SOCIAL ORGANIZATION OF THE NEW ZEALAND DUSKY DOLPHIN

A Dissertation

by

TIMOTHY MICHAEL MARKOWITZ

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2004

Major Subject: Wildlife and Fisheries Sciences

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Approved as to style and content by:

Bernd Würsig (Chair of Committee)	Frances Gelwick (Member)
Ted Friend (Member)	Gil Rowe (Member)
R. Douglas Slack (Member)	Alejandro Acevedo-Gutiérrez (Member)
Robert Brown (Head of Department)	

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ABSTRACT

Social Organization of the New Zealand Dusky Dolphin. (May 2004)

Timothy Michael Markowitz,

B.A., University of California, Santa Cruz;

M.S., University of California, Davis

Chair of Advisory Committee: Dr. Bernd Würsig

Social organization of dolphins in extensive societies has not been well studied. Off Kaikoura, New Zealand, thousands of dusky dolphins (*Lagenorhynchus obscurus*) gather, feeding nocturnally on deep scattering layer prey, resting and socializing diurnally. During 1997-2003, interval sampling was used to monitor large assemblages numbering hundreds (n=169), smaller mating groups (mean±s.e.=7±1.6 adults, n=42), mother-calf nurseries (mean±s.e.=13±1.6 adults, 1±0.5 juveniles, 4±0.7 calves and 1±0.4 neonates, n=41), and non-mating adult groups (mean±s.e.= 9±1.3 adults, 1±0.2 juvenile, n=37). Group size, distance from shore (east), ranging along shore (north), traveling, inter-individual distance, and noisy leaping peaked in winter (n=39), with dolphins maintaining closer proximity to each other in smaller, more restful groups, closer to shore during the spring-summer-autumn (n=234) reproductive seasons. Dolphin groups were found closest to shore (west) during early morning, spread out and leaping often. Resting peaked at midday in tight groups. Late in the day, dolphins spread out, moving eastward (offshore) in preparation for feeding. Large groups exhibited coordinated travel, with noisy leaps as a directional signal. “Mating of the quickest” occurred in groups of (median) 6 males chasing 1 female. Leaping rarely occurred in restful nurseries, which at times associated with Hector’s dolphins (*Cephalorhynchus hectori*). Other mixed-species groups included common dolphins (*Delphinus delphis*), southern right whale dolphins (*Lissodelphis peronii*), long-finned pilot whales (*Globicephala malaena*), and bottlenose dolphins (*Tursiops truncatus*). Killer whales (*Orcinus orca*) elicited predator assessment and evasion. Whale riding occurred with larger whales. Residence was seasonal, with 1,969±814.9 from a population of 12,626 dolphins spending 103±38.0 days in Kaikoura (mean±s.e., mark-recapture mortality, single-season lagged-ID emigration models, n=153 weeks). Dolphins (n=39) summering in Kaikoura migrated to the Marlborough Sounds in winter, where small, coordinated groups foraged diurnally on schooling fishes in shallow bays, often associated with sea birds and New Zealand fur seals (*Arctocephalus forsteri*). Aquaculture may threaten dusky dolphin foraging habitat in Admiralty Bay, where an estimated 220 dolphins gathered to feed each winter. Photo-identification research, enhanced by digital techniques, demonstrated a structured fission-fusion society. Dusky dolphins associated with preferred long-term (>1,000 days) hunting companions in Admiralty Bay and non-random casual acquaintances (200 days) in Kaikoura (lagged-association models).

DEDICATION

To Ken Norris,

Living on Mountain Time feels like the sands singing inside me.
Nature is the authority, Honesty the policy.
What an amazing journey of Discovery you encouraged me to take!

To Tom Smith,

Your Bounty is as boundless as the sea you sail,
Your character as strong as the great whales you saved,
Good as Gold, Mate!

Each day, I reflect on your lives,
The causes you made,
The lessons you imparted,
The immeasurable kindness you showed,
And your unforgettable, inexhaustible, winning spirits.

ACKNOWLEDGMENTS

This work would not have been possible without the assistance of many people who kindly contributed financial support, time, and effort to the work. Thank you, Bernd “Kahuna” Würsig, for your wisdom, guidance, inspiration, kindness, unwavering support, and consistent encouragement from the very beginning through all the many adventures of the past eight years. Thank you to all of the Würsigs for sharing the woofs, buzzes, hospitality, and warmth of your home with me. For your tireless efforts, I thank my respected colleague, research partner, and companion through much of the work, A.D. Harlin.

Work in Kaikoura was accomplished with the help of many hard-working Earthwatch volunteers and full-time field assistants including C. Littnan, S. “Boogie” Stanley, K. “the Pit” Mazzarella, A. “Avo” Acevedo, L. “Gravy Spice” McOmber, C. “Ginty” Owens, N. “QOH” Brown, K. “Band Camp” Andrews, H. “Disco” Peterson, and A. “Pookie” Murray. I am grateful to Kaikoura residents and businesses for their help, including the staff of Dolphin Encounter especially D., L., and R. Buurman, I. “Brady” Bradshaw, J. Wadsworth III, and D. “Doonie” Dawg; Whale Watch Kaikoura; J. Van Berkel and the rest of the good folks at the University of Canterbury Edward Percival Field Station; J. Hocking at Better Boats; M. Green and S. Howie at Kaikoura Marine; R. Peterson at West End Motors; and S. “Tutu” Johnson.

Local Marlborough residents were also extremely helpful and made me feel very welcome. Most especially, I wish to thank D. and L. Boulton of French Pass Sea Safaris, L. and Z. Battersby of Dolphin Watch Marlborough, I. and P. Montgomery of

Okiwi Bay Lodge, and the teachers and students of the French Pass School for their assistance. Research in the Marlborough Sounds was accomplished with the help of many excellent field staff who kindly volunteered their time, including C.J. McFadden, T. Brock, M. Merriman, L. Boren, H. and J. Markowitz, R. Honeycutt, B. and M. Würsig, S. Cheeks, R. Constantine, B. White, and S. Carlyle.

Field research was funded by the Earthwatch Institute Center for Field Research; the National Geographic Society Committee for Research and Exploration; Interdisciplinary Research Initiative grants from the Research Enhancement Program, Office of the Vice President for Research and Associate Provost for Graduate Studies, Texas A&M University; the Marlborough District Council; and the New Zealand Department of Conservation. I am also grateful to the Department of Conservation, especially A. Baxter, for logistical support including use of a towing vehicle for launching at French Pass and a second research vessel for surveys of Pelorus Sound. I was supported during analysis and writing by the Tom Slick Fellowship, College of Agriculture, Texas A&M University, and by the Texas Institute of Oceanography Graduate Fellowship.

I am so grateful to my awesome, eclectic, cool committee who brought their diverse insights and expertise to bear in helping me plan, conduct, analyze, and write up this work. Thank you B. Würsig, F. Gelwick, R. D. Slack, G. Rowe, T. Friend, and A. Acevedo-Gutiérrez for your sage advice and consistent support. Your many efforts and diligent work on my behalf are very much appreciated.

I also thank the many other faculty, staff, and colleagues at Texas A&M University who contributed helpful ideas and encouragement. Analysis was accomplished with the volunteer help of Marine Mammal Research Program interns and students from the departments of Marine Biology and Wildlife and Fisheries Sciences, Texas A&M University. Thanks also to my lab mates for your comradeship. G. Gailey and G. Hillman provided technical support with computer analysis. S. Gowans provided invaluable assistance and advice in selecting and calculating mark-recapture population estimates. J. Crenshaw helped me navigate the treacherous passages through the university bureaucracy. Thank you, K. “Homey” Plyer and “Max”, for putting up with all those long nights of typing and mental instability during the final stages of my write up.

Thank you, Wendy Jane Schrader, for the light you bring into my life.

Last, but really you were first, thank you to my wonderful family for always encouraging me to boldly go out there and do it! Thanks, Mom, for your spirit. Thanks, Jen, for your nature. Thanks, Dad, for introducing me to the amazing world of critters. Thank you for the music of your laughter, thank you for your strength, thank you for your love.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

FIGURE Page

FIGURE Page

FIGURE Page

CHAPTER I

INTRODUCTION

Dolphin Social Organization

There is a growing body of evidence supporting the notion that dolphins, unlike animals found in undifferentiated schools, herds, or flocks, maintain complex social networks with clearly established relationships between individuals (Norris 1994). Much remains to be learned about dolphin societies, many of which appear to be comprised of complex networks of relationships at the individual, subgroup, and group levels (Connor 2000). The dusky dolphin (*Lagenorhynchus obscurus*) is a species known for its particularly high degree of sociality and acrobatic aerial displays (Baker 1983). The flexibility of dusky dolphin grouping and activity in different ecological settings (Würsig *et al.* 1989, Würsig 1991) distinguishes this species as especially appropriate for examination of social organization in a mesopelagic dolphin species.

Like other social mammals, dolphins have relatively large, complex brains (Ridgway 1986), and demonstrate phenomenal learning capabilities (Herman 1980). Brain size within the family Delphinidae is particularly large relative to other mammals. For example, the encephalization quotients of *Tursiops* and *Lagenorhynchus* lie just below humans and roughly double those of gorillas, chimpanzees and orangutans (Jerison 1986). Highly convoluted, the dolphin brain has nearly twice the surface area of the human brain, but since the cortex is about half as thick, the total volume of the dolphin cerebral cortex is just over 80 percent that of the human brain (Ridgway 1986).

This dissertation follows the style and format of Marine Mammal Science.

While these and other differences, such as the development of brain centers related to sensory perception, suggest divergence in brain function between dolphins and humans, it would appear that there has been a general convergence toward cerebral hypertrophy in these two distantly related taxa (Jerison 1986). Strong evolutionary pressures favoring the development of unusually large brains relative to body size could include the importance of social knowledge and skills in survival and reproduction (Connor *et al.* 1992, Shane 1991).

Social organization is defined as the way in which members of a species interact with each other (Manning and Dawkins 1992). It describes the, "content, quality, and patterning of relationships" (Hinde 1976).

Social organization varies widely across cetaceans (Wells *et al.* 1999). Until recently, the most detailed studies of dolphin social organization have been conducted with just two genera, the bottlenose dolphin (*Tursiops* spp., reviewed by Shane *et al.* 1986, Wells 1991, Connor *et al.* 2000) and the killer whale (*Orcinus orca*, Fellerman *et al.* 1991, Baird 2000). This research, facilitated by knowledge of the two genera from captive studies, their relative accessibility to scientists, and their occurrence in relatively small, stable groups (Samuels and Tyack 2000), demonstrates complex social systems in species showing limited gregariousness. Similar to primates, bottlenose dolphins exhibit remarkable foraging flexibility (Wells *et al.* 1999), well-defined social age-ordered dominance hierarchies (Samuels and Gifford 1997, Shane *et al.* 1986), and cooperative coalitions and alliances for intraspecific competition (Connor *et al.* 1992). Killer whales live in matrilineal societies, with marked differences between different feeding cultures and dialects suggesting social transmission of vocal repertoires (Baird 2000).

Research on social organization of dolphins living in more extensive societies than these has been stalled by the technical and logistical difficulties of consistently identifying individuals and monitoring behavior in large groups. Although the level of detail achieved in studies of dolphins living in small groups may never be accomplished in such extensive societies, these obstacles can be overcome with the use of focal behavioral sampling (Mann 1999*a*, 2000) and modern digital techniques (Hillman *et al.* 2003, Markowitz *et al.* 2003*ab*, see Chapter VI).

New Zealand Dusky Dolphin Behavioral Ecology

A good candidate species for examining social organization in a more extensive dolphin society is the dusky dolphin. Like killer whales and bottlenose dolphins, dusky dolphins are found discontinuously distributed over a wide range, prefer coastal waters less than 2,000 m deep (Würsig *et al.* 1997) making them easily accessible to researchers, have large brains for their body size relative to other cetaceans and other mammals in general (Jerison 1986), and exhibit alternate foraging strategies in different environments with some evidence for cooperative hunting tactics (Würsig 1989, Würsig 1991). Unlike killer whales and bottlenose dolphins, dusky dolphins gather in groups of anywhere from two to over one-thousand (Würsig *et al.* 1997).

Worldwide, dusky dolphins are distributed in temperate waters of South America (Argentina, Chile and Peru), South Africa (and Namibia), and New Zealand, with their range centering at about 42º S. They are a coastal/mesopelagic species, most often occurring in water less than 2,000m deep (Würsig *et al.* 1997). In New Zealand, dusky dolphin distribution ranges from the coastal waters about the South Island to the lower North Island and east to the Chatham Islands, shifting south in summer and north in winter (Gaskin 1968).

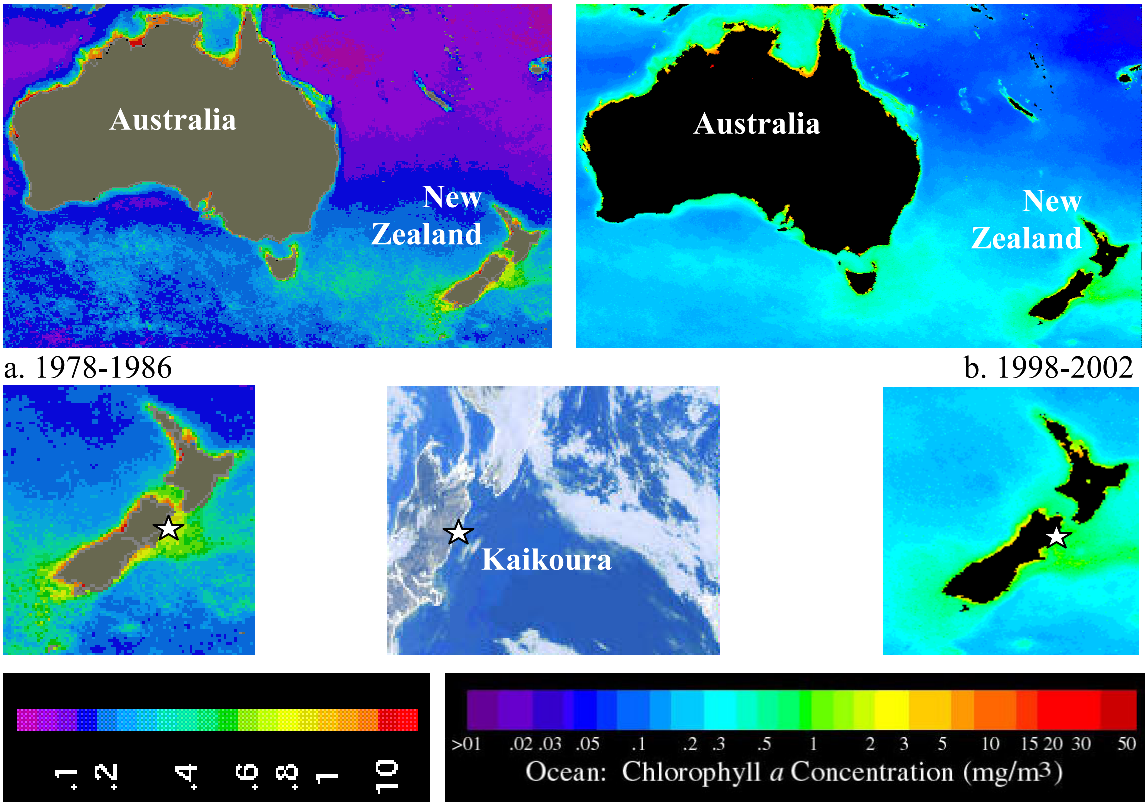
At present, there is a great deal of confusion regarding the taxonomy of the dusky dolphin. Recent genetic evidence (Würsig *et al.* 1997) suggests the genus *Lagenorhynchus* may be a collection of loosely related species thrown together due to similar morphological traits (Webber 1987). Further, the level of divergence of dusky dolphin populations in South America and New Zealand is currently under investigation (Harlin *et al.* 2003).

Sexual maturity is reached at the early age of 7-8 years in dusky dolphins, perhaps due to their relatively small adult size, centering at 1.7-1.8m in length (Würsig *et al.* 1997). The large active testes of male dusky dolphins, often greater than 1kg in weight, during the summer breeding season suggest sperm competition indicative of a promiscuous mating system (Cipriano 1992). Gestation length has been estimated to be approximately 11.4 months (Cipriano 1992), and lactation lasts about 18 months (Leatherwood and Reeves 1983). Thus, weaning appears to occur earlier than the 3 years of age at which it has been observed in bottlenose dolphins (Wells *et al.* 1987). As in Argentina (Würsig and Würsig 1980), calving in New Zealand occurs during the early summer, from November to mid-January (Cipriano 1992). In general, New Zealand dusky dolphins are somewhat smaller than those living off the coasts of South Africa and South America (Table 1). Calves (<1 year old) are generally 1.2m in length or less; juveniles (1-2 years old) are generally between 1.3-1.5m in length (Cipriano 1992). Dusky dolphins are also unusually long-lived for a small dolphin species, living to estimated ages of 30 years or more (Cipriano 1992).

Table 1: Summary of estimated New Zealand dusky dolphin life history parameters (estimates from Leatherwood and Reeves 1983, Cipriano 1992, Würsig *et al.* 1997)

Parameter	**Estimate**
Gestation length	11.4 months
Lactation duration	18 months
Calving season	early summer (mid-Nov to mid-Jan)
Age at first reproduction	7-8 years old
Size at birth	0.97-1.02 m long
Size of infants (< 1 year old)	< 1.2 m long
Size of juveniles (1 to 2 years old)	1.3 to 1.5 m long
Size of subadults (3 to 8 years old)	1.55 to 1.6 m long
Size of adults (8 to 30+ years old)	1.65 to 1.86+ m long
Maximum Age	≥ 35-36 years

Just offshore and south of Kaikoura, New Zealand, is a major gathering place for dusky dolphins, where large groups of several hundred to over one thousand occur almost every day of the year (Würsig *et al.* 1997). These aggregations appear to coincide with Kaikoura's unique oceanographic features providing spatially and temporally predictable resources. Kaikoura is located at roughly the same latitude as the subtropical convergence, a mixing of Antarctic and tropical waters which shows higher year round primary productivity than either waters to the north or south (Boyd *et al.* 1999). In addition, the Kaikoura Canyon, adjacent to the Hikurangi Trench, brings deep, productive waters within 500 meters of the Kaikoura coastline, increasing nutrient availability near shore and resulting in a concentration of plankton, fish, squid, and marine mammals at this location (Lewis 1998). Consequently, the waters off Kaikoura have relatively high chlorophyll *a* concentrations compared to the rest of the region, as can be seen from space in satellite images (Figure 1).


a. 1978-1986

b. 1998-2002

Figure 1. Chlorophyll *a* (phytoplankton pigment) concentrations (mg*m^{-3}) based upon composite data from satellite images taken from a. 1978-1986 (Nimbus) and b. 1998-2002 (Seawifs) are shown for New Zealand and Australia. Note the color scale bars used differ between a and b. Close-up views below focus on the waters about New Zealand with the approximate location of Kaikoura on the east coast of the South Island indicated by a white star (satellite composite images from http://seawifs.gsfc.nasa.gov).

Whereas sperm whales (*Physeter macrocephalus*) that gather near Kaikoura forage throughout the day by diving hundreds of meters into the Kaikoura Canyon (Whitehead and Weilgart 2000), dusky dolphins generally wait to feed until their prey become more accessible in the evening. Dusky dolphins off Kaikoura feed largely on mesopelagic fishes and squid (Cipriano 1992) that rise with the deep scattering layer at night, leaving daylight hours for rest and social interaction (Würsig *et al.* 1997).

By comparison to Kaikoura, dusky dolphins are less reliably found in other near-shore areas about New Zealand. In the course of this study, many long days spent surveying other areas (off the southeast, west, and north coasts of the South Island) yielded relatively few dusky dolphin sightings, with one notable exception; Admiralty Bay in the Marlborough Sounds provides regular winter foraging habitat for 200-300 dusky dolphins (Markowitz *et al.* 2004). Consequently, this location, a shallow bay habitat, is the other main study site besides Kaikoura where research was conducted in this study.

Research Objectives

Spinner dolphins (*Stenella longirostris*) off the main Hawaiian islands, which feed nocturnally on deep scattering layer prey in a manner similar to dusky dolphins, exhibit considerable fluidity in subgroup structure (Würsig *et al.* 1994). Preliminary data suggest that dusky dolphins' membership in subgroups may be somewhat more stable (Cipriano 1992), with greater dyadic fidelity between social partners (Würsig 1982, 1986). However, the social relationships of New Zealand dusky dolphins have yet to be examined in any detail. This study represents the first dedicated attempt to investigate the social organization of this population, and one of the first studies of its kind with wide-ranging dolphins known to gather in both small and large groups.

Examining the social organization of a species requires investigation of the content and quality of relationships (quantifying behavioral interactions) as well as their patterning (which individuals are interacting) in space and time (Hinde 1976). In studies of cetaceans, it has become common to run the "gambit of the group" assuming that individuals within a group are interacting (Whitehead and Dufault 1999). This has led to a tendency among cetacean biologists to focus on group structure (examining who is together, where, and when), with little to no quantitative data on the behavior of individuals in those groups (Mann 1999*a*, 2000).

The goal of this research is to examine dusky dolphin social organization in a manner which focuses more completely on the content and quality (Connor 2000) as well as the patterning (Whitehead 1995, 1997) of social relationships. Unfortunately, it is impractical if not impossible to measure directly dyadic interactions between fast swimming individual dusky dolphins in groups ranging from a few to hundreds of members. Therefore, the research presented in this dissertation relies largely on focal group samples of behavior (Martin and Bateson 1993, Lehner 1996, Mann 1999*a*) for information on the content and quality of relationships (Chapters II-V), and photo-identification of distinctively marked individuals (Würsig and Jefferson 1990) for information on the patterning of relationships (Chapters VI-VII). Specifically, the objectives of this research were to:

1. compare behavior in groups by season and time of day; group size and composition; and habitat (Kaikoura versus Admiralty Bay);
2. record group and individual movements within and between days; across seasons; and over years;
3. examine abundance, residency, and association patterns of New Zealand dusky dolphins.

Overview of Chapters

The chapters of this dissertation fit into the framework of New Zealand dusky dolphin social organization as follows:

Chapter II investigates temporal variation in dusky dolphin social activities off Kaikoura by season and time of day. Although research on movement patterns and location of dusky dolphins has been conducted from shore-based stations in Kaikoura in the past (summarized by Würsig *et al.* 1997), this chapter reports the most systematically collected behavioral information to date from boat-based focal group follows.

Chapter III further details the content and quality of dusky dolphin relationships off Kaikoura, comparing the behavior of dolphins in large groups to smaller groups engaged in mating, caring for calves, and other activities. This chapter appraises social roles and strategies of dusky dolphins relative to group cohesion, breeding success, and parental care.

Chapter IV documents how dolphin behavior changes following winter migration from the deep-water habitat off Kaikoura to the shallow bays of the Marlborough

Sounds. In the process of examining dolphin groups foraging in the Marlborough Sounds, this chapter also inspects the current and potential overlap between dolphin habitat and an expanding aquaculture industry (Markowitz *et al.* 2004).

Chapter V documents interactions between dusky dolphins and other species of marine mammals throughout New Zealand. Such heterospecific interactions generally occur within a social context, representing a regular, and possibly important, component of dusky dolphin social lives. Responses of dusky dolphin groups to a predator, the killer whale, are also described.

Chapter VI highlights the advances in digital photographic technology allowing more efficient photo-identification of individual dolphins (Markowitz *et al.* 2003*ab*). Particularly advantageous for identifying individuals within large groups such as dusky dolphins, digital photography holds promise for advances in photo-identification research with many other species as well.

Chapter VII examines the residency, abundance, migration, and social group structure of New Zealand dusky dolphins for the first time using photo-identification techniques. In the course of conducting this research, > 40,000 photographs were taken and > 3,500 individual dolphins were catalogued over a 7-year period. Much analysis remains to be completed, as this represents one of the largest, and most cumbersome, efforts of its kind ever undertaken. However, it is already yielding new insights into the patterning of dusky dolphin social relationships.

CHAPTER II

LIVES SHIFTING IN RHYTHM: DUSKY DOLPHIN SEASONAL AND DIURNAL BEHAVIOR OFF KAIKOURA

Sunshine, storm, cold, heat, forever withstanding, passing, carrying…
The fluid vacuum around and ahead still entering and dividing…
Whoever you are! Motion and reflection are especially for you…
Whoever you are! You are he or she for whom the earth is solid and liquid,
You are he or she for whom the sun and moon hang in the sky,
For none more than you are the present and the past...

Figure 2. A dusky dolphin (*Lagenorhynchus obscurus*) leaping offshore of Kaikoura.

The law of the past cannot be eluded,
The law of the present cannot be eluded,
The law of the living cannot be eluded…
How beautiful and perfect are the animals!
How perfect the earth, and the minutest thing upon it!
What is called good is perfect, and what is called bad is just as perfect,
The vegetables and minerals are all perfect, and the imponderable fluids perfect;
Slowly and surely they have pass'd on to this,
and slowly and surely they yet pass on.

\- Walt Whitman, Leaves of Grass

Introduction

Life is dynamic. At sea, especially near the surface, the temporally shifting nature of life is particularly apparent. Although creatures living in such a moving medium must constantly adjust to an ever-changing environment, it is not totally unpredictable. On the contrary, near-surface life at sea is constantly pulsing with the predictable patterns of seasonal and diel variation (Lalli and Parsons 1995). Tides, light, and weather patterns provide a regular tempo to which plants and creatures respond (Davis 1987). Marine organisms, such as the dusky dolphin (*Lagenorhynchus obscurus*, Figure 2), react to these temporal patterns in the environment and to one another within an ecological framework, creating a symphony of diverse lives in rhythm with the sea.

Dusky dolphin behavior follows the predictable seasonal and daily pulses of the sea. Dusky dolphins living in different habitats alter their behavior and group structure in such a way as to most efficiently utilize available resources (Würsig *et al.* 1989, Markowitz *et al.* 2004, see also Chapter IV). It is not surprising, therefore, that they also adjust their behavior to fit seasonal and diurnal fluctuations in particular habitats (Würsig *et al.* 1991). The goal of this chapter is to examine seasonal and diurnal variation of dusky dolphin social behavior in one such habitat, off the east coast of New Zealand's South Island. Near Kaikoura, dusky dolphins can be found reliably most days throughout the year, making it an ideal site for studying both seasonal and diurnal patterns (Cipriano, 1992).

The geophysical periods of day and night (circadian), the tides (circatidal), phases of the moon (circalunar), and the seasons (circannual) provide the ecological and evolutionary basis for biological rhythms (Palmer 1976). Rhythmic behavior is often regulated by biological clocks evolved to fit environmental cycles (Enright 1970). Biological rhythms generally occur as an interaction of exogenous factors--environmental “zeitgebers” (“time givers”)-- and endogenous (“free-running”) timing mechanisms, regulated in mammals by neuroendocrine pathways involving the retina, the suprachiasmatic nuclei of the anterior hypothalamus, and the pineal gland (Nelson 1995). This chapter will investigate the ways in which the social activities of dusky dolphins are organized with respect to seasonal and daily cycles, testing the hypotheses that seasonal variation in behavior is linked to the timing of reproduction and that diurnal variation is tied to nocturnal feeding.

Seasonal Patterns: Dusky Dolphins Moving with the Turning of the Seasons

All marine mammals exhibit seasonal breeding patterns, which in turn can influence feeding (including fasting) and movement (including long range migration) patterns (reviewed by Boyd *et al.* 1999). For species that breed seasonally, endocrine profiles tied to photoperiod influence sexual and parenting behavior (Ketterson and Nolan 1994), which can be important for raising young in environmental conditions favorable for development. Some animals have annual biological clocks, which can run freely without exogenous input but can be entrained, or calibrated, by appropriate environmental stimuli related to the seasons (Pengelley and Asmundson 1971).

While dusky dolphins occur near Kaikoura year-round, their distribution throughout New Zealand generally shifts with changing water temperatures, north in winter and south in summer (Gaskin 1968). Results of dusky dolphin photo-identification research (Markowitz *et al.* 2004) indicate seasonal residency of individuals off Kaikoura and regular seasonal migrations of individuals north to winter foraging habitat in the Marlborough Sounds (see Chapters IV and VII). Sea surface water temperatures in Kaikoura during this study ranged from 8-11°C in winter to 12-18°C in summer (Figure 3). Daylight hours range from roughly 9:00-17:00 local time in winter to 4:00-22:00 in summer. Salinity (mean ± se = 35.9 ± 0.11 ppt, n = 289) did not vary between seasons.

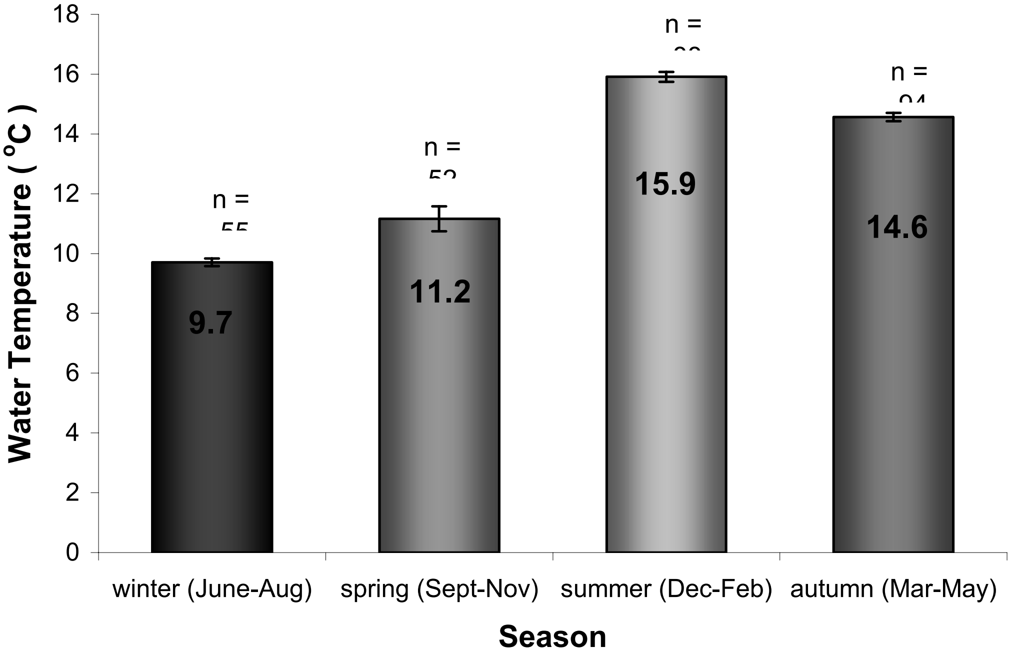


Figure 3. Sea surface water temperatures measured at each dolphin group encouter in Kaikoura are compared by season. Mean values are shown with one standard error of the mean (n values represent the number of measurements taken during independent samples from group encounters on different days).

Satellite data on chlorophyll *a* concentrations indicate that although Kaikoura is a particularly productive region throughout the year, it is most dramatically so in spring and less so during the winter non-breeding, when chlorophyll *a* concentrations increase to the north (Figure 4).

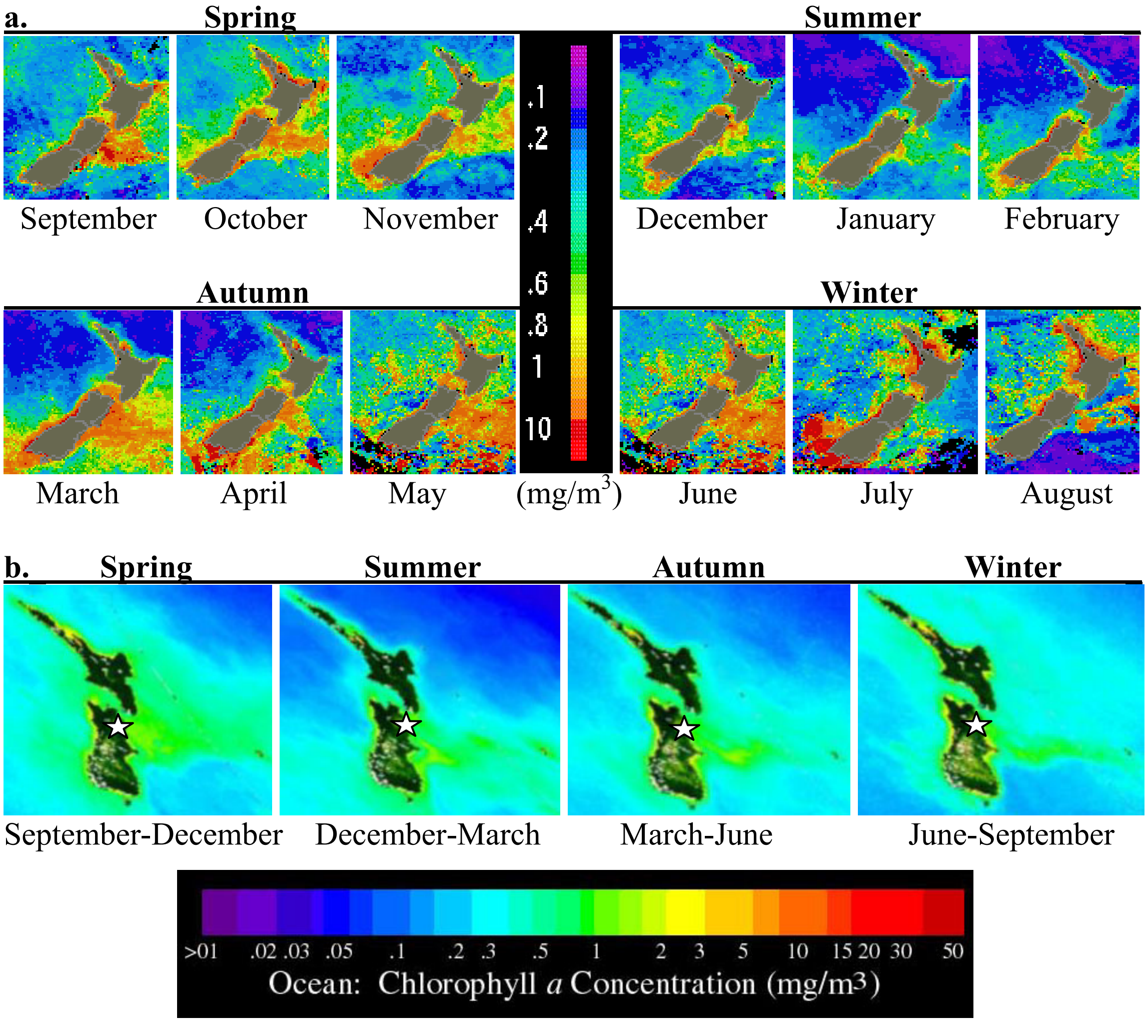


Figure 4. Data from satellite images show chlorophyll *a* (phytoplankton pigment) concentrations ($mg*m^{-3}$) in New Zealand waters by season. Composites of satellite data are presented: a. by month from 1978-1986 (Nimbus), and b. by season from 1997-2002 (Seawifs) for comparison. Note the color scale bars used differ between a and b (satellite composite images from http://seawifs.gsfc.nasa.gov). For reference, the approximate location of Kaikoura is indicated by a star on the second set of larger images (b).

Although dolphins do not undergo the long-distance migrations between feeding and calving grounds exhibited by baleen whales (Wells *et al.* 1999), all dolphins studied to date show seasonal mating and calving, with gestation lengths generally ranging from 10-16 months (Perrin and Reilly 1984). Post mortem examinations of net-caught dusky dolphins in Kaikoura show seasonal peaks in adult male testis size and newborn calves (Cipriano 1992), indicating seasonal reproduction (see Chapter I, Table 1), timed such that calves are born into the warmest part of the year in spring and summer (Würsig *et al.* 1997). I hypothesize that seasonal variation in dusky dolphins' social behavior off the coast of Kaikoura will be linked to their annual reproductive cycle. The following predictions are derived from this general premise and its correlaries regarding mating, parental investment, and calf development.

Predictions Regarding Seasonal Variation in Behavior

Shore-based research conducted from the cliffs south of Kaikoura (e.g. Cipriano 1992) indicating larger dusky dolphin group sizes in winter than in summer suggest differences in prey availability and/or predation risk between seasons (Würsig 1989). Although dolphins typically engage in sexual behavior for social as well as reproductive reasons (Wells *et al.* 1999), seasonal estrus means that the frequency of sexual behaviors related to reproduction should follow a regular seasonal pattern. Based on the findings from previous shore-based and post-mortem research (Cipriano 1992), I predict that with respect to group size and reproductive status:

- Group size peaks in winter.
- Sexual activity peaks seasonally in summer.

- Observation of neonatal calves is limited to spring and summer.

Developing calves and their mothers are not likely to swim as efficiently nor as rapidly as adult dolphins. In addition to the physical and energetic limitations on calves swimming, mothers with calves incur energetic costs due to lactation and increased drag through assisted locomotion of calves (Waite 1988, Johnson and Norris 1994). Radio and theodolite tracking data indicate that dusky dolphins range further along the coast in the winter (Würsig *et al.* 1991). Thus, dolphin groups should rest more and travel less over a shorter range during the calving season, spring and summer. Bowriding may represent boisterous play behavior and/or a mode of efficient transport when dolphins are traversing large distances, and is therefore most likely when dolphins range further in winter, and least likely when mothers with young calves are present in spring-summer. Therefore, I predict that with respect to ranging and movement:

- Dolphin groups range less along shore during the calving season.
- Dolphins travel less and rest more during the calving season.

Dusky dolphins seek protection from predators by grouping more tightly and swimming close to shore (Würsig *et al.* 1997). As calves are likely to be most vulnerable to predation by killer whales and deep-water sharks, I predict that with respect to protection from predators:

- Dolphin groups are found closer to shore during the calving season.
- Groups maintain closer inter-individual proximity during the calving and breeding season.

Leaping is a high-energy activity. Different types of leaps may have different functions. In Argentina, dusky dolphins may use noisy leaps near surface fish schools to frighten and corral the fish, and possibly as a signal to recruit other dolphins to coordinated feeding. Clean headfirst re-entry leaps are utilized most during feeding to facilitate rapid return to fish herding below the surface. Acrobatic flips are frequently seen as a post-feeding and possibly social-bonding "celebration" (Würsig 1984). In Kaikoura, dolphins feed at night, yet leaping is frequently seen during the daytime. How do these leaps function in non-feeding contexts? If noisy leaps act as a long-range signal to other dolphins, then one might expect it to be used in a non-feeding context to convey something over a large distance. Such "shouts" would be less expected if they might disturb group members. In a non-feeding context, clean leaps could facilitate locomotion relative to social-sexual encounters. Boisterous, showy acrobatic "celebrations" should be least common around very young calves. Therefore, I predict that with respect to leaping activity:

- Noisy leaping occurs least when calves are newborn (spring-summer).
- Noisy leaps are used most when groups are larger and spread further (winter).
- Clean leaping is more common during the breeding season (summer).
- Acrobatic flips occur least when calves are younger (spring-summer).

In summary, predictions regarding seasonal variation in dusky dolphin group size and reproductive status, ranging and movement, protection from predators and leaping activity are based on previous findings and on what is known about the seasonal breeding and calving cycle of dusky dolphins (Cipriano 1992). Table 2 reviews these predictions, with the expected ranking of each parameter by season.

Table 2: Expected ranking of parameters by season
(greater sizes, numbers, distances, and frequencies denoted by larger numbers)

Behavioral category	**Winter**	**Spring**	**Summer**	**Autumn**
group size	4	2	1	3
calves	1	4	3	2
mating	1	2	4	3
ranging	4	1	2	3
distance from shore	4	2	1	3
behavioral state	travel	rest	rest/mill	mill/travel
inter-individual distance	4	1	2	3
noisy leaps	4	1	2	3
clean headfirst re-entry	1	2	4	3

Diurnal Patterns: A Day in the Life of a Dusky Dolphin

At sea, one of the most prominent diel cycles is the vertical movement of deep scattering layer (DSL) organisms. The DSL, a sound-reflecting layer of plankton and associated biota, was noted in the early 20th century during sonar scans for its appearance as a false ocean floor (Lalli and Parsons1993). Vertical migration of plankton follows a regular circadian rhythm, likely evolved as a defense against visual predators, as plankton rise in the water column at night and descend during the day (Longhurst 1976). This cycle, in turn, influences the daily feeding and movement pattern of predators at higher trophic levels. For example, dive profiles for shallow-diving Northern fur seals and Antarctic fur seals show a diel pattern, tracking the vertical migration of their prey (Wells *et al.* 1999). Hawaiian spinner dolphins also fit their feeding to DSL migrations (Benoit-Bird and Au 2003), moving offshore at the end of each day to feed at night when their DSL-associated prey is closest to the surface (Würsig *et al.* 1994).

A day in the life of a dusky dolphin occurs in rhythm with these predictable diel patterns. Dusky dolphins in Kaikoura feed at night on prey that rises each evening with the DSL (Würsig *et al.* 1997). Mesopelagic predators, such as lanternfishes and squid follow the DSL as a predictable source of food. These fishes and squid in turn become prey for dusky dolphins. Stomach content analyses of stranded and net-caught dusky dolphins in Kaikoura (Cipriano 1992) revealed that their diet consists mainly of lanternfishes (family *Myctophidae*), and also includes hoki (*Macruronus novaezelandie*), red cod (*Physiculus bacchus*), hake (*Merluccius australis*), and 2 genera of squid from the Cranchidae family (*Nototodarus* sp. and *Todaroides* sp.). Radio-tracking and theodolite studies indicate that dusky dolphins move offshore in the evening to feed on these prey items (Würsig *et al.* 1991).

I hypothesize that diurnal variation in dusky dolphins' social behavior off the coast of Kaikoura will be tied to their diel schedule of nocturnal feeding. The following predictions are derived from this general premise and its correlaries regarding rest, coordinated activity, and social interaction.

Predictions Regarding Diurnal Variation in Behavior

Although dolphins exhibit hemispheric sleep, they rest on a regular diel cycle (reviewed by Wells *et al.* 1999). Since dusky dolphins in Kaikoura feed during the middle of the night (Würsig *et al.* 1997), they most likely return from feeding still active in the early morning, rest during the middle of the day, and become more active in preparation for feeding late in the day, as has been found with Hawaiian spinner dolphins (*Stenella longirostris longirostris*, Norris and Dohl 1980). Theodolite tracking research indicates dusky dolphins rest more in the middle of the day (Barr and Slooten 1998), and move offshore late in the day (Cipriano 1992). Bow-riding behavior is more likely during active periods than during periods of rest. As dolphins move offshore in the evening, spreading out in a parallel formation would allow them to search a larger area of water per unit time for prey and/or potential predators (Norris and Dohl 1980).

Therefore, I predict that with respect to movement patterns:

- Dusky dolphins in Kaikoura rest most in the middle of the day, and are more active (travel and/or mill) early and late in the day, following and preceding nocturnal feeding.
- Dolphins move offshore late in the day in preparation for night foraging.
- Dolphins engage in bow-riding more often during active periods early and late in the day, than during less active periods near midday.
- Dolphins spread out in parallel formation (reduced competition and enhanced search pattern) as they move to forage late in the day.

During daytime resting periods, dusky dolphins should seek to minimize risk of predation. Dusky dolphins seek refuge from predators during resting periods near shore (Würsig and Würsig 1980, Würsig *et al.* 1991). Tighter grouping in a circular formation represents the most likely defensive posture (Hamilton 1971).

Therefore, I predict that with respect to predators:

- Dolphin groups are found closer to shore after night feeding for protection from predators, particularly at midday.
- Groups maintain closer inter-individual proximity during rest periods (especially midday).
- Groups are most likely to assume a defensive roughly circular-shaped formation during rest periods (midday).

Resting dolphins generally swim slowly with minimal aerial activity (Wells *et al.* 1999). While some group “scouts” or “sentinels” may engage in leaping during rest periods, the frequency of leaping should be lowest when dolphins are resting and highest during more active periods. Leaps that facilitate rapid movement from the surface into the water column (headfirst re-entry leaps) should represent a higher proportion of leaps when dolphins are most active.

Therefore, I predict that with respect to leaping activity:

- Leaping occurs most frequently during active periods (early, late) and least frequently during resting periods (midday).
- Clean headfirst re-entries represent a higher proportion of leaps during socially active periods (early, late) than during resting periods (midday).

In summary, predictions regarding diurnal variation in ranging and movement, protection from predators, and leaping activity were based on previous findings and on what is known about the diel feeding-resting cycle of dusky dolphins (Würsig *et al.*1997). Table 3 recaps these predictions, with the expected ranking of each parameter by time of day.

Table 3: Expected ranking of parameters by time of day
(greater sizes, numbers, distances, and frequencies denoted by larger numbers)

Behavioral category	**early**	**morning**	**midday**	**afternoon**	**late**
travel/mill	3	2	1	2	3
rest	1	2	3	2	1
distance from shore	3	2	1	2	3
bow-riding	3	2	1	2	3
inter-individual distance	3	2	1	2	3
formation	-	-	circular	-	parallel
leaping frequency	3	2	1	2	3
main leap type	re-entry	-	noisy	-	re-entry

Methods

Data Collection

Research Effort

From 1997 to 2003, over 1,500 hours of research, conducted on 223 days in the Kaikoura region from small 4.2-5.5m vessels with 25 to 85 hp outboard motors, resulted in 568 dusky dolphin group encounters. This data set was supplemented with additional information on the location of dolphin groups by season and time of day collected from larger dolphin tour vessels on 357 tours in 1994-1996.

Dolphin groups were located with the help of a shore-based "look-out" team, as well as dolphin tour operators. Shore-based teams were generally posted at two locations, Ota Matu and the Kaikoura Peninsula lookout (Figure 5), as described by Cipriano (1992), Würsig *et al.* (1991, 1997), and Brown (1999). Once a group was located, the vessel approached slowly, assuming a position at no-wake speed alongside the group. Encounter- and leave-times were recorded for all dolphin groups. During group observations, the vessel was driven parallel and at a matched speed to the dolphins (Würsig and Jefferson 1990) to minimize disturbance while maintaining a clear view of dolphin behavior.

Defining and Describing Groups

When conducting focal group observations, it is important to explicitly define the rules for inclusion of individuals in the group (Martin and Bateson 1993). In this study, dolphin groups were defined by spatial proximity according to the "10-m chain rule"

(Smolker *et al*. 1992). Under this definition, dolphins were considered part of a group so long as they were within 10m of a nearest neighbor. This "distance measures" definition of group was chosen over a "coordinated activity" definition for its simplicity and because it does not rely on any explicit or implicit assumptions about the behavior of a group's members (Mann 1999*a*). Such an approach is particularly valuable in studies of social organization, where the diversity of behaviors exhibited within a spatially and temporally associated group are of interest (Mann 2000).

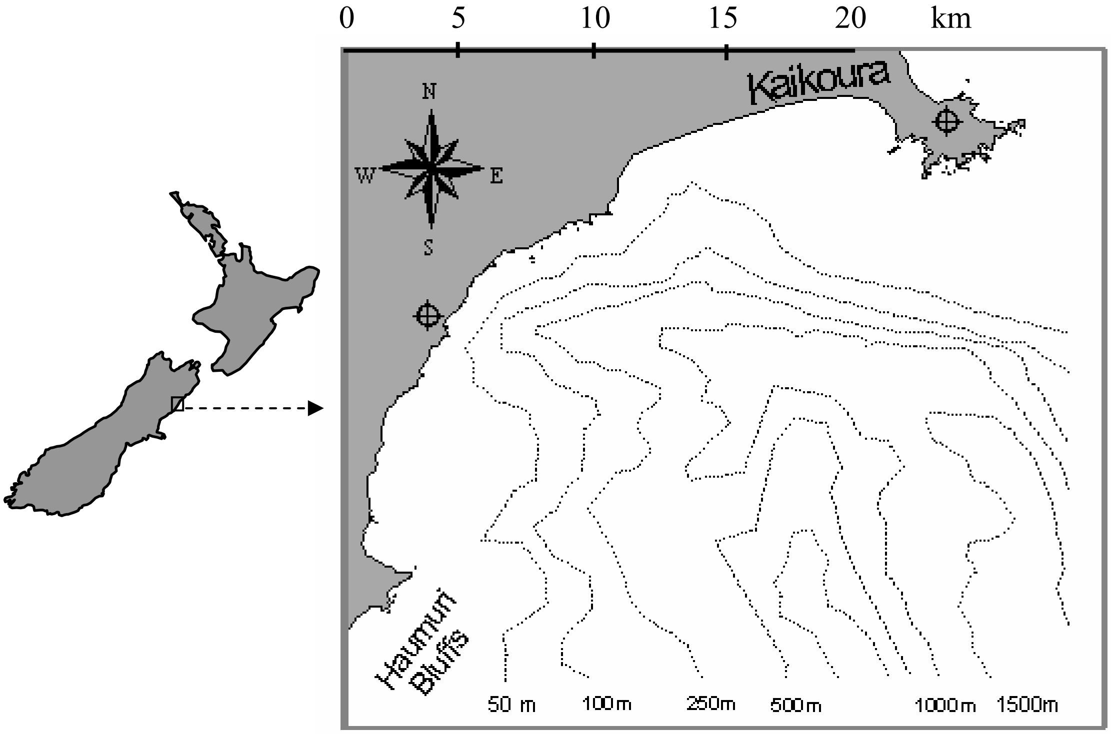


Figure 5. The study site in the Kaikoura region of New Zealand's South Island is shown with a sketch of isobaths (depths in m). Locations of shore stations from which dolphin groups were spotted are shown by "⊕" marks (scale bar in km is shown at the top).

Group location and tracks of group movements were estimated using longitude, latitude and time data recorded by a Garmin 12X global positioning system (GPS) from the vessel as it was positioned alongside the group. Time and location data were recorded at two-minute intervals and later downloaded to computers for analysis.

Experienced observers made estimates of group size based on consensus. Group size for large groups was classified as belonging to one of five categories (50-99, 100-249, 250-499, 500-1000, or >1,000). Group size for smaller groups was estimated by noting the maximum number of individuals observed at or near the surface at one time, as well as by noting distinctively marked individuals missed during counts when surfacing was asynchronous (see Chapter VI). The presence or absence of juvenile, calf, and neonatal age classes were noted for large groups, and a count of these younger animals made for smaller groups. Juveniles were defined as noticeably smaller than adults swimming independently. Calves were smaller dolphins swimming in consistent close proximity to an adult. Neonatal (newborn) calves were recognized by their fetal folds.

Focal Group Behavioral Sampling

Focal group behavioral samples were conducted during 40-minute recording sessions (n = 289), with each session divided into twenty 2-minute sample intervals. Each 40-minute sample came from an independent group encounter for a given day. Behavioral observations were quantified with instantaneous and all-occurrences recording (Martin and Bateson 1993). At the start of each session, a note taker recorded the date, time, and group number, and started a stopwatch, set to 2-minute intervals. Subsequently, the remaining crew, comprised of 1-2 experienced observers and 1-3 trained volunteers, called out dolphin behaviors, which were recorded by the note taker on a data sheet. All observers were trained using video records of dolphin behavior, scoring >95% inter-observer reliability prior to data collection.

Instantaneous sampling was used to document behavioral state, inter-individual proximity, group swimming formation, group speed, group heading, and the number of bow-riding dolphins. At a signal from the stopwatch, a single assessment was made for each of the above measures every two minutes. Except for the number of bow-riding dolphins counted by trained volunteers, experienced researchers made all instantaneous assessments.

Following Shane (1990), behavioral state was defined as travel, mill, rest, and feed (Table 4). Because groups were defined by spatial proximity, not by behavior, it was possible for group members to be in more than one behavioral state per sample. Therefore, all observed behavioral states were noted for each interval.

Table 4: Dusky dolphin behavioral states examined

Behavioral State	Definition
Travel	Steady, directed movement at moderate to rapid speed.
Mill	Variable or interweaving movement.
Rest	Very slow, rhythmic surfacing, often with eyes partly closed.
Feed	Chasing fish or other prey (regardless of movement pattern).

In order to document the inter-individual spatial proximity, or spread between dolphins in groups, the mode distance between nearest neighbors was recorded by instantaneous sample. Mode nearest neighbor distance in adult dolphin body lengths was classified as either < 1 body length (< 1.8m), 1-3 body lengths (1.8 to 5.4m) or > 3 body lengths (> 5.4 to10m). Group formation was recorded instantaneously as circular (equally spread from side to side and head to tail), linear (spread further head to tail than side to side), parallel (spread further side to side than head to tail), echelon (triangular or "v" formation with relatively few leaders and followers fanned out behind), or none for each interval (Weaver 1987). The number of dolphins riding the bow of the research vessel was recorded at each instantaneous sample. Only dolphins <1m from the boat and within 45° of the bow were counted.

Dusky dolphin aerial activity, comprised of noisy leaps, clean headfirst re-entries, and acrobatic flips, was recorded by all-occurrences sampling (Figure 6). The number of leaps observed per interval was recorded by type for all sampling intervals. This allowed examination of the total number of leaps, variation in the number of leaps per interval, and the number of intervals with leaping per sample. Noisy leaps (Figure 6a) and acrobatic leaps (Figure 6b) often occurred in repetitive bouts (Martin and Bateson 1993). For these behaviors, the number of leaps per bout was recorded. Noisy leaps were defined as all breaches or slaps resulting in a loud splash that were not acrobatic leaps (Figure 6a). Acrobatic leaps were defined as head-over-tail flips or somersaults with a splash (Figure 6b). Dolphins used headfirst re-entry leaps to catch a breath and re-enter the water cleanly in a vertical direction (Figure 6c).

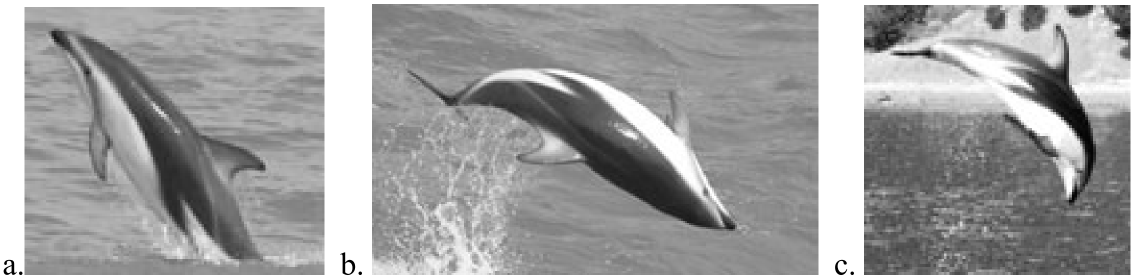


Figure 6. All occurrences of aerial behavior were recorded, with leaps (other than porpoising) divided into the three following types: a. noisy leaps (“breaches” and “slaps” that make a splash), b. acrobatic leaps (“flips” or “somersaults”), and c. headfirst re-entry leaps (“clean” vertical leaps). Leap types a and b occurred in bouts; the number of leaps per bout were documented for these behaviors.

Data Analysis

Data were sorted for analysis by season and time of day. Seasons were defined using the same designations as Cipriano (1992); winter = June-August, spring = September-November, summer = December-February, and autumn = March-May. For examination of diurnal patterns, the day was divided into time blocks as follows: “early” < 9:00, “morning” = 9:00-10:59, “midday” = 11:00-12:59, “afternoon” = 13:00-15:00, “late” > 15:00. The start time for each behavioral sample was used to assign it to a time of day category.

Location and time data were downloaded and manipulated using GPS Utility v. 4.04.7, and plotted using ArcView v 3.2. Behavioral data were transposed to Microsoft Excel spreadsheets, with tallies of instantaneous samples, number of bowriding dolphins, number of intervals with bowriding, number of leaps, leap bouts, and intervals with leaping. These were used to calculate proportions of intervals in which behaviors were observed and mean values per 2-minute interval for all samples.

Statistical analyses were conducted comparing mean values from samples of independent group encounters on different days using SPSS v. 11.0.1. Data were arcsine transformed to reduce heterogeneity of variance (Lehner 1996) using the formula 2*arcsine(x^{-2}). They were then tested for normality using Kolmogorov-Smirnov and Shapiro-Wilk statistics, and tested for homogeneity of variance using the Levene statistic. Means for variables with a normal distribution and homogenous variance were compared by MANOVA, using Tukey tests for post-hoc comparisons (behavioral state and swimming formation). Nonparametric data (all other variables) were compared using Kruskal-Wallis, applying the non-parametric sequential Bonferroni table-wide technique for post-hoc comparisons (Rice 1989).

Results

Seasonal Variation: Behavior of dusky dolphins in different seasons

Group Size and Reproductive Status

The estimated number of dolphins in large groups was greatest in winter and lowest in summer (Figure 7). No large groups under 250 dolphins were noted during winter months, and no large groups comprised of over 1,000 dolphins were noted in summer.

