Dynamics of mother-offspring common dolphins (*Delphinus* sp.) engaged in foraging activities in the Hauraki Gulf, New Zealand

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Nicolas de la Brosse
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Abstract

This study investigated the dynamic of mother-offspring common dolphins (*Delphinus* sp.) engaged in foraging activities in the Hauraki Gulf, New Zealand. While previous studies have demonstrated the importance of Hauraki Gulf waters for feeding and nursing common dolphins, no previous study has systematically assessed the dynamics of mother-offspring pairs engaged in foraging activities. During 228 hr of survey time, a total of 49 independent focal groups were recorded between March and July 2009. All observations were conducted from the surface using the platform of opportunity, *Dolphin Explorer,* a 20 m tour boat. Variables examined included group size, composition, offspring presence, predominant behavioural state, foraging strategies employed, associated species, mother-offspring relationship, and location of offspring within groups. This study tested the hypothesis that foraging strategies employed by mother-offspring pairs would be influenced by environmental and anthropogenic parameters, group size, and associated species. It also examined the influence of associated species and foraging strategies on the mother-offspring dynamic within focal groups.

Sighting Per Unit Effort (SPUE) and Offspring Per Unit Effort (OPUE) varied by month, with SPUE and OPUE being highest in March and July, respectively. Mother-offspring pairs predominantly engaged in cooperative foraging strategies (97%), and were less likely to engage in individual strategies. Cooperative feeding groups likely provide better protection to young and vulnerable dolphins, as well as a more prolific food supply to lactating females and their offspring. Water depth, sea surface temperature and group size had no influence on foraging strategies employed by mother-offspring pairs. Groups comprising immature dolphins typically altered their behaviour more frequently in presence of vessels, with presumed mothers keeping their offspring away from boats in 80% of encounters. However, a limited sample size likely impeded the statistical significance of this observation. Behavioural changes and potential vessel avoidance during foraging activity may occur as a response of perceived threat. Cooperative foraging strategies employed by focal groups had no significant influence on the location of the young. Offspring were observed in echelon position during 93.6% of the time dolphins foraged, and were never separated from their assumed mother during individual foraging strategies. Echelon position may enhance better predatory protection, as well as learning during foraging activities.

Mother-offspring pairs were observed in association with Australasian gannets (*Morus serrator*) and Bryde's whales (*Balaenoptera brydei*) during 68.4% and 8.4% of encounters, respectively. Prevalence of dolphin cooperative feeding is likely to attract and benefit associated species. While neither species were found to affect the foraging strategies employed by mother-offspring pairs, diving gannets did affect the position of mother-offspring pairs within feeding groups, with offspring typically located on the peripheral edge of the focal group. Conversely, no such affect was detected for associated feeding involving Bryde's whales. Since mothers permit offspring in the centre of mono-specific feeding groups, it seems plausible that the use of peripheral regions maybe associated with the presence of mixed-species feeding aggregations. This apparent shift in mother-offspring position is unexplained, although may represent perceived risk by the assumed mother. Results presented here extend our knowledge of foraging behaviour and mother-offspring common dolphin dynamics in the Hauraki Gulf, New Zealand.

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1.1. Taxonomy

Taxonomy of the common dolphin (genus *Delphinus*) has been very controversial since the description of *D. delphis* by Linnaeus in 1758. Since the mid-1990s, an increasing number of studies have described over two dozen nominal species world-wide (Hershkovitz 1966; Gaskin 1992; Perryman and Lynn 1993; Heyning and Perrin 1994; Rosel et al. 1994; Carwardine 1995; Westgate 2005; Natoli et al. 2006). Currently, two species of common dolphin are recognised: The short-beaked (*D. delphis*) and the long-beaked form (*D. capensis*). These species were described based on divergences of colour pattern, body length and cranial morphology of specimens observed in Northeast Pacific Ocean (Heyning and Perrin 1994). Further evidence confirmed that the two morphotypes were genetically distinct in the Northeast Pacific populations, as well as a population from the Black Sea (Rosel et al. 1994). Moreover, the existence of other potential sub-species has remained contentious over the years, using cranial and rostrum features to identify different morphotypes. Only *Delphinus capensis tropicalis*, first identified as a nominal third species of common dolphin (van Bree 1971), has been confirmed as a sub-species of the long beaked form, following examination of both tooth counts and rostral length/zygomatic width ratio (Jefferson and van Waerebeek 2002).

For many years, the short-beaked form was considered to be the only species of *Delphinus* occurring within New Zealand waters (Gaskin 1972; Neumann 2001c; Burgess 2006). Prior to a recent study (Stockin 2008), the molecular genetics of this population had not been systematically examined. Meanwhile, pigmentation (Stockin and Visser 2005) and skull morphometry (Amaha 1994) of New Zealand common dolphins revealed similarities with both *D. delphis* and *D. capensis*. As investigations remain ongoing, common dolphins identified within the present study are defined as *Delphinus* sp.

1.2. Distribution and abundance

Common dolphins are present throughout the world's oceans, although largely restricted to warm temperate, subtropical and tropical marine habitats (Evans 1994; Perrin 2002b). Some authors agree that distribution of common dolphins is not directly influenced by water

temperature, but reflect more that of prey species, which directly are influenced by water temperature (Banks and Brownell 1969; Selzer and Payne 1988; Bräger and Schneider 1998; Neumann 2001c). *Delphinus* ranges from 40 to 60 ºN to approximately 50 ºS (Selzer and Payne 1988; Jefferson et al. 1993; Evans 1994; Lucas and Hooker 2000).

D. delphis (Figure 2a) has a wide but discontinuous distribution, with local variants existing in the Mediterranean Sea (Gihr and Pilleri 1969), Black Sea (Tomilin 1957), from southern Norway to West Africa in the Eastern Atlantic Ocean (Gihr and Pilleri 1969; van Bree and Purves 1972), from Newfoundland to Florida in the Western Atlantic, from southern Canada to the Pacific coast of South America, in the central North Pacific Ocean (but not off Hawaii), from Japan to Taiwan (Nishiwaki 1972) and around New Caledonia, Tasmania and New Zealand in the Western Pacific Ocean (Gaskin 1968b; Bell et al. 2002; Bilgmann 2007). The species is possibly absent from the South Atlantic and the Indian Oceans (Rice 1998). The distribution of *D. capensis* (Figure 2b) remains poorly understood. Some individuals have been observed in West Africa, from Venezuela to Argentina, from southern California to central Mexico and off Peru, around Korea, southern Japan and Taiwan in the Western Pacific Ocean, and around Madagascar and South Africa (van Bree 1971; Pilleri and Gihr 1972). Investigations into the taxonomy of New Zealand common dolphins remain ongoing, with the current assumption being that only the short-beaked form is present within these waters.

In New Zealand waters, *Delphinus* is present around much of the coastline, although thought to be primarily concentrated off the eastern coast of the North Island, based on sighting and stranding records (Stockin and Orams 2009). Hotspots identified include the eastern Northland coast, the Bay of Plenty (Neumann 2001c), the Hauraki Gulf (Stockin et al. 2008b), and Cook Strait (Stockin and Orams 2009). The southern limit is considered to be around the Banks Peninsula (Gaskin 1968a), although distribution is known to vary seasonally (Gaskin 1968a; Bräger and Schneider 1998; Neumann 2001c), with the southern distribution likely more restricted during the austral winter months (Gaskin 1972).

(a)
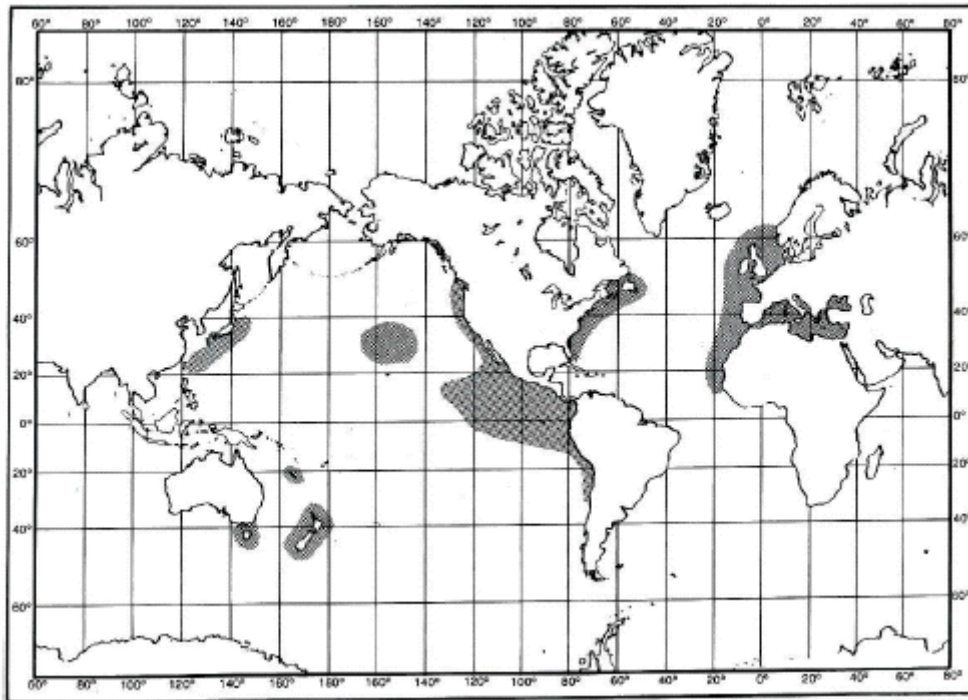
(b)
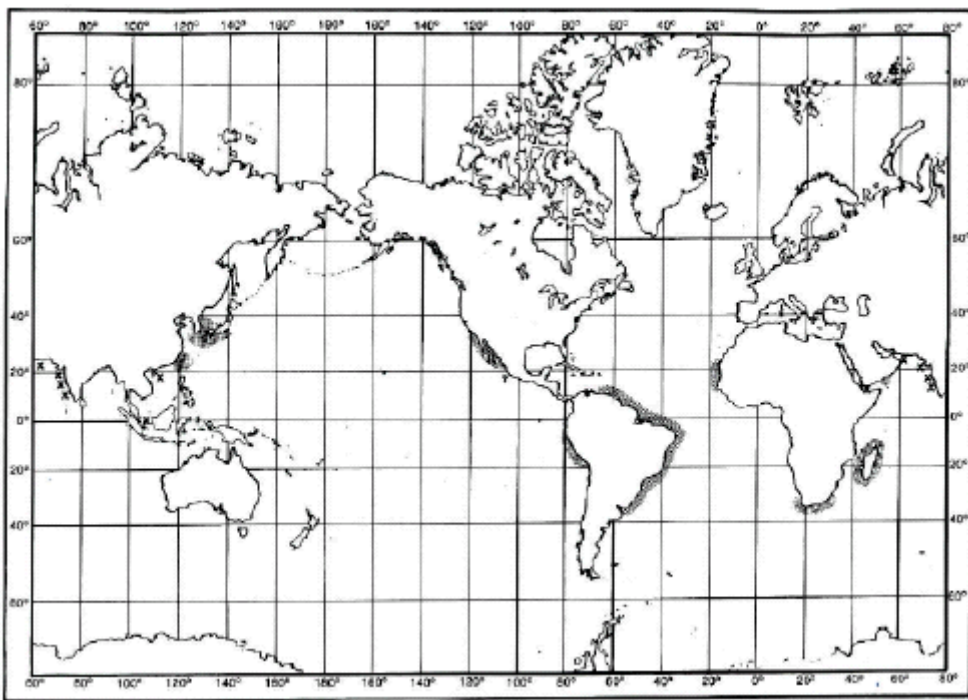
Figure 2: Approximate known distribution of the (a) short-beaked (*D. delphis*) and (b) long-beaked (*D. capensis*) common dolphin (Source: Heyning and Perrin, 1994).

The distribution of cetaceans has been related to a variety of environmental parameters, including sea surface temperature (Fraser 1934; Gaskin 1968a; Au and Perryman 1985), sea surface salinity (Selzer and Payne 1988), patterns of sea floor relief (Evans 1975; Hui 1979; Hui 1985), and oceanographic features of a region via links in the food web (Selzer and Payne 1988). Distribution of some populations varies with migrations, depending on oceanographical conditions (Forney and Barlow 1998). In Canada, common dolphins (*D. delphis*) move seasonally into higher latitude temperate regions when relatively warm summer waters allow the species to extend its range polewards (Gaskin 1992). Scarcity of common dolphins in some parts of the world is affected by inter-species competition (Evans 1975). For example, in the Eastern Tropical Pacific, spotted (*Stenella attenetua*) and spinner dolphin (*S. longirostris*) have been reported to occur in some areas apparently not occupied by common dolphins (Perrin 1972), possibly indicating competitive exclusion.

Delphinus is often considered mesopelagic, with most groups occurring over the continental shelf and beyond (Gaskin 1992). It is within such habitats that the species has mostly been reported to forage on the deep scattering layer (Evans 1971; Gaskin 1992). Nevertheless, they have occasionally been recorded into shallow inshore waters (Selzer and Payne 1988; Gaskin 1992; Bernal et al. 2003; Ramírez-Carroz and González-Fernández 2004; Stockin 2008). Previous studies report the presence of common dolphins in depths between 26 and 5,121 m (Winn 1982), but tending to occur more often between 100 and 1,000 m, with some peaks in population abundance around shelf edges and deeper waters (Selzer and Payne 1988; Cañadas et al. 2002; Cañadas and Hammond 2008). Areas of steep sea floor relief often induce upwelling, offering nutrient-rich waters carried upward towards the surface and providing greater feeding opportunities for species such as common dolphins (Au and Perryman 1985).

Despite being the most frequent species observed throughout the world's oceans (Gaskin 1992), no succinct abundance estimates are available. Most authors believe that the population reaches a few million (Perrin 2002b). The status of *Delphinus* was believed to be generally stable, but declines in populations have been identified both in the Mediterranean and Black Seas (Viale 1994; Stanev 1996; Bearzi et al. 2003; Bearzi et al. 2008; Cañadas and Hammond 2008). Direct and indirect threats include fisheries interactions and pollution. The accidental capture (by-catch) in fishing nets is widely considered to be one of the main threats to the species (Kirkwood et al. 1997; Tregenza and Collet 1998). Within New Zealand, common dolphins are known to be captured in the commercial jack mackerel (*Trachunus*

novaezelandiae) trawl fishery (DuFresne et al. 2007; Rowe 2007) and incidentally killed within inshore recreational set nets (Stockin et al. 2009b). Furthermore, other impacts have been identied from persistent organochloride pollutants (Stockin et al. 2007) and tourism (Stockin et al. 2008a).

Common dolphins are known to be highly mobile (Evans 1971) and have a very large geographical range. Such movements can vary seasonally and possibly inter-annually on a local scale. This makes any population estimates problematic to conduct. However, in the northern hemisphere, some abundance estimates have been established within particular areas. For the Eastern Tropical Pacific, an estimate of 3,127,203 (CV = 0.26) individuals was reported (Gerrodette et al. 2008). In the Black Sea, aerial surveys estimated 50,000 common dolphins (Yukhov et al. 1986), while ship-based line-transects proposed 96,000 animals (Sokolov et al. 1997). In the Northeastern Atlantic Ocean, a survey yielded an estimate of 75,450 (CV = 0.67), found almost exclusively in the Celtic and the North Sea (Hammond et al. 2002). In the Southwest Pacific, no abundance estimate is available, including in New Zealand and Australian waters. Recent efforts using photo-identification (Neumann et al. 2002; Filby 2006) reveal relative abundance and density estimates as the only measure of *Delphinus* abundance within these waters.

1.3. Biology and morphology

Common dolphins have a long rostrum sharply demarcated from the melon, an erect dorsal fin, and pointed pectoral fins (Nishiwaki 1972; Gaskin 1992; Evans 1994). Common dolphin colour patterns constitute the most distinct feature (True 1889), with their elaborate pigmentation pattern of white, grey, yellow and black being the clearest diagnostic features of *Delphinus*. The four-part crisscross pattern is organised as follows: A white belly region, representing a total lack of pigmentation, a buff to pale yellow anterior thoracic patch, a grey flank patch, and a black dorsal-most area (Mitchell 1970; Perrin 1972; Perrin 2002a) (Figure 3). Nonetheless, many colour variations exist, such as the dorsal fin – varying from black or grey with a black border to white with a black border (Neumann et al. 2002) or extent of grey on the tail stock, shape of the grey or yellow lines on the lower sides and intensity of the bluff thoracic patch (Perrin 2002a). Anomalous pigmentation of common dolphins (Perrin et al.

1995; Fertl et al. 2004; Stockin and Visser 2005) and colour development with age (Amaha 1994) have also been reported in previous observations. Many authors believe that some of those variations of colour patterns support the existence of several species and sub-species of common dolphins (Perrin 2002a). In addition, it has been reported that colouration may vary with geographical locations (Amaha 1994; Heyning and Perrin 1994).

Figure 3: Pigmentation pattern on a common dolphin (*Delphinus* sp.) in the Hauraki Gulf, New Zealand (Photo: N. de la Brosse).

Significant sexual dimorphism is documented for populations, with males being on average approximately 9% larger in body length (Westgate 2005). Recent studies in the Northeastern Pacific, reported that total body length of the short-beaked form ranged from 172 to 201 cm for males (n = 28), and from 164 to 193 cm for females (n = 37). In the same region, the body length of the long-beaked species varied from 202 to 235 cm (n = 15) and from 193 to 224 cm (n = 10) for males and females, respectively (Heyning and Perrin 1994). In addition to the body length, the presence of prominent post anal humps in mature males has been claimed to serve as a sexual recognition (Neumann 2001b; Murphy and Rogan 2006), as well as pigmentation of the area adjacent to the genital slit (Evans 1994). However, this last criterion has not always been successful, as the genital blaze is only apparent on a small number of individuals (Neumann 2001b). The long-beaked common dolphin can reach weights of up to 135 kg, and up to 100 kg for the short-beaked form. Physical maturity is considered to be attained after sexual maturity, and is defined when skeletal growth stops, following the fusion

of the vertebral epiphyses with the centra (Chivers 2002). In New Zealand, male and female common dolphins have been reported to grow to 240 and 233 cm, respectively (Stockin and Orams 2009).

Sexual maturity of any cetacean has been reported to vary with several parameters, including health of the animal, quality and quantity of food available and contaminants (Miller 2007). Age and size at sexual maturity even differ within populations of the same species, with common dolphins exhibiting great variation (Collet and Girons 1984; Whitehead and Mann 2000). Generally, female common dolphins tend to become sexually mature earlier than males. In the North Atlantic, females reach sexual maturity around eight years, while males are sexually mature at 11 years of age (Westgate 2005). Other studies in the same location showed that females were sexually mature between six and seven years of age and at lengths of ca. 190 cm, and males between five and seven years and approximately 200 cm (Collet 1981; Collet and Girons 1984; Perrin and Reilly 1984). In the North Pacific, Ferrero and Walker (1995) reported females averaging eight years of age and 10.5 years for males. As a general rule, it is assumed that female cetaceans start to reproduce when at about 85 to 94% of their mean total body length (Whitehead and Mann 2000). There is currently no life history data available for New Zealand *Delphinus*.

The reproductive rate recorded for common dolphins varies between regions and populations. In the Western North Atlantic, the annual pregnancy rate was estimated to be between 5 and 33% of females on any given year (Westgate and Read 2007). In the Northeast Atlantic, an annual pregnancy rate of 26% was determined (Murphy 2004), while 75% of females were observed to be pregnant in the Black Sea (Perrin and Reilly 1984). In the Eastern Tropical Pacific, 30.4% of lactating females were simultaneously recorded pregnant (Danil and Chivers 2007).

For the majority of cetaceans, reproduction has a seasonal component. For most of the mysticetes, breeding occurs as a discrete phase of each year, with others aspects – mainly feeding – being reduced or halted entirely. Seasonal reproduction is least obvious in the offshore tropical odontocetes. The primary reasons for this seasonal variability are prey availability, energy demands and temperature of the water (Whitehead and Mann 2000). Seasonal peaks in ovulation and birth have been reported in number of odontocetes, including the harbour porpoise, *Phocoena phocoena* (Read 1990), striped dolphin, *Stenella*

coeruleoalba (Miyazaki 1984) and bottlenose dolphin, *Tursiops truncatus* (Urian et al. 1996). In temperate waters, common dolphins have been reported to reproduce seasonally, with calving peaks occurring from May to June off France (Collet 1981), May to August off Great Britain (Sabin et al. 2002), May to September in the Northeast Atlantic (Murphy 2004), June to August in the Black Sea (Tomilin 1957), July to August off Spain (López et al. 2002) and in the Western North Atlantic (Westgate and Read 2007). However, no seasonality in female reproduction was observed in the Eastern Tropical Pacific region, with calving occurring year-round (Danil and Chivers 2007).

Very little is known about the reproductive biology of common dolphin in the Southwest Pacific. In New Zealand waters, common dolphin breeding is considered seasonal (Neumann 2001b) although in the Hauraki Gulf, calves are present year-round (Schaffar-Delaney 2004, Stockin et al. 2008b), though most prevalent in the austral summer months of December and January (Schaffar-Delaney 2004; Stockin et al. 2008b). The high number of offspring observed year-round strongly suggests that the Hauraki Gulf plays an important role as a nursing area for common dolphins (Schaffar-Delaney 2004; Stockin et al. 2008b). In this region, 70% of groups were reported to contain immature animals, 25% of which were neonates (Stockin et al. 2008b). Potential reasons for this include the sheltered and warm waters of the Hauraki Gulf. Areas with calm seas and warmer waters have been reported to be favoured by mothers and their offspring, as it reduces energy consumption (Evans 1987; Elwen and Best 2004). Being sheltered by the Coromandel Peninsula and Great Barrier Island, the waters of the Hauraki Gulf appear to be relatively calm on most days (Bercusson and Walsby 1999), with variation in water temperatures which are not as wide as in other areas inhabited by delphinids, and physical characteristics of the water remaining relatively stable throughout the year (Schaffar-Delaney 2004).

