COMPARATIVE SOCIOECOLOGY OF THE DUSKY DOLPHIN (*LAGENORHYNCHUS OBSCURUS*) IN NEW ZEALAND

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ABSTRACT

Behaviour and social groupings of animals are often closely tied to habitat structure. Ecological factors (e.g., predation pressure, resource distribution) and social pressures profoundly influence behaviour and social organization. This study examined the socioecology of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, one of the most productive submarine canyon habitats in the world, supporting marine mammal populations and a thriving tourism industry. Behavioural data were collected during 332 dusky dolphin group follows from a small research vessel and onboard 174 dolphin tours during 2006-2009. Continuous and interval sampling were used to document behavioural states, behavioural events, and changes in group composition. Data from small groups (n=197) were compared with similar data collected from 67 small group encounters with Hector's dolphins (*Cephalorhynchus hectori*) in the same habitat. In winter, dusky dolphins formed larger groups that ranged more widely and small groups that primarily rested during the day near shore. Although resting, small groups increased dispersion and swam in parallel formation in winter. In summer, dolphins formed small groups for calf-rearing, mating and resting. Groups with calves were the largest and most stable of these small groups, and were found closest to shore, in relatively shallow water, often near river mouths. In mating groups, rapid chases decreased intromission rates as competition among males increased. Sexual selection may favour traits improving male success in behavioural contests as well as sperm competition in this species. Apparent mechanisms for female choice included 'escape' strategies that prolonged chases. Hector's dolphins formed smaller groups with higher fission-fusion rates, less cohesion, and fewer social bond reinforcement behaviours than dusky dolphins. Interactions with tour vessels had short-term effects on the behavioural state, heading, dispersion, and leaping rate of large dusky dolphin groups. Resting was disrupted during tour interactions and dolphins increased travel away from approaching tour vessels following tour interactions. Assertive approach methods reduced the duration of swimmer-dolphin interactions, particularly in summer when dolphins may be sensitised to high levels of tourism. These large-brained, highly social mammals form intricate societies that are responsive to changes in habitat, predation pressure and resource distribution. Understanding these responses is vital for protection of dolphins in the wild.

DEDICATION

This dissertation is dedicated to my mentor

Dr. Daisaku Ikeda

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CHAPTER 1

INTRODUCTION

Socioecology

The ecology of an organism has a profound influence on its social structure (Clutton-Brock and Harvey 1977, Emlen and Oring 1977). Temporal variation in predation pressure or the abundance and distribution of food can determine group size (Wells et al. 1999) as well as social unit size in fission-fusion societies (Dunbar 1992). Socioecological studies examine this relationship between ecological factors and social behaviour (Emlen and Oring 1977, Vehrencamp 1983, Terborgh and Janson 1986, Norris 1994a, Emlen 1995, Kappeler and van Schaik 2002, Wittemeyer et al. 2005, Gowans et al. 2008).

For many species, group size, composition, and behavioural budgets are closely tied to habitat type. Troops of baboons (*Papio* sp.) located in highly arid climates exhibit more complex social organization and consistent subgroup structures than troops in other locations (Henzi and Barrett 2005). In African elephant (*Loxodonta africana*) societies, levels of association are organized in ‘tiers’ with stable matriarchal family associations the least likely, and third tier associations the most likely, to be affected by seasonal and interannual variability in resources (Wittemeyer et al. 2005). Variation in vegetation structure influences the association of male and female lions (*Panthera leo*), with increased vegetation leading to decreased hunting success in male lions and higher levels of association with females in order to scavenge from female hunts (Funston et al. 1998). Identifying the relationships between key ecological factors and social behaviour in different species can contribute to conservation efforts and our understanding of sociality in animals.

Marine Mammal Social Organization

The social organization of a species includes the content, quality and patterning of relationships in space and time (Hinde 1976). Studies of social organization examine the temporal and spatial variability in group composition (social structure) as well as the behaviour of individuals within groups. The marine environment is highly variable and complex with often patchy distribution of resources (Steele 1978, Tiselius 1993, Stewart and Jones 2001). Marine mammals balance the physical challenges of being homeothermic, air breathing animals whose prey is located at depth with spatial and temporal resource variability in an aquatic environment. The social structure of marine mammals in response to these fluctuations can range from temporary feeding or thermal aggregations to life-long social bonds (Wells et al. 1999).

