and the same type of variation is found when considering the size of newborn calves. A relatively wide range of lengths at birth have been recorded, from a minimum of 75cm (Harrison *et al.*, 1969; Mitchell, 1975; Gaskin, 1992) up to 105cm (Perrin and Reilly, 1984), with numerous intermediate values averaging between 80 and 90cm (Bryden, 1972; Collet, 1981; Perrin and Reilly, 1984; Evans, 1994; Ferrero and Walker, 1995; Perrin, 2002; Jefferson *et al.*, 1993; Whitehead and Mann, 2000; Danil and Chivers, 2003). Such small sizes don't remain for very long

Plate 2. Mother-calf pair of common dolphins. The size of the calf compared to that of the adult suggests its very young age.

as delphinids' postnatal growth is very rapid and almost linear for the first year (Bryden, 1972; Perryman and Lynn, 1993; Read *et al.*, 1993).

In the North Pacific, common dolphins gain on average 20 to 25cm in the first six months of life, and about 40 to 45cm within the first year (Ferrero and Walker, 1995). By the age of two years, common dolphins' growth starts to slow but they do not reach asymptotic length before the age of seven (Ferrero and Walker, 1995). The male growth curve through age two is also slightly steeper than that portion of the female growth curve, meaning that over that period of time males gain more length than females (Ferrero and Walker, 1995). Higher growth rates have been reported for common dolphins in the Eastern Tropical Pacific and could reflect different adaptive strategies to temperate and tropical ocean habitats (Danil and Chivers, 2003).

Another characteristic of newborn common dolphins is their colouration. In some cetacean species, important colour differences exist between mothers and their calves. In the beluga whales (*Delphinapterus leucas*) for example, adult females are white but give birth to dark grey calves (Sims *et al.*, 2003). Spotted dolphin calves are born without any speckles but they acquire them as they grow older (Herzing, 1997). Common dolphin calves look much like their mothers: the intricate criss-cross pattern is already present, but pigmentation is not yet fully developed and young individuals are usually of lighter colour than adults (Gaskin, 1972) (Plate 3). They also lack distinct patches on their dorsal fins; however these will increase in contrast with age (Heyning and Perrin, 1994).

Newborn dolphins can also be identified as such by the presence of foetal lines on their body (Plate 4). These vertical lines are located symmetrically on each side of the trunk and lack pigmentation (McBride and Kritzler, 1951). They are produced by the folded posture of the foetus as it lies in the uterus, and the fact that they occur on both sides of the body indicates that the foetus shifts this flexure from side to side (McBride and Kritzler, 1951; Wells, 1991a). Foetal folds are particularly visible on bottlenose dolphin calves, which bear a series of five to seven of these lines (McBride and Kritzler, 1951; Cockroft and Ross, 1990; Mann and Smuts, 1999). In this species, they have been reported to disappear by about three months of age, although individual variations may


Courtesy of Nicola Clark

Plate 3. Newborn common dolphin showing the typical criss-cross colouration that characterises the species but with a lighter pigmentation than the adult it accompanies.

Courtesy of Karen Stockin

Plate 4. Young calves usually bear white markings on either side of their trunk called foetal folds, which can be observed on this common dolphin calf.

occur (Mann and Smuts, 1999). Foetal lines are present on most dolphin newborns, including common dolphins (Neumann, 2001).

Foetal folds are not the only remains of the neonatal folded posture. Dolphins are usually born with soft and bent pectoral and dorsal fins (Plate 5), while the fluke is curled downwards (McBride and Kritzler, 1951). For bottlenose dolphins, the fins stiffen and straighten during the first two weeks of postnatal development and do not appear to impair swimming abilities (McBride and Kritzler, 1951). Similar development would be expected in most odontocetes but whether it occurs at the same rate is still to be investigated.

Several criteria have been used within cetacean research in order to differentiate newborn calves from older individuals. Along with size, the different aspects of newborn anatomy, such as calf colouration (used in studies of bottlenose dolphins: Bearzi *et al.*, 1997; Grellier *et al.*, 2003; beluga whales: Sims *et al.*, 2003; spotted dolphins: Herzing, 1997), the presence of foetal folds (Hector's dolphins *Cephalorhynchus hectori*: Bejder, 1997; bottlenose dolphins: Connor *et al.*, 1996; Bearzi *et al.*, 1997; Grellier *et al.*, 2003; spinner dolphins: Norris *et al.*, 1994; spotted dolphins: Herzing, 1997), the observation of a folded dorsal fin (bottlenose dolphins: McBride and Kritzler, 1951; Mead and Potter, 1990; Fernandez, 1992; Bearzi *et al.*, 1997; Thayer *et al.*, 2003; spinner dolphins: Norris *et al.*, 1994), or a curled tail fluke (bottlenose dolphins: McBride and Kritzler, 1951; Fernandez, 1992; spinner dolphins: Norris *et al.*, 1994), have all been used to estimate the age of calves, whether they are used separately, combined, or along with other behavioural characteristics.

- Lactation and weaning

In all cetacean species, the newly born calf is highly dependent upon its mother for food and starts nursing on the fat-rich milk she produces within a few hours after birth (Caldwell and Caldwell, 1972). Compared to domesticated mammals, cetacean milk is rather high in fat and protein while relatively low in lactose (Harrison, 1969), and its composition seems to be influenced by the species habitat as well as by the stage of lactation (Peddemors *et al.*, 1989).

Plate 5. Newborn common dolphin showing a bent dorsal fin characteristic of its young age.

The female's nipples are located on her ventral side, about three quarters of the way from the rostrum to the tail tip. As a consequence, in order to suckle her young, a mother will have to roll on her side or let the calf swim under her (Cockroft and Ross, 1990). Either way, nursing takes place underwater, usually close to the surface (Harrison, 1969), probably so the calf can easily reach the surface for a breath between nursing bouts. While nursing occurs mostly in 'infant position' (with the calf swimming underneath its mother) (Mann and Smuts, 1998), some females have been observed rolling on their side to facilitate nursing (McBride and Kritzler, 1951; Cockroft and Ross, 1990; Wells, 1991a; Johnson and Norris, 1994; Gubbins *et al.*, 1999; Mann and Smuts, 1999). When side presentations do occur, they seem to be limited to the first few weeks of life; the calf being forced to roll under the mother thereafter (McBride and Kritzler, 1951; Cockroft and Ross, 1990; Gubbins *et al.*, 1999).

The exact rate at which a calf suckles is quite difficult to establish, as the observation of a calf in nursing position does not systematically imply that milk is transferred or that the individual in the position of the mother is a female (Whitehead and Mann, 2000). Nonetheless, different studies have been able to show that nursing frequency decreases as calves grow older (McBride and Kritzler, 1951; Harrison, 1969; Cockroft and Ross, 1990; Nordensten *et al.*, 2003). The length of nursing bouts is limited by the amount of time a calf can remain submerged and thus are relatively short during the first few weeks of life (Harrison, 1969). As the calf's nursing efficiency increases, it will be able to nurse for longer periods of time (Cockroft and Ross, 1990; Nordensten *et al.*, 2003); although overall, bout length also tends to decrease with age (Cockroft and Ross, 1990; Reid *et al.*, 1995). As infants slowly increase their fish intake, nursing events become less numerous. Odontocetes wean their offspring gradually, allowing infants to acquire the necessary foraging skills before they are completely dependent on solid food (Oftedal, 1997). With time, the infant will develop accurate feeding strategies and will spend more time foraging (Whitehead *et al.*, 2000). In the wild, weaning can be hard to determine but is usually marked by the absence of 'infant position' swimming and a significant drop in mother-calf association (Mann *et al.*, 2000).

Lactation is relatively costly for female dolphins (Whitehead and Mann, 2000). Producing milk implies high metabolic demands that they can satisfy by either increasing the quantity of prey eaten, or by selecting food of higher calorific value

(Bernard and Hohn, 1989). It has been shown that the diet of lactating female common dolphins is different to any other age and/or sex class, and is likely to be related to the specific requirements involved in lactation (Young and Cockroft, 1994).

The length of time for which calves nurse is extremely variable between species, as well as among individuals within a population, and appears to be influenced by a number of factors (Harrison, 1969; Perrin and Reilly, 1984; Whitehead and Mann, 2000). In most cetacean species, calves nurse for much longer than is required for survival (Tyack, 1986), and it has been suggested that such prolonged periods of lactation may be linked to the importance of social learning in these species (Brodie, 1969). Different values have been reported for common dolphins and there seems to be a disagreement on the length of their lactation period. Whereas Bryden (1972) reported a lactation duration of four months, later observations suggested that common dolphins calves usually nurse for longer periods: lactation periods of six months (Leatherwood *et al*., 1982; Perrin and Reilly, 1984), 10 months (Collet, 1981; Gaskin, 1992), 16 months (Danil and Chivers, 2003) and even up to 19 months (Perrin and Reilly, 1984) were found in different studies. Evans (1994) reported that common dolphin calves in the Eastern Pacific start taking fish anywhere between two and three months of age, but weaning is unlikely to be achieved for another few months as calves have milk and squid in their stomach up to about one year of age. Whitehead and Mann (2000) suggested that the lactation period of six months reported for common dolphins could be the result of dubious data. In comparison, most other odontocetes usually suckle for 12 to 18 months (Whitehead and Mann, 2000). The variation in values reported for common dolphins remains to be explained, but Perrin and Reilly (1984) suggested that it could potentially be linked to the year in which the assessment took place, to the state of exploitation of the population studied, and to the differences that exist between stocks. Other factors identified to influence the duration of lactation include milk composition, feeding strategies and food availability, the reproductive state of the mother, and degree of conflict between optimal length for the mother and optimal length for the calf. Weaning tends to occur earlier when milk contains a high percentage of fat (Bonner, 1984). Interestingly, it has been reported that common dolphin milk is richer in protein than in calcium (Peddemors *et al*., 1989). Also, in bottlenose dolphins, which wean at a later age, milk fat content is much lower than values reported for common dolphins (Cockroft and Ross, 1990). Considering feeding strategies, the duration of lactation is likely to be related to the difficulty of methods used to find and catch food (Whitehead and Mann, 2000). Such factor will determine the amount of time required for a calf to learn to feed itself efficiently and therefore how long it has to rely on its mother for food (Whitehead and Mann, 2000). The availability of food could have the same type of impact on the length of lactation, as a mother might speed up an infant's learning to forage where fish resources are plentiful (Caldwell and Caldwell, 1972). The lactation period also seems to depend on the age of females (Marsh and Kasuya, 1991; Whitehead and Mann, 2000). Many of the explanations available on the variations in age at weaning between and within species do not go beyond the stage of hypotheses and further investigations are required in order to understand patterns of calves' feeding dependency. As for the particular case of common dolphins, the exact lactation time for different subpopulations has yet to be confirmed.

- Sexual maturity

As with all other cetacean life history parameters, the age and size at sexual maturity varies between species, between populations of the same species, and even within populations (Collet and Girons, 1984; Bryden and Harrison, 1986; Whitehead and Mann, 2000; Perrin, 2002). Overall, female common dolphins tend to reach sexual maturity before males do. The youngest age and size were recorded in the Black Sea with females reaching sexual maturity between two and four years of age and length of 150-170cm, while males are sexually mature at three years of age and 170-180cm (Perrin and Reilly, 1984). In the North Pacific, different results were obtained with females averaging seven years of age and about 170cm at sexual maturity, and 10 years of age and about 180cm for males (Hui, 1979b; Ferrero and Walker, 1995; Perrin, 2002). For the Eastern Tropical Pacific, Danil and Chivers (2003) showed that females reach sexual maturity at a mean of 8.1 years and 185.9cm in length, and Perrin and Reilly (1984) showed that males reach sexual maturity around six or seven years of age and at an approximate length of 200cm. Finally, in the North Atlantic, females were found to be sexually mature between six and seven years of age and at lengths of about 190cm, and males between five and seven years and about 200cm (Collet, 1981; Collet and Girons, 1984; Perrin and Reilly, 1984; Evans, 1994).

As a general rule, female cetaceans start to reproduce when at about 85 to 95% of their mean adult body length (Whitehead and Mann, 2000), and this is consistent with the data available on common dolphins. It is assumed that before reaching such length, the potential benefits of producing an offspring are outweighed by the demands on the mother's growth (Whitehead and Mann, 2000).

The variation observed in age and length at sexual maturity can be explained by biological and ecological factors, as well as by the different ageing methods used across studies (Collet and Girons, 1984; Wells *et al*., 1987; Ferrero and Walker, 1995). Most of the variation between species in age at first reproduction is likely to be the result of a different growth rate (Whitehead and Mann, 2000). Within a species, climate, duration of lactation, diet, exploitation, date of birth and order of birth (Bryden and Harrison, 1986), habitat (Bryden, 1972) and population density (Perrin, 2002) have been identified to potentially affect age at sexual maturity.

3.2. Reproductive ecology

- Mating system

The mating system of a species refers to the strategies used by both males and females in order to reproduce. Five generalised systems have been identified in animals: monogamy where one male mates with one female in a breeding season (Alcock, 1998), polygyny where a single male controls the access to a group of females (Wells *et al*., 1987; Alcock, 1998), polyandry where one or two sexually mature females bear the young for the whole group (Wells and Norris, 1994; Alcock, 1998), polygynandry where males mate with sexually mature females and both sexes have multiple partners (Wells and Norris, 1994), and promiscuity where mate choice is absent and both males and females mate randomly (Wells and Norris, 1994). Determining the mating system of cetacean species represents a challenge, as certain measures are uneasy to access in an aquatic environment, and female choice might be playing a more important role than in other species (Whitehead and Mann, 2000). Considering the fluid association patterns that characterise delphinid species, including common dolphins, the lack of male parental care and the relative large size of males testes, it seems that dolphins' mating system is rather polygamous than monogamous (Wells *et al*., 1987). Although it doesn't seem very likely that a male dolphin would be able to guard a particular female during her entire period of receptivity (Wells *et al*., 1987), polygyny has been suggested for a few cetacean species (Evans, 1987). Within a polyandrous system, long term associations between individuals would be favoured, which does not appear to be the case in cetaceans (Wells *et al*., 1987). Wells and Norris (1994) suggested that Hawaiian spinner dolphins are polygynandrous. Several studies have also supported the hypothesis of promiscuity (Würsig and Würsig, 1980; Evans, 1987). Other mating systems could also have evolved due to the particular environment cetaceans live in (Whitehead and Mann, 2000). While monogamy and polyandry can apparently be excluded from the mating systems of delphinids, further investigations are required in order to test the hypotheses of polygyny and promiscuity (Wells *et al*., 1987).

- Calving and mating

In all wild populations of delphinids studied to date, mating and calving have been reported to occur seasonally (Perrin and Reilly, 1984; Tyack, 1986; Evans, 1987; Whitehead and Mann, 2000). Even though females are capable of giving birth throughout the year, births usually take place during one or two fairly restricted periods (Bryden and Harrison, 1986; Tyack, 1986; Urian *et al*., 1996). The duration of the peak calving season, although occurring in all species, varies in length and can be spread over a few weeks in some populations, while births will take place over a few months in others (Whitehead and Mann, 2000).

Seasonal peaks in births have been observed in all populations of common dolphins worldwide, including New Zealand, and have been estimated to spread over an average of four months (Whitehead and Mann, 2000). Two trends can be identified when looking at the breeding season of common dolphins, with either one single peak in the late spring or summer months (Gaskin, 1972; Jefferson *et al*, 1993; North Eastern Pacific: Leatherwood *et al*., 1976; Ferrero and Walker, 1995; Danil and Chivers, 2003; North Eastern Atlantic: Collet, 1981; Evans, 1987; Black Sea: Sleptsov, 1940; Gaskin, 1992; Evans, 1987; Mediterranean: Universidad Autónoma de Madrid and Alnitak, 2002), or two annual peaks, one in the spring and autumn (Jefferson *et al*., 1993; North Eastern Pacific: Evans, 1987; Evans, 1994; Ferrero and Walker, 1995). Southern California is the only location for which most common dolphin births have been recorded in the midwinter months (Evans and Bastian, 1969; Harrison *et al.*, 1969; Harrison *et al.*, 1972). Around New Zealand, groups of common dolphins that include newborn calves are more likely to be sighted during the summer months (Webb, 1973b; Constantine, 1995; Bräger and Schneider, 1998; Neumann, 2001). Sightings of neonates during winter in populations that show a summer breeding season (Universidad Autónoma de Madrid and Alnitak, 2002) support the fact that female common dolphins are able to breed year round.

Similar patterns are found in most odontocete species and births are usually distributed as follows:

- mainly during the summer months (spinner dolphins: Harrison *et al.*, 1969; Atlantic white-sided dolphins *Lagenorhynchus acutus*: Evans, 1987; Pacific white-sided dolphins: Evans and Bastian, 1969; Harrison *et al.*, 1969; Evans, 1987; bottlenose dolphins: ; Wells *et al.*, 1987; Hansen, 1990; Connor *et al.*, 1996; Urian *et al.*, 1996; Bearzi *et al.*, 1997; Kasuya *et al.*, 1997; Grellier, 2000; Thayer *et al.*, 2003; dusky dolphins: Würsig and Würsig, 1980; Cipriano, 1992),
- spread over spring and summer (bottlenose dolphins: Evans, 1987; harbour porpoises: Read and Hohn, 1995; spinner dolphins: Evans, 1987; Risso's dolphins: Evans, 1987),
- birth peaks restricted to spring for a few populations (bottlenose dolphins: Asdell, 1964; Harrison *et al.*, 1972; Mead and Potter, 1990; Fernandez and Hohn, 1998; Dudzinski, 1999; spotted dolphins: Harrison *et al.*, 1969),
- bimodal spring and fall birth peaks observed occasionally (spotted dolphins: Evans, 1987; Herzing, 1997; bottlenose dolphins: Scott *et al.*, 1990; striped dolphins: Evans, 1987),
- and no exclusive winter breeding season reported for any species.

In all animal species, it is widely accepted that breeding seasonality is used as a means to increase calf survival. A number of different factors that could influence the survival of newborn dolphin calves have been identified and their variation may explain the seasonality of reproduction in odontocetes (Thayer *et al.*, 2003). These include: availability of food (Barros and Odell, 1990; Urian *et al.*, 1996; Mann *et al.*, 2000; Whitehead and Mann, 2000; Danil and Chivers, 2003), oceanographic and climatic parameters (Perryman and Lynn, 1993; Ferrero and Walker, 1995; Mann *et al.*, 2000), day length (Ridgway, 1972; Mann *et al*., 2000), water temperature (Ridgway, 1972; Wells *et al*., 1987; Urian *et al*., 1996; Bearzi *et al*., 1997; Mann *et al*., 2000; Whitehead and Mann, 2000), and predation pressure (Wells *et al*., 1987; Mann and Smuts, 1998). Besides explaining timing in births, some of these factors are also likely to reflect the variations that exist between and within species.

For many cetacean species, studies have shown a change of habitat during the peak birth period and an extensive use of shallow areas during that time (for example in southern right whales *Eubalaena australis*: Payne, 1976; Elwen and Best, 2004b; humpback whales *Megaptera novaeangliae*: Smultea, 1992; dusky dolphins: Cipriano, 1992; bottlenose dolphins: Würsig and Würsig, 1977; Wells *et al*., 1987; Wells, 1991a; Mann *et al*., 2000; Hector's dolphins: Bräger *et al*., 2003). Common dolphins have been reported to move further inshore during what appears to be the main reproductive season (Bräger and Schneider, 1998; Neumann, 2000). However, whether these movements are exclusively determined by reproductive needs, or whether they are food-related, remains unknown.

Breeding seasonality implies timing of mating activities, and therefore the mating season of any given species should be influenced by the need to give birth during the appropriate season, as well as by the gestation period. Investigating mating seasonality can be achieved by either analysing biological variables related to reproduction (such as testosterone and progesterone levels, ovulation or testes size) or by observing mating behaviours. Mature common dolphins seem to go through seasonal patterns of sexual activity, with males presenting variation in spermatogenesis, and females ovulating seasonally (Ridgway, 1972; Collet and Girons, 1984). As would be expected, these cycles differ from stock to stock in duration and timing (Collet and Girons, 1984; Evans, 1994). During seasonal rut, male common dolphins present a significant increase in testicular size, prostate and muscles associated with reproductive organs (Evans and Bastian, 1969; Wells, 1984). Male seasonality has been suggested for other cetacean species (striped dolphins: Tomilin, 1957; harbour porpoises: Read and Hohn, 1995; spinner dolphins: Wells, 1984; dusky dolphins: Van Waerebeek and Read, 1994). Some of these studies managed to show that the seasonal maximum in testis size and activity occurred at the same time as the peak period of sexual activity and conception (Wells, 1984; Van Waerebeek and Read, 1994). Less is known about the cycle of reproductive activity in female dolphins but they seem to go through a number of periods of receptivity, associated with multiple ovulations (Wells, 1984). Patterns of behavioural sexual activity can also be used to identify mating seasons, as they are known to follow seasonal variations in some species (Evans and Bastian, 1969). Although it can prove difficult to distinguish social from sexual behaviours in cetaceans (Evans and Bastian, 1969; Norris and Dohl, 1980b; Wells, 1984), a variety of studies have managed to show that the occurrence and frequency of courtship behaviours are closely linked to copulatory events (Puente and Dewsbury, 1976), as well as ovulation in females and high testosterone levels in males (Wells, 1984).

- Calf development and mother-calf relationships

Very little is known about calf development and mother-calf relationships in common dolphins. The review of the literature presented here relies heavily on data available for bottlenose dolphins, as most studies on the subject have concentrated on that species.

Unlike most mammalian species which produce altricial offspring, female cetaceans give birth to precocial young that possess many of the sensory and locomotion abilities necessary for survival (Whitehead and Mann, 2000; Evans, 1987). This is likely to be highly important for species living in a marine environment, as females will have less means to keep their calves close to them (Whitehead and Mann, 2000). Although dolphin calves are able to swim quickly after birth (Wells and Norris, 1994), they will improve their motor coordination in the first few months of life (Cockroft and Ross, 1990; Mann and Smuts, 1999). The movements of young calves are usually exaggerated and characterised by wriggling, tilting and rapid course changes (Johnson and Norris, 1994; Fellner and Bauer, 1999). They also appear to be buoyant during that newborn period (Mann and Smuts, 1999), making submergence difficult (Cockroft and Ross, 1990). This pattern is quickly superseded and increase in diving depths has been reported after the second week of life for bottlenose dolphin calves (Mann and Smuts, 1999). The development of their musculature is also marked by their surfacing behaviour (McBride and Kritzler, 1951). During the first few days, newborn bottlenose dolphins tend to present ‘corklike’ surfacing as they come up for breath (McBride and Kritzler, 1951; Peddemors, 1990; Mann and Smuts, 1999). In the following two or three weeks, calves will still surface with most of the torso clearing the water and the jaw angled at approximately 30° from the water surface (McBride and Kritzler, 1951; Peddemors, 1990; Mann and Smuts, 1999). From then on, older infants and adults will roll at the surface without bringing the jaw fully out of the water (McBride and Kritzler, 1951; Peddemors, 1990; Mann and Smuts, 1999). The observation of chin-up surfacing may prove useful in estimating the age of young calves in the wild, and has been used as such in a variety of studies (for example in Connor *et al*., 1996; Herzing, 1997; Thayer *et al*., 2003). Infant bottlenose dolphins also quickly show a highly developed physical control and this can be attested by their precocious sexuality, especially in males (Caldwell and Caldwell, 1972). Male bottlenose dolphins have been observed involved in sociosexual rubbing within the first two weeks of life (Mann and Smuts, 1999) and most of them will have mounted their mothers within the first three weeks (Caldwell and Caldwell, 1972). Such behaviours have also been reported in spotted dolphins (Herzing, 1997). This early development of sexual behaviour, many years before the onset of sexual maturity, suggests that it is important in the social lives of the animals (Wells *et al*., 1987). Besides sexual behaviours, calves rapidly develop a diverse repertoire of other displays including different body slaps, spy hops and reciprocal chases with other calves (Johnson and Norris, 1994; Connor *et al*., 2000).

Improvement in swimming efficiency is also reflected by the changes that occur in mother-calf relationships, as the acquisition and development of behavioural skills progressively lead the calf to independence from the mother (Cockroft and Ross, 1990; Mann and Smuts, 1999). Bottlenose dolphin calves synchronise breathing and swimming with their mothers soon after birth (Mann and Smuts, 1999) and throughout the early period of life, they will be kept very close alongside their mothers (Evans, 1987). The distance between common dolphins' mothers and calves at sea has been estimated to one-fourth that between dolphins of adult size (Perryman and Lynn, 1993). It is during these first few weeks of life that calves are particularly vulnerable and face high mortality rates (Wells *et al*., 1987; Hersh *et al*., 1990; Small and Demaster, 1995; Mann *et al*., 2000), resulting in a 'U-shaped' mortality curve characteristic of most mammalian populations (Ralls *et al*., 1980). During this period, mother bottlenose dolphins have proved to be very protective of their offspring, herding them from any potential hazards (McBride and Kritzler, 1951; Mann and Smuts, 1999). For example, mother-calf pairs have been reported to stay clear of feeding aggregations during the newborn period, as the 'boisterous' activity involved may potentially be dangerous for calves (Würsig, 1986). Mothers will also keep their calves in close proximity (Evans, 1987; Mann and Smuts, 1999; Keiko *et al*., 2003), and not tolerate any separations (Whitehead and Mann, 2000). However, as calves grow older, the bond with the mother weakens (Evans, 1987) and they start to separate more frequently, spend more time away from their mothers and at greater distances (Evans, 1987; Taber and Thomas, 1982; Cockroft and Ross, 1990; Reid *et al*., 1995; Mann and Smuts, 1998, 1999; Keiko *et al*., 2003; Schneider *et al*., 2003; Grellier *et al*., 2003). As calves get more control over their movements, mothers will also decrease their role in maintaining proximity to their offspring, while calves will increase their role in maintaining proximity to their mothers (Taber and Thomas, 1982; Reid *et al*., 1995; Fellner and Bauer, 1999; Mann and Smuts, 1999).

After birth, mothers and calves are in nearly constant contact; rubbing is very frequently initiated by the calf (Mann and Smuts, 1999), and play only occurs with the mother as partner (Kuczaj *et al*., 2003). With age, rubbing behaviour tends to decrease (Mann and Smuts, 1999) and social play involving association with other calves is observed more often (Evans, 1987; Mann and Smuts, 1999; Kuczaj *et al*., 2003). These early interactions with the mothers will teach calves important behavioural and social skills, and will then be extended to a more social context involving different participants (Kuczaj *et al*., 2003). Within the first few weeks of life, bottlenose dolphin mother-calf pairs are also characterised by a high degree of coordinated breathing, with most infant surfacing bouts overlapping with those of the mother (Mann and Smuts, 1999). As calves grow older and reach high levels of motor coordination, they will start to establish their own breathing rate (Cockroft and Ross, 1990) and breathing synchrony will decrease (Mann and Smuts, 1999). With age, dolphin calves also tend to favour 'infant position' swimming (underneath the mother) rather than 'echelon position' swimming (alongside the mother), which requires more mobility as the calf has to break from this position in order to take breaths (Mann and Smuts, 1999). The changes in swimming position throughout the calf's early stage of life indicate the development of skilful swimming and diving (Mann and Smuts, 1999; Keiko *et al*., 2003). These observations fit with the increase in nursing efficiency discussed earlier. In bottlenose dolphins, all patterns of calf behaviour, mother-calf proximity and spatial relationships with the mother have proved to change as a function of calf age and mark the improvement of motor coordination and swimming efficiency during the first few months of the calf's life (Mann and Smuts, 1999).

It is during that same period of time that dolphin calves develop social skills, for example, through increased levels of social play. However, motor and social development do not occur over the same length of time, and Caldwell and Caldwell (1972, p. 429) noted that 'although the period of intensive care involving constant body contact is measured in weeks, the social bond between mothers and their offspring is measured in years'. During the close associations characteristic of the postnatal period, calves not only learn to swim efficiently but also learn to recognise their mother, which is essential for their survival (Cockroft and Ross, 1990). In bottlenose dolphins, the mother starts whistling immediately after birth and this may continue for several days (Evans, 1987). Such behaviour is presumed to provide the calf with a strong acoustic imprinting stimulus and is therefore likely to play an important role in recognition of the mother (Evans, 1987). However, social learning needs to extend far beyond that period as newborn dolphin calves are highly undeveloped socially (Wells and Norris, 1994). Mother-calf relationships even extend past weaning and in bottlenose dolphin populations, calves are likely to remain with their mothers for any length of time between three and eight years (Shane *et al*., 1986; Wells *et al*., 1987; Scott *et al*., 1990; Bearzi *et al*., 1997; Grellier *et al*., 2003). Spotted dolphin calves have been reported to stay with their mothers for at least three years (Herzing, 1997) and killer whale calves may associate with their mothers all the way into adulthood (Bryden and Harrison, 1986). These long periods of social dependency emphasise the importance of mother-calf relationships in the development of calves (Grellier *et al*., 2003). During that time, mothers will improve the survival of their calves by transmitting important information relating to feeding strategies and resource distribution, recognition of the population home range and limits, predator avoidance, and patterns of social interactions (Wells *et al*., 1987; Grellier *et al*., 2003). These social aspects of dolphin calves' development are as necessary as reaching motor coordination, in order to take a step towards independence (Wells *et al*., 1987).

- Allomaternal behaviour

In cetaceans, allomaternal behaviour refers to the care of the young by animals other than the mother (Whitehead and Mann, 2000). Although such behaviour has never been investigated in *Delphinus delphis*, it appears to be common in odontocetes (Tyack, 1986) and has been reported for a few different species (bottlenose dolphins: Caldwell and Caldwell, 1972; Mann and Smuts, 1998; Keiko *et al*., 2003; sperm whales: Whitehead, 1996; spinner dolphins: Johnson and Norris, 1994; killer whales: Haenel, 1986; harbour porpoises: Anderson, 1969). Soon after birth, allomothers tend to show great interest in the calves and can often be seen swimming in association with mother-calf pairs (Evans, 1987). While separated from their mothers, calves will often be accompanied by allomothers and during that time, they will swim in echelon position, play and occasionally engage in petting or rubbing bouts (Mann and Smuts, 1998). In wild and captive bottlenose dolphins, allomothers have been observed herding calves from hazards (Essapian, 1962; Mann and Smuts, 1998) and in both populations, allonursing has been reported although it seems to be very rare (Mann and Smuts, 1998; Whitehead and Mann, 2000).

Mann and Smuts (1998) investigated allomaternal behaviour in a wild population of bottlenose dolphins and assessed the potential benefits and costs involved for each of the participants: the allomother, the mother and the calf. They showed that immature females are more likely to be attracted to the young than any other sex and /or age class (Mann and Smuts, 1998). It has been proposed that these females practice allomothering as a way to learn to parent, which would be highly beneficial when comes their turn to calve, especially in a species characterised by high first-born mortality and high offspring investment (Mann and Smuts, 1998; Whitehead and Mann, 2000). The fact that experienced females are unlikely to escort calves unless they are kin (Mann and Smuts, 1998) enhances the idea that allomothers are not purely altruistic but benefit from accompanying a calf (Whitehead and Mann, 2000), either through the gain of mothering skills, or by indirect increase of their fitness (Mann and Smuts, 1998). In their study, mothers also appeared to be quite tolerant towards other individuals accompanying their calves, which suggested that allomothering did not generate high costs for them (Mann and Smuts, 1998). However, it didn't seem to have high direct benefits either, as mothers didn't spend more time foraging when their calves were accompanied, and were not engaged in affiliative behaviours with allomothers significantly more than with any other individual (Mann and Smuts, 1998).

Nevertheless, calves were likely to gain direct benefit from allomothers, such as reduced predation risk and improved social experience, which in turn would benefit the mothers through increased infant survival and reproduction (Mann and Smuts, 1998).

4) Conclusion and hypotheses

For many years, our knowledge of delphinids' life history and reproductive parameters has exclusively relied on post-mortem examination of carcasses made available through whaling and scientific kills, fishery by-catch reports, and stranding events (Bryden and Harrison, 1986). Because stranding and by-catch data are widely available for common dolphins, their reproductive biology has been extensively studied, and is as well understood as that of any other cetaceans (Evans, 1994). However, it is only recently, with the development of long term studies of individually identified animals, that investigations on the behavioural reproductive patterns of live specimens have been conducted. The possibility of keeping small cetaceans in captivity has generated numerous observations in that field (Harrison, 1969; Evans, 1994), with most of the work concentrating on the bottlenose dolphin (Evans and Bastian, 1969; Samuels and Tyack, 2000). Information on dolphins' reproduction in their natural environment has remained rather sparse and only a small number of detailed studies are available, again mainly focusing on coastal resident populations of bottlenose dolphins (for example: Wells *et al.*, 1987; Mann and Smuts, 1999). For common dolphins, behavioural reproductive patterns have rarely been described and investigations have been limited to breeding seasonality, mainly relying on stranding and by-catch data, and captive observations of courtship behaviour. Little information is actually available on the reproductive ecology of common dolphins in their natural habitat, and even though studies of wild populations are starting to emerge, none has yet focused on describing that particular aspect of their life history. When considering the wide range of studies that have been carried out on the reproduction of bottlenose dolphins, it becomes fairly easy to identify the gaps in knowledge of common dolphins. Such aspects as ecological breeding habits, mating season, maternal care, calf behavioural development and allomaternal behaviour have never been investigated for any common dolphin population. Therefore, many questions remain to be answered in order to reach a better understanding of the species. These questions include:

- How does the pelagic habitat of common dolphins influence their breeding habits?
- What are the differences between groups with and without calves? Do they make different uses of certain locations? Do they behave differently?
- Can a mating season be identified based exclusively on observations of courtship and mating behaviours?
- What is the typical behaviour of common dolphin calves? How does the behaviour of calves change with age? Is their behaviour comparable to the descriptions made for bottlenose dolphin calves?
- Does allomaternal behaviour occur in common dolphins?
- Do mother-calf pairs segregate from other dolphins?

Considering this lack of data on common dolphin reproductive ecology, investigating these specific questions will significantly increase our knowledge of the species, and will enable to fulfil the general research objectives set for this study. Therefore, these questions were used as the framework for the research project presented in the following chapters, and lead to the creation of specific hypotheses, which were then tested empirically using data collected during field observations. These hypotheses are presented below, grouped by the specific research question they investigated.
(Note: only the test hypothesis is presented here. The null hypothesis corresponds to the reverse statement)

4.1. Influence of environmental variables on group type

The presence of different age classes within groups of common dolphins could be influenced by the ecological parameters that characterise their habitat. In order to investigate whether group type (determined by the age class of the youngest member of the group) varies according to different oceanographic conditions, the following hypotheses were tested:
H 1: group type is affected by water depth.
H 2: group type is affected by water temperature.

Although common dolphin breeding seasonality has been investigated previously, it has been shown to vary between locations. The existence of a breeding season in the study area was therefore tested by:

H 3: group type is affected by the time of the year.

4.2. Influence of group size on group type

In order to investigate whether the number of common dolphins within a group had an influence on the age class of its youngest member, the following hypothesis was tested:
H 4: group type is affected by group size.

4.3. Influence of group type on the behaviour of common dolphins

Common dolphins' behavioural characteristics could potentially be influenced by the presence of different age classes within groups. This was tested using:
H 5: common dolphins' activity state is affected by group type.
H 6: the association of common dolphins with other species is affected by group type.
H 7: the reaction of the dolphins to the approach of the boat is affected by group type.
H 8: the minimum distance between the dolphins and the boat is affected by group type.

4.4. Mating season

The possible identification of a mating season within the population of common dolphins that inhabits the study area was tested by:
H 9: the occurrence of behaviours related to mating is affected by the time of the year.
H 10: the frequency of behaviours related to mating is affected by the time of the year.

4.5. Development of common dolphin calves' behaviour

Changes in different criteria such as separations, swimming position, nursing events, breathing synchrony, dive time and minimum distance to the boat are likely to represent the evolution of calves' behaviour towards independence. A number of different hypotheses were therefore used in order to investigate such evolution.

Variations in calves' swimming position with age were tested using:
H 11: the age class of calves affects the occurrence of 'echelon position' swimming.
H 12: the age class of calves affects the occurrence of 'infant position' swimming.

H 13: the age class of calves affects the percentage of time spent in 'echelon position' swimming.
H 14: the age class of calves affects the percentage of time spent in 'infant position' swimming.

The potential changes in the characteristics of separations with the age of the calf were tested using the following hypotheses:
H 15: the age class of calves affects the occurrence of separations between mothers and calves.
H 16: the age class of calves affects the frequency of separations between mothers and calves.
H 17: the age class of calves affects the duration of mother-calf separations.
H 18: the age class of calves affects the percentage of time spent without the mother.
H 19: the age class of calves affects the distance of mother-calf separations.

To test the responsibility of both individuals in initiating and terminating separations and the eventual influence of age on this variable, the two following hypotheses were used:
H 20: the age class of calves affects the mothers' responsibility in proximity maintenance.
H 21: the age class of calves affects their own responsibility in proximity maintenance.

As common dolphin calves' dependence on their mothers' milk is expected to decrease with age, the following hypothesis was tested:
H 22: the age class of calves affects the occurrence of nursing events.

Variations in breathing synchrony between mother-calf pairs as calves age were tested using:
H 23: the age class of calves affects breathing synchrony.

The potential influence of calves' age on mothers' and calves' average dive time, as well as the differences between them, were assessed using the following hypothesis:
H 24: the age class of calves affects the mean time elapsed between breaths for both mothers and calves.

H 25: calves' mean dive times are significantly different from those of mothers.

If mothers get less protective towards their calves as they age, it could be reflected in changes in distances between the mother-calf pairs and the boat as a function of calves' age. To test such an assumption, the following hypothesis was used:
H 26: the age class of calves affects the minimum distance between mother-calf pairs and the boat.

4.6. Allomaternal behaviour

The occurrence and evolution of allomaternal behaviour in common dolphins was investigated using:
H 27: the age class of calves affects the occurrence of association with non-mother dolphins.
H 28: the age class of calves affects the frequency of association with non-mother dolphins.

4.7. Grouping patterns

In order to investigate whether pairs of mothers and their calves tend to associate with one another, and whether such pattern is influenced by the age of the calf, the following hypothesis was tested:
H 29: the age class of calves affects the presence and number of other mother-calf pairs with the focal pair.

Chapter 3: METHODS

1) Introduction

Because of the unique environment they live in, cetaceans' social behaviour can be quite challenging to study (Mann, 2000). Although aerial displays can often be observed, dolphins spend most of their time underwater and typically only appear to the human observer for short periods of time. In pelagic species such as the common dolphin, individuals are also usually found in relatively large and fast moving groups (Mann, 2000). Under these circumstances, keeping track of their movements and getting detailed descriptions of their behaviour is difficult. In order to thwart these difficulties and enhance our knowledge of the species, different observation techniques and sampling methods, particularly suited for cetacean species, have been developed and described (Mann, 1999; Whitehead *et al*., 2000).

Choosing the right methodology is a key factor in any research project. A wide range of definitions and methods are available to study whales' and dolphins' behaviour. It is important to assess the advantages and disadvantages of each and to choose the methods most appropriate for a particular study. Mann (1999, p.103) points out that 'the selection and appropriate use of sampling methods that yield unbiased estimates of behaviour are critical to the scientific validity of any study'. In order to make such a choice, different parameters need to be taken into account. Habitat, group size, rate of change in group membership, dive time, and the ability to identify individuals, are examples of the factors that can influence the study of a particular species (Mann, 1999). Thus, the different traits that characterise the behaviour and biology of a species have to be considered when choosing observational methods.

A further important criterion to be considered relates to the goals of the study. The methods used not only have to suit the species characteristics but also have to provide accurate data in order to answer the specific research questions formulated (Altmann, 1974). It is important to develop and refine definitions and fieldwork protocols, which can then be used consistently throughout the study. Such consistency increases the validity of data and can facilitate comparisons between studies (Mann, 1999). It can also enhance the internal validity of the study and reduce observational bias (Altmann, 1974). Ensuring that these requirements are fulfilled is a vital process, so that accurate observations can be made and reliable conclusions drawn.

This chapter reviews the different methods used in this study and its structure is summarised in figure 5. Firstly, the study location and the research platform are introduced. Secondly, the process of data collection is described, together with an overview of the different observational methods and definitions used. These are discussed in light of the knowledge of common dolphins' behaviour, and of mother-calf relationship studies conducted on other species. Thirdly, how the chosen methods relate to the different research questions addressed in this study is discussed, and finally, the statistical tests used to analyse the data collected in the field are presented.

2) <u>Location of study</u>

This study was conducted in the Hauraki Gulf, which is located on the East coast of the North Island, adjacent to Auckland City, New Zealand (36°-37°10'South, 174°40'-175°30'East) (Figure 6). The area was declared Marine Park in 1967, in order to conserve its many islands and the waters surrounding them (Hauraki Gulf Maritime Park Board, 1983). The Hauraki Gulf is a broad embayment, open to the North and partly protected in the East by the Coromandel Peninsula and Great Barrier Island, while landlocked to the South and West (Hauraki Gulf Maritime Park Board, 1983; Owen and Owen, 1999; Black *et al.*, 2000). It includes some 47 islands, as well as headlands and coastlines, spreading over 13,600 square kilometres of Pacific Ocean (Hauraki Gulf Maritime Park Board, 1983). Water depth within the Gulf averages between 40 and 45 metres, and water temperature covers an approximate 10-degree seasonal range, with summer highs of about 22°C and winter lows of about 12°C (Jillett, 1971; Hauraki Gulf Maritime Park Board, 1983; Bercusson, 1999). Tides in the Gulf are semi-diurnal, with two low tides and two high tides each day. The tidal range is about 1.8m on neap tides and 2.4m on spring tides (Hauraki Gulf Maritime Park Board, 1983; Bercusson, 1999). The Hauraki Gulf is home to a great variety of marine species, ranging from the microscopic plankton to some of the largest baleen whales, together with many different species of fishes, birds and dolphins (Bercusson, 1999).

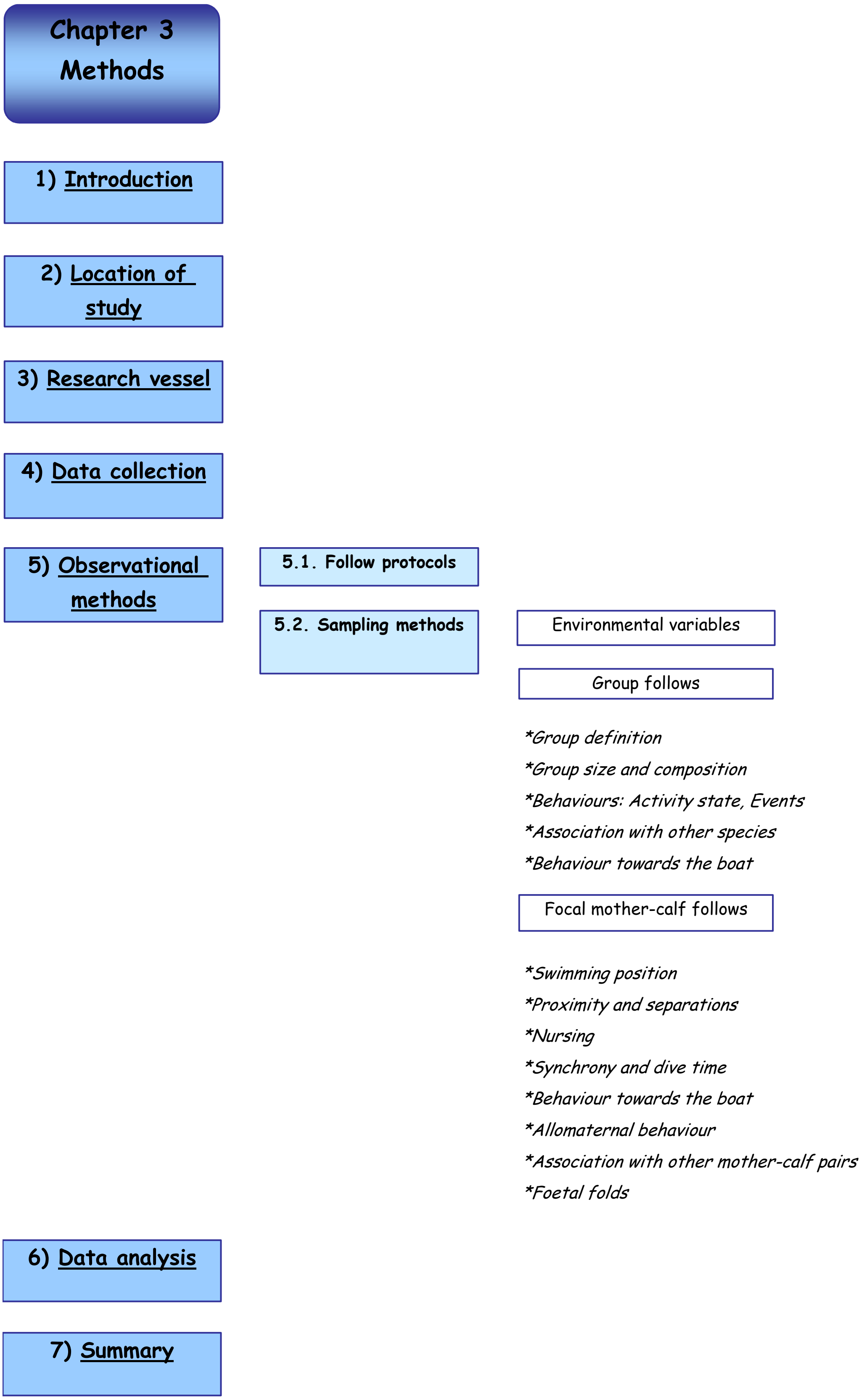


Figure 5. Structure diagram of the 'Methods' chapter.

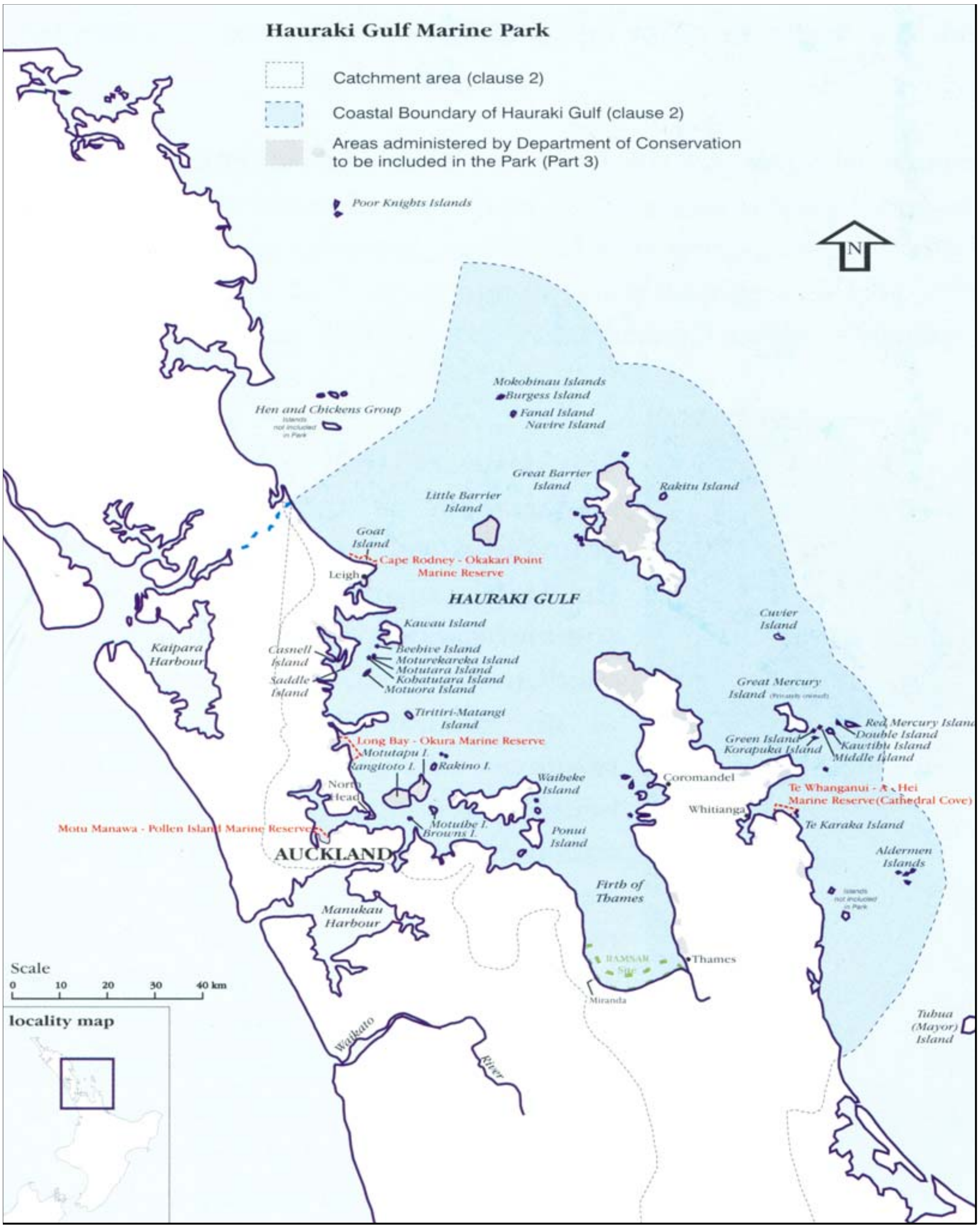


Figure 6. The Hauraki Gulf Marine Park on the East Coast of the North Island, New Zealand, where this study was conducted.
(Source: Department of Conservation, 2002)

3) Research vessel

All observations were made from onboard the commercial tourist boat 'Dolphin Explorer' (Plate 6). This operator has been conducting 'swim-with' and dolphin watching programs in the Hauraki Gulf since September 2000. 'Dolphin Explorer' operates under a permit (PER/02/03/00) issued by the Department of Conservation. This permit allows 'Dolphin Explorer' to approach dolphins and whales encountered in the Hauraki Gulf, according to the Marine Mammals Protection Regulations (Appendix 1). The species most frequently seen are common dolphins (*Delphinus delphis*) and Brydes whales (*Balaenoptera borealis*), while Sei whales (*Balaenoptera borealis*), fin whales (*Balaenoptera physalus*), bottlenose dolphins (*Tursiops truncatus*), and killer whales (*Orcinus orca*) can also be seen but on a less frequent basis. The permit also allows passengers of 'Dolphin Explorer' to swim with common dolphins under the following specific conditions:

- if the group of common dolphins encountered does not contain juveniles,
- if the group of common dolphins encountered is neither resting or feeding,
- if the group of common dolphins encountered is not located in the direct vicinity of a whale (300m).

The sea state is also considered by the skipper preceding each swim and swimming is not allowed if waves exceed half a metre.

Dolphin Explorer conducts daily trips (weather permitting, Beaufort Sea state ≤6), leaving downtown Auckland from pier 3 around 11am, and lasting five hours on average. From December 2002 to mid-February 2003, two trips were operated daily, with departure times of 8.00am and 1.30pm.