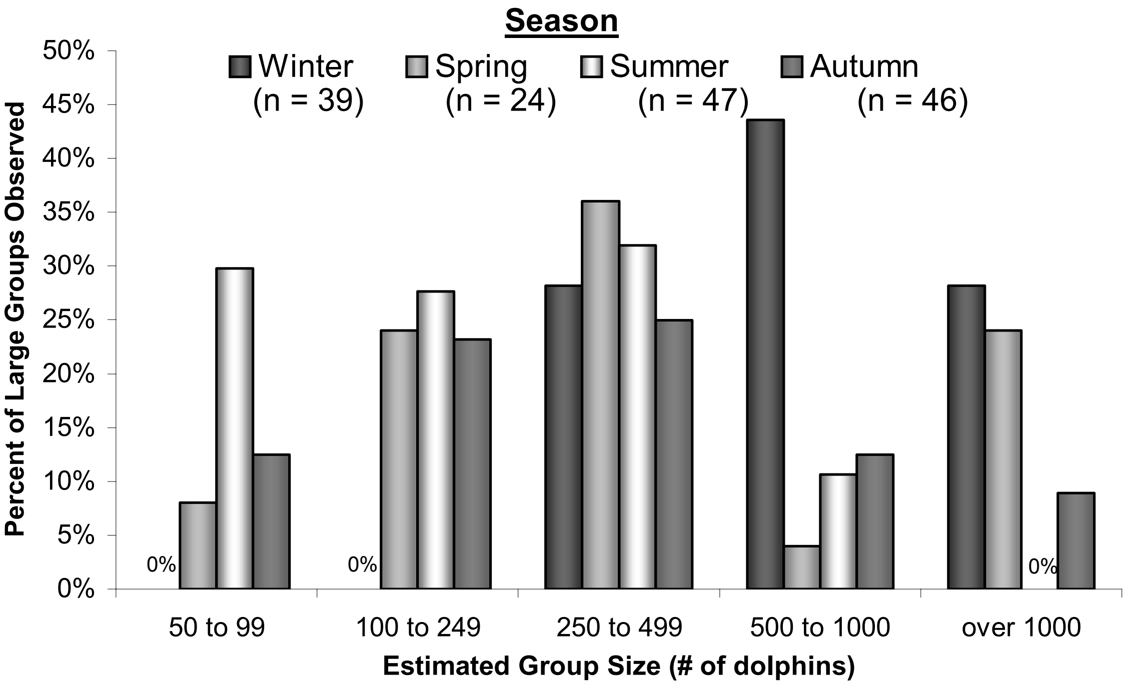


Figure 7. Estimated numbers of dolphins in large groups are compared by group size category. Bars represent the percent of total large groups encountered for each season.

Sexual activity, as indicated by percent of groups in which copulation was confirmed, peaked during summer and was lowest in winter (Figure 8).

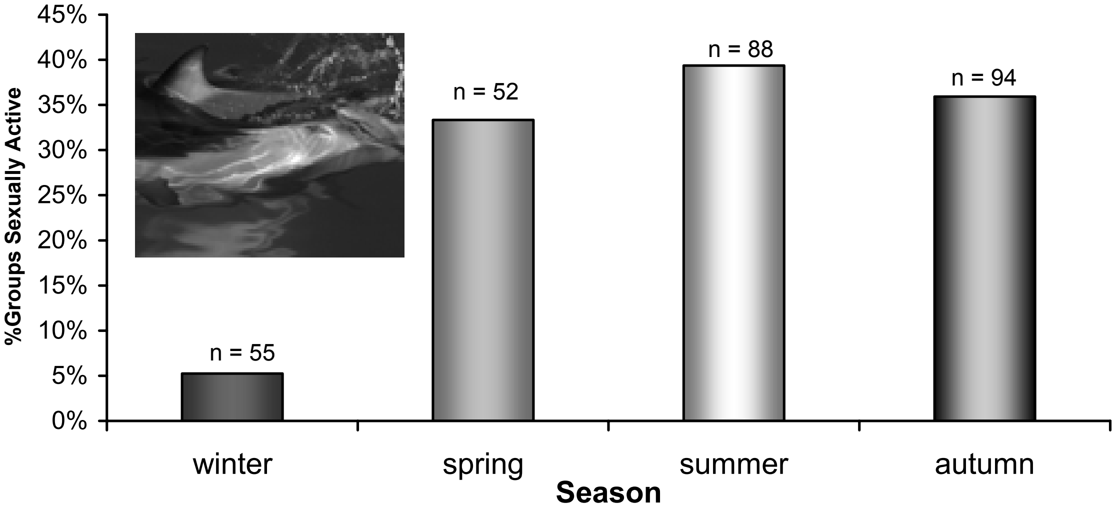


Figure 8. The percent of dusky dolphin groups exhibiting sexual behavior (as shown in the photograph) is compared by season.

Observation of calves peaked during the spring and summer months (Figure 9). No newborn calves (neonates) were observed during autumn and winter.

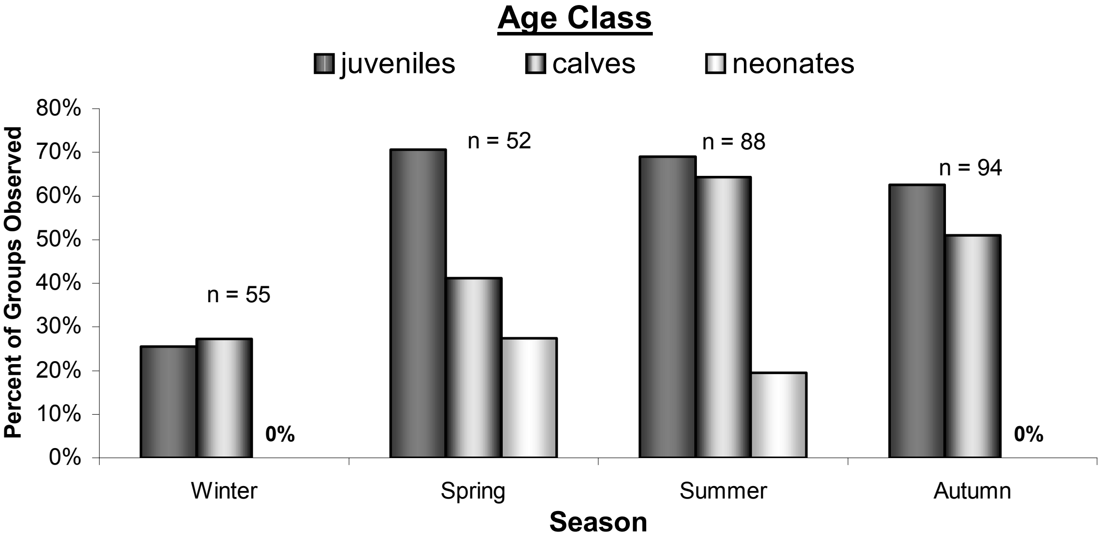
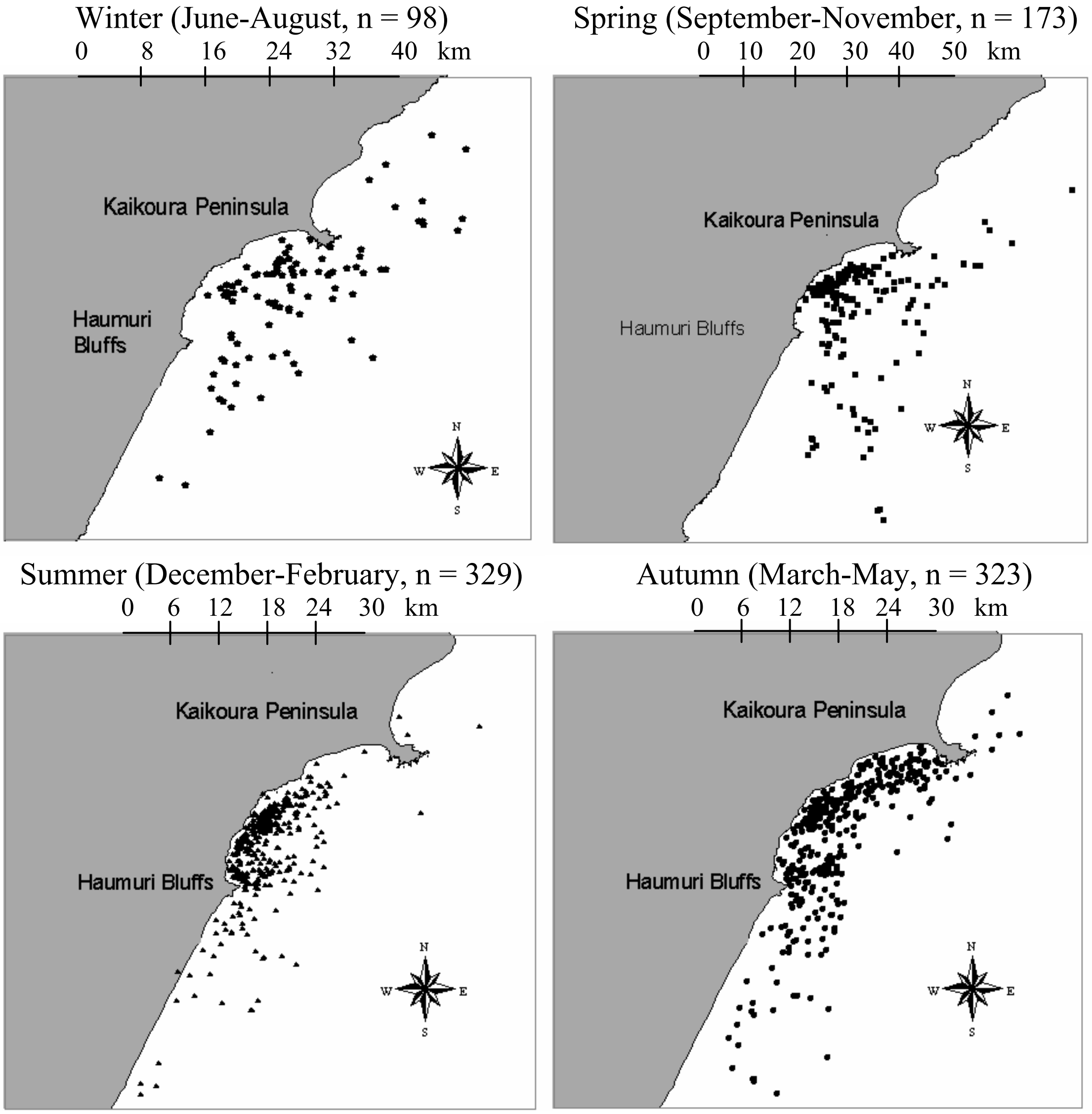


Figure 9. The percent of groups observed with juveniles, calves, and neonates are shown by season.

Ranging and Movement

Locations of dolphin groups varied between seasons (Figure 10), with significant differences in both longitude (Kruskal-Wallis, $H = 263.022$, $P < 0.001$) and latitude (Kruskal-Wallis, $H = 47.224$, $P < 0.001$) between seasons.


Winter (June-August, n = 98)

Spring (September-November, n = 173)

Summer (December-February, n = 329)

Autumn (March-May, n = 323)

Figure 10. Locations of dusky dolphin group encounters (n = sample size) in the Kaikoura region in 1995-2003 are shown by season (scale bars in km).

Groups were encountered furthest East, and hence furthest from shore, in Winter, followed by Spring, Autumn and Summer (Winter > Spring > Autumn > Summer, Bonferroni, $P < 0.001$), with dolphins ranging further north in Autumn and Winter than in Summer (Bonferroni, $P < 0.001$).

The daytime activity budget of dusky dolphin groups varied between seasons (MANOVA with arcsine transformed values, $F = 2.623$, $P = 0.005$), with dolphins traveling more ($F = 3.929$, $P = 0.009$) and resting less ($F = 3.103$, $P = 0.03$) during winter months than during breeding and post-calving seasons (Tukey post hoc comparisons, $P < 0.05$, Figure 11).

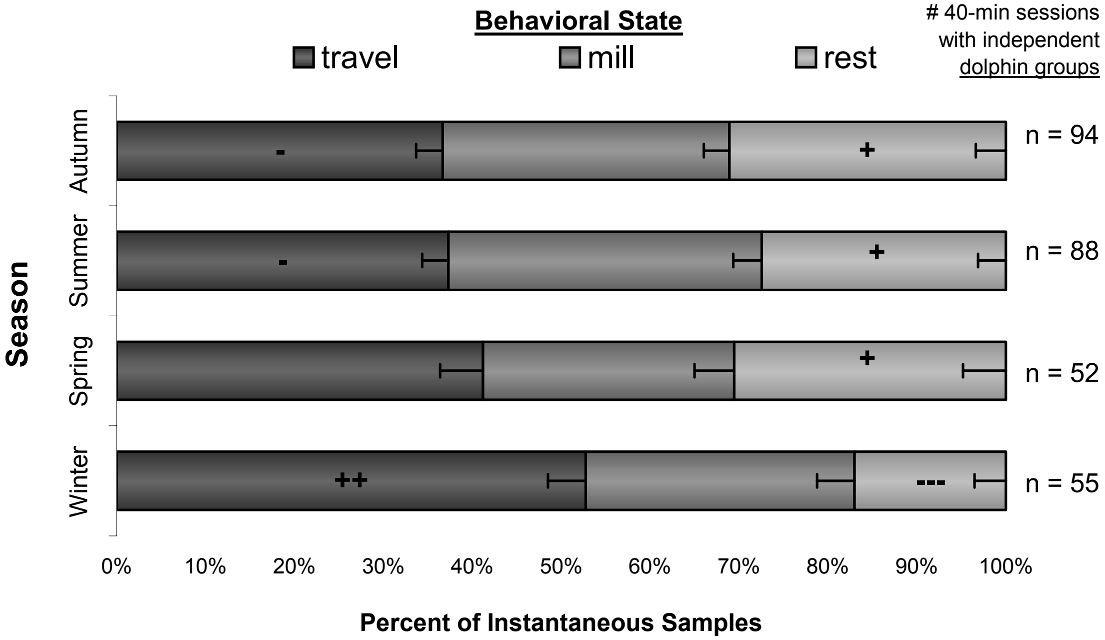


Figure 11. Daytime activity budgets of dusky dolphin groups during different seasons in Kaikoura are shown as percent of instantaneous samples traveling, milling, resting and feeding (mean values shown with 1 standard error of the mean). Significant differences between seasons are indicated by “+” and “-“ marks (Tukey, $P < 0.05$).

Spread and Formation

The spacing between dolphins in groups, measured every 2 minutes as the mode nearest neighbor distance in dolphin body lengths, changed with the seasons (Figure 12). The proportion of intervals with dolphins in close proximity (< 1 body length, Kruskal-Wallis H = 10.616, $P = 0.01$) and spread loosely (> 3 body lengths, Kruskal-Wallis H = 7.562, $P = 0.02$) differed significantly between seasons. During the spring and summer mating and calving seasons, dolphins more often maintained tighter proximity to each other within groups than in winter (Bonferroni post hoc comparisons, $P < 0.05$).

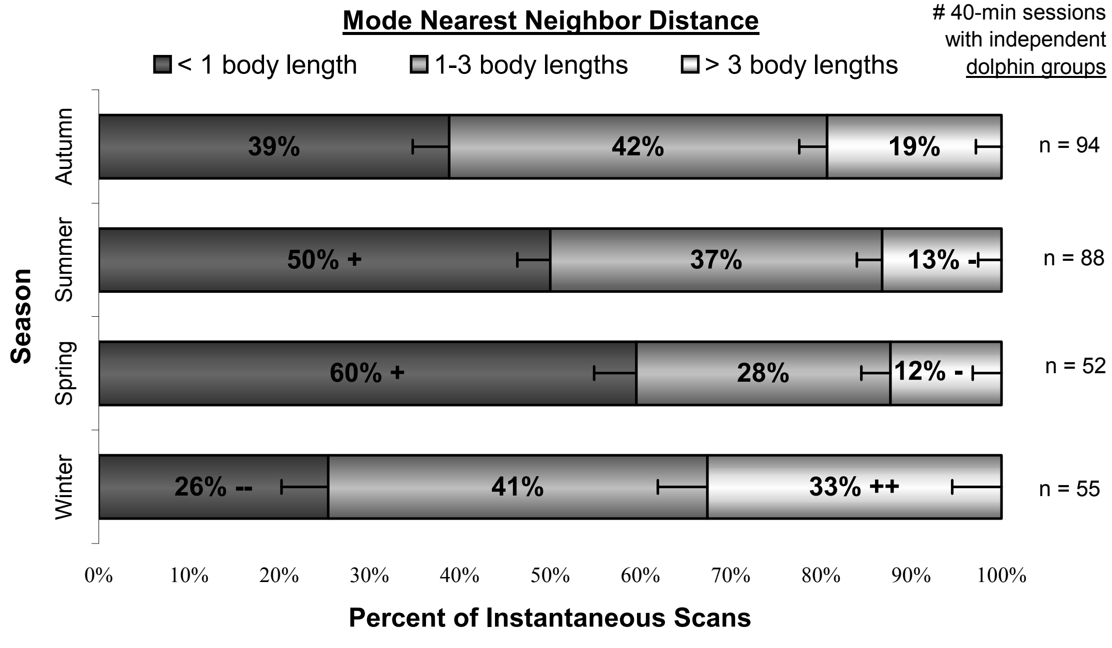


Figure 12. The proximity maintained between dusky dolphins in groups during different seasons in Kaikoura is shown by mode nearest neighbor distance in body lengths. Bars represent the percent of instantaneous samples most dolphins were < 1 body length (<1.8m), 1-3 body lengths (1.8 to 5.4m), and > 3 body lengths (>5.4 to 10m) apart (mean values shown with 1 standard error of the mean). Significant differences between seasons are indicated by "+" and "-" marks (Bonferroni, $P < 0.05$).

Leaping Activity

Leaping activity in dusky dolphin groups varied between seasons (Figure 13). The proportion of noisy leaps (Kruskal-Wallis $H = 19.909$, $P < 0.001$), clean headfirst re-entry leaps (Kruskal-Wallis $H = 34.708$, $P < 0.001$), and acrobatic flips (Kruskal-Wallis $H = 26.468$, $P < 0.001$) differed significantly between seasons. Noisy leaps were most common and re-entry leaps were least common in winter, while acrobatic flips were least common in spring (Bonferroni post hoc comparisons $P < 0.05$, Figure 12).

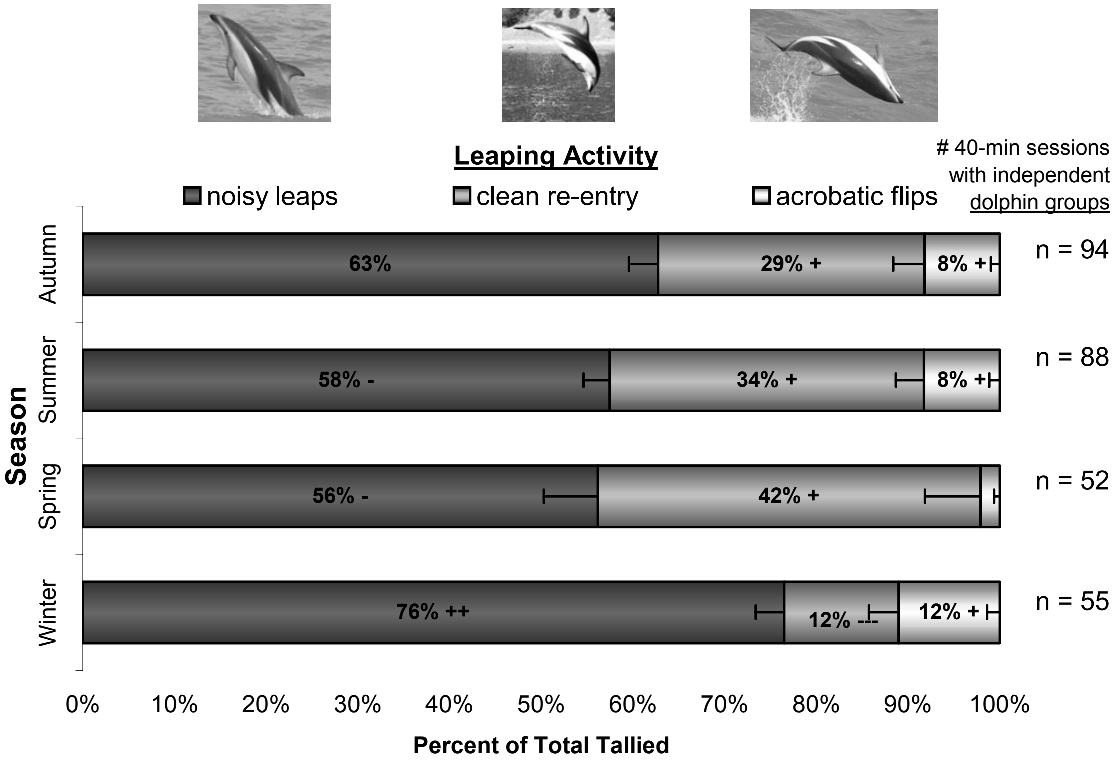


Figure 13. Proportions of leaps by type are compared between seasons. Bars represent the percentage of noisy leaps, clean headfirst re-entries and acrobatic flips (mean values shown with 1 standard error of the mean). Significant differences between seasons are indicated by "+" and "-" marks (Bonferroni, $P < 0.05$).

Diurnal Variation: Behavior of Dusky Dolphins at Different Times of Day

Unlike seasonal variation in grouping, group size and composition (by age class) did not vary by time of day.

<u>Ranging and Movement</u>

Dusky dolphin activity budget varied with time of day (MANOVA with arcsine transformed values, $F = 2.059$, $P = 0.02$). Although traveling was steady throughout the day, resting ($F = 4.148$, $P = 0.003$) and milling ($F = 2.442$, $P = 0.04$) varied significantly between time periods. Resting was noted most often at midday, and milling most often early and late in the day (Figure 14).

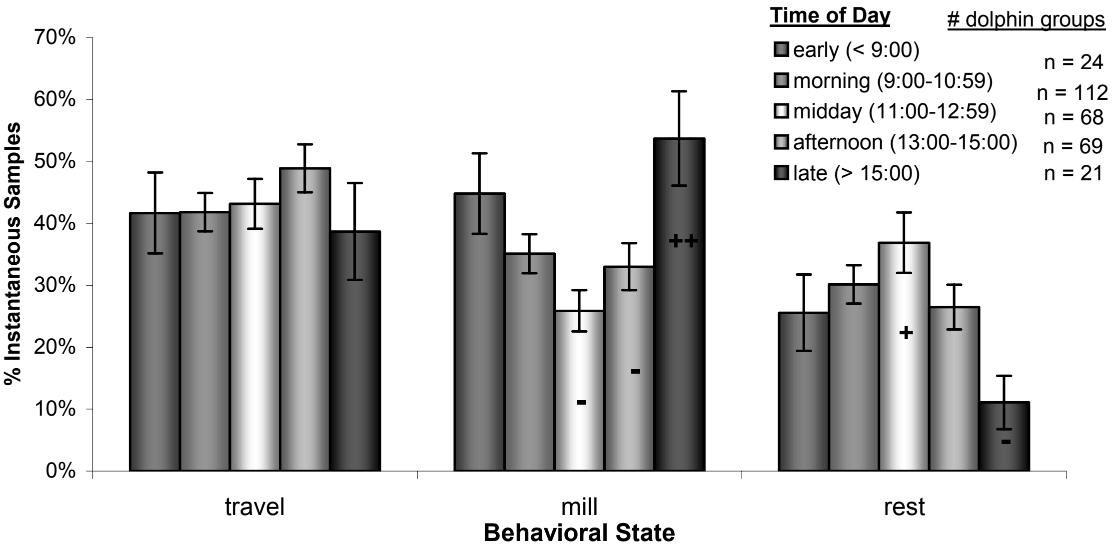


Figure 14. Activity budgets of dusky dolphin groups during different times of day in Kaikoura are shown as percent of instantaneous samples traveling, milling, resting and feeding (mean values shown with 1 standard error of the mean). Significant differences between seasons are indicated by "+" and "-" marks (Tukey, $P < 0.05$).

Group heading was more often westward (toward shore) during earlier time periods than late in the day (Kruskal-Wallis $H = 26.468$, $P < 0.001$) and more often eastward (offshore) during later time periods than early in the day (Kruskal-Wallis $H = 26.468$, $P < 0.001$). Late in the day, dolphin groups headed offshore (Figure 15), moving more often in an eastward direction than in a westward direction from 13:00 to 15:00 (Wilcoxon, $z = 2.385$, $P = 0.02$) and after 15:00 (Wilcoxon, $z = 3.623$, $P < 0.001$).

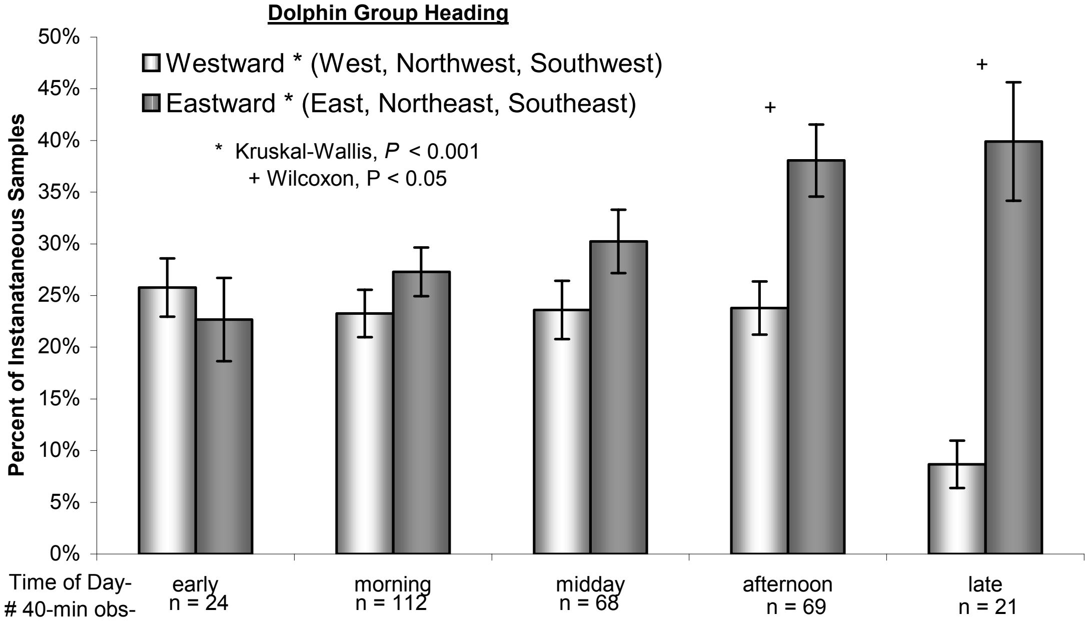


Figure 15. Compass heading of dolphin groups at instantaneous 2-minute samples are compared by time of day. Bars represent the proportion of samples with each heading (mean values shown with 1 standard error of the mean).

Consequently, dolphin group location was further westward late in the day and further eastward early in the day. Both longitude (Kruskal-Wallis, $H = 11.397$, $P = 0.02$) and latitude (Kruskal-Wallis, $H = 15.084$, $P = 0.005$) varied significantly by time of day, with dolphin groups located further east (Mann Whitney $U = 4114.5$, $P < 0.02$) and south (Mann Whitney $U = 3764$, $P < 0.001$) late in the day than early in the day (planned comparisons, Figure 15).

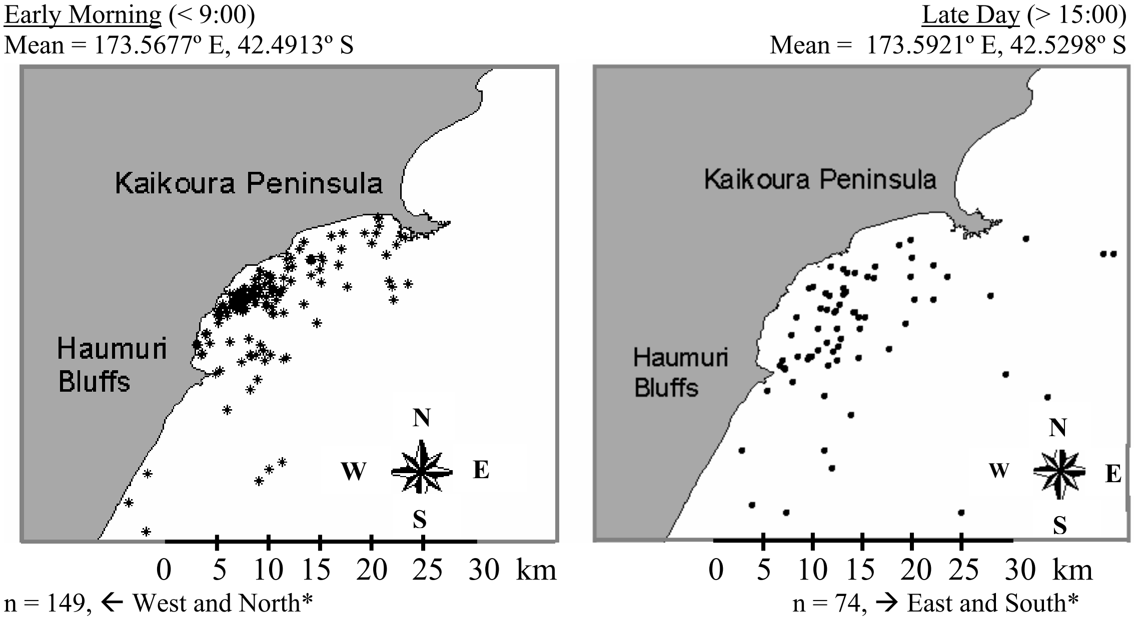


Figure 16. Positions of dolphin groups are shown by time of day (* $P < 0.05$). Positions for morning (n = 276), midday (n = 171), and afternoon (n = 218) are not shown as there were no significant differences between these time periods in either longitude or latitude.

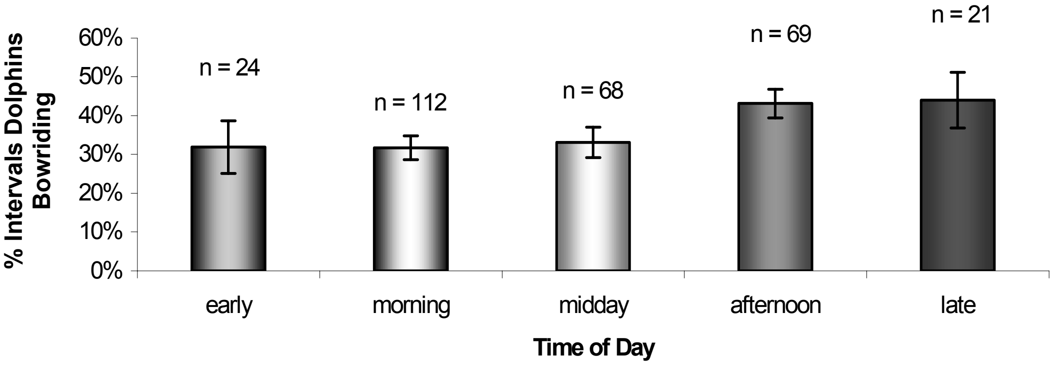


Figure 17. Bowriding behavior in dolphin groups is compared by time of day. Bars represent the percent of instantaneous samples dolphins engaged in bowriding (mean values shown with 1 standard error of the mean).

Bowriding, with dolphins engaged in surfing play and/or assisted travel on the front of the vessel, varied significantly between diurnal time periods (Kruskal Wallis *H* = 9.388, *P* = 0.05). Dolphins engaged in bowriding more in the afternoon and late in the day than during the early, morning, and midday periods (Figure 17).

Spread and Formation

As dolphins moved offshore late in the day, they spread out, maintaining a greater distance between individuals than during midday rest periods (Figure 18).

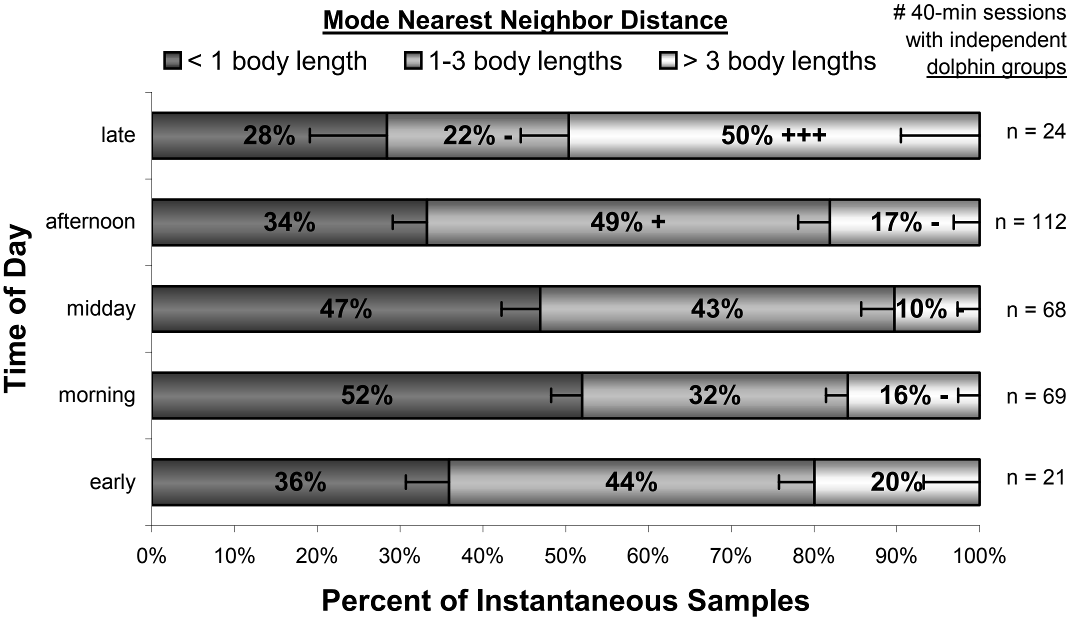


Figure 18. The proximity between dusky dolphins in groups during different times of day in Kaikoura is shown by mode nearest neighbor distance in body lengths. Bars represent the percent of instantaneous samples when dolphins were <1 body length, 1-3 body lengths, and > 3 body lengths apart (mean values shown with 1 standard error of the mean). Significant differences between times of day are indicated by "+" and "-" marks (Bonferroni, *P* < 0.05).

Mode nearest neighbor distance was significantly more often > 3 body lengths apart (Kruskal Wallis, *H* = 14.153, *P* = 0.007) and significantly less often 1-3 body lengths apart (Kruskal Wallis, *H* = 12.364, *P* = 0.02) late in the day than during the earlier afternoon (Bonferroni post hoc *P* < 0.05).

Swimming formation also varied by time of day (MANOVA with arcsine transformed values, *F* = 2.651, *P* < 0.001), with dolphins swimming in parallel or no formation as they spread out and moved offshore late in the day, and in circular or echelon formation during midday rest (Figure 19). The percent of instantaneous samples at which dolphins swam in circular (*F* = 5.361, *P* < 0.001), echelon (*F* = 4.757, *P* = 0.001), and no (*F* = 4.796, *P* = 0.001) formation differed significantly across times of day (Figure 16).

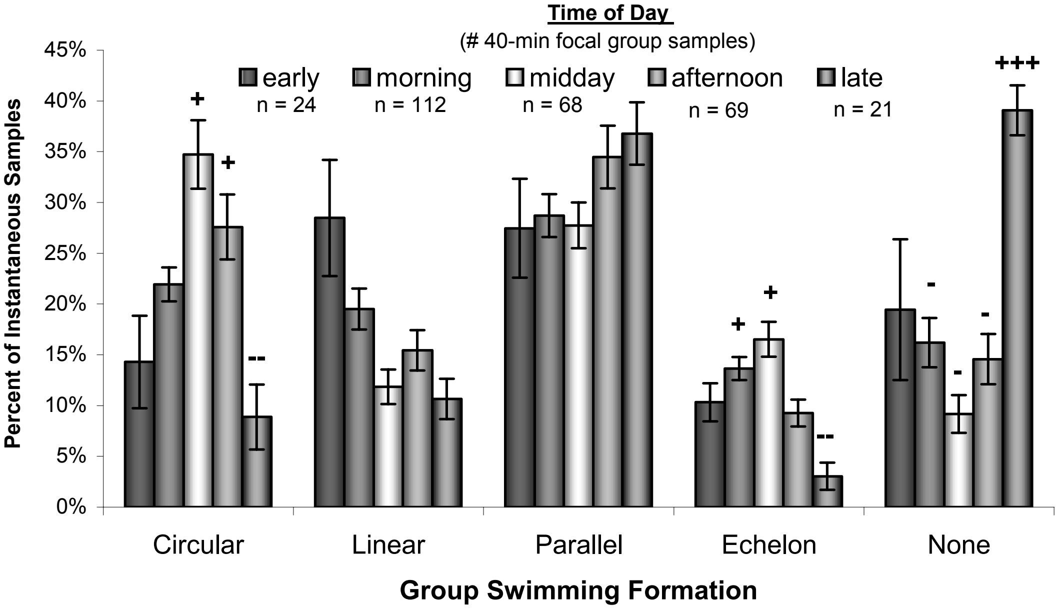


Figure 19. Group swimming formation is compared by time of day. Bars represent the percent of instantaneous samples when dolphins swam in circular, linear, parallel, echelon, and no formation (mean values shown with 1 standard error of the mean, +- *P* < 0.05, Bonferonni post hoc comparisons).

Leaping

Dusky dolphins engaged in more leaping activity in the morning and in the afternoon than in the late morning and at midday (Figure 20).

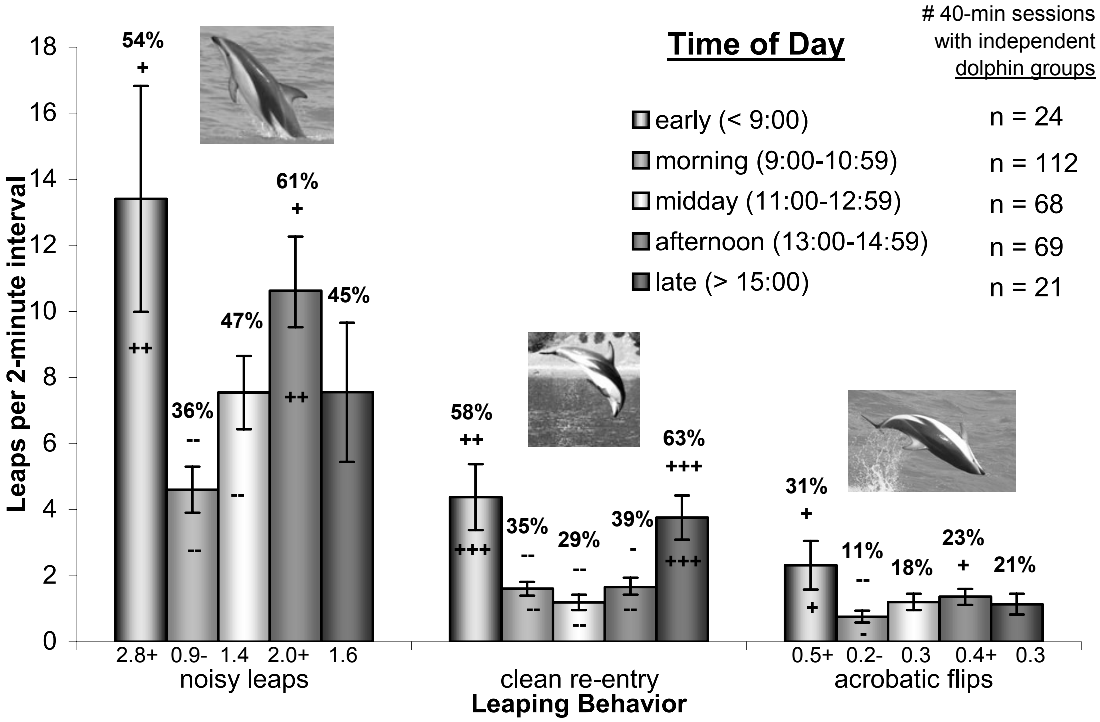


Figure 20. Leaping activity in dusky dolphin groups is compared by time of day. Bars represent the number of noisy leaps, clean headfirst re-entries and acrobatic flips tallied per 2-minute interval (mean values shown with 1 standard error of the mean). Data labels above bars indicate the mean percentage of intervals with leaps. Data labels below the bars indicate the number of bouts of noisy leaps and flips per interval. Significant differences are indicated by "+" and "-" marks (Kruskal-Wallis, Bonferonni post hoc, $P < 0.05$).

The mean number of noisy leaps (Kruskal Wallis $H = 15.700$, $P = 0.003$), clean headfirst re-entries (Kruskal Wallis $H = 20.562$, $P < 0.001$), and acrobatic flips (Kruskal Wallis $H = 11.187$, $P = 0.03$) tallied per 2-minute interval differed significantly between times of day. The percent of intervals in which noisy leaps (Kruskal Wallis $H = 15.990$, $P = 0.003$), clean headfirst re-entries (Kruskal Wallis $H = 17.565$, $P = 0.002$), and acrobatic flips (Kruskal Wallis $H = 14.114$, $P = 0.007$) were observed also varied between times of day, as did the number of leaping bouts for noisy leaps (Kruskal Wallis $H = 16.766$, $P = 0.002$) and acrobatic flips (Kruskal Wallis $H = 15.028$, $P = 0.005$).

Dolphins engaged in the highest proportion of clean re-entry leaps as they spread out and moved offshore late in the day, whereas noisy leaps comprised a larger proportion of leaps during the middle of the day and afternoon (Figure 21).

The proportion of noisy leaps (Kruskal Wallis $H = 20.021$, $P < 0.001$) and clean headfirst re-entries (Kruskal Wallis $H = 25.452$, $P < 0.001$) varied with time of day. The proportion of acrobatic flips did not differ significantly between different times of day.

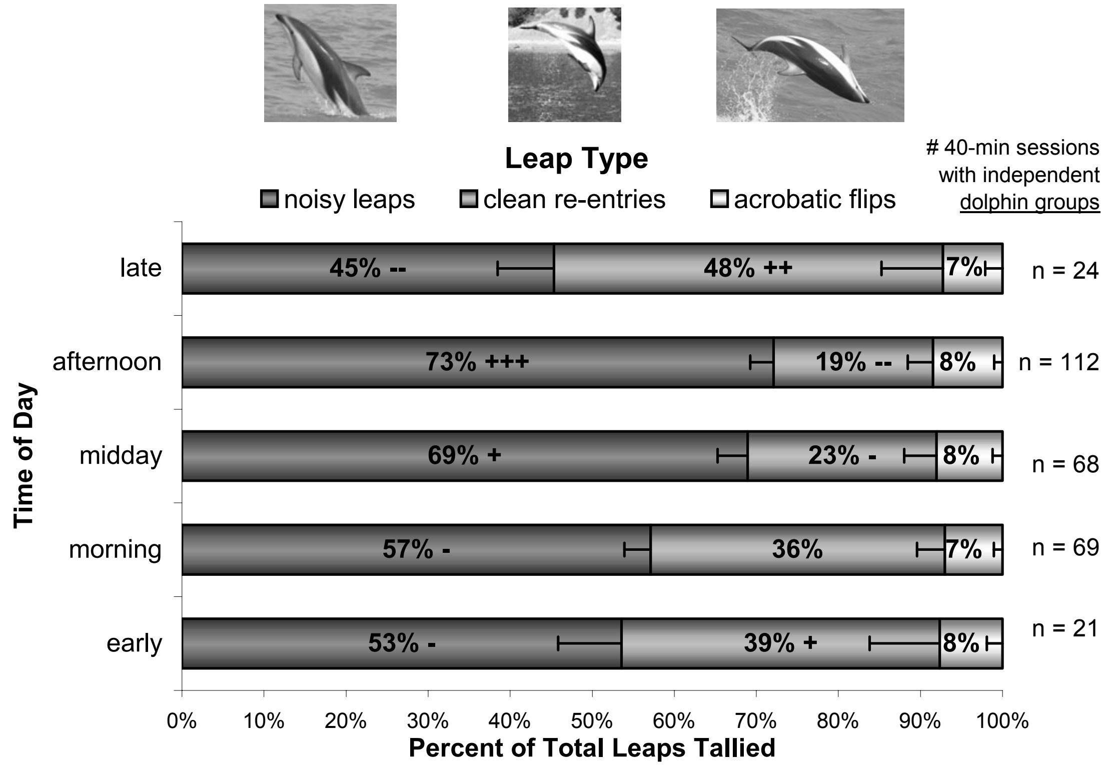


Figure 21. Proportions of leaps by type are compared between times of day. Bars represent the percentage of noisy leaps, clean headfirst re-entries and acrobatic flips out of the total number of leaps (mean values shown with 1 standard error of the mean). Significant differences are indicated by "+" and "-" marks (Bonferonni, $P < 0.05$).

Discussion

Seasonal Patterns

Group Size and Reproductive Status

Estimated group size for large groups followed the hypothesized seasonal pattern previously described for dusky dolphins in Kaikoura, with larger groups in winter and smaller groups in summer (Würsig *et al.* 1997). As predicted, mating activity peaked in summer, but also occurred at a relatively high rate in spring and autumn. Also as predicted, neonates were observed only in spring and summer, most frequently in the spring. Older calves were seen throughout the year, but were most common in summer, when they were noted in roughly two-thirds of groups encountered. These results are consistent with findings from post mortem specimens (Cipriano 1992) indicating a seasonal calving and breeding season peaking in the spring and summer.

Ranging and Movement

As predicted, dolphin groups were found further offshore (east) and ranging further along shore (north) in winter than in summer and autumn, when calves were present in greater numbers. This pattern concurs with previous studies (summarized by Würsig *et al.* 1997). Contrary to predictions, the tendency of the dolphins to be further alongshore and offshore remained through the spring, which heralded the arrival of the first newborn calves. In other words, the ranging of the dolphins did not decrease until most of the calves had already been born (in summer). During summer in particular, group sightings clustered in the relatively shallow and sheltered area near shore between

Goose Bay and the Haumuri Bluffs. This area, in the lee of the Haumuri Bluffs from southerly weather fronts, could potentially provide a calmer and more secure sanctuary for developing calves. In autumn, sightings shifted to more regularly include areas further north to the Kaikoura peninsula but generally remained within about 5km of shore and south of the peninsula. As predicted, resting was generally most prominent when calves were younger and found in a higher proportion of groups (spring-autumn), as compared with more frequent traveling in the non-calving, non-breeding season (winter). Observed seasonal variation in daytime ranging and movement patterns in Kaikoura are unlikely to be related to foraging directly, as the dolphins in Kaikoura feed almost exclusively at night (Cipriano 1992, Würsig *et al.* 1997).

Protection from Predators

As predicted, dolphins maintained closest inter-individual proximity and were found closest to shore in spring and summer, when calves would be most vulnerable to predation. Given that bunching and moving close to shore are observed in response to killer whales (Würsig *et al.* 1997), it follows that dolphins staying closer to each other and shore could represent groups assuming a generally more defensive "posture" when calves are present. The rarity of observed predation events (about 1-2 per year with some exceptions, e.g. Constantine *et al.* 1998) even during the calving season, suggests that these "defense measures" are reasonably effective (see Chapter V). Seasonal breeding may also influence inter-individual distance, as close physical proximity is more likely during periods of greater social/sexual activity, and is, at any rate, a prerequisite for mating.

Leaping

As predicted, noisy leaps were most prevalent when groups were largest in winter, indicating their importance as a long-range signal, possibly related to coordinated group movements at a time when they travel more extensively further offshore and along the coast. Such noisy leaps could also serve a "grooming" function, in which case the need to slough skin/parasites would presumably be greater in winter. Alternatively, noisy leaps could be an expression of internal physiological state, with dolphins engaging in more boisterous celebrations during winter months than other seasons. These interpretations are not mutually exclusive, and further research on the social contexts in which they occur most frequently give greater insight into their function (see Chapter III). Clean headfirst re-entry leaps were, as predicted, most common during the breeding season, and appear to function in mating interactions (Markowitz *et al.* 2000, see Chapter III). The showy, high-energy acrobatic flips generally occurred at a low-level, but as expected represented a smaller proportion of leaps in the spring when calves were youngest.

Seasonal Pattern Summary

The results of this study indicate that dusky dolphin behavior follows predictable seasonal patterns. Predictions derived from previous shore-based studies and examination of post mortem specimens (summarized by Würsig *et al.* 1997) were generally supported; however, the observed ranking was different than expected during at least one season for 7 out of 9 parameters (Table 5). Observed rankings were as expected in all cases for the winter non-breeding, non-calving season. Values differed from expected most often in the spring and autumn.

Table 5: Expected versus observed ranking of parameters by season
(greater sizes, numbers, distances, and frequencies denoted by larger numbers)

Behavioral category	**Winter**	**Spring**	**Summer**	**Autumn**
group size	4 ✓	2 ☒ **3**	1 ✓	3 ☒ **2**
calves	1 ✓	4 ☒ **3**	3 ☒ **4**	2 ✓
mating	1 ✓	2 ✓	4 ✓	3 ✓
ranging	4 ✓	1 ☒ **4**	2 ☒ **1**	3 ☒ **1**
distance from shore	4 ✓	2 ☒ **4**	1 ✓	3 ☒ **1**
behavioral state	travel ✓	rest ✓	rest/mill ✓	mill/travel ☒ **rest/mill**
inter-individual distance	4 ✓	1 ☒ **4**	2 ☒ **1**	3 ☒ **1**
noisy leaps	4 ✓	1 ✓	2 ✓	3 ✓
clean headfirst re-entry	1 ✓	2 ☒ **4**	4 ✓	3 ☒ **4**

(✓ = as predicted. ☒ = different from predicted, observed rankings in bold)

Contrary to expectations, the dolphins remained further offshore, ranged further along shore, maintained larger groups, and kept a greater spacing between individuals during the spring, when most calving occurred, than in subsequent seasons. Ranging, group size, and inter-individual distance did not diminish until most of the calves had already been born, in the summer and autumn. Thus, most discrepancies between expected and observed rankings (Table 5) can be explained by the dolphins' behavior in spring and winter being more similar than expected, and their behavior in autumn and winter being less similar than expected. These findings further calibrate understanding of seasonal variation in dusky dolphin behavior from that which could be inferred based on examination of post mortem specimens and observations made at a distance from shore-based stations (e.g. Würsig *et al.* 1991, Cipriano 1992, Brown 1999). Such advances highlight the different perspective provided by detailed observations during boat-based focal follows of dolphin groups (Mann 2000).

Diurnal Patterns

<u>Ranging and Movement</u>

As predicted, this study confirmed the dusky dolphin midday resting period reported by Barr and Slooten (1998). The diurnal pattern of midday rest with more active periods early and late in the day is similar to that of the Hawaiian spinner dolphin, another creature that feeds nocturnally on mesopelagic prey associated with the deep scattering layer (Würsig *et al.* 1994). Over the past few years, tour operators in Kaikoura have voluntarily regulated their activities in order to give the dolphins "vessel free" time during the hours of 11:00-13:00. This "midday break" appears to be well placed to allow dolphins to rest with minimal human distraction.

As for the Hawaiian spinner dolphin (Würsig *et al.* 1994), data from this study indicate dusky dolphins disperse and move offshore late in the day in preparation for nocturnal feeding. Norris and Dohl (1980) pointed out that dolphins that are spread in parallel formation, as dusky dolphins often are late in the day, can together search a larger area of water per unit time. Coordinated group searching has been reported for bottlenose dolphins, with dolphins swimming in formation in such a manner as to "comb" through the sea in search of prey (Bel'kovich *et al.* 1991).

To illustrate how this parallel spread might increase searching efficiency, a simple model of dusky dolphin searching power can be developed based on data from the current study: If 500 dusky dolphins (median large group size) swim in parallel at a mean inter-individual distance of 5.5 m (approximately 3 body lengths, or the minimum spread during most intervals late in the day), then the group would be spread over a distance of roughly 2.7 km. Assuming the group was moving at the mean speed for large groups (7 kmh^{-1}), then the group would scan an area of surface water 18.9 km^2 each hour, or 1 km^2 every 3.2 minutes. This simple analysis does not address searching in three dimensions. However, given that dolphins dive regularly as they move offshore, a coordinated group could efficiently scan through the water column to a depth of roughly 125m (Benoit-Bird *et al.* in press). By maintaining group cohesion even when spread widely, dolphins likely maintain acoustic contact (Mann 1999*a*) in the event that one or more individuals encounter an especially rich patch of prey or danger in the form of a potential predator.

Contrary to expectations, the dolphins returned closest to shore early in the day, maintaining closer spacing between individuals, similar to the midday rest period.

Protection from Predators

As expected, dusky dolphins maintained closer inter-individual proximity and were more often in a circular formation during the midday rest period (Barr and Slooten 1998) than at other times of day. This behavior likely provides maximum protection against predators when dolphins are at their most vulnerable because they are “half-asleep” (Wells *et al.* 1999). The dolphins remained closer to shore during this period than later in the day, but not as near shore as in the early morning hours.

Leaping

As predicted, leaping activity generally peaked during non-resting periods early and late in the day. However, noisy leaps made up a higher proportion of leaps in the middle of the day. During this time, active "scouts" or "sentinels" (Connor *et al.* 2000) on the edges of large resting groups engaged in leaping behavior, possibly to keep groups moving in a coordinated fashion and/or to watch for potential threats (see Chapter III). Alternatively, more active individuals might be more likely to swim to the edge of the group simply because they are more active. Clean headfirst re-entry leaps facilitate diving, and therefore might be most important in social-sexual interactions (Markowitz *et al.* 2000) and/or foraging (Markowitz *et al.* 2004). As predicted, these leaps were observed most in non-resting periods, especially late in the day as dolphins moved offshore in preparation for feeding. Acrobatic flips occurred most in the early part of the day. In Argentina, dolphins were engaged in more of these leaps following a successful feeding (Würsig 1984). Perhaps the acrobatic flips observed early in the morning in Kaikoura represent a similar "celebration" following a night of feasting.

Diurnal Pattern Summary

These findings confirm that dusky dolphin behavior in Kaikoura follows predictable diurnal patterns. Observed rankings of parameters matched the expected rankings presented in the introduction to this chapter in 27 of 35 cases (Table 6). Again, much can be learned where results differed from expected. Most notably, dolphin movement closest to shore during early morning following nocturnal feeding, and increased activity following midday rest and prior to moving offshore late in the day indicate that the dolphins “synchronized their watches” somewhat differently than aniticipated. These observations might be explained as dusky dolphins seeking shelter immediately following a night’s work, and “mobilizing” prior to moving offshore, as has been noted for Hawaiian spinner dolphins (Würsig *et al.* 1994).

Table 6: Expected versus observed ranking of parameters by time of day
(greater numbers, distances, and frequencies denoted by larger numbers)

Behavioral category	**early**	**morning**	**midday**	**afternoon**	**late**
travel/mill	3 ✓	2 ✓	1 ✓	2 ✓	3 ✓
rest	1 ✓	2 ✓	3 ✓	2 ✓	1 ✓
distance from shore	3 ☒ **1**	2 ✓	1 ☒ **2**	2 ✓	3 ✓
bow-riding	3 ☒ **1**	2 ☒ **1**	1 ✓	2 ☒ **3**	3 ✓
inter-individual distance	3 ☒ **2**	2 ✓	1 ✓	2 ✓	3 ✓
formation	-	-	circular ✓	-	parallel✓
leaping frequency	3 ✓	2 ☒ **1**	1 ✓	2 ☒ **3**	3 ✓
Main leap type	re-entry✓	-	noisy ✓	-	re-entry✓

(✓ = as predicted. ☒ = different from predicted, observed rankings in bold)

CHAPTER III

SOCIAL BEHAVIOR OF DUSKY DOLPHINS OFF KAIKOURA, NEW ZEALAND

Figure 22. Social interactions between dusky dolphins include re-entry leaps and high-speed chases.

…the individual is a member of a community of interdependent parts. His instincts prompt him to compete for his place in the community, but his ethics prompt him also to co-operate.