Gestation periods are different between species and among populations of the same species, and tend to increase with body size for marine mammals (Whitehead and Mann 2000). The shortest gestation length has been recorded for harbour porpoise and pygmy sperm whale (*Kogia breviceps*), lasting approximately 9 months (Harrison et al. 1969; Whitehead and Mann 2000), while the longest period (up to 15 or 16 months) has been observed in sperm whale (*Physeter macrocephalus*) and killer whale (*Orcinus orca*) (Harrison et al. 1969; Perrin and Reilly 1984; Marino 1997). Gestation of the common dolphin varies between regions, but generally ranges from 9.2 (Asdell 1964) to 11.5 months (Murphy 2004). Collet (1981)

estimated gestation at between 10 and 11 months for *D. delphis* from Northeast Atlantic, which is similar to the findings from the Black Sea (Perrin and Reilly 1984). In the Northwest Atlantic, gestation lasts for approximately 11.5 months (Westgate 2005), 11.1 months in central North Pacific (Ferrero and Walker 1995), and 11.4 months in the Eastern Tropical Pacific region (Danil and Chivers 2007). Calving intervals vary between 1.7 (Murphy 2004) and 2.1 years (Danil and Chivers 2007).

From captive and post-mortem observations of pregnant females, it appears that cetaceans tend to have one single calf at a time, with twins occurring occasionally and often resulting in non-viable calves (Harrison et al. 1969; Evans 1987; Whitehead and Mann 2000). One twin gestation of a stranded common dolphin (*D. delphis*) was recorded on the north western Spanish coast (González et al. 1999). At birth, common dolphins have several characteristics that differentiate them from older individuals. The size of newborn calves is the most striking feature, at a minimum of 75 cm (Harrison et al. 1969; Gaskin 1992) and a maximum of 105 cm (Perrin and Reilly 1984). Calves in the North Pacific gain on average 20 to 25 cm in the first six months, and approximately 40 to 45 cm within the first year (Ferrero and Walker 1995). Newborns appear like their mothers in most morphological aspects, with crisscross pattern and distinct hour glass colouration already present, although pigmentation is not yet fully developed and appears paler in the thoracic patch (Gaskin 1972). Dorsal fins tend to be pale, but increase in contrast with age (Heyning and Perrin 1994). Neonates are also characterised by bent pectoral and dorsal fins, in addition to the presence of foetal lines on their body (Figure 4). These vertical lines are located symmetrically on each side of the thorax (McBride and Kritzler 1951).

Within hours after birth, the newborn starts nursing on the lipid-rich milk the mother produces. Therefore, neonates will spend most of their time in *infant* position (Mann and Smuts 1998), nursing just under the surface (Harrison et al. 1969). The female's nipples are located on her ventral side, about three quarters of the way from her rostrum to the tail tip. Several studies have shown that nursing frequency decreases as calves age (McBride and Kritzler 1951; Harrison et al. 1969). As prey intake increases, nursing events become less frequent as calves progressively develop foraging skills and spend more time feeding independently.

Figure 4: Young calf with foetal folds visible on both sides of the body. White arrows point to three visible foetal folds (Photo: N. de la Brosse).

Lactating females require a greater quantity of high calorific prey to be eaten in order to produce relatively costly milk (Bernard and Hohn 1989). It has been suggested that lactation period may be linked to social learning in most cetacean species (Brodie 1969), lasting much longer than is required for survival. Estimates of the length of lactation vary with regions, with periods of six months recorded in the Black Sea (Perrin and Reilly 1984), to approximately 10 months in the Northeast Atlantic (Collet 1981; Murphy 2004), and even up to 16.5 months for the Eastern Tropical Pacific (Danil and Chivers 2007). Lactation length is likely to be related to prey availability, and the difficulty for calves in using methods to find and capture food (Whitehead and Mann 2000).

1.4. Behaviour

1.4.1. Social organisation

Living in groups is highly beneficial for individuals of social species. In general, group living enhances resource acquisition (Creel and Creel 1995), vigilance and defence against other predators, as well as improving the care of the offspring (Clutton-Brock 2002). Some species, such as the killer whale, have been reported to form permanent groups that they keep for their entire life (Bigg et al. 1990). Other delphinid species – including bottlenose (Smolker et al. 1992), dusky (*Lagenorhyncus obscurus*) (Würsig and Würsig 1980), spinner (Karczmarski et al. 2005) and common dolphins (Neumann 2001b; Bruno et al. 2004) live in a fission-fusion society, whereby group size and composition change as a result of individual movements. Social, ecological, demographic, and life history factors influence fission-fusion social dynamics of groups, whose composition may change on a daily or diel basis (Connor et al. 2000; Bearzi et al. 2005). Specific factors include food density and distribution, predator pressure, community size, presence and number of females, cooperative foraging, intra-specific competition and aggression, infant socialization, and social pressure to meet and interact with all individuals in the community (Doran 1997).

1.4.2. Mother-offspring relationships

After birth, mother and offspring are in near constant contact. Several factors explain the preference for close contact during the time of high dependence of offspring on their mothers. First, at young age, offspring show uncoordinated swimming, with exaggerated movements, characterised by wriggling, tilting and rapid course changes (Johnson and Norris 1994), and difficulties with submergence (Cockcroft and Ross 1990). Close proximity represent a means for mothers to control their offspring's movements (Fellner 2000). Mother-offspring pairs are also characterised by a high degree of coordinated breathing. As they grow, offspring will establish their own breathing rate (Cockcroft and Ross 1990) and synchrony will tend to decrease (Mann and Smuts 1999). Second, close proximity with the mothers provides accurate nursing and lactation, which is of importance during the newborn period (Trivers 1974). Finally, the low occurrence of separation allows newborns to develop their social skills and recognize their mothers (Mann and Smuts 1999).

Delphinus offspring of all age classes have been mostly recorded swimming side by side with their mothers, in *echelon* position (Fellner 2000; Schaffar-Delaney 2004). This position likely represents several advantages to the offspring, such as providing a ride with the pressure wave caused by the mother's body as she moves through the water (Norris et al. 1961). This is similar to the pressure created by a vessel when dolphins bow ride, a mechanism therefore, enabling offspring to conserve energy (Evans 1987). In addition, such a position would benefit offspring by allowing the coordination of movements, diving and synchronous breathing (Cockcroft and Ross 1990; Mann and Smuts 1999).

As offspring develop, their dependence on their mother decreases, and the role and responsibility on mothers in maintaining proximity will disappear (Trivers 1974). Thus, common dolphin offspring increase the occurrence and the frequency of separations as they change age class. In New Zealand, juveniles have been recorded to spend significantly more time separated from their mothers than newborns (Schaffar-Delaney 2004). Mann and Smut (1999) suggest that newborns have to learn to separate from their mothers at a young age in order to develop the locomotive skills necessary for survival. The improvement of their mobility will also enhance their ability to reunite with their mother, resulting in a greater level of independence (Mann and Smuts 1998; 1999). However, offspring are likely to extend their close relationship to the mother for several years. In bottlenose dolphin, offspring have been reported to remain close to the mother for between three and eight years (Shane et al. 1986; Wells et al. 1987; Bearzi et al. 1997; Grellier et al. 2003). These long periods of social dependency show the importance of mother-offspring relationships in the development of the newborn (Grellier et al. 2003). Mothers transmit important information relating to feeding strategies and resource distribution, recognition of the habitat, predator avoidance, and patterns of social interactions (Wells et al. 1987; Grellier et al. 2003).

1.4.3. Foraging behaviour

The foraging behaviour of dolphins is closely affected by the local ecology, and is likely to change with varying conditions (Shane 1990; Neumann 2001b). Ecological factors include time of day, season, water depth, water temperature, bathymetry, tide, and anthropogenic factors (Shane 1990). Delphinid species have developed some suitable foraging

specialisations to adapt to prey availability, habitats and ecological environment, thereby promoting their survival. Such foraging techniques are highly variable (Lynas and Sylvestre 1988; Acevedo-Gutierrez 2002; Visser 2005; Ford and Ellis 2006; Weiss 2006; Vaughn et al. 2007), and the energetic consequences of different strategies will have an important impact on the targeted food consumed (Bowen et al. 2002). Specialised feeding behaviour is required to detect and pursue prey, as well as to reduce intraspecific competition for resources (Partridge and Green 1985). Examples of this include cooperative hunting and strand feeding in killer whales (Guinet 1991; Hoelzel 1991; Baird and Dill 1995), and methods used by humpback dolphins (*Sousa plumbea*) to drive prey onto exposed sand banks at low tide (Peddemors and Thompson 1994). Feeding behaviours are shaped in response to habitat type and prey resources, and may also be population or site specific (Sargeant et al. 2005).

In contrast to other delphinids, foraging behaviour of common dolphins has been poorly documented. *Delphinus* show high variability in behavioural repertoires (Neumann 2001a; Stockin et al. 2009a), and adapt feeding strategies, according to the type of targeted prey and habitat within which they are feeding. Common dolphins have often been observed cooperatively driving fish into a tight bait ball (Würsig 1986; Gallo Reynoso 1991; Clua and Grosvalet 2001; Neumann and Orams 2003; Burgess 2006). In New Zealand, several distinct foraging strategies used by common dolphins from the western Bay of Plenty have been described (Neumann and Orams 2003). Individual strategies identified included *high-speed pursuits*, *fish-whacking*, and *kerplunking*, while cooperative methods included *carouselling*, *line-abreast* and *wall-formation*. *Carouselling* was the most frequently observed strategy employed by common dolphins in this region (Neumann and Orams 2003). Another similar study undertaken in the Hauraki Gulf, suggested that common dolphins in this neighbouring region exhibited greater plasticity in foraging strategies (Burgess 2006). Differences in foraging strategies recorded between these studies likely reflect the differing environments (oceanic *versus* coastal), as well differences in prey species and availability. Foraging activity was the predominant behaviour observed in the Hauraki Gulf (Stockin et al. 2009a), possibly due to the year round availability of prey. Stockin et al. (2008a) suggest 46.8% of the activity budget is attributed to foraging alone in the Hauraki Gulf, a value significantly greater than in the Bay of Plenty (16.2%). Furthermore, foraging activity in the Hauraki Gulf is not influenced by the time of day, possibly because of the abundance of food source throughout the day (Burgess 2006). This is contrary to findings from the Bay of Plenty, where dolphins

exhibit two diurnal peaks in feeding activity (Neumann 2001c). This all day feeding activity in the Hauraki Gulf likely reflects the productive waters (Stockin et al. 2009a).

Mixed-species aggregations have been documented world-wide during cetacean feeding behaviour (Frantzis and Herzing 2002). Numerous associations and interactions between delphinid species occur (Frantzis and Herzing 2002; Bearzi 2005), as well as associations of dolphins with other species, such as seabirds (Evans 1982). Other species regularly associated with common dolphins include bottlenose dolphins, striped dolphins, Risso's dolphins (*Grampus griseus*), pilot whales (*Globicephala macrorynchus*), harbour seals (*Phoca vitulina*), great shearwaters (*Puffinus gravis*), terns (*Sterna* sp), gannets (*Sula* sp), petrels (*Procellaria* sp), and a few baleen cetacean species (Evans 1982; Clua and Grosvalet 2001; Filby 2006).

In New Zealand waters, common dolphins are most frequently observed with Bryde's whales (*Balaenoptera brydei*) and Australasian gannets (*Morus serrator*) (Constantine and Baker 1997; O'Callaghan and Baker 2002; Neumann and Orams 2003; Burgess 2006; Stockin et al. 2008b; Wiseman 2008). Other species found in association include sooty shearwaters (*Puffinus griseus*), Buller's shearwaters (*P. bulleri*), white-faced storm petrels (*Pelagodroma marina*), sei whales (*B. borealis*) and minke whales (*B. acutorostrata*) (Neumann and Orams 2003; Burgess 2006; Stockin et al. 2008b). While mixed-species groups can result in a more efficient utilisation of the food resources for one or all participating species (Stensland et al. 2003), potential advantages of multi-specific groups to common dolphins within New Zealand waters remain unclear (Wiseman 2008; Stockin and Orams 2009).

1.4.4. Diet

Cetacean diet has been investigated through stomach content analyses (Santos et al. 2001; De Pierrepont et al. 2005; Beatson et al. 2007), use of stable isotopes (Walker and Macko 1999; Niño-Torres et al. 2006) and fatty acids (Iverson et al. 1997; Olsen and Grahl-Nielsen 2003; Learmonth 2006) of stranded or by-caught specimens. Common dolphins typically prey upon epipelagic shoaling fish e.g. mackerel (*Trachurus* sp.), anchovy (*Engraulis encrasicolous*), pilchard (*Sardina pilchardus*), herring (*Clupea harengus*), blue whiting (*Micromeristius poutassou*) as well as smaller mesopelagic fish and squids (Pascoe 1986; Overholt and

Waring 1991; Evans 1994; González et al. 1994; Young and Cockcroft 1994; Hassani et al. 1997; Silva 1999; Perrin 2002b; Brophy 2003; Santos et al. 2004; Lahaye et al. 2005; Pusineri et al. 2007). *Delphinus* is considered to be an opportunistic predator, although recent evidence suggests that prey species may not be as diverse as previously assumed for this species (Gibbs et al. 2000), with diet known to be geographically varied (Gaskin 1992).

Within New Zealand, only one quantitative dietary study has been completed (Meynier et al. 2008). In that study, at least 31 fish and seven cephalopod species were identified as prey for the New Zealand population. The prevalent prey were jack mackerel, anchovy (*E. australis*), arrow squid (*Nototodarus* sp), cardinal fish (*Epigonus* sp), grey mullet (*Mugil cephalus*), as well as pelagic species such as redbait (*Emmelichthys nitidus*), yellow-eyed mullet (*Aldrichetta forsteri*), scarpee (*Helicolenus percoides*), dwarf cod (*Austrophycis marginata*), and other mesopelagic fish such as lanternfish (*Myctophidae*). This concurs with additional observational data from common dolphins in the Bay of Plenty, showing common dolphins feeding on schooling fish including jack mackerel, kahawai (*Arripis trutta*), yellow-eyed mullet, flying fish (*Cypselurus lineatus*), parore (*Girella tricuspidata*) and garfish (*Hyporamphus ihi*) (Neumann and Orams 2003). The same fish species were also reported for the Hauraki Gulf, and an additional observation of New Zealand pilchard (*Sardinops neopilchardus*), a locally abundant species (Kendrick and Francis 2002).

Previous dietary studies of common dolphins suggest that they consume the most abundant, easily captured prey. Squid species are also commonly found in the Hauraki Gulf (Kendrick and Francis 2002), and could play an important role in the diet of common dolphins. Stockin and Orams (2009) found the remains of arrow squid as the most frequently recorded prey species in the stomachs of nine post-mortem carcasses of common dolphins that stranded in the Hauraki Gulf. Diet analyses conducted on *Delphinus* overseas suggest that lactating females might limit feeding on squid despite its high calorific value, as foraging on squid involve deep dives, and thus, separations from their offspring (Bernard and Hohn 1989). However, shallow waters of the Hauraki Gulf allow feeding on these energetic prey species without deep diving and limit separation with offspring, especially during lactation. Having such a large variety of prey types requires great adaptation in both foraging skills and predator avoidance accordingly.

1.5. Conclusion and hypotheses

This study aims to extend our knowledge of common dolphin behavioural ecology in the Hauraki Gulf, New Zealand. In particular, this research is designed to address the paucity in our understanding of mother-offspring dynamics in relation to feeding opportunities. Studies on common dolphin behaviour are limited, thus there have been no previous systematic efforts assessing the dynamics of mother-offspring pairs when engaged in foraging activities. Considering this lack of empirical data, several specific hypotheses were tested using data collected during field observations. These hypotheses are presented below (note: Only the test hypothesis is presented here. The null hypothesis corresponds to the reverse statement).

Environmental parameters:

H1: Distance from shore affects the foraging strategies employed by mother-offspring pairs.

H2: Water depth affects the foraging strategies employed by mother-offspring pairs.

H3: Sea surface temperature affects the foraging strategies employed by mother-offspring pairs.

H4: Group size affects the foraging strategies employed by mother-offspring pairs.

Anthropogenic parameters:

H5: Presence of mother-offspring pairs affects the reaction of foraging dolphins to the approach of boats.

H6: Presence of offspring affects the minimum distance between dolphins and the tour boat.

Associated species:

H7: Presence of Australasian gannets affects foraging strategies employed by mother-offspring pairs.

H8: Presence of Bryde's whales affects foraging strategies employed by mother-offspring pairs.

H9: Mother-offspring pairs limit interactions with Australasian gannets during foraging.

H10: Mother-offspring pairs limit interactions with Bryde's whales during foraging.

Foraging strategies:

H11: *Line-abreast* foraging affects the position of offspring within a group.

H12: *Carousel* foraging affects the position of offspring within a group.

H13: *Wall formation* foraging affects the position of offspring within a group.

H14: Mother-offspring pairs are less likely to engage in *individual* foraging strategies.

H15: Mother-offspring pairs avoid the central bait ball during *carouselling* feeding.

H16: The prevalence of *cooperative* strategies used by focal groups increases with the presence of offspring.

Foraging phases:

H17: Percentage of time offspring spend in echelon position decreases during *individual* foraging strategies.

H18: Percentage of time newborn/calf spends in infant position decreases during *individual* foraging strategies.

This study aims to contribute important knowledge and insight into socio-biology and behaviour of common dolphins. While the Hauraki Gulf may be an important feeding (Stockin et al. 2009a) and nursing area (Stockin et al. 2008b) for this species, it is also an important economic and recreational resource, supporting a variety of human activities, including recreational and commercial fishing, tourism and shipping. Some of those activities, including tourism, are known to impact the foraging behaviour of common dolphins (Stockin et al. 2008a). Common dolphins exhibit a degree of site fidelity to the Hauraki Gulf, a factor which may result in their susceptibly to cumulative impacts (Stockin 2008; Stockin and Orams 2009).

Chapter Two: Methods and Materials

Figure 5: Mother-calf common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand (Photo: N. de la Brosse).

2.1. Study site

This study was conducted in the Hauraki Gulf (Figure 6), a large, shallow, semi-enclosed coastal body of temperate water located on the east coast of North Island, New Zealand, approximately 20 km north of Auckland city (36° 51' S, 174° 46' E). In 1967, the Hauraki Gulf was declared a Marine Park in order to protect the islands and their surrounding waters (Hauraki Gulf Maritime Park Board, 1983). Approximately 47 islands are included in the Gulf, spreading over 13,600 km² of Pacific Ocean. The Hauraki Gulf is landlocked to the west and south, partly protected in the east by the Coromandel Peninsula and Great Barrier Island, and open to the north. Water depth in this region averages between 40 and 45 m, with a maximum depth of 53 m. Water temperatures in the Hauraki Gulf vary from approximately 12°C in austral winter to about 22°C in austral summer (Hauraki Gulf Maritime Park Board 1983).

An extremely productive area, the Hauraki Gulf exhibits a high diversity of biological fauna, influenced by a warm subtropical East Auckland Current, especially around the outer island groups (Stanton et al. 1997). In late austral winter and spring, the Hauraki Gulf exhibits high levels of nutrient availability associated with high levels of chlorophyll. This results from important upwellings produced by the prevailing westerly winds (Chang et al. 2003). In the austral summer, predominant easterly winds lead to downwellings and the movement of warm, nutrient poor waters towards the coast (Proctor and Greig 1989).