The 'Dolphin Explorer' is a 20-metre passenger catamaran, with a glass-over-ply construction, powered by two 350-horse power Scania diesel inboard engines. 'Dolphin Explorer' can reach a top speed of 22 knots, but cruising speed during dolphin trips is usually around 17 knots. 'Dolphin Explorer' offers two main viewing platforms: the top deck at an elevation of five metres above sea level, and the front deck at an elevation of two metres above sea level. The vessel has a capacity of 100 passengers, and usually has three crewmembers working onboard, with an additional fourth when the number of passengers exceeds 50.

Plate 6. 'Dolphin Explorer', the commercial tourist boat from which this study was conducted.

This operator allows students to come on board, free of charge, in order to complete their research projects. It constitutes the main research platform for a number of projects based in the Hauraki Gulf.

4) Data collection

All data were collected between the 18th of January 2003 and the 29th of February 2004. The search for the dolphins was conducted along two main routes (Figure 7):

- the 'Northern route' towards Kawau Island and Little Barrier Island,
- the 'Eastern' route towards the Coromandel Peninsula.

The decision on which route to follow was made daily by the crew depending on previous sightings, weather and any signs of bird activity, especially the Australasian gannet (*Morus serrator*). These birds can often be seen in association with common dolphins as they prey on the same fish species (Gallo, 1991; Neumann, 2001). While dolphins circle a school of fish, gannets dive from great heights into the 'fish ball' in order to feed. This was referred to as a 'work-up'. Therefore, sightings of diving birds strongly suggested the presence of dolphins in the same area. During each trip, continuous scans using hand-held binoculars were completed from the top deck of 'Dolphin Explorer' by myself, a crewmember, or any other researcher or volunteer working on the boat that day. These scans covered an area of 180° abeam of the vessel over approximately 8 kilometres in good visibility conditions (Beaufort sea state ≤ 3) and over approximately 3 miles otherwise. Sightings of the dolphins' dorsal fins and abnormal splashes at the surface were also used in order to locate the animals. However, the search relied mainly on sightings of diving aggregations of gannets; as such boisterous activity can be seen from greater distances.

Dolphins were approached according to the Marine Mammals Protection Regulations (Appendix 1) and international whale-watching guidelines (Mann, 2000). These recommendations have been set in an attempt to minimise boats' impact on dolphin behaviour. Once a group of dolphins was sighted, speed was reduced to reach a total stop approximately 400 metres away from the animals. It is assumed that this stop would give some time for the dolphins to habituate themselves to the presence of the boat, as recommended by Mann (2000). It also allowed the crew and researchers onboard 'Dolphin Explorer' to assess the dolphins' initial activity and direction of travel

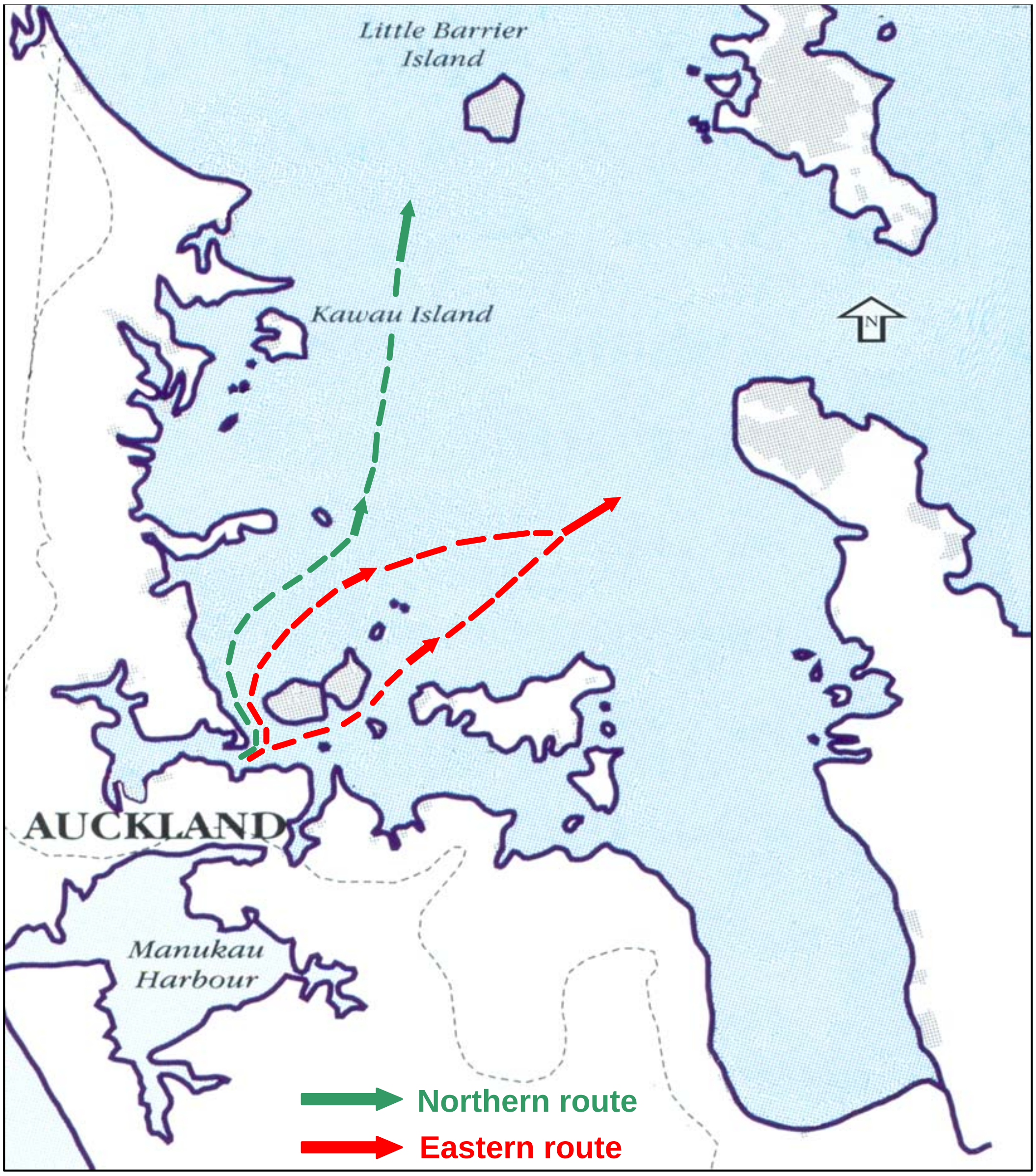


Figure 7. The two main routes taken by 'Dolphin Explorer' in search of common dolphins.

in order to approach them according to the protocols set under the Marine Mammals Protection Regulations. Specifically, ‘Dolphin Explorer’ would be piloted to parallel the course of the dolphins, slightly to the rear of the group. A slow and steady speed was also prefered. When sea conditions were calm and dolphins remained in the same area, engines were turned off in order to minimise disturbance to the animals.

Data collection started when the animals were assessed to be at around 200 metres distance from the boat. This distance provided time to record the necessary environmental variables (for example water depth and water temperature) before reaching the dolphins. As a frequent response from the dolphins to the presence of ‘Dolphin Explorer’ was to bow ride the pressure wave of the vessel, the bow of the boat represented the best viewing area. All observations were made from the port bow of ‘Dolphin Explorer’, as limited space and movement were available at the starboard bow due to the presence of the anchor. Data were recorded on an Olympus S725 Microcassette recorder, and later transferred on to Microsoft Excel data sheets.

The length of the observation sessions depended on the length of time ‘Dolphin Explorer’ would spend with a group of dolphins. The decision to leave the dolphins would always be made by the skipper and relied on different parameters. The length of the encounter was consistently taken into account as Neumann (2001) showed that common dolphins can start to react negatively to boats’ approaches after a 45-minute period. In the present study, an encounter was defined as a time period spent with the same group of dolphins. Increase in the dolphins’ swim speed, spatial avoidance (for example sudden changes in the dolphins’ direction of travel), and modification of their diving behaviour, have been described as potential signs of avoidance in previous studies (Janik, 1996; Nowacek *et al*., 2001; Jelinski *et al*., 2002; Lusseau, 2003). When such behaviour was observed, ‘Dolphin Explorer’ terminated the encounter. Finally, weather conditions, having other groups of dolphins in sight or having to return to the harbour also influenced the time spent with the animals. When leaving a group of dolphins, ‘Dolphin Explorer’ operated a 90° turn at idle speed until the dolphins were at a distance of 300 metres from the vessel as recommended by the Marine Mammals Protection Regulations (Appendix 1), and initial course was then resumed.

5) Observational methods

Observational methods refer to the protocols used during data collection. The systematic use of such protocols ensures that the information gathered in the field is consistent throughout the study and reduces bias. When choosing observational methods, two types of decisions must be made (Mann, 1999):

- the follow protocol: which individuals to focus on and for how long, and
- the sampling method: how behaviours are going to be recorded.

5.1. Follow protocols

The 'follow protocol' refers to the length of the observations and whether a group or an individual animal is going to be followed. Mann (1999) identified five different follow protocols that can be used to study cetaceans:

- surveys: minimum time is spent with the animals, the goal being to record general information on a high number of groups,
- group follows: a group of animals is monitored for an extended period of time,
- focal follows: one specific individual, or a pair, is monitored for an extended period of time,
- tracking: animals are monitored electronically (hydrophone, tagging),
- anecdote: descriptive report of an unusual event.

In this study, focal follows and group follows were combined in order to answer the research questions.

Mother-calf pairs were monitored using focal follows. Focal follows consist in sampling the behaviour of one individual or a pair within a group (Altmann, 1974; Mann, 1999). Focal animal data are ideal for studying behaviour, interaction and social relationships, and most studies of mothers and calves in cetaceans, and in other species, have relied on this protocol (for example, bottlenose dolphins: Smolker *et al.*, 1993; Mann and Smuts, 1998; Mann and Smuts, 1999; Fellner, 2000; Keiko *et al.*, 2003; southern right whales: Taber and Thomas, 1982; Thomas and Taber, 1984; vervet monkeys: Struhsaker, 1971; humans: Richards and Bernal, 1972). They allow the researcher to focus on a specific pair of individuals, to follow the stream of their behaviour, and help understand their social dynamics (Mann, 2000). In the present study, focal mother-calf follows represented the most accurate protocol to be used as they provide the best insight into their relationships (Mann, 1999). Conducting focal animal follows does not exclude the use of other types of protocols. When studying a group of animals, different methods can be combined as long as information is consistently and reliably recorded (Altmann, 1974; Mann, 2000). In this study, data on non-focal animals was collected during group follows. This type of follow protocol requires the sampling of a group as a whole. Gathering general information on the groups of dolphins encountered was necessary in order to have a broader view on the flow of events, and represented the basis for comparison between groups of dolphins with and without calves.

5.2. Sampling methods

Sampling methods refer to the procedures used to record behaviours within the different follow protocols (Altmann, 1974; Mann, 1999). *Ad Libitum* sampling has represented the most common sampling method for many decades. It consists of 'typical field notes' (Altmann, 1974), where the observer records what seems of interest without any systematic constraints (Mann, 1999). Nowadays, different methods are available and quantitative records are generally preferred to descriptive notes, as data can then be statistically analysed and may reveal correlations that would have otherwise remain undetected. The use of *Ad Libitum* sampling is still valuable in the case of rare events and anecdotal observations (Mann, 1999), and was utilised for such events in this study. However; more specific, structured sampling methods were mainly used, according to the particular research questions addressed by the present study.

- Environmental variables

The first type of data to be recorded when a group of dolphins was sighted concerned the characteristics of the area in which the animals were found. For each encounter, the following data were systematically recorded:

- date,
- time at which the animals were found, as well as the duration of the encounter,
- longitude and latitude at which they were found,
- water depth, and
- sea surface temperature.

The longitude and latitude were obtained using Global Positioning System (GPS), and position was read from the boat's depth sounder, along with the corresponding water depth. Sea surface temperature was measured from water obtained from the side of the boat, using a digital thermometer graduated in 0.1 degrees Celsius. In order to facilitate analysis and discussion of the data, dates were collapsed into months and seasons of observation. Following the accepted convention of the New Zealand oceanographic calendar (Paul, 1968), four three-months seasons were used:

- summer: January, February and March,
- autumn: April, May and June,
- winter: July, August, and September,
- spring: October, November, and December.

To investigate the influence of habitat on the breeding habits of common dolphins (hypotheses 1 to 3), the different types of groups (determined by the age class of the youngest member of the group) were compared on water depth, water temperature, months and seasons. Although it could be argued that water depth and water temperature are closely related and should not be analysed separately, the water temperature across the Hauraki Gulf on any one day tends to be relatively uniform (Paul, 1968) and therefore both factors may have differential influence on dolphins' behaviour.

- Group follows

During group follows, group composition, group activity and behaviours were continuously sampled; they were systematically recorded throughout the encounter (Mann, 1999) by repeatedly scanning the group from front to back. For each group, the minimum distance between the animals and the boat, their reaction towards the boat, and the other species associated with the common dolphins were also noted.

a. Group definition

An important first step when conducting group follows is to define what will be considered as a group (Mann, 1999). Depending on the context, a group can designate the functional association of different subgroups, a location-based aggregation, or a social unit. There are many different ways to define groups and Connor *et al.* (2000)

found no less than 11 different definitions within 17 studies on bottlenose dolphins. Most of the definitions found in the cetacean literature can be divided into two categories (Mann, 1999):

- those based on co-ordinated activities, and
- those based on distance measures.

The co-ordinated activities definition implies that individuals are considered as part of the same group if they are involved in the same activity or if they are travelling in the same direction as others. Mann (2000) raises the limits of this kind of group definition. Although being based on behavioural similarities, this approach has implicit assumptions about distance: dolphins involved in the same activity miles away will not be considered as part of the group, as they cannot be seen. Furthermore, it doesn't take into account the fact that dolphins in close association can be involved in different activities. She also puts forward that 'although co-ordinated movements and activities may be important to the animals for maintaining group membership, they are impractical to quantify reliably' (Mann, 2000, p.55). As a consequence, she recommends proximity-based definition to designate group membership (Mann, 2000).

When using distance as a criterion, individuals are considered as part of the same group if they are located within a certain area or within a certain distance of each other (Mann, 2000). Distance criteria can vary from one study to another, depending on the species and the characteristics of its association patterns, as well as on the researcher's choice. Some may chose to use a 10-metre 'chain rule' (Connor *et al*., 1992b; Smolker *et al*., 1992; Mann and Smuts, 1999; Mann *et al*., 2000), or a 100-metre 'chain rule' (Wilson *et al*., 1993) to identify group membership. This involves considering any animal that surfaces within such distance of any other animal within the group as a group member. Some may consider individuals as part of the same group when they are located within a 100-metre radius (Irvine *et al*., 1981; Wells *et al*., 1987; Corkeron, 1990), while others might set the distance criteria between individuals by using body length measures (Dorsey *et al*., 1989; Weinrich, 1991; Fertl, 1994). This approach also has its own limits, as firstly it does not take into account the animals' behaviour. Secondly, it can also prove difficult to designate a cut-off distance for group membership as dolphins are known to communicate over long distances (Tyack, 2000) and could be in acoustic proximity rather than in physical proximity.

The use of these definitions has different implications. When defining groups, researchers should make their choice according to the species he or she is working with. Definitions should capture the fluid or stable nature of the species society (Mann, 2000). It is therefore important to keep in mind that common dolphins tend to live in a very fluid fission-fusion society, meaning that group composition presents a high rate of variation over time (Norris and Dohl, 1980a; Wells *et al.*, 1999; Neumann, 2001). Some researchers chose to use a combination of both methods (for example, Mobley and Herman, 1985; Whitehead *et al.*, 1992; Mattila *et al.*, 1994; Brown and Corkeron, 1995; Defran and Weller, 1999) and such combinations have been successfully used to assess the ecology of common dolphins (Neumann, 2001).

After having considered the characteristics of the common dolphins' society, the previous use made of the two methods described above and their implications, the following group definition was used in this study:

> Dolphins were considered as part of the same group when they were observed in close proximity, within 200 metres of each other, and in apparent association, moving in the same direction or engaged in the same behaviour.

This definition excluded other groups that could have been utilising the same area, and even though their presence could be noticed, such distance prevented the assessment of the eventual presence of calves in these groups.

b. Group size and composition

The group size refers to the number of adult dolphins present in a group. A visual count, or estimate, was obtained by scanning the group continuously. The minimum number of animals was recorded for each group in one of the following six categories: 0-10 dolphins, 11-20, 21-30, 31-50, 51-100, more than 100 dolphins. Such categories were designed since reliable counts can be obtained for groups up to 30 animals (Neumann, 2001). As groups reach bigger sizes and the exact number of animals becomes difficult to obtain, the use of broader categories was favoured. Small categories were also preferred when possible in order to maximise the statistical analysis between group size and the different group types. By using large categories, a possible correlation between these two parameters may not be revealed. Similar categories have been used in studies of bottlenose dolphins (for example: Constantine *et al*., 2004), with the highest category being 31-50 animals, as bottlenose dolphins usually travel in smaller groups than common dolphins (Whitehead and Mann, 2000). In the present study, group size was compared across the different group types (determined by the age class of the youngest member of the group), which enabled hypothesis 4 to be tested.

Studying group composition allows the researcher to gain more detailed information on the structure of a group. Such data was of great importance in this study, as all research questions relied on the identification of the presence or absence of calves in the groups encountered. Many terms have been used in order to describe group composition: calf, newborn, infant, juvenile, subadult, adult, along with different definitions for each of them. Most studies combine biological criteria, such as small size, presence of foetal folds, or fins still folded, and behaviour of individuals in order to classify them into a specific age category (Connor *et al*., 1996; Bearzi *et al*., 1997; Herzing, 1997; Neumann, 2001; Constantine, 2002; Thayer *et al*., 2003). The behaviour of common dolphin calves has never been investigated and using the behaviours described in other species as criteria would lead to assumptions that common dolphins behave in the same way. Other features, such as foetal folds, may last months, resulting in positively biased estimates of birth dates (Caldwell and Caldwell, 1972; Cockroft and Ross, 1990). Therefore, the size of calves was strictly used to distinguish between four age categories. Because of the magnifying property of the water, the lengths of dolphins estimated at sea are significantly greater than the lengths of the same specimens recorded during necropsy (Read and Hohn, 1995). Therefore, rather than trying to estimate the total length of calves, the size of each calf was estimated as a proportion of its mother's size; a method which has previously been used in other studies (for example to assess the size of southern right whale calves: Thomas and Taber, 1984; bottlenose dolphins: Bearzi *et al*., 1997; Constantine, 2002; spotted dolphins: Herzing, 1997). In order to determine group composition, the following four age classes were used during the course of this study:

- newborns: designates young calves of typical newborn size, measuring less than half the size of the mother (Plate 7). Through necropsy, Evans (1975) only found milk in the stomachs of individuals of that size.
- infants: animals measuring around half the size of the mother (Plate 8), which corresponds approximately to six months of age (Ferrero and Walker, 1995; Danil

Plate 7. Common dolphin calf classified as a newborn.


Courtesy of Karen Stockin

Plate 8. Common dolphin calf classified as an infant.

and Chivers, 2003). Through necropsy, squid and milk were found in stomachs of individuals of this size (Evans, 1994).

- juveniles: animals measuring around two thirds of the mother's size (Plate 9), which corresponds approximately to one year of age (Ferrero and Walker, 1995; Danil and Chivers, 2003).
- adults: all other animals not included in the previous categories. Subadults were not taken into account as they would have been too difficult to discriminate visually from full-sized dolphins.

'Calves' was therefore use as a general term to designate non-adults dolphins. Continuous sampling was used in order to determine the presence and number of individuals for each of the four categories described above. Each group of common dolphins was then categorised into one of four group types, according to the size of the youngest individual sighted within a group:

- group type 1: the youngest dolphin in the group was a newborn,
- group type 2: the youngest dolphin in the group was an infant,
- group type 3: the youngest dolphin in the group was a juvenile,
- group type 4: the youngest dolphin in the group was an adult.

As one of the prerequisites of any study, a decision rule for following animals under changing conditions must be developed a priori (Mann, 1999, 2000). When group size and group composition changed within one encounter, explicitly when dolphins joined or left the group, the time and description of the change was noted. In order not to sample the same animals twice, the minimum number for each age class was recorded in the data set.

c. *Behaviours*

When sampling behaviour, a distinction must be made between states and events (Altmann, 1974; Martin and Bateson, 1993; Mann, 2000). Such a distinction is based on the duration of a given behaviour: events are usually regarded as instantaneous displays, while states are of appreciable duration. In reality, all behaviours require a certain amount of time and our choice between regarding behaviours as states or events depends upon the questions we are attempting to answer (Altmann, 1974). In the present

Plate 9. Common dolphin calf classified as a juvenile.

study and like most authors in the cetacean literature (Constantine, 1995; Mann, 2000; Neumann, 2001), behavioural events were referred to as behaviours of short duration such as discrete body movements (for example: head slap, leap…). Behavioural states were referred to as behaviours of long duration such as prolonged activities (for example: resting, feeding, travelling…).

Activity state

The activity state refers to the general behaviour of the dolphins when encountered. There are three main ways to record group activity state: point sampling, focal group sampling (also known as predominant group-activity sampling), and predominant activity sampling.

Point sampling entails scoring activity periodically, for example every three minutes (as used by Neumann, 2001). The use of point sampling is recommended for studies focusing on a species' activity budget and requiring data on the proportion of time spent in specific activity states, as well as on changes from one state to another (Mann, 1999). Such detailed information on common dolphins' activity state was not necessary in order to answer the questions addressed in the present study. Furthermore, recording activity state at set time points may have interrupted focal follows and therefore limited the possibility of answering other research questions. Focal group sampling involves recording the activity over half of the group is engaged in for a certain time interval (Mann, 1999, 2000). Predominant activity sampling involves recording the activity the whole group is engaged in over 50% of a certain time interval (Hutt and Hutt, 1970), and therefore requires precise sampling of each group member or some subset of the group. This is difficult to achieve when observing large groups of delphinids, as is the case for common dolphins in the Hauraki Gulf. Because focal group sampling only involves a global assessment of the group, it is the most appropriate method to record common dolphins' activity state. Altmann (1974) advises to restrain the use of focal group sampling to situations in which every member of the group is under continuous observation during the sample period. However, due to the particularity of the environment they live in, these conditions are never met with wild cetaceans and focal group sampling remains the most commonly used method to determine group activity in dolphins and whales (Mann, 2000). In this study, the activity of the groups encountered was therefore recorded using focal group sampling.

In order to describe dolphins' activity state, five main categories have been used by most researchers who have quantified cetaceans' behaviour: feeding, travelling, socialising, resting, and milling (Shane, 1990b). These categories fit with observations of the behaviour of common dolphins and have been successfully used on this species in the past (Neumann, 2001). Consistency in the methodology used across studies has been emphasised in the previous years, including for categories and definitions of activity states, as it allows unambiguous comparison of results (Shane, 1990b; Mann, 1999). For all these reasons, these five categories were used in the present study:

- socialising: Shane described socialising as 'some or all pod members in almost constant physical contact with one another, oriented toward one another, and often displaying surface behaviours (1990a, p.262). Dolphins are mainly involved in mating, rubbing and playing (Shane *et al.*, 1986).
- travelling: dolphins are all moving at a sustained speed in a persistent direction (Shane *et al.*, 1986; Shane, 1990a).
- feeding: dolphins are involved in an effort to capture and consume prey (Shane, 1990a). They can be seen herding a school of fish (feeding circles) or chasing the fish at the surface (feeding rushes).
- resting: dolphins are moving slowly at the surface in a co-ordinated manner, and in one particular direction (Shane *et al.*, 1986; Shane, 1990a). Individuals are usually within a few body lengths of each other (Neumann, 2001).
- milling: dolphins remain within a given area and are not moving in any definite direction. Individuals are continuously changing their heading (Shane *et al.*, 1986; Shane, 1990a).

For each group, behavioural state was sampled continuously throughout the encounter. At the end of each encounter and according to the behaviours displayed by more than 50% of the group (focal group sampling), one of the five activity states described above was assigned to the group. The percentage of observations of each activity state was compared across the different group types in order to test hypothesis 5.

Events

In the present study, behavioural events were sampled in order to provide indication of a possible mating season. Therefore, focus was only made on events relating to reproduction. It is known that dolphins' copulatory behaviours may be used in contexts outside reproduction (Wells, 1984). Nonetheless, seasonal changes in the occurrence of these behaviours may still indicate the presence of a mating season (Mann, 2000). Behavioural patterns related to reproduction have been shown to increase during mating seasons in different studies (McBride and Hebb, 1948; McBride and Kritzler, 1951; Puente and Dewsbury, 1976; Wells, 1984; Shane, 1990b).

Two main sampling methods are available to record behavioural events: incident sampling also known as all-occurrence sampling, and one-zero sampling. One-zero sampling consists of recording the occurrence or non-occurrence of specific behaviours during a certain time interval (Altmann, 1974; Mann, 1999). Whereas such method may be used to gain categorical information, it fails to provide frequencies of the behaviours recorded. All-occurrence sampling or incident sampling entails scoring all behavioural events of a specific type (Altmann, 1974; Martin and Bateson, 1993; Mann, 1999). This method provides accurate information about the rate of occurrence of behaviours. Mann (1999, p.115) points out that in order to use all-occurrence sampling, ‘the behaviours themselves must be obvious and attractive enough to alert the observer. In addition, the observer must be able to record all the events regardless of how many animals are present’. Shane (1990b) describes surface behaviours most closely related to socialising as being highly visible. Altmann (1974) adds that one also has to ensure that the behavioural events do not occur too frequently to be recorded. These conditions being fulfilled in the present study, and true frequencies being valuable in order to determine the existence of a mating season, all-occurrence sampling was used.

Courtship and copulatory behaviours have been described for a variety of dolphin species (bottlenose dolphins: McBride and Hebb, 1948; Puente and Dewsbury, 1976; common dolphins: Essapian, 1962; spinner dolphins: Wells, 1984), and some recurrent patterns have been identified. In his study on spinner dolphins, Wells (1984) describes six behavioural patterns with potential sexual connotations: genital-to-genital contact, beak-to-genital propulsion, other genital contact, non-genital contact, ventral presentations and chases. Puente and Dewsbury (1976) identified nine courtship patterns for bottlenose dolphins: vocalisation, mouthing, nuzzling, rubbing, stroking, displaying, leaping, chasing, and head butting. Some of these behaviours have also been classified as belonging to dolphins’ mating repertoire in other studies (Connor *et al.*, 2000; Reynolds *et al.*, 2000). In the first and only attempt to investigate courtship in common dolphins, Essapian (1962) describes the behaviour of a pair of captive dolphins and adds tail slapping and breaching to the list. He also notes that common dolphin courtship and mating behaviours are very similar to that of the bottlenose dolphins. Some of the behavioural categories named above contain detailed patterns that may be available to the observer studying captive dolphins, or in areas of great visibility. The mating behaviours observed in this study usually occurred during fast moving interactions. Moreover, water visibility made it difficult to distinguish between certain behaviours, such as rubbing and stroking. For these reasons and because data collection needs to be simplified when a significant amount of information is being collected (Mann, 2000), broader categories were used to record mating behaviours of common dolphins and the following behaviours were sampled:

- genital-to-genital presentations: two individuals swimming belly-to-belly, with genital areas sometimes seen in contact with each other. Even though intromission could rarely be observed, its occurrence conformed to this position.
- beak-to-genital contact: the tip of the rostrum of one dolphin is in contact with the genital slit of another individual. This behaviour was only coded as such when it involved two adults, as dolphin calves are known to nurse in the same position.
- non-genital contact: includes any other types of body contact between two dolphins, such as rubbing of the animals' bodies and pectoral fins, or rolling on each other at the surface.
- chase: one dolphin rapidly pursuing another.
- leap: one dolphin jumping out of the water.
- head slap: one dolphin slapping its head again the surface of the water.

Vocalisations and tail slaps were not taken into account in this study. The high-pitched sounds produced by the dolphins could only be heard when the dolphins were right underneath the bow, which restricted all-occurrence recording of that event. Tail slaps represent one of the main techniques used by dolphins while feeding (Neumann, 2001), and proved to be difficult to distinguish from social tail slaps. The existence of a mating season, as stated by hypotheses 9 and 10, was assessed by comparing the occurrence and frequency of these different behaviours across months and seasons.

d. Association with other species

Common dolphins are known to associate with birds and baleen whales for feeding purposes (Gallo, 1991; Neumann, 2001). Mothers and calves of different delphinid species have been reported to stay clear of feeding aggregations, as the intensity of the activities they involve may not be safe for calves (Würsig, 1986). The presence of other species within these aggregations appears likely to further increase this intensity. Therefore, the presence of other species with common dolphins was recorded in order to determine whether the different group types presented the same association pattern (hypothesis 6). For each group, the presence of birds or whales associated with the common dolphins was noted. Other species were considered as associated with the common dolphins if observed within the group under observation and involved in the same activity. Association patterns were tested using four different dependent variables:

- associations with any other species,
- associations with birds and whales,
- associations with birds only, and
- associations with whales only.

e. Behaviour towards the boat

In order to investigate whether the boat's approach had the same impact on different types of groups (hypotheses 7 and 8), the minimum distance between the boat and the dolphins, as well as the reaction of the animals towards the boat, were recorded for each group.

The dolphins' reaction was coded in one of the three following categories (Neumann, 2001):

- attraction: the dolphins are coming towards the boat, swimming at the bow for extended periods of time and staying around the boat even if stopped.
- avoidance: dolphins are continuously changing their heading away from the boat.
- neutral: no observable reaction or change in the behaviour of the dolphins can be noticed, they are not attracted to the boat and neither avoiding it.

The minimum distance to the boat was recorded in metres, and was coded as 0 when the dolphins were riding the bow. In order to measure such distance, different cues were used such as the length and width of the research vessel, as well as the average size of adult common dolphins. Although judging distances at sea can prove difficult, the use of these cues along with the author's previous involvement in projects requiring similar skills ensured the accuracy of measurements made in the present study.

- Focal mother-calf follows

During focal mother-calf follows, continuous sampling was used in order to collect data on proximity and separations between mothers and calves, synchrony and breathing rate of the pair, swimming pattern of the pair, allomaternal behaviour, and association with other mother-calf pairs (see Appendix 2 for an example of a focal mother-calf follow). Continuous sampling involves the systematic recording of behaviours that have been defined a priori (Altmann, 1974; Mann, 1999). Each occurrence of the behaviours of interest is recorded, along with information on its time of occurrence (Martin and Bateson, 1993). Continuous sampling is the richest source of information on social behaviour (Mann, 1999), and has consequently been used widely in the study of mother-calf relationships in different cetacean species (for example, southern right whales: Taber and Thomas, 1982; bottlenose dolphins: Mann and Smuts, 1998, 1999). Such data provide information on details, sequences, actors and recipients, rates and duration of behaviour for individual animals (Mann, 1999). Mann (1999) lists the different behaviours that can be recorded on a continuous basis. These include breathing frequency, dive times, surface-display rates, and synchronous surfacing, most of which are used to study mother-calf relationships (Mann and Smuts, 1999). However, when a great amount of information is recorded continuously, this method can prove very demanding for the observer. In such cases, Altmann (1974) recommends its use for one or two animals at most. Another option is to score frequencies within time blocks using point sampling. The observation session is then divided into short sample intervals (for example 30 seconds). At each sample point, the observer scores whether or not certain behaviours are occurring (Altmann, 1974; Martin and Bateson, 1993; Mann, 1999). For this study, continuous sampling represented the best option in recording mother-calf interactions. Mother-calf pairs would usually come in view only for short periods of time. Thus, to capture the flow of events, point sampling would have had to be used with very short sample intervals, which would be equivalent to using continuous sampling. Moreover, if the behaviours of interest occur outside the sample point, they would not be recorded. Once again, frequencies were necessary in order to answer most of the research questions relating to mother-calf relationships. The use of one-zero sampling was therefore restricted to recording the presence of foetal folds on the calves and the occurrence of nursing behaviours, as categorical data were sufficient to test the hypotheses relating to these topics.

When using continuous sampling, records need to be kept on the length of each sample period, as well as the amount of time during which the animals sampled are in view for that particular period (Altmann, 1974). For this study, the focal sample began as soon as a mother-calf pair was located and lasted as long as it remained sufficiently close for good visibility. The time at which the focal follow was initiated and terminated was recorded, providing the exact length of observation for each mother-calf pair.

Even though it has been reported that individuals accompanied by calves are not always the mothers, and not always females (Whitehead and Mann, 2000), the identification of mothers in different studies have relied on their regular association with calves (Wells *et al.*, 1987; Bearzi *et al.*, 1997). Therefore, in this study, mother-calf pairs were identified as such by the persistent presence of a smaller individual next to an adult sized dolphin. Focal follows were not achievable for every group containing calves as the sampling of a pair relied on the distance at which they would approach the boat. In fact, to be able to record accurately all occurrences of the behaviours of interest for this study, mother and calf pairs needed to be in a 15 metres circa around the boat. A decision rule was necessary when more than one mother-calf pair approached the boat, in order to choose which one would be sampled. In order to maximise the efficiency of the focal follow, the pair closest to the boat was followed. If, during the sampling of a pair, another mother and her calf approached the boat, their presence and the size of the calf was recorded, and the initial follow on the first pair continued.

For each mother-calf follow, the size of the calf was recorded under one of the three age classes described previously: newborn, infant or juvenile. Thomas and Taber (1984, p.43) pointed out that such a record provides ‘a basis for rough estimation of the relative ages of the calves and a means to associate behavior with age’, and was used in that manner in the data analysis.

a. Swimming position

Dolphin calves have been described to swim with their mothers in two main positions: ‘infant position’ swimming and ‘echelon position’ swimming (Mann and Smuts, 1999). In ‘infant position’, the calf swims underneath its mother with its head slightly touching her abdomen. Upon surfacing to breathe, the calf breaks this position to regain it afterwards. Echelon swimming refers to the calf swimming alongside the mother, paralleling her course, less than 30cm away from her side (Plate 10).

During mother-calf follows, the position of the calf was monitored continuously. Upon sighting of a mother-calf pair, their initial swimming position was noted as well as any changes occurring thereafter, along with the time of the change. These observations provided data on the occurrence and the time spent in each position for each mother-calf pair sampled, which were compared across the different age classes (hypotheses 11 to 14).

b. Proximity and separations

One of the goals of this study was to investigate whether the characteristics of separations between mothers and calves varied with the age class of the calf. In order to test hypotheses 15 to 19, the occurrence and the frequency of separation, the mean duration of separation, the mean distance of separation, and the proportion of time spent by the calf away from the mother were calculated for each focal follow and compared for the three age classes.

In their study on mother-infant separations in bottlenose dolphins, Mann and Smuts (1998) define separations as one animal departing from a two-metre radius of another. They found that two metres is the separation distance to which mothers reacted negatively during the first week of life of the newborn calf. This distance is thus considered biologically significant for bottlenose dolphins. As the significant separation distance for common dolphins is not known, separations were considered as an observable increase of distance, superior to one metre, between the mother and her calf. For each instance of mother-calf separation, the distance between them was recorded in metres, and in the same manner as previously described regarding the distance of dolphins to the boat. The maximum and average distances of separation were calculated afterwards for each mother-calf pair.

An important measure of mother-calf relationships is the extent to which their proximity is due to the movements of one member of the pair rather than the other (Hinde and

Courtesy of Gregory Lamare

Plate 10. Two mother-calf pairs of common dolphins swimming together. One of the calf is swimming in 'echelon position', while the other one can just be distinguished in 'infant position' underneath its presumed mother.

Atkinson, 1970; Martin and Bateson, 1993; Mann, 2000). In fact, separations will not bear the same meaning whether they are initiated and terminated by the mother or by the calf. In order to investigate which member of the mother-calf pair was responsible for maintaining proximity, the identity of who separated or rejoined the other member of the pair was consistently recorded. For each mother-calf follow, the following were recorded:

- number of separations initiated by the mother,
- number of separations initiated by the calf,
- number of mutual separations,
- number of rejoins initiated by the mother,
- number of rejoins initiated by the calf,
- number of mutual rejoins.

Responsibility in separations and rejoins could be identified when one individual within the pair moved away or toward the other pair member, actively increasing or decreasing the distance between the two. Mutual separations and rejoins corresponded to instances where both pair members were equally responsible. In 1970, Hinde and Atkinson proposed a mathematical function in order to summarise the contribution of both partners within a particular dyad in proximity maintenance. The use of this index has proved successful in previous studies of mother-calf relationships in cetaceans (southern right whales: Thomas and Taber, 1984; bottlenose dolphins: Mann and Smuts, 1998), and was therefore used in the present study. This function is calculated as follows:

$$\frac{Rc}{Rm+Rc} - \frac{Lc}{Lm+Lc} \qquad \underline{\qquad}$$

Rc = total number of rejoins by the calf.
Rm = total number of rejoins by the mother.
Lc = total number of leaves by the calf.
Lm = total number of leaves by the mother.
For each calf, the proximity index was calculated and then compared across the three age groups in order to test hypotheses 20 and 21.

As the amount of time spent away from the mother can be used as a sign of calves' independence (Mann and Smuts, 1999), the time at which the pair separated, along with the time at which they rejoined were recorded for each separation. This then allowed the calculation of the maximum and average durations of separation, as well as the proportion of time the calf spent without its mother over the length of the observation.

By comparing these data between the three different age classes, it was possible to consider whether proximity measures change with calf age. Such data have previously been used for this purpose in other studies (for example in Taber and Thomas, 1982; Mann and Smuts, 1998, 1999).

c. *Nursing*

Due to dolphins' particular anatomy, especially the fact that females don't have external nipples, true cases of nursing observed through transfer of milk from the mother to the calf prove difficult to witness (Mann, 2000). In the field, nursing can be inferred based on the calf's position and behaviour, and refers to the observation of the calf's rostrum in contact with the mother's mammary slit area for longer than two seconds (Mann and Smuts, 1998) (Plate 11). This definition was used in the present study in order to assess nursing events. For each calf observed, the occurrence of nursing position was recorded, and compared between newborns, infants and juveniles in order to investigate hypothesis 22.

d. *Synchrony and dive time*

Synchrony between mothers and calves was assessed through their surfacing pattern. Exact breathing synchrony occurs when the mother and calf break the surface of the water in perfect unison (Mann and Smuts, 1999). During synchronous breaths, the members of the pair are typically close and parallel or staggered in position (Mann and Smuts, 1999). Mothers and calves could also be seen surfacing one right after the other. This type of surfacing was recorded, but coded separately from synchronous breathing. Solitary surfacing was taken into account and referred to mothers and calves breaking the surface of the water for a breath on their own. Mothers' and calves' dive times were also considered in order to investigate potential differences between them, as well as between the three age classes. In order to answer the different questions relating to

Plate 11. Common dolphin calf in nursing position.

synchrony and dive time of mother-calf pairs (hypotheses 23 to 25), the following data were collected in the field:

- total number of breaths taken by the calf,
- total number of breaths taken by the mother,
- number of synchronous surfacings,
- number of overlapping surfacings,
- number of overlapping surfacings initiated by the calf,
- number of overlapping surfacings initiated by the mother,
- number of calf's solitary surfacings,

number of mother's solitary surfacings.The maximum and average dive times of both mothers and calves were calculated afterwards.

e. Behaviour towards the boat

In Monkey Mia, where bottlenose dolphins are hand fed from the beach, mothers have been seen herding their newborn calves away from the beach and tourists (Mann and Smuts, 1999). In another attempt to identify the potential impact of the boat on the dolphins, any sign of the mother herding her calf away from the boat was recorded. The minimum distance between the mother-calf pair and the boat was noted and compared across the three calf age classes (hypothesis 26). The minimum distance to the boat was recorded in metres, and was coded as 0 when the pair was bow riding.

f. Allomaternal behaviour

Allomaternal behaviour refers to the association or interaction between calves and non-mother dolphins (Mann and Smuts, 1998), and has been referred as such in many studies (Quiatt, 1979; Lee, 1987; Fairbanks, 1990; Stanford, 1992; Muroyama, 1994; Whitehead, 1996). However, such a term implies a benefit for the infant or the mother and has led Mann and Smuts (1998) to recommend the use of the term 'escorting' when the existence of such benefit is unknown. In order to investigate whether the occurrence and frequency of escorting behaviour in common dolphins varies with the age class of calves (hypotheses 27 and 28), the association of calves with non-mother dolphins was recorded using all-occurrence sampling. Two types of associations were considered:

- the calf is separating from the mother to swim rapidly with another adult but rejoining within a few seconds,
- the calf is seen swimming and surfacing with an adult other than the mother.

When a mother-calf pair was located and followed, particular attention was drawn to the mother's dorsal fin as it would allow her identification throughout the encounter. This also allowed recording the association of the calf with another dolphin. Individual common dolphins are known to have distinctive and unique colouration patterns on their dorsal fins (Neumann, 2001). Such colouration and the presence of other markings, such as nicks and notches, have been widely used to identify individual animals within different cetacean species (Würsig and Jefferson, 1990), and were used to identify the mother in the present study.

g. Association with other mother-calf pairs

Previous studies have shown that bottlenose dolphin mothers and calves are more likely to associate with other mother-calf pairs and adult females than with any other individual (Mann and Smuts, 1999). Groups of females only, most of them accompanied by calves, are usually called 'nursery groups'. Although Neumann (2001) described the presence of a postanal hump only observed on adult males, there are no easily observable differences between male and female common dolphins. Even if the ventral surface is visible when the animals are leaping out of the water, the male's postanal hump is difficult to observe, thus making it difficult to reliably identify nursery groups. Nevertheless, association patterns between the mother-calf pair under focal observation and other mother-calf pairs within the group were recorded. For each focal mother and calf, the presence of other pairs alongside or within a few body lengths was noted along with their number (Plate 10). Such a pattern was thereafter compared between the different age groups in order to test hypothesis 29.

h. Foetal folds

Foetal folds are characterised by white lines across the back of dolphin calves (Mann and Smuts, 1999) (Plate 4). The presence of such lines was recorded for each calf, using one-zero sampling, as information on the occurrence or non-occurrence of such pattern was sufficient in order to investigate differences between age groups. As foetal folds were observed occasionally on adult sized dolphins, such occurrence was also recorded, although not included in the comparative analysis as all adult dolphins were not sampled on this criterion.

6) Data analysis

Once observations are made, the investigation of how they relate to the hypotheses underlying the study is required in order to answer each specific research question. Towards that goal, the data collected in the field were analysed using statistical methods, as they provide relevant mathematical tools to describe, organise, analyse and interpret empirical data (Martin and Bateson, 1993; Gravetter and Wallnau, 2004). Because a wide variety of statistical analyses are available, each of them having different requirements, the choice of a specific test is challenging and must be made according to the type of data to be analysed, as well as the nature of the research questions addressed (Harris, 1998).

Depending on the characteristics of the variables studied, two basic types of tests can be used: parametric and non-parametric tests (Martin and Bateson, 1993; Harris, 1998). Parametric tests are based on specific assumptions regarding the nature of the population from which the data are drawn and can only be used if all of the following conditions are fulfilled (Martin and Bateson, 1993; Harris, 1998):

- normality: the variables studied follow a normal distribution,
- homogeneity of variance: the samples under investigation have approximately equal variances,
- additivity: the effects of different treatments or conditions are additive,
- level of measurement: the variables considered are measured on an ordinal scale,
- linearity: the associations between the dependent and the independent variables are linear.

In situations that do not conform to these requirements, non-parametric tests can be used, as they make fewer assumptions about population distribution and allow the use of nominal measurements (Harris, 1998). Nonetheless, these tests still require independence of observations and continuity in the variables studied. Martin and Bateson (1993) note that such assumptions are usually realistic when working with behavioural data. Because of their stronger sensitivity in detecting significant differences, the use of parametric tests is usually recommended (Harris, 1998; Gravetter and Wallnau, 2004). However, non-parametric tests are considered to be more robust and powerful under certain circumstances, due to their lower dependency on various assumptions (Martin and Bateson, 1993). To investigate whether parametric tests could be used in the present study, all variables were tested for normality. These tests showed that none of the variables followed a normal distribution. Further attempts to apply transformations to the data in order to approximate normality also proved unsuccessful. As a result, non-parametric tests were systematically used in order to analyse data. The different observations made in this study are considered to be independent, as each observed value was generated by a different group (group follows), or a different mother-calf pair (focal follows). However, it cannot be discounted that some animals might have been sampled more than once throughout the study period. Nevertheless, because the circumstances under which they were observed were different from one day to the other, it is considered that observations were independent from one another. When multiple groups were encountered on the same day, independence was ensured by the geographic distance between them. In fact, the distribution of common dolphin groups and the boat's search patterns were usually such that the dolphins of a specific sighting could not have been sampled twice in one day.

In order to choose the appropriate analyses, it is also important to consider how the different variables should be tested to conclude whether or not the hypothesis under investigation can be rejected (Harris, 1998). The hypotheses tested in this study involved the following analyses:

- H_1 to H_3: analyses of the relationship between environmental variables and group type (determined by the age class of the youngest member in the group),
- H_4: analysis of the relationship between group size and group type,
- H_5 to H_8: analyses of the relationship between behavioural variables and group type,
- H_9 and H_{10}: analysis of the relationship between time of the year and mating behaviours,
- H_{11} to $H_{24,}$ and H_{26} to H_{29}: analyses of the relationship between the age class of calves and their behaviours,
- $H_{25:}$ analysis of the differences between mothers' and calves' dive time.

These hypotheses were investigated by three methods:

- comparisons of the distribution of a dependent variable across all values of the independent variable; for example, to investigate whether the distribution of mean water depths varied according to group type,
- correlation in the distribution of the variables investigated; for example, to investigate the correlation between mean water depth and group type,
- comparisons of the mean values of the dependent variable within each independent variable; for example, to assess the difference in mean water depths between each group type.

Comparisons of distributions allow the investigation of whether the variations of a dependent variable are influenced by the values of an independent variable (Maleske, 1995). However, such analysis does not provide any information on the direction of influence or how the variables are associated. In order to further investigate the relationships between variables, the use of correlation coefficients appears beneficial as they enable description to the extent at which two variables vary together (Martin and Bateson, 1993). Both comparisons of distribution and correlation coefficients remain general analyses and the potential variation between the values within each independent variable is not considered. As a consequence, more detailed comparisons, using significant differences between mean values, were conducted.

Finally, in choosing statistical tests, one also has to consider the scale on which the data were measured. Four different levels of measurement are usually distinguished (Martin and Bateson, 1993; Harris, 1998; Gravetter and Wallnau, 2004):

- nominal scale: values are assigned to mutually exclusive, qualitative categories,
- ordinal scale: values are assigned to quantitative categories and organised in ordered sequences,
- interval scale: values are assigned to quantitative categories, the difference between two values can be quantified, and the zero point is arbitrary,
- ratio scale: properties of an interval scale with the additional feature of an absolute zero point.

In the present study, both nominal and ordinal scales were used. Data relating to the occurrence versus non-occurrence of a certain event produced values on a nominal scale and lead to the calculation of proportions; for example, the occurrence of mother-calf separations. Variables recorded on an ordinal scale resulted in quantitative data for which mean values could be obtained; for example, the frequency of mother-calf separations.

Considering the need for non-parametric tests, the analyses involved in testing the hypotheses previously stated, and the scale of measurement of both independent and dependent variables, five different tests were conducted in the present study, using the statistical software package SPSS: Kruskal-Wallis, Chi-Square for independence, Spearman rank correlation, Mann-Whitney and binomial tests.

In order to compare the distribution of a dependent variable across all values of an independent variable, Kruskal-Wallis tests and Chi-Square tests for independence were used, depending on the scale of measurement of the data. These non-parametric tests allow the evaluation of differences in the distribution of measurements between more than two categories of the independent variable (Gravetter and Wallnau, 2004). While Chi-Square tests for independence are used when the dependent variable is measured on a nominal scale, Kruskal-Wallis tests are used for dependent variables measured on an ordinal scale (Gravetter and Wallnau, 2004). Both tests produce a chi-square statistic, with degrees of freedom defined by the number of categories of the independent variable minus one in Kruskal-Wallis tests; and by the number of categories of the independent variable minus one, multiplied by the number of categories of the dependent variable minus one in Chi-Square tests for independence (Gravetter and Wallnau, 2004). The Chi-Square statistic is identified using the letter H in Kruskal-Wallis tests and the symbol X^2 in Chi-Square tests for independence. This statistic is compared to a critical value set for the level of significance chosen, and p indicates whether or not H and X^2 are significant (Gravetter and Wallnau, 2004).

Differences between distributions were further assessed using Spearman rank correlation test. This test can be used for both ordinal and nominal scales of measurement. The statistical relationship between two variables is indicated by the correlation coefficient r, and is described by two characteristics (Gravetter and Wallnau, 2004):

- direction: a relationship can be either positive or negative, which is specified by the sign of the correlation (+ or -). A positive relationship means that the two variables vary in the same direction. A negative relationship means that the two variables vary in opposite directions.

- degree: the magnitude of the coefficient indicates the degree to which two variables are correlated. A coefficient of ± 1.0 indicates a perfect correlation, whereas a coefficient close to zero shows that there is no association between the two measures.

While r informs on the direction and strength of the correlation, the p value indicates whether or not the coefficient found differs significantly from zero (Martin and Bateson, 1993).

Finally, values of the independent variables were compared two by two using Mann-Whitney tests for ordinal values and binomial tests for nominal values. These tests enable an evaluation of the difference between two measurements of an independent variable, whether they consist of means (Mann-Whitney test) or proportions (binomial test) (Gravetter and Wallnau, 2004). Mann-Whitney tests provide with a U value that represents the sum of ranks, and binomial tests result in a z value that corresponds to the standardised difference between two proportions. The p value indicates whether or not U and z are representative of significant differences between the two measurements (Gravetter and Wallnau, 2004). A very small value of U, close to zero, gives evidence that the two samples are very different (Gravetter and Wallnau, 2004). The reverse statement applies to binomial tests, with z values close to zero representing a lack of differences between two proportions (Gravetter and Wallnau, 2004).

In hypothesis testing, statistical tests are used to determine whether or not a null hypothesis can be rejected. In this process, two types of errors referred to as Type I and Type II errors, can be made and need to be considered (Martin and Bateson, 1993; Bart *et al.*, 1998; Gravetter and Wallnau, 2004). Type I error refers to rejecting a true null hypothesis. It can be minimised by using a low alpha level, which corresponds to the maximum probability of committing such error (Martin and Bateson, 1993; Bart *et al.*, 1998; Gravetter and Wallnau, 2004). For all tests used in this study, the level of statistical significance was set for $\alpha=0.05$, as it has been identified as an appropriate value to reduce Type I error (Bart *et al.*, 1998; Gravetter and Wallnau, 2004; StatSoft Inc., 2004) and represents the most widely used value in the study of behaviour (Martin and Bateson, 1993). When the results of the statistical analyses were significant for a lower alpha level (0.01), such value was reported.