\- Aldo Leopold, A Sand County Almanac

Introduction

Social Behavior

Group living offers many advantages to social mammals (Trivers 1985), such as dusky dolphins (Figure 22). Some of these advantages accrue without the need for cooperation or well-defined social relationships. For example, group members may gain protection from predators due to the confusion effect (Miller 1922), the selfish herd effect (Hamilton 1971), the dilution effect (Dehn 1990) and/or increased vigilance (e.g. prairie dogs, Hoogland 1981). These benefits require neither cooperation nor knowing one's neighbors well. They are merely a function of safety in numbers in the face of a potential threat. Similarly, increased foraging efficiency due to coordinated effort need not result from cooperation (Connor 2000). Mammals and birds generally spend less time engaged in vigilance and more time feeding in larger groups (Elgar 1989).

In some cases, groups of social mammals clearly cooperate for mutual and/or reciprocal advantage. Group defense against predators often involves a cooperative effort, as in ground squirrel colonies defending against rattlesnake attacks (Sherman 1977). The evolution of cooperation in mammals has been explained to occur as a result of immediate mutual benefit, kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971). Game theory models, based on a two-player "prisoner's dilemma" game show how reciprocity could be favored, given repeated interactions between individuals (Axelrod and Hamilton 1981). However, this sociobiological approach is overly simplified, and may not represent a realistic model for the organization of complex societies in nature (Norris 1994).

Marine Mammal Social Lives

Particularly in aquatic environments, prey resources are often spatially and temporally patchy. Feeding in groups in such an environment can increase foraging efficiency (Wells *et al.* 1999). At sea, marine mammals have few refuges from predators (Connor *et al*. 2000). In this environment, the safety in numbers due to the “selfish herd” effect (Hamilton 1971), increased vigilance, and group defense, can be particularly crucial to survival. Matriarchal groups of sperm whales, similar in many respects to those of African elephants (Lee 1987, Moss 1988), act together to care for calves and defend them from predators (reviewed in Whitehead and Weilgart 2000).

Dolphins are highly social, typically living in groups that may aid in capturing prey and predator defense (Würsig 1989).

Differences in social behavior of dusky dolphin populations in Argentina and New Zealand are related to differences in the aquatic environments, as is their feeding ecology in these two areas (Würsig *et al.* 1997). In Argentina, where large schools of southern anchovy (*Engraulis anchoita*) inhabit shallow waters, groups of 8-12 dolphins exhibit coordinated search patterns and hunting during the day, fusing to form large feeding aggregations. At night, the dolphins rest in small groups. In New Zealand, aggregations of hundreds of dolphins, comprised of smaller subgroups, follow the deep scattering layer (DSL), feeding mostly at night on mesopelagic fishes and squid brought close to shore at Kaikoura by a deep submarine canyon (Würsig *et al.* 1989). This variation in social relationships and coordinated foraging effort suggests a high degree of behavioral plasticity (Würsig 1991).

A great deal is now understood about how dusky dolphin distribution, movements and behavior vary by location, season, and time of day (Cipriano 1992, Würsig *et al.* 1997). However, there is still much to learn about dusky dolphins' social relationships. Nearly all aspects of their lives, from feeding to predator avoidance to care of offspring, involve a social component. Dusky dolphin society is characterized by remarkable flexibility, as the dolphins adjust their behavior and group size across locations to fit the local ecology. Small groups of 6 to 12 individuals engage in mating and rearing of young (Würsig *et al.* 1997). In Kaikoura, these smaller groups regularly band together into larger groups of hundreds, or even thousands, of individuals. Within this fission-fusion society, how do the dolphins coordinate their activities?

Coordinated Activities in Large Groups

The relatively well-studied societies of bottlenose dolphins (Connor *et al.* 2000) and killer whales (Baird 2000) provide insight into the social lives of dolphins . However, just because social organization is better understood in these two species, it does not necessarily follow that other dolphin societies are less well organized nor that they must be organized similarly. To draw upon a human analogy, the best-studied cetacean societies might be thought of as "floating villages" of relatively small groups within which individuals share kinship or close cooperative bonds. We know that in human societies, large groupings of people do not lack social order. On the contrary, it might be argued that some of the greatest social complexity and cultural advancements have occurred where people gather in large numbers. "Rome wasn't built in a day", nor was it built by a few villagers. Fewer studies have examined social behavior in more extensive dolphin societies such as those of common dolphins, spinner dolphins, and dusky dolphins, which can occur in groups of hundreds to thousands. I hypothesize that dusky dolphins in such large groups show highly coordinated, cohesive behavior, facilitating efficient group responses to changing circumstances. This hypothesis gives rise to the following specific predictions.

Predictions Concerning Large Group Behavior

As with large gatherings of people, dolphins in large groups are expected to be highly coordinated in their movements. In order to enhance cohesion, such dolphin traffic should travel more steadily and rapidly than smaller groups. Consequently, I predict that with respect to movement patterns:

- Large groups travel more than smaller groups.
- Movement of large groups is highly coordinated
    -Heading among group members is less variable than that in small groups.
- Mean and top swimming speeds of large groups are higher than in small groups.
- High-speed activities are more common in large groups than in small groups.

Given "safety in numbers", dolphins in larger groups are expected to be more spread out. Moving as a unit is expected to result in clearly delineated swimming formations. Swimming in a long head-to-tail alignment is likely to occur if some leaders travel faster, while others follow. Therefore, I predict that with respect to inter-individual proximity and swimming formation:

- Dolphins in large groups maintain greater inter-individual distances.
- Dolphins in large groups most often swim in linear formation.

Dusky dolphins are well known for their aerial acrobatics, engaging in perhaps a higher frequency and a wider variety of leaping than any other cetacean species (Würsig *et al*. 1997). Such showy aerial acrobatics likely involve at least some energetic cost, and may make dusky dolphins more conspicuous to potential predators. How do these leaps function in the lives of the animals? As they occur in this particularly gregarious species, it seems likely that at least some of these leaps serve a social purpose. For example, noisy leaps might serve as a signal to other dolphins. Würsig (1984) found that dusky dolphins feeding together on schools of anchovy in Golfo San José, Argentina, engage in a higher proportion of noisy leaps ("breaches" and "slaps") when prey are found, possibly stunning fish and/or recruiting other dolphins to the feeding effort. The greater the number of dolphins recruited to the feeding activity, the longer the feeding lasts, presumably due to the greater efficiency of a larger number of dolphins containing and herding the prey toward the surface (Würsig and Würsig 1980). As the feeding bout progressed, the dolphins engaged in a higher proportion of clean headfirst re-entry leaps. Such leaps, oriented in a vertical descent direction, likely function to enhance efficiency of diving in air breathing mammals working to herd prey below the surface. Following feeding, dusky dolphins in Argentina engage in a higher proportion of acrobatic leaps ("flips" or "somersaults"), which might be a form of celebration, cementing social bonds following a successful hunt (Würsig 1984).

In Kaikoura, New Zealand dusky dolphins almost never feed during daylight hours. Yet the leaps described by Würsig (1984) still occur at a high frequency. This suggests that these leaps serve important functions in non-feeding as well as feeding contexts. The observation of noisy leaping among non-feeding dolphins lends further support to the idea that this behavior acts as a signal, and is not merely to stun prey. If noisy leaps serve a similar signaling function in a non-feeding context, then it is expected that such behavior will influence the movements and behavior of other group members. They are likely to occur most often in large groups spread over larger distances, acting to coordinate group movements. They are likely to occur less often in small groups, especially in nurseries where calves are particularly vulnerable if detected by predators. Therefore, I predict that with respect to social interaction and leaping activity:

- Interactive behaviors and social-contact behaviors occur more in large groups than in nurseries and non-mating adult groups, but less than in mating groups.
- Long-distance signaling is important; noisy leaps and tail slaps occur more frequently in large groups than in smaller groups.

- If noisy leaps act to direct/coordinate large group movements, then changes in large group heading will be non-random with respect to leaping activity.

Kaikoura, New Zealand is one of the few places where “swim with dolphins” ecotourism is marketed on a large scale. Several studies at Kaikoura have focused on the effects of boating and diving tours, begun in 1989, on dusky dolphin movements and behavior. An increasingly popular attraction over the last 10 years, marine mammal tourism has become a multi-million dollar industry in New Zealand, with over 70 permits issued nation-wide. In Kaikoura, on the South Islands' East Coast, up to 7 vessels operating 3 times per day bring tourists to see dusky dolphins during peak season. Over 100 people per day swim with the dolphins. Tour vessels most often visit large pods ($\geq$ 50 individuals). Detailed shore-based studies of both short-term (Barr and Slooten 1998, Yin 1999) and long-term (Brown 1999) responses of dolphins to tour industry activities indicate that the effects of tours on the dolphins are minimal. However, if tour vessels disturb dolphins, then I predict that:

- Dolphins react to vessels with a “fight or flight” response, increasing swimming speed in the presence of a greater number of vessels.
- Dolphins change heading to avoid vessels (turning away from vessels more than toward vessels).

Competition in Small Mating Groups

Male-male competition for access to mates often takes the form of aggressive confrontation, in which mating success is largely determined by the outcome of either violent or ritualized/posturing combat (Eibl-Eibesfeldt 1961). Often, physical size and/or age can be an important factor in determining the outcome of male-male conflicts over mates, as in red deer (*Cervas elephus*, Clutton-Brock *et al*. 1979), African elephants (Poole 1989), rhesus macques (*Macaca mulatta*, Manson 1996) and elephant seals (*Mirounga angustirostris* LeBoeuf & Kaza 1981, *Mirounga leonina* McCann 1981, Modig 1996). The use of weapons can also be important in male-male competition for access to females, as is the case with African elephant (*Loxodonta africana* Poole 1989) and narwhal (*Monodon monoceros* Gerson and Hickey 1985, Brear *et al*. 1993) tusks, and elk antlers (Leslie and Jenkins 1985). Hormonal state can also play a role in male-male competition for mates. For example, male African elephants in musth can dominate males that they otherwise could not (Poole 1989), and the rut in red deer influences outcome of social conflicts between males (Lincoln *et al*. 1972).

Cooperation between males can also be important in the outcome of aggressive male-male competition for mates. Male lions form highly egalitarian alliances with both related and unrelated males to take over & maintain prides (*Panthera leo*) Grinnell *et al*. 1995). Male savanna baboons (*Papio anubis*) that form coalitions overthrow more dominant males and gain access to females (Packer 1977, Smuts & Watanabe 1989, Noë 1994). Extra-troop male langurs cooperate in raids to take over troops held by other males (Hrdy 1977). The level of cooperation exhibited by dolphins competing for access to mates can rival that of primates. For example, male bottlenose dolphins form coalitions and alliances (Connor *et al.* 1992), roughly analogous to those observed in baboons to obtain mates (Packer 1977, Noë 1994). These suggest lasting cooperative relationships based on reciprocal altruism (Trivers 1971) or by-product mutualism (Dugatkin *et al*. 1992) that benefit social partners in conflicts with other conspecifics (De Waal and Harcourt 1992). Male coalitions to gain access to mates have also been noted in Atlantic spotted dolphins (*Stenella frontalis*, Herzing 1996).

Non-aggressive competition between males for access to mates may take the form of sperm competition (Trivers 1985). In primates, testes mass relative to body mass is generally larger in species with multi-male groups than in monogamous species or single-male groups, indicating sperm competition (Harcourt *et al.* 1981). Among dolphins, the testis size relative to standard length is especially high in the genus *Lagenorhynchus*, suggesting sperm competition (Connor *et al*. 2000).

Female choice can also play an important role in reproductive contests (Trivers 1985). Showy characters can represent handicaps reliably demonstrating to females the fitness of males (Zahavi and Zahavi 1997), for example resistance to parasites (Hamilton and Zuk 1982). Courtship displays among lekking birds provide females an arena in which to select mates (Kruijt and Hogan 1967). Among cetaceans, the mating system of humpback whales (*Megaptera novaeangliae*) shares many features with that of lekking birds, with some evidence for female choice (Clapham 2000).

I hypothesize that small mating groups of dusky dolphins act as competitive breeding arenas. This hypothesis gives rise to the following specific predictions:

Predictions Concerning Small Mating Groups

The mating system of the dusky dolphin has generally been described as "promiscuous", meaning multi-mate polygynandrous. In the deep coastal waters of Kaikoura, New Zealand, dusky dolphins feed mostly at night, leaving greater time during the day for social-sexual activities. Mating, which occurs for social as well as reproductive reasons, is observed throughout the year. Testis mass accounts for as much as 5% of adult male body weight (4 kg) in the breeding season (Cipriano 1992). Sex size dimorphism is negligible. Therefore, aggressive male-male competition seems unlikely, and sperm competition seems likely (Kenagy and Trombulak 1986). Female choice could also play a role in mating success, particularly if male behavior in some way demonstrates fitness (Zahavi and Zahavi 1997). Smaller body size might also favor maneuverability or quickness (Connor *et al*. 2000), and could influence mating success. If this is the case, I predict that with respect to movement patterns:

- Mating groups engage in more milling than other groups.
- Movement of mating groups lacks coordination.
  - -Heading of group members is more often variable than in other groups.
- Mean and top swimming speeds in mating groups areslower than in large groups but faster than in nurseries and other small groups (especially burst/top speeds).
- High-speed activities are more common in mating groups than in other groups.

Assuming mating groups involve competition for mates (beyond sperm competition), I predict that with respect to inter-individual proximity and swimming formation:

- Dolphins in mating groups are tightly grouped, with males crowding to get access to females.
- Dolphins in mating groups most often lack swimming formation, an indication of uncoordinated competition.

Given that clean headfirst re-entry leaps allow dolphins to catch a breath and return rapidly to depth, it follows that dolphins might engage in a higher proportion of these leaps when chasing one another as well as when chasing prey (see Chapter IV). Such chases might be expected in play, agonistic interactions, or in a competitive social-sexual context. Therefore, I predict that with respect to social interaction and leaping activity:

- Interactive behaviors and social-contact behaviors occur most in mating groups, especially chases and behavioral precursors to copulation (e.g. inverted swimming).
- Re-entry leaps, allowing dolphins to catch a breath and return rapidly to depth, occur most in mating groups.
- If competition in mating groups involves more than just sperm competition, then multiple males attempt copulation with a single female but not all males present will succeed

Parental Care and Calf Development in Nursery Groups

The rearing of young plays an important role in shaping social relationships in many long-lived species, such as elephants (Lee 1987), lions (Heinsohn and Packer 1995), baboons (Altmann 1980), and macaques (Small 1990). In complex dolphin societies, as in those of other mammals, mothers invest a great deal of time and energy caring for their young (Johnson and Norris 1994). The polygynous-promiscuous mating systems of most dolphins (Würsig *et al*. 1989) make paternity uncertainty the rule, and, therefore, parental investment by the father is likely to be minimal (Trivers 1972). Because young are born large relative to their mothers and precocial, twinning is extremely rare in cetaceans (Whitehead and Mann 2000). Maternal investment involves energetic costs such as gestation, lactation, and assisting calves in locomotion (Waite 1988, Johnson and Norris 1994). Other costs might include trade-offs between time spent feeding or engaged in social activities and the need to care for young and defend them against predators (Mann and Smuts 1998). Females appear to keep track of calves using vocal signals. For example, female bottlenose dolphins and their calves produce highly individualized signature whistles that likely facilitate reunions when they become separated (Smolker *et al*. 1993).

To help offset the large demands of rearing young, mothers are sometimes assisted by social partners and relatives in their parental endeavor (reviewed in Riedman 1982, Packer *et al*. 1992). Alloparental behavior, while generally rare, appears to be widespread among odontocetes (reviewed in Whitehead and Mann 2000). Alloparenting has been observed in spotted dolphins, exhibited most often by sub-adult females

(Dudzinsky 1996); in killer whales (*Orcinus orca*), exhibited by adults of both sexes (Waite 1988); and in spinner dolphins, exhibited by animals of varying sex and age classes (Johnson and Norris 1994). Female bottlenose dolphins, which also engage in alloparental care (Shane 1990), exhibit high fidelity to social partners, maintaining associations over several years (Würsig and Harris 1990, Wells *et al*. 1987). Male bottlenose dolphins do not appear to assist in calf rearing activities (Wells *et al*. 1987). In addition to facilitating social bonds between caregivers, such relationships likely influence the incorporation of the developing calf into the social structure and are important for younger females "learning to parent" (Mann and Smuts 1998).

Predictions Concerning Nurseries

The social environments in which dusky dolphin calves are reared have yet to be described in detail. In New Zealand, "nurseries," usually comprised of between 6 and 12 adults and a smaller number of calves, have been identified. These groups appear to remain in shallow waters perhaps as protection from predators, such as killer whales and sharks (Würsig *et al*. 1997). Little else is known about the behavior, movements, and social relationships of dusky dolphins in "nurseries". Such "nursery" groups are also a prominent feature in bottlenose dolphin societies (Wells *et al*. 1987).

Calves are likely incapable of swimming as rapidly or at such sustained speeds as older dolphins. Maternal investment, involving energetic costs due to lactation and increased drag (Whitehead and Mann 2000), makes it likely that females with calves are more limited in their movements. This should favor resting, with slower mean and top swimming speeds, and a minimum of energetically costly high-speed activities. Given the high level of cooperation seen in many dolphin nurseries, it seems likely that these groups will swim in a synchronized manner. Therefore, I predict that with respect to movement patterns:

- Nurseries rest more than all other groups.
- Movement of nursery groups is generally coordinated: Heading of group members is less often variable than in mating groups, but more often variable than in large groups.
- Mean and top swimming speeds of nursery groups are slower than for all other groups.
- High-speed activities are least common in nurseries.
- Respiration rates are higher and swimming speeds are slower for adults accompanied by calves than for solo adults.

As calves are likely to be most vulnerable to predators, they are expected to maintain the closest proximity between individuals, and swim in such a formation as to be most prepared for danger. Circular swimming formations provide the greatest protection for individuals in the middle of the group, and are predicted by the "geometry of the selfish herd" (Hamilton 1971). Parallel formations facilitate searching, by allowing dolphins to effectively scan a larger area of water for potential predators (Norris and Dohl 1980). Swimming in parallel formation also allows mothers to keep calves between themselves and other group members, another form of defense. Therefore, I predict that with respect to inter-individual proximity and swimming formation:

- Dolphins in nursery groups maintain closer inter-individual proximity than do other groups.
- Dolphins in nursery groups most often swim in formation, either in parallel (searching), or circular (defensive).

Another potential purpose of nursery groups is that it provides a quieter, less boisterous environment for calves and their mothers to rest. If this is the case, then fewer boisterous social activities (especially high energy activities such as chases and leaping) should occur in nursery groups than other groups. Given the high level of cooperation seen in nursery groups of many species (Whitehead and Mann 2000), it is expected that nursery groups will include other attendants besides the mothers. Among primates, it is common for younger juveniles and subadults to seek access to offspring. Such behavior has also been observed in bottlenose dolphins (Mann and Smuts 1998). This may be important for developing relationships with newly born associates and for learning parenting skills employed later in life. Therefore, I predict that with respect to social interactions and leaping activity:

- Interactive behaviors and social-sexual contact behaviors occur least in nurseries.
- Leaping occurs at a very low rate, without a high proportion of re-entry leaps.
- If alloparenting occurs, then nurseries should include adult and/or juvenile "helpers" or attendants as well as mothers and calves.

Given high calf mortality (Whitehead and Mann 2000) and the tenuousness of early life, one would expect nursery groups to be particularly wary of human traffic, especially when calves are youngest. If this were the case, one would expect:

- Bowriding behavior in nurseries increases as calves mature.

Adults Forming Small Groups for Non-reproductive Purposes

The function of non-sexually active small groups of adults in Kaikoura is unknown. Perhaps they are formed to establish and maintain social bonds important in other contexts (e.g. feeding, mating, calf care).

Predictions Concerning Adult Non-mating Groups

As these groups are unlikely to be competing as in mating groups, they are not expected to swim as fast nor to exhibit as many high-speed behaviors as mating groups. Similarly, their movements should be more coordinated than mating groups and more restful than large groups, although not as restful as nursery groups as they are not under the same physical and energetic constraints. Therefore, I predict that with respect to movement patterns:

- Non-mating adult groups mill less and rest more than mating groups, but rest less than nurseries.
- Movement of non-mating adult groups is coordinated.
  -Heading of group members is less often variable than in mating groups.
- Mean and top swimming speeds are lower than large groups and mating groups but higher than nurseries.
- High-speed activities are more common than in nurseries, but less common than in large groups and mating groups.

As they lack safety in numbers, small adult groups should maintain closer proximity between individuals than large groups. However, as they are not actively engaged in mating, and as they are less vulnerable than calves, adult groups should spread out more than mating groups and nurseries. If they are comprised of one or more leaders, with others following casually behind, then an echelon formation would be predicted. Therefore, I predict that with respect to inter-individual proximity and swimming formation:

- Adult non-mating groups maintain closer inter-individual proximity than large groups, but spread out more than mating groups and nurseries.
- Dolphins in adult groups swim in echelon formation, as they fan out behind a leader or leaders.

If these groups serve to facilitate social bonding, then social-interactive behaviors in non-mating adult groups are expected more than in nursery groups, but less than in mating groups and in the busier large groups. Therefore, I predict that with respect to social interaction and leaping activity:

- Interactive behaviors and social-sexual contact behaviors occur more than in nurseries but less than in large and mating groups.
- Leaping occurs at a very low rate, without a high proportion of re-entry leaps.

In summary, predictions regarding behavior in different social groups were developed from what was previously known about dusky dolphin large groups, mating groups, nurseries, and non-mating adult groups in Kaikoura (Würsig *et al*. 1997). Table 7 reviews these predictions, with the expected ranking of each parameter by social group type.

Table 7: Expected ranking of parameters by social group
(greater numbers, proportions, and frequencies denoted by larger numbers and words)

Behavioral category	**Large**	**Mating**	**Nurseries**	**Adult**
behavioral state	travel	mill	rest	rest
uncoordinated movement	1	4	2	3
swimming speed	4	3	1	2
high-speed bursts	3	3	1	2
inter-individual distance	3	1	1	2
swimming formation	linear	none	parallel	echelon
interactive & social	3	4	1	2
noisy leaps	3	2	1	2
clean headfirst re-entry	2	3	1	2

Methods

Data Collection

Group Definition

From 1997-2003, 568 groups were located on 223 days in Kaikoura as described in chapter II with the help of shore based teams. Groups were defined using the "10-m chain rule" (Smolker *et al*. 1992). This inter-individual proximity definition of groups varies importantly from those employed in some cetacean research in that it merely requires individuals to be spatially and temporally clustered, and does not necessarily require them to be behaving similarly (Mann 1999*a*). To draw a human analogy, individuals belonging to a group of college students under this definition might be engaged in activities as diverse as feeding, napping, studying and exercising so long as they were all within the same dorm room. Such a spatial and temporal definition of groups is particularly appropriate for a study of social behavior as it allows examination of interactions between individuals behaving quite differently.

Social groups were divided into four types: large groups ($\geq$ 50 individuals), nursery groups (< 50 individuals with calves), mating groups (< 50 individuals with confirmed sexual activity), and adult groups (< 50 individuals with neither calves nor sexual activity).

Focal Group Sampling Procedure

During 289 focal group follows with 169 large groups, 42 mating groups, 41 nurseries, and 37 adult groups, data were collected during 40-minute behavioral sampling sessions divided into 2-minute intervals as detailed in chapter II. Instantaneous sampling was used to document behavioral state, inter-individual proximity, group swimming formation, group speed, group heading (variable if dolphins within the group were headed in different directions), and the number of bow-riding dolphins (see Chapter II, Table 4). As the focus of the present study was the nature and context of social behavior in dolphin groups, no blanket "social" category was employed for behavioral state (as in Shane 1990). In other words, for the purpose of this study, all groups examined were considered "social"; the question was *how* the dolphins were associating. Noisy leaps, clean headfirst re-entries, and acrobatic flips, were recorded by all-occurrences sampling, with the number of leaps per bout and per interval documented (see Chapter II, Figure 5).

In addition to the instantaneous and all-occurrences recording described in chapter II, one-zero sampling was used to compare interactive and social-contact behaviors between groups. One-zero sampling documents whether or not a behavior is observed during an interval (Martin and Bateson 1993). One-zero scores do not provide accurate estimates of either frequency or duration (Altmann 1974). For this reason, some researchers have cautioned against the use of such a sampling protocol (e.g. Mann 1999*a*). However, if results are interpreted carefully, one-zero sampling is not only an acceptable protocol providing a meaningful measure of the "amount" of behavior, but often the only practical method for recording intermittent behaviors (Martin and Bateson 1993). While duration and frequency measures of the same behavior are often poorly correlated, one-zero sampling provides a weighted measure relative to both duration and frequency (Rhine and Linville 1980).

High speed, interactive, and social contact behaviors were recorded by one-zero sampling. High-speed behaviors were used as an indication of brief and/or sustained rapid movement (Figure 23).

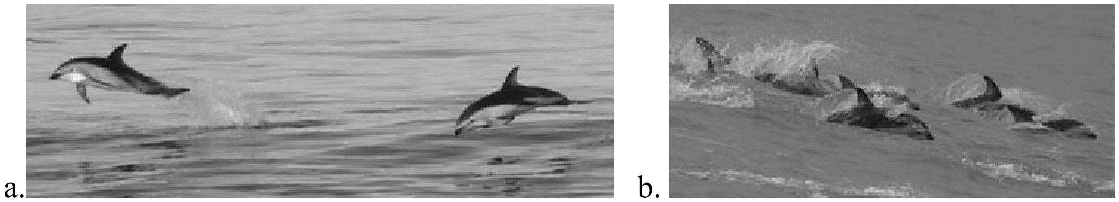


Figure 23. High-speed behaviors documented by one-zero sample were: a. porpoising ("clean" lateral leaps) and b. speed bursts ("slicing"). Speed bursts by only some individuals within the group ("some slicing") and simultaneous speed bursts by all group members ("group slicing") were documented separately.

Porpoising was defined as a clean lateral leap. Such low horizontal leaps, with minimal slapping or splashing, generally occur at moderate to high speeds (Bel'kovich *et al*. 1991). Porpoising allows dolphins to catch a breath and re-enter the water oriented in a relatively horizontal direction of travel. As air is about 800 times less dense than water, such leaps may also function to briefly reduce drag; porpoising spotted dolphins were estimated using aerial photogrammetry to leap 6.8 m on average, resulting in a minimum "airspeed" of 29.5 km/hr (Au *et al*. 1988). While such leaps are discrete events, many dolphins engage in them simultaneously over short periods, making it impossible to count all-occurrences or measure accurately by instantaneous sampling. Speed bursts were defined as rapid movement along the surface resulting in spray as the dolphins "sliced" through the water. Generally, such "slicing" was observed in conjunction with swimming speeds of 16-22 km/hr, often brief and intermittent. For each interval, observers noted whether some, all, or none of the members of the group displayed "slicing" bursts of speed.

Interactive behaviors included tail slapping, playing with kelp, bubble blowing play, chasing, eye outs (also called "spy hopping") and inverted (or "belly up") swimming (Figure 24). As the term suggests, these behaviors occurred in an interactive context without necessarily involving physical contact between individuals.

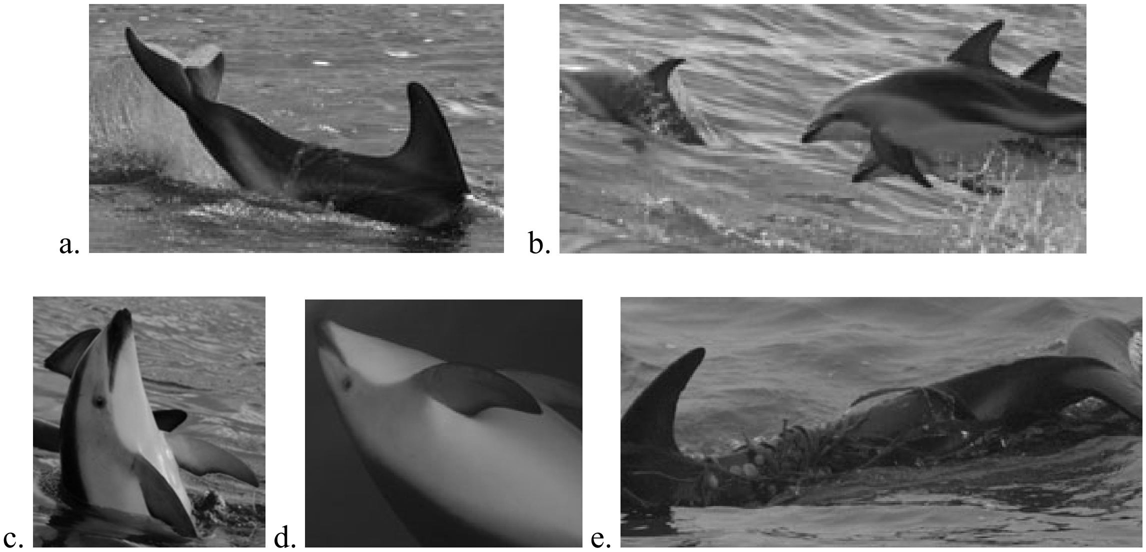


Figure 24. Interactive behaviors, documented by one-zero sample at 2-minute intervals, included: a. tail slap, b. chasing, c. eye out (or "spy hop"), d. inverted (or "belly up") swim, e. playing with kelp, and bubble blowing play (not pictured).

For interacting bottlenose dolphins, tail slapping, in which the dolphin hits the surface of the water with the ventral surface of the flukes, is generally considered an act of aggression (Shane *et al*. 1986). Dragging kelp and blowing bubbles are often observed as a form of play among dolphins. Chasing, defined as rapid movement and changes in direction with one or more individuals following another closely, may occur in the context of play, competition, or mating. Dolphins can see well both in and out of water (Herman *et al*. 1975). They use eye outs, in which they pause with the head elevated perpendicular to and above the surface of the water, to see above the surface (Tyack 2000). Such spy hopping allows dolphins to see further and to see things of interest, such as people on boats, that are above the surface.

Social-sexual contact behaviors examined in this study are shown in Figure 25. As evidenced by observation of social-sexual interactions during non-estrous breeding seasons (Chapter II), with other species (see Chapter IV), and with same sex partners, dusky dolphins engage in mating and other contact behavior for social as well as reproductive reasons (similar to bottlenose dolphins, Connor *et al*. 2000). Although not discrete events, social-sexual contact behaviors occur rapidly and infrequently. Therefore neither continuous nor instantaneous sampling methods could adequately document these behaviors, and one-zero sampling was employed. Social rubbing (Connor *et al*. 2000, defined as any touching of the body), ventral presentation (or two dolphins swimming “belly-to-belly”), and sexual approach (approaching another dolphin with the penis out), often preceded mating. However, copulation was noted only if intromission was confirmed. Social contact behaviors were the most difficult behaviors to observe at a distance, limiting research teams’ ability to detect all social-contact behaviors in large groups spread out over a distance. However, within a radius of roughly 20m, all near surface social-sexual contact could reliably be documented.

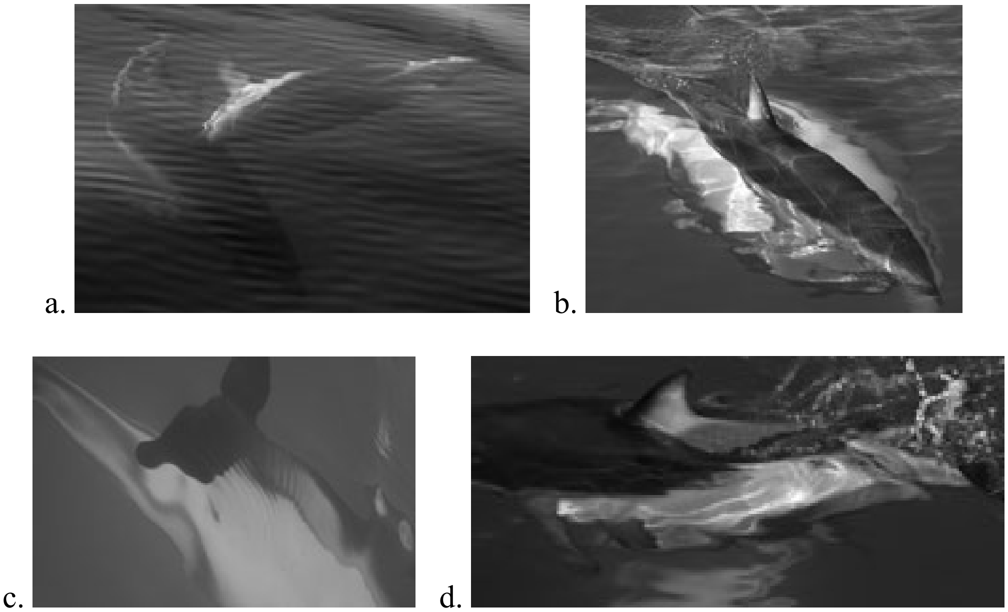


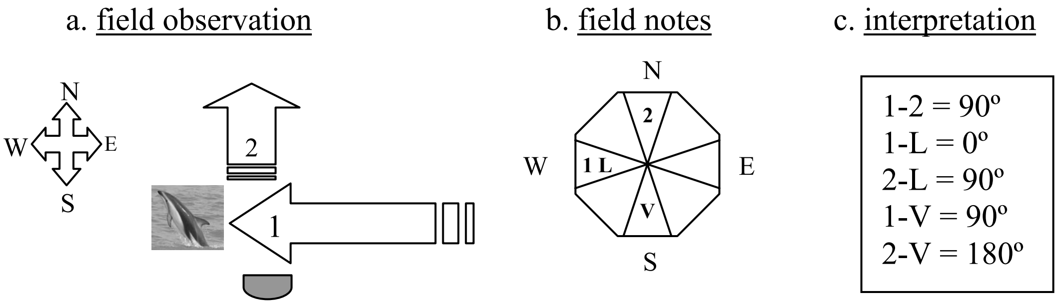
Figure 25. Social-sexual contact behaviors documented by one-zero sample at 2-minute intervals in this study were: a. social rub, b. ventral presentation ("belly-to-belly swim"), c. sexual approach with penis out, and d. confirmed copulation (intromission). Small groups were classified as mating groups if either b and c or d were observed.

Additional Methods Used to Examine Particular Social Group Types

Large Groups

Additional data were collected on behaviors maintaining group cohesion as well as responses to boat traffic in large groups. Factors influencing changes in heading were examined, in order to investigate how group unity is maintained and whether it is strained by human disturbance. In large pods, all occurrences of changes in pod heading > 45° were noted, including the first and second heading, the location of greatest leaping activity, and the location of vessels (Figure 24).

Additional data on dolphin-tour interactions in large groups were collected on 31 trips during 77.5 hours on Dolphin Encounter tour boats. These supplemental data included the number and duration of swim drops, the number of swimmers per drop, and vessel activity during swims.


a. field observation

b. field notes

c. interpretation

Figure 26. At each change of heading > 45 degrees in large groups, data were collected as shown on the initial and second heading of the group in relation to noisy leaping activity and vessels. a. In this schematic, dolphin group heading is represented by arrows (initial = 1, changed = 2), with the photographed dolphin and gray boat representing the relative position of noisy leaping activity and a vessel. b. Data were collected on data sheets with the initial heading (1), changed heading (2), leaping activity (L), and vessels (V) noted as shown. c. In analysis, these notes were tabulated as shown.

Mating Groups

To learn more about the dusky dolphin mating (effort) system, behavioral observations were combined with the use of still photographs and digital video to identify and sex individuals (Figure 27). A Canon Optura digital video camera was used to record a total of 6.87 hours of above-water video of mating activity in 27 small mating groups. These data were used to examine mating group size, composition, and the involvement of particular individuals in mating activities. During digital video sessions with mating groups, volunteers continuously called out the location of dolphins plus social contact and interactive behaviors. This audio record proved to be every bit as valuable as the video record. As much as possible, the number of females and males in each group, and their position with respect to sexual and social interactions, were documented.

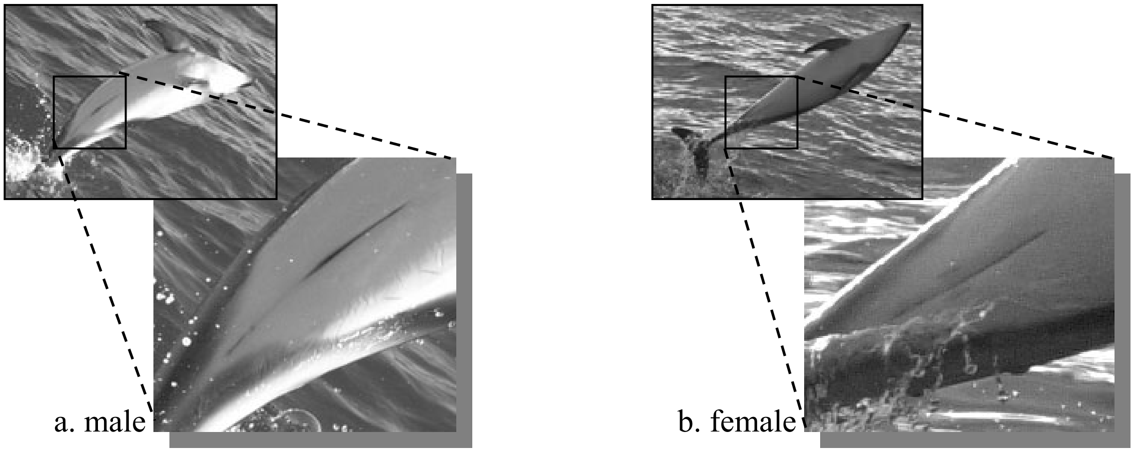

a. male
b. female

Figure 27. Dolphins were sexed using digital photographs (as shown), digital video, and observations in the field. A. Males were identified by the distance between the genital slit and anus. B. Females were identified by the lack of separation between the genital slit and anus, and by mammary slits.

Nurseries and Non-mating Adult Groups

In nursery groups, data were collected on the respiration rates and behavior of focal individuals in order to learn more about the costs associated with parental effort. Focal individual samples of resting respiration rate were conducted with 13 identifiable adults in nursery groups. During focal dolphin respiratory samples, a note-taker recorded times between blows and swimming speed while observers called every blow.

Sample sizes were limited due to the difficulty of this sampling technique; adults with (n = 4) and without calves (n = 9) were compared.

Data Analysis

Data were sorted for analysis by social group type. Behavioral data were transposed to Microsoft Excel spreadsheets, with tallies of instantaneous samples, one-zero samples, number of bowriding dolphins, number of intervals with bowriding, number of leaps, leap bouts, and intervals with leaping. These were used to calculate proportions of intervals in which behaviors were observed and mean values per 2-minute interval for all samples. To eliminate bias based on the number of individuals present in groups of varying sizes, variables for which frequencies were documented (leaping) were converted to proportional values within each sample. In order to do this, the number of noisy leaps, clean leaps, and flips were divided by the total number of leaps for each 40-minute sample.

Statistical analyses were conducted on values from samples of independent group encounters on different days using SPSS v. 11.0.1. As variances were heterogeneous (failing Levene's test) even when proportional dat were arcsine transformed (Lehner 1996), non-parametric statistics were used in these analyses. Data were compared across groups using Kruskal-Wallis, applying the non-parametric sequential Bonferroni table-wide technique for post-hoc comparisons (Rice 1989). Large group changes in direction with respect to leaping activity and vessels were examined by comparing heading with respect to the variable in question prior to and following the change using Wilcoxon signed-rank tests. Simple linear regression and Pearson Correlation were used to examine the relationship between number of vessels and large group swimming speed. Analyses of digital video of mating groups (detailed in McOmber 1999) were combined with still photographs and field notes to describe mating group composition and interactions. Bowriding activity in nurseries was compared by season, beginning with the spring calving season (Cipriano 1992, see also Chapter II).

Results

Social Group Comparisons

Movement Patterns

Activity budgets of large groups (>50 individuals) and smaller mating groups differed significantly from each other and those of small nurseries and non-sexually active adult groups (Figure 28). The proportion of 2-minute intervals (out of 20) dolphins engaged in traveling (Kruskal Wallis $H = 37.427$, $P < 0.001$), milling (Kruskal Wallis $H = 41.007$, $P < 0.001$), and resting (Kruskal Wallis $H = 25.135$, $P < 0.001$) varied significantly between these social groupings, with large groups traveling more, mating groups milling more and resting less, and nursery and adult groups resting more than other social groups (Post Hoc Comparisons, Bonferroni, $P < 0.05$, Figure 28). Feeding was observed <1% of intervals of dusky dolphin daytime behavior in Kaikoura.

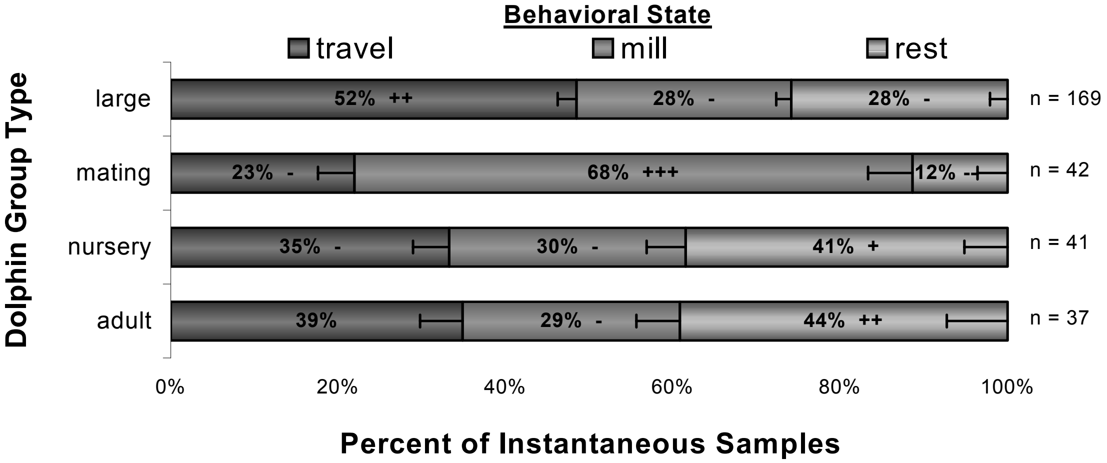


Figure 28. Daytime activity budgets of dusky dolphins in different social groups are shown as % samples traveling, milling, resting and feeding (mean values with 1 standard error of the mean). Data labels indicate the percent of all instantaneous samples during which each behavioral state was noted (+ - Bonferroni, $P < 0.05$). As all behavioral states observed within groups was noted, these percentages total more than 100%, but have been standardized per group (sample sizes indicated on the right) on the x-axis.

Variability in dolphin heading, defined as the proportion of instantaneous samples at which group members were headed in different directions (>45º different in the horizontal plane by compass bearing), varied significantly across social group types (Kruskal Wallis $H = 31.635$, $P < 0.001$). Mating groups were most likely to swim in an uncoordinated fashion, while large groups exhibited the least variability, indicating the most coordinated movement (Bonferroni, $P < 0.05$, Figure 29).

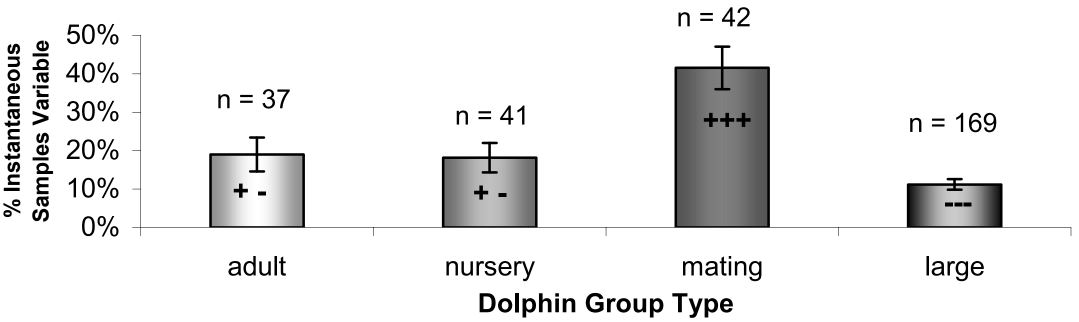


Figure 29. Bars represent the percent of instantaneous samples at which dolphins swam in variable headings (mean values with 1 standard error of the mean), compared between types of social groups. "+" and "-" indicate significant differences (Bonferroni, $P < 0.05$).

Mean (Kruskal Wallis $H = 10.633$, $P = 0.01$) and maximum (Kruskal Wallis $H = 10.375$, $P = 0.02$) estimated swimming speeds varied significantly between different dolphin social groups. Mean and top swimming speeds were fastest in large groups, and mean speeds were slowest in nurseries (Figure 30).

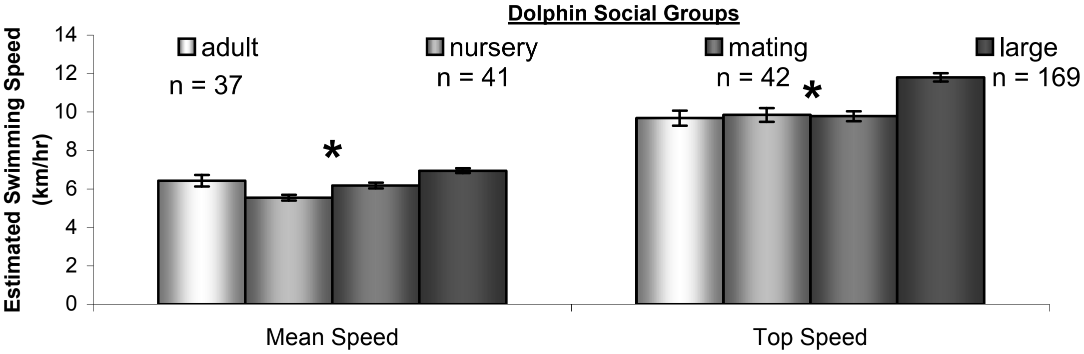


Figure 30. Mean and top speeds (km/hr, mean values with 1 standard error of the mean) are compared between social groups (* Kruskal Wallis, $P < 0.05$).

High-speed activity occurred most commonly in large groups and least commonly in small nurseries and non-sexually active adult groups (Figure 31). The percent of intervals with speed bursts (Kruskal Wallis $H = 29.839$, $P < 0.001$) and lateral porpoising (Kruskal Wallis $H = 62.620$, $P < 0.001$) varied significantly between social group types.

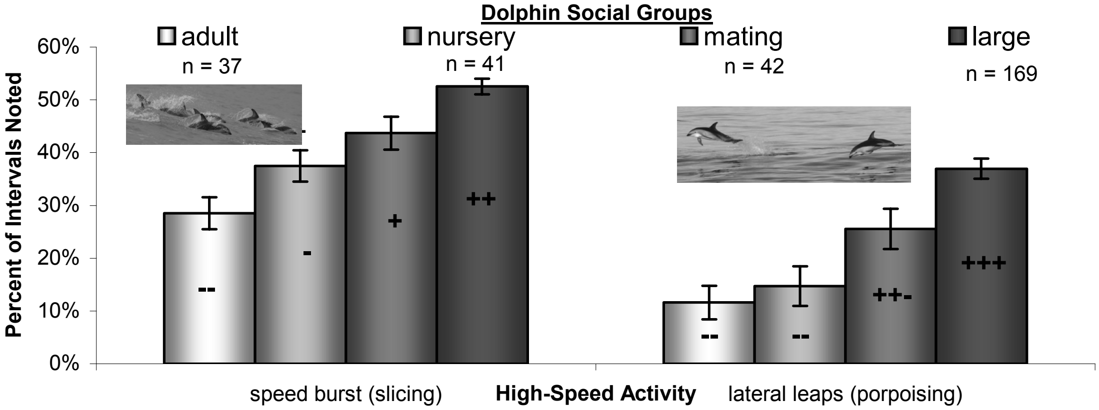


Figure 31. High-speed behaviors are compared between types of social groups. Bars represent the percent of intervals during which dolphins engaged in high-speed activities (mean values with 1 standard error of the mean). Significant differences are indicated by "+" and "-" marks (Bonferroni, $P < 0.05$).

Spread (Inter-individual Distance) and Swimming Formation

Inter-individual distance was greater in large groups than in small groups, with the closest proximity maintained between individuals in mating groups (Figure 32). Individuals were in close proximity (0-1 body lengths) less often (Kruskal Wallis H = 52.129, $P < 0.001$), and spread at a moderate (1-3 body lengths, Kruskal Wallis H = 28.481, $P < 0.001$) to large distance (> 3 body lengths, Kruskal Wallis H = 26.794, $P < 0.001$) more often in large groups than in smaller groups (Post Hoc Comparisons, Bonferroni, $P < 0.05$).

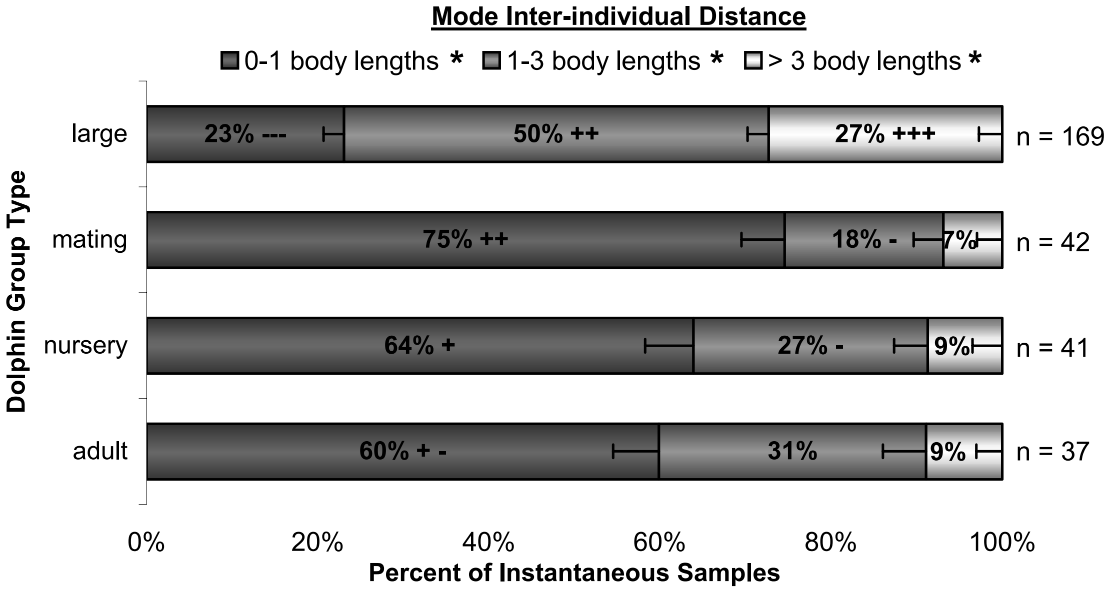


Figure 32. The proximity maintained between dusky dolphins in different social groups in Kaikoura is shown by mode nearest neighbor distance in body lengths. Bars represent the percent of instantaneous samples dolphins were <1 body length, 1-3 body lengths, and > 3 body lengths apart (mean values shown with 1 standard error of the mean). Significant differences are indicated by "+" and "-" marks (Bonferroni, $P < 0.05$).

Large groups, mating groups, nurseries, and adult groups differed in the proportion of intervals that dolphins were observed in various swimming formations (Figure 33). Observed frequencies of circular (Kruskal Wallis $H = 10.227$, $P = 0.02$) and linear (Kruskal Wallis $H = 14.036$, $P = 0.003$) formations varied between groups, with large groups swimming most often in these configurations. The propensity of dolphins to swim in parallel differed between group types (Kruskal Wallis $H = 20.780$, $P < 0.001$), with nursery groups most often and mating groups least often assuming this form. The frequency of echelon, or “v”, formations varied significantly (Kruskal Wallis $H = 15.046$, $P = 0.002$), most often exhibited by small non-mating adult groups. The frequency of associating dolphins lacking a clear swimming configuration varied significantly between groups (Kruskal Wallis $H = 14.036$, $P = 0.003$), with small mating groups least often swimming in formation.

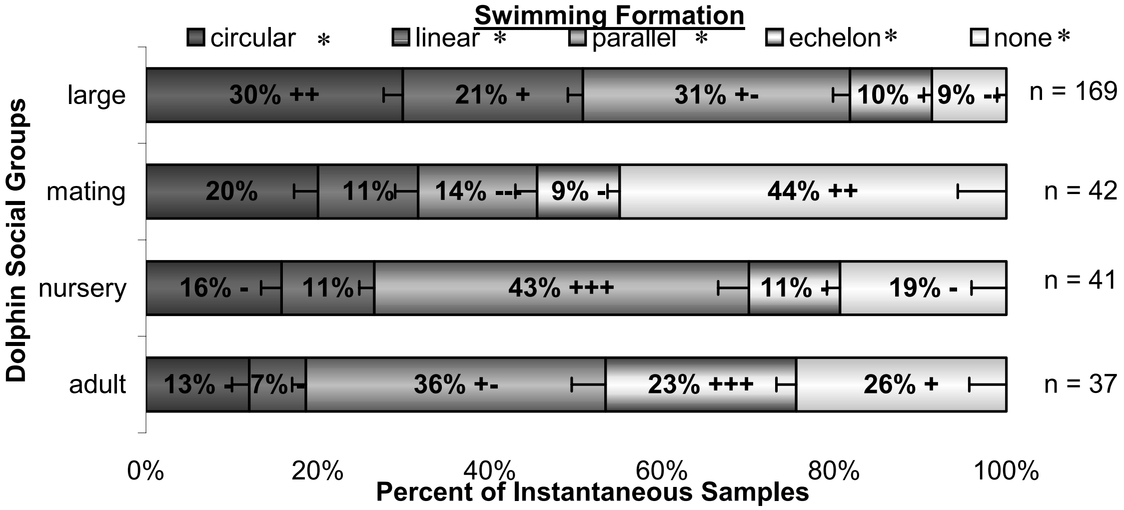


Figure 33. Group swimming formation is compared by social group type. Bars represent the percent of instantaneous samples dolphins when swam in circular, linear, parallel, echelon, and no formation (mean values shown with 1 standard error of the mean) Significant differences are indicated by “+” and “-“ marks (Bonferroni, $P < 0.05$).

Social Interactions

Interactive behaviors were noted during the highest proportion of intervals in mating groups and large groups (Figure 34). Inverted swimming (Kruskal Wallis $H = 56.264$, $P < 0.001$) and chasing (Kruskal Wallis $H = 44.197$, $P < 0.001$) occurred most frequently in mating groups. Tail slaps were most commonly noted in large groups (Kruskal Wallis $H = 89.493$, $P < 0.001$). Eye outs (spyhopping) was more common in large groups and mating groups than in non-sexually active adult groups (Kruskal Wallis $H = 19.546$, $P < 0.001$).

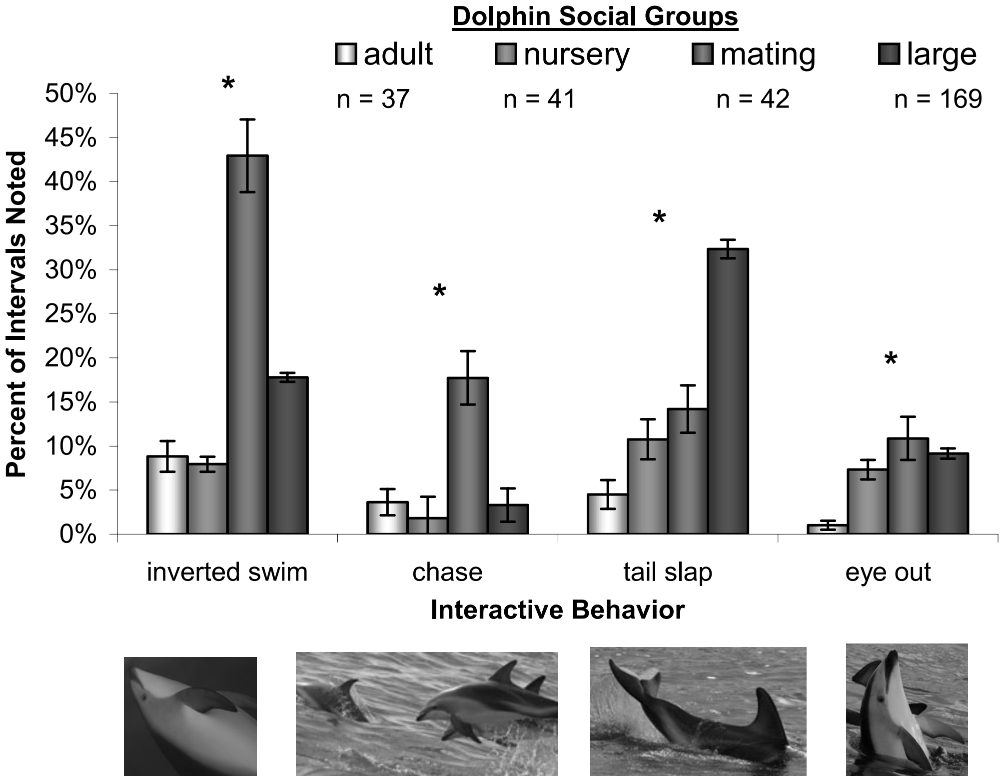


Figure 34. Interactive behaviors are compared between different social groups. Bars represent the percent of intervals during which dolphins engaged in interactive behaviors (mean values with 1 standard error of the mean). Significant differences are indicated by "*" marks (Kruskal Wallis, $P < 0.001$).