Cetacean social structures have evolved in a range of ecological frameworks particular to each species, with intraspecific variability dependent on both the species' behavioural plasticity and localized ecological pressures (Weilgart et al. 1996, Baird 2000, Clapham 2000, Connor et al. 2000, Rendell and Whitehead 2001, Hoelzel et al. 2007). Baleen whales form temporary aggregations of individuals that are based on resource availability or breeding activity (Wells et al. 1999, Clapham 2000), while some toothed whales form life-long highly stable associations with relatives and/or cooperative alliances with non-relatives (Connor et al. 2000, Baird 2000).

Dolphin Socioecology

Dolphins are large-brained social mammals with intricate social relationships (Ridgway 1986, Norris 1994a, Connor 2007). Many dolphin species (e.g., common dolphins, *Delphinus delphis*; spinner dolphins, *Stenella longirostris*; dusky dolphins, *Lagenorhynchus* *obscurus*) group in herds or ‘schools’ based on habitat characteristics, much like terrestrial herd mammals. Unlike herd mammals, however, threats (e.g., from predators) to dolphin schools are three-dimensional. Because terrestrial herds are able to localize predation threats in two dimensions, the behavioural response of group members to a predation threat is often limited to a particular location and a few members. Three-dimensional threats are more difficult for all group members to localize, and require a more complete group response (Norris and Schilt 1988, Norris 1994a). it has been proposed that this difference between two and three-dimensional threat localization may require cetaceans at times to forgo their mammalian individuality as the group responds to perceived danger (Norris 1994a).

Social patterns of behaviour for cetaceans described thus far are based on intricate, well defined relationships among small family groups of animals, such as sperm whales (*Physeter macrocephalus*) that form matriarchal groups much like African elephants (Weilgart et al. 1996); and bottlenose dolphins (*Tursiops* sp.) that exhibit fission-fusion social structures similar to those of chimpanzee societies (Connor et al. 1992). Most research on the behaviour, residency patterns and habitat use of dolphin groups, particularly in New Zealand, focuses on small resident groups of animals (e.g., Hector’s dolphins, *Cephalorhynchus hectori*, and bottlenose dolphins; Bräger et al. 2002, Bräger et al. 2003, Bejder et al. 1999, Constantine 2002, Lusseau 2002, Martinez et al. 2009) that are found close to shore and are therefore relatively accessible. The study of dusky dolphin socioecology will provide one of the few windows into a social system with both very large (thousands of individuals) and quite small (2-30 individuals) social groupings in a wide-ranging, semi-pelagic species (Wursig et al. 2007).

Dusky Dolphins

This study examines spatiotemporal variation in the behavioural ecology and social grouping patterns of the dusky dolphin (Figure 1.1), a small-bodied, seasonally breeding species of the southern hemisphere (Table 1.1). Dusky dolphins are found in the temperate waters off Southern Africa, South America and New Zealand. This species ranges in coastal and near shore waters, usually less than 2,000 m deep, in groups of tens to hundreds, migrating seasonally with changes in water temperature and prey availability (Würsig et al. 1997, Markowitz 2004). In New Zealand, dusky dolphins occur mainly off the South Island with greatest numbers along the east and south coasts (Gaskin 1968). Seasonal reproduction includes dramatic testis size increases in males during the breeding season (November to mid-January), indicating sperm competition and a promiscuous mating strategy (Cipriano 1992).

*Table 1.1: Selected life history parameters of the dusky dolphin (*Lagenorhynchus obscurus, *estimates from Leatherwood and Reeves 1983, Cipriano 1992, Würsig et al. 1997)*

Parameter	**Dusky Dolphin**
Gestation length	11.4 months
Lactation duration	18 months
Calving season	Early summer (mid-November to mid-January)
Age at first reproduction	7-8 years
Size at birth	0.97-1.02 m long
Size of adults	1.65 to 1.86+ m long
Maximum Age	≥ 35-36 years

Figure 1.1 The New Zealand dusky dolphin.

