

FORAGING ECOLOGY OF
COMMON DOLPHINS (*Delphinus* sp.)
IN THE HAURAKI GULF, NEW ZEALAND

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I dedicate this thesis to my best friends –
my twin sister, Sarah and my brother, Nathan.

Declaration

The work presented in this thesis is, to the best of my knowledge and belief, original except as acknowledged in the text. I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Elizabeth A. Burgess

December 2006

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To the amazing times and experiences on the voyages of *Aronui moana* (Great learning of the sea)...

*Thus within her kingdom lies,
Filling scenes for hungry eyes,
Also treasures of this natural world,
Which, if watched carefully, will be unfurled.*

- David Suzuki

Abstract

This study investigated the foraging ecology of common dolphins (*Delphinus* sp.) in the Hauraki Gulf Marine Park, off the east coast of Auckland, New Zealand. Like most species of small cetacea in the Southern Hemisphere, its foraging habits are poorly described. A total of 59 focal group follows of common dolphins were conducted between January and April 2006. Observations were conducted at the surface, recording the predominant behavioural state of the group, foraging phase, foraging strategy, group dispersion, group formation, swimming style, group heading, calf presence and associated species. All occurrences of fission-fusion events and surface behaviours were recorded. This study tested the hypothesis that foraging behaviour of common dolphins would be influenced by environmental and physical parameters, group size, calf presence and associations with other species. In the Hauraki Gulf, foraging behaviour was recorded during all common dolphin follows, with $14\% \pm 1.7$ (mean $\pm$ s.e.) of time spent feeding. Larger groups of dolphins spent more time foraging than smaller groups. Herding accounted for a large part of the foraging behaviour of common dolphins (mean $\pm$ s.e. = $28\% \pm 2.3$, $n = 54$). Larger groups were found to spend significantly more time herding than smaller groups. Herding was generally directed towards the nearest landmass. Common dolphins use a variety of foraging strategies, both individual and group coordinated strategies. High-speed pursuits ($n = 29$) and kerplunking ($n = 15$) were the only individual foraging strategies recorded. Coordinated feeding strategies employed were synchronous diving ($n = 50$), line-abreast ($n = 28$), carouselling ($n = 26$) and wall-formation ($n = 4$). Synchronous diving and carouselling were the most enduring strategies, accounting for a significant proportion of foraging behaviour (mean $\pm$ s.e. = $32\% \pm 0.05$ and $24\% \pm 0.08$ of instantaneous samples, respectively). Foraging strategies were typified by various group formations, dispersion between group members, swimming styles and breathing intervals. Foraging strategies were also observed to have different roles in dolphin foraging. Line-abreast and wall-formation were associated with herding. However, high-speed pursuit, kerplunking and carouselling were strategies synonymous with feeding. Foraging strategies were shown to be dynamic, with dolphin groups changing strategies within a foraging bout (mean $\pm$ s.e. = 3 strategies per foraging bout ± 0.4). Larger groups spent more time engaged in coordinated foraging strategies than smaller groups. Noisy surface behaviours and fission-fusion events were frequently seen in synchrony with

foraging behaviour. Calves present in a foraging group, typically assumed a central position in the group during herding, but remained on the periphery during feeding. When feeding, common dolphins frequently were associated with Australasian gannets (*Morus serrator*), shearwaters (*Puffinus* spp.) and Bryde's whales (*Balaenoptera brydei*). Observations on the predatory behaviour of each species suggested a temporary close association between birds, whales and dolphins. This study showed an association of Australasian gannet flocks ($n = 46$) and Bryde's whales ($n = 27$) with common dolphins, and described the nature of the joint aggregations of mixed-species feeding in the Hauraki Gulf. The behaviour of gannets and whales strongly coincided with that of the foraging dolphin group. Whales were recorded tracking behind foraging dolphins for up to one and a half hours ($\text{mean} \pm \text{s.e.} = 23 \text{ min} \pm 2.3$). Observations suggest that the relationship between gannets and whales with common dolphins was deliberate, and that these species take advantage of the superior ability of dolphins to locate and concentrate prey. The associations with gannets and whales had a significant impact on common dolphin foraging behaviour. Duration of the phenomenon was predicted to be a direct function of the quantity of prey fish available. The presence of a whale had a sizable impact on the diffusion of feeding aggregations.

Results from this study indicate that the benefits of coordinated team hunts implemented by common dolphins in the Hauraki Gulf are a key factor in their foraging ecology. Their cooperative foraging skills appear to not only benefit the common dolphin individual, but other species as well. Ultimately, their role as a social hunter and an abundant, apex predator in the ocean, suggests that the common dolphin is a strongly interacting species which may facilitate population viability of other species in the Hauraki Gulf ecosystem.

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Chapter One: INTRODUCTION

1.1 *Foraging ecology*

Foraging determines an organism's intake of resources - water, nutrients or energy. Expenditure of those resources on fitness-related activities determines the life-history patterns of an organism (survival, reproduction, growth). The allocation of a limited resource pool among competing life-history traits links foraging and life-history (Boggs, 1992). The evolutionary basis for individual feeding behaviour is generally considered in the context of optimal foraging theory (Partridge & Green, 1985). Optimal foraging theory states that organisms focus on consuming the most energy, while expending the least amount of energy. The understanding of many ecological concepts, such as adaptation, energy flow and competition, hinges on the ability to comprehend why animals select certain foraging strategies to attain certain food items (Krebs, 1978).

Predation impacts ecological attributes such as population structure and viability, as well as evolutionary phenomena such as foraging tactics (Endler, 1986; Norrdahl & Korpimäki, 2000). Many terrestrial predators chase their prey and capture them in full pursuit (e.g., cheetahs chase gazelles, dogs chase hares, falcons strike pigeons, and bats hunt moths; reviewed by Howland (1974)). In the aquatic environment, large vertebrate predators should have difficulty catching small prey because the overall manoeuvrability of small prey is likely to be superior to that of large predators in a viscous surrounding (Webb, 1976; Domenici, 2001). Yet, aquatic predators regularly catch their prey, using specialised locomotor and/or behavioural strategies to compensate for inequities in manoeuvrability between themselves and smaller, elusive prey (Maresh et al., 2004).

From an evolutionary perspective, the foraging behaviour of marine mammals is constrained by the challenges to exploit marine food as a warm-blooded, air-breathing, live-bearing animal (Elsner, 1999). Each one of those mammalian characteristics is an obstacle to life in the water. Therefore, cetaceans offer a good example of a group of animals in which adaptations related to foraging are generally acknowledged to have

played a central role in evolutionary radiations (Würsig, 1986; Baird, 2000; Connor, 2001; Mann & Sargeant, 2003).

1.2 Foraging behaviour of dolphins

Delphinid foraging strategies range from individual hunting manoeuvres to highly coordinated group activity (Würsig, 1986). The Delphinidae family includes at least 30 species of small (< 4 m long) toothed cetaceans, generally termed dolphins, and four species of larger (4 to 6 m) toothed cetaceans (Reeves et al., 2002). The smaller members of Delphinidae include bottlenose dolphins (*Tursiops* spp.), common dolphins (*Delphinus* spp.), and several species of the genera *Stenella*, *Lagenorhynchus* and *Cephalorhynchus*. Larger members of the family include the killer whale (*Orcinus orca*), and pilot whales (*Globicephala* spp.) (Leatherwood et al., 1983). The Delphinidae family is therefore represented by a large and relatively diverse group of cetaceans, which exhibit different modes of living and several different social systems. In a review of foraging strategies, Würsig (1986) emphasises the variability and, in some cases, complexity of feeding behaviours evident in dolphin species.

Dolphins can display a high degree of coordination among individuals while engaged in feeding manoeuvres. Fish may be trapped against shorelines, driven between dolphin groups, encircled in both shallow and open waters, chased or tossed onto beaches (Tayler & Saayman, 1972; Norris & Dohl, 1980b; Würsig, 1986). The manner in which food is gathered depends greatly on the type and accessibility of prey. Where the type of prey available is relatively constant, the foraging strategy may also be relatively unvarying from day to day and between seasons. Such consistency in foraging behaviour has been observed in Hawaiian spinner dolphins (*Stenella longirostris*), which feed at night on organisms associated with a rising deep scattering layer (Norris & Dohl, 1980a; Norris et al., 1985). Where prey types change, strategies of finding and securing prey must change accordingly. For example, populations of killer whales feeding on salmon often hunt in loosely coordinated groups (Bigg et al., 1976), while killer whales feeding seasonally on pinnipeds appear to use complicated strategies to isolate and attack particular vulnerable animals (Condy et al., 1978; Lopez & Lopez, 1985). Transient killer whales that predate on larger whale species (Tappy, 1979) also attack as a tight pod, harassing their prey from different angles and using different techniques. This behaviour may be comparable to wild dogs (*Lycaon pictus*) which

exhaust and finally bring down a wildebeest (*Connochaetes taurinus*) (Kleiman & Eisenberg, 1973).

The behaviour of dolphins is closely tied to local ecology, and behaviour patterns change according to ecological factors. Many studies have contributed insights into the relationship between behaviour and ecology (e.g., Shane, 1990; Neumann, 2001b). Dolphin behaviour can be influenced by several factors, including time of day, season, water depth, bathymetry, tidal flow, and human activities (Shane, 1990). Dolphins' responses to these ecological variables are somewhat unpredictable and can differ depending on the habitat in which the animals are studied. Ultimately, dolphins experiencing different prey availability, habitats and ecological environments are predicted to adapt suitable foraging specialisations.

1.3 Foraging specialisations in dolphins

Foraging specialisations allow animals to adapt to environmental variations and, thus, promote their survival. Diversity in foraging techniques is well documented for many species, including chimpanzees (*Pan troglodytes*) (Teleki, 1973; Wrangham, 1974; Goodall, 1986), spider monkeys (*Ateles geoffroyi*) (Chapman et al., 1995), baboons (*Papio* sp.) (Barton et al., 1996), humpback whales (*Megaptera novaeangliae*) (Whitehead, 1983; Clapham, 2000), lizards (*Ctenotus* spp.) (Craig et al., 2006) and stingless bees (*Plebeia tobagoensis*) (Hofstede & Sommeijer, 2006).

Specialised foraging behaviours provide an efficient means of detecting and pursuing prey (Partridge & Green, 1985), as well as reducing intraspecific competition for food resources. The use of foraging specialisations may evolve in response to physical difference in habitat, such as topography (Hoelzel et al., 1989), or variation in food supply (Partridge & Green, 1985). In addition to ecological factors, an individual's preference also plays a role in the selection of a foraging specialisation (Nowacek, 2002).

Foraging behaviours have been documented as variable and adaptable for many cetaceans, and show both inter- and intra- population variability (Sargeant et al., 2005). For example, lobtail and bubble-net feeding in humpback whales (*Megaptera novaeangliae*) (Hain et al., 1982; Weinrich et al., 1992), cooperative hunting and strand

feeding in killer whales (Guinet, 1991; Hoelzel, 1991; Baird & Dill, 1995; Guinet & Bouvier, 1995), bird-associated foraging and lunge feeding by minke whales (*Balaenoptera acutorostrata*) (Hoelzel et al., 1989), and extravagant methods used by humpback dolphins (*Sousa plumbea*) to push fish onto exposed sand banks at low tide (Peddemors & Thompson, 1994). Bottlenose dolphins (*Tursiops* spp.) are well known for their foraging diversity. They forage both in groups and individually (Shane et al., 1986), exploiting prey throughout the water column, on shore or above the water surface (Connor et al., 2000b). Bottlenose dolphins have even adapted their foraging behaviours to take advantage of human activity, by following fishing boats to obtain discarded fish (Leatherwood, 1975; Chilvers & Corkeron, 2001), visiting provisioning locations (Orams et al., 1996; Mann & Kems, 2003), and catching fish cooperatively using net fishers (Pryor et al., 1990; Simões-Lopes et al., 1998). Additional tactics include using their rostra to dig into the substrate (Rossbach & Herzing, 1997; Nowacek, 2002; Mann & Sargeant, 2003), smacking their tails on the water surface over shallow seagrass beds to disturb prey (Connor et al., 2000b; Nowacek, 2002), whacking fish with their tails (Shane, 1990; Nowacek, 2002), circling schools of fish then darting into the school to capture some fish (Hamilton & Nishimoto, 1977; Bel'kovich et al., 1991), surging partially or fully out of the water and onto the beach to catch single fish (Berggren, 1995; Mann & Sargeant, 2003), stirring up sediment to trap fish (Lewis & Schroeder, 2003), and other behaviours (e.g., Leatherwood, 1975; Würsig, 1986; Mann & Sargeant, 2003; Gazda et al., 2005).

Foraging behaviours apparently unique to populations, research sites, and/or individuals have steadily increased in the cetacean literature (Nowacek, 2002; Mann & Sargeant, 2003; Sargeant et al., 2005). Like other mammals, individual dolphins may use specialised foraging techniques that are shaped in response to habitat type or prey resources. Bottlenose dolphins are also well known for their diet breadth and versatile foraging behaviours which can be population or site specific (Sargeant et al., 2005). They serve as a prime example of a species with varied feeding strategies at numerous locations around the world. In South Carolina, fish are driven onto mudbanks by bottlenose dolphins, who temporarily beach themselves in the process (Rigley, 1983). In the Bahamas, bottlenose dolphins dive rostrum first into the sand and bury themselves up to their flippers, during benthic 'crater feeding' (Rossbach & Herzing, 1997). In Florida, they 'whack' fish into the air, with their tail flukes, stunning or killing the fish in the process (Wells et al., 1987). In Western Australia, bottlenose dolphins even forage with the aid of sponges worn over their rostra as tools during benthic foraging (Smolker et al., 1997; Mann & Sargeant, 2003). Bottlenose dolphins use

estuarine mud flats to trap fish in several areas of the south-eastern United States (Hoese, 1971; Rigley, 1983), the Colorado River Delta (Silber & Fertl, 1995) and Portugal (dos Santos & Lacerda, 1987). Finally, off the south Pacific coast of Costa Rica, the rare behaviour of 'food sharing' has even been observed between a male and a female bottlenose dolphin that was accompanied by a calf (Fedorowicz et al., 2003). Another delphinid species showing immense flexibility in their feeding strategies is the killer whale. Prey taken by killer whales cover an extensive spectrum from schooling fish to baleen whales (Baird, 2000). Specialisations on certain prey by certain pods have been well documented for the Pacific Northwest (Baird, 2000).

In summary, the types of foraging specialisations used by dolphins appears to be determined by the ecology and localised habitat types (Weiss, 2005). The dependency of dolphins on habitats that are conducive to their foraging technique(s) and the influence of habitat characteristics on foraging efficiency indicate a need to further understand the relationship between identified feeding areas and foraging specialisations of species (Hastie et al., 2003).

1.4 Cooperative feeding of dolphins

Cooperative or group hunting has been reported in several mammals (e.g., African wild dogs (*Lycaon pictus*): Creel & Creel, 1995) and even in one bird species (Harris hawks (*Parabuteo unicinctus*): Bednarz, 1988). Group hunts that are considered cooperative, range from simultaneous chases to hunts that are clearly coordinated (Kitchen & Packer, 1999). Cooperative hunting occurs when individuals coordinate actions, such that the probability of successful capture of prey is increased among all participants (Sargeant et al., 2005). Cooperative feeding is common among social carnivores and is generally thought to be a way of increasing hunting success (Kruuk, 1975). This is particularly relevant in aquatic environments where prey resources are often spatially and temporally dispersed. Feeding in groups in such an environment can increase foraging efficiency (Wells et al., 1999). Among cetaceans, many species of delphinids have been observed to feed cooperatively (Norris & Dohl, 1980b; Würsig, 1986; Evans, 1987; Similä & Ugarte, 1993; Fertl & Würsig, 1995; Fertl et al., 1997).

Coordinated feeding in dolphins is often opportunistically sighted and difficult to describe. Coordinated episodes have been described for bottlenose dolphins (Würsig,

1986; Bel'kovich et al., 1991), dusky dolphins (*Lagenorhynchus obscurus*) (Würsig & Würsig, 1980), killer whales (Similä & Ugarte, 1993), Atlantic spotted dolphins (*Stenella frontalis*) (Fertl & Würsig, 1995), Clymene dolphins (*Stenella clymene*) (Fertl et al., 1997), rough-toothed dolphins (*Steno bredanensis*) (Steiner, 1995) and common dolphins (Gallo-Reynoso, 1991; Clua & Grosvalet, 2001; Neumann & Orams, 2003). Accounts of apparent cooperative behaviour in feeding dolphins include fish being herded into a ball (Caldwell & Caldwell, 1972; Leatherwood, 1975; Rossbach, 1999), fish driven ahead of dolphins swimming in a crescent formation (Leatherwood, 1975; Würsig, 1986), against mud banks (Leatherwood, 1975) or trapped between dolphins attacking from either side (Würsig, 1986). A division of labour with role specialisation has even been described in cases of group hunting in bottlenose dolphins (Gazda et al., 2005).

A well-documented cooperative hunter is the killer whale. This species is known to exhibit varying degrees of cooperative foraging behaviour depending on the type of prey selected (Guinet, 1991; Guinet, 1992; Similä & Ugarte, 1993; Baird & Dill, 1995). Cooperative foraging in killer whales has been identified by observations of group movements, from synchronous respirations while chasing and encircling prey (Ljungblad & Moore, 1983) to divisions of labour in the attack (Tarpy, 1979) and the sharing of prey (Lopez & Lopez, 1985). Killer whales have been documented attacking gray whales (*Eschrichtius robustus*) (Baldrige, 1972), sperm whales (*Physeter macrocephalus*) (Pitman et al., 2001) and even blue whales (*Balaenoptera musculus*), using cooperative strategies (Tarpy, 1979). The ability to capture prey larger than the predator is the most commonly cited selective advantage of cooperative foraging in terrestrial social carnivores (Kleiman & Eisenberg, 1973). Schaller (1972) has shown that cooperatively hunting lions (*Panthera leo*) have a success rate of 30% compared with 15% exhibited by solitary lions.

1.5 Associated species with dolphins during foraging

Foraging as a group may also reduce an individuals' risk of predation by diluting the probability of their being attacked (Hamilton, 1971; Foster & Treherne, 1981), hampering the ability of predators to focus on them as targets (Neil & Cullen, 1974; Landeau & Terborgh, 1986), or by providing earlier predator detection (Powell, 1974; Lazarus, 1979). These hypotheses are not mutually exclusive and different selective

pressures may impinge upon different group participants (Morse, 1977; Cimprich & Grubb, 1994).

Social foraging doesn't just extend to monospecific groups, but also to heterospecific groups comprised of mixed-species foraging in close association. Some benefits of social foraging extend to both monospecific and heterospecific groups, but as monospecific group size increases, competition may begin to erode the advantages of sociality (Barnard & Thompson, 1985). However, members of mixed-species associations may be able to retain these advantages while being subjected less to competition for resources (Barnard & Thompson, 1985).

Mixed-species aggregations are documented in a variety of species, from fish (reviewed by Lukoschek & McCormick, 2002) and birds (Morse, 1970; Morse, 1977; Dolby & Grubb, 1998) to mammals such as ungulates, primates and cetaceans (reviewed by Stensland et al., 2003). In cetaceans, mixed-species groups are reported for more than 30 species (reviewed by Frantzis & Herzing, 2002) in various marine habitats (Saayman et al., 1972; Perrin et al., 1973; Würsig & Würsig, 1980; Au & Perryman, 1985; Polacheck, 1987; Selzer & Payne, 1988; Reilly, 1990; Shane, 1995). Numerous accounts of associations and interactions between different species of the family Delphinidae occur world-wide (reviewed by Frantzis & Herzing, 2002; Bearzi, 2005), but dolphins have also been observed in association with other species groups, particularly seabirds (reviewed by Evans, 1982).

Periodic associations between cetaceans and various seabird species, especially during bouts of feeding, have long been recognised by seafarers and exploited by whalers and fishermen. Many reports now exist in the literature (Evans 1982), although the nature of the associations vary considerably. Some authors have documented seabirds and cetaceans engaged together in intensive feeding activity (Brown, 1980; Clua & Grosvalet, 2001). Others simply note seabirds following cetaceans over a period of time (Evans, 1982).

Hypotheses proposed to explain the selective advantages of participating in social foraging associations have generally focused on foraging and anti-predation benefits (Morse, 1977; Bertram, 1978; Powell, 1985). For example, it has been suggested that foraging success is enhanced through copying (Krebs, 1973; Greig-Smith, 1978; Waite & Grubb, 1988), kleptoparasitism (Thompson & Barnard, 1983), flushing of prey from cover (Swynnerton, 1915; Barlow, 1974; Peres, 1992), or by allowing individuals to

reduce time allocated to non-foraging activities such as vigilance (Pulliam, 1973). An alternative explanation is that aggregations tend to occur when two species simply feed on the same prey resources (Tarasevich, 1957).

Mixed-species groups may lead to a more efficient utilisation of the food resources for one or all participating species (Stensland et al., 2003). One of the most well known associations in the marine environment is that of pelagic dolphins and schools of tuna (*Thunnus albacares*). These dolphin-tuna associations, sometimes also attract seabirds, other fish species and sharks (Au & Perryman, 1985; Au & Pitman, 1986; Au, 1991). During these associations, prey is driven towards the surface and is considered so abundant and diverse that dolphins and other species can feed from the fish school at the same time (Au & Pitman, 1986). The mixed-species group feeds, interacts and travels together for various periods of time (Au, 1991). These associations have been studied in the tropical Pacific (Perrin et al., 1973; Au & Pitman, 1986; Polacheck, 1987; Scott & Cattanch, 1998) and in the North-east Atlantic (Das et al., 2000).

In a review by Evans (1982), common dolphins were highlighted as a species that regularly associate with other species. Common dolphins have been observed in sympatric associations with other cetacean species, including bottlenose dolphins (*Tursiops truncatus*), striped dolphins (*Stenella coeruleoalba*), Risso's dolphins (*Grampus griseus*) and short-finned pilot whales (*Globicephala macrorhynchus*) (reviewed by Frantzi & Herzing, 2002; Bearzi, 2006). Various accounts of common dolphins feeding in association with other species have been recorded around the world. Common dolphins have been observed feeding in association with pinnipeds, such as Californian sea lions (*Zalophus californianus*) and harbour seals (*Phocena vitulina*) (Gallo-Reynoso, 1991; Bearzi, 2006). They have also been observed in association with a great variety of seabirds, including Cory's shearwaters (*Calonectris diomedea*), great shearwaters (*Puffinus gravis*), boobies (*Sula* spp.), terns (*Sterna* spp.), gannets (*Sula* spp.), gulls (*Larus* spp.), petrels (*Procellaria* spp.) and kittiwakes (*Rissa tridactyla*) (Evans, 1982; Pitman & Au, 1992; Pitman & Ballance, 1992; Clua & Grosvalet, 2001).

In New Zealand waters, common dolphins have been observed in mixed-groups with dusky dolphins (*Lagenorhynchus obscurus*) (Würsig et al., 1997; Markowitz, 2004a) and striped dolphins (Stockin, unpublished data), as well as a few baleen cetacean species, such as Bryde's whales (*Balaenoptera brydei*) (Constantine & Baker, 1997; O'Callaghan & Baker, 2002; Neumann & Orams, 2003), sei whales (*Balaenoptera*

borealis) and minke whales (*Balaenoptera acutorostrata*) (Neumann & Orams, 2003). In the Bay of Islands, Hauraki Gulf and Mercury Bay areas of the North Island, common dolphins have been observed in feeding associations with various seabird species, such as Australasian gannets (*Morus serrator*), sooty shearwaters (*Puffinus griseus*), Buller's shearwaters (*Puffinus bulleri*), flesh-footed shearwaters (*Puffinus carneipes*), fluttering shearwaters (*Puffinus garia*), white-fronted terns (*Sterna striata*), and white-faced storm petrels (*Pelagodroma marina*). Common dolphins associated and interacting with other species are mentioned by several authors (Constantine & Baker, 1997; O'Callaghan & Baker, 2002; Neumann & Orams, 2003; Schaffar-Delaney, 2004), but detailed descriptions or quantitative analysis of these mixed-species aggregations are rarely attempted.

1.6 The common dolphin

Common dolphins are distributed throughout the world's oceans but are restricted to temperate and tropical latitudes (Gaskin, 1968). However, like most other cetaceans, the common dolphin is not panmictic, and occurs as a series of geographically separate populations, which often show varying morphological characteristics (Jefferson & Van Waerebeek, 2002). On a global scale, the systematics and zoogeography of the genus *Delphinus* are subjects of ongoing investigation (e.g., Jefferson & Van Waerebeek, 2002), with over 20 different species having been suggested in the past (Carwardine, 1995). Two distinct species of common dolphin are now widely recognised: the short-beaked (*Delphinus delphis*) and the long-beaked common dolphin (*D. capensis*), distinguished morphometrically by Heyning and Perrin (1994) and genetically by Rosel et al. (1994). A subspecies of the long-beaked common dolphin has also been recognised (*D. capensis tropicalis*) which is endemic to the Indian Ocean (Jefferson & Van Waerebeek, 2002). In New Zealand waters, only the short-beaked common dolphin species is considered to occur, although this population is subject to morphological variation (Stockin & Visser, 2005), and is currently under taxonomic evaluation¹ (Stockin, unpublished data).

The short-beaked common dolphin (*Delphinus delphis*) is a small toothed cetacean from the family Delphinidae (Plate 1.1). Common dolphins are slender, with a typical body length of 1.8 to 2.3 m (Gaskin, 1992; Evans, 1994). However, larger individuals of up to 2.6 m (Evans, 1994), as well as smaller specimens (Perrin, 2002; Silva &

¹ Therefore, the common dolphin species investigated in this study will be referred to as *Delphinus* sp.

Sequeira, 2003) have been recorded. They are easily distinguished by their elaborate hourglass tri-colour pattern (Carwardine, 1995; Perrin, 2002) which has been described as one of the most complex of any cetacean (Mitchell, 1970).

There is relatively little information in scientific literature regarding the behaviour of free-ranging common dolphins. Where their behaviour has been investigated, it has primarily focused on animals in captivity, describing their social interactions and vocalisations (Evans, 1994; Kyngdon, 2000). Outside of the Mediterranean, it has been studied in few areas, and mostly in the context of abundance and distribution (Dohl et al., 1985; Selzer & Payne, 1988; Reilly, 1990; Gaskin, 1992; Chivers & DeMaster, 1994; Bearzi, 2001; Neumann, 2001b; Neumann et al., 2001; Stockin, unpublished data). Relatively little is known about groups living near or on the continental shelf edge, and the ecology and behaviour of offshore populations remain largely unknown (Evans, 1994).

Common dolphins are generally considered to be pelagic, with most groups occurring over the continental shelf and beyond (Gaskin, 1992). There they typically form large groups, sometimes numbering in the thousands (Cockcroft & Peddemors, 1990), although smaller coastal populations have been documented (Politi & Bearzi, 2001). The social organisation of common dolphins is largely unknown, although Evans (1975) and Bruno et al. (2002) suggest that the basic social unit for common dolphins contains less than 30 individuals. Overall, their behavioural ecology appears to resemble that of other pelagic dolphins, particularly some populations of spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) (Norris & Dohl, 1980b), suggesting that common dolphins could tend towards very fluid fission-fusion societies (Wells, 1991; Neumann, 2001b). In complex fission-fusion societies, the size and composition of groups changes rapidly as individuals frequently join and leave the group (Wells et al., 1987; Connor et al., 1992; Smolker et al., 1992; Smolker et al., 1993; Mann & Smuts, 1999). An ecological basis to the formation of fission-fusion societies may be foraging benefits to attain food that is spatially and temporally patchy (Goodall, 1986; Symington, 1990; Connor et al., 2000b).



Plate 1.1 A common dolphin in the Hauraki Gulf, showing typical lateral pattern with yellow and light grey side patches.

1.6.1 Diet and foraging behaviour

Common dolphins feed on a range of different prey items, varying between seasons and different geographic areas. The diet of common dolphins has been investigated through stomach content analyses of beached or by-caught specimens. Their prey includes epipelagic shoaling fishes as well as smaller mesopelagic fishes and squids (Perrin, 2002). Shoaling fish such as mackerel (Scombridae), sardines (Clupeidae) or anchovies (Engraulidae), and to a lesser extent cephalopods made up the majority of the stomach contents of stranded or incidentally caught common dolphins (Overholtz & Waring, 1991; Evans, 1994; Young & Cockcroft, 1994; Young & Cockcroft, 1995; Silva & Sequeira, 1996; Walker & Macko, 1999; Bearzi et al., 2003). While the feeding habits of common dolphins have been documented for various populations worldwide, (e.g., eastern United States (Overholtz & Waring, 1991), Portugal (Silva & Sequeira, 1996), Mediterranean Sea (Bearzi et al., 2003)), their diet within New Zealand waters is comparatively poorly known. Post-mortem analysis of the stomach contents of eight stranded common dolphins in the Hauraki Gulf, found the remains of eight fish species and at least two species of squid (Stockin et al., 2005). Arrow squid (*Nototodarus* sp.) and false trevally (Latarariidae) were the most frequently recorded species. Neumann and Orams (2003) observed common dolphins in the Bay of Plenty feeding on schooling fish, such as jack mackerel (*Trachurus novaezelandiae*). Another five fish species were identified from video-footage of dolphins chasing prey: kahawai (*Arripis trutta*), yellow-eyed mullet (*Aldrichetta forsteri*), flying fish (*Cypselurus lineatus*), parore (*Girella tricuspidata*) and garfish (*Hyporhamphus ihi*).

To be able to feed on such a large variety of prey, common dolphins exhibit a range of different feeding behaviours. Compared to other delphinids, such as bottlenose dolphins and killer whales, the foraging behaviour of common dolphins is not well-documented. Aspects of the behavioural repertoire of common dolphins are comparable to that of other delphinids, showing high variability (Würsig, 1986) and adapting hunting techniques specific to the habitat and targeted prey species. Information on feeding behaviours of common dolphins is mainly observed and documented *ad libitum* (Clua & Grosvalet, 2001; O'Callaghan & Baker, 2002). A study conducted in Mercury Bay, New Zealand, observed in detail the distinct foraging strategies used by common dolphins, and is the most thorough reference of the different methods used by common dolphins in the context of feeding (Neumann & Orams, 2003). Several distinct feeding methods were identified and described by Neumann and Orams (2003). Feeding methods employed by individual dolphins were

high-speed pursuits, fish-whacking, and kerplunking. Coordinated feeding strategies included carouselling, line-abreast and wall-formation. Temporary division of labour was observed during some coordinated feeding bouts in common dolphin groups, suggesting the importance of cooperation during foraging. Carouselling, which consisted of dolphins cooperatively surrounding a school of fish, was the most frequently observed foraging strategy in Mercury Bay (Neumann and Orams 2003). Carouselling has also been reported for common dolphins foraging in the Azores in mixed-species aggregations with tuna and seabirds (Clua & Grosvalet, 2001).

Since delphinid foraging behaviours are known to show variation between locations, this study aimed to extend the research on the foraging ecology of common dolphins to the Hauraki Gulf Marine Park.

1.6.2 Common dolphins and the Hauraki Gulf Marine Park

To date, only three studies have focused on New Zealand common dolphins (one conducted in the Bay of Plenty: (Neumann, 2001b), and two in the Hauraki Gulf: (Schaffar-Delaney, 2004; Stockin, unpublished data). In New Zealand, common dolphins are found around most coasts, and have been observed from the Bay of Islands in the north of the North Island, to Kaikoura on the east coast of the South Island (Gaskin, 1968; Constantine & Baker, 1997; Würsig et al., 1997; Bräger & Schneider, 1998). Their distribution in New Zealand has been described as meso-pelagic and it was suggested that their occurrence southward is more restricted in winter than in summer (Gaskin, 1972). Common dolphin sightings off the west coast have predominantly been reported during the summer season (Gaskin, 1972; Bräger & Schneider, 1998), though this may be an artefact of low sampling effort. Most reported sightings of common dolphins are from regions off the east coast of both the North and South Islands, especially in the eastern Cook Strait, Bay of Plenty, eastern Northland and Hauraki Gulf (Gaskin, 1972; Constantine & Baker, 1997; Neumann, 2001b; O'Callaghan & Baker, 2002).

The Hauraki Gulf Marine Park is utilised by a number of cetacean species (Hauraki Gulf Forum, 2004). Some species pass through the Gulf intermittently or during migration, while others appear to be resident or semi-resident in the Gulf. The cetacean community of the Hauraki Gulf is dominated by groups of common dolphins (O'Callaghan & Baker, 2002; Stockin, unpublished data).

The Hauraki Gulf is a broad embayment adjacent to the city of Auckland, North Island, New Zealand (36° 51' S, 174° 46' E). The Hauraki Gulf Marine Park was created by special legislation in 2000, in order to conserve its many islands, catchments and diversity within its environment (Hauraki Gulf Marine Park Act, 2000). Located next to metropolitan Auckland, the Gulf itself is important for commerce in New Zealand, serving the Port of Auckland (Hauraki Gulf Forum, 2004). It is also a significant area for the fishing and transport industries, as well as being important for recreation. Therefore, management of the Marine Park recognises the national significance of the Hauraki Gulf, aiming to protect natural resources while provide for recreational and economic activities, and also acknowledges cultural and historic value of the area to people and communities.

The Hauraki Gulf represents an unusual habitat for common dolphins because of its enclosed waters and predominantly level seabed of mud and broken shell, with an average depth of approximately 39-47 m (O'Callaghan & Baker, 2002). Internationally, the common dolphin is generally regarded as a deep-water pelagic species, found in depth ranges of up to 3500 m, in waters affected by upwellings (Reilly, 1990; Fielder & Reilly, 1994). Therefore, there are questions regarding why this particular population inhabits these comparatively shallow, sheltered waters in contrast to common dolphins studied elsewhere in world (Gaskin, 1992). Kenney and Winn (1986) proposed that cetacean distributions are determined by the distribution of the most important prey species. The Hauraki Gulf area has been identified as a significant area for common dolphin feeding activity (Schaffar-Delaney, 2004; Stockin, unpublished data). Therefore, the population of common dolphins in the Hauraki Gulf is a good subject for investigation with regard to their foraging ecology and behaviour.

