THE BEHAVIOUR AND ECOLOGY OF SHORT-BEAKED COMMON DOLPHINS (*Delphinus delphis*) ALONG THE EAST COAST OF COROMANDEL PENINSULA, NORTH ISLAND, NEW ZEALAND

- with a note on their interactions with humans

A dissertation presented in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
in Marine Science
at Massey University

by

Dirk R. Neumann

November 2001

This dissertation is my own composition.

All sources have been acknowledged.

No part of this work has been submitted

for another degree at Massey, or any other University.

Dirk R. Neumann

November 2001

ACKNOWLEDGEMENTS

Firstly, my deepest thanks to my chief supervisor, Senior Lecturer Dr. Mark Orams (Massey University), for his help, expertise, patience, and encouragement throughout my Ph.D. candidacy. The way in which he and his family made me feel at home in New Zealand went far above and beyond what I could have wished for. My heartfelt thanks therefore also extend to Renée, Daniel, and Brianna Orams. Thank you to my second supervisor, Dr. Liz Slooten (University of Otago) for her advice on the research project, and this thesis. Several people at Massey University deserve my thanks, especially Associate Professor John Monin, Mary Miller, Lynne Tunna, and Dr. Denny Meyer.

I am indebted to my volunteer research assistants who were (in chronological order) : Trine Baier Jepsen, Colleen Clancy, Paul Grant, Sandra Winterbacher, Jo Moore, Jodie Holloway, Birgit Klumpp, Christiane Knappmeyer, Tina Jacoby, Nikki Guttridge, Lindsey Turner, Karen Stockin, Chris Smith Vangsgaard, Aline Schaffar, Daphne Bühler, Patrice Irvine, Stefanie Werner, Fabiana Mourao, Deanna Hill, Miriam Brandt, and Johanna Hiscock.

I am grateful to Scott Baker (University of Auckland), Rochelle Constantine (University of Auckland), Kirsty Russell (University of Auckland), Mike Donoghue (Department of Conservation), Michael Uddstrom (National Institute for Water and Atmospheric Research), Ingrid Visser, Alexandra Leitenberger, Susana Caballero, Deborah Kyngdon, Sue Halliwell, Adrienne Joyce, and Vicky Powell for their help and input. A special thanks to Brett Orams for creating the fabulous diagrams illustrating dolphin behaviour. The Massey University Animal Ethics Committee was kind enough to grant permission for the genetic sampling conducted as part of this research.

Vital support for this project came from dolphin-tour operators Rod & Elizabeth Rae (Mercury Bay Seafaris, Whitianga), John Wharehoka & Karen Waite (Dolphins down under, Whakatane), Graeme Butler (Gemini Galaxseas, Tauranga), and the late Stephen Stembridge (Dolphin Explorer, Auckland).

This 3-yr research project was funded by : Massey University (MU) Doctoral Scholarship, MU College of Business research grant, MU Research Equipment Fund, MU research fund, Graduate Research

Fund (MU Department of Management and International Business), WADAP (Whale and Dolphin Adoption Project), and the Department of Conservation Science Investigation Programme. Additional financial support was provided by Konrad Kohlhammer. The support of my friends and family in Germany has also been invaluable and is greatly appreciated. I thank all of you for keeping your fingers crossed, and believing in me. Finally, let us not forget, that none of this would have been possible without the cooperation of the common dolphins, who were kind enough to allow me a glimpse into their daily lives. Thank you !

PUBLICATIONS

The following have been produced during the Ph.D. candidature, as a result of the research presented in this dissertation :

Publications in peer-reviewed journals

Neumann, D.R. (2001). Seasonal movements of short-beaked common dolphins *(Delphinus delphis)* in the northwestern Bay of Plenty, New Zealand: The influence of sea-surface temperature and "El Niño/La Niña". *New Zealand Journal of Marine and Freshwater Research, 35:,* 371-374.

Neumann, D.R. (2001). The activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquatic Mammals, 27 (2):* 121-136.

Neumann, D.R. & M.B. Orams. (2001). Feeding strategies of short-beaked common dolphins (*Delphinus delphis*), in the northwestern Bay of Plenty, New Zealand. *Marine Mammal Science,* under review.

Neumann, D.R., A. Leitenberger & M.B. Orams. (2001). Long-term tracking of common dolphins in New Zealand - a photo-catalogue of easily recognizable individuals. *New Zealand Journal of Marine and Freshwater Research,* under review.

Neumann, D.R., K. Russel, M.B. Orams, C.S. Baker & P. Duignan. (2001). The common dolphin's codpiece : A new tool for sexing *Delphinus delphis* at sea. *Aquatic Mammals,* submitted.

Other publications

January 1999-July 2001. Quarterly updates on common dolphin research in the Whale and Dolphin Adoption Project Newsletter, by D. Neumann.

April 1999. Massey University magazine, pp. 21-22 : "A passion for dolphins", by L. Granville. Article about the common dolphin research project.

March 2000. Spirits of the sea magazine, p. 3 : "Dolphins under human threat", by D. Neumann.

April 2000. New Zealand Fishing News, p. 30 : "Dolphin article irresponsible". Letter to the editor by D. Neumann.

March 2001. Marine mammals of the Bay of Plenty, by J. Berghan, edited by R. Constantine, pp. 11-16 : "Common dolphins", by D. Neumann.

Presentations at professional meetings

Neumann, D.R. 1999. Seasonal movements of short-beaked common dolphins *(Delphinus delphis)* in the northwestern Bay of Plenty, New Zealand: The influence of sea-surface temperature and "El Niño/La Niña". *13th Biennial conference on the biology of marine mammals, Wailea, Maui, Hawaii, USA, 28 November - 3 December, 1999.*

Neumann, D.R. and M.B. Orams. 2001. The effects of tourism on common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Southern Hemisphere Marine Mammal Conference, Philip Island, Victoria, Australia, 28 May - 1 June, 2001.*

Neumann, D.R. 2001. Activity budget and feeding strategies of short-beaked common dolphins (*Delphinus delphis*) in New Zealand. *14th Biennial conference on the biology of marine mammals, Vancouver, Canada, 27 November - 3 December, 2001.*

Public presentations and media appearances

10.3.2000. Public seminar, Mercury Bay area school, Whitianga, hosted by Forest and Bird Society. 60-min presentation on the biology of common dolphins.

14.3.2000 - TV3 News (6 p.m.) - "Love hurts", 3-min interview with Darren McDonald on the dangers dolphins face today.

14.3.2001 - Seaweek seminar, Auckland Museum, hosted by the Whale and Dolphin Adoption Project. 30-min presentation on common dolphins and swim-with-dolphin tourism. Hon. Sandra Lee, Minister of Conservation in attendance.

18.3.2001 - Radio New Zealand, Spectrum programme 1144, "Dirk and the dolphins". 20-min interview with David Steemson on dolphin biology and conservation.

18.4.2001 - Radio New Zealand, Kim Hill programme. 15-min live interview on dolphin biology and conservation.

21.4.2001 - Public seminar, Whakatane, hosted by Dept. of Conservation. 60-min presentation on common dolphins and swim-with-dolphin tourism.

4.7.2001 - Auckland Science Fair, Massey University, Albany. Two 45-min presentations on the biology of common dolphins and the logistics of field research.

ABSTRACT

This thesis provides new insights into the behavioural ecology of free-ranging short-beaked common dolphins (*Delphinus delphis*), in New Zealand. A preliminary assessment of common dolphin-human interactions was also carried out as part of this 3-yr field study (1998-2001). 166 surveys were conducted in the greater Mercury Bay area, on the east coast of Coromandel Peninsula, North Island, New Zealand. These led to 105 focal group follows, with a total of 118.2 h spent following common dolphins. Seasonal movements of common dolphins were uncovered, and are apparently tied to fluctuations in sea surface temperature.

Common dolphins appear to live in a fission-fusion society. Groups frequently merged and split again. The merging of groups was often accompanied by either sexual, or feeding activity. 408 individual dolphins were identified from photographs of their dorsal fins. No evidence of long-term associations between individuals was found. Resightings of identifiable dolphins indicate movement of individuals between Mercury Bay and the Hauraki Gulf, as well as between Mercury Bay and Whakatane.

This study provides the first activity budget for common dolphins in the wild. Common dolphins spent 55.6% of their time traveling, 20.4% milling, 16.2% feeding, 7.1% socialising, and 0.7% resting. This proportion did not change significantly by season, or from year to year. Common dolphins were found to feed on at least six different fish species. A number of different feeding strategies were employed to capture these fish. Some of these techniques had previously been observed in bottlenose dolphins and orca, but have never before been described for common dolphins.

The results of this study suggest that common dolphins can potentially be negatively affected by interactions with humans. Boat traffic appears to disturb some dolphin groups, especially those containing few individuals. However, commercial tourism appeared to have little impact on the dolphins, at this study site. Few attempts at swimming with common dolphins resulted in a sustained interaction, but unsuccessful attempts did not elicit an obvious negative response. Fishing poses the greatest threat of physical injury and possible mortality to common dolphins. Several key issues were identified, and their value in managing human-dolphin interactions is discussed.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF PLATES

1. INTRODUCTION

Delphinus delphis - common dolphin, or not-so-common dolphin ? That is the question !

> common *adj.* - [...] 3. of ordinary standard; average 4. prevailing; widespread 5. widely known or frequently encountered [...] (Hawks et al., 1986).

Using this definition, 'common' dolphin is a somewhat misleading name for *Delphinus delphis.* Common dolphins (Plate 1) can hardly be described as 'ordinary' or 'average' dolphins. They are indeed the prevailing dolphin species, in some areas, including the Bay of Plenty, New Zealand, but their worldwide distribution is nowhere near as widespread as that of the bottlenose dolphin, *Tursiops truncatus, T. aduncus.* Not many people frequently encounter common dolphins, because they are mainly found in the deep, open ocean. They are not widely known, either. The common dolphin is, in fact, a rather uncommon study subject (Table 1). To redress this, a 3-year study on their ecology and behaviour was conducted along the east coast of Coromandel Peninsula, New Zealand. The main objective of this study is to contribute to an understanding of the basic behavioural ecology of this species.

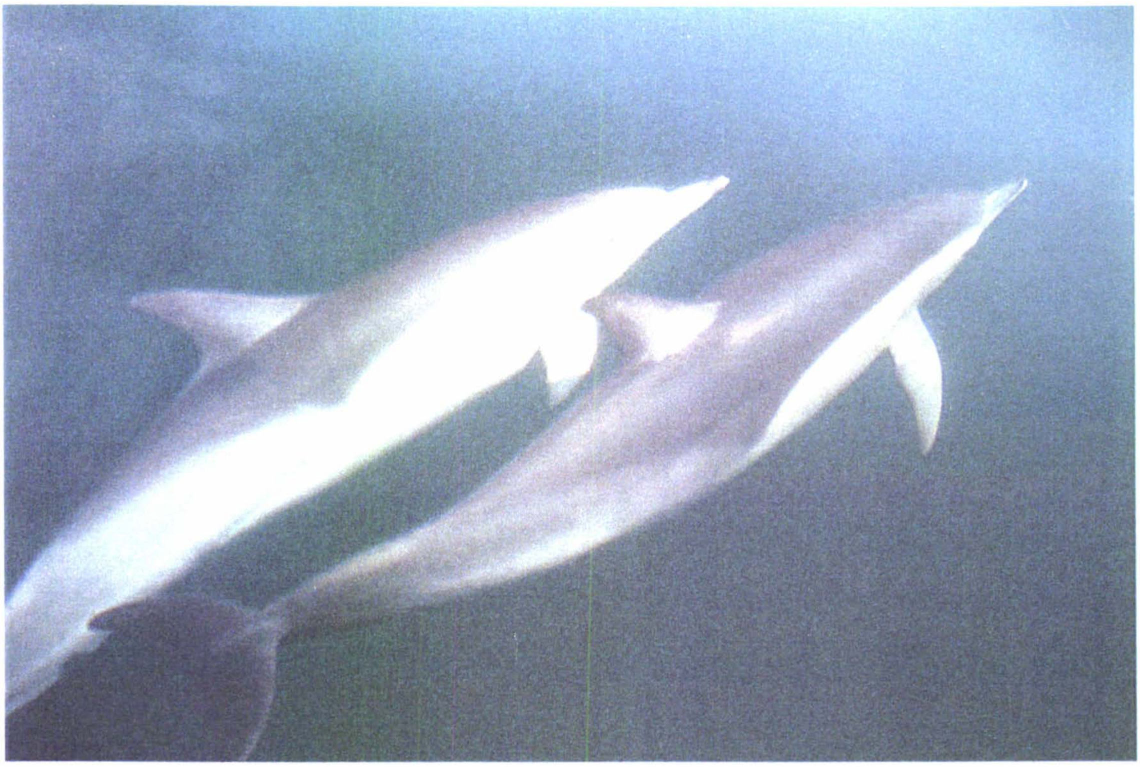


Plate 1. Common dolphins, *Delphinus delphis*, in Mercury Bay.

Table 1. Number of articles indexed in Biological Abstracts, that had a certain delphinid genus name in their title, and the number of these that also contained the word "behaviour" in the title. While this is certainly not an exhaustive list, it is an indication of the typical pattern that students of cetology are confronted with.

Dolphin genus	Number of articles on this genus	Number of articles including behaviour
Tursiops	313	24
Stenella	171	6
Orcinus	108	8
Lagenorhynchus	87	5
Delphinus	**49**	**1**
Cephalorhynchus	31	3

Common dolphins are the most frequently encountered cetacean species in the Bay of Plenty, yet no study has investigated this population to date. Prior to the start of this study, in late 1998, only a handful of studies had examined free-ranging common dolphins New Zealand-wide (Gaskin, 1968; Constantine, 1995; Slooten & Dawson, 1995). These studies did not focus exclusively on common dolphins, and only Constantine (1995) provided some insights into their behaviour. However, she primarily investigated the dolphins' (including bottlenose dolphins') reactions to commercial dolphin-tour operations. As a consequence, baseline data on common dolphin behaviour were not collected. Thus, a number of important questions about common dolphins remain unanswered.

These include:

1) Basic demographics of common dolphins:
How many are there ? Where do they go ? What is their social organisation ?

2) Baseline behaviour of common dolphins:
What do they typically do during daylight hours ? How do they interact with each other and their environment ?

3) Is the behavioural ecology of common dolphins comparable to that of other delphinids ?

In addition to providing insights into the basic behavioural ecology of common dolphins, this study also seeks to provide information to assist in the management and conservation of common dolphins. In order to do this successfully, it is of the utmost importance to properly understand the species' biology. Although common dolphins are abundant and not listed as a threatened species, they nevertheless face a number of human-made threats in their environment. Deaths in by-catch occur in the eastern tropical Pacific tuna fishery (Evans, 1994), and the jack mackerel fishery around New Zealand (Slooten & Dawson, 1995). Deliberate killing has also been reported from Australia (Gibbs & Long, 2001; Kemper et al., 2001).

Whale- and dolphin-watching tourism, while certainly less lethal, is also of growing concern. This form of marine ecotourism is booming world-wide (Orams, 1999), and common dolphins are targets for swim-with-dolphin operations around New Zealand (Constantine, 1999a). There is evidence that some cetaceans are negatively affected by the unsolicited human attention (Kruse, 1991; Constantine, 1995; Corkeron, 1995; Barr, 1997; Bejder et al., 1999). Therefore, a portion of this study is devoted to an investigation of the following question:

4) Are common dolphins affected by interactions with humans, particularly commercial swim-with-dolphin tourism ?

Identifying potentially negative effects will be valuable in addressing and mitigating harmful human impact (Valentine, 1990). This should contribute not only to the welfare of the dolphins, but also to the welfare of tourism operators, who rely on a healthy and 'happy' population of dolphins for their livelihood.

The great importance of baseline information for such an assessment is pointed out by Constantine (1999a, p. 5):

> One of the most important aspects of evaluating the effects of tourism on marine mammals, is the presence of pre-disturbance baseline data on the population size, habitat use, home range, and behavioural ecology of the target species.

Bejder and Dawson (1998, p. 2) concur:

> Despite the obvious need [for baseline data], no New Zealand cetacean population has received detailed study before being targeted by commercial whale or dolphin-watching operations. Hence, 'before and after' comparisons are impossible.

While there currently is some tourism-activity in the study area, it is very infrequent. The present study will therefore be a good approximation to a pre-impact situation, which could be used as 'before' data, especially in the light of the future commercial development of Mercury Bay (Auckland City Council, 2001) and the continued rapid growth of the New Zealand tourism industry (Tourism Strategy Group, 2001).

In an attempt to answer the general questions outlined above, specific hypotheses were developed based upon current knowledge, and then tested empirically. The findings are set forth in this thesis, as follows:

Chapter 2 includes a review of the literature on common dolphin ecology, behaviour, and their interactions with humans.

This leads to the creation of specific hypotheses, designed to address the general questions raised in this chapter. The methodology used to collect the relevant data to test these hypotheses is outlined in chapter 3.

The fourth chapter addresses questions regarding common dolphin ecology. Abundance, grouping patterns, habitat use, and seasonal movements are discussed.

Chapter 5 focuses on common dolphin behaviour, and provides the first activity budget for this species, information on daily and seasonal activity patterns, and a quantification of aerial behaviours and other behavioural events. Feeding strategies that were previously undescribed for common dolphins are also discussed.

Chapter 6 examines human influences on common dolphins, namely disturbances due to boat traffic, swimmers in the water, and interactions with recreational fishing.

The main findings and contributions to scientific knowledge are summarised in chapter 7. This final chapter also includes suggestions for future research and management recommendations.

In summary, this study aims to make a significant contribution to the scientific knowledge of free-ranging common dolphins. In addition, it also intends to provide practical guidelines for human-common dolphin interactions that will aid in the conservation of this species.

2. COMMON DOLPHINS

- a review of current knowledge

2.1 Introduction

The purpose of this chapter is to present an overview of the current scientific knowledge on common dolphin behavioural ecology. Areas lacking in detailed information are identified. Surprisingly, there is a paucity of literature on common dolphin behavioural ecology. As a consequence, relevant literature on other cetacean species is reviewed, in order to provide insight into issues that may also apply to common dolphin behaviour and ecology. In the first part of this chapter, the role of ecological factors such as season, sea-floor profile, and sea surface temperature in the distribution and abundance of dolphins are discussed (section 2.2). Patterns of group formation are also addressed. This is followed by section 2.3, which provides a general overview of delphinid behaviour. Available information on common dolphin foraging strategies is presented, along with comparisons to other species. The value of activity budgets in understanding a species' behaviour is pointed out. Section 2.4 reviews human-dolphin interactions, including the impacts of boat traffic, tourism, and fishing activities on dolphins and other cetaceans.

Specific hypotheses, intended to fill some of the gaps in the knowledge about common dolphins, are developed in the summary section 2.5. These form the foundation for the field research carried out in this study. The literature pertaining to the methodology for investigating these issues is reviewed under the relevant subheadings in chapter 3. The results are presented and discussed in chapters 4, 5, and 6.

2.2 Common dolphin ecology

The common dolphin is the archetypal dolphin first described by Linnaeus (1758), as *Delphinus delphis*. A century and a half later, the understanding of common dolphins was still limited to the very basics:

> The common dolphin is an efficient predator of all the European seas, and was a familiar companion to ancient Greek mariners. The body, measuring two to two-and-a-half meters, is dark grey-black on top, and white below, covered by a sheen that sparkles in all the colours of the rainbow, which, in death, naturally disappears. A 25 centimeter tall dorsal fin sits on top if its back, and its jaws are equipped with numerous teeth, all of them fangs. It is known that the common dolphin traditionally accompanies ships, which is probably what caused the ancient Greeks to tie the dolphin into their myths and legends.

> (Lackowitz, 1896, p. 344. Translated from German by D. Neumann).

Over the past 50 years, our understanding of common dolphins and other cetaceans has grown greatly (Samuels & Tyack, 2000). Today, three separate species of common dolphin are recognised, based on genetic and morphological differences. These are *Delphinus delphis*, the short-beaked common dolphin, *D. capensis*, the long-beaked common dolphin, and *D. tropicalis*, the tropical common dolphin (Heyning & Perrin, 1994; Rosel et al., 1994). Only the short-beaked species has been reliably documented for the southwestern Pacific (Bell et al., 2001).

Common dolphins are generally considered to be pelagic, with most groups occurring over the continental shelf and beyond (Gaskin, 1992). There, they form large groups, sometimes numbering in the thousands (Reilly & Fiedler, 1994). Overall, their behavioural ecology resembles that of other pelagic dolphins, particularly spotted (*Stenella attenuata*) and spinner dolphins (*S. longirostris*) (Norris & Dohl, 1980). Like these two species, common dolphins are also often found associated with tuna, which has led to great mortalities of common dolphins as by-catch in the commercial fishing industry (Evans, 1994).

The social organisation of common dolphin groups is largely unknown. Some delphinids show a high degree of philopatry to their natal group (especially killer whales, *Orcinus orca,* Baird, 2000), while others live in very fluid fission-fusion societies:

> Large schools of open ocean dolphins, such as Hawaiian spinner, pantropical spotted, striped, or Risso's dolphins, typically change composition from day to day. Within these ephemeral groupings, however, some long-term associations may be found, functional division of labour may be seen, and juvenile and nursery subgroups are evident. (Wells et al., 1991, p. 385).

The similarities to the lifestyle of spotted and spinner dolphins, suggest that common dolphins would also tend towards high group fluidity (Norris & Dohl, 1980).

To fully comprehend the behaviour and social organisation of a species, it is necessary to distinguish between males and females. Long-term studies on bottlenose dolphins, which tracked focal individuals of known sex, revealed sexual segregation of mature males from females (Wells, 1991), the formation of male coalitions (Wells, 1991; Connor et al., 1992), and differences in the activity budgets of males and females (Waples et al., 1998). Some cetaceans show pronounced sexual dimorphism, which allows researchers to determine an individual's gender in the field. Adult male sperm whales (*Physeter macrocephalus*) are considerably larger than their female counterparts (Whitehead & Weilgart, 2000). Mature male killer whales(*Orcinus orca*) are also larger than females, but can best be distinguished by their extremely tall dorsal fins (Baird, 2000).

Among most small delphinids, an individual's sex is much more difficult to determine. Often, the only dolphins for which gender can be presumed with any confidence, are those that are consistently accompanied by a dependent calf. Thus, they are recorded as females (Constantine, 1995; Mann, 2000).

Common dolphins are generally accepted to show very little sexual dimorphism, but Evans (1994) described sexually dimorphic differences in the colouration of the area adjacent to the genitals, for common dolphins from the northeastern Pacific. In some small odontocetes, the caudal peduncle becomes enlarged, posterior to the anus, forming a so-called 'peduncle keel', or 'postanal hump' (Jefferson et al., 1997). This has been demonstrated for spinner dolphins (*Stenella longirostris*) (Norris et al., 1994; Perrin & Gilpatrick, 1994), Fraser's dolphins (*Lagenodelphis hosei*) (Jefferson et al., 1997), and Dall's porpoises (*Phocoenoides dalli*) (Jefferson, 1990). In these species, the postanal hump is a secondary sexually dimorphic character which is highly exaggerated in sexually mature males, while it is less pronounced or absent in females and immature males. This is illustrated for spinner dolphins by photographs in Perrin (1972).

The life-span of wild common dolphins is unknown, but some individuals have survived more than 12 years in captivity and were already fully grown, when captured (D. Kyngdon, pers. comm., 15.1.1999). Common dolphins are believed to reach sexual maturity around six years of age, have a 10 month gestation period, and nurse their young for at least 10 months (Collet, 1981). The peak breeding period appears to be in the middle of summer (Collet, 1981; Ferrero & Walker, 1995). Seasonal parturition would result in higher numbers of newborn calves in dolphin groups at a certain time of year. Constantine (1995) observed a peak in the number of newborn calves in mid-summer (January) for common dolphins in the Bay of Islands.

Common dolphins have an almost world-wide distribution, and are found in most tropical, subtropical, and temperate seas. They appear to be particularly abundant in the eastern tropical Pacific (Au & Perryman, 1985; Evans, 1994). In New Zealand, common dolphins are seen regularly from the Bay of Islands in the North (Constantine & Baker, 1997) to Kaikoura in the South (Würsig et al., 1997). The distribution and movements of other delphinids have been reported to be influenced by a great number of variables including prey availability (Cockcroft & Peddemors, 1990), sea floor profile (Hui, 1979; Selzer & Payne, 1988; Gaskin, 1992; Gowans & Whitehead, 1995; Davis et al., 1998), thermocline (Reilly, 1990), oxygen minimum layer (Polachek, 1987), and sea surface temperature (Gaskin, 1968; Dohl et al., 1986; Shane, 1994). The time of year (Bräger, 1993; Barlow, 1995; Waples, 1995), time of day (Saayman et al., 1973; Shane, 1990a; Bräger, 1993; Waples, 1995), and tidal state (Würsig & Würsig, 1979; Hanson & Defran, 1993) can also have an effect on dolphin movements. However, there have been no studies in New Zealand which investigated these issues for common dolphins.

2.3 Common dolphin behaviour

There is a conspicuous lack of scientific literature on the *behaviour* of common dolphins. Where their behaviour *has been* investigated, it has primarily focused on animals in captivity, describing their social interactions and vocalisations (Evans, 1994). Very few studies have investigated common dolphin behaviour in the wild, and fewer still can claim to have collected data systematically over an extended period of time. Currently, there are very few such studies underway, worldwide, and most of their results have yet to be reported. The most comprehensive work is being conducted by the Tethys Research

Institute, Italy (Ferretti et al., 1998), and the Biscay Dolphin Research Programme, UK (Brereton et al., 1999).

What is relatively well known about common dolphins are their feeding habits. This knowledge is mostly not the result of first-hand observation, but has largely been inferred from stomach content analyses. A large sample size has been available for such studies, because common dolphins frequently die as by-catch in the tuna purse seine fishery. In one year alone (1988) over 15,000 common dolphins were estimated to have been killed in the eastern tropical Pacific (Evans, 1994). Their frequent association with tuna may be caused by a shared feeding ecology (Evans, 1994). Stomach contents from various locations showed that common dolphins appear to live on three major food groups (Pascoe, 1986; Evans, 1994; Young & Cockcroft 1994, 1995; Walker & Macko, 1999):

1) small schooling fishes, such as anchovies, and mackerel (*Scombridae*).

2) fishes from the deep scattering layer, such as deep sea smelt, and lanternfish (*Bathylagidae* and *Myctophidae).*

3) squid, also often associated with the deep scattering layer (*Cephalopoda*).

The deep scattering layer organisms would normally only be available to the dolphins during their nocturnal migrations towards the surface, which suggests much night-time feeding in common dolphins. This has also been inferred from acoustic data, collected by Goold (2000).

While the diet of common dolphins (*Delphinus delphis, D. capensis*) has been investigated in detail, comparatively little is known on how common dolphins go about capturing their prey. The feeding strategies of *Delphinidae* are known to be highly variable. Habitat, nature of the targeted prey, and learning of specialised hunting techniques lead to the use of many different foraging methods. Bottlenose dolphins (*Tursiops sp.*) are a prime example, with feeding strategies including circling schools of fish, then darting into the school to capture some (Hamilton & Nishimoto, 1977; Bel'kovich et al., 1991). 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 bury themselves up to their flippers in the sand, during benthic 'crater feeding' (Rossbach & Herzing, 1997). In Florida, they have been observed to 'whack' fish into the air, with their tail flukes, stunning or killing them in the process (Wells et al., 1987; Nowacek, 1999b). The flukes are also employed in 'kerplunking' where the dolphins lift them above the surface, and drive them down rapidly onto the surface and through the water, creating a characteristic splash, sound, and bubble-cloud underwater (Nowacek, 1999b; Connor et al., 2000a). There is even a possibility that bottlenose dolphins use sponges as tools during benthic foraging in Western Australia (Smolker et al., 1997).

Killer whales (*Orcinus orca*) are another delphinid species showing immense flexibility in their feeding strategies. 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). The importance of learning some of these specialised feeding techniques is particularly evident in the intentional stranding used in capturing pinnipeds from beaches (Guinet, 1991).

The feeding strategies of dolphins with a more pelagic distribution are much less well-known. Spotted dolphins (*Stenella frontalis*) have been reported to cooperatively surround schools of clupeid fish, and drive them to the surface (Fertl & Würsig, 1995). Dusky dolphins (*Lagenorhynchus obscurus*) have been observed to feed in a similar fashion in shallow, nearshore waters (Würsig & Würsig, 1980; Würsig et al., 1997). Off Kaikoura, New Zealand, common dolphins have been observed in mixed groups with dusky dolphins during the summer (Würsig et al., 1997). Possibly, the larger group size allows mixed-species groups a more efficient exploitation of food sources, or provides increased protection from predation.

Direct observations of common dolphin feeding behaviour are scarce, but the cooperative rounding up of small schooling fish, driven to the surface in a tight ball has been described (Würsig, 1986; Bel'kovich et al., 1991; Gallo, 1991). This type of cooperative feeding often attracts other predators, such as diving birds or pinnipeds, which likely feed on the same fish (Würsig & Würsig, 1980; Gallo, 1991; Wells et al., 1999).

The behavioural repertoire of common dolphins is likely to be comparable to that of other delphinids. Most 'tricks' that are frequently performed by bottlenose dolphins in captive displays have also been taught successfully to captive common dolphins (Evans, 1994). The vocalisations of common dolphins are more akin to those of several *Stenella* species, encompassing higher frequencies than those of bottlenose dolphins (Evans, 1994). Like most odontocetes, common dolphins can be presumed to use acoustic signals, both for communication (whistles), as well as hunting and orientation in their environment (echolocation clicks) (Norris et al., 1994, Moore & Ridgway, 1995). Various aerial behaviours such as leaps, breaches, and tailslaps that have been described for other delphinids (for example see Shane, 1990a) are also performed by common dolphins. These behaviours have variously been attributed to coordination of group activity (Norris et al., 1994), show of excitement, or agonistic displays (Connor et al., 2000b).

In this thesis, the behaviour of common dolphins was explored mainly through a time-budget of the predominant group activity. Activity budgets can provide valuable insights into how animals interact with each other and their environment. They provide information on how a population is affected by changes in habitat, food supply, reproductive efforts, and many other physiological, social, or environmental parameters. Activity budgets have contributed to a better understanding of a wide range of species: for example, birds (Mock, 1991; Stock & Hofeditz, 1996), squirrels (Wauters et al., 1992), antelope (Maher, 1997), moose (Miquelle, 1990), bighorn sheep (Goodson et al., 1991), otters (Ostfeld et al., 1989), and bats (Charle-Dominique, 1991). Studies on primates have linked variations in activity budgets to habitat differences (Isbell & Young, 1993; Watts, 1988; Defler 1996), food availability (Adeyemo, 1997), predation pressure (van Schaik et al., 1983), or sex and age of the animals (Marsh, 1981; Post, 1981; Baldellou & Adan, 1997). In cetaceans, activity budgets helped identify the behavioural patterns of killer whales (Heimlich-Boran, 1987), Atlantic white-sided dolphins, *Lagenorhynchus acutus* (Weinrich et al., 2001), and dusky dolphins (Würsig & Würsig, 1980). In bottlenose dolphins, activities fluctuated according to habitat, tidal state, time of year, group size, and gender of individuals (Shane, 1990a,b; Bräger, 1993; Hanson & Defran, 1993; Waples, 1995; Bearzi et al., 1999).

2.4 Common dolphins and their interactions with humans

Humans have been fascinated by dolphins since ancient times, and many have cherished encounters with these playful cetaceans. Throughout history, some wild dolphins have interacted with humans out of their own free will. These interactions mostly involved lone, sociable bottlenose dolphins, and the reasons for their behaviour remain unclear (Lockyer, 1990; Orams, 1997b). There are fewer reports of wild common dolphins interacting with people. This can probably be attributed to their less coastal distribution. However, in a highly unusual occurrence, a mother and calf common dolphin, and a second adult, were seen regularly in Whitianga harbour, from 1981 to 1987 (Doak, 1995). They could be observed on a daily basis from aboard the passenger ferry linking Whitianga and Ferry Landing (a three minute boat ride). The first calf was found dead after four years, but a second calf was born, apparently inside the estuary. Local witnesses all agree that the dolphins left the area suddenly, after this second calf had been killed. How the calf's death came about is unclear. Some blame an accidental boat strike, others natural causes, and still others a deliberate, malicious attack (R. Rae, pers. comm., 25.11.1998). If the latter is true, it may represent another instant in which some locals became 'fed up' with the attention drawn to their town by the dolphins' presence. Such a violent response towards dolphins in close contact with humans has been reported in antiquity by Pliny the younger (as cited in Orams, 1997, p. 318), and also took place in Opononi, New Zealand (North Shore Times Advertiser, 1995). In each case, some townspeople were apparently unhappy with the impact the presence of a lone, sociable bottlenose dolphin was having on their respective communities.

Through the second half of the 20th century, reports of human encounters with dolphins, and the 'marketing' of dolphins in films, television, and other media as highly intelligent, friendly, and even spiritual animals spawned an immense human interest in these creatures (Samuels & Tyack, 2000). Some even ascribe therapeutic effects to physical interactions with dolphins (Pacenti, 1999a,b). Many humans harbour a great desire to get close to these animals, perhaps even touch or communicate with them (Doak, 1981, 1988). This desire has been, and still is, commercially exploited on a great number of levels - the most direct being the exhibition of cetaceans in captivity (Yale, 1991; Samuels & Spradlin, 1995). As public awareness about issues regarding the well-being of captive cetaceans has increased, a new trend towards 'making contact' with dolphins in their natural environment has emerged (Amante-Helweg, 1996). This has contributed to the creation of a rapidly growing whale- and dolphin-watching industry around the world (Orams, 1999).

Cetacean tourism has great potential to increase people's awareness of a need for nature conservation, by using whales or dolphins as a touchstone species. A greater appreciation, combined with education, should benefit conservation (Orams, 1995, 1997a). Dolphin- and whale-watching also provide an economic use of cetaceans as a resource, which is non-lethal (Orams, 1999). The profitability of such ventures may even help turn around attitudes in nations that still perform whaling. In Iceland and Norway, for example, ex-whaling boats have been recommissioned as whale-watching boats, with whales still providing the income for former whalers (pers. obs.). In Tonga, the greater economic benefits of whale-watching compared to whale-hunting, may prevent a return to the consumption of humpback whale meat (*Megaptera novaeangliae*) in this South Pacific nation (Orams, 2001).

At first glance, cetacean-based eco-tourism seems like a highly desirable arrangement, with all sides benefiting: the tour operators have a source of income, the customers get close to cetaceans, and the cetaceans remain unharmed in their natural environment (Duffus & Dearden, 1990). Yet, many other so-called 'eco-tourism' ventures have proven to be detrimental to wildlife, when human actions were not carefully monitored and regimented (for example see Gunther, 1992; Stock & Hofeditz, 1996; Wünschmann, 1999). This also became apparent in situations in which wild bottlenose dolphins were provisioned with food. At Monkey Mia, Australia, calf mortality and aggressive behaviour increased (Wilson, 1994), while bottlenose dolphins at Tangalooma, Australia, showed increased aggression towards each other and towards humans until strict controls were put in place (Orams et al., 1996).

Adverse reactions to boat traffic have also been observed for both whales (Beach & Weinrich, 1989; Corkeron, 1995), and dolphins (Au & Perryman, 1982; Janik & Thompson, 1996; Nowacek, 1999a). These include longer dives, heading away from boats, and disruption of normal behaviour patterns. These may lead to short-term effects such as decreased foraging, resting, or socialising opportunities (Weir et al., 1996; Constantine & Baker, 1997; Nowacek, 1999a). The resulting long-term effects may be more detrimental and could include decreased survival rates, lower reproductive success, or permanent emigration (Kruse, 1991; Weir et al., 1996).

It appears that some cetaceans are affected primarily by the noise associated with boat traffic. Some dolphins and whales have shown avoidance reactions in response to the sounds produced by vessels and aircraft (Richardson et al., 1995; Würsig et al., 1998). Bowhead whales (*Balaena mysticetus*) left areas in which air-gun blasting was carried out during seismic surveying (Ljungblad et al., 1988). They also moved away from played-back sound recordings of drilling and dredging noises (Richardson et al., 1990). Pelagic spotted (*Stenella attenuata*) and spinner dolphins (*S. longirostris*) changed their headings away from approaching vessels when these were still as far as six miles away (Au & Perryman, 1982). Würsig et al. (1998) found similar reactions to approaching boats and survey planes by striped dolphins (*Stenella coeruleoalba*), while bottlenose (*Tursiops truncatus*) and spotted dolphins (*Stenella frontalis*) did not appear to avoid them. There are observations that suggest that beluga whales (*Delphinapterus leucas*) may begin to avoid vessels while they are still 35 kilometers distant (Myrberg, 1990).

High densities of boat traffic can cause bottlenose dolphins to increase the duration of their dives (Janik & Thompson, 1996; Nowacek, 1999a), or even displace them from preferred foraging locations (Allen & Read, 2000). Boat strikes on bottlenose dolphins have also been reported during times of increased pleasure boating activity in Florida (Wells & Scott, 1997). Corkeron (1995) found that groups of humpback whales (*Megaptera novaeangliae*) containing calves dived more frequently when whale-watching vessels were present. Aerial behaviours, such as pectoral slaps and breaches, also appear to be more frequent in the presence of whale-watching boats (Corkeron, 1995; Peterson, 2001). In some areas, cetaceans appear to become habituated to boat traffic (e.g., grey whales (*Eschrichtius robustus*) (Jones & Swartz, 1984)), while in others, there is evidence for sensitisation (e.g., bottlenose dolphins (Constantine, 1999b)).

Because cetacean tourism is almost always boat-based, there are legitimate concerns, that such ventures could be detrimental (Curran et al., 1996). In fact, the majority of approaches by tour boats to dusky dolphins in Kaikoura caused changes in behaviour, and disrupted feeding and resting activities (Würsig et al., 1997).

The popular swim-with-the-dolphins option, in New Zealand, adds another potential stressor to tourism-cetacean interactions, and bottlenose and common dolphins have both shown avoidance behaviour in reaction to swimmers (Constantine, 1995, 1999b; also see Samuels et al., 2000 for a review of in-water dolphin-human interactions).

To provide humans with the expected enjoyment of interacting with marine mammals, and yet ensure the continued welfare of these animals, such ventures must be developed with the greatest care (Shackley, 1992). To ensure the safety and welfare of both dolphins and tourists, the behavioural patterns of the targeted dolphins need to be well-understood. It is very much in the interest of both wildlife conservation, and tourism operators (who rely on a healthy population of dolphins for their livelihood) that such effects are identified early, so that steps can be taken to alleviate detrimental impact.

In New Zealand, four species of dolphins are targets of commercial dolphin-watching and swim-with-dolphin operations. In the Bay of Islands, the primary target species is the bottlenose dolphin (Constantine, 1995; Constantine & Baker, 1997). In Kaikoura, dusky dolphins are sought out by tourists (Barr, 1997), while Hector's dolphins draw tourists to Banks Peninsula and Porpoise Bay (Bejder, 1997; Bejder et al., 1999). In the Bay of Plenty/Coromandel area, common dolphins are the most abundant cetaceans, and therefore the prime target for dolphin-tours. This study is the first to focus exclusively on this species in New Zealand, and to address common dolphin-human interactions in this area.

Under the Marine Mammal Protection Act (1978) and the Marine Mammal Protection Regulations (1992, see Appendix 1), the Department of Conservation (DoC) is charged with ensuring that tourism operations do not detrimentally impact these animals. A licensing system administered by DoC has therefore been put into place. In June 2001, 100 permits were on file nationwide, with 10 of these in the application process. Cetaceans are the targets of 75 operations, while the remainder focuses on seals. Only 30 permits are being used by full-time exclusively marine mammal-based tourism operations. In the greater Bay of Plenty area there are currently (June 2001) seven licensed dolphin-tour operators who primarily interact with common dolphins: 1 Auckland, Hauraki Gulf; 1 Whitianga; 1 Whangamata; 2 Tauranga; and 2 Whakatane.

The tourism operation investigated in this study was Mercury Bay Seafaris in Whitianga, owned and operated by Rod and Elizabeth Rae since 1992 (Ryan, 1998). The 'Dolphin Quest' information pamphlet, given to patrons who book a dolphin tour with Mercury Bay Seafaris provides a good indication of the operators' attitude towards dolphin-watching:

> [Common dolphins] are better adapted to their medium than we are to ours. Treat them with respect and be prepared to learn from your encounter with the dolphins. [...] We swim with dolphins at their invitation, they do not make appointments !

On average, Mercury Bay Seafaris conduct 20 swim-with-dolphin trips a year, almost all of them between November and February. Only one trip a day is offered, typically lasting from 8 a.m. to 12 noon. The maximum number of customers on board is 10. The boat 'Seafari 2' is a 7.5 meter Stabicraft, powered by twin 90 hp Yamaha two-stroke outboard engines (Plate 2). Rod Rae is a very conscientious skipper who adheres to the Marine Mammal Protection Regulations (1992), and consistently approaches dolphin groups slowly and gradually from behind. He then follows the group and allows his customers to watch the dolphins. Only when the dolphins slow down and start milling around the boat are swimmers allowed to enter the water, which corresponds to the 'around-the-boat' method described by Constantine (1995). Most swimmers are equipped with a 3.5 mm wetsuit, mask, snorkel, and flippers, while some prefer to wear only a bathing suit.

There are a number of anthropogenic influences which have much more obvious effects on dolphins than tourism: Common dolphins are hunted directly in small artisanal fisheries along the coast of Peru (Read et al., 1988) and in the Black Sea (Celikkale et al., 1989). While common dolphins are protected, along with other marine mammals, in a number of countries, including Australia and New Zealand, there is some evidence that common dolphins are occasionally killed deliberately, in Australia (Gibbs & Long, 2001; Kemper et al., 2001). Shark-nets, which are intended to protect recreational swimmers and surfers from shark attacks at certain beaches, also pose a problem for dolphins. In South Africa, common dolphins are the species that die most frequently in shark-nets (Cockcroft, 1990; Peddemors, 1999). They

Plate 2. Seafari 2, Whitianga's only dolphin-tour boat (operated by Mercury Bay Seafaris), on a dolphin cruise.

also suffer mortalities as by-catch in the commercial tuna fishery in the eastern tropical Pacific (Evans, 1994), and in New Zealand are occasionally taken in mid-water trawls for jack mackerel (*Trachurus novaezelandiae*) (Slooten & Dawson, 1995). Anecdotal reports also suggest interactions between common dolphins and recreational fisheries in New Zealand, but their effects remain largely unknown.

However, not all human fishing activities are harmful to dolphins: There are unusual examples of cooperative fishing between bottlenose dolphins and shore-based artisanal fishermen in Mauritania (Busnel, 1973), Brazil (Pryor et al., 1990), and Australia (Orams, 1995): Indigenous fishermen attract the dolphins' attention by slapping the surface, the dolphins then herd fish towards the hand-held nets, and are rewarded with a portion of the catch. These interactions appear to benefit both dolphins and humans, and may have occurred for hundreds of years (Orams, 1995).

On the other end of the spectrum, dolphins have learned to exploit human fishing efforts: Bottlenose dolphins in Moreton Bay, Australia, forage to a great extent on the by-catch discarded from shrimp trawlers (Corkeron et al., 1990). Similar associations exist in the Gulf of Mexico (Leatherwood, 1975). Killer whales have also been reported to scavenge on the discarded by-catch of trawlers (Couperus, 1994), and in certain locations (including New Zealand), they actively 'steal' fish off long-lines (Secchi & Vaske, 1998; Visser, 2000). Neither cooperative nor commensalistic interactions with human fisheries have been reported for common dolphins.

Marine pollution is another anthropogenic factor threatening dolphin survival. Bottlenose dolphins have been shown to be potentially susceptible to the toxic effects of an oil spill (Smultea & Würsig, 1995). In some dolphins, the accumulation of heavy metals (Augier et al., 1993) and organochlorines (Cockcroft et al., 1990) reached physiologically dangerous levels. Common dolphin females periodically 'shed' large amounts of toxins stored in their blubber, by passing them on to their offspring during lactation. This may negatively affect the survival chances of their calves, especially their first-born offspring, which receive higher amounts of toxins, accumulated over the years leading up to their mothers' sexual maturity (Cockcroft et al., 1990). A similar mechanism may be responsible for low survival rates of first-born bottlenose dolphin calves in Sarasota Bay, Florida (Wells & Scott, 1990).

Very little is known about the potential influence of the anthropogenic factors mentioned above on the behavioural ecology of common dolphins. There is great potential for future research in this area. Because these anthropogenic influences were too many, and too varied to all be incorporated into this study, this dissertation focused mainly on the effects of tourism, and also provided some information on interactions between recreational anglers and common dolphins.

2.5 Summary and hypotheses:

This review showed that there are considerable gaps in the knowledge about common dolphins. General questions, such as: 'How do common dolphin groups form ? Where do they go ? Are their movements influenced by certain environmental variables ? Can males be distinguished from females ?' remain imperfectly, or completely unanswered. Their behavioural patterns, including feeding strategies, are also poorly understood. Little information is available on the effects of human activities on common dolphins. Constantine (1995) reported on the effects of tourism on common dolphins in the Bay of Islands, but did not provide baseline data for comparison.

To address some of these questions, specific hypotheses were created, which were then tested empirically, by using data collected during field observations.

2.5.1 Investigating common dolphin ecology:

Social organisation, particularly the stability of given groups over time, remains unclear. To test this issue, the following null-hypotheses were investigated:

H0 1a: The composition of groups, as indicated by group size, does not remain stable over time.

H0 1b: The composition of groups, as indicated by photo-identification resightings, does not remain stable over time.

The possibility of seasonal variation in dolphin abundance, was tested by:

H0 2: Average group size does not change significantly over time.

To find out more about potential variation in social organisation between groups, the following null-hypotheses were investigated:

H0 3: There is no difference in the sex ratio between groups.

H0 4: The number of calves in each group does not change significantly over time.

The presence or absence of sexual dimorphism in common dolphins was tested, using the following null-hypothesis:

H0 5: There are no external morphological differences between common dolphin individuals that could be attributed to their gender.

Reports from other locations suggest a seasonal breeding cycle for common dolphins, with most births occurring in mid-summer. To find out if this was also the case for common dolphins in the study area, the following null-hypothesis was tested:

H0 6: The number of newborns in each group does not change significantly over time.

The influence of seasonal, diurnal, and tidal variations on common dolphin habitat use was investigated through:

H0 7a: The presence of dolphins in the study area is not affected by the time of year.

H0 7b: The presence of dolphins in the study area is not affected by the time of day, H0 7c: The presence of dolphins in the study area is not affected by diurnal tidal fluctuations.

H0 8: Habitat use, indicated by the average distance from shore, does not change significantly over time.

Long-distance movements, habitat use, and site-fidelity were also documented by use of photo-identification records.

2.5.2 Investigating common dolphin behaviour:

Many questions on the behaviour of cetaceans, such as their feeding strategies, typical behavioural patterns, and the influence of environmental or demographic variables on their behaviour, have been investigated successfully for a number of species. However, for free-ranging common dolphins, most of these questions remain open. In order to address some of these issues, the following approach was taken:

Previous studies on the behaviour of small cetaceans have uncovered a number of variables that can influence the animals' behaviour. Activity budgets have proven useful tools in assessing these influences. Therefore, the first activity budget for free-ranging common dolphins was compiled as part of this study. The influence of various factors on the dolphins' behaviour was tested, using the following null-hypotheses:

H0 9: The time dolphins spend engaged in various activity states does not vary significantly between seasons or years.

H0 10a: The time of day does not affect the dolphins' activity budget.

H0 10b: Tidal fluctuations do not affect the dolphins' activity budget.

H0 11: There is no difference in the activity budgets of groups that are smaller than average, versus those that are larger than average.

The context and possible function of some behavioural events (e.g. breaching, tailslapping, etc.) performed by common dolphins, was investigated by quantifying various displays, recording the predominant group activity at the time, and the sequence in which behavioural events occurred.

While cooperative herding of fish has been reported for common dolphins (Würsig, 1986; Gallo 1991), some feeding strategies are used only infrequently, and long-term studies are therefore invaluable in obtaining a complete picture of a species' behavioural repertoire. Over the three years of this study, the feeding behaviour of common dolphins was investigated, including close visual observation of prey items. Qualitative descriptions of the strategies involved in capturing such prey were also completed. Comparisons to the feeding strategies of other cetaceans were then carried out.

2.5.3 Investigating human impact on common dolphins:

Part of this study was devoted to a preliminary assessment of the effects of a local small-scale tourism operation on common dolphins. Dolphins generally exhibit a great deal of behavioural plasticity and readily adapt to new challenges or requirements in their habitat, including human activities (Corkeron et al., 1990; Lockyer, 1990; Shane, 1990b). The activity budgets for bottlenose dolphins in the three different study areas used by Shane (1990b) and Waples (1995) exhibited differences that were attributed mainly to differences in habitat and prey availability. Because of this variability in behaviour, a comparison of activity budgets was considered to be a feasible way to examine potential differences in behaviour in response to tourism - especially within the same habitat, where most other potential influences (including that of the research boat) can safely be assumed to be identical for both samples. In addition, the influence of other boat traffic (including the research vessel) on the dolphins' behaviour was investigated, through the following null-hypotheses:

H0 12: There is no difference in common dolphin activity, before and after a boat approaches them to within < 100 meters.

H0 13: Dolphins remain equivocal towards boats for the duration of a follow, and show neither attraction nor avoidance.

H0 14: There is no difference in the activity budget of common dolphins between baseline data and data collected in the presence of the tour boat.

H0 15: Dolphins do not change their behaviour in response to swimmers entering the water from tour boats.

The results for the above research questions are presented and discussed in chapter 4 (ecology), chapter 5 (behaviour), and chapter 6 (human impact). The methodology used to collect the data necessary to answer these questions, is presented in the following chapter (chapter 3).

3. METHODS

3.1 Introduction:

The study of cetaceans in the wild presents a number of challenges which require observers to adapt their sampling regime to the unique characteristics of their study subjects and study location. Irrespective of these challenges, in conducting scientific research it is important that the collection of data is systematic and consistent so that valid and reliable results are produced. This chapter explores the various challenges, and discusses the choice of methodology, in the light of established research techniques. Firstly, the choice of study area and observation platform are explained, then the specific sampling protocols employed in this study are discussed. Further, definitions for a number of recorded variables are presented.

The choice of sampling protocol and even such apparently 'basic' concepts as the definition of 'groups' of study subjects, are rather contentious within the marine mammal research community (Mann, 1999). Methods used vary widely between studies, and no universally applicable formula exists for the collection of data on cetaceans in the wild. In this study, weighing the advantages and disadvantages of focal *group* versus focal *individual* sampling was one of the central issues that had to be resolved. Personal preferences and practical considerations undoubtedly also play a role in the choice of sampling methods, and therefore, it is possible that alternative sampling methods could have been utilised in this study. However, every effort was made to examine the 'pros' and 'cons' of various methodologies carefully, and the methods chosen are considered those best suited to study common dolphins under the circumstances found in the study area. A consideration of these methods and their alternatives is presented in this chapter as a rationale for the methods utilised.