Dolphins and Tourism

Ecotourism has been increasing world-wide for the last several decades. Communities are turning from direct harvest of species to instead capitalize on public interest to view wildlife in its natural habitat. Ecotourism is lucrative, with cetacean watching tourism generating more than US$1 billion per year with 13 million viewers annually (O'Connor et al. 2009). Although tourism can provide conservation benefits for wild animals, these interactions can also disrupt their lives. Appropriate management for sustainable wildlife tourism activities is a growing concern, particularly for cetaceans.

To assess the effects of tourism on dolphins, most research has focused on short-term behavioural responses to tours. Assessing long-term changes and biologically significant impacts that result from cumulative exposure to tourism is more problematic, although short-term responses can provide an indication for these more lasting consequences of tourism (Samuels and Bejder 2003). In some well-studied populations, dolphin tourism has been shown to change dolphin distribution and apparently increase calf mortality (Mann and Barnett 1999, Mann and Kemps 2003, Bejder et al. 2006a).

Short-term behavioural responses to tourism have been well-documented for a number of dolphin species. Dolphins respond with reduced resting, disrupted foraging, vessel avoidance, and higher fission rates for dolphin groups as individuals react to tour vessels, swimmers or provisioning (Constantine et al. 2004, Neumann and Orams 2005, Lusseau 2006, Bejder et al. 2006a, Dans et al. 2008, Markowitz et al. 2010b, Martinez 2010).

Dusky dolphin tourism occurs off the coasts of South Africa, Argentina and New Zealand. Tourism in South Africa and Argentina is largely unregulated (Markowitz et al. 2010b). Assessment of effects of tourism on dusky dolphins in Argentina showed dolphin foraging and socializing behaviour were disrupted by tourism interactions (Dans et al. 2008). In New Zealand, dusky dolphin tourism occurs primarily at Kaikoura and is regulated by the New Zealand Department of Conservation. Dusky dolphin tourism at Kaikoura has grown significantly since the 1980s (Markowitz et al. 2010b) with tourism interactions with dolphins monitored primarily from shore beginning in the 1990s (Barr 1997, Würsig et al. 1997, Yin 1999). Monitoring tourism interactions from research and tour vessels provided additional information on dusky dolphin responses to tourism (Markowitz 2004, Duprey et al. 2008). Although there have been no biologically significant impacts reported for dusky dolphins interacting with tour vessels at Kaikoura, some short-term behavioural responses have been noted including decreased swim speeds (Yin 1999, Markowitz 2004), higher leaping rates (Barr 1997), and changes in direction and behavioural state (Würsig et al. 1997).

Study Area

The Kaikoura Coast, South Island (42˚S, 173˚E) is an ecologically productive location in which dusky dolphins are found in high abundance year-round (Figure 1.2). The consistent presence of dolphin groups in this area supports a lucrative and expanding tourism industry. The Kaikoura Canyon, located just 500 m offshore the coastline south of Kaikoura, is 60 km long and up to 1200 m deep, providing a conduit to the Hikurangi Channel system (Lewis and Barnes 1999). This feature brings deep, productive water close to shore, resulting in a concentration of plankton, fish, squid, and pelagic seabirds and marine mammals (Figure 1.3; Lewis 1998).