The percent of intervals with social rubs (Kruskal Wallis, $H = 59.345$, $P < 0.001$) and ventral presentation (Kruskal Wallis, $H = 99.672$, $P < 0.001$) differed significantly across social group types. Social contact behaviors occurred in 4-5 times as many intervals in mating groups as in other group types (Figure 35).

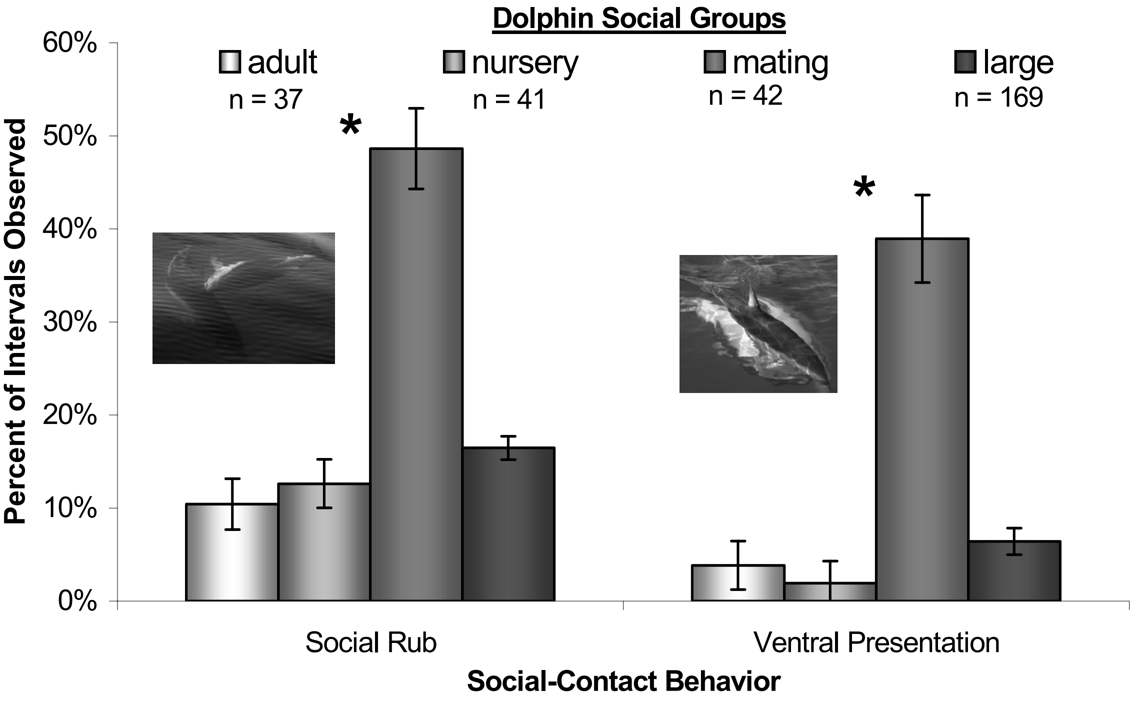


Figure 35. Social-contact behaviors are compared between different social groups. Bars represent the percent of intervals during which dolphins engaged in social-contact behavior (mean values with 1 standard error of the mean). Significant differences are indicated by "*" marks (Kruskal Wallis, $P < 0.001$).

Large, mating, nursery, and adult groups varied not only in the number of leaps counted but also in their prevalence, with different proportions of noisy leaps (Kruskal Wallis, $H = 78.666$, $P < 0.001$), clean headfirst re-entry leaps (Kruskal Wallis, $H = 82.613$, $P < 0.001$), and acrobatic flips (Kruskal Wallis, $H = 52.340$, $P < 0.001$) between group types (Figure 36). Large groups engaged in greater proportions of noisy leaps and acrobatic flips, while mating groups engaged in higher proportions of clean headfirst re-entry leaps than other groups (Post Hoc Comparisons, Bonferroni $P < 0.05$).

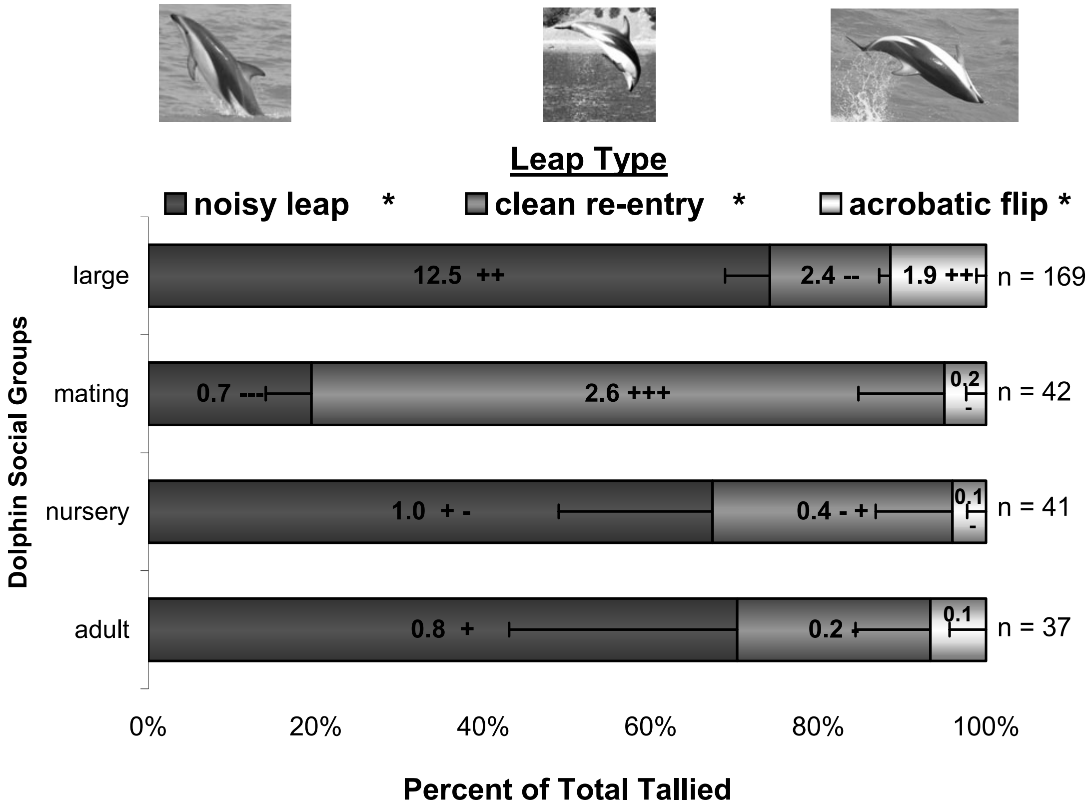


Figure 36. Proportions of leaps by type are compared between social group types. Bars represent the percentage of noisy leaps, clean headfirst re-entries and acrobatic flips out of the total number of leaps (mean values shown with 1 standard error of the mean). Data labels indicate the mean frequency of leaps per 2-minute interval. Significant differences in leap proportions between social groups are indicated by “+” and “-“ marks (Bonferroni, $P < 0.05$).

Results from Particular Social Groups

Large Groups

Large groups ranged in size from 50 to an estimated >1,000 dolphins. Group sizes tended to be largest with fewest calves and juveniles in winter and smallest with more juveniles and calves in summer (see Chapter II, Figure 8). Noisy leaps, which occurred most frequently in large groups, appeared to act at least at times as a signal, directing group movements. We noted in the field that such leaps often occurred around the periphery of the large groups. Large groups changing directional heading by at least 45 degrees most often turned away from dolphins engaged in noisy leaping (Figure 37). Thus the changed heading was significantly further away from noisy leaping activity than the initial heading (Wilcoxon signed ranks test, $z = 4.542$, $P < 0.001$, n = 169).

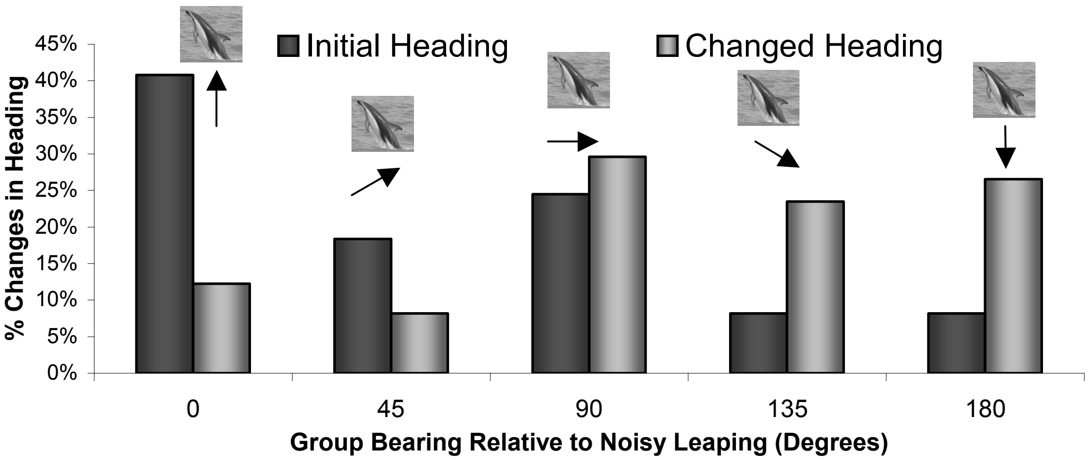


Figure 37. Changes in heading of large groups are examined with respect to noisy leaping activity. Bars compare the bearing of the dolphin group relative to leaping activity before versus after a change in heading ≥ 45 degrees.

Large groups had frequent visitation from other vessels in addition to the research vessel. Other vessels were present during 55 ± 4.8% of observation intervals (mean ± s.e., n = 169). Dolphin Encounter (the larger of the two commercial dolphin tours) vessels were present during 36 ± 4.2 % of observation intervals with large pods, New Zealand Sea Adventures (the smaller dolphin tour company) vessels were present 6 ± 1.7 % of time, Whale Watch (the only other cetacean tour company) vessels were present 9 ± 1.8 % of time, and other vessels (e.g. fishing vessels) were present 4 ± 0.8% of the time. No tour vessels were noted to be with nurseries (n = 61), and observation of vessels other then the research vessels with mating and small adult groups was rare (<<1 percent, n = 197). Tourists swam with the dolphins during 12 ± 1.7 % of observation periods with large pods, with an average of 11.8 ± 0.91 swimmers in the water at any one time (mean ± s.e., n = 169). Roughly two-thirds of passengers signed up for a swimming tour, but they spent less than 25 percent of the tour actually engaged in swimming with dolphins (n = 31). Vessel activity was minimal during approximately one-half of swims, which were almost always with large pods although calves were frequently present (Table 8).

Table 8. Data on dolphin swim tour activities collected onboard dolphin tour vessels

Mean Tour Length	2 hours, 7 minutes
Passengers	Mean # Swimmers = 11.5 Mean # Spectators = 6.4
Swim Drops	3.4 drops per trip 8.3 minutes per drop 10.8 swimmers per drop
Vessel Activity	Stationary = 59.6 % Engine Off = 47.9 %
Pod Description	> 90% swims with large pods Calves present 71.4 % of swims

Dolphin tour vessels most commonly visited large groups. If these groups were disturbed by vessel presence, then one might expect the dolphins to increase speed, a "fight or flight" response. However, the opposite response was observed. Mean and top swimming speed of dolphins decreased with increasing vessel presence (Figure 38).

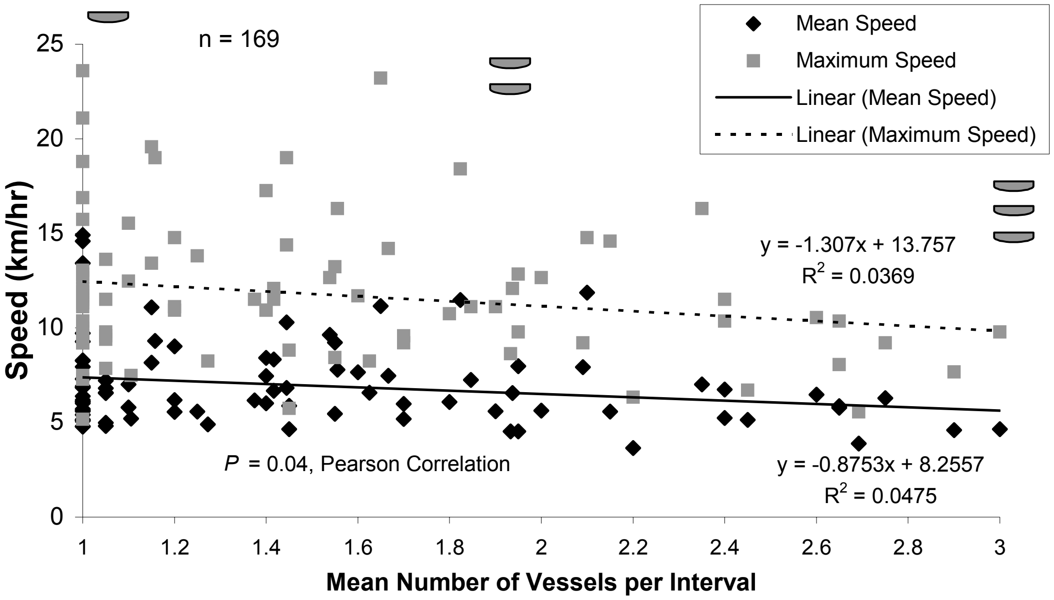


Figure 38. Estimated mean and maximum speeds of large groups are plotted by mean number of vessels present. Trend lines represent linear regressions.

Large groups changing heading showed no general tendency to turn away from or toward vessels. However, in particular, large groups were more likely to turn toward than away from the research vessel (Wilcoxon signed Ranks test, $z = 3.292$, $P = 0.001$, Figure 39). In comparison, dolphins did not turn toward or away from tour vessels more than would be expected by chance (Wilcoxon signed Ranks test, $z = 0.088$, N.S.). Dolphins in large groups engaged in bowriding at (mean ± s.e.) 49 ± 2.3% of instantaneous samples, versus 17 ± 3.2% in mating groups, 18 ± 4.2% in nurseries, and 17 ± 4.3% in adult groups. This further indicates that at least some members of large groups (mean ± s.e. = 2 ± 0.1) were drawn to interact with vessels about half the time.

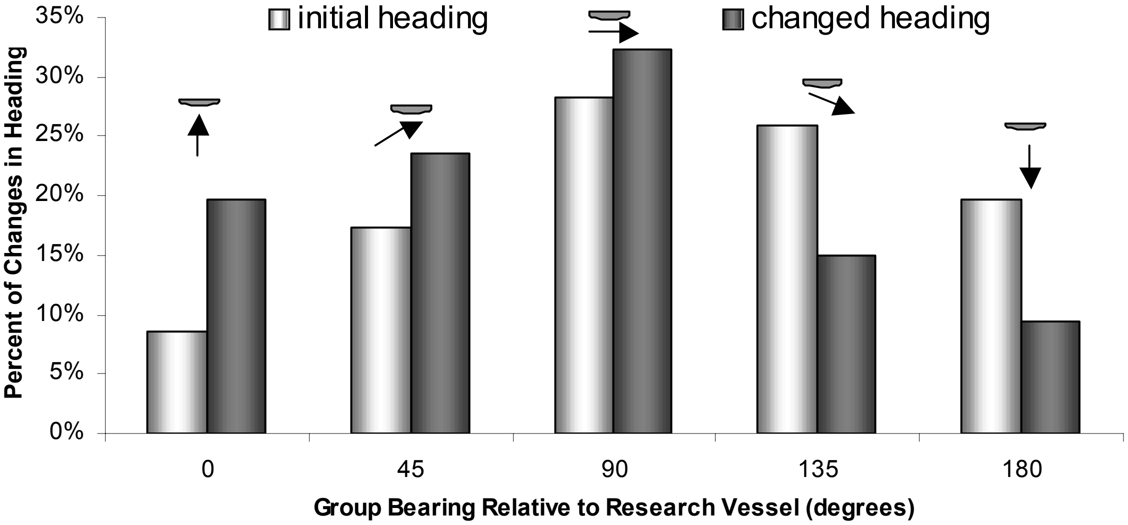


Figure 39. Changes in heading of large groups are examined with respect to the position of the research vessel. Bars compare the bearing of the dolphin group relative to the research vessel before versus after a change in heading ≥ 45 degrees.

Mating Groups

Small mating groups (n = 42) were comprised mainly of adult animals (median =7, range = 3 to 35), with fewer juveniles (median = 0.5, range = 0 to 6). Most groups were comprised of <10 males and a single female (median #: Males = 6, Females = 1). The mating period (period of highest sexual activity during the focal observation) ranged from 4 to 34 minutes (median =13 minutes). During mating periods, confirmed intromission occurred rapidly, with multiple partners. Inter-copulatory intervals ranged from 34 to 126 seconds (median = 49 seconds). Both males and females were observed to have multiple sexual partners over these short periods of time; however, single females more often mated with multiple males. In one exceptional case, a single male mated exclusively with two females over the course of one of these brief mating periods.

The number of individuals (males) confirmed in ventral presentation represented only 22%-75% of those present. During ventral presentation (swimming "belly-to-belly" as they do when copulating), all dolphins that could be sexed in the ventral up position were males. Usually one, rarely two, individuals were in the ventral down position. Those that could be sexed were all females. These same individuals were consistently chased. Re-entry leaps were commonly associated with chases, and occurred at high rates in mating groups.

Mothers with calves appeared to avoid mating group activities. Mothers with calves were observed in mating groups on just three occasions. In each case, a lone female with a very young calf was the object of the chase. These chases were particularly rapid, with both the mothers and the calves showing signs of distress. In one case, calf tossing was observed. In another, the female and calf were escorted away from mating activity by two other adults, apparently from their nursery group.

Nurseries

Calves made up 25 ± 3.0 % of nursery group membership (mean ± s.e., n = 61). In other words, on average, there were three older animals for each calf in nursery groups. Specifically, nursery groups were comprised of 13 ± 1.6 adults, 1 ± 0.5 juveniles, 4 ± 0.7 older calves, and 1 ± 0.4 neonates on average (mean ± s.e., n = 61).

In nursery groups, bow riding increased with calf maturation as the seasons progressed (Figure 40). Both the percent of instantaneous samples at which bowriding was noted (Kruskal Wallis $H = 17.261$, $P = 0.001$) and the mean number of bowriders per interval (Kruskal Wallis $H = 18.122$, $P < 0.001$) changed significantly between seasons (n = 41).

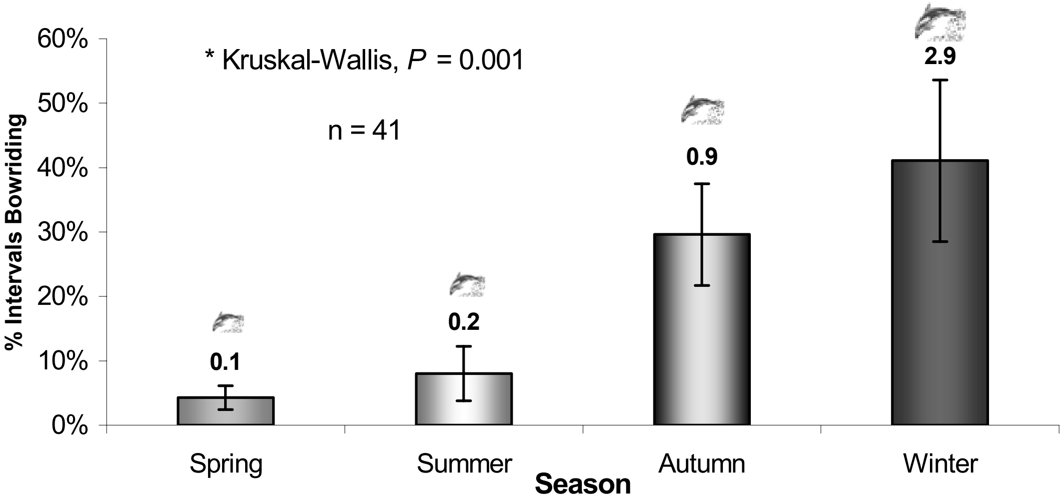


Figure 40. Bow-riding by members of nursery groups is plotted by season, beginning with the calving season and corresponding roughly to calf maturation. The percent of instantaneous samples with bow-riding dolphins are shown for each season. Bars represent mean values ± 1 standard error. Data labels indicate the mean number of bow riding dolphins per 2-minute instantaneous sample.

Contrary to expectations that nursery groups would be found closer to shore than other groups, no significant differences were found in mean positions between nurseries and other groups.

Resting respiration rates did not vary significantly between adults with calves and adults without calves in nursery groups. Failure to reject the null hypothesis in this case may be due to high variability combined with a low sample size (adults with calves $n = 4$, adults without calves $n = 9$) owing to the difficulty in obtaining focal individual data. Respiration rates (mean ± s.e.) were 5.7 ± 1.37 breaths per minute (inter-breath interval = 16 ± 4.1 seconds) for adults with calves, and 4.2 ± 0.24 breaths per minute (inter-breath interval = 22 ± 3.8 seconds) for adults without calves. Mean (± s.e.) resting swimming speeds were slightly lower (Mann-Whitney $z = 1.607$, $P < 0.05$) for adults with calves (3.2 ± 0.60 km/hr) than for adults without calves (4.4 ± 0.43 km/hr).

Small Non-mating Adult Groups

Small non-sexually active groups were comprised of (mean ± s.e.) 9 ± 1.3 adults and 1 ± 0.2 juveniles ($n = 37$). These groups were observed in Kaikoura in all seasons, and were generally restful.

Discussion

Large Groups

Movement Patterns

As hypothesized, cohesive, coordinated, steady movement characterized large groups of dusky dolphins. Such coordinated movements are likely to be important if the dolphins are to respond efficiently as a group to changes, including potential dangers, in their environment. As predicted, these large groups traveled more than other groups, exhibiting higher mean and top swimming speeds, with all group members generally moving in the same direction. It is not surprising, therefore, that high-speed activities were more common in large groups. Lateral leaps (or "porpoising") in particular likely increase the speed and efficiency of travel (Au *et al*. 1988).

Spread and Formation

As hypothesized, dolphins in large groups maintained a greater inter-individual proximity than in smaller groups. This is likely due to the greater "safety in numbers" resulting in the dolphins assuming a less defensive posture. Nevertheless, circular formations were a surprisingly regular feature in large groups. Although predators such as killer whales and sharks may attack from below, such formations likely provide protection from danger, especially for dolphins toward the middle of the group (Hamilton 1971). An interesting topic for future study would be to examine whether females with calves in large groups are found nearest the middle of the group. The linear (although not necessarily "single file") formation, predicted for groups traveling with some leaders and other stragglers, was observed most frequently in large groups, but was not as prevalent as might be expected, occurring less than one fourth of the time.

Social Interaction

Noisy leaps, which as predicted comprised an especially high proportion of leaps in large groups, appear to act as a long-range signal, directing group movement. Given that large groups of dusky dolphins form to reduce risk of predation, it stands to reason that certain individuals have "watch duty" while others rest. Unlike terrestrial mammals, dolphins need to remain active enough to surface and breathe regularly (breathing is a conscious activity), even while asleep. Dolphins accomplish this feat through hemispheric sleep, effectively keeping half the brain awake (Ridgway 1986). In elephants, a common behavior observed during resting periods is that certain individuals will "stand over" other recumbent individuals (Moss 1988, Brockett *et al*. 1999). When observing dusky dolphins resting in large groups, it is common to see active individuals on the outer edges of the groups. These individuals frequently engage in noisy leaping activity.

Zahavi and Zahavi (1997) suggest that stotting in impala represents a handicap, a reliable signal to the predator of the fitness and alertness of their prey. If the prey animal(s) can convince the predator that the energy obtained by successful prey capture is not worth the energy expended or that the probability of hunting success is sufficiently low, then the energy expended in leaping and the greater risk incurred by attracting the predator's attention are more than compensated by the energy saved in avoiding the predator and the reduced risk of being captured. It is possible that “noisy” leaping serves a similar purpose in dusky dolphins, but this seems unlikely because 1) it appears to occur frequently in the absence of potential predators; and 2) it does not appear to occur at an especially high frequency (in fact the frequency declines) when the dolphins are in close proximity of potential predators (at least killer whales).

Nevertheless, these leaps are loud (can be heard at least 300-500m from the source by humans, and probably even further), require significant energy, are usually repeated (>95 percent occur in bouts), and occur most often in large groups. This suggests that they represent a signal, but not to potential predators, as they rarely occur near killer whales. In foraging contexts, noisy leaps are correlated with location of prey, and it has been suggested that small foraging groups may recruit additional help in cooperative hunting of schooling fish (Würsig and Würsig 1980). However, during the daytime, foraging in Kaikoura is minimal (observed in <<1 percent of groups), and resting dolphins are generally not foraging. Therefore, noisy leaping might function to maintain group cohesion and coordinate movement. The “guard duty” or “scout” role could be combined with that of “traffic cop”, ensuring that the group stays together even when the majority of its membership is literally “half-asleep”.

Although strikingly apparent during resting periods, noisy leaps occur most frequently during more active periods (see chapter II). Signals with regard to group movement may be most important when groups are more “rapidly on the move”. Leaps on the sides of the group could effectively prevent individuals straying out to one side, leaps behind the group could serve to keep stragglers moving, and leaps in front of the group could signal individuals in front to change direction, or perhaps “herd” them in another direction. Data from this study provide support for the notion that noisy leaps in front of a group result in changes in direction away from the leaping.

The prevalence of tail slaps in large groups also highlights their potential importance as a long-range signal. These tail slaps appear to occur in high-energy contexts, although not necessarily in agonistic situations as is commonly observed in bottlenose dolphins (Shane 1990).

Other interactive and social-contact behaviors were noted less often in large groups than in mating groups, but more often than in nurseries and non-mating adult groups. Social-sexual interactions, chases, and play appear to represent a regular component of dolphin behavior in large groups, but do not occur with nearly the same intensity as in mating groups.

Response to Human Traffic

The results of this study with regard to the effects of human traffic on large dolphin groups concur with those of previous shore-based studies (Barr and Slooten 1998, Brown 1999), suggesting minimal impact of tours on dusky dolphins in Kaikoura. Using this boat-based approach, it was impossible to examine this question with comparisons to a “no-vessel” condition. However, even with the limited data available in this study, it appears that large groups do not generally respond to vessels with a “fight-or-flight” response indicative of acute stress (Selye 1937). The observation that large groups slowed down when more vessels were present and turned toward vessels at least as often as turning away would appear to indicate an affiliative response, if anything. Würsig *et al*. (1997) report from shore-based studies that the most common response of dusky dolphins to vessels was to ride the bow of approaching vessels. Changes in direction, and changed behavioral state from traveling to milling were also observed (Würsig *et al*. 1997). These findings are consistent with the vessel approach and decreased speeds observed in the presence of more vessels in this study. As most vessels visit large dolphin groups in Kaikoura, the effects on smaller groups also appear to be minimal. Limited dolphin tour permits, careful regulation, and the tendency of dusky dolphins to form large groups have contributed to the development of a sustainable dolphin tour industry with minimal impacts on the dolphins and substantial socio-economic benefits for the local community (Fairweather and Simmons 1998). However, as “minimal effects” do not necessarily mean “no effects,” continued monitoring of this growing industry is important to ensure long term sustainability.

Würsig *et al*. (1997) described dusky dolphin juvenile subgroups, similar to those described for spinner dolphins in Hawaii (Johnson and Norris 1994). Although juvenile groups were not observed as a distinct social unit in the course of this study, subgroups of juveniles were noted within larger groups. Future research could attempt to examine subgroups within the larger group envelope. Unfortunately, the dynamic, shifting nature of dolphins’ positions in large groups makes focal individual or subgroup observations problematic. Perhaps this challenge could be addressed with the use of digital video and sequential high-speed still photography, or other methodological advances.

Mating Groups

Movement Patterns

Although dusky dolphin sexual activity occurs throughout the year, it peaks during Austral summer. Mating occurred most frequently in small groups without calves. As hypothesized, social and high-speed activities occurred at a high rate in these groups. Mating groups were characterized, as predicted, by uncoordinated activity, engaging in more milling than other groups, often with a variable heading. In effect, the observed pattern appeared indicative of rapid, competitive, "every dolphin for themselves" interactions. It is likely that swimming speeds were severely underestimated for mating groups, given the highly variable heading, prevalence of high-speed behaviors, rapid chases with frequent changes in direction, and high degree of movement in the vertical as well as horizontal plane. Mating chases were often so quick that it was a challenge to keep the research vessel, to which mating groups appeared largely indifferent, in proximity to the group.

Spread and Formation

With the focus of the males in mating groups on gaining access to lone estrous females, mode inter-individual distance was minimal. Mating groups were least likely to have a swimming formation, again highlighting the lack of coordinated swimming in a competitive chasing context. This observation suggests that the interaction between males is mainly competitive, not cooperative. However, it is possible that some males cooperate to compete in these groups as in male bottlenose dolphins (Connor *et al.*

1992), given long-term association between males in mating and feeding groups has been noted (Markowitz *et al.* 2004, see Chapters IV and VII).

Social Interaction

Rather than physical strength, quickness and agility coupled with sperm competition appear to be the main factors in determining male reproductive success. Reproductive chases are extremely rapid, involving frequent changes in direction, male chasing strategies and female "escaping" strategies. This role of quickness in intra-sexual competition and mate choice is either unusual or has not been emphasized in the literature. Headfirst re-entry leaps, frequent in feeding groups, also occurred at a high rate in mating groups and likely play a role in male pursuit of females and/or females evading males.

Given the advantages of quickness in an anti-predator context, it is not surprising that quickness also plays an important role in dusky dolphin mating. Unlike bottlenose dolphins (Connor *et al*. 2000), males either singularly or cooperatively generally appear unable to monopolize females and therefore rely on quickness to gain access to mates. Mating groups are most commonly formed of single, presumably estrus females being chased by 4-8 males. Agonistic interactions, including jostling for position and mid-air collisions, were observed in these groups but not at a high rate. The absence of size dimorphism between sexes in dusky dolphins (van Waerebeek 1993) suggests that physical strength is relatively unimportant in the context of intra-sexual competition. Low rates of agonistic interactions, along with fewer threats from sharks, may partially explain the lower mark rate of dusky dolphin dorsal fins as compared to bottlenose dolphins. On average, relatively few males in mating groups successfully copulate with the female, indicating that whereas dusky dolphin mating might be considered "promiscuous," behavioral contests as well as sperm competition play their roles in reproductive success.

Mating chases appear to involve male-male competition but quickness may be more important than size or aggression in reproductive success. Extended chases provide a mechanism for females to ensure fitness of their mates. Although females might mate with multiple males in a manner of minutes, not all males engage equally in copulatory activities. Observations of harassment of mothers and calves suggest mate coercion in at least some cases. Protection of calves from conspecific harassment may be an important factor contributing to the formation of nursery groups. These observations suggest that strategies are employed both by females to ensure the fitness of their mates and by males to increase their chances of siring offspring. Female choice and male-male competition are likely important factors in dusky dolphin reproduction.

From the female perspective, the chase may represent a method to exercise a certain degree of choice in sexual partners (Whitehead and Mann 2000). Females may opt to evade unattractive males or those that fail to demonstrate requisite vigor/social skill. A number of observations suggest that females are not helpless or passive participants in dusky dolphin mating activity. Apparent avoidance strategies by females include rapid changes in direction (quickness and agility), re-entry leaps (which allow the female to dive below chasing males), and head-up braking maneuvers (which result in males “overshooting” the female when they are chasing from below). Although not involving flagrantly showy features, the quickness requirement could represent a form of “handicap” (Zahavi and Zahavi 1997), providing a reliable indication of the quickness, agility, and physical condition of candidate males with whom a female might copulate. According to sociobiological theory, mate choice can promote "good genes" which in turn increase the probability that the females' own offspring inherit these advantageous phenotypic traits such as quickness, social skills, or other attractive characters (Trivers 1985).

From the male perspective, intra-sexual competition appears to take on two main forms: physical chasing and sperm competition (Connor *et al*. 2000). In the chase, it appears that quick males may be highly favored (although this remains to be tested). This form of competition contrasts with the more typical model of violent or ritualized male-male combat (Eibl-Eibesfeldt 1961) in which size, age, strength (Clutton-Brock *et al.* 1979, Manson 1996, LeBoeuf & Kaza 1981, McCann 1981, Modig 1996), weapons (Gerson and Hickey 1985, Brear *et al.* 1993, Leslie and Jenkins 1985), and/or hormonal state (Poole 1989, Lincoln *et al.* 1972) are the most important determinants of male reproductive success. Male strategies include herding the female up against the surface of the water (swimming ventrum to ventrum), much as they herd fish. It is unclear whether male-male cooperation (as in bottlenose dolphins, Connor *et al.* 1992) is important in this regard, but it seems likely given that we have noted male-male winter hunting partners also together in mating groups during the summer (see Chapters IV and VII). Coercion of females (Connor *et al*. 2000) may also be a factor, and seems particularly apparent in chases of females with newborn calves. Males generally follow females closely, for example engaging in re-entry leaps following females as the chase proceeds at depth. The speed of these chases during the breeding season (peaking in summer, see Chapter II) clearly demonstrates fitness, in terms of quickness and agility, and motivation on the part of the males. Social sexual behavior at other times appears to be much more relaxed and is likely non-reproductive for the most part. The large testis size of dusky dolphins suggests sperm competition (van Waerebeek 1992) and might partially explain the frequency of non-reproductive mating (due to hormonal state).

Nursery Groups

The ratio of three older animals to every calf observed on average in dusky dolphin nursery groups is consistent with the notion that mothers have “help” in rearing calves, as noted for other dolphin species (Whitehead and Mann 2000). One juvenile was present on average, and other attendants may well have been subadults (not distinguished from adults in this study); therefore, it is possible that some of the attendants of mothers and calves were learning to parent and/or developing social bonds with some of their cohort’s newest members (Mann and Smuts 1998). Further, multiple calves were at times observed with a single adult, suggesting “babysitting”, as twinning is extremely rare in delphinids (Whitehead and Mann 2000).

Movement Patterns

As predicted, dolphins in nurseries rest more, swimming slower on average than those in other groups and engaging in relatively few bursts of speed. Furthermore, adults with calves swam at slower resting speeds than those without calves. Such slower swimming speeds could partially explain why nurseries form. Because it seems likely that calves are more vulnerable to predation, one might expect mothers with calves to always seek “safety in numbers” by joining large groups. However, if large groups respond by “running” at top speed from predators, which large groups of dusky dolphins do in response to killer whales (Constantine *et al.* 1998, see also Chapter V), then mothers and calves will be the least likely to keep up. Thus, paradoxically, mothers with calves in large groups might actually be less safe from predators than those in smaller groups. Contrary to *a priori* expectations, nurseries were not located significantly closer to shore compared to other groups; however, this concurs with the results of previous shore-based research (Cipriano 1992).

Spread and Formation

As predicted, dolphins in nursery groups maintained tight inter-individual proximity, likely facilitating both defense and care of calves. Parallel swimming formations were a prevalent feature of nursery groups, perhaps functioning to increase search efficiency for potential threats (Norris and Dohl 1980), and to keep calves protectively positioned with older animals on either side (Mann and Smuts 1998).

Social Interaction

As hyothesized, boisterous social interaction was minimal in nursery groups. Leaping was also minimal, making these groups least "obvious" to the casual observer, and possibly also to predators or marauding dolphins. More subtle interactions between mothers and calves, as documented for bottlenose dolphins (Connor *et al*. 2000), likely occurred at a relatively high rate.

Non-mating Adult Groups

Movement Patterns

Non-sexually active, adult groups were most similar to nurseries in their movement patterns. Although mean swimming speeds in adult groups were faster than in nurseries, they were generally restful and dolphins engaged in few high-speed activities. Such small, restful adult groups may function to establish and maintain social bonds important in other contexts such as mating, parenting, feeding, and predator avoidance. These groups could also represent members of mating groups that are "taking a long break" between mating periods, as observed in some focal follows of mating groups.

Spread and Formation

Inter-individual distance was similar to that observed in nurseries; dolphins generally maintained close proximity to one another although not as tight as in mating groups. Echelon formation, with followers spread out in formation behind a leader, was more common in non-mating adult groups than in others.

Social Interaction

Interactive and social-contact behaviors were generally minimal in non-mating adult groups. Leaping occurred at a very low rate, similar to nurseries. The function of these small, quiet groups of non-mating adults remains a mystery. Future research could endeavor to sex individuals in these groups, and examine group structure (see Chapter

VII), to determine whether these groups represent “bachelor herds”, “female bands”, or mixed-sex assemblages.

Social Group Comparison Summary

In summary, dusky dolphin behavior varied among social groups in Kaikoura in ways expected given coordination of large numbers of dolphins in large groups, competition for access to mates in small mating groups, and energetic and developmental constraints in nurseries. When comparing expected versus observed rankings of these social groups, 28 of 36 were ranked as predicted (Table 9). Most discrepancies can be explained by behavior in small groups which did not always follow predictions. Generally, behavior in small adult groups and nurseries was more similar than expected. The functions of these small adult groups are yet to be determined.

Table 9: Expected versus observed ranking of parameters by social group
(greater numbers, proportions, and frequencies denoted by larger numbers and words)

Behavioral category	**Large**	**Mating**	**Nurseries**	**Adult**
behavioral state	Travel ✓	Mill ✓	Rest ✓	Rest ✓
uncoordinated movement	1 ✓	4 ✓	2 ✓	3 ☒ **2**
swimming speed	4 ✓	3 ✓	1 ✓	2 ☒ **3**
high-speed bursts	3 ✓	3 ✓	1 ✓	2 ☒ **1**
inter-individual distance	3 ✓	1 ✓	1 ✓	2 ✓
swimming formation	Linear ✓	None ✓	Parallel ✓	Echelon ✓
interactive & social	3 ✓	4 ✓	1 ✓	2 ☒ **1**
noisy leaps	3 ✓	2 ☒ **1**	1 ☒ **2**	2 ✓
clean headfirst re-entry	2 ☒ **1**	3 ✓	1 ☒ **2**	2 ✓

(✓ = as predicted. ☒ = different from predicted, observed rankings in bold)

Over 1,000 dusky dolphins of a population numbering over 10,000 may be found off Kaikoura, New Zealand at any one time (see Chapter VII). Like people living in cities, dusky dolphin social groups follow predictable patterns related to crowd control, acquiring access to mates, and raising young. The dolphins' highly coordinated behavior in large groups, as well as the noisy leaping activity of apparent "sentinels" (Connor *et al.* 2000) or "traffic cops," indicate that even in large assemblages their behavior is socially regulated. Mating groups could be competitive arenas where "mating of the quickest" is the rule. As with other cetaceans (Whitehead and Mann 2000), dusky dolphins form nursery groups that provide restful, quiet social environments of relative safety for mothers and their developing offspring. Small groups of non-mating adults are similarly restful, and may allow dusky dolphins to develop and maintain social bonds in a less crowded and more relaxed social environment.

CHAPTER IV

DUSKY DOLPHIN WINTER FORAGING IN THE MARLBOROUGH SOUNDS: OVERLAP WITH AQUACULTURE*

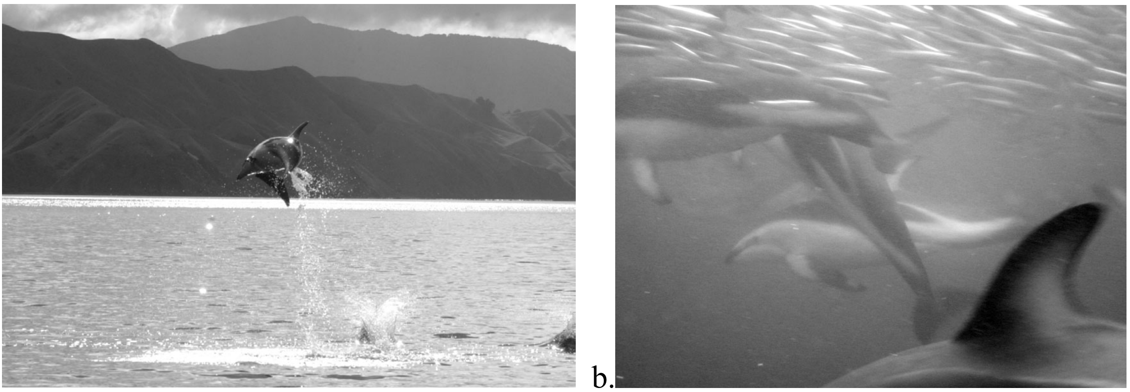


Figure 41. Dusky dolphins coordinate daytime foraging on schooling fishes in the Marlborough Sounds as shown a. above and b. below water (underwater photograph courtesy of D. Boulton).

> *Catching mobile and elusive prey calls for flexible behavior that can be rapidly and effectively adapted to changing circumstances.*
>
> *…foraging optimally requires accurate evaluation of so many aspects of a changing environment that conscious thinking about the situation may be the most effective procedure.*
>
> *Porpoises display such great versatility under a wide variety of conditions that they must think out solutions to some of the problems they solve so ingeniously.*
>
> \- Donald Griffin, Animal Thinking

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Introduction

Resource managers are faced with the task of balancing conservation of aquatic biota with a variety of human activities, including recreation, tourism, commercial fishing and aquaculture. The effects of human activities on wild dolphin populations vary depending upon the type of activity, its proximity to dolphin habitat, and the behavior and distribution of the animals themselves. Freshwater dolphins, such as the Yangtze River dolphin (or baiji, *Lipotes vexillifer*), often live in direct conflict with people for food and habitat, leading to especially drastic effects of human industries on these species (Zhou and Zhiang 1991). Coastal dolphin species, such as the New Zealand Hector's dolphin (*Cephalorhynchus hectori*), have been impacted by near-shore set-net fisheries. Incidental capture in fishing nets set within preferred Hector's dolphin habitat has resulted in a major decline in the species (Dawson 1991), and a reduction in the genetic diversity of some populations (Pichler *et al.* 1998).

Competition with humans for aquatic resources can impact aquatic mammals, likely exerting a greater influence on their populations than either directed hunting or incidental catch due to fishing (Crespo and Hall 2001). In addition to direct or indirect competition for resources, human-made structures such as those associated with aquaculture may compete with marine mammals for space in the coastal environment (Würsig and Gailey 2002). However, such effects of aquaculture on wild dolphins are rarely considered in models for managing the environmental impacts of marine farming (e.g. Henderson *et al.* 2001). In the course of research on dusky dolphin distribution and foraging behavior (Figure 41) in New Zealand waters, it became clear that the dolphins might be affected by habitat alteration due to aquaculture developments in the Marlborough Sounds region. The goals of this chapter are to examine dusky dolphin habitat use in the Marlborough Sounds, and to assess the potential impacts of an expanding marine farming industry on dolphins in the region. This study represents one of the first efforts to measure the degree of overlap between dolphin habitat and aquaculture, and examines the potential ecological consequences of marine farming activities for these apex predators and associated species.

The IUCN lists the dusky dolphin as a species for which currently available data are insufficient to assess conservation status (Whitehead *et al.* 2000). In South America, dusky dolphin populations have been impacted by unsustainable practices, including intentional dolphin harvest (Van Waerebeek 1992), incidental catch (Dans *et al.* 1997), and reduction of their principal prey species (Manzanilla 1988; McKinnon 1994). Currently, the impacts of human activities on New Zealand dusky dolphin populations, including large-scale ecotourism worth millions of dollars to local revenues, appear minimal (Barr and Slooten 1998; Brown 1999; Fairweather and Simmons 1998). This is in part due to the careful regulation of human-dolphin interactions by New Zealand resource management agencies, such as the Department of Conservation.

Occurring mainly in the continental shelf and slope waters along the coasts of Chile, Peru, Argentina, Western South Africa, and New Zealand, dusky dolphins adopt different foraging strategies in different habitats (Würsig *et al*. 1989). In Golfo San José, Argentina, the dolphins inhabit a shallow environment and depend primarily on schooling southern anchovy (*Engraulis anchoita*), which they hunt co-operatively in small groups during the day (Würsig and Würsig 1980). In Kaikoura, New Zealand, dusky dolphins gather in large groups and feed at night on lantern fish (family Myctophidae) and squid (*Nototodarus* sp. and *Todaroides* sp.) associated with the deep scattering layer. Daylight hours are used for resting, socializing, and reproduction (Würsig *et al.* 1997).

Water temperature can influence both delphinid thermal energetics and prey availability (Wells *et al*. 1999). Historic sightings suggest a shift in distribution of New Zealand dusky dolphins to the north in winter and south in summer (Gaskin 1968), correlated with seasonal changes in water temperature. A warmer, shallower, and relatively sheltered area roughly 200 km north of Kaikoura, the Marlborough Sounds represents winter habitat for some dusky dolphins.

As dusky dolphins migrate north from Kaikoura to the Marlborough Sounds (see Chapter VII), they encounter different aquatic environments, with differences in prey type, abundance and distribution. Many of the mesopelagic prey species utilized by dusky dolphins in deep water off Kaikoura are rare in the warmer, shallow Marlborough Sounds; instead, schooling fish such as pilchard (*Sardinops neopilchardus*) are locally abundant and may be concentrated in certain areas by tides and currents (Baker 1972). Consequently, dusky dolphins might be expected to alter their hunting tactics and feed during the day, cooperatively hunting schools of fish in a manner similar to the South American dusky dolphin populations.

Dusky dolphins inhabiting the Marlborough Sounds often find themselves in close proximity to people (Figure 42). A major port area and popular holiday spot, the

Marlborough region is host to a wide array of human uses. These include recreational boating, fishing, and diving; ferry and other large vessel activity; and extensive marine farming. Mussel farming is the largest aquaculture industry in New Zealand, and the largest commercial enterprise in the Marlborough region. In 2000, green-lipped mussels (*Perna canaliculus*) were grown in 520 farms around New Zealand, 455 of which are in the Marlborough Sounds (Gall *et al*. 2000). With increasing economic demand for mussels and the growth of mussel farming, greater information on potential impacts of this lucrative industry on marine ecosystems is required to ensure that it remains sustainable (Smaal 1991).

Figure 42. Dusky dolphins in the Marlborough Sounds live in close proximity to people. The dolphin pictured leaps to catch a breath during a bout of feeding in Admiralty Bay.

Shellfish mariculture can affect dolphin habitat use in a number of ways. For example, an oyster farm established in Shark Bay, Australia excluded mother-calf pairs of Indian Ocean bottlenose dolphins (*Tursiops aduncus*) from the farm area (Mann

1999*b*). Objects at the surface and lines in the water column (Figure 43) may impede dolphin movements, impacting the animals' ranging and foraging patterns (Würsig and Gailey 2002).

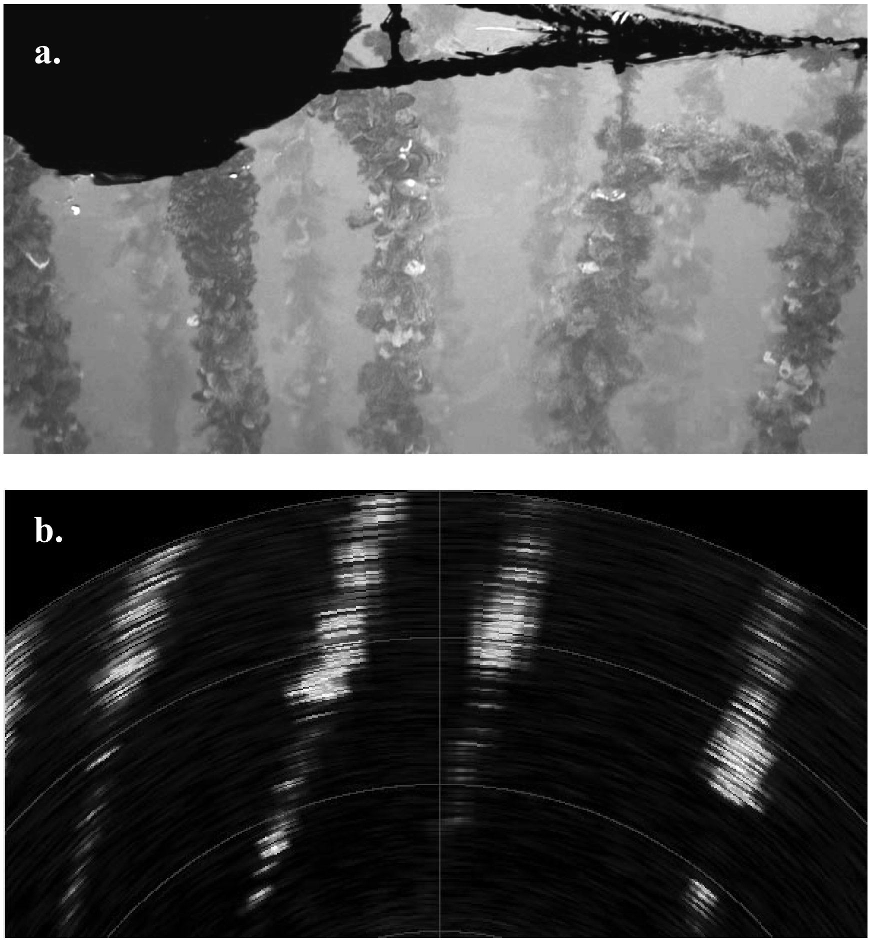


Figure 43. Marine farm lines seeded with green-shell mussels, possibly a physical obstruction to dolphin movements and/or a visual/acoustic barrier, are shown as (a) a photograph, and (b) a 675 KHz sector-scan sonar image. The space between vertical sections of lines varies, but is generally 0.2-1m.

In addition to the potential for physical obstruction by floats and lines, marine farms could have less direct effects on dolphins. Increased boat traffic due to aquaculture activity may increase noise levels that could disturb cetaceans, particularly when cetacean habitat use and marine farming are both concentrated in the same small areas (Richardson *et al*. 1995). Mollusk farming can cause biodeposition, faunal changes, and the introduction of new species or pathogens to marine ecosystems (Buschmann *et al.* 1996). Changes in the benthic communities beneath mussel farms, including increases in aerobic heterotrophic bacteria (La Rosa *et al.* 2001) and decreases in meiofauna (Mirto *et al*. 2000), result from the biochemical effects of accumulated faeces and pseudofaeces (Grant *et al*. 1995). Although mussel farming appears to influence water column biochemistry less than fish farming, mussels increase nitrogen levels (La Rosa, *et al.* 2002), and deplete chlorophyll *a* levels (Grange and Cole 1997, Ogilvie *et al*. 2000) within and around farms. Although these indirect trophic effects could impact dolphin habitat, we do not evaluate them for the present situation in the Marlborough Sounds. Rather, the purpose of this study is to examine the relationship between dolphin habitat use and aquaculture development in the area.

Recently, a further increase in green-lipped mussel farm development has been proposed in the Marlborough Sounds. To assess the potential impacts of such management changes on dusky dolphins, it is first necessary to collect basic information regarding the dolphins' ecology, including which local areas they inhabit most, how many of them use these areas, and how they utilize the habitat. This study aims to describe dusky dolphin occurrence and behavior, and measure the existing and potential overlap between dusky dolphin habitat use and marine farming, in the Marlborough Sounds.

Methods

Research Effort

During 6 successive winters from 1998-2003, 590 hours of boat-based research on 113 days in the Marlborough Sounds produced focal follow data from 870 dusky dolphin group encounters. All work was conducted from small, 4-6 m inflatable vessels with 25-85 hp outboard motors. During the first 3 winters, 1998-2000, observations of dusky dolphin groups were conducted in the Marlborough Sounds during exploratory non-systematic surveys. Areas examined included Queen Charlotte Sound, the outer Pelorus Sound, the greater Admiralty Bay area, and Current Basin. Mean search speed (± s.e.) was 17 ± 4.9 km/hr (n= 23). From 1998-2000, 119 hours of boat-based research on 23 days yielded 43 hours of focal follow information on 73 dusky dolphin groups.

During winter 2001, the greater Admiralty Bay and outer Pelorus Sound regions were divided into six zones and systematically surveyed to compare dusky dolphin use of different areas (Figure 44). In July-September 2001, 118 hours of boat-based research conducted on 27 days yielded 52 hours of focal follow data on 306 dusky dolphin groups. Surveys were conducted by ≥ 2 trained observers at mean (± s.e.) speeds of 16 ± 0.4 km/hr (n=27), along transect lines pre-programmed into a Garmin 12X global positioning system (GPS) receiver, spaced evenly at 1-1.5 km apart and drawn to within 500 m of shore. In this manner, research teams conducted 17 surveys of inner Admiralty Bay covering 405 km over 28 hours, 12 surveys of outer Admiralty Bay covering 503 km over 28 hours, 8 surveys of Current Basin covering 149 km over 8 hours, 3 surveys of Forsyth Bay covering 67 km over 3 hours, 4 surveys of Waitata Reach covering 195 km over 10 hours, and 3 surveys of Tawhitinui Reach covering 238 km over 11 hours. Queen Charlotte Sound was also surveyed for 12 hours over 2 days during winter 2001.

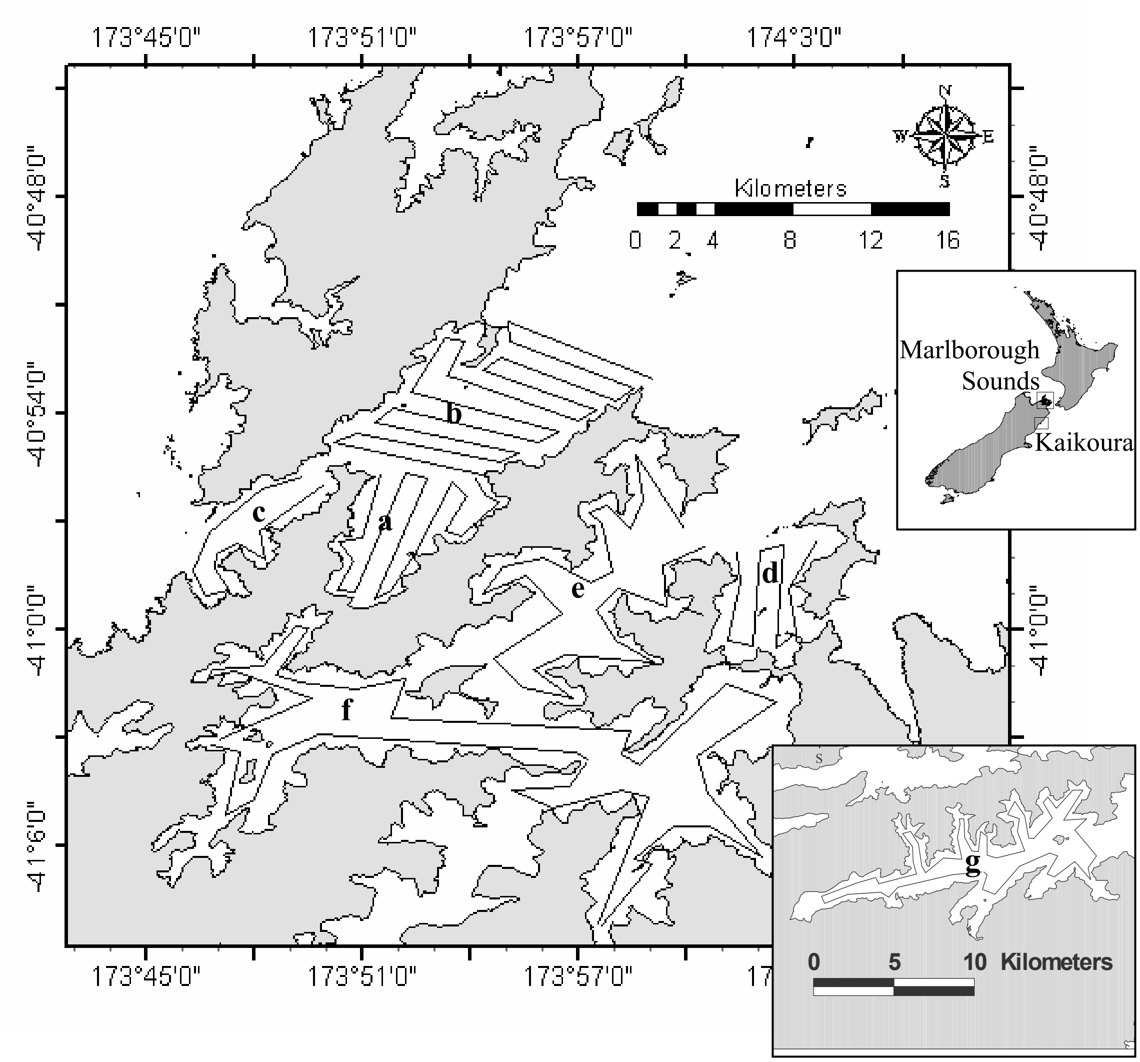


Figure 44. Line transect routes for 7 areas (a. inner Admiralty Bay, b. outer Admiralty Bay, c. Current Basin, d. Forsyth Bay, e. Waitata Reach, f. Tawhitinui Reach, and g. inner Queen Charlotte Sound) surveyed in the Marlborough Sounds during the winters of 2001-2003. Shaded areas represent land, and lines represent survey routes. For reference, the location of the Marlborough Sounds and Kaikoura are shown on a map of New Zealand.