2.2. Data collection

2.2.1. Research vessel

Non-systematic surveys were conducted in the Hauraki Gulf, Auckland from 18 March to 27 July 2009 inclusive. Weather permitting (Beaufort Sea State < 4), daily surveys were conducted from *Dolphin Explorer*, a commercial tour boat. *Dolphin Explorer* is a 20 m catamaran powered by two 350-horse power Scania inboard engines, with a cruising speed of approximately 19 kt. This vessel has been conducting *swim with* and *dolphin watching* programmes in the Hauraki Gulf since September 2000 under a Department of Conservation
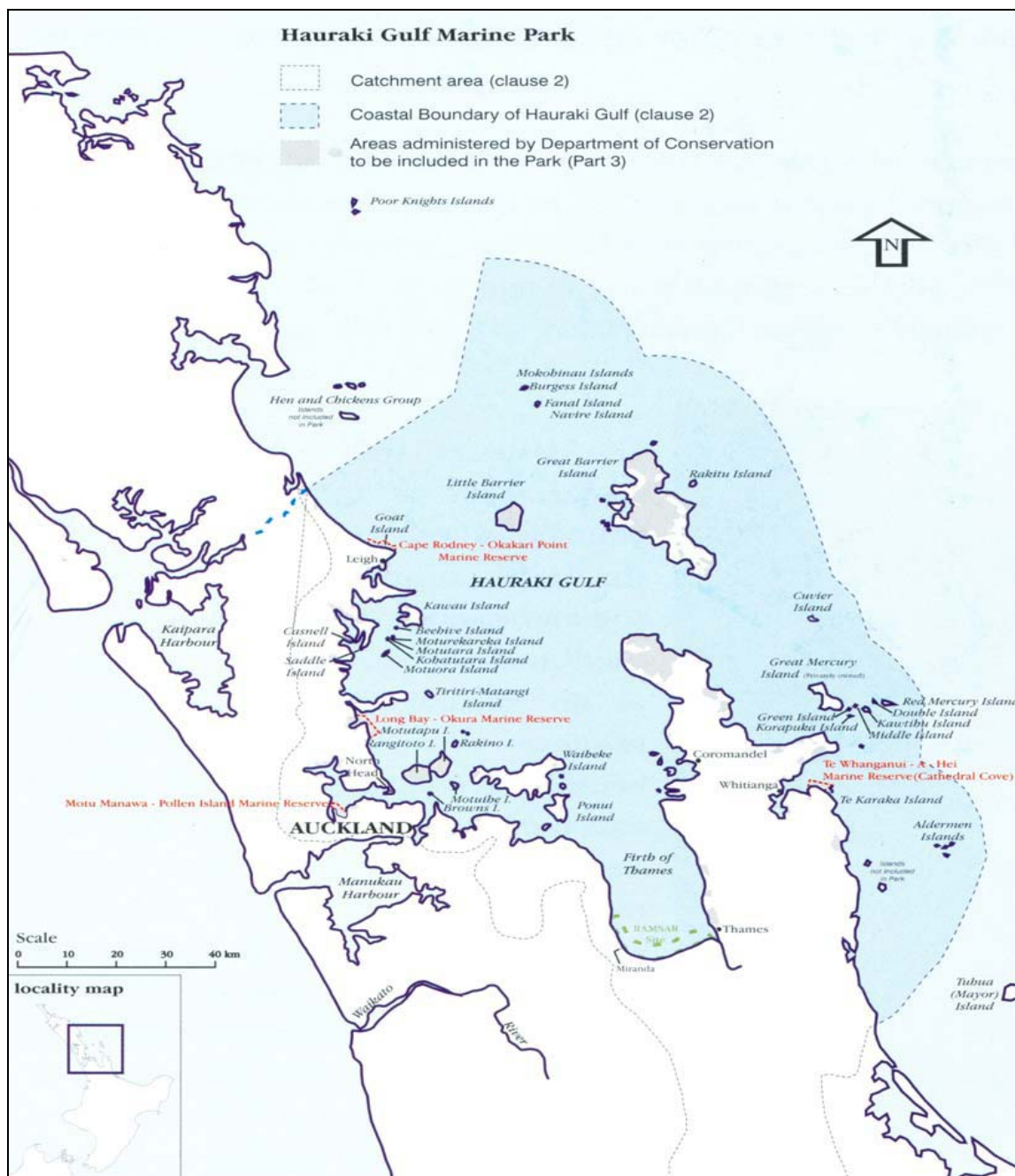
Figure 6: The Hauraki Gulf Marine Park, east coast of the North Island, New Zealand (Source: Department of Conservation 2002).

permit (PER/02/03/00). In the austral summer time, the vessel runs two daily trips of 4.5 hr, while only one trip is operated during the austral winter. The front deck, at an elevation of two metres above sea level, was used as the observational platform for this research. A number of previous studies have used this vessel as a platform of opportunity (PoO) to undertake research on marine mammal and marine birds within the region (Schaffar-Delaney 2004; Stockin 2008; Wiseman 2008). The cetacean species most frequently encountered by the tour operator are common dolphins (*Delphinus* sp.) and Bryde's whales (*Balaenoptera brydei*), observed during 90% and 75% of surveys, respectively. Bottlenose dolphins (*Tursiops truncatus*) and killer whales (*Orcinus orca*) can also be observed on a relatively regular basis in this region.

Survey routes onboard *Dolphin Explorer* were influenced by sea condition, weather forecast, as well as location of previous sightings and activities (presence of marine mammals and/or sea birds). Thereby, search effort for the dolphins was conducted along two routes:

-   The 'Eastern route', going toward the Coromandel Peninsula;
-   The 'Northern route', going toward Kawau Island and Little Barrier Island.

Experienced observers continuously scanned the horizon using hand-held binoculars (Pentax 8 x 40 magnification) for any signs of marine mammal activity. Each scan covered 180° abeam of the vessel, providing up to approximately 10 nmi visibility in good conditions. Splashes (i.e. dolphin jumping), blows, dorsal fins and bird aggregations, (especially Australasian gannets, *Morus serrator*) were used as sighting cues. This seabird is known to associate with common dolphins (Gallo Reynoso 1991; Neumann 2001c; O'Callaghan and Baker 2002; Burgess 2006; Stockin 2008; Stockin et al. 2008a; Stockin et al. 2008b; Wiseman 2008).

2.2.2. Approach and environmental data

Upon sighting dolphins, *Dolphin Explorer* would slowly approach the group according to the N.Z. Marine Mammals Protection Regulations (1992), in order to minimise any potential effects on dolphin behaviour (Mann et al. 2000). At a distance of approximately 300 m from the dolphin group, the vessel would stop to assess the dolphins' behaviour and course. Subsequently, *Dolphin Explorer* would approach the group at low and steady speed, on a

course parallel to the dolphins, slightly to the rear of the group. Once within approximately 100 m of the animals, start time and location of the encounter were recorded using a Global Positioning System, and environmental data (water depth, sea surface temperature, weather, wind and visibility) were logged. Focal group follows with instantaneous scan sampling of the predominant behaviour (Altmann 1974; Mann 1999a) was used to measure behaviour. Furthermore, the presence of any other vessel was recorded. Boat numbers, as well as the distance from the focal group were assessed, since vessel presence has been shown to impact on dolphin foraging activity (Lusseau 2003; Constantine et al. 2004; Stockin et al. 2008a).

Duration of focal follows depended upon time spent with dolphins. The decision to leave was taken by the skipper, in case of changes in dolphins' behaviour (i.e. increasing speed, spatial avoidance of the boat, change in direction of travel, change of diving behaviour), deteriorated weather conditions, and/or time to return to the harbour.

2.2.3. Defining dolphin groups

When conducting focal follows, it is important to define the rule of inclusion of individuals in the group (Mann 1999a). Two main ways have been identified to define dolphin groups. Firstly, individuals involved in the same coordinated activity or travelling in the same direction as other dolphins. However, this rule has limitations, considering that some animals could be involved in different activities, even though they are in close association. Furthermore, dolphins having the same activity far away will not be considered as part of the focal group (Mann et al. 2000). Secondly, spatial proximity of individuals is also used to describe a group, if animals are located within a certain distance of each other (Mann et al. 2000). The distance of individual inclusion in the group varies between studies, depending on the focal species and researcher's choice. As such, the 10 m *chain rule* has been commonly used (Connor et al. 1992; Smolker et al. 1992; Mann and Smuts 1999; Mann et al. 2000), as well as the 100 m *chain rule* (Wilson et al. 1993). Body length measures might also set distance criteria between individuals (Weinrich 1991; Fertl 1994). Nevertheless, those methods have shown limitations, as it does not take into consideration the animals' behaviour. Also, some species are known to communicate over long distances (Tyack 2000), and some individuals could be in acoustic proximity rather than spatial proximity. As such, in this

study, individuals located within a 100 m radius were considered to be part of the same group, with a number of animals observed in association, moving in the same direction and usually engaged in the same activity (Shane 1990; Stockin et al. 2009a).

2.2.4. Instantaneous scan sampling

During focal group follows of common dolphins, group composition, behaviours, foraging strategies (if feeding) and associated species were sampled every two minutes. Instantaneous scan sampling was used to record a group's current activity at pre-selected moments in time (Altmann 1974). This was considered more appropriate than individual group follows because groups were often large and individuals were rarely recognisable. Also, individuals frequently changed their position within the group, making it impossible to follow one individual continuously (Neumann 2001a).

At the start and the end of each encounter, group size and composition, behaviour, and associated species were recorded onto a standardised data sheet (see *Appendix 1*). Group size was estimated, based on a visual count or estimate, scanning the group continuously. For each group, the number of individuals was recorded in one of the following categories: 1-10, 11-20, 21-30, 31-50, 51-100, >100. According to Neumann (2001b), reliable counts can be done for groups of up to 30 individuals. Therefore, as groups reached greater numbers and exact counts became too difficult to assess, a broader range was used.

The following additional parameters were subsequently recorded every two minutes onto a separate data sheet (see *Appendix 2*).

a) Group composition

Many terms have been used to describe group composition, including newborn, infant, calf, juvenile, adult (Table 1). Those terms often relate to biological criteria, such as individual size, presence of foetal folds, folded fins, and behaviour (Connor et al. 1996; Bearzi et al. 1997; Herzing 1997; Neumann 2001b; Constantine 2002). In the present study, size and independence were the primary criteria used to determine the individual category. For

offspring, the total body length (TBL) was compared to that of the accompanying adults to identify the age class. Thus, group composition was described using four age categories. Note, sub-adults were not considered in the present study since sexual maturity could not be ascertained by TBL alone.

Table 1: Definition of age categories recorded for common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand.

Age categories	Definition
Newborn	Individual measuring less than half the size of the mother's body length, often with visible foetal folds, curled dorsal fin and lighter colouration (McBride and Kritzler 1951; Schaffar-Delaney 2004).
Calf	Animal measuring approximately half the size of the mother, and consistently observed in association with an adult animal (Fertl 1994; Ferrero and Walker 1995; Schaffar-Delaney 2004).
Juvenile	Animal measuring around two thirds of the length of the mother, frequently observed swimming in association with an adult animal, though not in the infant position, suggesting they are weaned (Ferrero and Walker 1995; Schaffar-Delaney 2004).
Adult	All other dolphins not included in any of the previous categories.

During foraging bouts, particular attention was paid to offspring position within the group. Offspring could either be located in the centre of the foraging bout, where feeding activity and fish ball occurred, or remain at the peripheral edge of the foraging group, away from the prevalent feeding activity.

b) Behaviour

In the present study, five categories of behavioural states were recognised (Table 2), derived from the descriptions used by Shane (1990), and adapted by Neumann (2001b) and Stockin et al. (2009a) for New Zealand common dolphins. Behavioural states were recorded every two minutes, using a continuous scan method (Mann 1999a) in order to identify the correct activity state. Describing behaviours requires a certain amount of time, as it refers to a prolonged activity state and not an isolated behavioural event (Altmann 1974; Martin and Bateson 1993; Mann 1999a; Schaffar-Delaney 2004). Short behaviours are referred to as events of short durations, such as body movements (e.g. head slap, tail slap, breach).

c) Foraging strategies

New Zealand common dolphins have been observed using several methods to capture prey (Neumann and Orams 2003; Burgess 2006). These methods fall into two primary categories:

- Coordinated feeding, in which dolphins are involved collectively in herding and pursuing prey.
- Individual strategies, in which a dolphin is involved in pursuing and/or capturing its prey in isolation of any other dolphin.

Neumann and Orams (2003) described the following methods employed by common dolphins when foraging: *High-speed pursuit* (Figure 7), *kerplunking* (Figure 8), *fish-whacking* (Figure 9), *line-abreast* (Figure 10), *wall formation* (Figure 11), *carouselling*, and *bubble-blowing* (Figure 12). During focal follows, only the predominant foraging strategy was recorded on the data sheet. The predominant feeding strategy was determined as the strategy state in which more than 50% of the animals were involved at each instantaneous sample.

Table 2: Definition of behavioural states recorded for common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand (Shane 1990; Neumann 2001b).

Behavioural states	Definition
Travel	Dolphins move at a sustained speed, in the same direction, making noticeable headway along a persistent compass bearing.
Mill	Dolphins remain in the same location, not moving in any definite direction, changing their heading, showing no surface behaviours, asynchronous breathing, and no apparent physical contact between individuals.
Rest	Dolphins move slowly at the surface. Individuals are usually within a few body lengths of each other.
Forage	Dolphins are involved in any effort to capture and consume prey, chasing prey at the surface, coordinated deep diving, and rapid circle swimming. Prey may be observed at the surface.
Socialise	Some or all group members are in constant physical contact with one another, oriented toward another, and often displaying surface behaviours. Dolphins are mainly involved in aspects of play, rubbing and mating.
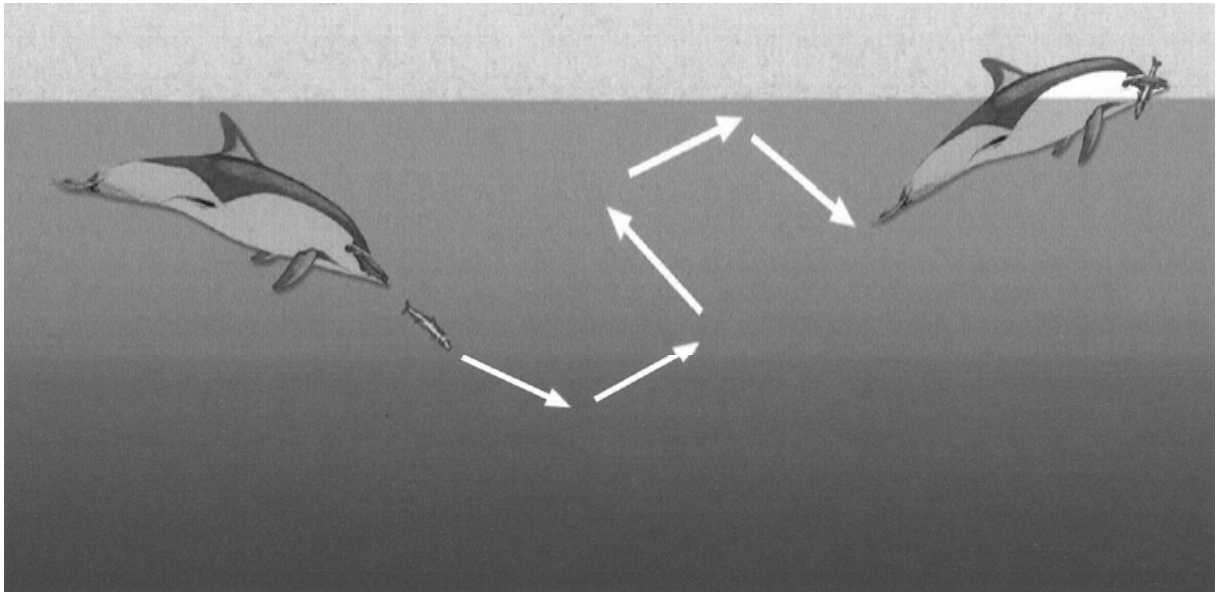
Figure 7: *High-speed pursuit*: Dolphin pursues solitary prey on a zig-zagging chase (Neumann and Orams 2003).
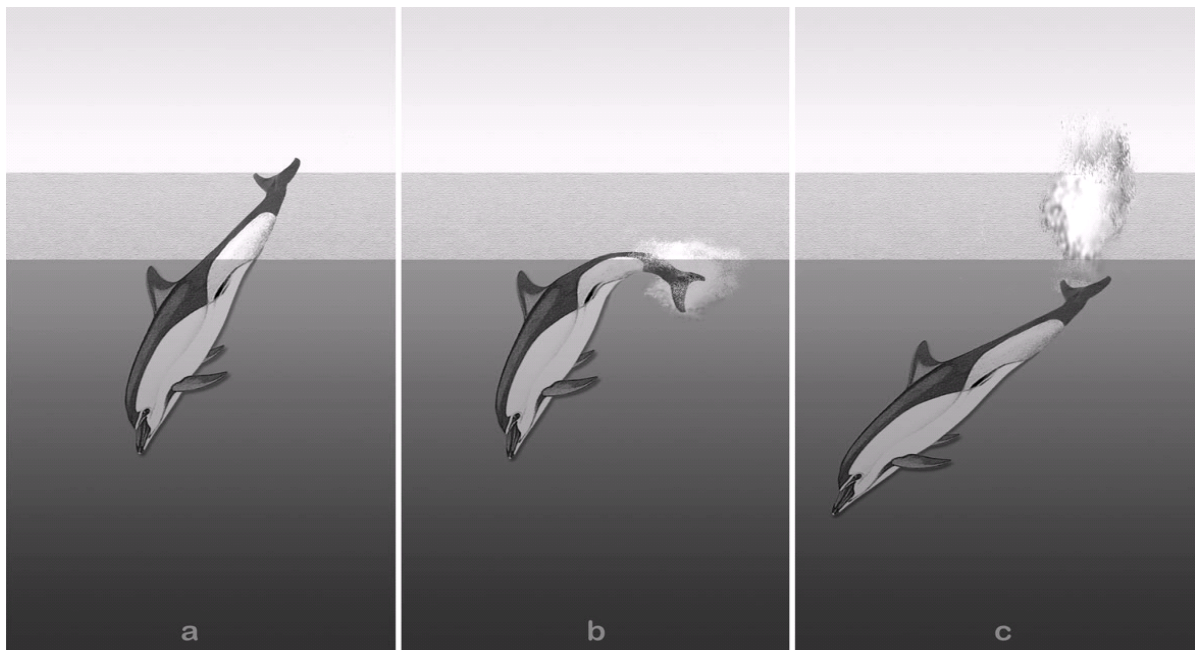
Figure 8: *Kerplunking:* a) Dolphin lifts flukes vertically above the surface, b) flukes are thrust down and forward, c) the dolphin straightens and dives, while cavitation splash is observed at the surface (Neumann and Orams 2003).
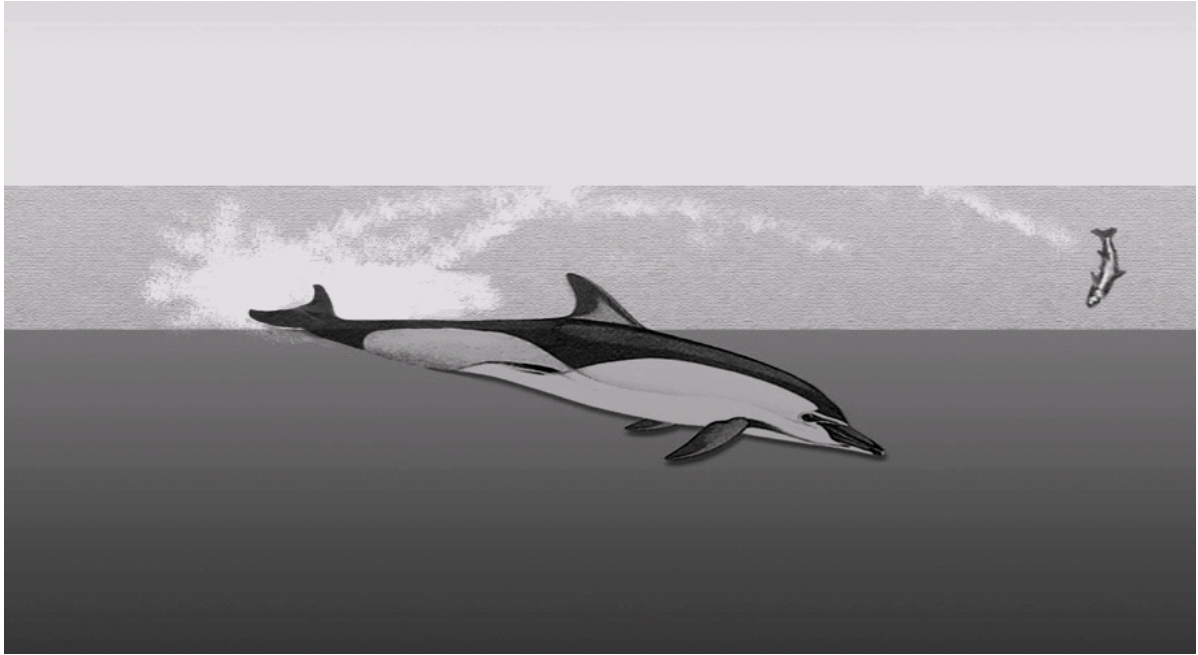
Figure 9: *Fish-whacking:* Dolphin stuns its prey by catapulting it through the air with its tail flukes (Neumann and Orams 2003).
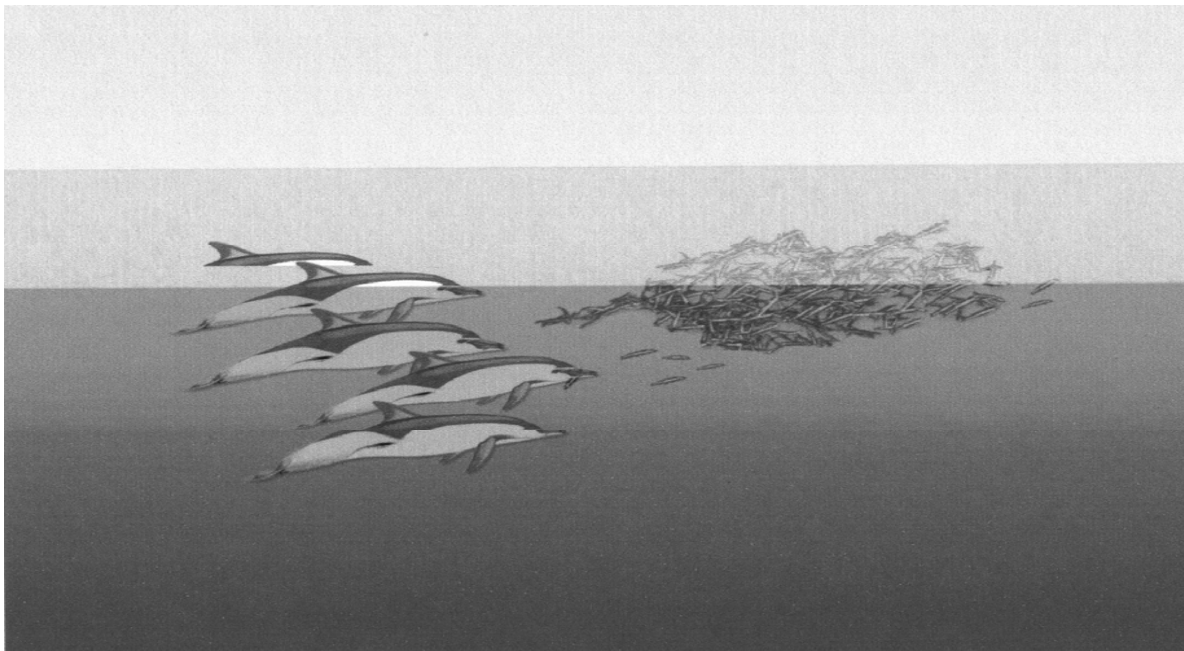
Figure 10: *Line-abreast:* Dolphins swim closely side-by-side, driving fish in front of them (Neumann and Orams 2003).
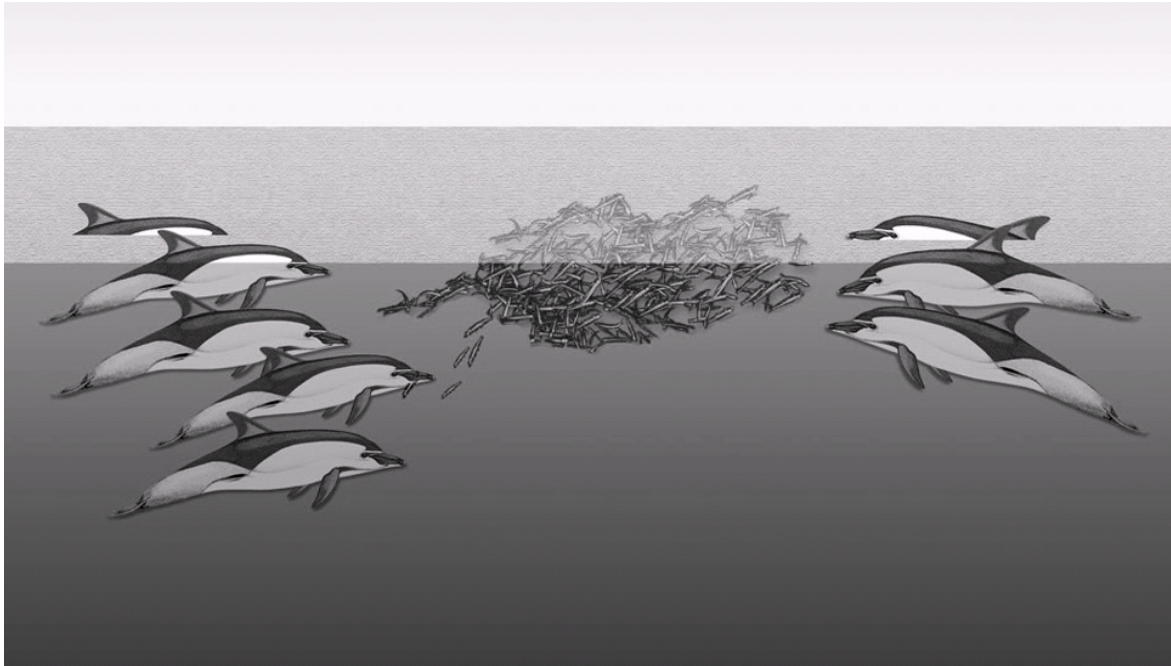
Figure 11: *Wall formation:* Dolphins drive fish towards another group of dolphins (Neumann and Orams 2003).
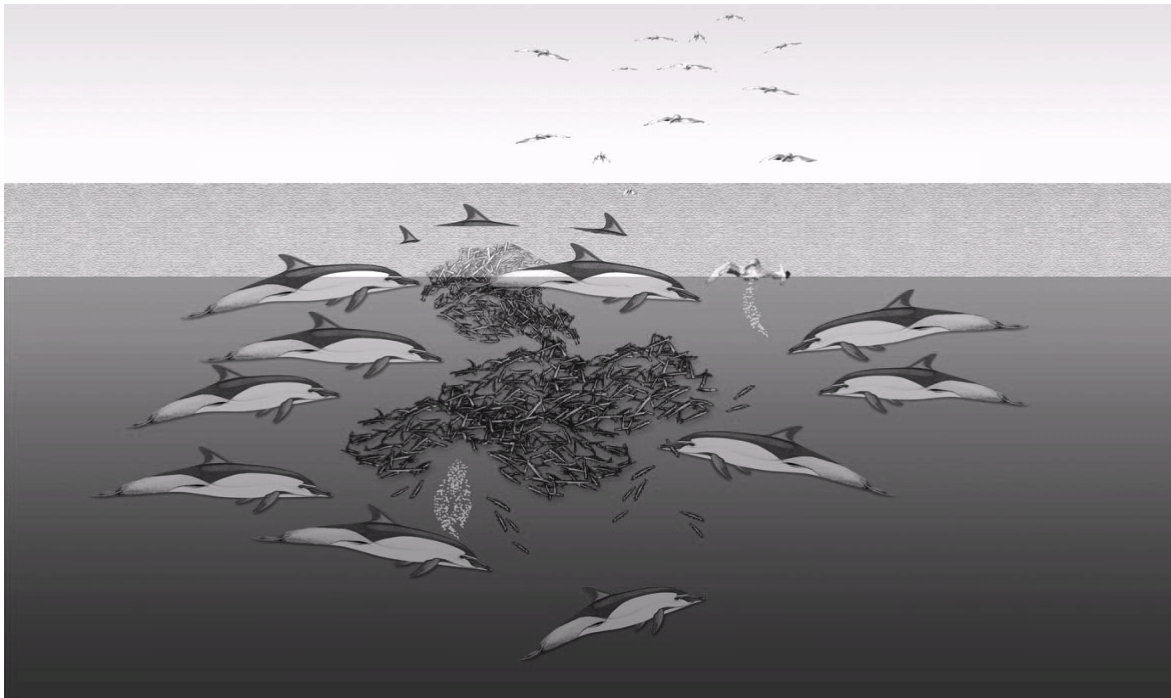
Figure 12: *Carouselling:* Dolphins cooperatively encircle a school of prey, trapping them against the waters surface. Note: Bubble-blowing underneath prey school (Neumann and Orams 2003).