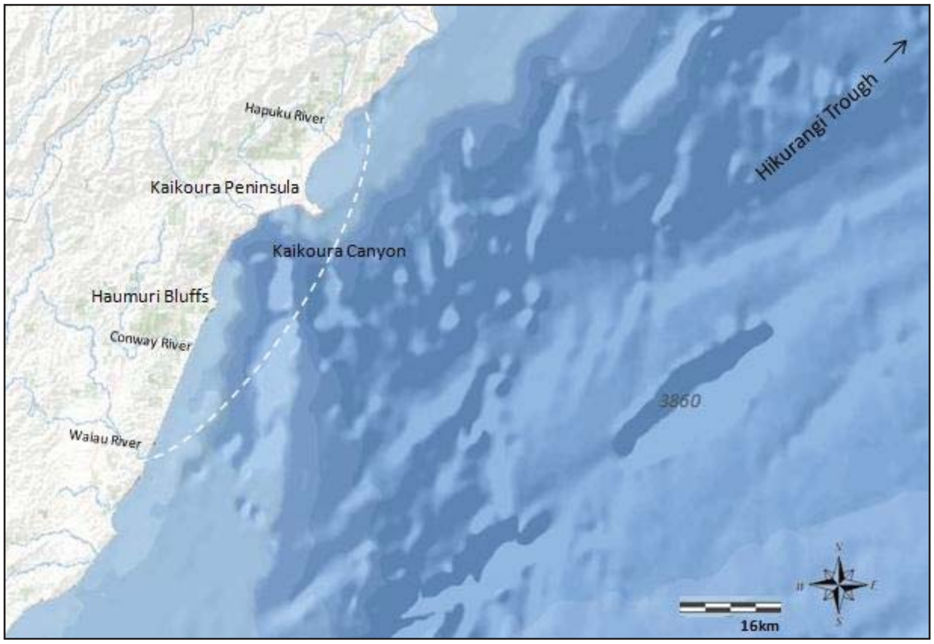


Figure 1.2. The study area (white dashed line) includes coastal areas from north of the Hapuku River south to the Waiau River, centered on the Kaikoura Canyon.

The Kaikoura Canyon is also adjacent to two significant oceanographic boundaries, the convergence zone between the Southland and East Cape currents of New Zealand (Carter and Herzer 1979, Chiswell 1996), and on a larger scale, the subtropical convergence (Boyd et al.

1999). The Kaikoura Canyon is one of the most productive canyon habitats in the world, with deep-sea biomass values reportedly 100-fold higher than previously reported for deep-sea habitats below 500 m (De Leo et al. 2010).

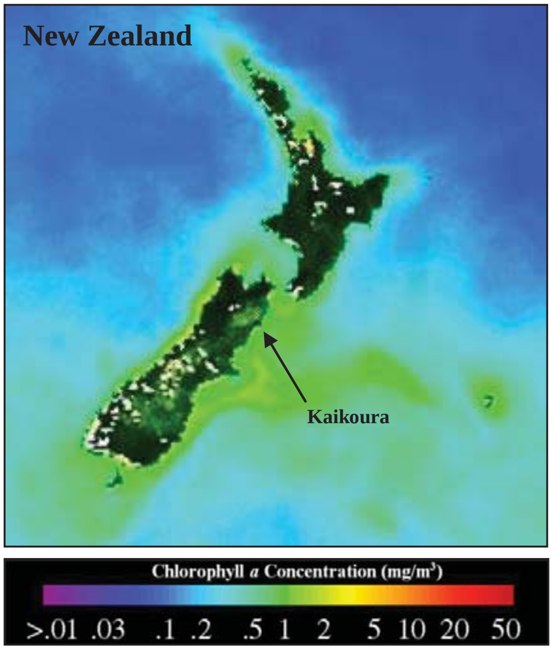


Figure 1.3. Seasonal Primary Productivity based on chlorophyll a concentration, summer 2010-2011 (http://oceancolor.gsfc.nasa.gov/SeaWiFS/).

Dusky Dolphin Research

Research on the foraging behaviour and grouping patterns of the dusky dolphin began in the 1970s in the Valdés Peninsula region of Argentina. Small groups of 6-15 dolphins join to form large cooperative feeding groups that concentrated schools of anchovy (*Engraulis anchoita*) in Golfo San José of the Valdés Peninsula. Leaping and social-sexual behaviours after the dolphins fed suggested strengthening of social bonds and 'play' behaviour (Würsig and Würsig 1980). Dusky dolphins in the Kaikoura Canyon habitat of New Zealand's South Island have a different strategy. Schools of dolphins including 200 to 300 individuals range in the canyon habitat throughout the day and feed on meso-pelagic fishes associated with the Deep Scattering Layer (DSL) at night. Such large groups of dolphins are sustained by the rich ecology of the canyon. The fission-fusion behaviour of dusky dolphins in this habitat is quite different when compared with the relatively shallow and protected waters of Golfo San José (Würsig et al. 1989).

Morphological studies from stranded specimens of the New Zealand dusky dolphin as well as genetic analyses further clarified the taxonomy of the dusky dolphin as monophyletic with the Pacific white-sided dolphin (*L. obliquidens*), with a suggestion that these species be organized into a new genus separate from other *Lagenorhynchus* spp. (Webber 1987, Harlin et al. 2003). Behaviour and occurrence patterns as well as life history and feeding ecology of dusky dolphins at Kaikoura were examined using theodolite tracking, radio-tagging, and post-mortem techniques (Cipriano 1992). The social structure, behaviour and ranging patterns of New Zealand dusky dolphins were investigated using behavioural sampling and photographic identification. Individual dusky dolphins ranged between the Kaikoura Canyon on the east coast and the west and north coasts of the South Island, with individuals in small bays of the Marlborough Sounds region socializing and foraging much like others of their species in Golfo San José, Argentina (Markowitz 2004, Vaughn et al. 2010).