During the winters of 2002 and 2003, the research effort was focused on the area with highest dusky dolphin sighting rates in the previous 4 winter seasons, the inner Admiralty Bay. Using the same inner Admiralty Bay survey route as in 2001 (Figure 44a), surveys were conducted at mean (± s.e.) speeds of 14 ± 0.4 km/hr (n = 31) in 2002 and 16 ± 1.0 km/hr (n = 17) in 2003. In June-August 2002, 218 hours of boat-based research in the inner Admiralty Bay on 42 days yielded 70 hours of focal follow data on 253 dusky dolphin groups. In July-August 2003, 102 hours of boat-based research on 17 days in the inner Admiralty Bay yielded 25.2 hours of focal follow data on 162 dusky dolphin groups. During 2003, additional data were collected during limited surveys in the outer Admiralty Bay, Current Basin, and Queen Charlotte Sound. Data were collected on 63 focal groups encountered during 9 incomplete surveys over 12.3 hours in the outer Admiralty Bay (Figure 44b), 4 focal groups encountered during 4 complete surveys over 3.8 hours in the current basin (Figure 44c), and 8 focal groups encountered during 4 complete surveys over 16.3 hours in Queen Charlotte Sound.

Search effort in summer was limited to 16 hours on 4 days in Queen Charlotte Sound (1999-2000) and 24 hours on 3 days in Admiralty Bay (2000-2001).

Dolphin Location and Movements

A dolphin group was defined as all individuals within 10 m of at least one other individual at a given time (i.e., the “10-m chain rule”, Smolker *et al.* 1992). Group size was defined as the largest number of individuals seen at the surface at any one time, and changes in group size were noted as they occurred (Mann 1999*a*). During focal group follows, the vessel was driven parallel to each group, matching the group heading and speed at such a distance as to minimize disruption of dolphin movements (Würsig and Jefferson 1990). Position and time data recorded with a Garmin 12X GPS receiver at 2-minute intervals were used to estimate the location and track the movements of each focal dolphin group. GPS Utility v. 3.40.6 software was used to download tracks, and to calculate the mean speed and average location of each group encountered. All occurrences of dolphins entering the boundaries of marine farms were noted, and total time spent in the farms was recorded with a stopwatch. During 2002 and 2003, all instances of dolphins coming within 200m of the existing farms and the total time spent within this proximity were additionally noted.

Positions of dolphin groups, survey track lines, and both existing and proposed marine farms were plotted and overlaid in ArcGIS, ArcMap v. 8.2 onto a base map by Eagle Technologies (Wellington, New Zealand). For accuracy, the 44 existing farms in Admiralty Bay were mapped by plotting GPS locations taken on site at the four corners of each farm. Proposed farms were traced by overlaying the Marlborough District Council June 2002 resource consent chart onto the base map in ArcGIS.

The observed number of dusky dolphin groups encountered within current farms in Admiralty Bay was compared to the number that would be expected to occur within the boundaries of the farms given a random distribution. To accomplish this, random points equal to the observed total number of encounters in inner Admiralty Bay were generated using the Random Point-In-Polygon Generation Program v.2 (VBA macro developed by M. Sawada 2002, *http://arcscripts.esri.com/details.asp?dbid=12098* for ArcGIS). These points were plotted in a polygon drawn around the boundaries of the inner Admiralty Bay in ArcGIS (Figure 45), and the number of random points falling in the farms was tallied. This process was replicated 50 times, and the resulting values compared to observed dusky dolphin group encounters in Admiralty Bay mussel farms. To examine whether dolphin use of the near shore environment was random with respect to marine farms, a second polygon was drawn from the shoreline to 400m from shore. This area includes all current farms, areas between the farms, areas inshore of the farms, and areas just slightly offshore proposed for extension of the existing farms. The number of dolphin groups encountered in this near shore region was tallied, and an equal number of points were then randomized within the polygon, again with 50 replications. The number of dolphin groups encountered in farms was then compared to the number expected given a random distribution in this near shore area.

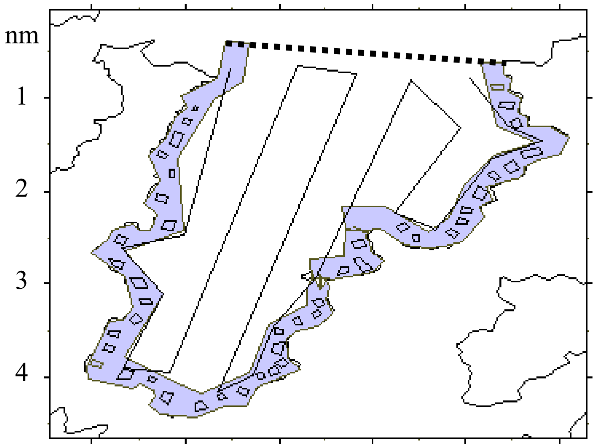


Figure 45. The distribution of dusky dolphin encounters survey (track lines) relative to marine farms (boxes) was compared to points plotted randomly in a polygon of the inner Admiralty Bay (bounded by dotted line). Distribution of sightings in a second near shore polygon (dark shading) was also compared to a random distribution.

Photo-identification of Individuals

Photo-identification of dusky dolphins using dorsal fin scars was conducted in the manner described by Würsig and Jefferson (1990). During 1998 and 1999, photographs were taken on 100 to 400 ISO slide film with a Nikon N90 camera and 80-200 mm and 100-300 mm lenses, and later digitized to aid in analysis. During 2000-2002, photographs were captured digitally with a Nikon D1 camera using 100-300 mm and 80-400 mm lenses and stored at high resolution on compact flash media. Of 18,758 dorsal fin photographs taken in the Marlborough Sounds during the six successive winters, 13,544 (72%) were suitable for analysis following the criteria of Markowitz *et al*. (2003a). Based on field estimates of group size, 85%, 97%, 93%, and 85% of dolphins encountered were photographed during the winters of 2000, 2001, 2002, and 2003 respectively. Mark rate, or the percentage of individuals with distinctive markings, was estimated by taking photographs of all dolphins at random and counting the number of photographs with marked versus unmarked individuals.

Photographs of distinctively marked dorsal fins were catalogued according to the number and location of notches and scars. Once non-marked and redundant images were removed, a total of 4,626 photographic records were collected of distinctive individuals in particular groups on different days. To date, 3,788 photographic records from 1998-2002 have been compared using the Finscan v. 1.5.4 Computer Assisted Dolphin Photo-Identification System, software that employs string and curve-based matching methods to present most likely identification matches in order of similarity (Araabi *et al*. 2000, Hillman *et al.* 2003). All assessments of individual identity were confirmed by eye. An additional 838 records from the most recent field season (2003) remain to be catalogued.

Mark-recapture population estimates were calculated using the POPAN module of SOCPROG v. 1.3 (developed in MATLAB by H. Whitehead, programs available at *http://is.dal.ca/~whitelab/index.htm*). “Closed” (Schnabel), “mortality”, “mortality + trend” and “re-immigration” models were run (Gowans *et al.* 2000; Whitehead 1990a). The Akaike Information Criterion (Akaike 1974) was used to determine the model that best fit the population for each estimate, and residual differences between expected and observed number of individuals were plotted and examined to ensure that capture probabilities were not heterogeneous (Gowans *et al.* 2000). Using a 1-week sampling interval, a population estimate was calculated for the five-year period (“re-immigration” model), and single-season population estimates (“mortality” model) were generated using only data from the best three photo-identification sampling seasons (2000-2002). A second population estimate, using a 1-year sampling interval, was generated for the 2000-2002 dataset (“mortality + trend” model).

Behavioral Sampling

For each group, feeding was noted if dolphins were seen apparently “pursuing fish or holding fish in their mouths” (Acevedo-Gutierrez and Parker 2000). Birds and other marine species associated with feeding were noted. During 2002 and 2003 surveys, all instances of birds and other species feeding without dolphins were also noted. When possible, the identity of the prey species was also recorded. Only those groups tracked for greater than ten minutes were included in analyses of feeding behavior.

Twenty minutes of behavioral observations were recorded at 2-minute intervals for focal groups followed for at least 1 hour. Most common behavioral state (defined as “travel”, “mill”, “rest”, and “feed”; Shane 1990), mode inter-individual distance (0-1 body lengths, 1-3 body lengths, or >3 body lengths), and number of birds associated with the group were recorded by instantaneous samples (Altmann 1974), also called “point samples” (Mann 1999*a*). In addition to the group assessment of behavioral state, specific behavioral events related to possible dolphin foraging were documented. All occurrences of clean headfirst re-entry leaps, noisy leaps, and acrobatic (somersault) leaps (Würsig and Würsig 1980) were recorded. When synchronous diving occurred, dive times were recorded with a stopwatch. Simultaneous bursts of speed by group members were recorded during each interval by one-zero sampling (Martin and Bateson 1993). These data were compared in SPSS v. 11.0 with information collected in a similar manner in Kaikoura from 1997-2003 (see Chapters II and III for details).

Results

Dusky Dolphin Locations

During all years, dusky dolphin groups wintering in the Marlborough Sounds were most commonly encountered in Admiralty Bay, where the mean group size was five dolphins. During the winters of 1998-2000, 25.5 hours of search effort in Admiralty Bay resulted in 36.5 hours of focal work with 62 dusky dolphin groups (2.4 group encounters/hour). By comparison, 33 hours of search effort in Queen Charlotte Sound yielded sightings of seven dusky dolphin groups with focal follows of 4.1 hours (0.2 group encounters/hour). Surveys from French Pass through Current Basin to Okiwi Bay over 23.5 hours yielded sightings of another 4 dusky dolphin groups with focal follows of 2.7 hours (0.2 group encounters/hour).

These findings are further supported by comparison of encounter rates between areas systematically surveyed in 2001 (Table 10). Over 99 percent of all sightings occurred in the inner and outer Admiralty Bay areas, where encounter rate was at least 16 times that of other locations. No dusky dolphins were encountered in Queen Charlotte Sound and three dolphin groups were encountered in Pelorus Sound in 2001.

Table 10. Dusky dolphin group sightings by location, winter 2001

Location	Groups/Survey	Dolphins/Group	Groups/hr	Inter-group distance
Inner Admiralty	12.5	5	7.5	1.9 km
Outer Admiralty	7.5	5	3.3	5.6 km
Current Basin	0	N/A	N/A	N/A
Forsyth Bay	0	N/A	N/A	N/A
Waitata Reach	0.25	6	0.1	N/A
Tawhitinui Reach	0.5	2	0.2	119 km

The inner Admiralty Bay area had by far the greatest number of sightings, with significantly more dolphin groups encountered per km of survey effort than the outer Admiralty Bay (Mann-Whitney, $U = 3276.5$, $P < 0.001$, median inner bay = 0.86 groups/km, outer bay = 0.26 groups/km). These sightings show a high level of overlap with proposed mussel farms in the Marlborough Sounds (Figure 46).

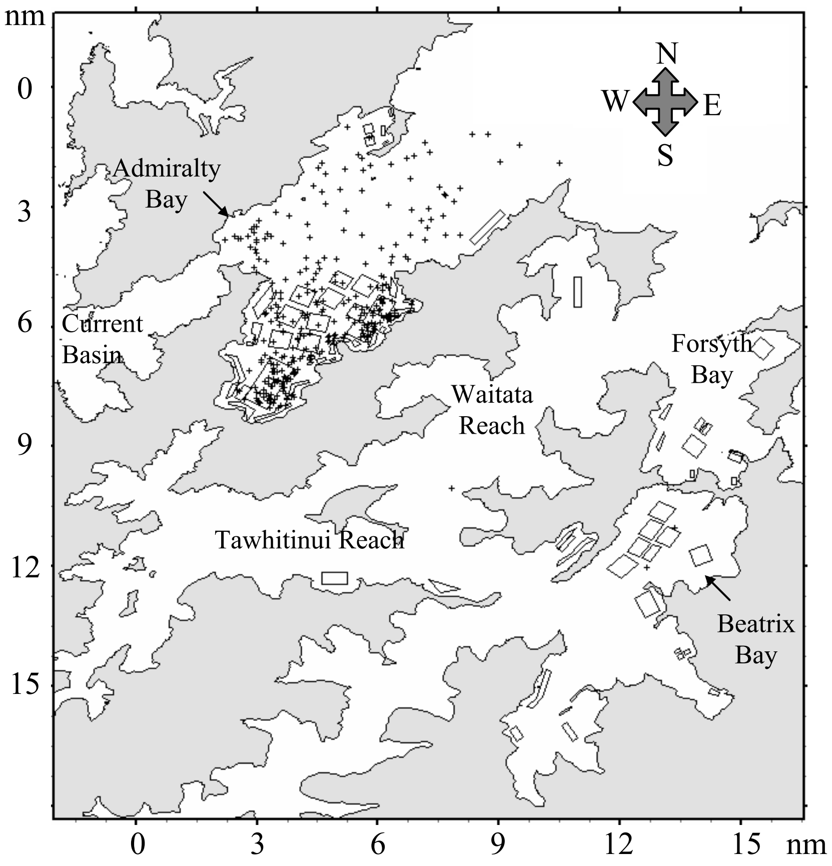


Figure 46. The average location (calculated using GPS Utility v. 3.40.6 software from positions downloaded every 2-minute with a Garmin 12X receiver) of each dusky dolphin group encountered each day (n = 306) during Winter 2001 surveys of six zones in the greater Admiralty Bay and outer Pelorus Sound regions is indicated by a plus mark with general location indicated. Boxes show proposed mussel farm developments and extensions of existing farms traced from the Marlborough District Council marine resource consent chart, June 2002. Only those proposed farm developments within the survey areas measuring >250m on a side are included.

During the three winters of systematic survey effort (2001-2003), 604 dolphin groups were encountered in inner Admiralty Bay (Figure 47). For groups encountered in the inner Admiralty Bay, 126 (21%) were in the near shore zone (<500m of shore, including the area of marine farms).

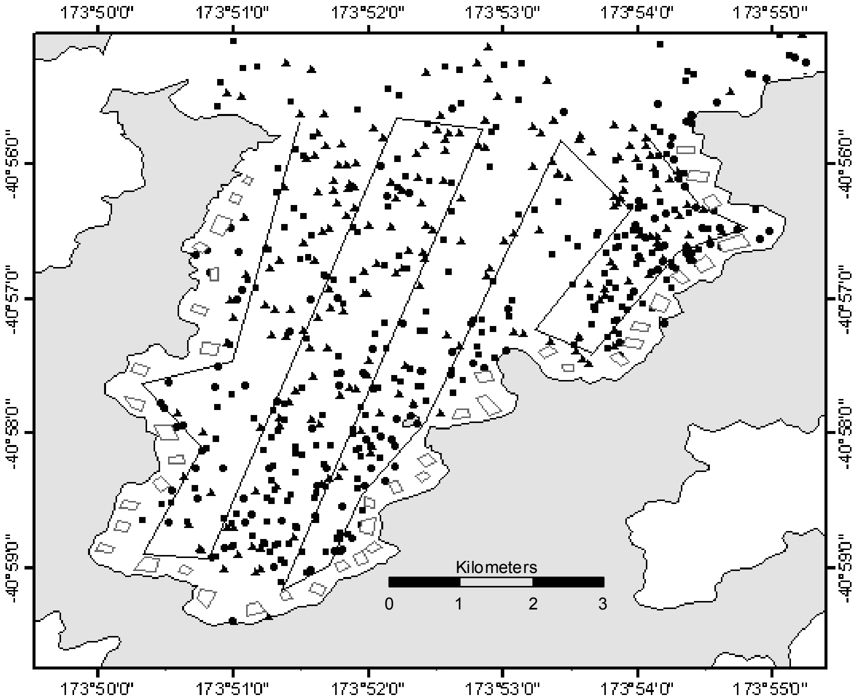


Figure 47. GPS positions of dolphin group encounters in Admiralty Bay during the winters of 2001 (squares, n= 213) 2002 (triangles, n = 253), and 2003 (circles, n = 138) are shown in relation to survey route and the position of 44 marine farms presently situated in the Bay.

Dusky dolphin habitat use showed some inter-annual variation, but remained consistently high in the inner Admiralty Bay. From 2001-2002, encounter rates in the Inner Admiralty Bay dropped from 7.5 to 3.3 groups/hour and mean inter-group distance increased from 1.9 to 4.4 km. In 2003, mean encounter rates in the inner (n = 17 complete surveys) and outer (n = 9 incomplete surveys) Admiralty Bay were equal, with 5.4 groups encountered per hour of survey effort. Again, encounter rates were considerably higher in Admiralty Bay during winter 2003 than in Current Basin (mean = 0.8 groups/hour, n = 4 surveys) and Queen Charlotte Sound (mean = 0.5 groups/hour, n = 4 surveys).

Although dusky dolphins used the inner Admiralty Bay extensively, they did not utilize the areas within the boundaries of existing marine farms along the edges of the bay as much as adjacent areas and other areas proposed for future farm development in the center of the bay. Over the course of the study, just one encounter occurred within a marine farm. When 604 points were plotted randomly in the inner Admiralty Bay (n = 50 replications), the mean number of points expected to fall in marine farms was 20 (95% C.I. = 18-21, standard deviation = 4.7, range = 11-30). When 126 points were plotted randomly in the near shore zone (n = 50 replications), the mean number of points expected to fall within the farms was 16 (95% C.I. = 15-17, standard deviation = 3.2, range = 10-23). Thus, if dolphin distribution in Admiralty Bay was random, an average of 20 of 604 encounters (with a minimum of 11) would be expected to occur within farm boundaries; and if dolphin distribution in the near shore environment was random, an average of 16 of 126 (with a minimum of 10) encounters would occur within farms.

Although just one group was encountered in farms, 13 groups were observed to enter farms at some point during focal follows, spending a total of 35.2 minutes in farms out of 182.9 hours focal follows in Admiralty Bay (0.32%). Correcting for area (dividing by the estimated total inner Admiralty Bay area outside farms = 28.5 km^2, and estimated total area inside farms = 0.85 km^2 respectively), dolphin groups were observed spending significantly more time per survey day (Wilcoxon Signed Ranks Test Z=5.777, $P < 0.001$, $n = 44$) outside farms (median = 4.6, mean $\pm$ s.e. = 5.0 $\pm$ 0.35 minutes/km^2) than inside farms (median = 0, mean $\pm$ s.e. = 0.1 $\pm$ 0.11 minutes/km^2). Areas near farms were used more often than areas inside farms (Figure 48a). During 69.7 hours of dolphin observation in winter 2002, dolphins were observed a total of 8.1 minutes inside farms (0.19%), but were tracked for 5.6 hours (8.0%) within 200m of the farms. Correcting for area (estimated total area within 200m of farms = 7.0 km^2, estimated total area in farms = 0.85 km^2), dolphin groups were observed spending significantly more time per survey day (Wilcoxon Signed Ranks Test Z=2.934, P= 0.003, n=28) within 200m of farms (median = 0.7, mean $\pm$ s.e. = 2.9 $\pm$ 1.07 minutes/km^2) than inside farms (median = 0, mean $\pm$ s.e. = 0.2 $\pm$ 0.06 minutes/km^2). During 25.2 hours of dolphin observation in winter 2003, dolphins were observed a total of 21.0 minutes (1.4%) in farms, but were tracked for 4.4 hours (17.4%) within 200m of the farms. In most cases, dolphins observed to enter the farms traveled rapidly up the lanes from one end of the farm to the other (Figure 48b). Feeding in a marine farm was noted on just one occasion, although feeding near farms was not uncommon (Figure 48c).

No dusky dolphins were encountered during summer surveys in Marlborough; however, residents report sporadic dusky dolphin occurrence throughout the year, and we have confirmed these sightings with photographs.

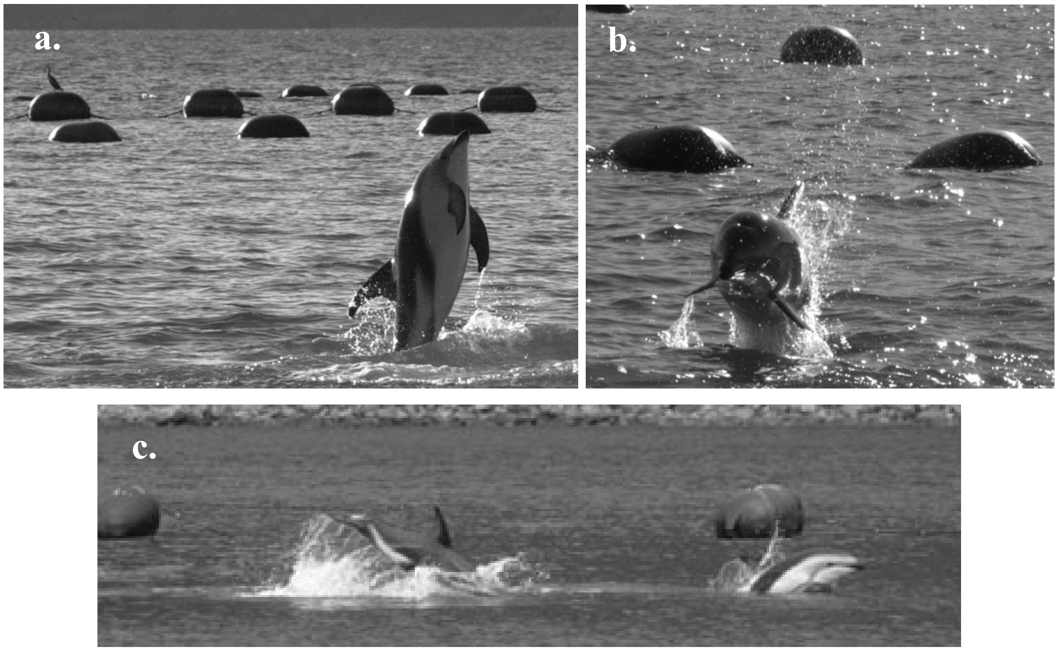


Figure 48. Dusky dolphins were often seen near mussel farms in Admiralty Bay, as shown here (a) noisy leaping and (b) feeding. Dolphins rarely entered the boundaries of farms and remained in them for brief periods (c), swimming rapidly up the “lanes” between lines and floats to the other side of the farm.

Photo-identification Information on Dusky Dolphin Abundance and Residency

The total number of marked individual dusky dolphins photographed in Admiralty Bay over the 5 winter seasons from 1998-2002 was 421, with an overall estimated mark rate of 76% (s.e. = 2.0%). Discovery curves for the 2 seasons of systematic surveys (2001 and 2002) demonstrate that >100 marked individuals were photographed in Admiralty Bay each year despite inter-annual variation, and that new individuals continued to be photographed throughout the winter seasons (Figure 49).

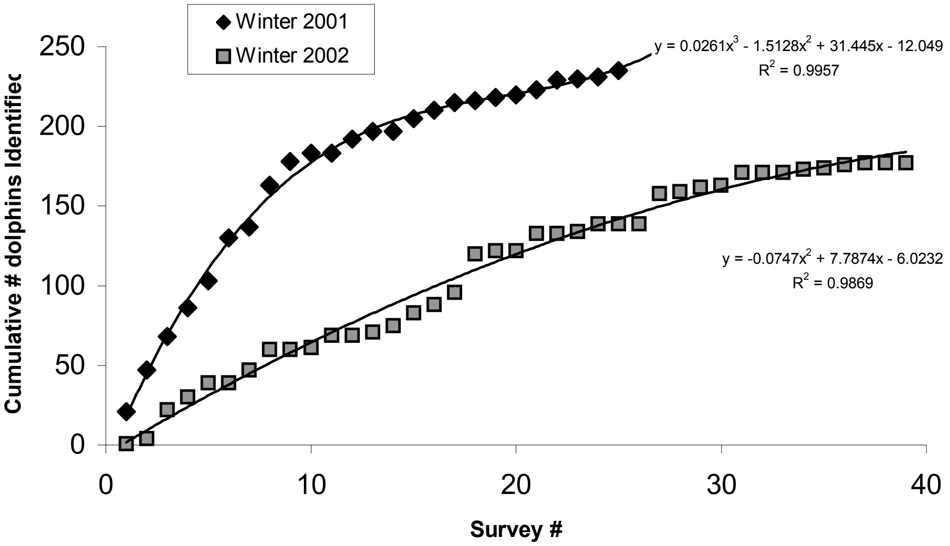


Figure 49. These discovery curves indicate the cumulative number of distinctively marked individual dusky dolphins photographed in Admiralty Bay by survey day over the course of the winters of 2001 and 2002.

Using a one-week sampling interval (n = 28), the estimated total population size of dusky dolphins in Admiralty Bay was 1,013 (s.e. = 186.7) during the five consecutive winters of 1998-2002, with an estimated mean population size of 220 (s.e. = 25.9) during any given week ("re-immigration" model). Single-season estimates ("mortality" model) were 152 (s.e. = 52.1, 95% c.i. = 113-223) in 2000 (n = 3 weeks); 272 (s.e. = 17.3, 95% c.i. = 249 -300) in 2001 (n = 13 weeks); and 179 (s.e. = 18.0, 95% C.I. = 164-198) in 2002 (n = 9 weeks). Using each season as a sampling unit ("mortality + trend" model), the estimated total population size was 1,090 (s.e. = 630.9, 95% C.I. = 693-1,291) dusky dolphins inhabiting Admiralty Bay over the 3 successive winters (2000-2002).

As the photo-identification catalog grew over the course of this study, it became clear that at least some dusky dolphins return to Admiralty Bay in successive winters. In

Winter 2000, 8% of individuals photographed at Admiralty Bay in 1998 and 1999 were re-identified in the bay. In Winter 2001, 15% of individuals photographed in previous seasons were photographically "re-captured" in Admiralty Bay. By winter 2002, 55% of marked individuals photographed in Admiralty Bay had been previously identified at the same location during one or more of the previous four winters. Preliminary comparisons to photographic records of dolphins in Kaikoura demonstrate that at least some ($n = 37$, see Chapter VII) dolphins photographed in Admiralty Bay during the winter were found in Kaikoura during summer.

Dusky Dolphin Use of Admiralty Bay as a Winter Foraging Habitat

Foraging and feeding were common activities of dusky dolphin groups in Admiralty Bay. Daytime feeding activity was noted in 72% of groups in Admiralty Bay as opposed to <1% of groups in Kaikoura. Behavioral data from 40-minute focal group samples demonstrate that dusky dolphin groups in Admiralty Bay fed during the daytime significantly more than groups in Kaikoura (Kruskal-Wallis, $H = 116.8$, $P < 0.001$). Dusky dolphin groups in Admiralty Bay spent roughly equal amounts of time feeding, resting, traveling, and milling, while dusky dolphins in Kaikoura groups spent 99% of their time during daylight hours resting, traveling, and milling (Figure 50).

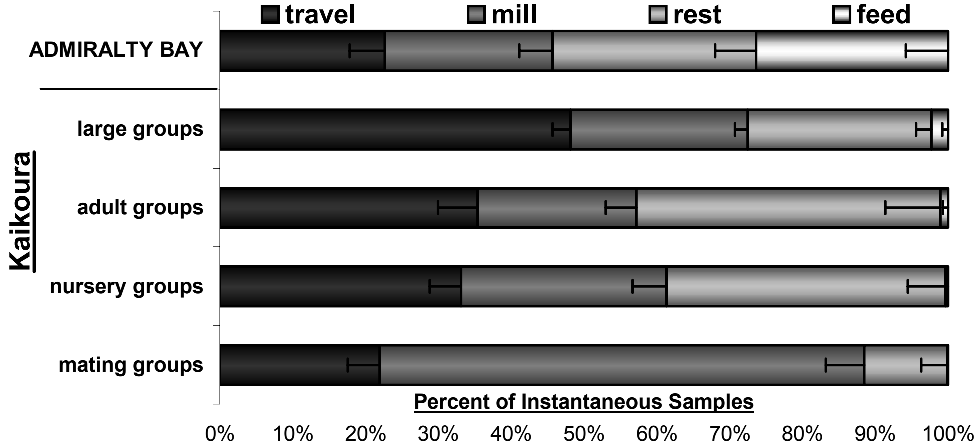


Figure 50. Daytime activity budgets of dusky dolphin groups in Admiralty Bay versus Kaikoura are shown as percent of instantaneous samples traveling, milling, resting and feeding (mean values from 40-minute samples of independent groups with standard error bars). Within Kaikoura, small adult, nursery, and mating groups are shown separately from large groups comprised of hundreds of individuals.

Prey species in Admiralty Bay included the New Zealand pilchard, yellow-eyed mullet (*Aldrichetta forsteri*), and sprat (*Sprattus antipodum*). The proportion of groups observed feeding (Figure 51) varied between years, with 83%, 59%, and 72% of inner Admiralty Bay groups feeding during 2001, 2002, and 2003, respectively. If frequency of observed feeding is related to prey availability, reduced feeding opportunities could account for the differences in encounter rate and estimated number of dolphins using the bay during the three winters (Table 11).

Table 11. Encounter rate, abundance, and feeding in Admiralty Bay 2001-2003

Year	Groups/Hour	Abundance (95%CI)	% Feeding
2001	7.5	272 (249-300)	83%
2002	3.3	179 (164-198)	59%
2003	5.4	TBA	72%

Estimated speed of group movements in Admiralty Bay was generally low, averaging (± s.e.) 4.4 ± 0.12 km/hr (n = 604). These slow swimming speeds in the horizontal plane of the water column may be related to increased foraging and/or diving activity in the vertical plane. Synchronous diving was more commonly noted in Admiralty Bay groups (79%) than in Kaikoura groups (16%), and was associated with feeding in 69% of cases observed in Admiralty Bay. The mean (± s.e.) duration of group dives from the last individual diving to first surfacing was 35 ± 1.9 seconds (n = 40), and the mean (± s.e.) dive duration for focal individuals was 68 ± 10.7 seconds (n = 10).

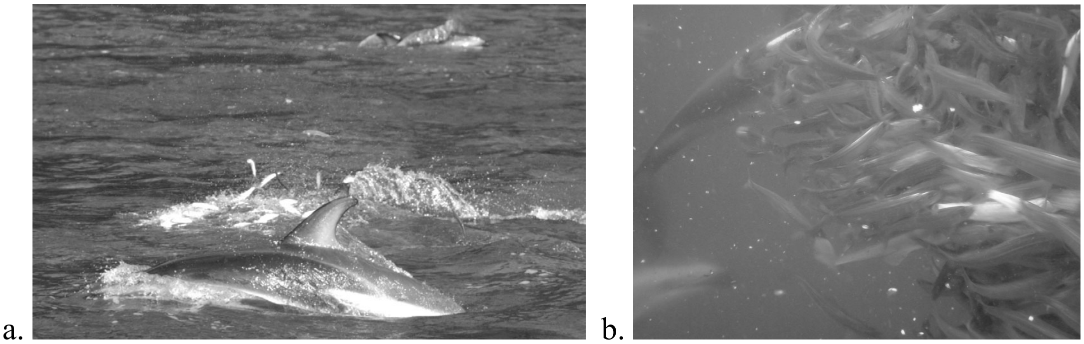

a. b.

Figure 51. Dusky dolphins fed on schooling fish by surrounding them in both the (a) horizontal and (b) vertical planes (underwater photograph courtesy of D. Boulton).

Dolphins hunting in groups (Figure 51) can increase prey encounter rate when searching for fish schools by spreading out over a wider area (Bel'kovich *et al.* 1991). Inter-individual distance was greater in Admiralty Bay groups (n = 24) than in Kaikoura groups (n = 115) of comparable size (Mean Admiralty Bay < 1 = 31%, 1-3 = 43%, > 3 = 26%; Mean Kaikoura < 1 = 67%, 1-3 = 24%, >3 = 9%). In Admiralty Bay, the mode body lengths between individuals in small groups was significantly less often < 1

(Mann-Whitney, $U = 273$, $P<0.001$), significantly more often 1-3 (Mann-Whitney, $U = 359$, $P=0.003$), and significantly more often >3 (Mann-Whitney, $U = 297.5$, $P<0.001$) than in Kaikoura.

Despite low mean swimming speeds, synchronous bursts of rapid movement, often observed when dolphins chased fish schools (Figure 51a), were more commonly noted (Kruskal-Wallis, $H = 17.97$, $P = 0.001$) in Admiralty Bay groups (median = 10%, mean $\underline{+}$ s.e. = 10.8 $\underline{+}$ 2.83 % of intervals, n = 24 independent groups) than in Kaikoura groups (small groups median = 0%, mean $\underline{+}$ s.e. = 4.1 $\underline{+}$ 1.47% of intervals, n = 115 independent groups, large groups median=0%, mean $\underline{+}$ s.e. = 2.4 $\underline{+}$ 0.51 % of intervals, n = 149 independent groups). Leaping also varied between regions, with dusky dolphins engaging in a greater proportion of headfirst re-entry leaps, allowing them to catch a breath and descend again rapidly as might be expected when herding fish, in Admiralty Bay than in Kaikoura (Kruskal-Wallis, $H = 72.45$, $P < 0.001$). Re-entry leaps comprised 97% of documented aerial behavior for Admiralty Bay groups (n = 24), as compared to 15% in large groups (n = 149), 76% in mating groups (n = 41), 28% in nursery groups (n = 39), and 15% in other small groups (n = 35) in Kaikoura.

Seabirds may use dolphins to find food (Figure 52), and vice versa, as the number of birds in the vicinity of a pod was positively correlated with the proportion of intervals that dolphins engaged in feeding activity (linear regression: $y = 12.619x + 0.3419$, $R^2 = 0.8854$). Birds most frequently observed feeding with dusky dolphins were Australasian gannets (*Sula serrator,* 87%, Figure 52a), shearwaters (*Puffinus* Spp., 26%, Figure 52b), and white-fronted terns (*Sterna striata* 13%). During winter 2002 surveys, 59% of bird groups observed feeding (n = 241) did so in association with feeding dusky dolphins, and 96% of dolphin groups observed feeding (n = 148) versus 52% of dolphin groups not feeding were accompanied by birds.

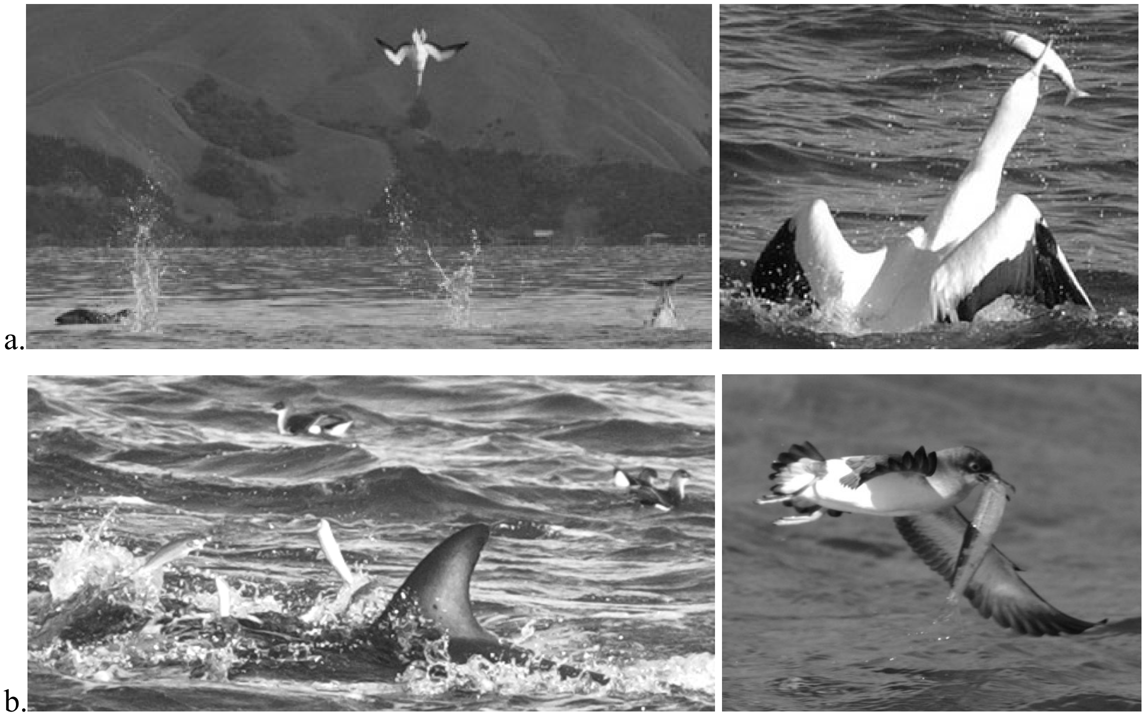


Figure 52. Birds in Admiralty Bay feed in association with dusky dolphins. a. An Australasian gannet plunges deep into the middle of a fish ball surrounded by dolphins, and surfaces with a fish. b. Fluttering shearwaters gather around feeding dolphins with fish near the surface, and fly away with fish.

Feeding aggregations also attracted other marine predators including marine mammals and predatory fish and sharks, such as barracuda and spiny dogfish (Figure 53). New Zealand fur seals (*Arctocephalus forsteri*) were noted during 9% of observations and common dolphins (*Delphinus delphis*) on three occasions (see Chapter V).

Figure 53. Other marine predators including (a) New Zealand fur seals and (b) spiny dogfish (underwater photographs courtesy of D. Boulton) fed in association with dusky dolphins.

Discussion

Within the Marlborough Sounds, dusky dolphins are concentrated in Admiralty Bay, the same area with the greatest proposed increase in marine farming. Admiralty Bay is a small area, the inner bay measuring roughly 5 km wide across the mouth by 7 km long, and yet it is preferred winter foraging habitat for hundreds of dusky dolphins. Behavioral data indicate that dusky dolphins spend roughly 25 percent of the time in Admiralty Bay actively feeding, and much of the remaining time searching for prey, as indicated by relatively large distances between individuals, slow swimming speeds, and regular diving. Unusual oceanographic features of the area, most notably the adjacent French Pass with currents at times exceeding 12 km/hr, likely act to increase local productivity and concentrate prey in Admiralty Bay.

The great interest in Admiralty Bay for marine farm development may also be due in part to the concentration of resources, as well as the lack of human traffic in this remote location. Less than 20 people live in the town of French Pass, and mussel farming is worth millions of dollars in annual revenue. While Admiralty Bay may represent a “Not In My Back Yard” space for most human residents and recreational users in the Marlborough region, hundreds of dolphins remain in the bay through the winter months, making their living during this time by hunting schooling fishes in small groups.

Dolphin use of Admiralty Bay showed inter-annual variation, apparently linked to the local abundance and distribution of prey. Although prey abundance was not measured directly, encounter rates, mark-recapture abundance estimates, and the percent of groups feeding followed a similar pattern, suggesting that the distribution of schooling fish accounts for observed inter-annual differences. A more even spread of sightings between the inner and outer Admiralty Bay in 2003 than in 2001 indicates that prey may have been more widely distributed in the greater bay region during 2003, or possibly more scarse in general.

Although dolphins are able to pass through existing marine farms in Admiralty Bay, they do not use this habitat as much as the surrounding habitat. Comparison of dolphin encounter rates in farms to those expected with a random distribution indicates that dolphins avoid the areas within farm boundaries. Randomization of points in the near shore environment provides similar results, demonstrating that this finding cannot be attributed to dolphin preference for mid-bay habitat. Further, dolphins were observed to spend significantly more time per unit area adjacent to mussel farms and in the middle of Admiralty Bay than in the farms themselves. These findings indicate that the 44 existing inner Admiralty Bay farms, occupying < 1 km^2 total area, already influence dolphin distribution and habitat use. The proposed 200m extensions of existing farms and the establishment of larger mid-bay farms would likely further limit dolphin access to winter foraging areas in Admiralty Bay (Markowitz *et al.* 2004).

It is beyond the scope of this study to model the potential population level impacts of large-scale changes to this habitat on dusky dolphin survival and reproduction. Genetic analyses indicate that the population of dusky dolphins in New Zealand is a large and healthy one (Harlin *et al*. 2003), and this is substantiated by preliminary mark-recapture estimates for Kaikoura (see Chapter VII). Nevertheless, a winter foraging community comprised of at least hundreds, and over the long-term perhaps thousands, of dolphins could be threatened by such dramatic changes to the Admiralty Bay habitat as have been proposed. Such potential effects should be carefully considered when reviewing marine farm applications.

To date, there are few studies of the effects of aquaculture on wild dolphin populations. The results of this study suggest that dusky dolphin winter foraging could be impacted by proposed aquaculture developments in the Marlborough Sounds. Although more difficult to measure than intentional and incidental take, habitat loss and degradation is one of the major threats to wild cetacean populations (Whitehead *et al*. 2000). Impacts due to changes in dolphin habitat should be carefully monitored and minimized wherever possible.

Objects such as floats and lines at the surface and in the water column could impair dusky dolphin foraging by directly impeding dolphin movements or by acting as visual or acoustic obstructions (Figure 43). When foraging co-operatively, dusky dolphins converge on an area where fish have been found, and begin working together to encircle and herd fish into a ball often against or near the surface (Würsig 1986). Just as large scale development of lion (*Panthera leo*) hunting grounds on the African savanna would likely interfere with a pride's ability to capture antelope, it should come as no surprise that dolphin groups hunting fish are hampered by physical obstacles in their preferred foraging habitat (Würsig and Gailey 2002). Floats and lines could also disrupt echolocation, as objects placed between an echolocating dolphin and a small target, such as a fish, can interfere with the dolphin's ability to detect the target (Au 1993).

Introduction of additional mussel farms could also have indirect trophic effects on dolphins and other apex predators in the marine environment. Because mussels feed on phytoplankton (Gall *et al*. 2000), it is not surprising that mussel farms significantly impact phytoplankton levels (Grange and Cole 1997). In Beatrix Bay, roughly 16 km East of Admiralty Bay, phytoplankton levels within mussel farms were found to be significantly lower than outside of farms (Ogilvie *et al*. 2000). Sediment chemistry and benthic community composition are also influenced by mussel farms, mainly due to the accumulation of faeces and pseudofaeces beneath the farms (Mirto *et al*. 2000). At present, the consequences of microbiotic changes caused by shellfish aquaculture are unknown for predators at higher trophic levels, including dolphins.

This study shows how management decisions regarding one relatively small area, such as Admiralty Bay, can potentially have far-reaching demographic and ecological consequences. Some, if not all, of the hundreds of dolphins inhabiting Admiralty Bay during the winter months spend their summers in Kaikoura, where they rest, reproduce, and interact with tourists supporting a multi-million dollar ecotourism industry during the day. Dusky dolphins switch from a nocturnal feeding strategy in the deep-water habitat off Kaikoura to diurnal feeding when they migrate to the shallower Marlborough Sounds. Due to the prevalence of seabirds, predatory fish, and other marine mammals feeding in association with dusky dolphins, impacts of aquaculture developments on dolphin foraging are likely to influence the ecology of these other apex predators as well.

Conservation is not only important when species hover on the edge of extinction (Würsig *et al.* 2002). Further the impacts of human activities are not limited to those involving dramatic scenes of intentional or unintentional over-harvest of apex predators. Management of coastal areas for mariculture and other uses should be informed by studies on the use of the habitat by marine animals, and the potential impacts of coastal developments on the animals and their habitats. The question is not whether there will be any further development of a lucrative and generally environmentally friendly marine farming industry in the Marlborough region and elsewhere. The real question is whether the potential impacts of aquaculture on areas of particular ecological importance to creatures living in the coastal environment will be factored into decisions regarding the placement and management of marine farms.

CHAPTER V

INTERACTIONS BETWEEN DUSKY DOLPHINS AND OTHER MARINE MAMMALS IN NEW ZEALAND

> *A merry school of porpoises, a square mile of them, suddenly appear, tossing themselves into the air in abounding strength and hilarity, adding foam to the waves and making all the wilderness wilder. One cannot but feel sympathy with and be proud of these brave neighbors, fellow citizens in a commonwealth of the world, making a living like the rest of us.*
>
> \- John Muir, Travels in Alaska

Figure 54. New Zealand dusky dolphins interact with other species of marine mammals including S. right whale dolphins (*Lissodelphis peronii*), common dolphins (*Delphinus delphis*), long-finned pilot whales (*Globicephala malaena*), bottlenose dolphins (*Tursiops truncatus*), Hector's dolphins (*Cephalorhynchus hectori*), killer whales (*Orcinus orca*), New Zealand fur seals (*Arctocephalus forsteri*), sperm whales (*Physeter macrocephalus*), S. right whales (*Eubalaena australis*), and humpback whales (*Megaptera novaeangliae*).

Introduction

Like many other animals, dusky dolphins form mixed-species groups (Figure 54). Such interspecific associations are most likely when there is a high degree of overlap in preferred habitat, and may enhance foraging or predator avoidance. Various dolphin species engage in mating, care-giving behavior and even stranding with heterospecifics.

Odontocetes demonstrate a variety of social systems, some of which appear remarkably convergent with those of terrestrial mammals (Connor *et al*. 1998). Studies with birds indicate that the degree and character of interspecific associations often depend upon overlap of preferred habitat of the species in question, with residents usually, but not always, the nuclear species to which others are attracted (Gram 1998). The two most common explanations for the formation of heterospecific groups are increased foraging efficiency and enhanced protection from predators (Morse 1977). These two driving forces in the formation of mixed species groups are not necessarily mutually exclusive. For example, golden plovers (*Pluvius dominica*) in lapwing flocks (Barnard *et al*. 1982) and Thomson's gazelles (*Gazella thomsoni*) in mixed herds with Grant's gazelles (Fitzgibbon 1990) are able to spend more time foraging due to the decreased need for vigilance gained through interspecific association.

Species in mixed assemblages are known to increase their ability to find and capitalize on food resources. Fieldfares (*Turdis pilaris*) and redwings (*Agelaius phoeniceus*) both increase their net energy intake when they flock together (Barnard and Stevens 1983). Great tits increase their feeding rate when in mixed-species flocks

(Sasvari 1992). Great egrets (*Casmerodius albus*), little blue herons (*Florida caerulea*), and tricolored herons are attracted to snowy egrets (*Egretta thula*) in tropical mixed-species flocks, and increase their foraging success by increasing their proximity to this species (Caldwell 1981). A variety of fish species increase their foraging efficiency by following other fish that flush or expose prey items in the course of their own search for food (Matthews 1998). Birds can develop positive associations with more effective foragers regardless of species, leading to an increased preference for heterospecifics. They may learn to utilize new food types and acquire foraging techniques through interactions with other species (Sasvari and Hegyi 1998). Fish have also been observed to increase opportunities for feeding through social observation of heterospecifics (Pitcher 1986).

Predator defense may be improved in heterospecific assemblages by increased predator detection, the dilution effect, and cooperative anti-predator behavior. While tropical rainforest primates may more readily find food in mixed-species groups or may aggregate at common food resources (Gautier-Hion *et al*. 1983), the driving force is most commonly an increase in the probability of predator detection (Struhsaker 1981). Associating in mixed-species groups reduces the vulnerability of red colobus and diana monkeys (*Cercopithecus diana*) to both land predators, such as chimpanzees (Dunbar 1997), and aerial predators, allowing them to utilize different parts of the forest canopy (Bshary and Noë 1997). Mixed-species herds of zebra (*Equus quagga*) stay together when threatened by potential predators with the numerically inferior species bunched within the larger group, suggesting these zebras benefit through “safety in numbers”

(Keast 1965). Thompson's and Grant's gazelles similarly band together to decrease vulnerability to attacks by cheetahs (Fitzgibbon 1990). For some fish, mixed species shoals can provide increased protection from predators due to the dilution effect without increasing competition for food resources as much as in large, monospecific schools (Pitcher 1986). Mixed-species groups may also work together to actively defend against predators, as in mobbing of owls by smaller birds (Pavey 1998). Both fish (Pitcher 1986) and birds (Yorio and Quintana 1997) have been observed to share in nest defense with hetero-specifics.

Among dolphins, group living offers calves protection from predators and increased opportunities for social learning (Wells 1991). It also plays an important role in acquiring mates (Connor *et al*. 1998), and in foraging (Wells *et al*. 1999). Mixed species associations may offer some similar advantages.

Interactions between dolphins and other species have been widely noted (reviewed by Connor *et al*. 2000). In the eastern tropical Pacific, bottlenose dolphin (*Tursiops truncatus*) mixed species associations, often with short-finned pilot whales (*Globicephala macrorhynchus*), increased with distance from shore (Scott and Chivers 1990). Mating between heterospecifics has been reported for several species of dolphins and sometimes results in hybridization between different dolphin species (Baird *et al*. 1998). Dolphins engage in care giving behavior directed toward other species (Caldwell *et al*. 1962; Baird 1998). Dolphins also have been reported to strand with heterospecifics on occasion (Pilleri and Knuckey 1969). However, not all interactions between cetaceans are necessarily affiliative. Some interactions between different species of odontocetes involve harassment (Weller *et al*. 1996), violence (Ross and Wilson 1996), and predation (Constantine *et al*. 1998). Interactions between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins included both affiliative, aggressive, and sexual behavior (Herzing and Johnson 1997).

In Argentina, dusky dolphins (*Lagenorhynchus obscurus*) associate with southern right whales (*Eubalaena glacialis*), southern sea lions *(Otaria flavescens*), Risso's dolphins *(Grampus grisseus*) and bottlenose dolphins (Würsig and Würsig 1980). In New Zealand, dusky dolphins have previously been observed with sperm whales(*Physeter macrocephalus*), killer whales (*Orcinus orca*), southern right whale dolphins (*Lissodelphis peronii*), common dolphins (*Delphinus delphis*), Hector's dolphins (*Cephalorhynchus hectori*), a humpback whale(*Megaptera novaeangliae*), and a lone sociable bottlenose dolphin (Würsig *et al*. 1997). Here, I report the context and character of interactions between dusky dolphins and ten other species of marine mammals, including one known predator, the killer whale. My goal is to examine the relationship between the formation of observed polyspecific associations and ecological factors, and the possible role of such mixed-species groups in foraging, predator defense and the rich social lives of dolphins.

Methods

Associations between dusky dolphins and ten other species of marine mammals were documented in New Zealand from 1994 to 2003, with observations of the context and character of interactions between species recorded during 1997 to 2003. From 1997 to 2003, inter-specific interactions were noted during research efforts in Kaikoura on the east coast (see chapters II and III for research effort details), the Marlborough Sounds on the north coast (see chapter IV), and the Westport/Jackson Bay areas (two 1-week surveys in 1998 and 1999) on the west coast of New Zealand's south island. Additional data from 1994-1996 were provided by staff onboard tour boats operated by the Dolphin Encounter company. Experienced observers noted the presence of other species and the location of dusky dolphin pods on 174 trips in 1994-1995 and 265 trips in 1995-1996. These boat-based efforts were augmented by tracking of dolphin groups from shore stations, with boat and shore teams in constant radio contact.

All interactions between dusky dolphins and other marine mammals were noted. The locations of dusky dolphin associations with other species were recorded using a Garmin 12XL global positioning system (GPS) receiver. Time and length of interactions and longitude-latitude encounter positions were noted for all groups. During the focal follows, GPS track information was downloaded at 2-minute intervals to derive information on movement patterns (including mean speed). Environmental parameters, including surface water temperature, were recorded.

For each group, the number and age classes of both dusky dolphins and associated marine mammal species were noted. When fewer than 50 dolphins were present in a pod, a count was made of the number of adults, juveniles, and calves present. Larger group sizes were categorized as 50-99, 100-249, 250-499, 500-1000, and > 1000. Interactions between dusky dolphins and most other marine mammals were generally rare events and the character of these interactions varied widely with the species in question. Therefore, it was difficult to develop a systematic behavioral sampling protocol for examining these interactions. In some instances, data were collected using the focal group 2-minute interval sampling methods outlined in chapters II and III. More commonly, research teams kept a “running log” characterizing each these interactions by noting the behaviors of the species in question. Behaviors documented in this manner included behavioral state, sudden bursts of speed, approach and avoidance, bow riding, and whale riding. Synchronous dive times were recorded with a stopwatch. In the case of smaller numbers of heterospecifics interacting with large groups of dusky dolphins, it was noted whether the two species maintained distinct subgroups or intermingled.

Location and time data were downloaded and manipulated using GPS Utility v. 4.04.7. Positions were plotted using ArcView v 3.2 and overlaid on bathymetric charts to examine the spread of interactions between dusky dolphins and each other species, the distance from shore and along shore at which interactions occurred, and water depths in which they took place.

Results

Interactions with Other Dolphins

<u>Hector's Dolphins (Cephalorhynchus hectori)</u>

Würsig *et al*. (1997) reported that interactions between dusky dolphins and Hector's dolphins are rare. Data from this study agree with this assessment. Hector's dolphins were observed in association with dusky dolphins on 17 occasions in Kaikoura and just once in Queen Charlotte Sound (Figure 55).

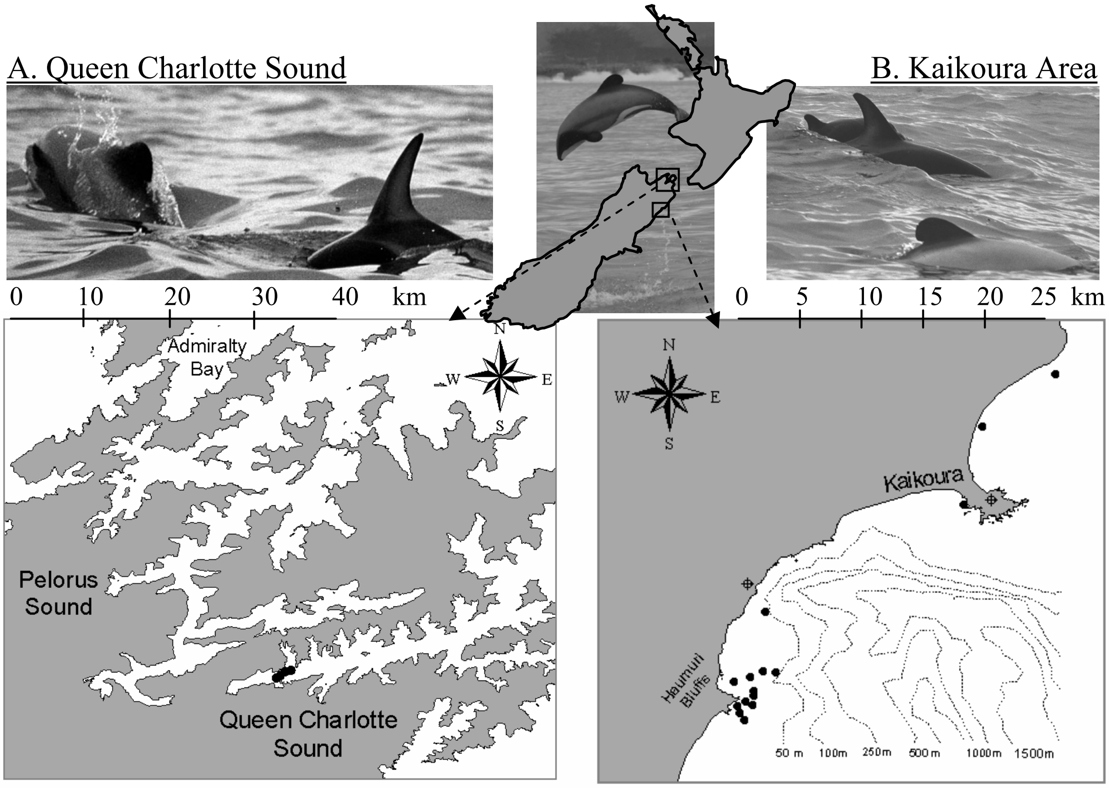


Figure 55. Locations of interactions between dusky dolphins and Hector's dolphins (pictured) in (a) Queen Charlotte Sound and (b) Kaikoura are shown as squares. A. The track of a single group over a period of 3.6 hrs is shown. B. Photograph shows mothers and calves in one of four mixed nurseries. ⊕ marks indicate shore-based lookout stations.