1.6.3 Conservation status of the common dolphin

The conservation status of the common dolphin is listed as 'lower risk' in the 2006 IUCN Red List of Threatened Animals (IUCN, 2006). However, the recent decline observed in the Mediterranean subpopulation was acknowledged, and the status of common dolphins for that particular area is classified as 'endangered' (Bearzi, 2003).

Within New Zealand, common dolphins are not listed as a priority species for conservation management, nor are they identified as a species of significance under

the stated action plan to further develop planning and management for cetaceans in the Hauraki Gulf marine area (Suisted & Neale, 2004). This status is not, however, based on any empirical understanding of the abundance, distribution or life history of the species in the area. Further research is needed to clarify the biological and ecological significance of common dolphin conservation in the Hauraki Gulf.

While common dolphins are still regarded as abundant worldwide and are not listed as a threatened species (with the exception of the Mediterranean), they do face a number of anthropogenic threats, especially involving the fishing industry. For example, large numbers have been killed in by-catch associated with yellow-fin tuna (*Thunnus albacares*) fishery in the eastern tropical Pacific (Evans, 1994). Worldwide, the common dolphin represents the most prominent by-caught species every year for both the pelagic purse-seine and drift net fisheries (Evans 1994). Around New Zealand, by-catch of common dolphins associated with the jack mackerel (*Trachurus novaezealandiae*) fishery has been reported (Slooten & Dawson, 1995). Other potential threats to common dolphin populations include over fishing of food resources which disrupts prey distribution, affecting ecosystem dynamics and thereby affecting cetacean communities (Viale, 1994; Bearzi et al., 2003). Common dolphins are also subjects for commercial dolphin-watching operations, with research suggesting that dolphin foraging behaviour is sensitive to disturbance from such operations in the Hauraki Gulf (Stockin, unpublished data).

1.7 *Objectives of this study*

Studies on the foraging behaviour of cetaceans can contribute to the information on predator-prey relationships which leads to a better understanding of the functioning of marine ecosystems. Research on common dolphins in New Zealand has been limited, and there has been no systematic effort to assess their foraging ecology within the Hauraki Gulf. This project aimed to better understand these biological aspects by conducting a dedicated study investigating common dolphin foraging ecology within the Hauraki Gulf. Aside from providing new data on the ecology of the common dolphin, this study sought to provide data that will be useful in efforts to promote the conservation of biodiversity in the Hauraki Gulf Marine Park. Outcomes from this research will hopefully contribute to sustainable management of the Hauraki Gulf Marine Park and cetaceans in New Zealand.

The specific aim of this study was to investigate the foraging ecology of common dolphins within the Hauraki Gulf Marine Park. This research:

- investigated the foraging activity of dolphin groups;
- addressed whether certain foraging strategies were predominantly used to capture prey;
- investigated the influence of group size, calf presence and environmental factors on foraging behaviour;
- aimed to document and understand the role of common dolphins foraging behaviour in mixed-species feeding aggregations within the Gulf.

1.8 *Ecological significance of this study*

New Zealand is known to have a rich and diverse fauna of marine mammals, with almost half of the world's whale and dolphin species having been reported in New Zealand waters (Baker, 1999).

The waters of the Hauraki Gulf, off the city of Auckland, were classified as a Marine Park (*Hauraki Gulf Maritime Act 2000*) in acknowledgment of its significant biological diversity. The Hauraki Gulf Marine Park is also an economic and recreational resource, supporting commercial fishing and recreational boating. Resource managers are faced

with the task of balancing the conservation of aquatic biota with a variety of human activities, including recreation, tourism, commercial fishing and shipping. In order to do this successfully, it is important to understand the biology and ecological role of significant species.

The Hauraki Gulf is used by a variety of cetacean species of which common dolphins are the most frequently encountered and they are sighted year-round. The Gulf is considered an important foraging area for common dolphins (Stockin, unpublished data) and effective prey capture is fundamental to an individual's survival, making the Gulf a potentially significant area for common dolphin populations. Furthermore, common dolphins represent an abundant², top-order predator whose feeding ecology could potentially have a significant role in the ecosystem of this Marine Park. Ultimately, a better understanding of the feeding ecology of common dolphins within the Gulf will augment the wise management and use of the Hauraki Gulf Marine Park.

² Common dolphins have been assumed to be abundant in the Hauraki Gulf, however, their actual population status is unknown.

Chapter Two: METHODS

2.1 *Study area*

This study was conducted in the Hauraki Gulf (36° 25' S to 36° 55' S, 174° 40' E to 175° 30' E), a large, shallow, semi-enclosed coastal sea off the east coast of the North Island, New Zealand, adjacent to the city of Auckland (36° 51' S, 174° 46' E). The Hauraki Gulf is a broad embayment, open to the north, while landlocked to the south and west, and partly protected in the east by Great Barrier Island and the Coromandel Peninsula (Figure 2.1). It extends from Bream Head to Cape Colville, approximate latitude 36° 55' S to 36° 30' S. The Gulf area includes approximately 47 islands spreading over 13,600 km² of Pacific Ocean (Hauraki Gulf Maritime Park Board, 1983).

The Hauraki Gulf is within a warm temperate region, influenced by the subtropical East Auckland Current, particularly around the outer island groups (Stanton et al., 1997). Circulation patterns within the Gulf are dominated by the influence of wind direction and strength upon surface water movements. Water temperatures in the Gulf vary approximately 10°C seasonally, with summer highs of about 22°C and winter lows of about 12°C (Hauraki Gulf Maritime Park Board, 1983).

Tides in the region are semi-diurnal, with two low tides and two high tides in each 24 h period (Bercussion, 1999). The tidal range is approximately 1.8 m on neap tides and 2.4 m on spring tides (Hauraki Gulf Maritime Park Board, 1983). Water depth within the Gulf averages between 40 and 45 m, with a maximum depth of 53 m.

2.2 *Surveys in the Hauraki Gulf*

Non-systematic surveys for common dolphins were conducted in the Hauraki Gulf from January to April 2006. Weather permitting, daily surveys were conducted from the research boat, *Aronui moana* (a 5.6 m *Stabi-craft* vessel powered by a 90 hp four-stroke outboard engine) (Plate 2.2). Observations were only made under calm weather conditions (Beaufort sea state 0-3) with good visibility across the survey area (see Appendix 1).

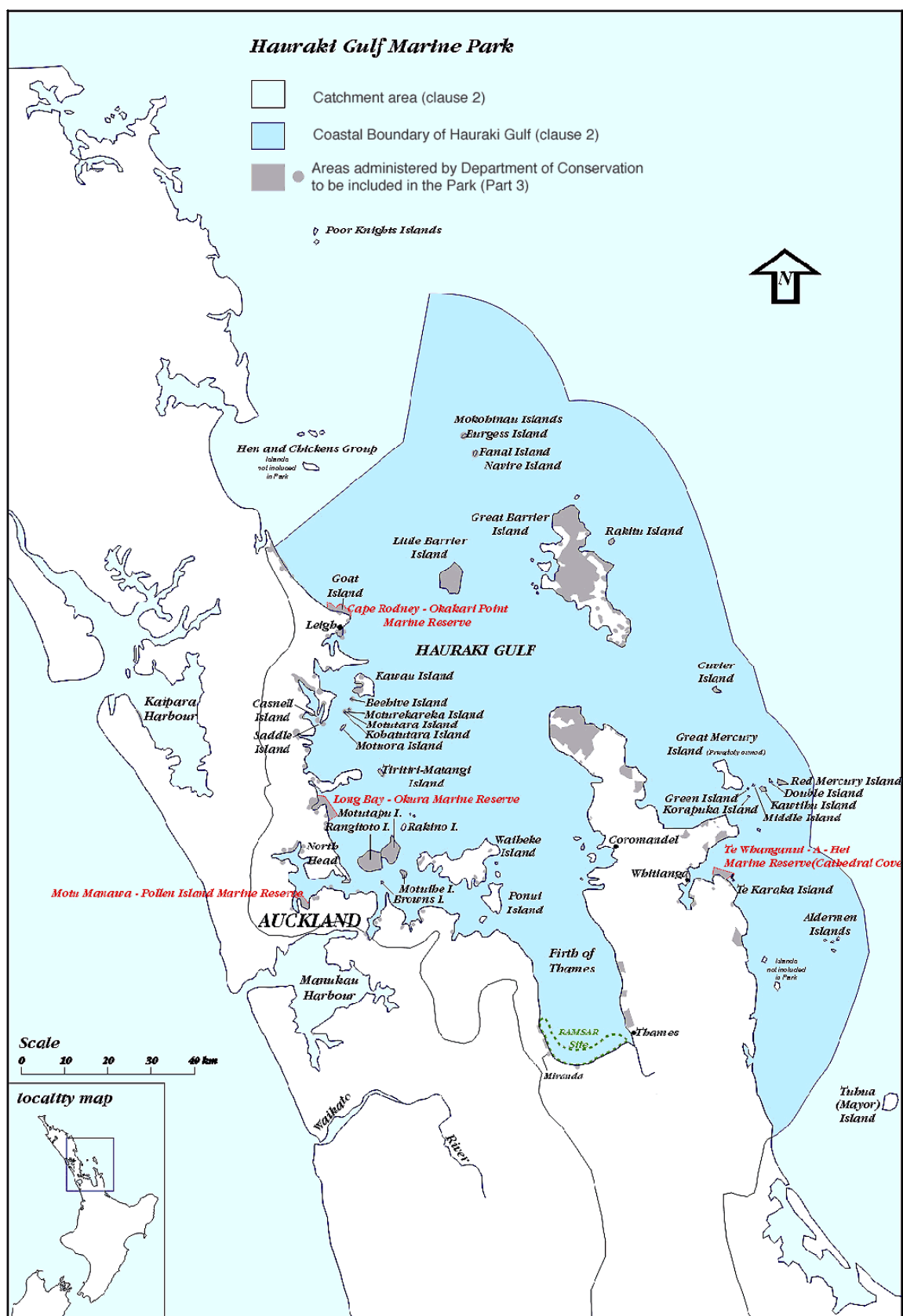


Figure 2.1 Map of the Hauraki Gulf Marine Park on the east coast on the North Island, New Zealand, where this study was conducted (Source: Department of Conservation, 2002).



Plate 2.1 The research vessel, *Aronui moana*, used in this study to observe common dolphins in the Hauraki Gulf.

The primary objective was to record the behaviour of focal groups of common dolphins (Mann, 2000) during daylight hours. The vessel was randomly navigated across the study area until observers noticed visible signs of dolphins. Any evidence of dolphin activity was investigated for the presence of dolphin groups, including aggregations of birds. Once a common dolphin group was located, observations and data collection began with that focal group. Observations were conducted on every dolphin group encountered, regardless of behavioural state, to allow for a random sample and to reduce bias towards sampling dolphins that were feeding. The method used to sight the dolphins was recorded (i.e., presence of circling gannet flocks) in an effort to identify searching bias towards conspicuous behaviour or associated species.

Two observers were onboard - Observer 1 (trained observer) had the role of recording all data observations, while Observer 2 (primary researcher, E. A. Burgess) continually watched the dolphin group and assessed all dolphin behaviours (see *section 2.5.1*). Once a group of dolphins was located, a sighting sheet was completed (see *Appendix 2*) - recording date, time, latitude and longitude, observers onboard and weather conditions (see *section 2.4*). The dolphin group was then approached slowly to within 300 m of the group. Assessments were made of the group size (see *section 2.3*), dolphins behavioural state (see *section 2.5.1a*) and direction of travel. Then a slow approach was made in accordance with the Marine Mammal Protection Regulations, and as per standard protocols described by Mann (2000).

The research boat approached slowly and was manoeuvred carefully, in order to minimise its potential effects on the dolphins' behaviour. During group observations, the vessel was driven parallel and at a matched speed to the dolphins (Würsig & Jefferson, 1990) to minimise disturbance while maintaining a clear view of dolphin behaviour. If the group was milling, stationary, or moving at slow speed for a period of time then the boat was either placed in neutral or the engine was turned off. If the dolphins were travelling, they would on occasion approach the boat and bow-ride. On these occasions, both speed and course of the boat remained consistent allowing the dolphins to determine the length of time they would bow-ride, rather than the boat being driven to either initiate or maintain contact. Differences in the group's behavioural state resulted in varying distances being maintained from the focal group, but where possible, a distance of 50 m was maintained. A focal group follow observation was then initiated, and data on the behaviour of the dolphin group was collected (see *section 2.5*).

2.3 Defining common dolphin groups

The objective of this study was to record the behaviour of focal groups of common dolphins (Altmann, 1974). When conducting focal group observations, it is important to explicitly define the rules for inclusion of individuals in the group (Martin & Bateson, 1993). In this study, dolphin groups were defined by spatial proximity according to the '10 m chain rule' (Smolker et al., 1992). Under this definition, any numbers of dolphins were considered part of a group so long as they were within 10 m of a nearest neighbour. This 'distance measures' definition of a group was chosen over a 'coordinated activity' definition for its simplicity and because it does not rely on any assumptions about the behaviour of a group's members (Mann, 1999; Mann, 2000). Such an approach is particularly valuable in studies where the diversity of behaviours exhibited within a spatially and temporally associated group are of interest (Mann, 2000).

Since common dolphins are known to live in fission-fusion societies (Neumann, 2001b), the splitting of group members required a rule to address situations when one or more animals leave the group. In circumstances of fission, observers may be tempted to stay with the larger or more active group. Because this is likely to bias data collection, a decision rule for following animals under changing conditions must be developed (Mann, 2000). This was addressed by creating the following *a priori* rule: When the focal group split into two or more separate groups, the follow was continued with the group that stayed on a course parallel to the research vessel, regardless of whether it was the larger or smaller group. This was possible because the two groups never simultaneously deviated from their previous course. This rule was also employed to avoid harassment of the dolphins.

Throughout the study, photo-identification was opportunistically taken following methods outlined by Würsig and Würsig (1977). Photographs of the dorsal fins were randomly taken using a digital SLR camera (*Canon EOS 20D*) equipped with a 90-300 mm lens. In accordance with the Hauraki Gulf Common Dolphin catalogue (Stockin, unpublished data) maintained by Massey University, individuals were photographed using the left side of the dorsal fin. Photo-identification contributed to efforts to avoid re-sampling the same group of dolphins. Previous studies surveying the distribution and abundance of common dolphins in the Hauraki Gulf (Stockin, unpublished data) reveal that common dolphins are present year-round, and that an average of three independent groups can be found within the Gulf at anyone one time. By taking into

account the distance travelled and time elapsed between encounters, efforts were made to ensure samples originated from independent groups. Where feasible, examination of photo-identification involving distinctive individuals helped to confirm sample independence.

2.4 Collection of data on physical and environmental factors

All dolphin sightings were accompanied by records of the following temporal and environmental variables: date, time, latitude and longitude coordinates, distance offshore, water depth, water temperature, fish seen visually or on the fish finder (*Hummingbird Matrix 65x GPS fishing system*), vessels within 100 m of the dolphins, cloud cover, Beaufort sea state, visibility and tidal state.

During the follow, location (latitude and longitude) and time data were continually recorded using a *Garmin 76S* hand-held global positioning system (GPS) from the vessel as it was positioned alongside the dolphin group. Location coordinates and temporal data were later downloaded onto a personal computer (*IBM Thinkpad R51* using the software program *ExpertGPS version 2.3.9*) for analysis. The distance from shore was calculated from the GPS track coordinates using the mapping program *ExpertGPS version 2.3.9*.

Water depth and sea surface temperature were determined using the depth-sounder and thermometer (*Hummingbird Matrix 65x GPS fishing system*) onboard the research vessel. The depth-sounder also had a 'fish-finder' mode which could be used to highlight schools of fish. This mode was used during group follows, by recording the depth range of fish schools and a category of fish density at each instantaneous sample. However, these data were unreliable, as fish readings were heavily influenced by the speed of the vessel. Therefore, these data were not included in analyses.

Any vessel that approached within 100 m of the focal group was noted. Since vessel presence has been shown to impact on dolphin foraging behaviour (Lusseau, 2003; Constantine et al., 2004) those observations with other vessels present were either excluded from the analyses, or the length of the follow session was reduced and vessel data excluded from the data set.

Weather conditions were recorded at the beginning and ending of each dolphin encounter. During the group follow session, any extreme changes in weather were also noted. The categories of variables recorded for each focal group sighting are listed in *Appendix 1*.

Finally, observations were also scored for temporal variability by being assigned to a period in the day and tidal cycle, though these variables were confined to daylight hours. The day was divided into time blocks as follows: *early* before 0900 hours; *morning* between 0900-1059 hours; *midday* between 1100-1259 hours; or *afternoon* after 1300 hours. The start time for each behavioural sample was used to assign the group follow session to a time category. Likewise, the start time was used to assign a stage of the tidal cycle to each session accordingly: *high* sightings occurred 30 min either side of high tide; *ebb* sightings occurred > 30 min after high tide; *low* sightings occurred 30 min either side of low tide; or *flood* sightings occurred > 30 min after low tide.

2.5 Follow protocol and sampling method

Once a dolphin group was encountered (as defined by the dolphin group being a distance of less than 300 m from the boat), data collection commenced. The group follow session was terminated when visual contact with the focal group was lost and not regained within three consecutive two minute intervals (6 minutes), or the weather conditions deteriorated (e.g., poor visibility, Beaufort sea state > 3), or the follow length had reached 2 hours. This 'cut-off' time was based on observations by Neumann (2001b) who recorded avoidance behaviour in common dolphin groups during longer follows. Encounter- and departure-times, and corresponding location coordinates were recorded for all dolphin groups.

Three sampling methods were used for the collection of behavioural data in the present study (Altmann, 1974): (1) instantaneous scan sampling of focal-group activity; (2) all-occurrence sampling of events in a focal group; and (3) continuous sampling of particular activities performed by the focal group during a given observation period.

2.5.1 *Instantaneous scan sampling*

Instantaneous sampling (Altmann, 1974) is a technique used to record a group's current activity at pre-selected moments in time. This method was used to sample behavioural states (behaviour patterns of relatively long duration), but was not applicable for recording behavioural events (behaviours of discrete duration) (Mann, 1999).

Instantaneous sampling of focal common dolphin groups was recorded for sessions lasting 20 minutes or longer, with each session divided into two minute sample intervals ($n \geq 10$ instantaneous samples). At the start of each session, Observer 1 recorded initial data (date, time, environmental variables and group number - see *Appendix 2*), before starting the clock timer set at two minute intervals. Subsequently, Observer 2 called out the behavioural states which were recorded by Observer 1 onto a standardised data sheet (see *Appendix 3*). In order to maintain consistency in the interpretation of behavioural states, only Observer 2 (E. A. Burgess) assessed behaviour.

Behavioural state was scored by using widely accepted focal group scan sampling methodology (Altmann, 1974), and assigning a predominant group activity after an instantaneous scan of the group. Predominant group activity was defined as the activity that 50% or more of the group members were simultaneously engaged in.

Instantaneous scan sampling was used to document behavioural state, foraging phase, group dispersion, group formation, swimming style and group heading. At the signal from Observer 1, a single assessment was made for each of the above measures.

A primary use of instantaneous sampling is to estimate the proportion of time that individuals devote to various activities. For analysis, the proportion of time was calculated from the percentage of samples in which a given activity (state) was recorded.

(a) *Behavioural states and foraging strategies*

Five categories of activity state were recognised in the present study (Table 2.1). Definitions were derived from the descriptions used by Shane (1990) for bottlenose dolphins, and adapted by Neumann (2001b) and (Stockin, unpublished data) for New Zealand common dolphins.

Foraging behaviour was divided into three 'phases' - *herding*, *diving* and *feeding* (Table 2.2). This allowed for a distinction between dolphins expending energy marshalling fish versus capturing fish. Thus, whenever 'foraging' was recorded during instantaneous sampling, the foraging phase was also noted.

New Zealand common dolphins have been observed to use several distinct methods in the pursuit and capture of prey (Neumann & Orams, 2003). Two main categories were distinguished: (a) *individual* foraging strategies in which a dolphin pursues and/or captures fish on its own. Other group members could be present, but do not in any way aid or interfere with the individual's feeding effort; (b) *coordinated* foraging strategies in which several dolphins collectively herd or pursue fish. Under each of the two categories, several foraging strategies were investigated for common dolphins, as defined by Neumann and Orams (2003): *high-speed pursuit*, *fish-whacking*, *kerplunking*, *line-abreast*, *wall formation*, *carouselling* and *bubble-blowing* (Table 2.3, Figure 2.2-2.6). If the use of a strategy was clearly identified in the group during foraging, it was recorded at each instantaneous sampling interval. If more than one strategy was observed, both were recorded with the predominant strategy highlighted on the data sheet.

Table 2.1 Definitions of behavioural states used to assess common dolphins in the Hauraki Gulf, based on behavioural states used by Shane (1990) and Neumann (2001a).

Behavioural state	Definition
Rest	Moving very slowly and/or drifting in one direction. Resting lacked the active components of the other behaviours described.
Mill	Moving in varying directions in one location (no net movement in a particular direction), showing no surface behaviours, asynchronous breathing, and no apparent physical contact between individuals; usually staying close to the surface.
Travel	Dolphins moving at a sustained speed, in the same direction, making noticeable headway along a consistent compass bearing.
Forage	Dolphins involved in any effort to capture and/or consume prey as evidenced by chasing fish on the surface, coordinated deep diving, and rapid circle swimming (but not chasing another dolphin). Typically no contact between individuals (as often observed when socialising). Prey sometimes observed during the foraging bout.
Socialise	Some or all group members in almost constant physical contact with one another (except mothers and calves), oriented toward one another, and often displaying surface behaviours; no obvious forward movement. Typically involved aspects of play and mating with other dolphins.

Table 2.2 Definitions for phases used to describe foraging behavioural state of common dolphins in the Hauraki Gulf.

Behavioural state	Definition
Herding	Dolphins were coordinated in their swimming, maintaining constant speeds and with obvious directional changes.
Diving	Coordinated deep diving, often with fluke-up dive behaviours, synchronous surfacing patterns.
Feeding	Dolphins were observed either pursuing and/or capturing prey showing rapid changes in direction and sudden bursts of speed.

Table 2.3 Definitions of foraging strategies used by common dolphins in New Zealand, derived from Neumann and Orams (2003).

Foraging strategy	Definition
<i>Individual strategies</i>	
High-speed pursuit	Dolphins are seen individually pursuing single prey items at the surface, zig-zagging across the surface with bursts of speed.
Fish-whacking	Dolphins 'whack' fish with their tail flukes, launching the prey into the air, the dolphin then captures the stunned fish as it re-enters the water.
Kerplunking	Rapid tail fluke movement at the surface of the water, creating a percussive 'kerplunk' sound on the water.
<i>Coordinated strategies</i>	
Line-abreast	Dolphins form a tight line with individuals side-by-side, driving fish in front of them.
Wall formation	A group of dolphins drive fish toward another group of dolphins, trapping the fish in the centre.
Carouselling	Dolphins surround a school of fish and trap them at the surface, forcing the fish into a densely packed 'bait ball'. Some individuals patrol the edges of the school, while others dash through the centre.
Bubble-blowing	Dolphins release bubbles of air under water, in an apparent attempt to startle fish.

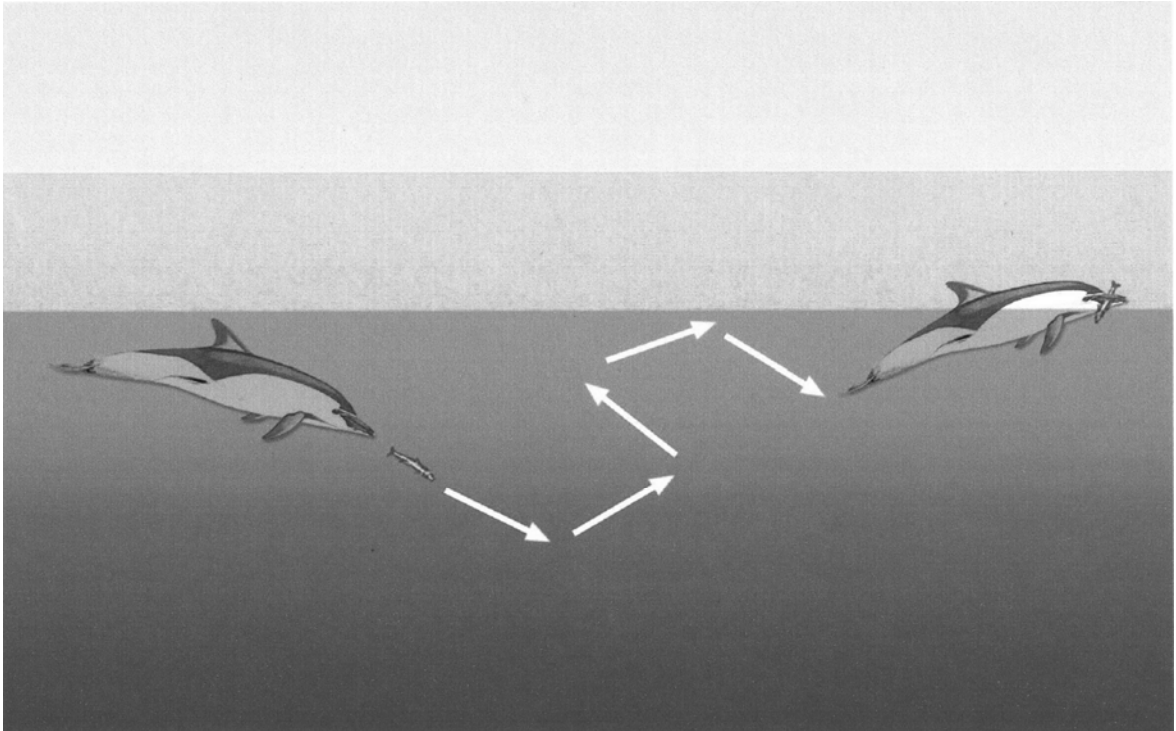


Figure 2.2 High-speed pursuit: dolphin pursues a solitary fish on a zig-zagging chase (Source: Neumann and Orams, 2003).

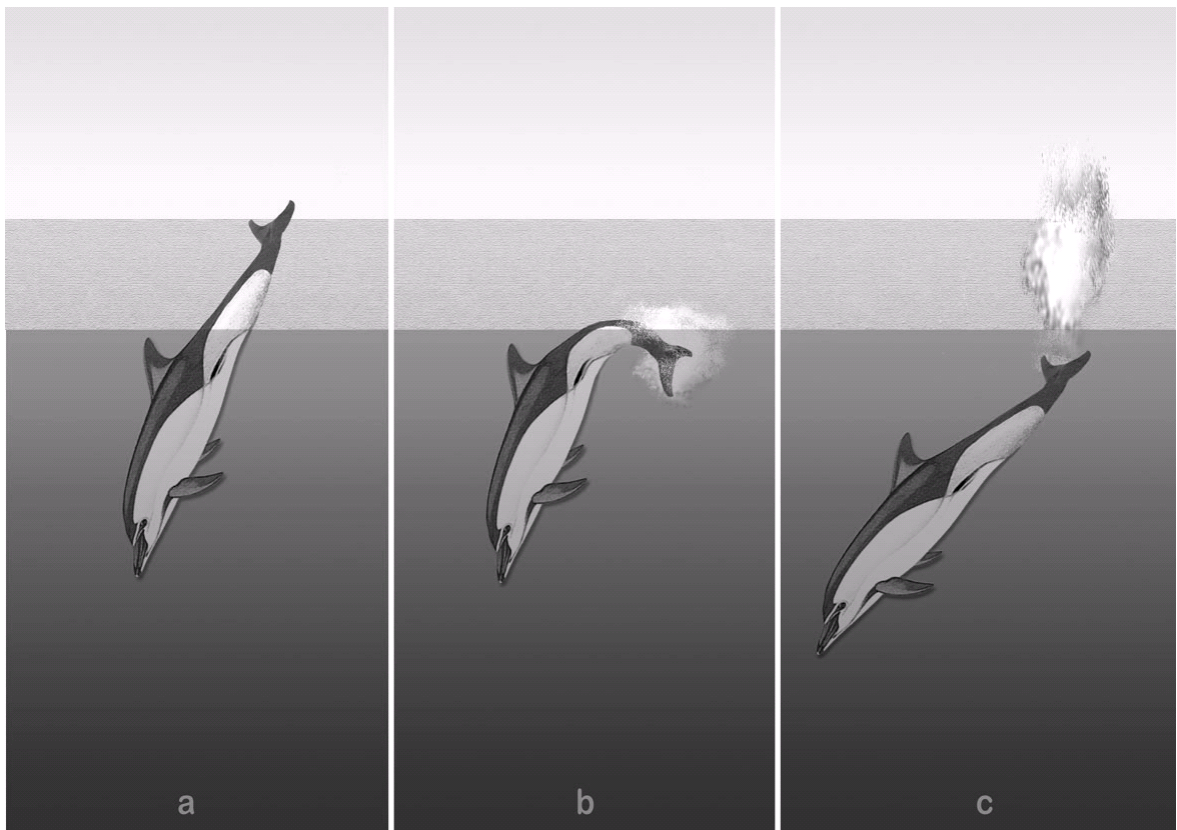


Figure 2.3 Kerplunking: a) dolphin lifts flukes vertically above the surface, b) flukes are brought down and forward, c) the dolphin straightens and dives, while cavitation splash is seen at the surface. (Source: Neumann and Orams, 2003).

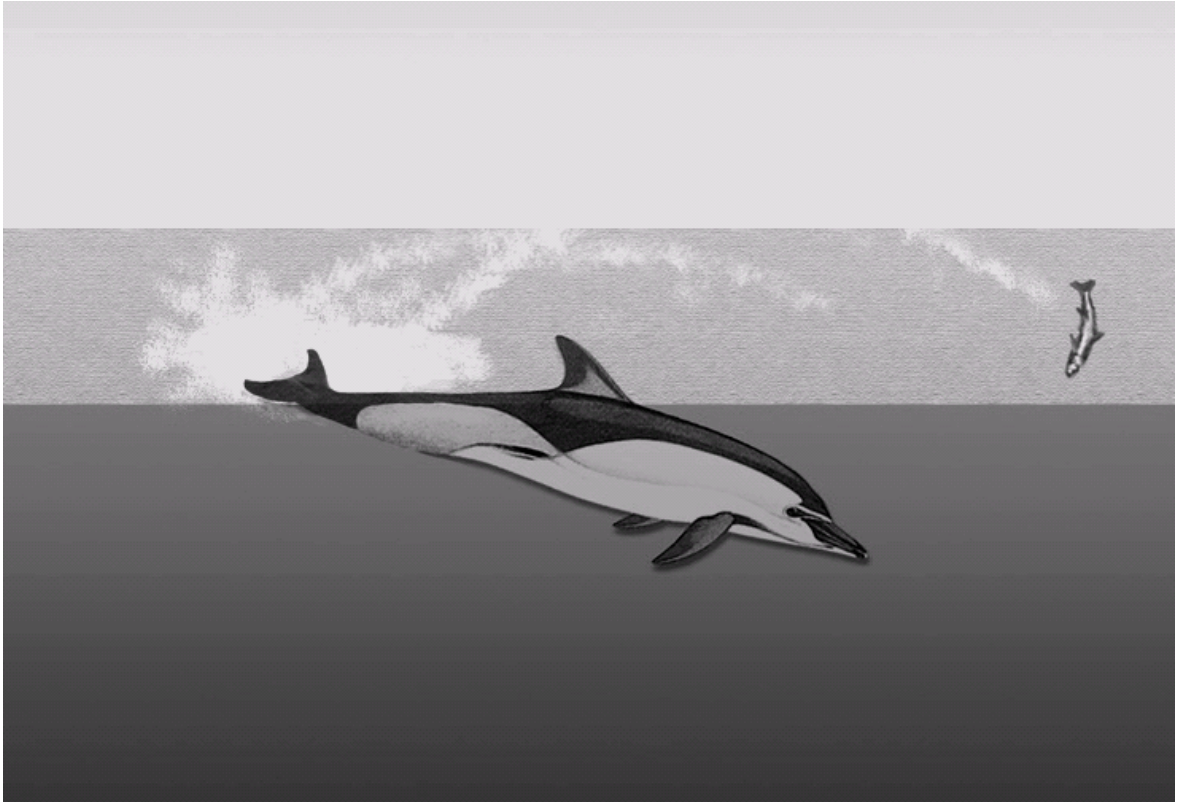


Figure 2.4 Fish-whacking: dolphin stuns its prey by catapulting it through the air with its tailflukes (Source: Neumann and Orams, 2003).