Type II error is closely related to the power of a statistical test to correctly reject a false null hypothesis. In fact, Type II error corresponds to the failure to accept the test hypothesis when the null hypothesis is false and is represented by the symbol β (Martin and Bateson, 1993; Bart *et al.*, 1998; Gravetter and Wallnau, 2004). This type of error can be minimised in two ways. Firstly, the characteristics of both the data to be analysed and the hypotheses to be tested need to be considered in order to select the most appropriate statistical tests (Martin and Bateson, 1993). This procedure was completed in this study and has been described in the preceding paragraphs. Secondly, the use of large samples will increase the power of a test and therefore reduce Type II error (Bart *et al.*, 1998; Gravetter and Wallnau, 2004; StatSoft Inc., 2004). Large samples may be especially challenging to obtain when working with wild animals such as dolphins. Some mathematical formulas have been created in order to calculate the sample size necessary to answer a specific question (Bart *et al.*, 1998; StatSoft Inc., 2004). However, these methods require making estimates of unknown population parameters, such as the difference expected between two variables under investigation (Bart *et al.*, 1998). For example, calculating the sample size required to compare the behaviour of calves of different age classes would have involved making assumptions on the differences between them, which did not appear appropriate. In this study, the sample size used for each analysis was reported with each of the results obtained and taken into account in their interpretation. When the sample size was not considered to be representative of the population studied, mention was made and the results of the statistical analyses disregarded.

All studies contain a certain level of sampling errors as a sample is very unlikely to provide a perfect estimation of the population it represents (StatSoft Inc., 2004). However, these errors must be minimised. Type I and Type II errors were considered in this study and different means were used to reduce their potential occurrence.

A procedure identified to improve the interpretation of the results of hypothesis testing is the calculation of confidence intervals (StatSoft Inc., 2004). Such calculation provides information about the precision of the data, as it gives a degree of confidence for each estimates obtained (Bart *et al.*, 1998; StatSoft Inc, 2004). For each of the values of the different independent variables tested in the present study, confidence intervals were calculated using the most common level of 95%, therefore indicating the interval having a 95% probability of including the mean (Bart *et al.*, 1998; Harris, 1998). Depending on the type of data for which confidence intervals are calculated, different formulas are available (Bart *et al.*, 1998). For continuous data such as water depth of water temperature, confidence intervals were calculated using the normal distribution formula. For counts, such as the number of dolphins per group, confidence intervals were calculated using the Poisson distribution formula. Because such a formula is not symmetrical, the lower and upper values of the confidence interval around the sample mean may not be of equivalent distance. For percentages, confidence intervals were calculated using the binomial distribution. Confidence intervals were presented as raw values in result tables and as vertical bars within graphs.

7) Summary

A wide range of data was collected in the field in order to investigate the several hypotheses addressed in this study. Group follows allowed to gather the necessary information in order to test hypotheses relating to group type and mating season. They involved the collection of data on group size, on the presence of different age classes within groups of common dolphins, on behavioural states and events, on the behaviour of dolphins towards the boat, and on their association with other species. Hypotheses on calf behavioural development and mother-calf relationships were analysed using data recorded during focal mother-calf pair follows. They included information on the calves’ swimming position, on proximity and separations between mothers and calves, on nursing events, on breathing synchrony and dive time, on the behaviour of mother-calf pairs towards the boat, on the association with other mother-calf pairs, and on the presence of foetal folds. Within each of these follow protocols, the nature of the data that needed to be collected was considered, along with the different sampling techniques available, and lead to the selection of a variety of methods, including continuous sampling, one-zero sampling, all-occurrence sampling, *Ad Libitum* sampling, and focal group sampling. The same approach was used in order to accurately choose the statistical analyses conducted on the data. All of the methods used in the present project are widely accepted in the field of study of animal behaviour and have been used in the same manner in previous studies of different cetacean species.

Chapter 4: RESULTS

1) Introduction

This chapter summarises the results of the statistical analyses conducted on the empirical data collected in the field (Figure 8). Each result is presented in relation to the corresponding hypothesis it aimed to test. The data used for each of these analyses is summarised in graphs and tables, which are included in the relevant paragraphs of this chapter. Observations resulting from *Ad Libitum* sampling are also used to illustrate the mathematical results.

In the first section of this chapter, the time spent on the field and details on the data collected during that time are described. Using descriptive statistics, the characteristics of common dolphin groups encountered throughout the study are then presented. The following sections relate directly to the results of the different analyses conducted for each group of hypotheses. These begin with an investigation of the influence of environmental variables, namely water depth, water temperature and season, on group type. The influence of group size on group type is then considered. The influence of group type on different aspects of common dolphins' behaviour is then assessed, and focus is more specifically made on behavioural activity state, on the association with other species and on the reaction to the boat. The potential existence of a mating season within the population of common dolphins studied is then discussed. The last sections of this chapter refer to the behavioural development of calves and mother-calf relationships. Hypotheses relating to changes in separation patterns, mother-calf proximity, nursing occurrence, breathing patterns, dive time, distance to the boat, with the age class of calves are investigated. The results of the analyses regarding escorting behaviour and grouping patterns are then described, followed by some observations of other traits characteristic of common dolphin calves. Finally, the results of the analyses conducted in this study are summarised.

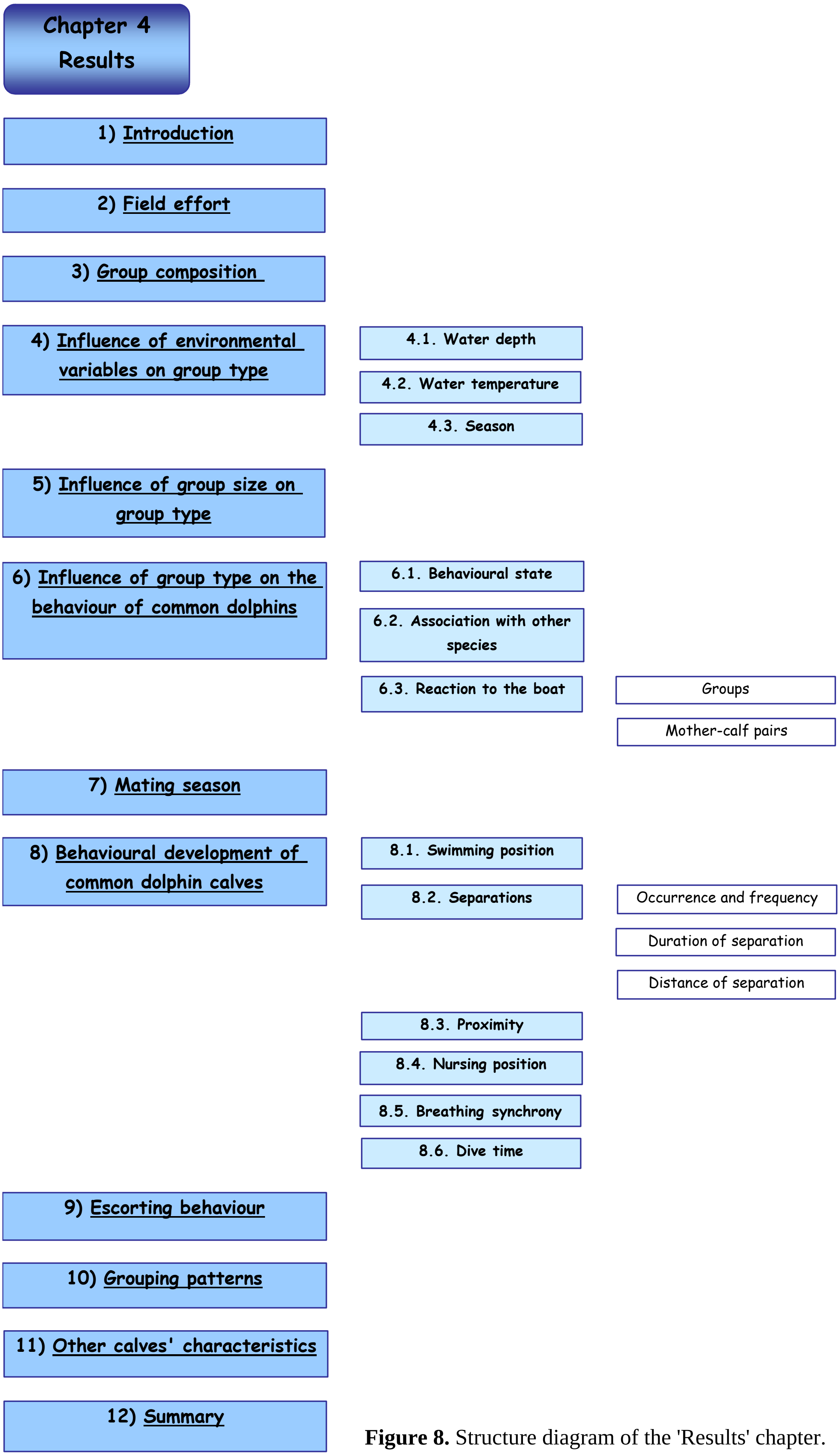


Figure 8. Structure diagram of the 'Results' chapter.

2) Field effort

From the 18th of January 2003 to the 29th of February 2004, 221 trips were conducted onboard 'Dolphin Explorer', representing a total of 1,105 hours spent on effort (Table 1). Common dolphins were sighted on 185 of these trips, and a total of 348 groups were encountered. In some cases, the small amount of time spent with groups of dolphins, the large distances kept between the animals and the boat, as well as weather conditions limiting visibility precluded the accurate assessment of group type. As a result, those groups for which the presence or absence of calves could not be investigated were excluded from the data set. Focal group follows were conducted on 320 groups of common dolphins, resulting in 131 hours and 46 minutes of observations (Table 2). The mean duration of group follows was 24.78 minutes (SD=18.363 minutes, ranging from one minute to 140 minutes). Within these groups, observations of 311 mother-calf pairs yielded two hours, 56 minutes and 18 seconds of focal follows. A total of 35 focal follows were conducted on mothers and newborn calves, 136 on mothers and infants, and 140 on mothers and juveniles. The mean duration of focal follows was 1.84 minutes (SD=1.811 minutes, ranging from 0.233 minutes to 8.46 minutes).

3) Group composition

Of the 320 groups of dolphins encountered in this study, the size category of the smallest calf could be determined for 245 groups. Newborns represented the youngest individual in 41 groups (16.7%), infants in 100 groups (40.8%), and juveniles in 48 groups (19.6%). 56 groups were composed of only adults (22.9%) (Graph 1). Including the 75 groups for which the categorisation of the smallest calf was not possible but presence of calves could however be confirmed, a total of 184 groups with calves (82.5%) and 56 groups without calves (17.5%) were sighted.

The overall number of calves in each group ranged from zero to 12 with a mean of 3.68 per sighting (SD=2.656, n=180). Observations of high numbers of calves were rare and groups of common dolphins usually contained only one or two calves (Graph 2). The number of newborns in each group ranged from zero to four with a mean of 1.44 per sighting (SD=0.634, n=41). The number of infants in each group ranged from zero to

	JAN 03	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
Dolphin Explorer trips	10	18	20	26	20	20	20	18	14
Trips with researcher onboard	8 (80%)	12 (66.67%)	19 (95%)	20 (76.92%)	13 (65%)	13 (65%)	13 (65%)	14 (77.78%)	12 (85.71%)
Trips with researcher onboard and common dolphins sighted	8	10	16	15	10	11	13	14	9

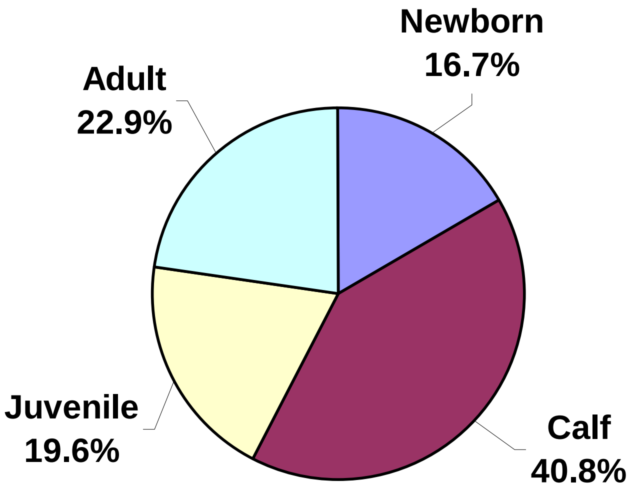
	OCT	NOV	DEC	JAN 04	FEB	TOTAL
Dolphin Explorer trips	21	20	23	23	13	266
Trips with researcher onboard	19 (90.47%)	19 (95%)	23 (100%)	23 (100%)	13 (100%)	221 (83.08%)
Trips with researcher onboard and common dolphins sighted	19	12	17	20	11	185

Table 1. Summary of the research effort throughout the study period.

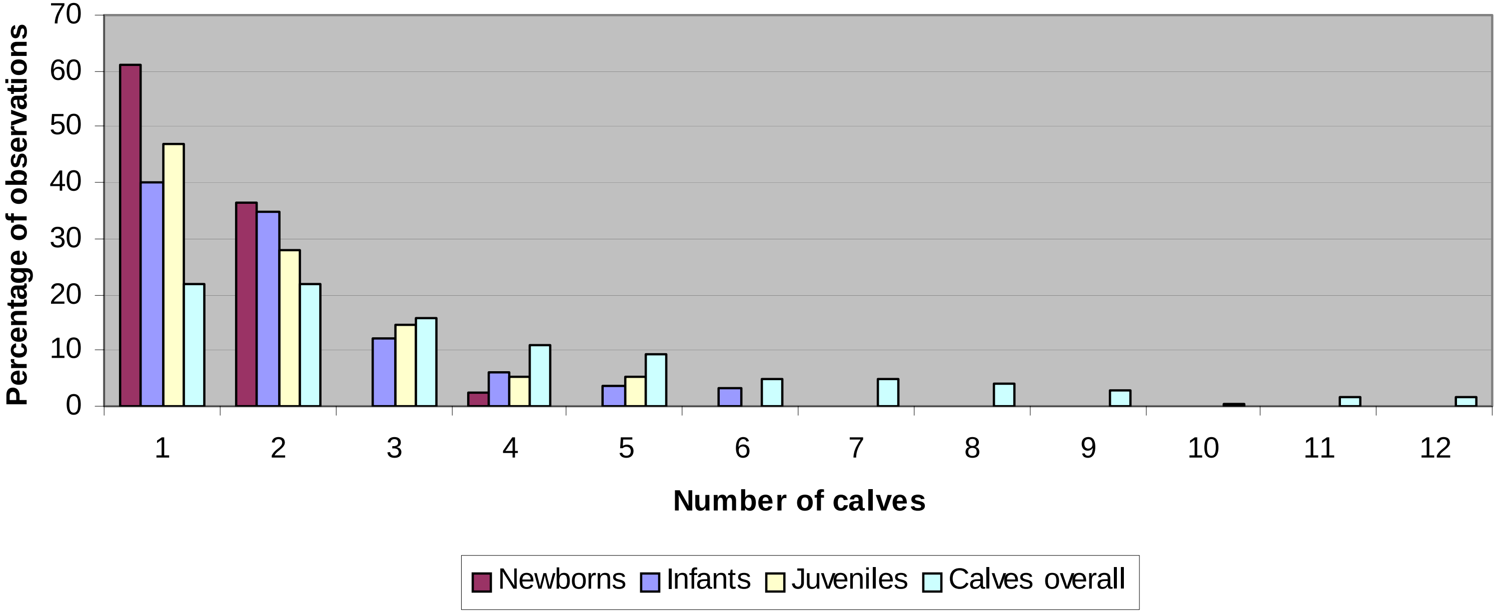
	JAN 03	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP
Total number of groups encountered	11	24	33	21	23	21	25	34	12
Number of group follows	9 (81.81%)	24 (100%)	32 (96.96%)	19 (90.47%)	20 (86.95%)	18 (85.71%)	23 (92%)	31 (91.17%)	10 (83.33%)
Length of group follows	4h55min	8h03min	12h48min	11h	9h11min	9h39min	13h47min	10h36min	3h41min
Number of focal follows	5	25	25	40	24	14	24	22	6
Length of focal follows	*	*	*	16min38sec	16min48sec	23min44sec	8min55sec	7min53sec	5min09sec

	OCT	NOV	DEC	JAN 04	FEB	TOTAL
Total number of groups encountered	40	12	33	37	22	348
Number of group follows	39 (97.5%)	7(58.33%)	32 (96.96%)	36 (97.3%)	20 (90.90%)	320 (91.95%)
Duration of group follows	15h04min	3h20min	9h28min	11h48min	8h26min	131h46min
Number of focal follows	33	8	37	22	26	311
Duration of focal follows	42min59sec	6min02sec	18min08sec	23min32sec	6min30sec	2h56min18sec

Table 2. Summary of groups encountered and follows conducted throughout the study period.



Graph 1. Percentage of observations of each group type throughout the study.



Graph 2. Number of newborns, infants, juveniles and calves, as a percentage of total observations.

six with a mean of 2.08 per sighting (SD=2.08, n=130). The number of juveniles in each group ranged from zero to five with a mean of 1.93 per sighting (SD=1.93, n=136).

4) Influence of environmental variables on group type

4.1. Water depth

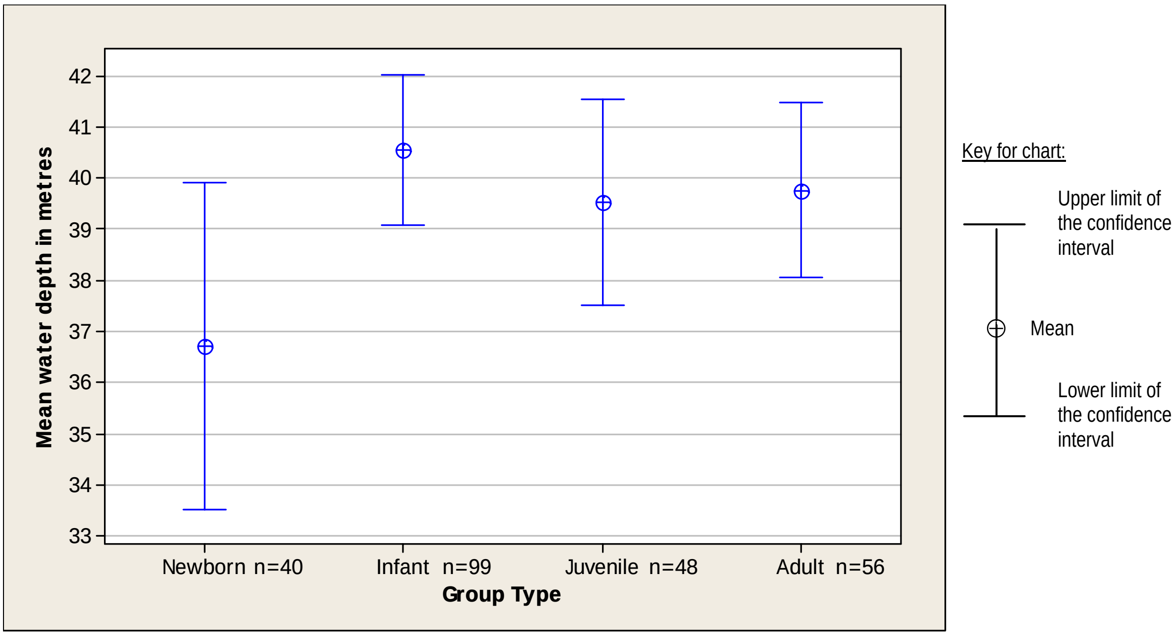
The water depths at which common dolphins were found ranged from 8.5 to 54.3 metres, with a mean of 39.68 metres (SD=7.45m). The mean water depth was calculated for each group type and the following results were obtained (Graph 3):

- youngest member of the group was a newborn: mean water depth was 36.7 metres (ranging from 8.5m to 51.4m, SD=9.98m, n=40),
- youngest member of the group was an infant: mean water depth was 40.5 metres (ranging from 11.6m to 51.8m, SD=7.42m, n=99),
- youngest member of the group was a juvenile: mean water depth was 39.5 metres (ranging from 20.9m to 50.7m, SD=6.94m, n=48),
- groups composed of adults only: mean water depth was 39.7 metres (ranging from 25.3m to 54m, SD=6.38m, n=56).

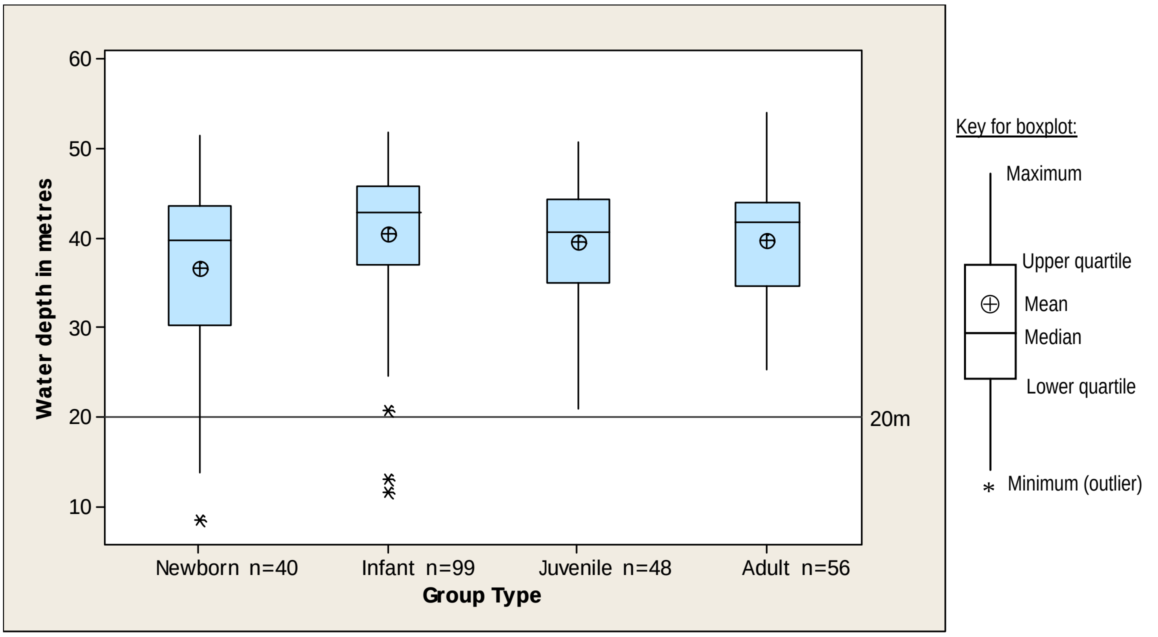
The distribution of mean water depth did not appear to vary according to group type (H=5.945, df=3, p>0.05; r=0.014, n=243, p>0.05). Therefore, hypothesis 1 '*Group type is affected by water depth*' cannot be accepted.

However, because of the difference in mean water depths between group type 1 (newborn) and the other group types (Graph 3), Mann-Whitney tests were performed between groups. These tests revealed a statistically significant difference between group type 1 (newborn) and group type 2 (infant) (U=1505.5, p<0.05). Groups of common dolphins in which the youngest member was a newborn were found in significantly shallower waters than groups for which the youngest member was an infant.

Comparative boxplots of the distribution of water depths according to group type also shows that only groups with newborns or infants occurred in water depths under 20 metres (Graph 4). This observation was tested statistically (Table 3). A Chi-Square test for independence found a significant difference in the distribution of common dolphin



Graph 3. Mean water depth for each group type (refer to key for explanation of chart symbols[1]).



Graph 4. Distribution of water depths for each group type (refer to key for explanation of boxplot symbols).

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[1] For explanation of chart symbols throughout the 'Results' chapter, refer to 'Key for chart' on this page.

Group type		Occurrence in water depths under 20 metres
Newborn	Mean	8
	n	40
	SD	0.267
	Lower confidence interval	1.57
	Upper confidence interval	20.39
Infant	Mean	2
	n	99
	SD	0.141
	Lower confidence interval	0.25
	Upper confidence interval	7.11
Juvenile	Mean	0
	n	48
	SD	0
	Lower confidence interval	0
	Upper confidence interval	7.397
Adult	Mean	0
	n	56
	SD	0
	Lower confidence interval	0
	Upper confidence interval	6.375

Table 3. Occurrence of common dolphin groups under 20 metres of depth as a percentage of total observations for each group type.

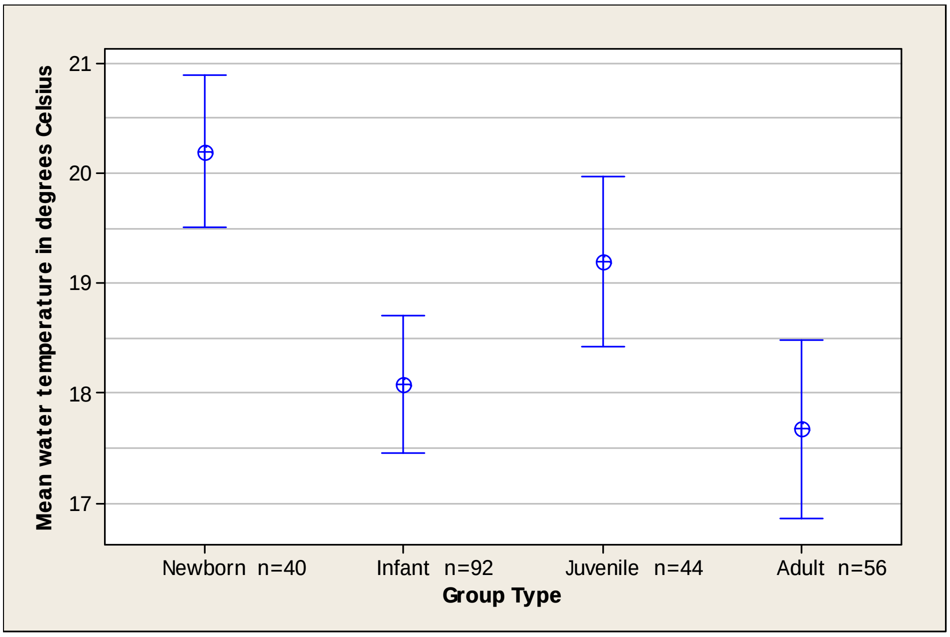
groups under depths of 20 metres according to group type ($X^2=8.065$, df=3, $p<0.05$). Although not very strong, the negative correlation coefficient gives an indication on the direction of the relationship between the two variables ($r=-0.160$, $n=243$, $p<0.05$), with a decreasing tendency of occurrence in waters shallower than 20 metres as the age class of the youngest calf in the group increases. Due to small sample size, differences between group types could not be tested.

4.2. Water temperature

The water temperature in which common dolphins were found ranged from 13.4 to 24.5°C, with a mean of 18.7°C (SD=2.94°C). The mean water temperature was calculated for each group type and resulted in the following (Graph 5):

- youngest member of the group was a newborn: mean water temperature was 20.2°C (ranging from 14°C to 23.7°C, SD=2.17°C, n=40),
- youngest member of the group was an infant: mean water temperature was 18.1°C (ranging from 13.4°C to 23.7°C, SD=3.01°C, n=92),
- youngest member of the group was a juvenile: mean water temperature was 19.2°C (ranging from 14.1°C to 23.3°C, SD=2.53°C, n=44),
- groups composed of adults only: mean water temperature was 17.7°C (ranging from 13.5°C to 22.6°C, SD=3.03°C, n=56).

The difference in mean water temperatures across group types was significant ($H=20.492$, df=3, $p<0.01$). The Spearman rank correlation coefficient of -0,170 ($n=232$, $p<0.05$) indicates that as the age class of the youngest member of the group increases, the mean water temperature tends to decrease. Mean water temperatures were significantly higher for groups with newborns than for groups with infants ($U=1107.5$, $p<0.01$) or with adults only ($U=625$, $p<0.01$). The difference between groups with newborns and groups with juveniles was only significant for a level of significance of $\alpha=0.10$ ($U=691$, $p>0.05$). Considering these results, test hypothesis 2 '*Group type is affected by water temperature*' can be accepted.



Graph 5. Mean water temperature for each group type.

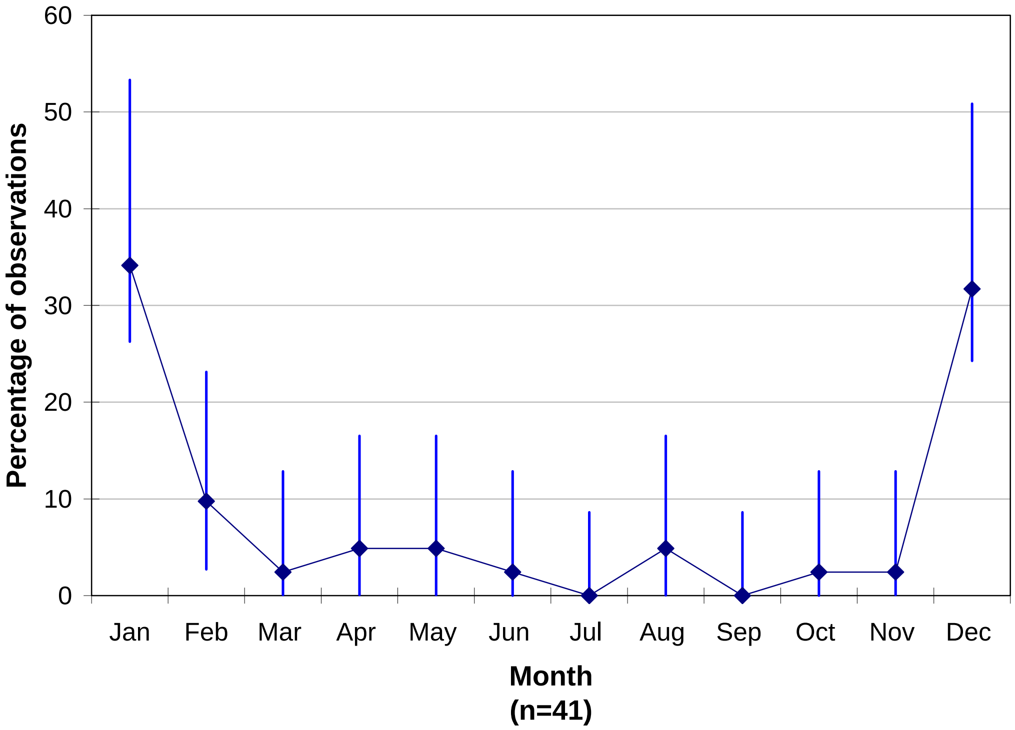
4.3. Season

Whether they contained newborns, infants, or juveniles, groups of common dolphins with calves were encountered in all seasons. It seems likely that some births do take place during winter, as newborn calves were sighted during that season. Nevertheless, the different types of common dolphin groups did not appear to be observed at the same rate year-round, which is suggestive of breeding seasonality for the species. These observations were tested statistically by comparing the percentage of occurrence of the four group types against the time of the year. The distribution of the different group types was found to vary significantly across months (X^2=73.197, df=33, $p<0.01$), as well as across seasons (X^2=22.282, df=9, $p<0.01$). In order to further investigate these patterns, the percentage of observations of each group type was calculated and compared across months as well as seasons.

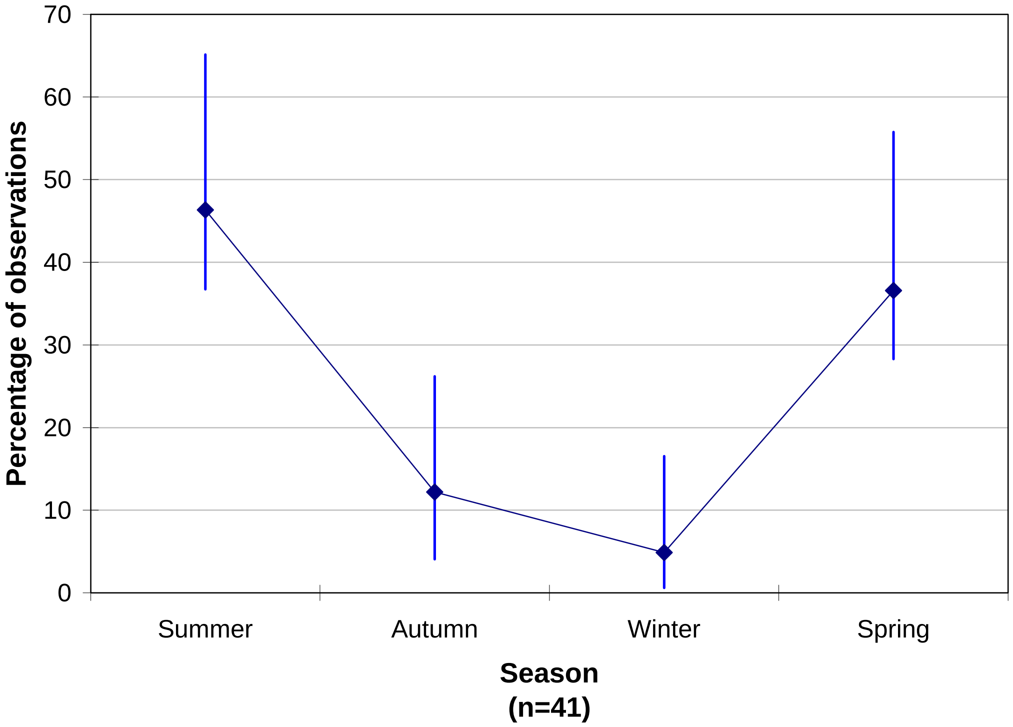
Chi-Square tests for independence indicated that the occurrence of group type 1 (newborn) varied significantly with the time of the year, whether coded in months (X^2=43.944, df=11, $p<0.01$) (Graph 6) or in seasons (X^2=12.347, df=3, $p<0.01$) (Graph 7). Binomial tests were used to compare seasons more specifically. There were significantly more groups with newborn calves sighted in summer and spring than in winter (between summer and winter: z=3.18, $p<0.01$; between spring and winter: z=-3.08, $p<0.01$), which is likely to be due to the peaks observed in December and January (Graph 6). The same significant pattern was found for the distribution of the mean number of newborns sighted per season (H=12.084, df=3, $p<0.01$), between summer and winter (U=1897, $p<0.01$), and between spring and winter (U=1516, $p<0.01$) (Table 4).

The percentage of observations of group type 2 (infant) did not vary according to the month of the year (X^2=18.244, df=11, $p>0.05$) (Graph 8), or according to the season (X^2=5.460, df=3, $p>0.05$) (Graph 9). The distribution of the mean number of infants sighted across seasons was not significant either (H=0.409, df=3, $p>0.05$) (Table 4).

Chi-Square tests for independence did not show any significant differences in the distribution of observations of group type 3 (juvenile) according to months (X^2=13.990, df=11, $p>0.05$) (Graph 10) or seasons (X^2=5.185, df=3, $p>0.05$) (Graph 11).



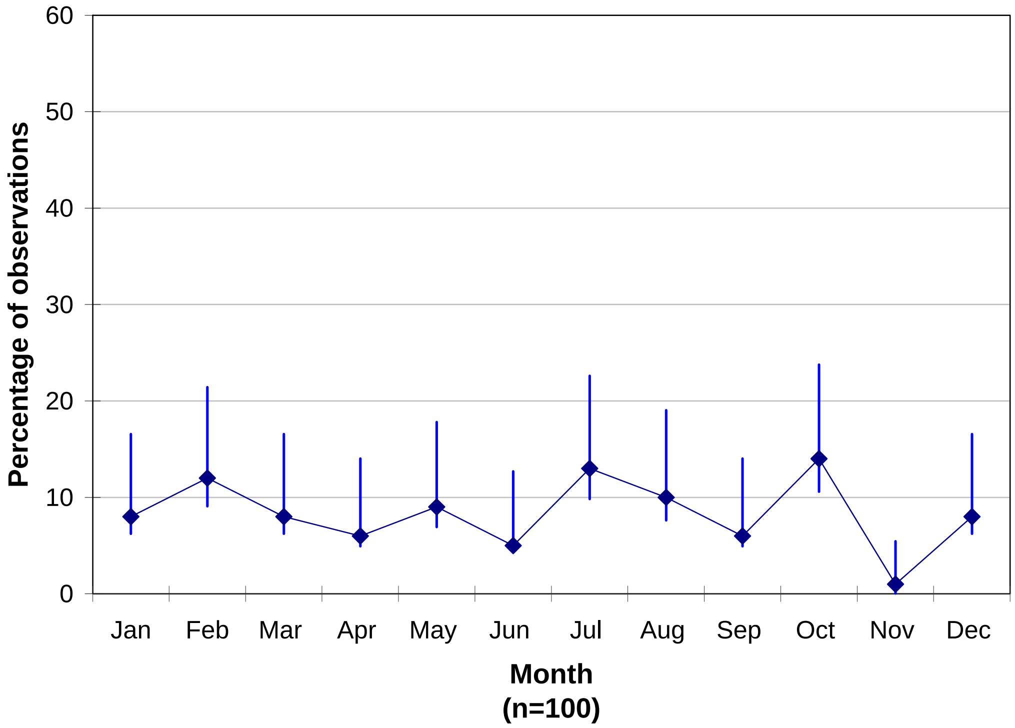
Graph 6. Occurrence of group type 1 (newborn) per month as a percentage of total observations of group type 1.



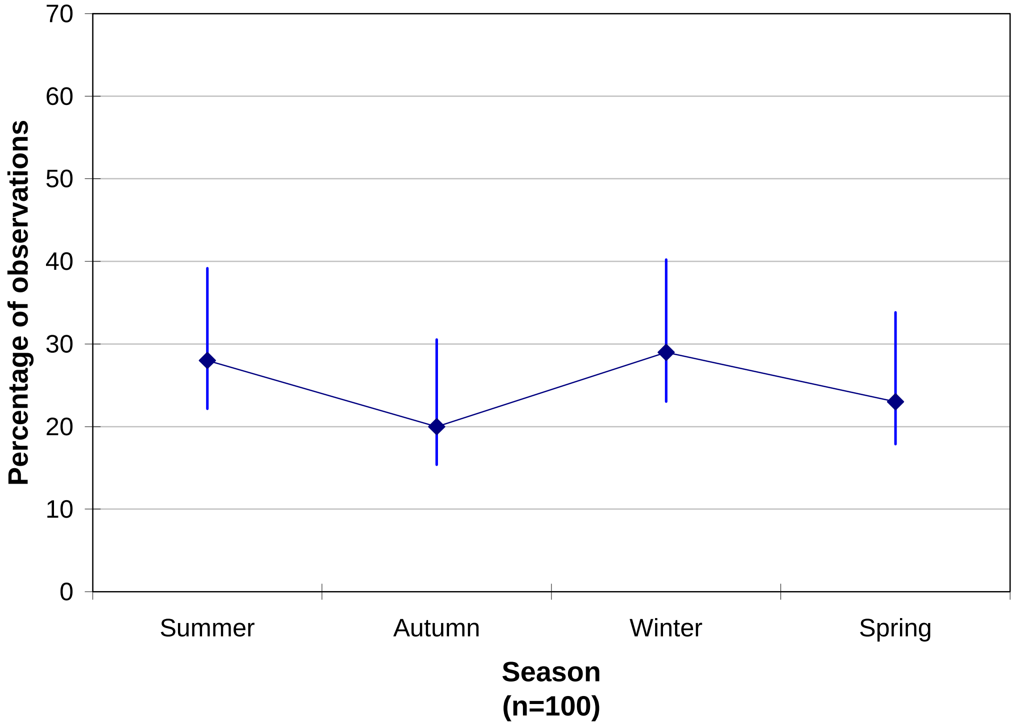
Graph 7. Occurrence of group type 1 (newborn) per season as a percentage of total observations of group type 1.

Calf age class		Summer	Autumn	Winter	Spring
Newborn	Mean	0.29	0.16	0.04	0.4
	n	83	44	56	68
	SD	5.595	0.479	0.187	0.792
	Lower confidence interval	0.2	0.07	0.01	0.26
	Upper confidence interval	0.43	0.33	0.13	0.56
Infant	Mean	1.14	1.2	1.14	1.0625
	n	77	42	56	64
	SD	1.493	1.353	1.445	1.296
	Lower confidence interval	0.93	0.92	0.9	0.84
	Upper confidence interval	1.41	1.6	1.46	1.35
Juvenile	Mean	1.23	1.45	0.72	1.0625
	n	75	44	54	64
	SD	1.290	1.547	1.089	1.180
	Lower confidence interval	1	1.14	0.53	0.84
	Upper confidence interval	1.5	1.86	0.99	1.35

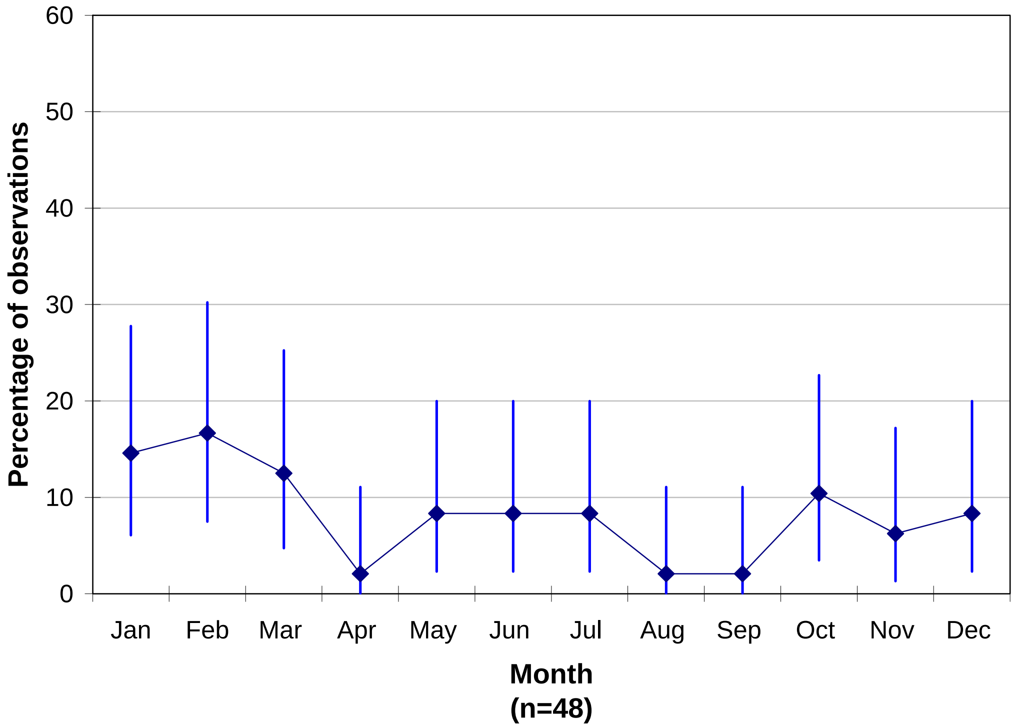
Table 4. Mean number of newborn, infant and juvenile common dolphins sighted per season.



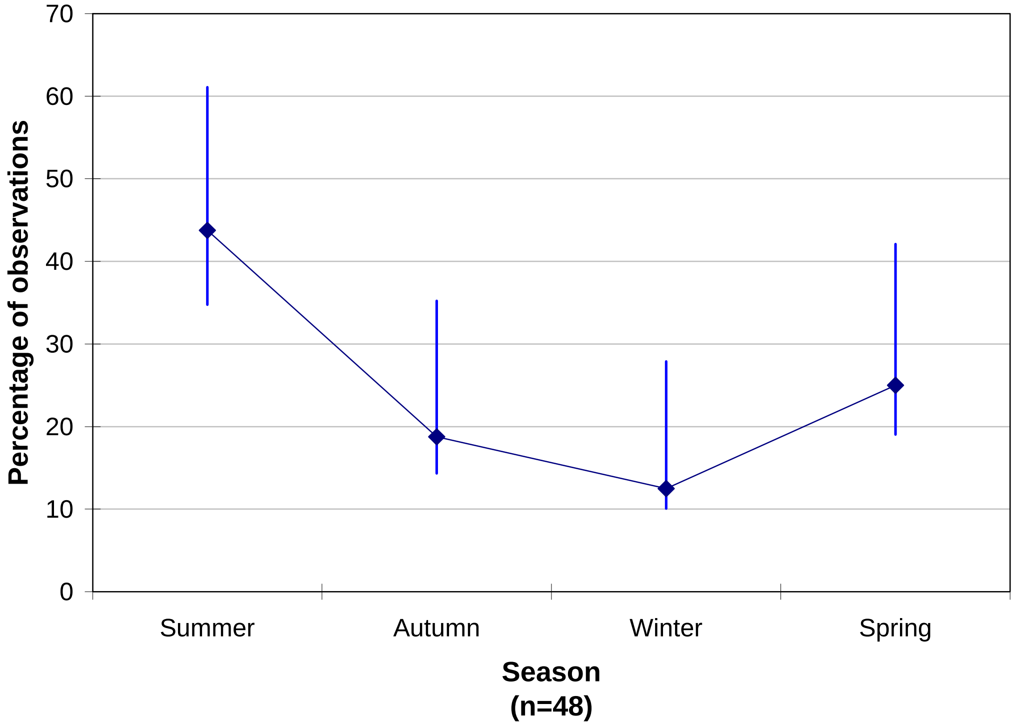
Graph 8. Occurrence of group type 2 (infant) per month as a percentage of total observations of group type 2.



Graph 9. Occurrence of group type 2 (infant) per season as a percentage of total observations of group type 2.



Graph 10. Occurrence of group type 3 (juvenile) per month as a percentage of total observations of group type 3.



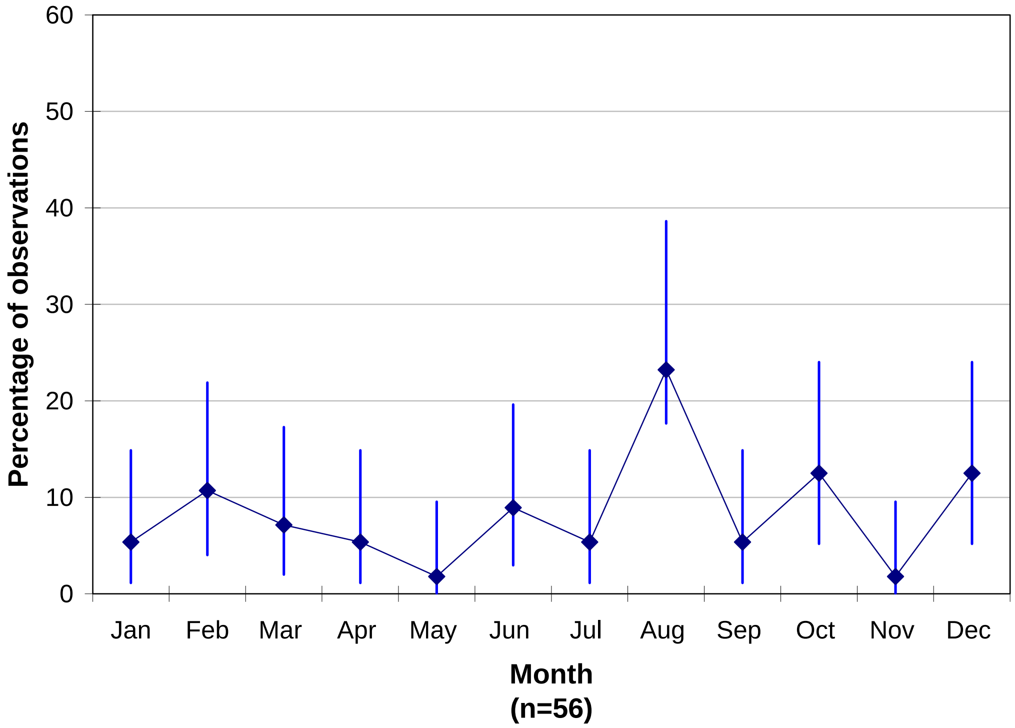
Graph 11. Occurrence of group type 3 (juvenile) per season as a percentage of total observations of group type 3.

Nevertheless, groups with juveniles occurred more frequently in summer than in winter ($z=2.20$, $p<0.05$). There was a significant difference in the mean number of juveniles sighted according to seasons ($H=9.107$, $df=3$, $p<0.05$), with higher numbers sighted in summer and autumn than in winter (between summer and winter: $U=1492$, $p<0.01$; between autumn and winter: $U=861$, $p<0.05$) (Table 4).

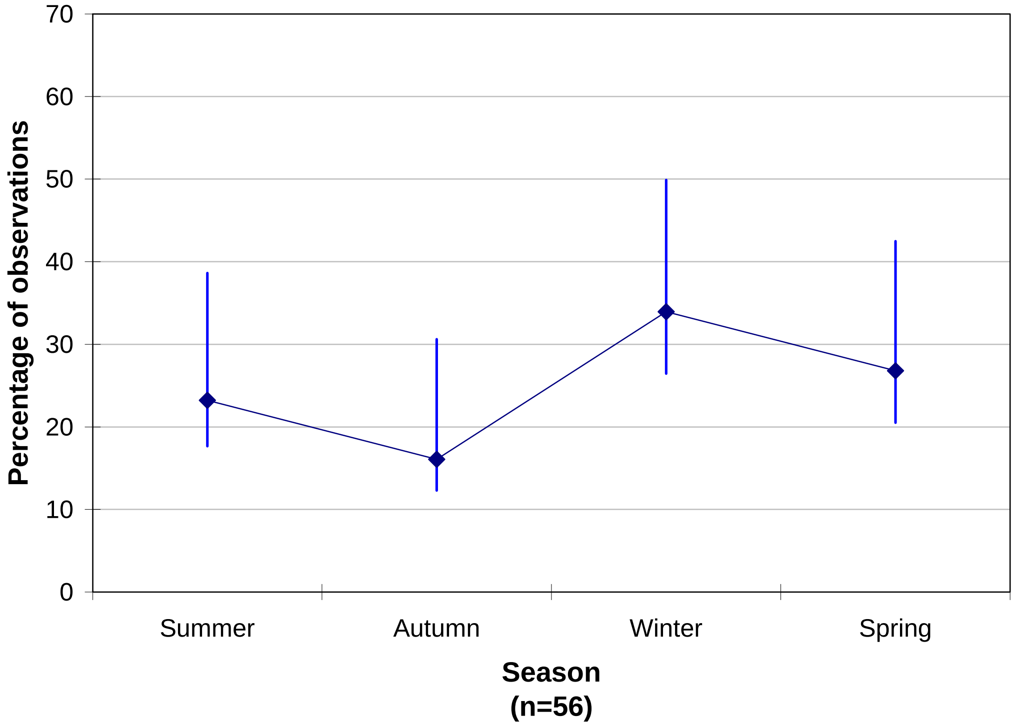
There was no significant difference in the percentage of observations of group type 4 (adult) according to the time of the year in months ($X^2=18.874$, $df=11$, $p>0.05$) (Graph 12) or in seasons ($X^2=5.965$, $df=3$, $p>0.05$) (Graph 13). The winter peak observed on graph 13 lead to a binomial comparison between winter and autumn which proved to be significant ($z=-2.43$, $p<0.05$). Groups without calves are therefore more likely to be sighted in winter than in autumn.

Because only group type 1 (newborn) varied significantly across months and seasons, we cannot accept hypothesis 3 '*Group type is affected by the time of the year*'. Nevertheless, a more specific hypothesis, such as '*Time of year influences the frequency of observation of groups in which the youngest calf was a newborn*' can be accepted.