d) Mother-offspring relationships

Continuous sampling appears to be the richest source of information on social behaviour (Mann 1999a), especially during mother-offspring follows. Each occurrence of behaviour along with information on its timing of occurrence is recorded using this method (Martin and Bateson 1993). Such a method has been used widely in the study of mother-offspring relationships in different species, including New Zealand common dolphins (Schaffar-Delaney 2004). The present study focused on mother-offspring relationships within foraging groups. During each encounter, the predominant foraging strategies used by common dolphins were recorded every two minutes during focal follows, alongside mother-offspring data.

Continuous scanning was also conducted to locate mother-offspring pairs throughout the encounter. It has been reported that individuals accompanied by offspring are not always the mothers, and not always females (Whitehead and Mann 2000). Yet, persistent association of individuals with offspring can be identified as mother-offspring pairs (Wells et al. 1987; Bearzi et al. 1997). Therefore, mother-offspring pairs were identified by regular presence of a smaller individual next to an adult size common dolphin.

Dolphin offspring have been reported to swim in two main positions when associated with their mother: Infant and echelon position (Mann and Smuts 1999). In infant position, the young swims underneath the mother with its head slightly touching her abdomen. This position is broken when surfacing to breathe. In echelon position, the young swims alongside its mother, paralleling her course and less than 30 cm away from her side. Separation also occurs, with offspring swimming away from the mother. In this study, offspring were considered separated from their mother when the distance between mother and offspring exceeded one metre (Schaffar-Delaney 2004). Calf position relative to the mother was recorded every two minutes on the data sheet (*Appendix 2*).

e) Associated species

Common dolphins are known to associate with other species during feeding activities (Gallo Reynoso 1991; Neumann 2001b; Schaffar-Delaney 2004; Burgess 2006). In the Hauraki Gulf, they have been mainly observed in aggregations with Australasian gannets and Bryde's whales (Burgess 2006; Stockin et al. 2008b; Wiseman 2008). Mother-offspring pairs of different delphinid species have been reported to stay away from feeding aggregations, as the intensity of such activities may not be considered safe for offspring (Würsig 1986). In order to test the impact of such feeding associations on mother-offspring pairs, presence, number and behaviour of Australasian gannets and Bryde's whales were recorded every two minutes. Since whales surfaced irregularly and the vessel remained with the dolphin group at all times, data (number and behaviour) were noted and then recorded in the next interval sample. Data concerning Australasian gannets were recorded at every time interval. Behaviour states of associated species were described using the following criteria (Table 3).

Table 3: Definitions of behavioural states of species associated with common dolphins (*Delphinus* sp.) in the Hauraki Gulf.

Associated species	Behavioural state	Definition
Australasian gannet *Morus serrator*	Tracking	Birds persistently flying above dolphin group, maintaining pace and course of dolphins.
	Circling	Birds flying in circle above foraging dolphins.
	Diving	Birds dive from up to 30 m high, entering the water at great speed.
Bryde's whale *Balaenoptera brydei*	No interaction	Whale is not orientated toward dolphin group, and is either resting or travelling away from the dolphins.
	Foraging	Whale either vertically lunge feeding, or rolling laterally with expanded ventral pleats.
	Tracking	Whale is tracking behind dolphins and maintaining high speed and direction.

2.3. Statistical Analyses

Statistical analyses were conducted using *Minitab* (v.15) and *GraphPad Instat* (v.3). Normality and equal variance tests were undertaken on all data sets. Tests revealed none of the variables followed a normal distribution. Further attempts to apply transformations (i.e. *log* and *square root*) proved unsuccessful. Where assumptions of parametric tests failed, a non-parametric test was used. For all analyses, statistical significance between variables was assumed at the P = 0.05 level. If significant differences were detected, a relevant *post-hoc* comparison was performed to isolate these differences.

Focal group follows formed the basis for foraging activities data. Proportions of samples for each foraging behaviour over the sampling session were calculated for each focal group follow. Proportions of time spent in each foraging strategy for each sample were also calculated in presence and absence of associated species. Sightings Per Unit Effort (SPUE) was calculated as the number of common dolphin sightings per 60 min of search effort. Similarly, Offspring Per Unit Effort (OPUE) was calculated as the number of offspring common dolphin sightings per 60 min of search effort.

Group size data were pooled in three categories small ($\leq$ 20 individuals), medium (from 21 to 50 individuals) and large (> 51 individuals). Also, distance between dolphins and vessels were pooled in two categories (< 50 m and $\geq$ 50 m) due to limited sample size. Data on foraging strategies employed by mother-offspring pairs were analysed to determine the influence of water temperature, depth and group size. For each foraging strategies, non-parametric Mann-Whitney tests were applied to test hypotheses when only two variables were compared. When three or more variables were compared (i.e. group size), non-parametric Kruskal-Wallis tests were used (Zar 1996). The effect of associated species on mother-offspring's location within the foraging group was further tested using a Pearson Chi-square or Fisher's Exact test when data were too few.

The proportion of time offspring spent in each position in the group for each focal follow was compared for every foraging strategy, using Mann-Whitney test. Individual foraging strategies data were pooled in order to test the prevalence of such strategies used by common dolphins in presence of offspring. The same process was repeated for cooperative strategies.

Chapter Three: Results

Figure 13: Common dolphin (*Delphinus* sp.) in the Hauraki Gulf, New Zealand (Photo: N. de la Brosse).

3.1. Field effort

Data were collected between 18 March and 27 July 2009, during 57 independent boat-based surveys on *Dolphin Explorer*. This represented 228 hr of survey time, resulting in a total on-effort time of 198 hr (Table 4). Effort was greatest during April and lowest in May and June.

Common dolphins (*Delphinus* sp.) were sighted during 89.5% of survey trips (n = 51), resulting in a total of 86 independent encounters. Sighting Per Unit Effort (SPUE) and Offspring Per Unit Effort (OPUE) varied by month (Table 5), with SPUE being highest in March (0.58) and lowest in April (0.29), and OPUE being highest in July (0.38) and lowest in May (0.24) (Figure 14). The mean time spent with common dolphins was 21.4 min (SD = 14.7 min, range = 1 – 84 min). A total of 49 independent focal follows were conducted, representing 13.8 hr of focal effort.

Table 4: Monthly summary of surveys and on-effort search time (hr) in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009.

Month	Number of Surveys	Effort: Survey Time (On-Effort)
March	13	52 (42.6)
April	16	64 (57.0)
May	8	32 (29.1)
June	8	32 (27.5)
July	12	48 (41.8)
Total	57	228 (198.0)

Table 5: Monthly analysis of common dolphin (*Delphinus* sp.) sightings in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Note: SPUE = Search Per Unit Effort, OPUE = Offspring Per Unit Effort.

	Number of Sightings		Sighting Rates	
Month	All *Delphinus*	Offspring	SPUE	OPUE
March	25	15	0.58	0.35
April	17	16	0.29	0.28
May	9	7	0.31	0.24
June	9	7	0.32	0.25
July	24	16	0.57	0.38
Total	84	61	Mean = 2.09 SE = 0.06	Mean = 1.51 SE = 0.03
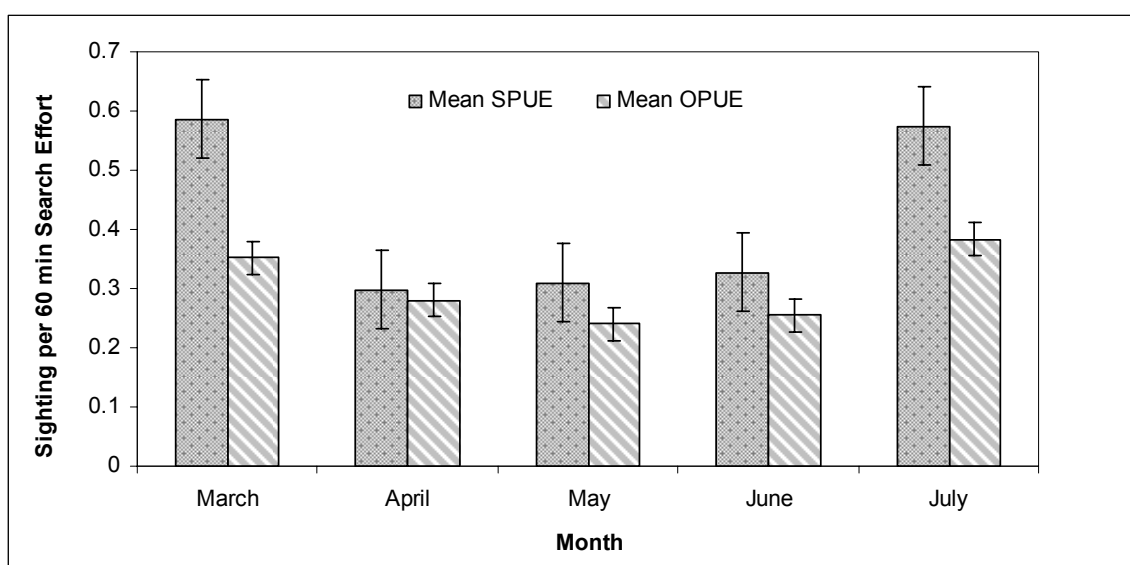
Figure 14: Mean SPUE and OPUE of common dolphin (*Delphinus* sp.) sightings in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Note: Bars represent Standard Error (SE).

3.2. Group composition

Out of the 86 groups of common dolphins sighted, offspring were observed 72% of the time (n = 62). Mother-offspring encounters varied each month (Figure 15), and were more frequently sighted in April (94% of the time). Juveniles and calves were observed 34.4% (n = 142) and 29.8% (n = 123) of the time during focal follows, respectively. Newborns were never observed during any surveys.
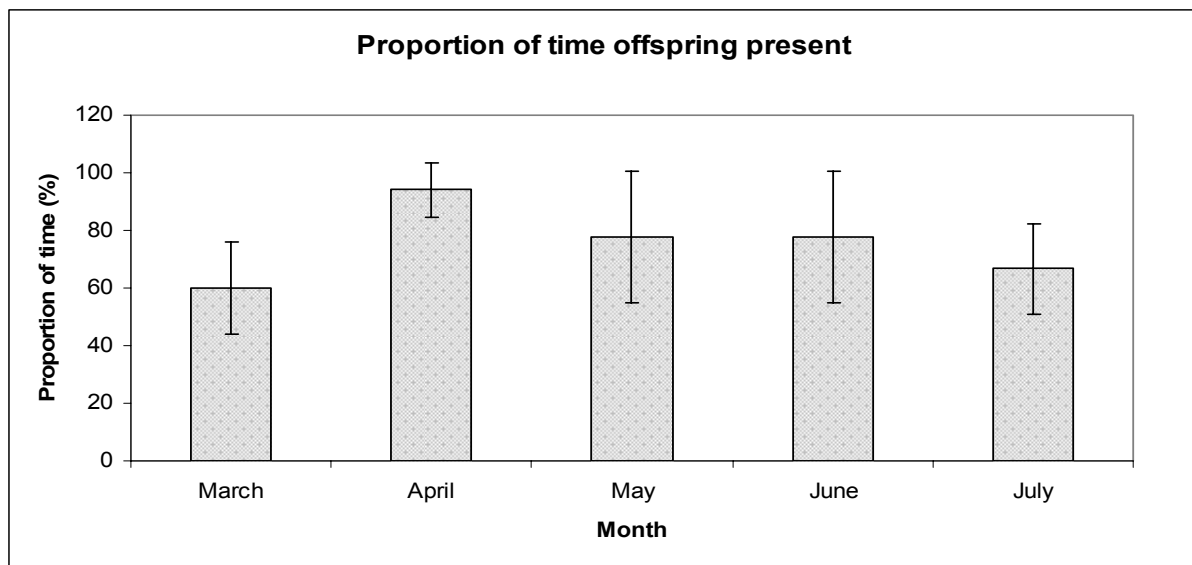
Figure 15: Proportion of time mother-offspring common dolphin pairs were observed during each month in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