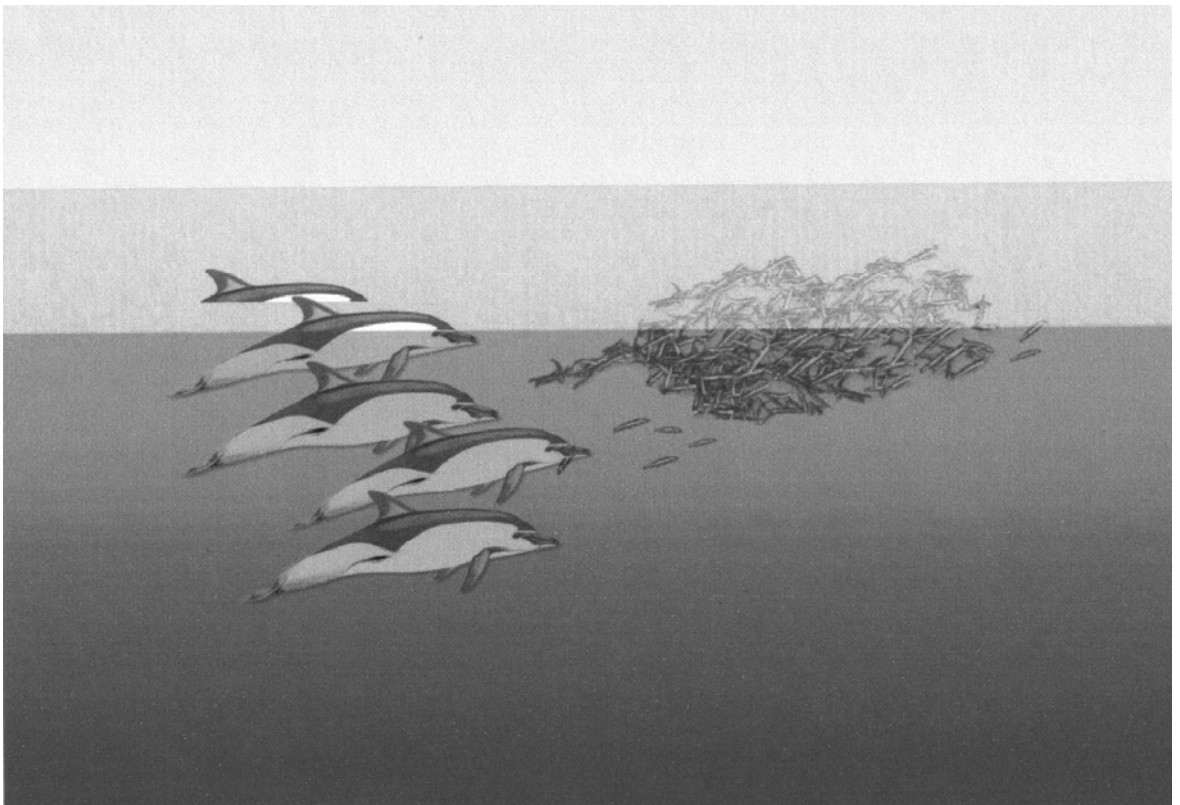


Figure 2.5 Line-abreast: dolphins swim closely side-by-side and drive fish in front of them (Source: Neumann and Orams, 2003).

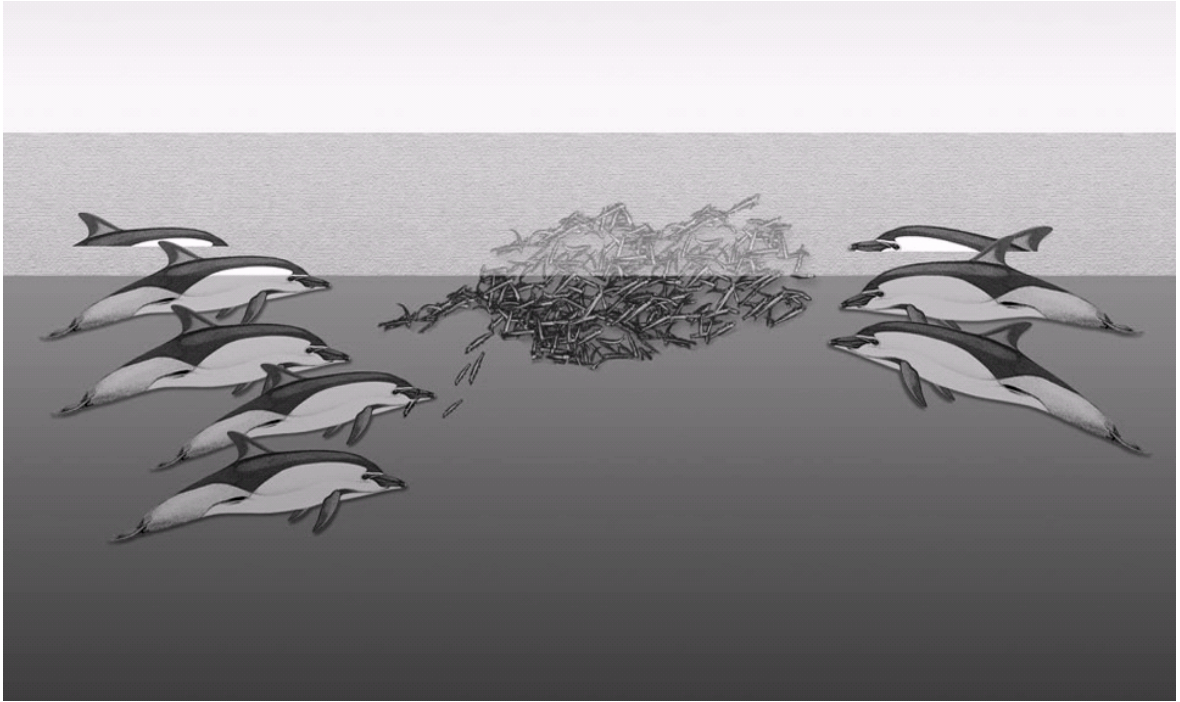


Figure 2.6 Wall formation: dolphins drive fish towards another group of dolphins (Source: Neumann and Orams, 2003).

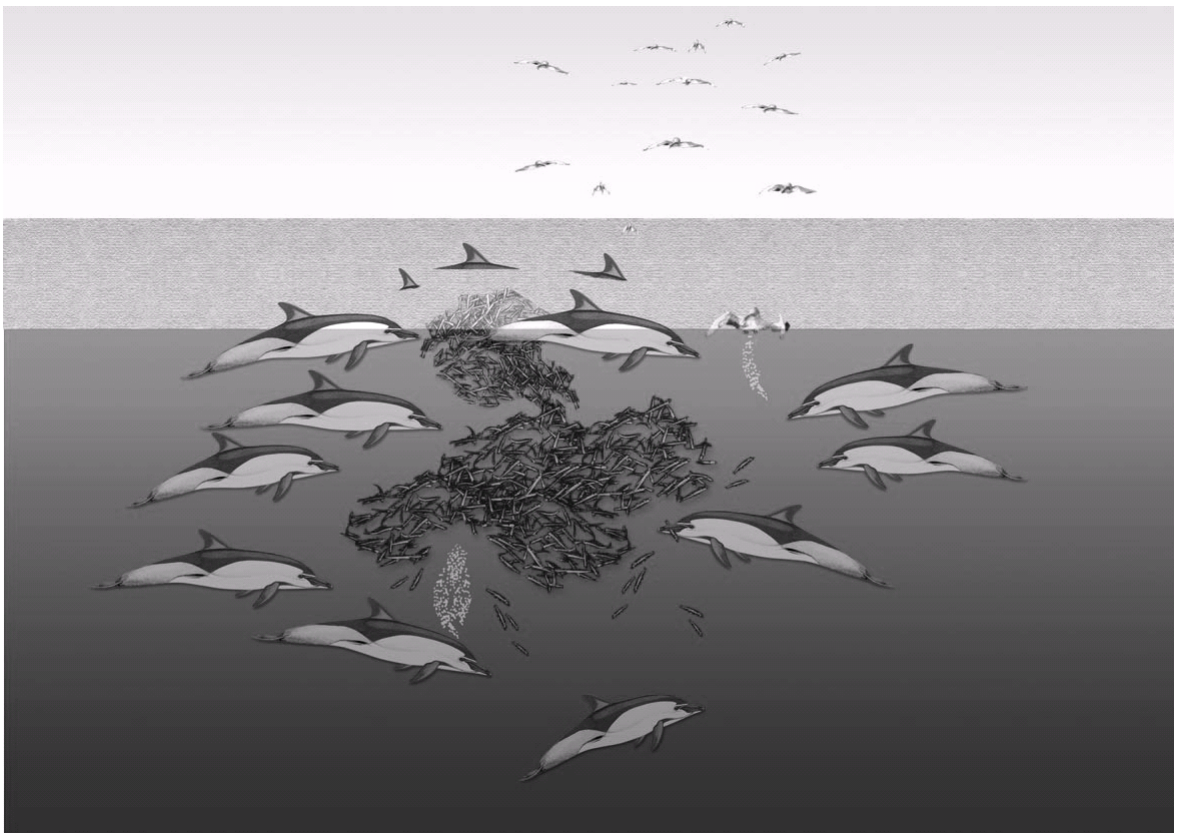


Figure 2.7 Carouseling: dolphins cooperatively encircle a school of fish and trap them against the surface. Also, showing bubble-blowing underwater (Source: Neumann and Orams, 2003).

(b) *Describing the dolphin group*

Group size

When a group of common dolphins was encountered, data on the group size and age-class composition were collected. Group size was estimated based on the maximum and minimum number of individuals observed at or near the surface at any one time, following the '10 m chain rule'. For analysis purposes, group size was then further classified as belonging to one of seven categories 1-10, 11-20, 21-30, 31-50, 51-100, 101-200, >200.

Presence of calves

Group composition was assessed using the presence/absence of adult, juvenile, calf and neonatal age classes, and counts of calves made for smaller groups. Juveniles were defined as animals that were noticeably smaller than adults but swimming independently. Calves were smaller dolphins (two-thirds or less the length of an adult) swimming in consistent close proximity to an adult. Neonatal (newborn) calves were recognised by their foetal folds, curled dorsal fin and lighter colouring. (McBride & Kritzler, 1951; Schaffar-Delaney, 2004). For statistical analysis, only the presence or absence of calves (including neonates) in dolphin groups was used.

Group formation

The two-dimensional geometry of the group was recorded during the group follows. Group formation was recorded instantaneously as: *diamond* (equally spread from side to side and head to tail); *linear* (spread further head to tail than side to side) (Plate 2.2); *parallel* (spread further side to side than head to tail); *echelon* (triangular or "v" formation with relatively few leaders and followers fanned out behind); *circular* (dolphins spiralled inwards or outwards in circular pattern); or *random* (no obvious formation) for each interval (Markowitz, 2004a).



Plate 2.2 A common dolphin group porpoising in a tight, linear formation.

Group dispersion

Dispersion was defined as the spatial proximity between dolphins in groups or the mode distance between nearest-neighbours. The two-dimensional spread of the dolphin group at each sample was classified as follows: *tight* referred to individuals less than one body length apart (< 2 m); *moderate* designated a separation of greater than one and less than three body lengths (2 to 6 m); or *loose* referred to group members spread over greater than three body lengths apart (> 6 m) (Markowitz, 2004a).

Swimming style

Swim style was assessed at each instantaneous sample during focal follows using the following categories: *slow* swimming referred to dolphins swimming at less than three knots with obvious easy surfacing behaviour; *steady* swimming the dolphins had pace (> 3 knots) with clear re-entry into the water and no splash; *accelerate* swimming the dolphin exhibited bursts of speed with rapid movement and significant spray as the dolphins “sliced” through the water; *porpoising* the dolphins showed consecutive low horizontal leaps with minimal splashing at moderate to high speeds (Plate 2.2); or *dive* which meant the dolphins were submerged during the sampling interval.

Surfacing pattern

During the two-minute period preceding the instantaneous time point, continual observations were made of the group's overall breathing pattern. If members of the group were observed breathing regularly at the surface then *frequent* surfacing was recorded at the next instantaneous sample; *infrequent* surfacing referred to irregular surfacing patterns, such that only a few representative members of the group were seen at the surface; *long downtimes* referred to occasions where animals were only sighted once or twice during the two minute period; if the group was not sighted during the two minute period then *dive* was recorded.

(c) *Describing associated species*

The behavioural state of associated species in the vicinity of the dolphins was also instantaneously collected at each two minute interval during focal follows. An *associated species* was defined as any species observed within a defined radius of the focal group of dolphins. Distances varied between taxa e.g., birds ≤ 200 m, cetaceans ≤ 500 m. Australasian gannets or Bryde's whales within their respective radius were observed at each time interval, and their behavioural state (Table 2.4) and the number of individuals recorded. Observations of associated species were achieved, without detriment to the dolphin follow, by the assistance of the auxiliary observer, while the primary observer (E. A. Burgess) remained focused on the focal dolphin group. Since whales surfaced irregularly and the vessel remained with the dolphin group at all times, the distance of the whale from the dolphins and direction of travel were noted and then recorded in the next interval sample. The presence of all bird species and any other marine species was recorded at every instantaneous sample, and species were identified using established field guides (Heather & Robertson, 1996; Baker, 1999). Bryde's whales were distinguished by the presence of diagnostic longitudinal ridges on the rostrum or the area between the blowhole and the tip of the head. Without confirmation of seeing these ridges, whales were cautiously referred to as *like-Bryde's* whales (termed used by Wiseman, pers. comm).

(d) *Describing mixed-species feeding aggregations*

The presence or absence of mixed-species feeding aggregations was noted during each instantaneous scan sample (see *section 2.5.3b* for the definition of a mixed-species feeding aggregation).

Table 2.4 Definitions of behavioural states used to describe species associated with common dolphins in the Hauraki Gulf.

Associated species	Behavioural state	Definition
Australasian gannet	Following	Birds persistently flying above dolphin group, maintaining pace and direction of the dolphins.
	Circling	Birds circling directly above foraging dolphins, generally the birds are not making any net movement.
	Diving	Birds dive straight down from up to 30 m high, with their wings stretched backwards, entering the water to catch fish at tremendous speed. This is a feeding behaviour.
	Resting	Birds sitting inactive on the water's surface, generally forming rafts of individuals drifting together.
Bryde's whale or like-Bryde's whale	Following	Whale is orientated towards the dolphin group, approaching from 180° behind, diving directly towards the dolphins, as determined by blow and dorsal fin orientation.
	Approaching	Whale is orientated towards the dolphin group, approaching from 180° ahead, diving in a direct line towards the dolphin determined by blow and dorsal fin orientation.
	No interaction	Whale is not orientated towards the dolphin group, diving away from the dolphins, as determined by blow and dorsal fin orientation.
	Present	Whale is present in the vicinity of the dolphins, but it was unclear which direction the whale was heading.
	Feeding	Whale seen capturing fish, either vertically lunge feeding or rolling laterally with expanded ventral pleats.

2.5.2 All-occurrences incident sampling

(a) *Fission and fusion*

Many animal populations can be classified as fission-fusion societies, whereby groups form and separate over time (Symington, 1990; Whitehead et al., 1991; Chilvers & Corkeron, 2002). Neumann (2001b) observed frequent occurrences of splitting-up and coming together of common dolphin groups. During this study, distinct dolphin groups were identified according to the '10 m chain rule' (see *section 2.3*). Therefore, splitting and joining events within and between dolphin groups were defined spatially. A *fission* event was defined as the separation of individuals from the focal group into two or more distinct subgroups, by distancing themselves greater than 10 m from the edge of the group in a direction away from the previous course. A *fusion* event was defined as the amalgamation of the focal group with another dolphin group previously separated by greater than 10 m. All incidents of fission and fusion involving the focal dolphin group were recorded.

(b) *Surface behaviours*

Common dolphin surface behaviour (e.g., leaps, head slaps, tail slaps and breaches) was recorded by all-occurrences sampling. It was possible to record all occurrences of surface events in a group, because such behaviours are obvious, and unlikely to be missed or under-represented. Furthermore, surface behavioural events never occurred too frequently to record.

Incident sampling was used to record all occurrences of surface behaviour events of all individuals within the group during an entire sampling session. The type of surface behaviour observed and the count of repetitive occurrences were recorded, as well as the time of the event. This allowed the occurrence of surface behaviours to be overlaid with behavioural state data collected during scan sampling methodology. Individual animals could not be identified, though distinctions between subjects during consecutive events could be made. Table 2.5 lists the surface behaviours recorded during group follows. Other behaviours, e.g., bow-riding, social rubbing, play, fluke-up diving, inverted swimming, logging and defecation events were also recorded. However, analyses focused on the 'noisy' surface behaviours that involved loud

splashes on the water and could potentially serve a communicative purpose during foraging (Neumann, 2001b).

(c) *Prey species*

Whenever prey was visible, descriptions were noted and attempts were made to identify the fish to species-level. Recreational fishing boats were also opportunistically encountered fishing in the vicinity of feeding dolphins. These fishing boats were approached, and enquiries were made about species they were catching.

Table 2.5 Definitions of surface behaviours recorded in common dolphins in the Hauraki Gulf, after Shane (1990).

Behavioural event	Definition
Chin slap	Dolphin emerges partly out of the water, as far as mid-body, and then comes down forcing the head and anterior body to break the water's surface.
Tail slap	Tail flukes barely clear the surface before bringing them down, creating a downward suction, and a loud, percussive sound. The dolphin is either in the normal or inverted position.
Side slap	Dolphin comes partly out of water, turning laterally to slap down on its side.
Back slap	Dolphin emerges from the water, as far as mid-body, and then slaps back dorsally against the water.
Leap	Entire body clears with water before a head-first re-entry, allowing the dolphin to catch a breath before re-entering the water cleanly in a vertical direction.
Breach	Dolphin lifts its entire body out of the water, and then hits the water with a loud 'smack'.

2.5.3 Continuous sampling

This study recorded the duration of particular behavioural states, such as (a) when synchronous diving behaviour was obvious in the group, the duration of synchronous dives was recorded; and (b) when mixed-species feeding aggregations occurred, the duration of feeding bouts was recorded.

(a) Foraging dive duration

The correspondence between surface (observable) and subsurface (often unobservable) behaviour is unknown for most studies of cetaceans, but such information could help in assessing the biases in relying on surface behaviour alone (Mann, 1999). Subsurface behaviour is particularly valuable in cetacean foraging studies, where some animals are known to forage at depths and not during surfacing bouts. Therefore, foraging dives were distinguished in this study as part of the foraging phases (see *section 2.5.1a*). When synchronous diving behaviour occurred, dive times were measured. This was only recorded when the group was clearly engaging in coordinated subsurface activity, which was suspected to be in the foraging state. Time was recorded from when all group members submerged and no dolphins were visible at the surface, until the group reappeared at the surface. Since this diving behaviour was coordinated within a group, it was possible to record diving duration at a group level rather than an individual's diving pattern.

(b) Feeding bouts involving mixed-species aggregations

Mixed-species feeding aggregations are known to occur in the Hauraki Gulf, with the foraging behaviour of common dolphins being central to the formation of such feeding bouts. A *mixed-species feeding aggregation* was defined as the simultaneous presence of more than one species (i.e., dolphins, birds and occasionally whales) that participate in large-scale feeding while the dolphins forage. Feeding bouts with birds were defined as the duration of feeding, as timed from the onset of more than five birds simultaneously diving until no birds are diving in the vicinity of dolphins.

(c) *Underwater observations*

Observational sampling in cetacean behaviour can be extremely difficult, and all sampling methods have some limitations. To obtain adequate data, 'it is practical and advisable to use more than one sampling method' (Mann, 2000). In this study, attempts were made to collect continuous data on subsurface behaviour of common dolphin groups using an underwater video camera. Making use of such equipment was hoped to help address the bias in relying on surface behaviour, and to further investigate the sub-surface foraging behaviour of common dolphins. Unfortunately, this method was not successful in this study, as lack of visibility while maintaining a suitable distance from dolphins, meant that decent video recordings were hard to achieve. With time constraints, the decision was made to focus on collecting data through surface observations.

2.6 *Statistical Analyses*

Statistical analyses were conducted using the software *Minitab version 13* and *SAS version 9.1*. Normality and equal variance tests were conducted on all data sets. Where assumptions of parametric tests failed, a non-parametric test was used (see *Appendix 4*). 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. Tukey's test was used for post-hoc testing on parametric data, while Dunn's method was used on non-parametric data (see *Appendix 4*).

Since the dolphins' behaviour may be altered initially by the presence of the research boat, the first minutes of observation may not accurately reflect natural behaviour. Therefore, before data were statistically analysed, the first 10 minutes of observations were discarded. This allowed a 'settling down' period in the group's behaviour (Mann, 2000).

Focal group follows with instantaneous scan sampling formed the basis for activity budget data. To avoid pseudo-replication, each focal group follow, not each data point, was treated as an independent sample. Proportions of instantaneous samples for each

behavioural state over the sampling session were calculated for each focal group follow. Foraging behaviour was the main focus of the present study. Therefore, data on behavioural states resting, milling, travelling and socialising were pooled together as *non-foraging*. This revised data set satisfied the assumptions of parametric tests, passing tests of normality and equal variance.

Feeding bouts by foraging dolphins and feeding bouts during mixed-species aggregations were distinguished as single events when three or more sampling intervals (i.e., 6 min) recording non-foraging or no feeding activity separated feeding sequences.

Data on behavioural states and foraging phases were analysed to determine the influence of time of day, tidal cycle, water temperature, depth, distance from shore, dolphin-sighting region (physical or environmental factors), group size and calf presence on foraging activity. Data were compared using the one-way analysis of variance (ANOVA) for parametric data, or Kruskal-Wallis ANOVA for non-parametric data sets (see *Appendix 4*). Pearson's product moment correlation for parametric data, or Spearman's rank correlation for non-parametric data was used to examine the relationship between continuous physical variables and foraging activity (see *Appendix 4*).

Records of dolphin group dynamics during behavioural states were analysed using proportions of instantaneous samples in which each descriptive parameter was observed. Descriptive statistics were compiled for the most frequently recorded parameter during each foraging phase.

All occurrence data was analysed to identify behavioural synchrony, and to determine whether the occurrence of surface behaviours corresponded with certain behavioural states. Fission-fusion events and noisy surface behaviour records were converted into a rate of occurrence by calculating the number of events per hour of behavioural state observations. This data set was analysed for differences between foraging and non-foraging behaviours using the Mann-Whitney test, and compared across all behavioural states using the Kruskal-Wallis ANOVA.

Data on the descriptive parameters of common dolphin groups during foraging strategies were summarised by calculating the mean percent of instantaneous samples for each parameter during focal follows. Each foraging strategy was described by the

most frequently encountered foraging state, group formation, group dispersion, swimming style and surfacing pattern used by dolphin groups. Changes in the foraging strategy between individual and coordinated strategies within a foraging bout, due to group size and calf presence were tested using the CATMOD procedure (SAS 1996). This categorical data modelling method uses a maximum-likelihood estimator to obtain a chi-squared approximation of the probability for each factor in the model. This statistical analysis has been previously used on bottlenose dolphin behavioural data by Constantine et al. (2004). The data were also tested to determine whether there was an interaction effect between the independent variables 'group size' and calf presence'.

The effect of associated species on dolphin foraging behaviour was tested using the CATMOD procedure (SAS 1996), which compared the proportions of all behavioural states for gannet and whale presence using a maximum likelihood estimator. The count data were tested to determine whether there was an effect of gannet and whale presence on the phases of foraging in common dolphins. A full factorial model was used for the analysis, which included an interaction variable between 'gannet presence' and 'whale presence'. The effect of whale lunge feeding on dolphin foraging behaviour was also examined using the maximum-likelihood CATMOD model, examining dolphin foraging behaviour before and after a whale lunge feeds through the dolphin group.

Chapter Three: RESULTS

3.1 *Common dolphin observations in the Hauraki Gulf*

A total of 75 common dolphin groups were encountered over 30 days surveying in the Hauraki Gulf, between 11 January and 19 April 2006. Field effort consisted of over 271 h, with 55 h 20 min (20.4%) devoted to focal follows. Focal follow data were collected from 59 independent groups, which were used in the following analyses.

Focal group follows were considered independent samples, based on the number of focal follows which were conducted each day. There were, on average, 2.18 follows per day (s.e. = 0.3, range = 1 – 6 follows per day) and the mean distance between consecutive focal groups was 8.7 km (s.e. = 1.1, range = 1.2 - 20.3 km). The mean duration of focal group follows was 56.3 min (s.e. = 3.8, range = 20 - 134 min). During these follows, 1712 instantaneous samples were recorded. Foraging behaviour was recorded in all focal group follows, with a total of 82 surface feeding bouts observed. The searching method used was not suspected of pre-disposing sampling effort towards dolphin groups feeding with gannet flocks, as 71.2% of groups (n = 42) were sighted without the aid of birds.

Weather conditions during focal group follow sessions were typically fine (77.9%, n = 46) with Beaufort 1 sea conditions (37.5%, n = 22, range = Beaufort 0 – 3), good visibility (38.9%, n = 23, range = excellent – fair visibility) and oktas 3 cloud cover (22.0%, n = 13, range = oktas 0 – 8). Sea surface temperature and depth during foraging was recorded for all 59 groups of dolphins. Temperature data were not normally distributed (see *Appendix 4*). A non-parametric Kruskal-Wallis ANOVA showed that the differences were significant between the months surveyed ($H_{3,59} = 26.80$, $P < 0.001$). Over the course of this study, temperatures varied by only 1-2 °C between January and April. However, water temperature was significantly higher in February and lowest in April (Table 3.1).

Table 3.1 Descriptive statistics for the measurements of sea surface temperature for each month surveyed in 2006 (total n = 59).

Data set		Sea surface temperature (°C)				Dunn's test
		mean (± s.e.)		min.	max.	
January	n = 9	20.6	± 0.24	20	22	n.s.
February	n = 15	21.6	± 0.24	20	24	> Mar, Apr *
March	n = 28	20.0	± 0.15	19	21	< Feb *
April	n = 7	19.6	± 0.20	19	20	< Feb, Mar *

Note. Sample sizes for each category are given as 'n'. Significance levels are indicated with an asterisk:
 * P < 0.05; ** P < 0.01; *** P < 0.001.

Of the 59 focal group follow sessions, four regions were identified based on their proximity to and bearing from landmasses. These were defined as *inner Hauraki Gulf*, *central Hauraki Gulf*, *Coromandel Peninsula* and *Kawau Island* (Figure 3.1). The depth of water at each dolphin observation was significantly different between the identified regions (Kruskal-Wallis ANOVA, $H_{3,59} = 25.10$, $P < 0.001$; Figure 3.2). Post-hoc Dunn's comparison analysis identified the Kawau Island region as significantly deeper than the other regions (mean ± s.e. = 50.6 m ± 0.9, n = 4, range = 49 - 52 m), while inner Hauraki and Coromandel regions were significantly shallower depths (inner Hauraki, mean ± s.e. = 36.2 m ± 1.2, n = 23, range = 22 - 47 m; Coromandel Peninsula, mean ± s.e. = 39.8 m ± 1.1, n = 16, range = 30 - 46 m). Mean water depth recorded at all dolphin sightings was 39.7 m (s.e. = 0.7, n = 59, range = 22 - 52 m) and the mean distance from the nearest shoreline was 4.91 nautical miles (s.e. = 0.29, n = 59, range = 1.15 - 10.84 Nm). Water depth showed a positive correlation with the distance from the shore (Figure 3.2).

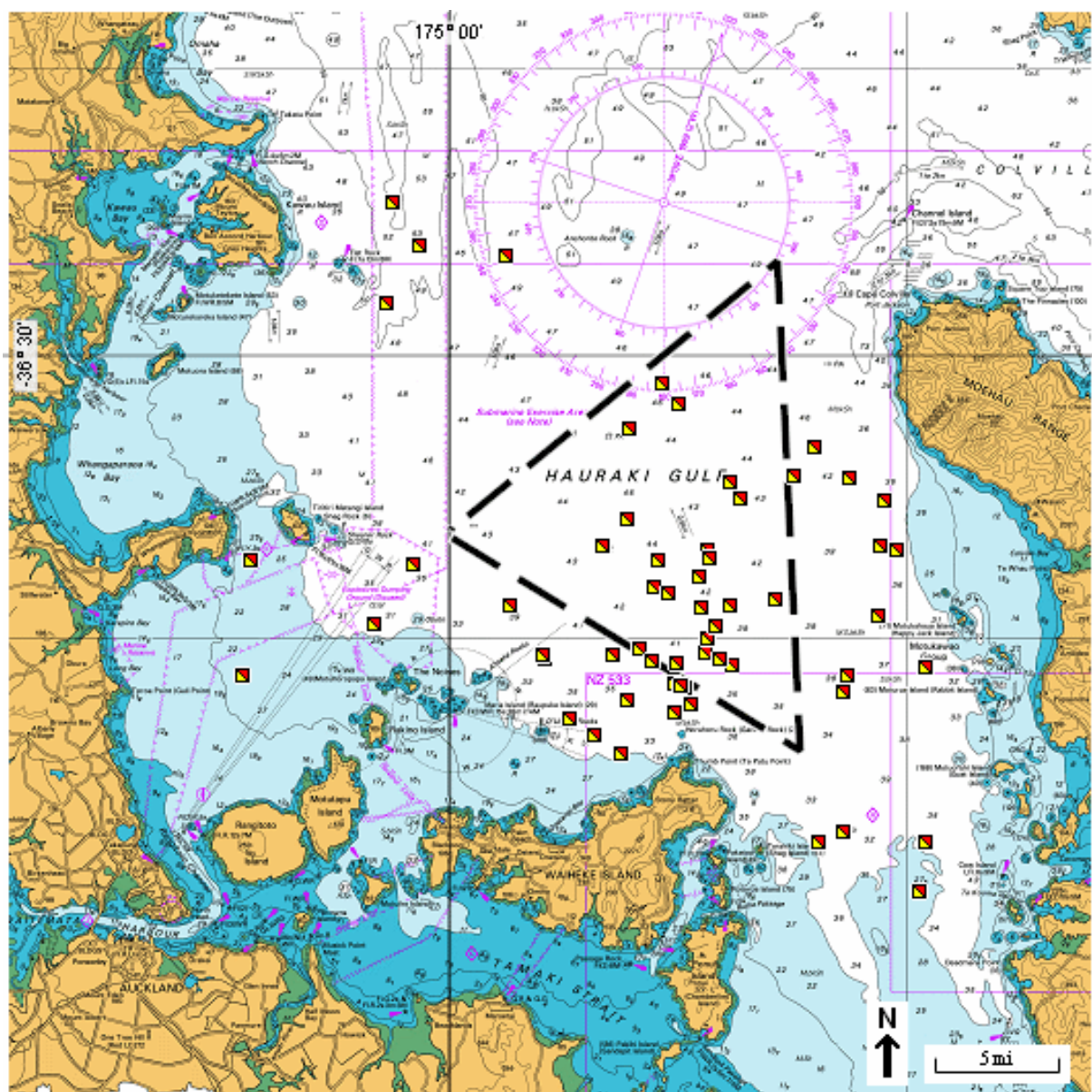


Figure 3.1 Map of the Hauraki Gulf showing coordinates of common dolphin sightings observed for focal group follows during this study. The triangle defines four dolphin-sighting regions - central Hauraki Gulf (centre of the triangle), inner Hauraki Gulf (south-west of the triangle), Coromandel Peninsula (east of the triangle) and Kawau Island (north-west of the triangle). Each dolphin sighting, as marked by the symbol  on the map, was assigned to one of these regions (total n = 59).

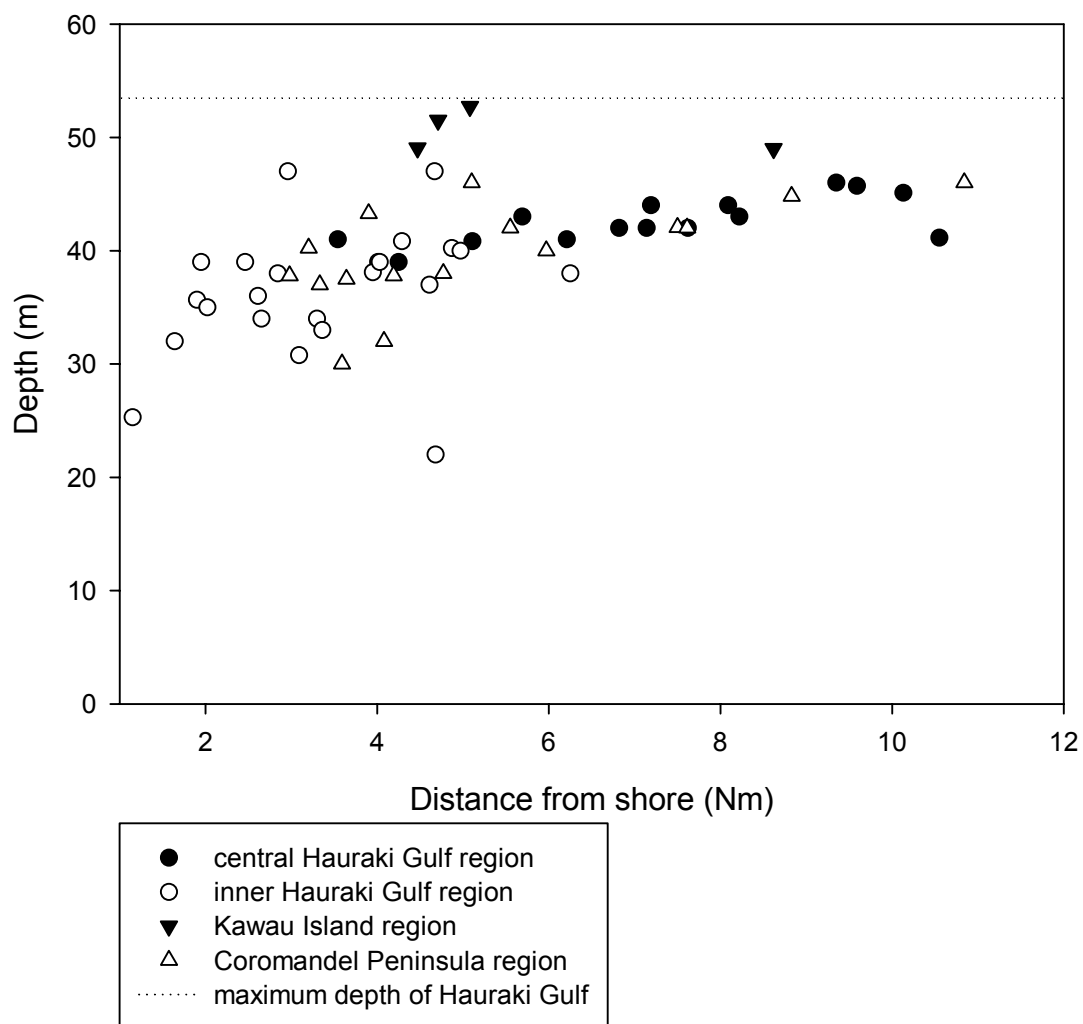


Figure 3.2 Correlation between the distance from shore and water depth for each common dolphin focal group follow identified by region within the Hauraki Gulf (Spearman's rank correlation, $r^2_{57} = 0.29$, $P < 0.001$).