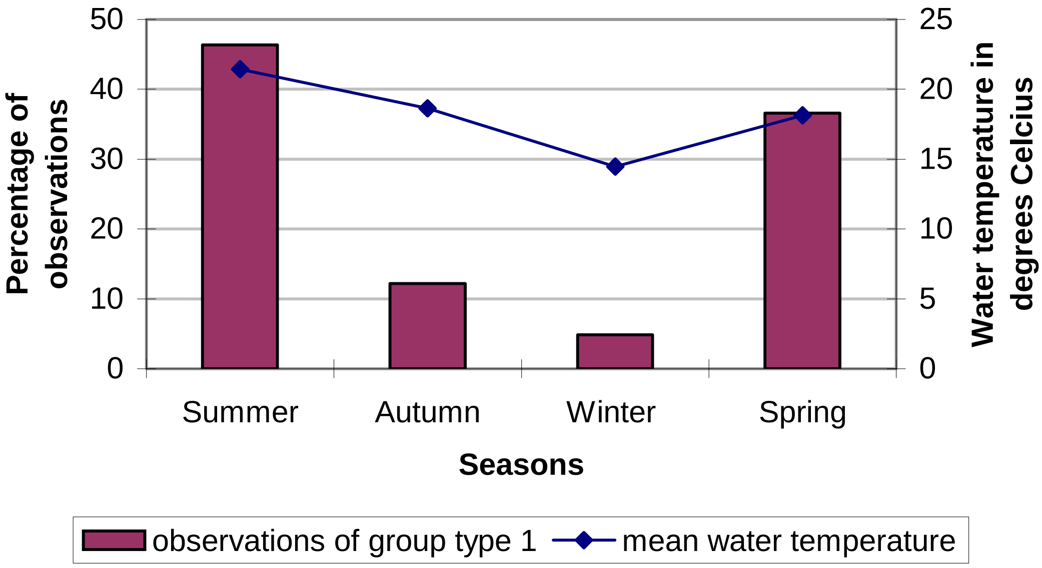
Because the potential influence of months and seasons on the occurrence of different group types could have been related to sea surface temperature, the latter was tested against time of the year. Water temperature varies significantly across months ($H=261.384$, $df=11$, $p<0.01$) and seasons ($H=217.635$, $p<0.01$). Graphs 14 to 17 provide an overview of the inter-relationships between these three variables. Sightings of groups with newborns proved to be the highest in spring and summer, which also corresponded to the seasons of highest water temperatures. Their occurrence appeared to be the lowest during the cold months of winter. No significant pattern can be observed for groups with infants, which is consistent with the fact that their occurrence did not seem to vary seasonally. The occurrence of groups with juveniles showed a similar pattern to that of groups with newborns, as they were observed more frequently during the season of warmest water temperatures (summer) and were less likely to be encountered during the season of coldest water temperatures (winter). In contrast, groups containing only adults showed higher occurrence during the coldest season of the year. It therefore seems likely that the influence of season on the occurrence of the different group types is mediated by the seasonal variations in sea surface temperature.



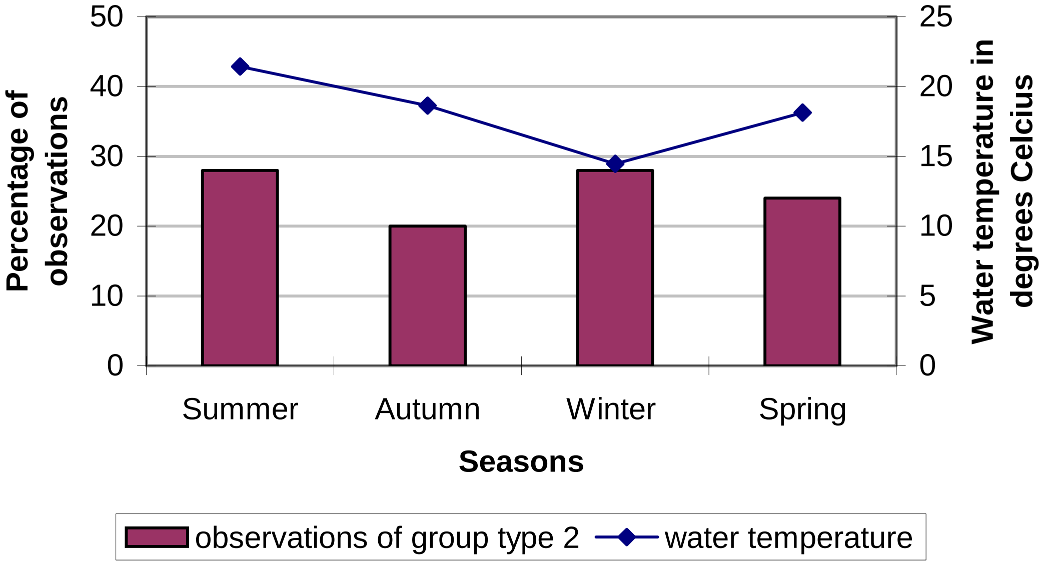
Graph 12. Occurrence of group type 4 (adult) per month as a percentage of total observations of group type 4.



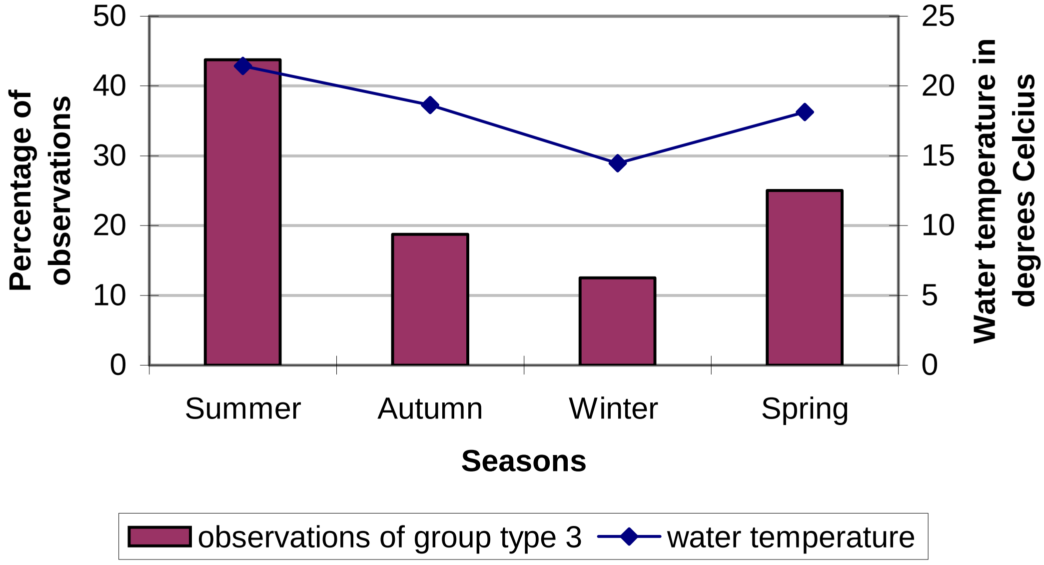
Graph 13. Occurrence of group type 4 (adult) per season as a percentage of total observations of group type 4.



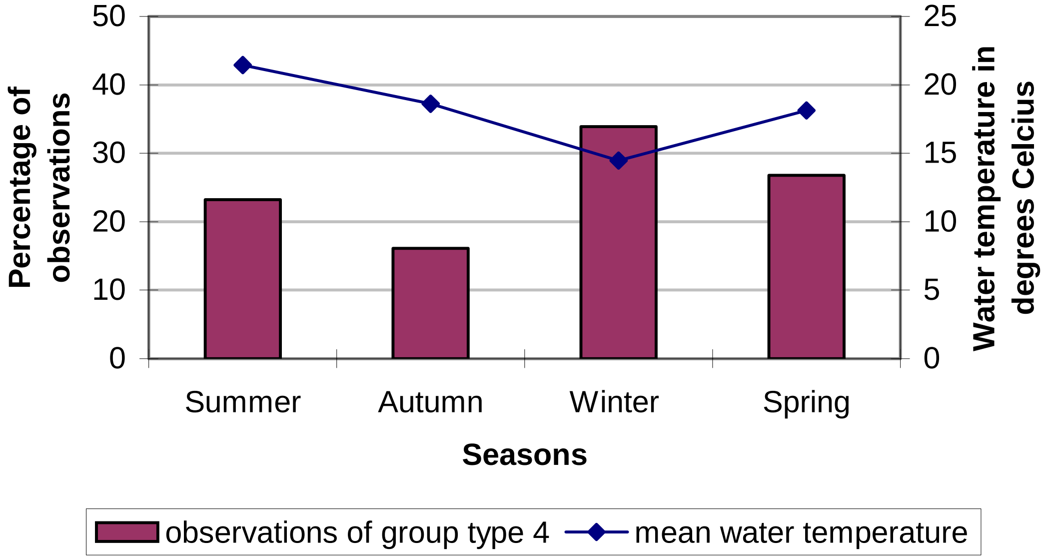
Graph 14. Occurrence of group type 1 (newborn) per season as a percentage of all observations of group type 1, and mean water temperature per season.



Graph 15. Occurrence of group type 2 (infant) per season as a percentage of all observations of group type 2, and mean water temperature per season.



Graph 16. Occurrence of group type 3 (juvenile) per season as a percentage of all observations of group type 3, and mean water temperature per season.



Graph 17. Occurrence of group type 4 (adult) per season as a percentage of all observations of group type 4, and mean water temperature per season.

5) Influence of group size on group type

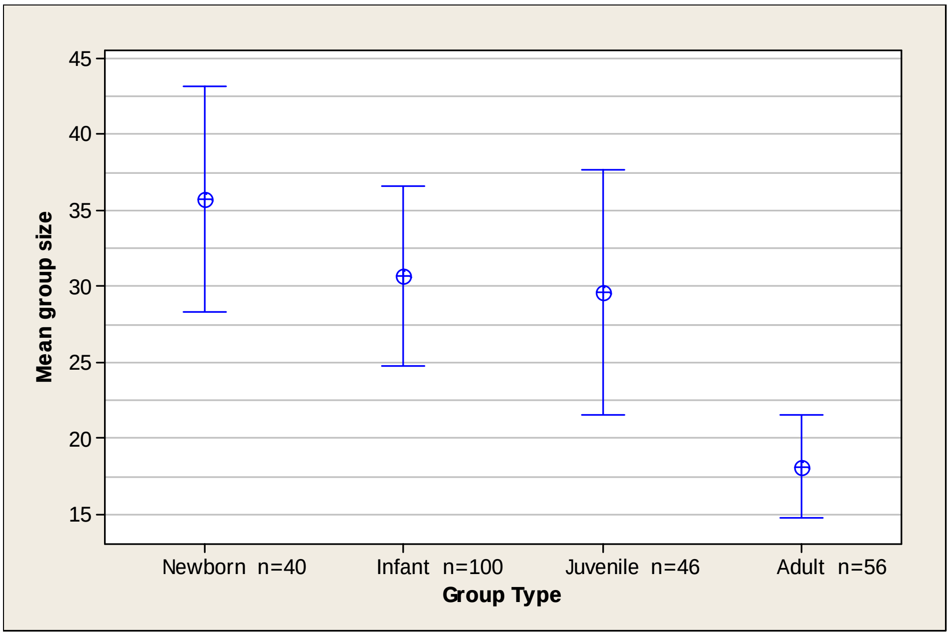
Common dolphin groups of a wide range of sizes were encountered throughout the study, and numbers varied from only two individuals up to approximately 450 animals. When large aggregations were sighted, dolphins were often seen travelling at high speed with many members of the group leaping out of the water. Both extremes of the range were rarely observed and groups usually contained around 30 dolphins (mean=33.1, SD=35.81). In order to assess the potential effect of group size on the presence of calves of different age classes, variations in group size were investigated across the four group types (newborn, infant, juvenile, adult).

Mean group size was calculated using the mid-point of the group size category recorded for each encounter. As groups over 100 individuals (group size category 6) were mostly made of 150 common dolphins, this value was used in the calculation of mean group size. Graph 18 illustrates that mean group size tends to decrease as the age class of the youngest member of the group increases. These two variables proved to be negatively correlated ($r=-0.306$, $n=242$, $p<0.01$), and a significant difference was found in the distribution of group size according to group type ($H= 25.460$, $df=3$, $p<0.01$). Groups were significantly smaller when composed of adults only (between adult and newborn: $U= 482.5$, $p<0.01$; between adult and infant: $U=1961.5$, $p<0.01$; between adult and juvenile: $U=949.5$, $p<0.05$), and significantly larger when the youngest member of the group was a newborn (between newborn and infant: $U=1402$, $p<0.01$; between newborn and juvenile: $U=640$, $p<0.05$). As a result, hypothesis 4 '*Group type is affected by group size*' can be accepted.

6) Influence of group type on the behaviour of common dolphins

6.1. Behavioural state

Out of the five behavioural states identified in this study, feeding was more frequently observed than any other activity with an occurrence of 44% of all encounters (difference between feeding and travelling: $z=6.26$, $p<0.01$; between feeding and milling, $z=5.71$, $p<0.01$; between feeding and socialising: $z=11.65$, $p<0.01$; feeding and resting: $z=10.06$, $p<0.01$). Feeding usually involved high levels of surface activity, with



Graph 18. Mean group size for each group type.

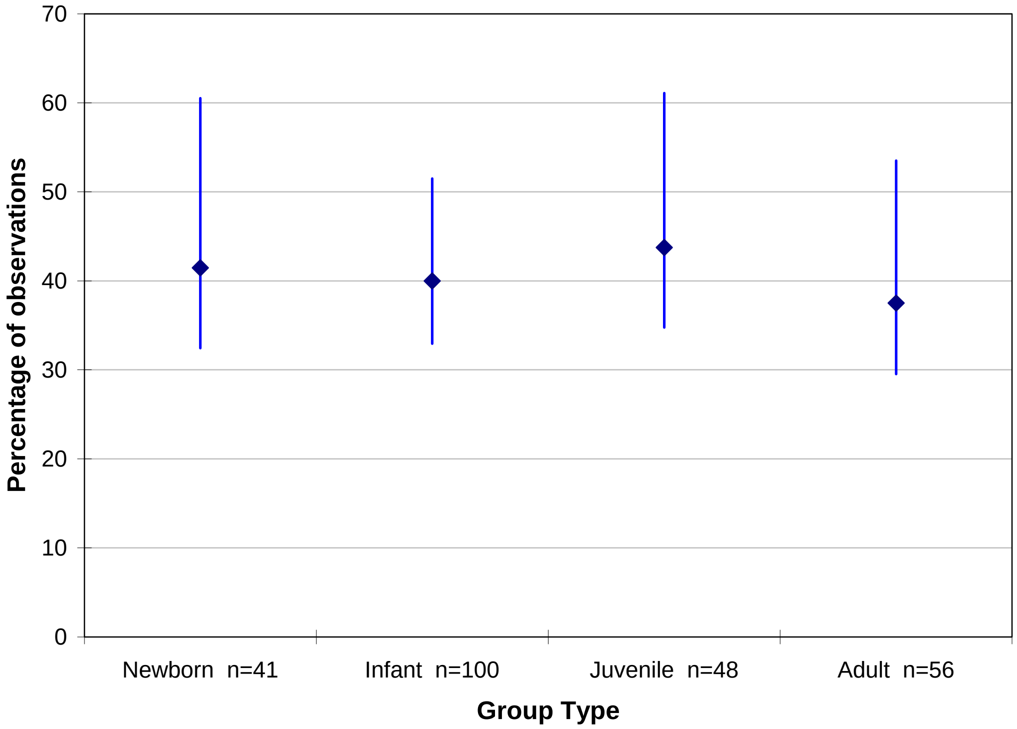
dolphins swimming in fast circular movements, most often in association with diving birds, and sometimes with baleen whales, usually Bryde's whales, lunge feeding in close proximity. All age groups were observed actively involved in feeding activities, and on many occasions, newborn calves were seen leaping underneath the diving birds and participating in circling a school of fish along with other individuals.

The potential influence of the age class of the youngest member of common dolphin groups on the occurrence of different behavioural states was assessed by comparing the distribution of these two variables. The Chi-Square test for independence and the correlation test used towards that goal failed to find a significant difference ($X^2=9.323$, $df=12$, $p>0.05$) or correlation ($r=0.024$, $n=245$, $p>0.05$) between them. In order to test each of the five behavioural states individually, the occurrence of feeding, travelling, milling, resting and socialising was calculated as a percentage of total observations (Graphs 19 to 23), and compared across group types.

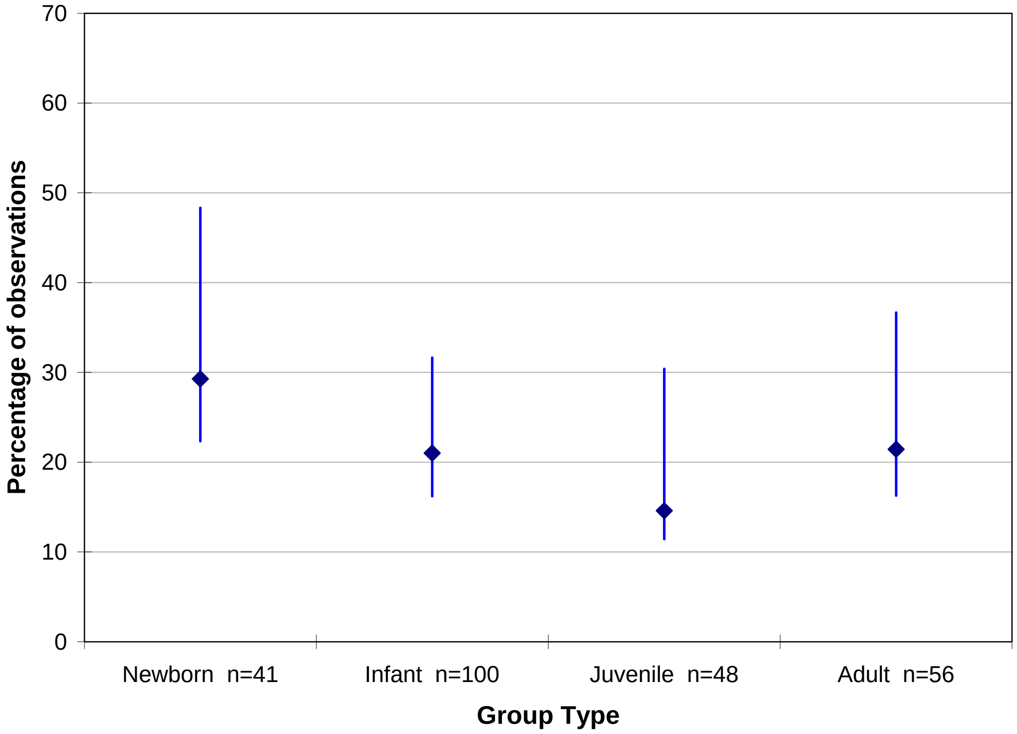
The occurrence of feeding behaviour was not significantly different according to group type ($X^2=0.445$, $df=3$, $p>0.05$). The age class of the youngest member of the group did not seem to influence the distribution of any other behavioural states either, as the percentage of observations for each of them didn't prove to vary significantly across the different group types (travelling: $X^2=2.857$, $df=3$, $p>0.05$; milling: $X^2=2.150$, $df=3$, $p>0.05$; socialising: $X^2=3.241$, $df=3$, $p>0.05$; resting: $X^2=2.302$, $df=3$, $p>0.05$). Therefore, hypothesis 5 '*Common dolphins activity state is affected by group type*' cannot be accepted.

6.2. Association with other species

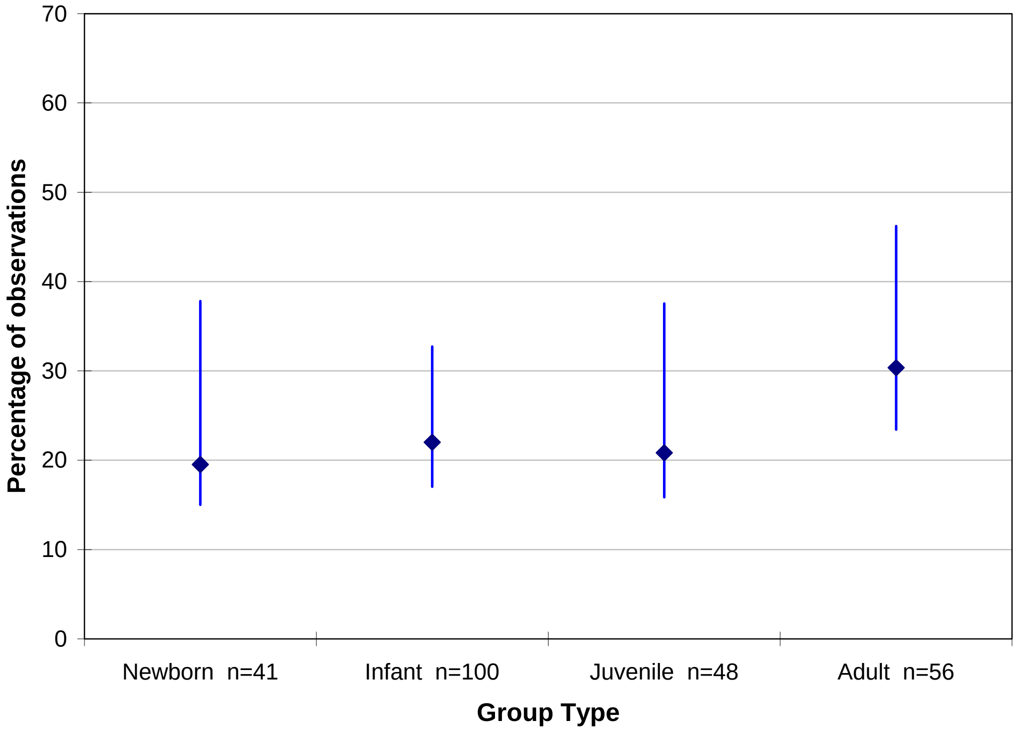
For the present study, it was hypothesised that the association of common dolphins with other animal species would be affected by group type. The observations made in the field do not tend to support this statement, as the frequency of observations of such associations did not vary significantly according to group type ($X^2=5.606$, $df=3$, $p>0.05$; $r=-0.034$, $n=244$, $p>0.05$) (Graph 24). The peak that can be observed in the percentage of association for group type 3 (juvenile) resulted in a significant difference with group type 4 (adult) ($z=2.43$, $p<0.05$), and groups with juveniles were more likely to be seen associated with other species than groups only containing adult individuals.



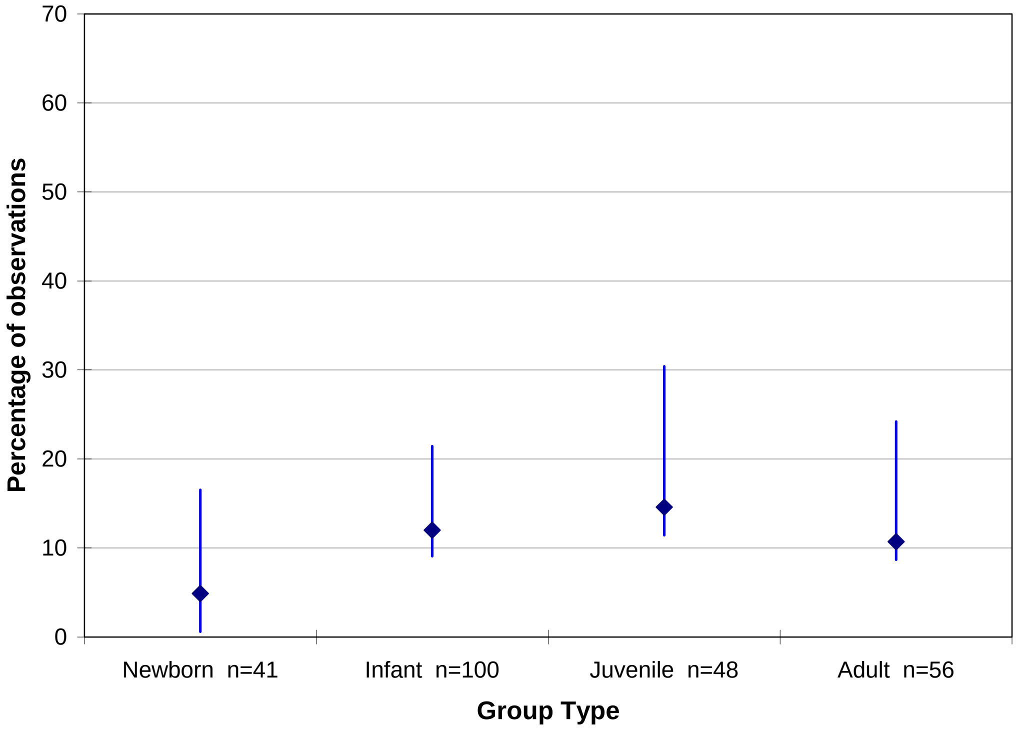
Graph 19. Occurrence of feeding as a percentage of total observations for each group type.



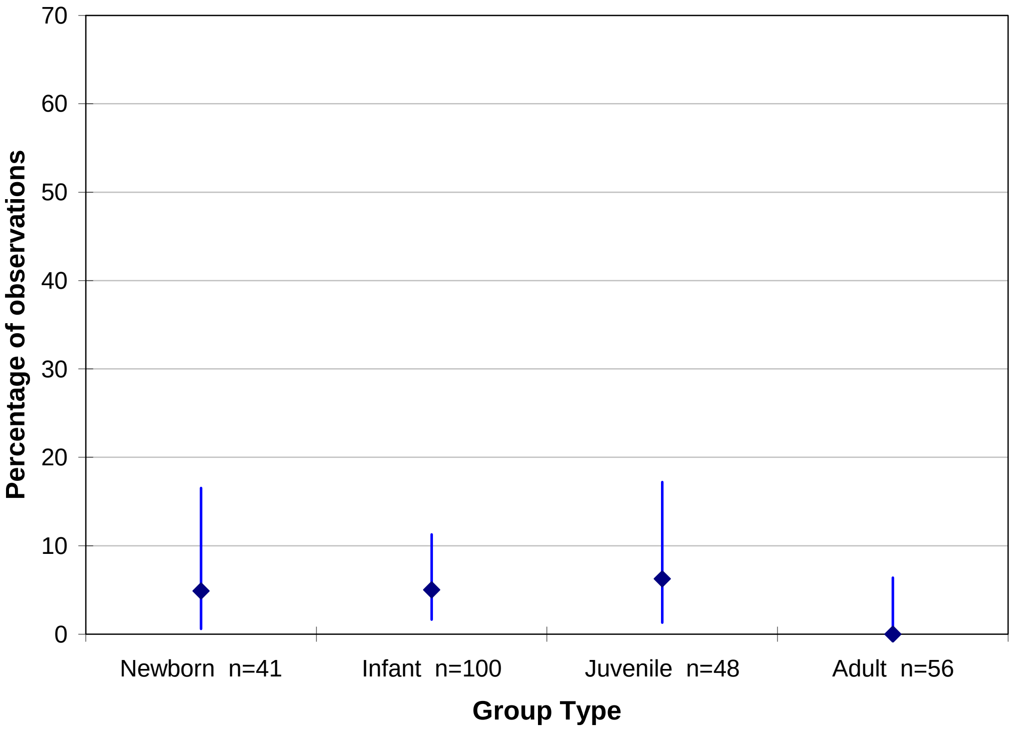
Graph 20. Occurrence of travelling as a percentage of total observations for each group type.



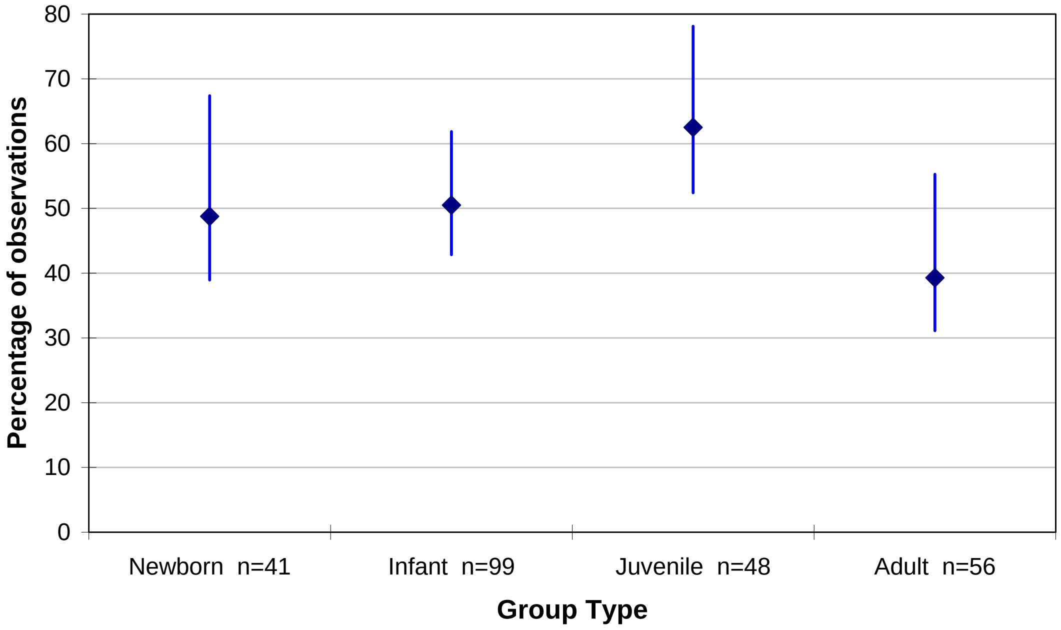
Graph 21. Occurrence of milling as a percentage of total observations for each group type.



Graph 22. Occurrence of resting as a percentage of total observations for each group type.



Graph 23. Occurrence of socialising as a percentage of total observations for each group type.



Graph 24. Occurrence of association with other species as a percentage of total observations for each group type.

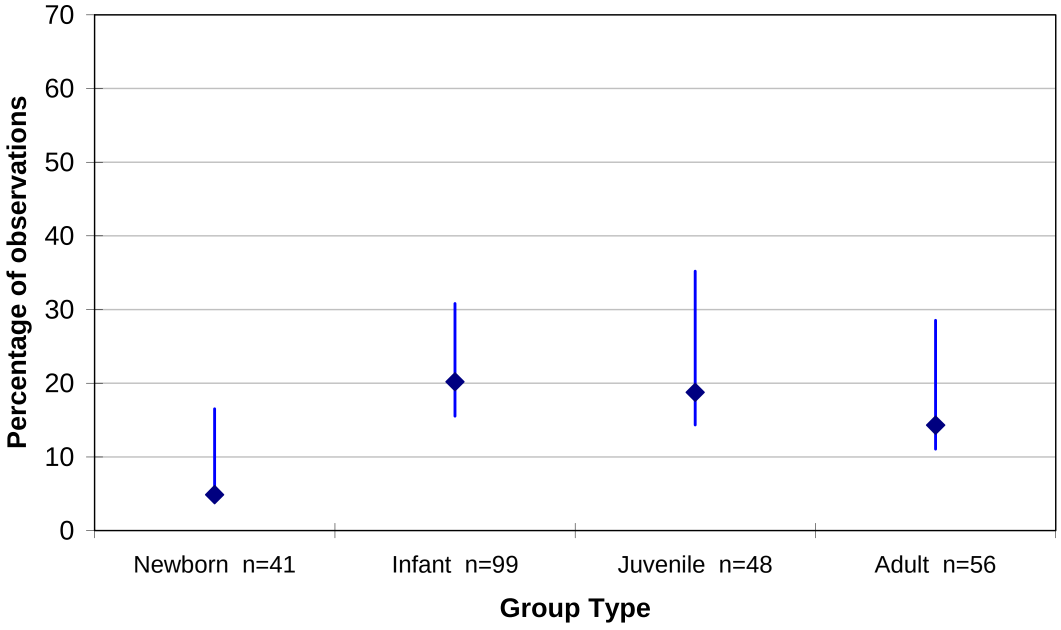
The three different patterns of association were also investigated (Graphs 25 to 27). The percentage of observations of association with birds and whales did not appear to vary according to the age class of the youngest member of the group ($X^2=5.471$, df=3, $p>0.05$; $r=0.049$, $n=244$, $p>0.05$). Nevertheless, associations with birds and whales was significantly less frequent for groups with newborns, than for groups with infants ($z=-2.92$, $p<0.05$) or with juveniles ($z=-2.11$, $p<0.05$). As for the associations with birds only, and with whales only, they both appeared to vary independently from the influence of group type (birds only: $X^2=7.726$, df=3, $p>0.05$; $r=-0.082$, $n=244$, $p>0.05$; whales only: $X^2=1.423$, df=3, $p>0.05$; $r=0.042$, $n=244$, $p>0.05$). Binomial tests were used in order to assess the two peaks in the percentage of observations of association with birds only for group type 1 (newborn) and 3 (juvenile). Both were significantly higher than the percentage obtained for groups containing only adults (between group type 1 and 4: $z=2.16$, $p<0.05$; between group type 3 and 4: $z=2.25$, $p<0.05$). Association with birds only occurred more frequently when the youngest member of the group was either a newborn or a juvenile, than when the groups were composed of adults only.

Although some significant variations were found between certain group types, the results of the Chi-Square tests for independence and of the Spearman rank correlation tests tend to show that the variations in association with other species are not related to the age class of the youngest member of the group. Therefore, hypothesis 6 '*The association of common dolphins with other species is affected by group type*' cannot be accepted.

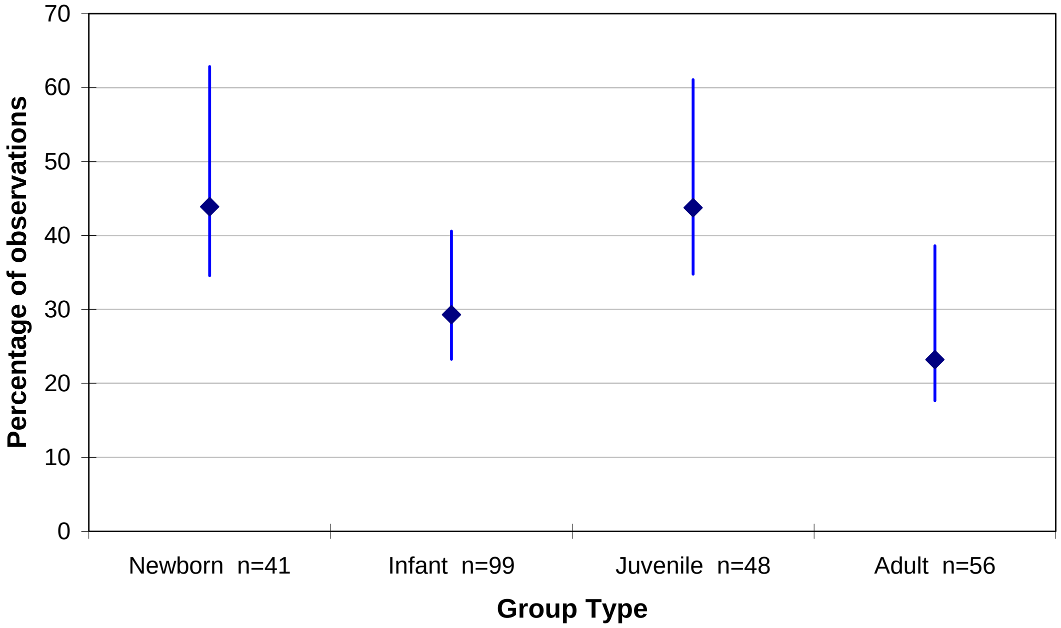
6.3. Reaction to the boat

- Reaction of groups to the boat

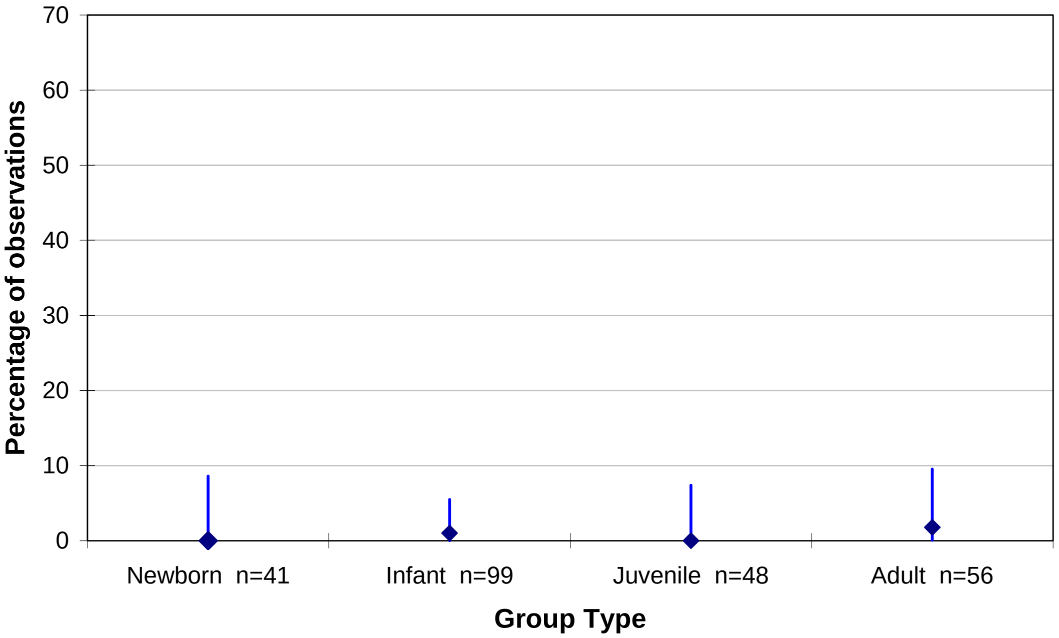
Common dolphins reacted to the approach of the boat ('Dolphin Explorer') by riding the bow wave of the vessel in 66% of all encounters. Therefore, the minimum distance to the boat was likely to be less than one metre. Even though dolphins were generally attracted to the boat, they also proved to sometimes show no distinctive changes in their behaviour. This lack of reaction was most commonly observed when the dolphins were feeding. Observed avoidance of the boat was rare and was only seen on four occasions.



Graph 25. Occurrence of association with birds and whales as a percentage of total observations for each group type.



Graph 26. Occurrence of association with birds only as a percentage of total observations for each group type.



Graph 27. Occurrence of association with whales only as a percentage of total observations for each group type.

Both the reaction of the dolphins to the boat and the minimum distance between the animals and the vessel were compared across the different group types encountered.

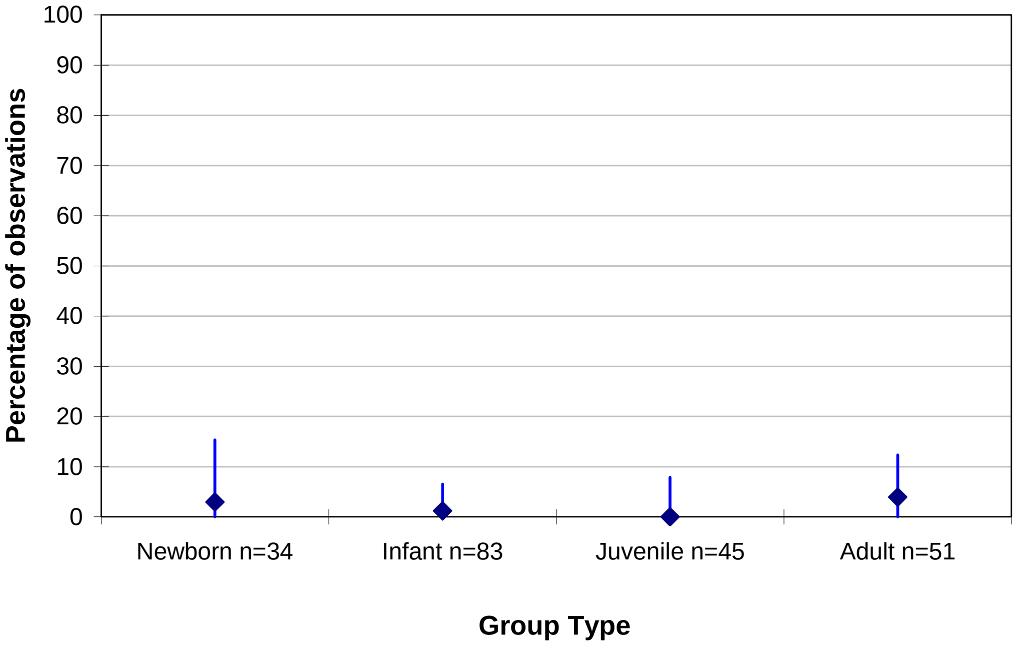
The behavioural reaction of common dolphins towards the approach of the boat did not vary (X^2=4.112, df=6, p>0.05); neither was it correlated (r=-0.028, n=213, p>0.05) with group type. Each of the three possible reactions (attraction, neutral, and avoidance) was also tested independently and their occurrence for each group type is summarised in graphs 28 to 30. Avoidance did not vary according to group type (X^2=2.430, df=3, p>0.05). The dolphins did not show any obvious reaction to the boat in 33% of all encounters, and the occurrence of such a response was not significantly different across the different group types (X^2=1.804, df=3, p>0.05). Finally, the percentage of observations of attraction was the highest of all reactions (66%) and did not vary according to whether the youngest member of the group was a newborn, an infant, a juvenile or whether groups only contained adult individuals (X^2=1.480, df=3, p>0.05).

As the results of the analyses show that occurrence of avoidance, attraction or neutral behaviour towards the boat was not affected by the age class of the youngest member of the group, hypothesis 7 '*The reaction of the dolphins to the approach of the boat is affected by group type*' cannot be accepted.

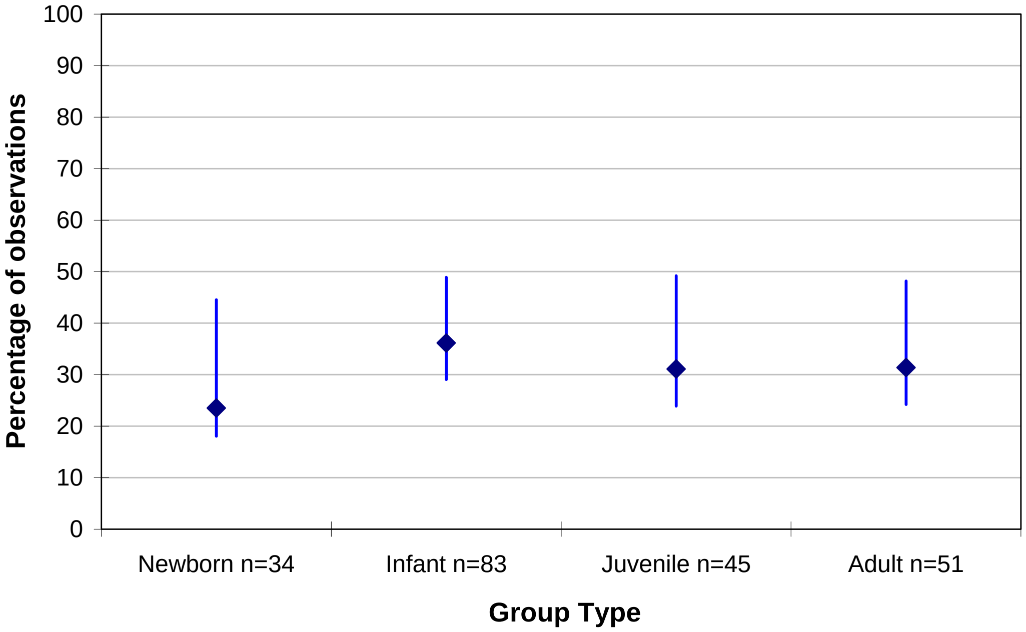
The mean minimum distance to the boat was calculated for each group type, and as shown by graph 31, averaged less than one metre for all group types. The slight variations between the different groups did not result in significant differences (H=4.685, df=3, p>0.05). The age class of the youngest member of the group did not influence the distance at which the dolphins would approach the boat, and as a consequence, hypothesis 8 '*The minimum distance between the dolphins and the boat is affected by group type*' cannot be accepted.

- Reaction of mother-calf pairs to the boat

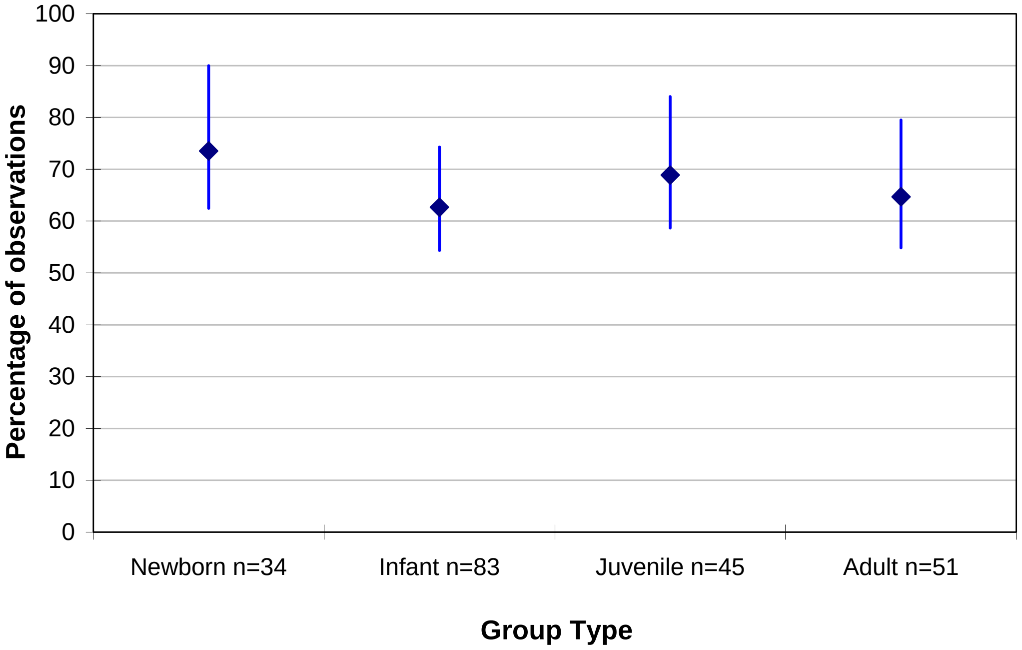
On two separate occasions, the presumed mothers of two infants appeared to herd their calves away from the boat. In both cases, the infants were approaching the back of the boat on their own when the presumed mothers interposed themselves between the boat and the calves, and chased them away from the vessel. One of these chases involved a



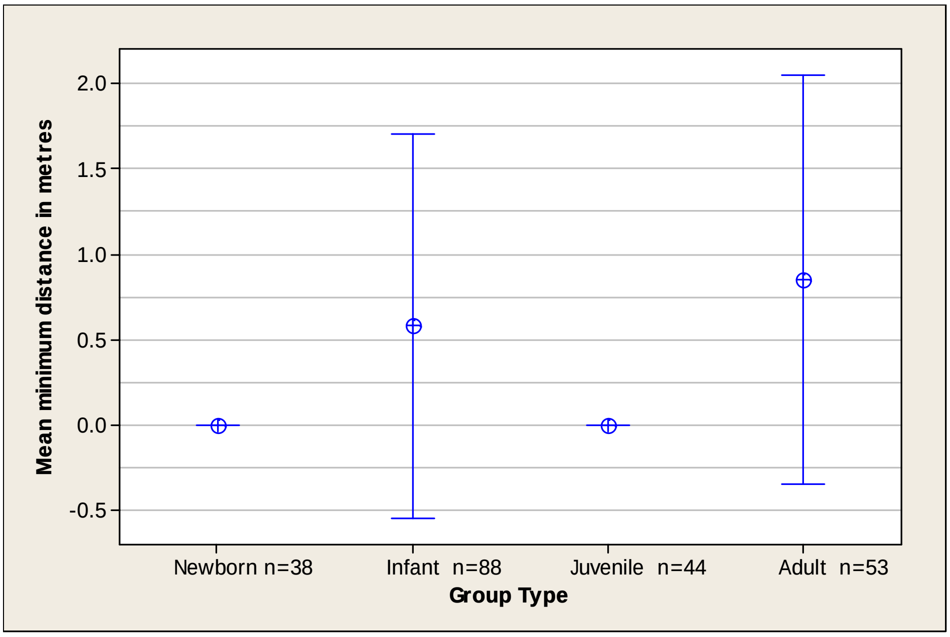
Graph 28. Occurrence of avoidance of the boat as a percentage of total observations for each group.



Graph 29. Occurrence of neutral reaction to the approach of the boat as a percentage of total observations for each group type.



Graph 30. Occurrence of attraction to the boat as a percentage of total observations for each group type.



Graph 31. Mean minimum distance to the boat for each group type.

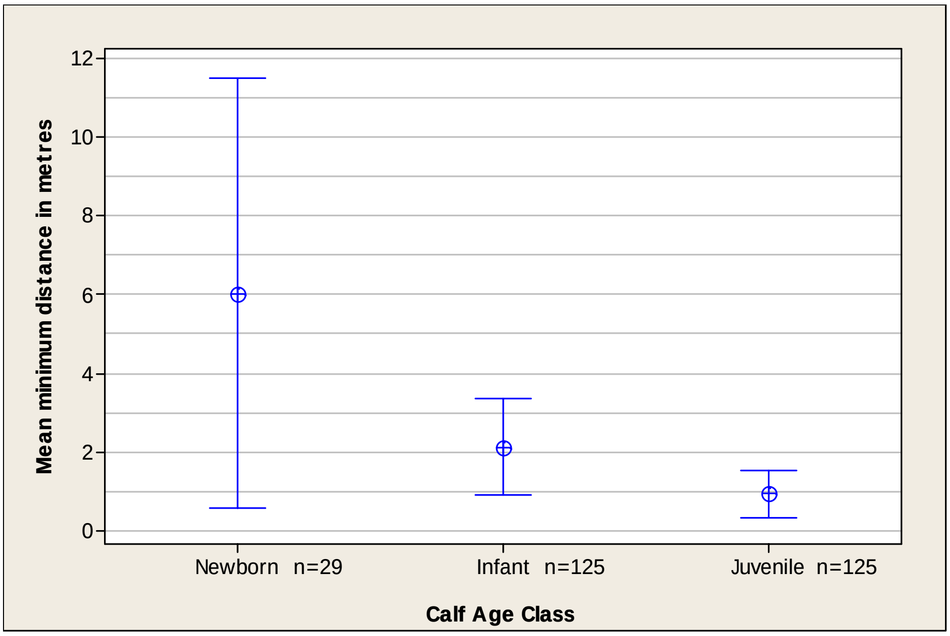
bite attempt from the presumed mother towards the infant. Besides these two events, many mother-calf pairs did initiate close approaches to the boat, at distances that allowed to conduct focal follows, without any specific reaction. Nevertheless, it seemed that mother-calf pairs only came to the bow for short periods of time and would spend less time bow riding than other individuals in the group. The potential influence of calf age class on the minimum distance between mother-calf pairs and the boat was investigated statistically.

The mean minimum distance between mother-calf pairs and the boat was calculated for each calf age class, and resulted in the greatest distance for newborn calves (Graph 32). The apparent decrease with age class revealed by the graph was statistically confirmed ($H=6.623$, $df=2$, $p<0.05$; $r=-0.195$, $n=279$, $p<0.01$). The mean minimum distance to the boat was significantly higher for newborns than for juveniles ($U=1512$, $p<0.05$). From these results, it appears that the distance at which mother-calf pairs approached the boat was dependent on the age class of the calf, and that mothers were more likely to approach at closer distances with older aged calves. Therefore, hypothesis 26 '*The age class of calves affects the minimum distance between mother-calf pairs and the boat*' can be accepted.