Group size varied, with groups of up to 10 individuals most frequently observed (24.4%; n = 21), while groups of 51 to 100 individuals were the least recorded (9.3%; n = 8) (Figure 16). Mother-offspring pairs were mostly present in groups comprising 21 to 30 individuals (24.2%; n = 15), while small groups (1-10) were predominant (50%; n = 12) when offspring were absent (Figure 16). Due to limited data, statistical analyses could not be conducted to test differences between each group size category. However, once categories were pooled (Small, Medium, Large), Fisher's Exact test revealed that group size differed significantly in presence or absence of offspring (χ^2 = 11.485; df = 2; p = 0.003). Group size varied monthly, with large groups tending to be more frequent towards winter (Figures 17 and 18). Nevertheless, no statistical analyses were possible to confirm significant differences due to a limited sample size.
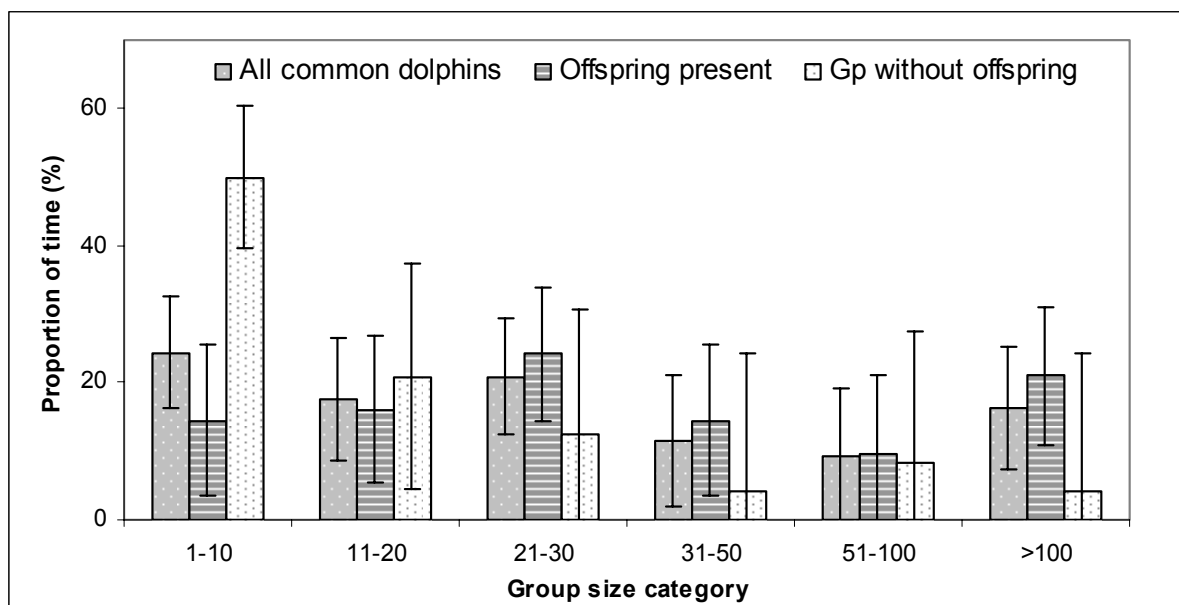
Figure 16: Proportion of time common dolphins (*Delphinus* sp.) were observed in each group size category in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).
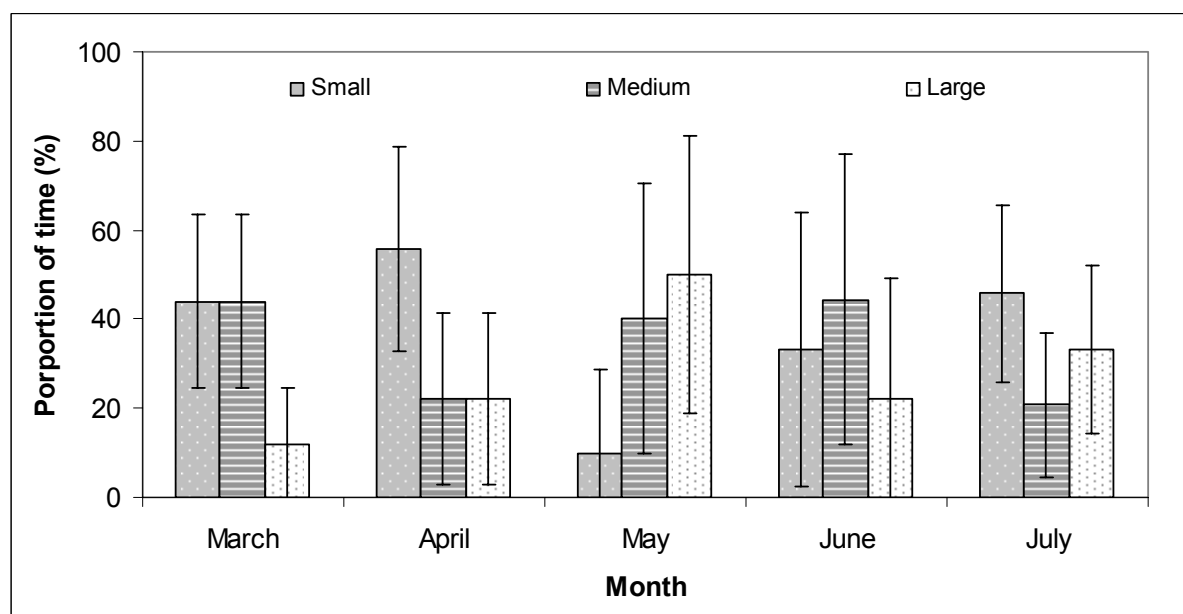
Figure 17: Proportion of time common dolphins (*Delphinus* sp.) were observed in each group size category for each month in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).
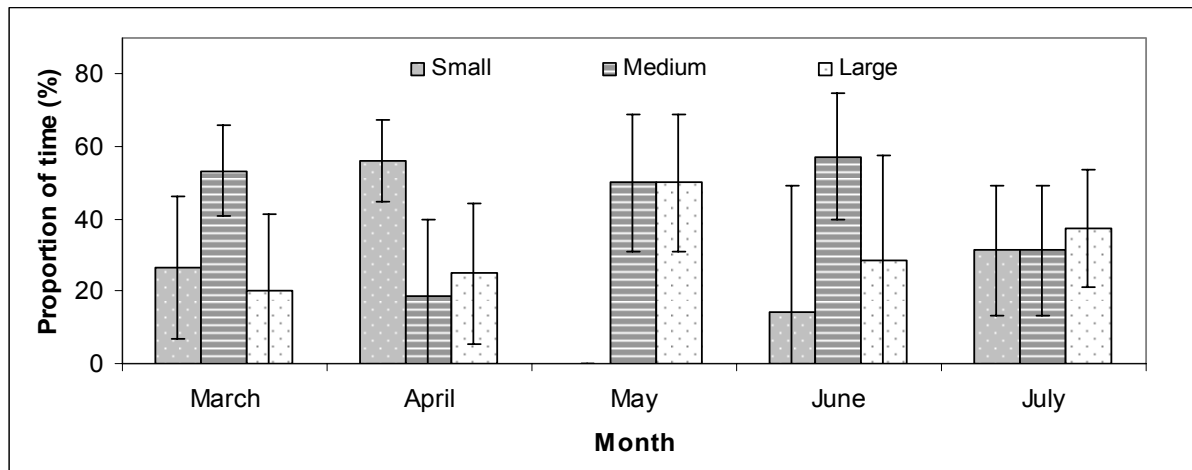
Figure 18: Proportion of time mother-offspring pairs were observed in each group size category each month in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

3.3. Influence of environmental variables on mother-offspring pairs' foraging strategies

Mother-offspring pairs were primarily observed foraging using cooperative strategies (97%), while mother-offspring pairs rarely engaged in individual strategies (n = 6). *Line-abreast* was the most frequently used strategy by mother-offspring pairs, accounting for 62% of observations, while *kerplunking* occurred the least, accounting for just 0.5% (Figure 19).
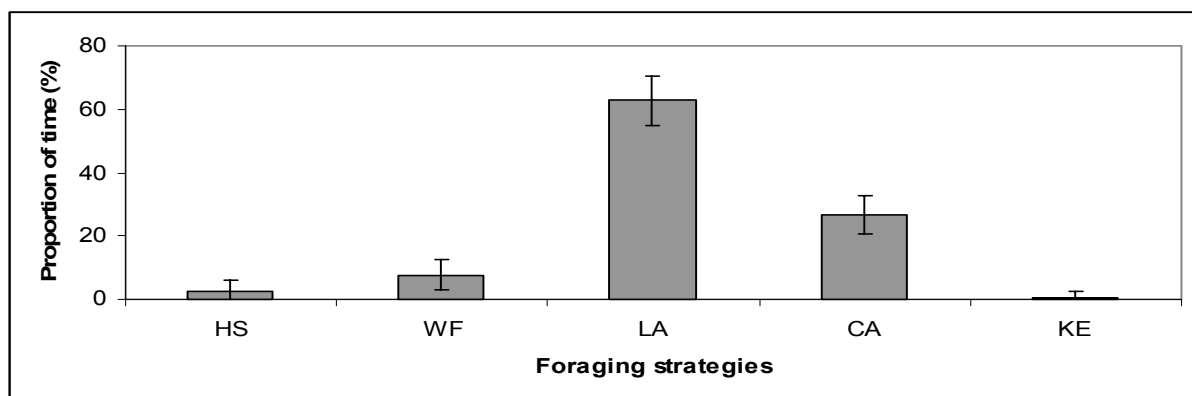
Figure 19: Proportion of time mother-offspring pairs spent in each foraging strategy in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE). Note: HS = *high-speed pursuit*, WF = *wall formation*, LA = *line-abreast*, CA = *carouselling*, KE = *kerplunking*.

3.3.1. Water depth

Common dolphins were encountered in water depths ranging from 12.0 to 52.5 m (mean = 36.5; SE = 9.46). No significant difference in water depth was detected when comparing sightings of groups containing adults only against groups with offspring (Mann-Whitney U: U = 580; p = 0.116). The mean depth in which common dolphins and mother-offspring pairs were observed was calculated for each month. In autumn, common dolphin groups occurred in deeper waters than in winter (Figure 20). Water depths where common dolphin groups with offspring occurred differed significantly between months (Kruskal-Wallis: H = 27.190; df = 4; p < 0.0001). Small sample size prevented statistical analysis of water depth where sightings of groups containing adults only differed monthly.
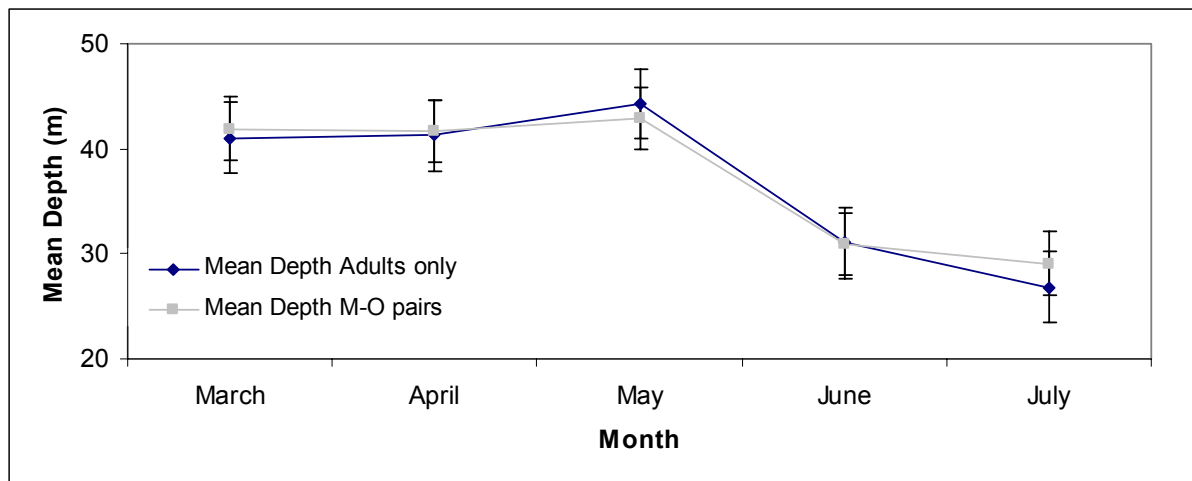
Figure 20: Monthly mean water depths (m) for common dolphin (*Delphinus* sp.) groups containing adults only and mother-offspring (M-O) pairs sighted in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

In order to assess the influence of water depth on foraging strategies of mother-offspring pairs, depths at which each foraging strategy occurred were compared. A Kruskal-Wallis test revealed no significant differences when testing the influence of water depth on the foraging strategies employed by mother-offspring pairs in the Hauraki Gulf (H = 4.617; df = 4; p = 0.3289). Therefore, foraging strategies employed by mother-offspring pairs in that area are not affected by water depth, and the hypothesis '*water depth affects the foraging strategies employed by mother-calf pairs*' was rejected.

3.3.2. Water temperature

The sea surface temperature (SST) that common dolphins were sighted in ranged from 13.1 to 23.5 °C, (mean = 18.3; SE = 3.53). The mean SST recorded when adult common dolphins only and mother-offspring pairs were sighted was calculated for each month, depicting an expected seasonal decline as months flow into the austral winter (Figure 21).
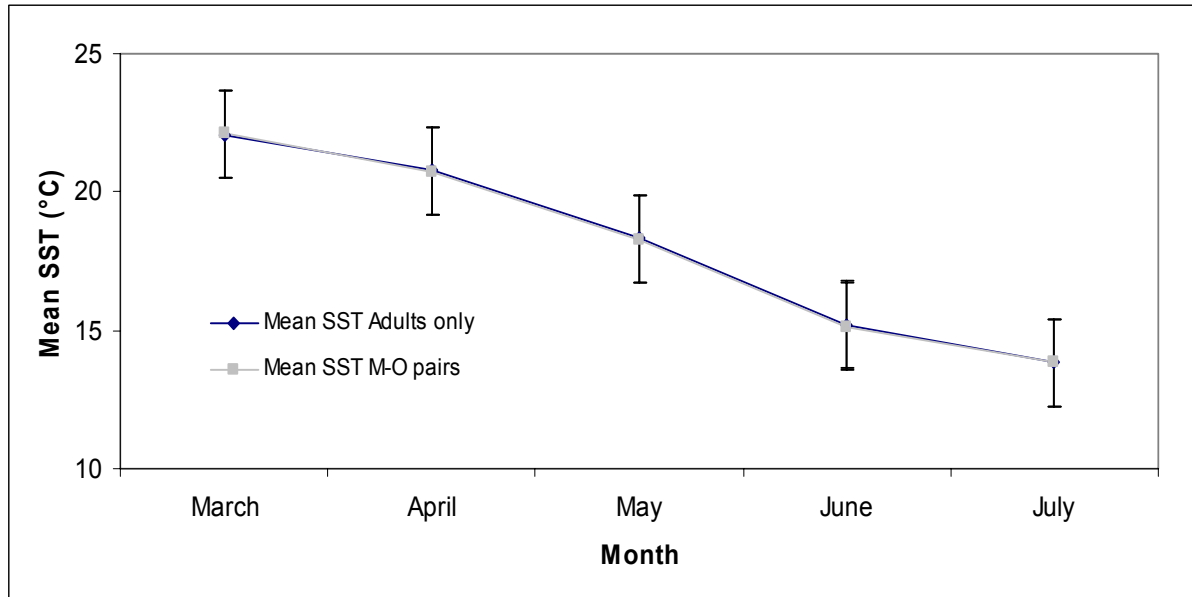
Figure 21: Monthly mean SST (°C) of adult common dolphins (*Delphinus* sp.) only and mother-offspring (M-O) pairs sighted in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

Individual strategies such as *high-speed pursuit* and *kerplunking* occurred more often when water temperatures were higher, while mother-offspring pairs engaged more frequently in cooperative strategies as SST declined (Figure 22). However, a Kruskal-Wallis test revealed SST had no significant affect on foraging strategies employed by mother-offspring pairs (H = 8.491; df = 4; p = 0.075). Therefore, the hypothesis '*sea surface temperature affects the foraging strategies employed by mother-offspring pairs*' could be rejected despite the prevalence of cooperative strategies employed by mother-offspring pairs as the SST declined.
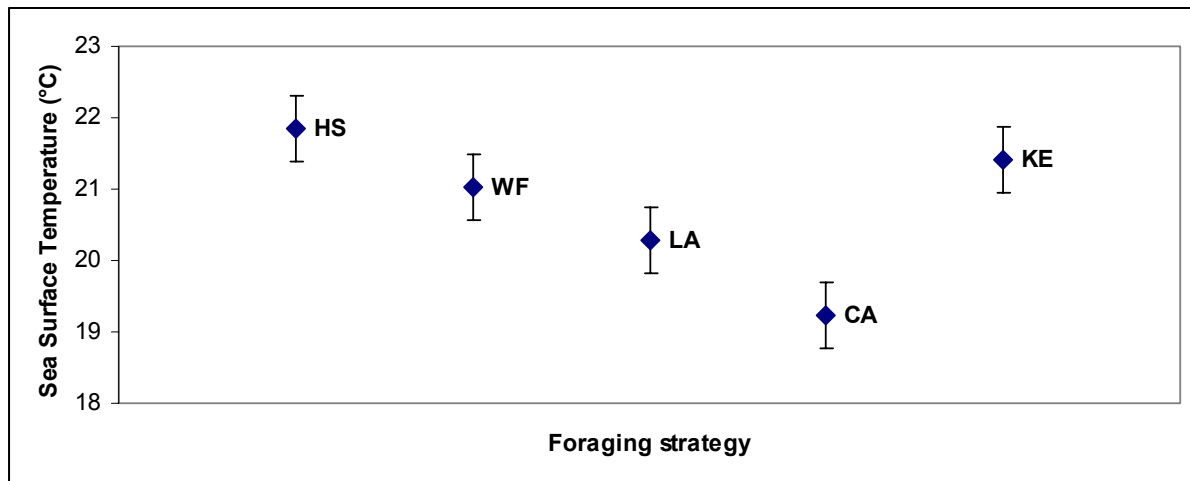
Figure 22: Mean SST (°C) for foraging strategies employed by mother-offspring pairs observed in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE). Note: HS = *high-speed pursuit*, WF = *wall formation*, LA = *line-abreast*, CA = *carouselling*, KE = *kerplunking*.

3.3.3. Group size

A non-parametric Kruskal-Wallis test revealed no significant difference when testing the impact of group size on the prevalence of *high-speed pursuit* (Kruskal-Wallis: H = 0.7801; df = 2; p = 0.677), *kerplunking* (H = 2; df = 2; p = 0.368), *line-abreast* (H = 1.061; df = 2; p = 0.588), *wall formation* (H = 2.756; df = 2; p = 0.252) and *carouselling* (H = 0.0352; df = 2; p = 0.983) foraging strategies (Figure 23). Thus, those foraging strategies employed by mother-offspring pairs are not affected by the group size in the Hauraki Gulf and thus, the hypothesis '*group size affects the foraging strategies employed by mother-offspring pairs*' was rejected.

3.4. Influence of anthropogenic parameters on mother-offspring pairs

3.4.1. Reaction of foraging dolphins

Common dolphins were observed interacting with one or more vessels in 10.5% of encounters (n = 9), and were engaged in foraging activities during 4.6% of the time. Statistical analyses were not possible due to a limited sample size, and the hypothesis '*presence of mother-offspring pairs affects the reaction of foraging dolphins to the approach o boats*' could not be tested. However, in presence of interacting vessels, foraging common dolphins were recorded

to change behaviour 50% of the time when offspring were present in the group, while behaviour always remained consistent when dolphins were feeding in the absence of offspring.

3.4.2. Minimum distance between dolphins and boat

Once again, the limited data prevented statistical analysis and the hypothesis '*presence of offspring affects the minimum distance between dolphins and the boat*' could not be tested. Nevertheless, mother-offspring pairs were observed 5.8% of the time (n = 4) interacting with one or more vessels, and maintained a distance greater than 50 m in 80% of interactions. In contrast, when no offspring were present in the group, common dolphins were always observed within 50 m of other vessels.

3.5. Influence of associated species on mother-offspring pairs

3.5.1. Influence on foraging strategies

Australasian gannets (*Morus serrator*) and Bryde's whales (*Balaenoptera brydei*) were observed in association with common dolphins during 51% and 7.5% of focal follows, respectively, and were primarily associated with dolphins engaged in foraging activities (81.6% of gannet encounters and 87.1% of Bryde's whales encounters). Common dolphins were recorded feeding in association with Australasian gannets during 75.5% of focal follows, and 11.8% of the time with Bryde's whales. Therefore, associated feeding was predominant in the Hauraki Gulf, especially with gannets. Comparably, mother-offspring pairs associated with gannets (68.4%) and Bryde's whales (8.4%) at a similar rate during focal follows.

A Mann-Whitney test revealed that foraging strategies employed by mother-offspring pairs did not significantly differ in presence of Australasian gannets. *High-speed pursuit* (U = 205; p = 0.302), *line-abreast* (U = 191.5; p = 0.400), *wall formation* (U = 219.5; p = 0.859) and *carouselling* (U = 206.5; p = 0.607) strategies were not affected by the presence of Australasian gannet (Figure 24). *Kerplunking* strategies could not be statistically tested due to too few data. Therefore, the hypothesis '*presence of Australasian gannets affects the foraging strategies employed by mother-offspring pairs*' was rejected.
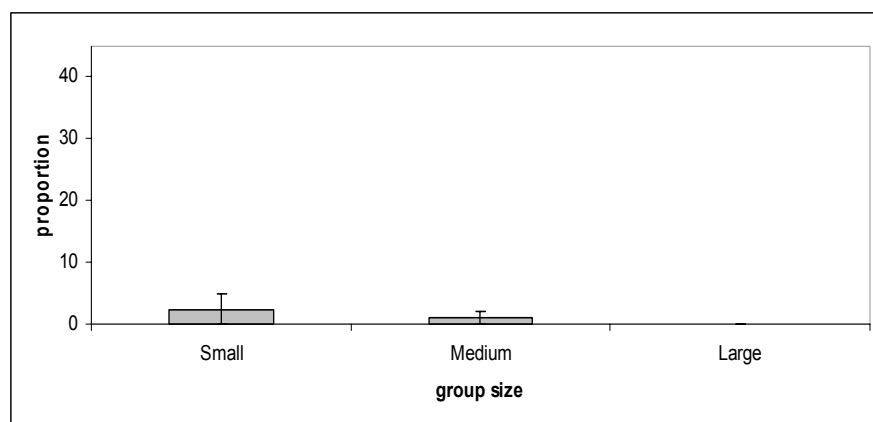
High-speed pursuit
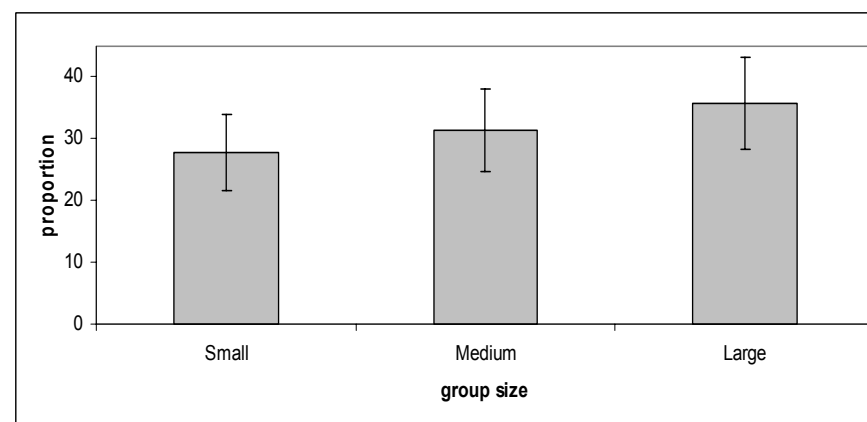
Line-abreast
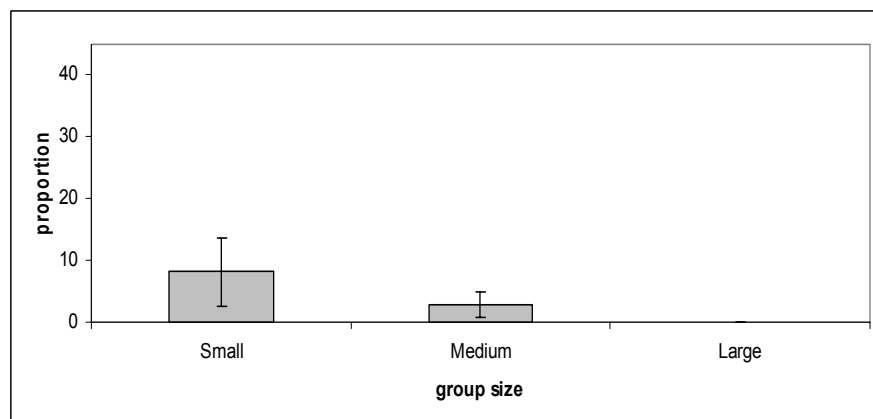
Wall formation
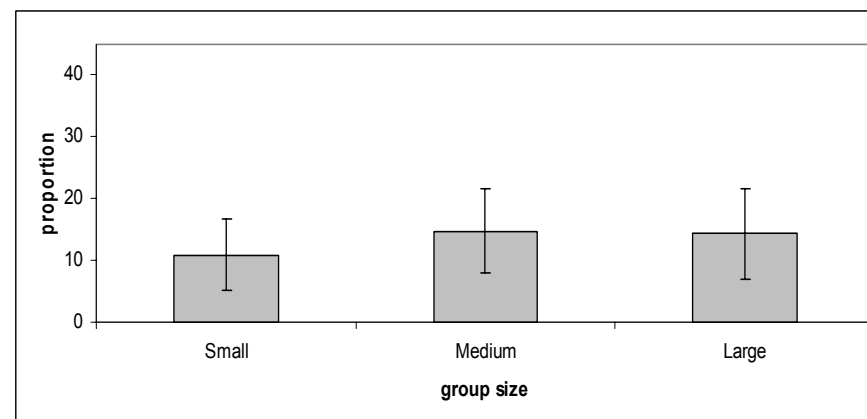
Carouselling

Figure 23: Influence of group size on foraging strategies employed by mother-offspring pairs in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

Similarly, foraging strategies employed by mother-offspring pairs did not significantly differ in presence or absence of Bryde's whales. *Line-abreast* (U = 56.0; p = 0.124), *wall formation* (U = 85.0; p = 0.475) and *carouselling* (U = 84.0; p = 0.615) foraging strategies were not affected by the presence of Bryde's whales (Figure 25). *High-speed pursuit* and *kerplunking* strategies could not be statistically tested due to too few data. Therefore, the hypothesis '*presence of Bryde's whales* affects the *foraging strategies employed by mother-offspring pairs*' could be rejected.

