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

A thesis presented in fulfilment of the requirements for the degree of

Master of Science
(Zoology)

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Albany, New Zealand


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2006

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.

A handwritten signature in black ink, appearing to read 'Elizabeth A. Burgess', with a stylized, cursive script.

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 ± 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 (mean \pm s.e. = 23 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 (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 (Tarpay, 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 & Kemps, 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: 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, 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 Frantzis & 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, 2004) 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 gavia*), 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*



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

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).

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 of 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.