Work with large groups of dusky dolphins continued at Kaikoura (summarized in Würsig and Würsig 2010). Movement and vocalization patterns for dusky dolphins (Yin 1999, Brown 1999), interactions with predators (Srinivasan and Markowitz 2010), foraging ecology of dolphins in large groups (Dahood and Benoit-Bird 2010) as well as some interactions of dolphins with the growing tourism industry at Kaikoura (Barr and Slooten 1998, Duprey et al. 2008) were investigated. In recent studies of small satellite groups of dolphins at Kaikoura, the occurrence patterns and habitat use of nursery groups of mothers and calves (Weir et al. 2008) and the behavioural development of calves in these groups (Deutsch 2008) were investigated. Genetic analyses indicated familial relationships of dolphins in these nursery groups, with some evidence for matrilines, whereas New Zealand dusky dolphins found in other small groups at Kaikoura and in the Marlborough Sounds region were not related (Shelton et al. 2010). As was reported by Markowitz et al. (2004) a male bias was confirmed by genetic analyses for small foraging groups in Admiralty Bay (Shelton et al. 2010), with some males foraging together in Admiralty Bay also associated in mating groups chasing females at Kaikoura (Markowitz et al. 2010a). In the Marlborough Sounds region, surface and underwater behaviour of small foraging groups of dusky dolphins have been examined in detail (Pearson 2009, Vaughn et al. 2008, Vaughn et al. 2010, Vaughn et al. 2011).

Research Objectives

A socioecological framework proposed for delphinids suggests that semi-pelagic species, such as the dusky dolphin, will form larger groups with changing partners when compared with coastal species (Gowans et al. 2008). The objectives of this research are to investigate the influences of habitat on social grouping patterns and behaviour of dusky dolphins at Kaikoura, New Zealand. Behaviour and fission-fusion interactions of dolphins in large and small groups is examined and compared with the sympatric Hector’s dolphin, typically found near shore in shallow water habitat adjacent to the Kaikoura Canyon. As the formation of large groups of dusky dolphins at Kaikoura supports a thriving tourism industry, no investigation of their behavioural ecology would be complete without a thorough examination of tourism interactions.

Summary of Chapters

The comparative socioecology of dusky dolphins in New Zealand is examined as follows:

In Chapter 2, the influence of ecological features, season and time of day on the grouping patterns and behaviour of dusky dolphins are examined. Questions I address include:

1. What habitat features influence the behaviour and distribution of dusky dolphins in the Kaikoura Canyon area?
2. How do behaviour and social grouping vary with season and time of day?
3. Do dusky dolphins conform to a socioecological model proposed for cetaceans?

Locations, behavioural state, and social-sexual behaviours are compared for individuals in large and small groups with continuous sampling for dolphins in small groups providing detailed information on durations and frequencies of behaviour.

In Chapter 3, small groups of dusky dolphins are examined more closely, with questions related to the composition and function of different social group types (e.g., mating competition, calf-rearing). Questions I address include:

1. Do social behaviours and grouping patterns vary with group composition, reproductive effort and parental investment?
2. Do water depth, distance from shore and distance from river mouths influence behavioural displays and fission-fusion rates?
3. Are different social group types found in different microhabitats?

In Chapter 4, I compare the social organization and behaviour of the sympatric Hector's dolphin with dusky dolphin groups of similar size. Questions I address include:

1. Do habitat use and grouping behaviour differ between Hector's and dusky dolphins in the Kaikoura Canyon Area?

2. How does behaviour vary between these two species?
3. Do differences in behaviour, habitat use and grouping patterns conform to a socioecological model proposed for cetaceans?

In Chapter 5, I begin the examination of tourism interactions with dusky dolphins at Kaikoura observed from a small research vessel. A before-during-after approach is used to examine the influence of tour vessels on behaviour and movement patterns of individuals in large groups.