3.5.2. Influence on location of offspring within foraging group

When common dolphins were feeding in the absence of any associated species, mother-offspring pairs were recorded in the centre of the foraging group during 90% of focal follows. When associated with Australasian gannets, mother-offspring pairs were found in the centre during only 24.6% of focal follows. Instead, during 75.4% of the time, mother-offspring pairs remained at the peripheral edge of the foraging group (Figure 26). They remained predominantly in this position when gannets were diving (81.8%), and were only likely to be observed in the centre of the foraging group when gannets were circling above the foraging focal dolphin group (33.3%). Pearson Chi-square test revealed that mother-offspring position within foraging groups was significantly affected by the presence of Australasian gannets (χ^2 = 35.419; df = 1; p < 0.0001). Therefore, the hypothesis '*mother-offspring pairs limit interactions with Australasian gannets during foraging*' was confirmed.

During associations with Bryde's whales, mother-offspring pairs were recorded 50% of the time in the centre of the foraging group (Figure 26). Fisher's Exact test revealed no difference in the position of mother-offspring pairs within groups when feeding in association with Bryde's whales. Therefore, the hypothesis '*mother-offspring pairs limit interactions with Bryde's whales during foraging*' could be rejected.

Figure 24: Influence of Australasian gannets on foraging strategies employed by mother-offspring pairs in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).
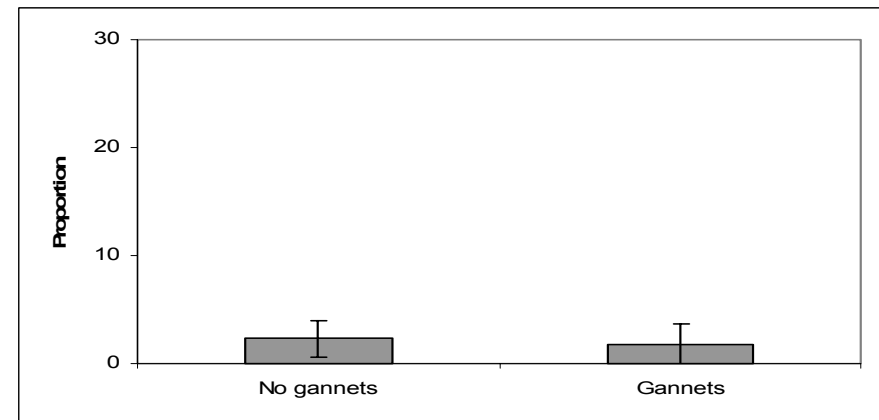
Wall formation
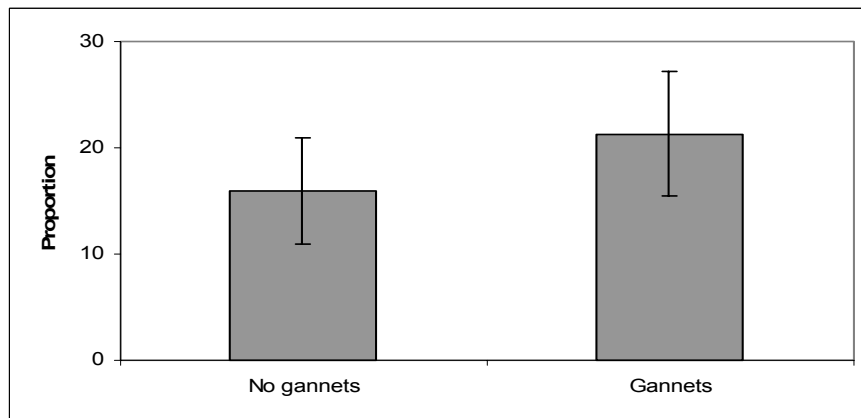
Line-abreast

Carouselling
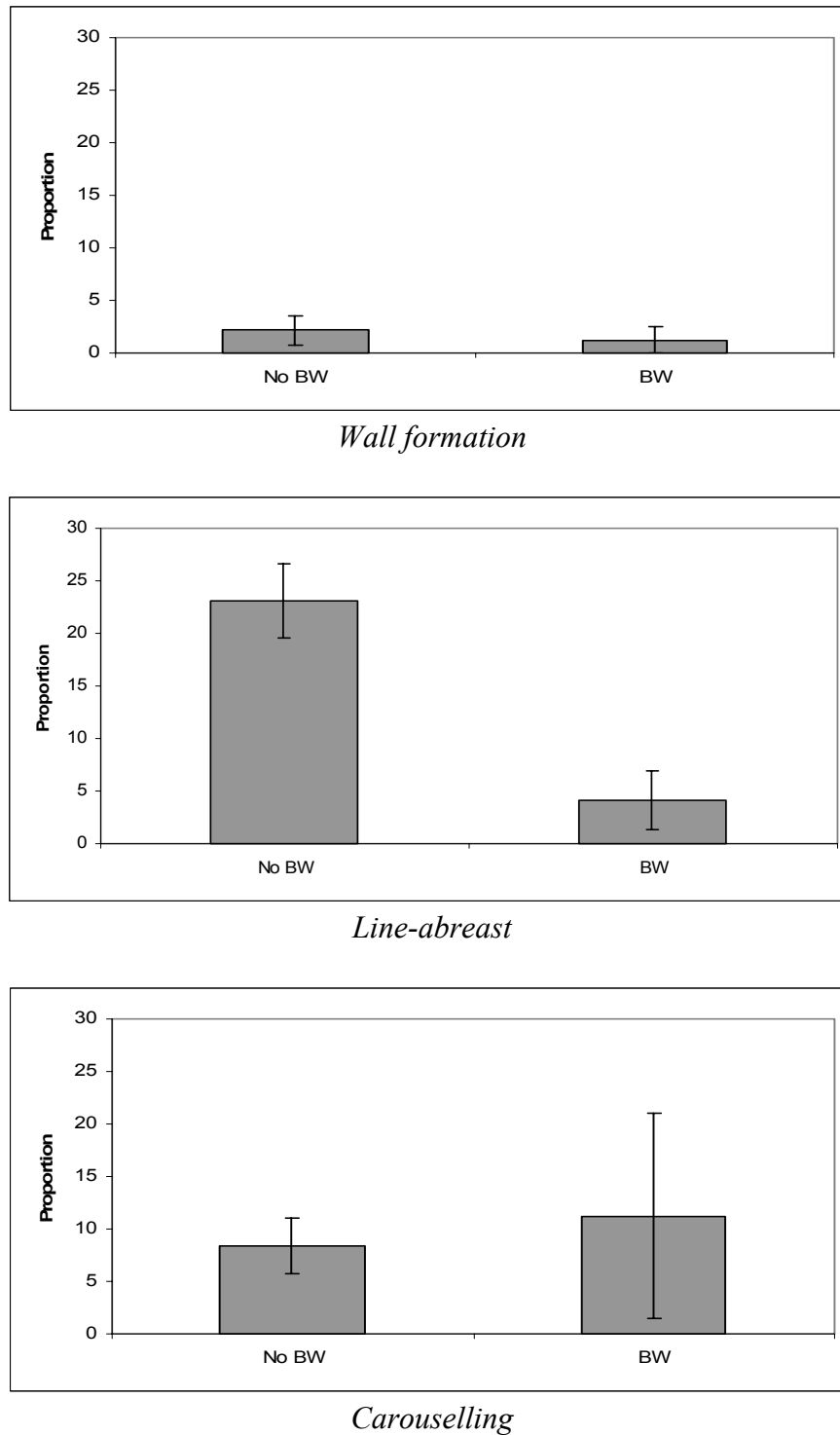
Figure 25 : Influence of Bryde's whales on foraging strategies employed by mother-offspring pairs in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE). Note: No BW = no Bryde's whale present, BW = Bryde's whale present.
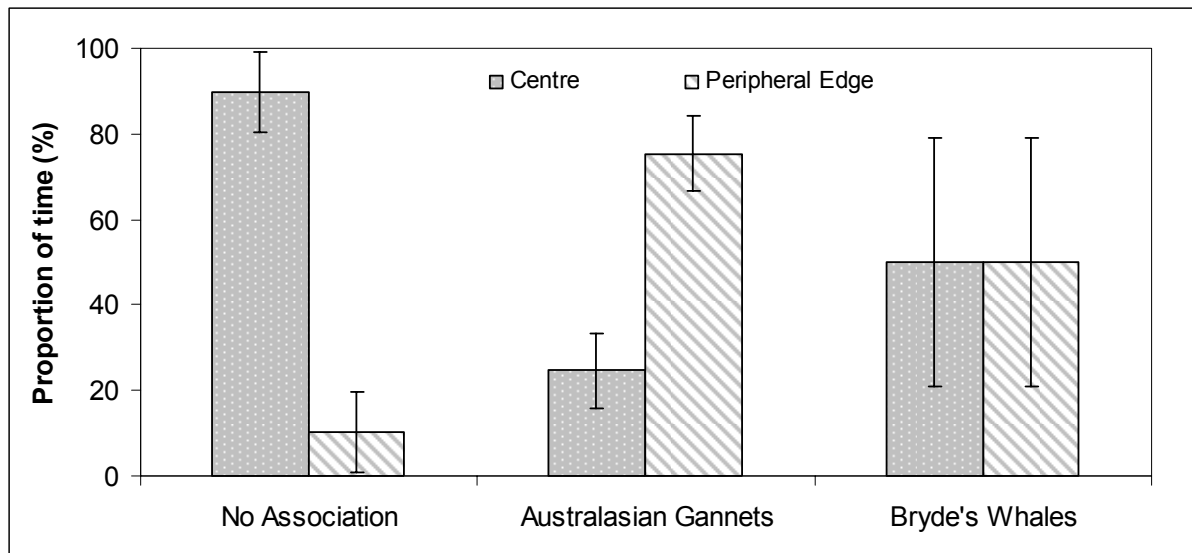
Figure 26: Proportion of time mother-offspring pairs spent in each position within foraging groups in presence and absence of associated species in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

3.6. Foraging strategies

3.6.1. Position of offspring within group

Line-abreast was the most frequently recorded foraging strategy employed by common dolphins in the Hauraki Gulf. This strategy did not significantly affect on the position of mother-offspring pairs within a group (Mann-Whitney U: U = 169; p = 0.370). Thus, the hypothesis '*line-abreast foraging strategy affects the position of offspring within a group*' was rejected. Similarly, *carouselling* had no significant affect on the position of offspring within foraging groups (U = 75.5; p = 0.259), and so the hypothesis '*carousel foraging affects the position of offspring within a group*' was also rejected. Limited data prevented this test being repeated for *wall formation* foraging strategy on position of offspring within a group. However, descriptive statistics suggest no difference, as offspring were recorded 50% of the time at the peripheral edge of foraging groups when dolphins were engaged in *wall formation* (Figure 27).
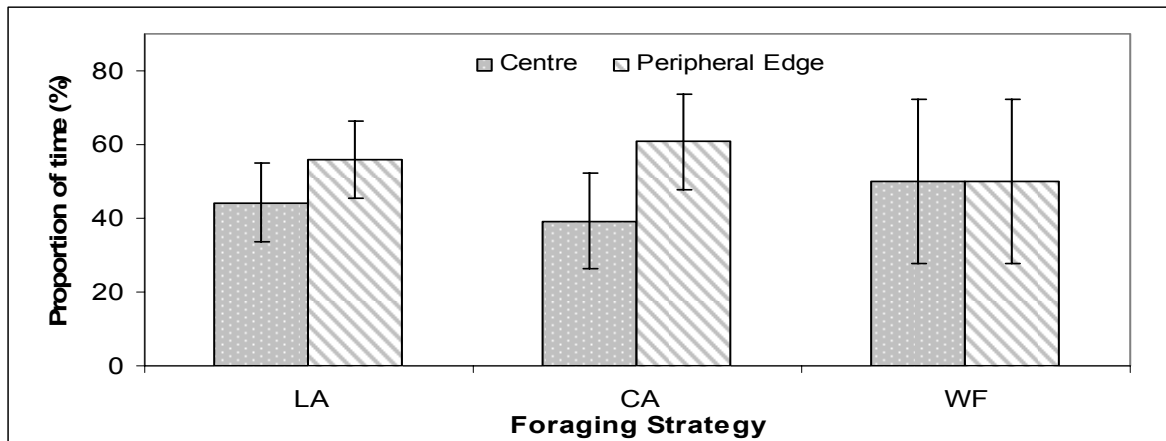
Figure 27: Position of mother-offspring pairs within foraging groups for each foraging strategy recorded in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE). Note: LA = *line-abreast*, CA = *carouselling*, WF = *wall formation*.

3.6.2. Presence of offspring on foraging strategies employed

A Mann-Whitney test revealed a highly significant difference between strategies employed by mother-offspring pairs (U = 1.00, p < 0.0001), showing that cooperative strategies were predominantly used by mother-offspring groups during feeding activities (Figure 28). The hypothesis '*mother-offspring pairs are less likely to engage in individual foraging strategies*' was confirmed.
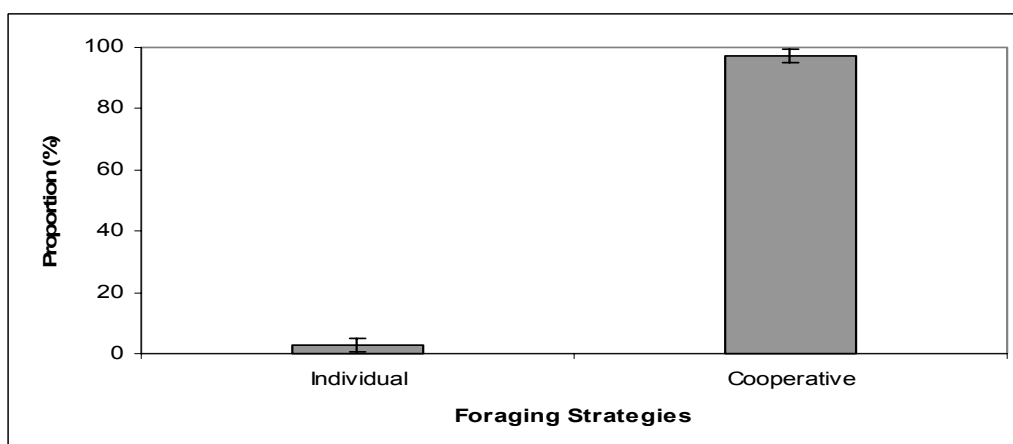
Figure 28: Mean foraging strategies employed by mother-offspring (M-O) pairs in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

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Despite the greater frequency of cooperative strategies used by common dolphins in the presence of offspring, prevalence of cooperative strategies was not affected by the presence of offspring (Figure 29). A non-parametric Mann-Whitney test revealed no significant difference in the occurrence of cooperative strategies in presence or absence of offspring (U = 393.5; p = 0.108). Therefore, the hypothesis '*the prevalence of cooperative strategies used by focal group increases with the presence of offspring*' was rejected.
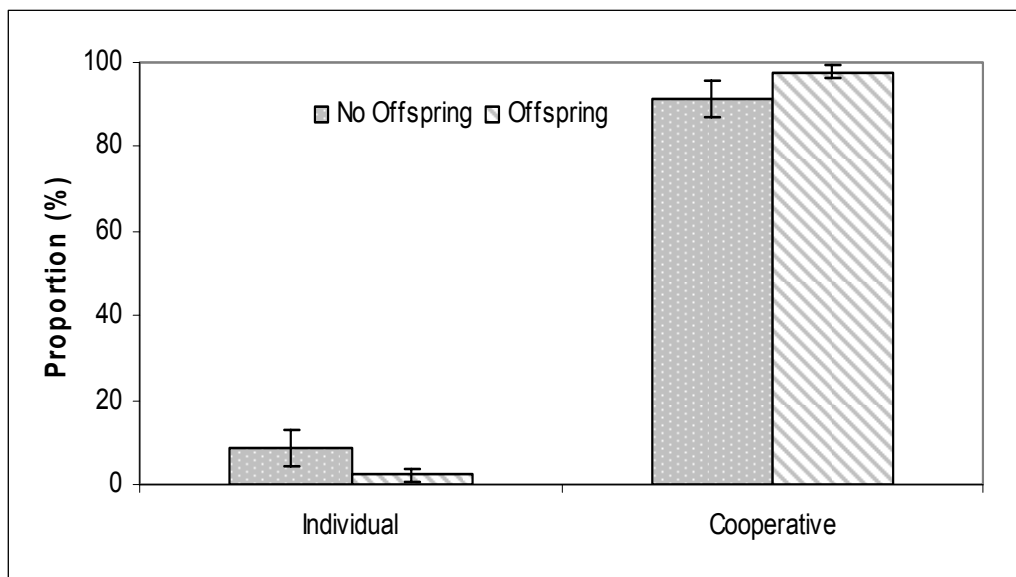
Figure 29: Proportion of foraging strategies used by common dolphins (*Delphinus* sp.) in the presence and absence of offspring in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

3.7. Mother-offspring relationships during foraging activity

Offspring were observed in echelon position 93.6% (n = 88) of the time during foraging behaviour. When common dolphins were engaged in individual strategies, offspring were never observed separate from their presumed mother. However, mother-offspring pairs were separated 6.7% of the time (n = 6) when using cooperative strategies (Figure 30).
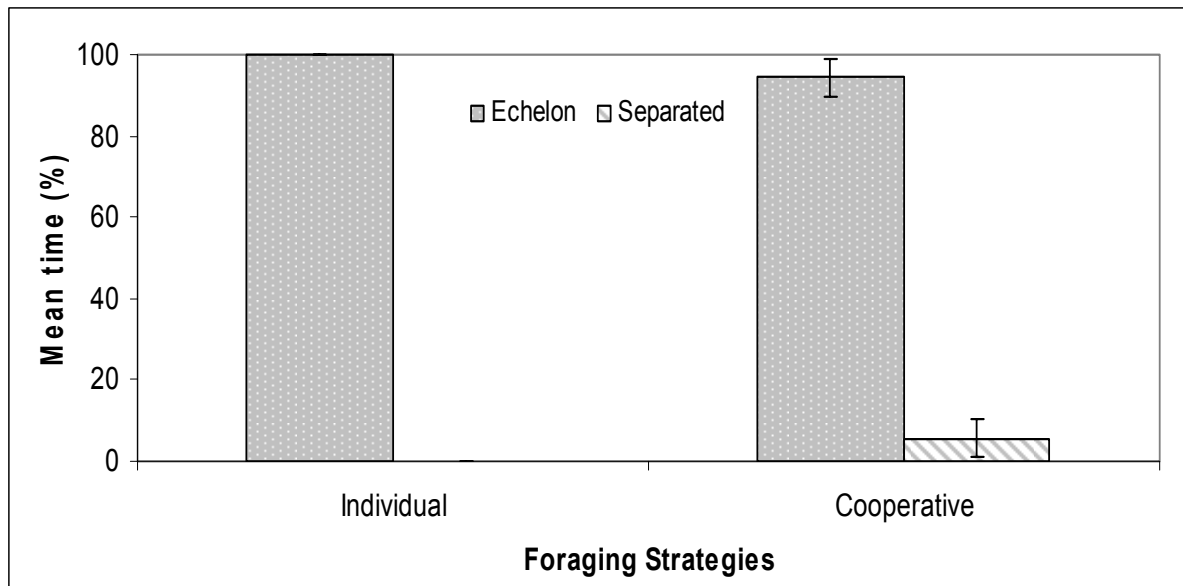
Figure 30: Position of offspring in relation to their presumed mother during foraging strategies recorded in the Hauraki Gulf, New Zealand between 18 March and 27 July 2009. Bars represent Standard Error (SE).