7) <u>Mating season</u>

The potential existence of a mating season within the population of common dolphins studied was investigated by comparing the distribution of mating behaviours across months and seasons. Due to small sample sizes for each of the behaviours recorded, the frequency of mating behaviours could not be calculated. For the same reason, the occurrence of mating behaviours could not be tested individually and were therefore grouped in two categories based on whether they involved genital contact or not. This categorisation was based on the demonstration that variation in behaviours involving genital contact are more likely to be related to sexual hormone changes than behaviours that do not involve genital contact (Wells, 1984).

The percentage of observations of mating behaviours as a whole, showed seasonal variations that, although were not significant across months ($X^2=18.807$; $df=11$; $p>0.05$), proved to be significant across seasons ($X^2=8.867$, $df=3$, $p<0.05$)



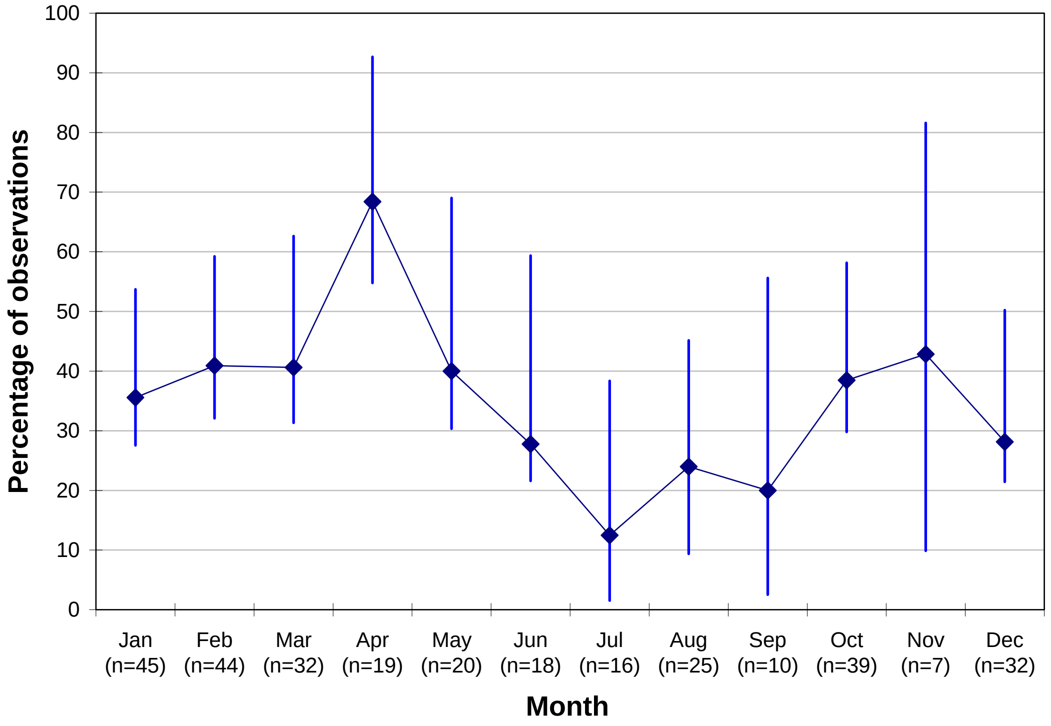
Graph 32. Mean minimum distance to the boat for each calf age class.

(Graphs 33 and 34). Observations of mating behaviours peaked in April, a second moderate increase occurred in October and November, and observations were the lowest from July to September, which corresponds to winter. Further analysis of these patterns was conducted using the distribution of mating behaviours between seasons. The percentage of observations of mating behaviours was found to be lower in winter than in any other season (between winter and summer: $z=2.67$, $p<0.01$; between winter and autumn: $z=3.08$, $p<0.01$; between winter and spring: $z=2.16$, $p<0.05$). The differences between other seasons did not appear to be statistically significant. Mating behaviours were observed less often in winter than in any other season.

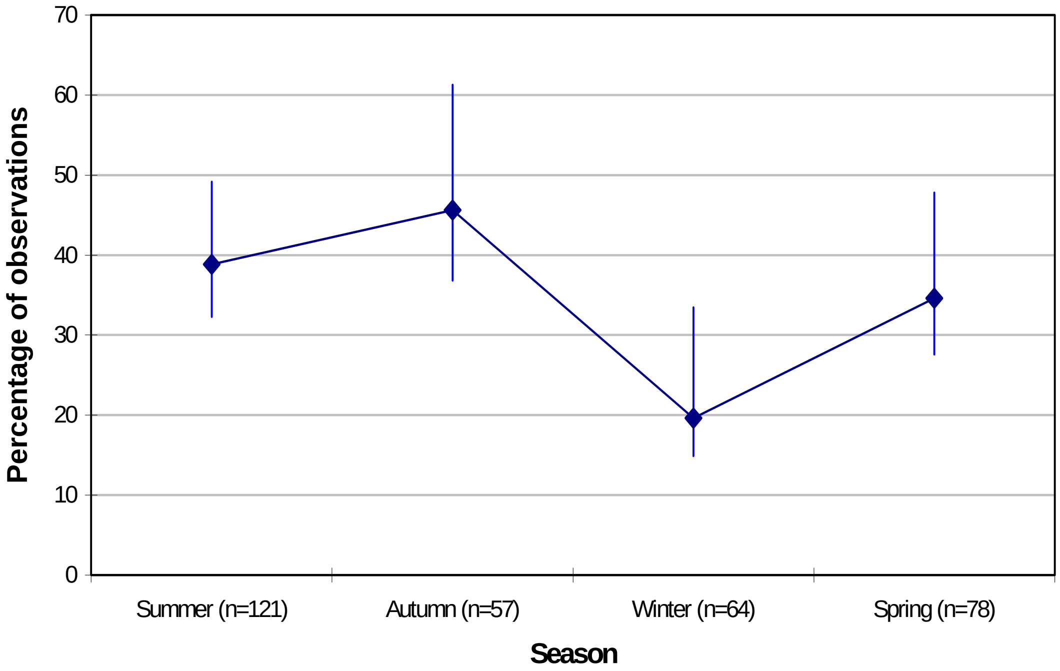
The variations in the percentage of observations of mating behaviours involving genital contact followed a similar pattern to that of mating behaviours considered as a whole, with a peak in April as well as in October and November. Although these variations did not result in significant differences across months ($X^2=19.418$, $df=11$, $p>0.05$) (Graph 35), the percentage of observations of mating behaviours involving genital contact varied significantly across seasons ($X^2=9.627$, $df=3$, $p<0.05$) (Graph 36). Binomial tests revealed that mating behaviours with genital contact were less frequently observed in winter than in any other season (between summer and winter: $z=1.98$, $p<0.05$; between autumn and winter: $z=3.05$; $p<0.01$; between spring and winter: $z=-2.81$, $p<0.01$).

The percentage of observations of mating behaviours not involving genital contact did not appear to vary according to the time of the year, whether coded in months ($X^2=10.905$, $df=11$, $p>0.05$) (Graph 37) or in seasons ($X^2=5.964$, $df=3$, $p>0.05$) (Graph 38). However, observations of mating behaviours without genital contact appeared to be higher in summer than in winter ($z=2.09$; $p<0.05$).

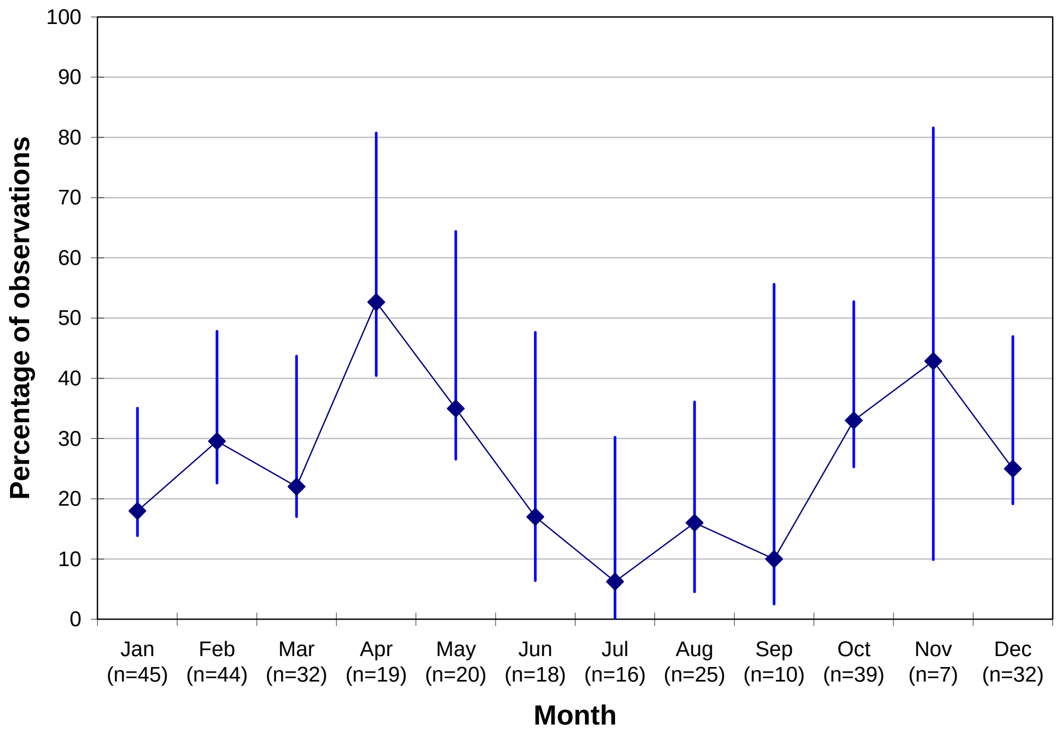
As the occurrence of mating behaviours as a whole and the occurrence of mating behaviours involving genital contact have proved to vary according to seasons, hypothesis 9 '*The occurrence of behaviours related to mating is affected by the time of the year*' can be accepted. The data collected in this study did not allow the investigation of hypothesis 10 '*The frequency of behaviours related to mating is affected by the time of the year*'.



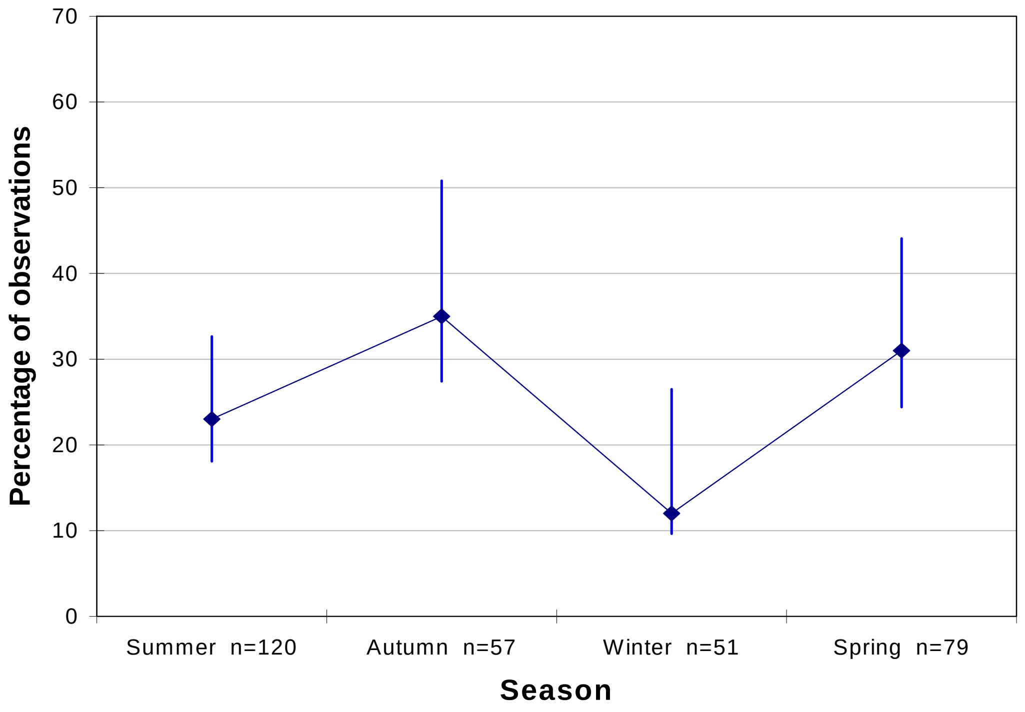
Graph 33. Occurrence of mating behaviours as a percentage of total observations per month.



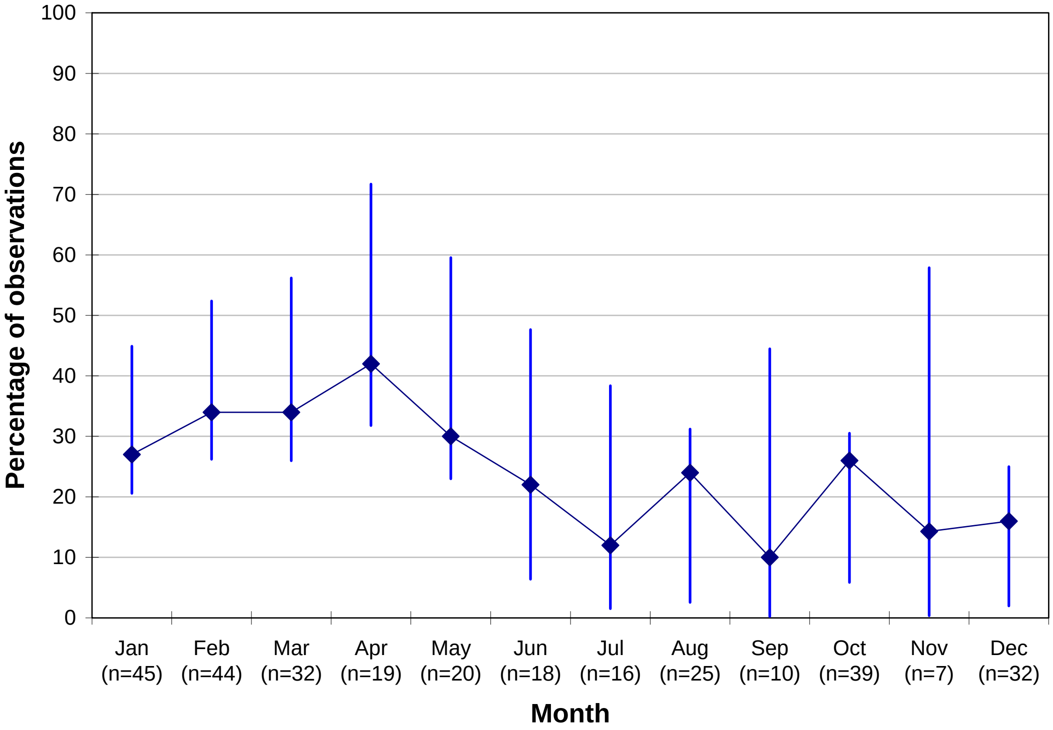
Graph 34. Occurrence of mating behaviours as a percentage of total observations per month.



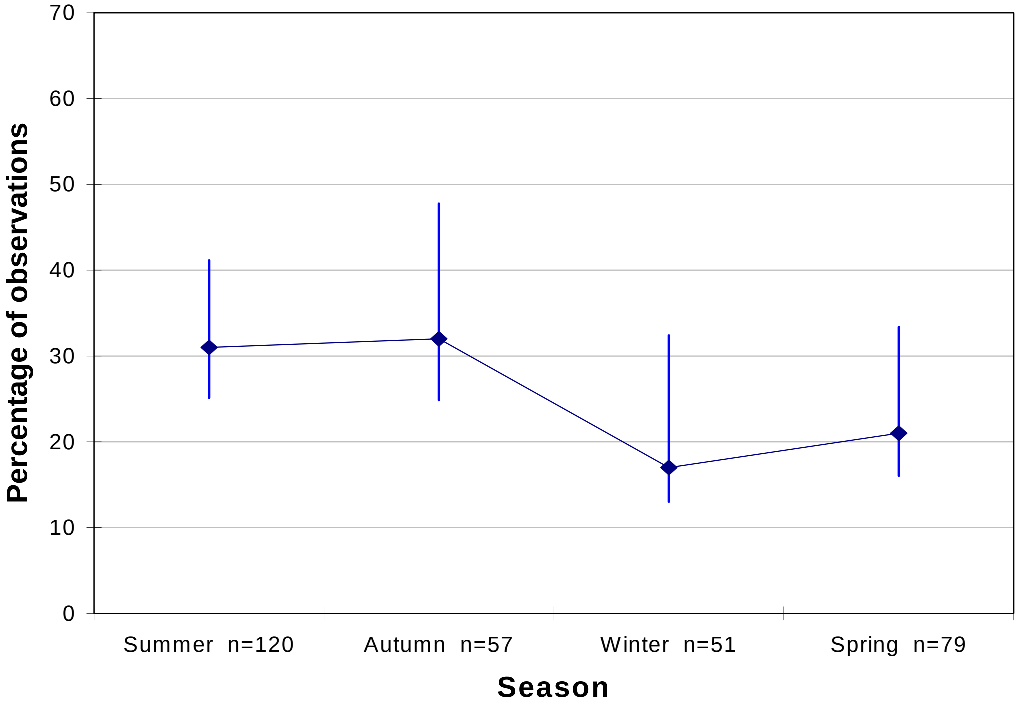
Graph 35. Occurrence of mating behaviours involving genital contact as a percentage of total observations per month.



Graph 36. Occurrence of mating behaviours involving genital contact as a percentage of total observations per season.



Graph 37. Occurrence of mating behaviours without genital contact as a percentage of total observations per month.



Graph 38. Occurrence of mating behaviours without genital contact as a percentage of total observations per season.

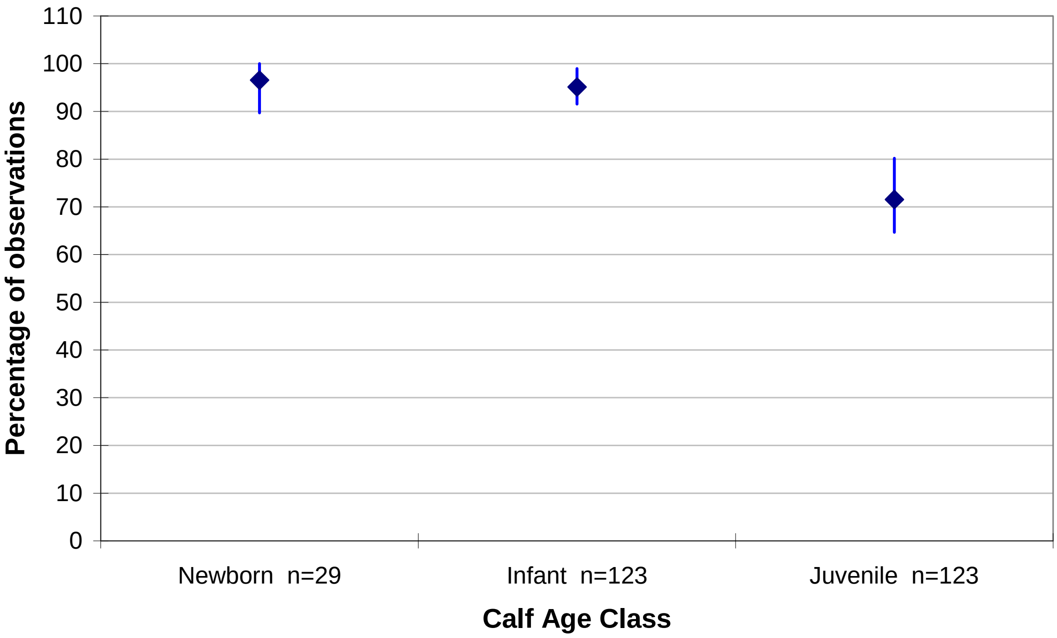
8) Behavioural development of common dolphin calves

8.1. Swimming position

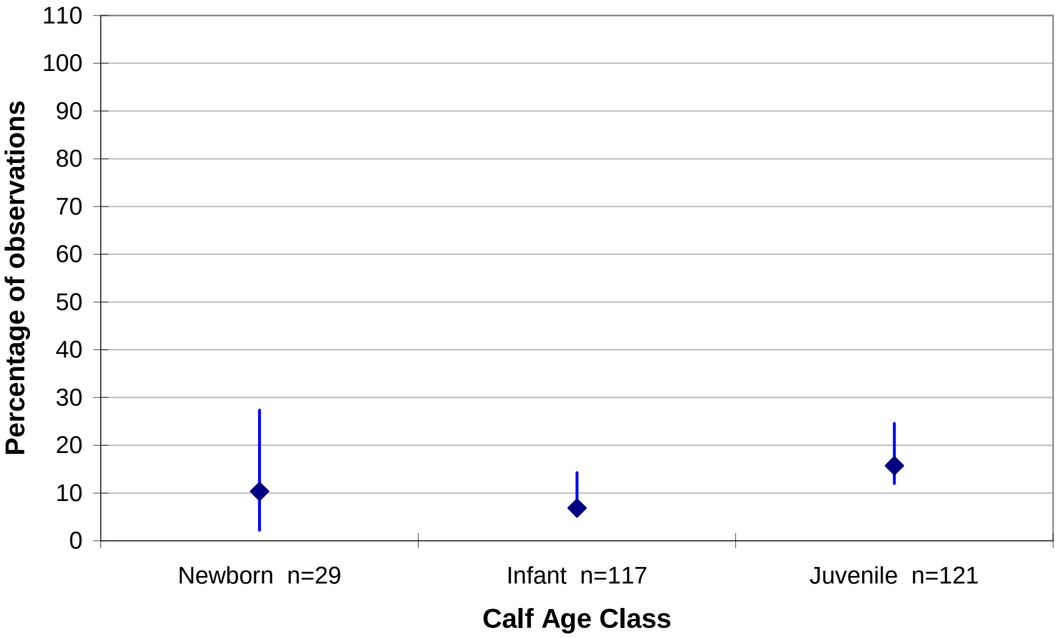
In most mother-calf pairs sighted in this study, calves were swimming in ‘echelon position’. Whether contact was made with the mother while swimming in this position was hard to establish, but newborns generally swam in very close proximity to their presumed mothers. On one occasion, an infant was clearly seen swimming in contact with an adult dolphin assumed to be its mother, with its back against hers, possibly supporting the calf. As for ‘infant position’, observations were less frequent. In order to investigate the variations in calves’ swimming position across the different age classes, the occurrence of ‘echelon position’ and ‘infant position’ swimming was calculated as a percentage of total observations for newborns, infants, and juveniles (Graphs 39 and 40), and compared across the three age classes. The mean proportion of time spent in each position was also calculated for each age class (Graphs 41 and 42), and compared across the three age classes.

The occurrence of ‘echelon position’ swimming appeared to decrease significantly as calves’ age class increased ($X^2=29.922$, df=2, $p<0.01$; $r=-0.317$, n=275, $p<0.01$), with observations of ‘echelon position’ being more frequent for newborns and infants than for juveniles (difference between newborns and juveniles: $z=4.72$, $p<0.01$; difference between infants and juveniles: $z=5.23$, $p<0.01$) (Graph 39). ‘Echelon position’ was therefore less likely to be observed with older aged calves. The slight increase in observations of ‘infant position’ swimming with calf age class did not yield any significant results at the level of significance of $\alpha=0.05$ ($X^2=4.713$, df=2, $p>0.05$; $r=0.112$, n=275, $p>0.05$), but did at the 0.10 level (Graph 40). Nevertheless, the percentage of observations of ‘infant position’ swimming did show a significant increase between infants and juveniles ($z=-2.19$, $p<0.05$), and, even though no definite conclusions can be drawn on the overall variation of occurrence of ‘infant position’ with age class, it appears that such a swimming position is more likely to be observed in juveniles than in infants.

As the likelihood of observing ‘echelon position’ decreased across age classes, hypothesis 11 ‘*The age class of calves affects the occurrence of ‘echelon position’* e



Graph 39. Occurrence of 'echelon position' swimming as a percentage of total observations for each calf age class.



Graph 40. Occurrence of 'infant position' swimming as a percentage of total observations for each calf age class.

swimming' can be accepted. Although the results obtained tend to show that the occurrence of 'infant position' decreases across ages classes, this pattern remains to be confirmed and hypothesis 12 '*The age class of calves affects the occurrence of 'infant position' swimming*' cannot be accepted.

Calves of all age classes spent more time swimming in 'echelon position' than in 'infant position' with their mothers (U=3176.5, $p<0.01$). The variations that can be observed on the graphs (Graphs 41 and 42) are very similar to the ones found for the occurrence of each swimming position, with a decreasing trend for 'echelon position' swimming and an increasing trend for 'infant position' swimming with age class. The decrease in the mean percentage of time spent in 'echelon position' was statistically significant (H=50.134, df=2, $p<0.01$; r=-0.593, n=140, $p<0.01$). Further assessment of the potential differences between each age class was conducted. Newborns and infants spent significantly more time in 'echelon position' with their mother than juvenile common dolphins did (difference between newborns and juveniles: U=115, $p<0.01$; difference between infants and juveniles: U=700, $p<0.01$). The variations in the mean percentage of time spent in 'infant position' did not prove to be significant (H=0.725, df=2, $p>0.05$; r=0.025, n=140, $p>0.05$).

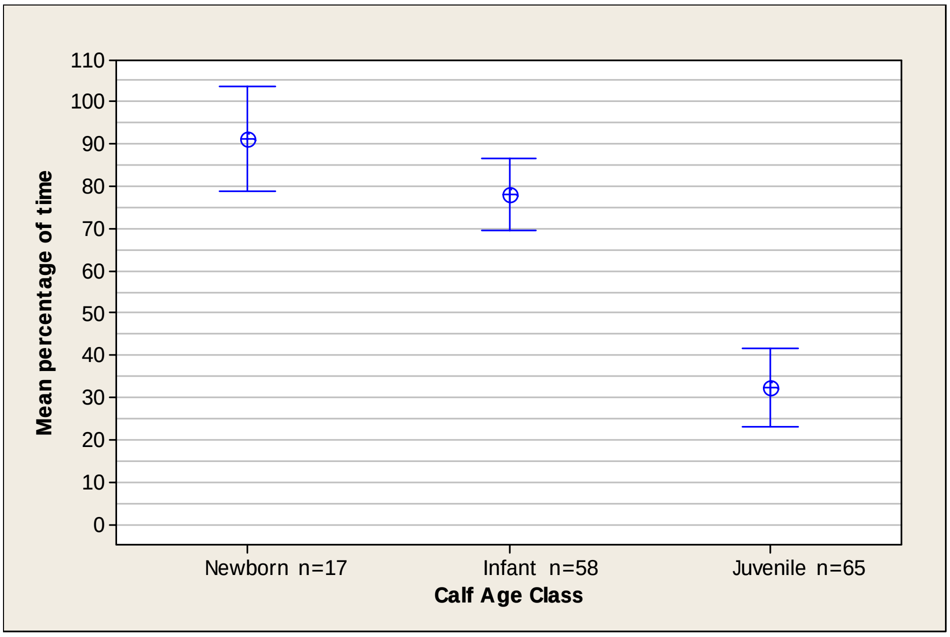
In view of the results obtained here, hypothesis 13 '*The age class of the calves affects the percentage of time spent in echelon position*' can be accepted. The decrease in the mean percentage of time spent in 'infant position' across the age categories was not found to be statistically significant, and therefore hypothesis 14 '*The age class of the calves affecst the percentage of time spent in infant position*' cannot be accepted.

8.2. Separations

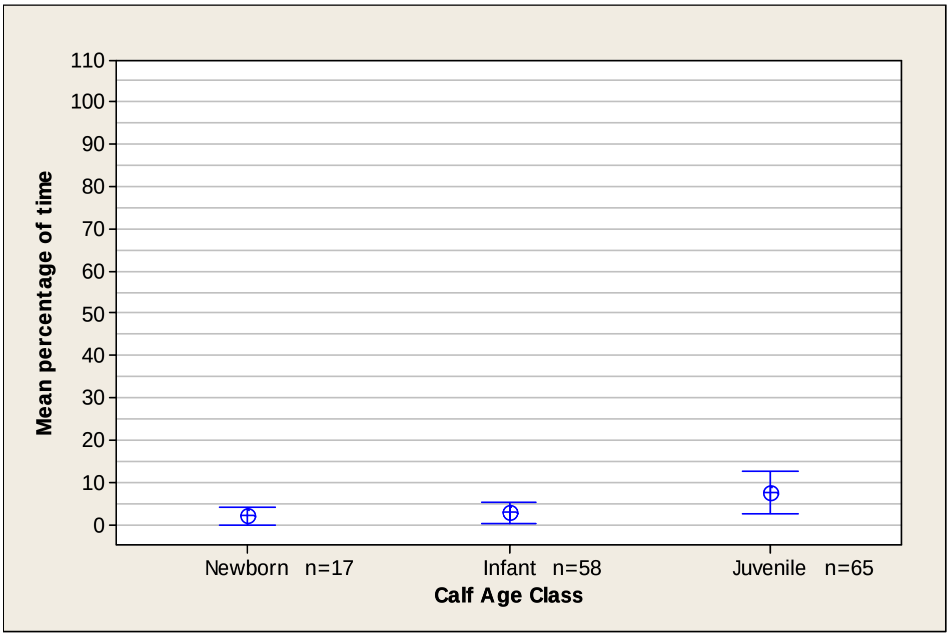
- Occurrence and frequency

The influence of calf age class on separations between mothers and calves was first assessed by considering their occurrence and frequency.

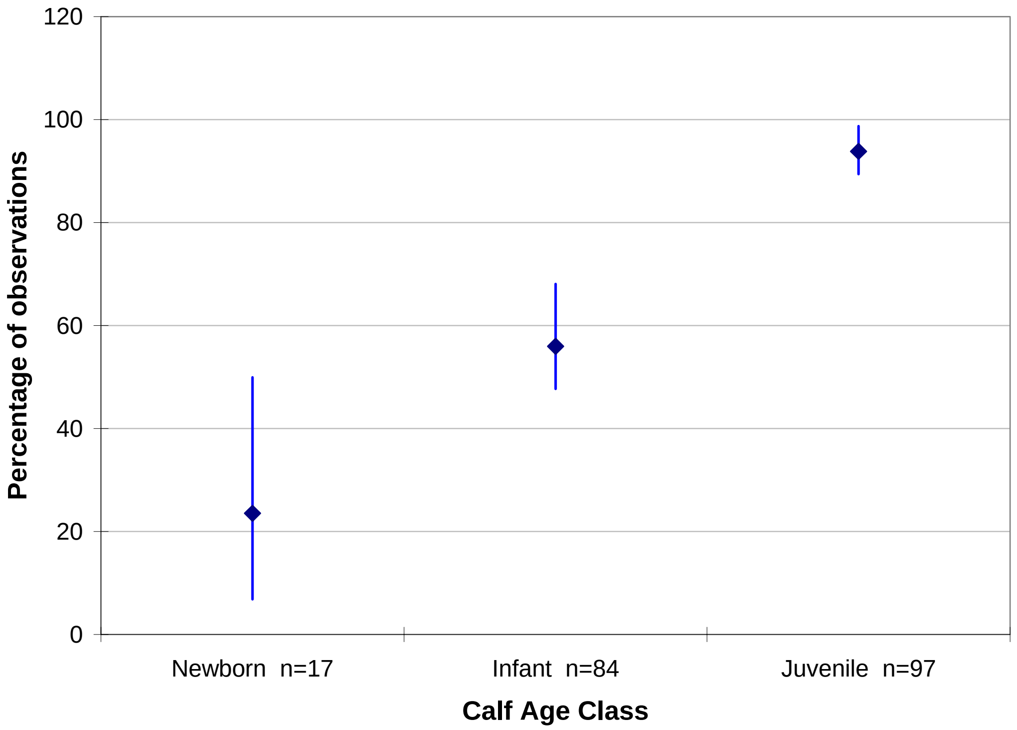
The occurrence of separations showed a linear increase with calf age class (Graph 43), and statistical analysis confirmed this observation (X^2=53.105, df=2, $p<0.01$; r=0.515,



Graph 41. Mean percentage of time spent in ‘echelon position’ swimming for each calf age class.



Graph 42. Mean percentage of time spent in ‘infant position’ swimming for the each calf age class.



Graph 43. Occurrence of mother-calf separations as a percentage of total observations for each calf age class.

n=198, p<0.01). Frequencies were calculated per five-minute interval in order to facilitate data analysis. An analysis of the mean frequency of separations showed a similar pattern (Graph 44). Mother-calf separations were more frequent with older aged calves (H=33.448, df=2, p<0.01; r=0.543, n=110, p<0.01).

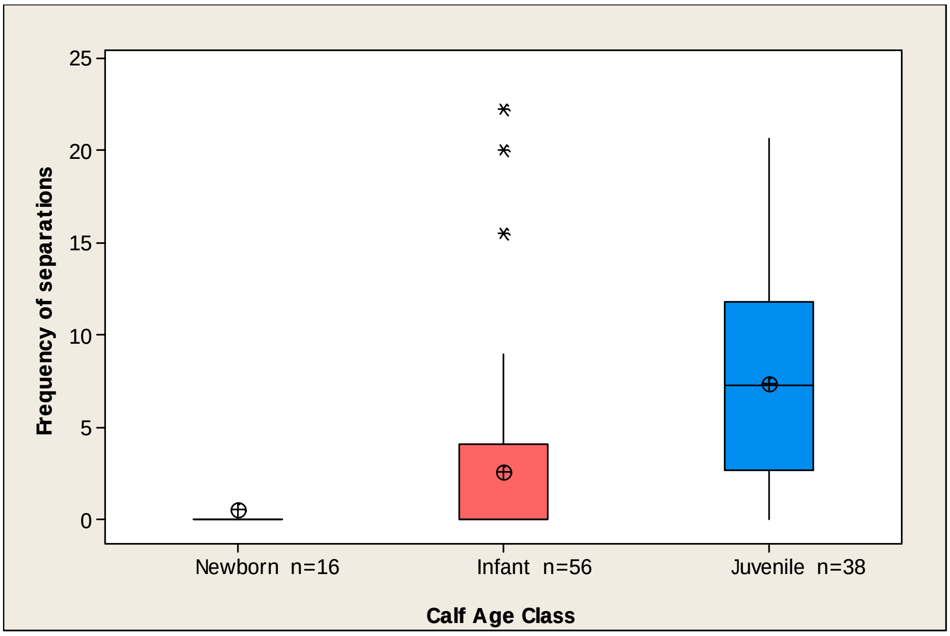
As a consequence of these results, hypothesis 15 '*The age class of calves affects the occurrence of separations between mothers and calves*' and hypothesis 16 '*The age class of calves affects the frequency of separations between mothers and calves*' can be accepted. Mother-calf separations were more likely to be observed and occurred more frequently with common dolphin calves of older age classes.

- Duration of separation

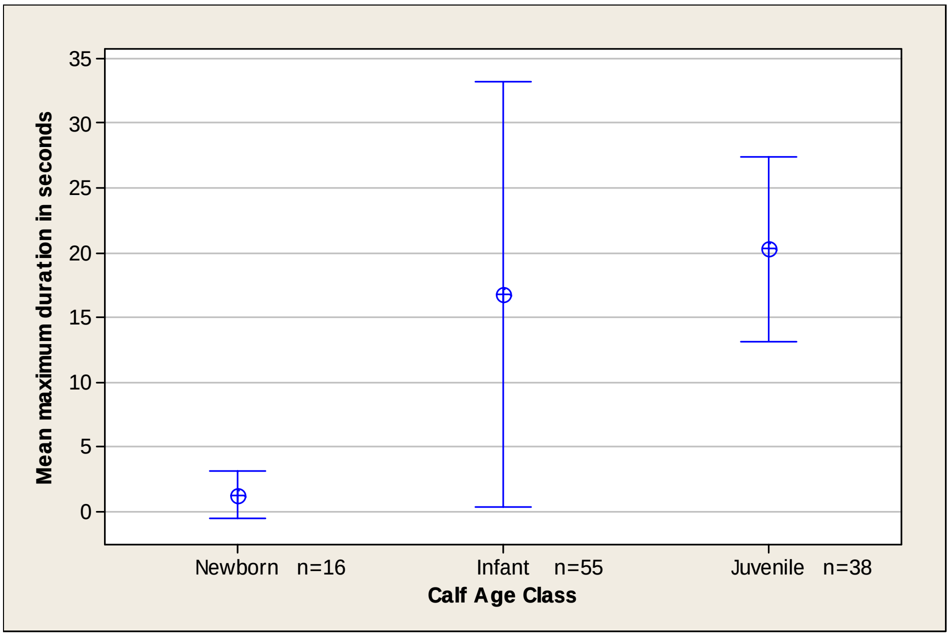
The maximum length of time for which a mother-calf pair was separated was considered in order to test the influence of calf age class. Using the average duration of separation would have involved the calculation of the mean of an already averaged value, which represents a non-valid procedure in statistics (Gravetter and Wallnau, 2004). The mean maximum duration of separation was therefore calculated for newborns, infants, and juveniles (Graph 45), and compared across the three age classes.

The mean maximum duration of separation between mothers and calves was found to vary significantly according to the age class of calves (H=27.670, df=2, p<0.01). Correlation was also significant, with a coefficient of 0.501 (n=109, p<0.01). These results lead to the conclusion that the maximum length of time a calf spends away from its mother increases with age class. Therefore, hypothesis 17 '*The age class of calves affects the duration of mother-calf separations*' can be accepted.

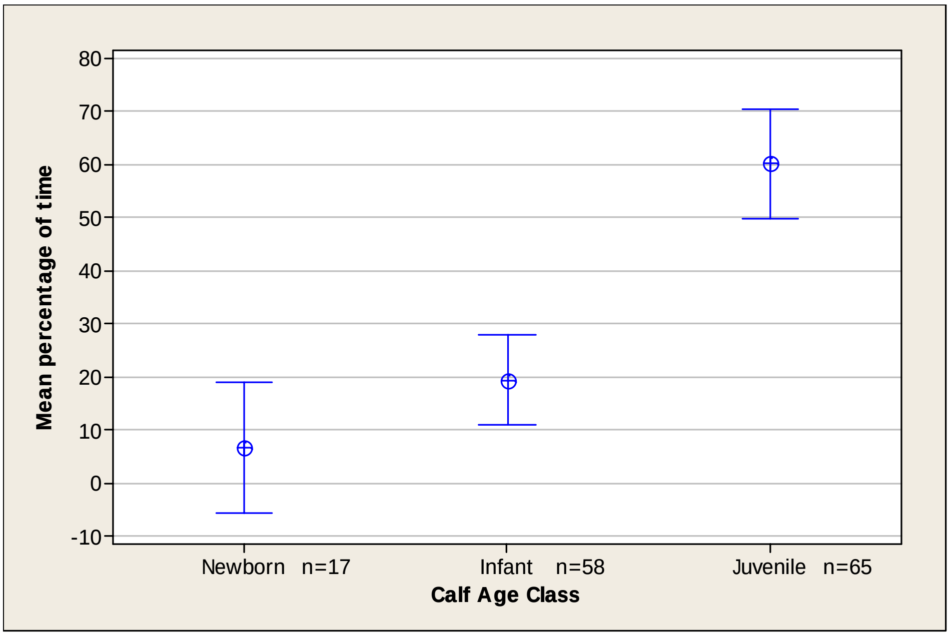
In order to investigate whether calves spent more time away from their mother with age, the mean percentage of time spent without her was calculated for each calf type (Graph 46) and compared across all age classes. The comparison of the variations of both variables showed a significant difference between them (H=46.132, df=2, p<0.01). The direction of the relationship was tested using Spearman rank correlation coefficient, which showed that the two variables vary together (r=0.571, n=140, p<0.01). These



Graph 44. Mean frequency of mother-calf separations per five-minute interval for each calf age class (for explanation of symbols in boxplots see ‘Key to boxplot’ on page 95).



Graph 45. Mean maximum duration of mother-calf separations for each calf age class.



Graph 46. Mean percentage of time spent without mother for each calf age class.

analyses lead to the conclusion that the mean percentage of time calves spent without their mothers increases with the age class of the calves considered. In light of these results, hypothesis 18 ‘*The age class of calves affects the percentage of time spent without the mother*’ can be accepted. Older calves spend more time away from their mother than young calves do.

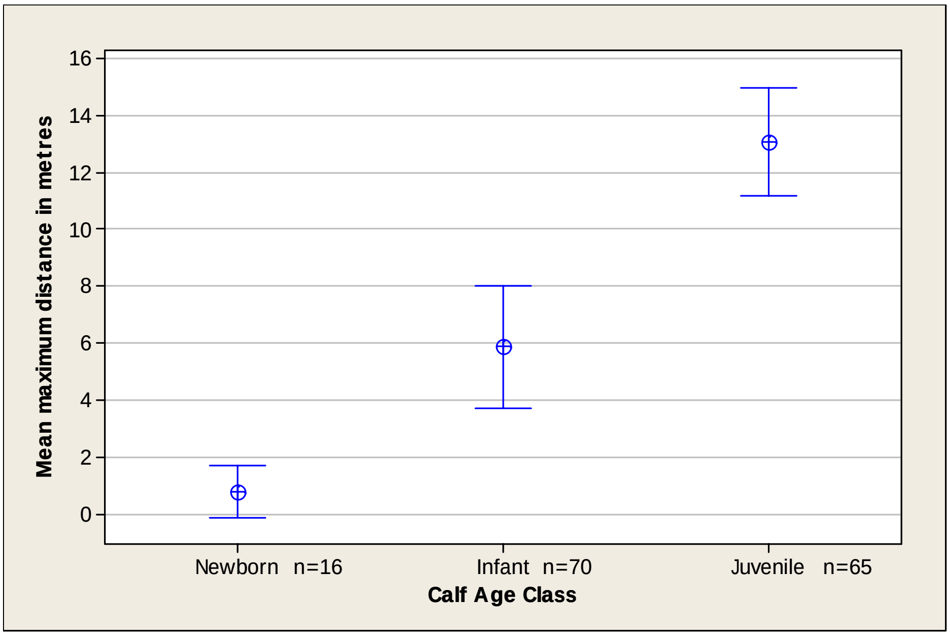
- Distance of separation

For the same reason as described above, the mean maximum distance of separation, rather than the mean average distance, was used in the analysis of influence of calf age class on the distance of mother-calf separations. This distance was calculated for each calf class.

Graph 47 shows a linear increase in the mean value of the maximum distance of separation with the age class of calves. Such variation in the distribution of mean maximum distance of separation according to calf age class proved to be statistically significant (H=45.888, df=2, p<0.01). The analysis of the correlation between the two variables also confirmed statistically the observation of the graph: as the age class of the calves increases, the mean maximum distance of separation increases as well (r=0.553, n=151, p<0.01). Older calves tend to separate over greater distances than younger calves do. Therefore, hypothesis 19 ‘*The age class of calves affects the distance of mother-calf separations*’ can be accepted.

8.3. Proximity

In the present study, responsibility of both mothers and calves in maintaining proximity with the other was assessed by using the Hinde index. Identifying the initiator of approaches and leaves within mother-calf pairs proved to be challenging and could only be established for a very few separations per focal follow. This was not considered as being representative of the underlying relationships between mothers and calves. The focal follows conducted in this study did not provide sufficient data to calculate the Hinde index and therefore, hypotheses 20 ‘*The age class of calves affects the mothers’ responsibility in proximity maintenance*’ and 21 ‘*The age class of calves affects their own responsibility in proximity maintenance*’ could not be investigated.



Graph 47. Mean maximum distance of mother-calf separations for each calf age class.

8.4. Nursing position

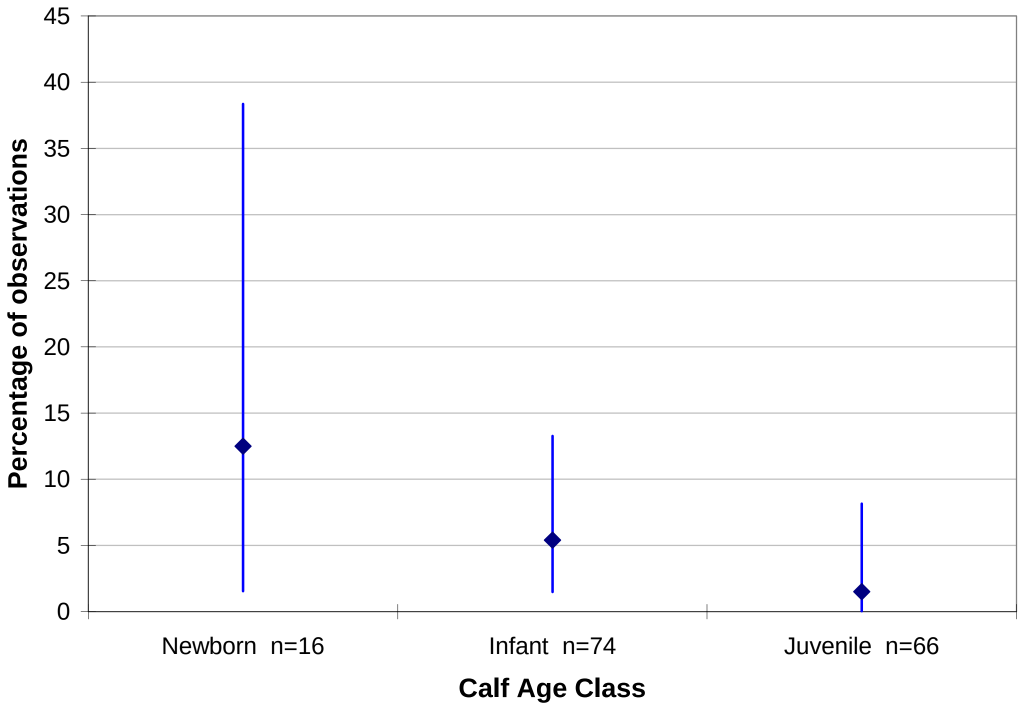
Out of the 311 focal follows conducted in this study, nursing position was only recorded on eight occasions. This low number of observations is likely to reflect only a small proportion of actual occurrence of nursing. Calves were seen in nursing position, (rostrum against mammary slit) with both the mother turning on her side, belly orientated towards the calf, and with the calf swimming underneath the mother (Plate 10). The percentage of observations of nursing position was calculated for each calf age class (Graph 48) and compared across them. A Chi-Square test for independence failed to find a significant difference in the percentage of observations of nursing position according to calf age category ($X^2=3.903$, df=2, $p>0.05$). Such a result is likely to be due to the rare observation of this behaviour. Occurrence of nursing position and calf age category appeared to be negatively correlated, which supports the decrease in observations between the different calf age classes shown by graph 48, but this correlation appeared to be relatively weak and was only significant at the 0.10 level ($r=-0.148$, $n=156$, $p>0.05$).

The data collected in the present study did not allow acceptance of hypothesis 22 '*The age class of calves affects the occurrence of nursing events*'.

8.5. Breathing synchrony

The influence of calf age on breathing synchrony was investigated by comparing the mean percentage of synchronous surfacing, calves' solitary surfacing, and overlapping surfacing across the different age classes. Each breathing pattern was calculated as a mean percentage of the total number of breaths for each calf type (Graphs 49 and 51), along with its mean frequency of occurrence per five-minute interval (Graphs 50 and 52).

Analysis of the distribution of synchronous surfacing demonstrated that the mean percentage of observations of such a breathing pattern tend to decrease with older aged calves ($H=8.235$, df=2, $p<0.05$; $r=-0.268$, $n=110$, $p<0.01$) (Graph 49). Differences between age classes were investigated more specifically, and significant decreases were found between newborns and juveniles ($U=202$, $p<0.05$), and infants and juveniles

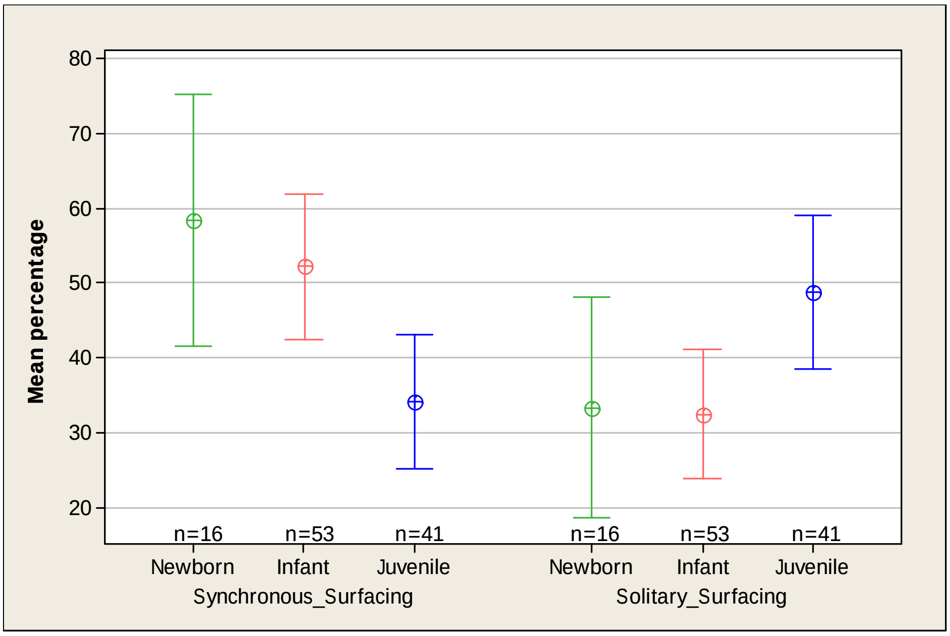


Graph 48. Occurrence of nursing position as a percentage of total observations for each calf age class.

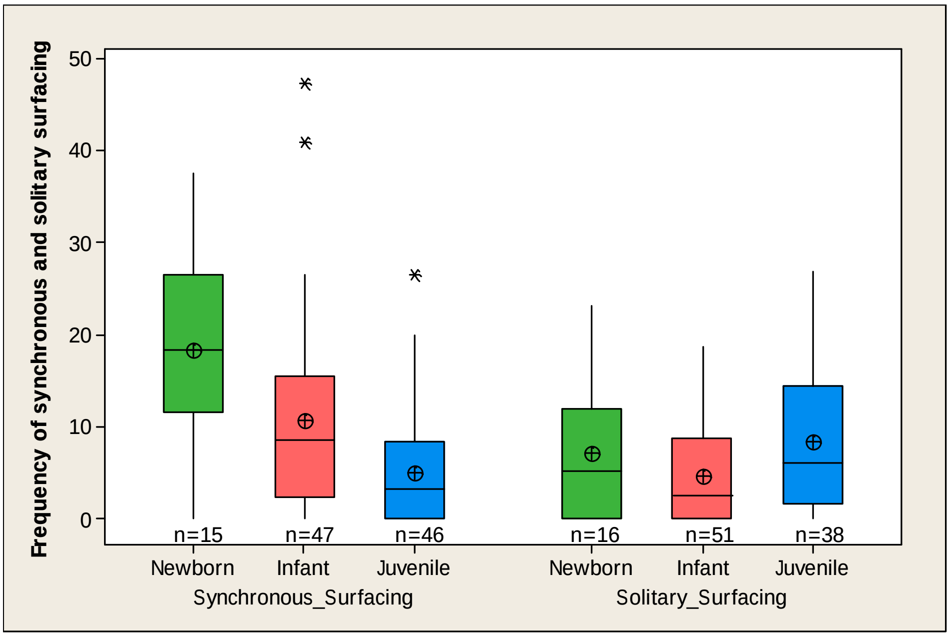
($U=775.5$, $p<0.05$). These results show that young common dolphin calves are more likely to be observed in breathing synchrony with their mothers than older individuals. The frequency of synchronous breathing per five-minute interval also proved to decrease with older aged calves ($H=24.279$, $df=2$, $p<0.01$; $r=-0.465$, $n=108$, $p<0.01$) (Graph 50). Significant differences existed between all calf classes (between newborn and juvenile: $U=75.5$, $p<0.01$; between infant and juvenile: $U=694.5$, $p<0.01$; between newborn and infant: $U=182$, $p<0.01$). It can therefore be concluded that synchronous breaths between mothers and calves become less frequent as calves reach older age classes.