In Chapter 6, I further refine the investigation of tourism/dolphin interactions with an examination from tour vessels of swimmer placement, approach methods, swimmer-dolphin associations and detailed interactions between individual tour vessels and groups of dolphins on the behaviour and movement patterns of dolphins in large groups. Proposed changes in management of the tourism industry at Kaikoura resulting from the recommendations of this research are also discussed.

In Chapter 7, I summarise my findings and provide conclusions based on the results presented in each chapter.

This research was conducted with financial support from a New Zealand Department of Conservation research contract and a doctoral scholarship from Massey University. Colleagues conducted simultaneous behavioural observations of dusky dolphins from shore and assessed encounter rates with dusky dolphin groups during surveys south of Kaikoura. In consultation with my doctoral supervisors, I developed all research topics and protocols for this dissertation, and all data reported herein were collected by me and research assistants. Systematic survey data for dusky dolphin groups south of the Haumuri Bluffs were collected in association with S. Dufresne, as referenced in the text for all chapters in which these data were used. Findings from Chapters 5 and 6 were previously reported in a contract report to the New Zealand Department of Conservation as referenced in the text for these chapters. Co-author D. Lundquist assisted with data collection from tour vessels reported in Markowitz et al. (2009b) to the New Zealand Department of Conservation and in Chapter 6.

CHAPTER 2

SOCIOECOLOGY OF THE NEW ZEALAND DUSKY DOLPHIN: LIFE ON THE EDGE OF THE KAIKOURA CANYON

INTRODUCTION

Social Mammal Responses to Habitat Variability and Resource Distribution

Behaviour and social groupings of animals are closely tied to habitat structure for many species including baboons (*Papio* sp., Henzi and Barrett 2005), lions (*Panthera leo*, Funston et al. 1998) and bovids (Family Bovidae, Estes 1974). Seasonal variability in resources affects social grouping patterns and behaviour (e.g., African elephants, *Loxodonta africana*, Wittemeyer et al. 2005). In addition to influencing food availability, seasonal variability in environmental parameters can modify predation pressure (Wells et al. 1999). Like social groupings for terrestrial animals, cetacean social organization has evolved in conjunction with localized ecological pressures (Weilgart et al. 1996, Baird 2000, Clapham 2000, Connor et al. 2000, Rendell and Whitehead 2001, Markowitz et al. 2004, Hoelzel et al. 2007).

Dolphin species are found in a wide variety of habitats, including coastal (<100 m depth and within several km of shore), neritic (< 200 m in depth but not influenced by surf zone or coastal water), and pelagic (deep water areas over the open ocean that are less influenced by season) habitats (Gowans et al. 2008). In coastal habitats, where prey availability tends to be most predictable and predation risk lowest, dolphins form smaller groups, with stable long-term partnerships (Wells et al. 1999). Dolphins inhabiting neritic environments form larger groups, range more widely and have changing social partners (Gowans et al. 2008).

Dusky dolphins (*Lagenorhynchus obscurus*), which inhabit both the coastal and neritic realms as well as wandering occasionally into the "semi-pelagic" zone, modify social grouping and diel activity patterns dramatically as they move between shallow bays and deep water habitats (Würsig et al. 1989, Markowitz et al. 2004). At the edge of the Kaikoura Canyon, dusky dolphins typically rest in coastal and neritic habitats in the daytime, moving offshore to feed in deeper water at night (Würsig et al. 2007). This provides a special location to examine the interaction between dusky dolphin social grouping patterns, behaviour and habitat use.

Social and Behavioural Flexibility of Dusky Dolphins

Dusky dolphins, like many other marine and terrestrial species, exhibit seasonal and diurnal behavioural rhythms (Markowitz 2004). In Golfo San Jose and Golfo Nuevo on the Patagonian coast of Argentina (42°S, 64°W), dusky dolphins form feeding groups of tens to hundreds of animals and forage during the day, primarily on anchovies (*Engraulis anchoita*; Würsig and Würsig 1980, Koen-Alonso et al. 1998, Vaughn et al. 2010). In the deep waters of the Kaikoura Canyon off the east coast of New Zealand's South Island (42°S, 173°E), dusky dolphins gather in large assemblages of hundreds of individuals, feeding at night on prey associated with the deep scattering layer (Würsig et al. 1989). Smaller peripheral groups of dusky dolphins are usually found in the vicinity of large groups. When a large group is not present in the area, nursery and other small groups are typically not found (Markowitz 2004), although there appear to be exceptions described below.