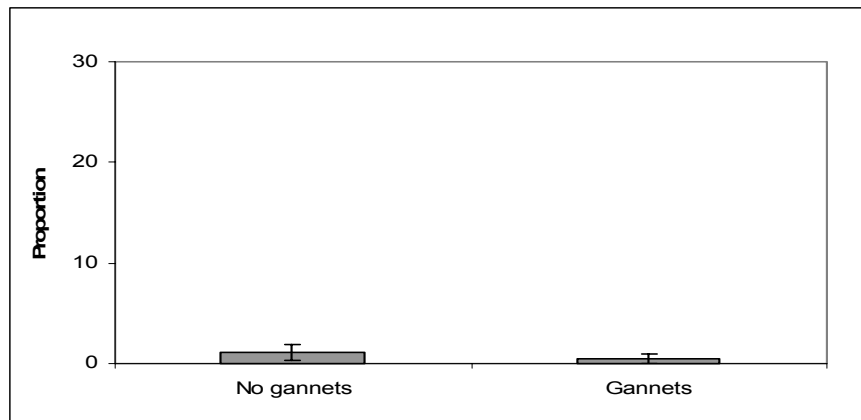Despite this, Fisher's Exact test revealed no significant difference of position between individual and cooperative strategies ($p = 1.00$, relative risk = 0.943). As such the hypothesis '*percentage of time offspring spend in echelon position decreases during individual foraging strategies*' was rejected. Offspring were never recorded in infant position during focal follows. Therefore, the hypothesis '*percentage of time calf/newborn spends in infant position decreases during individual foraging strategies*' could not be examined.

Chapter Four: Discussion

Figure 31: Travelling common dolphins (*Delphinus* sp.) in the Hauraki Gulf, New Zealand (Photo: N. de la Brosse).

4.1. Mother-offspring pairs foraging strategies

4.1.1. Environmental variables

The use of foraging specialisations may evolve in response to physical difference in habitat, such as topography (Hoelzel et al. 1989). This can be explained by the distribution and abundance of small fish, as well as the type of fish species, which are strongly tied to a number of environmental factors, such as changes in seafloor topography. Some authors have reported the presence of common dolphins along seafloor reliefs and submarine canyons (Hui 1979; Polacheck 1987; Selzer and Payne 1988; Gaskin 1992; Gowans and Whitehead 1995), showing that undersea topography is a significant physical feature influencing common dolphins. However, foraging strategies employed by mother-offspring pairs in the present study were not found to be affected by water depth in the Hauraki Gulf. This is surprising given that similar delphinids, such as dusky dolphins (*Lagenorhynchus obscurus*), have been reported to use different foraging strategies in New Zealand, varying with the seafloor topography. In the shallow waters of Admiralty Bay, dusky dolphins use different foraging tactics to those reported off Kaikoura, where the deep oceanic waters support a vertically-migrating scattering layer (Würsig et al. 1997; Benoit-Bird et al. 2004). In Admiralty Bay, the main prey targeted by dusky dolphins include schooling fish, such as anchovy (*Engraulis australis*) and pilchards (*Sardinops sp.*) (Vaughn et al. 2007), while dusky dolphins consume primarily small squid (*Nototodarus* and *Todaroides* spp.) and lanternfish (*Myctophid* spp.) in Kaikoura (McFadden 2003). Such disparity between the feeding tactics of these two regions likely reflects differences in prey type and availability.

In the Bay of Plenty, Neumann (2001c) suggested that common dolphin foraging could be influenced by seamounts and rapidly changing seafloor relief, which may provide shelter or create nutrient upwelling conditions that increase localised fish abundance and type. However, with a largely flat seafloor, and relatively shallow waters that are predominantly uniform in depth, the physical characteristics of the Hauraki Gulf may explain why foraging strategies employed by mother-offspring pairs are not affected by water depth. Despite the non-significant affect of water depth on foraging strategies used by mother-offspring pairs, the observations made from the present study reveal that pairs were almost never engaged in individual strategies in shallower waters.

During the present study, sea surface temperature (SST) was highest in March, declining over a range of 10°C until the austral winter month of July. SST is known to influence both delphinid thermal energetics and prey availability (Wells et al. 1999). Throughout the duration of the present study, SST was not found to affect the foraging strategies of mother-offspring pairs within the Hauraki Gulf. However, it should be noted that not all seasons were included within the present study, which may explain the lack of statistical resolution. Off the north-western Bay of Plenty, common dolphins were reported to move seasonally in correlation with SST, El Niño and La Niña Southern Oscillation patterns (Neumann 2001c). It was suggested that offshore shifts during winter months were likely to be a consequence of prey movement, which was an indirect effect of SST. Prey distribution, abundance and availability are affected by the ocean climate, which can vary considerably at different spatial and temporal scales (Stockin et al. 2008b).

The Hauraki Gulf is known to be a productive area (Booth and Sondergaard 1989; Stanton et al. 1997; Chang et al. 2003), with the same prey species occurring in abundance throughout the year (Kendrick and Francis 2002). However, delphinids may change feeding tactics intra-annually owing to changes in prey abundance, distribution, or schooling behaviours, as prey patterns are likely to be affected by water temperature (Baird 2000; Ballance et al. 2006). In this study, *high-speed pursuit* and *kerplunking* foraging strategies typically occurred in higher water temperatures, while mother-offspring pairs were engaged more frequently in cooperative strategies as sea temperature decreased. Individual strategies demand high energy, due to bursts of speed, rapid directional changes and exhausting foraging events such as tail slapping. In cooler waters, energy is necessary to maintain the blubber reserves, and thus individual foraging strategies may be overly costly, especially for a lactating female or her offspring, with higher calorific requirements. Cooperative strategies are believed to increase the feeding efficiency of delphinids, and thus maybe more energetically beneficial for mother-offspring pairs when water temperatures decline throughout the winter months.

4.1.2. Group dynamics

In the present study, group size had no significant effect on mother-offspring pairs foraging strategies in the Hauraki Gulf. Large groups including mother-offspring pairs were never

observed foraging individually, while large groups were dominant when cooperative foraging occurred, especially when mother-offspring pairs were engaged in *line-abreast* and *carouselling* strategies with the rest of the group. Furthermore, group size increased towards the end of the study period, as winter approached. This is consistent with Stockin et al. (2008b), who observed larger group sizes more frequently during the winter months, possibly representing a seasonal effect. Arguably, common dolphins may form larger groups as the water temperature drops, in order to increase feeding efficiency, thus providing a significant benefit to group members including mother and offspring. Both Schaffar-Delaney (2004) and Stockin et al. (2008b) reported that common dolphin groups with calves tended to be significantly larger than groups composed of adults only in the Hauraki Gulf. Previous studies suggested that the Hauraki Gulf is an important calving and nursery area for this population (Schaffar-Delaney 2004; Stockin et al. 2008b). It seems likely that larger groups may provide a protected environment within which early postnatal development and learning may occur (Wells et al. 1987). An additional advantage derived from larger nursery groups may include alloparental behaviour. Allomaternal care for offspring has been previously suggested for several cetaceans, including humpback dolphins (*Sousa chinensis*) (Karczmarski 1999), bottlenose dolphins (*Tursiops truncatus*) (Mann and Smuts 1998; Grellier et al. 2003), and sperm whales (*Physeter macrocephalus*) (Gordon 1987). Given the risks that offspring face from predators, it is likely that the presence of a nearby adult is of general benefit to the offspring.

4.1.3. Prevalence of cooperative foraging

The results of the present study reveal that mother-offspring pairs mostly feed cooperatively in the Hauraki Gulf. This is consistent with prior observations reported for common dolphins in New Zealand waters (Neumann 2001b; Burgess 2006). However, on further examination, it is apparent that *line-abreast* was the dominant foraging strategy used by mother-offspring pairs during the present study, with *high-speed pursuits* barely observed. This differs somewhat with previous studies of foraging common dolphins in the Hauraki Gulf and the Bay of Plenty, where *high-speed pursuit* was regularly observed (27.9% and 28.4%, respectively), with *line-abreast* strategy occurring on a less frequent basis (10.3% and 27.6%, respectively). However, both Burgess (2006) and Neumann (2001b) examined all foraging

groups irrespective of age composition, while the present research focused only on groups containing mother-offspring pairs. This may explain differences reported here and possibly indicate that in the presence of offspring, common dolphins predominantly feed in cooperation. Within the present study, the prevalence of cooperative strategies used by focal groups was not affected by the presence of offspring. Nevertheless, despite the lack of statistical significance, focal groups were almost never observed feeding individually when offspring were present, while individual foraging was more frequently recorded in the absence of offspring. These results suggest that mother-offspring pairs are less likely to engage in individual foraging strategies, possibly due to the cost involved in those techniques, and potentially, limitations encountered by offspring (e.g., exposure to predation, higher demand of energy to chase food, or lower agility and manoeuvrability).

Cooperative feeding occurs when individuals synchronize actions, such that the chance of successful prey capture is increased among all participants (Sargeant et al. 2005). Prey studies suggest common dolphins feed on highly mobile and often patchily distributed species, such as pilchard and anchovy (Young and Cockcroft 1994; Clua and Grosvalet 2001; Neumann and Orams 2003; Meynier et al. 2008; Stockin et al. 2008b). In the Hauraki Gulf, schooling fish, such as the New Zealand pilchard (*S. neopilchardus*) are locally abundant (Kendrick and Francis 2002). Dietary studies of common dolphins suggest that they consume the most abundant, easily captured prey. The dispersion of this targeted food could, therefore, explain the cooperative feeding used by common dolphins in this region, as previously hypothesized by Burgess (2006).

Cooperative feeding has been widely described in the past, offering numerous benefits (e.g., Fertl and Würsig 1995; Neumann and Orams 2003; Gazda et al. 2005; Burgess 2006; Vaughn et al. 2007). The prevalence of cooperative feeding when mother-offspring pairs were present could directly profit the mother, by providing a large density of food within a confined area. Calves and juveniles are highly dependent upon their mother for food, nursing on the fat-rich milk produced. Lactation is relatively costly for dolphins, and lactating females have high metabolic demands in order to produce milk (Whitehead and Mann 2000). Therefore, nursing dolphins have to either increase the amount of food eaten, or select food of high calorific value (Bernard and Hohn 1989). In a previous study on dusky dolphins, Vaughn et al. (2007) suggested that coordinated feeding could increase the feeding efficiency of the individuals, as probably less energy is required to capture prey from bait balls that are closer to the surface.

As such, cooperative strategies are therefore, more likely to be energy efficient to lactating females.

In contrast, individual foraging strategies (e.g., *high-speed pursuit* and *kerplunking*), which demand bursts of speed and lifting the tail clear of the water, are energetically costly to lactating females. Additionally, cooperative feeding could benefit offspring during the weaning stages by facilitating the development of feeding skills. For example, capturing prey that are concentrated and condensed at the waters surface as a result of coordinated feeding efforts would likely be beneficial to an inexperienced dolphin. Limited hunting and locomotory skills of young dolphins could potentially prevent individual feeding without the support of other experienced dolphins within the pod.

Potentially, cooperative feeding could also provide protection to offspring. A previous study comparing the diet of lactating females and weaned common dolphin calves suggested that calves did not usually feed with adults (Young and Cockcroft 1994). Würsig (1986) suggested that feeding aggregations and large number of individuals could potentially be dangerous for offspring, as it involved 'boisterous' activity, as well as contact and socio-sexual activity. While dolphins feed, large predatory sharks or even killer whales (*Orcinus orca*) could render offspring highly vulnerable (Würsig 1986). However, the present study, in addition to a previous study examining mother-calf behaviour (Schaffar-Delaney 2004), do not support this hypothesis, as feeding was the most frequently observed behaviour of all sightings, with its occurrence not related to group type. Furthermore, Norris and Dohl (1980) suggested that predation risk is the principal factor driving group formation in cetaceans. Large predators such as sharks or killer whales have been widely reported to predate on dolphins (Heithaus 2001a;b). Wells (1986), examined bottlenose dolphins living on the west coast of Florida, reported 22% of non-calves bore scars from unsuccessful shark attacks. Others similar reports of shark predation on dolphins have been detailed within a number of studies (Norris and Dohl 1980; Long and Jones 1996; Mann and Watson-Capps 2005; Heithaus and Dill 2006; Wirsing and Heithaus 2008). The killer whale may be the most widely distributed cetacean species and likely represents a threat to common dolphins (Jefferson et al. 1991). Potential predators, including sharks – broadnose sevengill (*Notorhynchus cepedianus*), shortfin mako (*Isurus oxyrinchus*), white (*Carcharodon carcharias*), bronze whaler (*Carcharhinus brachyurus*), blue (*Prionace glauca*), and smooth hammerhead (*Sphyrna zygaena*) sharks, in addition to killer whales are frequently observed in the Hauraki Gulf and have been reported

as a predatory threat in this region (Stockin et al. 2008b). Evidence for predation attempts on common dolphins comes not only from occasional observations of attacks, but also from scars on living individuals (Visser 1999; 2000). Certainly, offspring, by their small size, potential ignorance, and limited mobility, are ideal prey due to their vulnerability to such predators. As such, individual foraging strategies could arguably expose offspring to additional risks of predation.

Foraging in cooperation may enable better protection of offspring, as group effects may increase vigilance, signalling the early approach of a predator. Upon an attack, an aggressive defence by other group members (e.g., Whitehead and Glass 1985; Mann 1999b; Coscarella and Crespo 2009) or tight bunching of adults with offspring in the centre (e.g., Palacios and Mate 1996; Weller et al. 1996) may improve survivability of younger group members. This later behavioural response has previously been observed in sperm whales under predation by sharks or killer whales (Best 1979). As such, cooperation seems plausible as a mechanism to increase foraging efficiency yet maintain vigilance for predators.

4.1.4. Associated species

Mixed-species associations were widely observed in the present study, especially during feeding bouts. In the Hauraki Gulf, feeding seems to play a major role in the aggregations of species (Stockin et al. 2009a). It is believed that primary benefits of feeding in aggregate with cetaceans include reduced predation (Bertram 1978; Norris and Schilt 1988) and increased foraging success. Previous local research suggests common dolphins provide an excellent foraging opportunity for other marine predators, especially seabirds and other cetaceans (Burgess 2006; Baker and Madon 2007; Wiseman 2008; Stockin et al. 2009a).

The degree that seabirds benefit from feeding with cetaceans depends on cetacean feeding tactics. Cetaceans that feed at depth do not usually attract seabirds (Evans 1982). In contrast, seabirds take advantage of cetaceans when they feed near the surface (Bräger and Schneider 1998). Association between seabirds and common dolphins has previously been examined by Stockin et al. (2009a) in the Hauraki Gulf. In the present study, association with seabirds, especially the Australasian gannet (*Morus serrator*), was recorded to occur in 75.5% of

encounters. Gannets were observed to be feeding in association with foraging mother-offspring groups in 68.4% of encounters. This is relatively consistent with previous findings, as Stockin et al. (2009a) reported approximately 80% of foraging common dolphin groups were associated to Australasian gannets. This large proportion of associations could be explained by the search methodology used to locate dolphins in the present study, where gannets were commonly used as sighting cues to find dolphin groups. However, this hypothesis was refuted by Stockin et al. (2009a), as a similar proportion of foraging associations were recorded using an independent platform and different search methodology, suggesting that the area is indeed an important feeding area for this species and not just a bias in search methodology. Nevertheless, gannets have been widely observed in association with delphinid species, since they feed on similar species and often take advantage of dolphins herding prey toward the surface (Robertson 1992; Schaffar-Delaney 2004; Burgess 2006; Vaughn et al. 2007; Stockin et al. 2009a).

Results from this study suggest that feeding aggregations between gannets and common dolphins did not affect the foraging strategies employed by mother-offspring pairs. Nonetheless, gannets were rarely observed during individual foraging strategies, suggesting such solitary feeding by common dolphins may not be beneficial to gannets. Mother-offspring pairs were more typically involved in cooperative foraging strategies in presence of gannets. It is likely that in most of the cases, common dolphins were already engaged in cooperative foraging strategies before seabirds were associated, herding and trapping the fish ball toward the surface. Such tactics would benefit gannets, which would then join and associate with the feeding bout, taking advantage of the concentrated and high amount of prey near the surface. Although, in the absence of dolphins, predatory fish such as yellowtail fish (*Seriola lalandei*) were observed skimming the surface in feeding aggregations with gannets, and were probably responsible for herding the prey near the surface, creating the feeding aggregation with gannets. Cooperation during hunting has been documented in yellowtail, observed surrounding and herding prey in a tight group towards the shore (Schmitt and Strand 1982).

Cooperative foraging is likely to attract gannets, and may offer advantages to both dolphins and gannets. Diving gannets and herding dolphins associated together may provide a greater ability to maintain bait ball cohesion and density, forming an opposing barrier (from above and below), to enhance optimal feeding. Moreover, cooperative foraging strategies were possibly more frequent when gannets were present in order to protect offspring. Diving

gannets could potentially appear as a threat to young and vulnerable dolphins that lack good locomotory skills. When diving, gannets break the surface at high speed (145 km/hr, Farr Biswell 2007). As such, the potential for injury to perhaps less agile members of the group is higher than groups comprising adults only. As discussed previously, group effect of cooperative feeding could yield a better protection of offspring.

As with previous studies (Burgess 2006; Stockin et al. 2009a), Bryde's whale (*Balaenoptera brydei*) was the most frequent cetacean recorded in association with common dolphins. These species were recorded together in 11.8% of encounters during the present study. Bryde's whales fed in association with foraging mother-offspring pairs during 8.4% of focal follows. Mixed-feeding aggregations including only whales and common dolphins were rare. Whales that foraged amongst feeding common dolphins appear to be attracted to the feeding session from relatively far distances. Burgess (2006) and Wiseman (2008) suggest that whales may take advantage of the ability of the dolphins to locate and concentrate food in the Hauraki Gulf. Results of the present study reveal Bryde's whale presence does not affect foraging strategies employed by mother-offspring. Burgess (2006) reported that common dolphins changed foraging behaviour before and after a whale lunge feeding event. Seemingly, whales spend a substantial amount of time 'tracking' or following the dolphins, but only a brief period of time actually engaged within actual feeding.

Mothers may not perceive Bryde's whales as a threat to their offspring. In several occasions, common dolphins, including young individuals, were observed bow riding the pressure wave created by the whale. Bryde's whales were mostly only ever observed feeding in association with cooperatively foraging dolphins. Cooperative feeding techniques used by common dolphins may benefit the whales, as prey is herded and maintained in a concentrated baitball. This hypothesis has been suggested in several studies (e.g., Neumann and Orams 2003; Burgess 2006; Wiseman 2008; Stockin et al. 2009a). In contrast, individual strategies are unlikely to be advantageous for whales, since dolphins chasing at high-speed, tend to be in pursuit of more dispersed prey (Neumann and Orams 2003). The large body size of Bryde's whales is likely to limit agility and manoeuvrability during such a pursuit (Webb and de Buffrènil 1990). Instead, whales often track behind the dolphins as they herd prey together. Once prey are concentrated, and frequently driven to surface waters, whales would typically lunge feed through the centre of the feeding bout. This lunge feeding is likely to be a direct consequence of the common dolphins' foraging strategy. Considering the high metabolic

demands of Bryde's whales and the scattered prey distribution within the Gulf waters, it seems reasonable to suggest that the whales may regularly take advantage of common dolphin foraging behaviour in order to maximise their foraging efforts via a single lunge feeding event. As such, the common dolphin has been described as a critical associated species for the Bryde's whale (Burgess 2006).

Carouselling strategy was the dominant foraging tactic employed by common dolphins when a Bryde's whale was associated within a feeding bout. A previous study revealed that dolphins spent more time herding in the presence of whales (Burgess 2006). Bryde's whales could seemingly consume in a single lunge event, an entire school of fish carefully herded by the dolphins. One or perhaps two lunges by an individual whale through the aggregation typically destroyed the bait ball, dispersing the prey and breaking up the hunt. Therefore, despite the apparent lack of impact on foraging strategy employed by mother-offspring pairs, Bryde's whales are likely to cause disruption by interrupting cooperative foraging activities. Such disturbance could potentially reduce food intake of mother-offspring pairs.

4.2. Dynamic of mother-offspring pairs during foraging activity

4.2.1. Location within feeding groups

The position of offspring within a focal group was likely to be indirectly affected by the foraging strategies employed by other common dolphins within the group. As discussed previously, some foraging strategies employed by dolphins benefit and attract other species (e.g. seabirds) that join feeding bouts and have an impact on mother-offspring location within the group.

Mother-offspring pairs were observed to be in the centre of the foraging group in 90% of focal follows when dolphins were feeding alone. Since mothers allow offspring in the centre of mono-specific feeding groups, it seems that the use of peripheral regions may be associated with the presence of mixed-species aggregations. Results presented here suggest that gannets most likely affect the location of young dolphins within a group during foraging activity. Offspring were observed to be at the peripheral edge of foraging groups during 75.4% of

encounters when gannets were present. This apparent shift in mother-offspring location within a feeding group may be a consequence of perceived risk by the mother. Typically, the centre of a foraging group is where most of the activity occurs, with the tight bait ball concentrated in this location usually by a large number of active dolphins and diving birds. As discussed previously, gannets diving at high velocity could be perceived as an injury risk by mother-offspring pairs. Therefore, in presence of gannets, mother-offspring pairs typically remain on the peripheral edge of the group, with no direct involvement in the foraging activity. An alternative and/or additional reason for this could also be linked with the involvement of other predatory species, namely sharks, often observed during the present study, and known to frequently join mixed-feeding aggregations (Au and Perryman 1985; Au 1991). Like other associated species described, sharks were typically observed in the centre or at close proximity to the feeding bout, where prey were most condensed. The vulnerability of offspring to those associated predatory species may drive mothers to maintain their offspring at the peripheral edge, away from the feeding frenzy. This would still allow offspring to be in a visual and/or vocal proximity to the rest of the foraging group, and would still facilitate the learning of foraging techniques while remaining at a potentially safer distance.