The mean percentage of calves' solitary surfacing was not found to vary significantly according to calf age class ($H=5.640$, $df=2$, $p>0.05$) (Graph 49). It is worth noticing that the *p* value was nonetheless very close to significance ($p=0.06$), and would have been so if using an alpha value of 0.10 as level of significance. Further comparisons of the different calf types showed that juveniles were seen surfacing by themselves significantly more often than infants ($U=804$, $p<0.05$). The same trend was found in the Spearman rank correlation test, which even though it did not result in a high coefficient, proved to be positively significant ($r=0.205$, $n=132$, $p<0.05$). The Kruskal-Wallis analysis of the frequency of calves' solitary surfacing according to age provided inconclusive results, as the *p* value exactly equalled 0.05 ($H=5.991$). Nevertheless, the frequency of solitary surfacing proved to be significantly higher for juveniles than for infants ($U=681.5$, $p<0.05$) (Graph 50), which fits with the increase observed in occurrence of solitary surfacing between infants and juveniles. Although the frequency of solitary surfacing appeared to decrease between the age classes of newborn and infant, this difference was not significant ($U=337$, $p>0.05$), and may be due to an anomalie in the data.

Comparing the frequency of synchronous and solitary surfacing for each calf type also reveals some interesting differences. For newborns and infants, the frequency of synchronous breaths with their mothers was higher than the frequency of solitary surfacing (newborns: $U=42$, $p<0.01$; infants: $U=765$, $p<0.01$). The reverse pattern was found for juveniles, with a higher frequency of solitary surfacing compared to synchronous surfacing ($U=633.5$; $p<0.05$).



Graph 49. Occurrence of synchronous and calves' solitary surfacing as mean percentages of all breaths for each calf age class.



Graph 50. Mean frequency of synchronous and calves' solitary surfacing per five-minute interval for each calf age class (for explanation of symbols in boxplots see 'Key to boxplot' on page 95).

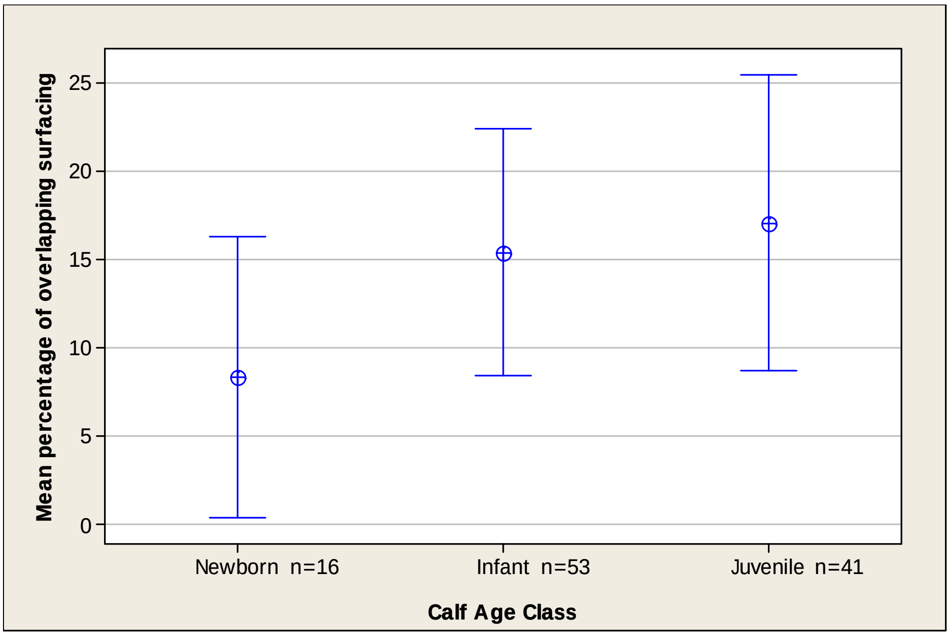
The mean percentage of overlapping surfacing appeared to be relatively stable across the different age classes (H=1.117, p>0.05; r=0.088, n=110, p>0.05) (Graph 51). Similar results were found for the frequency of overlapping surfacing, as it did not appear to vary significantly according to whether the calf followed was a newborn, an infant, or a juvenile (H=0.407, p>0.05; r=0.060, n=108, p>0.05) (Graph 52). The identity of the initiator of overlapping surfacing was also tested across the different age groups in order to investigate the potential influence of calf age. The different values obtained for these two variables are summarised in Table 5. Both the percentages of observations of 'calf after mother' and 'mother after calf' surfacing didn't appear to vary with the age class of calves (H=1.680, df=2, p>0.05; r=±0.005, n=34, p>0.05).

Considering the significant decrease in the mean percentage and frequency of synchronous surfacing with older aged calves and the significant increase in occurrence and frequency of calves' solitary surfacing between infant and juvenile common dolphins, hypothesis 23 '*The age class of calves affects breathing synchrony*' can be accepted.

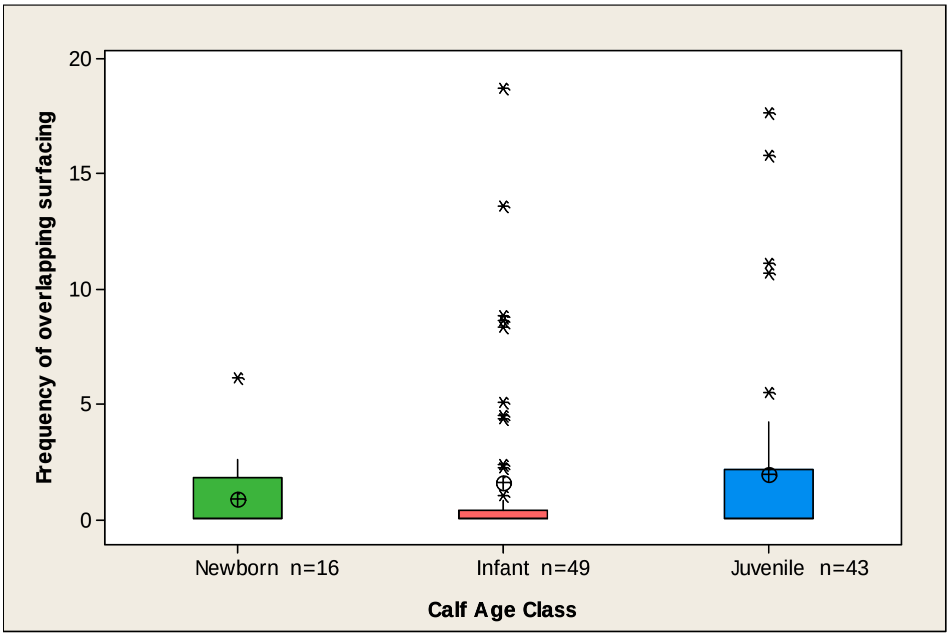
8.6. Dive time

Within each focal follow conducted in this study, the time interval between breaths was calculated for both mothers and calves by dividing the total length of observation by the total number of breaths for each partner of the pair. Mean values were obtained thereafter for each age class (Graph 53).

Kruskal-Wallis tests found significant differences in the distribution of the mean time interval between breaths for both mothers and calves according to calf age class (mothers: H=11.259, df=2, p<0.01; calves: H=9.976, df=2, p<0.01). Correlation between these variables also proved to be significant, and show that as the age class of common dolphin calves increases, the mean time interval between breaths increases not only for calves (r=0.285, n=90, p<0.01), but also for mothers (r=0.373, n=81, p<0.01). The mean time between breaths was significantly shorter for newborns than for infants (U=146.5, p<0.01) and juveniles (U=133, p<0.01). The mothers of juveniles had greater mean time intervals between breaths than did the mothers of infants (U=384.5, p<0.05) and of newborns (U=70.5, p<0.01). The results obtained here prove that the variations



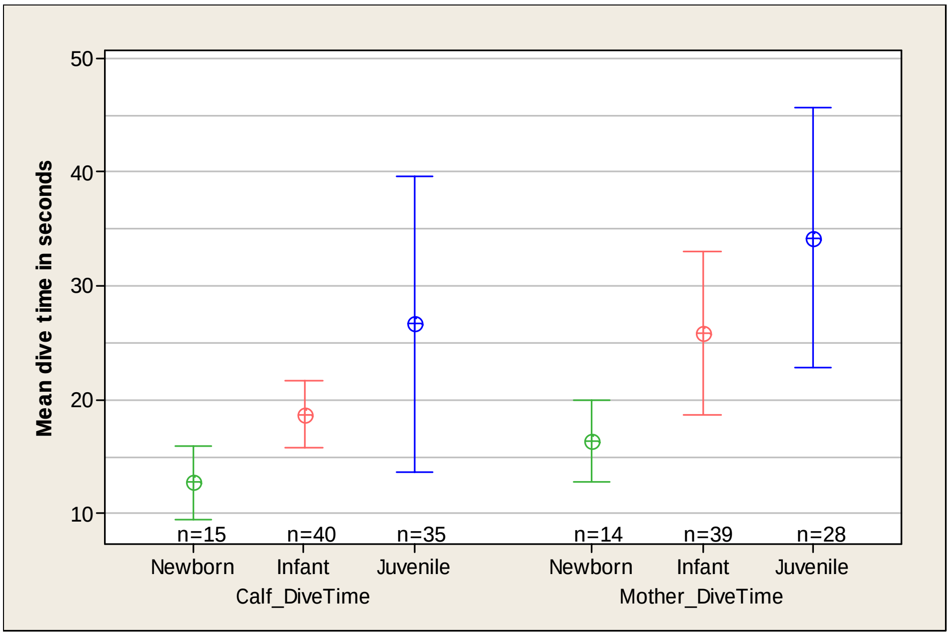
Graph 51. Occurrence of overlapping surfacing as a mean percentage of all breaths for each calf age class.



Graph 52. Mean frequency of overlapping surfacing per five-minute interval for each calf age class (for explanation of symbols in boxplots see 'Key to boxplot' on page 95).

Calf age class		Calf after mother' surfacing	Mother after calf' surfacing
Newborn	Mean	25	75
	n	4	4
	SD	50	50
	Lower confidence interval	-54.6	-4.56
	Upper confidence interval	104.56	154.56
Infant	Mean	56.25	43.75
	n	16	16
	SD	47.87	47.87
	Lower confidence interval	30.74	18.24
	Upper confidence interval	81.76	69.26
Juvenile	Mean	42.86	57.14
	n	14	14
	SD	43.22	43.22
	Lower confidence interval	17.91	32.19
	Upper confidence interval	67.81	82.09

Table 5. Two patterns of overlapping breaths calculated as a mean percentage of total observations of overlapping surfacing, and summarised for each calf age class.



Graph 53. Mean dive time of mothers and calves for each calf age class.

in mean time spent underwater by both mothers and calves are influenced by the age class of calves. Therefore, hypothesis 24 '*The age class of calves affects the mean time elapsed between breaths for both mothers and calves*' can be accepted.

As can be seen on graph 53, mothers' mean dive time was greater than that of calves. Another illustration of such a pattern is given by figure 9, which represents the breathing frequency of a mother-infant pair during a focal follow. This pattern was observed across all age classes. In order to investigate whether these differences were significant, a Mann-Whitney test was used. The values obtained show that the time between breaths was indeed significantly longer for mothers than for calves (U=4.049, p<0.05), and lead to the acceptation of hypothesis 25 '*Calves' mean dive times are significantly different from those of mothers*'.

Comparisons of the difference in mean dive times between mothers and calves were conducted across the three age classes in order to assess the evolution of such difference. A difference of 4.91 seconds between means was found between mothers and newborns, 7.51 seconds between mothers and infants, and 14.06 seconds between mothers and juveniles (Graph 54). Although the difference in mean inter-breath interval between mothers and calves appears to increase, such observation was not supported by statistical analysis (H=4.001, df=2, p>0.05; r=0.188, n=80, p>0.05), and no definite conclusion can be drawn.

9) Escorting behaviour

Although each calf was predominantly accompanied by a specific adult individual presumed to be the mother, associations with non-mother dolphins were also observed. On one specific occasion, an infant was observed interacting with a juvenile for eight minutes while the rest of the group was feeding approximately 50 metres away. They were seen swimming together with the infant in 'echelon position', as well as a few metres apart, and were involved in fast swimming and chases. After these eight minutes, an adult dolphin assumed to be the mother of the infant left the feeding group and joined the calves. The infant immediately resumed 'echelon position' swimming with the adult dolphin, while the juvenile followed them a couple of metres behind.

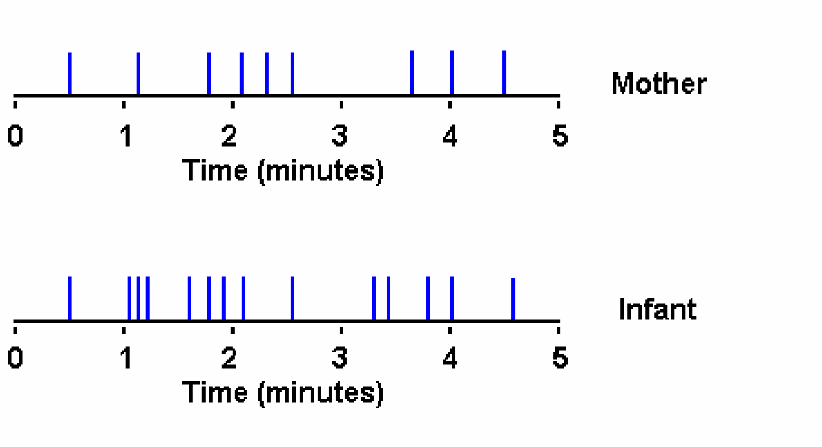
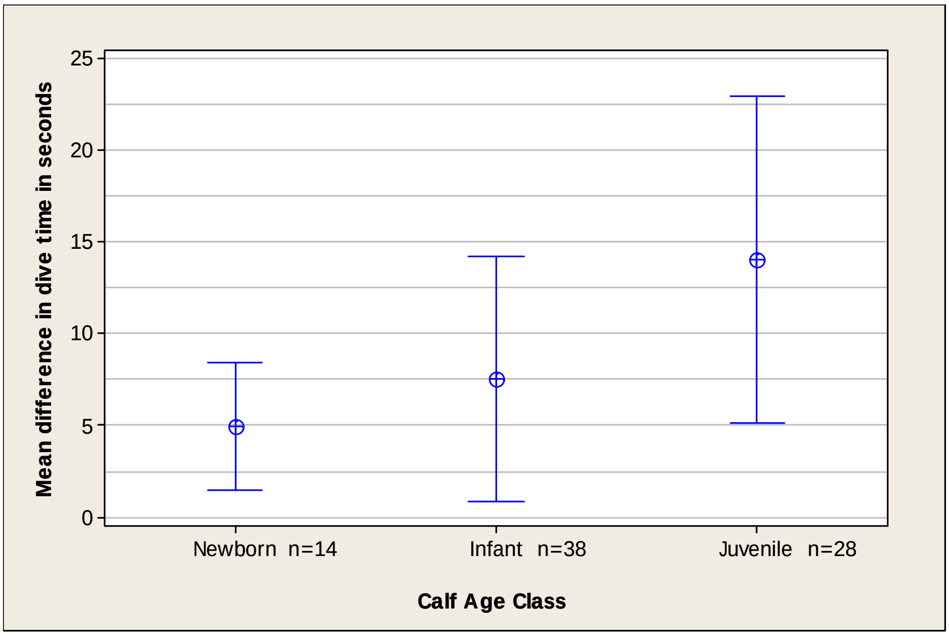


Figure 9. Breathing frequency of a mother-infant pair during the length of a focal follow.



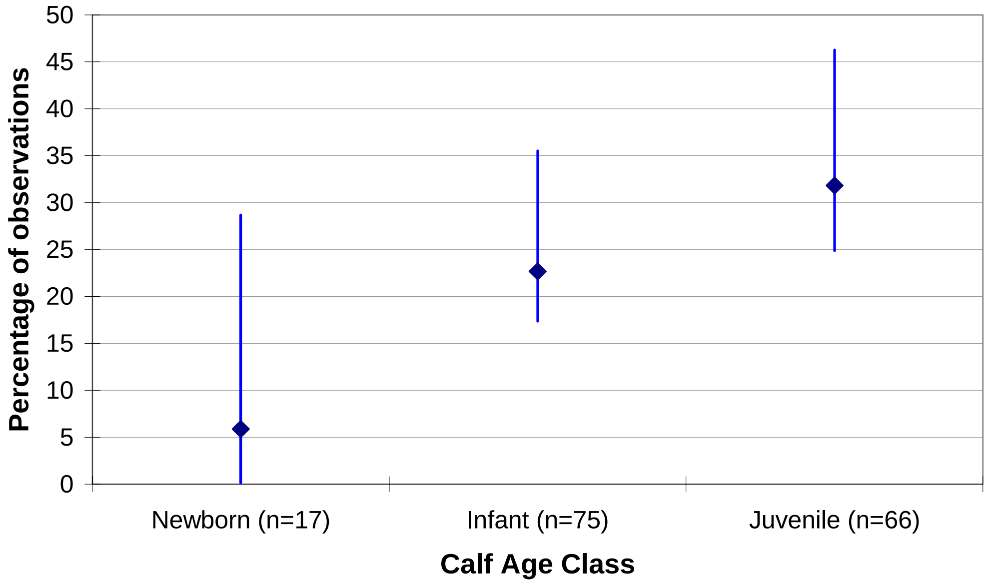
Graph 54. Difference between the mean dive time of mothers and calves for each calf age class.

For each calf age class, the occurrence of association with non-mother dolphins was calculated as a percentage of total observations (Graph 55). Due to a small sample size, the frequency of escorting behaviours could not be calculated. The data collected showed an increase in the occurrence of escorting behaviours with older aged calves. The results of the statistical tests investigating this observation appeared to be divided. The Chi-Square test for independence did not show a significant difference in the distribution of observations of associations with non-mother dolphins according to calves' age class ($X^2=5.204$, df=2, $p>0.05$). However, significance would have been reached for an alpha value of 0.10, and the positive Spearman rank correlation coefficient, although not very high, proved to be significant ($r=0.170$, $n=158$, $p<0.05$). Further investigation of differences between age classes, using binomial tests, showed that newborn calves were less likely to be seen associated with non-mother dolphins than infants ($z=-2.79$, $p<0.01$) and juveniles ($z=-6.65$, $p<0.01$). These different results tend to show that the likelihood of calves being associated with non-mother dolphins increased with older aged calves.

Considering the low Spearman rank correlation coefficient obtained and the lack of significance of the Chi-Square test for independence for $\alpha=0.05$, hypothesis 27 '*The age class of calves does affect the occurrence of association with non-mother dolphins*' cannot be accepted. Nevertheless, newborn calves were less likely to be seen associated with non-mother dolphins than infant and juvenile common dolphins did. The data collected in this study did not appear to be sufficient to test hypothesis 28 '*The age class of calves does affect the frequency of association with non-mother dolphins*'.

10) Grouping patterns

In this study, the occurrence of nursery groups could not be investigated, as the presence of male dolphins within groups could never be excluded. Nevertheless, few observations support the existence of associations of mother-calf pairs within common dolphins. On one occasion, a group comprised of only two mother-infant pairs was sighted. No other dolphins were present in the area at that time. Another interesting observation was made, in that when groups of common dolphins encountered contained more than one calf, mother-calf pairs were often seen swimming with one another. As a



Graph 55. Occurrence of escorting behaviour as a percentage of total observations for each calf age class.

result, mother-calf pairs subject to focal follows for this study were accompanied by other pairs in more than 40% of all observations (Table 6).

In order to investigate whether the occurrence of associations between mother-calf pairs was influenced by the age class of calves, the percentage of observations of such events (Table 6) was compared across the different age classes. These percentages did not appear to vary significantly ($X^2=0.657$, df=2, $p>0.05$), or to be correlated ($r=-0.045$, $n=254$, $p>0.05$) with calf age class. The number of other mother-calf pairs sighted with the one under focal observation ranged from zero to four, with a mean of 0.53 (SD=0.81). For each focal follow, the number of other mother-calf pairs together with the one followed was taken into account as a mean percentage of all other mother-calf pairs present in the group (Table 6). Variations in the mean percentage of other mother-calf pairs accompanying the focal pair did not prove to be significantly related, nor to be correlated to the age class of calves ($H=0.14$, df=2, $p>0.05$; $r=-0.07$, $n=253$, $p>0.05$).

As both the percentage of observations of associations between mother-calf pairs and the mean percentage of other mother-calf pairs accompanying the focal pair seem to vary independently from calf age category, hypothesis 29 ‘*The age class of calves affects the presence and number of other mother-calf pairs with the focal pair*’ cannot be accepted.

11) Other calf characteristics

A behaviour in which young common dolphin calves seemed to be consistently engaged in, consisted of fast swimming in circles, with the mother as the central point. As adult dolphins would be travelling in one particular direction, infants could also often be seen venturing in different directions at high speed, while returning to their mother regularly. Pairs of juveniles were observed swimming together on several occasions, sometimes involving chases between them. Calves were never seen displaying aggressive behaviours.

‘Corklike’ surfacing by common dolphin calves was observed in the present study, and was exclusively displayed by newborn calves. In order to take a breath, newborns would

Calf age class		Percentage of observations of association between mother-calf pairs	Mean percentage of other mother-calf pairs accompanying the focal pair
Newborn	Mean	52	17.15
	n	29	29
	SD	50.9	21.57
	Lower confidence interval	41.0	8.95
	Upper confidence interval	74.2	25.36
Infant	Mean	46	22.87
	n	112	111
	SD	50	34
	Lower confidence interval	38.8	16.48
	Upper confidence interval	56.7	29.27
Juvenile	Mean	43	24.42
	n	113	113
	SD	49.8	36.65
	Lower confidence interval	36.0	17.59
	Upper confidence interval	53.7	31.25

Table 6. Grouping patterns summarised for each calf age class.

lunge out at the surface, sometimes almost leaping out of the water. Infants and juveniles presented the same breathing pattern as adult dolphins.

Although contact between mothers and calves was difficult to identify, rubbing bouts between them were observed on five occasions and involved calves of all three age classes. One of these bouts was part of a highly social interaction between an infant and its presumed mother. The mother-infant pair was observed for 6 minutes and 28 seconds, within which the infant kept rolling belly up under its mother, and several rubbing bouts using pectoral fins were observed.

Foetal folds on common dolphin calves generally appeared as two white lines in an inverted V shape under the dorsal fin, and a white circle around the head of the animal, just behind the blowhole. Of the 279 calves for which the presence or absence of foetal folds could reliably be identified, 49 of them did bear these marks. While 60% of all newborns for which the presence of foetal folds could be identified had foetal folds, 14% of all infants and 11% of all juveniles had foetal folds. Using a Chi-Square test for independence, the difference between these percentages revealed to be significant according to calf age class ($X^2=42.229$, df=2, $p<0.01$). Newborns were significantly more likely to be observed with foetal folds than infants and juveniles (between newborns and infants: $z=4.84$, $p<0.01$; between newborns and juveniles: $z=5.24$, $p<0.01$). The percentage of observations of foetal folds appeared to decrease with older aged calves, which is supported by the correlation coefficient ($r=-0.260$, $p<0.01$). White markings, that could have been the remains of foetal folds, were also observed on six adult individuals.

12) **Summary**

The results of the statistical analyses conducted on the data gathered during field observations proved to give some interesting insights into the characteristics of groups with calves, as well as on calves' behavioural development and mother-calf relationships. Only a few hypotheses couldn't be tested due to small sample sizes. The different findings resulting from data analysis are pinpointed here:

- a large proportion of common dolphin groups contained calves (82.5%),
- group type didn't seem to be affected by water depth, although only groups with newborns or infants were found under 20 metres of depth,
- the mean water temperature tended to be higher with the presence of young calves in the group,
- groups with newborn calves were more likely to be encountered in the summer and spring,
- group size varied significantly according to group type. Group size tended to decrease as the age class of the youngest calf in the group increased,
- the occurrence of the five different activities in which the dolphins could be involved did not appear to vary according to group type,
- there was no significant difference in the patterns of associations with other species across the different types of groups,
- there was no relationship between the reaction of the dolphins to the boat, or the minimum distance to the boat, and group type,
- mothers and calves of older age classes approached the boat at closer distances than mothers and younger calves did,
- observations of mating behaviours varied with the time of the year, and were significantly lower in winter. Mating behaviours involving genital contact were less likely to be observed in winter than in any other season. The occurrence of mating behaviours without genital contact appeared to be higher in summer than in winter.
- the occurrence of 'echelon position' and the mean percentage of time spent in this position decreased with calves' age class. The variations in occurrence of 'infant position' and in the mean percentage of time spent in this position with age class did not prove to be significant.
- the occurrence and mean frequency of separations increased with the age class of calves,
- the mean maximum duration and distance of separations increased with the age class of calves,
- calves of older age classes tend to spend more time away from their mothers,
- the mean proportion and frequency of synchronous breathing decreased as calf age class increased. Although juveniles breathed more frequently on their own than infants did, no definite conclusions could be drawn on calves' solitary surfacing. Overlapping surfacing appeared to remain stable across all age classes.

- mean dive times of both mothers and calves showed a significant increase with the age class of the calves. Mothers' mean dive time also proved to be higher than that of calves.
- although newborn calves were less likely to be seen associated with non-mother dolphins than infant and juvenile common dolphins, no definite conclusions could be drawn on the occurrence of escorting behaviour across the different age classes,
- associations between mother-calf pairs appeared to be frequent but did not seem to be related to the age class of calves,
- the occurrence of foetal folds on calves decreased as the age class they belonged to increased.

Chapter 5: DISCUSSION

1) Introduction

The purpose of this chapter is to discuss the results of the statistical analyses in light of the knowledge available on common dolphins and other cetacean species. The significance of each of the results obtained in this study is reviewed and compared to previous studies conducted on similar subjects. The structure of this chapter is summarised in figure 10.

Firstly, the results relating to the influence of environmental variables on the occurrence of common dolphin groups of different types are discussed. The breeding seasonality of the common dolphins in the Hauraki Gulf is reviewed, and discussed in regards to variations in water temperatures. This leads to the discussion of the existence of a mating season. The variations in water depths according to the different group types are then considered. The role of the Hauraki Gulf for the population of common dolphins under investigation in this study is also considered.

Secondly, the social organisation and behaviours that characterise the different group types of common dolphins are discussed. The advantages relating to larger group sizes and to associations of mother-calf pairs within groups are put in perspective with the results obtained in this study. The observations of groups with newborns involved in feeding activities and associated with other species are then discussed. The reaction of common dolphin groups, and of mother-calf pairs, to the boat as well as their implications, are investigated.

Thirdly, the development of common dolphin calves is discussed. The importance and meaning of the changes observed in mother-calf relationships are investigated by considering different aspects of their behaviour: mother-calf separations, escorting behaviour, swimming position, synchrony and breathing patterns, dive time and nursing. The occurrence of foetal folds on calves of different age classes is also reviewed. Other behavioural characteristics of common dolphin calves observed during this study are discussed using information available for other species.

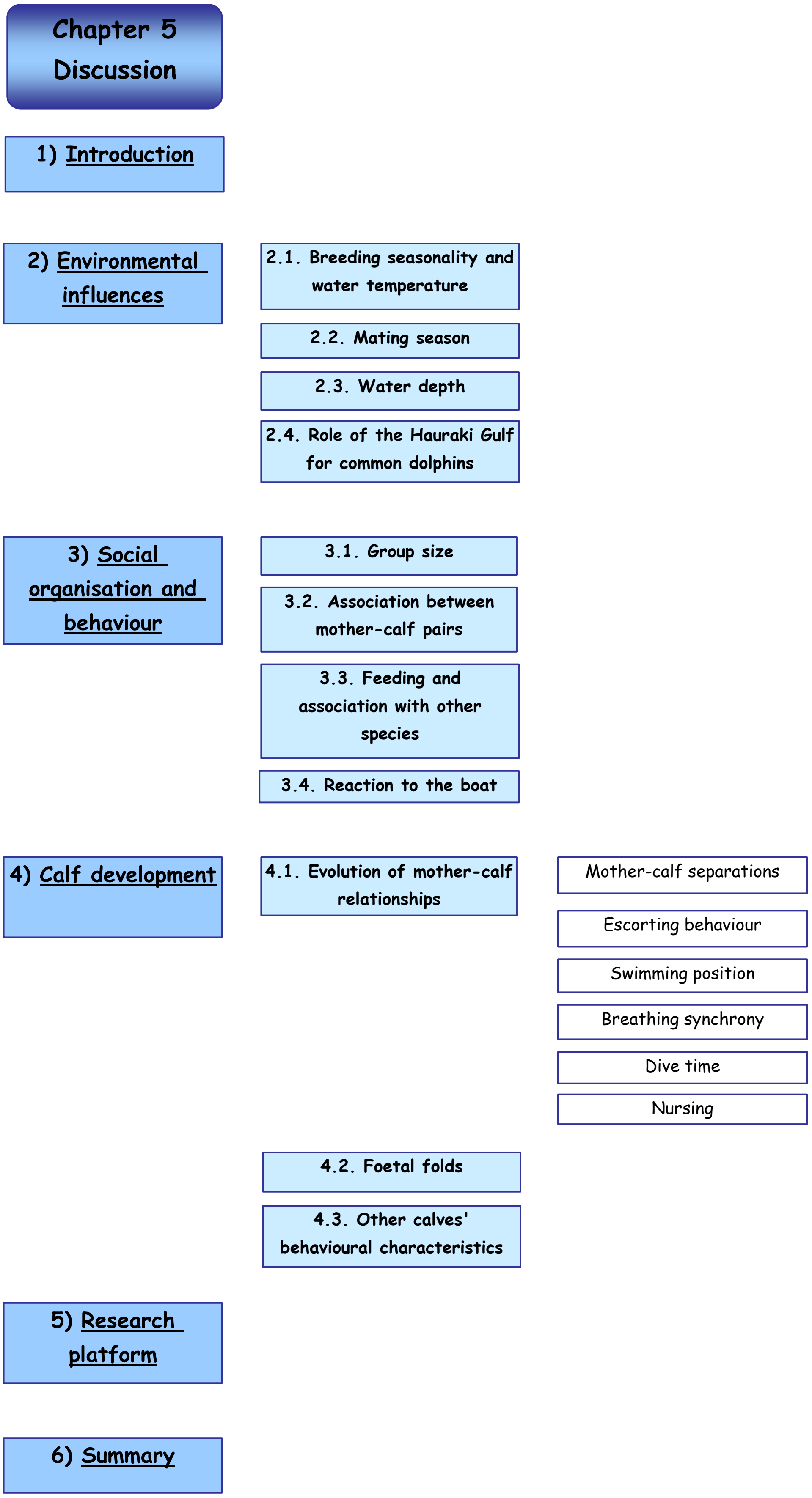


Figure 10. Structure diagram of the 'Discussion' chapter.

Fourthly, the advantages and disadvantages of the research platform used in the course of this study are reviewed.

Finally, the different topics discussed in this chapter are summarised.

2) Environmental influences

2.1. Breeding seasonality and water temperature

The results of the present study show that the common dolphins encountered in the Hauraki Gulf tend to breed seasonally. A large majority of groups containing newborn calves were sighted during spring and summer (82.9%), with a peak over the months of December and January. This is consistent with previous observations made in New Zealand (Constantine, 1995; Bräger and Schneider, 1998; Neumann, 2001), and in other locations worldwide (Gaskin, 1972; Jefferson *et al.*, 1993; Northeastern Pacific: Leatherwood *et al.*, 1976; Ferrero and Walker, 1995; Danil and Chivers, 2003; Northeastern Atlantic: Collet, 1981; Evans, 1987; Black Sea: Sleptsov, 1940; Gaskin, 1992; Evans, 1987; Mediterranean: Universidad Autónoma de Madrid and Alnitak, 2002). The occurrence of groups with juveniles also showed seasonal variations, with higher proportions in the summer than in the winter. Back-projected birth dates have been used to assess breeding seasonality in previous studies (Perryman and Lynn, 1993; Danil and Chivers, 2003) and may allow to further investigate this observation. Because individuals of juvenile size would be approximately a year old, their higher occurrence during the summer months compared to winter suggests that they were born around the same time the previous year. This observation further supports the existence of a breeding season orientated towards summer.

Reproduction concentrated to some specific part of the year appears to be advantageous for a species when the environment it inhabits changes seasonally (Bronson, 1989). For cetaceans, it has been shown that areas with the widest range of oceanographic parameters, such as those of high latitudes (Evans, 1987; Bronson, 1989; Urian *et al.*, 1996), usually show the strongest seasonality in births (Norris and Dohl, 1980a; Perryman and Lynn, 1993; Ferrero and Walker, 1995; Whitehead and Mann, 2000). The peak in sightings of newborn calves spread over two months is consistent with the results of previous studies conducted on populations of common dolphins found at similar latitude in the Northern Hemisphere (Collet, 1981; Ferrero and Walker, 1995), and contrasts with the broader breeding seasons reported for latitudes closer to the equator (Perryman and Lynn, 1993). This peak is likely to be related to oceanographic conditions favourable for calves' survival over the late spring and early summer within the Hauraki Gulf. The observation of calves of all age classes throughout the year, and more specifically of newborns during the winter months, emphasises the ability of female common dolphins to give birth year round. However, the survival rate of individuals born outside the main breeding season may be lowered (Fernandez and Hohn, 1998).

Breeding seasonality appears to be highly influenced by environmental factors such as water temperature, as most births tend to occur during the warmest months of the year (Ridgway, 1972; Evans, 1987; Wells *et al.*, 1987; Bronson, 1989; Urian *et al.*, 1996; Bearzi *et al.*, 1997; Mann *et al.*, 2000; Whitehead and Mann, 2000). Studies conducted on different populations of bottlenose dolphins have found that the peak in births usually coincide with the peak in water temperatures (Würsig, 1978; Wells *et al.*, 1987; Hansen, 1990; Wells, 1991a; Urian *et al.*, 1996; Bearzi *et al.*, 1997). A similar pattern was found in this study, as the peak in sightings of newborn common dolphins corresponded to the months of highest water temperatures in the Hauraki Gulf. Furthermore, groups containing newborn calves were found in temperatures significantly warmer than groups with infants and groups composed of adults only. The difference with groups containing juveniles was of lower extent, as these groups were also mostly found during the summer months. Groups containing only adult common dolphins were sighted more frequently during winter, which represents the coldest season of the year. These observations suggest that giving birth in warmer waters is likely to be beneficial for female common dolphins, either directly or through increased calf survival. Mann *et al.* (2000) showed that female bottlenose dolphins' reproductive success is indeed influenced by a breeding season, and it has been suggested by several authors that warmer waters represent a physiological advantage for both mothers and calves (Würsig, 1978; Wells *et al.*, 1987; Wells, 1991a; Mann *et al.*, 2000; Whitehead and Mann, 2000). During the crucial period following birth, living in waters of relatively high temperatures is assumed to allow both members of the pair to lose the least energy to thermal regulation (Whitehead and Mann, 2000), especially since calves are born with very little insulating blubber (Wells, 1991a). It seems likely that water temperature exerts the same type of influence on the population of common dolphins observed in the Hauraki Gulf, and the benefit of warmer waters would explain the breeding seasonality observed in this study.

Water temperature is also likely to have an influence on other environmental factors, such as prey availability, which has been identified to potentially affect timing in births in many mammal species, including dolphins (Evans, 1987; Bronson, 1989; Barros and Odell, 1990; Boyd, 1991; Urian *et al*., 1996; Mann *et al*., 2000; Whitehead and Mann, 2000; Danil and Chivers, 2003). In fact, because reproduction represents a high energetic cost for females, it has been hypothesised that they will synchronise the period of greatest energy demands with peaks in food availability (Bronson, 1989; Urian *et al*., 1996; Whitehead and Mann, 2000). In bottlenose dolphins, nutritive requirements of mothers have been identified to be the highest during late gestation and early lactation (Urian *et al*., 1996). Calves might also benefit increased survival when food supply is adequate for lactating mothers (Urian *et al*., 1996). Being the warmest time of the year, late spring and early summer months might also be the most abundant food-wise. The combination of warm water with longer days and calmer weather appears to favour the production of phytoplankton, which is an important component of the diet of fish and squid, which are in turn fed upon by dolphins (Evans, 1987). Therefore, the breeding seasonality observed in common dolphins might also be the result of variation in availability of food resources, and such a suggestion has already been made for the North Pacific population of common dolphins (Danil and Chivers, 2003). It has also been put forward that seasonal variation in climate and prey availability will not exert an independent influence on the timing of births, but instead are most probably organised in a complex of interacting factors (Bronson, 1989; Urian *et al*., 1996). This is likely to be the case for the common dolphins of the Hauraki Gulf.

It can be concluded that the breeding season identified in this study corresponds to the higher water temperatures of late spring and early summer, and is likely to be related to changes in the environment that are beneficial for mothers and their young calves.

2.2. Mating season

The existence of a breeding season in most cetacean populations studied to date suggests that successful mating occurs during a restricted part of the year (Würsig and Würsig, 1980). Seasonal changes in the frequency of mating activity have been reported for different species such as the bottlenose dolphin (McBride and Hebb, 1948; McBride and Kritzler, 1951; Puente and Dewsbury, 1976; Shane, 1990b), and the spinner dolphin (Wells, 1984). Because observations of newborn calves within groups of common dolphins varied seasonally and appeared to peak in the late spring and early summer, it would be expected that mating behaviours present the same type of variation. Considering that the gestation period of common dolphins is usually between 10 and 11 months (Harrison, 1969; Harrison *et al.*, 1969; Gaskin, 1972, 1992; Perrin and Reilly, 1984; Ferrero and Walker, 1995), although not precisely known for the New Zealand population, births between December and February would be the result of successful mating between January and April. Previous observations of common dolphins in the Cook Strait, New Zealand, reported copulation during the months of February and March (Webb, 1973b). Although observations in mating behaviours appeared to peak in April, the only significant difference found in this study consisted in a decrease during the winter months compared to any other seasons. A similar pattern was found when considering mating behaviours involving genital contact separately. The mating season projected by the analysis of peaks in sightings of newborn calves does not correspond to months of significantly higher occurrence of mating behaviours.

These results could be explained by two factors. Firstly, it appears possible that mating behaviours were not accurately recorded. Common dolphins being a fast moving species, behaviours related to mating may occur rapidly, impeding all-occurrence sampling. In addition, during sightings of common dolphins, attention was focused on locating calves and determining group composition. Therefore, a defficiency in the sampling of mating behaviours cannot be excluded. Secondly, observations of mating behaviours may not always be related to successful copulation. Male and female dolphins seem to go through physiological changes that limit conception to a specific part of the year (Würsig and Würsig, 1980). Seasonal variations in the spermatogenesis of male common dolphins have been previously reported (Ridgway, 1972; Collet and Girons, 1984). Therefore, the observation of mating behaviours throughout most of the year does not appear to be contradictory to the existence of a breeding season. Dolphins are also known to use mating behaviours in a wide variety of contexts that are not always related to reproduction (Wells, 1984; Wells *et al.*, 1987). For example, it has been suggested that sexual behaviours displayed by dolphins could also be used to maintain group cohesiveness and social structure (Wells, 1984; Dawson, 1985). Therefore, their use as courtship and mating behaviours can be difficult to distinguish from their use as communicative and social signals (Norris and Dohl, 1980a). The results from this study did not allow the identification of a mating season for the common dolphins in the Hauraki Gulf. Future studies concentrating more specifically on mating behaviours may enable to find a correspondence with the identified breeding season.

2.3. Water depth

Mothers and calves of different cetacean species have been observed to make extensive use of shallow waters during the main breeding season (for example, southern right whales: Payne, 1976; Elwen and Best, 2004b; dusky dolphins: Cipriano, 1992; bottlenose dolphins: Würsig and Würsig, 1977; Wells *et al.*, 1987; Wells, 1991a; Mann *et al.*, 2000; Hector's dolphins: Bräger *et al.*, 2003), and has even proved to significantly affect the reproductive success of female bottlenose dolphins (Mann *et al.*, 2000). Several authors have suggested that such habitat utilisation could have evolved in order to reduce the risk of predation (Norris and Dohl, 1980a; Evans, 1987; Wells *et al.*, 1987; Wells, 1991a; Scott *et al.*, 1990; Connor, 2000; Bräger *et al.*, 2003). Both sharks and killer whales have been identified as the main predators of dolphins and whales (Wells *et al.*, 1980; Evans, 1987; Connor, 2000), and it seems that shallow waters provides better detection, and therefore better avoidance, of these predators (Mann *et al.*, 2000). Würsig and Würsig (1980) suggested that the loud background of low water depths might mask, or at least reduce, noises produced by mother-calf pairs from killer whales. It is understandable that predator avoidance will be important during the breeding season, as calves are highly vulnerable to threats during the first few months of life (Mann *et al.*, 2000). Once again, a combination of factors might explain the use of shallow waters by mother-calf pairs. Different authors have also suggested that inshore movements in the summer time might be driven by higher prey density in these areas (Wells *et al.*, 1987; Bräger and Schneider, 1998; Mann *et al.*, 2000).

Common dolphins are as likely as any other species to be preyed upon by sharks and killer whales. Many different species of sharks, such as mako (*Isurus oxyrinchus*), hammerhead (*Sphyrna zygaena*) and great white (*Carcharodon carcharias*), are frequently sighted in the waters of the Hauraki Gulf (Owen and Owen, 1999), and killer whales are also encountered on occasions. Predation of killer whales on common dolphins has been reported for both the Hauraki Gulf (O'Callaghan and Baker, 2002), and other locations around the New Zealand coast (Visser, 1999). Yet, this study has shown that groups of common dolphins containing newborn calves did not appear to favour shallow waters. While the mean water depth of groups with newborns was 36.7 metres, female bottlenose dolphins and their newborn calves have mostly been found in waters less than 10 metres deep (Würsig and Würsig, 1980; Mann *et al*., 2000). This difference could be a result of the specific habitat that characterise each species. Shallow waters are part of bottlenose dolphins' range, as they are usually described as a coastal species (Connor *et al*., 2000). On the other hand, common dolphins, which are more likely to inhabit open waters (Evans, 1987), might have to travel long distances in order to reach such shallow waters. The suggestion that predator avoidance is the main explanation for mother-calf pairs using very shallow waters was made as a result of studies focusing on coastal species, and especially on the bottlenose dolphin. However, this strategy might not be an efficient option for pelagic species such as the common dolphin.

It is also important to note that water depths that are 'shallow' will be different for coastal and pelagic species of dolphins. In fact, the depths in which common dolphins are found in the Hauraki Gulf are already significantly lower than for most other populations worldwide (O'Callaghan and Baker, 2002). But even under these circumstances, the distribution of the different group types did not seem to be affected by water depth. The large majority of groups with young calves were encountered at similar depths to groups without calves. However, it is interesting to note that the few common dolphin groups observed under 20 metres of depth all contained newborn calves or infants. The use of the shallowest part of the Hauraki Gulf could potentially benefit mother-calf pairs of common dolphins, as they might offer temporary secure waters for births to take place or runs of key preys for lactating females. However, the low occurrence of observations of groups with calves in waters under 20 metres suggests that they only visit these areas occasionally or that they rapidly return to deeper waters. An underestimation of the occurrence of inshore presence of common dolphins due to search patterns can also not be excluded.

2.4. Role of the Hauraki Gulf for common dolphins

The fact that groups of common dolphins containing newborn calves were found in warmer waters suggests that females are selective towards the environment in which they raise their young. Another trait that has been identified as being favoured by mothers and their calves is a preference for areas with calm seas, as it will reduce their energy consumption (Wells *et al*., 1980; Evans, 1987; Elwen and Best, 2004a). Being sheltered from much of the oceanic weather by the Coromandel Peninsula and Great Barrier Island, the waters of the Hauraki Gulf appear to be relatively calm on most days (Hauraki Gulf Maritime Park Board, 1983; Bercusson, 1999), which contrasts with the more usual open ocean habitat of common dolphins. It is also interesting to note that the variation in water temperatures observed in the Hauraki Gulf are not as wide as in other areas inhabited by delphinids (seasonal variation of 17°C: Wells *et al*., 1987; 20°C: Bearzi *et al*., 1997; 25°C: Hersh *et al*., 1990), and all the physical characteristics of the water in the Hauraki Gulf appear to remain relatively stable throughout the year (Jillett, 1971; Hauraki Gulf Maritime Park Board, 1983). For these reasons, the waters of the Hauraki Gulf may be ‘attractive’ for mother-calf pairs of common dolphins. The high percentage of groups with calves encountered in this study further supports this hypothesis.

Within the Mediterranean region, the Alboràn Sea has been identified as an important breeding ground for common dolphins, as 46.4% of all groups included calves (Universidad Autónoma de Madrid and Alnitak, 2002). In that particular study, calves were defined as individuals half the size of adults or less (Ana Cañadas, personal communication), which corresponds to the categories ‘newborns’ and ‘infants’ used in this study. In 57.5% of groups sighted in the Hauraki Gulf, the youngest member was either a newborn or an infant. This high percentage could be explained by the fact that the common dolphins of the Hauraki Gulf have an unusually high breeding success rate or that the species comes to the area especially to breed. In order to appreciate the exact role of the Hauraki Gulf for common dolphins, comparisons of the occurrence of groups with calves in other areas along the coast of New Zealand appear necessary.

Comparisons with the data collected by Neumann (unpublished data) in Mercury Bay were attempted but the distribution of observations made within both studies was considered to be too different to draw any accurate conclusions. Nevertheless, the high percentage of groups with calves strongly suggests that the Hauraki Gulf plays an important role as a calving ground for common dolphins.

The high occurrence of common dolphins throughout the year suggests that the Hauraki Gulf offers more than just a calving ground for the species. The availability of food within the area is another factor to investigate. Even though the Hauraki Gulf is characterised by a fairly level sea bed, which represents an unusual habitat for common dolphins (O'Callaghan and Baker, 2002), the many headlands and islands produce a persistent up- and down-welling within the Gulf, which introduce nutrients into the surface layers (Black *et al*., 2000). The region is also affected by the East Auckland current (Jillett, 1971), which brings nutrient-rich oceanic waters into the Gulf (Sharples, 1997; Zeldis *et al*., 1998). These oceanographic conditions, as they increase nutrients levels and therefore food availability, have been identified as optimal for the presence of abundant marine life (Walford, 1958). For common dolphins, it will probably represent greater feeding opportunities (Evans, 1974; Au and Perryman, 1985) and contribute to their presence in the area. The potential benefit of these high levels of food for mother-calf pairs must be considered and could also explain their high occurrence in the Hauraki Gulf. As the distribution of dolphins and whales is mostly determined by food availability and suitable conditions for reproduction (Townsend, 1935; Sverdup *et al*., 1942), which both appear to be fulfilled by the waters of the Hauraki Gulf, this area is likely to provide common dolphins, whether they are accompanied by calves or not, a highly beneficial habitat.

3) <u>Social organisation and behaviours</u>

3.1. Group size

In the present study, groups of common dolphins with calves were found to be significantly larger than groups without calves. Furthermore, group size was highest for groups that contained newborn calves with a mean of 35.75 dolphins per group, and the smallest for groups made up of only adult individuals with a mean of 18.13 dolphins per group. Groups with newborns were significantly larger than groups with infants or juveniles, which in turn were larger than groups of adults. Similar accounts of decreasing group size with increasing calf age are recurrent in the cetacean literature (Winn, 1982; Wells *et al*., 1987; Scott *et al*., 1990; Bearzi *et al*., 1997; Mann *et al*., 2000; Whitehead *et al*., 2000), but have not been documented for common dolphins. The only information previously available on the subject relates to early observations of Black Sea common dolphins aggregating into larger groups during parturition (Tsalkin, 1938).

It could be suggested that these observations result from the fact that larger groups are more likely to contain individuals of different age categories. However, the tendency of finding newborns calves in larger groups in different dolphin species suggests that it benefits for mother-calf pairs. Wells (1991b) even related survivorship of bottlenose dolphin calves in Sarasota Bay, Florida, to group size. The functions of cetaceans groups are numerous (Connor, 2000), and larger groups could be advantageous for female common dolphins and their calves in many different ways.

Larger groups could provide mother-calf pairs with more efficient protection from predators. It has been previously suggested that the larger groups formed by pelagic species present an effective way to prevent attacks (Wells *et al*., 1980), and could represent an alternative strategy to the use of shallow waters for common dolphins. Being part of a group appears to provide mother-calf pairs with a safe environment (Brown *et al*., 1966; Dohl *et al*., 1974), as it offers effective defence against predators (Wells *et al*., 1987; Connor, 2000; Fellner, 2000). In fact, living in groups will decrease the risk of predation through increased vigilance and heightened awareness of surroundings (Evans, 1987; Wells, 1991a; Alcock, 1998; Connor, 2000; Fellner, 2000), as well as through confusion and dilution effect (Alcock, 1998; Connor, 2000; Fellner, 2000). The overall predation risk to an individual will be lowered by the presence of other members of the same species (dilution effect). For any predator, tracking a specific prey will also be of greater difficulty within a group, which will therefore reduce the capture rate per attack (confusion effect). Group living might also enable certain members of the group to reduce their own vigilance levels and devote more time to other activities, such as care of the young (Connor, 2000). Safety in numbers is a common hypothesis in the study of animal behaviour, and the different advantages of group living will be enhanced as the number of group members increases (Alcock, 1998). Larger groups provide individual group members with more eyes, more ears, and in the case of dolphins, more echolocation clicks (Wells, 1991a), which will increase efficiency in predator surveillance (Norris and Dohl, 1980a; Wells *et al*., 1980).

Larger groups may also benefit mothers and their calves by increasing feeding efficiency. It has been suggested that the location of food resources will be facilitated by higher numbers of individuals within a group through increased awareness (Shane, 1990a; Connor, 2000; Fellner, 2000). In species practicing cooperative hunting, such as the common dolphin (Neumann, 2001), larger groups may benefit their members in two other ways (Connor, 2000). Firstly, they may improve the defence of food resources and enable the capture of larger schools of prey (Connor, 2000). And secondly, larger groups will allow the division of labour (Connor, 2000). Easy access to prey is very likely to benefit lactating females (Bronson, 1989; Urian *et al*., 1996; Whitehead and Mann, 2000), and could explain why newborn common dolphin calves and their mothers are found in the largest groups.

Larger groups could also provide increased hydrodynamic efficiency (Connor, 2000; Fellner, 2000), and the opportunity for social learning for calves (Norris and Dohl, 1980a; Johnson and Norris, 1986; Wells, 1991a).