3.2 Pilot work:

During November and December 1998, several dolphin test-surveys were conducted aboard commercial tour boats out of Whitianga, Tauranga, and Whakatane. These test surveys were used to assess the suitability of potential study areas, and also to fine-tune observational methodology. *Ad libitum* observations of dolphin behaviour were carried out on these trips to compile a basic ethogram. Various data recording methods were then tested for their potential use. These trips also allowed an assessment of the commercial dolphin-watching/swimming operations, from both the operators' and the tourists' perspective.

Eventually, Whitianga was chosen as study site, because its low level of dolphin-tourism provided a unique opportunity to record common dolphin behaviour in the absence of tour boats, as well as a chance to test these results against some tour-boat interactions. A common problem with most tourism-impact studies on cetaceans is that there are no pre-tourism baseline data. Whitianga presented the nearest possible approximation to a pre-tourism situation, thanks to the low frequency of commercial dolphin-watching trips. The collected data therefore provide valuable baseline information, especially in the face of future multi-million dollar developments in Whitianga which have the potential to affect local marine life (see chapter 7). Furthermore, of the potential study sites, Whitianga provided the easiest and safest boat launching facilities, and Mercury Bay waters appeared to be the least hazardous.

During the pilot-phase of this study (and beyond) Rod and Elizabeth Rae, Whitianga's dolphin tour operators since 1992 (trading as 'Mercury Bay Seafaris'), freely shared their own experiences with common dolphins, and made a log of dolphin-sighting locations available, which was very valuable in the analysis of the dolphins' seasonal movements.

3.3 Observation platform:

Observations were conducted from 'Aihe' a 5.5 meter centre-console, rigid-hull inflatable boat, with a 90 hp outboard engine (Plate 3). This may, in some cases, have influenced the nature of observations, because the behaviour of dolphins and other cetaceans has been shown to be affected by boat traffic to varying extents (Acevedo, 1991; Kruse, 1991; Corkeron, 1995; Nowacek, 1999a). To get a true baseline reading of how dolphins behave without boats present, some studies have been successful in conducting land-based observations (Janik & Thompson, 1996; Bejder et al., 1999). Unfortunately, due to the offshore distribution of common dolphins, this was not an option in this study. However, boat-based studies can still provide valid information on dolphin behaviour, by adhering to established approach and follow-protocols, which are intended to minimise disturbance (Bearzi et al., 1999; Mann, 2000). Würsig & Würsig (1979) found no apparent impact on the activity or direction of movement of bottlenose dolphins, during boat-based follows. Bearzi et al. (1999, p. 1069) reported:

> In the event of close approaches (less than 5-10 meters), the animals [bottlenose dolphins] would usually submerge (or occasionally come closer to inspect the boat or attempt to bowride), but the general behavioral activity and direction of movement did not seem to be significantly affected.

Plate 3. Aihe, the 5.5 m RIB research vessel (with the author at the helm).

Slow and predictable driving off to one side of the group, along with gradual approaches, helps to minimise the research vessel's impact. Mann (2000, p. 53) recommends:

> Experienced observers avoid sudden turns, accelerations, and decelerations, approaching the animals head-on, or zooming up from behind; such maneuvers are prohibited by most whale-watching guidelines designed to reduce harassment. Maintaining a steady speed so as to keep pace with the animals helps to maximize their visibility and minimize disrupting their behaviour.

To increase the likelihood of observing unaffected dolphin behaviour, focal group follows were conducted in strict adherence to the above recommendations and the Marine Mammal Protection Regulations (1992, R18, see Appendix 1), which stipulate among other things:

> (a) Persons shall use their best endeavours to operate vessels, vehicles, and aircraft so as not to disrupt the normal movement or behaviour of any marine mammal.
>
> (b) Contact with any marine mammal shall be abandoned at any stage if it becomes or shows signs of becoming disturbed or alarmed. [...]

> (e) No sudden or repeated change in the speed or direction of any vessel or aircraft shall be made except in the case of an emergency. [...]
>
> (k) No person, vehicle, or vessel shall cut off the path of a marine mammal or prevent a marine mammal from leaving the vicinity of any person, vehicle, or vessel.

While researchers of some previous studies reasoned that dolphins were habituated to the research vessel, and therefore did not examine their vessels' potential impact (e.g., Waples, 1995; Nowacek, 1999a), this study attempted to take the dolphins' reaction to the research vessel into account (see chapter 6).

3.4 Study area:

Over three summer seasons, from December 1998 to March 2001 (with the exception of the winter months May-August each year), observations were conducted in the greater Mercury Bay area, based from Whitianga (36 degrees 50' South, 175 degrees 42' East), on the east coast of Coromandel Peninsula, North Island, New Zealand (Figure 1). In March and April 2001, additional observations were carried out in a 40 kilometer radius out to sea from Whakatane (37 degrees 56′ South, 177 degrees 05′ East), central Bay of Plenty, North Island, New Zealand (Figure 1).

3.5 Volunteer research assistants:

This study would not have been possible without the help and dedication of 19 volunteer research assistants from 10 different countries. Two volunteers at a time joined the research project for 6-10 week periods, before being relieved by the next two volunteers. Almost all of them were biology students who took the opportunity to get hands-on fieldwork experience. Once a group of dolphins had been found, one of the volunteers would take over the helm (after having received careful theoretical and practical instruction on how to drive the boat in the presence of dolphins), and the other would record data onto the data sheet. These roles were alternated from one sighting to the next. This allowed the author to keep his eyes on the dolphins continuously, and also to photograph individuals for identification purposes. Volunteers called out the time points, immediately after which the focal group was scanned, and the data to be recorded was dictated to the volunteer in charge of the data sheet. To avoid the potential pitfalls of inter-observer variability during data collection, the data reported here exclusively represent the principal

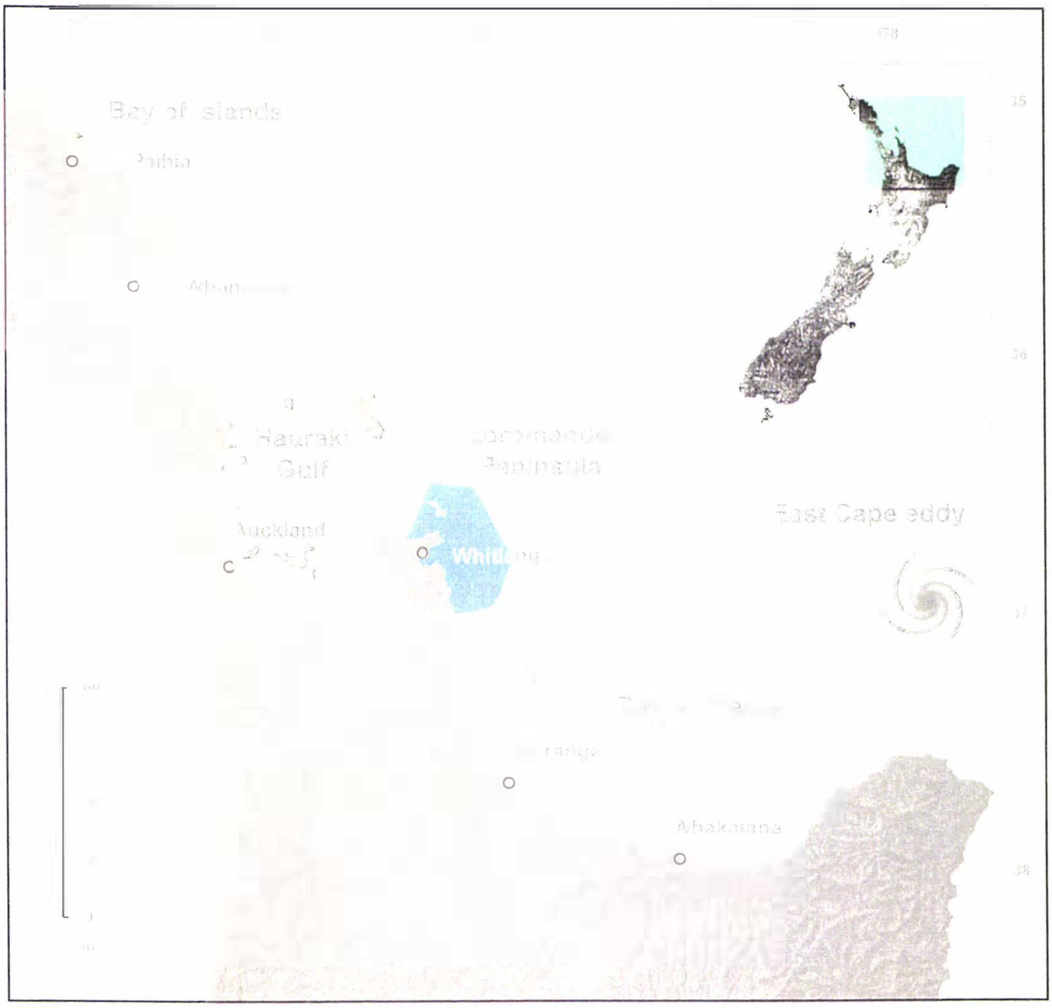


Figure 1. The northeast coast of New Zealand's North Island.
The study area is indicated in dark blue.

investigator's judgment. This was particularly important for the distance estimates, as they varied widely between observers.

3.6 Surveys:

The search for dolphins was conducted along two main search routes, a northern one and a southern one (Figure 2). Because the entire study area could not be covered on one tank of fuel, surveys alternated between the two transect lines. The first group of dolphins encountered on these surveys served as the focal group, and the remainder of the transect was then abandoned on most occasions. When information was obtained that dolphins had been sighted in a specific area, the transect line was left to seek out such groups. During searches, the waters were continuously scanned for signs of dolphins (mostly with the naked eye from a height of 1.5 to 2.5 meters above the sea surface, sometimes aided by Minolta binoculars with a 7x magnification), particularly dorsal fins and splashes, but also feeding gannets because of their known association with feeding common dolphins (Gallo, 1991). Typically, this allowed for a 3-6 kilometer search radius around the boat, depending on sea conditions.

A small number (n=7) of winter surveys (May-August) were conducted during the first field season (1998/1999), but did not yield any sightings of common dolphins. During the winter season, sea conditions in the study area are typically not suitable for small open boats. A complete lack of dolphin sightings in winter (either due to the dolphins' absence or difficulties in spotting them because of rough seas) was also reported by the commercial dolphin-tour operators (R. Rae, pers. comm. 25.11.1998). Winter surveys were therefore abandoned for the remainder of the study and excluded from data analysis. It follows that the results presented in this thesis are indicative of common dolphin behaviour for most of the year (September – April) but not an entire annual cycle.

Surveys were only conducted in sea conditions of Beaufort 2 or less. Upon sighting a group of dolphins, their location was recorded using a hand-held Garmin 35 GPS, the number of animals in the group was counted or estimated, and the predominant group activity at the first contact was recorded. This was done at whichever distance the dolphins were first spotted (typically ranging between 200-500 meters), before approaching closer for group follow and photo-ID purposes. All information was logged by hand, onto a standardised data sheet (Appendix 2).

Because boat-based estimates of dolphin numbers may not have been representative of dolphin abundance in the study area (e.g. because additional groups may have been present without being encountered),

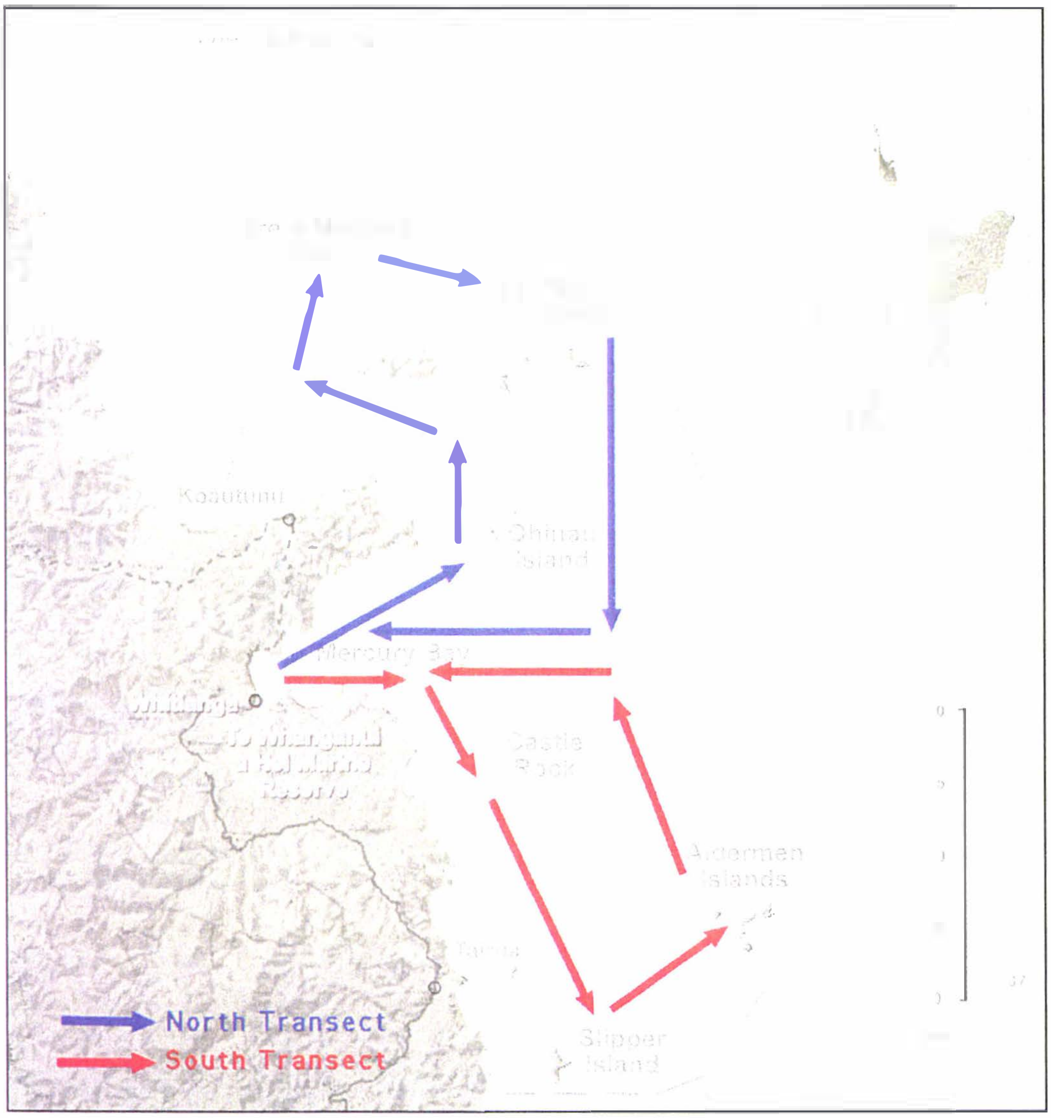


Figure 2. The Mercury Bay study area, including typical transect routes.

two aerial surveys were undertaken from a single-engine Piper Cherokee 4-seater airplane. Their purpose was to provide a more reliable estimate of dolphin abundance in the study area. Counts were to be based upon aerial photographs taken from 200 meters elevation. However, this attempt was abandoned because those animals that were below the surface at the time when photographs were taken, could not be counted, even though water clarity was good and theoretically should not have presented a problem.

3.7 Definition of group:

Common dolphins in the study area were consistently encountered in ‘groups’, and since each ‘group’ was used as the basic unit for analysis, this term requires a formal definition. There is no universally accepted formula for defining a ‘group’ of cetaceans. The species studied, the conditions under which observations are conducted, and the observer’s personal preference all play a part in defining a ‘group’ of study subjects. As a result, definitions vary widely between studies. In assessing 17 studies on bottlenose dolphins, Connor et al. (2000b) found no less than 11 different definitions for ‘group’.

Most definitions rely on either the proximity of animals to each other, or coordination in their behaviour, or a combination of the two. In his thesis on Hector's dolphins (*Cephalorhynchus hectori*) Bejder (1997, p. 13) states: "A group was defined as dolphins in close contact (< 20 meters) with each other." In a study on bottlenose dolphins, Hanson & Defran (1993, p. 130) use a definition that makes implicit assumptions about proximity, which is dependent on their equipment: "A focal group was defined as the aggregation of dolphins viewed within the field of the binoculars during the course of an observation interval." Constantine (1995, p. 15) combines a proximity measure with similarities in behaviour, following the methods of Fertl (1994): "A pod was defined as any number of dolphins moving in a similar direction or engaged in similar behaviours and each of them within five dolphin lengths of any other member of the pod." Shane (1990a, p. 247) is more vague about proximity, and focuses on behaviour: "A pod was defined as any group observed in apparent association, moving in the same direction, and often, but not always, engaged in the same activity". Mann (1999, p. 116) does not believe similarities in activity to be useful in defining a 'group':

> I recommend proximity-based measures, because this method is quantifiable and does not rely on behavioral sampling to determine group membership. 'Coordinated-behavior' definitions make implicit assumptions about proximity, because observers cannot assess the activities of animals who are kilometers away.

One of the problems with proximity-based definitions is the cut-off level. What is the biologically significant distance that would separate a congregation of dolphins into distinct groups ? Whitehead et al. (2000, p. 67) point out the problem:

> Common definitions for grouping involve separations from tens to hundreds of meters, yet most cetaceans can communicate over ranges of kilometers.

After considering all of the above, and after observing common dolphin grouping patterns during the pilot study, it was decided that Reynolds et al.'s (2000, pp. 112-113) description fit the common dolphin pattern rather well:

> Groups (and subgroups) of dolphins represent congregations - that is, relatively temporary collections of individuals in the same general area and often engaged in similar activities.

Therefore, a combination of proximity-measure and the direction of movement was used to define a group: In this study, a group of dolphins was defined as an aggregation of all the dolphins within visual range (3-6 kilometers), as long as they were simultaneously moving in the same direction, when traveling.

3.8 Number of animals in the group:

A visual count, or estimate, of the number of animals in the sampled group was one of the basic variables recorded at each time point. Estimates were always based on the minimum number of animals positively identified as different individuals, and can therefore be considered conservative. The surfacing patterns of the dolphins were closely observed to identify if a new animal had come to the surface, or if the same animal was being counted twice. This method produced very reliable counts for groups of up to 30 animals. For larger groups, the margin of error became increasingly greater. When estimated numbers exceeded 50 individuals, a subsection of the group was focused on, and the animals in this subgroup were counted, and then extrapolated to the total group.

To gain a more detailed picture of the demographics in each group, these estimates were broken down into three size-based categories:

newborns - young calves that still showed fetal folds (Plate 4), or such animals that were of typical newborn size (80-120 centimeters; Evans, 1994), without the folds being apparent.

calves - animals ranging in size from circa 130-160 centimeters, as long as they were still traveling in the typical calf position alongside an adult individual.

adults - any animal not belonging to one of the two categories above. These were apparently fully grown individuals (180 to 220 centimeters in length), physically mature, but not necessarily sexually mature (Collet & St. Girons, 1984). Immature animals, that were not yet fully grown, but were larger than calves, and did not travel in the typical calf position alongside an adult individual, were also included in this category. A further separation of these individuals into a fourth 'juvenile' category was not undertaken, because the visual estimation of the small relative size differences between adults and juveniles was exceedingly difficult, and might have been inconsistent between sightings, as a result of varying distances from the boat.

3.9 Environmental variables:

In addition to the above, sea-state, including wind direction and wind speed, sea surface temperature (measured 30 centimeters below the surface with a hand-held swimming pool thermometer) and the time of the nearest low-tide were also recorded for each sighting. The group's latitude/longitude coordinates were recorded with a hand-held GPS, and later the depth at these locations was taken from the area's navigational charts.

Plate 4. A common dolphin calf featuring fetal folds (light-coloured stripes below the dorsal fin). These are the result of the fetus's tightly-folded position in the womb.

3.10 Photo-identification:

To gain a better understanding of a population's size, its movements, and relationships among the animals, it is necessary to distinguish between individual animals reliably over time. This can be achieved by tagging them, or by using naturally occurring distinctive features of certain individuals.

Würsig & Würsig (1977) discovered that bottlenose dolphin individuals could be reliably identified over several years, from photographs of their dorsal fins. This non-intrusive method of 'photo-identification' has now been well-established for dolphins and other cetaceans (Würsig & Jefferson, 1990). It is based on the observation that each animal's dorsal fin has a unique shape and unique pattern of nicks, notches, and scars. Compared to most bottlenose dolphins, the majority of common dolphins showed very few nicks and notches in their dorsal fins, which made photo-identification much more difficult. However, these dolphins showed a great variability in fin colouration. It ranged from black all over to almost completely white, the most common pattern being a blackish dorsal fin, with a white, or light-grey patch in the centre (Plate 5). Observations of captive common dolphins in Marineland, Napier, New Zealand, confirmed that these colour patterns are stable over long periods of time (several years, D. Kyngdon, pers. comm., 15.1.1999). However, they are not necessarily exact mirror images on either side of the fin; therefore, right-side and left-side views had to be analysed independently for those fins that did not also feature a distinctive outline (Plate 6). The uniqueness of the dorsal fin's outline (including nicks and notches), combined with its colour pattern, were used for identification in this study.

In some rare cases, other distinguishing features were used to identify individual dolphins. Common dolphins have been reported to occasionally suffer from a genetic defect, in which the typical hourglass pattern along the flanks is not expressed (Perrin et al., 1995). The patch behind the eye, instead of being ochre-coloured is grey, which gives the animals an overall resemblance to bottlenose or spinner dolphins (Plate 7). A handful of grey-sided individuals were encountered during this study, and they were identified mainly based upon the extent of the lateral grey patch, its hue, and any distinctive patterning of this patch. One individual that featured an otherwise completely normal colour pattern was identified based upon a line of black pigmentation, circa five centimeters wide, running at an angle from behind the dorsal fin, along the left side of its body halfway towards its venter (see 'Black body-line' in Appendix 3).

Physical deformities can also be useful in identifying individuals (for example see the bottlenose dolphin 'Quasi' in Constantine (1995, p. 20) which suffers from a spinal deformity)). Two common dolphins were

Plate 5. Common dolphin dorsal fins, illustrating the variety of fin colouration from completely black to completely white.

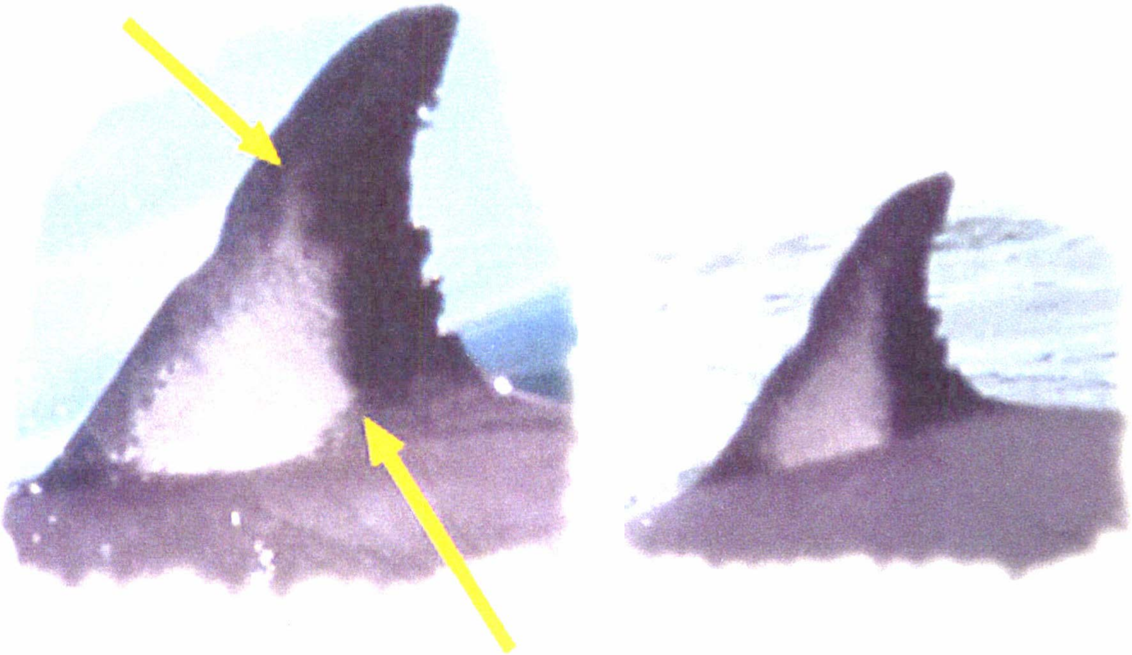


Plate 6. The dorsal fin colour pattern is not always an exact mirror image on either side of the fin. The image on the left is actually the right-side view, flipped over for easier comparison. Arrows indicate areas where the colouration differs between the two sides.

Plate 7. In some common dolphin individuals, the light-coloured yellowish lateral patch behind the eye is not expressed. Instead, this area is grey, giving the animal an overall resemblance to bottlenose or spinner dolphins.

distinguishable by the front third of their upper jaws being turned upwards at a 90 degree angle, giving them a somewhat 'duck-billed' appearance (see 'Platypus' in Appendix 3). These two individuals were separated from each other, based on differences in dorsal fin pigmentation, and by the fact that their bent upper jaws were slightly rotated in opposite directions, to the left in one, to the right in the other. What caused this deformity remains unknown. It could be the result of a fracture, or a congenital deformity. One of the grey-sided individuals featured a distinct bend to the left, of the front third of its rostrum, but as opposed to the 'duck-bills' this involved both the upper and lower jaw, which still closed properly upon each other. Another dolphin carried a deep, well-healed triangular cut in the dorsal part of its peduncle, circa 30 centimeters anterior to the tail flukes. Viewed laterally, a 'V'-shape of skin and muscle was missing, approximately down to a level just above the spine (Plate 8). From the appearance of the injury, a boat strike must be considered the most likely cause. All of the above animals appeared otherwise completely healthy, and well-nourished.

Common dolphins were photographed or video-taped to document unique features. Purely visual confirmation of previously photographed individuals was considered acceptable for a very small number of animals whose features were so extremely obvious, that confusion with any other individual was highly unlikely (animals for which a resighting was scored on that basis were: ‘Platypus’, ‘Black body-line’, and ‘Left-bent greysides’).

Photographs or video of individuals were obtained by opportunistically photographing animals that came close to the boat during group follows. Photos were taken with a Canon EOS 300 camera and a Tamron 35-200mm zoom lens on Fujichrome 100 ASA slide film. Freeze-frames of video footage came from a Sony 900 E digital Handycam and were later transferred to a Macintosh laptop computer for analysis. Unfortunately, the resolution of video-images was only acceptable for identification when the dorsal fin filled almost the entire frame (Plate 9).

Projected slides were separated into four categories of ‘identifiability’: 1) ‘blatantly obvious’, 2) ‘easy’, 3) ‘distinguishable’, 4) ‘too average-looking’ (Plate 10). Only crisp pictures that were completely in focus and allowed the examination of one or more distinct characters, were used in the analysis. Category 4 was therefore excluded. To determine whether or not identifiable individuals had been sighted more than once, the remaining photographs were then systematically checked against each other, by simultaneous projection using two slide projectors side-by-side. Any potential matches were re-checked by volunteers. Matches that were not rejected at this stage were then re-checked by the author several months later, using both projection and

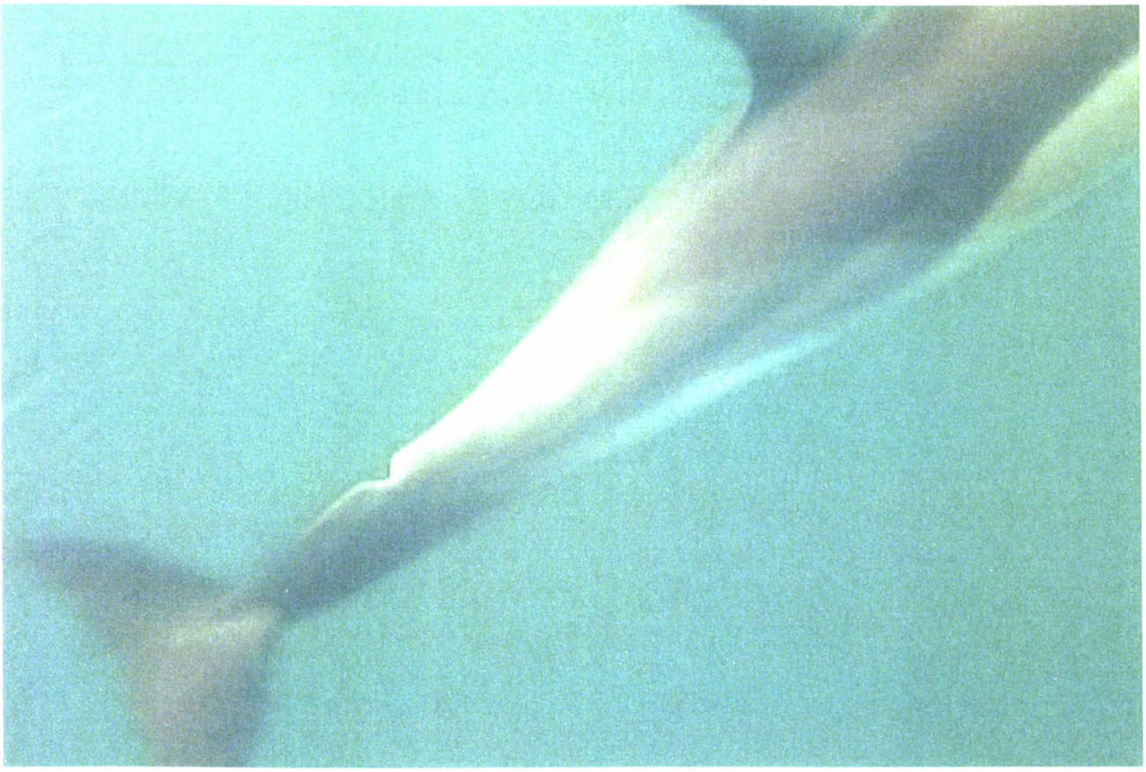


Plate 8. V-shaped cut on the peduncle of a common dolphin. Shape and position of the cut are suggestive of contact with a boat propeller.

Plate 9. Examples of poor (left) and good (right) resolution in still images captured from digital video. While the colour pattern of the animal on the left is very distinct, the dorsal fin's outline is too pixelated. Such images could therefore not be used for photo-identification.

a) b) c) d)

Plate 10. The varying degrees of distinctiveness among common dolphin dorsal fins. Examples for : a) blatantly obvious, b) easy, c) distinguishable, d) too average. Category d) was therefore excluded from photo-identification.

a 2.5x magnification slide viewer. This process was designed to eliminate the possibility of falsely matching two separate individuals as a resighting. Once the photo catalogue was complete, it was also checked for potential matches against the photo catalogues created by Nicolle Van Groningen, University of Bergen, Netherlands (January-July 1998 in the Whakatane area, containing 108 individuals; unpublished data), and Alexandra Leitenberger, University of Vienna, Austria (November 2000-March 2001 in the Hauraki Gulf, containing 500 individuals; Leitenberger, 2001).

3.11 DNA-sampling:

During the second half of the third and final field season (2000/01), exfoliated skin was collected from nine bow-riding common dolphins, in an attempt to genetically determine the gender of these individuals from DNA isolated from their skin samples. A sampling permit is required for such research in New Zealand, and was obtained from the Department of Conservation Hauraki Conservancy (applied for in February 2000, granted in March 2001). Samples were obtained by using a slightly modified skin-swabbing technique which has been applied successfully to genetic sampling of other small cetaceans, namely Hector's dolphins (Pichler et al., 1998) and dusky dolphins (Harlin et al., 1999). A piece of the 'soft' part of velcro was glued to the tip of a 1.5 meters wooden broomstick. A five centimeter piece of the 'hard' part of velcro was folded back onto itself, so that one side stuck to the soft velcro on the broomstick, while the other faced outward. Latex gloves were worn while handling velcro to avoid contamination. This apparatus was then scraped firmly across the backs of bow-riding dolphins. When pieces of skin remained attached to the hard velcro, these were transferred immediately for preservation to a Falcon tube containing 70 percent ethanol. DNA was then extracted from these samples by K. Russell at the University of Auckland, using a simple chelex extraction method, followed by polymerase chain reaction using x-y-related primers (Gilson et al. 1998). The results were then interpreted visually, based on the banding patterns on an electrophoresis gel. This analysis was carried out 'blindly', i.e. K. Russell analysed numbered samples, without knowing which of the sampled individuals had been observed to carry a postanal hump.

3.12 Sampling the behaviour of free-ranging cetaceans:

While it is comparatively easy to study cetacean anatomy or their behaviour in captivity,

> Researchers studying the behavior of cetaceans at sea face several unusual challenges. Many cetaceans swim rapidly, range

> over long distances on a daily basis, and have seasonal migrations of thousands of kilometers. Cetaceans are difficult to follow because they disappear during dives and do not leave long-lasting traces, such as tracks, scats, or dens. (Mann, 1999, p. 102).

A great variety of observational methods have been employed to overcome these challenges (reviewed by Mann, 1999). For delphinids, they range from surveys which provide snapshots of cetacean abundance and distribution (for example see Dohl et al., 1986; Reilly, 1990; Hui, 1994; Reilly & Fiedler, 1994), to detailed long-term studies that include the capture and tagging of individuals (Wells, 1991). Boat-based research is the norm for studies of dolphins, and the systematic following of groups or individuals has contributed greatly to a better understanding, particularly of bottlenose dolphins (Wells et al., 1987; Shane, 1990a,b; Connor et al., 1992; Waples, 1995; Smolker et al., 1997; Bearzi et al., 1999; Nowacek, 1999a). However, the boats' effects on the dolphins must also be considered and minimised by careful approaches, maintaining steady speeds, and remaining parallel to the dolphins (Mann, 2000).

The behaviours sampled by researchers can be separated into behavioural *states* and behavioural *events* (Altmann, 1974; Martin & Bateson, 1993). Single behavioural displays of short duration (e.g.

tailslaps, breaches) are classified as events, while on-going behaviours of longer duration (e.g. resting, feeding, socialising) are considered states (Martin & Bateson, 1993; Mann 2000). Behavioural *events* can often be sampled continuously, especially when they are rare and conspicuous (Waters & Whitehead, 1990; Slooten, 1994). Activity budget data of behavioural *states* has been collected widely by the use of instantaneous scan-sampling, most commonly at 3-minute time intervals (Shane, 1990a,b; Waples, 1995; Bearzi et al., 1999). While a complete ethogram for common dolphins has yet to be published, their behavioural repertoire is sufficiently similar to that of bottlenose dolphins to follow the use of established definitions when categorising behavioural states as either traveling, milling, feeding, resting, or socialising (Shane, 1990a; Waples, 1995; Reynolds et al., 2000).

3.12.1 Sampling behaviour during focal group follows:

The observational sampling of cetacean behaviour can be extremely difficult, and no one sampling method can provide adequate data without having some shortcomings. As a result, "It is practical and advisable to use more than one sampling method." (Mann, 2000, p. 63). In this study, visual observations were aided by documenting some behaviours on video, using a Sony 900 E digital handycam. A custom-built underwater housing on a 2 meter stainless steel pole also allowed for underwater filming, while the observer remained on board the research vessel. The original descriptions of the behavioural sampling techniques discussed here can be found in Altmann (1974) and Martin and Bateson (1993), while the terminology used below follows Mann (1999). The pilot phase of the study (Nov-Dec 1998) proved helpful in choosing the appropriate sampling techniques. It became clear that focal individual follows would be too difficult to carry out, because of the large size of dolphin groups, constant movement of individuals within the group, and difficulties in clearly distinguishing between individuals. The number of variables recorded on the data sheet was condensed to a manageable format (Appendix 1), and after attempts at continuous behavioural sampling proved dissatisfying, 3-minute interval sampling provided encouraging results.

One of the preferred options in behaviour sampling is to follow a focal individual, because this tends to provide the most accurate information, and data based on the "natural unit for analysis" (Mann, 1999, p. 117). Focal animal sampling is best suited to small and stable groups, and is dependent on the presence of readily identifiable group members. Therefore, this was not the most appropriate option in this study, because groups were often large (> 50 individuals) and individuals were rarely recognisable from natural markings in the field, with many group members possessing similar features (although a number could be distinguished later in the laboratory, when looking at highly detailed photographs). Secondly, individuals frequently changed their position within the group. It would not have been possible to follow one individual consistently without driving the boat through the group, potentially causing considerable disturbance. Therefore, a focal group follow protocol was chosen for data collection. To minimise potential biases, it strictly followed Mann's (1999, p. 110) recommendations:

> [When conducting a focal group follow] an estimate of predominant group activity *can* be achieved by explicitly scan sampling over 50 percent of the individuals, rather than by 'watching' the group.

This was accomplished by instantaneous scan-sampling at 3-minute intervals. Mann (1999, p. 105) also states that, "The sampling protocol must include a 'decision rule' for when one or more animals leave the group". 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 represented the larger or the smaller group. This was possible because the two groups never simultaneously deviated from their previous course. This rule was employed to avoid harassment of the dolphins. The dolphins that separated from the focal group may have done so because of the presence of the research vessel. To avoid any undue stress on these animals, they were not followed. Additionally, this rule was advantageous in assessing the effects of tourism on common dolphins (chapter 6). The tour boat would always stay with those dolphins which continued to travel on the boat's course, rather than change its course to follow other animals. Therefore, the animals that were sampled were those most likely to be impacted by the tour boat.

3.12.2 Instantaneous scan sampling:

To establish how much time common dolphins spent on various activities during a follow, the focal group was scanned every three minutes and data recorded on the following variables:

Activity state: The behavioural state which more than 50 percent of the animals were involved in at each time point (= instantaneous sampling of predominant activity). Five categories of activity state were defined as follows, closely modeled after the definitions used by Shane (1990 a), Hanson and Defran (1993), and Waples (1995) for bottlenose dolphins:

resting - the dolphins stay close to the surface, and close to each other. They surface at regular intervals in a coordinated fashion, either not propelling themselves at all, or moving forward very slowly.

milling - the dolphins are swimming along, but frequent changes in direction prevent them from making noticeable headway in any one direction and they remain in the same general area. Often different individuals in the group will be swimming in different directions at a given time, but their frequent directional changes keep them together.

traveling - the dolphins propel themselves along at a sustained speed, all heading in the same direction and making noticeable headway along a certain compass heading.

feeding - the dolphins are seen either capturing fish, or pursuing fish. The herding of fish was also included in this category, as it was invariably followed by at least some fish captures.

socialising - any physical interactions taking place among the members of a group (except mothers and calves), including chasing each other, body contact, and copulation. Often accompanied by aerial behaviour.

The above categories were chosen after the pilot phase of this study, during which it became clear that any observed activity states could be classified accurately under one of the above definitions, fulfilling the requirement set forth by Martin & Bateson (1993, p. 60): "More important still, the criteria used to define a category should unambiguously distinguish it from other categories, particularly those it resembles most closely". The distinction between socialising, traveling, resting, and feeding/foraging, is widely accepted and forms the basis of most activity budgets on cetaceans (Mann, 2000). Shane

(1990a) and Waples (1995) also included 'milling', which appeared useful to classify some of the observed common dolphin behaviour. Further distinctions, including mixed behaviours, did not appear to fit the common dolphin pattern. Waples (1995) and Hanson & Defran (1993) included 'play' as a separate activity category. Play with objects (e.g. seaweed) was very infrequent for common dolphins, and such episodes were of short (< 1 minute) duration. Therefore, they were scored as events in this study.

3.12.3 Continuous sampling of behavioural events (incident sampling):

In addition to the instantaneous scan-sampling of behavioural states, continuous focal group sampling was carried out for behavioural events. Continuous sampling of an entire group is possible when observations are limited to a number of highly visible and infrequent behaviours of short duration (Waters & Whitehead, 1990; Slooten, 1994; Mann, 2000). This was applicable to the following:

- **aerial behaviour,** including: leap, breach, spyhop, tailslap, chest slap (see below for definitions).
- **bodily contact,** including: biting, pectoral touch, body touch, rolling together at the surface while maintaining body contact, belly-to-belly contact, and copulation. The latter two were both classified as 'sex'. Intromission could rarely be confirmed, but the body-positions for

belly-to-belly contact were identical with those for confirmed copulations (Plate 11).

- play: This included carrying seaweed in mouth or on body parts, and harassing seabirds floating on the surface.

- **chuffing:** a rapid, forceful exhalation.

- **bubble-blow:** a burst of bubbles is released from the blowhole while submerged.

- abrupt **directional changes** while traveling.

- abrupt **changes in breathing interval**, e.g. prolonged diving.

- **reactions to swimmers** entering the water: did some dolphins show a visible reaction to swimmers, e.g. by approaching or avoiding them ?

- **fission and fusion** of groups: when some animals joined or left the focal group, the time for that event was noted, along with the number of animals in the focal group before and after the event.

- **boat avoidance**: the entire group suddenly changed direction away from the research vessel or the tour boat, and/or dived for a prolonged period of time; and exhibited this behaviour consistently during renewed approaches by the boat. When this behaviour occurred three times in a row within three minutes, it was scored as boat avoidance, and the focal group follow was terminated to avoid harassing the dolphins.

Plate 11. Sex. Two common dolphins in the typical belly-to-belly mating position.

3.12.4 Definitions of specific behavioural events:

leap - jump in which the dolphin clears the surface with the entire body and enters the water again, head-first without much splashing.

breach - jump in which the dolphin clears the surface with its entire body and then crashes onto the surface (mostly on its side, or its back) creating a loud noise and a big splash.

chest slap - essentially a partial breach in which only the front half of the body clears the surface and is brought down rapidly onto the surface in a bowing motion, creating a loud smacking sound and a splash (Plate 12).

head slap - same as chest slap, but here only the head clears the surface and is slapped onto the surface in a nodding motion.

tailslap - the tail flukes are raised above the surface, and then brought down rapidly onto the surface, creating a loud smacking sound.

chase - one dolphin rapidly pursuing another dolphin

spyhop - the animal is in a vertical position in the water and raises its head above the surface, at least far enough to expose the eyes, and after a brief 'look around' slips back below the surface.

rolling together - 2 animals are in bodily contact and spin around their axis and/or each other at the surface.

chuff - a brief, noisy, forceful exhalation

bubble blow - the animal releases a large volume of air through its blowhole while submerged, in one short burst.

whistle - high-pitched whistle-like vocalisations, heard above the surface without the aid of a hydrophone.

play - behaviour without an apparent purpose, other than perhaps to 'amuse' the dolphin. Two forms of play were observed and scored in this category. They were: carrying seaweed in mouth, or on body parts (Plate 13), and poking seabirds floating on the surface with rostrum.

long dive - the pattern of breathing intervals changes abruptly and the animals stay submerged for at least twice as long as they did on the previous dive.

change of heading - the entire group - while traveling - suddenly changes its heading by more than 90 degrees from one surfacing to the next.

Sequences of behavioural events - On certain occasions, some of the above behavioural events occurred temporally close together, and may therefore be connected. When 2 or more of these events occurred in succession, and each event was separated by less than 2 minutes from the preceding one, then these were considered a sequence, following the methodology used by Slooten (1994).

Plate 12. Chest slap. Sequence illustrating how a common dolphin rears up above the surface (left), to slam its upper body onto the surface a fraction of a second later (right), creating a big splash and loud smacking sound.

Plate 13. Play. Common dolphin carrying a piece of seaweed on its dorsal fin during an episode of playing.

3.13 Vessel impact:

In most boat-based studies, it is difficult to estimate to what degree the dolphins might be affected by the boat's presence. Land-based observations have quantified interactions between dolphins and boats, which varied according to the boats' and the dolphins' behaviour (Acevedo, 1991; Janik & Thompson, 1996; Bejder et al., 1999). Nonetheless, research on the effects of boat traffic on dolphin behaviour can also be conducted successfully by observers who are aboard a vessel themselves (Würsig & Würsig, 1979; Constantine, 1995; Nowacek, 1999a; Peterson, 2001). While some researchers reasoned that dolphins were habituated to their research vessels and therefore did not examine their vessels' potential impact (e.g. Waples, 1995; Nowacek, 1999a), the dolphins' reaction to the research vessel, as well as the tour boat, were taken into account in this study. This was accomplished by collecting the first data point from the distance at which dolphins were first spotted (between 200-500 meters from the focal group). While it is possible that the dolphins' behaviour was already affected at this distance (which has been demonstrated for other cetaceans (e.g. see Myrberg, 1990), including dolphins (Au & Perryman, 1982)), it is generally assumed that vessel impact is low or absent at distances of 400 meters or more (Constantine, 1995; Constantine & Baker, 1997). The research vessel then proceeded to within < 100 meters of the nearest dolphin, for easier recording of behaviour, and photo-identification. This slow and steady approach typically took 30-90 seconds. By the time of the second data point, the vessel was therefore considerably closer to the animals, and any behavioural changes in response to this approach could then be tested by comparing the first and second data points of each focal group follow.

Data on the following variables were recorded at every 3-minute instantaneous scan sampling time point and tested for correlations with boat approaches, or swim attempts:

Spread: This was the area over which the group was spread out, estimated as the distance between the 2 group members that were farthest apart from each other.

Heading: When the animals were traveling, their magnetic compass heading was read off the boat's compass.

Speed: The animals' speed was recorded based upon the speed showing on the boat's speedometer. Speeds of less than 5 kph were recorded as 'slow'.

Boats: The number and types of boats present within 400 meters of the dolphins.

Boat distance: The distance between boats present (including the research vessel) and the dolphin(s) closest to them. If the animal closest to the boat was bow-riding, the distance was scored as 0. Boat distance information can therefore also be used to estimate the maximum possible distance for the dolphin farthest away from the boat, calculated as boat distance + group spread.

3.14 Statistical analysis

To avoid pseudoreplication, each focal group follow - not each individual data point - was treated as an independent sample. This cut the sample size from n=2364 (data points) to n=105 (sightings). Chi-square contingency tables, linear regressions, and analyses of variance were used to test the statistical significance of results, in accordance with Sokal & Rohlf (1981), Zar (1984), and Norman & Streiner (1994). Statistician Dr. D. Meyer (Massey University) was kind enough to advise on the suitability of tests, and accuracy of results.

3.15 Summary

The methods used in this study followed established and widely accepted sampling techniques used in studies of small cetaceans. These methods were evaluated during the pilot phase of this study, and were adapted to the unique characteristics of common dolphins. This led to scan-sampling of the predominant group activity state at 3-minute intervals, while behavioural events were recorded continuously. Data were also collected on group size, location, reactions to boats and swimmers, along with basic environmental variables.

4. COMMON DOLPHIN ECOLOGY

- Habitat use, demographics, and group formation in common dolphins

4.1 Introduction:

This chapter examines several questions about common dolphin ecology, including preferred areas of use, fluctuations in dolphin abundance, and mechanisms governing group formation. The results section (4.2) first examines average numbers of individuals, and the influence of environmental parameters on sighting success. Then, the dolphins' seasonal movements are explored, followed by the question of sexual dimorphism in common dolphins, which leads to the issue of variations in the sex ratio of dolphin groups.

The discussion (4.3), focusses mainly on diurnal and seasonal factors which may influence dolphin movements and abundance, as well as the roles of prey availability and predator avoidance in group formation. The summary (4.4) concludes that common dolphins appear to live in a fission-fusion society, like many other pelagic dolphin species. Photo-identification of individuals suggests that they are not resident in the study area for extended periods of time.

4.2 Results:

4.2.1 Field effort:

166 trips were conducted, which resulted in 105 focal group follows. 641 hours were spent on effort; 118.2 hours of these were spent following common dolphins. The mean duration of focal group follows was 67.5 minutes (SD=39.55, range= 15 to 195 minutes). 72 focal follows were considered baseline data, with only the research vessel present; while 33 focal follows were conducted with the tour boat present for all or part of the follow. The entire data set was used to calculate the results in this chapter. It was further augmented by Rod and Elizabeth Rae, who shared their data on 204 sighting locations for common dolphin groups from 1992-1998. This brought total sample size for analysis of seasonal movements to n=309.

4.2.2 The numbers of adults, calves, and newborns in each group:

Over the three study seasons, the number of individuals in each encountered group ranged from three to circa 400, with a mean of 57.3 (SD=50.78, n=105). Mean group size varied seasonally, with the largest groups encountered in early spring, and late summer (Figure 3). However, there was no significant correlation between group size and time of year (r=0.13, df=7, p>0.1). Null-hypothesis *H0 2: Average group size does not change significantly over time*, can therefore not be rejected.

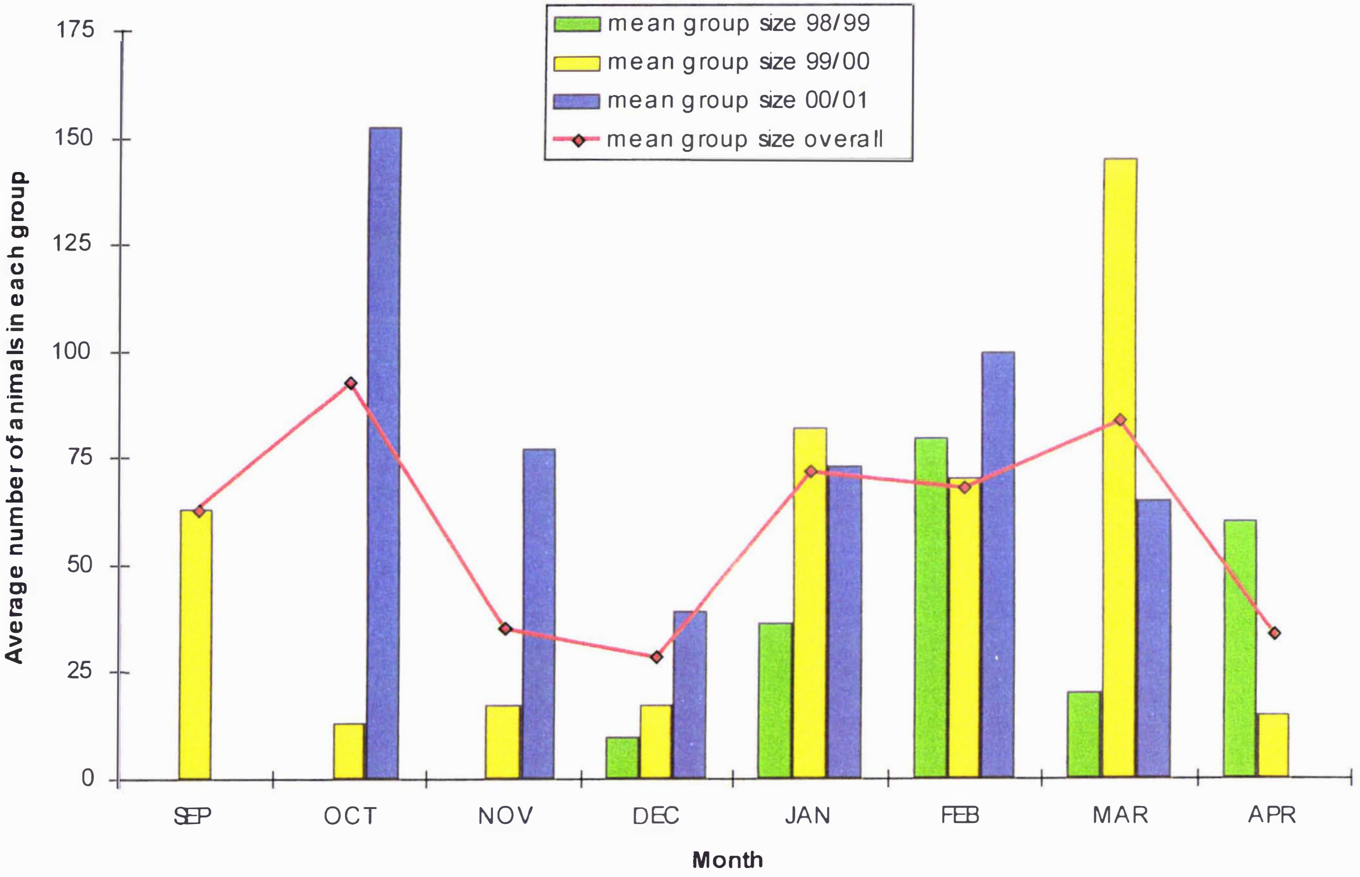


Figure 3. Average group size over the months of the study season.