Bryde's whales, in contrast, did not seem to affect the location of mother-offspring pairs within the foraging group. Indeed, within the present study, common dolphins were frequently observed riding the pressure wave created by a travelling whale. Aggressive behaviour of Bryde's whales toward common dolphins has never been reported, and thus potentially mothers might not consider the presence of a whale as a menace to their offspring. As most Bryde's whales within the Hauraki Gulf are solitary (Wiseman 2008), it is possibly easier for mother-offspring pairs to keep track of a slower solitary whale, as opposed to several high speed diving gannets. In most mixed-species feeding aggregations, Bryde's whales tracked behind dolphins as they herded prey species. Once the dolphins had corralled the prey, whales were recorded to lunge feed through the centre of the feeding frenzy. When this event was occurring, dolphins were typically forced to scatter and move away from the bait ball, before continuing to restructure the often diminished and dissipated bait ball. Thus, it is possible that the involvement of Bryde's whales in association feeding with common dolphins is considered only brief and that factor explains why no effect of Bryde's whale presence was observed on the location of mother-offspring pairs within the feeding group. However, while position may not be affected, it is not possible to dismiss a significant impact on the acquisition of prey during foraging bouts due to increased competition for food.

4.2.2. Mother-offspring relationships

This study shows the prevalence of close proximity between offspring and their mother during foraging activity, with immature dolphins reported in echelon position during 93.6% of feeding bouts. Whitehead and Mann (2000) suggested that separations between mother and offspring are largely the result of the foraging behaviour of the mother, especially two aspects of foraging: Rapid accelerations to chase prey and deep diving. A previous study of spotted dolphins (*Stenella attenuata*) proposed that lactating females may be constrained from deep diving for squid since this required mothers leaving their calves (who are less competent divers) at the surface (Bernard and Hohn 1989). In a relatively shallow region such as the Hauraki Gulf, mother-offspring separations may be less affected by deep diving, since offspring might be able to stay within the diving ranges of their respective mothers to feed. Furthermore, the fact that offspring were rarely separated from their mother in the Hauraki Gulf could be further explained by the low occurrence of individual strategies used in presence of immature dolphins. Yet, the results presented here could not confirm the hypothesis that the percentage of time offspring spends in echelon position decreases during individual foraging strategies. Furthermore, expectations that rapid accelerations to chase prey would likely yield an increase in mother-offspring separations could not be demonstrated in this area. Such feeding events would primarily occur during individual foraging strategies, such as *high-speed pursuit* strategy. The lack of individual foraging strategies data might explain why no differences in mother-offspring relationships between individual and cooperative strategies were observed during the present study.

Close proximity of echelon and infant positions between mother and offspring offers several advantages to young dolphins. Firstly, the protection of offspring from predators is a function of the close physical association between mothers and young dolphins, sometimes lasting for three to six years from birth in species such as bottlenose dolphins (Navarro 1990). Lactating females are also known to exhibit punitive behaviour toward offspring that stray too far or too long, further demonstrating the parental care involved in protecting infants from predators (Chirighin 1987). Presence of other predators (e.g. sharks, killer whales) during common dolphin foraging occurs regularly in the Hauraki Gulf (Stockin et al. 2008b), with offspring highly vulnerable if separated from their mothers. As such, individual strategies may expose offspring to elevated risks if mothers separated in order to chase prey at high speed. When

foraging in close proximity, mother-offspring pairs could potentially appear as one large animal due to disruptive colouration, as has been proposed in other delphinids (Cockcroft and Ross 1990; Würsig et al. 1990).

Moreover, several cetacean biologists have recently described culture within different species of delphinidae (Deeke et al. 2000; Rendell and Whitehead 2001; Krützen et al. 2005). Some of the strongest evidence for social learning comes from bottlenose dolphins (Janik 2000) and killer whale studies (Deeke et al. 2000). An offspring must be able to forage successfully before being completely weaned. According to Mann and Sargeant (2003), learning to forage appears to be a slow process, warranting the overlap between nursing and foraging for the first years of life. By remaining in close proximity of the mother (i.e., infant or echelon position), offspring can suckle, learn to forage and be protected from predation risks.

4.3. Vessel presence

Data collected within the present study were too few to permit statistical analysis of boat effects on reaction of foraging mother-offspring pairs. Impact of boats on dolphins' behaviour has previously been documented for mother-offspring pairs (Wells 1991; Nowacek et al. 2001; Lusseau 2003; Schaffar-Delaney 2004; Lusseau 2006). Schaffar-Delaney (2004) revealed mothers exhibit longer dive times in response to boat traffic, which was interpreted as a means of avoidance (Nowacek et al. 2001). Mothers are also reported to herd their calves away from boats (Wells 1991; Lusseau 2006). In the present study, offspring were never observed in close proximity of another vessel. Mothers tended to keep their young at a relatively far distance (> 50 m) from any boat during foraging. As mothers lead their offspring to bow-ride during non-foraging activities, it is not likely that the boat is perceived as a threat. Instead, it may be perceived as another variable for mother-offspring pairs to navigate around during what is already a hazardous time. Thus, mothers may choose to keep their young at a greater distance from the boat when foraging in order to limit any potential separation from their calves. Also, occasionally, the bait ball was observed to 'take cover' under the boat. In such situations, mothers may try to keep their offspring away from the boat, likely to prevent any collision between the young, inexperienced dolphins and the boat.

When interacting with vessels, groups with offspring showed more behavioural changes than groups comprising adults only. Mother-offspring pairs may perceive foraging as a stressful behaviour, since vulnerability to predatory threats may increase as vigilance decreases when engaged in foraging. One or more vessels present during a foraging bout may add further stress to mother-offspring pairs, as anthropogenic interaction could also be perceived as a distraction which could affect offspring survival. For example, dependent calves and their mothers could be perceived as more vulnerable to boat strikes due to their lower manoeuvrability (Nowacek et al. 2001). Mortality of common dolphins as a result of boat strike has been previously reported by Stockin et al. (2009b). Female dolphins 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). Furthermore, fishing boats were also observed in close proximity to foraging common dolphins including offspring. Commercial trawl fisheries are known to incidentally kill common dolphins around New Zealand waters (DuFresne et al. 2007; Rowe 2007; Stockin et al. 2009b). Lesions from net entanglement were observed on a number of carcasses recovered from the Hauraki Gulf, with the area also used by recreational set net fishermen (Stockin et al. 2009b). Despite a lack of statistical significance, the observations made in the present study have important conservation implications for the species, which are enhanced by the high percentage of groups with offspring found within Hauraki Gulf waters.

Every year, the Hauraki Gulf is highly frequented by recreational vessels encountering common dolphin groups including young individuals (Bercusson and Walsby 1999). Recreational vessels and tourism activities have previously been reported to impact some populations, exhibiting changes in behaviour (e.g. Lusseau 2003; Constantine et al. 2004; Neumann and Orams 2006; Stockin et al. 2008a), area avoidance and declines in relative abundance in some occasions (Lusseau 2005; Bejder et al. 2006). In the Hauraki Gulf, Stockin et al. (2008a) observed that tourism activity focused on common dolphins does have impacts on their behaviour. Considering the importance of the Hauraki Gulf as a nursery area, efforts should be made to increase public awareness about boat handling around dolphin groups containing offspring.

Chapter Five: Conclusion

Figure 32: Spy hopping common dolphin (*Delphinus* sp) in the Hauraki Gulf, New Zealand (Photo: N. de la Brosse).

5.1. Summary

This study provides important first insights into the foraging behaviour of common dolphin (*Delphinus* sp.) mother-offspring pairs, describing the dynamics of such pairs within feeding groups. The significant findings of this study indicated that:

- In the presence of offspring, common dolphins predominantly forage using cooperative as opposed to individual strategies. This may provide a more prolific food supply to lactating females and their offspring, without the need for mother-offspring separation.

- Foraging strategies employed by mother-offspring pairs in the Hauraki Gulf are not affected by water depth, a likely consequence of the uniformity in topography evident within the study area.

- Cooperative strategies employed by mother-offspring group are more frequently observed in the austral winter, as water temperature decreases.

- Group size may not directly affect mother-offspring foraging strategies in the Hauraki Gulf, although larger group sizes occurring throughout the winter months appear to result in more frequent cooperative foraging strategies being used.

- Mother-offspring pairs primarily engage in *line-abreast* strategies. This is similar to groups containing adults only.

- Australasian gannets (*Morus serrator*) do not affect foraging strategies employed by mother-offspring groups, but affect the position of mother-offspring pairs within the feeding group.

- Bryde's whales (*Balaenoptera brydei*) do not affect foraging strategies employed by mother-offspring pairs, nor influence the position of mother-offspring pairs within the feeding group.

- Separation between mother and offspring are limited during foraging activity, a likely consequence of protection. Cooperative strategies likely favour close proximity between mother and offspring pairs, enhancing predatory protection for the young as well as facilitating an apprenticeship of foraging skills.

- Foraging mothers typically herd their young away from vessels, not likely a direct consequence of the vessel itself but more likely a cumulative response to various unpredictable variables being monitored during dynamic feeding events by the mother.

- Foraging behaviour of mother-offspring pairs may be affected by boat presence.

5.2. Limitations and significance of the study

It is important to acknowledge a series of parameters which limit the findings presented within this study. Firstly, data analysed were collected in a specific habitat, with enclosed and shallow waters. This region provides a different habitat from most other common dolphin populations studied worldwide. Dolphin behaviour is likely influenced by habitat, thus a difference in water depth, topography and oceanography could invariably affect mother-offspring foraging strategies used. As such, mother-offspring pairs inhabiting offshore areas may behave differently to those reported here. Conclusions from this study should, therefore, only be considered applicable for common dolphins inhabiting Hauraki Gulf waters.

Furthermore, all the data reported herein refer to above water observations, and therefore do not take into consideration the foraging strategies and mother-offspring dynamics of the dolphins sub-surface. As such, accuracy of the data may be affected by sampling constraints, since extended periods of time during deep dives are not accounted for during foraging events.

Underwater observations were not possible from *Dolphin Explorer* due to the lack of appropriate visibility. Underwater observations would only be possible from a short distance from the feeding dolphins, which may impact behaviour being monitored. Also, land-based theodolite surveys were not possible since dolphin distribution was wide and occurrence close to shore was not predictable. Thus, boat-based surveys were necessary to undertake the present research.

Even if efforts to limit anthropogenic interaction and impact on dolphins were made, conducting observations from a vessel obliges the researcher to take into consideration its potential impact on the animals. Thus, interactions with common dolphins during focal follows, possibly influenced the focal animals themselves, including any mother-offspring dynamics and strategies under observation.

The frequency of multispecies groups encountered during this study may be an overestimate owing to the use of binoculars to detect seabirds and whales when locating common dolphins. A random-based survey design, as detailed by Stockin (2008), which does not use binoculars to detect indicator species, would equal the probability of observing both single- and

multispecies groups. However, the present study focused on foraging groups, consequently mixed-species aggregations were likely to be an artefact of foraging dolphins. Thus, the search methodology employed in this study increased the probability of detecting feeding activity.

Mother and calf relationships have previously been studied in bottlenose dolphins (*Tursiops truncatus*) living in a controlled environment such as captivity (Cockcroft and Ross 1990; Peddemors 1990; Gubbins et al. 1999) or in areas where dolphins are provisioned (Mann and Smuts 1998; Mann and Smuts 1999). These environments provide easy access, enhancing greater opportunities to observe behaviours that cannot be monitored in wild populations. Even if common dolphins were found in relatively shallow waters in the Hauraki Gulf, the conditions to observe the dolphins, combined with the fast movements that characterise the species, were rather challenging compared to that of controlled habitats. Thus, the possibility to observe mother-offspring pairs for extended periods of time were limited, resulting in the short focal follows presented herein.

Additionally, conducting the research from a platform of opportunity limited the time of observation. The tour vessel had a strict time schedule to adhere to, and consequently duration of encounters was sometimes very limited. In many studies, short encounters are not taken in consideration since observations may not reflect the general behaviour of the dolphins. In this study, data collection was dependent on the opportunistic platform, and so it was decided that all data, regardless of focal follow duration, would be analysed. Results obtained in this study may have been affected by this limitation. Moreover, in numerous cases, the boat continued searching for further cetaceans, with some common dolphins bow riding, while the main group remained foraging. In an attempt to limit anthropogenic impact on foraging dolphins, the boat often remained at a distance (> 50 m) off the central feeding activity. As such, on occasion, further foraging data could have been collected, and perhaps some mother-offspring pairs could have been overlooked. However, regardless of environmental parameters and associated species present, such a bias would have remained consistent throughout the entire study.

Finally, difficulties in tracking all mother-offspring pairs occurred when focal groups were large. Sometimes, offspring were dispersed in large groups, and several researchers would

have been required to track all pairs. Since only one researcher (Nicolas de la Brosse) was conducting the surveys, some activities and behaviours may have been overlooked.

Despite the limitations described, the present study contributes to a better understanding of the species in many ways, providing further knowledge and insight into common dolphin socio-biology and ecology. Previous research on common dolphin behaviour has been mostly confined to New Zealand waters (Neumann 2001b; Neumann and Orams 2003; Schaffar-Delaney 2004; Neumann and Orams 2005; Burgess 2006; Stockin 2008; Stockin et al. 2008a;b; Stockin et al. 2009a; Stockin and Orams 2009). While foraging behaviour and mother-calf dynamics has been examined within the Hauraki Gulf prior, no previous study has been undertaken on mother-offspring strategies and dynamics within foraging events. Considering the importance of this region for feeding (Burgess 2006; Stockin et al. 2009a) and nursing (Schaffar-Delaney 2004; Stockin et al. 2008b), in addition to the feeding impacts detailed from tour boat interactions (Stockin et al. 2008a), this is critical. This study provides first insights into the dynamics and strategies employed by foraging mother-offspring pairs. Such information is of management value. This population inhabits inshore waters adjacent to the city of Auckland, where higher levels of anthropogenic influence are likely to be experienced as a direct consequence of habitat choice.

The Hauraki Gulf Marine Park is an important economic and recreational resource, supporting a variety of human activities, including commercial fishing, recreation, tourism and shipping. All those anthropogenic pressures affect common dolphin population confined in the Hauraki Gulf. Coastal anthropogenic impacts have been reported in this region, resulting from contaminants such as PCBs and OC pesticides (Stockin et al. 2007). Marine pollutants have some important biological effects on common dolphins, especially in the early developmental stages of life (Reijnders and Aguilar 2002). Common dolphins are also affected by set nets in this area (Stockin et al. 2009b). In addition, a previous study reported the impact of tourism in this region, where common dolphins were significantly less likely to continue foraging and less likely to continue resting after the approach of tour boats (Stockin et al. 2008a).

New information yielded from the present research will provide valuable insights which will enable the Department of Conservation to appropriately manage the expanding tourism industry in this region. The Hauraki Gulf Marine Park Act (2000) has already acknowledged the region as a significant coastal and marine ecosystem. However, there is a strong argument

for further recognition of its importance to species such as the common dolphin, that rely on this region for vital biological processes. New Zealand common dolphins are poorly understood, subject to a range of untested assumptions and yet continue to remain a *low priority* from a research and management perspective (Suisted & Neale 2004). The use of the region for feeding and nursing is of notable management importance, particularly considering vessel avoidance by mother-calfs reported by Schaffar-Delaney (2004), and given the apparent impact of vessel disturbance on foraging dolphins (Stockin et al. 2008a). In the present study, mother-offspring pairs were observed to change behaviour and to avoid interaction with boats during foraging activities. Since common dolphins are the most abundant cetaceans in the Hauraki Gulf (Stockin et al. 2008b), they remain the primary target for both commercial tour boats currently operating in the area. Thus, future dolphin tourism needs careful monitoring in this area.

5.3. Future research

Further investigations examining the diving profile of common dolphins foraging in presence of offspring in the group would extend our current knowledge of common dolphins foraging behaviour. Diving behaviour is an important process during feeding activity, as dolphins often dive to herd prey toward the surface. It is believed that dive time may be affected by the presence of offspring, although further study is required to examine such a hypothesis.

Underwater investigations would certainly improve the precision of observations reported here. Additional information concerning offspring dynamics within the feeding group, as well as position in relation to the mother might be collected using an underwater camera. Such a technique could also provide further information on prey and other predators involved in association feeding. Offspring responses to the presence of other predators (e.g. diving gannets or sharks) remain unclear, as only surface behaviour was recorded in the present study. However, parameters such as visibility may still affect future underwater investigations.

In order to avoid human interaction and impact during data collection, alternative methods would be worth developing. Collecting data from a boat always has an impact – even low –

on dolphin behaviour. Using a small remote controlled 'blimp' carrying a camera could be very advantageous in that no interaction between the researcher and the dolphins would occur, and thus dolphin behaviour would, therefore, not be affected by anthropogenic presence. Control would be monitored from a vessel, located several hundred metres away from the focal group. Also, some parameters would be easier to study from above, such as mother-offspring location within a group, or relationship between mother and offspring. However, such a sampling method would be very expensive to develop and to acquire, and more reliant upon prevailing winds.

Focal follows of mother-offspring pairs undertaken from a research vessel may enhance more accurate observations rather than from a platform of opportunity. As previously discussed, a platform of opportunity has a limited amount of time available to observe dolphins via focal group follows. Therefore, surveys from an independent research vessel would enable increased sample durations, allowing for greater habituation of dolphins to the vessel.

Finally, the conclusions of the present study are limited only to common dolphins studied in the Hauraki Gulf. Further research on an offshore population would allow comparisons to be drawn with dolphins inhabiting open, oceanic waters. Different environmental variables (e.g., depth, temperature, currents, food resources) and predators may occur, and are likely to influence and alter mother-offspring foraging strategies and dynamics.

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Appendix 1
Dolphin sighting datasheet used in this study.

GENERAL DATA	Encounter No: HG….
Observers:	Start Time:
Date:	Finish Time:
Research vessel:	Survey period:
Survey No:	Waypoint:

ENVIRONMENTAL DATA	Weather: ○ ☁ 🌧 ≋
Water Depth (m):	Beaufort: 1 2 3 4
SST (°C):	Visibility: Excell Good Poor

VESSEL DATA

No. Vessel present:

Closest Vessel distance: 0-50   51-100   101-150   >150

ON APPROACH

Focal grp size: 1-10   11-20   21-30   31-50   51-100   >100

Grp Composition:

Adults	Juvs	Calves	New

	ComDolp	AusGt	BryW	Other
Behav.	T M R F S	Foll Circ Div	R F T	
No.				

END OF ENCOUNTER

Focal grp size: 1-10   11-20   21-30   31-50   51-100   >100

Grp Composition:

Adults	Juvs	Calves	New

	ComDolp	AusGt	BryW	Other
Behav.	T M R F S	Foll Circ Div	R F T	
No.				

Appendix 2
Focal group follow datasheet used in this study.

Time	Ind. Focal Offspring	Focal Gp State	Focal Gp Strategy	Ass.Sp. AustGt	Ass.Sp. BryW	Offspring Position	Offspring Moth-Offsp Pos.	Behaviour	Observations
	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:02	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:04	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:06	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:08	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:10	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:12	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:14	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:16	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:18	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:20	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:22	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:24	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:26	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:28	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		
00:30	J C N	T M R / F S	HS WF LA / Car Ker	Track Circ / Div	R F T	Centre / Periph	Ech Inf / Sep		

Appendix 3

Table of statistical results for tests of normality, and the non-parametric tests applied in this study. Note: df = degree of freedom

Data	Normality Test	Statistical Test	Test Statistic (W, H, χ²)	df	N	p
Group size, presence offspring	Fail	Fisher's Exact	11.485	2	86	0.003
Depth, presence offspring	Fail	Mann-Whitney	580.000	1	86	0.116
Depth offspring present, months	Fail	Kruskal-Wallis	27.190	4	86	< 0.0001
Depth, foraging strategies	Fail	Kruskal-Wallis	4.617	4	86	0.329
SST, foraging strategies	Fail	Kruskal-Wallis	8.491	4	95	0.075
Group size, HS	Fail	Kruskal-Wallis	0.780	2	5	0.677
Group size, KE	Fail	Kruskal-Wallis	2.000	2		0.368
Group size, LA	Fail	Kruskal-Wallis	1.061	2	65	0.588
Group size, WF	Fail	Kruskal-Wallis	2.756	2	8	0.252
Group size, CA	Fail	Kruskal-Wallis	0.0352	2	15	0.986
Gannet, HS	Fail	Mann-Whitney	205.000	1	5	0.302
Gannet, LA	Fail	Mann-Whitney	191.500	1	60	0.400
Gannet, WF	Fail	Mann-Whitney	219.500	1	7	0.859
Gannet, CA	Fail	Mann-Whitney	206.500	1	16	0.607
BW, LA	Fail	Mann-Whitney	56.000	1	66	0.124
BW, WF	Fail	Mann-Whitney	85.000	1	7	0.475
BW, CA	Fail	Mann-Whitney	84.000	1	16	0.615
Gannet, location offspring	Fail	Pearson Chi-square	35.419	1	65	< 0.0001
BW, location offspring	Fail	Pearson Chi-square	0.079	1	8	0.779
LA, location offspring	Fail	Mann-Whitney	169.000	1	72	0.370
CA, location offspring	Fail	Mann-Whitney	75.500	1	6	0.259
Individual strat, Cooperative strat	Fail	Mann-Whitney	1.000	1	94	< 0.0001
Cooperative strat, offspring presence	Fail	Mann-Whitney	393.500	1	185	0.108
Position offspring, foraging strategies	Fail	Fisher's Exact	0.943	1	61	1