The effect of group size also appears to have its own limits and may induce higher costs than benefits over a certain size (Connor, 2000). Therefore, the number of individuals within a group is likely to increase until reaching an optimum. For common dolphin groups containing newborns in this study, the mean group size was 35.75. This could represent an approximate optimal group size for the common dolphins in the Hauraki Gulf.

Because of the high vulnerability of the newly born calves and the high energy costs endured by parturitioning and lactating females, the different advantages of group living appear to be of primary importance for the calves' survival and are likely to explain why newborn common dolphins are found in larger groups.

3.2. Asssociation between mother-calf pairs

Investigations of mother-calf pairs' association patterns in cetaceans have shown that they do not randomly form groups with any other individuals of the same species, but usually aggregate with other females of similar reproductive status within nursery groups (Tyack, 1986; Whitehead and Mann, 2000). Observations supporting the existence of nursery groups have been reported for several odontocete species (bottlenose dolphins: Shane *et al.*, 1986; Wells *et al.*, 1987; Scott *et al.*, 1990; Bel'kovich, 1991; Mann and Smuts, 1999; Dall's porpoises and harbour porpoises: Read and Hohn, 1995; dusky dolphins: Würsig and Würsig, 1980; Hawaiian spinner dolphins: Johnson and Norris, 1994), including common dolphins (Doak, 1981; Neumann, 2000; Silva and Sequeira, 2003). The benefits of group living previously discussed are likely to apply to nursery groups, as they will, for example, reduce the predation risk per individual calf (Whitehead and Mann, 2000). Yet, associations between mother-calf pairs also seem to have other advantages. Connor (2000) suggested that nursery groups would allow female bottlenose dolphins to decrease the risk of male harassment through the dilution effect. These groups are also likely to provide a secured environment within which mothers will be able to teach their calves the skills necessary for survival, as well as protect them from adverse stimuli (Wells *et al.*, 1987; Bel'kovich, 1991). Due to the difficulty of identifying the sex of wild common dolphins, the existence of true nursery groups only made of females and calves could not be investigated in this study. Nevertheless, associations of mother-calf pairs within groups of common dolphins were assessed. Mother-calf pairs under focal observation appeared to be accompanied by at least one other mother-calf pair in more than 40% of all observations. It has been suggested that mother-calf pairs may be attracted to one another due to the similar level of dependence of their calves, which also engage similar requirements for the mothers (Wells *et al.*, 1987). This could explain the frequent association of mother-calf pairs of common dolphins. The advantages of these associations could be similar to those of nursery groups. The occurrence of mother-calf pairs associations, as well as the percentage of other mother-calf pairs in the group found to accompany the focal pair, did not vary with the age class of the calves considered. Although mother-calf pairs of common dolphins were frequently observed swimming with one another, this study only took into account close associations and therefore may underestimate their actual occurrence. Further studies should concentrate on investigating the distribution of mother-calf pairs within groups of common dolphins in order to assess whether or not they tend to form discrete subgroups.

3.3. Feeding and association with other species

The results obtained in this study suggest that female common dolphins may make use of a specific habitat in order to optimise the survival of their young. However, the calves' protection does not only relate to the selection of appropriate environmental conditions, and more active strategies could be reflected in mothers' behaviour. An example would be in their reaction towards potential hazards or in the type of activities mother-calf pairs are involved. A previous study comparing the diet of lactating females and weaning calves in common dolphins suggested that calves did not usually feed with adults (Young and Cockcroft, 1994). Würsig (1986) postulated that feeding aggregations could potentially be dangerous for calves, as it involves 'boisterous' activity, as well as much contact and socio-sexual activity. While dolphins are feeding, large predatory sharks might also be attracted to the area and could render calves highly vulnerable (Würsig, 1986). The observations made of common dolphins in the Hauraki Gulf do not support this contention, as feeding was observed in 41% of all sightings and its occurrence did not appear to be related to group type.

Because the search for dolphins in this study relied mainly on visible signs of feeding activities, the high percentage of observations of this particular behavioural state does not provide an accurate representation of the activity budget for common dolphins. Nevertheless, the results obtained can still be expected to reflect whether or not feeding occurred differentially across group types. Common dolphin groups with newborn calves were seen feeding as often as any other group type, and calves of all ages, including newborns, were observed involved in actively surrounding a school of fish. Common dolphins feeding activities appear to be quite intense and even more so when feeding aggregations involve diving birds and lunge feeding whales. The overall rate of association of common dolphin groups with other species did not appear to vary according to group type either. Considering the vulnerability of calves during the first few months of life and previous results reported for the species, the presence of newborns within feeding groups of common dolphins and high levels of association with other species were unexpected. Association with birds, most frequently the

Australasian gannet, was as high for groups with newborns as groups containing older calves, and even higher than for groups only made up of adult individuals. This difference between group types could be explained by the fact that groups with calves were usually larger than adult groups, and small groups were less likely to be seen feeding.

The analysis of association with birds and whales reveals interesting results. In fact, groups with newborns associated with whales and birds in only 5% of all encounters, which is significantly lower than groups for which the youngest member was either an infant or a juvenile. Association with whales only was rare and is likely to be explained by the fact that the presence of whales with common dolphins was usually limited to feeding situations, to which birds were also highly attracted. The high frequency with which common dolphin groups including newborns were seen feeding, as well as the high rate of association with birds, could be explained by the fact that feeding was more likely to involve larger groups. However, observations of young calves actively involved in feeding activities suggest that these situations may also involve other benefits for mother-calf pairs. It can be suggested that if common dolphins highly rely on ‘work ups’ to hunt their prey, learning the feeding process at a young age would be advantageous. The rare association of groups including newborns with whales and birds might be related to the fact that these situations could potentially involve higher costs than benefits for the young, and further suggest that under certain circumstances, feeding aggregations might not be safe for calves. This is supported by the observation of an infant common dolphin, associated with a juvenile at the periphery of a feeding group, and later rejoined by the presumed mother.

3.4. Reaction to the boat

Female cetaceans are known to be highly protective of their young and to strongly respond to any situation perceived as a threat (McBride and Kritzler, 1951; Norris *et al*., 1977; Doak, 1995; Mann and Smuts, 1999). The impact of the presence of boats on dolphins’ behaviour has been documented for both groups as a whole (Janik and Thompson, 1996; Nowacek *et al*., 2001; Jelinski *et al*., 2002; Lusseau, 2003; Constantine *et al*., 2004) and mother-calf pairs (Wells, 1991a; Nowacek *et al*., 2001). In response to boat traffic, mothers were observed to have longer dive times, which was interpreted as a means to avoid boats (Nowacek *et al*., 2001). Mothers have also been seen herding their calves away from boats (Wells, 1991a). In the present study, the reaction of common dolphins did not differ according to group type. In response to the approaching vessel, dolphins frequently took position at the bow, obtaining propulsive power from the moving vessel (Fejer and Backus, 1960; Williams *et al*., 1992). The minimum distance between the dolphins and the boat did not seem to be influenced by group type either. Yet, the distance between the boat and mother-calf pairs varied significantly across the different age classes. The distance to the boat was the greatest for mothers and newborns, and significantly decreased with increased age of the calves. Although the majority of mother-calf pairs did approach the boat without any obvious reaction, presumed mothers were observed steering their calves away from the vessel on different occasions. Therefore, it appears that under certain circumstances mothers could perceive the boat as a threat. For example, dependent calves and their mothers could be more vulnerable to boat strikes due to their lower manoeuvrability (Nowacek *et al*., 2001). These results have important conservation implications for the species, which are enhanced by the high percentage of groups with calves found in the Hauraki Gulf. Because mothers and calves represent the nucleus of any mammal society (Eisenberg, 1986), their protection is likely to ensure the prosperity of the population as a whole. For that reason, the New Zealand Department of Conservation have forbid 'swim with dolphins' programs to occur when groups contain juveniles. In light of the results obtained in this study, this prohibition can only be supported, and the further inclusion, within the Marine Mammals Protection Regulations, of specific guidelines regarding dolphin mother-calf pairs should be considered. Every year, and especially during summer, the Hauraki Gulf is highly frequented by recreational boats that are likely to encounter common dolphins during their journey (Bercusson, 1999). Efforts should be made to properly inform the public of the risks of boat mishandling around groups of dolphins containing newborn calves.

4) <u>Calf development</u>

4.1. Evolution of mother-calf relationships

- Mother-calf separations

As bottlenose dolphin calves grow older, it appears that their competence in negotiating the marine environment consistently improves (Mann and Smuts, 1999). This improvement is reflected in different aspects of their behaviours, including mother-calf separations. In fact, the rate, proportion, duration and distance of separations between bottlenose dolphin calves and their mothers have all proved to increase as a function of calf age (Cockcroft and Ross, 1990; Reid *et al.*, 1995; Mann and Smuts, 1998, 1999; Gubbins *et al.*, 1999; Grellier *et al.*, 2003; Keiko *et al.*, 2003). Behavioural changes of the same order have also been reported for beluga whales (Schneider *et al.*, 2003), southern right whales (Taber and Thomas, 1982), and killer whales (Haenel, 1986). The results obtained in the present study show a similar tendency for common dolphin calves. Both the occurrence and frequency of separations appeared to increase with the age class of the calves considered. While newborns were only seen separating in 24% of all focal follows and on average less than once per five-minute interval, separations occurred in most observations of juvenile animals (94%) with a mean frequency of more than seven separations over the same time interval. Considering the vulnerability of young calves, it could be argued that 24% represents a relatively high occurence of separations for newborn common dolphins. Considering similar observations on bottlenose dolphins calves, Mann and Smuts (1999) suggested that newborns rapidly have to learn to separate from their mothers at a young age, as it will allow them to gain the locomotor skills necessary for their survival. This is likely to apply to common dolphin calves as well. The age class of common dolphin calves was also found to have an influence on the duration and distance of separation. Calves were observed separating for longer periods of time as the age class to which they belonged increased. As a result, the percentage of time they spent without their mothers increased in a similar manner. The maximum distance at which a calf would separate from its mother showed a significant increase with older aged calves, and when newborn calves did separate from their mothers, it was always over relatively short distances of five metres or less.

In the literature on bottlenose dolphins, the preference for close contact during the time of high dependence of calves on their mothers has been explained by the influence of different factors. Firstly, close proximity between mothers and calves allows the accurate provision of maternal care and nursing opportunities, which appear to be highly important during the newborn period (Trivers, 1974). Secondly, it is also during this period that calves' swimming abilities appear to be the least coordinated (Cockcroft and Ross, 1990; Mann and Smuts, 1999), and close proximity is therefore likely to represent a means for mothers to control their calves' movements (Fellner, 2000). The lack of such control has been reported to lead to calves' death in different studies (Tavolga and Essapian, 1957; Dudok van Heel and Meyer, 1974; Johnson and Norris, 1994). Thirdly, the lower occurrence and frequency of separations observed for the youngest calves could also be due to an imprinting period during which newborns learn to recognise their mothers (Mann and Smuts, 1999). For these different reasons, calves' survival during the first few weeks following birth appears to be highly related to close contact with their mothers. This is also likely to explain why mothers of different mammal species are known to show great responsibility in proximity maintenance during the newborn period (Trivers, 1974). As calves grow older and their dependence on their mothers decreases, the role of mothers in maintaining proximity will diminish (Trivers, 1974). Observations supporting the existence of a similar pattern in cetaceans have been reported for bottlenose dolphins (Reid *et al.*, 1995; Fellner, 1999; Mann and Smuts, 1999) and southern right whales (Taber and Thomas, 1982). The data collected in this study did not allow the investigation of the role of common dolphin mothers and calves in proximity maintenance.

As calves grow older, they will improve their locomotor abilities as well as their skills in reuniting with the mother, which will allow them to gain more independence and to separate more frequently, for longer periods of time and over greater distances (Taber and Thomas, 1982; Reid *et al.*, 1995; Mann and Smuts, 1998, 1999; Gubbins *et al.*, 1999). Because this pattern of increasing independence is found in most mammalian species (Gubbins *et al.*, 1999), it is also likely to explain the results of observations made on common dolphin calves.

- Escorting behaviour

The importance of close proximity between mothers and their young calves is further illustrated by the foraging behaviour of female spotted dolphins. Diet analyses conducted on the species suggested that lactating females restrain from feeding on squid, as this would involve deep dives and therefore separations from their calves, which are less proficient divers (Bernard and Hohn, 1989). For other cetacean species that mainly rely on deep-sea preys, changes in diet might not be possible. An efficient alternative to close proximity could then be to leave their calves at the surface with another member of the group that will provide care while mothers are feeding (Papastravrou *et al.*, 1989). This type of behaviour has proved to be used by sperm whales (Whitehead, 1996), and is usually referred to as allomaternal or escorting behaviour. Besides deep dives, other situations are likely to necessitate separations between mothers and calves. As discussed earlier, feeding aggregations could sometimes represent a threat for calves and it might be advantageous for females to rely on other individuals to look after their calves while they are feeding (Würsig, 1986; Evans, 1987). This behaviour has been reported for dusky dolphins (Würsig and Würsig, 1980), and killer whales (Haenel, 1986), and was observed on one occasion in this study. In this observation, the individual escorting the infant common dolphin was a juvenile. It would have been interesting to determine the sex of the juvenile animal as immature females are known to frequently occupy the role of escorts in other species (bottlenose dolphins: Mann and Smuts, 1998; killer whales: Haenel, 1986). Unfortunately, the possibility of identifying the sex of wild common dolphins is rather limited, as no obvious sexual dimorphism exists (Cawardine, 1995). This observation suggests that the use of escorting might enable mother common dolphins to separate from their calves without enduring the costs of leaving them unattended. However, because of the singularity of this event, no definite conclusion can be drawn and this observation remains anecdotal. All other occurrence of escorting recorded in this study is more likely to be representative of social behaviour rather than of a specific strategy used by mothers in order to be able to separate from their calves. The occurrence of escorting proved to significantly increase between newborns and older aged calves. As escorting implies separations between calves and their mothers, this increase in associations with non-mother dolphins is consistent with the increase in occurrence and frequency of separations, and is also likely to be related to changes in locomotor skills and independence. These associations could also play an important role in establishing social bonds with other members of the group. This increase in sociality is likely to explain the observations of juvenile common dolphins swimming with one another.

- Swimming position

The improvement of calves' swimming abilities demonstrated by the increase in frequency, distance and duration of separations across calf age classes could also be reflected by changes in the use made of 'echelon' and 'infant position'. In the present study, common dolphin calves of all age classes spent more time in echelon than in infant position. This observation is consistent with previous results obtained for bottlenose dolphin calves (Fellner, 2000).

'Echelon position' swimming appears to be highly beneficial for dolphin calves as it allows them to ride the pressure wave caused by the mother's body as she moves through the water (Norris and Prescott, 1961; Lang, 1966; Wells, 1991a). Wells (1991a) observed that bottlenose dolphin calves do not beat their tail as fast when swimming in 'echelon position' compared to what would be expected during high-speed travel. The hydrodynamic advantages of this position are likely to be similar to those involved in bow riding the pressure wave of moving vessels (Gubbins *et al*., 1999). By reducing the cost of swimming, 'echelon position' will enable calves to conserve energy (Norris and Prescott, 1961; Brodie, 1977; Prescott, 1977; Evans, 1987; Gubbins *et al*., 1999; Dearolf *et al*., 2000). Norris and Prescott (1961) suggested that 'echelon position' might also benefit young calves by allowing the coordination of their movements, breathing and diving with their mothers. Most studies conducted on bottlenose dolphin calves have shown that the percentage of time spent in 'echelon position' is very high at first but tend to decrease as a function of calf age (Tavolga and Essapian, 1957; Cockcroft and Ross, 1990; Wells, 1991a; Reid *et al*., 1995; Gubbins *et al*., 1999; Mann and Smuts, 1999; Keiko *et al*., 2003). Similar results were obtained in the present study: newborns and infants spent more time in 'echelon position' than juvenile common dolphins did. The use of 'echelon swimming' will be especially important during the first few months of life as it will aid swimming at a time when calves present the lowest levels of motor coordination (Cockcroft and Ross, 1990; Mann and Smuts, 1999). As calves grow older and gain greater locomotor skills, their ability to swim on their own will increase

(Cockcroft and Ross, 1990) and their reliance on ‘echelon position’ swimming will be lowered (Gubbins *et al*., 1999). The increase in calf size might also reduce the ability of mothers to carry calves in their pressure wave (Gubbins *et al*., 1999). Juvenile common dolphins still spent 32.4% of their time in echelon position, which is higher than the values reported for bottlenose dolphins. In fact, Mann and Smuts (1999) found that two month-old bottlenose dolphin calves only spent 10.6% (±11.4%) of their time in echelon position. This difference could be explained by the fact that focal follows were usually conducted while mother-calf pairs of common dolphins were bow riding, which may have an influence on calves’ swimming position. Nevertheless, the lower time spent in ‘echelon position’ by juveniles compared to younger aged calves is likely to represent their lower dependence on ‘echelon swimming’.

Changes in the percentage of time spent in ‘infant position’ have also been related to the improvement of locomotor skills; as such a position implies that calves are able to remain underneath their mothers (Mann and Smuts, 1999). Bottlenose dolphin calves have been reported to spend more time in ‘infant position’ as they age (Tavolga and Essapian, 1957; Cockcroft and Ross, 1990; Reid *et al*., 1995; Gubbins *et al*., 1999; Mann and Smuts, 1999; Keiko *et al*., 2003). Although the data collected in this study tend to show a slight increase in the mean percentage of time spent in ‘infant position’ by common dolphin calves of different age classes, the results of the statistical analyses did not allow any definitive conclusions. Nevertheless, juvenile common dolphins were more likely to be observed in ‘infant position’ than infants, which suggest that higher use of this position may be made by older aged calves. Such a pattern remains to be confirmed. The mean percentages of time spent in ‘infant position’ obtained in this study appear to be relatively low when compared to the values reported for bottlenose dolphin calves (Mann and Smuts, 1999), and these results could be related to a lower occurrence of infant position swimming while the dolphins are bow riding. Mann and Smuts (1999) suggested that ‘infant position’ swimming facilitates nursing and would explain the switch to infant position operated by young calves as soon as motor coordination has improved. Yet, an increase in time spent in ‘infant position’ does not automatically imply an increase in nursing. The percentage of time spent in ‘infant position’ is known to gradually increase over at least the first year of life (Reid *et al*., 1995; Gubbins *et al*., 1999; Keiko *et al*., 2003), a period over which both the rate and bout duration of nursing events have shown to decrease (McBride and Kritzler, 1951;

Cockcroft and Ross, 1990; Reid *et al*., 1995; Nordensten *et al*., 2003). It seems likely that 'infant position' swimming also involves other advantages for older aged calves, and could potentially represent an efficient alternative to 'echelon position' swimming when the size of calves prevents them from being carried in their mothers' pressure wave. The hydrodynamic benefits of 'infant swimming' remain to be investigated (Mann and Smuts, 1999).

- Breathing synchrony

Synchrony also appears to be an important component of mother-calf relationships during the newborn period, and has been investigated in bottlenose dolphins using observations of mothers and calves surfacing in perfect unison (Cockcroft and Ross, 1990; Peddemors, 1990; Mann and Smuts, 1999). These studies found a decline in the proportion of synchronous breaths as a function of calves' age (Cockcroft and Ross, 1990; Peddemors, 1990; Mann and Smuts, 1999). The same approach was utilised in the present study and resulted in similar observations. The mean proportion of synchronous breaths appeared to be lower for juveniles than for younger aged calves, and the frequency of this behaviour showed a consistent decrease across the different age classes. The decline in synchronous breaths has previously been related to an improvement in motor coordination (Peddemors, 1990; Mann and Smuts, 1999). This is further supported by the tendency of an increasing proportion in calves' solitary surfacing between infants and juvenile common dolphins. The frequency of solitary breaths also appeared to be significantly higher for juveniles than for infants. For newborn and infant common dolphins, the frequency of synchronous breaths with their mothers was found to be higher than the frequency of solitary surfacing, emphasising the importance of synchrony for these two age classes. The opposite pattern was observed for juveniles, with a mean frequency of 4.9 synchronous breaths per five-minute interval, compared to mean frequency of 8.5 solitary breaths over the same time interval. The proportion and frequency of overlapping surfacing were also assessed but did not appear to vary across the different age classes. The results obtained in this study suggest that synchrony is particularly important for common dolphin calves of young age. Synchrony between mother dolphins and their calves has been suggested to serve different functions such as, energy conservation, predator avoidance, social learning, and better swimming control (Fellner, 2000). All these factors have previously been identified as playing an important role in the survival of newborn calves and are likely to explain the higher levels of synchrony observed in newborn common dolphins, as well as the decrease observed across the different age categories.

- Dive time:

As dolphin calves appear to better negotiate their environment due to enhanced locomotor skills as they grow older, an improvement in their diving ability would also be expected. An increase in dive time with older aged calves was demonstrated for common dolphins in this study. In fact, the mean dive time was 12.7 seconds for newborn common dolphins, 18.6 seconds for infants, and 26.6 seconds for juveniles. A similar increase has previously been reported for captive bottlenose dolphin calves (Cockcroft and Ross, 1990) and southern right whales (Thomas and Taber, 1984). Mothers' dive times were also monitored and were found to be significantly higher than those of calves. This observation emphasises the calves' lower ability to remain underwater for long periods of time compared to adult individuals. Although the difference between mothers' and calves' dive times seemed to increase across the different calf categories, statistical analyses did not reveal any significant variations. The fact that calves usually take more breaths than mothers has been observed in bottlenose dolphins (McBride and Kritzler, 1951; Würsig, 1978; Mann and Smuts, 1999), grey whales (Norris *et al.*, 1977), and sperm whales (Whitehead, 1996). It also appeared that mothers' dive time was affected by the age class of their young and mothers of juvenile common dolphins showed greater time between breaths than mothers of newborns or of infants did. Such a pattern does not seem to have been investigated for other cetacean species. Mothers' diving ability could be lowered by the high energetic costs they endure in the weeks following birth, and would gradually recover as calves dependence on their nursing and care diminishes. Considering the importance of synchrony for newborn calves, it seems more likely that mothers will decrease their breathing frequency in order to allow their young calves to coordinate their movements with theirs. Mothers would then increase their dive time as a function of their calves' diving progress. Monitoring mothers' dive time while they are separated from their calves may enable further investigatiom this hypothesis.

- Nursing:

In the course of their development, dolphin calves will acquire the necessary foraging skills that will allow them to catch prey and to become less dependent on their mothers for food (Oftedal, 1997). This process is in part reflected by the changes in nursing patterns, and research conducted on bottlenose dolphin calves in captivity have shown that both the rate and bout duration of nursing events tend to decrease as a function of calf age (McBride and Kritzler, 1951; Cockcroft and Ross, 1990; Reid *et al.*, 1995; Nordensten *et al.*, 2003). Transfer of milk between mothers and calves appears to be difficult to observe in cetaceans and nursing is usually inferred from the position of the calf, with its rostrum pressed against the mother's mammary slit (Whitehead and Mann, 2000). Although the data collected in this study showed a decrease in the percentage of observations of nursing position across the different calf age classes, this pattern did not prove to be statistically significant. This result is likely to be related to the fact that nursing position was only observed in 4% of all focal follows conducted in this study. The low occurrence of observations of nursing position could be related to the fact that female common dolphins may only rarely suckle their young while bow riding. It also appears possible that the duration of focal follows might not have been long enough to accurately represent the occurrence of nursing position in common dolphin calves. Although the nursing rate of common dolphins is likely to follow the general pattern of a decrease with age observed in other species, obtaining exact data on the subject may allow identification of patterns that are specific to the species, as well as to determine weaning age. Unfortunately, this kind of information may prove difficult to obtain on wild populations of common dolphins.

4.2. Foetal folds

The presence of foetal folds on common dolphin calves of different age classes was also investigated in this study. Because foetal folds result from the folded posture of the foetus as it lies in the uterus (McBride and Kritzler, 1951), they are particularly visible on newborn calves and have been described as a predominant feature of their physical appearance in the weeks following birth (McBride and Kritzler, 1951; Mann and Smuts, 1999). They gradually disappear as calves grow older and are rarely observed on bottlenose dolphin calves over three months of age (Cockcroft and Ross, 1990; Mann and Smuts, 1999). Foetal folds were observed on 60% of common dolphin newborn calves subject to focal follows, and only on 14% of infants and 11% of juveniles. The decrease observed between newborns and older aged calves proved to be significant, which is consistent with the results reported for bottlenose dolphins. As 40% of newborns did not have foetal folds, the observations made in this study suggest that a rather large proportion of common dolphins are born without these marks. The presence of distinguishable white markings, remains of foetal folds, on some adults also suggests that their presence on certain individuals may extend beyond the first year after birth. Mann and Smuts (1999) suggested that individual differences and eventually the health of the animals could have an influence on the visibility of foetal folds on bottlenose dolphin calves. Cockcroft and Ross (1990) recommended that foetal folds should not be included in the definition of newborn bottlenose dolphins, as the great variation of their presence on calves may lead to biased results. Although the occurrence of foetal folds showed a decrease across the different calf types, the observations made in this study supports this recommendation and suggest that foetal folds may not always be an accurate criterion to distinguish newborn common dolphins from older aged calves.

4.3. Other calves' behavioural characteristics

Besides the behaviours typically recorded during focal follows of mother-calf pairs, calves sometimes executed displays that are worth discussing. The observation of an infant common dolphin consistently rolling belly up under its presumed mother throughout the focal follow raises the question of a possible mounting attempt. Young male bottlenose dolphins are known to be sexually precocious and often engage in sexual activity with older individuals, including their mothers (McBride and Kritzler, 1951; Caldwell and Caldwell, 1972; Schroeder, 1990; Mann and Smuts, 1999). Similar observations have been recorded for young male killer whales (Haenel, 1986). It would have been interesting to identify the sex of the infant common dolphin involved in this observation, but unfortunately it did not prove possible. Even though no conclusion can be drawn from this event, it suggests that early socio-sexual behaviours may occur in common dolphins. Following observations of sexual behaviours displayed by young bottlenose dolphin calves before the attainment of sexual maturity, Wells *et al.* (1987) suggested that these behaviours are likely to play an important role in the social lives of the animals. It could indeed represent the process by which male calves learn sexual patterns (Caldwell and Caldwell, 1972).

A behaviour observed more consistently in the course of this study involved calves darting away and back from the presumed mother, and rapidly swimming around her. Similar behavioural patterns have been reported for spinner dolphin calves (Johnson and Norris, 1994) but no explanations were proposed. It could be suggested that these behaviours may be representative of calves' urge to explore the environment, combined with the need to remain in close proximity with their mothers.

Finally, some of the behaviours that have been reported for calves in other species were never observed in common dolphins. It has been reported that by three weeks of age, bottlenose dolphin calves will display a diverse repertoire of behaviours including chin slaps, spy hops, jaw claps, belly slaps, playful chases with other infants and exchange of objects (Connor *et al.*, 2000). Johnson and Norris (1994) also reported that spinner dolphin calves are usually the most active members of the group. Besides the occasional reciprocal chases between juvenile common dolphins, none of the other behaviours were observed to be displayed by common dolphin calves. As the search for common dolphins mainly relied on signs of feeding activities, common dolphin groups were seen feeding in most encounters, a context which might not be appropriate for the occurrence of displaying. On the other hand, socialising, which is defined as dolphins being involved in surface behaviours (Shane, 1990a), was only observed in 4% of all encounters. The rarity of calves' displays in common dolphins could also be explained by the fact that displaying may not be common in this particular species. In fact, adult common dolphins were rarely seen engaged in surface behaviours. The observations of common dolphins in a wider variety of context may help to clarify this issue.

5) **Research platform**

In the present study, all observations were made from onboard the commercial tourist boat 'Dolphin Explorer'. The use of 'Dolphin Explorer' as a research platform proved to have both advantages and disadvantages in the collection of the data required for this particular research project.

Due to the size and stability of ‘Dolphin Explorer’, trips took place in most weather and therefore on most days of the study period, offering the opportunity to observe the animals regularly on a year-round basis. This is particularly important when investigating seasonal variations, as was the case in this study. The elevation of ‘Dolphin Explorer’ above sea level provided enhanced visibility of the surroundings, which facilitated the location of the animals over great distances. This elevation, combined with the presence of experienced crew continuously scanning the area, resulted in a relatively high success rate in finding the animals. Common dolphins were sighted on more than 80% of the trips conducted onboard the vessel, resulting in a total of 348 encounters over the 14 months of this study. Group follows were conducted on 320 of these encounters, which represents a relatively large sample that may not have been possible to obtain from another platform. When ‘Dolphin Explorer’ was with a group of dolphins, the elevation of the vessel also offered a broader view of the group, which represented an advantage in determining group composition. The construction of the boat, and especially the presence of two hulls, also proved to offer a great opportunity to view large numbers of dolphins bow riding and to closely follow their behaviours, including those of mother-calf pairs. For these different reasons, ‘Dolphin Explorer’ represented a beneficial research platform from which to conduct this project.

However, certain aspects of this study could have been improved by utilising a different research platform. Firstly, the use of a large boat such as ‘Dolphin Explorer’ appears to offer limited manoeuvrability around the dolphins, and therefore reduces the possibility of approaching a mother-calf pair. Although ‘Dolphin Explorer’ could be positioned in the direction of mother-calf pairs, focal follows could only be conducted accurately if they approached the boat at close distances. This resulted in focal follows of rather short duration, and mostly involving bow riding. The influence of bow riding on mother-calf relationships cannot be neglected and has been raised for some of the results obtained in this study. The use of a smaller boat may have allowed the researcher to remain with mother-calf pairs for longer periods of time, and to observe them in different contexts. Secondly, due to the commercial scope of the trips conducted by ‘Dolphin Explorer’, common dolphin groups that offered better sighting opportunities for passengers were usually favoured, resulting in a shorter viewing time for certain groups. Areas of greater sighting opportunities were also favoured. The use of an independent research vessel might have allowed the researcher to spend more time with groups that were considered of interest for the present study, and to explore other parts of the Hauraki Gulf such as its shallow regions. Thirdly, the search pattern used by the crew of ‘Dolphin Explorer’ in order to find common dolphins lead to their frequent observation in a feeding context. Observations of mother-calf pairs in a wider variety of other situations would have been interesting and may have been possible from a different platform. Finally, the potential impact of the boat on the dolphins’ behaviour cannot be discounted.

Although the use of a different research platform could have been advantageous in different ways, especially regarding focal follows of mother-calf pairs, the observations conducted from ‘Dolphin Explorer’ resulted in sufficient data to reliably test most of the hypotheses investigated in this study.

6) Summary

Many of the variables used to characterise common dolphin groups have proved to vary according to the age class of the youngest member of the group. The specific features of groups containing newborns discussed in this chapter have proved to represent conditions identified as favourable for the survival and growth of young calves in other species, and are likely to serve the same purpose for common dolphins. The advantages of warmer waters for mothers and their newborn calves, through thermoregulation and higher food availability, are likely to have lead the common dolphins of the Hauraki Gulf to mainly give birth during late spring and early summer. The peak in sightings of newborns calves did not appear to correspond to a peak in sexual activity. Although water depth did not prove to be affected by group type, observations of common dolphin groups with newborns and infants under depths of 20 metres suggest the potential advantages of shallow waters for these groups. The oceanographic conditions of Hauraki Gulf are likely to be highly beneficial for common dolphins, and due to the high percentage of groups with calves, this area is likely to represent an important calving ground for the species.

The changes in social and behavioural organisation across the different group types are also likely to reflect the importance of certain conditions in calves’ development. Groups of common dolphins with newborn calves were found in larger groups, which may benefit mother-calf pairs in many ways, including enhanced protection against predators and greater feeding opportunities. Similar benefits may also lead mother-calf pairs of common dolphins to associate with one another within groups. The high occurrence of groups with newborns involved in feeding activities and associated with other species, suggests that feeding aggregations may be highly important in teaching the calves to hunt prey. Nevertheless, certain observations also suggest that not all of these aggregations might be safe for calves. The greater distances to the boat kept by mothers and their newborn calves suggests that the boat could represent a threat during the period of high vulnerability for the calves.

The changes observed in all aspects of mother-calf relationships across the different age classes are likely to reflect the high dependence of newborn common dolphins on their mothers, as well as the improvement of their locomotor skills and the gradual gain in independence of older aged calves. Although the occurrence of foetal folds decrease with older aged calves, the variations observed led to the recommendation of their exclusion as a criteria to distinguish newborns from older calves. Anectodal observations made in this study, along with previous reports in different species, suggested early socio-sexuality in common dolphin calves. The rarity of displaying by common dolphin calves distinguish them from other species, and may be due to a specific characteristic of the species or to the context of observations made in this study.

After discussing the advantages and disadvantages of the use of a commercial tourist boat ‘Dolphin Explorer’ as a research platform in this study, it appeared that its use involves limitations for the collection of data on mother-calf pairs, but overall allowed testing of the hypotheses investigated in this study.

Chapter 6: CONCLUSION

The structure of this chapter is summarised in figure 11.

1) Summary

This study was the first to focus on female reproductive strategies and mother-calf relationships in common dolphins. Its main objective was to contribute to the understanding of the reproductive ecology of the species through the investigation of four general research questions outlined in the introduction chapter. The data collected during field observations in the Hauraki Gulf have provided answers to each of these questions as follows:

1) Do the common dolphins in the Hauraki Gulf display reproductive seasonality?

This question was addressed by investigating both breeding and mating seasonality of the common dolphins found in the Hauraki Gulf. The existence of a breeding season was assessed through seasonal variations in sightings of groups containing newborn calves. The results of this study showed that common dolphins breed seasonally, as 82.9% of groups with newborns were sighted during spring and summer, with particularly high occurrence in the months of December and January. The existence of a mating season was assessed through seasonal variations in occurrence of mating behaviours. Although observations of these behaviours differed between seasons, these variations did not relate to the peak in sightings of newborn calves. The breeding seasonality displayed by the common dolphins that inhabit the Hauraki Gulf can be explained by the variations in environmental conditions that are fundamental for calves' survival.

2) What are the specific characteristics of common dolphin groups containing calves?

In order to answer this question, groups of common dolphins categorised according to the age class of their youngest member were examined in relation to a series of criteria including water temperatures and water depths, the number of animals in the groups,

Figure 11. Structure diagram of the 'Conclusion' chapter.

their behavioural state, their associations with other species, and their reaction to the boat. As a result of this examination, the following conclusions can be drawn:

● Common dolphin groups with newborns were found in water temperatures higher than groups with infants or groups made up of only adults. Warmer waters are likely to increase the survival of young calves through thermoregulation and higher food availability; factors that are also likely to explain breeding seasonality.

● All group types were found in similar water depths. This result is inconsistent with the fact that all other cetacean species studied to date have been found to extensively use shallower waters when accompanied by young calves, most probably as a strategy to avoid predators. This study suggests that such strategy may not be efficient for a pelagic species such as the common dolphin. However, on the occasions where groups of common dolphins were sighted under 20 metres of depth, the fact that they always included either newborns or infants suggests that there may be potential advantages of this habitat for mothers and their young calves.

● Groups containing newborn calves were found to be larger than any other group types, with a mean of 35.75 dolphins per group. Large groups have been identified to decrease the risk of predation and to enhance feeding efficiency, which are likely to be advantageous for mother-calf pairs during the newborn period.

● The activity budget of the different group types was found to be similar. The observation of small calves involved in feeding activities suggests the importance of learning the hunting process at a young age. However, groups with newborns were only seen associated with whales and birds in 5% of all encounters, suggesting that mothers may stay clear of certain feeding aggregations when they have newborn calves.

● The reaction of the dolphins to the boat, as well as the minimum distance to the boat, was not different according to group type. However, when considering mother-calf pairs individually, it appeared that the minimum distance to the boat was the greatest for mothers and their newborn calves, and consistently decreased with the age of the calves considered. These results may represent the protective behaviour of mothers towards their calves, especially in the first few months following birth, in a situation that is perceived as threatening by mothers.

The results obtained in this study have shown that some of the variables that characterise groups of common dolphins vary according to the age class of the youngest member in the group. These variations are likely to reflect the high vulnerability of newborn calves and the strategies used by the mothers in order to increase their survival.

3) What is the role of the Hauraki Gulf for female common dolphins?

This question was investigated by two means. Firstly, the proportion of groups that contained calves was considered and comparisons with other populations of common dolphins were attempted. Only a minority of common dolphin groups encountered in the Hauraki Gulf contained only adult individuals, and 82.5% of the groups were accompanied by at least one calf. The youngest member of the group was a newborn in 16.7% of the groups, an infant in 40.8% of the groups and a juvenile in 19.6% of the groups. These percentages are much higher than what has previously been reported for the population of common dolphins found in the Alboràn Sea. Secondly, the oceanographic characteristics of the Hauraki Gulf were compared to those of other areas that have been identified as important breeding and calving ground for cetaceans. The Hauraki Gulf appears to provide common dolphins with a calm sea area, little variation in the characteristics of the water, including water temperature, and great feeding opportunities, which have all proved to play a significant role in calves' survival in previous studies. These results suggest that the Hauraki Gulf is an important calving ground for common dolphins.

4) What are the behavioural patterns that describe the relationships between calves of different age and their mothers?

In order to investigate the evolution of mother-calf relationships in common dolphins, calves belonging to different age categories were compared on several aspects of their behaviours including, separations from the mother, associations with non-mother dolphins, swimming position, breathing patterns, dive time, and nursing position.

Older aged calves separated from their mothers more frequently, over greater distances and over longer periods of time. They were also more likely to associate with other dolphins than younger calves were. Juvenile common dolphins spent less time in 'echelon position' than newborns or infants did, and were also more likely to be seen swimming underneath their mothers than infants were. Younger calves presented the larger proportion of synchronous breaths with their mothers, and the smallest proportion of solitary breaths. They also spent less time under water than older aged calves. Mothers of juveniles were found to have greater dive times than mothers of newborns or infants. Finally, the analysis of nursing position did not appear to provide reliable results due to the rarity of observations of this behaviour. All of the behaviours characterising mother-calf relationships changed as a function of the age category of the calves considered, reflecting the improvement of calves' motor skills, allowing them to gradually gain more independence from their mothers.

2) Limitations and significance

This study has been limited by a series of factors that must be outlined in order to appreciate the significance of the results obtained. For example, the fact that common dolphins in the Hauraki Gulf inhabit shallower waters than other populations worldwide needs to be considered. As the habitat occupied by a species is likely to influence its behaviour, the hypothesis that common dolphins, and more specifically mother-calf pairs, found in offshore waters may behave differently cannot be rejected. Therefore, the conclusions drawn in this study only apply to common dolphins in the Hauraki Gulf and should not be considered in this context.

Previous studies conducted on mother-calf relationships in bottlenose dolphins have all taken place in a controlled environment, either in captivity (McBride and Kritzler, 1951; Cockcroft and Ross, 1990; Peddemors, 1990; Reid *et al*., 1995; Gubbins *et al*., 1999; Nordensten *et al*., 2003), or in areas where dolphins are provisioned (Mann and Smuts, 1998, 1999; Mann *et al*., 2000). As these environments provide easy access to the dolphins for extended periods of time, they offer greater opportunities to observe behaviours that cannot be monitored with wild populations. Mann and Smuts (1999, p.555) acknowledged the fact that 'in the absence of the provisioning area, comparable data on newborns would have taken many years to obtain'. Although the common dolphins found in the Hauraki Gulf inhabit relatively shallow waters for the species, the conditions for observations are still rather challenging compared to that of controlled habitats. These conditions, combined with the fast movements that characterise common dolphins, limited the possibility to observe mother-calf pairs for extended periods of time and resulted in short focal follows. The fact that this study was conducted from a commercial tourist boat has also contributed to the short amount of time spent with each mother-calf pair.

Conducting observations from a boat also obliges the researcher to consider its potential impact on the animals. In the present study, mothers and their newborn calves were less likely to approach the boat at close distances, which resulted in a small number of focal follows conducted on newborn common dolphins, compared to the sample size obtained for juveniles and infants.

The controlled environments in which mother-calf pairs of bottlenose dolphins have been observed have also enabled focal follows on the same individuals over time, and therefore the witness of the growth of calves and the ability to obtain longitudinal data. These types of data are likely to be the most reliable and efficient approach to the study of mother-calf relationships, as they allow the researcher to consider individuals' differences (Martin and Bateson, 1993). In the present study, longitudinal data could not be collected. In fact, the population of common dolphins in the Hauraki Gulf is likely to contain a few hundred individuals and the chances of resighting the same female with her calf over the time frame of this study were relatively low. Therefore, each focal follow conducted in this study is likely to represent a different mother-calf pair.

Nevertheless, captivity and provisioned areas also involve disadvantages in the study of mother-calf relationships. Both environments have proved to have an impact on the dolphins' behaviours (Cockcroft and Ross, 1990; Mann and Smuts, 1999; Mann *et al.*, 2000), and Mann and Smuts (1999) indicated that calves of provisioned females experience greater mortality than calves of non-provisioned females. Limiting studies to captive and provisoned animals also highly restricts the range of species that can be investigated. The results obtained for common dolphins suggest that an alternative to longitudinal data on a small number of calves could be to focus on obtaining cross-sectional observations for a larger sample. In fact, the present study has provided significant results, similar to what had previously been obtained for bottlenose dolphins, and therefore show that studying mother-calf relationships in wild populations of dolphins can be achieved. Such a conclusion has great implications for future studies to take place.

This study contributes to a better understanding of common dolphins in many ways. In fact, it provides information on a topic never investigated before for the species, and in which our knowledge has been highly restricted to bottlenose dolphins. More specifically, this study specifies the conditions that appear to be of great importance for the survival of common dolphin calves, as well as the behaviours that characterise the period of high vulnerability. Considering the fundamental role that mothers play in sustaining dolphin societies, this type of information is crucial in protecting the population as a whole.

By increasing our understanding of the habitat use made by female common dolphins and their calves, the results of this study have also lead to a better appreciation of the potential effects of different threats. The Hauraki Gulf is under the influence of the ever-growing city of Auckland. Considering the importance of the Hauraki Gulf for common dolphins demonstrated in this study, an increase in pollution, commercial fisheries, tourist operations, and the number of recreational boats, could potentially impact the welfare of this population.

This study also provides baseline data on common dolphins' breeding patterns that will enable future assessment of the potential effect of changes in their habitat. Baseline data have been identified as particularly useful in assessing the impact of ecotourism on dolphins (Bejder and Dawson, 1999; Constantine, 1999). 'Dolphin Explorer' is presently the only commercial operator offering 'swim with' and dolphin watching trips out of Auckland, but further commercial permits are likely to be issued in the years to come. The information gathered in this study will allow the investigation of the impact of a growing number of commercial and recreational boats in the area.

3) Future research

Considering that the collection of longitudinal data on a species that forms large populations such as the common dolphin is highly improbable, future research should concentrate on obtaining focal follows of longer duration and for higher numbers of calves. Increasing the strength of the sample would increase confidence in the results obtained in this study.

Observations made in this study suggested that shallow waters could potentially be advantageous for mother-calf pairs, but these observations were too rare to draw any conclusion. Therefore, a focus should also be made on investigating the shallow parts of the Hauraki Gulf, especially during the summer time, in order to assess the exact use made of these areas by mothers and their calves.

The distribution of mother-calf pairs within common dolphin groups could not be investigated in detail in this study. The frequent associations observed between these pairs require further attention. Such an approach would also allow a better description of the position of mother-calf pairs within feeding aggregations and therefore to allow greater understanding of their dynamics.

As most common dolphin groups observed in the present study were involved in feeding activities, efforts shoud also be made to record the behaviour of mother-calf pairs in a wider variety of contexts. Such observations would allow the investigation of whether the activity budget of common dolphins varies with group type, but also to eventually witness different behaviours displayed by calves.

The population of common dolphins in the Hauraki Gulf seems appropriate as a site to expand our knowledge on mother-calf relationships in the species, and the use of a different research platform is likely to enable such studies to take place. However, future research should also be undertaken on other populations of common dolphins around the coast of New Zealand, in order to assess the proportion of calves in other areas and therefore to better understand the role of the Hauraki Gulf for the species.

Finally, the use of cross-sectional data to investigate mother-calf relationships should be considered for other populations of common dolphins, as well as other species of cetaceans worldwide. In fact, this kind of study would allow us to increase our knowledge on the population dynamics of a wide range of species, and enhance our understanding of cetacean societies as a whole.

4) Management recommendations

In light of the results obtained from this study, a number of different recommendations can be made which could enhance the conservation of the species.

Firstly, considering the high proportion of common dolphin groups containing calves in the Hauraki Gulf, decisions regarding the development of dolphin-based tourism in the area should take into account the implications of these findings. For example, the potential impact of additional marine mammal tourism operations could have on the population of common dolphins in the Hauraki Gulf should be assessed before further permits are issued. Due to the small number of groups without calves, no further ‘swim with the dolphins’ permits should be issued for the Hauraki Gulf, as it could significantly increase the pressure exerted on these groups.

Secondly, accurate definitions of calves should be used within the Marine Mammals Protection Regulations, especially in the frame of ‘swim with dolphins’ operations. The term ‘juvenile’ contained by these regulations should be clarified by stipulating that a juvenile dolphin is identified as any individual smaller than the one it accompanies. Considering the high vulnerability of young common dolphin calves demonstrated in this study, the misinterpretation of these regulations (which currently offer no definition for ‘juvenile’) is likely to have detrimental consequences for the dolphins.

Thirdly, considering that mothers and their newborn calves kept the greatest distance to the boat, specific guidelines regarding approaches towards groups containing newborn calves should be included in the regulations. The use of ‘best endeavours to operate vessels, vehicles and aircraft so as not to disrupt the normal behaviour of any marine mammal’ (Appendix 1) should be emphasised for this type of group. Within groups of dolphins that contain newborn calves, individual mother-calf pairs should not be approached intentionally; this fact should also be integrated into these regulations.

Fourthly, efforts should be made to educate the public on the Marine Mammals Protection Regulations. The waters of the Hauraki Gulf are frequently visited by numerous recreational boats which are likely to encounter common dolphins on their journey. Due to the vulnerability of young calves, boat owners should be made aware of the risks of boat mishandling and swimming around groups of dolphins containing small calves.

5) Conclusion

In conclusion, answering the four general research questions set at the beginning of this thesis has lead to a significant increase in our understanding of common dolphins' reproductive ecology. This study has resulted in an improved appreciation of the importance of the strategies used by female common dolphins in order to protect their young, and the role we, in turn, can take to ensure their survival.

This study has also emphasised that the study of mother-calf relationships in wild populations of pelagic delphinids is indeed possible. Consequently, it has demonstrated the additional opportunity to enhance our understanding of cetacean societies in the years to come.

Considering the time frame of this study and the challenges represented by both the species and the research platform used, the results obtained represent an important advancement in our knowledge of common dolphins, and hopefully provides an inspiration for future studies.

REFERENCES

Alcock, J. (1998). The evolution of mating systems. In P. Farley (Ed.), *Animal Behavior* (6th ed.) (pp. 483-521). Massachusetts: Sinauer Associates.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *49*, 227-267.

Alzieu, C., Duguy, R., and Babin, P. (1982). Delphinidae pathology : Fetal and neonatal contamination by PCB's cutaneous ulcerative lesions. *Revue des Travaux de l'Institut des Pêches Maritimes, Nantes*, *46*, 157-166.

Anderson, S. (1969). Epimeletic behavior in a captive harbour porpoise, *Phocaena phocaena*. In G. Pilleri (Ed.), *Investigation on Cetacea*, *Vol. 1* (pp. 203-205). Berne: Braine Anatomy Institute.

Asdell, S.A. (1964). *Patterns of mammalian reproduction*. London: Cornell University Press, Constable & Co Ltd.

Au, D. W. K., and Perryman, W.L. (1985). Dolphin habitats in the Eastern Tropical Pacific. *Fishery Bulletin*, *83*, 623-644.

Baillie, J., and Groombridge, B. (1996). *1996 IUCN Red List of Threatened Animals*. Gland, Switzerland: International Union for the Conservation of Nature and Natural resources.

Banks, R. C., and Brownell, R.L. (1969). Taxonomy of the common dolphins of the Eastern Pacific Ocean. *Journal of Mammalogy*, *50*, 262-271.

Barabash, I.I. (1935). *Delphinus delphis ponticus* subsp. n. Bull (in Russian). *Moskovskogo Obshchestva Ispytateley Prirody (Biological Division)*, *44*, 246-249.

Barros, N.B., and Odell, D.K. (1990). Food habits of bottlenose dolphins in the Southeastern United States. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 309-328). San Diego: Academic Press.

Bart, J., Fligner, M.A., and Notz, W.I. (1998). *Sampling and statistical methods for behavioral ecologists*. Cambridge: Cambridge University Press.

Bearzi, G. (2003). *Delphinus delphis (Mediterranean subpopulation)*, *2003 IUCN Red List of Threatened Species*. Retrieved March 15, 2004 from the World Wide Web: http://www.redlist.org/

Bearzi, G., and Notarbartolo di Sciara, G. (1995). A comparison of the present occurrence of bottlenose dolphins, *Tursiops truncatus*, and common dolphins, *Delphinus delphis*, in the Kvarneric (Northern Adriatic Sea). *Annales (Annals for Istrian and Mediterranean Studies)*, *7*, 650-668.

Bearzi, G., Notarbartolo di Sciara, G., and Politi, E. (1997). Social ecology of bottlenose dolphins in the Kvarneric (Northern Adriatic Sea). *Marine Mammal Science*, *13***,** 650-668.

Bearzi, G., Reeves, R.R., Notarbartolo di Sciara, G., Politi, E., Cañadas, A., Frantzis, A., and Mussi, B. (2003). Ecology, status and conservation of short beaked common dolphins *Delphinus delphis* in the Mediterranean Sea. *Mammal Review*, *33*, 224-252.

Bejder, L. 1997. *Behaviour, ecology and impact of tourism on Hector's dolphins (Cephalorhynchus hectori) in Porpoise Bay, New Zealand*. Master's thesis, University of Otago, Otago, New Zealand.

Bejder, L., Dawson, S.M., and Harraway, J.A. (1999). Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science*, *15*, 738-750.

Bel'kovich, V.M. (1991). Herd structure, hunting, and play: Bottlenose dolphins in the Black Sea. In K. Pryor and K. Norris (Eds.), *Dolphin Societies: Discoveries and Puzzles* (pp.17-78). Berkeley: University of California Press.

Bercusson, L. (1999). *The Hauraki Gulf: From Bream Head to Cape Colville*. Auckland: Shoal Bay Press.

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

Black, K. P., Bell, R.G., Oldman, J.W., Carter, G.S., and Hume, T.M. (2000). Features of 3-dimensional barotropic and baroclinic circulation in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *34*, 1-28.

Bonner, W.N. (1984). Lactation strategies in pinnipeds: problems for a marine mammalian group. *Symposium of the Zoological Society of London*, *51*, 253-272.

Boyd, I.L. (1991). Environmental and physiological factors controlling the reproductive cycles of pinnipeds. *Canadian Journal of Zoology*, *69*, 1135-1148.

Bräger, S., and Schneider, K. (1998). Near-shore distribution and abundance of dolphins along the West Coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *32*, 105-112.

Bräger, S., Harraway, J.A., and Manly, B.F. (2003). Habitat selection in a coastal dolphin species (*Cephalorhynchus hectori*). *Marine Biology*, *143*, 233-244.