The one observed interaction between dusky and Hector’s dolphins in the Marlborough Sounds occurred during the winter (7 June 1999), when dusky dolphins migrate north to the area (see chapter IV), in the Grove Arm of Queen Charlotte Sound (Figure 55a). A group of 14 dusky and two Hector’s dolphins engaged in social play and milling in close proximity (< 1 body length) to one another. They remained together for at least 3.6 hours, moving very little (just 1.8 km) during this time (Figure 55a).

Hector's dolphins are found year-round in Kaikoura. Yet their degree of association with dusky dolphins appears also to be highly seasonal, coinciding with the time of year when dusky dolphins are typically found closest to shore. All observed associations between Hector's and dusky dolphins occurred during summer (76%) and autumn (24%). These interactions occurred near shore, at water depths generally less than 30 meters (Figure 55b). Roughly half (53%) of these interactions occurred in small groups, comprised of 5-19 dusky dolphins (mean = 7) and 2-8 Hector’s dolphins (mean = 4). Dusky dolphin calves were present during 88% of these interactions in small groups. Mixed nursery pods with calves of both species present were observed in 4 cases (Table 12). In one instance, a small pod including neonates of both species with visible fetal folds, was observed very near shore to the north of the Kaikoura peninsula. Swimming speeds of this nursery ranged from 5 to 10 km*h $^{-1}$, as they engaged in quiet social activity and rested along the shoreline. Small numbers of Hector's dolphins (1 to 12) also joined large pods of dusky and common dolphins near the Haumuri Bluffs on 8 occasions (47%).

Table 12: Composition of mixed nurseries of dusky and Hector's dolphins

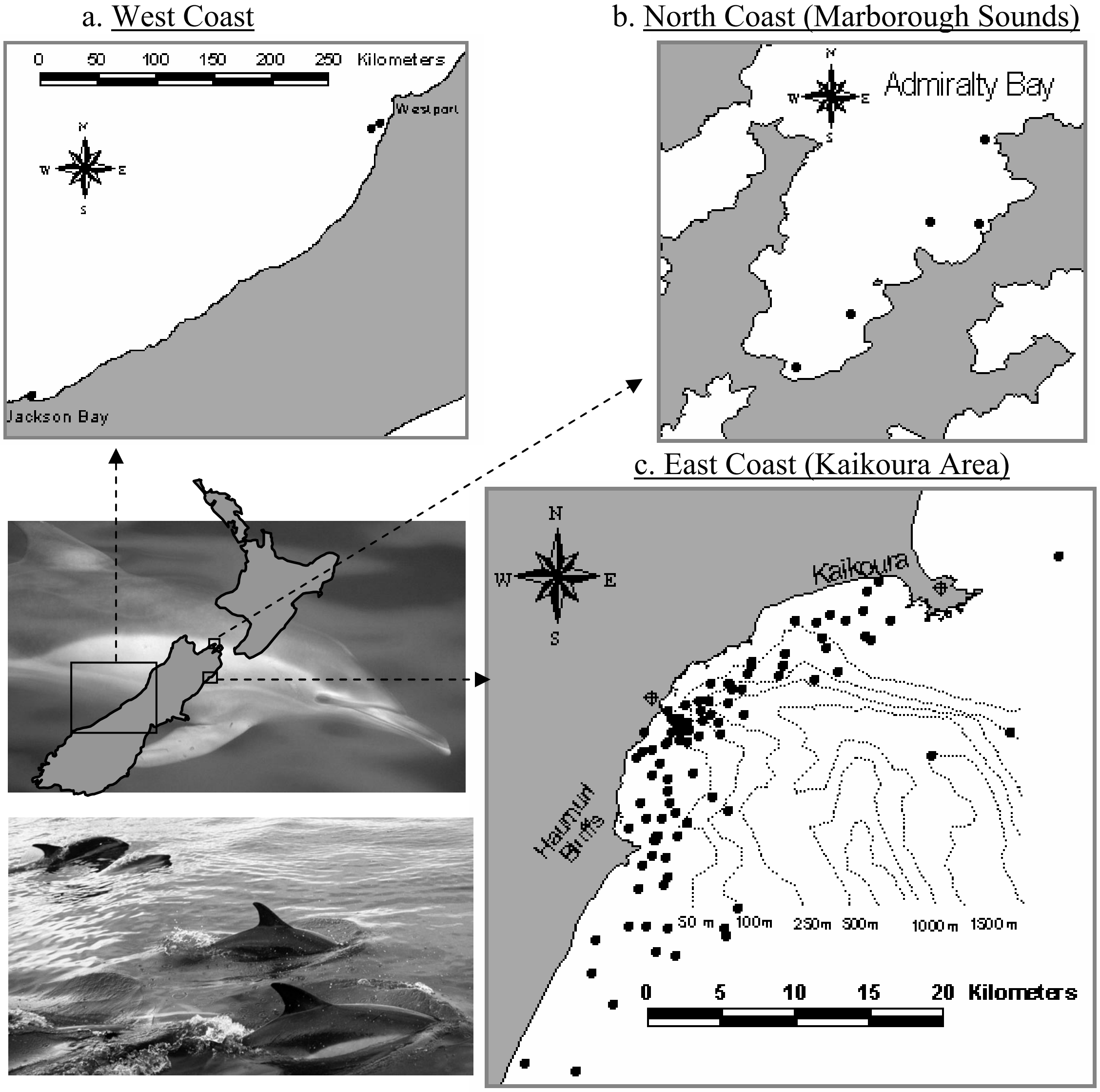
	Dusky Dolphins			**Hector's Dolphins**		
Date	Adults	Juveniles	Calves (neonates)	Adults	Juveniles	Calves (neonates)
24 Dec 97	3	1	3 (2)	3	0	2 (1)
11 Jan 98	19	3	5	3	0	1
14 Jan 98	10	0	2	1	0	1
14 Jan 00	6	3	2	2	0	1

Short-beaked Common Dolphins (Delphinus delphis)

Common dolphins were observed to interact with dusky dolphins more than any other marine mammal species in New Zealand. Interactions between the two species included mating and feeding together. The occurrence of mixed common and dusky dolphin groups was apparently tied to intermediate water temperatures, with the more tropical common dolphins preferring warmer temperatures and the more temperate dusky dolphins preferring cooler temperatures. Mixed dusky dolphin and common dolphin groups were observed in the warm waters of the north (n = 5) and west (n = 3) coasts as well as in the Kaikoura area (n = 161), mostly near shore in water < 100m deep (Figure 56).

West Coast (Westport-Jackson Bay)

Common dolphins were more commonly observed than dusky dolphins during surveys of the west coast. Three mixed groups were encountered in the Pancake Rocks (South of Westport) and Jackson Bay areas (Figure 56a), comprised of 6-30 common dolphins (mean = 16) and 2-11 dusky dolphins (mean =7). These groups engaged in traveling, with members of both species riding the bow of the research vessel. The mean surface water temperature during these encounters was 18.7° C, the warmest for any dusky dolphin encounters in the course of this study.


a. West Coast

b. North Coast (Marborough Sounds)

c. East Coast (Kaikoura Area)

Figure 56. Locations of dusky dolphin and common dolphin mixed groups on the west (a), north (b), and east (c) coasts of New Zealand's South Island are shown as dots. Photographs show a common dolphin calf that was accompanied by dusky dolphin adults in Admiralty Bay, and common dolphins in a large group of dusky dolphins in Kaikoura. ⊕ marks indicate the locations of shore-based lookout stations.

North Coast (Marlborough Sounds)

Of five mixed dusky dolphin-common dolphin groups encountered in Admiralty Bay during spring 2001 and winter 2003 (Figure 56b), three groups exhibited coordinated feeding by both species (see chapter IV), and mating between the two species was observed in the other two. In one instance, a very small common dolphin, apparently a calf or very young juvenile (Figure 56), maintained close proximity to an adult dusky dolphin for over 40 minutes. As all other photo-identification records of the adult dusky dolphin accompanying this young common dolphin showed no record of a juvenile/calf, this association/adoption appears to have been a short-term one.

Kaikoura

All observations of common dolphins in the Kaikoura area (n = 161) occurred in the context of mixed-species associations with dusky dolphin pods (Figure 56c). Unlike the west coast, common dolphins were always the numerically inferior of the two species in Kaikoura mixed-pods, with a median of 3 common dolphins present in the pods (range = 1 to 40). Just two observations (1.2%) were made of common dolphins in pods of less than 50 dusky dolphins in Kaikoura, and both were in highly social mating groups. Common dolphins were observed in fairly distinct sub-units within the larger dusky dolphin groups during 12.7% of observations. Dusky and common dolphins were frequently observed mating with each other (28.6% of mixed groups encountered). Apparent hybrids of the two species, as described by Würsig *et al.* (1997), were observed on 25 March 1998 in a group of 500-1000 dusky dolphins. Common dolphins and dusky dolphins engaged in bowriding together during 20.6% of mixed group encounters, often with dusky dolphins apparently displacing the common dolphins over time.

Unlike Hector's dolphins, common dolphins do not occur in Kaikoura year-round, but seasonally, coinciding with the highest water temperatures (Figure 57).

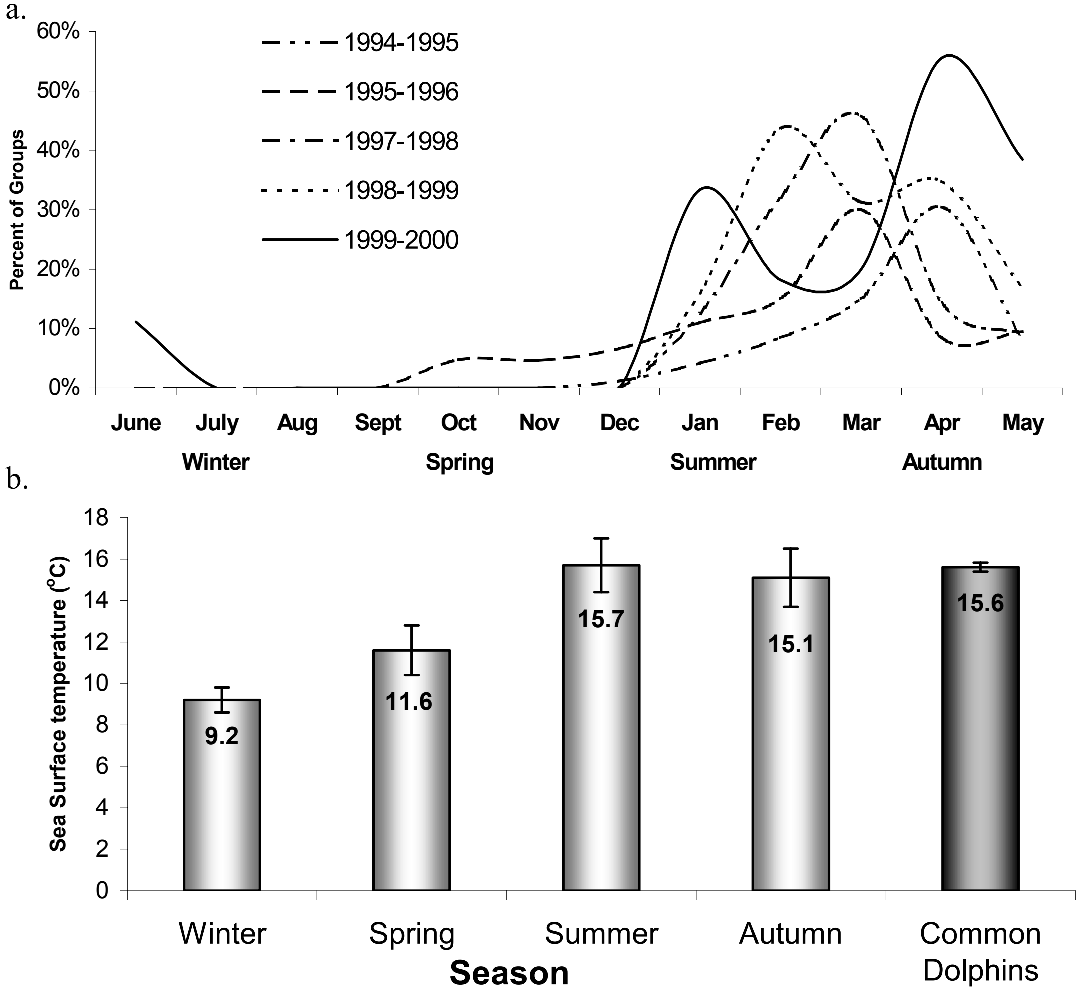


Figure 57. a. Seasonality of common dolphin interactions with dusky dolphins in Kaikoura is shown for 5 years by % of dusky dolphin groups with common dolphins present by month. b. Surface water temperatures are compared by season and to those recorded with common dolphins present. Bars represent mean values (indicated on data labels) with 1 standard error of the mean.

Southern Right Whale Dolphins (Lissodelphis peronii)

All observed associations between southern right whale dolphins and dusky dolphins in Kaikoura occurred in early spring, in September (n = 9) and October (n = 5). Southern right whale dolphins, generally an oceanic species (Gaskin 1968), joined large groups of dusky dolphins traveling > 10km offshore and ranging along the coast (Figure 58). Southern right whale dolphins made up a relatively small portion (median = 16 dolphins) of dusky dolphin groups from 250 to over 1,000. Traveling rapidly as subgroups within the larger dusky dolphin groups, the southern right whale dolphins occasionally engaged in porpoising.

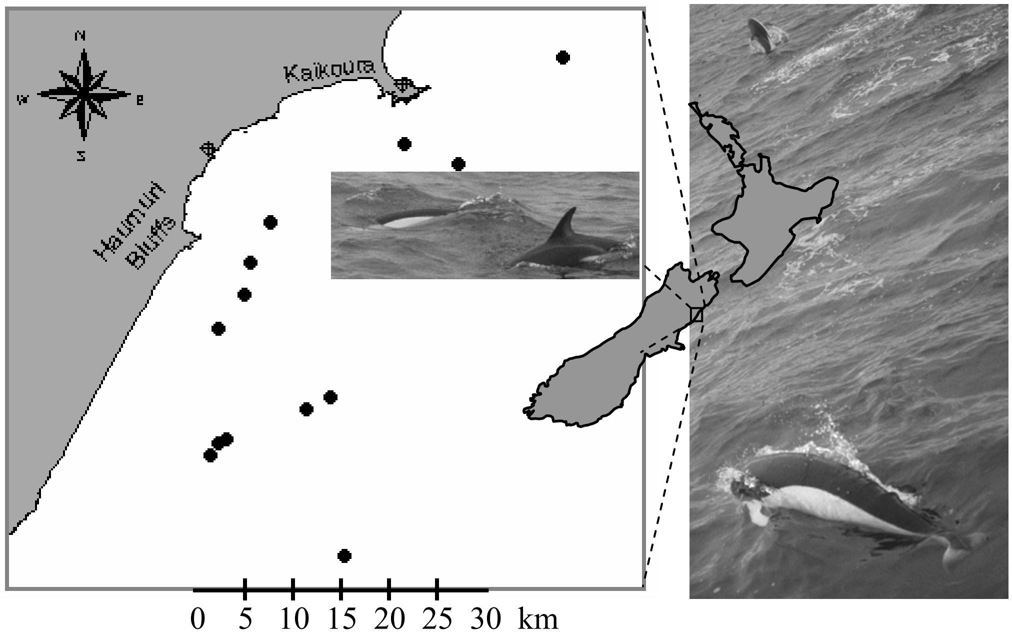


Figure 58. Distribution of mixed species associations of southern right whale dolphins and dusky dolphins (pictured) are plotted as filled circles. ⊕ marks indicate the locations of shore-based lookout stations.

<u>*Long-Finned Pilot Whales* (Globicephala melaena)</u>

Long-finned pilot whales were observed traveling through the Kaikoura area on six occasions in the course of this study, always in the company of bottlenose dolphins. On five of these days during two successive summers, the mixed groups found > 10km offshore in > 50m deep water also included dusky dolphins (Figure 59). .

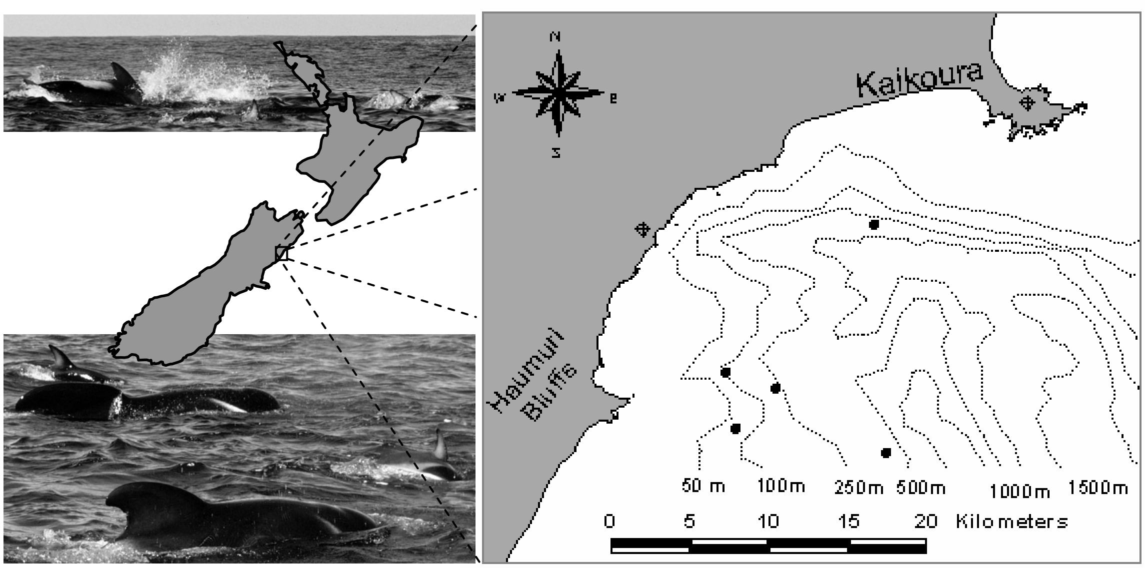


Figure 59. Dusky dolphins swam rapidly within mixed groups of long-finned pilot whales (pictured) and bottlenose dolphins in Kaikoura at the locations shown. ⊕ marks indicate the locations of shore-based lookout stations.

These mixed groups were comprised of 20-50 pilot whales, 6-20 bottlenose dolphins, and 2-5 dusky dolphins. These mixed assemblages moved steadily through the area at mean speed of 9.5 km*h^{-1}, with the pilot whales diving regularly. The pilot whales and bottlenose dolphins, while traveling in one large group, maintained distinct subgroups. The dusky dolphins swam rapidly between these subgroups, never staying with any one for long, and leaping very little. They showed much more interest in the groups than in attendant vessels, and were not observed to engage in bowriding. The pilot whales, by contrast, approached vessels at times, with a pilot whale calf spyhopping in one instance.

Bottlenose Dolphins (Tursiops truncatus)

In addition to the interactions between dusky and bottlenose dolphins described above, Müller *et al*. (1998) describe interactions between dusky dolphins and a lone sociable bottlenose dolphin, named "Maui", who resided for a time in Kaikoura (Figure 60a). While the dusky dolphins appeared to avoid Maui when she first arrived in the area in 1992, they gradually became habituated to her presence. She departed from Kaikoura to take up residence in the Marlborough Sounds at roughly the same time of year that dusky dolphins would be expected to shift northward in 1994, 1995, and 1996 (Müller *et al*. 1998). Recent photographic evidence (see chapters IV and VII) indicates that some dusky dolphins move from Kaikoura to Marlborough between seasons, so Maui may have traveled with dusky dolphins up to the Marlborough Sounds.

Direct interactions between bottlenose dolphins and dusky dolphins in the Marlborough Sounds were observed on only two occasions, with apparent chasing of dusky dolphins by bottlenose dolphins (track lines shown in Figure 60b). As few interactions were seen between the two species in an area of high dusky dolphin concentration during winter months (see chapter IV), it is possible that the larger bodied bottlenose dolphins, which traveled in groups of up to approximately 100 individuals, displaced dusky dolphins.

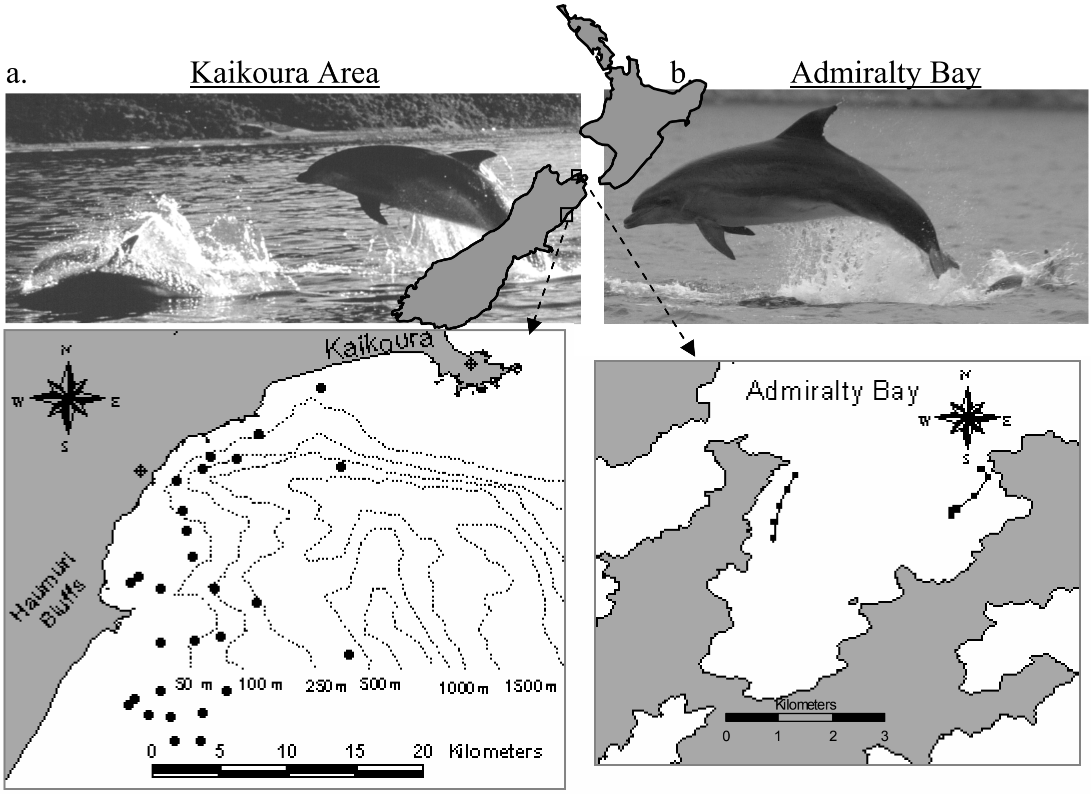


Figure 60. Locations of dusky and bottlenose dolphin interactions in (a) Kaikoura and (b) Admiralty Bay are shown as filled circles (track lines indicated for b). Photographs show chasing of dusky dolphins by (a) a lone sociable bottlenose dolphin “Maui” in Kaikoura (photo courtesy of B. Todd) and (b) a bottlenose dolphin in Admiralty Bay. ⊕ marks indicate the locations of shore-based lookout stations.

Killer Whales (Orcinus orca)

Killer whales travel through the Kaikoura area periodically, and have been observed to prey upon dusky dolphins in Kaikoura (Constantine *et al*. 1998). Interactions between killer whales and dusky dolphins in Kaikoura (n = 33) peaked during the dusky dolphin calving season in the spring (21%), summer (55%) and autumn

(21%), and were relatively rare during the winter (3%). The majority of these interactions occurred in the deepest water near shore (Figure 61). Tour operators reported two predation events during spring 1995 and another in summer 2000.

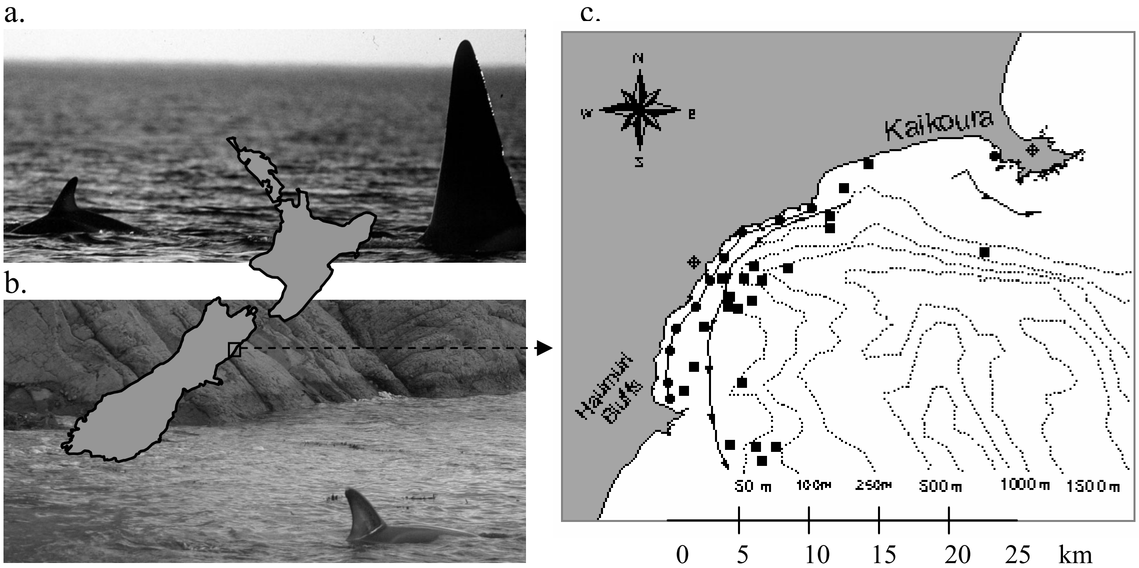


Figure 61. A. Dusky dolphin “scouts” engaged in apparent mobbing behavior, approaching and swimming rapidly around killer whales. B. Dusky dolphins sought refuge in the shallows from killer whales patrolling just offshore. C. Locations of interactions between killer whales and dusky dolphins in the Kaikoura area are shown as squares. Filled circles show locations of dolphins with killer whales nearby (arrows indicate the approximate track of the killer whales). ⊕ marks indicate the locations of shore-based lookout stations.

Dusky dolphins appeared to employ a number of strategies in response to killer whales. The most common response was rapid speed burst (15-20 km*h^{-1}) behavior, and movement very close to shore (Figure 61b). Small groups of adult dusky dolphins (mean = 6) were also observed to approach killer whales, swimming rapidly around and in front of them (Figure 61a), before departing at high speed. The particularly rapid nature of these interactions suggest that the dolphins may employ a form of "mobbing" or "scouting" in defense against predation by killer whales.

On the morning of 17 February 1998, a group of 6 killer whales was observed following a dusky dolphin group comprised of 15 adults, 3 juveniles, and 2 calves (tracks shown on Figure 61c). The killer whales remained just behind and roughly 500m offshore of the dolphins, which engaged in rapid white-water travel and bursts of speed to the south along the shoreline (Figure 61c). Often the dolphins were within a few meters of shore, and they showed no sign of venturing into deeper water. The killer whales followed the dolphins in this manner for 1 hour, 45 minutes at a mean speed of 10.5 km/hr before eventually heading off further to the south and offshore. The dolphins remained within the relative shelter of the bay just north of the Haumuri Bluffs into the afternoon.

Whale Riding

Dusky dolphin interactions with great whales were only observed on seven days in Kaikoura, exhibited by adult dolphins, and generally took the form of "whale riding" behavior. Whale riding behavior is thought to be a precursor of bow riding, in which dolphins ride the pressure wave created by large whales as they travel (Norris and Prescott 1961, Leatherwood 1974, Würsig and Würsig 1979). Whale riding varied with the behavior of the whale in question. Dolphins followed whales traveling in the horizontal plane and followed whales diving in the vertical plane (Figure 62). In all observed instances (n = 7), dusky dolphins interacting with whales in Kaikoura swam rapidly around the whales' heads. The reaction of whales to this activity appeared to range from affiliative to indifferent to agonistic.

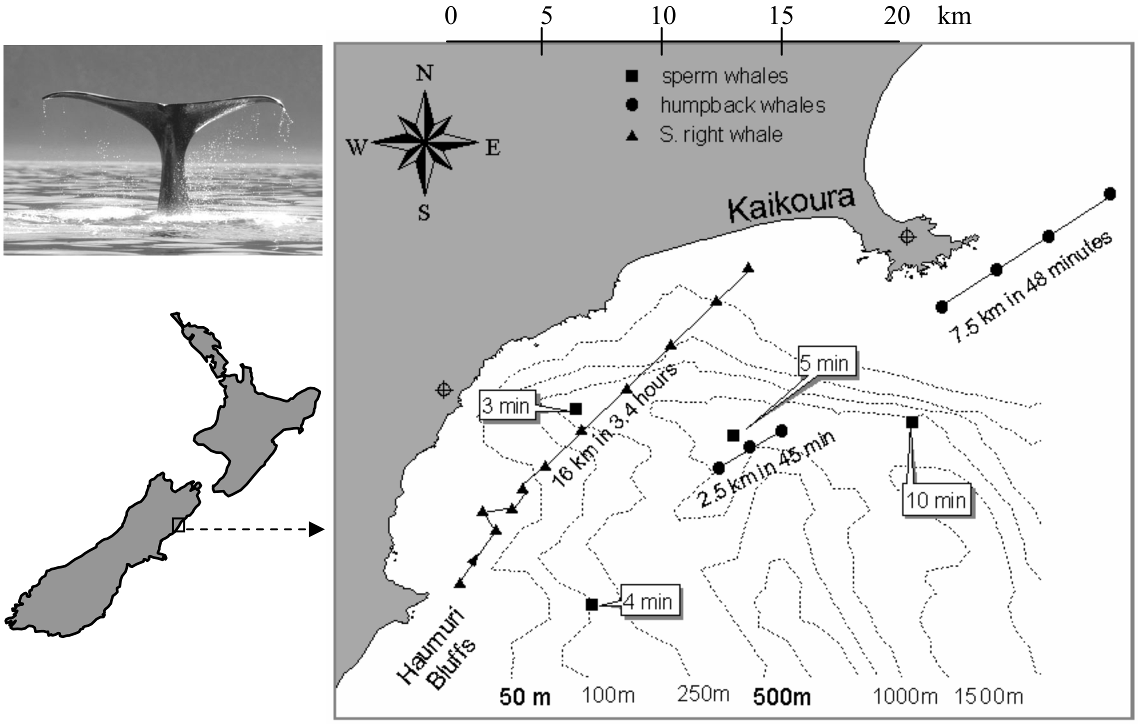


Figure 62. Locations of dusky dolphin interactions with great whales in Kaikoura are shown with data labels indicating the duration of the interaction and the distance traveled (except for sperm whales which were stationary while at the surface). Squares represent sperm whales, circles humpback whales, and triangles a southern right whale. ⊕ marks indicate the locations of shore-based lookout stations.

Sperm Whales (Physeter macrocephalus)

For sympatric species occurring year-round in the Kaikoura area, dusky dolphins and sperm whales rarely interact. Just four interactions between the two species were observed in the course of this study. Sperm whales feed on squid and other deep-sea prey during the daytime, by making sustained feeding dives. Between dives they generally stay at the surface for 5-10 minutes, and interactions between dusky dolphins and sperm whales occurred during this window of opportunity. All interactions occurred over deep water, from 100 to >1,000m depth (Figure 65), and most occurred in large groups during winter (Table 13) when dolphins were further offshore (see chapter II). Dolphins dove with the whale in 3 out of the 4 cases. In the fourth case, the dolphin group suddenly left the whale, which breached, at high speed (Table 13). When the research vessel caught up with the dolphins 35 minutes later, they had traveled 10.5 km to the north (indicating a mean speed of 18 km/hr).

Table 13: Dusky dolphin interactions with sperm whales

Date	# Dolphins (# riding)	Duration	Dolphin activity	Whale activity
17 Aug 1997	> 1,000 (15)	5 minutes	Speed burst	Breach
22 Feb 1999	4 (4)	10 minutes	Dive	Dive
15 July 2003	250-500 (10)	4 minutes	Dive	Dive
27 July 2003	500-1,000 (20)	3 minutes	Dive	Dive

Humpback Whales (Megaptera novaeangliae)

Dusky dolphins were observed to interact with humpback whales passing through the Kaikoura area on two occasions in the late autumn and early winter (Figure 62). On 23 May 1999, a group of 6 dolphins traveled steadily, whale riding with a lone humpback whale northeast along the coast at a mean speed of 9.4 km*h^{-1} for 48 minutes (Figure 63a). At the end of this period of steady travel, the whale turned on side, swiping through water with its tail flukes, and the dolphins left in a sudden high speed burst, moving offshore. The whale continued traveling northeast at a mean speed 8 km/hr for the next 25 minutes.

a.

b.

Figure 63. a. Dusky dolphins engaged in whale riding for 48 minutes, traveling steadily with a lone adult humpback whale. b. Interactions of a humpback whale mother and calf with dusky dolphins included inverted ("belly up") swimming by the whale.

On 20 June 2003, a humpback whale mother and calf were observed interacting in a different manner with a group of 20 dusky dolphins (Figure 63b). The humpback whales interacted with the dolphins as they mostly milled (70%, traveling 30%) around the whales for 32 minutes. The behavior of the whales during this interaction included inverted swimming (44% of intervals, Figure 63b), spy-hopping (4 times, 25% of intervals), waving pectoral flippers twice, and a single tail slap. A mean of 9.8 dolphins (standard deviation = 2.62) engaged in whale riding during 100% of instantaneous 2-minute samples throughout this interaction. Some also rode the bow of the research vessel (mean =1.6) at 40% of intervals. The dolphins steadily followed the whales to the north at a mean speed = 3.4 km*h^{-1}. They maintained close proximity clustered closely around the whale, spending 70% of intervals within 1 body length of each other and 30% spread 1-3 body lengths. The dolphins showed a high level of activity, engaging in speed bursts during 55% of intervals and porpoising during 15% of intervals. Other leaping activity occurred during 10% of intervals, 80% of which consisted of clean head-first re-entry leaps (1.7 every 2 minutes).

Southern Right Whale (Eubalaena australis)

On 19 Jan 1999, dusky dolphins followed a southern right whale passing through the Kaikoura area for the better part of the day (Figure 62). The dolphins engaged in whale riding, often in very close proximity to the head of the whale at a mean speed of 4.1 km/hr (Figure 64).

Figure 64. Dusky dolphins swam in very close proximity to a southern right whale.

Dolphins stayed with the right whale from 11:55-15:20. The whale was accompanied throughout this time by a small group of 24 adult dolphins, and briefly (33 minutes, 12:47-13:20) by a larger group (250-500 dolphins). Dolphins dove synchronously with the whale repeatedly. Dive times for the dolphins were among the longest recorded for dusky dolphins (mean=2.6 minutes, range = 0.9-6.4 minutes). Following these dives, the dolphins surfaced vertically out of the water, leaping synchronously. The right whale's dive times were longer than the dolphins (mean = 7.7 minutes, range = 5.8-10.3 minutes). The dolphins milled at the surface, until just before the whale surfaced. Prior to each surfacing of the whale, the dolphins increased their activity, with rapid speed bursts and circling in the area where the whale subsequently surfaced. While it was not clear from the vessel where the whale would surface, the dolphins clearly anticipated each surfacing, and apparently "tracked" the whale during its dives.

New Zealand Fur Seals (Arctocephalus forsteri)

Other than common dolphins, New Zealand fur seals interacted with dusky dolphins more than any other marine mammal. Many interactions between New Zealand fur seals and dusky dolphins involved feeding, with the fur seals apparently engaging in kleptoparasitism, capitalizing on the dolphins' coordinated foraging efforts. Some also involved social play, including chasing and bow riding together. Interactions were most commonly observed near shore and within 5-10 km of fur seal colonies (Figure 65).

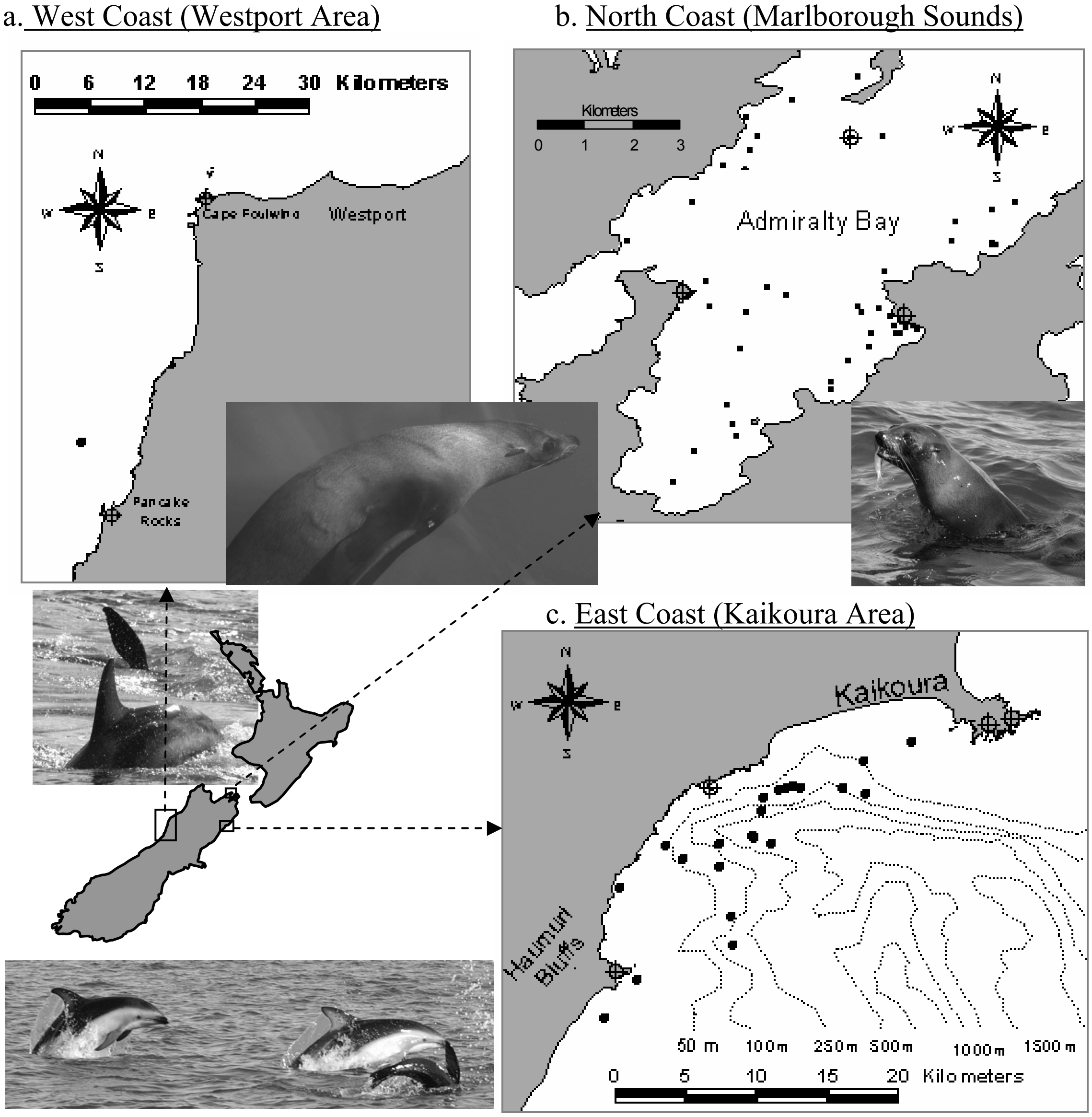


Figure 65. Locations of interactions between New Zealand fur seals and dusky dolphins on the (a) west, (b) north, and (c) east coasts of New Zealand's South Island are shown as filled circles. ⊕ marks indicate the locations of fur seal haul outs in each area (some on islands). Photographs show fur seals (a) bow riding, (b) feeding and (c) associating with dolphins.

In Kaikoura, most interactions (n=24) involved solitary fur seals (83% 1 seal, maximum 4 seals, mean = 1.2) and large groups of dusky dolphins (63%). Considering that daytime feeding was documented in <1% of dolphin group encounters in Kaikoura (see chapters II-IV), a high percentage of interactions with fur seals (25%) occurred in a feeding context. Social or interactive play between the seals and dolphins was noted in 21% of Kaikoura interactions.

In Admiralty Bay, 1-21 fur seals (mean = 2.4) interacted with groups of 1-25 dusky dolphins (mean =10). Most (96%) of these interactions involved feeding, (whereas only 72% of dolphin groups were observed feeding in Admiralty Bay, see chapter IV), with fur seals observed feeding on both the dolphins' prey (e.g. pilchard, Figure 65b) and on predatory fish (barracuda) attracted to the feeding activity.

Discussion

Although not an every day occurrence, heterospecific association is a regular feature of dusky dolphin social lives. Dusky dolphin associations with common dolphins, Hector's dolphins and southern right whale dolphins appeared to be related to seasonal changes in the degree of niche overlap between species, in which water temperature, distance from shore and water depth are likely important factors. Dusky dolphins were always the more numerous species in these mixed pods, and may have provided protection from predators for the other species involved. Interspecific mating between dusky and common dolphins, and mixed nursery pods of dusky and Hector's dolphins, were noted.

The formation of mixed-species groups depends first on co-occurrence of species within a given area. This, in turn, may be heavily influenced by ecological factors related to the preferred habitat types of the species in question. The high degree of seasonality in observed associations between dusky dolphins and common dolphins, Hector's dolphins, and southern right whale dolphins suggests that the extent of niche overlap between these species may change over the course of the year. Gaskin (1968) postulated that changes in the seasonal distribution of dolphins in New Zealand are linked to changes in sea surface temperature. Common dolphins appear to enter the Kaikoura area when surface water temperatures peak, and generally associate with large schools of dusky dolphins during that time. Associations between dusky dolphins and Hector's dolphins occur in shallow, near shore water, and so occur most frequently during the time of year when dusky dolphins are found closest to shore even though

Hector's dolphins can be found there year-round. By contrast, mixed dusky dolphin-southern right whale dolphin schools were observed offshore in deeper water, and hence occurred during late Winter-early Spring, when the dusky dolphins range further from shore. Dusky dolphin group sizes also reach their maximum at this time of year, often in excess of 1,000 individuals. Throughout their ranges in South America, South Africa, and New Zealand, dusky dolphins are restricted to waters less than 2000m deep (Würsig *et al*. 1997), which may effectively limit their interactions with the oceanic southern right whale dolphins.

Dusky dolphins in Kaikoura feed mainly at night on mesopelagic fishes and squid of the deep scattering layer, brought close to shore by a deep submarine canyon (Cipriano 1992). Since these prey are relatively abundant and evenly distributed, it seems unlikely that mixed-species assemblages provide a foraging benefit, as may be the case with mixed dusky dolphin-Risso's dolphin groups in Argentina (Würsig and Würsig 1980). Daytime feeding, by cooperatively herding schools of small fish, is common among dusky dolphins in Argentina but rarely observed in Kaikoura (Würsig *et al*. 1989).

Predator defense is more likely an important factor in the formation of these interspecific assemblages. Sightings of killer whales in Kaikoura coincide with the time of year when multi-species groups most commonly form between dusky and both common and Hector's dolphins. Defense against shark attacks may also be a factor. During the summer, two dusky dolphins were observed repeatedly ramming a blue shark with their rostrums. Common dolphins may use large dusky dolphin groups for enhanced predator detection and defense, and be tolerated by the dusky dolphins because they are not in competition for resources. Such a pattern has been observed in associations of olive colobus monkeys with diana monkey (*Cercopithecus diana*) groups (Whitesides 1989). Our only observations of dusky dolphins apparently displacing common dolphins occurred in the context of bowriding, with the small bow wave created by our tiny boat the limited resource.

The occurrence of mixed nursery pods of dusky and Hector's dolphins may be related to the vulnerability of calves to predation, with these heterospecifics cooperating in the defense of their young as is seen in birds (Yorio and Quintana 1997) and fish (Pitcher 1986). The reason Hector's dolphins do not associate more often with dusky dolphins may also be predation pressure. Hector's dolphins generally live in relatively small groups, preferring the near shore environment (Slooten and Dawson 1992) where reduced water clarity may help to prevent detection by predators. Thus, the relative safety in numbers offered Hector's dolphins in larger heterospecific pods may be balanced against the greater likelihood of being discovered by predators, with the scales tipped toward interspecific association when dusky dolphins venture into their preferred habitat. Such trade-offs have been documented in mixed-species groups of tadpoles, which benefit through increased vigilance and the dilution effect but are also more likely to be discovered by predators when associating with other species (Griffiths and Denton 1992).

The “flighty” behavior, especially the prevalence of rapid speed bursts, exhibited by dusky dolphins interacting with pilot whales and bottlenose dolphins is puzzling.

Given that agonistic, non-predatory interactions between different species of cetaceans have been reported to cause physical harm and distress (Ross and Wilson 1996; Weller *et al*. 1996), it is possible that the apparent wariness of the dusky dolphins around these larger species was not unwarranted.

Interactions between dusky dolphins and killer whales appeared to involve predator evasion, assessment, and harassment. “Scouting” and “mobbing” behavior have been reported for other marine mammals in response to sharks (Connor *et al*. 2000) and killer whales (Baird 2000).

Interactions between dusky dolphins and larger cetaceans were rare, and were generally playful. “Whale riding” was the most commonly observed interaction, with the dolphins accompanying whales over large distances and for prolonged periods in the horizontal plane, and also diving with the whales, apparently “riding” in the vertical plane. Whale responses to this behavior varied from apparently affiliative to indifferent to agonistic. In two instances, dolphins that had been associating with a whale appeared to take flight in response to an agonistic action of the whale (a breach by a sperm whale and a tail swipe by a humpback whale). Despite a high degree of range overlap, dusky dolphins and sperm whales were rarely observed interacting. Foraging sperm whales in Kaikoura may represent a less exciting stimulus than other whales for “whale riding” behavior, as they tend to move little in the horizontal plane lying relatively still at the surface while re-oxygenating between foraging dives.

Associating with other species may result in benefits other than increased foraging efficiency and predator avoidance. Mixed-species groups of Peruvian bats enhance thermoregulation by roosting in close proximity and facilitate ectoparasite removal by heterospecific allogrooming (Graham 1988). A variety of fish and ungulates reduce their parasite loads through association with cleaner species (Poulin and Grutter 1996). Some species of Amazon fish depend on mixed-species shoals in order to maintain their sexual-asexual mating system (Schlupp and Ryan 1996).

In the case of dolphins, it seems likely that interactions with heterospecifics are an important component of their social lives, the complexities of which are just beginning to be uncovered (Connor *et al*. 1998). For the highly social dusky dolphins, interaction with a number of other cetaceans would appear to be a regular part of their routine, which follows reasonably consistent seasonal trends from one year to the next. Mixed nurseries of Hector's and dusky dolphins could serve to introduce young dolphins to their neighbors and future social partners. Interactions between dusky dolphins and common dolphins may also play an as yet undetermined social role, given observations of mating and apparent hybrids between the two species.

CHAPTER VI

THE USE OF DIGITAL TECHNIQUES IN PHOTO-IDENTIFICATION OF NEW ZEALAND DUSKY DOLPHINS*

What is a camera… but a box of light?

- Ani DiFranco, Evolve

Figure 66. Photographs taken with still cameras from vessels are widely used to identify distinctive individuals in studies of wild, free-ranging cetaceans.

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*Portions of this chapter are reprinted with permission from Markowitz, T. M., A. D. Harlin, and B. Würsig. 2003a. Digital photography improves efficiency of individual dolphin identification. Marine Mammal Science 19: 217-223, and Markowitz, T.M., A.D. Harlin, and B. Würsig, 2003b. Digital photo-identification: A reply to Mizroch. Marine Mammal Science 19 (1): 608-612. Copyright 2003 by the Society for Marine Mammalogy.

Introduction

Methods for reliably identifying and monitoring individuals are critically important to understanding the behavior of animals (Martin and Bateson 1993). Naturally occurring distinctive features have proven particularly useful for studies of free ranging populations of marine mammals, especially in those cases where artificial marking could potentially harm animals or bias the collection of behavioral data (Wells *et al*. 1999). Since its first use in the 1970s (e.g., Würsig and Würsig 1977, Katona *et al*. 1979, Shane 1980, Payne *et al*. 1983), photo-identification has emerged as a dependable, non-invasive technique (Figure 66) for measuring social grouping, movements, residency, abundance, and life history of many cetacean species (summarized in Mann 2000). It has shown especially great utility for examining associations between individuals at different spatial and temporal scales (Whitehead 1997). Most photo-identification studies of dolphins and porpoises rely on nicks and cuts in the dorsal fin that provide long-lasting, individually unique markings (Würsig and Jefferson 1990); some body scars and pigmentation patterns also persist over many years and can be used for identification (Lockyer and Morris 1990).

Several techniques have been developed to standardize and facilitate comparison of photographic records, including tracing of dorsal fins onto standardized sheets and calculation of parameters such as the dorsal ratio (Defran *et al*. 1990, Kreho *et al*. 1999). With the advent of computer-aided photo-identification database sorting (Whitehead 1990b) and semi-automated photographic matching techniques (Hiby and Lovell 1990, Araabi *et al*. 2000, Hillman *et al*. 2003), catalogues of distinctively marked individuals are increasingly being maintained in a digitized format. These methods considerably decrease analysis time for large photographic catalogues (Araabi *et al*. 2000), and facilitate collaboration between researchers (Mizroch *et al*. 1990), increasing the speed, accuracy and efficiency of photo-identification efforts.

Digital photography holds promise as a seamless interface between the collection of photo-identification data and the latest computer-based analysis techniques. In order to assess whether digital image capture represents a reliable alternative to traditional film photography for individual dolphin identification, the efficiency of the two techniques was tested in the field with a wild dolphin population. This study aimed at comparing the practical effectiveness of digital photography versus traditional film photography for identifying individual dolphins. It was conducted without any *a priori* expectations, but rather with the simple goal of examining to what extent digital photography fails to reach, meets, or exceeds film standards in this research application (during both initial data collection and data analysis). Measures examined included the proportion of images collected suitable for analysis (based on image quality), and the efficiency with which these images could be analyzed quickly using a semi-automated computer photo-identification system.

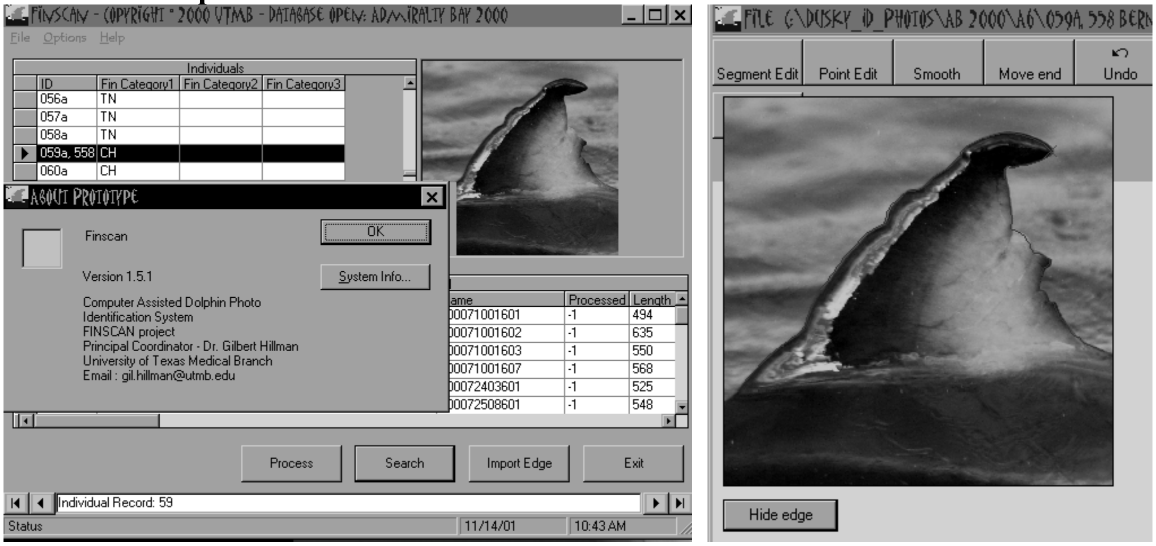
Methods

Over the past seven years, New Zealand dusky dolphins (*Lagenorhynchus obscurus*) were photographed for the purpose of individual identification, first with slide film and later using digital image capture, allowing a comparison of the efficiency of the two techniques. This research was conducted from small vessels using high-speed auto-focus cameras and variable focal length (zoom) lenses in the manner described by Würsig and Jefferson (1990). A sample of 22,962 photographs taken on film during 301 dolphin group encounters over a three-year period was compared to a sample of 32,759 images captured digitally from 737 dusky dolphin groups over a four-year period. The same photographers, in the same locations, and under comparable environmental conditions, collected images used in this analysis.

During 1997-1999 and some of 2002, dorsal fin photographs were taken with Kodachrome and TMAX 100-400 ISO film using a Nikon N-90 auto-focus camera with Nikkor 80-200 mm (f 2.8) and Tokina 100-300 mm (f 4.3) lenses. Following developing, images were mounted as slides. Photographic quality and distinctiveness were manually assessed using 8x to 15x magnifying lenses and light tables. Suitability of photograph quality for individual identification was judged based on clarity, contrast, angle, and the extent to which distinctive features were hidden or obscured, rating only “good” to “excellent” photographs as suitable (Friday *et al*. 2000). A photograph was deemed of suitable quality if distinguishing features could be recognized reliably in subsequent photographs, or the lack of distinguishing features could be concluded reliably. Suitable photographs were in sharp focus, with good contrast, within a few degrees of parallel to the dorsal fin, and unobscured (as in Slooten and Dawson 1992). All judgments as to the suitability of images for photo-identification were made by me and confirmed by a second experienced observer. The distinctiveness of individuals photographed was then examined to assess whether the features were adequate for reliable re-identification (Friday *et al*. 2000, Slooten and Dawson 1992). After this initial sorting, dorsal fins from suitable quality images were traced on paper, and later digitized using a Polaroid Sprintscan 35 plus slide scanner at 2700 pixels per inch.

During 2000-2003, digital images were acquired using Nikon D1 and D1H cameras with virtual ISO settings ranging from 200-1600 in “fine” resolution mode (2.6 megapixels), and either a Tokina 100-300 mm (f 4.3) or a Nikkor 80-400 mm (f 4.5-5.6) vibration reduction lens. In the field, digital images were temporarily stored on compact flash memory media as 1.2-1.3 megabyte compressed JPEG files, and then downloaded directly to a laptop computer for analysis. Downloaded digital images were cropped outside the edges of the dorsal fins and examined onscreen using Adobe Photoshop 4.0 software. Digital image quality and individual distinctiveness were judged by the same criteria as film images. The proportion of images of suitable quality for identification was calculated for all group encounters, with each group encountered on a different day considered to be statistically independent. Values for digital versus film photography were compared by Mann-Whitney test using SPSS v. 11 software.