3.2 Common dolphin foraging behaviour

Foraging and feeding behaviour were regular activities of common dolphins in the Hauraki Gulf. During this study, daytime foraging activity was recorded during all focal group follows of common dolphins ($n = 59$), with a total of 35.5 h of foraging behaviour observed. Dolphin groups spent significantly more time foraging than in the other behavioural states (travelling, socialising, milling and resting) (Kruskal-Wallis, $H_{4,59} = 167.60$, $P < 0.001$; post-hoc comparison, Dunn's test). Mean percentage of time spent foraging for all dolphin observations was 61.8% (s.e. = 2.7).

Common dolphin foraging activity did not significantly vary with time of day (one-way ANOVA, $F_{4,59} = 1.18$, $P = 0.329$). Most observations occurred during an ebbing tide (40.7%, $n = 24$), though tidal state did not significantly affect the percentage of time dolphins spent foraging (one-way ANOVA, $F_{3,59} = 1.09$, $P = 0.361$). There was no significant relationship between sea surface temperature and the proportion of time dolphin groups spent foraging (Pearson's product moment correlation, $r^2_{57} = 0.03$, $P = 0.168$).

The percentage of time spent foraging was not significantly affected by water depth (Pearson's product moment correlation, $r^2_{57} = 0.01$, $P = 0.540$) nor by the dolphin group's distance from the shore (Pearson's product moment correlation, $r^2_{57} = 0.02$, $P = 0.335$). There was also no significant difference in time spent foraging by the dolphins between the regions of the Hauraki Gulf identified in this study (one-way ANOVA, $F_{3,59} = 0.40$, $P = 0.756$).

Foraging activity budget for common dolphins differed significantly for each group size category (one-way ANOVA, $F_{4,59} = 3.00$, $P = 0.026$). Larger group sizes consisting of between 51 and 100 dolphins spent significantly more time foraging than other smaller groups, and consequently less time in non-foraging behaviours (Figure 3.3). Calf presence in the dolphin group did not significantly affect the proportion of time spent foraging (one-way ANOVA, $F_{1,59} = 1.54$, $P = 0.219$).

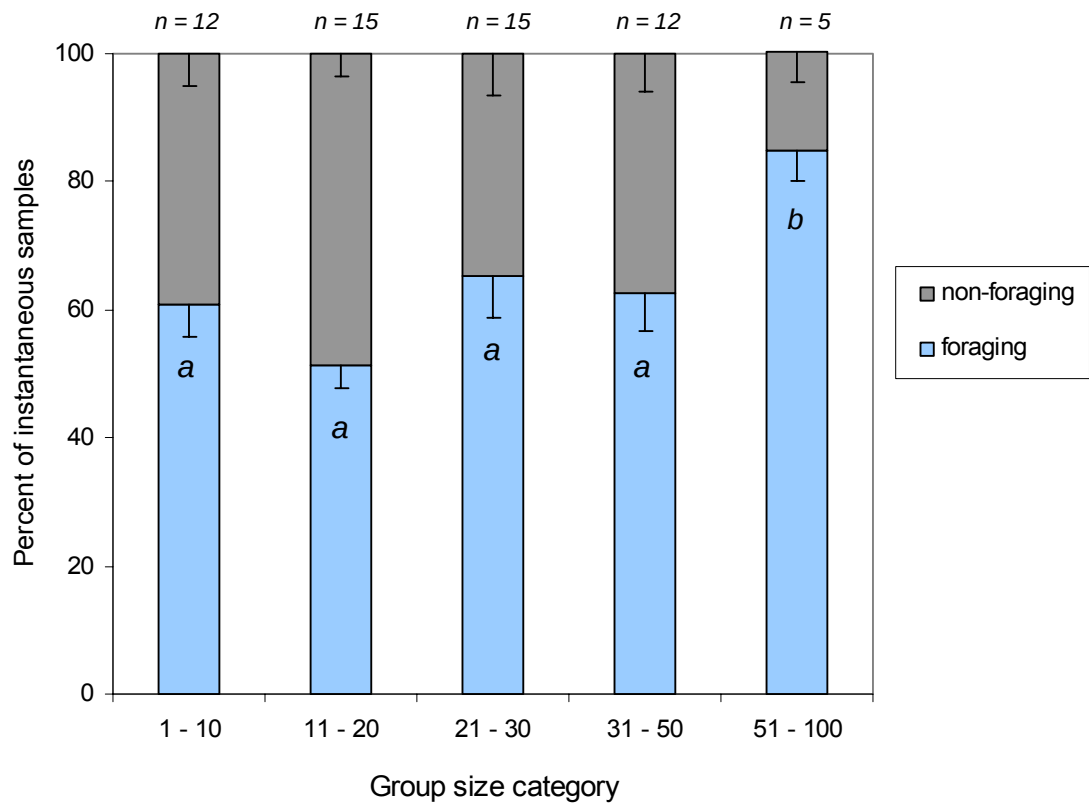


Figure 3.3 Daytime foraging activity budgets of common dolphins in different group size categories. Values are means with standard error bars. Sample sizes are given above each column (total n = 59). Significant differences are indicated by the letters 'a' and 'b' (Fisher's LSD test, $P < 0.05$).

3.2.1 Phases during foraging behaviour - herding, diving and feeding

Three phases during foraging behaviour were identified - *herding*, *synchronous diving* and *surface feeding*. For all dolphin foraging observations, the mean percentage of time spent herding was 27.6% (s.e. = 2.3), diving was 20.3% (s.e. = 2.0) and feeding was 13.7% (s.e. = 1.7). For all dolphin observations, the percentage of time spent in each foraging phase varied significantly (one-way ANOVA, $F_{2,59} = 15.66$, $P < 0.001$), with herding behaviour contributing to a greater proportion of time during foraging (Figure 3.4). Dolphins were observed to travel on average 1.93 km (s.e. = 0.24, range = 0.07 - 6.80 km) during herding behaviour. Distance covered significantly increased with time spent herding (Figure 3.5).

Herding behaviour was characterised by dolphin groups in a tight, parallel formation, swimming with steady speed and frequent surfacing events (Table 3.2). Groups engaging in synchronous diving during foraging were typified by tight dispersion with members in random formation and exhibiting long downtimes by remaining submerged between two-minute samples (Table 3.2). Feeding dolphins were characterised by bursts of rapid movement, with dolphins in tight, circular formation and surfacing infrequently (Table 3.2).

Table 3.2 Summary of the most frequently recorded parameter used during each foraging phase by common dolphin groups. Values are the percent of instantaneous samples recorded during foraging behaviour, presented as mean $\pm$ s.e. (total n = 59).

Descriptive parameter	Foraging phase		
	Herding n = 54	Diving n = 53	Feeding n = 54
Group formation	parallel 49.7% $\pm$ 0.05	random 36.5% $\pm$ 0.06	circular 47.1% $\pm$ 0.07
Group dispersion	tight 47.9% $\pm$ 0.04	tight 42.2% $\pm$ 0.06	tight 63.2% $\pm$ 0.05
Swimming style	steady 50.0% $\pm$ 0.04	dive 84.3% $\pm$ 0.03	accelerate 67.1% $\pm$ 0.05
Surfacing pattern	frequent 59.9% $\pm$ 0.04	long 37.3% $\pm$ 0.05	infrequent 49.9% $\pm$ 0.06

Note. Sample size (n) was calculated from the number of focal follows which recorded each foraging

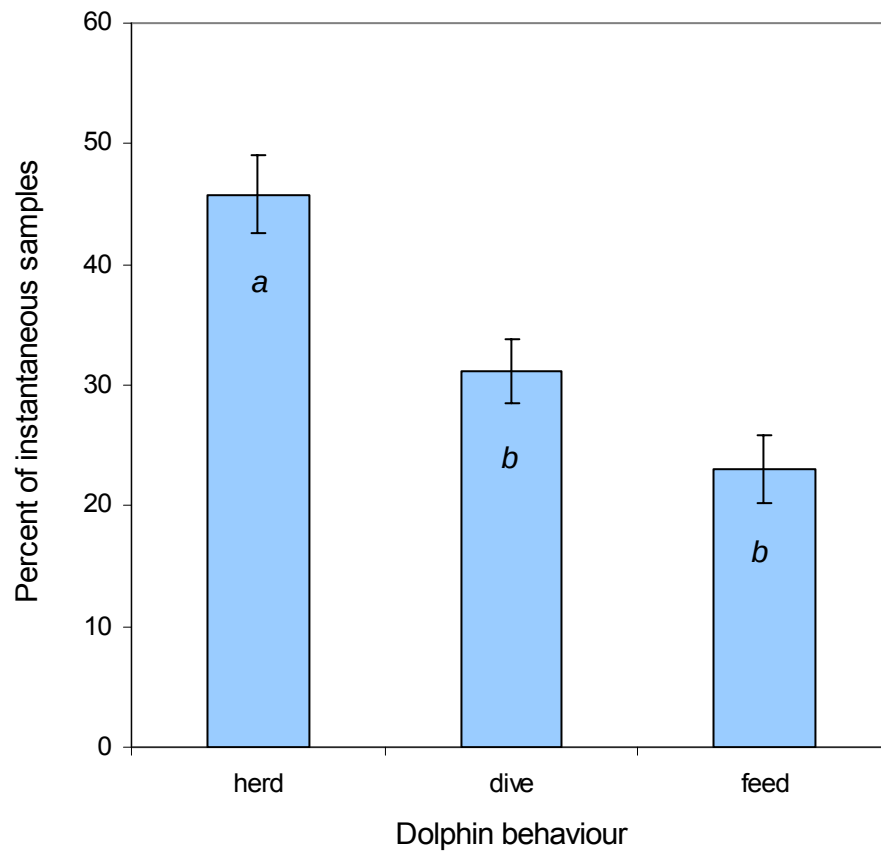


Figure 3.4 Foraging activity budget for common dolphins, showing the different behavioural phases by the percentage of time spent during foraging. Values are means with standard error bars ($n = 59$). Significant differences are indicated by the letters 'a' and 'b' (Fisher's LSD test, $P < 0.05$).

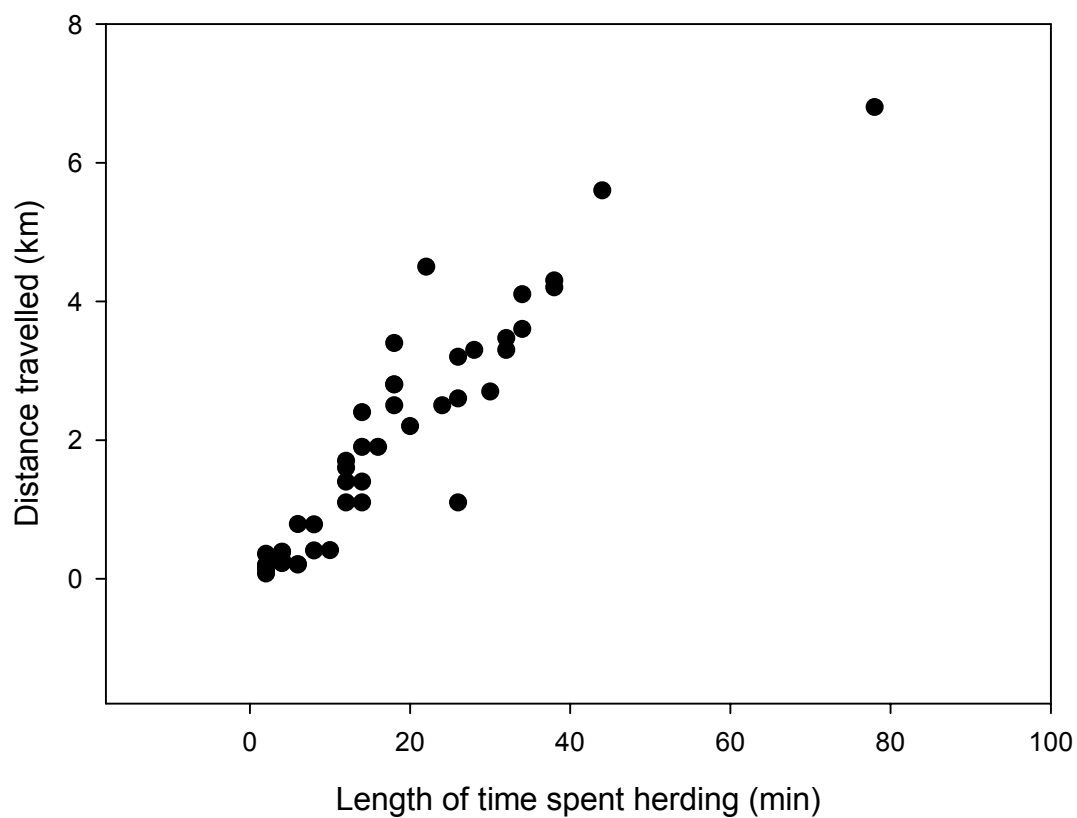


Figure 3.5 Correlation between the length of time dolphins spent herding and the distance travelled (Spearman's ranked correlation, $r^2_{52} = 0.86$, $P = < 0.001$).

Sea surface temperature was not significantly correlated with any of the phases observed during foraging behaviour (Spearman's ranked correlation, herding: $r^2_{57} = 0.02$, $P = 0.332$; diving: $r^2_{57} = 0.01$, $P = 0.673$; feeding: $r^2_{57} = 0.04$, $P = 0.123$). Water depth was positively correlated with the percentage of time dolphins spent feeding, so in deeper waters more feeding occurred during the foraging state (Figure 3.6). The proportion of time common dolphins spent feeding varied significantly between the four dolphin-sighting regions of the Hauraki Gulf identified in this study (one-way ANOVA, feeding: $F_{4,59} = 0.59$, $P = 0.646$). The percentage of time the dolphins spent diving and feeding was not significantly different between regions (Kruskal-Wallis ANOVA, diving: $F_{4,59} = 7.12$, $P = 0.060$; feeding: $F_{4,59} = 15.17$, $P = 0.002$) Dolphin groups in the Coromandel Peninsula and Kawau Island regions spent a greater proportion of time feeding, than those groups sighted in the inner and central Hauraki Gulf regions (Figure 3.7).

The swimming direction of the dolphins during herding behaviour was significantly different between the regions (one-way ANOVA, $F_{3,59} = 4.27$, $P = 0.009$). Dolphin groups foraging near Kawau Island were significantly different from the other regions (post-hoc comparison, Fisher's LSD test) in that they tended to herd in a $260^\circ \pm 44.2$ (mean $\pm$ s.e.) bearing or a westerly direction, while groups in the other three regions tended to herd in a south-easterly direction.

Further analyses were conducted to investigate the influence of group size and calf presence on the different phases of foraging behaviour. Group size was found to significantly affect the proportion of herding behaviour during foraging (one-way ANOVA, $F_{4,59} = 2.69$, $P = 0.041$), with larger groups spending more time herding (Figure 3.8). Diving and feeding behaviour was not significantly affected by group size (Kruskal-Wallis ANOVA, $H_{4,59} = 7.24$, $P = 0.124$; one-way ANOVA, $F_{4,59} = 2.04$, $P = 0.101$, respectively). In large group sizes, synchronous diving behaviour during foraging was observed more often than in smaller dolphin groups (Figure 3.8). While surface feeding behaviour was observed more often in medium-sized dolphin groups (21-30 dolphins) and less frequently in the larger dolphin groups (Figure 3.8). Those groups with calves present were found to have significantly longer herding periods than those dolphin groups without calves (one-way ANOVA, $F_{1,59} = 4.42$, $P = 0.040$). Diving and feeding behaviour was not significantly affected by calf presence (Kruskal-Wallis ANOVA, $H_{1,59} = 0.33$, $P = 0.568$; Kruskal-Wallis ANOVA, $H_{1,59} = 0.43$, $P = 0.513$, respectively).

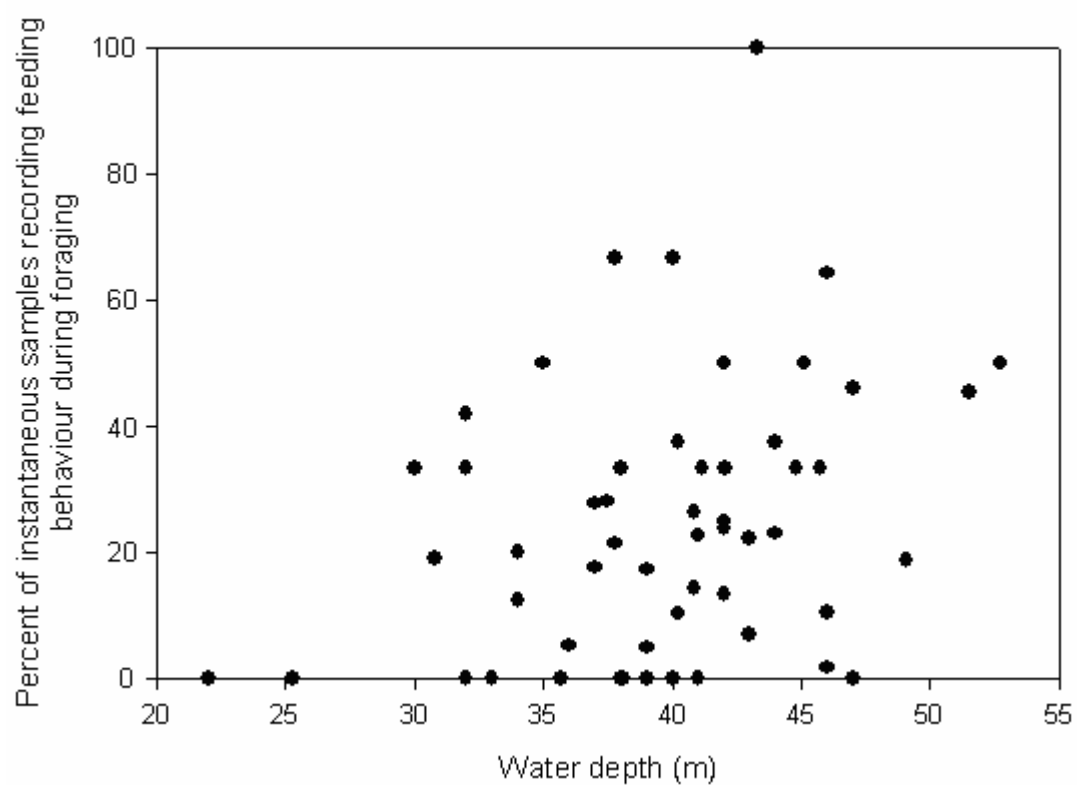


Figure 3.6 Correlation between water depth and the percentage of feeding behaviour recorded during the foraging activity of common dolphins (Pearson's product moment correlation, $r^2_{57} = 0.09$, $P < 0.001$).

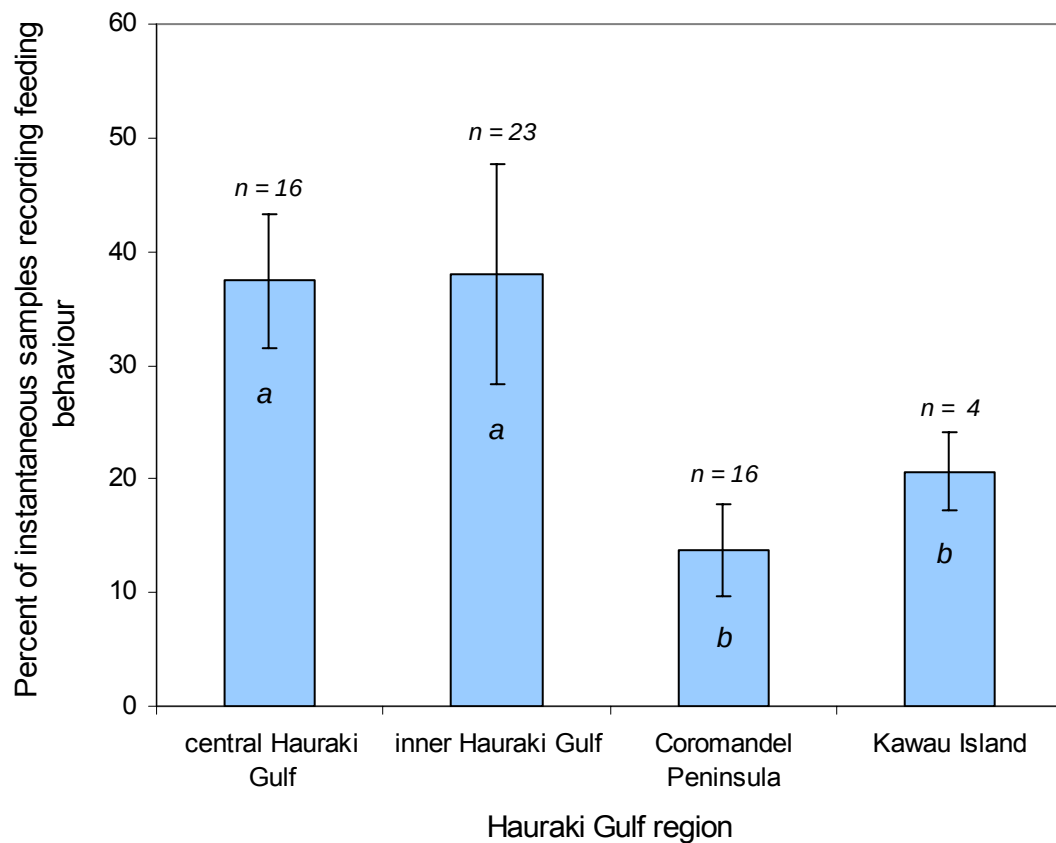


Figure 3.7 Proportion of time common dolphins spent feeding in different regions in the Hauraki Gulf (see Figure 3.1). Values are means with standard error bars. Sample sizes are given above each column (total $n = 59$). Significant differences are indicated by the letters 'a' and 'b' (Dunn's test, $P < 0.05$).

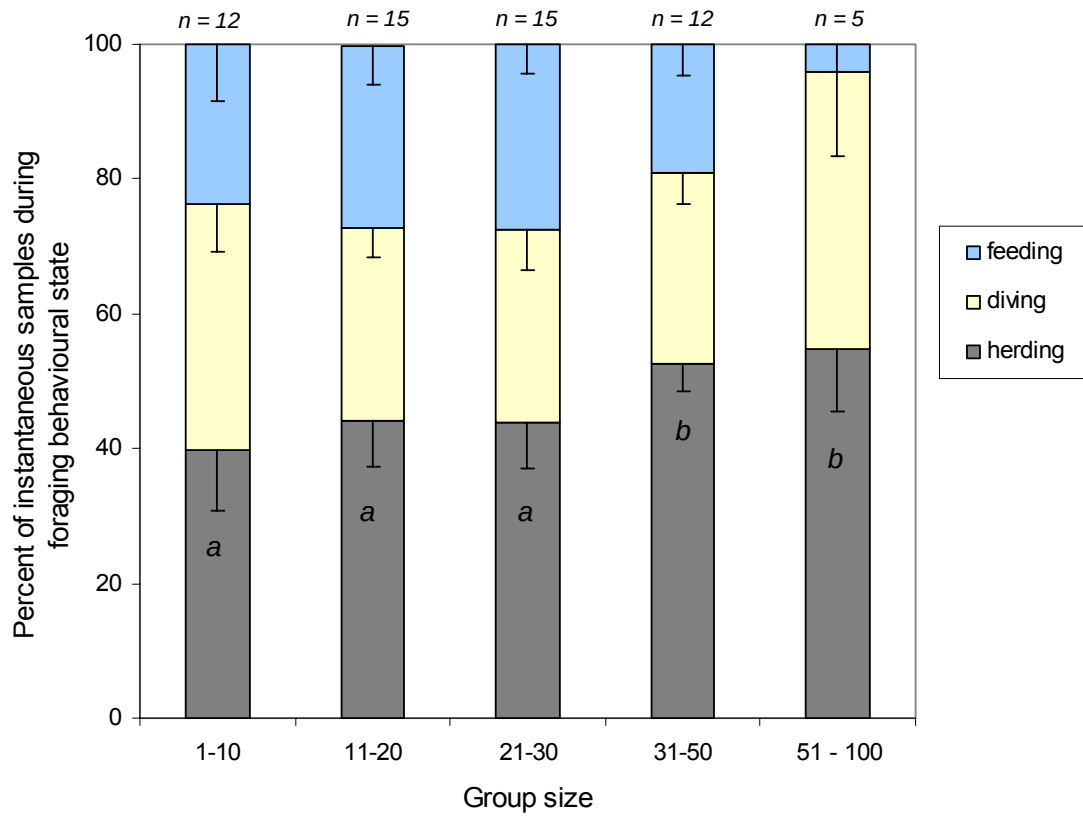


Figure 3.8 Foraging activity budget of common dolphins showing different foraging behavioural phases (herding, diving and feeding) by group size category. Values are means with standard error bars. Sample sizes are given above each column (total n = 59). Significant differences are indicated by the letters 'a' and 'b' (Fisher's LSD test, $P < 0.05$).

3.2.2 *Foraging strategies of common dolphins*

The foraging strategy most frequently observed was synchronous diving, where all dolphins within a group coordinated in deep diving underwater and re-surfacing together (Table 3.3). Dolphin groups spent a mean time of 50.1 seconds submerged during synchronous diving (s.e. = 4.10, n = 22). The foraging strategy least observed was the coordinated strategy, wall-formation. The individual foraging strategy most frequently seen was high-speed pursuit. Carouselling (Plate 3.1) and line-abreast foraging were also regularly observed as a coordinated strategy for foraging. The foraging strategies fish-whacking and bubble-blowing were not observed during this study.

The proportion of time during foraging behaviour that the dolphin group was observed in each foraging strategy (Figure 3.9). Synchronous diving and carouselling were the most enduring strategies, contributing to a significant proportion of foraging behaviour during focal follows (mean = 32.1% and 23.8% of instantaneous samples, respectively). Kerplunking was a more short-lived behaviour, accounting for 9.6% of foraging samples during follows (Plate 3.2). Wall-formation was a very brief and potentially transitory behaviour which only contributed to 0.3% of foraging samples in a focal group follow session. With so few groups engaging in wall-formation, hypothesis testing is limited owing to small sample sizes. However, the small sample size was unlikely to be a result of sampling bias, but rather because of the rarity of the behaviour.

Common dolphins frequently changed foraging strategies within a foraging bout, with 78.0% of groups observed altering their foraging strategy (n = 46). The mean number of changes from one strategy to another was 2.96 (s.e. = 0.37, range = 0 - 10) with a mean of 2.45 different strategies used within a foraging bout (s.e. = 0.15, range = 1-5).

Each foraging strategy was characterised by frequently observed behaviours in the common dolphin group (Table 3.4). Results suggest that coordinated foraging strategies (such as synchronous diving) are more significant for common dolphins in the Hauraki Gulf than individual foraging strategies. This was evident from the frequency of occurrence (Table 3.3) and the duration (Figure 3.9) of coordinated strategies in common dolphin foraging behaviour.

Table 3.3 Summary of the various foraging strategies used by common dolphins in the Hauraki Gulf during 59 focal group follow sessions.

	Number of observations	Percent of total focal group follow sessions
<i>Individual foraging strategy</i>		
high-speed pursuit	29	49.2%
kerplunking	15	25.4%
<i>Coordinated foraging strategy</i>		
carouselling	26	44.1%
line-abreast	28	47.5%
wall-formation	4	6.8%
synchronous diving	50	84.7%

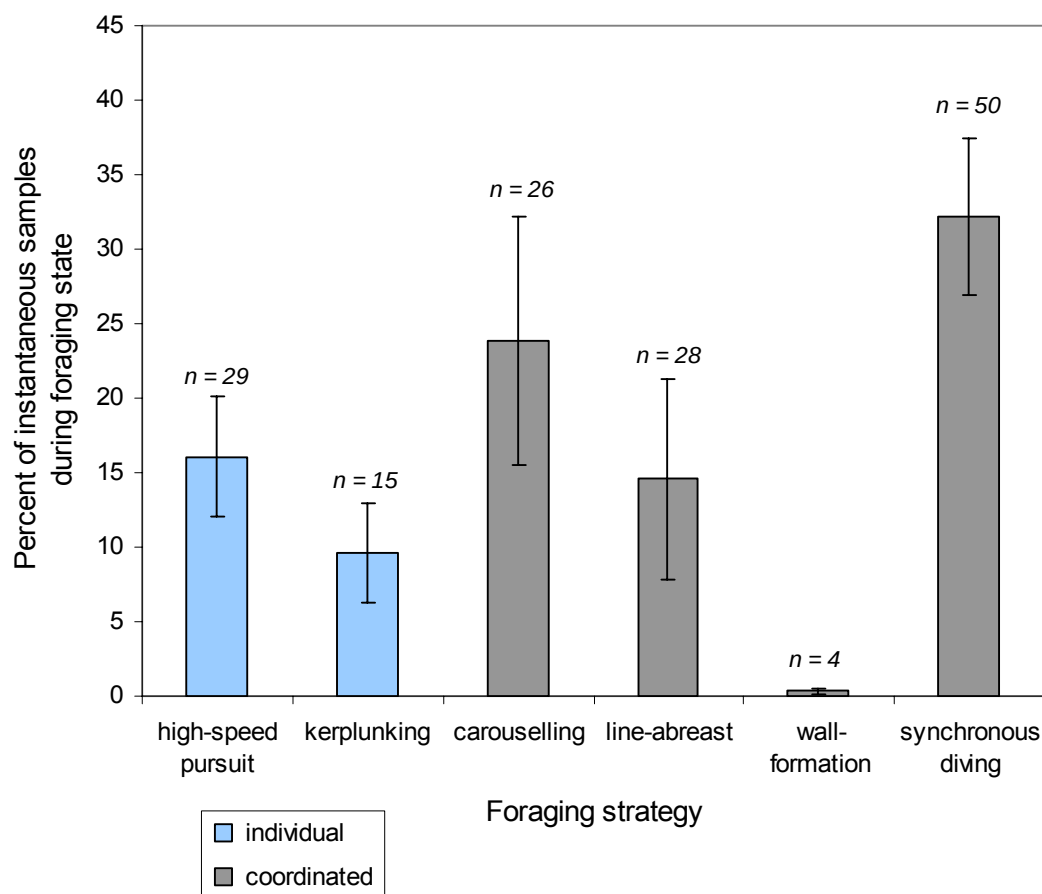


Figure 3.9 Proportion of samples in which common dolphin groups used the various foraging strategies during foraging behavioural state. Values are means with standard error bars. Number of observations are given above each column (total $n = 59$).



Plate 3.1 Common dolphins foraging using carouselling as a coordinated strategy, depicting tight formation and accelerated swimming.



Plate 3.2 A common dolphin using the foraging strategy, kerplunking, where the tail fluke is raised above the water surface, then brought back down to and below the water surface with force.

Table 3.4 Summary of the most frequently recorded parameter in each of the various foraging strategies used by common dolphins in the Hauraki Gulf. Values are the percent of instantaneous samples recorded in focal follows, presented as mean $\pm$ s.e. (total n = 59).

Descriptive parameter	Foraging strategy					
	individual			coordinated		
	High-speed pursuit n = 29	Kerplunking n = 15	Line-abreast n = 26	Carouselling n = 28	Wall-formation n = 4	Synchronous diving n = 50
Foraging state	feeding 75.1% $\pm$ 0.06	feeding 79.5% $\pm$ 0.08	herding 91.3% $\pm$ 0.05	feeding 78.4% $\pm$ 0.08	herding 60.0% $\pm$ 0.24	diving 100.0% $\pm$ 0.00
Group formation	random 45.5 $\pm$ 0.06	circular 64.7% $\pm$ 0.11	parallel 100% $\pm$ 0.00	circular 79.6% $\pm$ 0.08	parallel 35.0% $\pm$ 0.22	random 35.8% $\pm$ 0.06
Group dispersion	tight 46.1% $\pm$ 0.07	tight 63.8% $\pm$ 0.10	tight 88.1% $\pm$ 0.05	tight 79.2% $\pm$ 0.07	tight 70.0% $\pm$ 0.20	tight 33.6% $\pm$ 0.05
Swimming style	accelerate 85.2% $\pm$ 0.05	accelerate 49.9% $\pm$ 0.09	porpoising 17.7% $\pm$ 0.05	accelerate 48.4% $\pm$ 0.48	accelerate 15.0% $\pm$ 0.15	dive 86.1% $\pm$ 0.03
Surfacing pattern	frequent 55.1% $\pm$ 0.07	infrequent 49.2% $\pm$ 0.09	frequent 79.1% $\pm$ 0.07	infrequent 52.3% $\pm$ 0.08	frequent 80.0% $\pm$ 0.20	long downtime 36.0% $\pm$ 0.05

Note. Sample size (n) was calculated from the number of instantaneous samples recorded for each foraging strategy. Percentage values are calculated from counts within each

The probability of individual and coordinated foraging strategies in common dolphin foraging behaviour was significantly influenced by group size, with larger dolphin groups (50-100) showing a higher probability of coordinated strategies in their foraging behaviour (Figure 3.10; Table 3.5). Group sizes between 21 and 30 dolphins appear to have a more balanced trade-off between foraging strategies, with almost equal occurrences of the individual and group coordinated foraging strategies. The presence of calves did not significantly influence the probability of individual or coordinated foraging strategies. A full factorial model was used in the analysis as there was a significant interaction effect between the variables 'group size' and 'calf presence' (Table 3.5).

During this study, the foraging strategies of high-speed pursuits, line-abreast, carouselling and synchronous diving were observed in all of the four dolphin-sighting regions identified. Kerplunking behaviour was not observed in any of the observations near Kawau Island. However, the significance of this should be cautiously interpreted, as the sample size was small with only four focal group follow session conducted in that region. Similarly, wall-formation was only observed three times in the central Hauraki Gulf region and once off the Coromandel Peninsula.

Table 3.5 Summary of maximum likelihood CATMOD procedure results and levels of significance for data gathered on individual and coordinated foraging strategies by group size and calf presence, using a full factorial model (n = 59 sessions with 2148 instantaneous samples).

Source of variation	Data set		
	Foraging strategy category		
	df	χ^2	P
Group size	8	22.47	0.004 **
Calf presence	2	2.89	0.236
Group size x Calf presence	(6)	16.20	0.012 *

Note. Brackets indicate the interaction effect variable contains redundant parameters. Significance levels are indicated with an asterisk: * P < 0.05; ** P < 0.001; *** P < 0.0001.