The number of calves in each group ranged from 0 to 15 with a mean of 2.4 per sighting (SD=7.41, n=105) (Figure 4). The seasonal fluctuations of the number of calves in each group mirrored those for overall group size, and were also not significantly correlated (r=0.22, df=7, p>0.1). Null-hypothesis *H0 4: The number of calves in each group does not change significantly over time*, can therefore not be rejected.

The number of newborns in each group ranged from 0 to 12 with a mean of 1.8 per sighting (SD=4.63, n=105). Increasing numbers of newborns were observed, as the study season progressed, peaking in late summer (Figure 5). A simple regression shows a significant positive correlation between time of year, and the number of newborns (r=0.75, df=7, p<0.02). This means that null hypothesis *H0 6: The number of newborns in each group does not change significantly over time*, can be rejected.

4.2.3 Seasonal, diurnal, and tidal variations in sighting success:

While most sightings occurred in late summer, the success rate of encountering dolphins on surveys decreased over the field season (Figure 6). A simple regression shows a significant decrease in sighting success from September to April (r=0.68, df=7, p<0.05). This is probably a result of the dolphins' seasonal offshore movement,

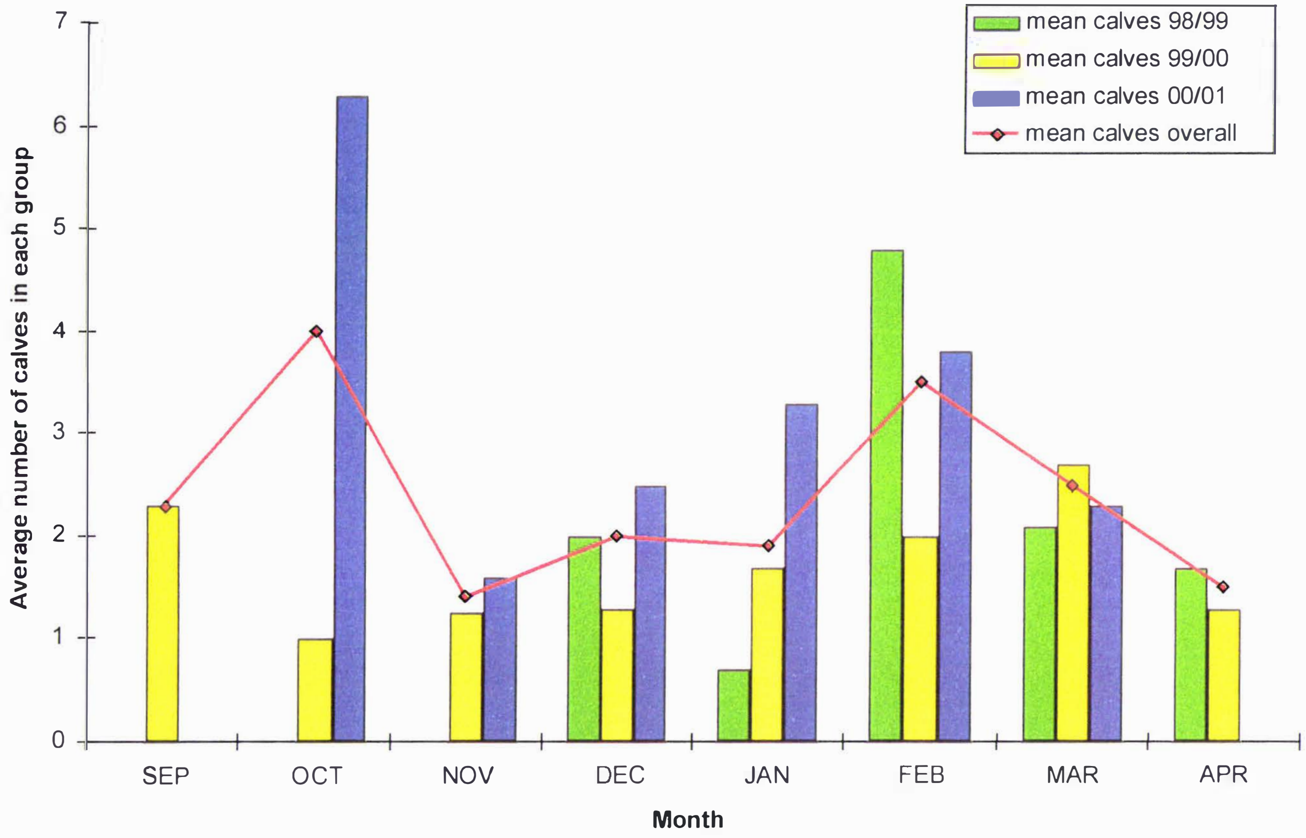


Figure 4. Average number of calves per group, over the months of the study season.

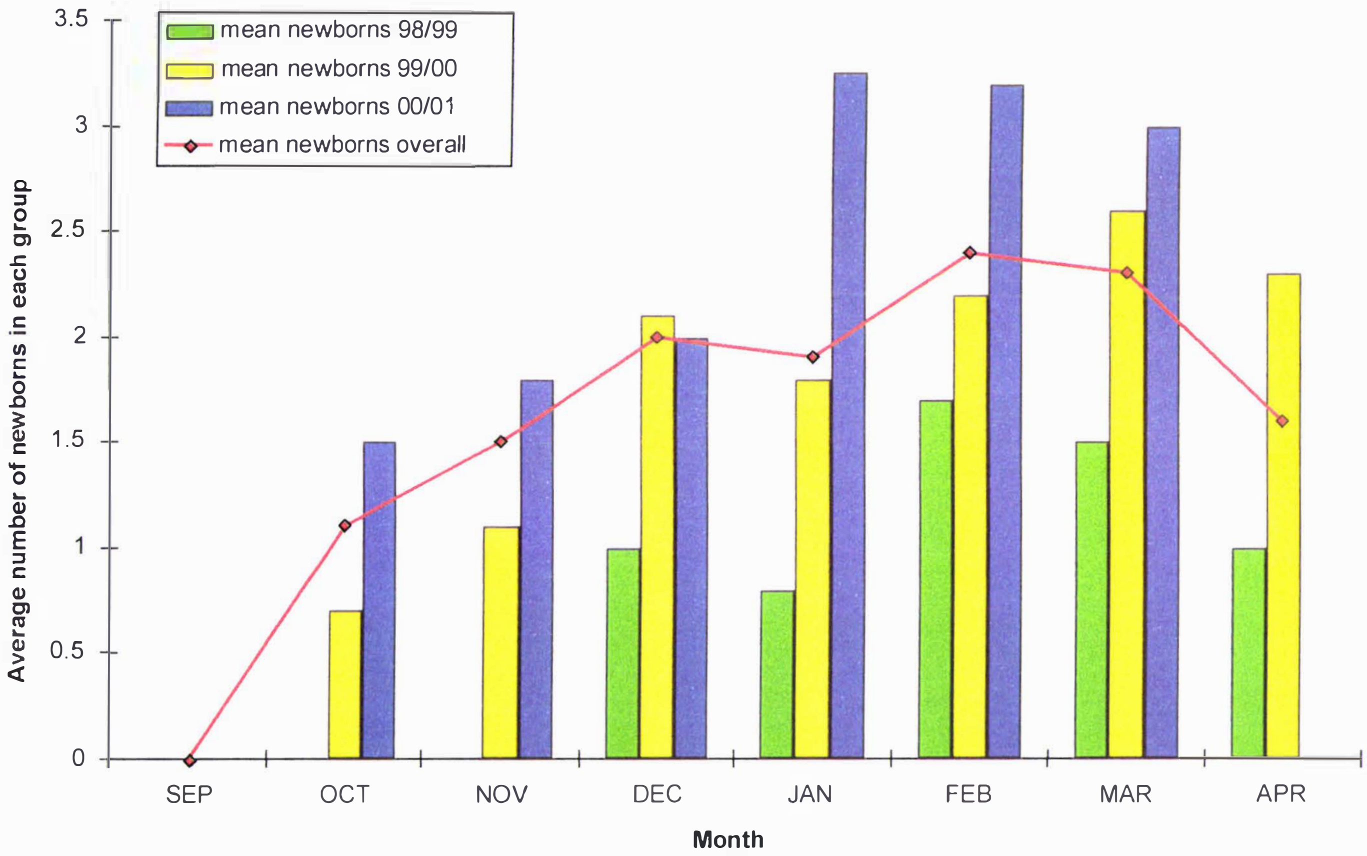


Figure 5. Average number of newborns per group, over the months of the study season.

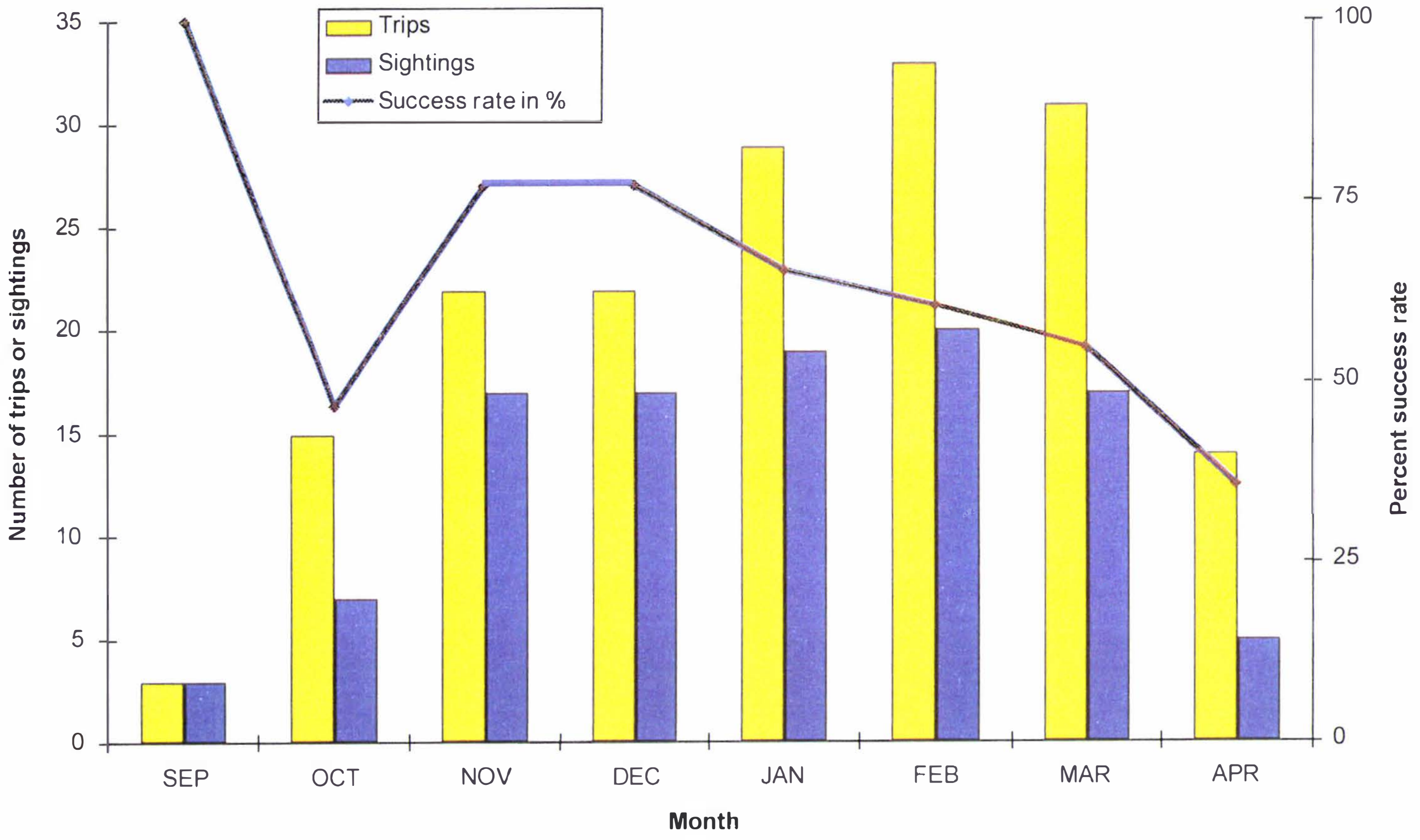


Figure 6. The number of survey trips vs. the number of dolphin sightings, over the months of the study season.

discussed below. The time of day also played a role in sighting success (Figure 7).

There is a noticeable decrease in sighting success rate over the time of day, i.e. the later in the afternoon, the less likely dolphins were to be found. The local dolphin tour operators have also observed this pattern, and as a result do not offer any dolphin-trips in the afternoon. Because of this, field effort was directed mainly towards morning hours. However, a chi-square test failed to show a significant association between time of day and sighting success (chi-square=3.47, df=3, p>0.1).

The New Zealand coastline is subject to a diurnal tidal flow with 2 high tides and 2 low tides in any 24-hour period. Therefore, the maximum time between a sighting and the nearest low tide could never exceed six hours. Most sightings occurred closer to the time of low-tide, rather than later (Figure 8). However, this association was not statistically significant (chi-square=0.92, df=2, p>0.1). These results show that null hypothesis *H0 7a: The presence of dolphins in the study area is not affected by the time of year,* can be rejected. The evidence is not sufficient to reject *H0 7b: The presence of dolphins in the study area is not affected by the time of day,* or *H0 7c: The presence of dolphins in the study area is not affected by diurnal tidal fluctuations.*

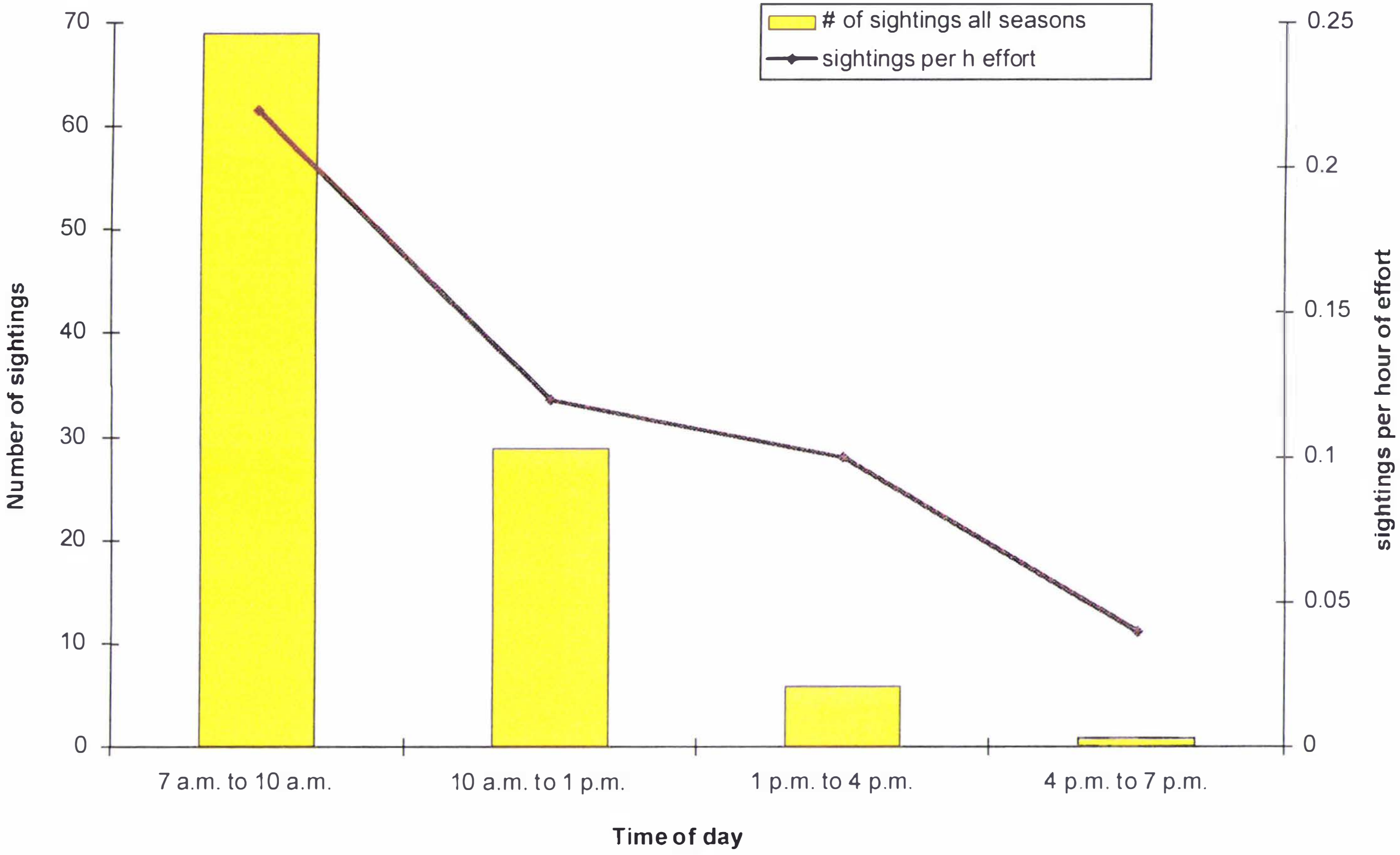


Figure 7. Variations in sighting success vs. time of day.

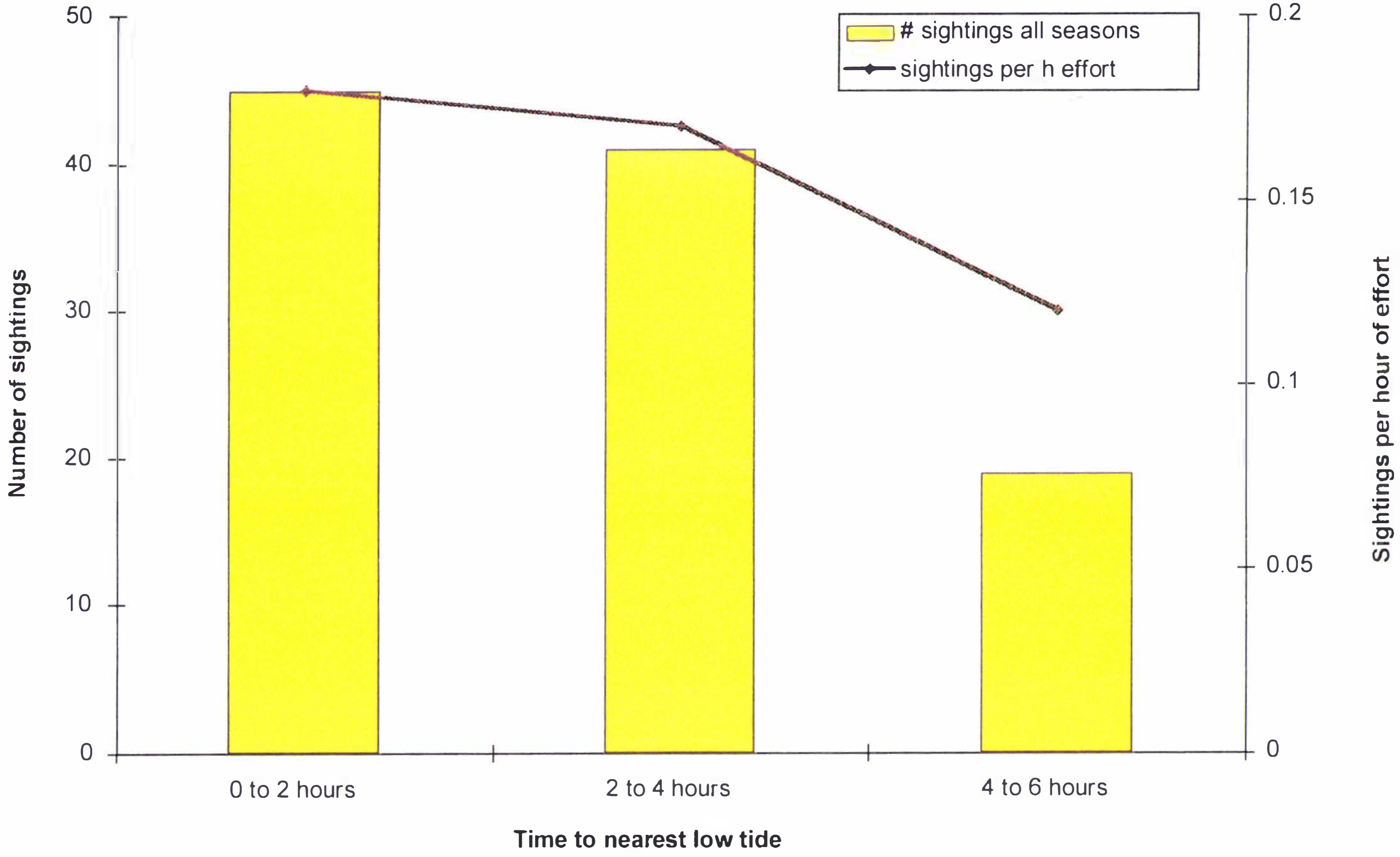


Figure 8. Variations in sighting success vs. the timing of low tide.

4.2.4 Seasonal movements:

Dolphins were found at a mean distance of 9.2 kilometers from shore in spring (SD = 4.12, n=89), 14.4 kilometers from shore in summer (SD = 4.42, n=162), and 19.1 kilometers from shore in autumn (SD = 3.86, n = 58) (Figure 9). A significant offshore trend progressing from spring to autumn was observable in eight of nine years between 1992 and 2001 (Figure 10, Table 2). Data from 1992/93 to 1997/98 represent sighting records made available by Rod and Elizabeth Rae (Mercury Bay Seafaris), while data from 1998/99 to 2000/01 were collected by the author. The 1994/95 season was the only year in which common dolphins did not show a significant offshore movement (r = 0.118, df = 46, p>0.05). Null-hypothesis *H0 8: Habitat use, indicated by the average distance from shore, does not change significantly over time*, can therefore be rejected

The seasonal offshore movement suggests a preference for warmer waters. Sea surface temperature in the study area fluctuates between 16 degrees C in winter and 23 degrees C in summer near shore, with a gradient to 2-3 degree C warmer waters 50+ kilometers offshore (Figure 11). Limited survey effort (because of poor weather conditions) during the winter months (June-August) did not yield any sightings of common dolphins, which suggests they spent most of their time

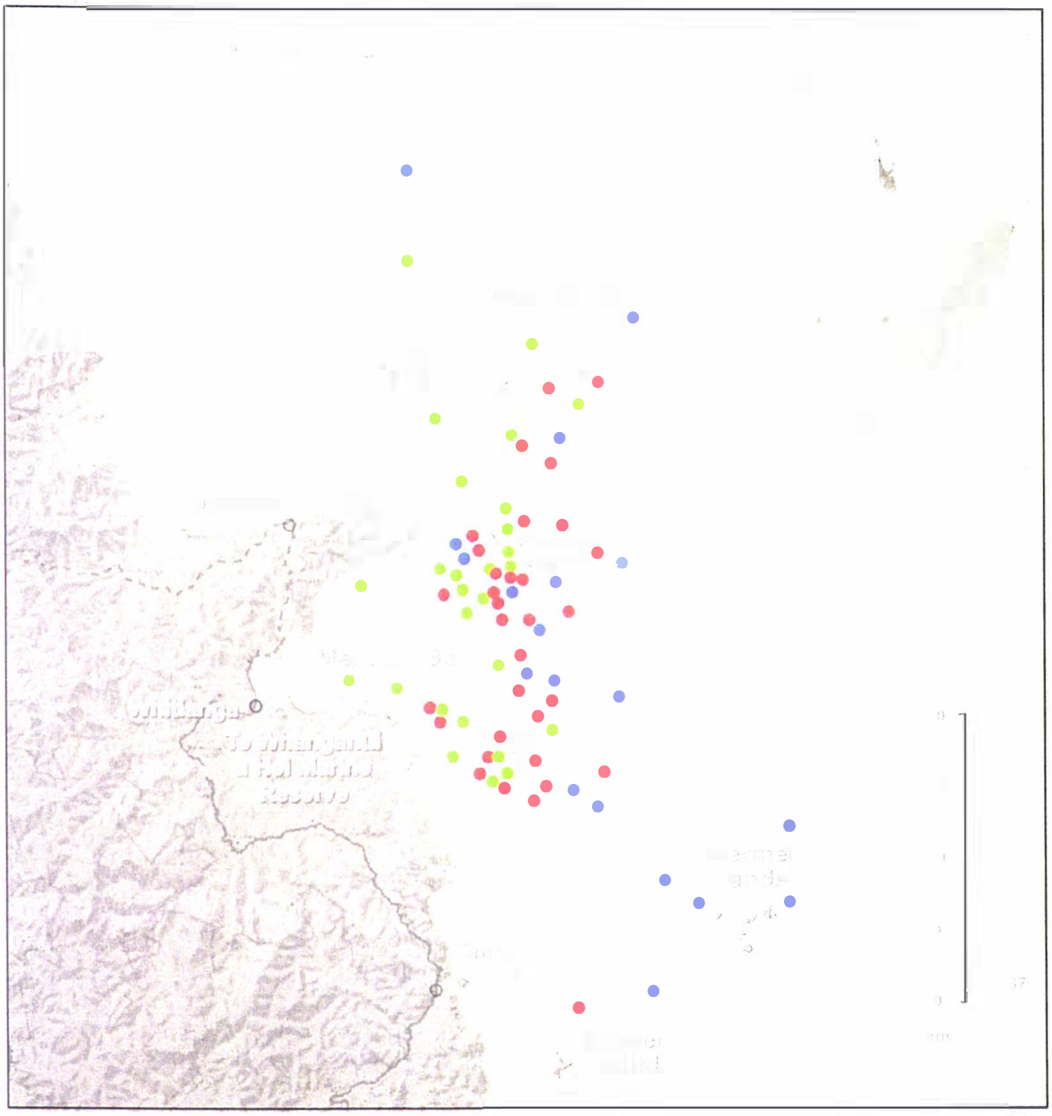


Figure 9. Locations of dolphin sightings illustrated by season : spring = green, summer = red, and autumn = blue.

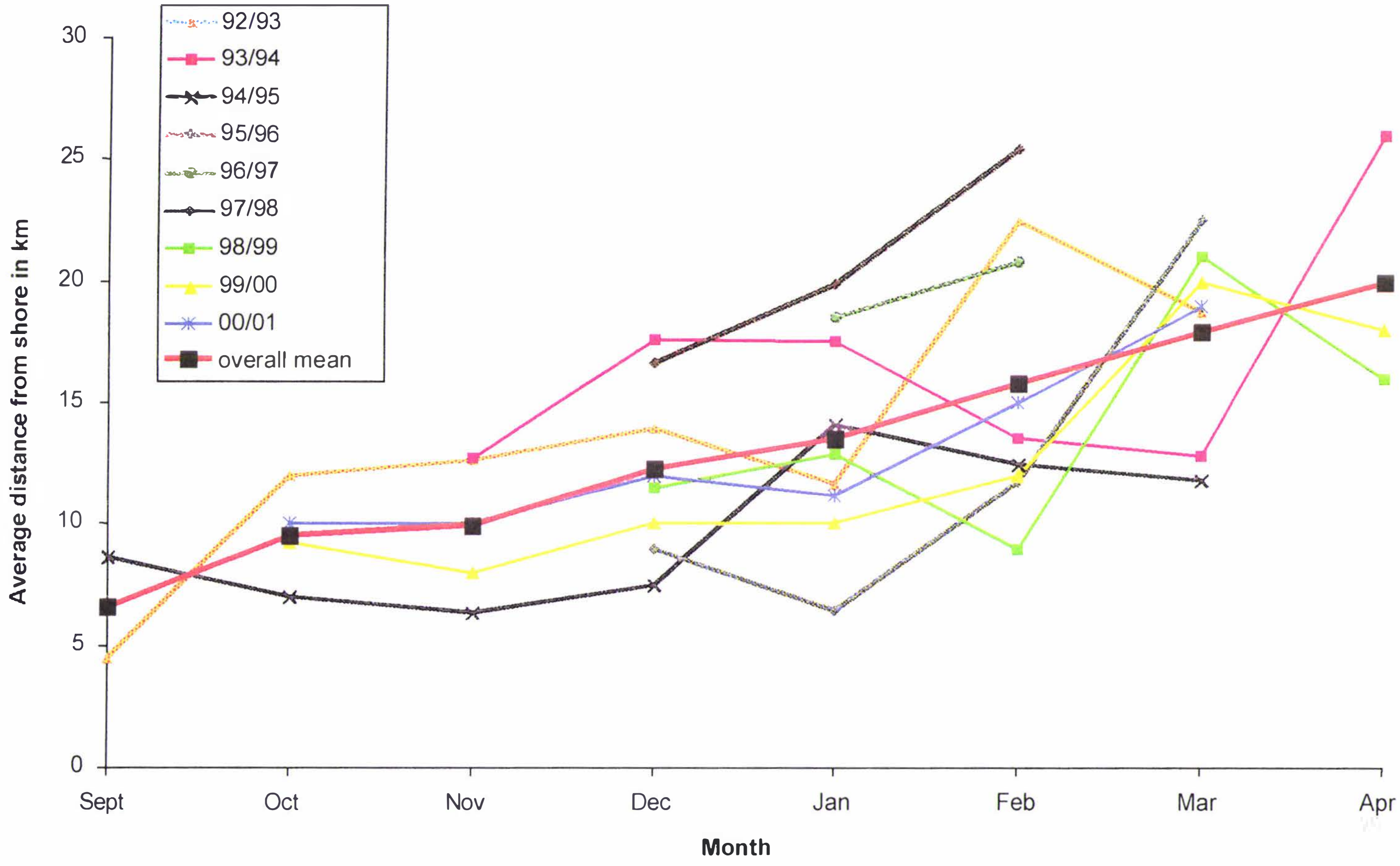


Figure 10. Mean distance from shore for common dolphin groups over the months of the study season, from 1992-2001.

Table 2. The statistical significance of common dolphins moving progressively farther offhore from spring to autumn, over consecutive years.

Year	**correlation r =**	**df**	*p*
1992/93	0.381	15	< 0.01
1993/94	0.295	62	< 0.02
1994/95	0.118	46	> 0.05 (ns)
1995/96	0.595	21	< 0.02
1996/97	0.402	27	< 0.02
1997/98	0.526	26	< 0.02
1998/99	0.530	23	< 0.02
1999/00	0.383	50	< 0.01
2000/01	0.452	30	< 0.01

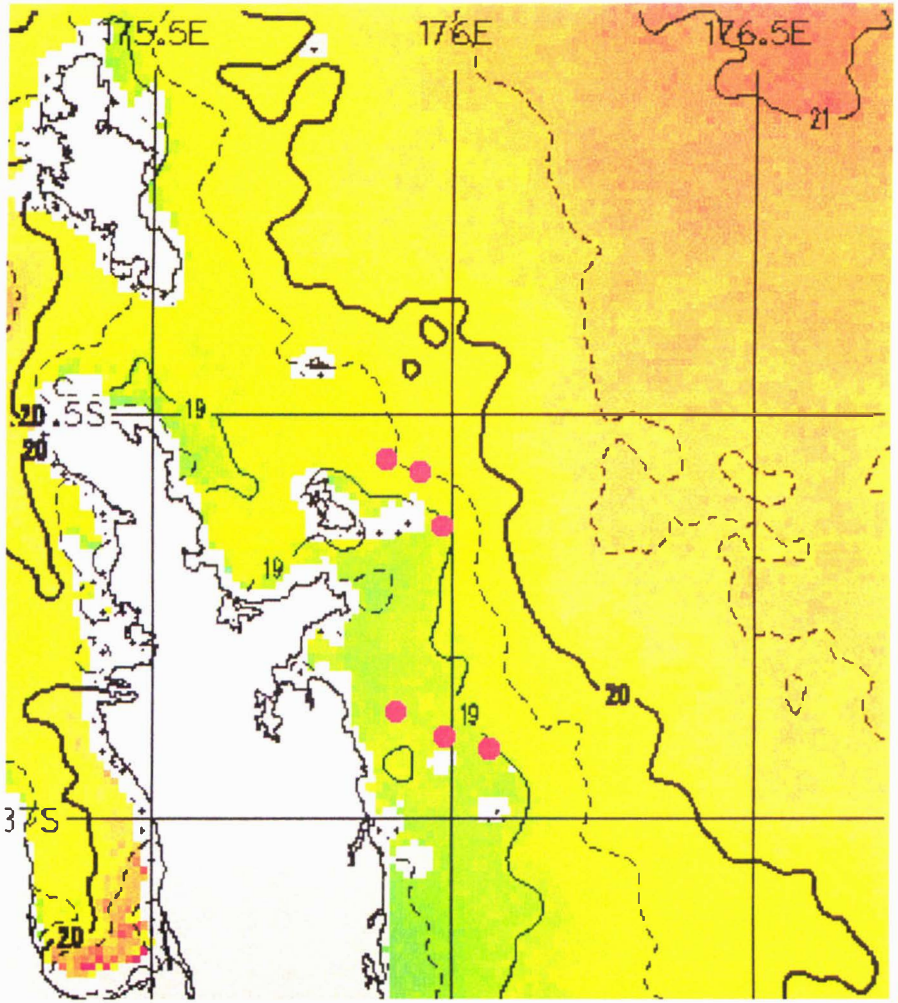


Figure 11. Chart created from satellite data, January 1998, illustrating the typical summer temperature gradient along the Coromandel coast. Note red dots, representing dolphin sighting locations during that month. © NIWA 1999.

outside the study area, in winter. Additional anecdotal evidence from local fishermen and charter boat operators also supports this conclusion (R. Rae, A. Hansford, pers. comm. 5.3.2000).

The dolphins' movement appeared to be strongly affected by the El Niño and La Niña Southern Ocean oscillation patterns. In January/February 1994, 1996, and 1999 when SST near shore was 2°C warmer than 'normal' (La Niña conditions (Jones, 2000)) the dolphins' mean distance from shore was only 6.2 kilometers (SD = 2.56, n = 54), whereas in years with 'normal' SST it was 11.5 kilometers (SD = 3.84, n = 47) (Figure 12). Additionally, in years with warmer than average SST, the dolphins' autumn offshore movement appeared to be delayed by about a month (Figure 13).

4.2.5 Group formation and composition:

The number of individuals in each group was rarely small enough to allow a picture to be taken of each individual. This precluded an assessment of the percentages of animals in each group that could be reliably identified versus those that could not. Therefore, although photo-identification is often used for mark-recapture analyses in estimating cetacean abundance (Wells & Scott, 1990), such an estimate would have been rather unreliable, based on the present data set. However, the number of common dolphins seen in the study area must

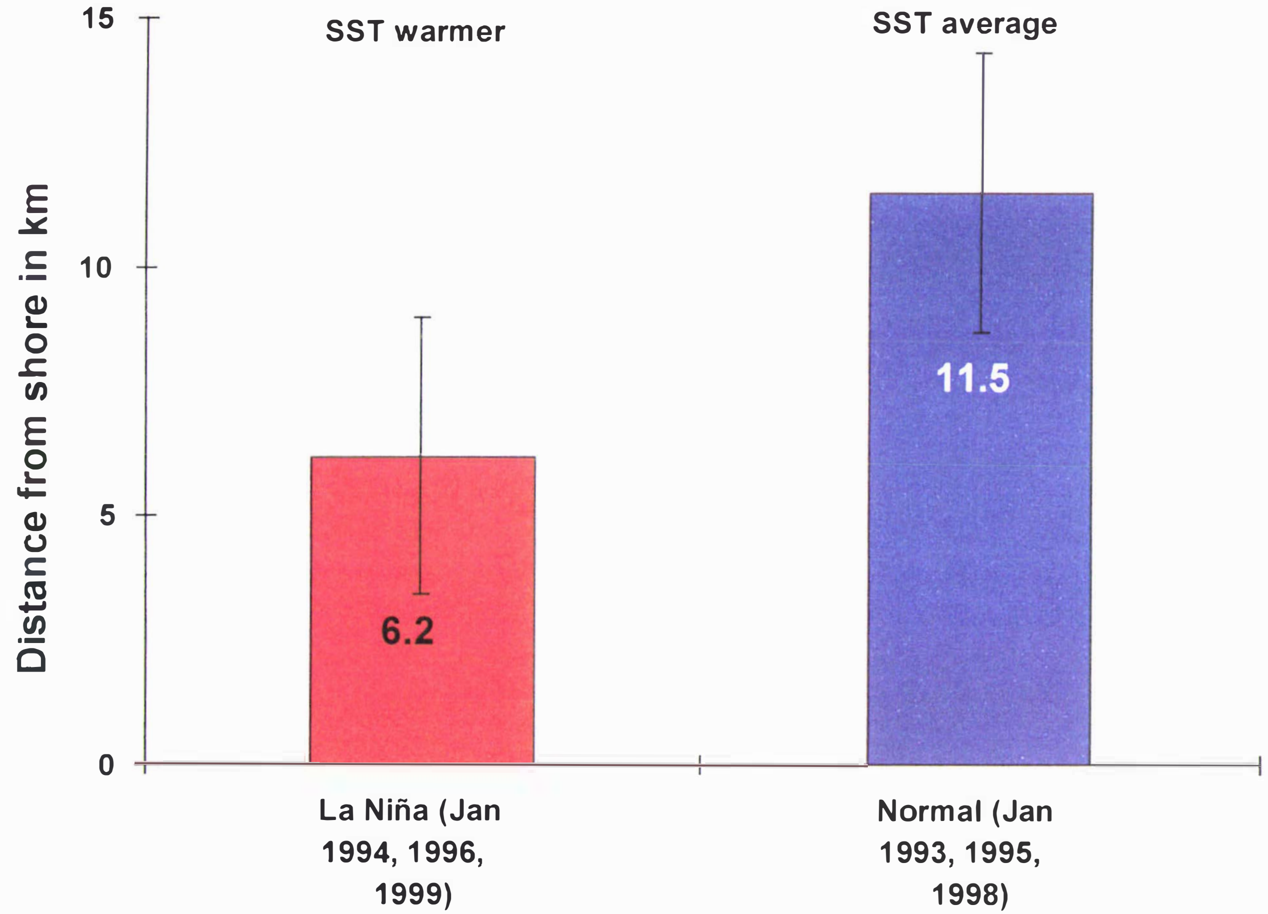


Figure 12. The dolphins' mean distance from shore during La Niña and "normal" conditions.

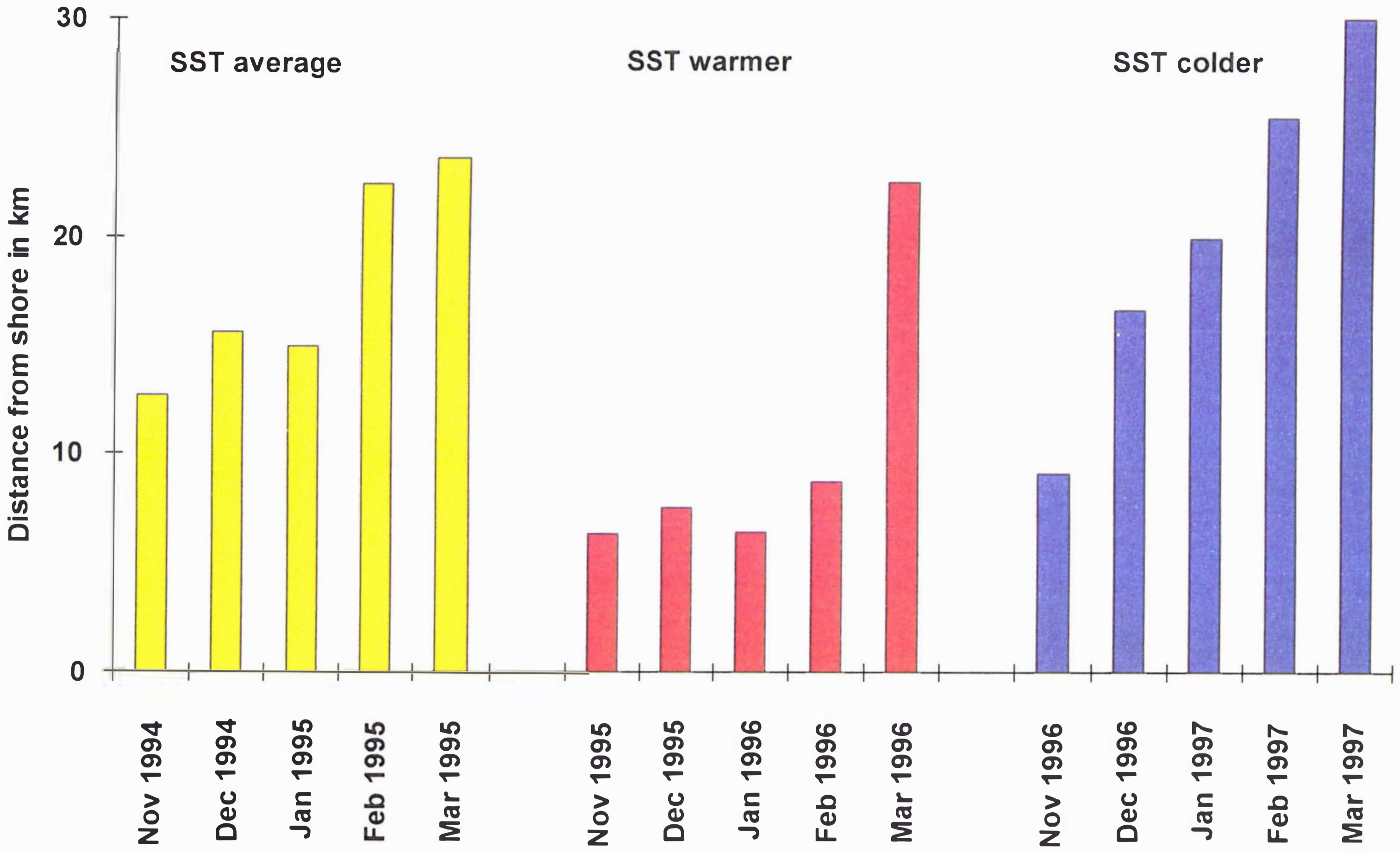


Figure 13. The dolphins' mean distance from shore in relation to variations in sea surface temperature (SST).

lie somewhere between 408 (number of identified individuals) and 6000 (cumulative total number of animals in focal groups).

The low rate of resightings (4.4 percent), and the fact that the number of identified individuals has not plateaued, suggest that the actual abundance probably tends towards the higher end of this range. The rate of identifying new individuals in each focal group did not decrease over the study period (Figure 14). It hovered around five individuals per sighting, peaking at 11 in October 2000. This increase was mainly due to superb sea conditions, improving photographic quality. The rate did drop off after October 2000, but this is not a significant decrease, seen over the entire study period ($r=0.31$, $df=14$, $p>0.1$). This, along with the lack of any indication that the number of identified animals was approaching an asymptote (Figure 15), points to a rather large, 'open' population of dolphins (Wells & Scott, 1990; Constantine, 1995; Bejder, 1997).

Group stability over a day - On 44 occasions groups of dolphins merged temporarily (fusion). On 45 occasions a group of dolphins split up into 2 or more separate, smaller groups (fission). Fusion was usually followed by a change in behaviour. 13 times (30 percent) fusion was followed by sexual activity among the members of the now enlarged group, 18 times (40 percent) it was followed directly by cooperative feeding (Figure 16). This change of behaviour occurred

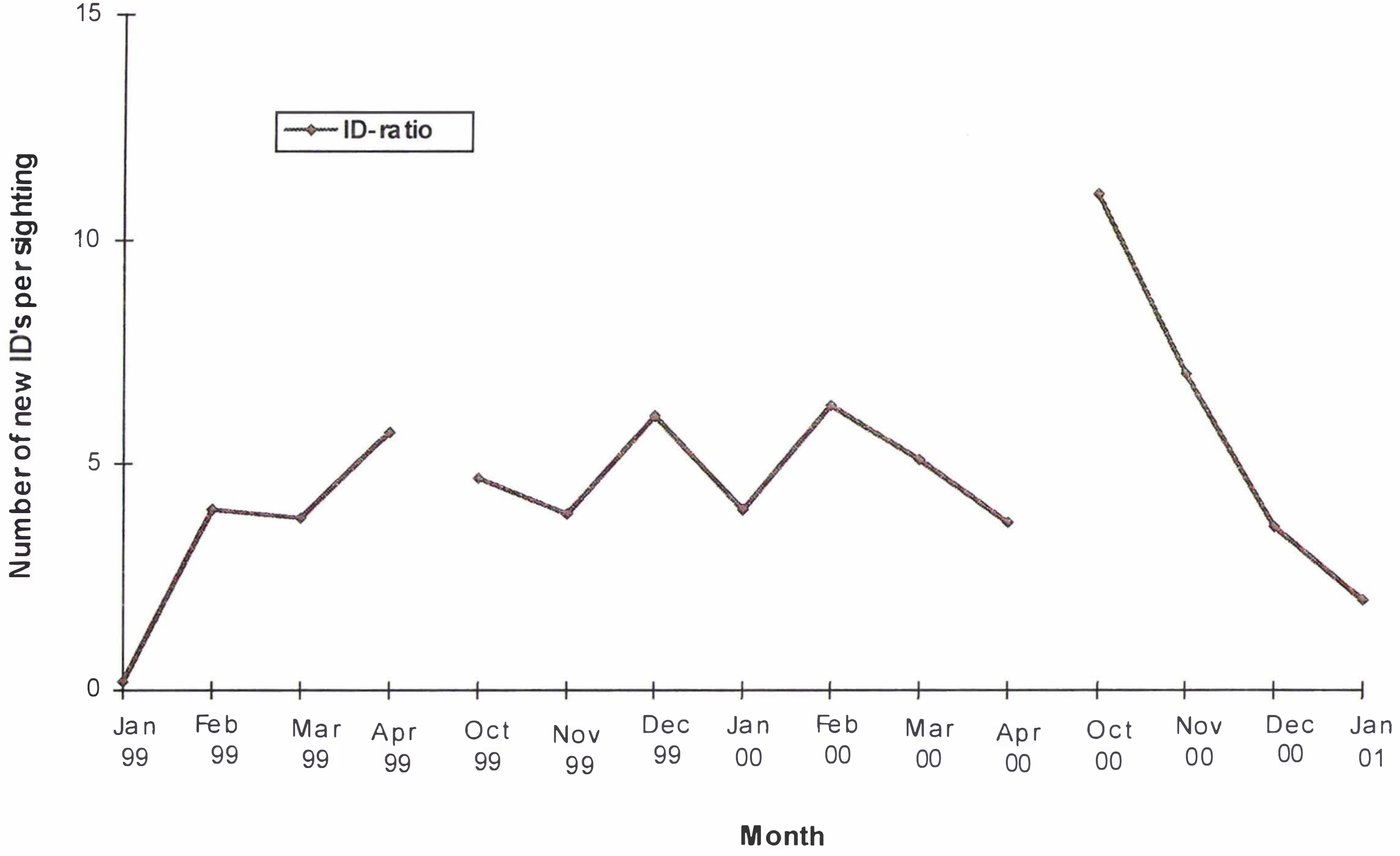


Figure 14. The rate of identifying new individuals over the course of the study.

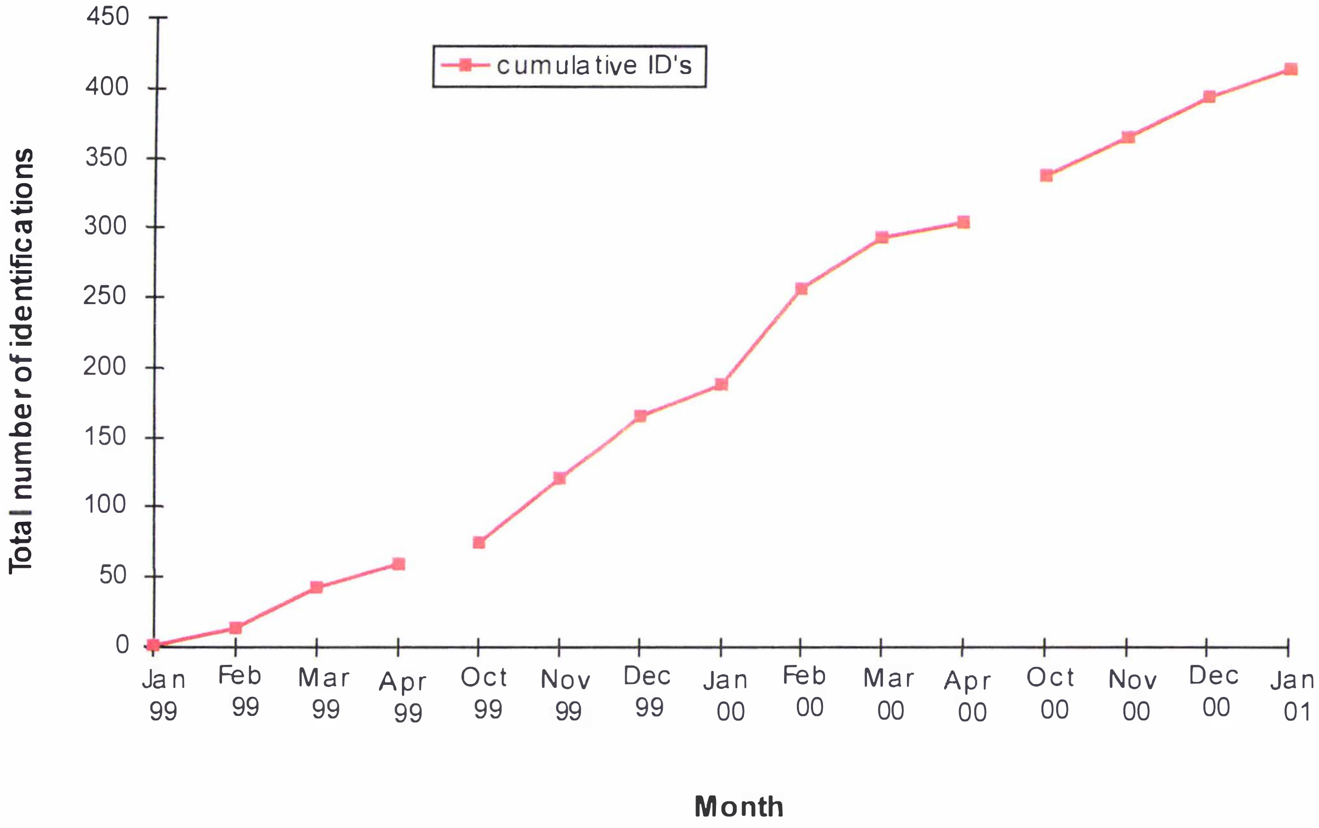


Figure 15. The cumulative number of identified individual common dolphins over the course of the study.

almost instantaneously after groups merged. In all cases the focal group was initially either milling or feeding, when it was joined by additional animals. The association between fusion and a change to either sexual or feeding behaviour is highly significant (chi-square=8.49, df=2, p<0.025).