To compare the effectiveness of digital and film images in computer analysis, images acquired digitally were tested against scanned slides using the Finscan Computer Assisted Dolphin Photo-identification System, Version 1.5.1 (Figure 67). This software matches images based on a mathematical description of the irregularities in the trailing edge of the dorsal fin (Kreho *et al.* 1999, Araabi *et al.* 2000, Hillman *et al.* 2003).



a. database input

FINSCAN - COPYRIGHT © 2000 UTMB - DATABASE OPEN: ADMIRALTY BAY 2000

ID	Fin Category1	Fin Category2	Fin Category3
056a	TN		
057a	TN		
058a	TN		
059a, 558	CH		
060a	CH		

ABOUT PROTOTYPE

Finscan

Version 1.5.1

Computer Assisted Dolphin Photo
Identification System
FINSCAN project
Principal Coordinator - Dr. Gilbert Hillman
University of Texas Medical Branch
Email : gil.hillman@utmb.edu

ame	Processed	Length
00071001601	-1	494
00071001602	-1	635
00071001603	-1	550
00071001607	-1	568
00072403601	-1	525
00072508601	-1	548

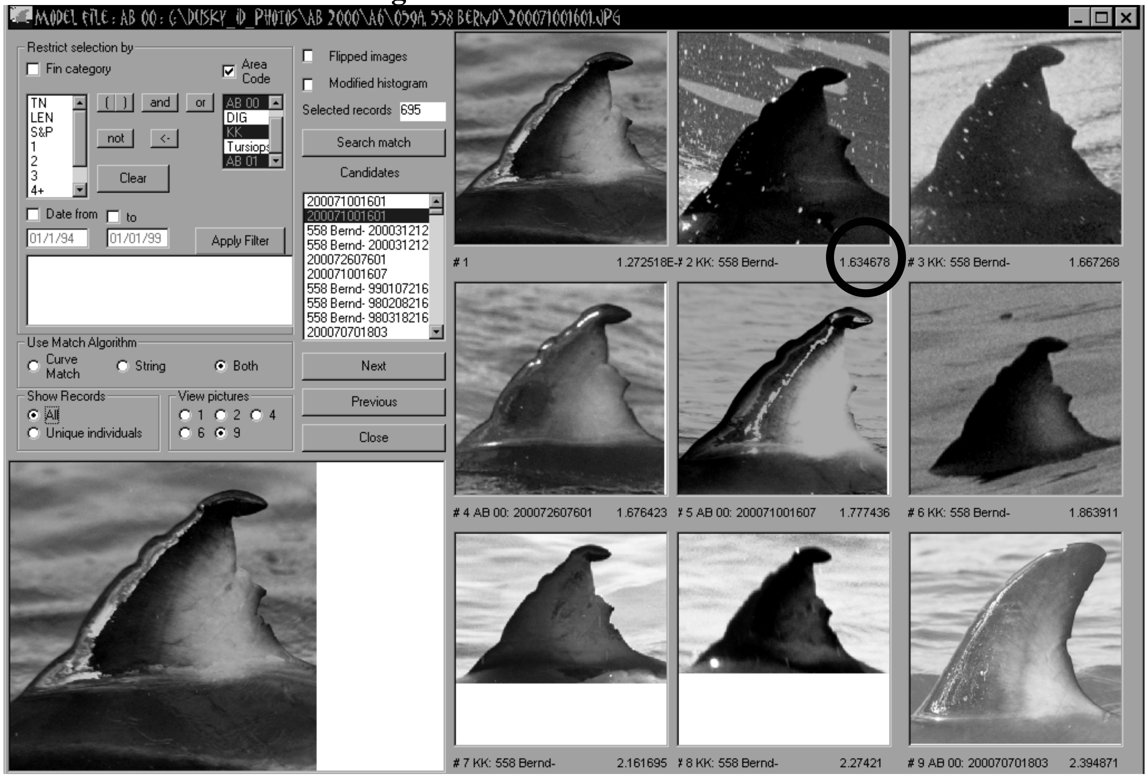
Individual Record: 59

Status 11/14/01 10:43 AM

b. fin outline

FILE G:\DUSKY_ID_PHOTOS\AB 2000\A6\059A, 558 BERN

c. semi-automated matching



MODEL FILE: AB 00: G:\DUSKY_ID_PHOTOS\AB 2000\A6\059A, 558 BERND\200071001601.JPG

Restrict selection by

☐ Fin category

☑ Area Code

TN
LEN
S&P
1
2
3
4+

AB 00
DIG
KK
Tursiops
AB 01

☐ Date from ☐ to

01/1/94
01/01/99

☐ Flipped images

☐ Modified histogram

Selected records 695

Candidates

200071001601
200071001601
558 Bernd- 200031212
558 Bernd- 200031212
200072607601
200071001607
558 Bernd- 990107216
558 Bernd- 980208216
558 Bernd- 980318216
200070701803

Use Match Algorithm

○ Curve Match ○ String ● Both

Show Records

● All
○ Unique individuals

View pictures

○ 1 ○ 2 ○ 4
○ 6 ● 9

1 1.272518E-

2 KK: 558 Bernd- 1.634678

3 KK: 558 Bernd- 1.667268

4 AB 00: 200072607601 1.676423

5 AB 00: 200071001607 1.777436

6 KK: 558 Bernd- 1.863911

7 KK: 558 Bernd- 2.161695

8 KK: 558 Bernd- 2.27421

9 AB 00: 200070701803 2.394871

Figure 67. Finscan software (Hillman *et al.* 2003) used to construct photo-identification catalog. Images were (a) input into a database, (b) traced by contrast with correction by eye, and (c) compared using curve and string matching to rank dorsal fin edges by similarity and compute the estimated percent difference between them (circled).

All images used in this test were judged to be of suitable photographic quality for analysis. To eliminate bias based on individual distinctiveness, a matched-pairs design was employed. We assembled one digital test group and one film test group from a sample of 20 known individuals for which there were at least two suitable quality digital and two suitable quality film records. An equal number of digital and film images were selected for each individual, making a total of 66 images in each test group.

Once each image was input at a standardized resolution of 300 x 300 pixels into a database (Figure 67a), an outline was snapped to the dorsal fin edge by contrast and then edited using the "segment edit" feature in Finscan (Figure 67b). Fin edges were processed and compared in the Finscan "search" mode (Figure 67c), using a combination of string and curve matching methods (Araabi *et al.* 2000, Hillman *et al.* 2003).

Each processed dorsal fin edge was compared by the Finscan system to the other 65 records in its test group. To examine the relative efficiency of digital and film records when compared to a larger catalogue, each record was tested a second time against 250 records of 100 individuals and a third time against 650 records of 250 individuals. For the second and third tests, the same records of individuals were added to each of the first two test groups. In all three tests, the Finscan system rank of the first correct match was noted for each record (circled in Figure 67c). In practical terms, this value represents the number of photographic records reviewed manually by an operator before the correct record was displayed by the Finscan system. The percent difference estimated by the Finscan system between each candidate image and its first correct match was also noted (circled in Figure 67c). Ranks and percent difference values for digital versus scanned film images were compared by Wilcoxon signed ranks tests using Systat v. 10 software.

Results

Digitally acquired images not only performed up to the slide film standard, but actually surpassed film on all measures examined. A greater proportion (Mann-Whitney $U = 131683.0$, $P < 0.001$) of digital images (median = 76%) were found to be of suitable photographic quality for analysis than film images (median = 50%). Consequently, a higher proportion (Mann-Whitney $U = 745193.5$, $P < 0.001$) of digital images (median = 50%) than slide film images (median = 22%) resulted in quality records of distinctively marked individuals (Figure 68). As there was no difference in percent suitability between successive years of film photography (1997, 1998, 1999) or digital photography (2000, 2001, 2002, 2003), these differences cannot be attributed to a change in researchers' level of experience.

In the field, more data were obtained per unit time with digital photography than with film photography. In 2002, when both digital (4,520 images) and film (1,941 images) cameras were used during a 2-month period, photographic records were obtained for a higher proportion of dolphins present using digital photography than film photography (Mann Whitney $U = 4879.0$, $P < 0.02$). An estimated 93 ± 1.3% of dolphins present were photographed using the digital camera versus 82 ± 3.5% of dolphins present using the film camera (estimates based on field counts of dolphins, mean group size = 6 dolphins). A complete photographic sample of all individuals present was obtained for an estimated 76% of groups using digital images (n = 150 groups) versus an estimated 64% of groups using film (n = 77 groups). Although more comparable results could possibly have been obtained using a bulk loader and large quantities of film in the field, the ability to capture a large number of images on a single small memory card had clear logistical advantages in the field.

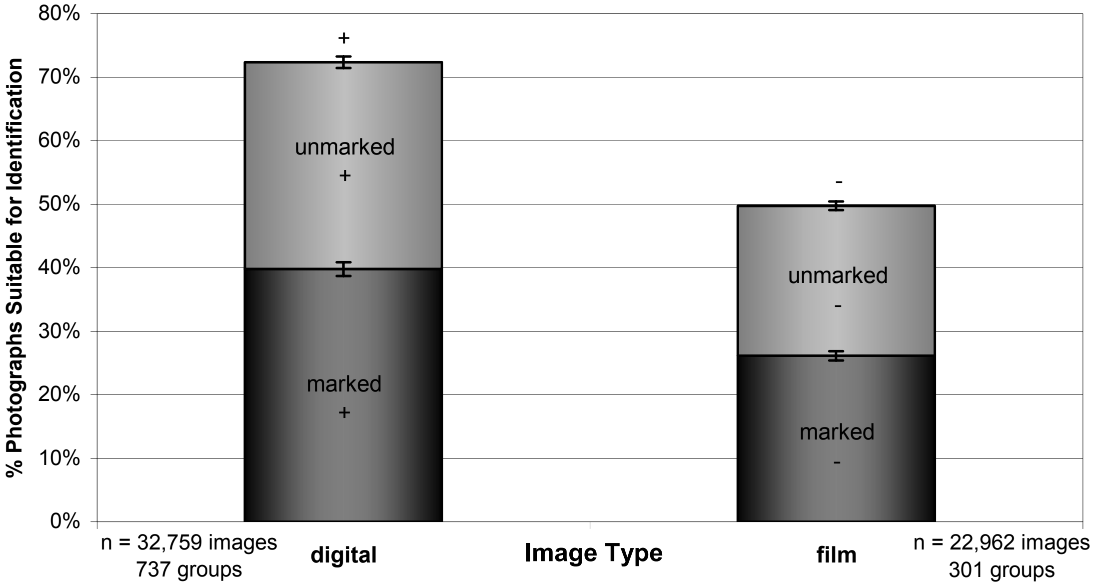
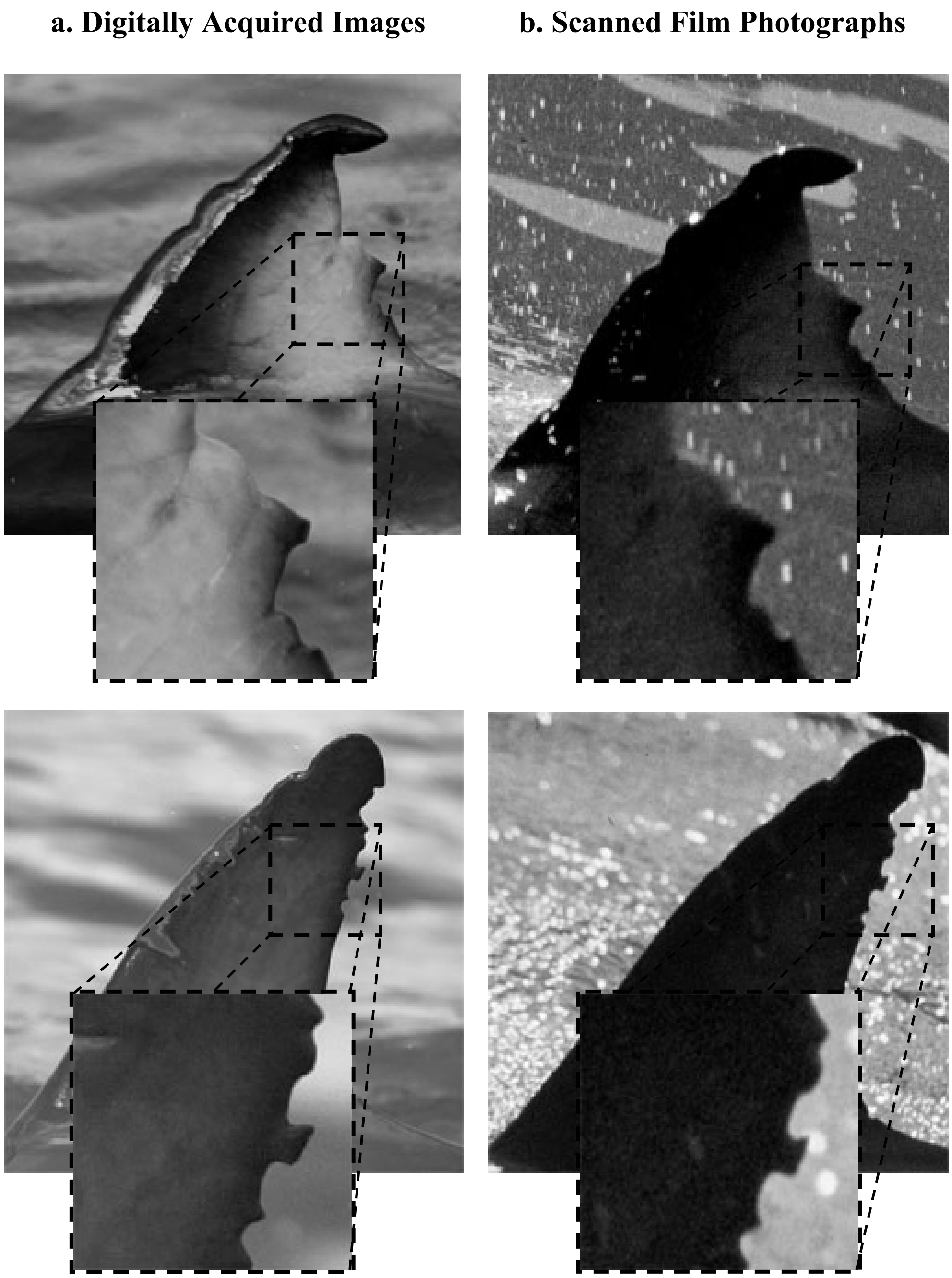


Figure 68. A higher proportion of digitally acquired images (+) than film images (-) were of suitable photographic quality for dolphin identification ($P < 0.001$ Mann-Whitney Test). Photographic quality was judged based on image clarity, contrast, angle, and the extent to which distinctive features were obscured, using light tables and 8x magnifying lupes for original film photographs and onscreen examination for digital photographs. Bars represent mean values for independent groups $\underline{+}$ 1 standard error. Results are subdivided into marked and unmarked categories depending on whether photographed individuals had distinctive features adequate for reliable re-identification.

Following this initial sort by photographic quality, digital images continued to demonstrate great utility for computer-based photo-identification analysis. The resolution and sharpness of digital images compared well to that of film images, particularly when I converted film images to digital format with a slide scanner for computer analysis as the quality of the scanned images was dependent on both the quality of the original image and the quality of the scan (Figure 69).



a. Digitally Acquired Images

b. Scanned Film Photographs

Figure 69. These photographs represent typical examples of (a) digitally acquired and (b) scanned slide film images of the same two individuals. Both sets of images were deemed suitable for photo-identification. Insets show close-ups of dorsal fin notch details. Digitally acquired images (a) were taken with a Nikon D-1 camera set at virtual ISO 800 in fine mode (resolution= 2,000 x 1,312 pixels). Film photographs (b) were shot on Kodachrome 200 slide film using a Nikon N90 camera, and scanned with a Polaroid Sprintscan 35 plus slide scanner.

Digital images outperformed scanned slides during all tests with the Finscan system. During trials with 65, 250, and 650 images comparing the first correct match presented for digital photographs and scanned slide film photographs, digital photographs were matched by the computer system significantly more rapidly than film photographs (Wilcoxon Tests: 65-- $Z = 1.913$, $P = 0.05$; 250-- $Z = 2.134$, $P = 0.03$; 650-- $Z = 2.062$ $P = 0.04$). Differences were more pronounced in tests with larger catalogues (Figure 70).

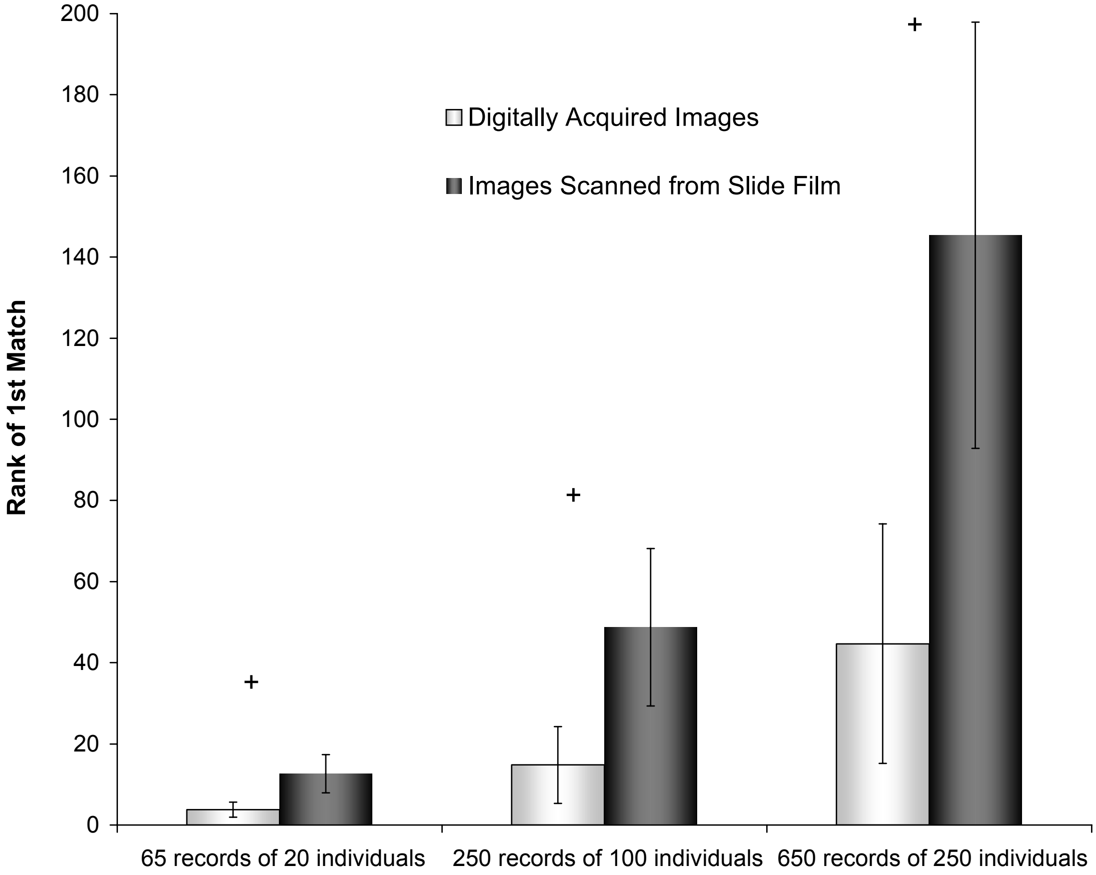


Figure 70. The ranks of the first correct dusky dolphin identification using Finscan semi-automated matching are compared for digital versus film dorsal fin images. Bars represent mean values of individuals tested (n = 20 individuals, matched pairs sets of digital versus film photographs) ± 1 standard error. Plus marks indicate significant differences at $P < 0.05$.

Using a standardized template of 300 x 300 pixels, Finscan selected the correct matching record as the first choice in the majority of digital image trials (68-79%), versus roughly half or fewer (36-53%) of the film photograph trials. Digital images were matched correctly in the first five choices in 73-90% of trials versus 42-63% of trials for film images. These differences in performance were again most pronounced with larger catalogues (Figure 71).

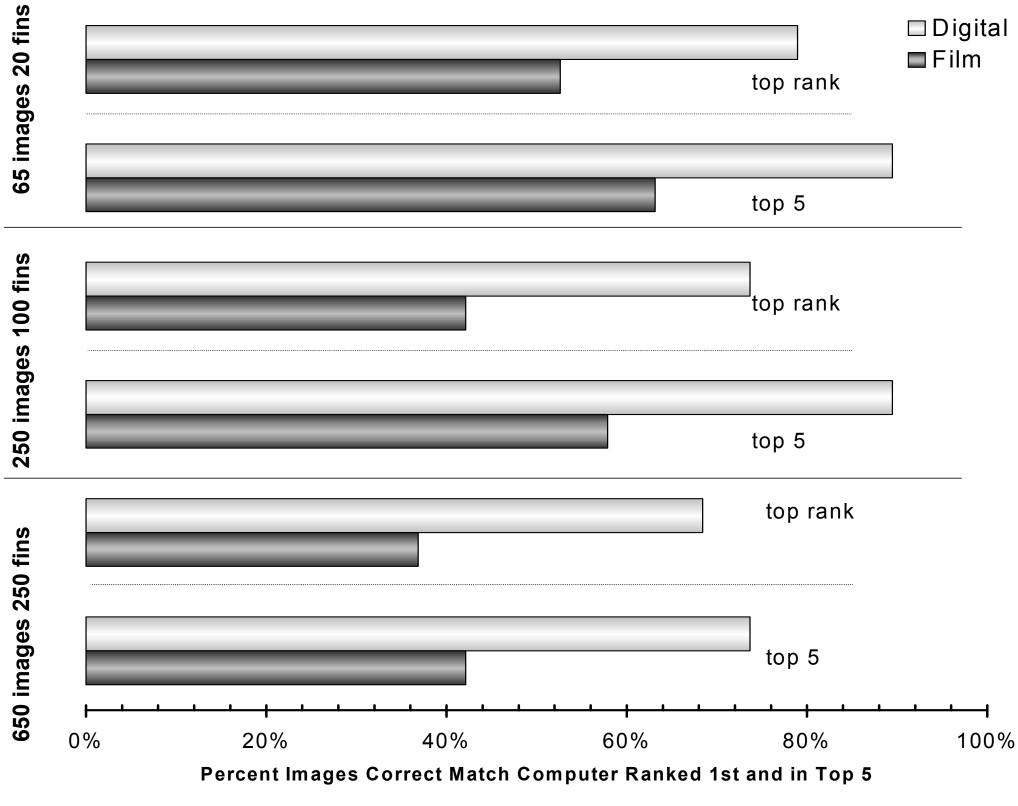


Figure 71. The percent of photographic records for which the computer correctly identified the individual dolphin as the first choice and within the top five ranked choices are compared for digitally acquired versus scanned film images (n = 20 individuals, matched pairs sets of digital versus film photographs).

The Finscan-estimated percent difference between the candidate and the first correct match for trials with 65, 250, and 650 candidates (Figure 72) was significantly lower for digital than for scanned slide film images (Wilcoxon Tests: 65-- *Z* = 2.173, *P* = 0.03; 250-- *Z* = 2.173, *P* = 0.03; 650-- *Z* = 2.455, *P* = 0.01).

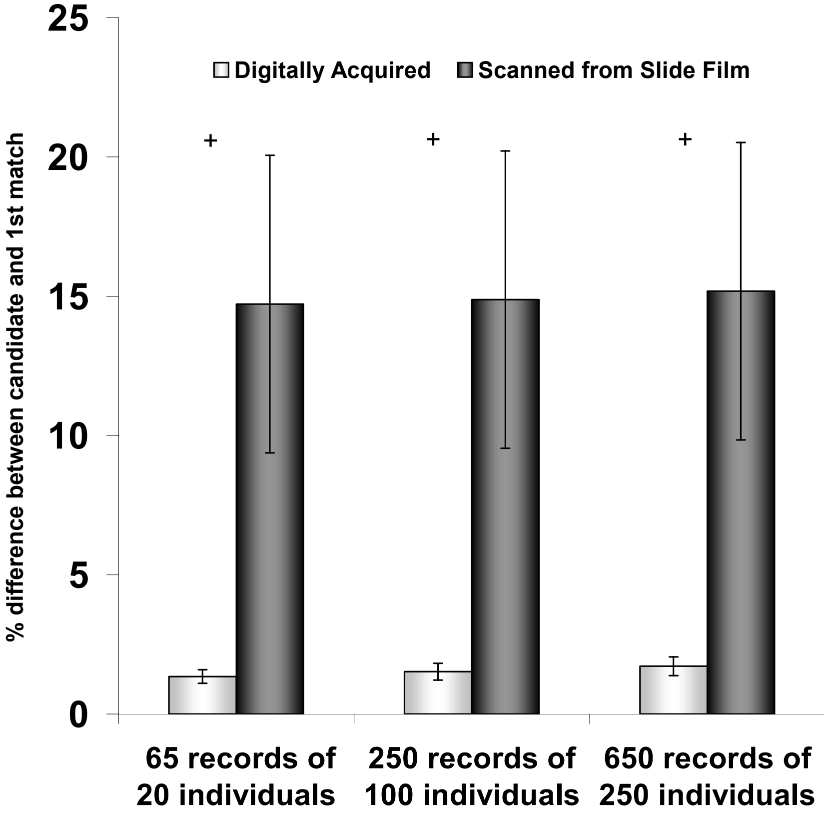


Figure 72. Estimated percent differences calculated by Finscan software between dorsal fin images and the first correct matches are compared for digital images versus film photographs (n = 20 individuals, matched pairs sets of digital versus film photographs). Bars represent mean values ± 1 standard error. Plus marks indicate statistically significant differences at P<0.05.

In practice, these results mean that the human operator would have to manually review fewer digital images than film images on average before the Finscan system presented the correct matching record. Digital images most clearly outperformed film images in the Finscan system when there were fewer possible correct matches. With just one or two matching records, the average estimated percent difference between correct matches was >10% for film images and <3% for digital images (Figure 73).

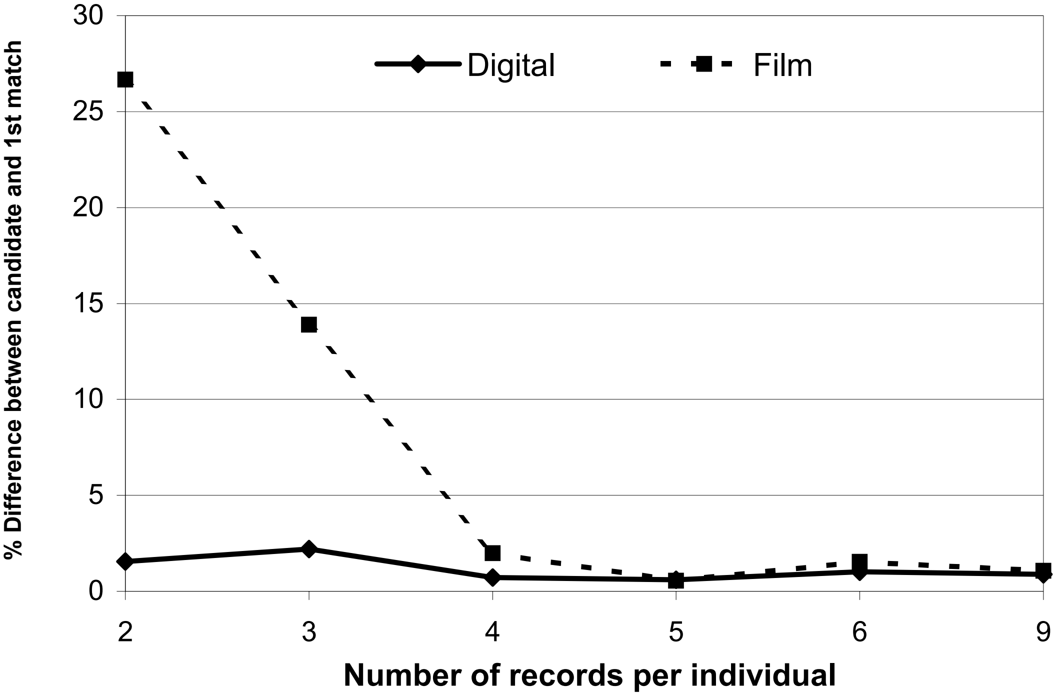


Figure 73. The number of records per individual (x axis) tested represents the number of possible correct matches per test. Mean estimated percent difference between the candidate fin and the first correct match as calculated by Finscan (y axis) is compared for film versus digital images (z axis) with respect to the number of matching records available in the catalog database.

In the worst case scenario during these trials, the greatest number of digital records presented by the Finscan system before the first correct match was 28 out of 65 candidates, 133 out of 250 candidates, and 402 out of 650 candidates. By comparison, as many as 64 of 65, 244 of 250, and 643 of 650 film images were presented before the correct matching record.

Discussion

These results confirm that digital photography can be used effectively in the identification of individual dolphins and indicate that it can even have greater utility than film photography in such research. A number of factors appear to contribute to these findings. In the field, the light sensitivity of the digital camera enabled use of high "virtual ISO" settings (e.g. 800-1600), promoting relatively high shutter speeds (e.g. 1/1000 sec or faster) while maintaining high F-stop values (small apertures, e.g. f 8 to f 11). This provided excellent image "freezing" and good depth of field for rapidly moving dolphins without the graininess of standard high-speed film (Würsig and Jefferson 1990). It also allowed collection of photographic data at lower light levels than would be possible using most films.

As the initial image capture is already in digital format, no information is lost when digital photographs are input into a computerized identification system such as Finscan (Araabi *et al*. 2000, Hillman *et al*. 2003). By comparison, the resolution at which film photographs can be utilized in such a system is limited by the resolution at which they are scanned. These problems can be overcome with the use of high-resolution scanners, but scanning adds additional time to analysis.

Suitability of photograph quality for identification was examined using 8-15x magnifying lupes and light tables for film photos versus onscreen examination of digital photographs. These two techniques were used to "level the playing field," by examining both the film and the digital media in their most original form. Had the film photographs been scanned and examined onscreen, the assessment might have been unfairly weighted against film due to the loss of resolution or quality during scanning. Similarly, had the digital photographs been printed and then examined (as advocated by Mizroch 2003), the assessment would have been weighted against the digital photographs due to the loss of resolution or quality during printing. Some might argue that “the odds were stacked” against film photographs in the Finscan analysis because it is computer based. Although such an assessment may be correct, computerized systems such as Finscan (Hillman *et al.* 2003) are becoming increasingly popular with researchers because they reduce analysis time substantially. For example, in this study, the use of Finscan rather than traditional manual matching saved approximately 1-2 hours per photographic record for dusky dolphins catalogs of 1,000-2,500 individuals. Therefore, this analysis presupposes that researchers switching to digital photography for individual dolphin identification would also be looking to computerize the photo-cataloging process, scanning film images of suitable quality prior to matching records.

In addition to improved image quality, increased range in optimal conditions, and maintained computer resolution, digital photography saves time, resulting in fewer “missed opportunities” in the field and increased analysis speed. Digital images allow for near-instant feedback after data acquisition in the field, unlike the days to weeks that development of silver-halide emulsions can take. Therefore, certain individuals were recognized more rapidly, allowing examination of social cohesion more efficiently. In the laboratory, thousands of additional hours were spent developing, sorting, slide mounting and labeling film images, whereas digital images were ready to be input into a Finscan database immediately following a rapid onscreen initial sorting process. Computer-based photo-matching systems for dolphin identification (e.g. Finscan, Araabi *et al*. 2000, Hillman *et al*. 2003) require analog film images to be converted into a digital format, which adds additional time to analysis and results in a loss of resolution. Digital technology reduces the time required to prepare images for computer-based analysis by up to 5 minutes per image (Markowitz *et al*. 2003a).

Ultra-high-speed films (e.g. ASA 1600, 3200) were not tested in this study, and may perform better than the standard high-speed films (ASA 100-400) tested. It is possible that use of such films could give results more comparable to digital photography than use of standard high-speed films (Mizroch 2003). However, the cost of these ultra-high-speed films is 4-10 times that of bulk-rolled standard high-speed films. If hundreds of rolls of film are shot per research season then the cost of this method would quickly exceed that of high speed, high resolution digital photography. For use in a computerized database, such films must also be scanned into digital format, degrading image quality and increasing analysis time.

Although this study focused on photo-identification of individual dusky dolphins, opportunistic field tests indicate that digital photography can also be effective with other dolphin species including bottlenose dolphins (*Tursiops truncatus*), Commerson's dolphins (*Cephalorhynchus commersonii*), and Hawaiian spinner dolphins (*Stenella longirostris longirostris*). For example, a small sample of 1,366 digital images of bottlenose dolphin dorsal fins taken during 11 group encounters in New Zealand from 2000-2001 yielded 74.3% of suitable photographic quality for analysis, and 70.1% distinctive enough for reliable re-identification due to the higher mark rate in this species. Body size, dorsal fin morphology, mark rate, swimming speed, behavior near vessels, and habitat preference vary between species, contributing to differences in photo-identification efficiency. Further research is recommended with different species to confirm the generality of these findings. More side-by-side film versus digital photo-identification efficiency tests should be conducted. Further testing will likely lend additional support for the use of digital photography in field research with cetaceans.

The results of this study comparing the efficiency of digital and film photography in the identification of individual dolphins cannot be generalized to all photo-identification efforts. However, researchers working with a variety of whale species (humpback whales, *Megaptera novaeangliae*, A. Pack pers. comm., P. Clapham pers. comm., sperm whales, *Physeter macrocephalus*, N. Jaquet pers. comm., western gray whales, *Eschrichtius robustus*, D. Weller pers. comm.) report that digital photographs are also very effective for identification of large whales. It remains to be seen how well digital cameras will fare under a variety of often harsh conditions in the field over many seasons. However, it is evident that under the right circumstances, digital technology holds great promise for enhancing and advancing photo-identification research.

Although the gap between the resolution of digital and film photographic media is closing, the absolute resolution of film remains generally higher than that of digital images. The purpose of this chapter is not to examine the absolute resolution of the two media. In fact, the highest resolution settings available on the digital cameras were not used in this study. Beyond a threshold level, higher resolution did not appreciably improve photographic quality in a way meaningful to the research on dusky dolphins. Fine resolution 2-3 megapixel jpeg files use 1-1.5 megabytes of memory per image, versus >10 megabytes per tiff file in the highest resolution (> 5 megapixel) mode. As results did not vary with changes in resolution, and increased file size decreased analysis speed due to processor, RAM, and hard drive limitations, the second highest resolution setting was chosen. This restraint will rapidly become obsolete as computer speeds and storage file sizes increase; however, as a rule the photographic features of the camera in question will be at least as important as the resolution. Further, when ordering a newer camera model for additional research, the Nikon D1H was chosen over the Nikon D1X, for its lower cost and higher number of frames per second despite slightly lower resolution. The optimal resolution settings will vary depending on the level of detail required to reliably document distinctive individuals, the distance from the camera to the subject, the number of photographs taken, the size of the photo-catalogue, and other particulars of each research project. However, resolution settings below 1-2 megapixels are not recommended.

The finding that digital images were more efficient than scanned film photographs when input into the Finscan system likely results from the more consistent high quality of digital images. This consistency and quality likely reduced variability in the outline of the dorsal fin edges, making discrimination and matching of features more rapid when multiple outlines were compared. This explanation is consistent with the finding that film images were more similar to digital images in matching efficiency when there were a greater number of possible correct choices. This is balanced by the finding that the difference in performance between digital and film images in the Finscan tests increased with catalogue size. If this trend holds true beyond the number of photographic records assembled for these matched tests, then the advantages of using digital photography in conjunction with semi-automated systems may be considerably more pronounced than demonstrated in this study. The use of digital photographs would likely also increase the efficiency of other automated computer-based photo-cataloging systems (e.g. right whale identification software, Hiby and Lovell 2001, Burnell and Shanahan 2001; grey seal identification software Hiby and Lovell 1990).

As with 35mm film cameras, the settings used on digital cameras (i.e., aperture, shutter speed, virtual ISO, image resolution, and white balance) will affect image quality. Researchers are encouraged to take time to familiarize themselves with the optimal settings for the new professional digital cameras as they have with film cameras. One advantage of digital cameras is the ability to adjust virtual ISO settings with changing light conditions in the field. No longer is it the case that 36 frames must be shot with the same setting and developed in the same conditions (e.g. "pushing" film).

Not all digital cameras are of equal suitability for photo-identification. Professional SLR digital cameras field-tested in this study are the equivalent to the Nikon F5 or Canon EOS 35mm film cameras. One can no more expect to obtain good photo-identification results with a point-and-shoot digital camera or video than with a similar film camera or video.

Film photography has long been and remains an effective tool for identifying individual whales and dolphins (e.g. Würsig and Würsig 1977, Würsig and Jefferson 1990). However, digital technology represents a leap forward that is already resulting in new scientific advances and discoveries. Questions and concerns regarding this new technology have been raised by researchers who have years of experience with film-based photo-identification systems (e.g. Mizroch 2003). Such skepticism is not surprising given a radically new approach to the identification of individual cetaceans at sea. Four years of photo-identification research conducted with digital cameras in the field resulted in increased efficiency of dolphin identification efforts. Digital photography consistently outperformed film photography in the proportion of images of suitable quality for analysis. Were this not the case, and digital photography performed just on par with film photography, the logistical advantages of digital photography would still be considerable. For example, long-term storage of multiple copies of photographs in digital format is inexpensive (about 5,000 images before cropping can be saved on a single compact disk), and takes up very little space compared to storage of slide film or prints. Multiple copies of photo-identification catalogues are good insurance against cataclysmic stochastic events, and storage on compact disks allows for easy transport between research field and laboratory sites, and for collaboration between research laboratories. There is no need to print digital images. Printing, even on state-of-the-art-printers, increases time, increases cost, requires considerably more archival space, and generally degrades photo resolution or quality (e.g. the onscreen resolution of the image files is higher than the resolution of the printed images appearing in this chapter).

Despite high start up costs, digital photography represents an economic alternative to film for large scale, long-term photo-identification research. Affordable and reliable archiving of images on compact disks and other computer memory media saves time, space, and money in the long run. As computer technology improves, the costs of digital photography are decreasing and the benefits to researchers increasing.

Concern regarding the cost of a digital system is legitimate; however, over the long-term, the initial investment in the digital camera is recouped by savings in film purchase and processing. Digital cameras replace analog film with re-usable memory cards that generally cost < $1 per megabyte. One of the greatest attributes of memory cards is that, unlike film, they are a renewable resource. Therefore, after the initial investment in a digital camera system (approximately 1.5x the cost of the equivalent film system), the costs associated with film are eliminated. More importantly, because memory cards do not require changing nearly as often as rolls of film, more photographic data can be collected in the field per unit time using digital media than using film. Few researchers would argue that more data collected per unit time in the field is anything but priceless.

In summary, comparison of the performance features of digital versus film photographs in dolphin photo-identification suggests that digital photography offers substantial advantages to researchers (Table 14).

Table 14. Performance of digital versus film photography in dolphin identification

Photo-identification Variable	Digital Photography	Film Photography
Images Acquired per Unit Time	>	<
Flexibility in Different Light Conditions	>	<
% Images Suitable Quality for Analysis	>	<
Sharpness and Detail of Images	>	<
Efficiency of Computer Matching	>	<
Handling, Sorting, and Analysis Time	<	>
Short-term Cost	>	<
Long-term Cost	<	>

CHAPTER VII

SEASONAL RESIDENCY, ABUNDANCE, MIGRATION, AND SOCIAL STRUCTURE OF NEW ZEALAND DUSKY DOLPHINS

> *…one could learn about these fleet, remote animals whose world was separated from ours by that most difficult of barriers, the sea surface… [to] provide the most precious of scientific treasures—little truths on which future understandings of the dolphins may be anchored.*
>
> \- Ken Norris, Dolphin Days

Figure 74. Much about the organization of dusky dolphin societies remains a mystery, due in part to the challenges of studying extensive social networks among mobile creatures in the marine environment.

Introduction

The goal of this chapter is to examine the residency, abundance, migration, and social structure of New Zealand dusky dolphins. Due to the extensive nature of dusky dolphin social lives (Figure 74), much remains to be done, both in terms of additional analyses and additional data collection, to provide detailed information on each of these parameters. Herein, I report preliminary results based upon examination of one of the largest photo-identification catalogs (in terms of the number of individuals) ever assembled for cetaceans in one location, with only the catalogs of individual humpback whales across oceans being larger (reviewed by Mann 2000). Analysis of photo-identification data on this scale is cumbersome, and remains incomplete.

Residency and Abundance

As a species, dusky dolphins occur in Kaikoura year-round (Würsig *et al.*1997). However, it is unknown whether individuals are resident in the area year-round or just seasonally. Genetic evidence indicates that the New Zealand dusky dolphin population is a large and healthy one (Harlin *et al.* 2003). By themselves, these population estimates for New Zealand dusky dolphins derived from haplotype frequencies may not provide an accurate estimate of dolphin numbers due to the degree of genetic overlap between New Zealand dusky dolphins and other populations globally. Although much analysis remains to be done, the photo-identification research conducted to date in Kaikoura can provide information on residency and abundance of dusky dolphins in the area.

Migration

Many cetaceans, especially the great whales that exhibit seasonal migrations between breeding/calving and feeding grounds, range over large distances (Wells *et al.* 1999). Information from radio and theodolite tracking studies indicate long-range movements of dusky dolphins (Würsig *et al.* 1991). Another source of information regarding movements comes from photo-identification of marked individuals as they move between different locations. In this chapter, findings related to seasonal movements of individuals are presented.

Social Structure

Analysis of social organization in complex fission-fusion societies includes a description of the quality of associations (Whitehead and Dufault 1999), and quantification of the structure of associations (Whitehead 1997). In chapters II-IV, the behavior of dusky dolphins in groups has been described (quality), but the membership of those groups (structure) has not. A goal of this chapter is to quantify social structure in dusky dolphin groups in Kaikoura and Admiralty Bay.

Methods

As many of the methods used in this study for collecting and cataloging identification photographs have already been detailed in the previous chapter, they will not be detailed here. Dolphins were approached and photographed following the methods and rationale of Würsig and Jefferson (1990). Suitability of photographs for identification was determined following standard criteria (Markowitz *et al.* 2003a). Mark rate was assessed by photographing dolphin dorsal fins at random and tallying the number of marked and unmarked records, and used as an adjustment factor to estimate actual numbers from those based on marked individuals only. All assessments of individual identity were confirmed by eye. Cataloging of photographic records was accomplished using the Finscan v. 1.5.4 Computer Assisted Dolphin Photo-Identification System, software that employs string and curve-based matching methods to present most likely identification matches in order (Hillman *et al.* 2003).

The number of months between re-sightings in Kaikoura within the same year and between subsequent years was calculated for all individuals. Lagged identification rates were used to further examine residency in Kaikoura and Admiralty Bay over time (Whitehead 1995). Population parameters for dolphins in Kaikoura were calculated using the “bigtemp” and “popan” modules in SOCPROG designed for large datasets. Mark-recapture population estimates were calculated using the POPAN module of SOCPROG v. 1.3 (developed in MATLAB by H. Whitehead, programs available at *http://is.dal.ca/~whitelab/index.htm*). “Closed” (Schnabel), “mortality”, “mortality + trend” and “re-immigration” models were run (Gowans *et al.* 2000; Whitehead 1990).

The Akaike Information Criterion (Akaike 1974) was used to determine the model that best fit the population for each estimate.

To examine migrations, photo catalogs from Kaikoura, Admiralty Bay (chapter IV), and the west coast were compared. Location data were downloaded and manipulated using GPS Utility v. 4.04.7, and plotted using ArcView v 3.2.

Association parameters for dolphins in Kaikoura and Admiralty Bay were estimated using the “assoc” module in SOCPROG. Lagged association rates were used to examine residency and associations over time, with the best-fit model determined based on log-likelihood values (Whitehead 1995). Half-weight indices were used to calculate coefficients of association in those cases where the probability of photographing individuals when separate was higher than the probability of photographing them when together (Cairns and Schwager 1987). In cases without such a bias, coefficients of association were calculated by simple ratio (Ginsberg and Young 1992). Mean and maximum coefficients of association were calculated for all pairs of dolphins, and compared between group types and years. Statistical comparisons were conducted using SPSS v. 11.0.1. Data were tested for normality using Kolmogorov-Smirnov and Shapiro-Wilk statistics. Means for variables with a normal distribution were compared by one-way ANOVA. Tukey tests were used for post-hoc comparisons. Average linkage cluster and sociograms were generated to examine association matrices (Whitehead and Dufault 1999).

Results

In Kaikoura, both the mean and overall mark rate (proportion of dolphins with markings suitable for identification) was 38% (± 1.2% s.e.), with a 95% confidence interval of 36-40%, for groups photographed at random (n = 337). A catalog of 2,494 was developed based on analysis of 4,551 photographic records from 1984 and 1990-2001 (Table 15). An additional 4,202 photographic records from Kaikoura (2,314 of them from Winter 2003) and 880 records from Admiralty Bay (all from Winter 2003) remain to be catalogued. Of the 2,494 individuals catalogued in Kaikoura, 669 (27%) were re-sighted on more than one day. Of these, 198 individuals were photographed in small groups and 641 were photographed in large groups. Unlike Admiralty Bay (see chapter IV), a relatively small proportion of individuals present were photographed in Kaikoura. The mean number of marked individuals photographed was 24 ± 1.2 in large groups (> 50 individuals) and 3 ± 0.08 in small groups (mean ± s.e.).

Table 15. Number of Kaikoura photo-identification records per year catalogued to date

Year	**'84**	**'90**	**'91**	**'92**	**'93**	**'94**	**'95**	**'96**	**'97**	**'98**	**'99**	**'00**	**'01**	**Total**
# ID	10	3	4	42	16	7	2	18	679	801	515	1,143	1,311	4,551

Seasonal Residency and Abundance in Kaikoura

Most re-sights of dolphins in Kaikoura occurred within the same year. For individuals identified repeatedly within a given year, sightings were seasonally clumped. Although not as pronounced, this pattern continued in successive years, with individuals most often photographed in Kaikoura in the same season. The means and 95% confidence intervals for months between re-sightings fall within three months for identifications within a year, 1 year, 2 years, 3 years, and 4-13 years apart (Figure 75).

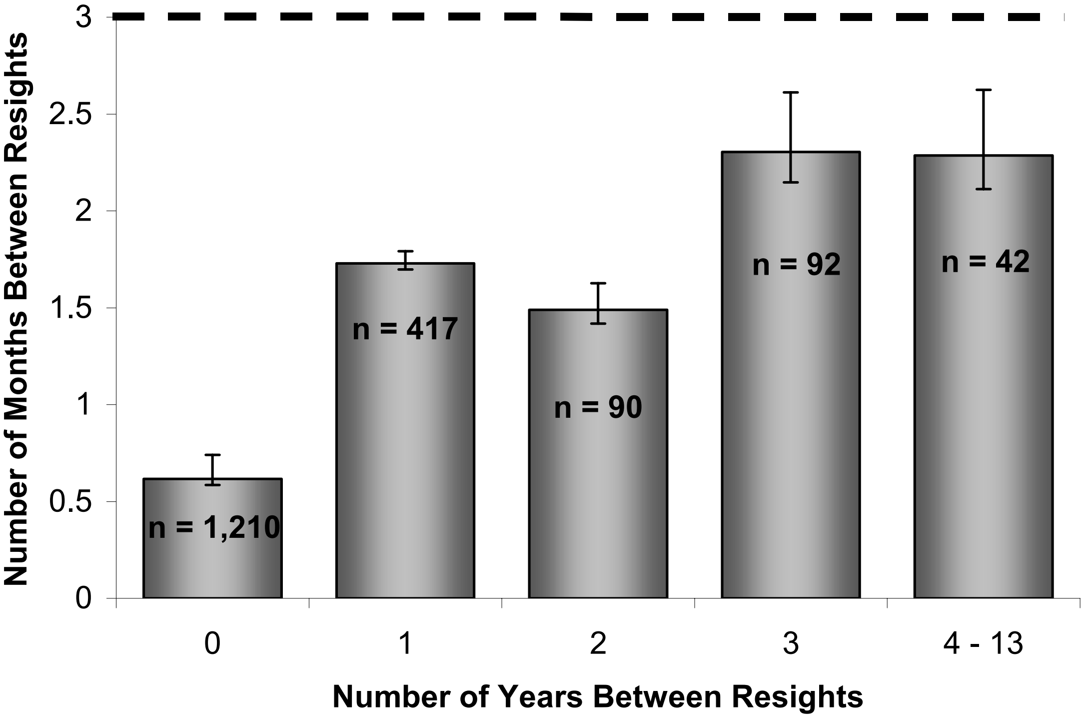


Figure 75. The seasonality of dusky dolphin residency in the Kaikoura area is shown by the number of months between re-sights of identified individuals. Data are shown by the number of years between re-sights, with "0" representing sightings of particular individuals in the same year, "1" representing sightings in successive years, and so on. Bars represent mean values, with 95% confidence intervals above and 1 standard error of the mean shown below. The dashed line at 3 months represents the a priori upper threshold for sightings in the same season.

Looking at the distribution of all re-identifications in Kaikoura, indicates a peak at 0-1 months with sightings decreasing beyond 2 months for re-identifications at 0, 1, 2, 3, and 4 - 13 years (Figure 76).

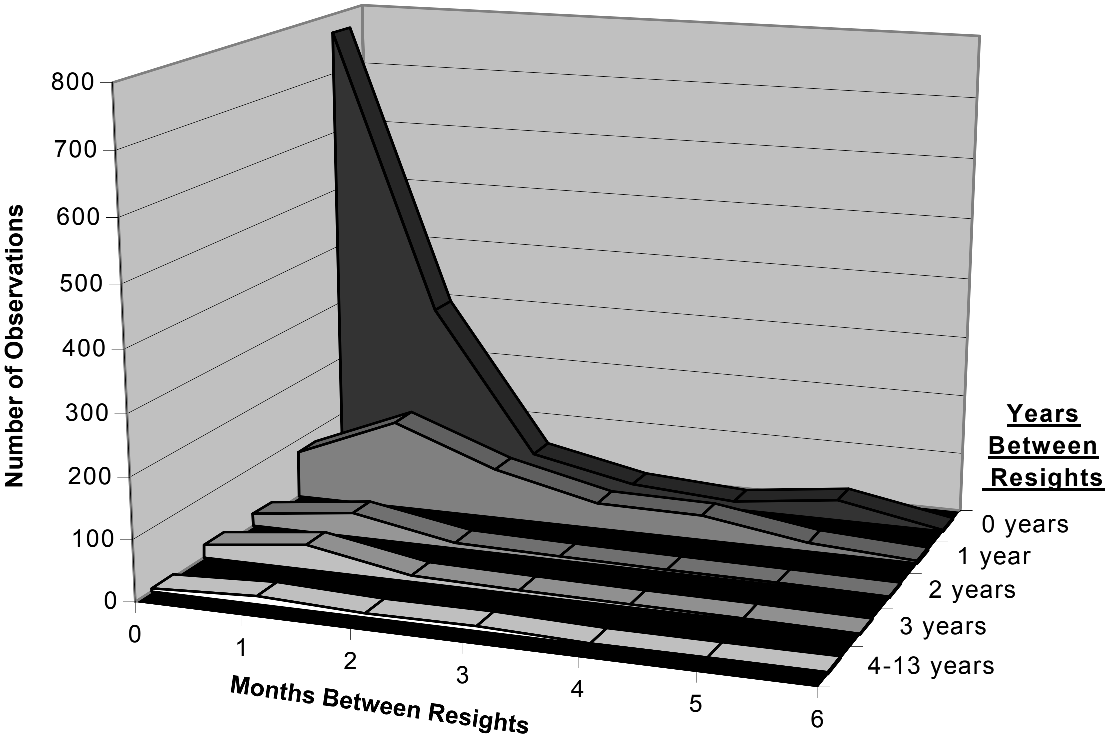


Figure 76. The seasonality of dusky dolphin residency in the Kaikoura area is shown with a frequency distribution of the number of months between re-sights of identified individuals. Data are shown by the number of years between re-sights, with "0" representing sightings of particular individuals in the same year, "1" representing sightings in successive years, and so on.

The seasonal pattern of re-identification is reflected in the lag time between re-identifications of the same individual, with peaks spaced regularly at 1-year intervals (Figure 77). This indicates that dolphins remained in Kaikoura for a season, left, and returned again at roughly the same season.

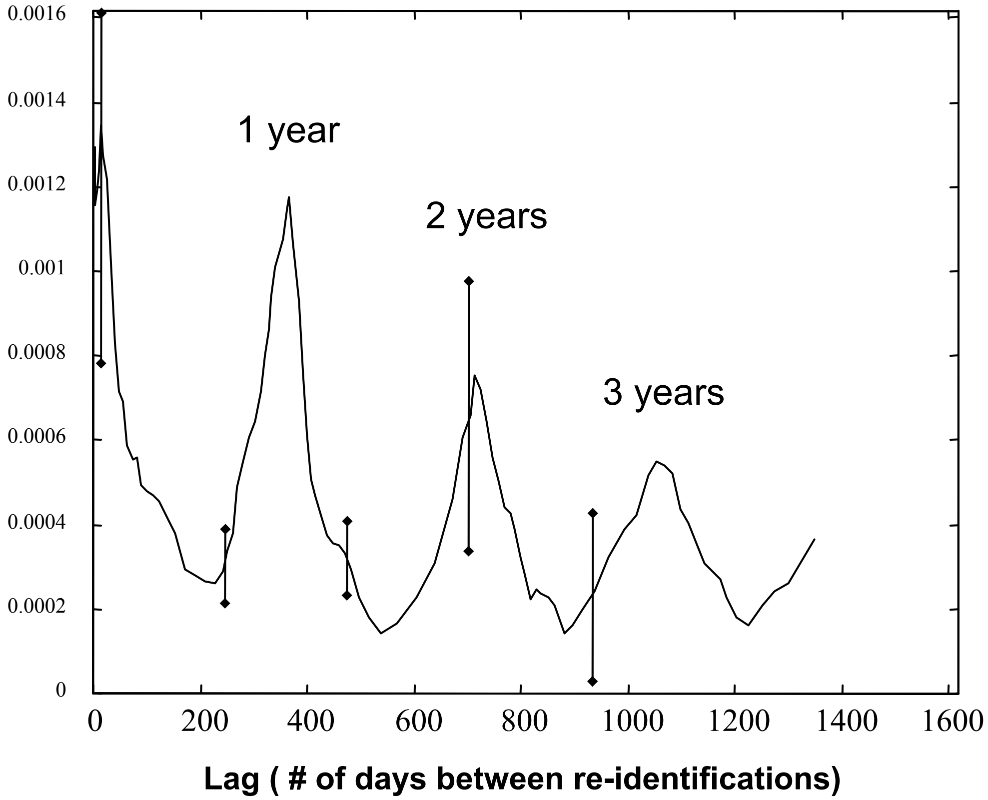


Figure 77. Lagged identification rates for individual dusky dolphins in Kaikoura show the probability that if a dolphin is photographically identified at time "0", it will be identified again at time x. Error bars show jackknifed standard errors. Data labels indicate the approximate location of annual (1-year) time lags.

The seasonal pattern of dolphin re-identification in Kaikoura held true for dolphins photographed 5 or more years apart (Table 16). Two individuals identified 13 years apart, were both photographed within just 1 month of the original record.

Table 16. Seasonality of re-identification of individuals in Kaikoura > 4 years apart

ID#	name	yrs	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
318	Angouh	5	92											97
1014	Martha	5			94,99									
437	Ramona	5	92											97
875	Amelia	6	92	98										
1276	Campigotto	6	92	98										
416	Bob	6				93	99					97		
734	Emiko	7	92,98,99				98							93,98
582	Holly	7	99	97	98									92,97
1486	Owen	7	92		99									
625	Brave	8	96,99		98,99,01	99,00								93,97,98
489	Buffy	8		01	97-01								93	97
570	Rebecca	8	99,00	99	93,98,01									
1434	Berkeley	8	92,00											
522	Dennis	9			00,01	00	98							92,97
327	Hanke	9	98,99	97										90,97,98
722	Michael	9	92,00	99,01	01									
3080	Stitch	9	92	99	99-01	99,00								
620	Chewy	9	92,00	96,97,01	01									
225	Apelila	13							84	97				
89	Aspen	13							84	97				
67	Ann	17	98,99	98	01	99,00			84		97		97	

(*Square fill represents season, ranging from lightest in summer to darkest in winter.*)

Looking at the scale of within a season (Figure 78), the best-fit model for re-identification rate indicates that on average dusky dolphins remained in Kaikoura for 103 ± 38.0 days (mean ± 1 standard error). At any given time, the average number of dusky dolphins present in Kaikoura was 1,969 ± 814.9 (mean ± 1 standard error).