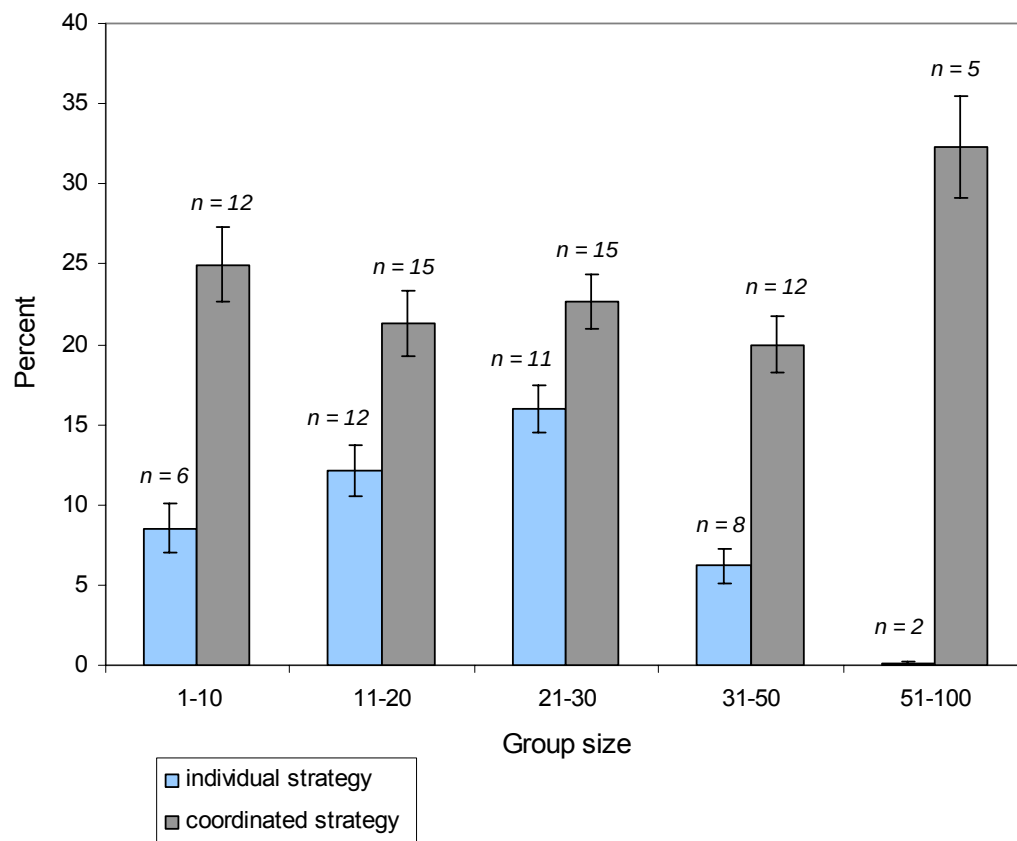


Figure 3.10 Occurrence of individual or coordinated foraging strategies by common dolphin groups, compared between group size categories. Values are maximum likelihood CATMOD probabilities with standard error bars. Sample sizes are given above each column.

3.2.3 Group dynamics during foraging behaviour

Tight dispersion between dolphins during herding behaviour was found to be significantly affected by group size (Kruskal-Wallis ANOVA, $H_{4,59} = 10.44$, $P = 0.034$, Figure 3.11), with larger group sizes being in close proximity (0-1 body lengths) more often (post-hoc comparison, Fisher's LSD test, $P < 0.05$). Moderate and loose dispersion during herding was not found to be significantly influenced by group size (moderate dispersion: Kruskal-Wallis ANOVA, $H_{4,59} = 7.59$, $P = 0.108$; loose dispersion: Kruskal-Wallis ANOVA, $H_{4,59} = 5.34$, $P = 0.254$).

For those common dolphin groups where calves were present ($n = 35$), the position of the calf during foraging behaviour was recorded whenever possible. The percentage of observations for each calf position was compared for each of the foraging phases (Figure 3.12). During herding the calves were generally positioned in the centre of the group (Chi-square test, $\chi^2_{1,95} = 4.65$, $P = 0.031$), but were generally separated by a short distance from the group during feeding (Chi-square test, $\chi^2_{1,95} = 5.725$, $P = 0.017$). The position of calves during diving phases of foraging was difficult to observe. During non-foraging behaviours, calves were typically sighted in the periphery of the group.

Fission and fusion events in common dolphin groups - where the focal group split into one of more groups, or the focal group joined another group, or another group joined the focal group - frequently occurred during focal follow observations (Figure 3.13). A total of 66 fission and 83 fusion events and were recorded during 55.3 h of focal follows. Fission events within common dolphin groups showed no significant difference between foraging and non-foraging behavioural states in the focal group (Mann-Whitney test, $U_{1,59} = 1859.00$, $P = 0.241$). A comparison across all behavioural states, showed that common dolphin groups were more likely to split into multiple groups during foraging and resting behaviours (Kruskal-Wallis ANOVA, $H_{4,59} = 18.86$, $P < 0.001$; Figure 3.13a). Whereas, fusion between dolphin groups was significantly influenced by foraging behaviour (Mann-Whitney test, $U_{1,59} = 2072.50$, $P = 0.011$). Common dolphin groups joined each other more frequently when the focal dolphin group was foraging, compared to the behaviours of travelling, milling, socialising or resting (Kruskal-Wallis ANOVA, $H_{4,59} = 26.71$, $P < 0.001$; Figure 3.13b).

Breaching, leaping, back slapping, side slapping, chin slapping and tail slapping behaviours all produced a loud sound when the dolphin fell back into the water onto its

belly, side, head or tail ('noisy' surface behaviours). A total of 247 noisy surface behaviour events were recorded during 55.3 h of focal follow observations. The most frequently recorded noisy surface behaviours were leaping ($n = 94$ events), tail slapping ($n = 48$ events), head slapping ($n = 46$ events) and breaching ($n = 42$ events) during the 55.3 h of observation. Incidences of noisy surface behaviour by common dolphins was not significantly different between foraging and non-foraging behaviour (Mann-Whitney test, $U_{1,59} = 1844.00$, $P = 0.362$). However, noisy surface behaviour was recorded more frequently during foraging and socialising behaviour, than other behavioural states (Kruskal-Wallis ANOVA, $H_{4,59} = 12.90$, $P = 0.012$; Figure 3.14).

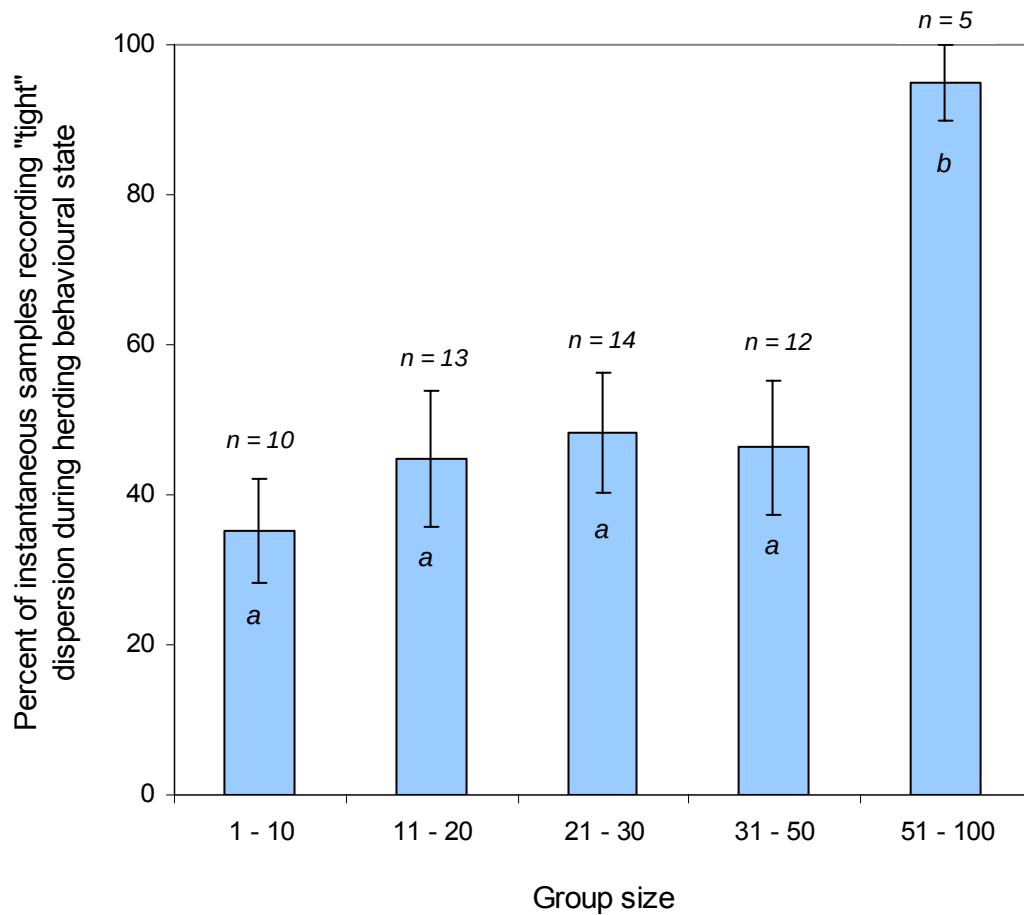


Figure 3.11 Proportion of samples in which common dolphin groups used 'tight' dispersion (0-1 body length between nearest neighbour) during herding behavioural state by group size category. Values are means with standard error bars. Sample sizes are given above each column (total n = 54 sessions with herding behaviour recorded). Significant differences are indicated by a cross (Fisher's LSD test, $P < 0.05$).

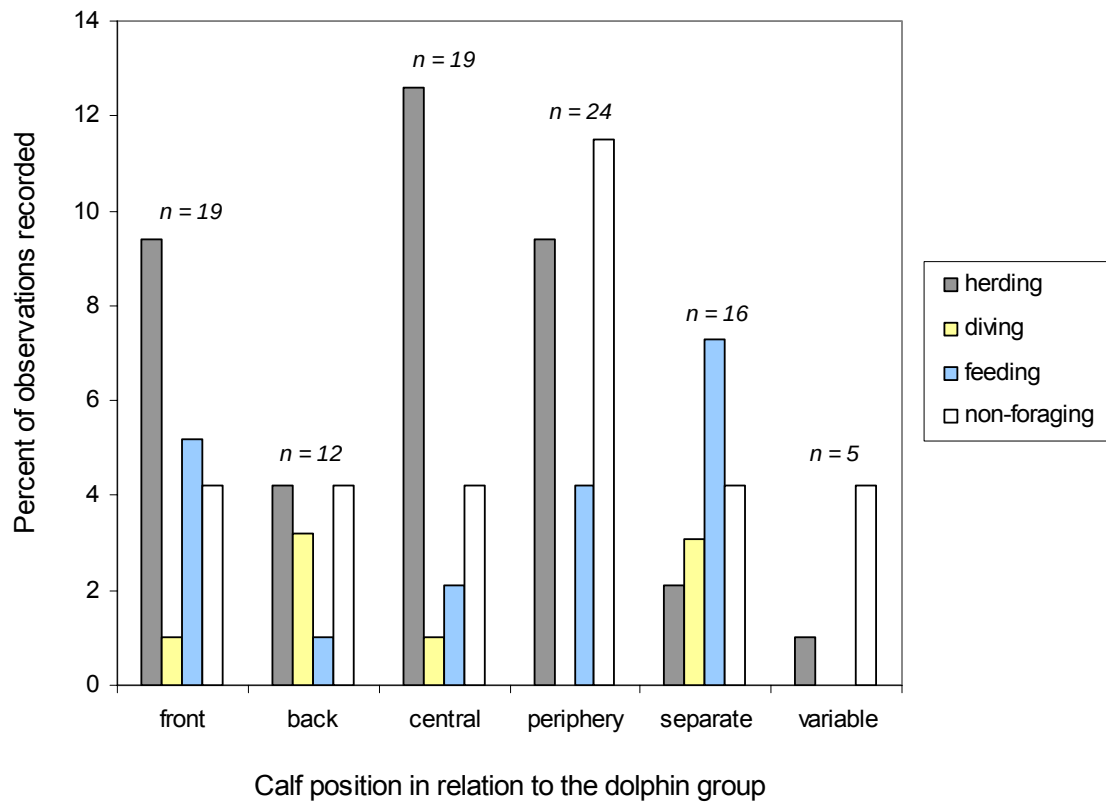


Figure 3.12 Position of calves within focal groups during the various phases of foraging behaviour in common dolphins. Sample sizes for each calf position are given above the columns (total $n = 95$ instantaneous observations in 59 focal follows).

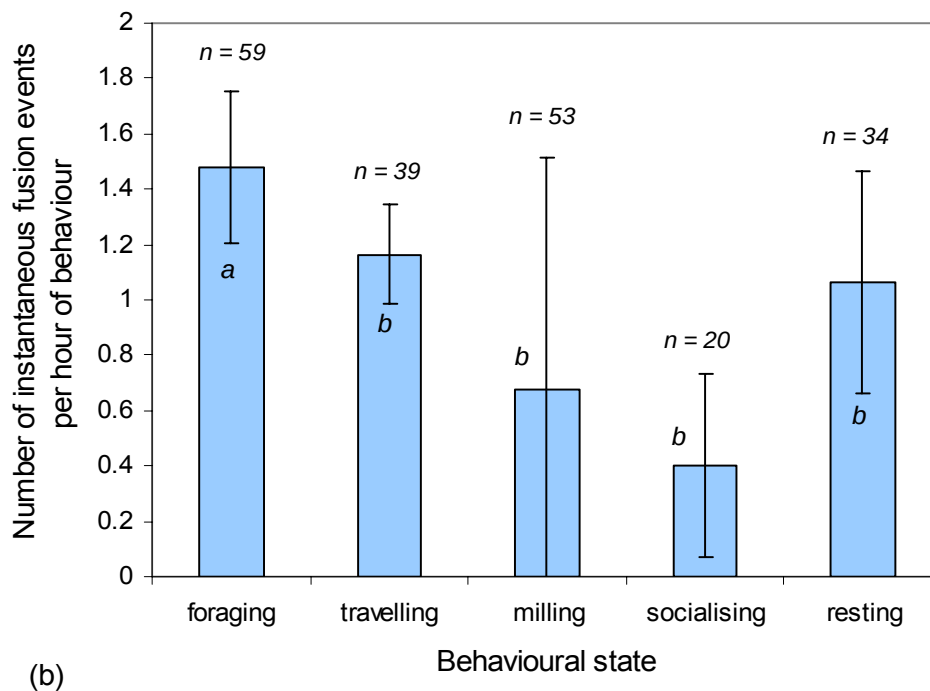
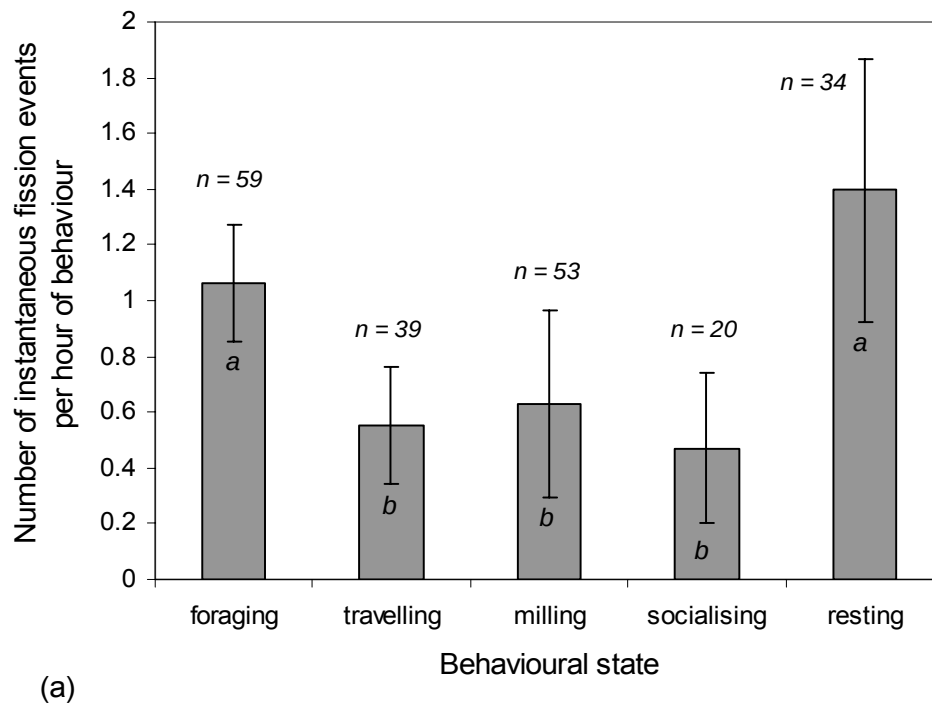


Figure 3.13 Records of (a) fission (group split) and (b) fusion (group join) in common dolphin groups during the various behavioural states. Values are means with standard error bars. Sample sizes are given above each column (total n= 59). Significant differences are indicated by the letters 'a' and 'b' (Dunn's test, P < 0.05).

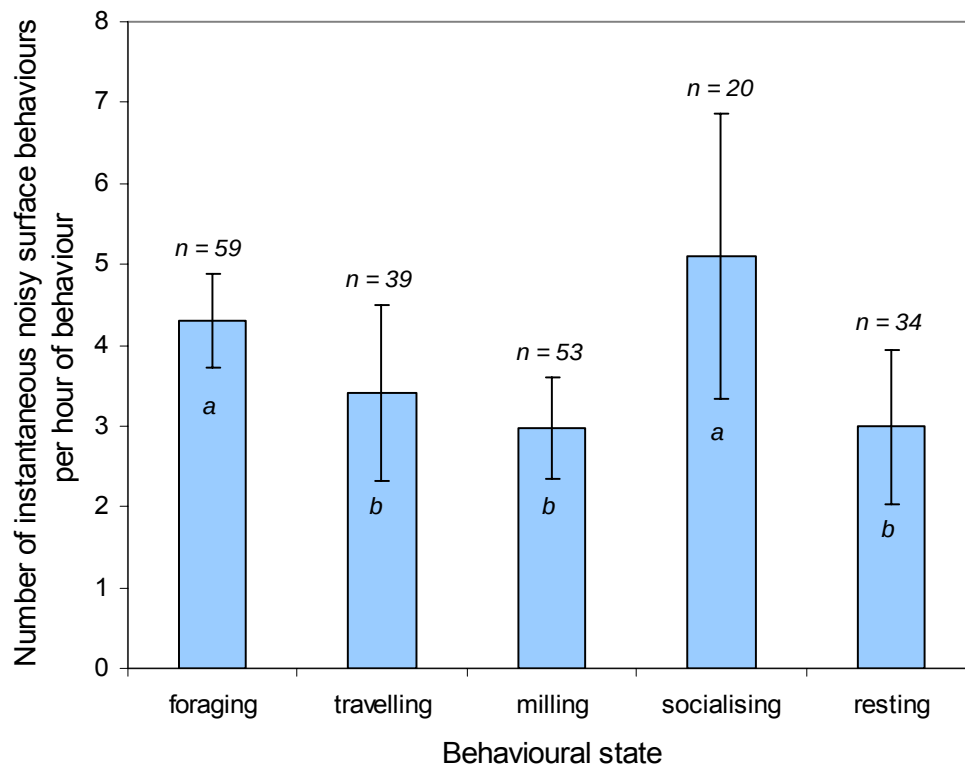


Figure 3.14 Records of noisy surface behaviour in common dolphin groups during the various behavioural states. Samples sizes for each behavioural state are given above the columns (total $n = 246$ instantaneous observations in 59 focal follows).

3.3 Species associated with foraging common dolphins

During focal follows, eight species were recorded in association with common dolphins in the Hauraki Gulf. These included seven avian species (Australasian gannet (*Morus serrator*) (Plate 3.3), flesh-footed shearwater (*Puffinus carneipes*) (Plate 3.4a), Buller's shearwater (*Puffinus bulleri*) (Plate 3.4b), sooty shearwater (*Puffinus griseus*), white-fronted tern (*Sterna striata*), red-billed gull (*Larus novaehollandiae*), and little blue penguin (*Eudyptula minor*)) and one or more cetacean species (Bryde's whale (*Balaneoptera brydei*) or like-Bryde's whale). Since observations for this study were restricted to the surface, analyses focused on those avian species with flight, and does not discuss the significance of little blue penguin, since this small, generally solitary, marine species would have been under represented in this study.



Plate 3.3 Australasian gannets (*Morus serrator*) were frequently observed feeding with common dolphins in the Hauraki Gulf.



(a) flesh-footed shearwater (*Puffinus carneipes*)



(b) Buller's shearwater (*Puffinus bulleri*)

Plate 3.4 Seabirds were frequently associated with common dolphins in the Hauraki Gulf.

3.3.1 Avian species

Australasian gannets were the most frequently encountered bird species interacting with common dolphins on 46 focal group follows (78.0%) (Plate 3.5, Figure 3.15). Gannets can be a conspicuous highlight of dolphin feeding activity, and were used to locate 28.8% of dolphin groups ($n = 17$) during this study. However, the majority of dolphin sightings (71.8%, $n = 42$) were not in the presence of gannets at the start of observations, and it is suspected that only a minor sampling bias exists in the presented data. When gannets were present, their behaviour varied significantly with the behaviour recorded for the dolphin group (Table 3.6). The birds spent significantly more time flying above and behind the dolphins during herding (Kruskal-Wallis ANOVA, $H_{3,22} = 30.08$, $P < 0.001$; post-hoc comparison, Dunn's test), and circling above foraging dolphins when the dolphin group dived or was engaged in feeding behaviour (Kruskal-Wallis ANOVA, $H_{3,34} = 25.12$, $P < 0.001$). A high proportion of diving behaviour by the gannets corresponded with surface feeding behaviour by the dolphins (Kruskal-Wallis ANOVA, $H_{3,35} = 44.97$, $P < 0.001$). When the dolphins were not engaged in foraging behaviour, gannets in the area spent significantly more time resting on the surface of the water, usually in rafts (Kruskal-Wallis ANOVA, $H_{3,33} = 17.75$, $P < 0.001$).

The size of Australasian gannet flocks associated with common dolphins was not influenced by dolphin group size (Chi-square test, $\chi^2_{16,59} = 21.77$, $P = 0.151$). However, gannet flock size was significantly related to the percentage of time dolphins spent feeding (Kruskal-Wallis ANOVA, $H_{4,59} = 14.30$, $P = 0.006$), with larger flocks recorded during observations with high proportions of feeding, and no gannets recorded during dolphin observations with low proportions of feeding behaviour (post-hoc comparison, Dunn's test).



Plate 3.5 A flock of Australasian gannets (*Morus serrator*) taking off after feeding in association with common dolphins.

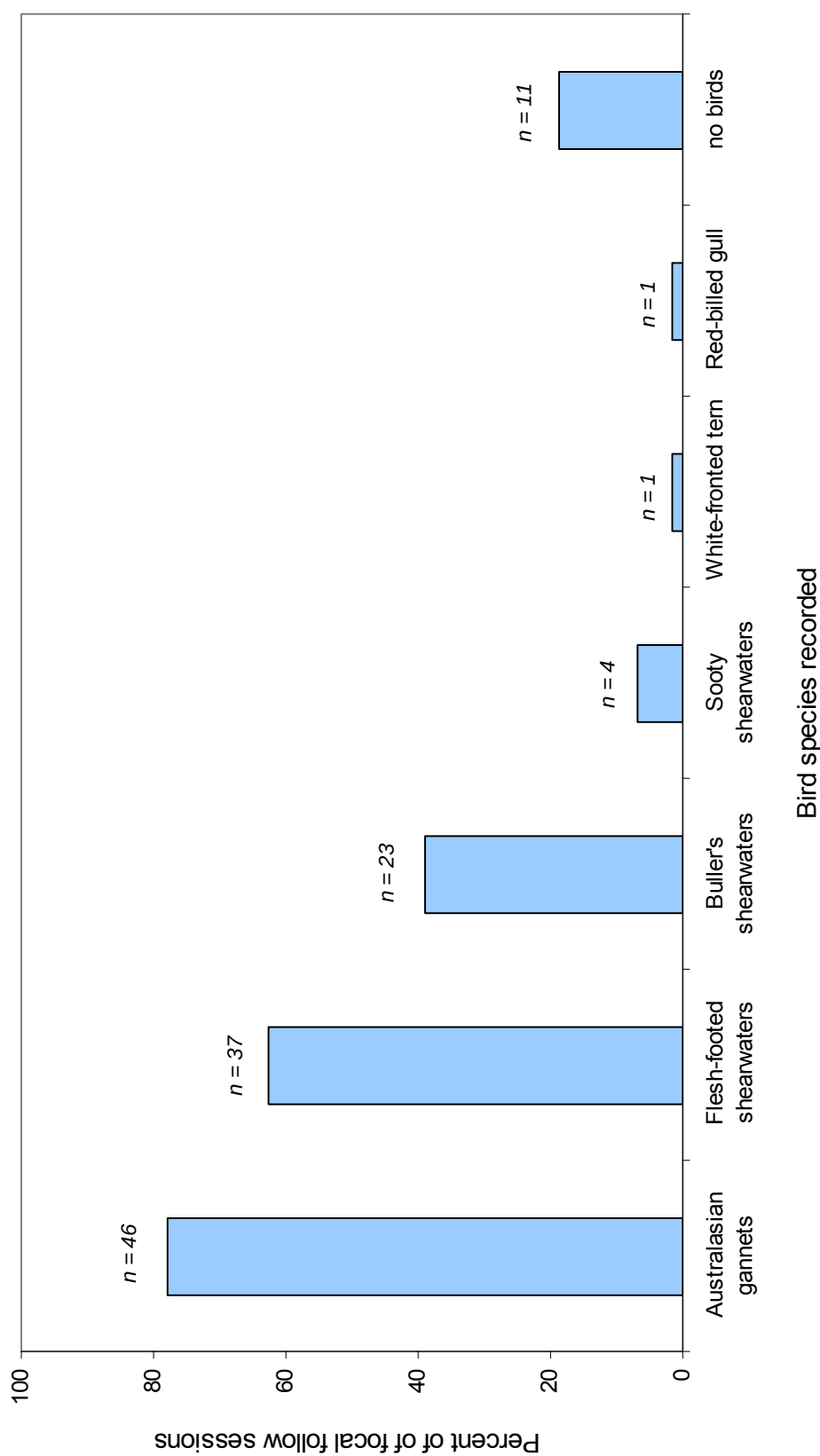


Figure 3.15 Frequency of each bird species recorded in flocks associated with common dolphins in 59 focal follow groups. Sample sizes are given above each column.

Table 3.6 Summary of the proportion of time common dolphin groups spent in each behavioural state and corresponding Australasian gannet behaviour during focal follow sessions. Values are percent instantaneous samples recorded during focal follows, presented as mean $\pm$ s.e. (total n = 46 focal follows with gannets present).

Gannet behaviour	<i>Dolphin behaviour</i>				Dunn's test
	herding	diving	feeding	non-foraging	
following	n = 22 64.8% $\pm$ 0.4	11.3% $\pm$ 0.3	7.2% $\pm$ 0.2	16.7% $\pm$ 0.3	herding > non-foraging, diving, feeding ***
circling	n = 34 18.5% $\pm$ 0.3	33.1% $\pm$ 0.3	42.5% $\pm$ 0.4	5.9% $\pm$ 0.2	feeding, diving > herding, non-foraging ***
diving	n = 35 14.4% $\pm$ 0.3	24.7% $\pm$ 0.3	58.9% $\pm$ 0.4	2.0% $\pm$ 0.1	feeding > diving, herding, non-foraging ***
resting	n = 33 20.8% $\pm$ 0.3	28.0% $\pm$ 0.4	8.6% $\pm$ 0.2	42.6% $\pm$ 0.4	non-foraging > diving, herding, feeding ***

Note. Sample sizes for each category are given as 'n'. Significance levels are indicated with an asterisk: * P < 0.05; ** P < 0.01; *** P < 0.001.

3.3.2 *Whale species*

Whales were observed to be present in the vicinity of the focal dolphin group on 27 focal follow sessions (45.8% of total number of sessions). Whales showed evidence of interacting with the dolphins on 21 follows (35.6% of total number of sessions), with lunge feeding events recorded during 15 observations (25.4% of total number of sessions). To further understand the importance of dolphin foraging behaviour for whale feeding interactions, only those sessions were analysed where both dolphins were foraging and whales were present (Figure 3.16). During such sessions, 91.3% ($n = 21$) of whale encounters interacted with foraging dolphins, with 65.2% ($n = 15$) of whales engaging in lunge feeding through the dolphin foraging group (Plate 3.6).

During the 21 focal follows with whales seemingly interacting, 38 lunge feeding events were recorded. The mean number of lunge events during a feeding session was 1.08 (s.e. = 0.35, $n = 12$, range = 0-3) for one whale present, and 2.78 (s.e. = 0.649, $n = 9$, range = 1-7) when more than one whale present. Whales were recorded following foraging dolphin groups for between 4 min and up to 1 h and 28 min (mean $\pm$ s.e. = 23.10 min $\pm$ 2.27, $n = 20^3$). When tracking the foraging dolphins, the whales generally maintained a distance of approximately 200 m behind the dolphin group.

Dolphin behaviour with the corresponding whale behaviour at each instantaneous sample was compared (Table 3.7). Whales spent significantly more time following when dolphins are observed herding (Kruskal-Wallis ANOVA, $H_{3,25} = 16.40$, $P < 0.001$). Likewise, whale lunging behaviour was typically recorded when the dolphins were confirmed feeding (Kruskal-Wallis ANOVA, $H_{3,15} = 36.00$, $P < 0.001$).

³ Note. Sample size = 20 and not 21 because one observation began with a whale lunge feeding and therefore, no behavioural data on the whale was able to be collected before the lunge event.

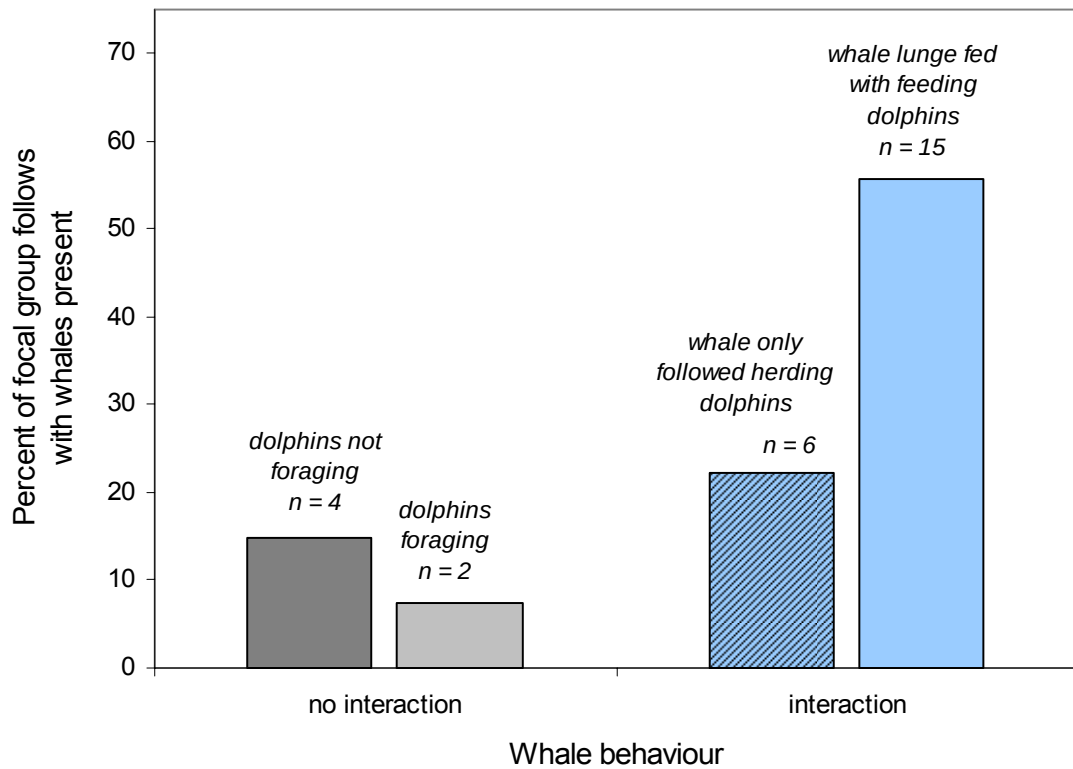


Figure 3.16 Proportion of behavioural interactions between common dolphins and Bryde's whales or like-Bryde's whales during focal group follows with whales recorded as present (total n = 27).



Plate 3.6 A Bryde's whale lunge feeding in association with foraging common dolphins in the Hauraki Gulf.

Table 3.7 Summary of the proportion of time common dolphin groups spent in each behavioural state and corresponding Bryde's or like-Bryde's whale behaviour during focal follow sessions. Values are percent of instantaneous samples recorded during focal follows, presented as means $\pm$ s.e. (total n = 27 focal follows with whales present).

Dolphin behaviour						
Whale behaviour		herding	diving	feeding	non-foraging	Dunn's test
follow / approach	n = 25	45.8% ± 0.3	20.7% ± 0.2	14.8% ± 0.2	18.6% ± 0.2	herding > diving, feeding, non-foraging ***
lunging	n = 15	8.3% ± 0.3	16.5% ± 0.2	75.2% ± 0.3	0.0% ± 0.0	feeding > diving, herding, non-foraging ***
no interaction	n = 15	19.6% ± 0.4	21.4% ± 0.4	0.0.714 ± 0.3	51.8% ± 0.5	non-foraging > diving, herding, feeding *
Note. Sample sizes for each category are given as 'n'. Significance levels are indicated with an asterisk: * P < 0.05; ** P < 0.01; *** P < 0.001						

Note: Sample sizes for each category are given as 'n'. Significance levels are indicated with an asterisk: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

3.3.3 Mixed-species aggregations during feeding

Of the 59 focal follow sessions, 57.6% ($n = 34$) of sessions recorded a mixed-species feeding aggregation during the follow. A total of 72 individual mixed-species feeding aggregation events were observed, of which 61 feeding aggregations were timed for their duration (mean $\pm$ s.e. = 4.31 min $\pm$ 0.62). Mixed-species feeding aggregations lasted from less than a minute to over 20 min before species dispersed.