There was an almost identical relationship between fission and sexual or feeding behaviour, as well. Groups split up significantly more often after bouts of sexual socialising or feeding (chi-square=9.61, df=2, p<0.01). Only 30 percent of the time did fission occur without a prior change in activity from either sex or feeding to traveling (Figure 16).

Group stability over months - Over 4000 photographs were taken from January 1999 to January 2001. In February and March 2001 a camera breakdown led to increased reliance on video and visual identifications. By April 2001 (Whakatane comparison) photographic effort was back to normal. A third of all pictures taken were eliminated immediately, because of poor picture quality, or the absence of critical body parts (in most cases the dorsal fin) from the picture. Of the remaining photographs, the majority was eliminated because the dorsal fin was not distinct enough to separate it reliably from similar-looking individuals. The lesser quality shots of circa 300 photos in which an individual had been photographed more than once during

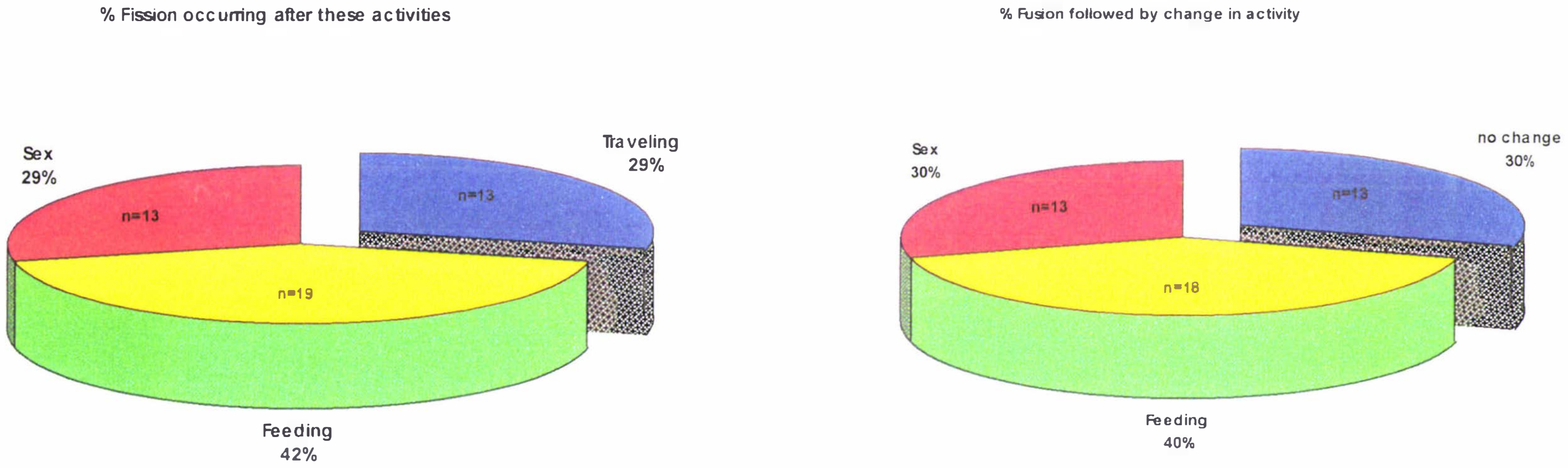


Figure 16. The relationship between fission (left), and fusion (right) of common dolphin groups and various activities.

the same sighting, were also excluded. This left a catalogue of 408 reliably identifiable individuals. These were catalogued chronologically, with consecutive numbers, and were also given a letter, identifying the season(s) in which the animal had been observed (e.g. 'A' for an animal that was seen only in the 1998/1999 season, 'BC' for an animal that was seen in 1999/2000, and also in 2000/2001). Thirty of these 408 belong to category 1 ('blatantly obvious'), 120 can be considered 'easy' (category 2), and the remaining 258 fit into category 3 ('distinguishable').

Eighteen identified dolphins were seen more than once over the course of this study (4.4 percent of catalogued individuals). Most were seen only twice, but 'Platypus' BC 208 was identified on five separate occasions, 'Stumpy' BC 209 on 4, and 'Black body-line' BC 91 three times. 11 resightings occurred over consecutive seasons, four matches were found between the Whitianga and the Whakatane study areas, and 2 individuals were matched between Whitianga and the Hauraki Gulf (Leitenberger, 2001) (Table 3). The interval between the first sighting and the most recent resighting ranged from 1 day (for 'Left-bent grey' C 374) to at least 983 days ('for Black body-line' BC 91) (Figure 17).

Five different anomalously pigmented common dolphins with grey lateral patches were seen in Mercury Bay. Leitenberger (2001) also reported five grey-sided individuals from the Hauraki Gulf. Only one of them matched a Mercury Bay animal, bringing the combined total to nine grey-sided individuals. These represent 1 percent of the individuals catalogued in the two study areas. A similar prevalence of this phenomenon was found by Perrin et al. (1995) off California. Two of the grey individuals in Mercury Bay were mothers accompanied by calves. In one of the pairs, the calf also had grey sides, whereas the other calf featured the typical hourglass pattern on its flanks. A mother-calf pair in which both animals were grey was also observed by Leitenberger (2001). Photographic analysis showed that this pair was not identical to the Mercury Bay pair. These associations show that grey sides can be inherited, but are probably a recessive feature, because one of the calves showed a normal colour pattern.

If two identified individuals were consistently resighted in each other's company, this would give some indication of the stability of group membership over time. Although 12 of the resighted individuals were found accompanied by another resighted individual during either their first or second sighting, none were seen together more than once.

An alternate indicator of group stability might be found in group size. If the observed groups were stable over time, the number of individuals counted at the first sighting should correspond to that of

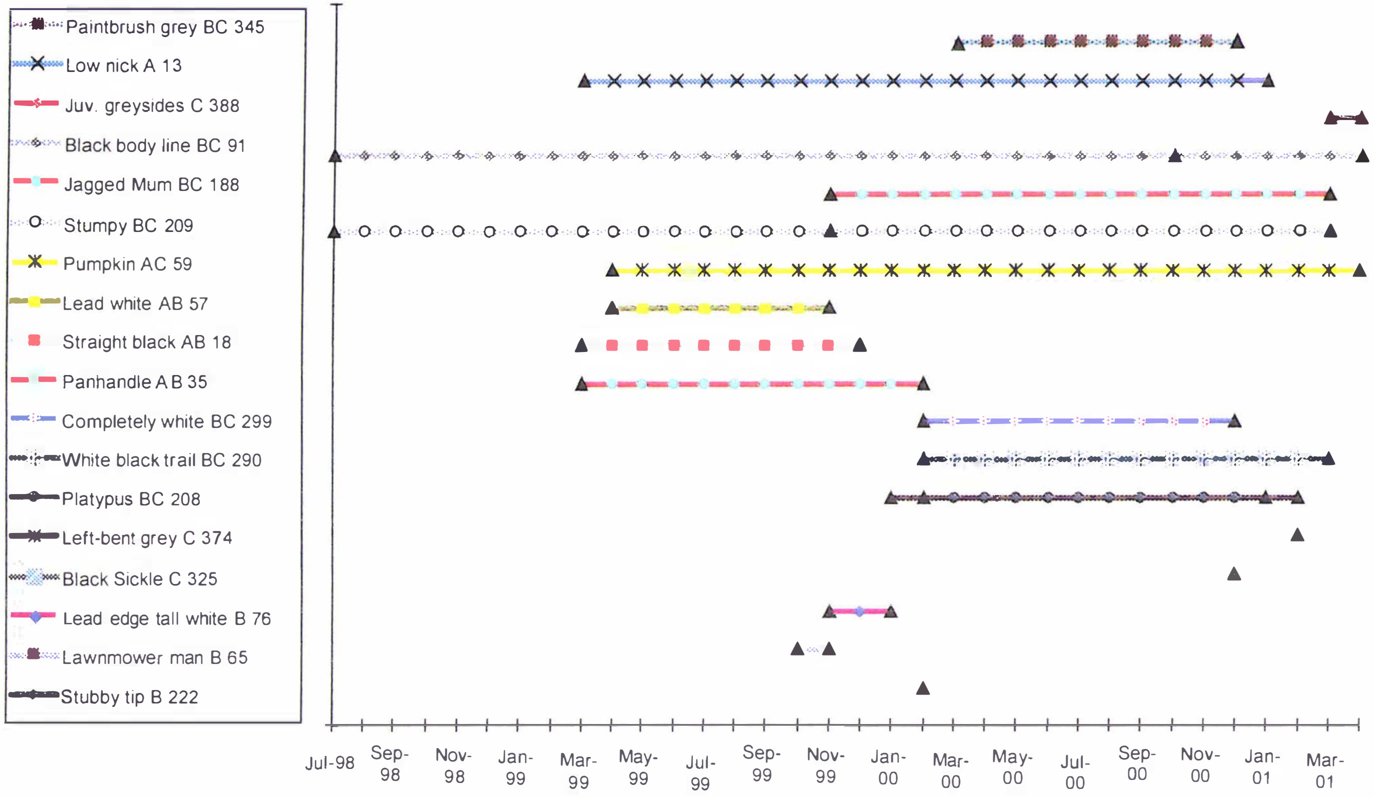


Figure 17. Duration of intervals between sightings, for individual dolphins that were sighted more than once over the course of the study. Black triangles indicate months of actual sightings. For individuals represented by a single triangle, first sighting and resighting occurred in the same month.

Table 3a. Resightings of identifiable individuals, part 1. Study seasons: A = 1998/1999, B = 1999/2000, C = 2000/2001; WHK = sighted off Whakatane (March/April 2001), all others seen in Mercury Bay.

Re-identified dolphin	**1.**	**2.**	**3.**	**4.**	**5.**
Within one season:					
A = A	none				
B = B					
Stubby tip B 222	4.2.00	9.2.00			
Lawnmower B 65	31.10.99	19.11.99			
Lead edge white B 76	2.11.99	28.1.00			
C = C					
Black Sickle C 325	21.12.00	26.12.00			
Left-bent grey C 374	18.2.2001	19.2.2001			
WHK = WHK					
Juv. greysides C 388	8.4.01	10.4.01			
Between two seasons:					
A & B					
Panhandle AB 35	22.3.99	11.2.00			
Straight black AB 18	17.3.99	25.12.99			
Lead white AB 57	3.4.99	1.11.99			
B & C					
Platypus BC 208	15.1.00	10.2.00	11.2.00	23.1.2001	19.2.2001
Black trail BC 290	4.2.00	3.3.01			
White BC 299	11.2.00	21.12.00			

Table 3b. Resightings of identifiable individuals, part 2. Study seasons: A = 1998/1999, B = 1999/2000, C = 2000/2001. Locations: WHT = Whitianga, WHK = Whakatane, AKL = Auckland (Hauraki Gulf). Italic print indicates individual was seen in a location other than Mercury Bay, *W* indicating Whakatane, *A* indicating Auckland.

Re-identified dolphin	1.	2.	3.	4.	5.
Between two places:					
WHT + WHK					
Pumpkin AC 59	1.4.99	*8.4.01 W*			
Stumpy BC 209	*July '98 W*	1.11.99	*24.3.01 W*	*30.3.01 W*	
Jagged Mum BC 188	13.11.99	*22.3.01 W*			
Black line BC 91	*July '98 W*	14.10.00	*10.4.01 W*		
WHT + AKL					
Low nick A 13	9.3.99	*20.1.01 A*			
Paintbrush grey BC345	7.3.00	13.12.00	*19.3.01 A*	*25.3.01 A*	

the second sighting. This was not the case for the resightings reported here, with two notable exceptions. For most resightings, the numbers for group size differed by more than 50 percent from one sighting to the next, even when the sightings were only 2-5 days apart. However, not so for sightings involving Platypus, and Left-bent grey: The group size for Platypus' sightings in 2000 was remarkably consistent, with an estimated 60 individuals on all three occasions (covering 27 days). That number changed to 200 individuals for the 2001 resightings, but was again consistent within the same season, with 200 animals also estimated another 27 days later. Left-bent grey was observed in a group of circa 150 animals on 18.2.2001, with the same number seen the following day.

This apparent consistency of group size over time, must be interpreted with great caution, as it could be purely coincidental. In fact, fission and fusion of groups appears to be a much more typical pattern. The formation of large groups, and the splitting into smaller factions could even be observed over a matter of hours (see above: 'Group stability over a day'). Whether or not the smallest observed groups represented stable social units that interacted, and temporarily merged with other such groups, still remains to be determined. However, this study has produced no evidence that would suggest the existence of long-term associations between certain individuals over several months or years. Therefore, null hypotheses *H0 1a: The composition of groups, as indicated* *by group size does not remain stable over time*, and *H0 1b: The composition of groups, as indicated by photo-identification resightings, does not remain stable over time*, cannot be rejected.

Predation as a factor in group formation - No direct predation was observed upon common dolphins. However, known dolphin-predators do occur in this area. They include large sharks, such as the great white (*Carcharodon carcharias*), tiger (*Galeocerda cuvieri*), mako (*Isurus oxyrhynchus*), and hammerhead shark (*Sphyrna zygaena*) (Cockcroft et al., 1989; Mann & Barnett, 1999; Heithaus, 2001), and killer whales (Visser, 1999). During dolphin surveys, two hammerhead, and two bronze whaler sharks (*Carcharinus brachyurus*) of medium size (1.5-2 meters) were observed in the study area. One very large shark (4.5-5 meters) was also encountered, likely either a mako, or a great white. Although hundreds of dolphin individuals were encountered over the course of this study, many of which could be studied from close range, only six animals were observed to carry scars from a predatory attack. Five of these were consistent with shark bites, while one animal showed bite scars of a different kind, with neat, round puncture holes. These were most likely inflicted by a medium-sized odontocete, possibly a small killer whale, a false killer whale (*Pseudorca crassidens*), or a pilot whale (*Globicephala melaena*).

One eyewitness reported a killer whale killing and devouring a common dolphin in the study area, prior to the start of this study (A. Hansford, pers. comm., 2.9.1999). Killer whales were seen twice over the course of this study (26.10.2000 + 27.12.2000), and it was notable that in spite of daily field effort, not one common dolphin was encountered for 10 days and six days following the respective killer whale sightings. The lack of dolphin sightings may possibly have been the result of dolphins avoiding the area, as long as it was frequented by killer whales. Similar avoidance responses by common dolphins to the presence of killer whales were reported by Visser (1999).

4.2.6 Sex ratio within groups:

So far, the only common dolphins that could be sexed on a regular basis, without capturing them, were those individuals that were consistently accompanied by a calf. Thus, these individuals were scored as females. In order to gain gender-data on individuals who were not apparent mothers, it was attempted to sex individuals from underwater video-footage of bow-riding dolphins. With the camera pointed at the dolphins' venters from below, a view of the animals' genital slits should have been possible. Unfortunately, these attempts proved futile, because unless the animals turned upside down in front of the camera, their bellies were always in the shade, and the genital slits were too inconspicuous to be seen under these lighting conditions. Evans (1994) described sexually dimorphic differences in the colouration of the area adjacent to the genitals for common dolphins from the northeastern Pacific. This 'genital blaze' was only apparent in a handful of individuals seen in this study, and could not be used as a reliable characteristic to distinguish between males and females. However, some individuals showed a clearly pronounced ventral peduncle keel, or postanal hump (Plate 14). This feature has been described as a sexually dimorphic character for spinner (Norris et al., 1994), and Fraser's (Jefferson et al., 1997) dolphins, where it only occurs in sexually mature males.

To test whether or not common dolphin individuals with a postanal hump were indeed always male, DNA-samples were collected from individuals in the wild. The presence or absence of a postanal hump in these animals was determined visually during sampling. DNA was successfully extracted from the skin of nine individuals that had been sampled by skin-swabbing. Genetic techniques can identify the gender of a sampled individual by their distinct banding patterns on an electrophoresis gel (Plate 15): one of the bands (the lower one) relates to the Y-chromosome, the other band is a control band indicating that PCR was successful. This analysis revealed that all postanal hump carriers were indeed male (Table 4).

Plate 14. The adult dolphins on the left (presumed males) feature a prominent postanal hump, while the adult dolphin on the right (presumed female) does not.

Plate 15. Genetic banding patterns on a gel, from a male (left, #3) and a female (right, #4) common dolphin. Note the additional band displayed for the male, which indicates the presence of a y-chromosome.

Table 4. Presence or absence of a postanal hump in skin-swabbed common dolphins, and the results of the genetic sexing of these individuals. All individuals except # 5 were of adult size (> ca. 1.8 m).

Sample number	Postanal hump	Genetic results for sex
1	yes	male
2	yes	male
3	yes	male
4	no	female
5	no, juvenile size	male
6	no	female
7	no	female
8	no, observed with calf	female
9	no	female

The success rate of obtaining visible pieces of skin on the velcro pads was circa 20 percent. The reason for this lies more in the difficulty of applying sustained, firm pressure onto the back of a fast-moving dolphin, than in the skin-capturing properties of the velcro. All sampled dolphins showed an immediate response to being scratched with the broomstick. They accelerated, dove, and/or veered off to the side, leaving the bow-wave. When multiple dolphins were bow-riding during sampling, all of them left the bow-wave, showing a coordinated flight response, even though they had not been touched physically. Eight of the sampled animals did return to bow-riding, within 30-90 seconds after having been scratched, while one remained visible in the focal group at a distance of 5-10 meters from the boat, but did not return to the bow-wave. No scratch marks resulting from the velcro were obvious on any of the sampled animals.

The hypothesis that only sexually mature male common dolphins possess a postanal hump was supported by the following evidence:

1) Dolphins with postanal humps were never accompanied by calves.

2) Dolphins that were consistently accompanied by calves (i.e. presumed females) never showed a postanal hump.

3) Calves and juveniles that had not yet reached adult size never carried a postanal hump.

4) An adult common dolphin found dead on 29.12.2000 in the Whitianga estuary had a postanal hump, and direct examination revealed that it was a male.

5) Photographs of dead common dolphins of known sex, published in Heyning and Perrin (1995, pp. 8-9) clearly show a postanal hump in all adult males, while it is absent in the adult females. These pictures also illustrate that a postanal hump is present in both the short-beaked (*Delphinus delphis*), and the long-beaked (*D. capensis)* common dolphin species.

6) Photographs taken by Dr. P. Duignan (pers. comm., 8.5.2001) during necropsies of stranded individuals in New Zealand indicate that a postanal hump was present in the only examined adult male (Plate 16), while it was absent in subadults and females.

7) Genetic analysis of skin samples that were collected from live common dolphins in the field confirmed that the postanal hump is almost certainly a secondary sexually dimorphic characteristic in common dolphins, only occurring in mature males (Table 4).

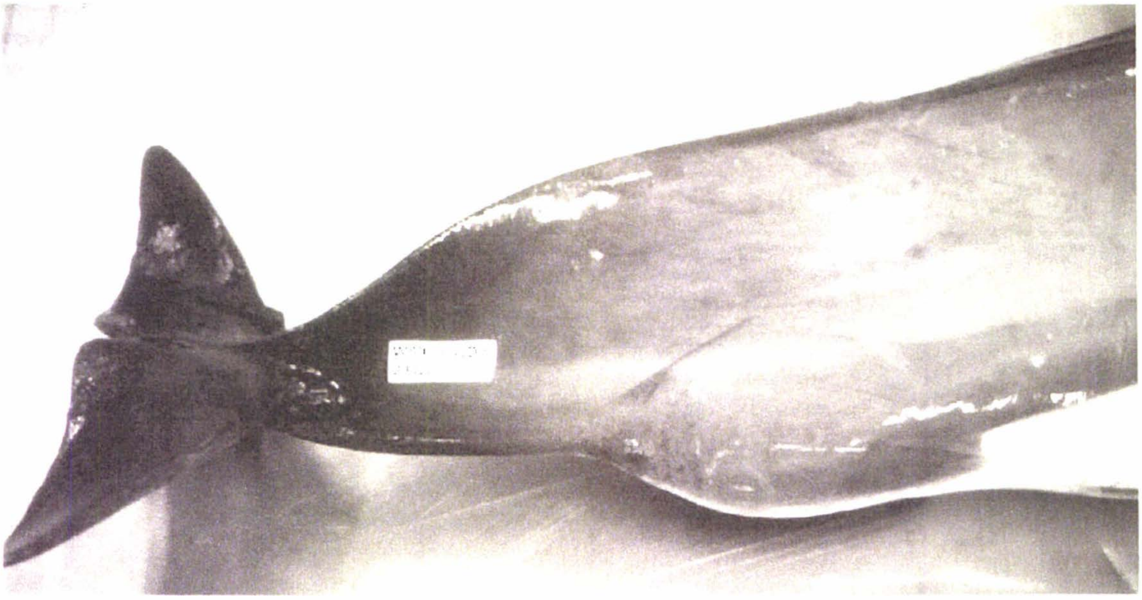


Plate 16. Close-up of the postanal hump of a mature male common dolphin (Photo by P. Duignan).

In light of the above, null-hypothesis *H0 5: There are no external morphological differences between common dolphin individuals, that could be attributed to their gender*, can be rejected.

Unfortunately, detailed quantitative data on the male-female ratio in most groups cannot be presented here. This is partly due to the fact that the possibility of using the postanal hump as a sexually dimorphic diagnostic character could only be proved genetically near the end of the study. Also, the presence or absence of individuals with a postanal hump could not be reliably determined for groups that included animals at a distance of > 100 meters from the boat. Nonetheless, the existence of at least three distinct types of groups became evident during focal group follows:

1) Nursery groups: These groups contained adults and juveniles without postanal humps, and a large proportion (20-50 percent) of calves and/or newborns. They never included mature males. At least four sightings fall into this category. Group sizes for these ranged between five and 20 individuals.

2) Mixed groups: The vast majority of sightings included juveniles, adult females and their calves, and at least some mature males. Group sizes ranged from three to 400 animals.

3) Male bachelor groups: These groups consisted exclusively of mature males, all sporting a postanal hump. At least two such groups were observed during this study. They contained nine and 15 individuals, respectively. The inter-individual distances in both of these groups were conspicuously small. During both follows the group spread never exceeded 20 meters.

While this information is very preliminary, it suggests that certain groups differ in their gender-composition. However, more systematic information should be collected before null hypothesis *H0 3: There is no difference in the sex ratio between groups*, can be rejected.

4.3 Discussion

4.3.1 The numbers of adults, calves, and newborns in each group

The mean group size of 57.3 individuals, and the range from 3-400 dolphins in each group corresponded closely with the findings of Leitenberger (2001) who observed a mean group size of 54 individuals, ranging from 2-400 animals per group. This suggests, that such numbers may be typical for common dolphins in coastal New Zealand waters.

Constantine (1995) found the occurrence of newborns to peak in January among common dolphins in the Bay of Islands. Numbers of newborns peaked in January-March in this study, which confirms this pattern of most births taking place in mid-summer, which has also been reported from the Eastern Atlantic (Collet, 1981).

4.3.2 Seasonal, diurnal, and tidal variations in sighting success

Sighting success dropped significantly towards autumn and winter. This can probably be explained by seasonal movements of common dolphins out of the study area. These are discussed in detail below (see 4.3.3 Seasonal movements).

There was a diurnal trend, indicating that fewer dolphin groups were encountered, as the day progressed into the afternoon. This could be the result of a change in activity, e.g. if the dolphins were resting more in the afternoon, they would have been less conspicuous to observers. Diurnal activity changes have been observed in bottlenose dolphins (Bräger, 1993; Waples, 1995) with feeding activity peaking in the morning, and the late afternoon, and more sedate behaviour during the middle of the day. Würsig & Würsig (1979) found bottlenose dolphins in Argentina to rest mainly in the mornings, and show more social and feeding behaviour in the afternoons. Hawaiian spinner dolphins show a distinct daily routine, with resting from morning to early afternoon, and most feeding activity taking place at night (Norris et al., 1994). Dusky dolphins in New Zealand appear to follow a similar pattern, with most resting and socialising occurring near shore during the day, and feeding largely occurring during the night (Würsig et al., 1997).

The dolphin-encounter rate, in this study, may also have dropped as a result of an afternoon offshore movement, possibly related to nocturnal feeding over the continental shelf (see below: 5.2.1 Discussion of observed activity patterns - Diurnal activity patterns). Conversely, sighting success may have dropped as a function of sea conditions. In the study area, wind speeds are typically low in the mornings, and increase throughout the day. Rougher sea conditions later in the day may thus have influenced the success of spotting dolphins in the afternoons.

While tidal currents could still influence the distribution of nutrients, prey, and hence dolphins in the study area, it is unlikely that common dolphins that consistently stayed in deep water (80 meters on average) would be greatly affected by tidal fluctuations. In contrast, some bottlenose dolphins can only venture into some of their preferred habitats during certain tidal states, e.g. when foraging in seagrass beds (Nowacek, 1999b) or in estuarine channels (Rigley, 1983).

4.3.3 Seasonal movements:

While common dolphins were encountered in the 500 km^2 study area on a regular basis over several months, this does not necessarily indicate that these dolphins are resident within the study area. The low frequency of individual resightings suggests that the observed common dolphins may indeed represent a succession of more or less transient dolphin groups over time (see below: 4.3.4 Group formation and composition).

Defran et al. (1999) found that bottlenose dolphins in the Southern California bight travel back and forth along the coast for distances of up to 470 kilometers and possibly beyond. They tend to frequent a very narrow corridor within 1 kilometer from shore and do not appear to mingle with bottlenose dolphins around the Channel Islands, 42 kilometers from shore (Defran & Weller, 1999). Defran et al. (1999) attribute the need to cover large distances in this area to low food abundance and patchy distribution.

Studies on dusky dolphins (Würsig & Würsig, 1980) and common dolphins (Cockcroft & Peddemors, 1990) have tied local seasonal fluctuations in the abundance of these species to the availability of their preferred prey. The distribution and abundance of small schooling fishes is strongly tied to a number of environmental variables, water temperature being one of great importance. Some fish species can only survive within a very narrow temperature spectrum (Rose & Leggett, 1988). Rapid drops in temperature can kill off entire fish populations (Hanekom et al., 1989). Conversely, a slight increase in sea surface temperature (SST), due to an El Niño event increased the reproductive output of herring (Tanasichuk & Ware, 1987). While data on the abundance and distribution of dolphin prey in the study area were not available, the dolphins' movements seemed to be closely linked to SST. While the waters were warm in spring and summer, dolphins were found relatively close to shore. As SST dropped in autumn, the dolphins were found increasingly farther from shore. Limited survey effort (due to a lack of customer demand for the tour operator, and more difficult weather conditions) during the winter months (June-August) did not yield any sightings of common dolphins, which suggests they spent most of their time > 35 kilometers from shore in winter, beyond the range of both the research and the tour boat. The warmer the water, the closer the dolphins came to the mainland: In Jan/Feb 1994, 1996, and 1999 when SST near shore was 2 degrees C warmer than 'normal' (La Niña conditions (Jones, 2000)) the dolphins' mean distance from shore was only 6.2 kilometers, whereas in years with 'normal' SST it was 11.5 kilometers.

A similar movement pattern has been reported by Goold (1998): in the Irish Sea, common dolphins also moved farther offshore in autumn as SST dropped. Barco et al. (1999) encountered five times as many bottlenose dolphins in their Virginia Beach study area in mid-summer when SST was warmest, than they encountered in spring and autumn. Reilly (1990) did not find any seasonal movements for common dolphins in the Eastern tropical Pacific (ETP), arguing that they occupied upwelling-modified habitats year-round. However, Reilly & Fiedler (1994) reported that when upwelling conditions in the ETP changed due to an El Niño in 1987, the dolphins' distribution shifted accordingly. Tershy et al. (1991) also found a decrease of common dolphin numbers in a nearshore study area as temperatures decreased from an El Niño to a La Niña condition. In the eastern Pacific (American west coast) during an El Niño, SST is typically warmer than usual, whereas in the western Pacific (e.g. New Zealand), it is colder. Constantine & Baker (1997) also found a correlation between common dolphin distribution and SST in the Bay of Islands. There, the trend was exactly reversed: common dolphins were found in shallow water in the winter months, when SST was lowest. In summer, when SST was highest, they were seen in deep water outside the Bay. It is possible that the oceanographic patterns in the Bay of Islands create a nutrient- and prey distribution very different from that in the much more exposed Mercury Bay area.

Common dolphins are found throughout a wide range of sea temperatures, from equatorial waters to temperate latitudes (Haug et al., 1981; Gaskin, 1992). As a result, it is unlikely that small fluctuations in SST would be the primary factor influencing their distribution. A more likely explanation is that SST affects the distribution of common dolphin prey species, in turn causing the dolphins' seasonal movements (Neumann, 2001a). That common dolphins follow the temperature-driven migrations of prey has been shown for the southeast coast of South Africa, where they follow the seasonal migration of pilchards (*Sardinops ocellatus*) (Cockcroft & Peddemors, 1990). Wells et al. (1990) observed a northward movement of bottlenose dolphins, which was apparently caused by an El Niño warm water influx. This movement of up to 600 kilometers allowed the dolphins to stay within their usual temperature range, and they subsequently even ventured into water that was colder than their previous habitat:

> Thus, the animals do not appear to have moved strictly in response to the northward movement of isothermal water masses. The northward-moving dolphins may have been responding more to the secondary effects of the warm-water incursion than to the movements of the warm water directly. Perhaps, the dolphins were following changes in the distribution of prey. [...] During the 1982-1983 El Niño event, fish species normally found in southern California and Mexican waters [...] were numerous in central and northern California. (Wells et al., 1990, pp. 428-429).

While the above line of evidence strongly suggests a seasonal offshore migration by common dolphins, it is important to consider an alternative explanation: the dolphins previously observed in the study area may have shifted farther north or south of the study area - still close to shore - while the dolphins now encountered farther offshore (and later rather *not* encountered in winter) are completely independent of the nearshore animals. This is based on the following line of reasoning:

1) The nearshore encounters simply represent the first group encountered on a survey, i.e. other dolphins may have been present farther offshore at the same time, without being recorded.

2) Simultaneous to the autumn-decrease in dolphin sightings in Mercury Bay, in March 2000, dolphin numbers off Whakatane (200 kilometers SE) increased considerably near shore (K. Waite and J. Wharehoka, pers. comm., 12.3.2000).

3) In bottlenose dolphins, distinct coastal and oceanic ecotypes exist sympatrically in the same region, but they are separated by differing habitat preferences (Defran & Weller, 1999).

That common dolphins are capable of along-shore movements from Mercury Bay to Whakatane is demonstrated by the photo-identification records compiled in this study. Commercial fishermen in Whitianga often report large numbers of common dolphins over the continental shelf (50+ kilometers offshore, A. Hansford, pers. comm., 15.10.1998). It is entirely possible that these dolphins are ecologically separate from the animals observed between the peninsula and up to 35 kilometers offshore. The data collected in this study cannot conclusively be used to determine which of these scenarios is most likely. Future satellite-tracking, genetic sampling, or increased photo-identification efforts could help clarify this issue.

4.3.4 Group formation and composition:

There was no indication that the number of identified animals was approaching an asymptote or that the discovery rate of identifying new individuals was dropping significantly over the period of this study. This points to a rather large, 'open' population of dolphins (Wells & Scott, 1990; Constantine, 1995; Bejder, 1997). The fact that few animals (4.4 percent of catalogued individuals) were seen more than once during the study is most likely representative of a succession of dolphins moving through the area and using the Mercury Bay habitat at different times, rather than residing in the area for extended periods of time. Intriguingly, resightings from one year to the next indicate that common dolphins in the greater Bay of Plenty may be following some kind of annual cycle, which brings them to Mercury Bay for at least a few days every year (Table 3).

However, the low resighting rate of individual dolphins in Mercury Bay may also be the result of an extremely large population being present (i.e. the same individuals may have been present, but were not documented, because only a small percentage of animals was photographed). Alternatively, common dolphins may be more difficult to identify than some other dolphin species (i.e. the same individuals may have been present, but it was impossible to prove because they belonged to photo-ID category d), lacking distinct features).

The merging of groups was, in most cases, directly followed by either sexual activity or feeding. When groups split into smaller groups, this fission occurred mostly directly *after* mating or feeding. This suggests that groups of dolphins seek out other groups specifically for the purposes of either mating or feeding. An increase in sexual activity upon the fusion of groups has also been observed by Slooten (1994) for Hector's dolphins, and by Würsig & Würsig (1979) for bottlenose dolphins. Affiliative sexual behaviour may be part of a social 'greeting ritual' marking the encounter of two groups, as is the case in bonobos (*Pan paniscus*), for example (Wrangham, 1993).

A change in activity to feeding was observed in the focal groups, after they joined another group which was already feeding. It seems likely that the focal group dolphins were alerted to the presence of prey by the feeding activities and vocalisations of the feeding group. Their foraging efforts may then have been exploited by the joining group. Both groups may profit in situations when dolphins herd a school of fish by so-called 'carouseling' (see chapter 5.1.7). Larger schools of fish may require a larger number of dolphins to control them. Würsig & Würsig (1980) also observed the joining of several groups of dusky dolphins during feeding bouts.

In summary, the frequent occurrence of splitting-up and coming together is an indication that the aggregations of dolphins observed in this study do not necessarily represent stable social units. Instead, common dolphins appear to live in a fission-fusion society, which is common among small, pelagic cetaceans (Wells et al., 1991).

The question remains if any of the smallest groups encountered are discrete units that interact and merge with various other small groups over time, while maintaining the same group membership after such interactions. Evans (1994) relates an observation, during which he observed the splitting-up of a group of 600 common dolphins into various subgroups. Once the group he was following had been reduced to 20 individuals, it did not split-up any further. He suggests that these 20 individuals may represent a stable core unit. Photo-identification did not produce any evidence for long-term associations between individuals in this study. This is analogous to the results reported by Slooten et al. (1993) for Hector's dolphins. Norris et al. (1994) proposed that 4-12 individuals might be the smallest reactive unit in spinner dolphin schools. They also discovered a very fluid fission-fusion society in this species, with a similar lack of association between identifiable individuals, as reported in this study. Wells et al. (1991, p. 387) propose that:

> Unlike very stable long-term associations of larger odontocetes, societies of many dolphins can be described as being built around repeated, rather than constant, associations among individuals or closely affiliated groups. Although specific composition of a group may change from day to day, the same individuals may come into contact with one another frequently

> over periods of years, resulting in a more extended and more loosely defined society.

This description may well apply to common dolphin societies. It is supported by the evidence collected in this study.

The most significant result of the photo-identification effort lies in providing a record for the spatial and temporal distribution of certain individuals. Thanks to resighting a number of individuals off Whakatane, that were previously identified in Mercury Bay (circa 200 kilometers distant), one can safely presume that common dolphins are very mobile in the greater Bay of Plenty area (Table 3).

Common dolphins have shown that they are able to cover such distances in relatively little time. Evans (1982) reported that a radio-tagged female common dolphin covered a distance of at least 270 nautical miles within 10 days. 'Black body-line' and 'Stumpy' were both documented by van Groningen off Whakatane during her January-July 1998 study (unpublished data). They were then spotted in Mercury Bay in season B ('Stumpy', 1.11.1999) and C ('Black body-line', 14.10.2000), respectively, and resighted off Whakatane in season C ('Stumpy', 24.3. + 30.3.2001; 'Black body-line', 10.4.2001). Local fishermen and dolphin-tour operators speculate that common dolphins in the Bay of Plenty have a nomadic lifestyle which takes them in an annual cycle from the East Cape north along the coast to Coromandel Peninsula, offshore from there, and back south towards East Cape. The observed matches between Whitianga and Whakatane would fit into such a pattern.

Common dolphins apparently do not restrict their movements to within the Bay of Plenty, however. Two Mercury Bay individuals were identified in the Hauraki Gulf (at least 100 kilometers distant by sea) by Leitenberger (2001) (Table 3). While some anecdotal information suggested that coastal topography and currents might separate Coromandel-dolphins from Hauraki Gulf-dolphins, there does not appear to be a firm boundary. Dolphin-movements from Mercury Bay to the coast north of Coromandel Peninsula have also been observed for bottlenose dolphins. Some individuals observed near Whitianga in October 1999, have been identified repeatedly in the Bay of Islands between 1994-1999 (Constantine, pers. comm., 19.11.1999).

Common dolphins in the Hauraki Gulf appear to be less transient than those in Mercury Bay. With very similar photo-identification effort, Leitenberger (2001) sighted 40 percent of her 500 catalogued individuals more than once (compared to 4.4 percent this study). 13.8 percent were seen three times or more, and frequently sighted individuals were seen throughout the entire 6-month study period. This suggests that at least some individuals appear to spend extended periods of time in the Hauraki Gulf. Future studies, comparing their sightings to Leitenberger's (2001) photo-catalogue, may be able to determine, whether these individuals, or even entire groups, are in fact long-term residents in the Hauraki Gulf.

Information obtained from the dolphin tour operators in Whakatane (K. Waite and J. Wharehoka, pers. comm., 12.3.2000) suggests that common dolphin abundance there increases in autumn, while it simultaneously decreases in Whitianga. Quite possibly, this could be due to an influx of individuals which were previously seen off Whitianga. Assuming that prey availability is the main driving force behind dolphin movements, Whakatane should then be more productive at that time of year, than Whitianga. This hypothesis is supported by surface geostrophic current data for the 1996/97 summer, which revealed a pattern by which planktonic organisms would be pushed towards the east coast of Coromandel Peninsula in early November. These currents then turned southeasterly in December, moving plankton towards Whakatane, and the East Cape (Chiswell & Booth, 1999).

Satellite images of phytoplankton concentration in Murphy et al. (2001) show high plankton concentrations along the east coast of the North Island, from September to November, which start to taper off in December. While the large-scale resolution of these images does not allow a conclusive comparison, in autumn, pockets of high phytoplankton concentration appear to linger in the eastern Bay of Plenty, and also along the northeast coast from Thames to Whangarei (including the Hauraki Gulf), but *not* along Coromandel Peninsula (Murphy et al., 2001). The East Cape eddy northeast of Whakatane is also likely to channel plankton and warmer water into the southeastern Bay of Plenty (Roemmich & Sutton, 1998). This means that the area off Whakatane and the Hauraki Gulf, might both be suitable habitats for dolphins throughout most of the year, while the conditions off Coromandel Peninsula are more ephemeral, and probably not suited to support a resident population. This may partly explain the higher rate of resightings found by Leitenberger (2001) in the Hauraki Gulf and the autumn resightings of individuals off Whakatane, which were seen in Mercury Bay in spring and summer (this study). Future research should now focus on the Whakatane and Hauraki Gulf areas, where photo-identification could assist in establishing whether individual dolphins spend extended periods of time there, especially during autumn and winter. Further, surveys of the East Cape eddy itself may reveal this location as a preferred offshore habitat for common dolphins. The boundary areas of such eddies are often areas of enhanced productivity (Murphy et al., 2001).

4.3.5 Reasons for group formation in common dolphins:

Living in a group does have its drawbacks, e.g. disease transmission, competition for food or other resources, or being more obvious to potential predators (Reynolds et al., 2000). These costs must be outweighed by the benefits, if group formation is to occur. Potential benefits include ready access to mates, better predator detection and defence, and cooperative exploitation of certain food sources. There appears to be a correlation between the cost/benefit ratio, and a dolphin population's habitat. Pelagic bottlenose dolphins form much larger groups than those living in a coastal, shallow water habitat (Reynolds et al., 2000). Predator and prey densities differ considerably between the two habitats, with large predators generally more numerous in deep water, and with more freedom of movement when stalking or attacking. Prey distribution is usually more patchy in the pelagic environment. Reynolds et al. (2000, p. 108) conclude:

> Thus, in coastal, shallow areas, small group size of dolphins is favoured - the costs of very large groups outweigh the benefits there. Not so in the offshore areas, where food resources are distributed patchily but are dense. In such settings, having many animals, potentially spread over a large area, may permit easier detection of a patch, and once a patch is found, there is enough to feed a large group. Here the benefits outweigh the costs of large group size.

This may also apply to spinner (*Stenella longirostris*), spotted (*S. attenuata*), and common dolphins, which are known to form the largest dolphin aggregations in the open water of the eastern tropical Pacific, often numbering several thousand individuals (Reilly & Fiedler, 1993).

The availability of prey probably determines the maximum group size, that is still beneficial to all the members in the group. As a cooperative effort, foraging should be facilitated by a large number of animals joining forces. This is only true, however, as long as prey is abundant enough for each group member to profit from its efforts. If prey are distributed in a large number of patches, each containing a small number of prey items, it probably becomes more efficient for the dolphins to forage in smaller groups. Indeed, a large group may be forced to split up and forage in separate areas to avoid competition. Scott & Cattanach (1998) suggest that common dolphins regularly split up into smaller groups at night, when prey species become more widely dispersed.

The role of predation in the group formation of common dolphins in Mercury Bay is more difficult to assess. The handful of scarred individuals observed in this study is much lower than the 21.9 percent of bottlenose dolphins that showed evidence of shark attacks in coastal Florida (Wells et al., 1987). In Australian waters the numbers are even higher, with over 35 percent of dolphins carrying shark scars in Moreton Bay (Corkeron et al., 1987), and 74 percent of all adults and juveniles shark-scarred in Shark Bay (Heithaus, 2001). There are four possible explanations for this:

1) The level of predation in Mercury Bay may be extremely low. If this were the case, it certainly would not be due to a lack of predators in the area. Mako and tiger sharks are frequently caught in gamefishing in this area, and hammerhead sharks occasionally occur here in groups of 50+ animals (A. Hansford, pers. comm., 3.1.2000). These sharks may specialise on different prey items in this area, but they are known to attack dolphins elsewhere (Cockcroft et al., 1989; Mann & Barnett, 1999; Heithaus, 2001). Killer whales have also been observed in the study area, and they are known to prey on common dolphins in New Zealand waters (Visser, 1999).

2) Common dolphins may get attacked quite frequently, but the injuries may heal extremely quickly without a trace. Bottlenose dolphins heal extremely fast (Orams & Deakin, 1997), but even so, one can still clearly identify the marks for the first few weeks, or months (depending on the severity) following an attack. It is possible that this healing process is faster still in common dolphins. Compared to bottlenose dolphins, the common dolphins in this study also showed much fewer rake marks - scars caused by other dolphins. Either

common dolphins have much fewer violent interactions with conspecifics, or their skin heals even more quickly than that of bottlenose dolphins.

3) Common dolphins may get attacked just as frequently, as bottlenose dolphins elsewhere, but the vast majority of these attacks may be fatal. Therefore, animals that might otherwise carry the signs of an attack, are removed from the population because of the attacks' success. This could indeed be the case: Because of its smaller body size, a 1.7 meter common dolphin would probably be less likely to survive an attack by a three meter shark, than a 2.7 meter bottlenose dolphin.

4) Common dolphins form much larger groups than the bottlenose dolphins for which shark-scar data are available, and this may represent a successful anti-predator strategy. Common dolphins were not sighted for several days immediately following killer whale sightings (24.10.2000, 10 days absent and 27.12.2000, 6 days absent), which may be an indication of active predator avoidance. Defence from shark attacks is one of the factors thought to contribute to school formation in spinner dolphins (Norris et al., 1994). Indeed, the daily activity pattern of Hawaiian spinner dolphins may be governed by strategies to avoid shark attacks, by seeking out shallow, sandy bays for resting during the day. These are locations that probably facilitate predator-detection by the dolphins (Norris et al., 1994). Würsig et al.

(1997) propose that predator avoidance is an important factor influencing the daily behavioural patterns and movements of dusky dolphins, as well. Dusky dolphins tend to rest in shallow waters, close to shore, during the day.

Leatherwood et al. (1971) also observed very low frequencies of shark bite scars on pelagic *Stenella* spp. and common dolphins. They also point out, that this could indicate that attacks are typically fatal, or conversely, that predation on healthy adults is low, because they are able to detect and escape from such predation attempts. Such a success could be explained, at least in part, by improved vigilance, which increases with group size (Scott & Cattanach, 1998).

While the maximum size of a group is probably determined by the availability of prey, there are likely selective pressures to form the largest possible group that can be sustained. Forming a group has obvious advantages: ready access to mates, cooperative foraging, but most importantly protection from predation (da Silva & Terhune, 1988). Common dolphin groups are much larger than those of bottlenose dolphins in the study area. Common dolphins are also much smaller than bottlenose, and therefore presumably more vulnerable to predation. Group formation may offset this disadvantage. The more animals in a group, the less likely it becomes for each individual to be taken by a predator ('dilution effect')

(McWilliams et al., 1994). Overall anti-predator vigilance increases, while the 'vigilance-workload' for each individual decreases (Jarman & Wright, 1993; Scott & Cattanach, 1998).

In summary, it is likely that group formation in common dolphins is governed by a need for predator defence, and an efficient exploitation of patchily distributed food sources. Available evidence suggests that common dolphins form particularly large groups in deep, open water, where there are no natural obstacles interfering with a predator attack (Reilly & Fiedler, 1993), and where prey are found in a small number of patches, but each patch contains a very high density of prey (Cockcroft & Peddemors, 1990).

4.3.6 Sex ratio within groups:

Genetic analysis revealed that sexually mature male common dolphins carry a postanal hump, as has been shown for some other delphinids (Jefferson, 1990; Jefferson et al., 1997; Norris et al., 1994). Therefore, the presence of a postanal hump can be used as a means of identifying sexually mature male common dolphins in the field (Plate 14). This is a valuable new tool, which will allow researchers to create a more complete picture of common dolphin social structure. Not only does it allow for the determination of the gender of another set of individuals in the group (besides those accompanied by calves), it also provides information on their reproductive status (i.e. sexually mature). While one can be fairly confident, that postanal hump-carriers are indeed always sexually mature males, it is possible that there may be some males in which the postanal hump is not evident, even though they are sexually mature. This issue could be addressed during necropsies that correlate external morphology with testes size, or sperm production.

The function of the postanal hump is not fully understood. Norris et al. (1994) hypothesised it could play a role in mimicking the S-posture used as a threat display by some reef shark species (p. 279): "What engaged our attention was that these humps are placed in exactly the same location as the claspers of adult male sharks."

While Norris et al. (1994) presented some evidence for mimicry of shark *behaviour*, the postanal hump's existence cannot be sufficiently explained by it. Norris et al.'s (1994) hypothesis does not explain, why the postanal hump would be much more exaggerated in eastern Pacific spinner dolphins than in Hawaiian spinner dolphins. It also fails to address the fact that Dall's porpoises show a postanal hump, while they are very unlikely to encounter any S-posturing reef sharks inside their distributional range. It is much more likely, that this is a character that allows female dolphins to assess the virility of potential mating partners. It could also play a role as a visual signal in establishing dominance hierarchies among males. Agonistic and affiliative displays that may be involved in courtship and competition for mates have been described for bottlenose dolphins (Connor et al., 2000b). The presence of the postanal hump may play a part in such displays, as a visual cue, in those species that are equipped with it.

Intriguingly, the postanal hump's morphology differs between spinner and common dolphins. In spinner dolphins the postanal hump consists mainly of connective tissue (Perrin & Gilpatrick, 1994), while it is composed of muscle in common dolphins (Lewis, 1991). Lewis (1991) also showed that the size of the postanal hump is positively correlated with testes size, which underlines its value as a display signal to potential mates. The fact that it consists of enlarged muscle tissue, located in the genital area, may also suggest that it might play a direct role in improving copulatory success.

In both Dall's porpoises (Jefferson, 1990) and spinner dolphins (Perrin & Gilpatrick, 1994) the development of the postanal hump in mature males is accompanied by a forward canting of the dorsal fin. This did not appear to be the case for common dolphins, although individuals with postanal humps did consistently carry very tall, triangular dorsal fins with a remarkably straight trailing edge (Plate 14). This is analogous to the situation in Fraser's dolphins (Jefferson et al., 1997). However, such dorsal fins were also observed on presumed females without postanal humps, who were closely accompanied by calves. Therefore, the two features do not appear to be directly correlated. The 'straightening' of dorsal fins could be a function of increasing age in both sexes, as straight fins were never observed on animals that were less than mature size. This hypothesis could be tested by correlating dorsal fin shape with the number of dentinal growth layers in the same individual.

The sex ratio did differ between groups, and three main types of groups could be distinguished: nursery groups (females and their immature offspring), mixed groups (animals of all ages and both genders), and all-male groups. Within some mixed groups, mature males were also spotted traveling in tight formation with each other (3-5 individuals, separated by no more than 1 meter from their nearest neighbour). Future research may determine whether this is consistently the case, and if such associations may, in fact, represent long-term coalitions. Leitenberger (2001) also reported nursery groups numbering 11-50 common dolphins, in the Hauraki Gulf. She often observed such groups in shallow (11-30 meters) water. Such a trend was not evident in this study.

The three types of groups observed in this study broadly correspond to the results of Wells (1991) and Connor et al. (2000b) for sex ratios in bottlenose dolphin groups:

1) Females are often associated with other females and their calves, forming groups that do not include adult males.

2) Mixed sex groups are observed, but their formation is generally restricted to the duration of a specific purpose (e.g. feeding, mating). Subadults of both sexes are more frequently associated with each other than adults. Bottlenose dolphins sometimes form groups that are composed exclusively of subadults. Such groups were not apparent among the common dolphins in this study.

3) All-male groups exist, and the individual members may consistently associate with each other for years, in so-called male alliances. These alliances usually consist of only two or three individuals, but the larger all-male common dolphin groups may be simply a function of the generally larger group sizes in this species, compared to coastal bottlenose dolphins.

4.4 Summary:

This chapter covered several aspects of common dolphin ecology, including their distribution, movements, and social organisation.

A number of significant findings were put forth:

* Common dolphins showed a seasonal offshore movement, which was most likely tied to changes in sea temperature (Neumann, 2001a).

* Resightings of individuals in the study area were scarce, suggesting a rather 'nomadic' lifestyle for common dolphins.

* No evidence for long-term associations between certain individuals was found.

* The sexually dimorphic character of the postanal hump (present only in males) was established, which provides a valuable new tool for sexing common dolphins at sea.

5. BEHAVIOUR OF COMMON DOLPHINS

5.1 Introduction:

This chapter examines the behavioural patterns of common dolphins. An activity budget is created, illustrating the various amounts of time common dolphins devote to five different activity states (travel, feed, mill, socialise, rest). The significance of each activity state is discussed, and compared to findings reported for other delphinids. Most time was spent on traveling, and substantial amounts of time were devoted to milling and feeding, while resting was observed only very rarely. Aerial behaviours were quantified, and potential explanations for the causes of these behaviours are offered. Qualitative descriptions of common dolphin foraging behaviour are also included in this chapter. Feeding strategies appear to be more varied than previously thought, and show interesting parallels to the behaviour of other delphinids.

5.2 Results:

5.2.1 Field effort:

The data which this chapter is based on, were collected simultaneously with the ecological variables discussed above (chapter 4). Field effort was therefore identical, with 105 focal group follows resulting from 166 surveys. Time devoted to these 166 trips was 641 hours, of which 118.2 hours were spent following common dolphins. The mean duration of these focal group follows was 67.5 minutes (SD=39.5, range= 15 to 195 minutes). 72 of the 105 focal follows were considered baseline data, with only the research vessel present, while 33 focal follows were conducted with the tour boat present for all, or part of the follow. Only baseline data (n=72) were analysed in this chapter.