Brodie, P.F. (1969). Duration of lactation in Cetacea: An indicator of required learning? *American Midland Naturalist*, *82*, 312-314.

Brodie, P.F. (1977). Form, function and energetics of cetacea: A discussion. In R.J. Harrison (Ed.), *Functional anatomy of marine mammals* (pp. 45-58). New York: Academic Press.

Bronson, F.H. (1989). *Mammalian reproductive biology*. Chicago: The University of Chicago Press.

Brown, D. H., and Norris, K.S. (1956). Observations of captive and wild cetaceans. *Journal of Mammalogy*, *37*, 311-326.

Brown, D.H., Caldwell, D.K., and Caldwell, M.C. (1966). Observations on the behavior of wild and captive false killer whales, with notes on associated behavior of other genera of captive delphinids. *Los Angeles City, Museum of Natural History, Contributions to Science*, *95*, 1-32.

Brown, M., and Corkeron, P. (1995). Pod characteristics of migrating humpback whales (*Megaptera novaeangliae*) off the East Australian Coast. *Behaviour*, *132*, 163-179.

Bryden, M.M. (1972). Growth and development of marine mammals. In R.J. Harrison (Ed.), *Functional anatomy of marine mammals* (pp.1-79). London: Academic Press.

Bryden, M.M., and Harrison, R.J. (1986). Gonads and reproduction. In M.M. Bryden and R.J. Harrison (Eds.), *Research on dolphins* (pp. 149-159). Oxford: Clarendon Press.

Caldwell, M.C., and Caldwell, D.K. (1972). Behavior of marine mammals. In S.H. Ridgway (Ed.), *Mammals of the sea: Biology and medicine* (pp 419-465). Springfield, IL: Charles C. Thomas.

Cañadas, A., Sagarminaga, R., and Garcia-Tiscar, S. (2002). Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. *Deep-Sea Research 1*, *49*, 2053-2073.

Carwardine, M. (1995). *Eyewitness Handbook: Whales, Dolphins and Porpoises.* London: Dorling Kindersley Limited.

Cipriano, F.W. (1992). *Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (Lagenorhynchus obscurus) off Kaikoura, New Zealand*. Doctoral dissertation, University of Arizona, Tucson, United States of America.

Cockcroft, V.G., and Ross, G.J.B. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 461-478). San Diego: Academic Press.

Cockcroft, V.G., and Peddemors, V.M. (1990). Seasonal distribution and density of common dolphins, *Delphinus delphis*, off the south-east coast of Southern Africa. *South African Journal of Marine Science*, *9*, 371-377.

Collet, A. (1981). *Biologie du dauphin commun, Delphinus delphis, en Atlantique Nord-Est*. Doctoral dissertation, University of Poitiers, France.

Collet, A., and Girons, H.S. (1984). Preliminary study of the male reproductive cycle in common dolphins, *Delphinus delphis*, in the Eastern North Atlantic. In W.F. Perrin, R. L. Brownell Jr and D.P. DeMaster (Eds.), *Reproduction in whales, dolphins and porpoises: Proceedings of the conference, Cetacean Reproduction, Estimating Parameters for Stock Assessment and Management, La Jolla, CA, 28 Nov. - 7 Dec. 1981* (pp. 355-360). Reports of the International Whaling Commission, special issue 6. Cambridge: International Whaling Commission.

Connor, R.C. (2000). Group living in whales and dolphins. In J. Mann, R. C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 199-218). Chicago: University of Chicago Press.

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

Connor, R. C., Smolker, R.A., and Richards, A.F. (1992b). Dolphin alliances and coalitions. In A.H. Harcourt and F. B. M. De Waal (Eds.), *Coalitions and alliances in humans and other animals* (pp. 415-443). Oxford: Oxford University Press.

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

Connor, R. C., Wells, R.S., Mann, J., and Read, A.J. (2000). The bottlenose dolphin: Social relationships in a fission-fusion society. In J. Mann, R. C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 91-126). Chicago: University of Chicago Press.

Constantine, R. (1995). *Monitoring the commercial swim-with-dolphin operations with the bottlenose (Tursiops truncatus) and common dolphins (Delphinus delphis) in the Bay of Islands, New Zealand.* Master's thesis, University of Auckland, New Zealand.

Constantine, R. (1999). *Effects of tourism on marine mammals in New Zealand*. Science for conservation, 106. New Zealand: Department of Conservation.

Constantine, R. (2002). *The behavioural ecology of the bottlenose dolphins (Tursiops truncatus) of Northeastern New Zealand: A population exposed to tourism*. Doctoral dissertation, University of Auckland, Auckland, New Zealand.

Constantine, R., Brunton, D.H., and Dennis, T. (2004). Dolphin watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. *Biological Conservation*, *117*, 299-307.

Corkeron, P.J. (1990). Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa edenis* in Moreton Bay, Australia. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 285-293). San Diego: Academic Press.

Cox, T.M., Read, A.J., Barco, S., Evans, J., Gannon, D.P., Koopman, H.N., Mc Lellan, W.A., Murray, K., Nicolas, J., Pabst, D.A., Potter, C.W., Swingle, W.M., Thayer, V.G., Touhey, K.M., and Westgate, A.J. (1998). Documenting the bycatch of harbor porpoises, *Phocoena phoconea*, in coastal gillnet fisheries from stranded carcasses. *Fishery Bulletin*, *96*, 727-734.

Dall, W.H. (1873). Description of three new species of Cetacea, from the coast of California. *Proceedings of the California Academy of Sciences*, *5*, 12-14.

Danil, K., and Chivers, S.J. (2003). Growth and reproduction of female short-beaked common dolphins, *Delphinus delphis*, in the eastern tropical Pacific. *Poster presented at the 15th Biennial Conference on the Biology of Marine Mammals. 14 – 19 December 2003, North Carolina, United States*.

Dawson, S.M. (1985). *The New Zealand whale and dolphin digest*. Auckland: Brick Row Publishing.

Dearolf, J.L., McLellan, W.A., Dillaman, R.M., Frierson Jr., D., and Pabst, D.A. (2000). Precocial development of axial locomotor muscle in bottlenose dolphins (*Tursiops truncatus*). *Journal of Morphology*, *244*, 203-215.

Defran, R.H., and Weller, D.W. (1999). The occurrence, distribution, and site fidelity of bottlenose dolphins (*Tursiops truncatus*) in San Diego, California. *Marine Mammal Science*, *15*, 366-380.

Department of Conservation (2002). *The Hauraki Gulf Marine Park*. DOC Fact Sheet. Auckland, New Zealand: Department of Conservation.

Doak, W. (1981). *Dolphin, dolphin*. Auckland: Hodder and Shoughton.

Doak, W. (1995). *Friends of the sea – solo dolphins in New Zealand and Australia*. Auckland: Hodder Moa Becket Publishing.

Dohl, T.P., Norris, K.S., and Kang, I. (1974). A porpoise hybrid *Tursiops x Steno*. *Journal of Mammalogy*, *55*, 217-221.

Dohl, T. P., Bonnell M.L., and Ford, R.G. (1986). Distribution and abundance of common dolphins, *Delphinus delphis*, in the southern California Bight: A quantitative assessment based upon aerial transect data. *Fishery Bulletin*, *84*, 333-343.

Dorsey, E.M., Richardson, W.J., and Würsig, B. (1989). Factors affecting surfacing, respiration, and dive behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea. *Canadian Journal of Zoology*, *67*, 7, 1801-1815.

Dudok van Heel, W.H., and Meyer, M.M. (1974). Birth in dolphins (*Tursiops truncatus*) in the Dolphinarium, Harderwijk, Netherlands. *Aquatic Mammals*, *2*, 2, 11-23.

Dudzinski, K. M. (1999). *An investigation of intraspecific behavior in bottlenose dolphins around Mikura Island* (Final JSPS Fellowship Report). Oxnard, California: Dolphin Communication Project.

Eisenberg, J.F. (1986). Dolphin behavior and cognition: Evolutionary and ecological aspects. In R.J. Shusterman, J.A. Thomas and F.G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 261-270). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Elwen, S.H., and Best, P.B. (2004a). Female southern right whales *Eubalaena australis*: Are there reproductive benefits associated with their coastal distribution off South Africa? *Marine Ecology Progress Series*, *269*, 289-295.

Elwen, S.H., and Best, P.B. (2004b). Environmental factors influencing the distribution of southern right whales (*Eubalaena australis*) on the southern coast of South Africa I: broad scale patterns. *Marine Mammal Science*, *20*, 3, in press.

Ersts, P. J., and Rosenbaum, H.C. (2003). Habitat preference reflects social organization of humpback whales (*Megaptera novaeangliae*) on a wintering ground. *Journal of Zoology, London*, *260*, 337-345.

Essapian, F. S. (1962). Courtship in captive saddle-backed porpoises, *Delphinus delphis*. *Zeirschrift fur Saugetierkunde*, *27*, 211-217.

Evans, P. G. H. (1980). Cetaceans in British waters. *Mammal Review*, *10*, 1-52.

Evans, P.G.H. (1987). *The natural history of whales and dolphins*. London: Christopher Helm.

Evans, W.E. (1974). Radio-telemetric studies of two species of small odontocete cetaceans. In W.E. Schevill (Ed.), *The whale problem* (pp. 385-394). Cambridge, Massachusetts: Harvard University Press.

Evans, W.E. (1975). *Distribution, differentiation of populations, and other aspects of the natural history of Delphinus delphis Linnaeus in the northeastern Pacific*. Doctoral dissertation, University of California, Los Angeles, California.

Evans, W. E. (1994). Common dolphin, white-bellied porpoise, *Delphinus delphis* Linaeus, 1758. In S.H. Ridgway and R. Harrison (Eds.), *Handbook of marine mammals, Vol. 5: The first book of dolphins* (pp. 191-224). London: Academic Press.

Evans, W.E., and Bastian, J. (1969). Marine mammal communication: social and ecological factors. In H.T. Andersen (Ed.), *The biology of marine mammals* (pp. 425-475). New York and London: Academic Press.

Fairbanks, L. A. (1990). Reciprocal benefits of allomothering for female vervet monkeys. *Animal Behaviour*, *40*, 553-562.

Fejer, A.A., and Backus, R.H. (1960). Porpoises and bow riding of ships under way. *Nature*, *188*, 700-703.

Fellner, W., and Bauer, G.B. (1999). Synchrony between a mother-calf pair of bottlenose dolphins (*Tursiops truncatus*). *Poster presented at the 13th Biennial Conference on the Biology of Marine Mammals. 28 November - 3 December 1999, Wailea, Hawaii.*

Fellner, W. (2000). *Synchrony between a mother-calf pair of bottlenose dolphins (Tursiops truncatus).* Bachelor's thesis, New College of the University of South Florida, United States.

Fernandez, S. (1992). *Composition de edad y sexo y parametros del ciclo de viva de toninas (Tursiops truncatus) varadas en el noroeste del Golfo de Mexico*. Master's thesis, Instituto Tecnical de Estudios Superiores Monterey, Guaymas, Mexico.

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

Ferrero, R. C., and Walker, W.A. (1995). Growth and reproduction of the common dolphin, *Delphinus delphis* Linnaeus, in the offshore waters of the North Pacific Ocean. *Fishery Bulletin*, *93*, 483-494.

Fertl, D. (1994). Occurrence patterns and behavior of bottlenose dolphins (*Tursiops truncatus*) in the Galveston ship channel, Texas. *Texan Journal of Science*, *46*, 299-317.

Forney, K.A., and Barlow, J. (1998). Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. *Marine Mammal Science*, *14*, 460-489.

Frantzis, A., and Herzing, D.L. (2002). Mixed-species associations of striped dolphins (*Stenella coeruleoaba*), short-beaked common dolphins (*Delphinus delphis*), and Risso's dolphins (*Grampus griseus*) in the Gulf of Corinth (Greece, Mediterranean Sea). *Aquatic Mammals*, *28*, 188-197.

Gallo, J.P. (1991). Group behavior of common dolphins *Delphinus delphis* during prey capture. Anales del Instituto de Biologia Universidad Nacional Autonoma de Mexico Serie Zoologia, 62, 253-262.

Gannier, A. (1995). *Les cétacés de Méditerranée nord-occidentale: estimation de leur abondance et mise en relation de la variation saisonnière de leur distribution avec l'écologie du milieu*. Master's thesis, Ecole Pratique des Hautes Etudes, Montpellier, France.

Gaskin, D.E. (1968). The New Zealand Cetacea. *Fishery Resources Bulletin (New Series)*, *1*, 1-92.

Gaskin, D.E. (1972). *Whales, Dolphins and Seals, with a special reference to the New Zealand region*. Auckland: Heinemann Educational Books.

Gaskin, D. E. (1992). Status of the common dolphin, *Delphinus delphis*, in Canada. *The Canadian Field-Naturalist*, *106*, 55-63.

Goold, J. C. (1998). Acoustic assessment of populations of common dolphin off the West Wales coast, with perspectives from satellite imagery. *Journal of the Marine Biological Association UK*, *78*, 1353-1364.

Gravetter, F.J., and Wallnau, L.B. (2004). *Statistics for the behavioral sciences* (6th ed.). Belmont, California: Wadsworth.

Grellier, K. (2000). Reproductive biology of the female bottlenose dolphins (*Tursiops truncatus*) using the Moray Firth, Scotland. Master's thesis, University of Aberdeen, Scotland.

Grellier, K., Hammond, P.S., Wilson, B., Sanders-Reed, C.A., and Thompson, P.M. (2003). Use of photo-identification data to quantify mother-calf association patterns in bottlenose dolphins. *Canadian Journal of Zoology*, *81*, 1421-1427.

Gubbins, C., Mc Cowan, B., Lynn, S.K., Hooper, S., and Reiss, D. (1999). Mother-infant spatial relations in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, *15*, 3, 751-765.

Haenel, N.J. (1986). General notes on the behavioural ontogeny of Puget Sound killer whales and the occurrence of allomaternal behaviour. In B.C. Kirkevold and J.S. Lockard (Eds.), *Behavioral Biology of Killer Whales* (pp. 285-300). New York: Alan Liss.

Hall, E.R. (1981). *The mammals of North America*, *Volume 2* (2nd ed.). New York: John Wiley and Sons.

Hall, M.A., and Boyer, S.D. (1990). Incidental mortality of dolphins in the tuna purse-seine fishery in the eastern Pacific Ocean during 1988. *Report of the International Whaling Commission*, *440*, 461-462.

Hansen, L.J. (1990). California coastal bottlenose dolphins. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 403-420). San Diego: Academic Press.

Harris, M.B. (1998). *Basic statistics for behavioral science research* (2nd ed.). Boston: Allyn and Bacon.

Harrison, R.J. (1969). Reproduction and reproductive organs. In H.T. Andersen (Ed.), *The biology of marine mammals* (pp. 253-348). New York: Academic Press.

Harrison, R. J., Boice, R.C., and Brownell Jr, R.L. (1969). Reproduction in wild and captive dolphins. *Nature*, *222*, 1143-1147.

Harrison, R. J., Brownell Jr, R.L., and Boice, R.C. (1972). Reproduction and gonadal appearances in some odontocetes. In R.J. Harrison (Ed.), *Functional anatomy of marine mammals* (pp. 361-429). London and New York: Academic Press.

Haug, T., Gullisken, B., and Christensen, I. (1981). Observations of the common dolphin *Delphinus delphis* L. in North-Norway. *Fauna*, *34*, 97-100.

Hauraki Gulf Maritime Park Board (1983). *The story of the Hauraki Gulf Maritime Park*. Auckland: Hauraki Gulf Maritime Park Board.

Heptner, V.G., Chapskii, K.K., Arsen'ev, V.A., and Sokolov, V.E. (1996). *Mammals of the Soviet Union. Vol: 2. Part 3. Pinnipeds and Toothed Whales*. Washington DC: Smithsonian Institution Libraries and the National Science Foundation.

Hersh, S.L., Odell, D.K. and Asper, E.D. (1990). Bottlenose dolphin mortality patterns in the Indian/Banana River system of Florida. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 155-164). San Diego: Academic Press.

Hershkovitz, P. (1966). Catalog of living whales. *United States National Museum Bulletin*, *246*.

Herzing, D. L. (1997). The life history of free-ranging Atlantic spotted dolphins (*Stenella frontalis*): age classes, color phases, and female reproduction. *Marine Mammal Science*, *13*, 576-595.

Heyning, J. E., and Perrin, W.F. (1994). Evidence of two species of common dolphin (Genus *Delphinus*) from the Eastern North Atlantic. *Contributions in Science*, *442*, 1-35.

Hinde, R. A., and Atkinson, S. (1970). Assessing the roles of social partners in maintaining mutual proximity, as exemplified by mother-infant relations in Rhesus monkeys. *Animal Behaviour*, *18*, 169-176.

Holt, R.S., and Sexton, S.N. (1990). Monitoring trends in dolphin abundance in the Eastern Tropical Pacific using research vessels over a long sampling period: Analyses of 1988 Data. *Report of the International Whaling Commission*, *40*, 471-476.

Honacki, J.H., Kinman, K.E., and Koeppl, J.W. (1982). *Mammalian species of the world*. Lawrence, Kansas: Allen Press.

Hui, C. A. (1979a). Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern California Bight. *Journal of Mammalogy*, *60*, 521-527.

Hui, C. A. (1979b). Correlates of maturity in the common dolphin, *Delphinus delphis*. *Fishery Bulletin*, *77*, 295-300.

Hui, C. A. (1985). Undersea topography and the comparative distributions of two pelagic cetaceans. *Fishery Bulletin*, *83*, 472-475.

Hutt, S.J., and Hutt, C. (1970). *Direct observation and measurement of behavior*. Springfield, Illinois: Charles C. Thomas.

Irvine, A.B., Scott, M.D., Wells, R.S., and Kaufmann, J.H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fishery Bulletin*, *79*, 671-688.

Janik, T., and Thompson, P.M. (1996). Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. *Marine Mammal Science*, *12*, 597-602.

Jefferson, T.A., Leatherwood, S., and Webber, M.A. (1993). *FAO Identification Guide: Marine Mammals of the World*. Rome: Food and Agriculture Organisation.

Jefferson, T.A., and Van Waersebeek, K. (2002). The taxonomic status of the nominal dolphin species *Delphinus tropicalis* Van Bree, 1971. *Marine Mammal Science*, *18*, 787-818.

Jelinski, D. E., Krueger, C.C., and Duffus, D.A. (2002). Geostatistical analyses of interations between killer whales (*Orcinus orca*) and recreational whale-watching boats. *Applied Geography*, *22*, 393-411.

Jillett, J.B. (1971). Zooplankton and hydrology of the Hauraki Gulf, New Zealand. *New Zealand Department of Scientific and Industrial Research, bulletin 204.*

Johnson, C.M., and Norris, K.S. (1986). Delphinid social organization and social behavior. In R.J. Schusterman, J.A. Thomas and F.G. Wood (Eds.), *Dolphin cognition and behavior: A comparative approach* (pp. 335-346). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Johnson, C.M., and Norris, K.S. (1994). Social behavior. In K.S. Norris, B. Würsig, R.S. Wells and M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 243-286). Berkeley: University of California Press.

Jonsgård, A. (1969). Age determination of marine mammals. In H.T. Andersen (Ed.), *The biology of marine mammals* (pp. 1-30). New York: Academic Press.

Kasuya, T., Izumisawa, Y., Komyo, Y., Ishino, Y., and Maejima, Y. (1997). Life history parameters of bottlenose dolphins off Japan. *IBI Reports*, *7*, 71-107.

Katona, S.K., Rough, V., and Richardson, D.T. (1993). *A field guide to the whales, porpoises and seals of the Gulf of Maine and eastern Canada – Cape Cod to Newfoundland*. New York: Scribner's Sons.

Keiko, M., Toru, H., Michio, K., Motoi, Y., and Masaaki, K. (2003). Change of position and proximity between mothers and their calves by the age of the calf in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Poster presented at the 15th Biennial Conference on the Biology of Marine Mammals. 14 –19 December 2003, North Carolina, United States.*

Kemper, C., Flaherty, A., Hill, M., Gibbs, S., and Long, M. (2001). Human interactions and cause of death of South Australian cetaceans. *Abstracts of the Southern Hemisphere Marine Mammal Conference. 29 May - 1 June 2001, Phillip Island, Victoria, Australia*.

Kenney, R.D., Payne, P.M., Heinemann, D.W., and Winn, H.E. (1996). Shifts in northeast shelf cetacean distributions relative to trends in Gulf of Maine/Georges Bank fish abundance. In K. Sherman, N.A. Jaworski and T. Smada (Eds.), *The Northeast Shelf Ecosystem: Assessment, Sustainability and Management* (pp.169-196). Cambridge: Blackwell Science.

Klinowska, M.M. (1991). *Dolphins, porpoises and whales of the world. The IUCN Red Data Book*. Cambridge: IUCN.

Kuczaj, S., Makecha, R., and Solangi, M. (2003). The ontogeny of social play in bottlenose dolphin (*Tursiops truncatus*) calves. *Poster presented at the 15th Biennial Conference on the Biology of Marine Mammals. 14 – 19 December 2003, North Carolina, United States.*

Lang, T.G. (1966). Hydrodynamic analysis of cetacean performance. In K.S. Norris (Ed.), *Whales, dolphins and porpoises* (pp. 410-434). Berkeley: University of California Press.

Leatherwood, S., Caldwell, D.K., and Winn, H.E. (1976). *Whales, dolphins and porpoises of the Western North Atlantic: A guide to their identification* (Report No. 396). Seattle, Washington: National Marine Fisheries Service.

Leatherwood, S., Reeves, R.R., Perrin, W.F., and Evans, W.E. (1982). *Whales, dolphins and porpoises of the eastern North Pacific: A guide to their identification* (Report No. 444). Seattle, Washington: National Marine Fisheries Service.

Lee, P.C. (1987). Allomothering among African elephants. *Animal Behaviour*, *35*, 278-291.

Lusseau, D. (2003). Male and female bottlenose dolphins *Tursiops* spp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology Progress Series*, *257*, 267-274.

Maleske, R.T. (1995). *Foundations for gathering and interpreting behavioral data*. Pacific Grove, California: Brooks/Cole Publishing Company.

Mann, J. (1999). Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, *15*, 102-122.

Mann, J. (2000). Unravelling the dynamics of social life: Long-term studies and observational methods. In J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 45-64). Chicago: University of Chicago Press.

Mann, J., and Smuts, B. (1998). Natal attraction: allomaternal care and mother-infant separations in wild bottlenose dolphins. *Animal Behaviour*, *55*, 1097-1113.

Mann, J., and Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*, 529-566.

Mann, J., Connor, R.C., Barre, L.M., and Heithaus, M.R. (2000). Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behavioral Ecology*, *11*, 210-219.

Marsh, H., and Kasuya, T. (1991). An overview of the changes in the role of a female pilot whale with age. In K. Pryor and K.S. Norris (Eds.), *Dolphin societies: Discoveries and puzzles* (pp. 281-285). Berkeley: University of California Press.

Martin, P., and Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge: Cambridge University Press.

Mattila, D.K., Clapham, P.J., Vasquez, O., and Bowman, R. (1994). Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominican Republic. *Canadian Journal of Zoology*, *72*, 1898-1907.

McBride, A.F., and Hebb, D.O. (1948). Behavior of the captive bottlenose dolphin, *Tursiops truncatus*. *Journal of Comparative Physiology and Psychology*, *41*, 111-123.

McBride, A. F., and Kritzler, H. (1951). Observations on pregnancy, parturition, and postnatal behavior in the bottlenose dolphin. *Journal of Mammalogy*, *32*, 251-266.

Mead, J.G., and Potter, C.W. (1990). Natural history of bottlenose dolphins along the central Atlantic coast of the United States. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 165-195). San Diego: Academic Press.

Mitchell, E. (1970). Pigmentation pattern evolution in delphinid cetaceans: An essay in adaptive coloration. *Canadian Journal of Zoology*, *48*, 717-740.

Mitchell, E. (1975). Report of the meeting on smaller cetaceans, Montreal, April 1-11, 1974. *Journal of the Fisheries Research Board of Canada*, *32*, 889-983.

Mobley, J. R., and Herman, L.M. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, *63*, 762-772.

Moore, S. E., and Ridgway, S.H. (1995). Whistles produced by common dolphins from the southern California Bight. *Aquatic Mammals*, *21*, 55-63.

Muroyama, Y. (1994). Exchange of grooming for allomothering in female patas monkeys. *Behaviour*, *128*, 103-119.

Mussi, B., Miragliuolo, A., and Bearzi, G . (in press). Short-beaked common dolphins around the island of Ischia, Italy (Southern Tyrrhenian Sea). *European Research on Cetaceans*, *16*.

Natoli, A., Cañadas, A., Vaquero, C., Politi, E., Fernandez-Piqueras, J., and Hoelzel, A.R. (in press). Phylogeography of Mediterranean and North Atlantic common dolphin populations. *European Research on Cetaceans*, *15*.

Neumann, D. R. (2001). *The behaviour and ecology of the short-beaked common dolphins (Delphinus delphis) along the East Coast of Coromandel Peninsula, North Island, New Zealand*. Doctoral dissertation, Massey University, Albany, New Zealand.

Neumann, D. R., Leitenberger, A., and Orams, M.B. (2002). Photo-identification of short-beaked common dolphins, *Delphinus delphis*, in north-east New Zealand: a photo-catalogue of recognisable individuals. *New Zealand Journal of Marine and Freshwater Research*, *36*, 593-604.

Nishiwaki, M. (1972). General biology. In S.H. Ridgway (Ed.), *Mammals of the Sea, Biology and Medicine* (pp. 3-204). Springfield, Illinois: Charles Thomas.

Nordensten, C., Mello, I., and Amundin, M. (2003). Reaction of three bottlenose dolphin dams with calves to other members of the group in connection with nursing. *Poster presented at the 17th European Cetacean Society Conference. 9 – 13 March, Las Palmas, Spain.*

Norris, K.S., and Prescott, J.H. (1961). Observations on Pacific cetaceans of California and Mexican waters. *University of California Publications in Zoology*, *634*, 291-402.

Norris, K.S., Goodman, R.M., Villa-Ramirez, B., and Hobbs, L. (1977). Behavior of California gray whale, *Eschrichtius robustus*, in southern Baja California, Mexico. *Fishery Bulletin*, *75*, 159-172.

Norris, K.S., and Dohl, T.P. (1980a). The structure and function of cetacean schools. In L.M. Herman (Ed.), *Cetacean behavior* (pp. 211-261). New York: John Wiley and Sons.

Norris, K.S., and Dohl, T.P. (1980b). Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. *Fishery Bulletin, United States*, *77*, 821-849.

Norris, K.S., Würsig, B., Wells, R.S., and Würsig, M. (1994). The Hawaiian spinner dolphin. Berkeley: University of California Press.

Notarbartolo di Sciara, G., Venturino, M.C., Zanardelli, M., Bearzi, G., Borsani, J.F., and Cavalloni, B. (1993). Cetaceans in the central Mediterranean Sea: distribution and sighting frequencies. *Bollettino di Zoologica*, *60*, 131-138.

Nowacek, S.M., Wells, R.S., and Solow, A.R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammal Science*, *17*, 4, 673-688.

O'Callaghan, T.M., and Baker, C.S. (2002). Summer cetacean community with particular reference to the Bryde's whales, in the Hauraki Gulf, New Zealand. *New Zealand: Department of Conservation, Science Internal Series, 55*.

Oftedal, O.T. (1997). Lactation in whales and dolphins: Evidence of divergence between baleen- and toothed-species. *Journal of Mammary Gland Biology and Neoplasia*, *2*, 205-230.

O'Shea, T.J., Brownell, R.L., Clark Jr, D.R., Walker, W.A., Gay, M.L., and Lamont, T.G. (1980). Organochlorine pollutants in small cetaceans from the Pacific and South Atlantic Oceans, November 1968-1976. *Pesticides Monitoring Journal*, *14*, 2, 35-46.

Overholtz, W. J., and Waring, G.T. (1991). Diet composition of pilot whales *Globicephala* sp. and common dolphins *Delphinus delphis* in the Mid-Atlantic Bight during 1989. *Fishery Bulletin*, *89*, 723-728.

Owen, W., and Owen, P. (1999). *William Owen's Hauraki Gulf: A fishing and cruising guide* (3rd ed.). Auckland: David Bateman.

Palka, D., Read, A., and Potter, C. (1997). Summary of knowledge of white-sided dolphins (*Lagenorhynchus acutus*) from US and Canadian Atlantic waters. *Report of the International Whaling Commission*, *47*, 729-734.

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

Pascoe, P.L. (1986). Size data and stomach contents of common dolphins, *Delphinus delphis*, near Plymouth. *Journal of the Marine Biological Association UK*, *66*, 319-322.

Paul, L. J. (1968). Some seasonal water temperature patterns in the Hauraki Gulf, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, *2*, 535-558.

Payne, R. (1976). At home with right whales. *National Geographic*, *149*, 322-329.

Peddemors, V.M. (1990). Respiratory development in a captive-born bottlenose dolphin *Tursiops truncatus* calf. *South African Journal of Zoology*, *25*, 1, 178-184.

Peddemors, V. M., de Muelenaere, H.J.H., and Devchand, K. (1989). Comparative milk composition of the bottlenosed dolphin (*Tursiops truncatus*), humpback dolphin (*Sousa plumbea*) and common dolphin (*Delphinus delphis*) from Southern African waters. *Comparative Biochemistry and Physiology Part A*, *94*, 639-641.

Perrin, W. F. (2002). Common dolphins *Delphinus delphis*, *D. capensis*, and *D. tropicalis*. In W.F. Perrin, B. Würsig and J. C. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (pp. 245-248). San Diego: Academic Press.

Perrin, W. F., and Reilly, S.B. (1984). Reproductive parameters of dolphins and small whales of the familly Delphinidae. In W.F. Perrin, R. L. Brownell Jr and D.P. DeMaster (Eds.), *Reproduction in whales, dolphins and porpoises: Proceedings of the conference, Cetacean Reproduction, Estimating Parameters for Stock Assessment and Management, La Jolla, CA, 28 Nov. - 7 Dec. 1981* (pp. 97-134). Reports of the International Whaling Commission, special issue 6. Cambridge: International Whaling Commission.

Perrin, W. F., and Brownell, R.L. (1994). A brief review of stock identity in small marine cetaceans in relation to assessment of driftnet mortality in the North Pacific. In W.F. Perrin, G.P. Donovan and J. Barlow (Eds.), *Gillnets and cetaceans* (pp.393-401). Reports of the International Whaling Commission, special issue 15. Cambridge: International Whaling Commission.

Perryman, W. L., and Lynn, M.S. (1993). Identification of geographic forms of common dolphin (*Delphinus delphis*) from aerial photogrammetry. *Marine Mammal Science*, *9*, 119-137.

Perryman, W.L., and Lynn, M.S. (1994). Examination of stock and schools of striped dolphin (*Stenella coeruleoalba*) in the eastern Pacific from aerial photogrammetry. *Fishery Bulletin*, *92*, 122-131.

Polacheck, T. (1987). Relative abundance, distribution and inter-specific relationship of cetacean schools in the Eastern tropical Pacific. *Marine Mammal Science*, *3*, 54-77.

Politi, E. (1998). Un progetto per i delifini in Mediterraneo. *Le Scienze*, *360*, 64-69.

Politi, E., Airoldi, S., and Notarbartolo di Sciara, G. (1994). A preliminary study of the ecology of cetaceans in the waters adjacent to Greek Ionian Islands. *European Research on Cetaceans*, *8*, 111-115.

Politi, E., and Bearzi, G. (in press). Evidence of rarefaction for a coastal common dolphin community in the eastern Ionian Sea. *European Research on Cetaceans*, *15*.

Prescott, J.H. (1977). Comments on captive births of *Tursiops truncatus* at Marineland of the Pacific. In S.H. Ridgway and K. Bernischke (Eds.), *Breeding dolphins: Present status, suggestions for the future* (pp. 71-76). Washington, DC: Marine Mammal Commission Report MMC-76/07.

Puente, A. E., and Dewsbury, D.A. (1976). Courtship and copulatory behavior of bottlenosed dolphins (*Tursiops truncatus*). *Cetology*, *21*, 1-9.

Quiatt, D. (1979). Aunts and mothers: adaptive implications of allomaternal behavior in non-human primates. *American Anthropol*ogist, *81*, 310-319.

Ralls, K., Brownell Jr, R.L., and Ballau, J. (1980). Differential mortality by sex and age in mammals, with specific reference to the sperm whale. In G.P. Donovan (Ed.), *Sperm whales* (pp. 233-243). Reports of the International Whaling Commission, special issue 2. Cambridge: International Whaling Commission.

Read, A. J., Wells, R.S., Hohn, A.A., and Scott, M.D. (1993). Patterns of growth in wild bottlenose dolphins, *Tursiops truncatus*. *Journal of Zoology, London*, *231*, 107-123.

Read, A. J., and Hohn, A.A. (1995). Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science*, *11*, 423-440.

Reid, K., Mann, J., Weiner, J.R., and Hecker, N. (1995). Infant development in two aquarium bottlenose dolphins. *Zoo Biology*, *14*, 135-147.

Reilly, S.B. (1990). Seasonal changes in distribution and habitat differences among dolphins in the Eastern Tropical Pacific. *Marine Ecology Progress Series*, *66*, 1-12.

Reynolds, J.E., Wells, R.S., and Eide, S.D. (2000). *The bottlenose dolphin: Biology and conservation*. Miami: University Press of Florida.

Rice, D.W. (1998). Marine mammals of the world. *Society of Marine Mammalogy Special Publication*, *4*, 231.

Richards, M.P.M., and Bernal, J.F. (1972). An observational study of mother-infant interaction. In N. Blurton-Jones (Ed.), *Ethological Studies of Child Behaviour* (chapter 7). London: Cambridge University Press.

Ridgway, S.H. (1972). Homeostasis in the aquatic environment. In S.H. Ridgway (Ed.), *Mammals of the sea: biology and medicine* (pp. 590-747). Springfield, Illinois: Charles C. Thomas.

Rogan, E., Baker, J.R., Jepson, P.D., Berrow, S., and Kieley, O. (1997). A mass stranding of white-sided dolphins (*Lagenorhynchus acutus*) in Ireland: biological and pathological studies. *Journal of Zoology*, *242*, 217-227.

Rosel, P.E., Dizon, A.E., and Heyning, J.E. (1994). Genetic analysis of sympatric morphotypes of common dolphins (genus *Delphinus*). *Marine Biology*, *119*, 159-167.

Samuels, A., and Tyack, P.L. (2000). Flukeprints: A history of studying cetacean societies. In J. Mann, R. C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: field studies of dolphins and whales* (pp. 9-44). Chicago: University of Chicago Press.

Schneider, L., Schamel, L., and Noonan, M. (2003). Behavioural landmarks in the development of neonatal beluga whales (*Delphinapterus leucas*). *Poster presented at the 17th European Cetacean Society Conference. 9 – 13 March, Las Palmas, Spain*.

Schroeder, J.P. (1990). Breeding bottlenose dolphins in captivity. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 435-446). San Diego: Academic Press.

Scott, M.D., Wells, R.S., and Irvine, B.A. (1990). A long-term study of bottlenose dolphins on the West coast of Florida. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 235-244). San Diego: Academic Press.

Selzer, L. A., and Payne, P.M. (1988). The distribution of white-sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) vs. environmental features of the continental shelf of the northeastern United States. *Marine Mammal Science*, *4*, 141-153.

Sergeant, D.E., St Aubin, D.J., and Geraci, J.R. (1980). Life history and Northwest Atlantic status of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*. *Cetology*, *37*, 1-12.

Shane, S.H., Wells, R.S., and Würsig, B. (1986). Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science*, *2*, 1, 34-63.

Shane, S.H. (1990a). Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 245-265). San Diego: Academic Press.

Shane, S.H. (1990b). Comparison of bottlenose dolphin behavior in Texas and Florida, with a critique of methods for studying dolphin behavior. In S. Leatherwood and R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 541-558). San Diego: Academic Press.

Sharples, J. (1997). Cross-shelf intrusion of subtropical water into the coastal zone of northeast New Zealand. *Continental Shelf Research*, *17*, 7, 835-857.

Silva, M. A., and Sequeira, M. (2003). Patterns in mortality of common dolphin (*Delphinus delphis*) on the Portuguese coast, using stranding records, 1975-1998. *Aquatic Mammals*, *29*, 88-98.

Sims, C., Rugh, D.J., and Hobbs, R.C. (2003). Developing a calving rate for beluga in Cook Inlet, Alaska, using aerial digital photography and videography. *Poster presented at the 15th Biennial Conference on the Biology of Marine Mammals. 14 –19 December 2003, North Carolina, United States.*

Sleptsov, M.M. (1940). Determination of the age of *Delphinus delphis* L. *Bulletin de la Société de Nature (Moscou)*, *49*, 43-51.

Small, R. J., and DeMaster, D.P. (1995). Survival of five species of captive marine mammals. *Marine Mammal Science*, *11*, 209-226.

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

Smolker, R.A., Mann, J., and Smuts, B.B. (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioral and Ecological Sociobiology*, *33*, 393-402.

Smultea, M. A. (1992). *Habitat utilization patterns of humpback whales (Megaptera novaeangliae) off the island of Hawaii* (Report No. PB92-182484). Washington: United States Marine Mammal Commission.

Sokolov, V.E., Yashin, V.A., and Yukhov, V.L. (1997). Distribution and numbers of the Black Sea dolphins surveyed from ships. *Zoologicheskii Zhurnal*, *76*, 3, 364-370.

Stanev, T. (1996). Distribution and numbers of dolphins in the Bulgarian sector of the Black Sea. *Proceedings of the Institute of Fisheries, Varna*, *24*, 177-182.

Stanford, C.B. (1992). Costs and benefits of allomothering in wild capped langurs (*Presbytis pileata*). *Behavioural and Ecological Sociobiology*, *30*, 29-34.

StatSoft Inc. (2004). Electronic Statistics Textbook. Tulsa, OK: StatSoft. Retrieved June 6, 2004 from the World Wide Web: http://www.statsoft.com/textbooks/stathome.html

Struhsaker, T. T. (1971). Social behaviour of mother and infant vervet monkeys (*Cercopithecus aethiops*). *Animal Behaviour*, *19*, 233-250.

Sverdrup, H.U., Johnson, M.W., and Fleming, R.H. (1942). *The oceans, their physics, chemistry and general biology*. Englewood Cliffs, New Jersey: Prentice-Hall, Inc.

Taber, S., and Thomas, P. (1982). Calf development and mother-calf spatial relationships in southern right whales. *Animal Behaviour*, *30*, 1072-1083.

Tavolga, M.C., and Essapian, F.S. (1957). The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. *Zoologica*, *42*, 3, 11-34.

Thayer, V. G., Read, A.J., Friedlaender, A.S., Colby, D.R., Hohn, A.A., McLellan, W.A., Pabst, D.A., Dearolf, J.L., Bowles, N.I., Russell, J.R., and Rittmaster, K.A. (2003). Reproductive seasonality of western Atlantic bottlenose dolphins off North Carolina, USA. *Marine Mammal Science*, *19*, 617-629.

Thomas, P. O., and Taber, S.M. (1984). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, *88*, 42-60.

Tomilin, A.G. (1957). *Mammals of the USSR and Adjacent Countries. Vol. 4: Cetaceans*. Moscow: USSR Academy of Science Publication House.

Townsend, C.H. (1935). The distribution of certain whales as shown by the logbook records of American whaleships. *Zoologica*, *1*, 1-50.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, *14*, 249-164.

True, F.W. (1889). Contribution to the natural history of the cetaceans, a review of the family delphinidae. *Bulletin of the U.S. National Museum*, *36*.

Tsalkin, V.I. (1938). Respredelinie obyknovennogo chemomorskogo del'fina (*D. delphis*) letne-osennii period. *Trudy Azova-Chernomomorskogo Nauchno-Issledovatel'skogo Instituea Rybnaga Khozyaista No. 2*.

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

Tyack, P.L. (2000). Functional aspects of cetacean communication. In J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 270-307). Chicago: University of Chicago Press.

Universidad Autónoma de Madrid and Alnitak (2002). *Identificación de las áreas de especial interés para la conservación de los cetáceos en el Mediterráneo español*. Memoria final. Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente.

Urian, K.W., Duffield, D.A., Read, A.J., Wells, R.S., and Shell, E.D. (1996). Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. *Journal of Mammalogy*, *77*, 394-403.

Van Bree, P.J.H. (1971). *Delphinus tropicalis*, a new name for *Delphinus longirostris* G. Cuvier, 1829. *Mammalia*, *35*, 345-346.

Van Bree, P.J.H., and Purves, P.E. (1972). Remarks on the validity of *Delphinus bairdii* (Cetacea, Delphinidae). *Journal of Mammalogy, 53*, 372-374.

Van Waerebeek, K., and Read, A.J. (1994). Reproduction of dusky dolphins, *Lagenorhynchus obscurus*, from coastal Peru. *Journal of Mammalogy*, *75*, 1054-1062.

Vella, A. (in press). *Delphinus delphis* (common dolphins) status in the central and southern Mediterranean around the Maltese islands. *European Research on Cetaceans*, *16*.

Viale, D. (1994). Cetaceans as indicators of a progressive degradation of Mediterranean water quality. *International Journal of Environmental Studies*, *45*, 183-198.

Vicente, N., and Chabert, D. (1978). Chemical pollutants in blubber tissue of a dolphin *Delphinus delphis* that grounded on the Mediterranean coast. *Oceanologie Acta*, *1*, 331-334.

Visser, I.N. (1999). A summary of interactions between orca (*Orcinus orca*) and other cetaceans in New Zealand waters. *New Zealand Natural Sciences*, *24*, 101-112.

Walford, L.A. (1958). *Living resources of the sea: opportunities for research and expansion*. New York: Ronald Press Co.

Webb, B. F. (1973a). Cetaceans sighted off the West coast of the South Island, New Zealand, summer 1970. *New Zealand Journal of Marine and Freshwater Research*, *7*, 1-2, 179-182.

Webb, B. F. (1973b). Dolphin sightings, Tasman Bay to Cook Strait, New Zealand, September 1968-June 1969. *New Zealand Journal of Marine and Freshwater Research*, *7*, 4, 399-405.

Weinrich, M.T. (1991). Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Canadian Journal of Zoology*, *69*, 3012-3019.

Wells, R. S. (1984). Reproductive behavior and hormonal correlates in Hawaiian spinner dolphins, *Stenella longirostris*. In W.F. Perrin, R. L. Brownell Jr and D.P. DeMaster (Eds.) *Reproduction in whales, dolphins and porpoises: Proceedings of the conference, Cetacean Reproduction, Estimating Parameters for Stock Assessment and Management, La Jolla, CA, 28 Nov. - 7 Dec. 1981* (pp. 465-472). Reports of the International Whaling Commission, special issue 6. Cambridge: International Whaling Commission.

Wells, R. S. (1991a). Bringing up baby. *Natural History*, *100*, 56-62.

Wells, R.S. (1991b). Reproductive success and survivorship of free-ranging bottlenose dolphins relative to group size and stability. *Abstracts of the Ninth Biennial Conference on the Biology of Marine Mammals. 5 – 9 December 1991, Chicago, United States*.

Wells, R.S., Irvine, A.B., and Scott, M.D. (1980). The social ecology of inshore odontocetes. In L.M. Herman (Ed.), *Cetacean behavior: Mechanisms and functions* (pp.263-317). Malabar, Florida: Robert E. Publishing.

Wells, R. S., Scott, M.D., and Irvine, A.B. (1987). The social structure of free-ranging bottlenose dolphins. In H.H. Genaways (Ed.), *Current Mammalogy* (pp. 247-305). New York and London: Plenum Press.

Wells, R.S, and Norris, K.S. (1994). Patterns of reproduction. In K.S. Norris, B. Würsig, R.S. Wells and M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 186-200). Berkeley: University of California Press.

Wells, R.S., Boness, D.J., and Rathbun, G.B. (1999). Behavior. In J.E. Reynolds and S.A. Rommel (Eds.), *Biology of Marine Mammals* (pp. 324-422). Washington: Smithsonian Institution Press.

Whitehead, H. (1996). Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behavioral Ecology and Sociobiology*, *38*, 237-244.

Whitehead, H., Brennan, S., and Grover, D. (1992). Distribution and behaviour of male sperm whales on the Scotian Shelf, Canada. *Canadian Journal of Zoology*, *70*, 912-918.

Whitehead, H., Christal, J., and Tyack, P.L. (2000). Studying cetacean social structure in space and time: Innovative techniques. In J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: Field studies of dolphins and whales* (pp. 65-87). Chicago: University of Chicago Press.

Whitehead, H., and Mann, J. (2000). Female reproductive strategies of cetaceans: life histories and calf care. In J. Mann, R. C. Connor, P.L. Tyack and H. Whitehead (Eds.), *Cetacean societies: field studies of dolphins and whales* (pp. 219-246). Chicago: University of Chicago Press.

Williams, T.M., Friedl, W.A., Fong, M.L., Yamada, R.M., Sedivy, P., and Haun, J.E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature*, *355*, 821-823.

Wilson, B., Thompson, P., and Hammond, P. (1993). An examination of the social structure of a resident group of bottlenose dolphins (*Tursiops truncatus*) in the Moray Firth, Northeastern Scotland. In P.G.H. Evans (Ed.), *European research on cetaceans: Proceedings of the sixth annual conference of the European Cetacean Society*. Cambridge: European Cetacean Society.

Winn, H. E. (1982). *A characterization of marine mammals and turtles in the mid and North American areas of the U.S. Outer Continental Shelf. Final Report of Cetacean and Turtle program (CeTAP)* (Report No. PB83215855). Washington DC: Bureau of Land Management, US Department of the Interior.

Würsig, B. (1978). Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine bay. *Biological Bulletin*, *154*, 348-359.

Würsig, B. (1986). Delphinid foraging strategies. In R.J. Schusterman, J. A. Thomas and F.G. Wood (Eds.), *Dolphin cognition and behavior: a comparative approach* (pp. 347-359). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Würsig, B., and Würsig, M. (1977). The photographic determination of group size, composition, and stability in coastal porpoises (*Tursiops truncatus*). *Science*, *198*, 755-756.

Würsig, B., and Würsig, M. (1980). Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. *Fishery Bulletin United States*, *77*, 4, 871-890.

Würsig, B., and Jefferson, T.A. (1990). Methods of photo-identification for small cetaceans. In P.S. Hammond, S.A. Mizroch and G.P. Donovan (Eds.*)*, *Individual recognition of cetaceans: Use of photo-identification and other techniques to estimate population parameters* (pp. 43-52). Reports of the International Whaling Commission, Special Issue 12. Cambridge: International Whaling Commission.

Würsig, B., Cipriano, F., Slooten, E., Constantine, R., Barr, K., and Yin, S. (1997). Dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand: status of present knowledge. *Report of the International Whaling Commission*, *47*, 715-722.

Young, D. D., and Cockcroft, V.G. (1994). Diet of common dolphins (*Delphinus delphis*) off the south-east coast of South Africa: opportunism or specialization? *Journal of the Zoological Society of London*, *234*, 41-53.

Yukhov, V.L., Petukhov, A.G., and Korkhov, A.I. (1986). Estimation of the abundance of Black Sea dolphins. *Biology of the Sea (Vladivostok)*, *6*, 64-68.

Zeldis, J., Sharples, J., Uddstrom, M., Pickmere, S. (1998). Fertilising the continental shelf: biological oceanographic studies on the northeastern New Zealand continental margin. *NIWA Water and Atmosphere*, *6*, 1, 13-16.

APPENDIX 1

An outline of the Marine Mammals Protection Regulations (1992) that are relevant to this study:

R. 18. CONDITIONS GOVERNING COMMERCIAL OPERATIONS AND BEHAVIOURS OF ALL PERSONS AROUND ANY MARINE MAMMAL -

Every commercial operation, and every person coming into contact with any class of marine mammal, shall comply with the following conditions:

(a) Persons shall use their best endeavours to operate vessels, vehicles, and aircraft so as not to disrupt the normal movement or behaviour of any marine mammal

(b) Contact with any marine mammal shall be abandoned at any stage if it becomes or shows signs of becoming disturbed or alarmed:

(c) No person shall cause any marine mammal to be separated from a group of marine mammals or cause any members of such a group to be scattered:

(d) No rubbish or food shall be thrown near or around any marine mammal:

(e) No sudden or repeated change in the speed or direction of any vessel or aircraft shall be made except in the case of an emergency:

(f) Where a vessel stops to enable the passengers to watch any marine mammal, the engines shall be either placed in neutral or switched off within a minute of the vessel stopping:

(i) No person shall disturb or harass any marine mammal:

(k) No person, vehicle, or vessel shall cut off the path of a marine mammal or prevent a marine mammal from leaving the vicinity or any person, vehicle, or vessel:

(l) Subject to paragraph (m) of this regulation, the master of any vessel less than 300 metres from any marine mammal shall use his or her best endeavours to move the vessel at a constant slow speed no faster than the slowest marine mammal in the vicinity, or at idle or “no wake” speed:

(m) Vessels departing from the vicinity of any marine mammal shall proceed slowly at idle or “no wake” speed until the vessel is at least 300 metres from the nearest marine mammal, except that, in the case of dolphins, vessels may exceed idle or “no wake” speed in order to outdistance the dolphins but must increase speed gradually, and shall not exceed 10 knots within 300 metres of any dolphin:

R. 20. SPECIAL CONDITIONS APPLYING TO DOLPHINS OR SEALS –

In addition to complying with the conditions set out in regulation 18 of these regulations, any commercial operation and any person coming into contact with dolphins or seals shall also comply with the following conditions:

(a) No vessel shall proceed through a pod of dolphins:

(b) Persons may swim with dolphins and seals but not with juvenile dolphins or a pod of dolphins that includes juvenile dolphins:

(g) A vessel shall approach a dolphin from a direction that is parallel to the dolphin and slightly to the rear of the dolphin.

APPENDIX 2

Example of a focal follow conducted on a mother-infant pair of common dolphins on the 8th of December 2003:

13h35m20 Three mother-calf pairs at the bow, including two infants and one juvenile. Start of focal follow on one of the infant and its mother. Infant is swimming in echelon position. No Foetal folds.
13h36m10 Synchronous breath.
13h36m17 Calf surfacing.
13h36m19 Mother surfacing.
13h36m25 Mother surfacing right after calf.
13h36m30 Calf separating for an approximate distance of five metres.
13h36m35 Calf rejoining the mother and synchronous breath.
13h36m43 Calf surfacing.
13h36m48 Mother surfacing.
13h36m50 Out of view.
13h37m06 Mother and infant back at the bow.
13h37m12 Mother surfacing.
13h37m18 Calf surfacing.
13h37m27 Calf surfacing right after mother, then separating for an approximate distance of two metres.
13h37m46 Calf rejoining, mother surfacing.
13h37m48 Calf surfacing, then separating for for an approximate distance of five metres.
13h37m58 Calf rejoining.
13h38m00 Calf for for an approximate distance of five metres.
13h38m06 Calf surfacing.
13h38m10 Calf rejoining.
13h38m15 Synchronous breath.
13h38m22 Mother surfacing.
13h38m25 Calf surfacing.
13h38m40 Mother and calf left the bow, end of focal follow.