Australasian gannets played an important role in mixed-species feeding aggregations with common dolphins (Plate 3.7). The presence of flesh-footed shearwater, Buller's shearwater (Plate 3.8) and Bryde's or like-Bryde's whales were significantly influenced by the presence of gannets (Table 3.8).

Table 3.8 Summary of species associated with common dolphin in which various combinations of species pairs co-occurred.

Species	co-occurring with:				
	Australasian gannet	Flesh-footed shearwater	Buller's shearwater	Sooty shearwater	Bryde's or like-Bryde's whale
Australasian gannet	χ^2 – $n = 46$	15.97 *** $n = 35$	10.65 ** $n = 23$	1.21 $n = 4$	6.20 * $n = 25$
Flesh-footed shearwater	χ^2	– $n = 37$	9.48 * $n = 20$	0.28 $n = 3$	7.50 ** $n = 22$
Buller's shearwater	χ^2		– $n = 23$	0.22 $n = 2$	5.75 * $n = 15$
Sooty shearwater	χ^2			– $n = 4$	0.03 $n = 2$
Bryde's whale	χ^2				– $n = 27$

Note. χ^2 is the Chi-square statistic of interaction, $df = 1$, n = sample sizes. Significance levels are indicated with an asterisk: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.



Plate 3.7 A flock of Australasian gannets (*Morus serrator*) following and diving in association with feeding common dolphins in the Hauraki Gulf.



Plate 3.8 A flock of shearwaters (*Puffinus* spp.) feeding with common dolphins in the Hauraki Gulf.

Analyses of mixed-species aggregations focused on Australasian gannets and Bryde's or like-Bryde's whales as associated species. The flock size of gannets would have meant a substantial impact from this species during mixed-species aggregations. Gannet flocks consisting of over 200 birds were observed in association with foraging dolphins, with the majority of gannet flock sizes between 10 and 50 gannets (30.5% of focal follows, $n = 18$). Furthermore, gannet flocks observed near foraging dolphins were dynamic, with aggregations changing in size from less than 10 birds in the vicinity to over 100 birds within minutes. Whale interactions with the dolphins were also focused on in the mixed-species aggregation analyses. The body size of a Bryde's whale (length = 12.2 - 15.3 m, weight = 12 - 20 tonnes (Carwardine, 1995)) and their dynamics as lunge feeders (Arnold et al., 2005), meant that they potentially had a substantial impact on dolphin foraging.

The time frame of foraging behaviour leading to mixed-species feeding aggregations with common dolphins was different for whales and gannets (Figure 3.17). Generally, whales spent a substantial amount of time following or tracking the dolphins, but only a brief time feeding. Conversely, gannets started following the dolphins later in their herding progression and then spent a substantial amount of time feeding with the dolphins. The length of time mixed-species feeding aggregations lasted was roughly equal to the length of gannet's feeding (Figure 3.17).

The length of time gannets followed common dolphin groups was significantly correlated with time gannet flocks spent diving (Figure 3.18) i.e., gannet flocks investing more time in following dolphins potentially had a greater foraging return. The length of time whales followed the dolphins was not significantly correlated with the number of feeding lunges (Figure 3.19). However, often it was suspected that more than one whale was in the area but due to irregular diving patterns and only opportunistic photo-identification of the whales, it was not possible to affirm single whale behaviours.

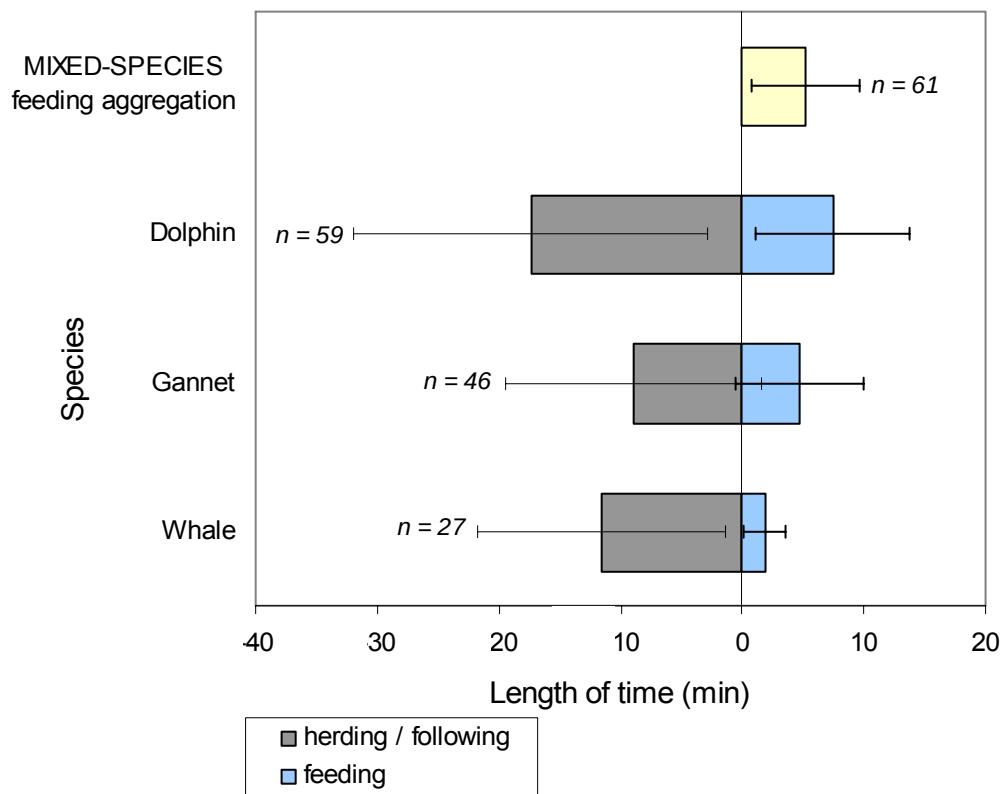


Figure 3.17 Time common dolphins spent herding and then feeding, compared with time Australasian gannets and Bryde's or like-Bryde's whales spent following dolphins and then feeding in mixed-species feeding aggregations. Time zero is the onset of feeding. Values are means with standard error bars. Sample sizes are given above each column (total $n = 59$).

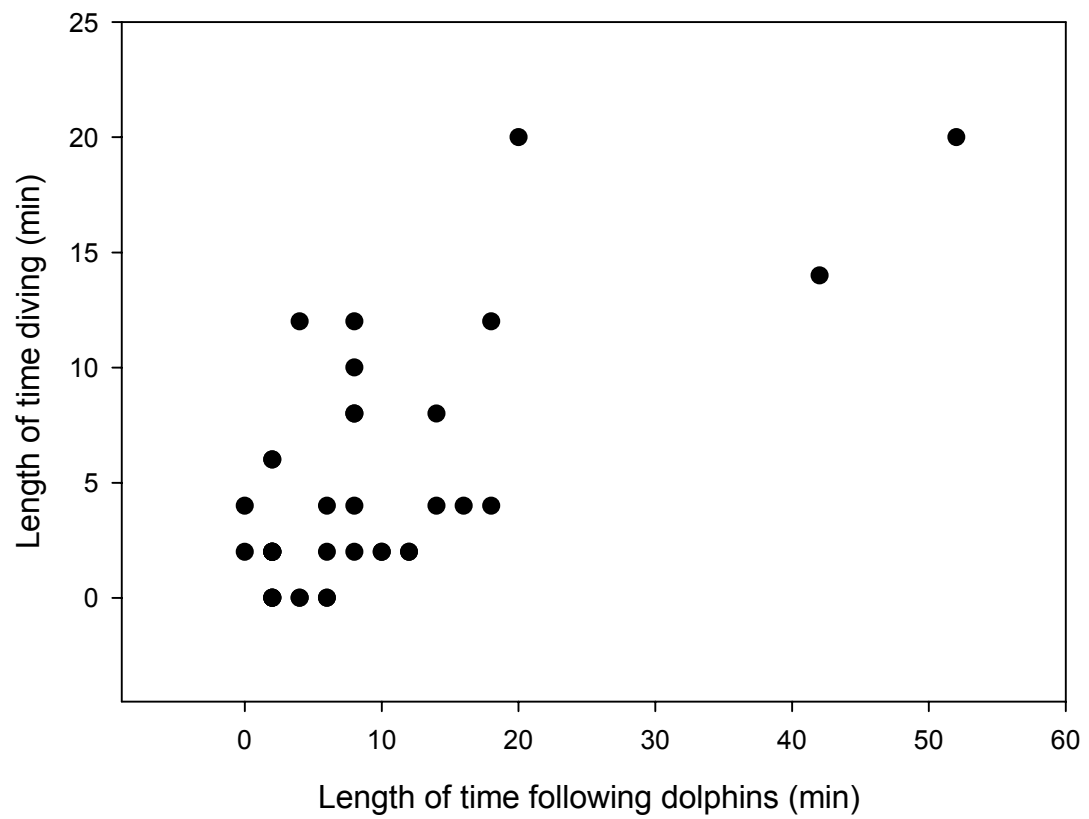


Figure 3.18 Correlation between the length of time Australasian gannets follow dolphins and the length of time gannets spent diving (Spearman's ranked correlation, $r^2_{44} = 0.49$, $P < 0.001$).

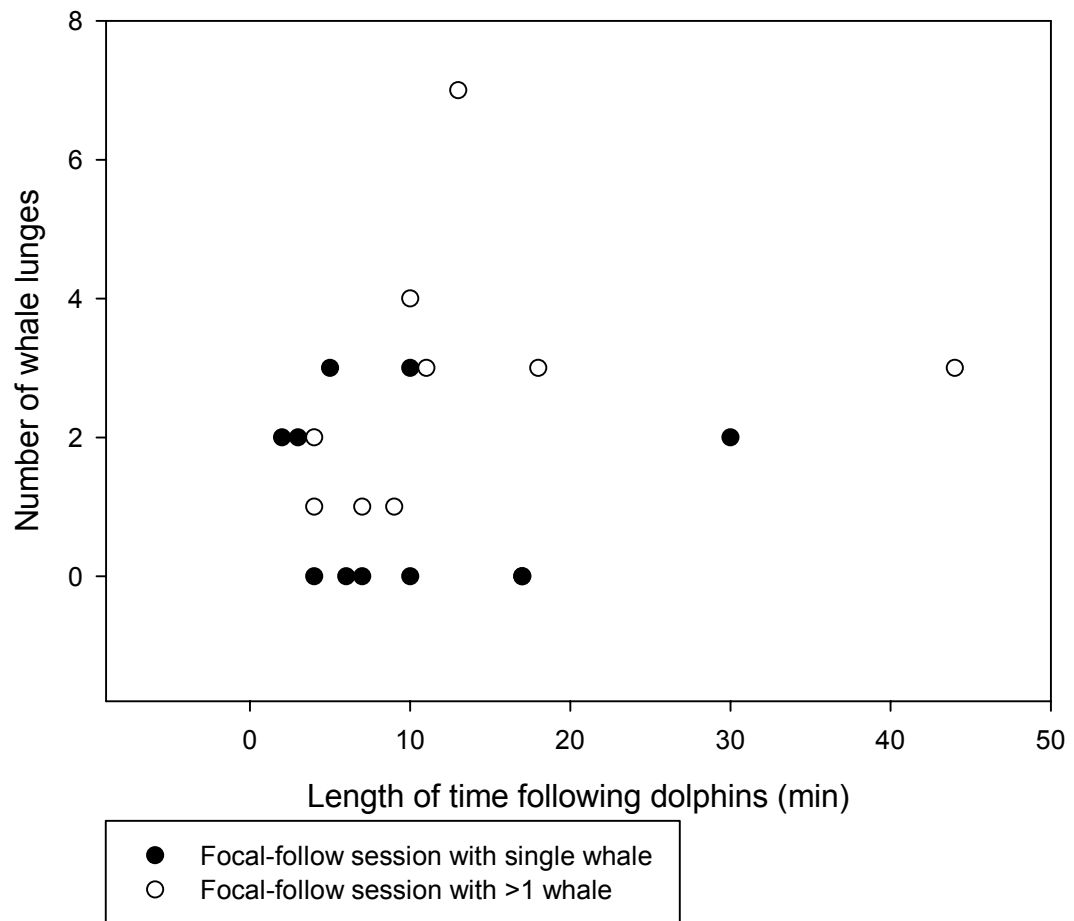


Figure 3.19 Correlation between the length of time whales follow dolphins and the number of feeding lunges (Spearman's ranked correlation, $r^2_{18} = 0.03$, $P = 0.421$).

3.3.4 Influence of associated species on common dolphin foraging behaviour

Analysis showed a significant difference in dolphin foraging behaviour depending on the presence or absence of both whales and gannets (Table 3.9). Data were tested using a full factorial model, but no significant interaction effect was found. Dolphin diving behaviour occurred less frequently in the presence of gannets, while dolphin feeding behaviour occurred more frequently in the presence of gannets (Figure 3.20). The probability of dolphins conducting herding behaviour was higher in the presence of whales, while dolphin non-foraging behaviour showed a lower probability in the presence of whales (Figure 3.21).

Dolphin foraging state data were also analysed to examine the affect of a whale lunging during feeding. Foraging behaviour of dolphins before and after a whale lunge feeding event was significantly different (maximum likelihood CATMOD analysis, $\chi^2_{3,59} = 11.11$, $P = 0.011$). The probability of dolphins engaging in herding and feeding behaviour decreased, while synchronous diving and non-foraging behaviour increased after a whale lunging event (Figure 3.22).

Table 3.9 Summary of maximum likelihood CATMOD results and levels of significance for data gathered on common dolphin foraging behavioural states - herding, diving, feeding, non-foraging by whale and gannet presence (n = 59 sessions with 1453 instantaneous samples).

Source of variation	Data set		
	Foraging states		
	df	χ^2	P
Whale presence	3	61.43	< 0.0001 ****
Gannet presence	3	34.29	< 0.0001 ****
Whale x Gannet presence	3	3.84	0.051

Note. Significance levels are indicated with an asterisk: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

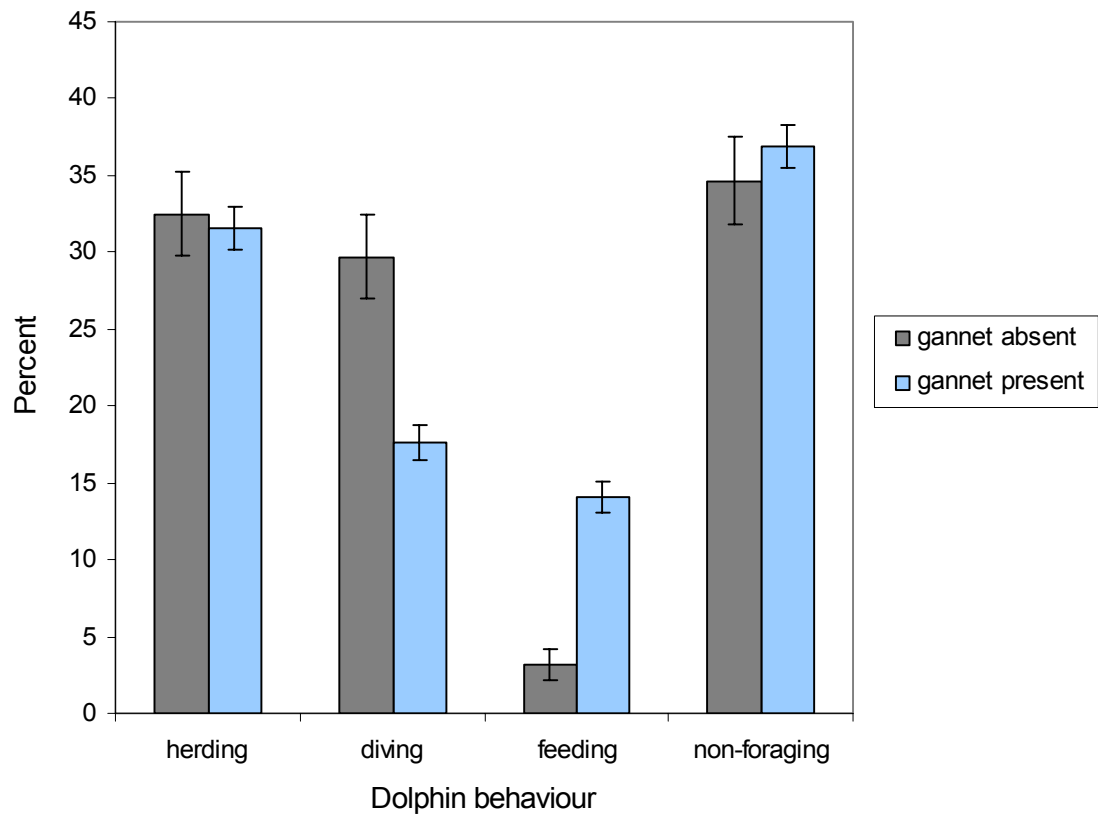


Figure 3.20 Probability of observing herding, diving, feeding and non-foraging behaviour of common dolphin groups by the presence of Australasian gannets. Values are maximum likelihood CATMOD probabilities with standard error bars (n = 59 sessions with 1453 instantaneous samples).

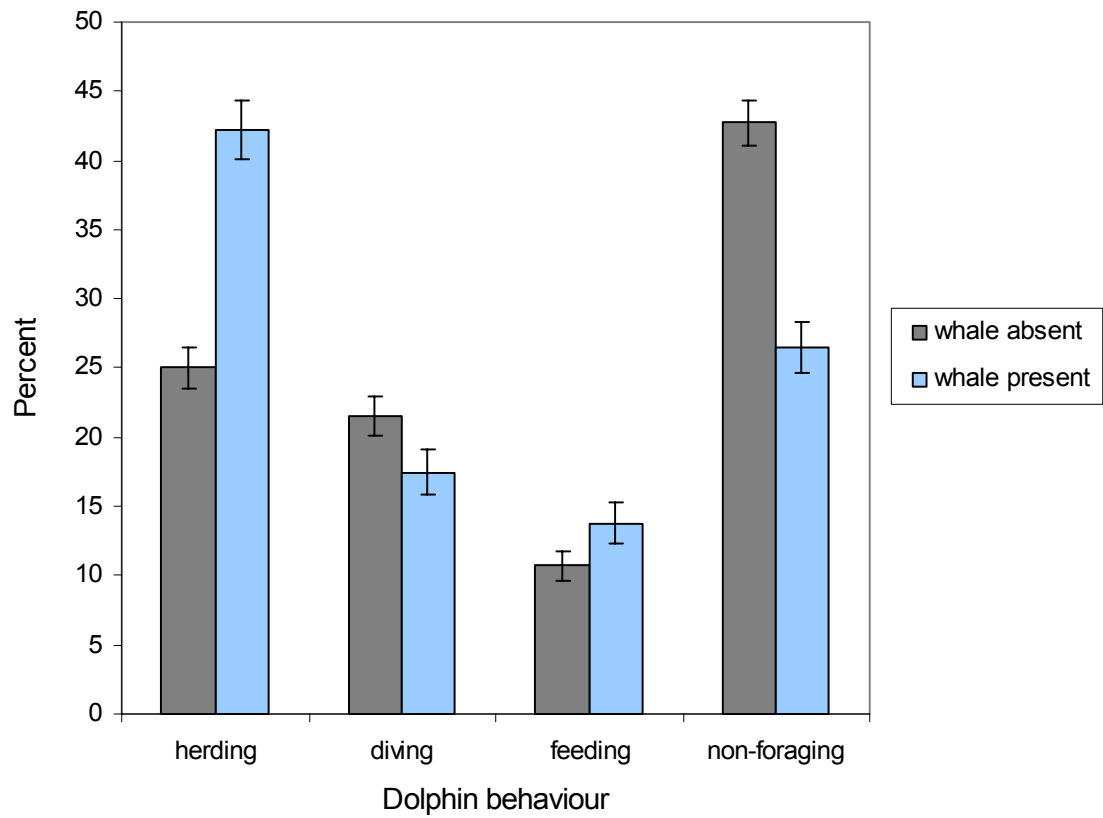


Figure 3.21 Probability of observing herding, diving, feeding and non-foraging behaviour of common dolphin groups by the presence of Bryde's or like-Bryde's whales. Values are maximum likelihood CATMOD probabilities with standard error bars (n = 59 sessions with 1453 instantaneous samples).

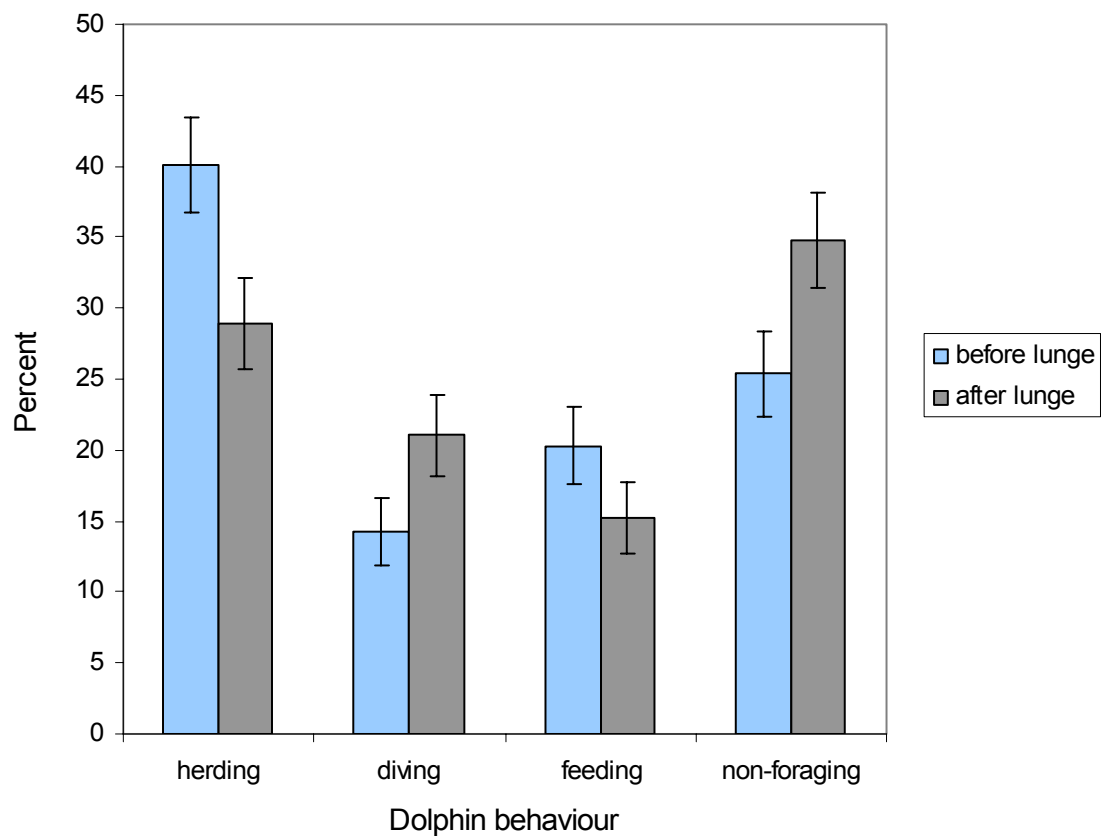


Figure 3.22 Probability of observing herding, diving, feeding and non-foraging behaviour of common dolphin groups before and after a feeding lunge by a Bryde's or like-Bryde's whale. Values are maximum likelihood CATMOD probabilities with standard error bars (n = 20 sessions with 421 instantaneous samples).

3.3.5 Fish observations

Since this study was limited to surface observations, only 11 sightings of prey species at or near the surface were made. These observations included seeing the concentrated fish 'bait ball' below the surface (n = 2), fish in the mouth of a common dolphin (n = 1), fish in the bill of shearwaters (n = 2), and fish fleeing at the surface during a whale's vertical lunge through the 'bait ball' (n = 6). All sightings were of small (approximately 10-15 cm in duration), slender fish presumed to be *Sardinops* sp.

Fishing boats anchored next to feeding dolphins in 'work-up' frenzies (mixed-species feeding aggregations) frequently caught 'snapper' (n = 4). Fishing charters in the Hauraki Gulf often target the dolphins for their fishing, with consistent catches of snapper, as well as John dory (*Zeus faber*) and red gurnard (*Chelidonichthys kumu*). Further anecdotal information from charter boats also suggest sharks participate in these mixed-species feeding aggregations. Kahawai (*Arripis trutta*) and trevally (*Pseudocaranx dentex*) are noticeably absent when fishing near dolphin 'work-ups' (M. Brown, pers. comm.).

Chapter Four: DISCUSSION

4.1 *Foraging behaviour in the Hauraki Gulf*

Common dolphin groups were frequently encountered in the Hauraki Gulf Marine Park, suggesting that the Gulf is an ecologically significant area for this species. Common dolphins occur year-round in the Gulf, and it appears that site-fidelity is likely to be relatively high for this species, although photo-identification to confirm residency is still in its infancy (Stockin, unpublished data). The year-round presence of this species in the study area may be related to productive feeding grounds, rich enough in prey to support their feeding requirements (Bearzi, 2005). This hypothesis is supported by the relatively high amounts of time that common dolphins observed in this study spent foraging in the Hauraki Gulf (62% of total time) compared to other behavioural states. Previous studies also observed feeding more frequently than any other activity for common dolphins in the Hauraki Gulf year-round (Schaffar-Delaney, 2004).

Observations of the different phases of foraging behaviour (herding, synchronous diving and surface feeding) in this study were important in increasing the understanding of dolphin foraging ecology in the Hauraki Gulf. In the literature, dolphin behavioural observations tend to focus on a broad category of 'feeding' (Shane, 1990; Neumann, 2001b; Bel'kovich et al., 1991; Felleman et al., 1991; Similä & Ugarte, 1993). Feeding is usually defined as an activity category during which animals are observed to chase, throw, capture and eat fish, or swim in specific patterns that gain them access to fish (Nowacek, 2002). However, this study further defined 'herding' and 'synchronous diving' behaviour as important components of foraging, and subsequently these states were identified and quantified. Herding and diving behaviours are significant because it is during these states that an animal potentially expends a lot of energy in order to reach the moment of prey capture and achieve an energy intake. Considering the complex societies of dolphins and their high level of cooperation to aggregate fish, it is important that herding or diving behaviours are considered separately when investigating foraging, because prey capture is only the end result of highly variable foraging strategies.

4.2 Foraging activity budget of common dolphins

Food availability is often a dominant factor in determining an animal's activity budget (e.g., Goodson et al., 1991; Stock & Hofeditz, 1996; Adeyemo, 1997; Baldellou & Adan, 1997). Other activities can be assumed to become more frequent, only after nutritional needs have been satisfied (Doenier et al., 1997).

Common dolphins in the Hauraki Gulf were confirmed feeding 14% of total time, and suspected foraging in synchronous diving behaviour 20% of total time. These results may have been subjected to a sampling bias as non-systematic survey methods were used to find dolphin groups, and more rigorous survey techniques are needed. However, these results are comparable to (Neumann, 2001b) for the Bay of Plenty, New Zealand. Neumann (2001b) reported common dolphins spent 17% of total time dedicated to feeding activity, though he did not specifically document diving. Bearzi (2001) reported that common dolphins in Santa Monica Bay, California spent about 30% of total time feeding or diving, which is just slightly less than the combined feeding and diving budget (34%) found for the Hauraki Gulf in this study. Neither Neuman (2001a) nor Bearzi (2001) categorised herding behaviour during foraging activity. The time spent feeding by common dolphins in the Hauraki Gulf is also comparable to studies of other dolphin species, such as bottlenose dolphins in Florida (17%, Shane, 1990), and Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off New England (10%, Weinrich et al., 2001).

Neumann (2001a) reported that common dolphins spent most of their time travelling (55%), and concluded that daily and seasonal movements of dolphins were likely to be governed by the distribution and availability of prey. This is in contrast to the Hauraki Gulf, where foraging behaviour was more frequently recorded. Such a discrepancy may be an artefact of the definitions used in each of the studies. Neumann (2001a) recorded data for five states: resting, milling, socialising, travelling and feeding. The definition for 'feeding' was specific in identifying those samples where an 'animal chases or captures prey items close to the surface'. However, the current study used a more general definition of 'foraging' and included herding behaviour in its definition, not just focusing on 'feeding'. Under the definitions used by Neumann (2001a), herding behaviour during foraging could possibly have been categorised as 'travelling', and subsequently may have over-represented this behaviour. Alternatively, the comparatively higher proportion of time devoted to travelling in the Bay of Plenty

compared to the Hauraki Gulf may be truly represented, and indicative of the more open seas off the east coast of the Coromandel when compared to the relatively enclosed waters of the Hauraki Gulf. The waters of the Bay of Plenty may have significantly different prey availability and dynamics.

Neumann (2001b) predicted that a common dolphin weighing 100 kg (Collet & Saint-Girons, 1984) required about 5 kg of prey per day, based on calculations modelled from bottlenose dolphins requiring 4-6% of their body weight in food a day (Shapunov, 1971; Shane, 1990). It is unknown exactly how much prey is captured in a feeding bout, and speculative as to whether or not 14% of a common dolphin's daily activity budget would be sufficient to catch that amount of prey. Combining the effort of herding (28%), synchronous foraging dives (20%) and confirmed surface feeding (14%), a significant proportion of the day was devoted to foraging activity. Prolonged surface feeding sessions were observed for over 30 mins, while on other occasions the dolphins were involved in short 2-5 min bouts of 'snacking'. On most occasions the dolphin groups would spend time herding or corralling the prey before surface feeding commenced.

Prey abundance is probably the critical factor, especially when food resources are rarely uniformly distributed throughout the marine environment (Partridge & Green, 1985). When dolphins devote time to cooperatively herd schools of fish, individual prey intake at the time of feeding is probably high and would require little time. Herding behaviour constituted a large proportion of time spent foraging, with the period of confirmed prey capture at the surface being approximately half the amount of time devoted to herding the prey. Furthermore, large distances are covered by the dolphin group during herding behaviour. This is ecologically significant, as it appears the dolphin group invests a significant amount of time and potentially energy, before reaching the point of prey capture. It is therefore, reasonable to speculate that any disturbance to the group during herding behaviour could have a significant impact on their foraging success.

Common dolphins appeared to be to be rather opportunistic feeders, with prey items varying, according to whichever species happens to be in great abundance at a given time (Young & Cockcroft, 1994). Fish species that were observed to be taken by common dolphin in the Bay of Plenty were kahawai (*Arripis trutta*), jack mackerel (*Trachurus novaezelandiae*), yellow-eyed mullet (*Aldrichetta forsteri*), flying fish (*Cypselurus lineatus*), parore (*Girella tricuspidata*) and garfish (*Hyporhamphus ihi*)

(Neumann & Orams, 2003). These fish are also found in the Hauraki Gulf (Kendrick & Francis, 2002). In this study, prey items taken by common dolphins in the Hauraki Gulf were small, slender schooling fish, suspected to be pilchards (*Sardinops* sp.). Schooling fish, such as the New Zealand pilchard (*Sardinops neopilchardus*), are locally abundant (Kendrick & Francis, 2002) and may be concentrated in certain areas by tides and currents (Baker, 1972). Common dolphins might be expected to alter their hunting tactics to cooperatively hunt schools of fish. Dietary studies of common dolphins suggest that they consume the most abundant, easily captured prey, and that their diet may be a reliable and accurate indication of the abundance and distribution of local, neritic resources (Young & Cockcroft, 1994). Thus, during the period of this study, locally abundant pilchards appear to be the most significant prey item for common dolphins in the Hauraki Gulf.

Several studies on stomach contents of *Delphinus* sp. identify the importance of various species from the deep scattering layer in their diet, particularly squid (Young & Cockcroft, 1994; Young & Cockcroft, 1995; Walker & Macko, 1999). Squid and myctophid lanternfish are normally available to dolphins only during their nocturnal migrations towards the surface. Common dolphins off southern California dove to feed on organisms in the deep scattering layer throughout the night, when the deep scattering layer was closest to the surface (Evans, 1971). Acoustic data by (Goold, 2000) has inferred that common dolphins do undertake night-time feeding. Presumably, the diurnal movement patterns of prey would strongly affect the way dolphins apportion their time each day. Squid species are found in the Hauraki Gulf (Kendrick & Francis, 2002), and could play a role in the diet of common dolphins. Stockin et al. (2005) found the remains of arrow squid (*Nototodarus* sp.) as the most frequently recorded prey species in the stomachs of eight post-mortem carcasses of common dolphins from the Hauraki Gulf. The high percentage of time devoted to diving during foraging activity during the day, could be suggestive of dolphins foraging on squid deeper in the water column. However, this is unconfirmed as prey was not observed during diving bouts and dietary investigation was not undertaken. Since this study was restricted to daylight hours, the possibility of feeding activity during night hours needs to be investigated.

4.3 Foraging behaviour and environmental or physical variables

Common dolphin foraging behaviour is flexible, and the dolphins observed in this study were generally active all day. There were no peaks in feeding activity during the day,

such as that observed for bottlenose dolphins with feeding activity peaking in the morning and afternoon (Shane et al., 1986). In various locations, dolphin species are known to exhibit two diurnal peaks in feeding activity - one in the early morning, and one in the late afternoon (Bräger, 1993; Hanson & Defran, 1993). Neumann (2001b) found a high frequency of early-morning feeding for common dolphins, but did not find a feeding activity peak in the late afternoon. He predicted that if common dolphins take advantage of the nocturnal migration of squid as they do elsewhere (Young & Cockcroft, 1994; Young & Cockcroft, 1995; Scott & Cattanach, 1998), then this second feeding peak could appear around dusk or shortly thereafter. In the Hauraki Gulf, foraging activity of common dolphins was not influenced by the time of day. This may be because the dolphins within this region are taking advantage of a food source that is in abundance throughout the day. Or as highlighted by Neumann (2001b), further investigations need to be conducted to understand the foraging dynamics into twilight and nocturnal hours.