5.2.2 Activity budget:

The time spent in each activity category during a sighting was calculated from the 3-minute interval samples. During focal group follows, common dolphins spent most of their time traveling, and the least amount of time was devoted to resting (Table 5). This was consistent throughout the three study seasons. The differences in time devoted to each behaviour were highly significant, while there was no significant difference between the activity budgets of different years (Table 6). Overall, common dolphins spent 55.6 percent of their time traveling, 20.4 percent milling, 16.2 percent feeding, 7.1 percent socialising, and 0.7 percent resting (Figure 18).

Seasonal changes in activity - While the time spent in each activity category varied between spring, summer, and autumn (Figure 19),

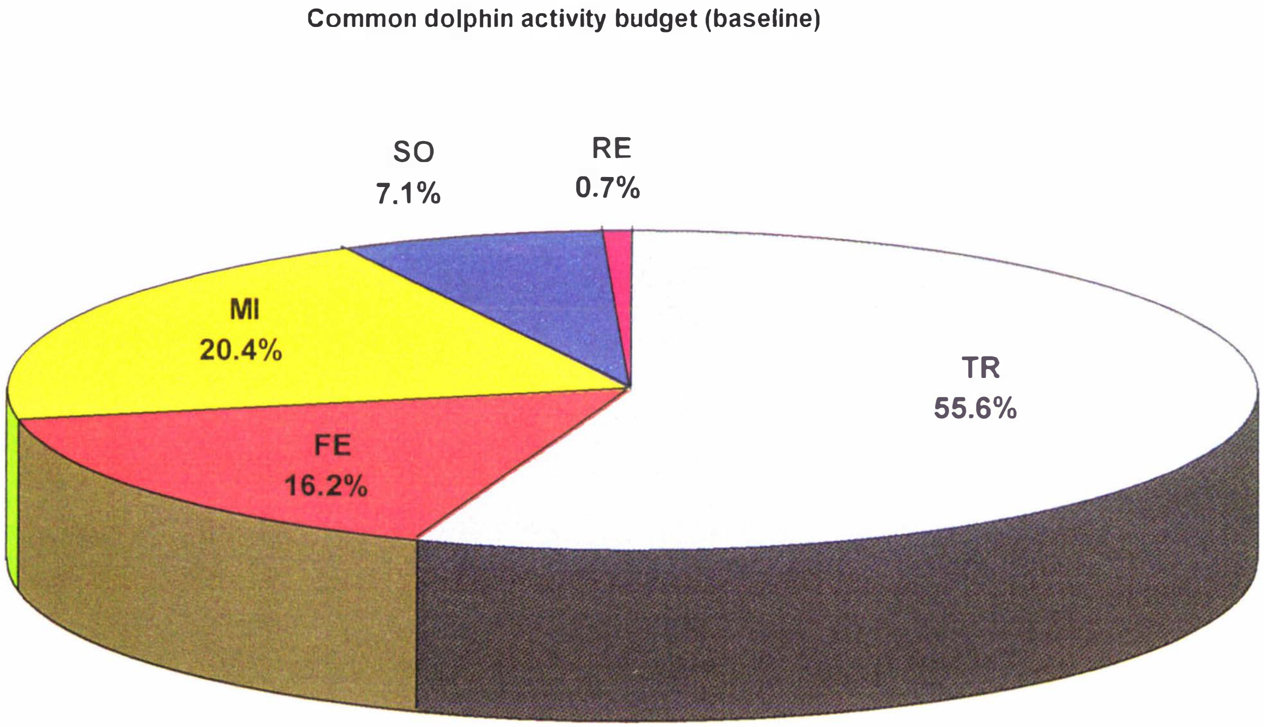


Figure 18. The activity budget of common dolphins. Legend: TR=travel, FE=feed, MI=mill, SO=social, RE=rest.

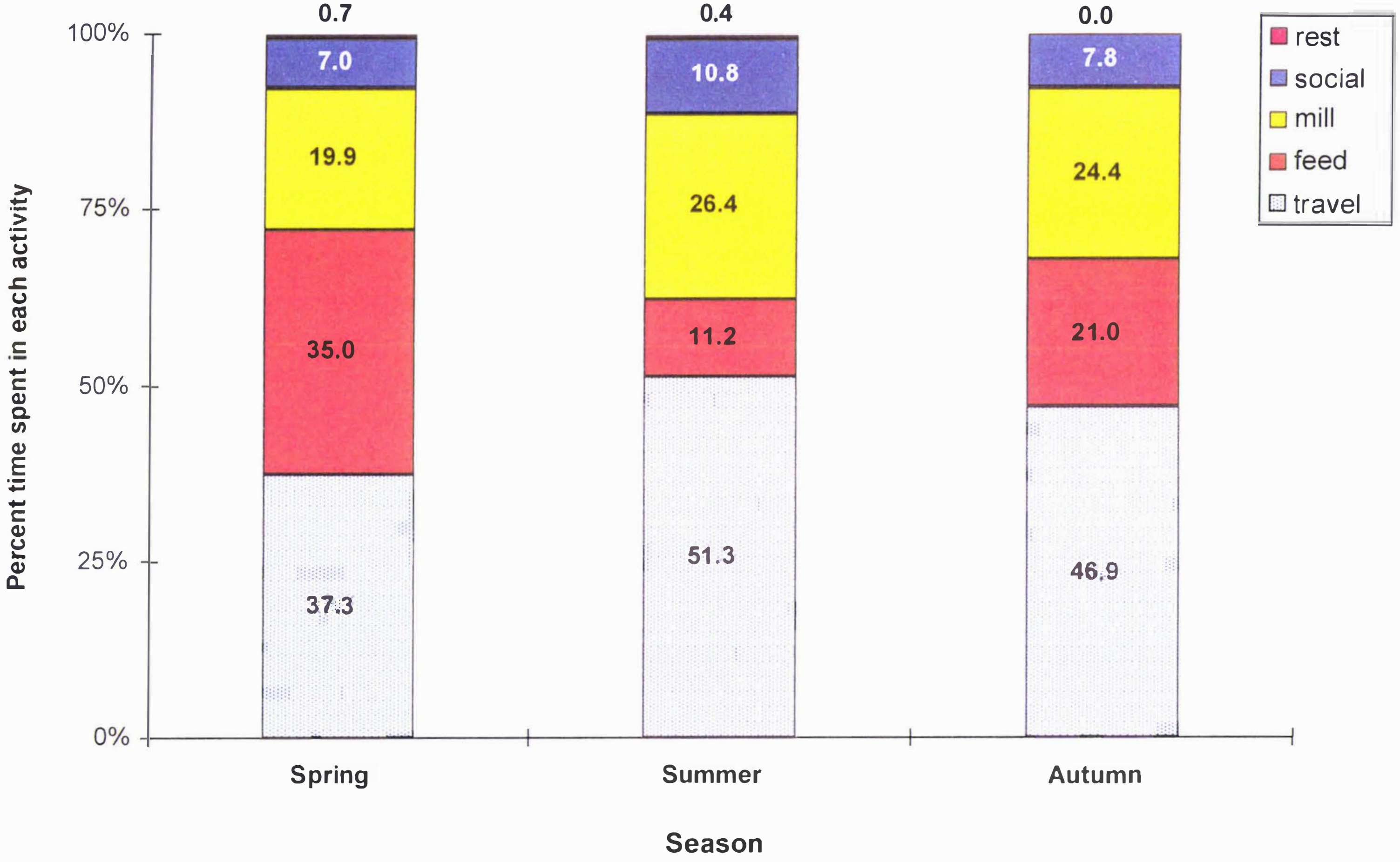


Figure 19. Seasonal variations in the activity budget of common dolphins.

there was no statistically significant relationship between activity budget and the time-of-year (Table 6).

Therefore, null hypothesis *H0 9: The time dolphins spend engaged in various activity states does not vary significantly between seasons or years,* cannot be rejected.

Activity and time of day and time of low tide - There was no apparent relationship between activity budget and the timing of low tide (chi-square = 0.82, df=2, p>0.1). All activities seemed to be evenly distributed throughout the day, with the exception of feeding. Most feeding bouts (44 percent, n=68) were observed in the hours between 7-10 a.m., however, due to the lesser amount of field effort in the afternoons, this did not prove to be statistically significant (chi-square = 3.53, df=3, p>0.1). Null hypotheses *H0 10a: The time of day, or tidal fluctuations do not affect the dolphins' activity budget*, and *H0 10b: Tidal fluctuations do not affect the dolphins' activity budget,* can therefore not be rejected.

Interestingly, when resting was observed, it always occurred between 10:35 a.m. and 11:50 a.m. The small sample size (n=4) precludes any statistical analysis, but it would be worthwhile to examine this time-frame more closely in the future, to find out if this might be a preferred resting period for common dolphins.

Table 5. Amount of time (in min) spent in the five activity states traveling (TR), feeding (FE), milling (MI), socialising (SO), and resting (RE), over the three years of the study (baseline data only; excludes behaviour sampled in the presence of the tour boat).

	TR	**FE**	**MI**	**SO**	**RE**	**Total min.**
1998/99	784	201	96	54	12	1147
1999/00	1071	291	531	204	12	2109
2000/01	810	285	348	81	9	1533
TOTAL:	**2665**	**777**	**975**	**339**	**33**	**4789**
percent	**55.6**	**16.2**	**20.4**	**7.1**	**0.7**	

Activity and group size - A breakdown of the activity budget by group size showed that larger groups seemed to spend more time on traveling, milling, and socialising, at the expense of feeding and resting, compared to groups that were smaller than the average group size of 57.3 individuals (Figure 20). This trend was, however, not statistically significant (Table 6). *H0 11: There is no difference in the activity budgets of groups that are smaller than average, versus those that are larger than average*, can therefore not be rejected.

5.2.3 Frequencies of various behavioural events:

While the predominant group activity was recorded only every three minutes, a continuous log was kept of any conspicuous behavioural events. The most frequently observed event was breaching (Table 7). The frequencies listed here, represent behaviour-bouts by individuals, i.e. if an animal breached 12 times in succession, this was only scored as 1 breaching bout. Conversely, if another animal breached only once, this was also scored as '1' in this table.

Most kinds of behavioural events were evenly distributed across the four activity states of feeding, milling, socialising, and traveling, with one exception: 'Rolling together' occurred significantly more often during socialising than during any other activity state (chi-square = 10.34, df=3, $p<0.02$). While sex was one of the factors that defined socialising,

Table 6. Analysis of Variance testing for significant differences in the dolphins' activity budget, based on various sources. The > 0.05 *p*-values indicate that there was no significant relationship between variations in activity budget and e.g. the time of year (source = season). The proportions of the 5 activities were calculated, and then transformed with an arcsin square root transformation, to satisfy the assumptions of an ANOVA (Sokal & Rohlf, 1981).

Source	**df**	F	*p*
activity	4	66.08	0.000
year	2	0.05	0.951
season	2	0.08	0.916
boat (tour or research)	1	0.78	0.403
group size	1	0.05	0.953
activity*season	8	1.38	0.328
activity*boat	4	1.09	0.421
season*boat	2	0.06	0.942
Error	8		
Total	29		

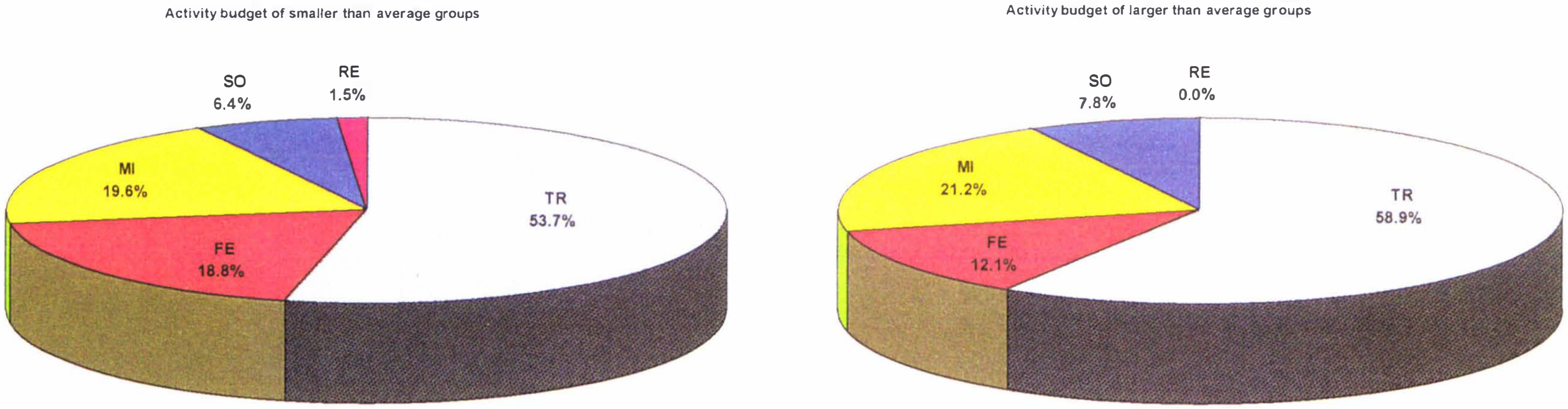


Figure 20. The activity budgets of groups that were smaller than average (<57 individuals, left), vs. those that were larger than average (>57 individuals, right). Legend: TR=travel, FE=feed, MI=mill, SO=social, RE=rest.

it also occurred regularly during the other activity states (i.e. when less than 50 percent of the group were socialising), and was not significantly correlated with socialising (chi-square = 5.21, df=3, p>0.1).

Resting was eliminated from this analysis, because no behavioural events were observed during resting, which is basically due to the definition of resting as a quiescent activity state and was highly coordinated (i.e. when resting was the predominant group activity, 100 percent of group members were resting).

'Playing' only occurred five times over the course of the study. The objects involved in play were pieces of seaweed (twice) and seabirds (three times). Common dolphins sneaked up on unsuspecting shearwaters that were resting on the surface, and poked them with their rostrum. The shearwaters invariably took flight, and on two occasions the dolphins accelerated and raced underneath the shearwaters during the take-off phase. The remains of a bird have been found in the stomach of a beached common dolphin in Australia (F. McKnight, pers. comm., 17.6.2001). The possibility that these episodes of play may therefore actually represent opportunistic predation attempts, cannot be entirely dismissed.

Playing with seaweed involved one animal carrying fronds of a brown alga first in its beak, and then on its dorsal fin (Plate 13). The second

Table 7. Frequency of bouts of behavioural events over the three years of the study.

	1998/1999	1999/2000	2000/2001	Total
leap	8	25	4	37
breach	6	90	38	134
chest slap	6	5	10	21
head slap	3	8	3	14
tail slap	3	36	38	77
chase	7	13	2	22
sex	14	47	30	91
rolling together	0	5	3	8
chuff	8	8	17	33
bubble blow	7	1	14	22
whistle	2	0	2	4
spyhop	4	0	1	5
play	1	2	2	5
swim faster	2	4	0	8
long dive	6	21	4	31
change of heading	5	23	8	36

episode involved social play: An adult common dolphin carried a frond of seaweed (probably *Sargassum*), in its beak. It then released the seaweed, and rotated its body to the right, to catch it with its left flipper. After carrying it draped across the flipper for half a minute, the dolphin shook it off, only to catch it again with its tailflukes. There, the seaweed stayed for another 10 seconds, before it became dislodged. Another dolphin swimming behind it, grasped the seaweed in its jaws, and the dolphin that played with it initially, changed direction and swam towards that animal. Both then dove out of sight, swimming side by side, and it is unknown if, or how long, this episode of playing continued.

5.2.4 Sequences of behavioural events:

Sometimes behavioural events occurred in close timely vicinity, and may therefore be somehow connected. If 2 or more of these events occurred in succession and each event was separated by less than 2 minutes from the preceding one, then these were considered a sequence, following the methodology used by Slooten (1994). In the sequences obtained by this method, intervals between the first, and the succeeding behaviour ranged from 2-110 seconds.

It is rather difficult to properly quantify behavioural sequences. Breaching and chasing both appear to be closely linked to sexual behaviour, because they frequently followed or preceded sex. Breaching by one animal was also frequently followed by breaching of a second (sometimes third and fourth) animal. Table 8 is an attempt to illustrate how frequently a behavioural event was followed or preceded by any other event. A visualisation of these relationships is provided for the five most frequent behavioural events: leaping (Figure 21), breaching (Figure 22), sex (Figure 23), chuffing (Figure 24), and tailslapping (Figure 25).

5.2.5 Prey:

The information obtained on common dolphin prey species in this study is rather sketchy, because no dead animals were available for an analysis of stomach contents. Even though the dolphins were frequently observed feeding, visual identification of their prey was extremely difficult. However, underwater video-footage showed that schools of jack mackerel (*Trachurus novaezelandiae*) were preyed upon on at least four different occasions (Plate 17). Prey identification was possible from the surface, when dolphins chased fish very close (< 1 meter) to the boat. This revealed that at least twice common dolphins chased schools of juvenile (up to 30 centimeters in length) kahawai (*Arripis trutta*). Yellow-eyed mullet (*Aldrichetta forsteri*) were also identified to be taken on 2 separate occasions. Several times dolphins chased flying fish (*Cypselurus lineatus*), and at least once there

Table 8. Matrix indicating sequences of behavioural events. Events in the first column were followed by the events in rows x amount of times, e.g. go to 'breach' in the *first column* and proceed across the corresponding row, and you will find it was *followed* by a leap on 3 occasions, by breaching of another animal on 20 occasions, etc. If you go to 'rolling together' in the *top row* and go down the column, you will find that it was *preceded* by a chase on one occasion.

	leap	**breach**	**chest slap**	**head slap**	**tail slap**	**chase**	**sex**	**rolling together**	**chuff**	**bubble blow**	**whistle**	**spyhop**	**play**	**swim faster**	**long dive**	**change heading**
leap	**2**	3		2		4	4									
breach	3	***20***			12		11		2							
chest slap			**2**		2				1	1						
head slap	1	1		***1***												
tail slap	2	9		1	***11***		3									
chase	2						9	1								
sex	4	11			4	5	***10***		4		2		2			
rolling together	1					1	2									
chuff		1			3		1		**3**	1				1		
bubble blow		2				1			3							
whistle										1		1				
spyhop										1						
play	1	2				1										
swim faster																
long dive		1														
Change heading		3												1		

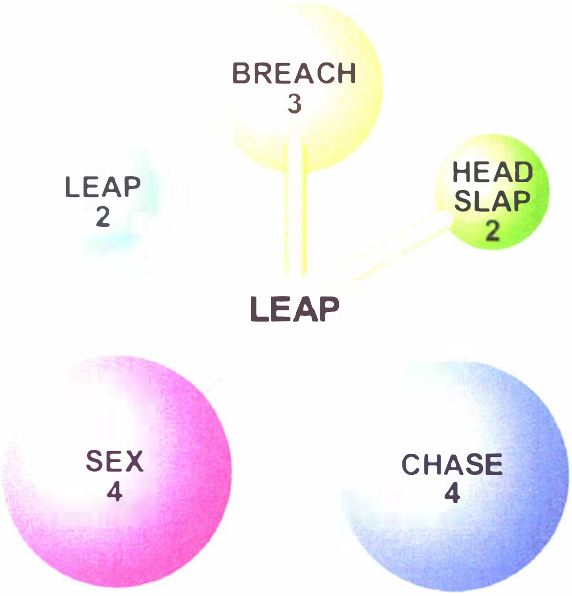


Figure 21. The frequency at which the behavioural event 'leap' was followed by other behaviours.

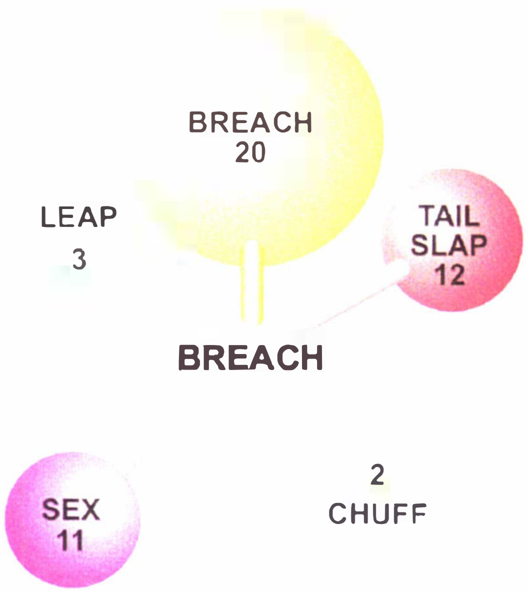


Figure 22. The frequency at which the behavioural event 'breach' was followed by other behaviours.

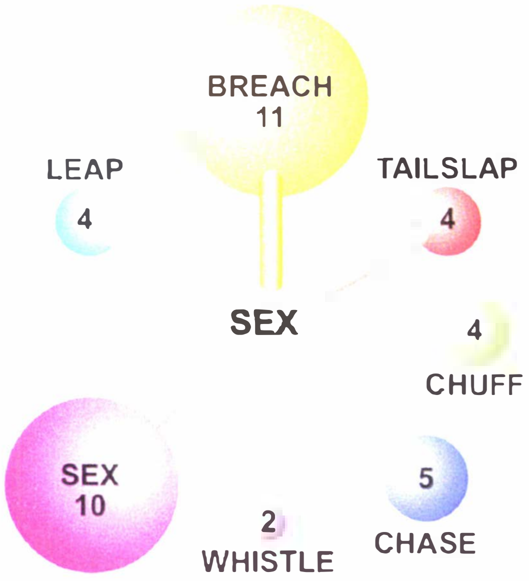


Figure 23. The frequency at which the behavioural event 'sex' was followed by other behaviours.

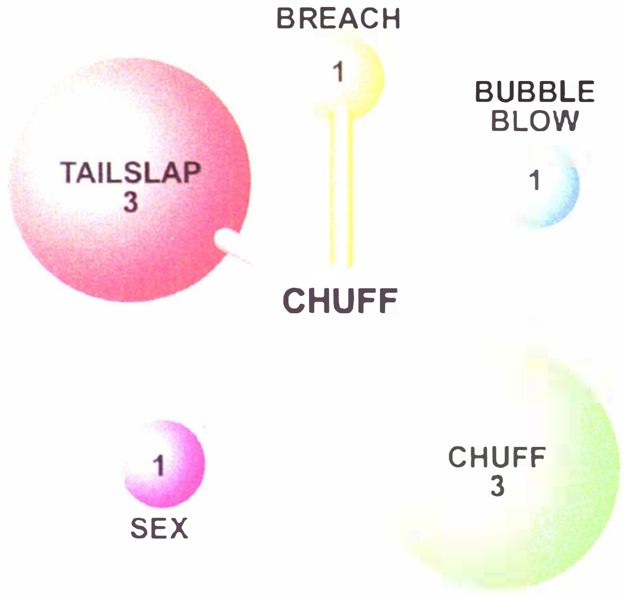


Figure 24. The frequency at which the behavioural event 'chuff' was followed by other behaviours.

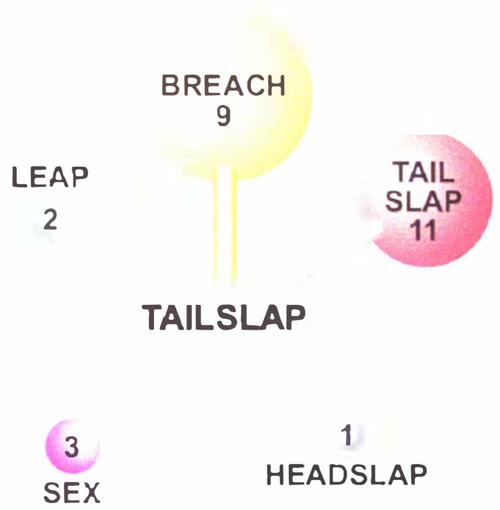


Figure 25. The frequency at which the behavioural event 'tailslap' was followed by other behaviours.

was a successful capture. Once, the dolphins rounded up a school of parore (*Girella tricuspidata*), and once two animals were observed each catching a garfish (*Hyporamphus ihi*). The visual identification of these species was based on Francis (1996). The sizes of the above prey items ranged from circa 15 centimeters (the smallest jack mackerel), to circa 40 centimeters (the largest yellow-eyed mullet) in length.

5.2.6 Associated species:

There are other species that associate with feeding common dolphins, because they feed on some of the same prey species. Their most frequent associates were Australasian gannets (*Morus serrator*) (Plate 18). Sooty shearwaters (*Puffinus griseus*) were the second-most frequent associates, mainly in combination with gannets. Once, gannets and shearwaters were joined by white-fronted terns (*Sterna striata*) (Table 9). Shearwaters and terns are less likely to capture live dolphin-prey, but they readily consume any 'scraps' left by the dolphins or gannets (pers. obs.).

There were only four occasions on which common dolphins were found in association with other cetaceans: Once with a sei whale (*Balaenoptera borealis*), once with a Bryde's whale (*Balaenoptera edeni*), once with two minke whales (*Balaenoptera acutorostrata*, or possibly the Antarctic minke whale, *B. bonarensis*), and once with a single minke

Plate 17. School of jack mackerel (*Trachurus novaezelandiae*), one of the fish species common dolphins were seen preying upon.

Plate 18. Australasian gannet (*Morus serrator*), a diving bird often associated with feeding common dolphins, competing with the dolphins for the same fish.

whale (Table 9). On all of these occasions gannets were also present, and the dolphins were feeding. Minke whales were seen on six further occasions without dolphins present. Bottlenose dolphins were spotted 12 times during the study, but never within five kilometers of common dolphins. On a further 2 occasions, large (> 80 individuals) mixed groups of bottlenose dolphins and false killer whales (*Pseudorca crassidens*) were observed, again nowhere near any common dolphins.

5.2.7 Feeding strategies:

Common dolphins were observed to use several distinct methods in the pursuit and capture of prey. Two main categories were distinguished:

1) individual feeding strategies in which a dolphin pursues and/or captures fish on its own. Other group members may be present, but do not in any way aid, or interfere with the individual's feeding effort.

2) cooperative feeding strategies in which several dolphins collectively herd or pursue fish. In such cases, groups of common dolphins often joined other groups already engaged in feeding. They separated again shortly after feeding had stopped.

'Carouseling' was the most frequently observed feeding strategy, and cooperative feeding was more prevalent than individual feeding (Table 10). For the first four months of this study, there was no differentiation

Table 9. Interspecific associations. Number of times common dolphins were accompanied by different species, when feeding.

gannets only	gannets and shearwaters	gannets, shearwaters, and terns	shearwaters only	sei whale and gannets	Bryde's whale and gannets	minke whales and gannets
10	28	1	2	1	1	2

between various feeding strategies in the data collection. This is reflected in the 12 feeding bouts with undetermined strategy.

Individual feeding strategies -

High-speed pursuit: Common dolphins were often seen individually pursuing single prey items. The prey was seen at the surface, trying to evade the dolphins by fast swimming, and rapid changes in direction. The pursuing dolphins were observed zig-zagging across the surface at speeds of 15-30 kph (Figure 26). Infrequently, common dolphins inverted themselves to a 'belly-up' position during such pursuits. On three occasions of upside-down chases, it was possible to determine the pursued species visually (based on Francis, 1996). Twice, the dolphins were chasing garfish (*Hyporamphus ihi*), and on another occasion flying fish (*Cypselurus lineatus*). Garfish and flying fish are both often found right at the air-water interface. Bottlenose dolphins are often seen swimming rapidly upside-down when pursuing fish close to the surface (Bel'kovich et al., 1991; Connor et al., 2000b). A possible explanation for this behaviour is that dolphins may rely heavily on vision to capture their prey during the final chase-and-catch phase, and "since a dolphin's vision field points down, and the fish stays up at the surface, the animal turns upside down to see its prey better" (Bel'kovich et al., 1991, p. 60).

Table 10. Frequencies of various feeding strategies observed during feeding bouts.

Individual feeding strategy	Number of observations	percent of observations
high-speed pursuit	19	27.9 %
fish-whacking	1	1.5 %
kerplunking	2	2.9 %
Cooperative feeding strategy		
carouseling	26	38.2 %
line abreast	7	10.3 %
wall formation	1	1.5 %
strategy not determined	12	17.6 %

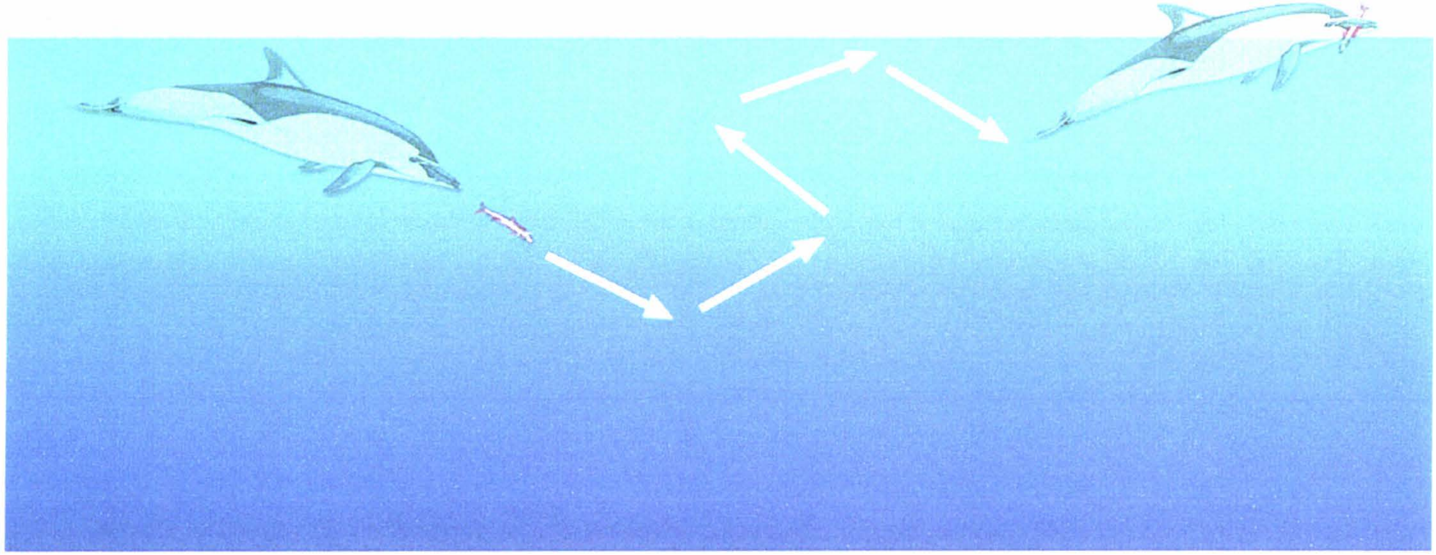


Figure 26. High-speed pursuit – an individual dolphin pursues a solitary fish on a zig-zagging chase.

Fish-whacking: Fish-whacking has been described in detail for bottlenose dolphins in Florida (Wells et al., 1987; Nowacek, 1999b). There, dolphins occasionally 'whack' fish with their tail flukes, launching them into the air in the process, and sending them flying across the surface for some distance (Figure 27). Upon re-entering the water, the dolphin then captures and consumes the fish. This very behaviour was displayed by a common dolphin off Whakatane. Circa 250 dolphins were seen spread out over 2 kilometers. Three small subgroups containing 5-10 individuals each, were actively chasing fish at the surface. Individuals were zig-zagging at high speed near the surface, and small fish could be seen jumping in front of them. One of the dolphins, its right side turned towards the surface, caused a big splash with a swipe of its tail-flukes, that sent a fish (mullet shape, circa 20 centimeters long) flying through the air over a distance of circa four meters. The dolphin was seen proceeding at high speed to where the fish hit the water. It could not be determined, if the fish was then actually consumed. Only 20 seconds later, the same individual performed another fish-whack, again in the same attitude, right side at the surface, hitting a fish with the downstroke of its tailflukes, launching the fish (same shape and size as above) over a distance of five meters. This time, the fish could be seen clearly, after it hit the surface. The fish floated motionless, and the dolphin immediately swam over and consumed it.

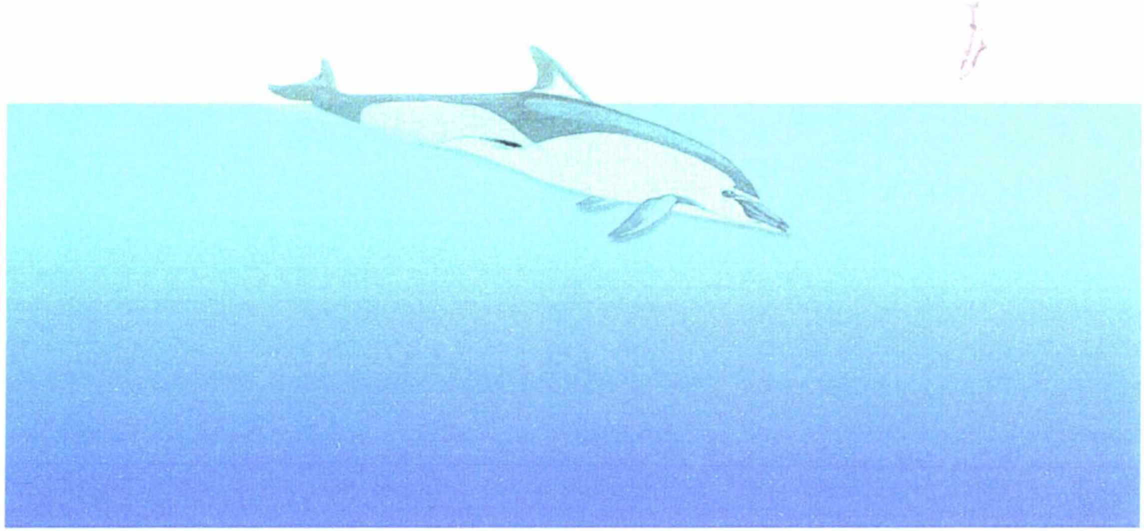


Figure 27. Fish-whacking – a dolphin catapults a fish out of the water, using its tailflukes.

On three other occasions, fish were found floating at the surface, directly after an intensive feeding bout. Once, a 90 centimeter barracouta (*Thyrsites atun*) - stunned; on another occasion a rough leatherjacket (*Parika scaber*) - dead; yet another time three porcupinefish (*Allomycterus jaculiferus*) - dead and inflated. The fact that they were left floating at the surface, rather than consumed, suggests that they are usually not prey items of common dolphins. The large size of the barracouta, and the protective spines of the leatherjacket and the porcupinefish make them unlikely targets for a common dolphin. More likely they were killed as 'innocent by-standers' during the dolphins' frantic feeding activity. Although no fish-whacking was directly observed during these feeding bouts, it may still have occurred, perhaps underwater, resulting in these casualties.

Kerplunking: Nowacek (1999b) and Connor et al. (2000a) described a specific, rapid tail fluke movement used by bottlenose dolphins while foraging in shallow waters in coastal Florida, and Western Australia, respectively. This behaviour was termed 'kerplunking', because of the characteristic percussive sound associated with it. Their descriptions of the bottlenose dolphins' behaviour also fits a behaviour observed in common dolphins in this study: In a 'kerplunk' the dolphin's body axis is angled away from the surface at circa 60-70 degrees . It then raises its peduncle high above the water, almost completely vertical, then brings the tailflukes down rapidly to the surface and continues the movement underwater, moving the flukes down and forward (Figure 28). This creates two distinct sounds and splashes: First, when the flukes initially hit the surface, there is a soft, smacking sound, accompanied by a small splash, angling away from the tail flukes at circa 45 degrees . This is followed by a much louder, lower frequency sound (the 'lunk' of kerplunk), as water rushes in to fill the void created by the downward fluke stroke. This cavitation also causes a second, much larger, vertical splash. The common dolphin kerplunks differed from those described by Connor et al. (2000a) for bottlenose dolphins in the following ways:

1) The dolphins exposed their entire peduncle above the surface, up to the level of the trailing edge of the dorsal fin, but the dorsal fin never broke the surface [*vs.* dorsal fin exposed above the surface (Connor et al., 2000a)].

2) The dolphins did not pivot when raising their peduncle, but remained stationary [*vs.* typical pivoting of 90 degrees (Connor et al., 2000a)].

3) The typical height of the cavitation splash was circa 2 meters [*vs.* 3-4 meters (Connor et al., 2000a)].

This behaviour differed considerably from 'tail slapping', a behaviour often seen in social contexts. When tail slapping, common dolphins are typically traveling with their body parallel to the surface. Only the most posterior part of the peduncle is raised above the surface, and the tailflukes are brought down towards the surface at a flatter angle, creating a louder, smacking sound. Also, the downward movement of the tailflukes is stopped immediately, once they hit the surface, *not* continuing down and forward, and therefore *not* creating a cavitation splash.

On two separate occasions, kerplunking was observed in common dolphins during a feeding bout. First, a large group of common dolphins (circa 300 individuals) was observed herding a school of jack mackerel (*Trachurus novaezelandiae*) in Mercury Bay. The dolphins circled the fish, with some individuals darting through the school at high speed. After 20 minutes, feeding activity gradually eased. Dolphins were no longer 'carouseling' the fish, and the group started to scatter. At this point, at least 10 individuals, each separated by 30-100 meters from the next, were observed to kerplunk. The most active of these 'kerplunkers' was focused upon, and seen to perform 16

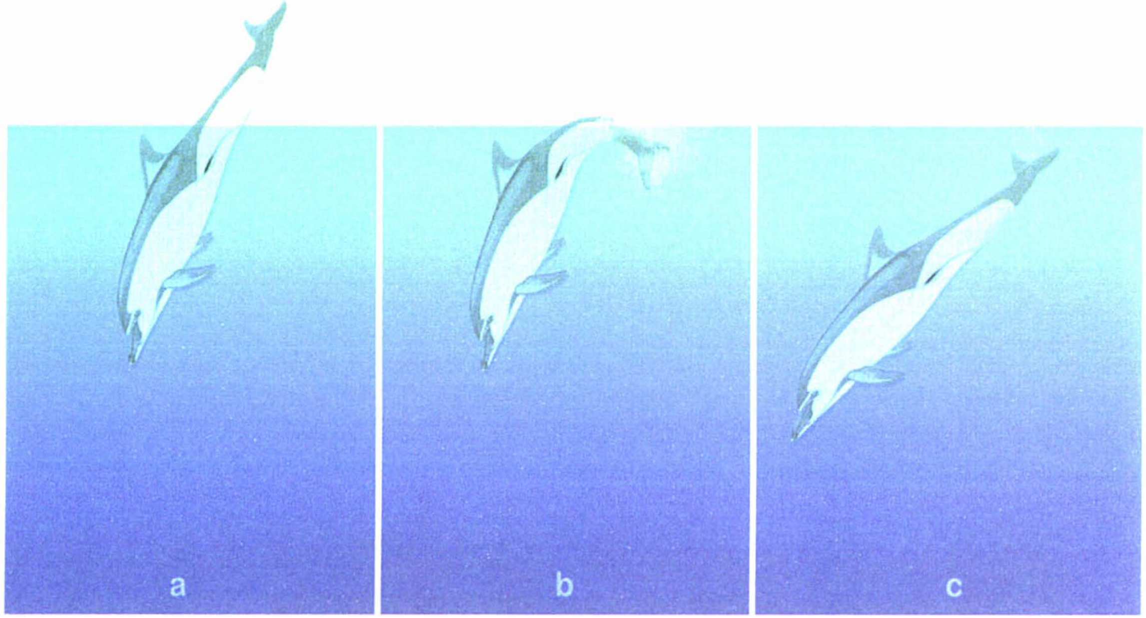


Figure 28. Kerplunking – a) dolphin is oriented vertically, with tailflukes extended above the surface; b) dolphin brings tailflukes down rapidly, and moves them forward towards its venter, creating a bubble-cloud underwater; c) dolphin 'straightens out', while a large vertical splash can be seen above the surface.

'kerplunks' in a bout lasting eight minutes. Every second or third kerplunk was followed by a dive typically lasting 30 seconds, after which the dolphin resurfaced within 10 meters of its kerplunking station. By the end of this 8minute period, all of the 'kerplunkers' had changed their activity to traveling, and followed the other members of the group, who had started to move offshore five minutes earlier.

In a separate incident off Whakatane, a group of 20 dolphins was observed pursuing a school of unidentified fish. The dolphins did not herd the fish into a tight ball, but individual dolphins were seen to chase and capture fish along the trailing edge of the school. This was a slow-speed pursuit, with dolphins and fish moving along at circa 7 kph. Separated from the main group by about 20 meters, one dolphin remained in one location and started lagging behind. The front half of its body was angled downward, and it swept its head from side to side. After 20 seconds of this behaviour, it performed 2 kerplunks in rapid succession, but remained in the same position at the surface. After an interval of another 20 seconds, a third kerplunk was performed, followed immediately by a deep dive. It surfaced again 40 seconds later, then caught up with the remainder of the group, resuming the slow-speed chase.

Cooperative feeding strategies -

Line abreast: When employing this strategy, common dolphins form a tight line, with individuals swimming side by side, separated by no more than one dolphin-body width. The fashion in which the dolphins are organised is reminiscent of a line of infantry soldiers marching into battle (Figure 29). This behaviour was observed on seven occasions, with the line moving forward at high speed (> 15 kph), and often porpoising in the process. The line of dolphins thus drive fish in front of them. There appears to be an element of tiring the prey in this process. Actual consumption of fish is only observed after > five minutes of chasing, and is accompanied by a decrease in speed. Fish are then easily picked off from the trailing edge of the school by the dolphins. This strategy is also employed by bottlenose dolphins. Bel'kovich et al. (1991) called it "driving fish in front".

Wall formation: Bottlenose dolphins often drive fish into shallow water, or against other obstacles, to restrict their maneuverability. In some cases, other dolphins serve as such an obstacle. Bel'kovich et al. (1991) have described this strategy as "wall formation", with a number of dolphins driving fish towards other dolphins, effectively trapping the fish (Figure 30). This kind of behaviour was observed only once in this study. A group of nine adult dolphins were traveling along, spread out over circa 40 meters. Two animals could be seen swimming

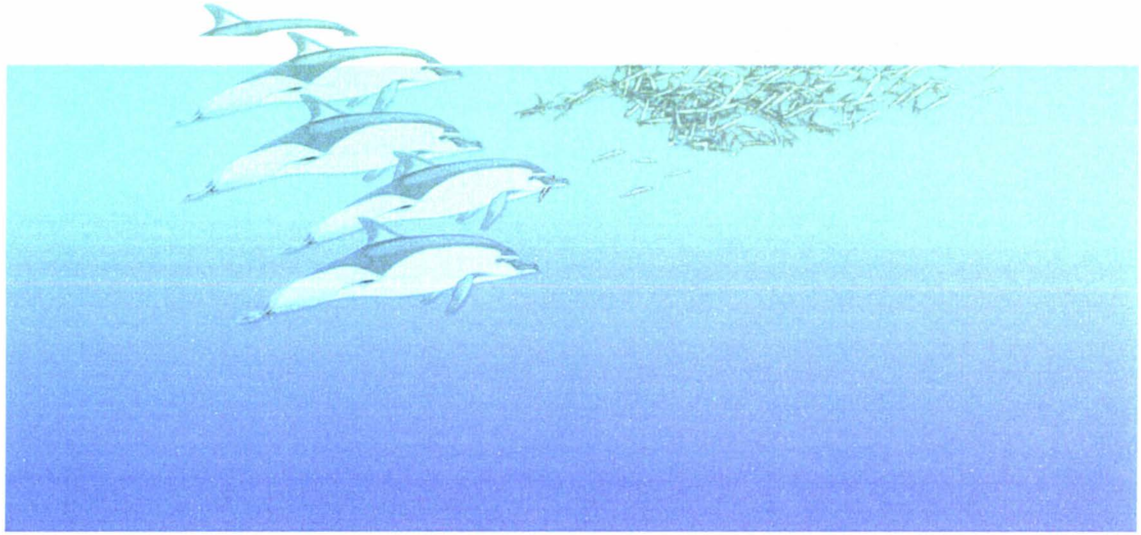


Figure 29. 'Line abreast' formation – dolphins swim closely side-by-side and drive fish in front of them.

away from the others at high speed (these two shall now be referred to as the 'drivers').At the same time, the remaining seven dolphins assumed a 'line abreast'-formation, but continued traveling at slow speed (circa 6 kph) (these seven shall now be referred to as the 'receivers'). After the 'drivers' were about 200 meters distant from the 'receivers' they started heading towards the 'receivers' at moderate speed, on a head-to-head collision course. As the two factions were separated by less than 10 meters, some fish could be seen swimming ahead of the 'drivers', towards the 'receivers'. The fish did not end up 'crashing' into the wall formed by the 'receivers', however. Both, 'receivers' and 'drivers' dove, while still separated by more than five meters. All of the dolphins remained submerged for circa one minute, presumably pursuing the fish, which may have tried to escape to greater depths. After re-surfacing, traveling was resumed, and there were no further indications of feeding behaviour.

Carouseling: The vast majority of feeding bouts appeared to be cooperative, with the dolphins actively herding a school of fish, and trapping it against the surface (Figure 31). This strategy has also been documented for dusky (Würsig & Würsig, 1980), spotted (Fertl & Würsig, 1995), and bottlenose dolphins (Würsig & Würsig, 1979; Bel'kovich et al., 1991), as well as killer whales (Similä & Ugarte, 1993). Bel'kovich et al. (1991) provide a good description of this behaviour,

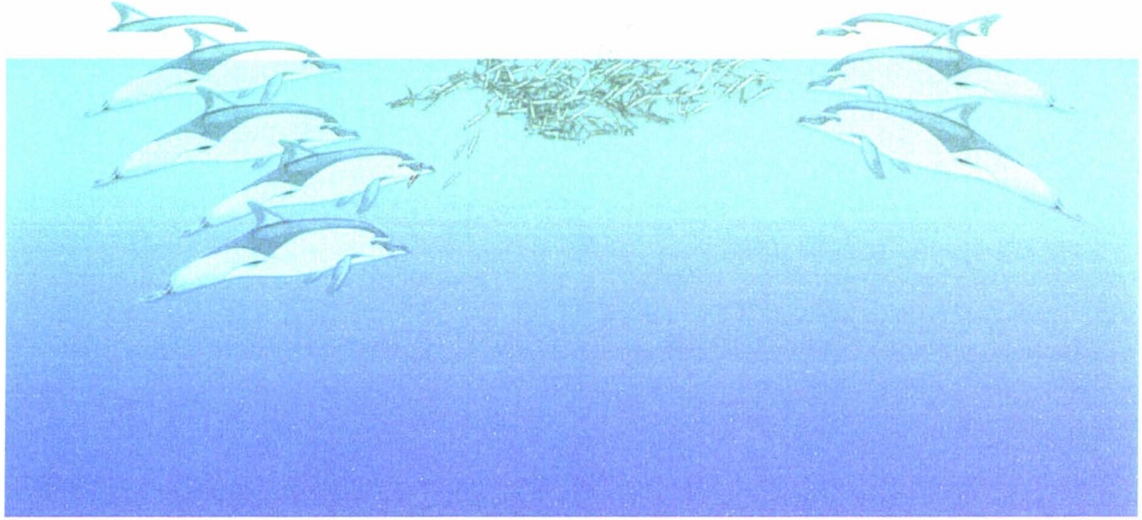


Figure 30. 'Wall formation' – dolphins form a 'line abreast', driving fish towards other dolphins, trapping the fish in the centre.

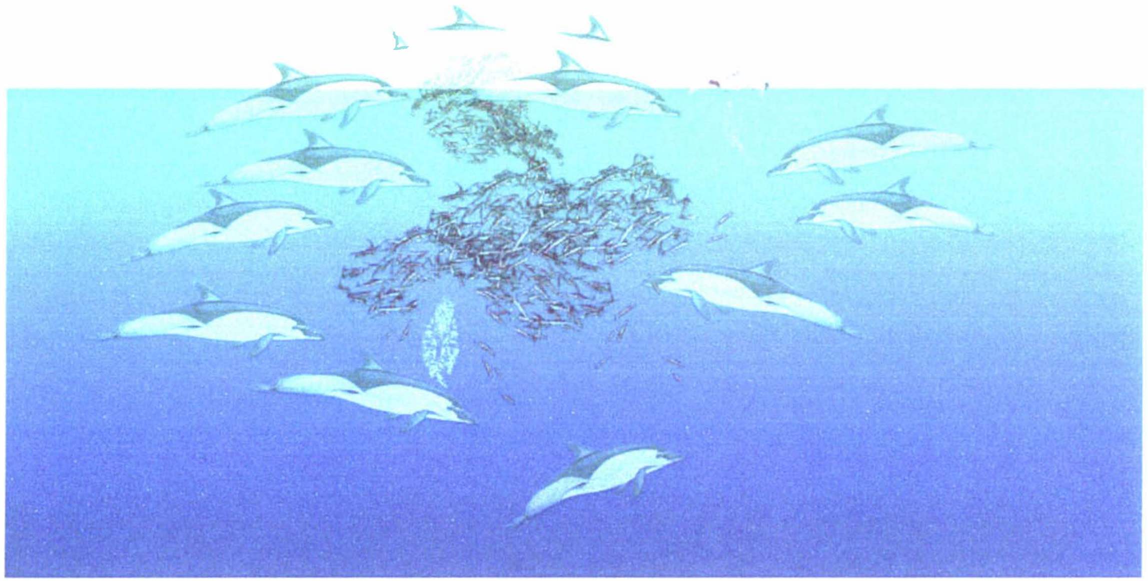


Figure 31. 'Carouseling' – dolphins cooperatively surround school of fish; individuals circling around the school keep the fish tightly packed, while others dash into the centre to capture fish (centre right); one individual is pictured 'bubble-blowing' (bottom left), which scatters the fish in the vicinity; gannets circle overhead and also dive for fish.

which they termed "carouseling". The common dolphin 'carousels' observed in this study, follow a very similar pattern. First, a number of dolphins (10-40 individuals) dive simultaneously, and force a large number of schooling fish to the surface. Then, the same individuals, aided by additional group members (if present) start circling the school horizontally, gradually tightening the circle, and thus forcing the fish into a densely packed 'meatball'. Some of the individuals involved in this process swim clockwise, while others swim counterclockwise. Some individuals also pass underneath the school, from time to time, effectively blocking off all escape routes. Once the fish are tightly concentrated, the majority of dolphins will continue to patrol around the fish, while two or three individuals at a time dart through the middle of the school at high speed, capturing fish in the process. In an attempt to escape these dolphins, some of the fish rush into the paths of the patrolling group, who will readily capture these fish. After 2-4 passes through the centre of the school, the 'darting' dolphins resume patrolling around the fish, while other dolphins take their turn at rushing through the school. This suggests a sequential division of labour among the dolphins. The smallest number of dolphins observed in this form of cooperative feeding was 15 individuals, which may represent the minimum number necessary to control fish in this fashion. Groups numbering less than 15 were never observed to 'carousel' fish. They either pursued them individually, or formed a line abreast.