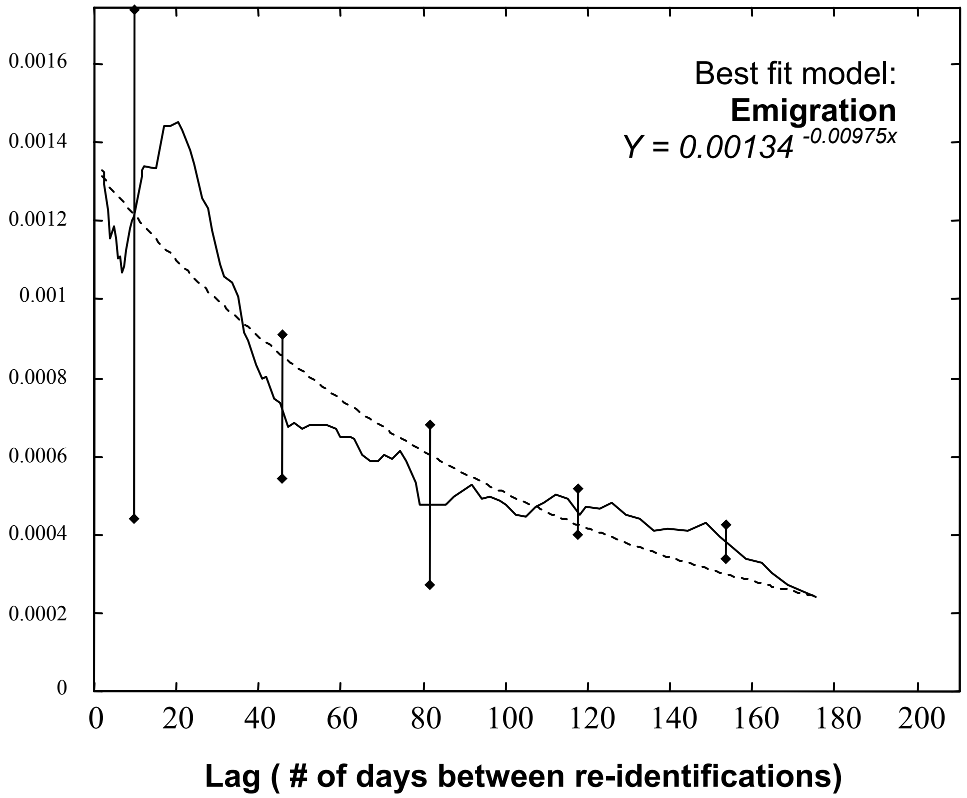


Figure 78. Lagged identification rates for individual dusky dolphins in Kaikoura within a season show the probability that if a dolphin is photographically identified at time "0", it will be identified again at time x. Error bars show jackknifed standard errors. The dashed line and text box show the best-fit model.

The "mortality" model, which assumes a constant population with mortality and/or permanent emigration balanced by birth and/or permanent immigration, was selected as the most appropriate model based on the Akaike criterion (Akaike 1974). Using a 1-week sampling period (n = 153 weeks) the estimated population size for Kaikoura was 12,626 individuals (not including calves, which are generally unmarked).

Migration between Kaikoura and Other Regions

West Coast

Surveys of the West Coast conducted during 2 1-week periods in February 1999 and February 2000 yielded very few sightings of dusky dolphins. Therefore, the photographic sample for the west coast is too poor to draw any conclusions beyond the recognition that at least some individuals make the journey between the east and west coasts of New Zealand's South Island. Of 12 marked individuals identified during surveys of the west coast of New Zealand's South Island, three (25%) matched photo-identification records from Kaikoura. These three individuals were photographed on the west coast in February and in Kaikoura (on the East Coast) during March and April (Table 17). One of these individuals (*) was also photographed in Admiralty Bay (on the north coast) during the following winter (Figure 79).

Table 17. Individuals photographed in Kaikoura and on the West Coast
(Dates 3 individuals were photographed, West Coast locations)

Kaikoura	West Coast	West Coast Location
March 2001	1 February 1999	Westport
April 1999, April 2000*	8 February 2000	Jackson Bay
April 1999, March 2001	16 February 2000	Westport

These data indicate that at least some dusky dolphins travel approximately 800 km to more than 1,000 km between locations around New Zealand's South Island within a single year (Figure 79).

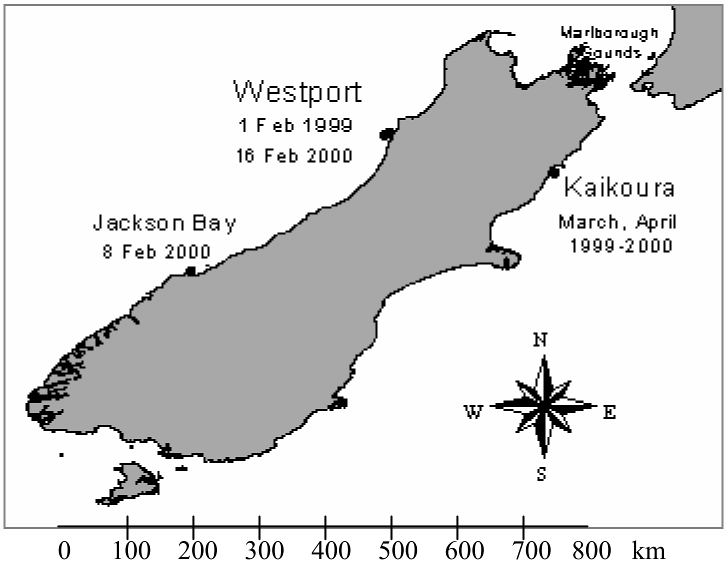


Figure 79. Locations of re-sightings between the east and west coasts of New Zealand's South Island indicate that individuals make long-range movements in the course of a year (Data labels indicate dates the same individuals were photographed at different locations; scale bar shows distances in km).

North Coast

When the photo-identification catalog for Kaikoura was compared to that for Admiralty Bay, 37 individuals were found to have been photographed in both locations. Most of these individuals were photographed in Kaikoura during the summer and autumn, and re-identified in Admiralty Bay during the winter (Table 18). In one instance, a pair of male dolphins was observed hunting fish together in Admiralty Bay during the winter and chasing a female together in a mating group in Kaikoura during the summer.

Table 18: Individuals photographed in (K) Kaikoura and (A) Admiralty Bay by season

SUMMER			AUTUMN			WINTER			SPRING		
Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
			K98				A01,02	A01, 02			
	K98, 99	K98		K99, 00	K01	A02	A00, 01	A01, 02	K97, A01		K97
		K01	K01				A01	A01			
			K98	K00			A01				
				K99	K98		A00				
	K99	K01	K98		K98	A99	A00				
K97-99	K98	K97			A98			A03			
K98		K01	K00	K00			A00				
K98	K99	K98, 01	K98-01	K00			A00	K97			
			K00	K00			A00				
K97	K98	K98			A98						K98
K97					A98	A02	A00	A02			
					K00		A00				
	K00						A00, 02	A02			
			K01				A00, 01	A01			
			K01		A98						
		K01	K01			A99	A02	A02			
K97		K99				A99					
						A99					
					K00	A02	A01, 02	A01, 02			
			K99				A00, 02				
			K01	K00	K00	K00	A00				
K98	K99			K99			A00, 02	A02			
			K01			A02	A01	A01			
			K98			A02	A00, 02	A02			
K97		K98					A00				
	K98	K01				A02	A00, 02				
			K01			A99					
			K00				A00				
	K98	K98					A00				
K97							A00				
				K99		A02	A01, 02	A01, 02			
		K98	K99, 01					A01			
		K98					A01	A01			
K98							A01, 02	A01			
				K97, 98			A01	A01			
			K01				A01				

(Each row represents 1 individual, n = 37; two-digit numbers indicate years.)

Sightings in the Marlborough Sounds are highly seasonal, with high local abundance in Admiralty Bay (see Chapter IV). Residency in Admiralty Bay being limited to a short season is supported by analyses of photo-identification data. Lagged identification rates indicate the length of the season in Admiralty is short for dusky dolphins, with a mean (± 1 standard error) residency of 83 ± 62.5 days (Figure 80). For more information on the distribution of sightings, movement patterns, and behavior of dusky dolphins in Kaikoura and Admiralty Bay, see chapters II-IV. In addition to re-sights in Admiralty Bay, one individual photographed in Kaikoura in Autumn 1998 was identified again in Queen Charlotte Sound the following spring.

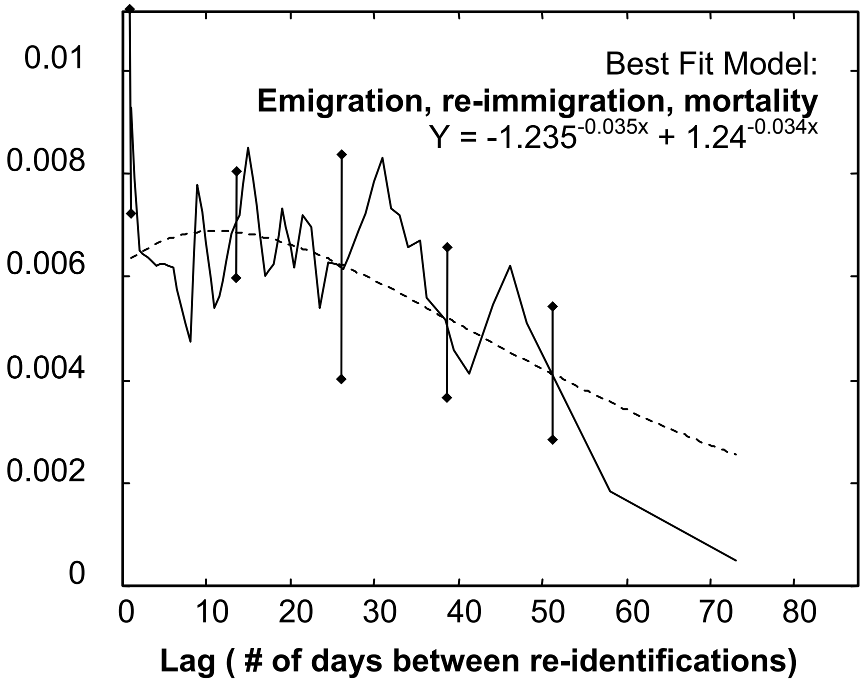


Figure 80. Lagged identification rates for individual dusky dolphins in Admiralty Bay within a season, show the probability that if a dolphin is photographically identified at time "0" it will be identified again at time x. Bars show 1 standard error (jackknife). The dashed line and text box show the best-fit model.

Social Structure

Kaikoura Large and Small Groups

Lagged association rates, which estimate the probability that two individuals currently associating will still be associating at various time lags later(Whitehead 1995), indicate non-random associations between dolphins in Kaikoura at the level of casual acquaintances lasting to approximately 200 days (Figure 81).

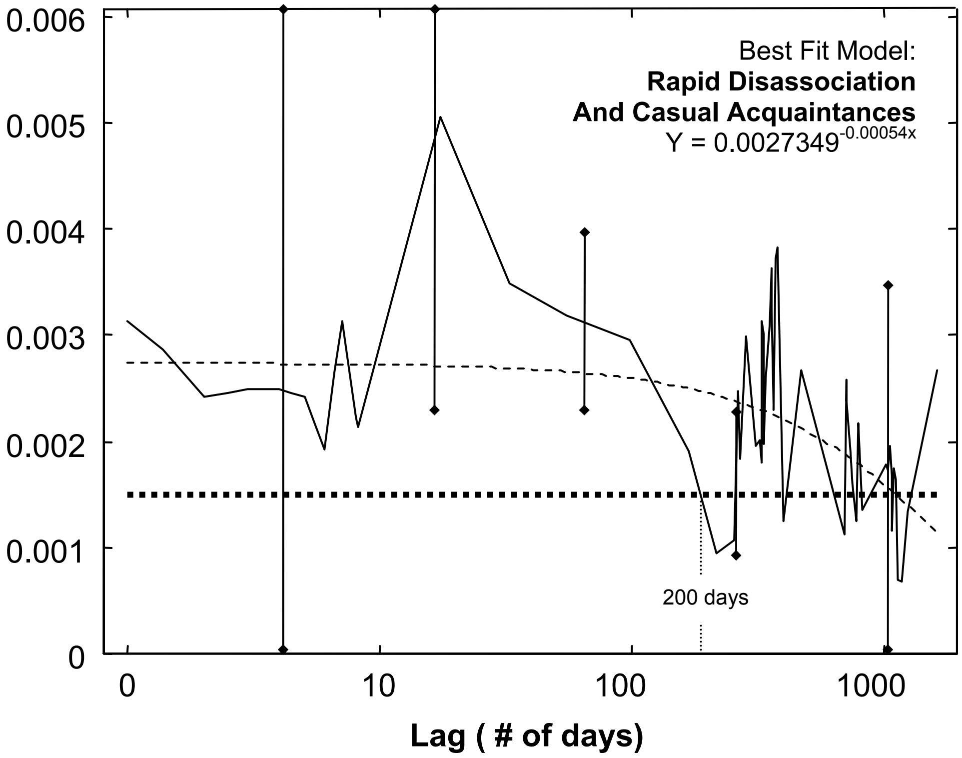


Figure 81. Lagged association rates for Kaikoura from 1997-2001 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. Bars show 1 standard error (jackknife). The bold dotted line at the bottom of the figure shows the null model for random associations. All associations above this line are non-random. The dashed line curve shows the best-fit model (based on log likelihood ratio) for this dataset, with a brief description of this model provided in the text box.

Within a single field season, dusky dolphins in Kaikoura maintain associations above random at the level of casual acquaintances throughout the season (Figure 82).

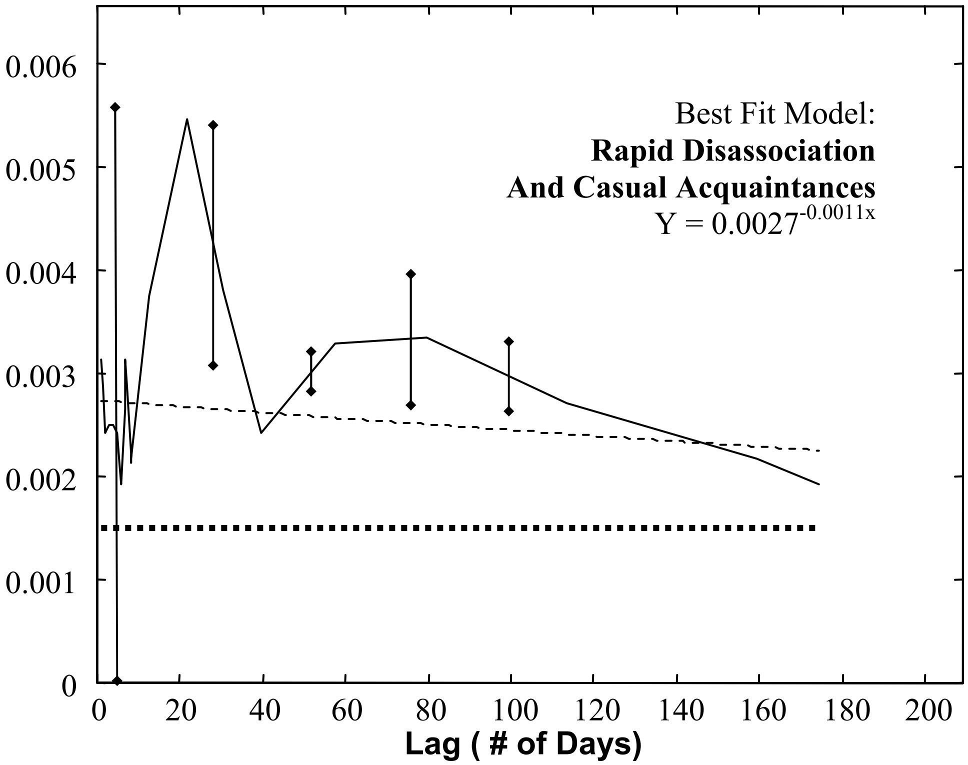


Figure 82. Lagged association rates for Kaikoura from 1997-2001 within a single year indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. Bars show 1 standard error (jackknife). The bold dotted line at the bottom of the figure shows the null model for random associations. All associations above this line are non-random. The dashed line curve shows the best-fit model (based on log likelihood ratio) for this dataset, with a brief description of this model provided in the text box.

As a small proportion of individuals present in groups were photographed in Kaikoura, association data were biased toward photographing individuals separately. Given this bias, the half-weight index was chosen as the most appropriate measure of association (Cairns and Schwager 1987). Using this index, the mean (± s.e.) coefficient of association for individuals photographed at least twice in Kaikoura (n = 669) was 0.03 ± 0.00079. The mean (± s.e.) coefficient of association for a given individual and his/her closest associate was 0.57 ± 0.00735 (Figure 83).

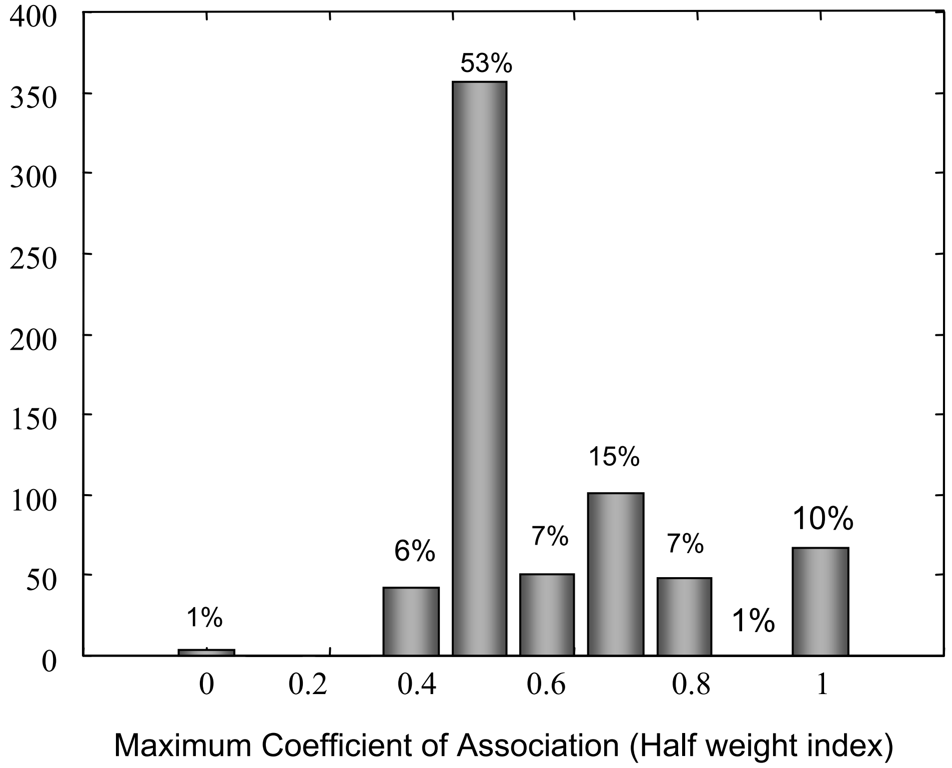


Figure 83. The maximum coefficients of association (closest association, half-weight index) for individuals photographed at least twice in Kaikoura during 1997-2001 are shown as bars, with number of individuals on the y-axis and percent of the total shown as a data label.

Coefficients of association were higher for large groups (mean ± s.e. = 0.04 ± 0.0012) than for small groups (mean ± s.e. = 0.03 ± 0.0014) in Kaikoura. Mean (± s.e.) coefficients of association between individuals and their most frequent associates were 0.60 ± 0.00735 in large groups and 0.48 ± 0.0163 in small groups. These results indicate steadier co-occurrence of individuals in large groups than in small groups (Figure 84).

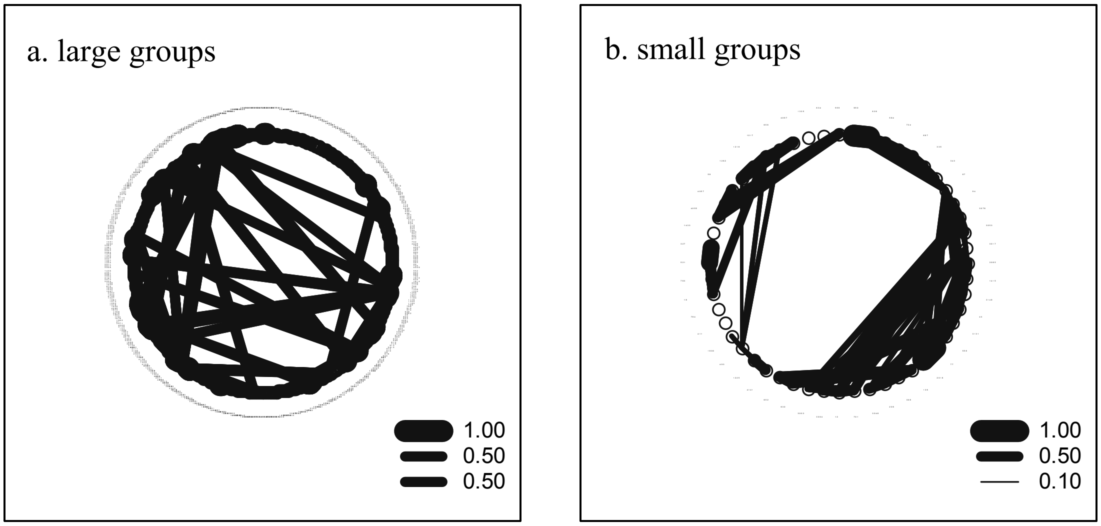
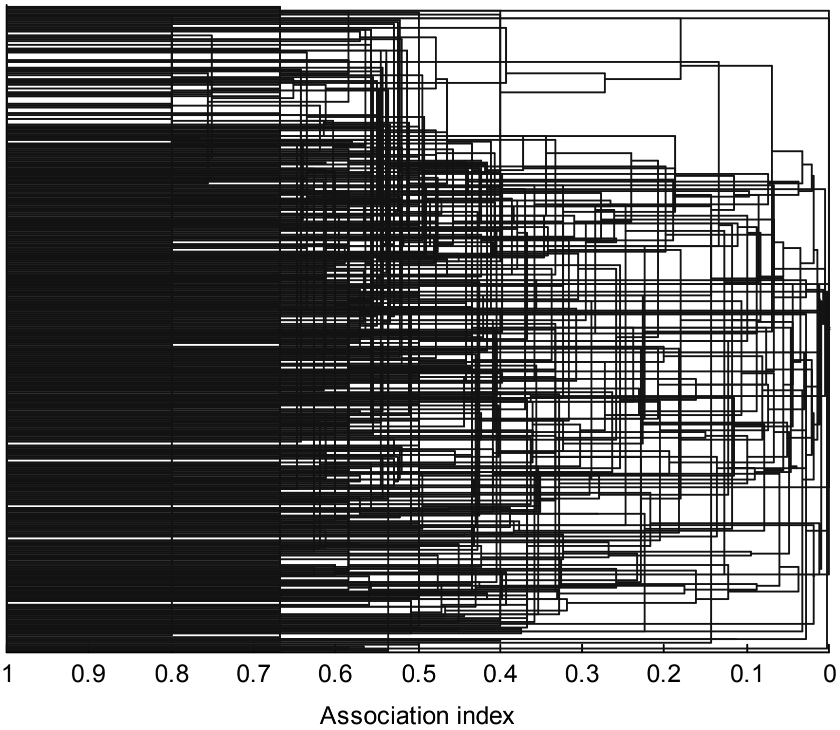


Figure 84. These sociograms show associations between individuals in (a) large versus (b) small groups in Kaikoura during 1997-2001. Half-weight coefficients of association were used in this analysis. Due to the high number of casual associates in large groups, only associations > 0.5 are shown for Kaikoura.

While associations between individuals in Kaikoura were non-random within a season, they showed no strong clustering pattern in either large or small groups (Figure 85).

a. large groups



b. small groups

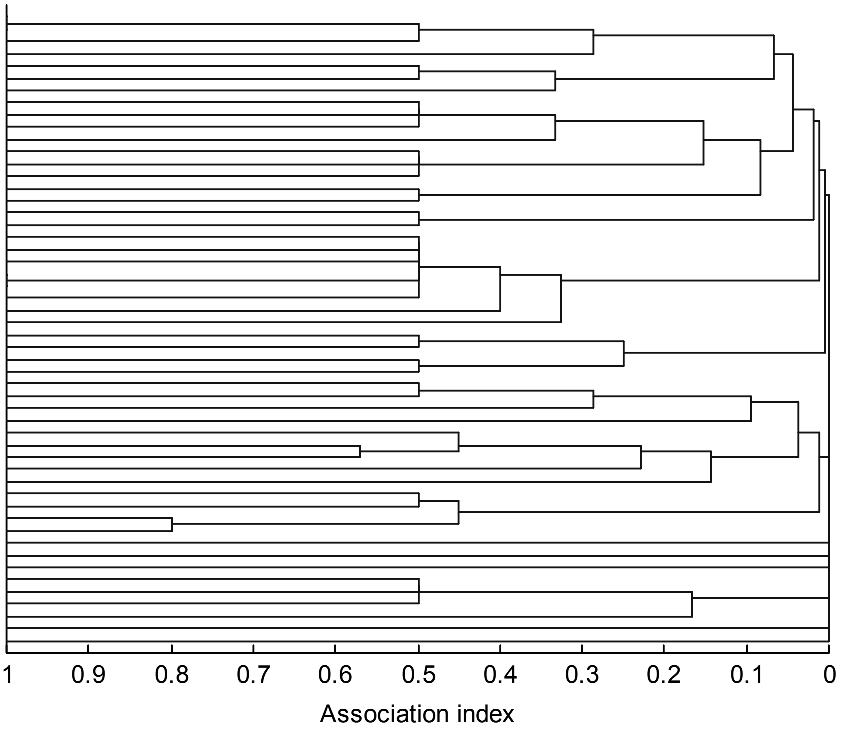


Figure 85. These diagrams, based on half-weight indices for individuals photographed at least twice during 1997-2001, show the extent to which associations clustered in (a) large and (b) small groups in Kaikoura.

Admiralty Bay Feeding Groups

Lagged association rates for feeding groups in Admiralty Bay indicate lasting stronger, longer lasting associations between individuals than in Kaikoura. Dolphins in Admiralty Bay associated non-randomly for over 1,000 days (Figure 86). In the short term, these associations appear to occur at the level of "casual acquaintances", possibly due to the splitting and joining of subgroups during foraging and feeding. In the long term, associations between individuals in Admiralty Bay stabilize indicating "constant companions" over successive years.

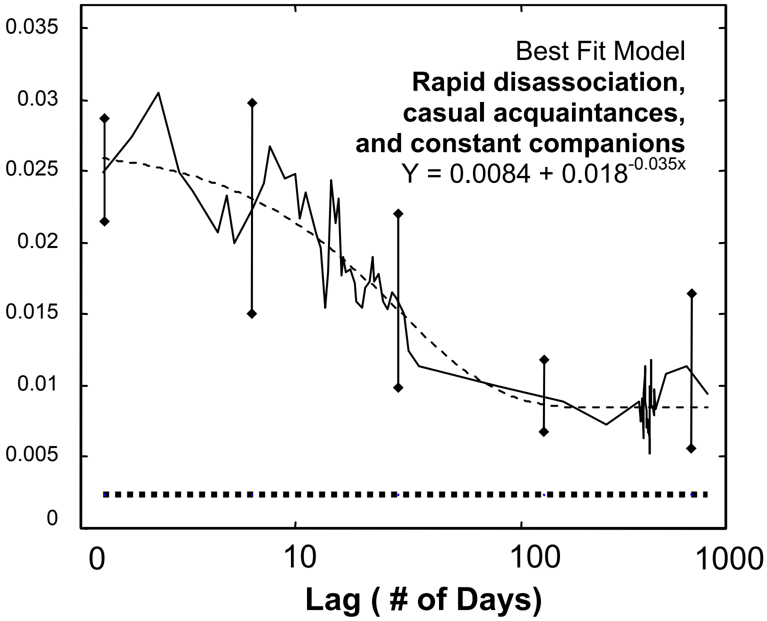


Figure 86. Lagged association rates for Admiralty Bay from 1998-2002 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x. Bars show 1 standard error (jackknife). The bold dotted line at the bottom of the figure shows the null model for random associations. All associations above this line are non-random. The dashed line curve shows the best fit model (based on log likelihood ratio) for this dataset, with a brief description of this model provided in the text box.

Within a single winter season, dolphins associated non-randomly, showing stronger ("2 levels") casual acquaintances than in Kaikoura, but no "constant companions" (Figure 87).

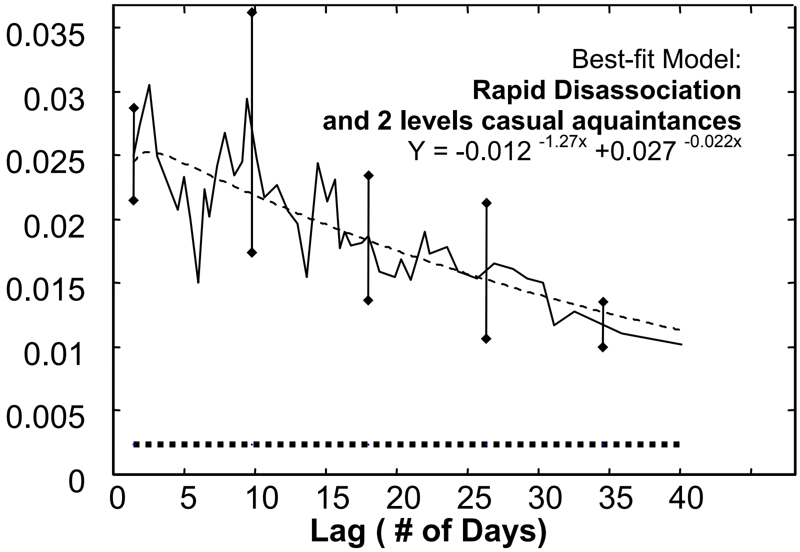


Figure 87. Lagged association rates within a season for Admiralty Bay from 1998-2002 indicate the probability that dolphins photographed together at time 0 will be photographed together again at time x during the same winter. Bars show 1 standard error (jackknife). The bold dotted line at the bottom of the figure shows the null model for random associations. All associations above this line are non-random. The dashed line curve shows the best fit model (based on log likelihood ratio) for this dataset, with a brief description of this model provided in the text box.

On average 4 ± (0.12) of 5 dolphins present in Admiralty Bay groups were photographically identified. As a high proportion of dolphins present in groups were photographed in Admiralty Bay (85-97% see Chapter IV), the probability of photographing dolphins separately was no greater than the probability of photographing them together (Cairns and Schwager 1987). Therefore, the simple ratio, which is statistically unbiased when the sample is random (Ginsberg and Young 1992), was used to calculate coefficients of association between individuals in Admiralty Bay. The mean coefficient of association in Admiralty Bay was 0.01 ± 0.00048. The mean (± s.e.) coefficient of association between individuals and their most frequent associates across all years in Admiralty Bay was 0.51 ± 0.0149 (Figure 88).

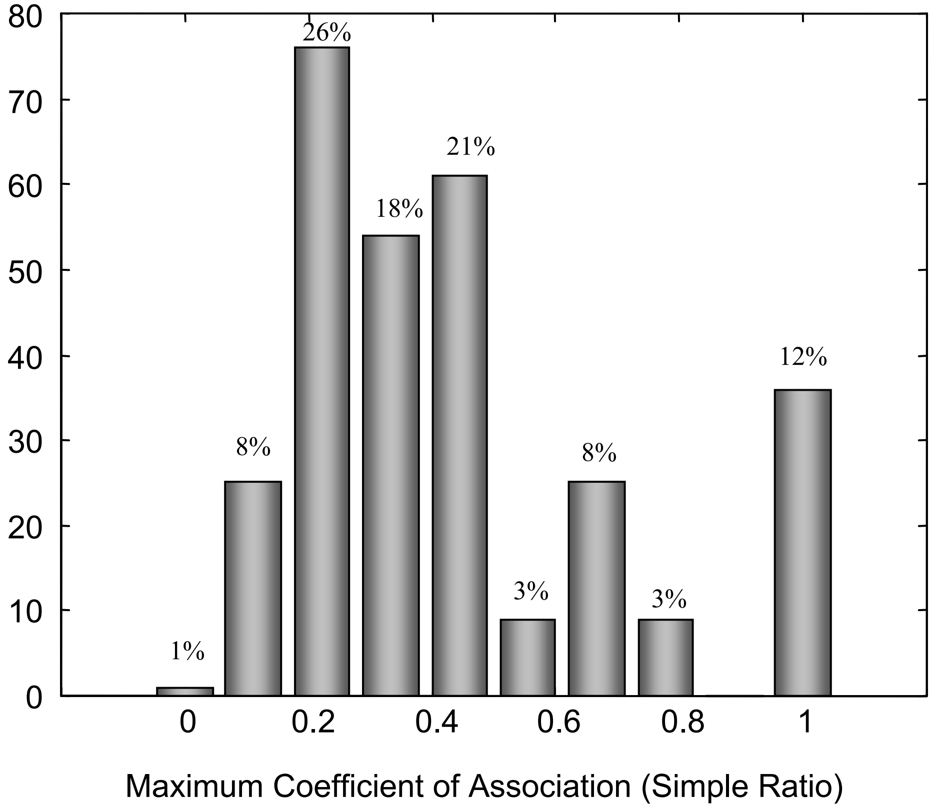


Figure 88. The maximum coefficients of association (closest association, simple ratio) for individuals photographed at least twice in Admiralty Bay during 1998-2002 are shown as bars, with number of individuals on the y-axis and percent of the total shown as a data label.

Dolphins wintering in Admiralty Bay showed inter-annual variation in the tightness of closest associations (Figure 89), with the lowest level of association observed during the year with the lowest feeding and lower sighting rates indicating fewer prey (see Chapter IV). Despite having a greater number of potential associates during 2001, associations were tighter than in 2002.

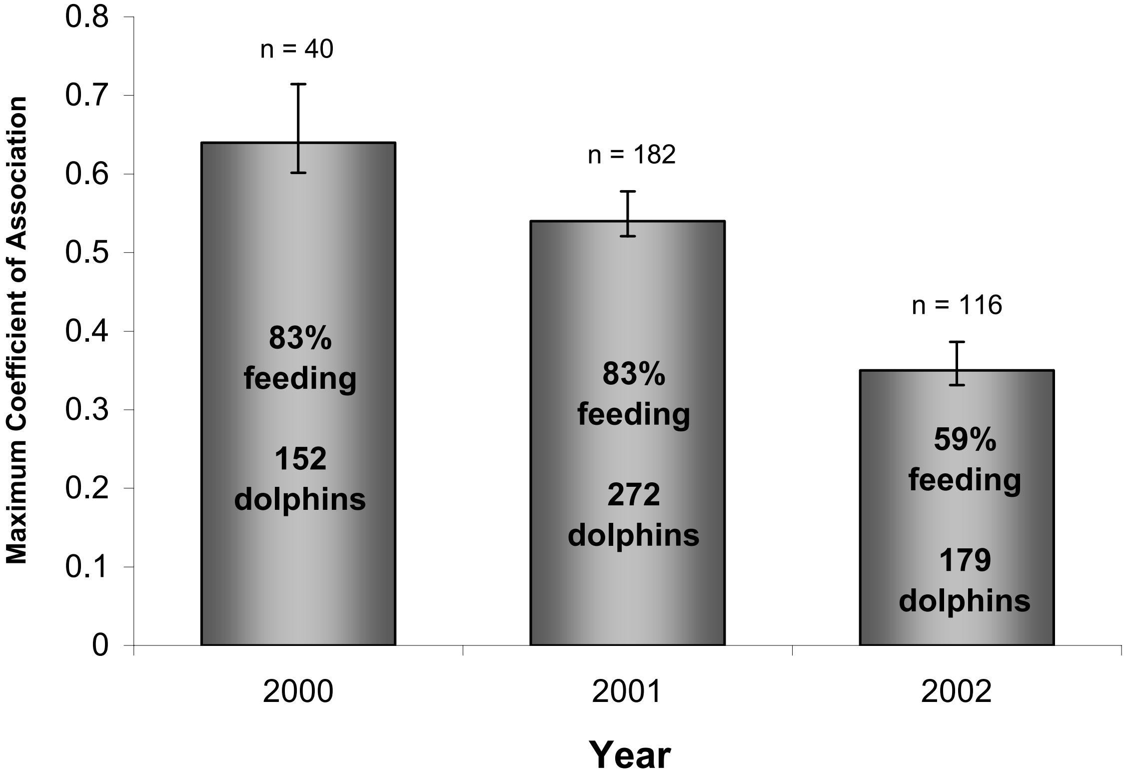


Figure 89. The maximum coefficient of association (closest associate) calculated by simple ratio is compared for dusky dolphins encountered in three successive winters in Admiralty Bay. Only dolphins photographed on more than 1 day per season were used in this analysis. Data labels indicate sample sizes, the percent of groups observed feeding, and the estimated population size during each winter season. Bars represent mean values, with 95% confidence intervals shown above and 1 standard error of the mean shown below.

Greater networks of more strongly associated dolphins were present in Admiralty Bay in 2000 and 2001 than in 2002 (Figure 90). In 2000, a social group of 7 individuals were seen consistently (# re-sights per individual ranged from 3 days to 6 days) hunting together in the same small area within the inner Admiralty Bay (Figure 91). Although this group split and rejoined, 2 pairs of dolphins were always seen together.

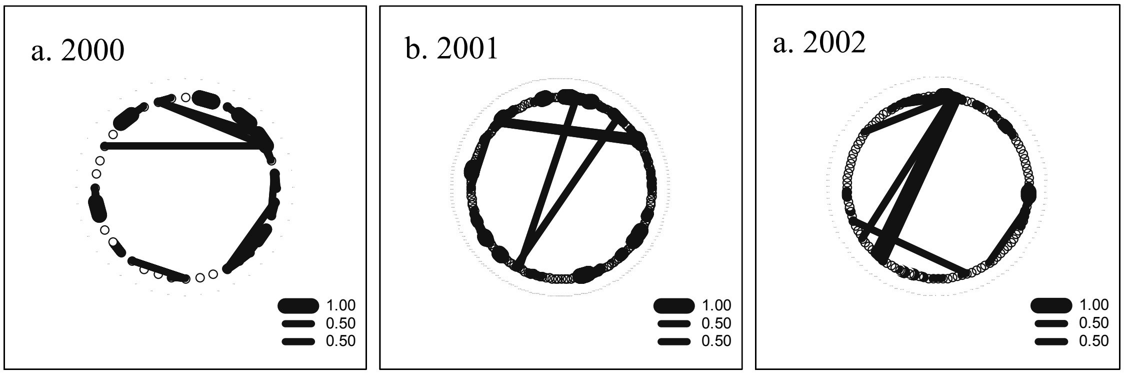


Figure 90. These sociograms (simple ratio coefficients of association) show associations between individuals in Admiralty Bay during (a) 2000, (b) 2001, and (c) 2002.

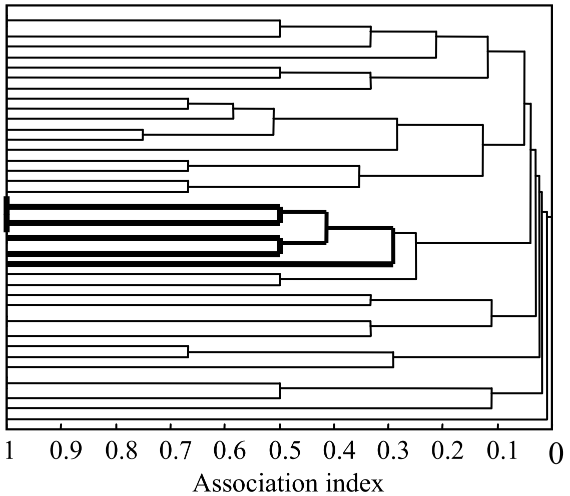


Figure 91. This diagram, based on simple ratio indices for individuals photographed at least twice in Admiralty Bay during winter 2000, shows the extent to which associations clustered. Bold lines show a group consistently observed feeding together in a narrow range. Bold vertical lines at the 1 level indicate pairs of constant companions.

Associations appeared to be more tightly clustered in 2001 than in 2002 (Figure 92). Additional data from 2003 combined with random permutations of the dataset should help clarify whether networks of tighter associations consistently occur in years when dolphin groups are feeding more.

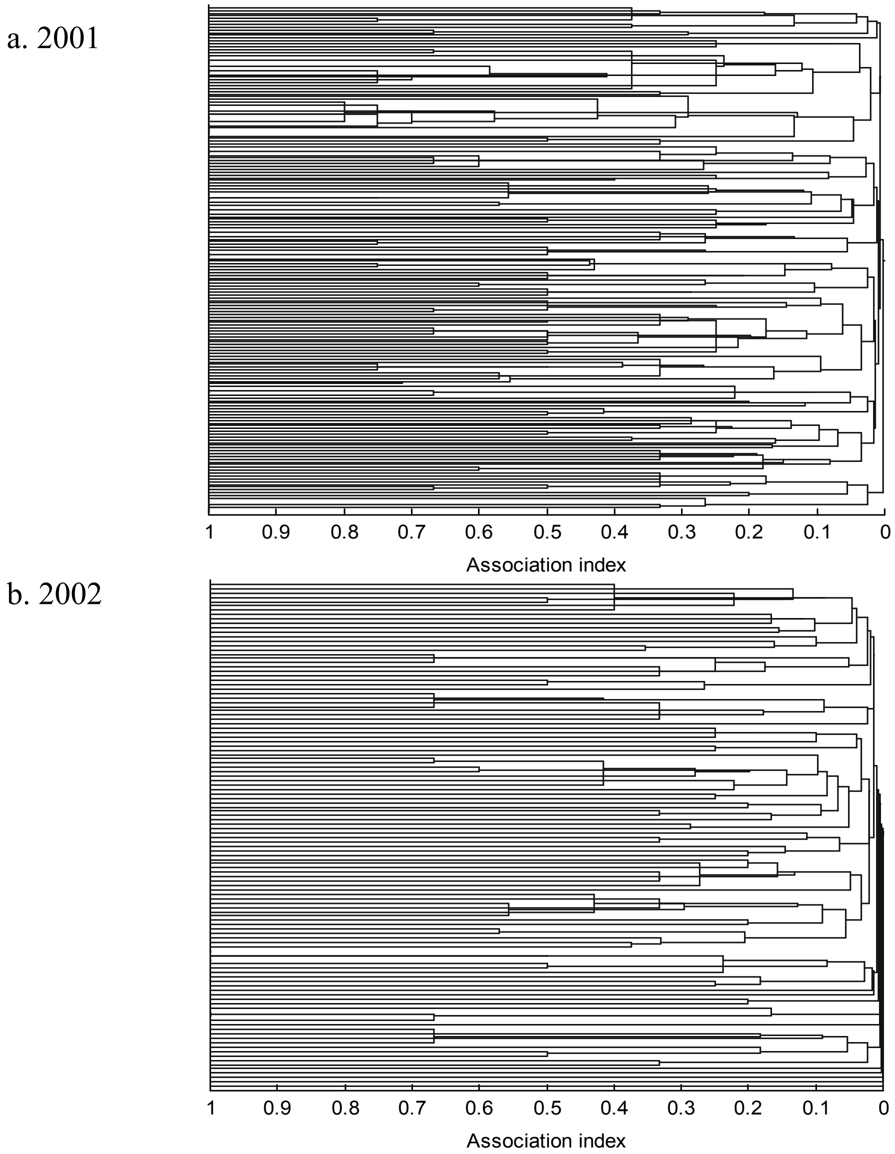


Figure 92. These diagrams, based on simple ratio indices for individuals photographed at least twice in Admiralty Bay, show the extent to which associations clustered during the winters of (a) 2001 and (b) 2002.

Discussion

Seasonal Residency and Abundance in Kaikoura

Dusky dolphins, as a species, are found in Kaikoura year-round. However, based on this preliminary analysis, it appears that particular individual dolphins are present in Kaikoura seasonally. Taken together, these results indicate that dusky dolphins are seasonally resident in Kaikoura, remaining in the area on average for 3.4 ± 1.27 months (mean ± s.e.), and returning at roughly the same season in subsequent years.

At any given time the estimated mean number of dolphins residing in Kaikoura was just under 2,000 out of an overall population of over 12,000. The high degree of variability in this estimate (standard error = 815) is most likely due to seasonal variation in the number of dolphins present, as larger group sizes are typically observed during winter months (see chapter II).

Given that dusky dolphins as a species can be found year-round in Kaikoura, there would seem to be a plentiful food supply to support large numbers during all seasons. This begs the question, why do they leave? One possibility is that mothers with growing calves head for better thermal conditions to the north when the water temperature drops. However, this only represents a portion of the population, and the majority of dolphins re-sighted in Admiralty Bay during winter are adult males (Markowitz *et al.* 2004). Perhaps either the summer residents displace the winter residents or vice versa, but here again there are no data available. Thus, like so many other scientific revelations, the finding that dusky dolphins as individuals are seasonally resident in Kaikoura while the species is present year-round leads inevitably to more unanswered questions.

The high level of seasonal residency may mean that particular individual dusky dolphins are only present in Kaikoura to interact with tour vessels for one-third to one-fourth of any given year. In combination with careful management and the relatively large number of dolphins, this regular seasonal turnover may limit the impacts of year-round dolphin swimming and watching eco-tourism, which generates considerable local revenue (Fairweather and Simmons 1998) and appears to be sustainable at present levels (Barr and Slooten 1998, Brown 1999).

A potential confounding factor in this analysis is the difference in effort between the seasons. Dolphins are more difficult to photograph in the larger, rapidly moving groups in winter than in the smaller more restful groups of summer (see chapter II). Further, the conditions in winter are not as often conducive to boat-based research (southerly fronts from the Antarctic make for more days with rough seas), and the number of daylight hours during which photographic data may potentially be collected is reduced (from as many as18 in summer to as few as 8 in winter). I hope to address this sampling bias with further photo-cataloging efforts. An additional 2,314 photographic records obtained in Kaikoura during this past winter using high-resolution digital photography should yield better information on seasonal residency.

Migration between Kaikoura and Other Regions

Although photo-identification sample sizes from regions around New Zealand other than Kaikoura and the Marlborough Sounds are poor, the observation that dolphins are re-sighted in locations as distant as Jackson Bay indicates long-range movements. If such movements are the rule and not the exception, then it is possible that most of the dusky dolphins in New Zealand pass through Kaikoura at some point during the year. If this is the case, and given a high rate of seasonal turnover, the population estimate for Kaikoura may approximate the total number of dusky dolphins in New Zealand waters. Alternatively, it may represent only a portion of the New Zealand population. This second possibility would concur with genetic estimates of population size at > 20,000, although these may be inflated as they are based on gene frequencies and some haplotypes are shared between New Zealand and other regions globally (Harlin *et al.* 2003).

To date, 37 individuals photographically identified in Kaikoura during summer and autumn have been re-identified in Admiralty Bay during winter. The proportion of dolphins traveling between the two regions is probably higher than this would indicate due to the relatively sparse and incompletely analyzed sample from Kaikoura. Additional photo-catalog work for dolphins in Kaikoura should help to confirm this migration trend. Comparing the mean number of dolphins present in Kaikoura at any given time and the overall population size to those of Admiralty Bay (see chapter IV) indicates that the number of dolphins using Admiralty Bay at any given time and the estimated total number are roughly 10% those in Kaikoura.

Where the dolphins residing in Kaikoura during the winter months come from and go to during the summer remains a mystery. The best guess at present is that they follow the continental slope and are found around the Chatham Islands and/or off the coast of Dunedin in the summer. Unfortunately the sea conditions in both of these regions are not particularly conducive to small vessel photo-identification research (as is clear from stories of fishing adventures off the Chatham Islands and my research team's own adventures off Dunedin). One possible way to address this question would be to attach satellite transmitters to dusky dolphins during the winter in Kaikoura and/or during the summer off Dunedin. A similar approach on the west coast would be invaluable as dusky dolphins are difficult to locate in this area.

Social Structure

As postulated by Würsig *et al.* (1997), dusky dolphins in New Zealand show a fluid fission-fusion society. Dusky dolphin associations within the complex of large groups and small adult, nursery, and mating groups in Kaikoura are clearly not static over time. This does not mean, however, that New Zealand dusky dolphins are without social structure. Non-random associations at the level of casual acquaintances last over half a year on average in Kaikoura.

Further analysis of associations in small groups by group type may help clarify social structure in Kaikoura. In particular, future analyses and additional field research could provide an indication of whether large groups are randomly assembled and disassembled, or aggregations comprised of smaller stable social units that join and split off together. Several anecdotal observations suggest the latter is the case, but this "hunch" awaits statistical confirmation.

In Admiralty Bay, the picture of dusky dolphin social structure is quite a bit clearer, due to the more complete photo-identification samples obtained within small feeding/foraging groups in this region. Within a single winter season, dolphins foraging in Admiralty Bay associate non-randomly at the level of casual acquaintances. Over successive seasons, dolphins returning to Admiralty Bay associate non-randomly at the level of constant companions, indicating stable long-term associations between hunting partners. The observation of one pair of males associating in small groups in both Admiralty Bay during the winter and in Kaikoura during the summer suggests that associations may be maintained in different locations and that associates may travel together between regions. Further, behavioral observations (Chapters II-IV) of these dolphins hunting schooling fish together in Admiralty Bay and chasing a female together in Kaikoura indicates that dusky dolphins may cooperate in different ecological and social contexts (although costs and benefits of cooperative/coordinated effort were not examined in this study).

Combining the results from this chapter with those of previous chapters, it is apparent that New Zealand dusky dolphins live in a well-organized society, which is neither altogether different from nor altogether similar to those of other dolphins. In Kaikoura, the daily pattern of behavior somewhat resembles that of Hawaiian spinner dolphins (Würsig *et al.* 1994). In Admiralty Bay, the same individuals behave more like dusky dolphins in Golfo San José, Argentina, indicating that variation in social organization may have more to do with habitat type than global scale population differences (Markowitz *et al.* 2004). In Kaikoura, features of dusky dolphin social lives include small restful nurseries, competitive "mating of the quickest" groups, and large aggregations that travel in a highly coordinated manner. Dusky dolphins adjust their social grouping and behavior to changing circumstances as they move large distances between varying habitat types. They appear to have preferred social partners including long-term stable companions, but also live gregariously within a complex network of associations, which extends even beyond their own species to include other marine mammals.

A popular misconception is that all dolphins are alike in the way they lead their social lives, following the best documented patterns of bottlenose dolphins (Connor *et al.* 2000). The results of this study show clearly that this is not the case. As a gregarious, small-bodied, wide-ranging species, the dusky dolphin shares a great many attributes with other dolphin species. Further research on dolphins with this sort of lifestyle could offer an excellent counterpoint to what is known regarding the better-studied bottlenose dolphin and killer whale societies. As one of the first studies of the social organization of dolphins living in such a metropolitan society, this research naturally opens more doors than it closes cases with definitive answers. The advent of digital technology, with its many advantages for photo-identification research promises to enable many further studies of complex dolphin social relationships. Many questions, including the meaningfulness of associations in large groups comprised of hundreds of individuals, the stability of social structure in mating groups and nurseries, the stability of associations over long periods of time, and the consistency of associations between different habitats, warrant further investigation.

CHAPTER VIII

CONCLUSION

When encountering a group of 500 dusky dolphins (*Lagenorhynchus obscurus*) racing by, churning up the sea, and launching themselves into the air, one is immediately confronted by the highly dynamic nature of such characters. Even when resting half-asleep, dusky dolphins never just sit still in the water, and of course, the water itself is constantly moving around them. It is often difficult to watch a single dolphin for longer than a few seconds. An understandable response would be to conclude that the lives of these dolphins lack any real organization, but it is now clear that dolphins in motion are very well organized.

Dusky dolphins social lives follow regular seasonal and diurnal rhythms. Seasonal variation in behavior of dolphins off Kaikoura appears tied to seasonal breeding and calving, likely related to fluctuations in water temperature and productivity. Diurnal variation in dusky dolphin behavior off Kaikoura is linked to the diel cycle of nocturnal foraging. Seasonal residency and migration coincide with predictable changes in behavior and group structure. Dusky dolphins migrating between deep- and shallow-water habitats change from nocturnal to diurnal foraging strategies, with clear effects on activity budgets and grouping. Knowledge of dusky dolphin behavioral ecology has conservation and management applications, as evidenced by the case of Admiralty Bay, a previously unrecognized important winter foraging habitat for dusky dolphins. Regular seasonal turnover of individuals approximately every 3 months off Kaikoura results in roughly 1,000-2,000 dolphins from a population >10,000 present at any one time. Abundance in Admiralty Bay peaks in winter, averaging 220 individuals.

Difficulties in analyzing a cumbersome photo-identification data set were partly offset by the use of digital photographic techniques. This allowed the first detailed analysis of social structure for this population, demonstrating long-term non-random associations between individuals, with casual aquaintances in Kaikoura lasting throughout a season (to 200 days) and some evidence for constant companions (lasting >1,000 days) as well as casual acquaintances (within a season) within foraging groups in Admiralty Bay. Dusky dolphin social stucture follows a fission-fusion pattern similar to that described on a somewhat smaller scale for bottlenose dolphins in Shark Bay, Australia (*Tursiops aduncus*, Smolker *et al.* 1992) and Sarasota Bay, Florida, USA (*Tursiops truncatus*, Wells *et al.* 1987). This social structure is similar to that of chimpanzees (*Pan troglodytes*) and spider monkeys (*Ateles* sp., Connor *et al.* 2000) . Dusky dolphin social structure and behavioral ecology are perhaps even more strikingly similar to those of spinner dolphins (*Stenella longirostris longirostris*) off the main Hawaiian islands, with groups splitting and joining as they move offshore to forage at night on DSL-associated species and inshore to rest and socialize during the day (Würsig et al 1994).

As one of the first efforts to examine the social organization of the dusky dolphins, this study provides a different perspective on factors important to the survival and reproduction of this mesopelagic dolphin. Particularly in highly social species, young inherit far more than just genes from their parents. The “ecological and social legacies that accompany genes" have been termed the "ontogenetic niche" (West and King 1987), and provide an important reminder of the role of developmental processes in the cultural evolution of wild-animal societies (Boyd and Richerson 1985). Social inheritance of dominance rank in matrilineal hierarchies, a common feature among many primates, depends heavily on alliances between unrelated females as well as kin (Chapais 1992). Studies of a number of wild-animal populations, including killer whales (Baird 2000) and sperm whales (Rendell and Whitehead 2003), demonstrate the cultural transmission of behavior (Whitehead 2002). Social/cultural indices may be at least as important as genetic measures in determining meaningful population boundaries for conservation and management of social marine mammals (Rendell and Whitehead 2003).

Much remains to be examined regarding the social organization of dusky dolphins. This study of social behavior provides information that could be used to build hypotheses for more detailed examination of particular social groups. For example, longitudinal research incorporating focal individual follows of mothers and calves in nurseries over longer sampling periods could provide a more thorough account of parenting effort and calf development (Mann 1999*a*). Further research on male-male relationships and roles in mating groups (as in bottlenose dolphins, Connor *et al.* 2000) could provide further evidence for or against a "mating of the quickest" system. Additional detailed investigation of dusky dolphin social organization in Admiralty Bay could include the roles of different individuals in foraging groups, examining how foraging activities are coordinated. Satellite telemetry could be employed to further understand and/or confirm long-range movements of dusky dolphins in areas difficult to access by small vessels. The timing and location of tag attachment could be planned so as to maximize the chances of documenting new, but suspected movements (e.g. between Kaikoura in winter and areas south off the Chatham Islands and Otago in summer). Continued photo-identification efforts, now that a catalog of distinctive individuals is established, should provide long-term data on residency, abundance, mirgration, and social structure invaluable to this sort of research (Mann 2000). The continued use of digital techniques adopted midway through this research should increase the efficiency and speed of data collection and analysis (Markowitz *et al.* 2003*ab*).

As with most science, the discoveries made during this study lead to further questions, promising many future insights into the social lives of dusky dolphins. The proliferation of myths about dolphins has resulted in people treating them as magical beings, sort of like "floating hobbits" (Pryor and Norris 1991). As entertaining as many fantastic dolphin tales can be, the social lives of these creatures in nature are yet more fascinating. The dusky dolphins of New Zealand (known in some circles as "Middle Earth") are in fact much less sedentary and inhabit a wider social and ecological realm than most would imagine of "floating hobbits", although they certainly enjoy the sort of gregarious lifestyle the title implies (Figure 93).

Figure 93. Gregarious and wide-ranging, dusky dolphins lead active social lives.

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VITA

Timothy Michael Markowitz

1355 Livingston Ave. Telephone: (650) 355-6184
Pacifica, CA 94044 U.S.A. email: tim_markowitz@yahoo.com

Education and Academic Awards Summary:

Ph.D. Wildlife & Fisheries Sciences, Texas A&M University.	G.P.A. 4.0
Research Excellence Award, TIO & Tom Slick Fellow.	Degree Awarded: 2004
M.S. Animal Science, University of California, Davis.	G.P.A. 3.6
Harris Fellow.	Degree Awarded: 1996
B.A. Double Major, University of California, Santa Cruz.	Academic College Honors
Environmental Studies and Creative Writing Honors.	Degree Awarded: 1993

Peer Reviewed Publications:

Brockett, R., T.S. Stoinski, J. Black, T.M. Markowitz, and T.L.Maple. 1999. Nocturnal behavior in a group of unchained, female African elephants. Zoo Biology 18: 101-109.

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Television Appearances during Ph.D. Research:

Dolphins: The Ultimate Guide- Discovery Channel, *The Aquanauts*- Animal Planet, and *National Geographic Explorer*- National Geographic Television.

Leadership Positions during Ph.D. Research:

Principal Investigator- New Zealand Dolphins Project, Earthwatch Institute.
Internship Coordinator- Marine Mammal Research Program, Texas A&M Galveston.