Efforts were made to conduct all field work and dolphin observations within the summer/autumn season. From the present study, sea surface temperatures peaked in February and then declined in the autumn months of March and April. However, the mean temperatures recorded in each month only varied by just over one degree Celsius. Water temperature can influence both delphinid thermal energetics and prey availability (Wells et al., 1999). Over the months this study was conducted, there was no significant effect of temperature on foraging activity. For such a relationship to be adequately examined, research needs to be extended over several years. This was achieved for common dolphins in the Bay of Plenty, New Zealand, where it was found that foraging effort did not appear to change seasonally, rather it was the foraging location that changed with decreasing water temperatures in autumn (Neumann, 2001b).

Tidal currents can affect dolphin behaviour directly by assisting or impeding travel and indirectly by influencing prey movements. The Hauraki Gulf experiences only a moderate tidal flow from a tidal range of 2-3 m, and no influence of tidal cycle was found on common dolphin foraging behaviour for this area.

Common dolphin groups were encountered throughout the Hauraki Gulf area, though in the present study, groups were not sighted close inshore. Dolphins groups were observed at least one nautical mile from the nearest shoreline and as far offshore as 11 nautical miles. The water depth does not vary substantially in the Hauraki Gulf, and

exhibits an almost level seabed as noted by O'Callaghan and Baker (2002). One region was, however, significantly different in depth profile, as dolphin groups sighted near Kawau Island experienced deeper waters than those groups sighted in the south-eastern regions of the Gulf. There was no significant influence of water depth or distance from shore on the overall foraging time of common dolphins in the Hauraki Gulf. However, when foraging behaviour was segregated and analysed as each of the different phases of foraging, significant influences of water depth were found. As water depth increased, foraging dolphin groups were found to spend increasingly more time feeding at the surface. An increase in the proportion of time spent feeding at the surface in deeper water, might suggest an increase in the amount of prey available, such that the group's feeding time is extended. Alternatively, a greater proportion of surface observations combined with an increase in synchronous diving, might demonstrate that the majority of feeding takes place at the surface with the dolphin group using the water surface as a barrier against which they can trap schooling fish in the deeper waters. This behaviour of common dolphins making prey rise to the surface during foraging has also been documented elsewhere in the Azores Islands and in the eastern Pacific (Au & Pitman, 1986; Clua & Grosvalet, 2001).

Dolphin sightings near Kawau Island and the Coromandel Peninsula also spent a greater proportion of time feeding when compared to dolphin groups sighted in the inner and central Hauraki Gulf regions. Sightings near Kawau Island were found to be in deeper waters than sightings from other areas. However, this may not explain the increase in feeding activity near the Coromandel Peninsula where water depth was not significantly different from other areas. Increased feeding activity may suggest that these areas are potentially more abundant in prey species. Distribution and abundance of small fishes is strongly tied to a number of environmental variables, such as changes in the seafloor topography. Some authors have reported the presence of common dolphins along sea floor reliefs, submarine canyons and escarpments (Hui, 1979; Polacheck, 1987; Selzer & Payne, 1988; Gaskin, 1992; Gowan & Whitehead, 1995), showing that undersea topography, rather than water depth, is the most significant physical feature influencing the distribution of common dolphins. Neumann (2001b) suggested that common dolphin distribution in the Bay of Plenty may be influenced by foraging opportunities around seamounts. Rapidly changing seafloor relief (e.g., seamounts) may provide shelter or create nutrient upwelling conditions, increasing localised fish abundance. Therefore, topography rather than water depth may be a stronger influence on foraging activity of common dolphins. However, such influences may not be relevant due to the predominantly flat seafloor of the Hauraki Gulf. It is also

possible that prey species, such as pilchards, are more abundant in these areas which are more distant from the urban areas of Auckland city. Urban catchments with related run off and significant recreational fishing pressure in the inner Hauraki Gulf could render these locations less conducive for prey abundance.

Common dolphin groups tended to herd in the direction of the nearest landmass, such that dolphin groups near Kawau Island headed in a westerly direction while groups near the centre of the Gulf, Waiheke Island and the Coromandel Peninsula tended to herd in a south-easterly direction. It is hypothesised that by herding towards the land rather than away, the dolphins could potentially be using a geographical barrier to corral schooling fish. However, a criticism of this hypothesis is that the common dolphins never approached closer than one nautical mile from land during this study. Whether the land still potentially acts as a barrier for corralling fish at that distance is unknown, and potentially further observations over longer periods may reveal otherwise.

In this study, the environmental and physical variables recorded showed a significant effect in certain aspects of common dolphin foraging activity. In other studies on dolphins, such variables have been reported to influence dolphin behavioural states and activity budgets (Shane 1990). While significant variables were identified, the current study was perhaps limited by data collected over a short time period. The collection of more observations throughout the year, may contribute to a better understanding of these environmental and physical variables and their role in common dolphin foraging behaviour in the Hauraki Gulf.

4.4 Foraging behaviour and group dynamics

The proportion of time spent foraging was strongly influenced by group size of common dolphins in the Hauraki Gulf. Larger groups comprising of 50 to 100 dolphins spent a longer time devoted to foraging activity than smaller groups (< 50). This increase in foraging activity with group size may occur because of the fission-fusion nature of common dolphin societies (Neumann, 2001b), as groups merge to form larger aggregations for the purpose of foraging. Previous studies have shown that dolphin species which inhabit open areas with patchy resources usually form large groups (Würsig & Würsig, 1980; Zemel & Lubin, 1995; Scott & Cattanach, 1998; Wells et al.,

1999). Dolphins potentially feed in larger groups in presence of large fish schools and when resources are patchily distributed.

Herding was an important phase of foraging for these larger groups. Groups of common dolphins with over 30 members were observed to devote more time to herding during foraging. Herding may potentially be more purposeful to larger groups than smaller groups of dolphins, as a large cooperative group would have a greater ability to concentrate prey, particularly when prey is sparsely distributed. Therefore, a selective advantage toward group living would be cooperation in large, collective groups to herd prey, thereby providing a significant benefit to group members. Herding in larger groups provides an advantage in that more dolphin members can potentially cover a wider area to corral prey, while not sacrificing spacing between herding dolphins. Dispersion between individuals during herding was found to be tight in larger group sizes. Tighter dispersion is potentially more favourable during herding, so that the chances of prey escaping are reduced. Smaller dolphin groups were more loosely dispersed, potentially sacrificing the distance between individuals in order to still have the ability to cover a wider area to corral prey. Group geometry was not random but has functional significance which varies depending on the dolphins' activity. Herding groups were tightly dispersed in a parallel formation, indicating that a cooperative effort between individuals was important. This group formation has been observed in other species, e.g., bottlenose dolphins (Shane, 1990) and dusky dolphins (Markowitz, 2004a). Herding behaviour in dolphins may also potentially be influenced by food availability, which was not investigated in this study. To further understand the effectiveness of herding as a foraging method, then feeding rates, food size and efficiency need to be determined.

The presence of calves in the group was not shown to significantly affect the amount of time devoted to foraging activity overall. However, calf presence did influence the herding behaviour of the group during foraging, with groups spending significantly more time herding when calves were present. Schaffer-Delaney (2004) found that in the Hauraki Gulf, common dolphin groups with calves present tended to be significantly larger than groups composed of adults only. This study showed that larger groups, tended to spend more time herding. Therefore, the influence of increased herding behaviour with calf presence may be a consequence of a larger group size. The statistical analyses used were not able to test for an interactive effect of both group size and calf presence on the proportion of time spent herding. However, an explanation of extended herding in groups with calves could be related to the increased

energetic requirements of lactating mothers (Cockcroft & Ross, 1990b). It has been shown that the diet of lactating female common dolphins is different from any other age and/or sex class, and is likely to be related to the specific requirements involved in lactation (Young & Cockcroft, 1994). Devoting more time to herding, may facilitate the aggregation of more prey and the ability of lactating females to obtain additional food (Cockcroft & Ross, 1990a; Young & Cockcroft, 1994).

Würsig (1986) argued that dolphins, such as bottlenose dolphins and killer whales use feeding methods that must be based on the animals' learning where, when, and how to find prey. Since learning has been shown to play an important role in dolphins (Defran & Pryor, 1980), and there is an extended period of mother-calf association (Schaffar-Delaney, 2004), it is plausible that calves learn foraging behaviour from mothers and other adults, by remaining central to the group during prey herding leading up to a feeding bout. This was evident in the foraging of common dolphin groups observed in the Hauraki Gulf, where calves typically assumed a position central or at least close to the group during the herding of prey. Yet, it is interesting that calves tend to assume a position on the outside separated by a short distance from the group during feeding. This study showed that during feeding bouts, calves were still very close to the group, and were not in 'babysitter' groups separated by a distance of a few hundred metres as has been reported for bottlenose dolphins (Shane, 1990). Würsig (1986) postulated that keeping calves separate was a means of protecting vulnerable calves from 'boisterous' activity and predators during the height of feeding. It is possible that common dolphins employ a similar strategy, since calves were frequently sighted on the outskirts of the group during feeding. Interestingly, Young and Cockcroft (1994) found that in the diets of common dolphins off southern Africa, there was little relationship between the diet of lactating females and weaning calves, with the prey species consumed by calves having more in common with diet of non-lactating females than with that of lactating females. These findings are similar to conclusions drawn for dusky dolphins, where 'nursery groups' consisting of small groups of subadults between one and three years old and calves did not feed with adults and were encountered some way from any central feeding activity (Würsig, 1986). These records of dietary divisions between mothers and calves, combined with the observations of common dolphin calves on the outskirts of feeding frenzies in the Hauraki Gulf, suggest that mothers may at times separate from their calves during feeding frenzies. However, further research would be required to verify such interactions. Current analyses are underway investigating the diet of New Zealand common dolphins (Stockin,

unpublished data), and this may prove useful in determining the validity of this hypothesis.

Dolphins typically live in schools that are not permanent units of a specific size (Norris & Dohl, 1980b). The term 'fission-fusion' is used to include those societies in which individuals form temporary groups that frequently aggregate or separate into larger or smaller units (Connor et al., 2000b). Fission-fusion societies usually form among animals with a low predatory pressure that use patchy resources variable in space and time (Scott & Cattanach, 1998). The findings from this study suggest that common dolphins in the Hauraki Gulf appear to live in a fission-fusion dynamic. These fluid societies allow individuals to select their group size and habitat depending on activity and ecological conditions (Gygax, 2002; Stensland et al., 2003). For common dolphins, it appears that foraging and prey availability are central to fission-fusion events. Neumann (2001b) also found a relationship between foraging states and fission-fusion events between groups. A variety of advantages of foraging in a group have been suggested for many species (see Stensland et al. 2003 for a list of species), including dolphins (Kenney, 1990; Scott & Chivers, 1990). A high concentration of food can facilitate the fusion of different social units for mutual protection and prey detection until the resource is reduced or exploited. Alternatively, a more uniform food distribution and a smaller amount of prey may induce competition among conspecifics for limited resources (Würsig, 1986).

Discrete surface behaviours may serve aggressive, social, sexual, alimentary, exploratory, play, or assisted-locomotion functions (Shane, 1990). Surface behaviours may have various functions depending on the context in which they occur (Würsig & Würsig, 1979). Therefore, this study made no attempt to understand the statistical association between surface behaviours and environmental factors. However, the synchrony between noisy surface behaviours and foraging activity was evident. Most of the aerial behaviours, such as breaching, tail slapping and head slapping, are highly conspicuous, both above and below the water. Besides being visually conspicuous, such aerial behaviours also include an acoustic component. While dolphins appear to primarily communicate with each other acoustically through various squeaks and whistles, these are considered very directional sounds, and Norris et al. (1994) proposed that aerial displays may be useful in communication through an omnidirectional sound. Spinner dolphins appear to use aerial behaviour to coordinate group activity and movements (Norris et al., 1994). Würsig & Würsig (1979) noted an increase in aerial behaviour associated with feeding and socialising. Other observers

have provided correlative data for bottlenose dolphin surface behaviour and feeding activity elsewhere in the world. Acevedo-Gutiérrez (1999) hypothesised that aerial behaviour in bottlenose dolphins may be directly related to prey capture, rather than being a social facilitator. Goodwin (1985) specifically linked bottlenose dolphin leaps with feeding. Saayman et al. (1973) associated leaping, splashing and slapping with feeding (Tayler & Saayman, 1972). In this study, it appears likely that active surface behaviour could serve a similar purpose in common dolphins.

4.5 *Foraging strategies and cooperation*

Dolphins use a variety of foraging specialisations to detect and pursue prey (e.g., Rendell & Whitehead, 2001; Nowacek, 2002; Mann & Sargeant, 2003). Observations of foraging marine mammals have been limited due to the difficulties of viewing subsurface behaviour and the non-representative nature of behaviour observed at the surface (Nowacek et al., 2001). Therefore, detailed descriptions of cetacean behaviours, particularly subsurface behaviours known to be essential to successful foraging, have eluded researchers. Furthermore, few studies have examined behaviour in more extensive dolphin societies such as those of common dolphins. This study found that synchronous diving behaviour constituted a major part of suspected foraging activity. Unfortunately, this study was limited to surface observations, and while synchronous diving was recorded, a thorough understanding of the functions and specific strategies used by dolphin groups under the water remains unclear. Neumann and Orams (2003) highlighted that bubble-blowing behaviour was mainly performed below the water's surface and was observed in their study using underwater video camera equipment. Due to various circumstances, underwater video recording is difficult. Factors such as camera angle, distance and visibility often provide inconclusive pictures. Therefore, no observations of bubble-blowing by dolphins in this study, may have been an artefact of observations being restricted to the surface. Underwater video cameras have previously been used by researchers to record subsurface foraging behaviour of common dolphins, though camera use has been restricted to filming during feeding bouts when prey fish have already been schooled into a tight bait ball and activity is concentrated in a localised area for easy viewing (Clua & Grosvalet, 2001; Neumann & Orams, 2003). During carouselling behaviour, Neumann and Orams (2003) recorded footage of underwater bubble-blowing by individual dolphins as a potential strategy to startle the schooled fish and separate

individual fishes from the school during the feeding frenzy. Observations in the Hauraki Gulf suggest that diving or subsurface behaviour also has a function before intense feeding has commenced, and potentially dolphins will synchronously dive to corral prey from deeper waters.

Common dolphins use a variety of strategies during foraging, and those observed in the Hauraki Gulf were equivalent to the foraging strategies of common dolphins described by Neumann and Orams (2003). The strategies most frequently observed were high-speed pursuit, carouselling and line-abreast. Neumann and Orams (2003) also commonly observed high-speed pursuit and carouselling in common dolphins, though only a small number of groups used line-abreast. A higher frequency of kerplunking was also observed in this study than was reported for common dolphins in the Bay of Plenty (Neumann and Orams 2003). Studies on bottlenose dolphins found that kerplunking was associated with habitat and dolphins only used kerplunking in shallow water (Nowacek, 2002). However, Hamilton and Nishimoto (1977) reported similar behaviour to kerplunking in bottlenose dolphins while circling schools of mullet. In this study, common dolphins were observed using kerplunking in over 20 m depth. In the deeper waters near Kawau Island, dolphin groups were not observed to use kerplunking, although this was more likely to be an artefact of a small sample size from this region ($n = 4$). Kerplunking appeared to be an important strategy used in conjunction with carouselling. The fluke movement of kerplunking creates a considerable cloud of air bubbles under water (Connor et al., 2000a). These observations of kerplunking during carouselling, support the hypothesis proposed that it has a function in startling fish or creating a visual and acoustic barrier to prey (Neumann & Orams, 2003). However, Neumann and Orams (2003) concluded that kerplunking could be considered an alternate strategy, used particularly in non-coordinated, solitary feeding with animals at some distance from other group members. However, observations from this study disagree, suggesting that kerplunking was used in close association with other group members, and may potentially contribute to a cooperative effort to school fish.

The amount of time common dolphins spent in each foraging strategy varied statistically. More time was spent synchronously diving or carouselling than the other foraging strategies. In comparison, line-abreast, high-speed pursuit and kerplunking were used by the dolphins for relatively short periods. Perhaps the strategies of high-speed pursuit and kerplunking, which demand bursts of speed and lifting the tail clear of the water, are relatively exhausting and can only be maintained for short periods.

Another explanation may be the dispersal of prey, such that these strategies are only worth maintaining while prey are tightly schooled and concentrated. Line-abreast foraging may also be potentially exhausting since the group generally maintains a high speed and often is observed porpoising. Wall-formation was only observed for very brief periods and may potentially be viewed as a transitory period where the 'drivers' and 'receivers' come together before using an alternative foraging strategy.

Each foraging strategy typically coincided with certain group formations, dispersion between group members, swimming styles and breathing intervals. Foraging strategies were also observed to have different roles in dolphin foraging. Line-abreast and wall-formation were generally associated with the herding phase of group foraging. Some prey capture may have occurred during this herding behaviour, but the majority of the group were coordinated in directed swimming. However, high-speed pursuit, kerplunking and carouselling were synonymous with surface feeding and prey capture. It was evident in this study, that foraging strategies were not exclusive, and dolphin groups changed strategies within foraging bouts and sometimes used both a coordinated and individual strategy simultaneously. For example, dolphins foraged using the line-abreast strategy which was then preceded by carouselling, or line-abreast then high-speed pursuit, or line-abreast then wall-formation, or carouselling then high-speed pursuit, or both carouselling and kerplunking simultaneously. This raises questions about the communication involved between members of a large group to cooperate in switching between foraging strategies, while maintaining a benefit to all members of the group.

Common dolphin groups are typically large, and their reliance on abundant, easily captured, shoaling pelagic prey thus has obvious energetic benefits and promotes cooperative foraging. Cooperative hunting occurs when individuals coordinate actions, such that the probability of successful capture of prey is increased among all participants (Sargeant et al., 2005). Coordinated strategies were more frequently observed than individual strategies in the foraging behaviour of common dolphins in the Hauraki Gulf. Cohesive and cooperative patterns and movement tended to characterise foraging groups of common dolphins in this study. The structured patterns observed with groups of dolphins indicate that foraging is truly cooperative, not just a group of animals aggregating at a common resource. Several authors have documented accounts of coordinated feeding in delphinid species, such as Atlantic spotted dolphins (*Stenella frontalis*) (Fertl & Würsig, 1995), Clymene Dolphin (*Stenella clymene*) (Fertl et al., 1997), bottlenose dolphin (*Tursiops truncatus*) (Rossbach, 1999) and dusky dolphin

(*Lagenorhynchus obscurus*) (Würsig & Würsig, 1980). While such feeding activity in dolphins has been well-described, reports are generally descriptive without analysing the importance of such coordinated activity to delphinid species over time.

Cooperative hunting has almost exclusively been reported for social mammalian carnivores (MacDonald, 1983). In common dolphins, larger groups were observed to use coordinated strategies more frequently than smaller groups of dolphins during this study. All species that exhibit social hunting behaviour also live in groups (Schaller, 1972). However, most investigators have argued that factors other than cooperative foraging, such as food dispersion (MacDonald, 1983) or kinship advantages (Rodman, 1981) may be more critical to the development and maintenance of social groups. The hypothesis that food dispersion may be responsible for the adaptation of cooperative foraging in common dolphins is plausible. Prey species identified during this study were small schooling fish, suspected to be pilchards. From previous studies, small schooling fish were targeted by common dolphins both in New Zealand (Neumann & Orams, 2003) and elsewhere (Clua & Grosvalet, 2001; Young & Cockcroft, 1994). Schooling pelagic species of fish, such as pilchard and anchovy, are known to have high mobility and are patchy in their distribution (Hobday, 1992). Cooperative techniques are, therefore, effective at aggregating high concentrations of prey.

Connor (2001) proposes that foraging specialisations are becoming more common in discovery among marine than terrestrial mammals. Connor (2001) outlined a series of hypotheses to explain this difference, suggesting that the terrestrial and marine habitats may differ in prey diversity, biomass, seasonality, predator mobility or rewards in foraging efficiency acquired through practice. Leatherwood (1975) hypothesised that the wide range of feeding behaviours exhibited by dolphins in different locales represents a 'plasticity' necessary for animals with limited ranges and faced with changing food resources. Individual and subgroup variation in foraging behaviours among cetaceans have been gaining increasing attention (e.g., Rendell & Whitehead, 2001; Nowacek, 2002; Mann & Sargeant, 2003; Sargeant et al., 2005). This study identifies plasticity in common dolphin foraging with members of a group modifying their behaviour to suit changing dynamics during the hunt. Some feeding strategies were used only infrequently, while others were regularly observed. Long-term studies are therefore invaluable in obtaining a complete picture of a species' behavioural repertoire. Markowitz (2004a) suggests that larger groups of animals may harbour some of the greatest social complexities. Few studies have examined social behaviour in more extensive dolphin societies, such as those of common dolphins. Gazda et al.

(2005) predicts that a division of labour with role specialisation may turn out to be more common in group-hunting marine mammals than in terrestrial mammals.

4.6 *Mixed-species feeding aggregations*

Feeding seems to play a major role in the associations of species observed in the Hauraki Gulf. During feeding, common dolphins appear to work cooperatively to herd large schools of bait fish into tight aggregations, where other species such as birds and whales take advantage of this food source. Mixed-species aggregations were commonly encountered in the Hauraki Gulf. Dolphin species that inhabit open areas with patchy resource usually form large groups (Scott & Cattanach, 1998; Wells et al., 1999; Zemel & Lubin, 1995) and opportunities for multi-species aggregations of marine mammals at sea increase where prey and habitat overlap (Norris & Dohl, 1980b). The cooperative hunting of large groups of common dolphins within the Gulf appears to provide a foraging opportunity for other marine predators. Stensland et al. (2003) hypothesises that for mixed-species groups to occur, the participating species should be social animals with loosely formed groups. Species with very stable social groups may be less likely to accept individuals of other species. Therefore, the fission-fusion nature of common dolphin groups in the Hauraki Gulf, present the ideal loosely associated social predator, whereby birds and whales can seek the company of these cooperatively foraging dolphins. In an area with a large number or high density of predators, there would be an even higher benefit to join another species to form a mixed species group. While not all foraging dolphin groups were accompanied by seabirds or other species, results suggest that the feeding behaviour of common dolphins does have a "strongly interactive" role in the marine ecology of the Hauraki Gulf Marine Park.

4.6.1 *Australasian gannet and shearwater associations*

Seabirds are good indicators and indeed signal the existence of a high level of predatory activity. A review by Stensland et al. (2003) illustrates the generality of the cetacean-seabird phenomenon, with associations occurring in many areas of the world and between many genera of both groups.

Flocks of Australasian gannets (*Morus serrator*) accompanying dolphin schools are a conspicuous sight in the Hauraki Gulf. Both species appear to have certain prey species in common and often feed in close association with each other. Diet studies on gannets from the east coast of the North Island found that the most frequently taken prey species were pilchard, anchovy and jack mackerel (Wingham, 1985). Associations between common dolphins and Australasian gannets in New Zealand have also been reported in the Bay of Islands (Constantine & Baker, 1997), in the Bay of Plenty (Neumann & Orams, 2003) and in the Hauraki Gulf (O'Callaghan & Baker, 2002; Schaffar-Delaney, 2004). Australasian gannets are active underwater predators, commonly using pursuit plunging and pursuit diving. Gannets were observed to hover, looking downward, above dolphin groups. The behaviour of the gannet flock strongly coincided with that of the foraging dolphin group. If the dolphins were herding, the flock of gannets was seen following close behind the foraging dolphin group. If the dolphins were feeding, the birds stayed circling, and then began diving for prey amongst the feeding dolphins. If the dolphins did not commence feeding, the birds usually responded to this quickly by departing. Seabirds were thought to initiate these associations by actively joining the dolphins and their observed behaviour of following herding dolphins indicates that such associations are potentially formed deliberately, rather than merely opportunistically.

Gannet flocks varied in number from a few to more than two hundred, which is probably linked to the abundance of prey. Flock size was not influenced by the number of dolphins present, but by the amount of time the dolphin group spent feeding. An increase in feeding time by the dolphins might suggest a greater availability of prey, which would in turn entice more gannets to the area. Greater numbers of birds over time, is also likely to be related to increased detection of feeding activity from a distance with accumulating bird numbers, and time for birds to relocate to the feeding site. In situations where dolphin groups spent a small proportion of time feeding, gannets were absent from the area. There was also a relationship between the amount of time gannets spent following dolphins and the length of time gannets engaged in diving. Gannets investing in more time and energy flying behind foraging dolphins were potentially rewarded with a longer time feeding. Gannets might follow dolphins longer when they can see more fish, which would potentially extend their feeding time. Ultimately, there appears to be a benefit for gannets to use dolphins for foraging.

Dolphin groups spent more time feeding in the presence of gannets compared with dolphin groups which did not have gannets present during feeding. This might suggest

that gannets selectively choose to associate with dolphin groups that have high levels of feeding activity. Theoretically, gannets could have had a sizeable impact on the feeding aggregation, with flocks of over 200 birds observed. Gannet flocks spent a significant amount of time feeding with the dolphin group, from almost the initiation of a concentrated feeding frenzy by the dolphins through until the dispersal of the prey. They are therefore a strong indicator of concentrated prey aggregation. It is understandable that fishermen often target gannets to find 'work up' or 'boil up' activity (M. Brown, pers. comm.). In the presence of gannets, dolphin groups showed significantly less diving behaviour during foraging. This is reasonable considering that the gannets, while being impressive divers, are restricted in their diving depths and could presumably most easily capture prey at the top of the water column. A decreased diving behaviour in the dolphins would suggest that prey has been concentrated near the surface and within diving reach of foraging gannets.

Feeding gannet flocks without the presence of dolphins were encountered, though the dispersion of gannets was noticeably different in each scenario. In mixed-species feeding aggregations with dolphins, the hovering flock and diving gannets were tightly dispersed, suggesting a high concentration of prey. However, in the absence of dolphins, feeding gannet flocks were widely dispersed and covering a greater area, suggesting prey was loosely dispersed or patchily distributed. Predatory fish, such as kahawai, were observed skimming the surface in feeding aggregations with gannets, and are probably responsible for herding the prey closer to the surface, creating the feeding aggregation. Cooperation during hunting has been documented in marine piscivorous fish (Schmitt & Strand, 1982). Yellowtail fish (*Seriola lalandei*) were observed cooperatively foraging on jack mackerel using elaborate and dynamic foraging sequences, comparable to dolphin foraging strategies. Yellowtail formed parallel lines, surrounded prey in u-shaped formations, herded prey towards the shore, and then encircled prey which responded by aggregating into a tight group (Schmitt & Strand, 1982). Cooperative hunting behaviours in fish have been speculated for some time (Schmitt & Strand, 1982), yet were unconfirmed, probably because opportunities to witness foraging behaviours of large piscivorous fish in open water are rare. Schmitt and Strand (1982) conclude that a high level of coordination may be used by other open water piscivorous fish, yet for logistic reasons, has received little attention. Observations in the Hauraki Gulf of kawahai suggest that this fish species may also foster cooperative foraging behaviours.

Gannets appear to play an important role in mixed-species feeding aggregations in the Hauraki Gulf. The presence of gannets significantly influenced the presence of shearwaters and whales. Gannets could potentially serve as both a visual or acoustic cue for other species in the area signalling feeding activity. The large numbers of gannets circling approximately 30 m above foraging dolphins would be a conspicuous sight above the water surface. Alternatively, the noise created by diving gannets plummeting into the sea could potentially be heard for a significant distance, alerting other species. Such cues may also be used within the species, since the number of gannets within the vicinity of feeding dolphins would change from a few birds to large flocks within a very short period.

Shearwater species were also recorded in association with common dolphins in the Hauraki Gulf. Flesh-footed and Buller's shearwaters were the most frequently encountered shearwater species. Shearwaters mainly feed on a mixture of squid, small fish and occasionally zooplankton (Heather & Robertson, 1996). Since these prey groups are rarely at the surface during daylight hours and shearwaters are mainly a surface feeder with rare brief immersions during foraging, daytime feeding would be dramatically enhanced by underwater predators such as dolphins forcing potential prey within their reach. The rapidity with which these birds gathered over feeding dolphins and the fact that they accompanied dolphins even away from food, indicates that such opportunities are valuable to the shearwaters. Shearwaters most probably ate scraps of fish flesh left by the dolphins and to a lesser extent whole fish, and hence were probably little competition for the mammals. During this study, observations indicated that during daylight hours, at least, feeding dolphins apparently provided a source of food for shearwaters.

It is less easy to establish any possible advantage to the dolphins from such interactions. Previous researchers have suggested the possibility that seabirds initially located the prey and cetaceans were subsequently attracted to the site. Evans (1982) reviewed published accounts of associative behaviour between the two taxa and concluded both that the seabirds are more likely to benefit and that most associations are probably opportunistic or incidental. Bird-dolphin associations in Sanibel Island, Florida were always initiated by the birds (Shane, 1990). In contrast, Würsig and Würsig (1980) proposed that dusky dolphins used sightings of feeding bird flocks to lead them to sites where other dolphins were already feeding. Tyack (1976) found that birds in Argentina associated with bottlenose dolphins only when the latter were feeding. On the contrary, during this study, none of the observations suggested that

dolphins were seeking groups of gannets or shearwaters, it was the birds that followed the dolphin groups. Furthermore, nothing in the birds' behaviour at the feeding sites could be interpreted as being of benefit to the feeding dolphins. Markowitz (2004a) also reported similar cases of birds following dolphins to potentially enhance their foraging success. Observations in the Hauraki Gulf suggest that associations were deliberate and intentional. Birds often ceased their random flight and headed directly for the focus of dolphin activity. Gannets would also circle directly above travelling groups of dolphins. Fish were apparently herded by the dolphins into a dense ball that remained just below the sea surface and thus within reach of the birds. The formation of such dense, almost spherical shoals by the prey fish, making predation so easy for dolphins, would seem to be a response of the fish to the threat from underwater rather than from above. In conclusion, the feeding associations witnessed were formed by the action of seabirds joining a group of feeding dolphins, seeking to benefit from the resulting concentrated fish and fish debris. The impact of the seabirds on the number of fish available was unquantified, yet observations suggest that the seabirds had a negligible impact on the dolphins, as the two species foraged simultaneously for significant period of time. Therefore, no disadvantage to either group was apparent and the relationship is probably commensal, i.e., beneficial in one direction only. However, in the case of large gannet flocks, the relationship may be regarded as kleptoparasitic.

4.6.2 Bryde's or like-Bryde's whale associations

Bryde's whales are among the largest predators on earth, yet little is known about their foraging behaviour at depth (Reeves et al., 2002). These whales obtain their prey by lunge-feeding, an extraordinary biomechanical event where a large amount of water and prey are engulfed and filtered (Reeves et al., 2002; Arnold et al., 2005; Goldbogen et al., 2006).

When dolphins were foraging in the vicinity of a whale, there was a high probability that the whale would follow the dolphin group in pursuit of a foraging opportunity. Whales were often observed tracking behind dolphin groups as they herded prey species. Once the dolphins had corralled the prey, whales were then recorded lunge feeding through the centre of the feeding frenzy of dolphins. When dolphins were not foraging, whales in the vicinity did not approach closer to the dolphin group. It was evident that Bryde's or like-Bryde's whales in the Hauraki Gulf were selective towards their

interaction with common dolphins and appeared to make obvious decisions about using the foraging dolphins for feeding opportunities.

Clua and Grosvalet (2001) proposed a model to describe the mixed-species feeding aggregations between common dolphins and tuna. It comprised of four stages: a preparation phase, an intensification phase, a mature phase, and a dispersion phase. In the preparation phase, common dolphins concentrate the prey fish with rapid circular movements. Intensification begins with the structuring of the 'bait ball' with a few dolphins foraging on the periphery and shearwaters foraging at the surface. At the mature phase, giant tuna penetrate the ball with vertical trajectory while dolphins scattered. Finally in the dispersion phase, the ball has diminished, with some dolphins continuing to foraging on the terminal ball while most predators disperse. In this study, whales appeared to lunge feed at the mature phase, when potentially the concentration of prey fish was optimal. One or two lunges by a whale through the aggregation appeared to destroy the school of prey, and the hunt tended to break up. Thus, the involvement of the Bryde's or like-Bryde's whale in Hauraki Gulf mixed-species feeding aggregations with common dolphins was only brief, yet potentially had a significant impact on foraging behaviour. It is unlikely that dolphins benefit from this association, and that the relationship is kleptoparasitism. Based on the sheer volume of the throat pouch of a baleen whale (Plate 4.1), the whale would be able to consume the entire school of fish, which had been carefully herded by common dolphins - in a single gulp. A whale lunging through the dolphin group had a significant impact on common dolphin behaviour. After a lunge feeding event, dolphins were less likely to engage in herding or feeding activity, and were more likely to deep dive or be in a non-foraging state. Deep diving may be an attempt by the dolphins to corral or capture the remains of the prey. It was obvious that once a whale had lunged through the aggregation, foraging by the dolphins ceased shortly after.

As a large baleen whale, Bryde's whales face extraordinary consequences of an extreme body size (Calder, 1984). Mechanical principles predict that large body size will decrease agility and manoeuvrability (Webb & de Buffrenil, 1990). To circumvent these effects, balaenopterid foraging behaviour incorporates the selection of dense aggregations of small prey (Weihs & Webb, 1983) and increased attacking speed during lunges (Goldbogen et al., 2006). Considering their high metabolic demands, it is therefore reasonable to expect that Bryde's whales might regularly exploit common dolphin foraging behaviour in order to maximise their foraging efforts in a single lunge feeding event. Results also showed that dolphins spent more time herding in the



Plate 4.1 A Bryde's whale vertically lunge feeding in association with common dolphins in the Hauraki Gulf, showing size of throat pouch. Note the rostral ridges confirming the species as Bryde's whale.

presence of whales, suggesting that potentially whales may approach dolphin groups which appear to bring a high foraging benefit (i.e., the longer dolphins spent herding, the more prey that may potentially be schooled).