The method of darting through the centre of the 'meatball' to capture fish was sometimes combined with, or substituted by, another method, aimed at startling the fish, and separating individual fish from the school. This was achieved by releasing air-bubbles from the blowhole underwater. While this should not be treated as an entirely separate feeding strategy, it is curious enough to warrant a detailed description:

Bubble-blowing: Thanks to the underwater video camera, the subsurface behaviour of common dolphins could be filmed during four feeding bouts. During three of these feeding sessions, common dolphins were observed to blow bubbles underwater, in an apparent attempt to startle fish they had herded. On all three occasions the fish were visually identified as jack mackerel (*Trachurus novaezelandiae*), and a number of dolphins (between 15-50 individuals) were circling them, keeping them tightly packed. During two of these encounters, an individual was seen positioning itself below, and on the edge of the school, then releasing a short burst of bubbles from its blowhole (Figure 31). As the bubbles rose towards the school, the fish reacted with a quick burst of speed, heading away from the bubbles. While their reaction was coordinated, some of the fish (those that reacted quicker than others, or swam farther away from the bubbles) were left separated from the school, and quite literally swam into the jaws of waiting dolphins. Two individuals caught a startled fish during the first occasion, one individual during the second. The 'bubble-blower' did not itself pursue any fish immediately following the bubble-blow, on these two occasions. This suggests that cooperation during feeding is highly evolved, featuring division of labour. It could be considered an example of reciprocal altruism, whereby the 'altruist' is repaid for his bubble-blowing services at a later stage, by swapping roles. In one instance, however, a dolphin was observed using the same technique, but chasing, and successfully capturing one of the fish it had startled, itself. Here, the dolphin also positioned itself near the edge of the school, and released bubbles. The fish reacted by heading away from the disturbance. A handful of fish broke out of the protective envelope of the school, and darted away to greater depths. The dolphin pursued one of them at high speed for circa 15 meters, caught, and swallowed it.

It is possible that bubble-blowing is a more common feature of common dolphin feeding behaviour, than the three examples above would suggest. Due to various circumstances, the camera could not be deployed during every feeding session. Even when it was, factors such as camera angle, distance, visibility, etc. often provided inconclusive pictures.

5.3 Discussion

5.3.1 Discussion of observed activity patterns:

Traveling and feeding - The activity budget showed that dolphins spent most of their time traveling (55.6 percent). This is no surprise, because daily and seasonal movements are likely governed by the distribution and availability of prey. Food resources are rarely uniformly distributed throughout the environment. This necessitates travel between foraging locations. Because of this connection between traveling and feeding, the two activities are discussed here in the same section.

Access to special habitats or conspecifics could also play a role in common dolphin travel. The search for mating opportunities influences the movement patterns of bottlenose dolphins (Waples et al., 1998). Many baleen whales seek special environments to give birth and to mate (Rice & Wolman, 1971; Clapham, 1996). Some bottlenose dolphin mothers seek sheltered, shallow bays, during the first few weeks of their calves' lives (Barco et al., 1999). However, such behaviours were not evident for common dolphins in this study.

Food availability is the single most important factor in determining an animal's activity budget (for example see Goodson et al., 1991; Shepherdson et al., 1993; Westerterp et al., 1995; 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 spent 16.2 percent of their time feeding. In bottlenose dolphins, daily food requirements have been calculated to range between 4-6 percent of body weight (Shapunov, 1971; Shane, 1990b). Assuming the same kind of range for common dolphins and a typical adult weight of 100 kg (Collet & St. Girons, 1984) this would work out to about five kilograms of prey per day. Whether or not 16.2 percent of a common dolphin's daily activity budget would be sufficient to catch that amount of prey is a matter of speculation. However, this number is well within the range of feeding activity reported for bottlenose dolphins in Florida by Shane (1990a, 17 percent), and Waples (1995, 13 percent). Pacific coast bottlenose dolphins spent 19 percent of their time feeding (Hanson & Defran, 1993), while Atlantic white-sided dolphins off New England (*Lagenorhynchus acutus*) spent only 9.5 percent feeding (Weinrich et al., 2001). Such variations may partly be a result of varying diurnal activity patterns: All of these activity budgets (including this study) are based on data collected during daylight hours. The amount of time devoted to various activities at night, still remains to be determined.

Milling - Milling, "a somewhat ambiguous category" (Reynolds et al., 2000, p. 132), was the second-most frequent activity (20.5 percent), but its role is difficult to assess. All that is noticeable from the surface during milling, is that the group does not make significant progress in any one direction. Their heading frequently changes, and they are not observed to feed, socialise, or rest during those times. Again, the value reported here is comparable to that reported by Waples (1995) for bottlenose dolphins, who spent 14 percent of their time milling. Milling has been widely used as a behavioural category in studies of dolphin behaviour (Shane et al., 1986; Reynolds et al., 2000), but few attempts have been made at explaining its biological significance. Milling could mark a stage of foraging, when dolphins have reached a promising location and are now investigating a given area more closely for prey. Conversely, milling could be a brief rest-stop between bouts of traveling, or it could represent a transitional stage between traveling and resting/socialising/feeding. This idea is supported by studies that associated milling with other behaviours, such as feeding, socialising, or playing (Shane et al., 1986). One could argue that milling is probably caused by all of the above, and happens to manifest itself to the observer in the characteristic non-directed movement classified as 'milling'. Various amounts of time that have here been recorded as milling, should therefore probably be considered to represent part of the time budget of the remaining four activities. However, since it was not apparent, which milling bouts might be associated with which other activity, milling was retained as a separate category.

Socialising - The focal group's activity was scored as socialising (7.3 percent) when more than 50 percent of the group were involved in conspecific interactions. These primarily involved sexual behaviour, signaled by belly-to-belly contact (with or without actual intromission). Chasing one another (which in rare cases included bites directed at the tailflukes, pectoral, or dorsal fin) was also scored as a social activity. How much time can be devoted to socialising probably depends on how easily other more immediate requirements (e.g., food) can be satisfied. One might expect the time devoted to socialising to increase when prey is particularly abundant, and/or when females are receptive. Time devoted to socialising varied seasonally in this study, but did not show a consistent trend. Since data on dolphin prey abundance in this area, or on the reproductive state of female individuals were not available, it could not be determined, whether these were correlated to the frequency of socialising.

Common dolphins engaged much more often in sexual contact than would be required for breeding. Homosexual behaviour and sexual activity by immature animals were observed frequently. This suggests that sexual behaviour in common dolphins might be used to establish and reinforce social bonds. The fact that sexual activity was observed frequently after two groups merged, may also indicate the use of sex as an affiliative, appeasing gesture. This kind of socio-sexual affiliative behaviour has also been documented among some primates (bonobos, *Pan paniscus*, Wrangham (1993), *Homo sapiens*, Pfaus (1996)), and other cetaceans (spinner dolphins, *Stenella longirostris*, Norris et al. (1994)). Bottlenose dolphins also exhibit non-reproductive sexual behaviour (Connor et al., 2000b), and perhaps even use mounting to establish dominance hierarchies (Östmann, 1991).

Resting -

Only 0.7 percent of time was spent resting. In studies on bottlenose dolphins it ranged between 2-3 percent (Waples, 1995; Hanson & Defran, 1993), while it was apparently not observed in a study on Atlantic white-sided dolphins (Weinrich et al., 2001). The low frequency of resting observed in this study, could be a sampling artifact, i.e. resting dolphins were present in the study area but were not spotted during surveys. When they rest, common dolphins show virtually no conspicuous surface activity, which makes it very difficult for an observer to spot such groups. Common dolphins may also generally rest in smaller groups, which would compound the problem, because smaller groups are more difficult to spot over long distances than are larger groups. In fact, the group sizes for the sightings that featured resting, were on the smaller side, ranging from 12-40 individuals. Alternatively, common dolphins may rest primarily at night, when no surveys were conducted. However, this is somewhat unlikely, because common dolphins in other locations are known to be active at night, preying on species of the deep-scattering layer (see section 5.3.3 on prey below).

An alternate possibility, would be that the dolphins' resting behaviour is disturbed by the presence of the research vessel. The dolphins may detect the boat, before the observers detect the dolphins, and by the time data collection begins, the dolphins' behaviour will have changed to an activity other than resting. Two of the resting bouts were observed at the beginning of a follow, but it took 12 minutes of the boat being present, before the dolphins changed their behaviour. The two remaining bouts occurred mid-way through one-hour follows, which suggests that at least on these occasions, the boat's presence did not interfere with the dolphins' readiness to rest.

Seasonal changes in activity - Common dolphin behaviour did not indicate a consistent relationship between the time-of-year and certain activities. Bräger (1993) attributed a seasonal increase in feeding activity by bottlenose dolphins in coastal Texas to higher energy requirements in colder winter waters and/or decreased availability of prey. Bighorn sheep increased their foraging time, when the nutrient value of available food decreased in winter (Goodson et al., 1991). Adeyemo (1997) found that green monkeys traveled more, to forage throughout a greater area, when food was less abundant during the dry season. For common dolphins in this study, foraging effort itself does not appear to change seasonally. It is rather the foraging location that changes with decreasing water temperatures in autumn (Neumann, 2001a; also see chapter 4 this study).

Diurnal activity patterns - Common dolphins were encountered much more frequently in the morning, than in the afternoon (Figure 7). This could be a result of:

1) dolphins spending most of their afternoons outside the study area, or

2) dolphins remaining in the study area, but becoming less conspicuous to the observers because they were either engaging in more sedate activities (e.g., resting), or had split into smaller groups, or both. Smaller groups are more difficult to spot over long distances than are larger groups. Scott & Cattanach (1998) reported an increase of mean group size of common dolphins in the eastern Pacific from morning to early afternoon, followed by a decrease in the evening. This does not seem to have been the case in this study area.

Hawaiian spinner dolphins show a distinct diurnal pattern in their behaviour (Norris et al., 1994). Nocturnal feeding in deep water is followed by resting throughout the morning in sheltered bays. Socialising and aerial behaviour then become the predominant group activity in the early afternoon, which is followed by traveling to the dolphins' hunting grounds. Nocturnal feeding upon species of the deep scattering layer also appears to play a major role in this species (Norris et al., 1994), as has been documented for common dolphins (Young & Cockcroft, 1994, 1995; Scott & Cattanach, 1998). Bottlenose dolphin activity appears to be less structured, but in various locations they exhibit two diurnal peaks in feeding activity - one in the early morning, and one in the late afternoon (Bräger, 1993; Hanson & Defran, 1993). There was also a high frequency of early-morning feeding for common dolphins in this study, albeit not significantly more than later in the day. Feeding activity could peak again in the late afternoon, but this does not appear to occur within the study area. If one assumes that common dolphins here also feed on species of the deep-scattering layer as they do elsewhere (Young & Cockcroft, 1994, 1995; Scott & Cattanach 1998), then this second feeding peak could well appear around dusk or shortly thereafter, once the deep-scattering layer rises close to the surface. One group of dolphins observed in the late afternoon, was traveling at a sustained high speed directly towards the continental shelf, and never deviated from this heading.

This follow had to be abandoned because of the increasing distance from shore, but if the dolphins maintained the same speed and heading, it would have put them right over the continental shelf (200 meter isobath) at sunset. This is where deep-scattering layer species would presumably be abundant. In a study based on acoustic recordings of common dolphin sounds, Goold (2000) found acoustic contact to peak in the middle of the night, and reach a low in the late afternoon, before it started to increase again around dusk. He attributed this to increased sound production during night-time feeding.

5.3.2 Behavioural events:

The major difficulty in interpreting behavioural events, is that their causes can hardly ever be determined. While the recorded events themselves are highly obvious, the behaviours leading up to a behavioural event may be much less conspicuous, or may happen entirely outside the observer's view. Thus, the immediate context of behavioural events is often very sketchy, and the interpretation of their function is therefore rather speculative.

Very few attempts at classifying cetacean behaviour by sequence analysis have been made. In a very detailed analysis of behaviour sequences of Hector's dolphins, Slooten (1994) found that most behavioural events that would intuitively be labeled as sexual (e.g.

penis out) were indeed strongly associated with sexual activity states. As in this study, she also found that belly-to-belly contact (possible copulation) was often followed or preceded by breaching ("noisy jump" in her terminology). In contrast, "chasing" in Hector's dolphins did not appear to be connected to sexual behaviour. Chasing was often observed as a prelude to sex, with the chaser copulating with the chased individual after a brief high-speed pursuit (Table 8).

Most of the aerial behaviours, such as breaching, chest-slapping, and tail-slapping are highly conspicuous, both above and below water. Melville (1851, p. 474) gives this description for breaching in sperm whales (*Physeter macrocephalus*):

> Rising with his utmost velocity from the furthest depths, the sperm whale thus booms his entire bulk into the pure element of air, and piling up a mountain of dazzling foam, shows his place to the distance of seven miles and more. In those moments, the torn, enraged waves he shakes off, seem his mane; in some cases, this breaching is his act of defiance.

Besides being visually conspicuous, such aerial behaviours also include an acoustic component, and with these properties lend themselves to display purposes. Breaching could be a form of mating display. In many species males advertise their physical fitness to potential mates by energy-demanding displays (for example see Sandegren, 1976; Pfaus, 1996). Mostly, these occur as a direct contest with other males and also help to establish social hierarchies (for example see Le Boeuf, 1974). While physical combat between two animals was not observed, it is possible that breaching could be used both as a mating display, and in hierarchical contests. The former, because breaching frequently occurred just before, or just after sex; the latter, because breaching by one animal was often followed by breaching of a second or more individuals (Table 8). Cousteau & Paccalet (1988, p. 225) offer the following interpretation in a discussion of breaching by great whales:

> In certain situations, breaching may simply be a way of saying to any whales in the vicinity, 'Here I am! Just listen to the racket I'm making as I land!' This would be especially useful when high winds or rough seas interfere with their ability to locate one another by underwater sound emission. In other cases, more complex forms of social interaction may be involved. Breaching could conceivably mean 'I'm challenging you' or 'I'm stronger than you'. During courtship, rival males may hold 'breaching matches' to decide which one will mate with a female.

It is possible, that breaching may fulfill such a 'contest' function in common dolphins, in some cases. In one case, in this study, two common dolphins traded breach for breach until they had breached 15 times each. Dolphins might be able to assess both the virility and the strength of another individual, based on subtle differences between breaches (e.g. height, loudness of splash, interval between breaches, etc.). However, if aerial behaviour were a form of mating display, one would expect only sexually mature animals to engage in it. Aerial behaviour was performed by all age classes and either sex. This has also been pointed out by Norris et al. (1994) for spinner dolphins.

While dolphins appear to communicate with each other primarily acoustically through various squeaks and whistles, these are very directional, and in some contexts the somewhat less refined, but omnidirectional aerial displays may be called for (Norris et al., 1994). Spinner dolphins appear to use aerial behaviours to coordinate group activity and movements (Norris et al., 1994). While common dolphins were never observed to spin around their axis, during leaps, almost all the aerial behaviour described by Norris et al. (1994) was also present in this species, and may serve a similar purpose. However, unlike for Hawaiian spinner dolphins, no clear correlation between aerial behaviour and certain activity states, or time of day was found in this study. Acevedo-Guttierez (1999) hypothesised that aerial behaviour in bottlenose dolphins may be directly related to prey capture, rather than being a social facilitator. No evidence for increased aerial behaviour during feeding was found for common dolphins, in this study.

Breaching may not only play a role in intra-specific communication, it might also be used in communication with other species. Unlike sophisticated acoustic signals, aerial displays are rather blunt and might not be too difficult for other species to interpret (even though this *Homo sapiens* seems to have difficulties interpreting it !).

Many ungulates have a means of signaling to would-be predators that they have been detected. In deer, this appears to be by snorting (Caro et al., 1995). They may also advertise their fitness to potential predators, effectively signaling that they would be extremely costly to catch, and that the predator would therefore be well-advised to select a different potential victim. Stotting in gazelles - a display in which the animal repeatedly leaps up high into the air, seemingly bouncing off all four legs at once - is a good example for this kind of inter-species signaling (Caro, 1986).

In relation to predators, breaching could also alert other individuals in the group to the presence of a threat. Deer accomplish this through foot-stomping (Caro et al., 1995). Even though no known dolphin-predators (sharks, killer whales (Cockcroft et al., 1989; Mann & Barnett, 1999; Visser, 1999; Heithaus, 2001)) were ever observed in the vicinity of the dolphins, sharks would not have been spotted, unless they had been very close to the surface and near the research vessel. However, no apparent defensive tactics, e.g. closing ranks, or taking flight were ever associated with aerial displays.

If aerial behaviour is indeed used in inter-specific communication, some of these displays may have been directed at the research vessel. Corkeron (1995) and Peterson (2001) observed that humpback whales (*Megaptera novaeangliae*) which were close to whale-watching boats showed a significantly higher frequency of aerial behaviours, than those whales not in the vicinity of a vessel.

After breaching, 'sex' was the second-most frequently observed behavioural event. From the high frequency of sexual behaviour, one may infer that common dolphins have a highly promiscuous mating system, although admittedly not all sexual events could have resulted in pregnancies. In the three-dimensional ocean environment, it would be very difficult for males to monopolise females. Although some male bottlenose dolphins appear to achieve this by forming male alliances and 'sharing' a female (Connor et al., 1992). Another indication for a promiscuous mating system in common dolphins lies in testes size. Mature common dolphins have some of the largest testes found in any delphinid (P. Duignan, pers. comm., 8.5.2001), suggesting possible sperm competition (Kenagy & Trombulak, 1986). The roles of courtship, competition, and female choice remain entirely unknown for common dolphins. Future work focusing on the behaviour of sexually mature males, which can be recognised by their postanal hump (see above, 4.3.3 Group formation and composition), combined with genetic testing of paternity, may shed some light on this subject.

5.3.3 Prey:

Studies of the stomach contents of dead common dolphins in other areas reveal a relatively opportunistic diet, consisting of small scombrids (e.g. mackerel), anchovies, mullet, but also squid, lanternfish, and other species typical of the deep-scattering layer (Young & Cockcroft, 1994, 1995; Walker & Macko, 1999). In Mercury Bay, six different prey species were identified in 11 sightings, suggesting that common dolphins here also show a rather opportunistic feeding pattern.

Unfortunately, it was impossible to conduct night-time observations during this study, and therefore the importance of various species of the deep-scattering-layer in the diet of Mercury Bay common dolphins, particularly squid, could not be determined. Squid and myctophid lanternfish are known to undertake diurnal vertical migrations, rising closer to the surface at night, when they thus become available to the dolphins. Squid is commercially harvested in this area, and common dolphins have been spotted by crew members of squid boats during nocturnal fishing, which suggests that squid also play a role in the diet of Mercury Bay common dolphins (S. Morrison, pers. comm., 12.4.2000)

Ferretti et al. (1998) observed a separation of ecological niche between sympatric bottlenose and common dolphins in their study area in the Eastern Ionian sea. Common dolphins tended to focus on surface feeding on pelagic schools of small fish (as observed in this study), whereas bottlenose dolphins appeared to engage mainly in deep-water foraging. Surface feeding was never observed for bottlenose dolphins in Mercury Bay, even though four of the six prey species taken by common dolphins also appear on the menu of bottlenose dolphins in the nearby Bay of Islands (Constantine & Baker, 1997). These were: kahawai (*Arripis trutta*), yellow-eyed mullet (*Aldrichetta forsteri*), parore (*Girella tricuspidata*), and garfish (*Hyporamphus ihi*). However, there appears to be no overlap in bottlenose and common dolphin habitat in the Mercury Bay study area. When sighted, bottlenose dolphins were never more than 500 meters from the coastline, in depths ranging from 5-30 meters. In fact, they seemed to 'hug' the mainland coastline in their traveling patterns, whereas common dolphins were never found closer than two kilometers to the mainland, in depths ranging from 12-200 meters. Although it is highly speculative, it might be worthwhile to consider the possibility that common dolphins in the study area are displacing bottlenose dolphins from part of their ecological niche. Perhaps the greater abundance of common dolphins in Mercury Bay (compared to the Bay of Islands) forces bottlenose dolphins to exploit other food sources in this area. Some of the bottlenose dolphins encountered in Mercury Bay have actually been identified as visitors from the Bay of Islands, based on natural markings on their dorsal fins (R. Constantine, pers. comm., 19.11.1999).

The two locations where common dolphins were found most often (around Castle Rock, and south of Ohinau Island, Figure 9), present areas of high sea floor relief, which common dolphins have been shown to prefer in various studies, probably because fish tend to concentrate there (Hui, 1979; Selzer & Payne, 1988). Fish often aggregate around any kind of structure, fixed or floating, possibly for shelter (T. Mulligan, pers. comm., 30.10.1998). Areas of rapidly changing seafloor relief (e.g. seamounts) can also act as such structures. Depending on upwelling-conditions such areas may not only provide shelter, but may also be richer in nutrients. The dolphins' offshore-movement in autumn is probably linked to seasonal movements of their prey, which are governed by changes in sea surface temperature (Neumann, 2001a).

5.3.4 Associated species:

The close link between gannets and common dolphins is remarkable. The frequencies for associations with gannets reported by Constantine & Baker (1997) for common dolphins in the Bay of Islands are similar to those reported in this study. Both species appear to have certain prey species in common and often feed in close association with each other. The same kind of association has been reported between common dolphins in the Gulf of California, and boobies (*Sula* sp.), close relatives of gannets (Gallo, 1991). By encircling schools of fish and pushing them to the surface, the dolphins bring the fish within easy reach of the gannets. This is not a completely one-sided affair, though. On a handful of occasions, a flock of feeding gannets was encountered, without any dolphins initially present. Five to 10 minutes later a group of common dolphins arrived and joined in the feeding. This indicates, that dolphins are possibly alerted to the presence of prey by the splashing sounds of gannets diving after fish. Gallo (1991) suggests that either species can act as an 'information centre' which attracts the attention of the other. A Bryde's whale that fed among the dolphins appeared to be attracted to the feeding session from a fair distance. It is difficult to estimate whether the low frequency of associations between common dolphins and baleen whales (3.8 percent of sightings) truly shows that they are rarely found together, or if this is a function of baleen whales being scarce in the study area. Leitenberger (2001) found baleen whales in the vicinity of common dolphins during 11.6 percent of her observations in the Hauraki Gulf. During all of these sightings, the common dolphins were feeding. Such associations are unlikely to benefit the dolphins, who will probably only be left with the 'scraps', when competing directly with baleen whales. Based on the sheer volume of their throat pouch, the larger baleen whales should be able to consume an entire school of fish - which has been carefully herded by common dolphins - in a single gulp. This may have been the case in the Bryde's whale observation, when feeding activity ceased completely, very shortly after the whale appeared.

5.3.5 Feeding strategies:

"Carouseling" was the most frequently observed feeding strategy. This suggests, that it might be the most efficient method for preying on small, schooling fish in the open ocean. Indeed, dusky dolphins (Würsig & Würsig, 1980), spotted dolphins (Fertl & Würsig, 1995), bottlenose dolphins (Würsig & Würsig, 1979; Bel'kovich et al., 1991), and common dolphins in the Gulf of California (Gallo, 1991) have all been observed to herd fish in this fashion, in similar habitats.

There are also interesting parallels between the common dolphin behaviour observed in this study, and killer whales (*Orcinus orca*) herding herring in Norwegian waters. Not only do the killer whales herd the herring cooperatively by 'carouseling', they also use bubbleblows to startle the fish, and they stun or kill some of the herring with tail fluke movements that could be described as 'underwater fish whacking' (Similä & Ugarte, 1993; Domenici et al., 2000). The description in Domenici et al. (2000, p. 283) of the orcas' behaviour almost sounds like a combination of the decriptions given above, for 'carouseling' and 'fish-whacking' in common dolphins:

> The whales cooperatively herded herring into tight schools close to the surface. During herding and feeding, killer whales swam around and under a school of herring, periodically lunging at it and stunning the herring by slapping them with the underside of their flukes, while completely submerged. [...] When killer whales slapped the herring successfully, disoriented herring appeared on the video at approximately the time of maximum fluke velocity, in synchrony with a loud noise. This noise was not heard when the tail-slaps 'missed' the target, suggesting that the herring were stunned by physical contact. Killer whales then ate the stunned herring one by one.

While common dolphins were not seen using any "underwater tail-slaps", the observations of fish-whacking indicate, that they may also be capable of using this technique. Only few (n=4) underwater observations of feeding behaviour were conducted in this study, and future research may reveal that common dolphins also stun prey with underwater tailslaps.

There is some speculation that bottlenose dolphins may use fish whacking to 'soften' the fish, or that it may be a form of playing with food (Reynolds et al., 2000), but it is certainly effective in stunning or even killing the fish outright (Nowacek, 1999b).

The use of air-bubbles in prey capture appears to be a convergent strategy among Odontocetes and Mysticetes. Humpback whales (*Megaptera novaeangliae*) are well-known for concentrating prey with bubble-nets, -curtains, or -clouds (Hain et al., 1982). The bubble-blowing used by common dolphins appears to be an effective technique designed to overcome the fish's defence mechanisms. In this study a Bryde's whale was observed using the same method, when pursuing the same prey:

On one occasion, a Bryde's whale joined a group of circa 70 common dolphins who were herding jack mackerel. Several dozen gannets were also diving in amongst the dolphins. The group had been feeding for 15 minutes before the whale arrived, suggesting that the whale may have been alerted to the presence of prey, either by the dolphins' vocalisations, or the sounds of diving gannets. Our boat was drifting about 20 meters from the ring of circling dolphins, which had a diameter of about 10 meters. The whale headed towards the centre of the aggregation, but dove about 50 meters away from it. Circa four minutes after the whale sounded, a dense white mass of air bubbles rose to the surface, no more than five meters from the bow of the boat. It was a rectangular 'bubble-bed', circa five meters by two meters in size. Curiously, the individual bubbles appeared to be exceedingly small, with a diameter no greater than that of a human thumb nail - considerably smaller than the bubbles created by common dolphins, which were about 4-times that size. These bubbles were extremely tightly packed, creating the impression of one white, foaming mass. As the bubbles broke the surface, so did the whale, circa 30 meters ahead of the bubbles, near the centre of the feeding activity. Its left side was turned towards the surface, its throat pleats were extended, and the whale was slowly closing its jaws. The whale then rolled over to expose its blowholes, exhaled, inhaled, and sounded. The tight ring of dolphins had now broken up, and many could be seen zig-zagging in front of the whale, suggesting that they were chasing fish that had just escaped the whale. The dolphins abandoned feeding and started to travel north only two minutes later, while the whale could be seen heading west, surfacing at 5-6 minute intervals.

The Bryde's whale was almost certainly responsible for creating the observed 'bubble-bed', because nothing like it had been observed previously, or since, when Bryde's whales were absent from such feeding sessions. That these bubbles are somehow employed in the whale's feeding strategy can be deduced from the fact that the whale was seen with extended throat pleats immediately after the bubbles rose to the surface.

Groups of common dolphins often joined other groups already engaged in feeding, and separated again shortly after feeding had stopped. This could be caused by active recruitment. Once a food source has been located, common dolphins may recruit other animals in the area (presumably acoustically) to join in the feeding effort. This could be beneficial to all the dolphins involved, if a larger number of individuals was necessary to control the prey. Bel'kovich et al. (1991) believe this to be the case in bottlenose dolphins, where designated 'scouts' alert other group members to the presence of prey. However, additional dolphins that join a feeding group may also represent uninvited guests. If characteristic feeding sounds are perceived by another group of dolphins, they could minimise their own search effort, and take advantage of the successful foraging efforts of other individuals. If this were the case, one might expect to see overtly aggressive behaviour towards such 'newcomers', in an attempt to defend and monopolise the food source. This was not the case in any of the interactions observed in this study.

Kerplunking was observed directly in connection with other feeding activity. The dolphins' orientation in the water, the apparent sonar (or visual) scanning, and the dives immediately following kerplunking suggest that it is most likely a strategy employed in startling fish, thus making them easier to capture. While Nowacek (1999b) and Connor et al. (2000a) reason that it helps bottlenose dolphins reveal the location of prey hiding in shallow water seagrass beds, this was certainly not the case for the common dolphins. Here, the kerplunks were used in the presence of small schooling fish in waters 50-100 meters deep. However, kerplunking in bottlenose dolphins may not be restricted to shallow water, either. Hamilton & Nishimoto (1977) reported tailslaps with a vertical body orientation being used by bottlenose dolphins while circling schools of mullet. The mullet reacted to those slaps with flight from the centre of the school. The fluke movement in kerplunking creates a considerable cloud of air bubbles underwater (Connor et al., 2000a), which suggests that this behaviour could possibly be used in a fashion analogous to 'bubble-blowing' described above - using a different method to essentially produce the same effect. It may be an alternate strategy, used particularly in non-cooperative, solitary feeding, as all incidents involved animals at some distance from other group members.

The wide variety of different feeding strategies described here suggests that common dolphins show a very high degree of behavioural plasticity when it comes to feeding, akin to that already documented for other delphinids, especially killer whales and bottlenose dolphins. It is unlikely, however, that the observed feeding strategies represent the complete spectrum of common dolphin hunting behaviour. Future studies that will observe common dolphins for even longer periods, and studies conducted on other populations elsewhere, are bound to add even more to our understanding of common dolphin foraging behaviour.

5.4 Summary:

This chapter examined several aspects of the behaviour of common dolphins. An activity budget was created, and the influence of seasonal, diurnal, and demographic factors on the dolphins' behavioural patterns were tested (Neumann, 2001b). A quantification of aerial behaviours was also carried out, along with observations on the dolphins' foraging behaviour.

Several significant findings were produced in this chapter:
The first activity budget for common dolphins was established as a baseline, against which future research can test the effects of a number of variables, including human impact. This activity budget was comparable to those reported for bottlenose dolphins from different locations.

The qualitative descriptions of feeding strategies uncovered behaviours never before described in common dolphins, including evidence for division of labour. Much of the discussion on feeding behaviour was based on a limited number of observations (e.g., two observations of 'kerplunking', one of 'fish-whacking'), and the interpretation may therefore be considered somewhat speculative. However, the parallels to similar behaviours in other species lend support to these speculations.

6. COMMON DOLPHINS AND HUMANS

6.1 Introduction:

In this chapter, the interactions between common dolphins and humans are analysed. The results regarding the impacts of boat traffic and swimming with dolphins are presented first. A number of case studies then highlight unusual reactions by the dolphins, and also address the effects of recreational fishing on common dolphins. These findings are discussed in section 6.3, followed by a brief summary (section 6.4).

Boat traffic appeared to affect mostly smaller than average groups of common dolphins, which showed active boat avoidance. The presence of swimmers did not have any obvious negative effects on the dolphins, but the likelihood of achieving sustained interactions between swimmers and common dolphins was much lower than that reported for other dolphin species. Common dolphins showed signs of considerable disturbance in response to recreational boat traffic that was not conducted in a slow and careful manner. There was some evidence that recreational fishing can contribute to physical injuries among common dolphins.

6.2 Results:

6.2.1 Impact of boat traffic:

Dolphins changed their activity in 24.7 percent (n=26) of encounters in response to an approaching boat; 19 times (26.3 percent) in response to the research vessel, seven times (21.2 percent) in response to the tour boat. Overall, activity did not change more often than expected during boat approaches, compared to the frequency of activity changes during the remainder of focal group follows. The exponential distribution of bout duration was calculated to account for the probability at which some of these behavioural changes would have occurred at that time, regardless of the approaching boat (Haccou & Mellis, 1992). A chi-square goodness-of-fit test was then used to assess the effect of boat approaches (chi-square=1.4, df=1, p>0.1). As a result, null hypothesis *H0 12: There is no difference in common dolphin activity, before and after a boat approaches them to within < 100 meters*, cannot be rejected. However, the activity change from feeding to traveling occurred significantly more often during boat approaches than during other times (chi-square = 5.42, df=1, p<0.02) (Table 11).

Attraction and avoidance - In 45.7 percent (n=48) of encounters, some of the observed dolphins were attracted to the boat, and started bow-riding. Bow-riding occurred more frequently with the tour boat (51.5

percent, n=17), than with the research vessel (43.1 percent, n=31). While this trend is not statistically significant (chi-square=0.835, p>0.1, df=1), it can probably be attributed to the fact that the tour boat displaces more water, and thus is potentially more attractive to dolphins for the purpose of bow-riding. The members of a group frequently took turns bow-riding, with some dolphins engaging in it repeatedly, while others did not join in, at all. When bow-riding occurred, it lasted 11.3 minutes on average (SD=10.51, range=3 to 48 minutes).

After this period of initial attraction, the dolphins behaved 'neutrally' for the remainder of the observation, in most cases (meaning they showed no further apparent response to the boat). In some cases, however, the dolphins exhibited boat avoidance behaviour. They abruptly changed their heading away from the path of the boat, and continued to do so, if the boat adjusted its heading to follow the dolphins. Sometimes, the dolphins combined this with long co-ordinated dives, putting a large distance between themselves and the boat while traveling below the surface.

When exhibited, boat avoidance occurred 48.6 minutes (SD=22.63, range= 12 to 110 minutes) into a focal group follow, on average. Boat avoidance was shown by 31.4 percent of focal groups (n=33). Only 24.2 percent (n=8) of follows during which the tour boat was present

Table 11. Changes in predominant group activity in response to approaching boats. Activity states: traveling (TR), feeding (FE), milling (MI), socialising (SO).

Change in activity from-to:	research vessel	tour boat	total
MI-TR	4	1	5
MI-FE	1	0	1
MI-SO	0	1	1
FE-TR	6	4	10
FE-MI	1	0	1
TR-MI	3	0	3
TR-FE	2	1	3
SO-MI	2	0	2

resulted in boat avoidance, whereas 34.7 percent (n=25) of baseline follows caused boat avoidance. This significant difference (chi-square=2.71, $p<0.1$, df=1) can be explained by variations in group size between the two samples. Groups containing fewer than the average 57.3 (SD=50.78, range=3 to 400) individuals, were significantly more likely to exhibit boat avoidance, than larger groups (chi-square=3.67, df=1, $p<0.1$) (Figure 32).

Groups that showed boat avoidance, contained an average of 44.1 individuals (SD= 46.33, range= 3 to 250), whereas groups that showed no boat avoidance were made up of 63.3 individuals, on average (SD=50.65, range= 5 to 400). Larger than average focal groups were encountered more frequently with the tour boat present, than in its absence. A percentage of 69.4 (n=50) of groups in the baseline-sample were smaller than average, while that was only the case for 45.5 percent (n=15) of groups in the tour boat-sample. Considering that smaller than average groups showed a much higher avoidance rate (40 percent) than larger groups (17.5 percent), this would account for the more frequent boat avoidance in the baseline sample.

Calves and newborns were present in similar numbers in both, groups that showed avoidance and groups that showed none, and their presence or absence did not appear to influence whether or not boat avoidance occurred (chi-square = 0.56, df=1, $p>0.1$). Boat avoidance

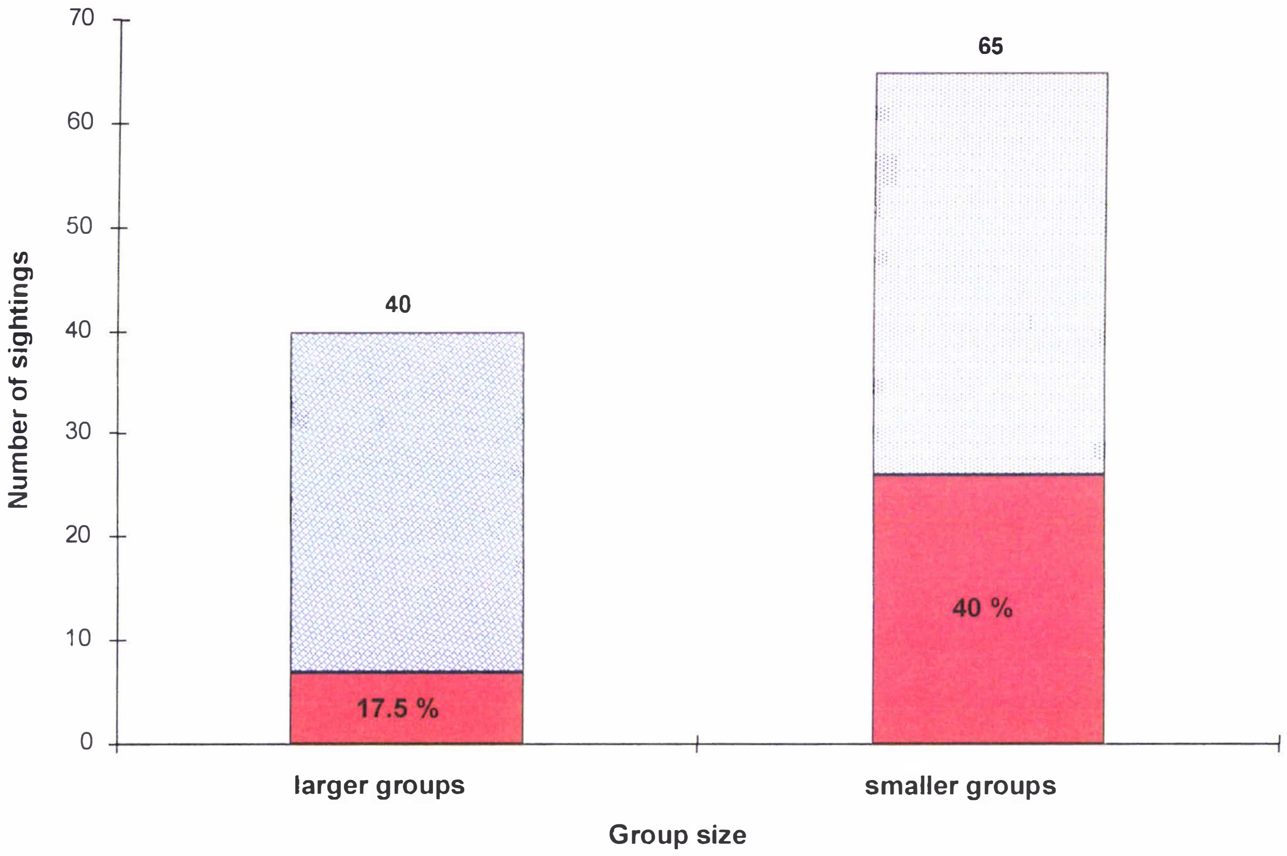


Figure 32. The relationship between group size and boat avoidance. Number of sightings of groups > 57 individuals (left) and groups < 57 individuals (right), with incidence of boat avoidance for each group size in red.

did not occur more frequently than expected in correlation to any particular activity state (chi-square = 2.58, df=4, p>0.1). Therefore, group size seems to be the chief factor contributing to boat avoidance, with larger groups being more boat-tolerant.

The above observations indicate, that null hypothesis *H0 13: Dolphins remain equivocal towards boats for the duration of a follow, and show neither attraction, nor avoidance*, should be rejected.

6.2.2 Activity budget:

The activity budget for focal group follows that were conducted while the tour boat was present, differs from that in the absence of the tour boat. Dolphins spent higher percentages of their time traveling, and socialising, at the expense of the remaining three categories (Figure 33). However, an ANOVA comparing the non-tour and with-tour data sets failed to show a statistically significant difference between their respective activity budgets (F=0.78, df=1, p>0.4) (Table 6).

Therefore, null hypothesis *H0 14: There is no difference in the activity budget of common dolphins, between baseline data, and data collected in the presence of the tour boat*, cannot be rejected.

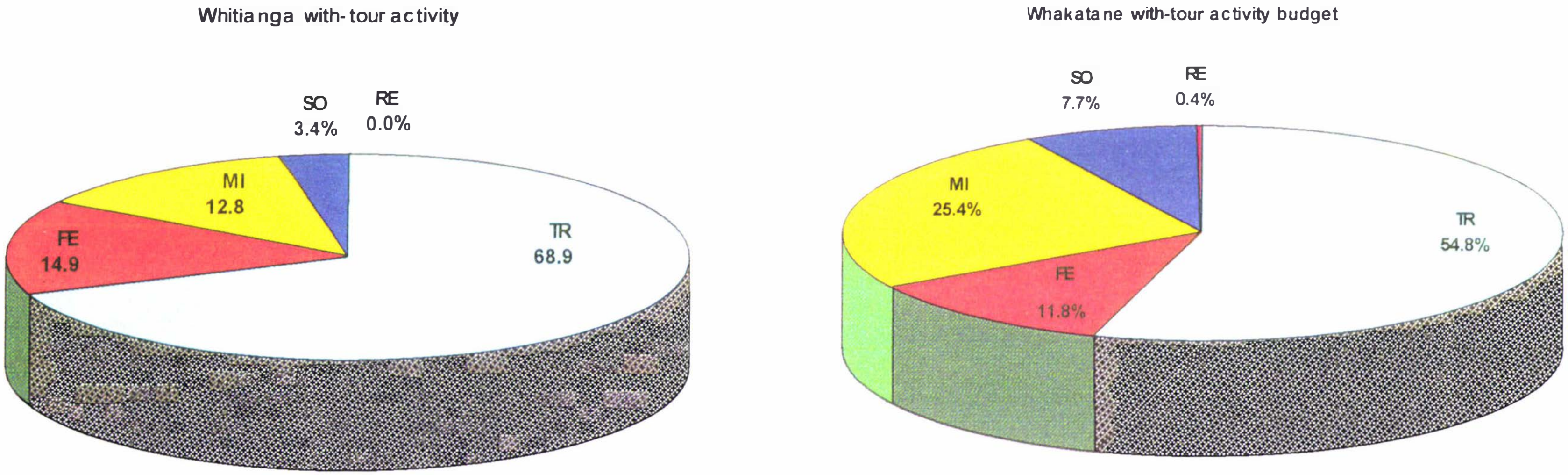


Figure 33. The activity budget of common dolphins in the presence of commercial dolphin-tour boats : Whitianga (left) and Whakatane (right). Legend: TR=travel, FE=feed, MI=mill, SO=social, RE=rest.

6.2.3 Swimming with dolphins in Mercury Bay:

Swimming with dolphins was attempted on 15 of the 33 tour boat trips. A percentage of 46.6 (n=7) of these resulted in an interaction with the dolphins, i.e. some of the dolphins approached and investigated the swimmers and were clearly visible to them underwater. 39 separate swim attempts were undertaken during those 15 trips, resulting in an average of 2.6 (SD=1.44, range= 1 to 5) swim attempts per trip.

Dolphins were interactive during eight swim attempts (20.5 percent). The mean duration of these interactions was three minutes (SD=1.6, range=1 to 10 minutes).

The dolphins' activity influenced the success of swim attempts. Dolphins were most interactive, when the predominant group activity was 'social', and least interactive when it was 'travel' or 'mill' (Table 12). Swim attempts were more successful, the larger the dolphin group was (Table 13). Calves or newborns were not present during swim attempts, as it is a violation of existing regulations to swim with them and the tour operator adhered to this requirement on all occasions observed in this study.

Unsuccessful swim attempts were always the result of the dolphins maintaining their initial activity, 'ignoring' the swimmers, and moving out of their underwater field of vision. On no occasion did the dolphins show apparent avoidance, by changing direction to head away from the swimmers, nor did they change their behavioural state when swimmers entered the water.

Dolphin behaviour did not show a consistent response during each trip, i.e. even though dolphins may not have showed any interest in the swimmers during the first or second swim attempt, they sometimes interacted with them during a later attempt (Table 14).

The behaviour of swimmers in the water appeared to influence the outcome of a swim attempt. No interactions took place when swimmers splashed noisily on the surface, while the success rate improved considerably when swimmers did repeated 'duck-dives' (Table 15).

During a typical interaction, some of the dolphins in the focal group (up to 50 percent) approached the swimmers to within three meters, never any closer than that. They then proceeded to inspect the swimmers visually, any one individual making up to five close passes beside swimmers. When swimmers tried to approach the dolphins by swimming towards them, the dolphins adjusted their distance to maintain the initial 'safety distance', typically about five meters. Fast approaches by swimmers often had the opposite of the desired effect, and resulted in an increase of that 'safety distance'. The only aerial

Table 12. Dolphin activity and success rate of swim attempts.

Dolphin activity	Interactive swims	Swim attempts	Success rate
SO	1	2	50%
FE	2	7	28.6%
MI	2	12	16.7%
TR	3	18	16.7%

Table 13. Relationship between the number of dolphins in a group and the success of swim attempts.

Group size	attempts	interactions	success rate
< 15	3	0	0%
15-30	7	1	14.3%
31-50	15	3	20%
51-100	8	2	25%
> 100	6	2	33.3%

Table 14. Sequence of swim attempts that led to interactions.

Swim attempt	**1.**	**2.**	**3.**	**4.**	**5.**
# interactions	2	3	2	0	1

Table 15. Behaviour of swimmers and outcome of swim attempts.

Behaviour of swimmers	attempts	interactions	success rate
splashing	7	0	0%
quiet snorkel	26	5	19.2%
duck-diving	6	3	50%

behaviours observed during swim-interactions were tailslapping (n=4), and chuffing (n=3). Neither of these was significantly correlated to swim-interactions (chi-square = 0.65, df=2, p>0.1).

During interactions, group spread increased on four occasions, and did not change on the four other occasions. No decrease in spread was observed. This could be a function of human activity artificially 'stretching' a group of dolphins. With swimmers in the water, the tour boat will always be stationary. When the dolphins are traveling, most group members will move on, while some may linger around the boat, investigating it, or the swimmers. Thus the distance between the leaders of the group and the 'interactive' dolphins would increase. Once that distance exceeded an estimated 150 meters, the interactive dolphins would terminate the interaction and catch up with the remainder of the group. Situations in which the dolphins were milling, feeding, or socialising (i.e. more likely to remain in a given area) would account for the cases in which group spread did not change.

6.2.4 Swimming with dolphins in Whakatane:

In March and April 2001, 15 focal group follows were conducted in the Whakatane area. These resulted from 16 surveys, 74 hours on-water effort, and represent 17.6 hours of following common dolphins. During 12 of these follows, the local tour boat (Te Tahi), a 12 meter twin-diesel-engine catamaran, was present and carried 4-20 passengers. The three focal follows in the absence of the tour boat were excluded from the analysis below, to consider only data for the potential tourism impact situation.

Interestingly, the activity budget for Whakatane resembles the baseline budget more than it does the Whitianga tourism sample (Figure 33). This could be a function of the smaller sample size, or it may re-emphasise the fact that there really is no significant difference between the activity budgets of baseline versus tourism-impact situations.

On nine of the 12 trips, swimming with dolphins was attempted. A percentage of 75 (n=7) of these resulted in an interaction with the dolphins. Thirty-nine separate swim attempts were undertaken during these nine trips. Dolphins were interactive during 18 swim attempts (46.2 percent). The mean duration of these interactions was 3.6 minutes (SD=1.6, range=1 to 14 minutes).

The trends that were observed for swim interactions in Mercury Bay, also held true for Whakatane, with the exception of a lower swim success rate during feeding, and a slightly less clear correlation between larger dolphin group size providing better swim success (Tables 16-19). Common dolphins only rarely showed an apparent response to swimmers. When they did, it was always an 'attraction' response, with dolphins approaching and investigating swimmers.

Table 16. Dolphin activity and success rate of swim attempts in Whakatane.

Dolphin activity	**Interactive swims**	**Swim attempts**	**Success rate**
SO	2	2	100%
FE	1	6	16.7%
MI	9	15	60%
TR	6	16	37.5%

Table 17. Relationship between the number of dolphins in a group and the success of swim attempts in Whakatane.

Group size	attempts	interactions	success rate
< 15	0	-	-
15-30	8	2	25%
31-50	11	6	54.5%
51-100	15	7	46.7%
> 100	5	3	60%

Table 18. Sequence of swim attempts that led to interactions in Whakatane.

Swim attempt	**1.**	**2.**	**3.**	**4.**	**5.**
# interactions	5	7	3	3	1

Table 19. Behaviour of swimmers and outcome of swim attempts in Whakatane.

Behaviour of swimmers	attempts	interactions	success rate
splashing	8	2	25%
quiet snorkel	21	9	42.8%
duck-diving	10	7	70%

However, considering the low frequency of dolphins changing their behaviour, and the small sample size, additional data should be collected before null hypothesis *H0 15: Dolphins did not change their behaviour in response to swimmers entering the water from tour boats*, can be rejected.

6.2.5 Human impact on common dolphins *can* be traumatic - evidence from case studies:

The above evidence suggests that common dolphins were only slightly affected by the presence of either the tour boat or the research boat. This could partly be due to the fact that both the skippers of the tour boat and of the research boat were aware of the Marine Mammal Protection Regulations (1992, Appendix 1) and attempted to follow these regulations (Figure 34). The tour boat's strict adherence to these regulations during data collection may have been influenced by the skipper's awareness of being observed. However, during several interviews, the operators of 'Mercury Bay Seafaris' conveyed the impression that their observed behaviour around the dolphins was typical of their conduct.

Recreational boating and fishing are very popular in Mercury Bay, which potentially brings common dolphins in contact with humans who are either unaware of the guidelines governing their behaviour

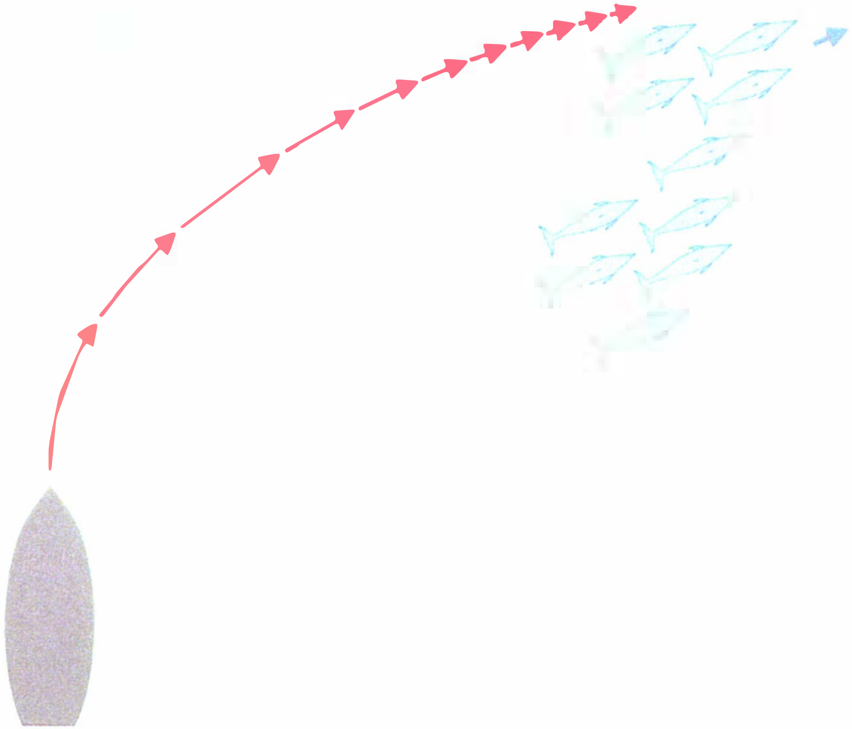


Figure 34. Recommended style of approaching dolphins : Off to one side, parallel, and gradually slowing down to the dolphins' speed.

around marine mammals, or who choose deliberately to disregard these guidelines. The dolphins *were* affected dramatically by boat traffic that was *not* conducted cautiously, and in strict adherence to the Marine Mammal Protection Regulations (1992). Such incidences were infrequent (5.7 percent of all observations, n=6); however, the sometimes extreme responses of the dolphins warrant a detailed description of these occurrences:

Dolphins, recreational boaties, and anglers -

Case # 1, 6.1.1999. Herding of dolphins: During a focal group follow of 50 common dolphins, the research vessel unintentionally herded the group against the tour boat. The dolphins were traveling parallel to the tour boat, and spread over circa 100 meters to the starboard side. The research vessel 'Aihe' approached from circa 200 meters off to the starboard to within 30 meters parallel to the tour boat. The dolphins did not swim to the starboard of the research vessel, but remained in the space between the two boats. As 'Aihe' had approached to within 50 meters, the group's spread had also decreased to 50 meters. As 'Aihe' continued its approach, the dolphins accelerated from circa 10 kph to circa 15 kph. When both boats started to match that speed, the dolphins came even more closely together, with the distance between animals decreasing to about 1 dolphin-body width. They then accelerated very dramatically to circa 25 kph, with all the animals rapidly porpoising away from the boats and out to deeper water. After this incident, neither the research nor the tour boat attempted to continue following the group.