Whales' initiation of feeding with dolphins does not necessarily provide evidence that they 'seek' dolphins out, considering that the foraging range of different species may overlap when food is abundant and available. However, non-foraging behaviour by dolphins was noticeably higher in the absence of whales. This suggests that whales may take advantage of the ability of the dolphins to locate food in the Hauraki Gulf and that these encounters may not be causal, especially when considering the amount of time spent by whales following dolphins during herding before the commencement of feeding activities. Whales were recorded tracking behind foraging dolphins for up to one and a half hours. This implies that the relationship between whales and common dolphins was deliberate, and that whales may take advantage of the superior ability of dolphins to concentrate prey. Furthermore, dolphins use echolocation as a principal means of locating prey, whereas baleen whales are presumed to rely mostly on their vision (Norris, 1969). Whales may have a better chance of finding resources that are patchily distributed in the open ocean by exploiting the more sophisticated food-finding ability of dolphins. Kennedy et al. (2001) proposed that the strongest environmental cue for foraging in right whales was the density of prey within small, exploitable patches in the whale's immediate vicinity. It was presumed that feeding is the principal underlying drive in a right whale's decision making, as well as other factors (e.g., reproduction and social considerations), and movements of whales reflected adaptive responses to the distribution of prey (Kennedy et al., 2001). Unlike most baleen whales, Bryde's whales are generally considered to be non-migratory. As a consequence, they do not have access to abundant prey (such as, krill) found in the sub-Antarctic waters. Given the potential residency of Bryde's whales in the Hauraki Gulf (N. Wiseman, pers. comm.), their potentially high energetic demands, and the scattered prey distribution within the Gulf waters, common dolphins may be a critical species for the Bryde's whale.

Baleen whales have been observed interacting with dolphins, although these associations tend to be viewed as opportunistic and brief. Stockin and Burgess (2005) reported the opportunistic feeding of a humpback whale with bottlenose dolphins off the east coast of Australia. Minke whales and common dolphins were observed together in Santa Monica Bay, California, although no reason for their association was given (Bearzi, 2005). Minke whales have previously been recorded within the Hauraki Gulf,

although relatively infrequent, and not in the presence of common dolphins (Stockin, unpublished data). Neumann and Orams (2003) reported common dolphins in association with a sei whale (*Balaenoptera borealis*), two encounters with minke whales (*Balaenoptera acutorostrata*) and a single encounter with Bryde's whale lunge feeding with feeding common dolphins in the Bay of Plenty, New Zealand. This is the first study to explicitly quantify Bryde's whales seeming to deliberately spend time tracking dolphins for a foraging benefit. Furthermore, the significance of occurrence of whales using common dolphins in the Hauraki Gulf, concurs with that reported by Stockin (unpublished data), and when compared to findings in the Bay of Plenty (Neumann & Orams, 2003), suggest that the Hauraki Gulf Marine Park is a significant foraging area in which these two species cohabit.

There is much that remains unknown about the habits of Bryde's whales. Bryde's whales are currently listed as 'data deficient' by the IUCN Red List of Threatened Animals (IUCN, 1996). In New Zealand, Bryde's whales are considered 'nationally critical' under the Marine Mammal Action Plan (Suisted & Neale, 2004). Considering the conservation status of Bryde's whales, this study indicates that broad regional changes in common dolphin abundance, might be expected to profoundly impact the Hauraki Gulf population of Bryde's whales. This study attempts to set forth a hypothesis concerning the strength of association between common dolphins and Bryde's whales. Questions relative to the possibility that Bryde's whales might frequently use common dolphins to obtain food, may be critically important in managing the Hauraki Gulf.

4.6.3 Other species associations

The role of other underwater predators in mixed species aggregations was not addressed in this study. Since observations were restricted to the surface, the investigation of other species interactions below the surface was not possible. Observations of recreational vessels fishing near mixed-species aggregations involving common dolphins provide some insight and raises questions for future research.

Recreational fishermen in the Hauraki Gulf often locate dolphin and gannet aggregations, which they call 'work-ups' or 'boil-ups', as potentially good fishing spots. Using hook and line, fishermen can readily catch John dory (*Zeus faber*), red gunard (*Chelidonichthys kumu*) and more frequently snapper (*Pagrus auratus*) around 'work-ups' of dolphin and birds (M. Brown, pers. comm.). During this study, snapper were observed being caught by fishermen anchoring very near mixed-species feeding aggregations with common dolphins. It is reasonable to predict, knowing the well-documented interaction between dolphins and tuna fish (Au, 1991; Pitman & Au, 1992; Das et al., 2000; Clua & Grosvalet, 2001), that common dolphins feeding in the Hauraki Gulf would attract a variety of predatory fish, including snapper.

Snapper has an extremely varied diet and appear to occupy a very broad feeding niche in Hauraki Gulf (Godfriaux, 1969; Colman, 1972). Godfriaux (1969) recorded 99 food items from 10 phyla in the diet of snapper caught in the Hauraki Gulf, with crustaceans, polychaetes, echinoderms, molluscs, teleost fish formed the main snapper food groups. Snapper feed on prey proportionate to their size. Snapper less than 14 cm long fed mainly on polychaetes and crustaceans (mysids and megalopa larvae), those 15-40 cm long on brachyurans and echinoderms. Large snapper, over 40 cm long fed less on polychaete worms, phiuroids and mall crustacens, and fed more on echiurids, crabs, hermit crabs, and particularly molluscs and fish (Godfriaux, 1969; Colman, 1972). Fish occurred in the diet of about 7% of all snapper examined in the Hauraki Gulf, mainly in the larger snapper (Colman, 1972). Snapper fed on both demersal and pelagic fish. The pelagic fish identified were pilchard (*Sardinops neopilchardus*), anchovy (*Engraulis australis*) and jack mackerel (*Trachurus novaezelandiae*) (Colman, 1972). Whether snapper were feeding on pelagic fish in mid water or near the bottom is unknown, and no literature makes reference to their association with feeding dolphins.

The feeding ecology of snapper suggests that these fish, at a medium to large size would be capable of taking advantage of small schooling fish corralled by common dolphins. The same prey fish of dolphins are part of the snapper diet, yet it is uncertain whether snapper are capable of eating live, undamaged fish, or whether they feed on injured or damaged fish from the dolphin-gannet feeding frenzy. Aquarists suspect that snapper at 27 cm (legal fishing size) would be able to at least bite at and possibly ingest half a small schooling fish, such as pilchard, with larger snapper at sizes of over 35 cm being capable of potentially eating the entire prey fish (Senior aquarist, Kelly Tarlton's Aquarium, pers. comm.). Recreational fishermen routinely use pilchards for bait when targeting large snapper (M. Francis, pers. comm.). Snapper feed on the same species of small, schooling fish as those targeted by common dolphins (Neumann & Orams, 2003), and those snapper associating with dolphins are potentially much larger than in other schools. This relationship was also found in tuna, where fish associating with feeding dolphins were much larger than tuna found in other types of aggregations (Ballance et al., 2006). The presence of snapper near 'work-ups' and the known lack of specialisation in the diet of snapper suggest that snapper may use mixed-species feeding aggregations for feeding opportunistically.

There exists the possibility that common dolphins may also take advantage by opportunistically feeding on snapper in the feeding frenzy. A study on bottlenose dolphins in the Bahamas observed dolphins following and feeding on lane snapper (*Lutjanus synagris*) inshore at particular times of the year (Rossbach & Herzing, 1997). Lane snapper is in a different family (Family Lutjanidae) to the snapper found in New Zealand waters (Family Sparidae). But while the two species are unrelated, they may be morphologically and ecologically similar (L. J. Paul and M. Francis, pers. comm.). While the potential of ingesting snapper during a feeding aggregation exists, further investigation into common dolphin diet in the Hauraki Gulf needs to be conducted.

Ultimately, understanding the dimension of underwater interactions, the species involved and their role in mixed-species aggregations requires further investigation, and results will undoubtedly show a further complexity to this phenomenon in the Hauraki Gulf.

4.7 *Ecological significance and conservation perspective of this study*

To date, conservation work has generally employed a triage approach, in that species receive protection only after it has been demonstrated that there is a pressing need for such protection (Hooker & Gerber, 2004). Many of the conservation efforts around the world, therefore, focus on threatened or rare species (Soulé et al., 2005). This focus has driven much of the legislation on conservation, which often lists species as a mechanism to initiate efforts to protect them (e.g., the United States *Endangered Species Act 1973* and the United States *Marine Mammal Protection Act 1972*).

In New Zealand, the *Marine Mammal Protection Act 1978* provides conservation, protection and management of marine mammals within New Zealand waters and within New Zealand fisheries. The *Marine Mammal Action Plan (2004)* serves to underpin the *Marine Mammal Protection Act* and provides specific outputs with regard to the conservation of marine mammals that the Department of Conservation can systematically work to achieve (Suisted & Neale, 2004). As highlighted in the Action Plan, the main aim and focus of marine mammal conservation in New Zealand is a species-led approach. The Action Plan identifies species that are threatened with extinction or that have been depleted or otherwise adversely affected by human activities or unusual natural events, and lists these marine mammal species as a priority for conservation. With advancing science in the discipline of conservation biology, and as ecologists further understand many of the ecosystem consequences of species interactions and community dynamics (Terborgh et al., 1999), it is warned that protective legislations and action plans are not reflecting the many advances in population biology and community ecology (Soulé et al., 2005). Ultimately, there has been an increasing emphasis on the need to use ecosystems, communities, and assemblages, rather than single species, as the basis for conservation. The results of this study highlight such a case for the common dolphin in the Hauraki Gulf Marine Park ecosystem.

Common dolphins play a role as a top predator in the Hauraki Gulf marine ecosystem. The foraging behaviour of common dolphins suggests that they are a strongly interactive species that contributes substantially to the foraging success of other species. Such interactions may suggest that common dolphins significantly contribute towards the maintenance of ecological and species diversity. The idea that some species interact more strongly than others is not new. Paine (1966) first used the term

'keystone' for particularly strong interactors: those, for example, whose activities maintain species and habitat diversity and whose effects are disproportionate to their abundance (Kotliar et al., 1999). Whether or not the ecological role of the common dolphin in the Hauraki Gulf warrants the label of 'keystone' species, its interactions with seabirds and the nationally critical Bryde's whales appears to be ecologically significant. Soulé et al. (2005) proposes that population densities of strongly interactive species must not be permitted to fall below thresholds for ecological effectiveness, and that the geographical ranges of such species should be as large as possible (Conner, 1988; Soulé et al., 2005). To achieve these goals, strongly interactive species at least need to be recognised by managers. In the Marine Mammal Action Plan for 2005-2010, site plans are recognised for the management of discrete sites or areas important to marine mammals. Marine mammal site plans are intended to give a holistic approach, addressing a wider range of marine mammal issues. At present, common dolphins are not listed as a management concern in the Hauraki Gulf site plan nor in the New Zealand Marine Mammal Action Plan.

Conservation management is not only important when species hover on the edge of extinction. Strongly interactive species in abundance may prove to be pivotal for the survival of other species and in maintaining the health and viability of whole ecosystems. Policymakers, managers and guiding action plans should take a holistic approach (rather than traditional, single-species recovery models) that provide recognition to both the species of concern and to the entire ecosystem.

Chapter Five: CONCLUSIONS and IMPLICATIONS FOR FUTURE RESEARCH

5.1 *Summary*

This thesis provides important insights into common dolphins that forage in the Hauraki Gulf, off the east coast of Auckland, New Zealand. Its main objective was to contribute to the understanding of the foraging ecology of the species, through the investigation of four general research questions outlined in *section 1.7*. The significant findings of this research showed that:

- The Hauraki Gulf is an important foraging area for common dolphins, with foraging behaviour frequently observed in dolphin groups.
- Common dolphin foraging behaviour is flexible, with several different foraging strategies identified. Foraging strategies tend to be cooperative and dynamic.
- Larger common dolphin groups spent more time devoted to foraging activity, and formed tightly aggregated groups.
- Dolphin groups sighted in areas distant from Auckland city and its catchments, spent a greater proportion of their time foraging.
- Herding was a significant phase in common dolphin foraging behaviour.
- Surface behaviours and fission-fusion events of common dolphins were synchronous with foraging in the group.
- Seabirds and Bryde's whales were frequently associated in mixed-species feeding aggregations with common dolphins, and these species take advantage of the superior foraging ability of dolphins.
- Behaviour of Australasian gannets and whales strongly coincided with that of the foraging common dolphin group.
- Common dolphins are a strongly interactive species in the Hauraki Gulf Marine Park.
- Common dolphins are potentially a 'keystone' species in the Hauraki Gulf Marine Park with several other species, including the critically threatened Bryde's whales, benefiting from their presence in abundant numbers.

5.2 *Future research*

This study has provided background information about the foraging behaviour and ecology of common dolphins in the Hauraki Gulf. However, it should be highlighted that observations were restricted to the summer/autumn season, and longer-term investigations throughout the year are needed to gain further insight into the potential seasonal changes in foraging behaviour. Future research should continue to collect data on the foraging activity of common dolphins across New Zealand, with particular attention to information on mixed-species associations. Other potential areas for expanding our knowledge on common dolphins include:

5.2.1 *Underwater foraging investigation*

The correspondence between surface (observable) and subsurface (often unobservable) behaviour is unknown for most studies of cetaceans. This study focused on understanding the foraging behaviour of common dolphins at the surface. However, the marine environment poses a third dimension of depth and therefore, with regards to marine mammal behaviour, observations at the surface are only a fraction of their activity. Synchronous diving was shown to be an important part of foraging for common dolphins in the Hauraki Gulf. Underwater observations are fraught with difficulties and challenges, such as poor visibility and keeping up with the dolphin group. However, previous studies have had success in documenting underwater activity when the dolphins were carouselling the schooling prey, using underwater video recording (Neumann & Orams, 2003) or using observers free-diving (Clua & Grosvalet, 2001). Implementing similar techniques during mixed-species aggregations in the Hauraki Gulf may provide insight into the subsurface behaviour of common dolphins, prey species identification, density of prey, and potentially identify any other marine predators involved in the aggregation, such as snapper, sharks or other predatory fish.

5.2.2 *Nocturnal foraging investigation*

Research on the diets of cetaceans can contribute to the information on predator-prey relationships in the marine food web ecosystem. Linking diet with the ecology of prey species, information on prey distribution, and habitat, can in turn, further provide new insights regarding cetacean distribution, movements, and trophic relationships.

Unfortunately, observations were not feasible during night-time hours to investigate the hypothesis that common dolphins feed on prey nocturnally, such as squid. Stockin et al. (2005) found the remains of arrow squid (*Nototodarus* sp.) as the most frequently recorded prey species in the stomachs of eight post-mortem carcasses of common dolphin from the Hauraki Gulf. While examining nocturnal activity budgets of common dolphins would be interesting, conducting field observations at night would be challenging and restrictive. Conducting field observations of dolphins at night would be challenging and restrictive. Alternative methods to address the question of nocturnal predation include continued dietary analyses of necropsied common dolphins. A problem with dietary studies based on stomach contents of stranded animals is the inherent delay between feeding and the stranding event. Collection of faecal samples is another means of investigating diets (Smith & Whitehead, 2000), however, collection of faecal samples from dolphins is challenging (Hooker et al., 2001). Furthermore, both stomach-content and faecal analyses provide detail on only the most recent few meals and may be biased because of the increased retention of certain less digestible dietary items (such as fish otoliths and squid beaks) (Smith & Whitehead, 2000). Recently, two new techniques (fatty acid signature analysis and stable-isotope analysis) have been used to assess aspects of diet using blubber and skin samples, respectively (Iverson et al., 1997; Iverson, 1993). Interpretation of diet using these analyses is based on tissue samples that reflect the average composition of food resources that have been assimilated over periods of days to months (Tiezen, 1978; Kirsch et al., 1998). There is the potential to use biopsy samples of beach-cast or by-caught dolphins to investigate trophic relationships between dolphins and their prey using these techniques. Information attained may provide useful information about sources and processes within an ecosystem (Hooker et al., 2001; Davenport & Bax, 2002).

5.2.3 *Linking predator and prey distribution*

Future work should focus on collecting detailed information on the distribution patterns of prey within the study area to allow direct comparison between predator and prey distribution. The relationship between search patterns and the distribution of food has rarely been documented for large free-ranging animals (Ward & Saltz, 1994). In marine systems, the spatial distribution of fish prey is poorly known at small temporal and spatial scales, making comparison between predator search effort and prey density extremely difficult. Marine predators also mainly forage beneath the surface, so that observations of feeding are rare (Heithaus et al., 2002). Quantitative analysis of

movement paths can therefore, provide an important technique to overcome these challenges and improve our understanding of the foraging strategies of marine predators.

5.2.4 Foraging specialisations in individuals

Much remains to be examined regarding group organisation of social dolphin species, such as the common dolphin. Group-living cetaceans may rely on each other for survival, but the costs and benefits of group living are unlikely to be shared equally among all group members. Researchers are now beginning to identify the individual's role in foraging strategies (Mann & Sargeant, 2003; Sargeant et al., 2005). This study encourages future studies of foraging variation at the individual level that can better address roles of specialisation, niche partitioning and habitat use, life history and social influences. Such studies are critical to understanding the importance of foraging areas to dolphins, species often heavily influenced by coastal development and habitat loss. It is also possible that a division of labour with role specialisation will also turn out to be more prevalent in group-hunting marine mammals (Gazda et al. 2004), such as common dolphins than in terrestrial mammals.

5.2.5 Acoustic communication during foraging

The acoustic ecology of foraging bottlenose dolphins was recently investigated by Nowacek (2005). Paul (1969) made the first acoustic recordings of common dolphins in the Hauraki Gulf. His opportunistic recordings and observations suggested that the common dolphins were attracted to the research fishing vessel by the noise of the echo-sounder equipment being used. During this study, observations of highly coordinated and cooperative foraging behaviour, raises questions about communication within the dolphin group. Acoustic recordings using a hydrophone were made during this study. Unfortunately, time did not permit the analysis of acoustic recordings to be attempted for inclusion in this thesis. Recordings were made during foraging and non-foraging behaviours of 20 focal group follows. Future analysis of these data is planned. Methods of analysis for acoustic recordings will be based on Ansmann (2005). Analysis of the resulting spectrograms will involve counting the number of whistles per time period, and recording whistle type and frequency range. These data will then be matched with the corresponding behavioural observations.

Such analyses will provide insight into the acoustic behaviour of common dolphins and help improve understanding its role during foraging.

5.2.6 Potential human interactions with foraging

Common dolphins are targets for tourism charters in the Hauraki Gulf. There is evidence that other cetacean species are negatively affected by such tourism operations (Corkeron, 1995; Constantine, 1995; Lusseau, 2003; Lusseau, 2006). Investigations are currently being undertaken to understand the effect of tourism vessels on common dolphins groups in the Hauraki Gulf (Stockin, unpublished data). Around New Zealand, by-catch of common dolphins associated with the jack mackerel (*Trachurus novaezelandiae*) fishery has also been reported (Slooten & Dawson, 1995). Stockin et al. (2005) found evidence of common dolphins entangled in gill nets in the Hauraki Gulf. In New Zealand, marine farms also have the potential to affect dolphin foraging in the coastal environment. Yet, as cautioned by Markowitz et al. (2004b) this issue has been largely omitted from aquaculture management models and data on the subject are minimal. Markowitz et al. (2004b) examines the potential overlap between dusky dolphin habitat use and New Zealand's growing green-lipped mussel farming industry. The Hauraki Gulf is a significant area for commercial and recreational fishing operations, and the Firth of Thames (south-east Hauraki Gulf) is considered a rapidly growing area for marine farming (Anon., 2006). Future researchers should consider investigating the interactions between commercial fisheries and recreational fishing practices, and foraging common dolphins in the Hauraki Gulf.

5.2.7 Importance as a strongly interacting species

Mixed-species feeding aggregations are a frequent occurrence in the Hauraki Gulf, and this phenomenon centres on the foraging behaviour of common dolphins. Future research should aim to identify the relative importance of these feeding aggregations in the foraging behaviour of Australasian gannets and Bryde's whales. The methodology of the present study focused on observations surrounding the common dolphins. Continued work should quantify these interactions from the perspective of the other species involved, by asking questions such as, how often gannets and whales feed with common dolphins, and by identifying the relative importance of dolphins to the foraging ecology of these species. Understanding the interaction strength among

species in the Hauraki Gulf ecosystem will assist management goals. This is particularly crucial for the Bryde's whale, currently listed as a critically threatened species in New Zealand. The Hauraki Gulf has a population of approximately 200-300 Bryde's whales (N. Wiseman, pers. comm.). Future research may potentially address the hypothesis that their presence within the Gulf may be attributed to their feeding association with common dolphins. Interspecific interactions of strongly interactive species have been shown to maintain diversity and resilience of an ecosystem (for review Soule et al. 2005). In the current state of the environment, where increasing numbers of species and ecosystems are depleting and degrading, it's more important than ever that science investigates species interaction webs (not just the threatened species in isolation), so that this knowledge can then be implemented in environmental policy and management.

5.3 *Conclusion*

Achieving the objectives outlined at the beginning of this thesis has lead to an increase in our understanding of common dolphin foraging ecology in the Hauraki Gulf. This has resulted in an improved appreciation of the importance of the foraging strategies used by common dolphins in order to attain food, a very fundamental concept to species survival.

This study makes a contribution to the biology of a poorly understood species, which has largely been neglected from a conservation management point of view in New Zealand.

It is hoped that this study inspires further research, and that such science will underpin environmental policies and management which will contribute to the future health and viability of cetacean populations in New Zealand.

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Appendix 1

List of definitions used to record environmental parameters.

Environmental parameter		Definition
Weather	Fine	predominantly sunny, no/few clouds
	Overcast	cloudy/grey with no visible sunshine
	Showers	light rain on and off with limited visibility
	Rain	heavy/continuous rain with dark skies
	Hail	hail showers/storms
	Fog	fog conditions
Cloud cover	0 - 8 oktas	Determined by how much of the sky is covered by clouds. The scale ranges from 0-8 oktas. If the entire sky is filled with clouds, then the cloud cover is 8 oktas.
Beaufort sea state (force)	0	smooth and mirror-like, wind calm (0-1kt)
	1	light ripple, light airs (1-3kt)
	2	small wavelets not breaking, light breeze (4-6kt)
	3	scattered whitecaps, gentle breeze (7-10kt)
	4	small waves, frequent whitecaps, moderate breeze (11-16kt)
	5	moderate waves, many whitecaps, fresh breeze (17-21kt)
	6	all whitecaps, some spray, strong breeze (22-27kts)
Visibility	Excellent	Surface water calm with no sun glare, or other environmental factors impeding ability to sight animals (visibility > 5 km).
	Very good	May be slightly uneven lighting conditions, or chop on water, but still relatively easy to sight animals (visibility > 5 km).
	Good	Light chop with scattered whitecaps, swell (2-4 m), or some glare, or other impediment (e.g. haze) in ≤10% of study area, dolphins can still be detected fairly easily.
	Fair	Choppy waves fairly frequent whitecaps, low-light conditions (e.g. heavy overcast, dawn, dusk), swell 4-6 m, or sun glare in 50% of study area, some animals likely to be missed.
	Poor	Numerous whitecaps, sun glare or haze in > 50% of study area, or swell >6m, rainy, foggy, impeding ability to sight animals, many animals likely to be missed.
	Unacceptable	Conditions > 6 Beaufort force, glare, haze, or other visibility impediment in 75% of study area, detection of animals unlikely unless observer is looking directly at place of surfacing.

Appendix 2

Dolphin sighting datasheet used in this study.

Survey period _____

HAURAKI GULF COMMON DOLPHIN PROJECT

Date _____	START time _____	Weather							
Observers _____	GPS waypoint _____	Beaufort _____							
	Water depth _____ m	Visibility <table border="1" style="font-size: small; text-align: center;"> <tr><td>exclnt</td><td>v.gd</td><td>gd</td></tr> <tr><td>fair</td><td>poor</td><td>unacpt</td></tr> </table>	exclnt	v.gd	gd	fair	poor	unacpt	
exclnt	v.gd	gd							
fair	poor	unacpt							
	SST _____ °C	Cloud cover _____ / 8							
		Tide state _____							

on approach...

Group size _____	—	1-10	10-20	20-30	30-50	50-100	100-200	>200										
Behav state _____																		
Dispersion _____	tight mod loose	Group composition: <table border="1" style="font-size: small; text-align: center;"> <tr><td>Ad</td><td>SubA</td><td>Juv</td><td>Calf</td><td>New</td></tr> <tr><td> </td><td> </td><td> </td><td> </td><td> </td></tr> </table>							Ad	SubA	Juv	Calf	New					
Ad	SubA	Juv	Calf	New														
Direction _____		<table border="1" style="font-size: small; text-align: center;"> <tr><td>AusGt</td><td>Fleshy</td><td>Buller</td><td>WFTrn</td><td>BryW</td></tr> <tr><td> </td><td> </td><td> </td><td> </td><td> </td></tr> </table>							AusGt	Fleshy	Buller	WFTrn	BryW					
AusGt	Fleshy	Buller	WFTrn	BryW														
Other assoc spp: _____		No.: _____																
		Behav: _____																

at the end...

Group size _____	—	1-10	10-20	20-30	30-50	50-100	100-200	>200										
Behav state _____																		
Dispersion _____	tight mod loose	Group composition: <table border="1" style="font-size: small; text-align: center;"> <tr><td>Ad</td><td>SubA</td><td>Juv</td><td>Calf</td><td>New</td></tr> <tr><td> </td><td> </td><td> </td><td> </td><td> </td></tr> </table>							Ad	SubA	Juv	Calf	New					
Ad	SubA	Juv	Calf	New														
Direction _____		<table border="1" style="font-size: small; text-align: center;"> <tr><td>AusGt</td><td>Fleshy</td><td>Buller</td><td>WFTrn</td><td>BryW</td></tr> <tr><td> </td><td> </td><td> </td><td> </td><td> </td></tr> </table>							AusGt	Fleshy	Buller	WFTrn	BryW					
AusGt	Fleshy	Buller	WFTrn	BryW														
Other assoc spp: _____		No.: _____																
		Behav: _____																

FINISH time _____	GPS waypoint _____	Weather							
		Beaufort _____							
		Visibility <table border="1" style="font-size: small; text-align: center;"> <tr><td>exclnt</td><td>v.gd</td><td>gd</td></tr> <tr><td>fair</td><td>poor</td><td>unacpt</td></tr> </table>	exclnt	v.gd	gd	fair	poor	unacpt	
exclnt	v.gd	gd							
fair	poor	unacpt							
	Water depth _____ m	Cloud cover _____ / 8							
	SST _____ °C	Tide state _____							

Focal data? <table border="1" style="font-size: small; text-align: center;"> <tr><td>Y / N</td></tr> </table>	Y / N	No. pages: _____
Y / N		
Photos? <table border="1" style="font-size: small; text-align: center;"> <tr><td>Y / N</td></tr> </table>	Y / N	IMG_# _____
Y / N		
Prey sample? <table border="1" style="font-size: small; text-align: center;"> <tr><td>Y / N</td></tr> </table>	Y / N	Species ID? _____
Y / N		
Vocals heard? <table border="1" style="font-size: small; text-align: center;"> <tr><td>Y / N</td></tr> </table>	Y / N	Acoustic recording # _____
Y / N		

COMMENTS:

TAIL SLAP	BREACH
HEAD SLAP	LEAP
SIDE SLAP	KERPLUNKING
PREY CAPTURE	DEFECATION
FLUKE-UP DIVE	

Appendix 3

Focal group follow datasheet used in this study.

Date:
Sighting No.:
Page No.:

BW=body; SS=sooty; BS=bulwer; WT=tern;
BP=penguin; GU=seagull
F=following; C=circling; D=diving; R=resting;
FB = following back

Time	State @	Strategy @	Dispers (1-3)	Compass Direction	Grp formation @	Aust. Gannets		Assoc Spp. @		Calf position @	Split / Join @	Work Up? Y / N	Dispers factor	Swim style (notes)	Surfac (%)
						No. (0-4)	Behav. @	Assoc Spp. @	No.						
	F Tv R M S	HSp W/F Lab Car ?	1 2 3		◆ Ab V Ln U ?			BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:02	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:04	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:06	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:08	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:10	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:12	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:14	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:16	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:18	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:20	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:22	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:24	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:26	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:28	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	
00:30	F Tv R M S		1 2 3					BW SS BS WT BP GU					1 2 3	□ dive; □ slow swim; □ accelerate swim; □ porpoise; □ bow-ridin	

Appendix 4

Table of statistical results for tests of normality and equal variance, and the parametric and non-parametric test applied in this study.

Data	Normality test	Equal variance test	Statistical test	Test statistic (F, H, U, r^2)	df	n	P	Post-hoc comparison
temperature, month	fail	P = 0.002	-	26.80	3	59	<0.001	Dunn's test
depth, Hauraki Gulf region	fail	P = 0.036	-	25.10	3	59	<0.001	Dunn's test
depth, distance from shore	fail	P = <0.001	-	0.29	57	59	<0.001	-
behavioural states	fail	P = <0.05	-	167.60	4	59	<0.001	Dunn's test
foraging behaviour, time of day	pass	P = >0.05	pass	1.18	4	59	0.329	n/a
foraging behaviour, tidal state	pass	P = >0.05	pass	1.09	3	59	0.361	n/a
foraging behaviour, temperature	pass	P = 0.523	pass	0.03	57	59	0.168	-
foraging behaviour, depth	pass	P = 0.536	pass	0.01	57	59	0.54	-
foraging behaviour, distance	pass	P = 0.349	pass	0.02	57	59	0.335	-
foraging behav., Hauraki Gulf region	pass	P = >0.05	pass	0.40	3	59	0.756	n/a
foraging behav., group size	pass	P = >0.05	pass	3.00	4	59	0.026	Fisher's LSD test
foraging behav., calf presence	pass	P = >0.05	pass	1.54	1	59	0.219	n/a
foraging phases	pass	P = >0.05	pass	15.66	2	59	<0.001	Fisher's LSD test
herding time, distance travelled	fail	P = 0.043	pass	0.86	45	47	<0.001	-
swimming dir., Hauraki Gulf region	pass	P = >0.05	pass	4.27	3	59	0.009	Fisher's LSD test
herding behav., temperature	pass	P = 0.244	pass	0.02	57	59	0.332	-
diving behaviour, temperature	fail	P = 0.039	pass	0.01	57	59	0.673	-
feeding behaviour, temperature	pass	P = 0.167	pass	0.04	57	59	0.123	-
herding behaviour, depth	pass	P = 0.683	pass	0.00	57	59	0.644	-
diving behaviour, depth	pass	P = 0.489	pass	0.06	57	59	0.062	-
feeding behaviour, depth	pass	P = 0.337	pass	0.09	57	59	0.019	-
herding behav., Hauraki Gulf region	pass	P = >0.05	pass	0.56	3	59	0.646	n/a
diving behav., Hauraki Gulf region	fail	P = 0.018	-	7.12	3	59	0.068	n/a
feeding behav., Hauraki Gulf region	fail	P = 0.01	-	15.17	3	59	0.002	Dunn's test
herding behaviour, group size	pass	P = >0.05	pass	2.69	4	59	0.041	Fisher LSD test
diving behaviour, group size	pass	P = >0.05	fail	7.24	4	59	0.124	n/a
feeding behaviour, group size	pass	P = >0.05	pass	2.05	4	59	0.101	n/a
herding behaviour, calf presence	pass	P = >0.05	pass	4.42	1	59	0.04	n/a
diving behaviour, calf presence	fail	P = 0.043	-	0.33	1	59	0.568	n/a
feeding behaviour, calf presence	fail	P = 0.002	-	0.43	1	59	0.513	n/a

Appendix 4 continued

Table of statistical results for tests of normality and equal variance, and the parametric and non-parametric test applied in this study.

Data	Normality test	Equal variance test	Statistical test	Test statistic (F, H, U, r^2)			df	n	P	Post-hoc comparison
feeding behaviour, water depth	fail	P = 0.035	pass	P = 0.17	Pearson's correlation	0.09	57	59	<0.001	-
herding behaviour, tight dispersion	fail	P = 0.021	-	-	Kruskal-Wallis ANOVA	10.44	4	59	0.034	Dunn's test
herding behav., mod. dispersion	fail	P = 0.032	-	-	Kruskal-Wallis ANOVA	7.59	4	59	0.108	-
herding behav., loose dispersion	fail	P = 0.040	-	-	Kruskal-Wallis ANOVA	5.34	4	59	0.254	-
fission freq., forage v non-forage	fail	P = < 0.05	-	-	Mann-Whitney test	1859.00	1	59	0.241	n/a
fission freq., behav. states	fail	P = < 0.05	-	-	Kruskal-Wallis ANOVA	18.85	1	59	< 0.001	Dunn's test
fusion freq., forage v non-forage	fail	P = < 0.05	-	-	Mann-Whitney test	2072.50	1	59	0.011	Dunn's test
fusion freq., behav. states	fail	P = < 0.05	-	-	Kruskal-Wallis ANOVA	6.48	1	59	0.011	Dunn's test
noisy behav freq., forage v non-fora	fail	P = < 0.05	-	-	Mann-Whitney test	1844.00	1	59	0.362	n/a
fusion freq., behav. states	fail	P = < 0.05	-	-	Kruskal-Wallis ANOVA	12.90	1	59	0.012	Dunn's test
gannet flock size, feeding behav.	fail	P = < 0.001	-	-	Kruskal-Wallis ANOVA	14.30	4	46	0.006	Dunn's test
gannet follow, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	30.08	22	3	<0.001	Dunn's test
gannet circle, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	25.12	34	3	<0.001	Dunn's test
gannet dive, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	44.97	35	3	<0.001	Dunn's test
gannet rest, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	17.75	33	3	<0.001	Dunn's test
whale follow, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	16.40	3	25	<0.001	Dunn's test
whale lunging, dolphin behaviour	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	36.00	3	15	<0.001	Dunn's test
whale no interaction, dolphin behav.	fail	P = > 0.05	-	-	Kruskal-Wallis ANOVA	10.81	10	15	0.013	Dunn's test
gannet following, gannet diving	pass	P = 0.401	fail	P = < 0.001	Spearman's correlation	0.49	44	46	<0.001	-
whale following, whale lunges	fail	P = < 0.001	pass	P = 0.36	Spearman's correlation	0.04	18	20	0.421	-