Case # 2, 15.1.1999. Zig-zagging through a group of dolphins: 'Aihe' had followed a group of 30 common dolphins with four newborns for 45 minutes, when a 4.5 meter, 50 hp outboard recreational boat arrived. The boat carried two adults and three children. The children crowded into the bow, and vocalised loudly. The boat was slowly and gradually approaching from behind the dolphins, and at first did not appear to influence the dolphins' behaviour.

After following the group for three minutes, with dolphins on either side of the recreational boat, the boat maintained a slow speed, but started zig-zagging through the group, in an apparent attempt at getting a closer look at the newborn calves. After two minutes of weaving through the group, the group's spread decreased from 70 meters to 30 meters, which was accompanied by a sudden change of direction, at a right angle away from the recreational boat, towards the research vessel, which was traveling 100 meters behind and parallel. Once the dolphins had crossed the bow of the research vessel, the group's spread increased again to circa 70 meters. The recreational boat discontinued its follow, while the research boat stayed with the group for another 30 minutes, during which no further boat avoidance was evident.

Case # 3, 10.2.2000. Fishing around dolphins: During a focal group follow of 150 dolphins, the research vessel was joined by a 5 meter, 90 hp outboard recreational fishing boat with two people on board. The dolphins were spread over circa 100 meters, and were traveling at circa 10 kph, with the research vessel following along the right rear edge of the group.

The fishing boat proceeded to drive straight through the centre of the group, with three lures trolling behind the boat, at a speed slightly faster than that of the dolphins. As the fishing boat reached the front of the group, the rear half of the group had gone on a long dive, staying submerged for two minutes (as opposed to breathing every 30 seconds, previously). The front half of the group split into two subgroups of about equal size. They both accelerated and headed away from the course the fishing boat was taking, porpoising away in opposite directions. The fishing boat then accelerated, but maintained its course and did not attempt to follow any of the dolphins. The research vessel remained with the group that had initially dived. Upon resurfacing, their behaviour changed to milling, with the group remaining very close together, within a spread of 40 meters. The milling continued for five minutes before traveling was resumed. The dolphins spread out again, and continued to head in the same direction and at the same speed as before the incident, but for the remaining 30 minutes of our group follow, they remained separated from the other half of the group, which had porpoised away in different directions.

Case # 4, 8.12.2000. Fishing amongst feeding dolphins: A group of 50 common dolphins had been feeding in the carousel formation in the presence of the research boat (with the engine turned off) for 10 minutes, before a 6 meter, 150 hp outboard recreational fishing boat arrived, with three people on board. They were trolling four lures over the stern, and proceeded to motor through the water in circles, at approximately 10 knots, in the centre of the dolphins' feeding formation. This immediately broke up the coordinated circling of the herded fish, and dolphins could be seen darting off in various directions, in a somewhat chaotic fashion.

After the recreational fishing boat had done 'doughnuts' in the same spot for a little over one minute, the group split into three subgroups. Two larger groups of circa 20 individuals each, rapidly porpoised away from the disturbance, one heading out to sea in a northeasterly, the other in a southeasterly direction. The group heading southeast, was then pursued by the fishing boat, which caused the group to double back. They eventually escaped in a northerly direction. A third group of 10 individuals, closely bunched together, swam rapidly towards the west, without porpoising. No attempt to follow any of these groups was undertaken by the research boat, to avoid further harassment.

The splitting-up of the group in this case, and the dolphins' rapid movement could be argued to be the result of pursuing their prey, which might have been scattered by the boat's approach. However, this is unlikely, because gannets continued to feed in the original carousel location, and did not follow the dolphins. The fish probably did scatter eventually, but only because the dolphins were forced to evade the fishing boat, which compromised their ability to herd the fish.

Physical injuries -

Some common dolphins in this study carried the marks of injuries that had been inflicted by humans. One individual, 'Pumpkin AC 59', had a large triangular part missing from the trailing edge of its dorsal fin (see Appendix 3). The fin had been carved in nearly the same manner as the fin of 'Pumpkin', a bottlenose dolphin in Sarasota Bay, whose injury is known to have been caused by a boat propeller (Reynolds et al., 2000). Another dolphin carried a deep, well-healed V-shaped cut in the dorsal part of its peduncle. A boat strike is considered the most likely cause of this injury (Plate 8). 'Stumpy', who is missing the top two thirds of its dorsal fin, may have sustained this injury as a result of contact with either a boat propeller or possibly monofilament fishing line (Appendix 3).

Case # 5, 25.12.1999. Wrapped in fishing line: During a focal group follow of 13 common dolphins in Mercury Bay, one individual was observed close to the boat with a 10 centimeter silvery lure protruding from the right corner of its beak. Monofilament line was still attached to the lure, and wrapped around the dolphin's body at least three times, just anterior to the dorsal fin (Plate 19). This suggests that the dolphin may have tried to free itself by spinning around its axis. As a result, the line either broke or was cut by the angler.

The line was cutting into the skin, and small pieces of the epidermis were peeling off in the dorsal area. Fronds of a brown alga (probably *Egregia* sp.) were wedged between the line and the dolphin's venter, suggesting that the animal had attempted to remove the line by scraping along a seaweed-covered surface.

The dolphin did not appear malnourished, and its behaviour did not differ from that of the other group members. However, with an estimated 1.6 meters, the animal was not yet fully grown, which makes it likely that the monofilament line will cut more deeply into the skin

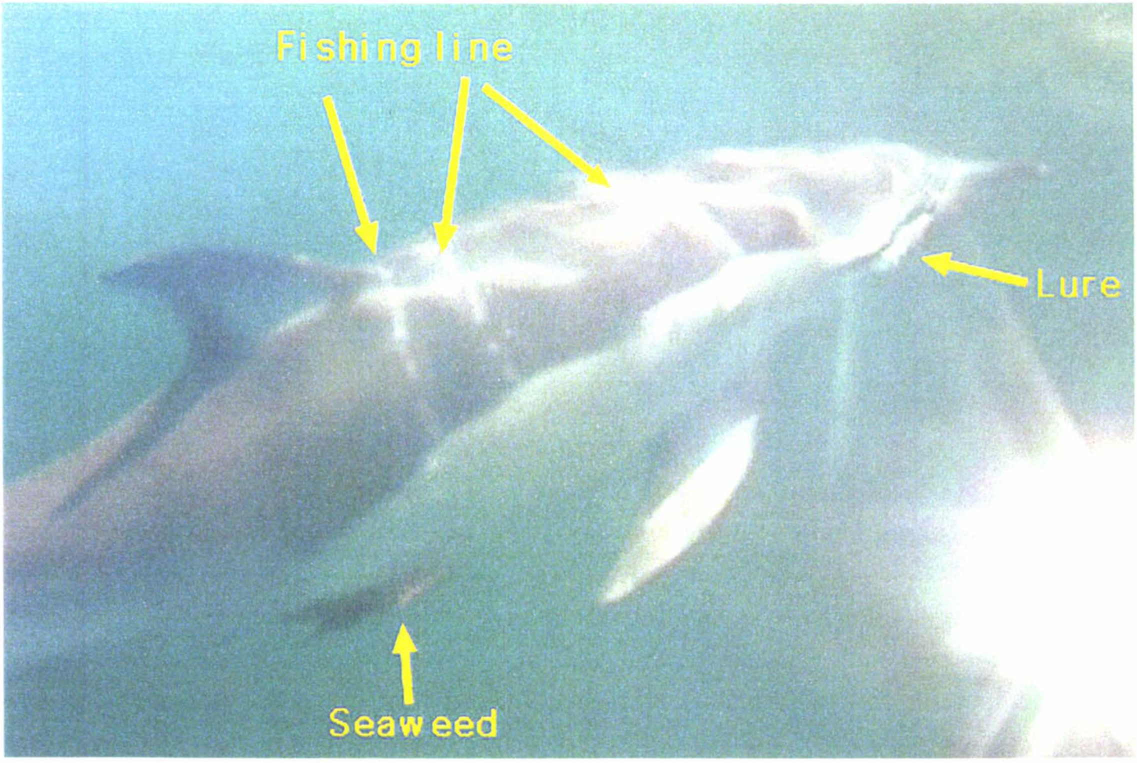


Plate 19. Common dolphin entangled in fishing line, seen on 25.12.1999 in Mercury Bay.

as the animal increases in bulk, resulting in a fatal injury. Several options for cutting the line were considered, but could not be attempted, because the dolphin could not be approached again closely after its initial pass at circa 1.5 meters from the boat. This dolphin was not resighted during the remainder of the study.

Case # 6, 6.4.2001. Possible stabbing victim: During a focal follow of 70 common dolphins near Moutohora Island, off Whakatane, an individual was spotted, that carried a hole in the base of its dorsal fin, about the diameter of a ping-pong ball. The hole penetrated into the tissue at the base on the left side of the fin, and extended through to the right side, where a cut on the leading edge indicated the exit wound.

The injury appeared well-healed, and the dolphin was in good physical condition. The shape and dimensions of the injury suggested that it was caused by a human-made object, possibly a grappling hook. This may have been used to free an entangled dolphin from a situation similar to the one described in case # 5, or it may have been used in a purely malicious attack.

6.3 Discussion

6.3.1 Impact of boat traffic:

The high frequency of changes in behaviour from feeding to traveling, in response to an approaching vessel is potentially serious, because it suggests that - on certain occasions - boat traffic can interfere with the dolphins' feeding behaviour.

Constantine (1995) reported that common dolphins changed their behaviour during 52 percent of boat approaches, while only 32 percent of bottlenose dolphin groups changed their activity. These figures cannot be compared directly with this study, because she added "bowride" to the five activity categories also used here. Bowriding was not scored as a separate activity category, because it did not fulfill the definition of a predominant group activity, at any time point (i.e. > 50 percent of the group being involved in a certain activity). In this study, bowriding was only observed during traveling. If one assumes, that this also applies to Constantine's (1995) study, then her "feeding to bowriding" would equate to "feeding to traveling" in this study. This would show a significant disruption of feeding activity for Bay of Islands common dolphins as well, with 10 of 17 feeding bouts disrupted by the boat's approach.

Although, it is tempting to score bowriding as a 'positive' response, with the dolphins finding the boat 'attractive', it may in the long run turn out to be detrimental to the dolphins, in those cases where it interferes with satisfying more basic requirements (e.g. food, rest). See Constantine (1995), for example, where feeding was abandoned in favour of bowriding.

Leitenberger (2001, p. 25) reported an interaction between a recreational powerboat and common dolphins, which resulted in the disruption of resting behaviour:

> One time a motorboat was performing high speed circles around a pod of resting dolphins containing juveniles. The dolphins showed avoidance behaviour by diving longer and moving away from the boat.

There are many more examples to underline that boats can have a potentially disruptive effect on the lives of dolphins and other cetaceans. Beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) apparently altered their headings to avoid boats, while they were still as far as 35 kilometers distant (Myrberg, 1990). Other species that showed similar avoidance behaviour towards approaching boats (albeit at shorter distances) include bowhead whales (*Balaena mysticetus*), spotted dolphins (*Stenella attenuata*), and spinner dolphins (*Stenella longirostris*) (Richardson et al., 1985, Au & Perryman, 1982).

Even if dolphins show a 'positive' response and approach boats, this could still have negative long-term effects, e.g. by keeping the dolphins from feeding or resting (Janik & Thompson, 1996). If dolphins become stressed due to boat traffic, it could have a negative impact on their physical fitness (Bejder et al., 1999). Because of the implications for cetacean conservation a number of studies are now addressing this problem (e.g. Nowacek, 1999a). Observed reactions reported in the literature range from an initial attraction to boats, for Hector's dolphins (Bejder et al., 1999), to changing direction and avoiding boats as far as six miles away, for spinner and spotted dolphins (Au & Perryman, 1982).

Orcas increased their travel speed when boats were present, but maintained their heading (Kruse, 1991). Bottlenose dolphins in a busy shipping channel showed changes in their behaviour when boats started to follow, rather than pass them (Acevedo, 1991). In Sarasota Bay, bottlenose dolphins dived longer as boats passed near to them (Nowacek, 1999a). Bottlenose dolphins in the Moray Firth appeared to take longer dives and/or move away from approaching boats (Janik & Thompson, 1996).

The reactions by common dolphins observed in this study, appear to correspond closely to those found by Bejder et al. (1999) for Hector's dolphins. Hector's dolphins showed an initial attraction to boats for bowriding, lasting up to 50 minutes. After 70 minutes, the dolphins were either avoiding the boat, or equivocal to it. The period of initial attraction was much shorter in common dolphins, and boat avoidance appeared to set in earlier, but the overall pattern of an attraction-neutral-avoidance sequence is the same.

Group size was significantly correlated with boat avoidance. Boat avoidance dropped from 40 percent for smaller than average groups to 17.5 percent for larger groups. As pointed out in 4.3.4., large groups form partly to provide better protection from predation. This is achieved by increasing group vigilance, and also by decreasing the likelihood of any one individual being taken (dilution effect). If this holds true, then dolphins traveling in large groups should have less cause to be disturbed by an unfamiliar entity, or potential threat (e.g. a boat) than dolphins traveling in smaller groups. This prediction was confirmed by the results of this study.

6.3.2 Activity budget:

The behaviour of dolphins did not appear to be affected significantly by the presence of the tour boat. This could be the result of:

1) The skipper's experienced and responsible handling of the vessel, and his adherence to the Marine Mammal Protection Regulations (1992). This would indicate that these regulations are indeed effective, when followed.

2) The frequency of dolphin-watching trips is too low to have an effect, in this area. Typically, around 20 trips were conducted over the entire summer. Furthermore, demographics indicate that any one common dolphin group does not spend extended periods of time in Mercury Bay (see 4.3.2 Group formation and composition). Therefore, it is unlikely that individual dolphins experience multiple tourist-trips during one season. This decreases the likelihood of either sensitisation or habituation to these trips.

3) Any behavioural changes caused by boat traffic were already exhibited in reaction to the research vessel, and were not compounded by the presence of a second vessel (i.e. the tour boat). This is supported by the finding that rates of boat avoidance did not increase in the presence of the tour boat.

While tourism-impact in Mercury Bay is diluted, by being spread over various groups during consecutive sightings, this dilution might be counteracted by the cumulative effects of tourism-exposure in different places. Movements by individual dolphins from Mercury Bay to the Hauraki Gulf, and from Mercury Bay to Whakatane were documented (see 4.3.2 Group formation and composition). Both locations feature a greater level of dolphin-tourism than Mercury Bay. This means that while individual dolphins may be exposed to tourism only briefly in one location, they will then be subject to tourism *again* in another location. However, so far there is no indication that common dolphin behaviour differed from the baseline behaviour observed in Mercury Bay, in either the Hauraki Gulf (Leitenberger, 2001), or off Whakatane (this study).

6.3.3 Swim impact:

Constantine (1995) reported a slightly higher rate of sustained interactions per swim attempts for common dolphins in the Bay of Islands (24 percent, vs. 20.5 percent this study; no statistically significant difference, z=1.48, p>0.05). The average duration of these interactions was noticeably longer (5.3 minutes, vs. 3 minutes this study; no statistically significant difference, z=1.84, p>0.05).

Leitenberger (2001) reported a 21 percent success rate for swim attempts with common dolphins in the Hauraki Gulf, which is almost identical to the 20.5 percent success rate observed in Mercury Bay (no statistically significant difference, $z=0.62$, $p>0.05$).

In contrast to this study, Leitenberger (2001) also observed active avoidance of swimmers, in 8.2 percent of in-water interactions, which is still much lower than the 38 percent avoidance reported for common dolphins in the Bay of Islands (Constantine, 1995; significant difference, $z=6.31$, $p<0.05$). No active avoidance of swimmers was apparent in this study. This is probably a direct result of the differing approach strategies immediately preceding a swim: Constantine (1995) observed an 86 percent avoidance rate when swimmers were placed in the path of the dolphins (Figure 35), rather than entered when dolphins were milling around the boat (Figure 36). Leitenberger (2001) found that none of the in-path placements in the Hauraki Gulf resulted in an interaction. Dolphins either ignored or avoided swimmers. This swimmer placement strategy was employed much less frequently in the Hauraki Gulf than in the Bay of Islands, and was never observed in Mercury Bay, which could explain the low rate or absence of swimmer avoidance in the latter two locations. Inter-observer differences in the interpretation of 'avoidance' may also be partly responsible for this variation.

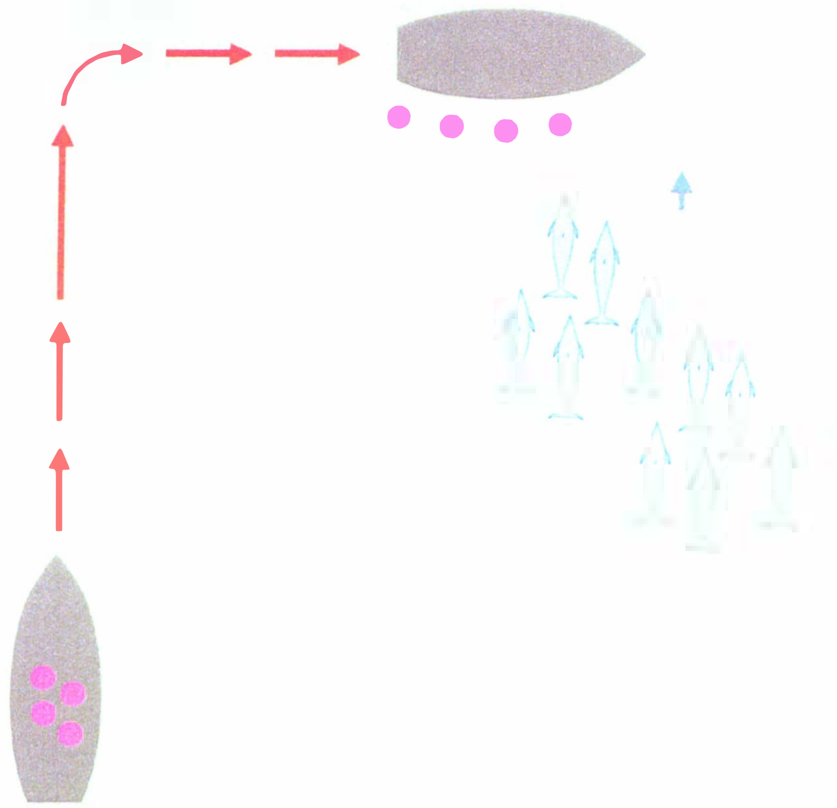


Figure 35. In-path placement ('J-hook') of swimmers : The boat accelerates to overtake the dolphins, 'hooks' around the front of the group, and places swimmers (= pink dots) in the dolphins' path.

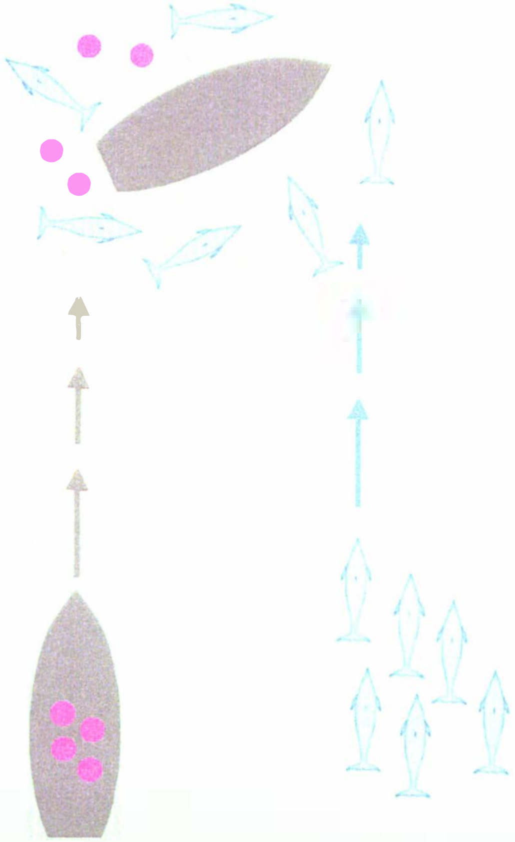


Figure 36. 'Around-boat' swimmer placement : The boat travels parallel to the dolphins, and as the boat slows down, the dolphins then start to mill around the boat, upon which swimmers (= pink dots) are placed in the water.

The relationship between the approach style of boats and swimmer avoidance in bottlenose dolphins reported by Constantine (1995) and Weir et al. (1996) illustrates that the more invasive approaches ('J-hook', in path, see Figure 35) caused higher rates of avoidance.

Variations in the influence of approach styles could not be assessed in this study, because swimmers were always placed in the water using the 'around boat' strategy (Figure 36), which showed the highest success rate in the Bay of Islands, with common dolphins actively approaching swimmers on 75 percent of such attempts (Constantine, 1995). However, case studies # 1-4 of irresponsible boat maneuvering around common dolphins, indicate that this species can be easily disturbed, when the Marine Mammal Protection Regulations (1992) are not complied with.

Even when recommended approach and follow protocols were strictly adhered to, 31.4 percent of focal groups of common dolphins still showed boat avoidance after a period of time (48.6 minutes on average). The dolphins appeared to get 'fed up' with the constant presence of the boat nearby, and tried to distance themselves from it. It would be worthwhile to investigate if this is related purely to the presence of the boat or its engine noise. Focal group follows using sailing vessels could be conducted to address this question.

Under the current Marine Mammal Protection Regulations (1992), it is unlawful to attempt swims with groups that contain calves (which includes newborns and calves, in the definition used in this study). This requirement was based on the notion that the smaller, weaker, inexperienced calves would be more at risk from any potential danger than adults, and that mothers with young calves might perceive swimmers as potential threats, causing stress. It could not be assessed during this study, whether or not this would indeed be the case, because this regulation was always complied with by the tour operators, and no swims with calves were ever attempted.

Weir et al. (1996) recommended regulations for swimming with bottlenose dolphins in Australia, which would require tourists to hang on to so-called 'mermaid lines' (a rope attached to the stern of the boat), while the boat is moving through, or drifting near, a group of dolphins, enabling the patrons to view them underwater. This technique is used by a number of operators in Australia, and provides added safety for the swimmers, many of whom may not have had any previous experience with snorkeling. It is also intended to limit stress on the dolphins, by making it impossible for swimmers to approach and try to touch dolphins. While this may be an issue with bottlenose dolphins, the experience from this study indicates that common dolphins will maintain a three meter buffer zone between themselves and swimmers. Attempts by swimmers to decrease that distance are always doomed to failure, because of the much greater mobility of dolphins.

Once in the water, the degree of interaction with swimmers is entirely up to the dolphins, who cannot be forced to interact against their will, by free-swimming humans. Conversely, the mermaid line strategy may actually increase stress on dolphins, by providing swimmers with greater speed (when the boat is pulling them along), that they would otherwise not be capable of, and by tempting operators to drive through groups of dolphins to provide their patrons with a good view of the dolphins. On the other hand, this technique would be preferable to operations where swim attempts are carried out by repeatedly driving through, or around a group, to drop swimmers in the dolphins' path.

As in this study, Leitenberger (2001) also observed very poor success rates for swim attempts, when swimmers were noisy and splashing, while success increased with diving and active swimming. This also resulted in large groups of swimmers having a significantly lower chance of interacting with the dolphins, because large groups were consistently noisier, than small groups of swimmers. Avoidance of swimmers has also been shown in situations where swimmers were not boat-based: When swimmers entered the water from a beach within 200 meters of Hector's dolphins, the dolphins changed their heading away from the swimmers in 12.5 percent of swim attempts (Bejder, 1997).

Bottlenose dolphins in the Bay of Islands appear to have become more sensitive to swim attempts over six years of increasing tourism exposure (Constantine, 1999b). Swimmer avoidance increased significantly over consecutive years. These bottlenose dolphins are members of a relatively closed population, showing a high degree of site fidelity (Constantine, 1999b). Therefore, they are subject to repeated swim attempts time and again. Such a sensitisation is less likely to occur in the much more transient common dolphins, unless the cumulative effects of tourism in different locations are significant.

Leitenberger (2001) also found a significant increase in boat- and swimmer-avoidance over the 6-month period of her study. This is potentially serious, as these six months also represent the first six months in business, for the 'Dolphin Explorer Ltd.' tour operation. It is possible that common dolphins showed sensitisation to this new entity in their environment. Leitenberger's (2001) photo-identification effort had a much higher resighting rate, than this study. She encountered 40 percent of 500 catalogued individuals more than once; 13.8 percent were seen three times or more (Leitenberger, 2001). Frequently sighted individuals were observed throughout the entire study period, which suggests that at least some individuals may be present in the Hauraki

Gulf for extended periods of time. Their encounter rate with the tour boat would therefore be much higher than that for dolphins in Mercury Bay, making them susceptible to potential habituation or sensitisation. However, the increased avoidance rates observed towards the end of Leitenberger's November 2000 to April 2001 study, coincide with a decrease in average group size. As in this study, Leitenberger (2001) also found larger groups of common dolphins to be much more tolerant towards both boats and swimmers, than smaller groups. Therefore, she argues that the increase in avoidance rate is a function of the smaller group sizes she observed in her autumn sample. This supports the notion that common dolphins tend to find 'safety in numbers'.

Overall, common dolphins appear to be much less 'receptive' to contact with human swimmers, than the other species targeted by swim-with-dolphin tourism in New Zealand. This is illustrated by the brevity of interactions, the large distance common dolphins maintain to swimmers, and the low proportion of swim attempts resulting in a sustained interaction. The success rates for swim attempts with common dolphins ranged between 20.5 percent in Mercury Bay and 46.2 percent off Whakatane, which are lower than those reported for Hector's, dusky, and bottlenose dolphins, all of which ranged above the 50 percent mark (Bejder, 1997; Barr, 1997; Constantine, 1995). In this context, it is worthwhile to note that none of the incidences involving "wild sociable dolphins" reviewed by Lockyer (1990) and Orams (1997) included common dolphins.

While Doak (1981) reported interactions with free-swimming common dolphins, these are analogous to the brief encounters experienced by people on swim-with-dolphin tours, described above. They do not consistently involve the same individuals, or active solicitation of human contact by the dolphins. Even in the case of the common dolphin individuals which frequented the Whitianga estuary for several years, no in-water interactions with humans have been reported (Doak, 1995).

In contrast, sociable bottlenose dolphins sometimes actively seek human company, including physical contact (e.g. 'Opo' (Alpers, 1963)). It appears that common dolphins show a lesser tendency towards inter-specific associations with humans than do some other cetacean species. This would partly explain the lower success rate of swim attempts with common dolphins, compared to Hector's, dusky, and bottlenose dolphins (Bejder, 1997; Barr, 1997; Constantine, 1995).

Compared to the around 20 percent swim success rates for common dolphins found by Constantine (1995), Leitenberger (2001), and in Mercury Bay (this study), the 46.2 percent success rate off Whakatane appears unusually high. This could be a result of the small sample size (n=12), but if this trend were to be confirmed by a larger sample, the possibility of common dolphins having become habituated to dolphin-tourism, should be considered: Tour frequency out of Whakatane is high, and has been so for at least five years. If common dolphins indeed spend extended periods of time in that area (see 4.3.4 Group formation and composition), then the same individuals may frequently come in contact with the tour boat and swimmers. This idea is contrary to the potential for sensitisation, discussed above, regarding Leitenberger's (2001) findings for common dolphins in the Hauraki Gulf. The small sample size of the preliminary Whakatane investigation (this study), and the short-term nature of Leitenberger's (2001) study, do not allow for a conclusive assessment of either situation. However, it is important that the sensitisation vs. habituation issue be considered, and studied more closely for common dolphins. Bottlenose dolphins in the Bay of Islands are subject to intense tourism activities, and Constantine (1999b) found evidence for sensitisation of these dolphins to boats and swimmers over several years.

Compared to the Bay of Islands, dolphin tourism along the Coromandel Peninsula coast and in the Hauraki Gulf is still in its infancy. However, human use of these areas is bound to increase, with continued growth in the New Zealand tourism industry (Tourism Strategy Group, 2001), and multi-million dollar residential developments (Auckland City Council, 2001). Therefore, long-term monitoring of common dolphin populations should be undertaken to determine if this species becomes either habituated or sensitised to human contact.

6.3.4 Case study discussion:

While the impact of both the research and the tour boat on the dolphins' behaviour appeared to be relatively minor, dolphins did show definite "signs of becoming disturbed or alarmed" (Marine Mammal Protection Regulations, 1992, R18 b) when boat approaches were not slow and gradual. The splitting-up of groups into smaller subgroups was one of the observed responses. That boat traffic can split-up groups of common dolphins, and interfere with their feeding activities, has also been experienced by other researchers. Gallo (1991, p. 256) reported:

> [...] later the same day we observed the formation of another feeding swarm with 100-150 [common] dolphins, however, the ship cut the swarm in half, causing it to disband within minutes.

In Port Stephens, Australia, the presence of tour boats has been implicated in splitting groups of bottlenose dolphins up into smaller subgroups (Allen et al., 2001). Bottlenose dolphins in Sarasota Bay, Florida, avoided boats that passed within 20 meters by prolonging their dives (Nowacek, 1999a).

The decrease of inter-individual distances (i.e. 'bunching up' of a group) has been observed as a response to potential threats in spinner dolphins (Norris et al., 1994). Dusky dolphins (Barr, 1997) and Hector's dolphins (Bejder et al., 1999) also reacted to boat traffic by forming more compact groups. Bottlenose dolphins decreased group spread in response to running engines, regardless of the boats' behaviour (Cope et al., 1999). Dramatic decreases in group spread were also evident for common dolphins in this study, when boats traveled unpredictably around dolphins (Case # 2) or threatened to cut off their escape route (Case # 1). Bejder et al. (1999, p. 748) point out:

> Tightening of groups is often observed among dolphins in situations of surprise, threat, or danger (Johnson & Norris, 1986) and is interpreted as providing increased protection for the individual. Hence it may be that interactions with boats, even if not avoided, might be stressful.

The splitting of groups (Cases # 3 and 4) might be a more extreme response, shown when the dolphins may feel 'under attack'. It may have evolved as an anti-predator response, forcing the attacker to choose between groups, ensuring the survival of each member in those groups that do not happen to be pursued. Spinner dolphins leapt away in various directions in response to a predator attack, before rejoining in a compact group (Norris et al., 1994).

The interactions between dolphins and anglers can be quite deadly. A juvenile bottlenose dolphin in Florida, was entangled in fishing line, in a very similar fashion to the entanglement reported here, in case # 5. It eventually died from the constriction of its larynx by the line (Contillo et al., 1999). Apparently, the accidental foul-hooking of common dolphins is not an infrequent occurrence. A reliable source, who wishes to remain anonymous, assured the author that every year during the Whakatane gamefishing tournament, at least two or three common dolphins are foul-hooked.

Hooks that caught in the dorsal fin may account for some of the large nicks observed in some fins, and/or for those dorsal fins that have been partially cut off. On at least one occasion during the 2000 Whakatane gamefishing tournament, a dolphin was hooked in the rostrum, and reeled in by the angler. The hook was then removed successfully, with the dolphin still in the water, and the animal was released (J. Wharehoka, pers. comm., 7.4.2001).

This threat to the dolphins' welfare is the result of a common perception among recreational fishermen, that gamefish, particularly yellow-fin tuna, regularly associate with dolphins, especially while they are feeding. This may, or may not be the case in the Bay of Plenty, but anglers do seek out groups of dolphins to fish amongst them, and are encouraged to do so by the recreational fishing industry (Mossman, 2000; Neumann, 2000). No direct evidence for the presence of gamefish around dolphins was ever found during the present study.

While it must be considered rare, the intentional killing of common dolphins is not unheard of in Australia (Gibbs & Long, 2001; Kemper et al., 2001), and they used to be regularly harpooned in an artisanal subsistence fishery along the coast of Peru (Read et al., 1988). Commercial fisheries also contributed to the deaths of common dolphins in New Zealand. Slooten & Dawson (1995) estimated that 80-300 common dolphins were killed annually as by-catch in the 1980's in the commercial jack mackerel fishery. The impact on the population remains unknown, because there are no reliable estimates for common dolphin population size in New Zealand waters.

6.4 Summary:

While this investigation of dolphin-human interactions was admittedly preliminary, it nevertheless produced some valuable insights:

Common dolphins generally showed few behavioural changes in response to boat traffic, as long as boats were driven in a careful manner, consistent with the provisions of the Marine Mammal

Protection Regulations (1992). However, prolonged boat traffic (exceeding 48.6 minutes on average) caused apparent boat avoidance behaviour in 40 percent of groups containing less than 57 (= mean group size) individuals, while only 17.5 percent of larger groups showed any indication of boat avoidance.

Common dolphins showed no avoidance responses towards swimmers in the water, but were generally less inclined to interact with humans than the other three dolphin species (bottlenose, dusky, and Hector's) which are targets of swim-with-dolphin tourism in New Zealand. Few interactions with recreational boaties and anglers were observed, but these interactions are cause for concern, as the dolphins' behaviour changed dramatically, and evidence of physical injuries was also observed.

7. CONCLUSIONS

7.1 Summary

This study was the first long-term study focusing exclusively on the behaviour and ecology of free-ranging common dolphins in New Zealand. The main objective of this study was to make a significant contribution towards the scientific knowledge of common dolphin behavioural ecology, particularly the following main questions, which were put forth in the introduction (chapter 1):

1) Basic demographics of common dolphins: How many are there ? Where do they go ? What is their social organisation ?

Significant progress towards a better understanding of these factors has been made. The main findings - collected during 166 surveys, which led to 105 focal group follows, with a total of 118.2 hours spent following common dolphins - were:

* The mean duration of focal group follows was 67.5 minutes (SD=39.55, range= 15 to 195 minutes).

* Average group size was 57.3 (SD=50.78, n=105).

* There was no significant seasonal variation in group size.

* The number of newborn common dolphin calves peaked in late summer.

* Seasonal movements of common dolphins were described, and available evidence suggests that these are tied to fluctuations in sea surface temperature.

* Common dolphins appear to live in a fission-fusion society, like many other pelagic dolphin species. Groups frequently merged and split again. The merging of groups was often accompanied by either sexual, or feeding activity.

* Four-hundred-and-eight individual dolphins were identified from photographs of their dorsal fins. No evidence was found of long-term association between individuals. Resightings of identifiable dolphins indicate movement of individuals between Mercury Bay and the Hauraki Gulf, as well as between Mercury Bay and Whakatane.

* Common dolphins showed sexual dimorphism in the morphology of their peduncle. The discovery of using the presence of a postanal hump to identify sexually mature males visually in the field will be of great

value to future studies investigating the social organisation of common dolphins. Based on this characteristic, at least three different types of common dolphin groups were distinguished: nursery groups, male bachelor groups, and large mixed groups.

* Group formation and the size of common dolphin groups are probably determined by a combination of predator avoidance and prey availability.

The second general issue addressed in this study, concerned the behaviour of free-ranging common dolphins along the New Zealand coast:

2) Baseline behaviour of common dolphins: What do they typically do during daylight hours ? How do they interact with each other and their environment ?

These questions were addressed mainly by compiling an activity budget for common dolphins in the wild. This contribution will allow future researchers to use the present information as a baseline, and assess the influence of geographical variation, social organisation, numerous environmental factors, and human impact on the behaviour of common dolphins.

* Common dolphins spent 55.6 percent of their time traveling, 20.4 percent milling, 16.2 percent feeding, 7.1 percent socialising, and 0.7 percent resting. This proportion did not change significantly by season or from year to year. The size of groups did not have a significant effect on the activity budget of common dolphins; neither had the time of day or tidal fluctuations.

* Numerous events of aerial behaviour were recorded, with 'breaching' being the most frequently observed event. Aerial behaviours may be used in long-distance communication to co-ordinate group activity. There was no significant correlation between any behavioural event and a specific activity category, except for a positive correlation between 'rolling together' and socialising.

* Common dolphins were found to feed on at least six different fish species, which is consistent with reports of a varied diet in other locations. A number of different feeding strategies were employed to capture these fish. Some of these techniques had previously been observed in bottlenose dolphins and killer whales, but have never before been described for common dolphins. Six prey species of common dolphins were identified. They were: jack mackerel, kahawai, garfish, parore, yellow-eyed mullet, and flying fish. Six distinct feeding strategies were observed and described in detail. Three occur during individual feeding: high-speed pursuit, fish-whacking, and

kerplunking. Three involve cooperative feeding: carouseling, line abreast, and wall formation. Bubble-blowing is sometimes employed to startle fish during hunting.

Question 3 concerned the position of these findings within the broader context of cetacean research:

3) Is the behavioural ecology of common dolphins comparable to that of other delphinids ?

Within the bigger picture of cetology, this study has managed to confirm or establish for the first time, similarities to other cetacean species, in group formation (spinner and spotted dolphins), reactions to boat traffic (Hectors' dolphins), and feeding strategies (bottlenose dolphins, killer whales). The activity budget of common dolphins was comparable to the proportions of time allocated to various activities by bottlenose dolphins in other locations.

In addition, this study also intended to carry out a preliminary assessment of common dolphin-human interactions, and provide practical guidelines for such interactions that will aid in the conservation of this species:

4) Are common dolphins affected by interactions with humans, particularly commercial swim-with-dolphin tourism ?

The results of this study suggest that common dolphins can potentially be affected negatively by the actions of humans. Boat traffic appears to disturb the dolphins when the boat's path is not easily predictable and/or takes it through the group. Small groups of < 50 dolphins often started to avoid boats after behaving equivocal towards them for circa three quarters of an hour. While few attempts at swimming with common dolphins resulted in a sustained interaction, unsuccessful attempts did not elicit an obvious negative response. Fishing poses the greatest threat of physical injury and possible mortality to common dolphins. Several key issues were identified, which may be valuable in managing interactions with this species. These are outlined below under 7.3 Management recommendations.

This study faced a unique set of challenges, which have undoubtedly contributed to common dolphins being somewhat 'neglected' by field researchers in the past. The distribution of common dolphins is much less predictable than that of various other delphinids, which have therefore been studied in much greater detail. The fact that common dolphins were generally found at a fair distance from shore (routinely 20 kilometers or more), meant that the research project was very susceptible to adverse weather conditions. This also raised the amount of funding required, especially for fueling the research vessel. All of the above contributed to a comparatively low sample size, which might be considered the main shortcoming of this study. However, considering the limited budget, and the limited time-frame available to carry out this study, the results provide a significant contribution to knowledge regarding common dolphins.

In hindsight, both the Whakatane area, and the Hauraki Gulf would have been more suited as study areas, if the primary concern would have been to establish a large sample size. The number of sightings per unit of effort were much greater in those locations (Leitenberger, 2001; pers. obs.). However, these areas also show a high degree of dolphin-tourism. Therefore, the collection of baseline data for common dolphin behaviour - which was the main objective of this study - would have been much more difficult, if not impossible, in those areas.

7.2 Future research

Although this study addressed some of the issues associated with boat traffic, fishing, and tourism, it is essentially a study which provides baseline information on how common dolphins behave in the presence of comparatively little human impact. This makes it the kind of valuable pre-impact study that many authors have called for (Bejder & Dawson, 1998; Constantine, 1999a). This contribution may be put to the test very soon, because exposure to human activities is about to increase dramatically for the dolphins in Mercury Bay:

The Whitianga Waterways residential development will turn Mercury Bay into a watersports center over the next 10-20 years (Auckland City Council, 2001). This has the potential to impact dolphins and other marine life considerably in the area. Boat traffic may increase as much as ten-fold. Therefore, it is vital to continue research in this area, and to carefully monitor if/how dolphin behaviour is affected, so that appropriate conservation steps can be implemented. The present study can be used as a baseline against which this impact can be assessed.

Whitianga is the main centre on the northeast coast of Coromandel Peninsula, with direct access to Mercury Bay. Its coastline, fishing, tramping, and other outdoor activities attract a growing number of domestic and international visitors. Over the course of this study, the number of people who visited the Whitianga Tourist Information Centre rose by 13.6 percent (Table 20).

One of Whitianga's big drawcards is certainly marine tourism, which contributes considerably to the local economy. The combined turnover for all Whitianga-based on-water tourism ventures (including charter-boats, scenic boat trips, kayak hire, etc.) totaled NZ$ 114,540.- in the 2000/2001 financial year, up from NZ$ 80,390.- the previous year (Whitianga Tourist Information Centre, pers. comm., 28.4.2001).

In the 2000/2001 summer, the local dolphin tour operators carried 142 passengers on 21 swim-with-dolphin trips. One-hundred-and-ten of their customers were overseas tourists, 32 were from New Zealand. These numbers were also typical of the two preceding years.

Obviously, the number of visitors will affect the volume of boat traffic in Mercury Bay, but their impact will be somewhat limited by the number of charter boats available. Currently (June 2001) there are 23 licensed fishing or diving charters, two boats offering scenic tours, and one offering dolphin tours. In addition, there are up to 35 commercial fishing boats operating out of Whitianga. This number is reached

Table 20. Number of visitors to the Whitianga Tourist Information Centre each financial year, from 1998 to 2001 (numbers kindly provided by the Whitianga Tourist Information Centre).

April 1998 - March 1999	83,567
April 1999 - March 2000	89,730
April 2000 - March 2001	94,913

during the October/November scallop season, while there are 10 boats operating year round (5 long-liners, and 5 for crayfish).

Although substantial, this commercial activity is almost negligible compared to the volume of private recreational boating during the summer. One-hundred-and-ninety-five private vessels have permanent berths in the Whitianga marina. Most of them are used during December and January. From Boxing day (26 December) to the end of January each summer, the population of Whitianga swells from approximately 4,000 permanent residents to 35,000 (Whitianga Tourist Information Centre, pers. comm., 28.4.2001). This is due to an influx of people who own holiday homes in Whitianga. They come chiefly from the Hamilton and Auckland areas and routinely spend their summer holiday here.

A large proportion of these visitors bring their own pleasure boats to Whitianga. This raises the number of private boats launched from the Whitianga harbour boat ramp from 5-10 during a typical off-season day to 80-100 per day during the main holiday season (Whitianga harbourmaster, pers. comm., 30.4.2001). In late February each year, Whitianga hosts a 4-day gamefishing tournament, which offers NZ$ 200,000.- in prizes. In 2001, 240 boats entered the competition, carrying more than 1,200 anglers.

The amount of boat traffic is set to increase even further, as a result of the Whitianga Waterways development. A series of canals are being dug to create new waterfront properties with direct access to the harbour (Auckland City Council, 2001). The project is geared specifically towards recreational boaties. The headline on the cover page of the Whitianga Waterways brochure reads: "Reserve your own private mooring". Over the next 20 years, 1600 sections are going to be developed, 500 of which will have direct private access to a canal. A new public boat ramp will also be built, creating a convenient launching facility for the owners of the remaining sections (Hopper Developments, pers. comm., 3.5.2001). This would bring the total number of public boat ramps in Whitianga to three.

The Waterways development has the potential of increasing the volume of boat traffic in Mercury Bay by an order of magnitude. Furthermore, Whitianga is the largest, but not the only, location from which boats are launched into the area covered by this study. The boat ramps of Kuaotunu, Cook's Beach, Hahei, and Tairua are also exceedingly busy during the summer months. This is bound to have an impact on the local marine environment. As has been shown in this study, dolphins can be adversely affected by boat traffic, and they are susceptible to injury from recreational fishing activity. During times of very high pleasure boat density in Florida, bottlenose dolphins were injured in boat collisions (Wells & Scott, 1997).

Recreational fishing is the main driving force behind Mercury Bay boat traffic. A further increase of recreational fishing in this area, may even cause a decline in local fish abundance. The impact may be most critical for slowly reproducing game-fish species, such as marlin, sharks, and tuna. It would be desirable for future research to monitor the effects of the Whitianga Waterways development on the Mercury Bay fauna. Any negative impacts may then be identified early, and proper steps be taken to mitigate those effects.

In addition, this study has raised a number of further questions on the behavioural ecology of common dolphins, which beckon to be addressed:

1) A reliable estimate of common dolphin abundance in New Zealand waters would be of great value. Unfortunately, aerial surveys were not found to be very effective, in this study, but perhaps systematic shipboard transect surveys could accomplish this task.

2) The seasonal movements of common dolphins should be investigated in greater detail. Especially, the possibility of Whitianga-dolphins moving to Whakatane in autumn should be addressed. If this proves correct, then a second, independent population of common dolphins who consistently stay >20 kilometers offshore may be

discovered. Satellite-tracking, genetic sampling, or increased photo-identification efforts could help answer this question. Simultaneous observations in Mercury Bay and off Whakatane would also be helpful, when photo-identification records and abundance estimates can be compared for specific dates and seasons. Further, surveys of the East Cape eddy may reveal this location as a preferred offshore habitat for common dolphins.

3) Using the photo-catalogue in Appendix 3, researchers may now be able to track certain identifiable common dolphins around New Zealand, in the future. Such sightings may reveal the true extent of the dolphins' home range, and also provide information on the animals' longevity.

4) The question still needs to be addressed of what is the smallest social unit in common dolphin groups; including whether such units are stable over time, or if membership changes frequently. Admittedly, it will be exceedingly difficult to accomplish this, but one of the best ways to investigate this question would probably be by following a group of common dolphins for several days, 24 hours a day. Radio-tracking of individuals may help with this task.

5) The observed 'straightening' of dorsal fins could be a function of increasing age in both sexes. Dorsal fins with a straight trailing edge

were never observed on animals that were less than mature size. This hypothesis ('the older the dolphin, the straighter the dorsal fin') could be tested by correlating dorsal fin shape with the number of dentinal growth layers in the same individual. Such information would be most likely to come from stranded or by-caught specimens.

6) Exclusively all-male groups were observed, and within some mixed groups, mature males were also spotted traveling in tight formation with other mature males. Future research now has the tool (i.e. the presence of a postanal hump) to conduct behavioural observations that may establish whether this is consistently the case, and if such associations may, in fact, represent long-term coalitions.

7) The presence of a sexually dimorphic postanal hump will allow future researchers to determine the gender of sexually mature males, in the field. Thus, they may be able to identify differences in social organisation and activity patterns between the sexes. Behavioural observations, focusing on the now visually recognisable sexually mature males, combined with genetic testing of paternity, may also shed some light on the mating system of common dolphins.

8) Several anomalously pigmented individuals, featuring grey lateral patches were observed in this study. One grey-sided adult was accompanied by a grey-sided calf, while another was accompanied by

a calf with normal colour pattern. Genetic testing of such individuals may reveal how pigmentation patterns are inherited, and which genes carry the information for these patterns.

9) A detailed analysis of potential predation scars on common dolphins may help determine predation pressure and possibly identify potential predators. Tests on captive common dolphins could help answer the question, if their skin heals any more quickly than that of e.g. bottlenose dolphins. This should not include deliberately injuring animals. It could be accomplished by documenting the healing progress of natural rake marks.

10) Feeding sessions of common dolphins should be carefully observed, and possibly video-taped above and below the surface. This may reveal even more distinct hunting and feeding techniques. Now that its existence has been described, the importance of bubble-blowing during feeding could also be assessed.

11) It is not clear whether the boat avoidance observed in this study was the result of the boat's physical presence, its engine noise, or both. Focal group follows using sailing vessels as observation platforms could be conducted to help test this question.

12) Long-term studies in locations with a high level of common dolphin-tourism may be able to evaluate, whether common dolphins might tend to become either sensitised (as documented by Constantine (1999b) for bottlenose dolphins), or habituated to such human activity.

13) Acoustic monitoring of common dolphin vocalisations could be of great value in assessing human impact. Scarpaci et al. (1999) found that bottlenose dolphins whistled more when tour boats approached, in a likely attempt to maintain group cohesion.

14) When resting was observed, it always occurred between 10:35 a.m. and 11:50 a.m. Is this a preferred resting period for common dolphins ? Overall, very little time appeared to be devoted to resting. Do they rest more at night, or were they disturbed by the research vessel, and terminated resting bouts prior to its arrival ? If the latter were the case, boat traffic may have a serious negative impact on common dolphin well-being, interfering with a necessary physical maintenance behaviour. Land-based studies could help solve this question by establishing an activity budget in the absence of boats. However, this will prove extremely difficult because common dolphins are rarely found near shore. To err on the side of caution, interactions with common dolphins should be kept brief, in order to allow them the opportunity for maintenance behaviours once the boat has left.

15) Satellite-tracking devices, combined with a time-depth recorder could help identify when resting occurs, and for how long. They would also provide information whether and where nocturnal feeding may occur. Diurnal, and perhaps even seasonal movement patterns could also be identified in extreme detail.

However, this approach must be very carefully weighed against the welfare of individual dolphins. While some tracking devices can be affixed without capturing and restraining the dolphin (Stone et al., 1994), they only remain attached for a few hours, and will not provide the desired detail of information. The more permanent technique would involve the capture of an individual, and the attachment of a satellite transmitter by bolting it through the dorsal fin (Wells et al., 1998). This appears to have no negative long-term effects on bottlenose dolphins, but common dolphins may not be so resilient.

The stress of capture proved fatal for a number of common dolphins who were caught, and intended for display in oceanaria (K. Waite, pers. comm., 3.4.2001). Common dolphins also showed a much more intense fright and flight response to skin-swabbing (this study), than that reported for dusky dolphins (Harlin et al., 1999) or shown by Hector's dolphins in response to suction-cup tagging (Stone et al., 1994). At least one common dolphin appeared to have died from the stress of being hit by a biopsy dart (Bearzi, 2000). This indicates that common dolphins may be somewhat more ‘fragile’ than other dolphin species. Therefore, attempts at capture, tagging, or genetic sampling should not be undertaken lightly.

7.3 Management recommendations

This study has outlined some of the conflicts of interest between humans and dolphins. For example:

* Many humans like to observe dolphins in their natural habitat - and some pay money to do so, *but* that may disrupt the dolphins' normal activity patterns.

* Many humans like to catch fish, *but* they may harm dolphins in the process.

To minimise negative impact on common dolphins, the following should be considered in establishing management guidelines:

1) This study has shown that the Marine Mammal Protection Regulations (1992) are effective in minimising disturbance of common dolphins. Groups of dolphins should therefore always be approached in a cautious manner, consistent with these regulations. A slow and gradual approach from behind and slightly off to one side of the group is recommended. The group can then be followed by cruising at the same speed, parallel to the dolphins, off to one side, and towards the rear of the group.

2) When a group of dolphins shows any kind of disturbance, or consistently change their heading away from the following boat (i.e. boat avoidance), follows should be discontinued.

3) The amount of time spent with any group of common dolphins could be limited to a maximum of 45 minutes, to avoid reaching the average boat avoidance threshold. Permits for commercial common dolphin-watching operations could require the operators to not exceed this time limit in interactions with any one group of common dolphins.

4) If dolphins engaged in feeding are encountered, the engines should be turned off, and the dolphins be observed while the vessel is drifting.

5) Swim attempts did not appear to affect the dolphins, but operators may consider certain recommendations to increase customer satisfaction. These could include: not targeting small groups for swim attempts; instructing swimmers to refrain from splashing, and to attempt repeated dives below the surface.

6) Game-fishing with trolled lures should not be conducted in the vicinity of common dolphins, particularly when they are feeding. If anglers insist on fishing in the presence of common dolphins, their boat should follow a minimum distance (50-100 meters) behind the

group, and never attempt to drive through or in front of the group. If dolphins approach the boat, particularly for wake-riding, trolled lures should be removed from the water immediately. Education of recreational anglers upon this subject should be attempted, perhaps through talks and/or leaflets given to gamefishing clubs. These should include recommended 'etiquette' around dolphins and emphasise the fact that it is illegal (under the Marine Mammal Protection Regulations, 1992) to harass or injure any marine mammal.

In the particular case of Mercury Bay, the authorities may wish to consider the following, in order to reduce the adverse effects of increasing human aquatic activity:

1) To protect marine life from over-harvesting, and thus also protect the food chain that predators such as dolphins depend upon, the existing Te Whanganui a Hei marine reserve could be expanded, or new marine reserves established.

2) Fish stocks in and around Mercury Bay should be monitored carefully; and if necessary, the maximum catch quota per capita be adjusted accordingly.

4) Educate the public about the existing Marine Mammal Protection Regulations (1992) and a 'code of ethics' of how to behave around

dolphins. This must be carefully weighed, however, against the potential of increasing the exposure of dolphins to humans. Signage or pamphlets educating people about proper dolphin-watching 'etiquette', may call their attention to the presence of dolphins in the first place. They may then decide to specifically seek out dolphins, which they may not have done in the absence of the educational material.

In closing, the author would like to remind the reader of Melville's (1851, p. 398) prophetic statement:

> But still another inquiry remains; one often agitated by the more recondite Nantucketers. Whether owing to the almost omniscient lookouts at the mastheads of the whale ships, now penetrating even through Bering's straits, and into the remotest secret drawers and lockers of the world; and the thousand harpoons and lances darted along all continental coasts; the moot point is, whether leviathan can long endure so wide a chase, and so remorseless a havoc; whether he must not at last be exterminated from the waters, and the last whale, like the last man, smoke his last pipe, and then himself evaporate in the final puff.

In the century and a half since the publication of the epic "Moby Dick" (Melville, 1851), humankind has undergone a remarkable transformation from almost eradicating many of the great whale species, to actively protecting all cetaceans, in many areas around the world.

Today, common dolphins, thankfully, do not face a "thousand harpoons and lances darted along all continental coasts". However, there is no reason for complacency. Dolphins are facing a new set of challenges in their environment, some of which were outlined in this dissertation. It is the moral responsibility of all people to ensure the welfare and conservation of this and many other animal species.

An understanding of the behavioural ecology of each species is of paramount importance if conservation efforts are to succeed. Hopefully, this study was able to make a small contribution towards achieving that goal.

***

Personal communications

Rochelle Constantine - PhD candidate, Dept. of Biological Sciences University of Auckland (19.11.1999).

Dr. Padraig Duignan - Dept. of Veterinary Science, Masey University, Palmerston North (8.5.2001).

Avon Hansford - Longshore Marine, Whitianga (2.9.1999, 15.10.1998, 3.1.2000).

Hopper Developments - Waterways Development Office, SH 25, Whitianga (3.5.2001).

Deborah Kyngdon - Master's student, Dept. of Biological Sciences, Massey University, Plamerston North (15.1.1999).

Fiona McKnight - Master's Student, Dept. of Marine Sciences, University of Queensland, Australia (17.6.2001).

Shaun Morrison - deckhand aboard MV Hapuku, Whitianga (12.4.2000).

Dr. Timothy Mulligan - Dept. of Fisheries and Wildlife Management, Humboldt State University, Arcata, California, USA (30.10.1998).

Roderick Rae - Mercury Bay Seafaris, Whitianga (25.11.1998, 6.2.2000).

Kare Waite - Dolphins Down Under, Whakatane (12.3.2000, 3.4.2001).

John Wharehoka - Dolphins Down Under, Whakatane (12.3.2000, 7.4.2001).

Whitianga harbourmaster - The wharf, Esplanade, Whitianga (30.4.2001).

Whitianga Tourist Information Centre, Albert Street, Whitianga (28.4.2001).

***

REFERENCES

Acevedo, A. (1991). Interactions between boats and botlenose dolphins, *Tursiops truncatus*, in the entrance to Ensenada de la Paz, Mexico. *Aquatic Mammals, 17*, 120-124.

Acevedo-Guttierez, A. (1999). Aerial behavior is not a social facilitator in bottlenose dolphins hunting in small groups. *Journal of Mammalogy, 80*, 768-776.

Adeyemo, A.I. (1997). Diurnal activities of green monkeys *Cercopithecus aethiops* in Old Oyo National Park, Nigeria. *South African Journal of Wildlife Research, 27*, 24-26.

Allen, M.C. & A.J. Read. (2000). Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science, 16*, 815-824.

Allen, S., L. Möller, & E. Kniest. (2001). Assessing vessel impacts on bottlenose dolphins in Port Stephens. *Abstracts of the Southern Hemisphere Marine Mammal Conference, Phillip Island, Victoria, Australia, 29 May - 1 June 2001.*

Alpers, A. (1963). *Dolphins*. London: John Murray Publishing.

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour, 49*, 227-265.

Amante-Helweg, V. (1996). Ecotourists' beliefs and knowledge about dolphins and the development of cetacean ecotourism. *Aquatic Mammals, 22*,131-140.

Au, D.W. & W.L. Perryman. (1982). Movement and speed of dolphin schools responding to an approaching ship. *Fishery Bulletin, 80*, 371-379.

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

Auckland City Council. (2001). Developing the act. *Vision Hauraki Gulf Newsletter, 19*, 1-2.

Augier, H., W.K. Park & C. Ronneau. (1993). Mercury contamination of the striped dolphin, *Stenella coeruleoalba,* Meyen, from the French Mediterranean coasts. *Marine Pollution Bulletin, 26,* 306-311.

Baird, R. W. (2000). The killer whale - foraging specializations and group hunting. In J. Mann, R.C. Connor, P.L. Tyack & H. Whitehead (Eds.), *Cetacean Societies - Field studies of dolphins and whales* (pp. 127-153). Chicago: University of Chicago Press.

Baldellou, M. & A. Adan. (1997). Time, gender, and seasonality in vervet activity: A chronobiological approach. *Primates, 38,* 31-43.

Barco, S.G., W.M. Swingle, W.A. McLellan, R.N. Harris & D.A. Pabst. (1999). Local abundance and distribution of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Virginia Beach, Virginia. *Marine Mammal Science, 15,* 394-408.

Barlow, J. (1995). The abundance of cetaceans in California waters: Part I. Ship surveys in summer and fall of 1991. *Fishery Bulletin, 93,* 1-14.

Barr, K. (1997). *The impacts of marine tourism on the behaviour and movement patterns of dusky dolphins (Lagenorhynchus obscurus), at Kaikoura, New Zealand.* Master's thesis, University of Otago, Dunedin, New Zealand.

Beach, D.W. & M.T. Weinrich. (1989). Watching the whales : Is an educational adventure for humans turning out to be another threat for an endangered species ? *Oceanus, 32,* 84-88.

Bearzi, G. (2000). First report of a common dolphin (*Delphinus delphis*) death following penetration of a biopsy dart. *Journal of Cetacean Research and Management, 2,* 217-221.

Bearzi, G., E. Politi, & G. Notarbartolo di Sciara. (1999). Diurnal behavior of free-ranging bottlenose dolphins in the Kvarneric (Northern Adriatic sea). *Marine Mammal Science, 15,* 1065-1097.

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

Bejder, L. & S.M. Dawson. (1998). *Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand.* (Report SC/50/WW11). International Whaling Commission Scientific Committee.

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

Bel'kovich, V.M., E.E. Ivanova, O.V. Yefremenkova, L.B. Kozarovitsky, & S.P. Kharitonov. (1991). Searching and hunting behavior in the bottlenose dolphin (*Tursiops truncatus*) in the Black Sea. In K. Pryor & K.S. Norris (Eds.), *Dolphin Societies - discoveries and puzzles* (pp. 38-67). Berkeley: University of California Press.

Bell, C., C. Kemper, & R. Baudinette. (2001). Common dolphins in Australian waters : taxonomy through morphology. *Abstracts of the Southern Hemisphere Marine Mammal Conference, Phillip Island, Victoria, Australia, 29 May - 1 June 2001.*

Bräger, S. (1993). Diurnal and seasonal behavior patterns of bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science, 9,* 434-438.

Brereton, T.M., A.D. Williams, & R. Williams. (1999). Distribution and relative abundance of *Delphinus delphis* (common dolphin) in the Bay of Biscay. *Abstracts of the 13th biennial conference on the biology of marine mammals. 28 Nov - 3 Dec 1999, Wailea, Maui, Hawaii.*

Busnel, R.G. (1973). Symbiotic relationship between man and dolphins. *The New York Academy of Sciences Transaction Series, 11*, 112-131.

Caro, T.M. (1986). The functions of stotting in Thomson's gazelles: some tests of the predictions. *Animal Behaviour, 34*, 663-684.

Caro, T.M., L. Lombardo, A.W. Goldizen & M. Kelly. (1995). Tail-flagging and other antipredator signals in white-tailed deer: New data and synthesis. *Behavioral Ecology, 6*, 442-450.

Celikkale, M.S., H. Karacam, E. Duzgunes, S. Unsal & H.F. Durukanoglu. (1989). Size and distribution of dolphin populations in the Black sea.*Doga Turk Zooloji Dergisi, 13*, 189-196.

Chiswell, S.M. & J.D. Booth. (1999). Rock lobster *Jasus edwardsii* larval retention by the Wairarapa eddy off New Zealand. *Marine Ecology Progress Series, 183,* 227-240.

Clapham, P.J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. *Mammal Review, 26*, 27-49.

Cockcroft, V.G. (1990). Dolphin catches in the Natal, South Africa, shark nets, 1980-1988. *South African Journal of Wildlife Research, 20,* 44-51.

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

Cockcroft, V.G., G. Cliff & G.J.B. Ross. (1989). Shark predation on Indian ocean bottlenose dolphins, *Tursiops truncatus*, off Natal, South Africa. *South African Journal of Zoology, 24*, 305-310.

Cockcroft, V.G., A.C. de Kock, G.J.B. Ross & D.A. Lord. (1990). Organochlorines in common dolphins caught in shark nets during the Natal, South Africa, sardine run. *South African Journal of Zoology, 25*, 144-148.

Collet, A. (1981). *Biologie de Dauphin commun, Delphinus delphis, en Atlantique Nord-est* [Biology of the common dolphin in the northeastern Atlantic]. Doctoral dissertation, University of Poitiers, France.

Collet, A. & H. Saint Girons. (1984). Preliminary study of the male reproductive cycle in common dolphins, *Delphinus delphis,* in the eastern North Atlantic. In W.F. Perrin, R. L. Browell, Jr, & D.P. DeMaster (Eds.), *Reproduction in whales, dolphins and porpoises* (pp. 355-360). Reports of the International Whaling Commission, Special Issue 6.

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

Connor, R.C., M.R. Heithaus, P. Berggren, & J.L. Miskis. 2000a. "Kerplunking": Surface fluke-splashes during shallow-water bottom foraging by bottlenose dolphins. *Marine Mammal Science, 16*, 646-653.

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

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

Constantine, R.L. & C.S. Baker. (1997). *Monitoring the commercial swim- with-dolphin operations in the Bay of Islands.* Science for Conservation 56, Department of Conservation, New Zealand.

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

Constantine, R.L. (1999b). Increased avoidance of swimmers by bottlenose dolphins in the Bay of Islands, New Zealand. *Abstracts of the 13th biennial conference on the biology of marine mammals. 28 Nov - 3 Dec 1999, Wailea, Maui, Hawaii.*

Contillo, J., B.G. Mase, R. Ewing, & J. Tobias. (1999). Documented evidence of human interaction and mortality of a known resident bottlenose dolphin in Biscayne Bay, Florida. *Abstracts of the 13th biennial conference on the biology of marine mammals. 28 Nov - 3 Dec 1999, Wailea, Maui, Hawaii.*

Cope, M., D. Saint-Aubin, & J. Thomas. (1999). The effect of boat activity on the behaviour of bottlenose dolphins (*Tursiops truncatus*) in the nearshore waters of Hilton Head, South Carolina. *Abstracts of the 13th biennial conference on the biology of marine mammals. 28 Nov - 3 Dec 1999, Wailea, Maui, Hawaii.*

Corkeron, P.J. (1995). Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. *Canadian Journal of Zoology, 73*, 1290-1299.

Corkeron, P.J., R.J. Morris, & M.M. Bryden. (1987). Interactions between bottlenose dolphins and sharks in Moreton Bay. *Aquatic Mammals, 13*,109-114.

Corkeron, P.J., M.M. Bryden, & K.E. Hedstrom. (1990). Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. In S. Leatherwood & R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 329-336). San Diego: Academic Press.

Couperus, A.S. (1994). Killer whales (*Orcinus orca*) scavenging on discards of freezer trawlers northeast of the Shetland Islands. *Aquatic Mammals, 20*, 47-51.

Cousteau, J.Y. & Y. Paccalet. (1988). *Whales*. New York: Harry N. Abrams Publishers.

Curran, S., B. Wilson & P. Thompson. (1996). *Recommendations for the sustainable management of the bottlenose dolphin population in the Moray Firth*. Scottish Natural Heritage Review, Issue 56.

da Silva, J. & J.M. Terhune. (1988). Harbour seal grouping as an anti-predator strategy. *Animal Behaviour, 36*, 1309-1316.

Davis, R.W., G.S. Fargion, N. May, T.D. Leming, M. Baumgartner, W.E. Evans, L.J. Hansen & K. Mullin. (1998). Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science, 14*, 490-507.

Defran, R.H. & D.W. Weller. (1999). Occurrence, distribution, site fidelity, and school size of bottlenose dolphins (*Tursiops truncatus*) off San Diego, California. *Marine Mammal Science, 15*, 366-380.

Defran, R.H., D.W. Weller, D.L. Kelly & M.A. Espinosa. (1999). Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California bight. *Marine Mammal Science, 15*, 381-393.

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

Doak, W. (1988). *Encounters with whales and dolphins*. Auckland: Hodder and Stoughton.

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

Doenier, P.B., Delgiudice, G.D. & M.R. Riggs. (1997). Effects of winter supplemental feeding on browse consumption by white-tailed deer. *Wildlife Society Bulletin, 25,* 235-243.

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

Domenici, P., R.S. Batty, T. Similä & E. Ogam. (2000). Killer whales (*Orcinus orca*) feeding on schooling herring (*Clupea harengus*) using underwater tail-slaps: Kinematic analyses of field observations. *Journal of Experimental Biology, 203,* 283-294.

Duffus, D.A. & P. Dearden. (1990). Non-consumptive wildlife-oriented recreation : A conceptual framework. *Biological Conservation, 53,* 213-231.

Evans, W.E. (1982). Distribution and differentiation of stocks of *Delphinus delphis* Linnaeus in the northeastern Pacific. In *Mammals in the seas, Vol. 4.* (pp. 45-66). Rome: Food and Agriculture Organization of the United Nations.

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

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

Ferretti, S., G. Bearzi, & E. Politi. (1998). Comparing behavior of inshore bottlenose and common dolphins in the eastern Ionian sea through focal group surfacing pattern analysis. *Abstracts of the World Marine Mammal Science Conference, Monaco, 20-24 January 1998.*

Fertl, D.C. (1994). *Occurrence, movements, and behavior of bottlenose dolphins (Tursiops truncatus) in association with the shrimp fishery in Galveston Bay, Texas.* Master's thesis, A&M University, Galveston, Texas.

Fertl, D.C. & B. Würsig. (1995). Coordinated feeding by Atlantic spotted dolphins (*Stenella frontalis*) in the Gulf of Mexico. *Aquatic Mammals, 21,* 3-5.

Francis, M. (1996). *Coastal fishes of New Zealand, an identification guide.* Auckland: Reed Publishing.

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

Gaskin, D.E. (1968). Distribution of *Delphinidae* (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. *New Zealand Journal of Marine and Freshwater Research, 2,* 527-534.

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

Gibbs, S. & M. Long. (2001). Stomach contents of a killer whale (*Orcinus orca*) implicate human interactions in South Australia. *Abstracts of the Southern Hemisphere Marine Mammal Conference, Phillip Island, Victoria, Australia, 29 May - 1 June, 2001.*

Gilson, A., M. Syvanen, K. Levine, & J. Banks. (1998). Deer gender determination by polymerase chain reaction: Validation study and application to tissue, bloodstain, and hair forensic samples from California. *California Fish and Game 84:* 159-169.

Goodson, N.J., Stevens, D.R. & J.A. Bailey. (1991). Effects of snow on foraging ecology and nutrition of bighorn sheep. *Journal of Wildlife Managment, 55,* 214-222.

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

Goold, J.C. (2000). A diel pattern in vocal activity of short-beaked common dolphins, *Delphinus delphis. Marine Mammal Science, 16*, 240-244.

Gowans, S. & H. Whitehead. (1995). Distribution and habitat partitioning by small odontocetes in the Gully, a submarine canyon on the Scotian Shelf. *Canadian Journal of Zoology, 73*, 1599-1608.

Guinet, C. (1991). Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology, 69*, 2712-2716.

Gunther, K. (1992). Changing problems in bear management: Yellowstone National Park twenty years after the dumps. *Abstracts of the 9th Annual International Bear Conference, Missoula, Montana, February 1992.*

Haccou, P. & E. Meelis. (1992). *Statistical analysis of behavioural data.* New York: Oxford University Press.

Hain, J.H.W., G.R. Carter, S.D. Kraus, C.A. Mayo, & H.E. Winn. (1982). Feeding behaviour of the humpback whale, *Megaptera novaeangliae,* in the western North Atlantic. *Fisheries Bulletin, 80,* 259-268.

Hanekom, N., L. Hutchings, P.A. Joubert & P.C.N. van der Byl. (1989). Sea temperature variations in the Tsitsikamma Coastal National Park South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science, 8,* 145-154.

Hanson, M.T. & R.H. Defran. (1993). The behaviour and feeding ecology of the Pacific coast bottlenose dolphin,*Tursiops truncatus. Aquatic Mammals, 19,* 127-142.

Harlin, A.D., B. Würsig, C.S. Baker, T.M. Markowitz. (1999). Skin swabbing for genetic analysis : Application to dusky dolphins (*Lagenorhynchus obscurus*). *Marine Mammal Science, 15,* 409-425.

Haug T., B. Gullinksen, & I. Christensen. (1981). Observations of the common dolphin, *Delphinus delphis*, in north Norway. *Fauna (Oslo), 34,* 97-100.

Hawks, P., W.T. McLeod, & L. Urdang (Eds.). (1986). *The Collins dictionary of the English language, 2nd edition*. London: Collins.

Heithaus, M.R. (2001). Shark attacks on bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia: Attack rate, bite scar frequencies, and attack seasonality. *Marine Mammal Science, 17*, 526-539.

Heyning, J.E. & W.F. Perrin. (1994). Evidence for two species of common dolphins (genus *Delphinus*) from the eastern North Pacific. *Contributions in Science (Los Angeles), 442*, 1-35.

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

Hui, C.A. (1994). Lack of association between magnetic patterns and the distribution of free-ranging dolphins. *Journal of Mammalogy, 75*, 399-405.

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

Jarman, P.J. & S.M. Wright. (1993). Macropod studies at Wallaby Creek: IX. Exposure and responses of eastern grey kangaroos to dingoes. *Wildlife Research, 20*, 833-843.

Jefferson, T.A. (1990). Sexual dimorphism and development of external features in Dall's porpoise *Phocoenoides dalli. Fishery Bulletin, 88*, 119-132.

Jefferson, T.A., R.L. Pitman, S. Leatherwood, & M.L. Dolar. (1997). Developmental and sexual variation in the external appearance of Fraser's dolphin (*Lagenodelphis hosei*). *Aquatic Mammals, 23*, 145-153.

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

Jones, D.A. (2000). Seasonal climate summary southern hemisphere (winter 1999): a return to near-normal conditions in the tropical Pacific. *Australian Meteorological Magazine, 49*, 139-148.

Jones, M.L. & S.L. Swartz. (1984). Demography and phenology of gray whales, and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. In M.L. Jones, S.L. Swartz, & S. Leatherwood (Eds.), *The gray whale* (pp. 309-373). Orlando, Florida: Academic Press.

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

Kenagy, G.J. & S.C. Trombulak. (1986). Size and function of mammalian testes in relation to body size. *Journal of Mammalogy,* 67, 1-22.

Kruse, S. (1991). The interaction between killer whales and boats in Johnstone Strait, B.C. In K. Pryor & K.S. Norris (Eds.), *Dolphin Societies - discoveries and puzzles* (pp. 335-346). Berkeley: University of California Press.

Lackowitz, W. (1896). *Das Buch der Tierwelt - Lebensbilder und Charakterzeichnungen aus dem gesamten Tierreich.* Berlin: Verlagsanstalt Urania.

Leatherwood, S. (1975). Some observations of feeding behavior of bottlenose dolphins, *Tursiops truncatus*, in the northern Gulf of Mexico and (*Tursiops* cf. *T. gilli*) off southern California. *Marine Fisheries Review, 37*, 10-16.

Leatherwood, S., W.F. Perrin, R.L. Garvie, & J.C. LaGrange. (1971). *Observations of sharks attacking porpoises (Stenella spp. and Delphinus cf. D. delphis).* Technical Note No. 908, Naval Undersea Center, San Diego, California.

Le Boeuf, B.J. (1974). Male-male competition and reproductive success in elephant seals. *American Zoologist, 14*, 163-176.

Leitenberger, A. (2001). *The influence of ecotourism on the behaviour and ecology of the common dolphin (Delphinus delphis), in the Hauraki Gulf, New Zealand*. Master's thesis, University of Vienna, Austria.

Lewis, T. (1991). The development of a postanal hump in male common dolphins, *Delphinus delphis*. *Abstracts of the 9th biennial conference on the biology of marine mammals, Chicago, USA.*

Linnaeus, C. (1758). Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus differentiis, synonymis, locis. Editio decima, reformata. Stockholm: Royal Library.

Ljungblad, D.K., B. Würsig, S.L. Swartz & J.L. Keene. (1988). Observations on the behavioral responses of bowhead whales, *Balaena mysticetus*, to active geophysical vessels in the Alaskan Beaufort sea, USA. *Arctic*, *41*, 183-194.

Lockyer, C. (1990). Review of incidents involving wild sociable dolphins, worldwide. Pages 337-353 In S. Leatherwood & R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 337-353). San Diego: Academic Press.

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

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

Mann, J. & H. Barnett. (1999). Lethal tiger shark (*Galeocerdo cuvieri*) attack on a bottlenose dolphin (*Tursiops* sp.) calf: Defense and reactions by the mother. *Marine Mammal Science, 15,* 568-574.

Martin, P.R. & P. Bateson. (1993). *Measuring behaviour - an introductory guide, 2nd edition*. Cambridge: Cambridge University Press.

McWilliams, S.R., J.P. Dunn & D.G. Raveling. (1994). Predator-prey interactions between eagles and cackling Canada and Ross' geese during winter in California. *Wilson Bulletin, 106,* 272-288.

Melville, H. (1851). *Moby-Dick, or the white whale.* Reprint of the complete first edition. 1972. London: Penguin Books.

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

Mossman, S. (2000). Using the natural signs. *New Zealand Fishing News, March 2000,* 96-97.

Murphy, R.J., M.H. Pinkerton, K.M. Richardson, J.M. Bradford-Grieve & P.W. Boyd. (2001). Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research, 35,* 343-362.

Myrberg, A.A. (1990). The effects of man-made noise on the behaviour of marine mammals. *Environment International, 16,* 575-586.

Neumann, D.R. (2000). Dolphin article irresponsible. *New Zealand Fishing News, April 2000,* 30.

Neumann, D.R. (2001a). Seasonal movements of short-beaked common dolphins *(Delphinus delphis)* in the northwestern Bay of Plenty, New Zealand: The influence of sea-surface temperature and "El Niño/La Niña". *New Zealand Journal of Marine and Freshwater Research, 35,* 371-374.

Neumann, D.R. (2001b). The activity budget of free-ranging common dolphins (*Delphinus delphis*) in the northwestern Bay of Plenty, New Zealand. *Aquatic Mammals,* in press.

Norman, G.R. & D.L. Streiner. (1994). *Biostatistics - the bare essentials.* St. Louis: Mosby.

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

Norris, K.S., B. Würsig, R.S. Wells, M. Würsig, S.M. Brownlee, C.M. Johnson & J. Solow. (1994). *The Hawaiian spinner dolphin.* Berkeley: University of California Press.

North Shore Times Advertiser. (1995). *Opo: the true and shameful story*. Tuesday, January 10, 1995, p. 7.

Nowacek, S.M. (1999a). *The effects of boat traffic on bottlenose dolphins, Tursiops truncatus, in Sarasota Bay, Florida*. Master's thesis, University of California, Santa Cruz.

Nowacek, D.P. (1999b). *Sound use, sequential behavior and the ecology of foraging bottlenose dolphins (Tursiops truncatus)*. Doctoral dissertation, Woods Hole Oceanographic Institution.

Östmann, J. (1991). Changes in aggressive and homosexual behaviour among two male bottlenose dolphins (*Tursiops truncatus*) in a captive colony. In K. Pryor & K.S. Norris (Eds.), *Dolphin Societies - discoveries and puzzles* (pp. 304-317). Berkeley: University of California Press.

Orams, M.B. (1995). *Managing interaction between wild dolphins and tourists at a dolphin feeding program, Tangalooma, Australia - the development and application of an education program for tourists, and an assessment of "pushy" dolphin behaviour*. Doctoral dissertation, University of Queensland.

Orams, M.B. (1997a). The effectiveness of environmental education: Can we turn tourists into "Greenies" ? *Progress in Tourism and Hospitality Research, 3*, 295-306.

Orams, M.B. (1997b). Historical accounts of human-dolphin interaction and recent developments in wild dolphin based tourism in Australasia. *Tourism Management, 18*, 317-326.

Orams, M.B. (1999). *Marine tourism - development, impacts and management*. London: Routledge.

Orams, M.B. (2001). From whale hunting to whale watching in Tonga: A sustainable future ? *Journal of Sustainable Tourism, 9*, 128-146.

Orams, M.B. & R.B. Deakin. (1997). Report on healing of a large wound in a bottlenose dolphin (*Tursiops truncatus*). In N.K. Saxena (Ed.), *Recent advances in Marine Science and Technology, 96th Pacific Congress on Marine Science and Technology, Honolulu, Hawaii* (pp. 477-489).

Orams, M.B., G.J.E. Hill & A.J. Baglioni. (1996). Pushy behavior in a wild dolphin feeding program at Tangalooma, Australia. *Marine Mammal Science, 12,* 107-117.

Pacenti, J. (1999a). Is it safe to swim with captive dolphins ? *Naples Daily News, 16 May 1999,* 15A-16A.

Pacenti, J. 1999b. Dolphin therapy: Scientific breakthrough or snake oil? *Naples Daily News, 17 May 1999,* 6D-7D.

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

Peddemors, V.M. (1999). Delphinids of southern Africa: A review of their distribution, status, and life history. *Journal of Cetacean Research and Management, 1,* 157-165.

Perrin, W.F. (1972). Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. *Fishery Bulletin, 70,* 983-1003.

Perrin, W.F. & J.W. Gilpatrick. (1994). Spinner dolphin, *Stenella longirostris* (Gray, 1828). In S.H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals, Vol. 5: The first book of dolphins* (pp. 99-128). London: Academic Press.

Perrin, W.F., W.A. Armstrong, A.N. Baker, J. Barlow, S.R. Benson, A.S. Collet, J.M. Cotton, D.M. Everhart, T.D. Farley, R.M. Mellon, S.K. Miller, V. Philbrick, J.L. Quan, & H.R.L. Rodriguez. (1995). An anomalosuly pigmented form of the short-beaked common dolphin (*Delphinus delphis*) from the Southwestern Pacific, Eastern Pacific, and Eastern Atlantic. *Marine Mammal Science, **11**,* 241-247.

Peterson, H.A. (2001). Whale behavioural responses and human perceptions : An assessment of humpback whales (*Megaptera novaeangliae*) and vessel activity near Juneau, Alaska. *Abstracts of the Southern Hemisphere Marine Mammal Conference, Phillip Island, Victoria, Australia, 29 May - 1 June, 2001.*

Pfaus, J.G. (1996). Homologies of animal and human sexual behaviors. *Hormones and Behavior, 30,* 187-200.

Pichler, F., C.S. Baker, S.M. Dawson, & E. Slooten. (1998). Geographic isolation of Hector's dolphin populations described by mitochondrial DNA-sequences. *Conservation Biology, 12*, 676-682.

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

Pryor, K., J. Lindbergh, S. Lindbergh & R. Milano. (1990). A human-dolphin fishing cooperative in Brazil. *Marine Mammal Science, 6*, 77-82.

Read, A.J., K. van Waerebeek, J.C. Reyes, J.S. McKinnon, & L.C. Lehman. (1988). The exploitation of small cetaceans in coastal Peru. *Biological Conservation, 46*, 53-76.

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

Reilly, S.B. & P.C. Fiedler. (1994). Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. *Fishery Bulletin*, *92*, 434-450.

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

Rice, D.W. & A.A. Wolman. (1971). *The life history and ecology of the gray whale (Eschrichtius robustus).* Special Publication #3 of the American Society of Mammalogy.

Richardson, W.J., B. Würsig & C.R. Greene. (1990). Reactions of bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort sea. *Marine Environmental Research*, *29*, 135-160.

Richardson, W.J., C.R.J. Greene, C.I. Malme, D.H. Thomsen, S.E. Moore, & B. Würsig. (1995). *Marine Mammals and Noise.* San Diego: Academic Press.

Rigley, L. (1983). Dolphins feeding in a South Carolina salt marsh. *Whalewatcher*, *7*, 3-5.

Roemmich, D & P. Sutton. (1998). The mean and variability of ocean circulation past northern New Zealand: Determining the representativeness of hydrographic climatologies. *Journal of Geophysical Research, 103*, 13041-13054.

Rose, G.A. & W.C. Leggett. (1988). Atmosphere-ocean coupling and Atlantic cod migrations - effects of wind-forced variations in sea temperature and currents on nearshore distributions and catches of *Gadus morhua. Canadian Journal of Fisheries and Aquatic Sciences, 45*, 1234-1243.

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

Rossbach, K.A. & D. L. Herzing. (1997). Underwater observations of benthic feeding bottlenose dolphins (*Tursiops truncatus*) near Grand Bahama Island, Bahamas. *Marine Mammal Science, 13*, 498-503.

Ryan, C. (1998). Dolphins, canoes and marae - Ecotourism products in New Zealand. In E. Laws, B. Faulkner & G. Moscardo (Eds.), *Embracing and managing change in tourism* (pp. 285-306). London: Routledge.

Saayman, G.S., C.K. Tayler, & D. Bower. (1973). Diurnal activity cycles in captive and free-ranging Indian bottlenose dolphins (*Tursiops aduncus* Ehrenburg). *Behaviour, 44*, 212-233.

Samuels, A. & T.R. Spradlin. (1995). Quantitative behavioral study of bottlenose dolphins in swim-with-dolphin programs in the United States. *Marine Mammal Science, 11*, 520-544.

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

Samuels, A., L. Bejder, & S. Heinrich. (2000). *A review of the literature pertaining to swimming with wild dolphins.* Marine Mammal Commission, Contract No. T 74463123. Bethesda, Maryland.

Sandegren, F.E. (1976). Courtship display, agonistic behavior, and social dynamics in the Steller sea lion (*Eumetopias jubatus*). *Behaviour*, *57*, 159-171.

Scarpaci, C., P.J. Corkeron, & D. Nugegoda. (1999). Monitoring whistles produced by bottlenose dolphins (*Tursiops truncatus*) during approaches made by commercial dolphin-swim boats in Port Phillip Bay, Victoria, Australia. *Abstracts of the 13th biennial conference on the biology of marine mammals. 28 Nov - 3 Dec 1999, Wailea, Maui, Hawaii.*

Scott, M.D. & K.L. Cattanach. (1998). Diel patterns in aggregations of pelagic dolphins and tunas in the Eastern Pacific. *Marine Mammal Science, 14*, 401-428.

Secchi, E.R. & T.J. Vaske. (1998). Killer whale (*Orcinus orca*) sightings and depredation on tuna and swordfish longline catches in southern Brazil. *Aquatic Mammals, 24*, 117-122.

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

Shackley, M. (1992). Manatees and tourism in Southern Florida: Opportunity or threat ? *Journal of Environmental Management, 34,* 257-265.

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

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

Shane, S.H. (1994). Occurrence and habitat use of marine mammals at Santa Catalina Island, California from 1983-91. *Bulletin of the Southern California Academy of Sciences, 93,* 13-29.

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

Shapunov, V.M. (1971). Food requirements and energy ballance in the Black Sea bottlenose dolphin (*Tursiops truncatus ponticus* Barabasch). In K.K. Chapskii & E.E. Sokolov (Eds.), *Morphology and Ecology of Marine Mammals* (pp. 207-212). Jerusalem: Israel Programme for Scientifc Translations.

Shepherdson, D.J., Carlstead, K., Mellen, J.D. & J. Seidensticker. (1993). The influence of food presentation on the behavior of small cats in confined environments. *Zoo Biology, 12*, 203-216.

Similä, T. & F. Ugarte. (1993). Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Canadian Journal of Zoology, 71*, 1494-1499.

Slooten, E. (1994). Behavior of Hector's dolphin: Classifying behavior by sequence analysis. *Journal of Mammalogy, 75*, 956-964.

Slooten, E. & S.M. Dawson. (1995). Conservation of marine mammals in New Zealand. *Pacific Conservation Biology, 2*, 64-76.

Slooten, E., S.M. Dawson & H. Whitehead. (1993). Associations among photographically identified Hector's dolphins. *Canadian Journal of Zoology, 71*, 2311-2318.

Smolker, R.A., A.F. Richards, R.C. Connor, J. Mann, & P. Berggren. (1997). Sponge-carrying by Indian Ocean bottlenose dolphins: Possible tool-use by a delphinid. *Ethology, 103,* 454-465.

Smultea, M.A. & B. Würsig. (1995). Behavioral reactions of bottlenose dolphins to the Mega borg oil spill, Gulf of Mexico, 1990. *Aquatic Mammals, 21,* 171-181.

Sokal, R.R. & F.J. Rohlf. (1981). *Biometry, 2nd edition*. New York: Freeman & Co.

Stock, M. & F. Hofeditz. (1996). Time-activity-budgets of Brent Geese (*Branta bernicla bernicla*) on saltmarshes in the Wadden Sea: The impact of human disturbance. *Vogelwarte, 38,* 121-145.

Stone, G., J. Goodyear, A. Hutt & A. Yoshinaga. (1994). A new non-invasive tagging method for studying wild dolphins. *Marine Technology Society Journal, 28,* 11-16.

Tanasichuk, R.W. & D.M. Ware. (1987). Influence of interannual variations in winter sea temperature on fecundity and egg size in Pacific herring, *Clupea harengus pallasi*. *Canadian Journal of Fisheries and Aquatic Sciences*, *44*, 1485-1495.

Tershy, B.R., D. Breese & S. Alvarez-Borrego. (1991). Increase in cetacean and seabird numbers in the Canal de Ballenas during an El Niño-Southern Oscillation event. *Marine Ecology Progress Series*, *69*, 299-302.

Tourism Strategy Group. (2001). *New Zealand tourism strategy 2010*. Auckland: New Zealand Tourism Board.

Valentine, P.S. (1990). Nature-based tourism : A review of prospects and problems. In M.L. Miller & J. Auyong (Eds.), *Proceedings of the 1990 Congress on Coastal and Marine Tourism, Vol. 2* (pp. 475-485).

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

Visser, I.N. (2000). Killer whale (*Orcinus orca*) interactions with longline fisheries in New Zealand waters. *Aquatic Mammals, 26,* 241-252.

Walker, J.L. & S.A. Macko. (1999). Dietary studies of marine mammals using stable carbon and nitrogen isotopic ratios of teeth. *Marine Mammal Science, 15,* 314-334.

Waples, D.M. (1995). *Activity budgets of free-ranging bottlenose dolphins (Tursiops truncatus) in Sarasota Bay, Florida.* Master's thesis, University of California, Santa Cruz.

Waples, D. M., Wells, R.S., Costa, D.P. & G.A.J. Worthy. (1998). Gender differences in activity budgets of bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Abstracts of the World Marine Mammal Science Conference, Monaco, 20-24 January 1998.*

Waters, S. & H. Whitehead. (1990). Aerial behaviour in sperm whales, *Physeter macrocephalus. Canadian Journal of Zoology, 68,* 2076-2082.

Weinrich, M.T., C.R. Belt, & D. Morin. (2001). Behavior and ecology of the Atlantic white-sided dolphin (*Lagenorhynchus acutus*) in coastal New England waters. *Marine Mammal Science, 17,* 231-248.

Weir, J., W. Dunn, A. Bell & B. Chatfield. (1996). *An investigation into the impact of "Dolphin-swim Ecotours" in Southern Port Phillip Bay.* Report by the Dolphin Research Project Inc., Hampton, Victoria, Australia.

Wells, R.S. (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In K. Pryor & K.S. Norris (Eds.), *Dolphin Societies - discoveries and puzzles* (pp. 199-225). Berkeley: University of California Press.

Wells, R.S. & M.D. Scott. (1990). Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. *Reports of the International Whaling Commission, 12,* 407-415.

Wells, R.S. & M.D. Scott. (1997). Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science, 13,* 475-480.

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

Wells, R.S., L.J. Hansen, A. Baldridge, T.P. Dohl, D.L. Kelly, & R.H. Defran. (1990). Northward extension of the range of bottlenose dolphins along the California coast. In S. Leatherwood & R.R. Reeves (Eds.), *The bottlenose dolphin* (pp. 421-431). San Diego: Academic Press.

Wells, R.S., A.J. Westgate, H.L. Rhinehart, P. Cunningham, J. Whaley, D.P. Costa, A.J. Read, T. Hepburn, M. Baran, C. Koberna, & T. Cox. (1998). Gulliver's travels : First records of long distance movements of offshore bottlenose dolphins. *Abstracts of the World Marine Mammal Science Conference, Monaco, 20-24 January 1998.*

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

Westerterp, K.R., Donkers, J.H.H.L.M., Fredrix, E.W.H.M & P. Boekhoudt. (1995). Energy intake, physical activity and body weight: A simulation model. *British Journal of Nutrition, 73,* 337-347.

Whitehead, H.J. & L. Weilgart. (2000). The sperm whale - social females and roving males. In J. Mann, R.C. Connor, P.L. Tyack & H. Whitehead (Eds.), *Cetacean Societies - Field studies of dolphins and whales* (pp. 154-172). Chicago: University of Chicago Press.

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

Wilson, B. (1994). *Review of dolphin management at Monkey Mia.* Report to the Department of Conservation and Land Management, West Australia.

Wrangham, R.W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human Nature, 4,* 47-79.

Wünschmann, A. (1999). Können Touristen Natur rettten ? [Can tourists save nature ?]. *Journal of the World Wide Fund for Nature (WWF), Germany, 2/99*, 14-21.

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

Würsig, B. & T.A. Jefferson. (1990). Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission, Special Issue 12*, 43-52.

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

Würsig, B. & M. Würsig. (1979). Behaviour and ecology of the bottlenose dolphin, *Tursiops truncatus,* in the South Atlantic. *Fishery Bulletin, 77*, 399-413.

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

Würsig, B., F. Cipriano, E. Slooten, R. Constantine, K. Barr, & S. Yin. (1997). Dusky dolphins (*Lagenorhynchus obscurus*) off New Zealand : Status of present knowledge. *Reports of the International Whaling Commission, 47*, 715-722.

Würsig, B., S.K. Lynn, T.A. Jefferson & K.D. Mullin. (1998). Behaviour of cetaceans in the northern Gulf of Mexico relative to survey ships and aircraft. *Aquatic Mammals, 24*, 41-50.

Yale, P. (1991). *From tourist attractions to heritage tourism*. Huntingdon, UK: ELM Publications.

Young, D.D. & V.G. Cockcroft. (1994). Diet of common dolphins (*Delphinus delphis*) off the south-east coast of southern Africa: Opportunism or specialization? *Journal of Zoology (London), 234*, 41-53.

Young, D.D. & V.G. Cockcroft. (1995). Stomach contents of stranded common dolphins *Delphinus delphis* from the south-east of Southern Africa. *Zeitschrift für Säugetierkunde, 60,* 343-351.

Zar, J.H. (1984). *Biostatistical analysis, 2nd edition.* Englewood Cliffs, New Jersey: Prentice Hall.

Appendix 1

A synopsis of those Marine Mammal Protection Regulations (1992) that are relevant to this study :

R. 18. CONDITIONS GOVERNING COMMERCIAL OPERATIONS AND BEHAVIOUR OF ALL PERSONS AROUND ANY MARINE MAMMAL - Every commercial operation, and every person coming into contact with any class of marine mammal, shall comply with the following conditions:

(a) Persons shall use their best endeavours to operate vessels, vehicles, and aircraft so as not to disrupt the normal movement or behaviour of any marine mammal

(b) Contact with any marine mammal shall be abandoned at any stage if it becomes or shows signs of becoming disturbed or alarmed:

(c) No person shall cause any marine mammal to be separated from a group of marine mammals or cause any members of such a group to be scattered:

(d) No rubbish or food shall be thrown near or around any marine mammal:

(e) No sudden or repeated change in the speed or direction of any vessel or aircraft shall be made except in the case of an emergency:

(f) Where a vessel stops to enable the passengers to watch any marine mammal, the engines shall be either placed in neutral or be switched off within a minute of the vessel stopping:

Appendix 1.2

Marine Mammal Protection Regulations (1992), continued :

(i) No person shall disturb or harass any marine mammal:

(k) No person, vehicle, or vessel shall cut off the path of a marine mammal or prevent a marine mammal from leaving the vicinity of any person, vehicle, or vessel:

(l) The master of any vessel less than 300 meters from any marine mammal shall use his or her best endeavours to move the vessel at a constant slow speed no faster than the slowest marine mammal in the vicinity, or at idle or "no wake" speed:

R. 20. SPECIAL CONDITIONS APPLYING TO DOLPHINS OR SEALS -

(a) No vessel shall proceed through a pod of dolphins:

(g) A vessel shall approach a dolphin from a direction that is parallel to the dolphin and slightly to the rear of the dolphin.

APPENDIX 2

The data sheet used to record the information presented in this study, and how it was filled in :

DATE : 17.10.2000 LOW TIDE : 4:33 a.m. WEATHER : 10 kn SW, 1 m swell ID-FILE : Film 72: 1-15

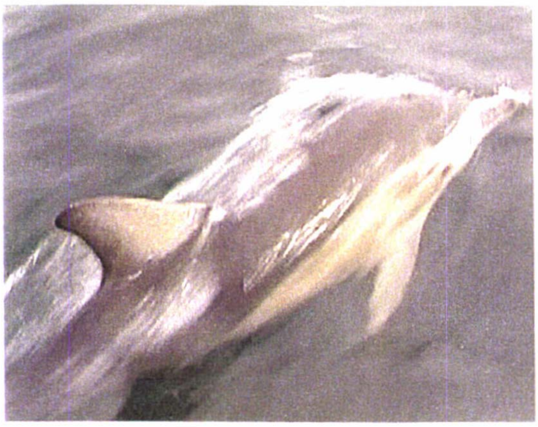
Time	Location	Depth	Temp.	Adults	Calves	Babies	Activity	Spread	Heading	Speed	Boats	Distance	Notes
12:55	36-47-29/ 175-47-42	50 m	19 C	40	3	6	TR	150	120	7 kph	Aihe	0	
12:58				40	3	6	TR	200	180	7	Aihe	10	
13:01				40	3	6	FE	100	var.	var.	Aihe	20	Gannets also FE
13:04	36-47-34/ 175-47-22	50 m	19 C	40	3	6	FE	100	var.	var.	Aihe	20	
13:07				40	3	6	FE	100	var.	var.	Aihe	30	
13:10				40	3	6	TR	100	90	5	Aihe	5	
13:13	36-47-40/ 175-47-20	50 m	19 C	40	3	6	TR	150	90	5	Aihe	5	
13:16				40	3	6	TR	100	150	5	Aihe	10	
13:19				40	3	6	MI	70	var.	slow	Aihe	10	

Appendix 3.1

Dolphin individuals resighted within the same study season (all individuals observed in the Mercury Bay study area, except WHK = seen off Whakatane) :

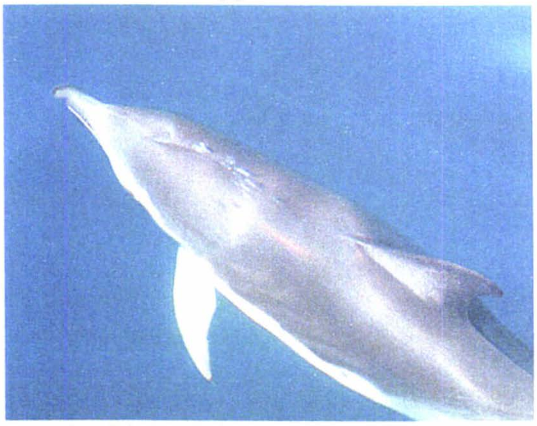
B 222, seen on :
4.3.2000 + 9.3.2000

B 65, seen on :
31.10.1999 + 19.11.1999

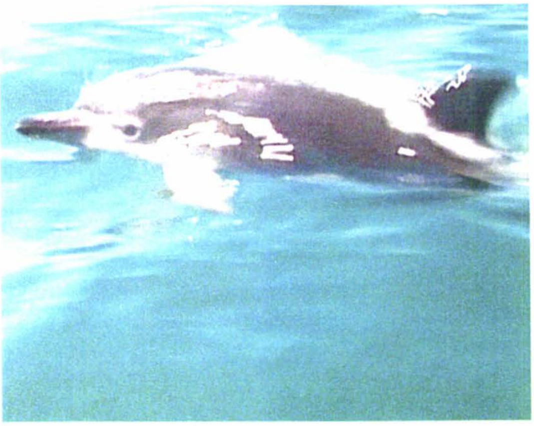


B 76, seen on :
2.11.1999 + 28.1.2000

C 325, seen on :
21.12.2000 + 26.12.2000



C 374 'Left-bent grey', seen on :
18.2.2001 + 19.2.2001



C 388, seen on :
8.4.2001 (WHK) + 10.4.2001 (WHK)

Appendix 3.2

Dolphin individuals resighted over two consecutive study seasons :

AB 35, seen on :
22.3.1999 + 11.2.2000

BC 208 'Platypus', seen on :
15.1./10.2./11.2.2000, 23.1./19.2.2001

AB 18, seen on :
17.3.1999 + 25.12.1999

BC 290, seen on :
4.2.2000 + 3.3.2001

AB 57, seen on :
3.4.1999 + 1.11.1999

BC 299, seen on :
4.2.2000 + 21.12.2000

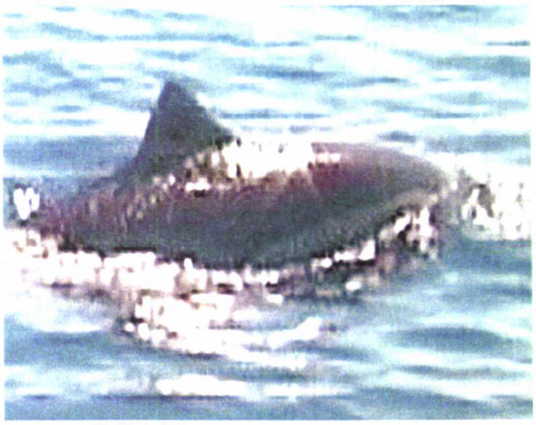
Appendix 3.3

Dolphin individuals resighted in two different locations (sightings off Whakatane indicated by W, sightings in the Hauraki Gulf indicated by A, all others are Mercury Bay):

AC 59 ‘Pumpkin’, seen on :
1.4.99 + 8.4.01 W

BC 91 ‘Black body-line’, seen on :
Jul ‘98 W + 14.10.00 + 10.4.01 W

BC 188 ‘Jagged Mum’, seen on :
13.11.99 + 22.3.01 W



BC 209 ‘Stumpy’, seen on :
Jul ‘98 W, 1.11.99, 24.3.01 W, 30.3.01 W

A 13, seen on :
9.3.99 + 20.1.01 A

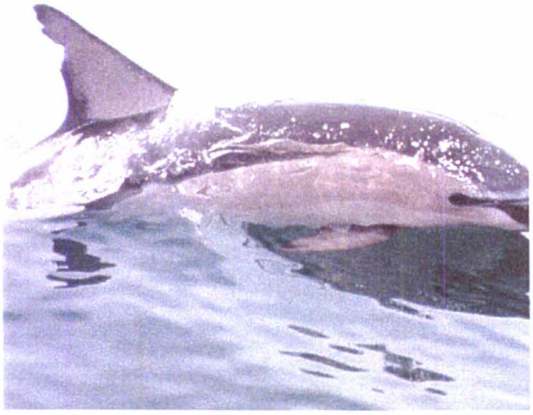
BC 345 ‘Paintbrush grey’, seen on :
7.3.00, 13.12.00, 19.3.01 A, 25.3.01 A

Appendix 3.4

Dolphin individuals that were seen only once, but are easily identifiable :


B 9, seen on :
10.10.1999

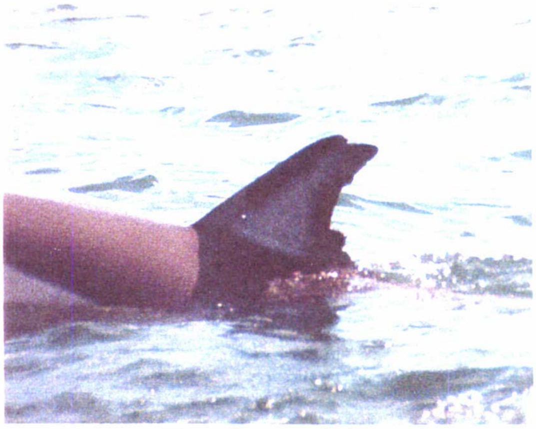

B 13, seen on :
1.11.1999


B 24, seen on :
5.11.1999


B 101, seen on :
8.2.2000

Appendix 3.5

Dolphin individuals that were seen only once, but are easily identifiable :



C 322, seen on :
16.10.2000

C 323, seen on :
16.10.2000

C 335, seen on :
24.11.2000

C 348, seen on :
8.12.2000