The social organization of dusky dolphins at Kaikoura is likely driven by predation risk and dolphins' distribution and movement patterns may be influenced primarily by killer whale predation (*Orcinus orca*) and less so by deep water sharks (reviewed by Srinivasan and

Markowitz 2010). Nursery groups are particularly vulnerable to predation with extensive injuries to calves sighted in the Kaikoura Canyon area presumably from killer whale or shark attacks (Constantine et al. 1998, Weir et al. 2010, W.Markowitz, personal observation). Killer whales frequent the Kaikoura Canyon in spring and summer during the breeding season (Visser 2000, Markowitz 2004, Dahood et al. 2008). The seasonal distribution and abundance of sharks (including the great white shark, *Charcharadon carcharias*, the shortfin mako, *Isurus oxyrinchus*, the sevengill, *Notorhynchus cepedianus*, and sleeper shark, *Somniosus pacificus*) that may prey on dusky dolphins at Kaikoura is not well studied, but shark abundance appears to be currently low at least in summer (Srinivasan and Markowitz 2010).

Large groups of dolphins off Kaikoura move offshore late in the day to prepare for nocturnal foraging (Markowitz 2004, Benoit-Bird et al. 2004, 2009), feeding primarily on lanternfishes (family Myctophidae) and squid (*Nototodarus* spp.) associated with the deep scattering layer (Cipriano 1992, Cipriano and Webber 2010, Dans et al. 2010). Past studies indicated that individual dusky dolphins are seasonally resident in the Kaikoura area, and are capable of using relatively large areas throughout any given year, with individuals moving seasonally between Kaikoura on the east coast, the Marlborough Sounds on the north coast, and the west coast of New Zealand's South Island (Markowitz et al. 2004, Markowitz 2004).

Effects of Social and Ecological Pressures on Behaviour

The spatial and temporal distribution of critical resources likely predicts patterns of behaviour (Emlen and Oring 1977). Evaluation of changes in behaviour can be used to indicate social and environmental factors that increase stress. For large-brained social mammals living in a complicated web of social relationships, social pressures can match or even exceed ecological pressures as a source of stress (Sapolsky 1994).

Research Goals and Predictions

This chapter examines how the behaviour and grouping patterns of dusky dolphins off Kaikoura are related to spatiotemporal variation in habitat use. Seasonal and diurnal variation in ranging patterns and behaviour for large and small (<50 individuals) groups are assessed, with reference to water depth, distance from shore and distance from river mouths.

Across a wide range of species, individuals tend to form large, wide-ranging groups in open environments and smaller, more localised groups in more complex, limited spaces (Estes 1974, Wells et al. 1999, Brashares et al 2000, Gowans et al. 2008). Dolphins move to shallow waters or increase group size to avoid predation (Saayman and Taylor 1970, Würsig and Würsig 1979). As group size decreases and predation risk increases (Turner and Pitcher 1986, Hamilton 1971), individuals should reduce dramatic or noisy behavioural displays that 'call attention' to the group. For dolphins, behaviours that result in percussive splashes such as leaps or tail slapping (defined below) constitute 'noisy' behaviour.

Larger, more cohesive social groups are likely to form when prey availability is reduced. Associating in larger groups increases prey detection and reduces predation risk as groups range more widely to increase prey encounter rates (Charnov 1976, Krebs and Davies 1993). Seasonal reductions in prey availability are likely to affect dusky dolphin social grouping patterns, particularly in winter. Dusky dolphins may form stable social groups for resting during midday, as foraging in the Kaikoura Canyon area occurs primarily at night (Markowitz 2004, Benoit-Bird et al. 2004, 2009).

According to theory on predator-prey dynamics, given abundant resources larger groups of individuals should form to reduce predation risk via the dilution effect (Hamilton 1971), confusion effect (Neill and Cullen 1974) and increased vigilance (Pulliam 1973, Krauss and Rukston 2002, Davies et al. 2012). Both large and small groups of dusky dolphins form at Kaikoura with smaller group formation an alternative taken by certain individuals perhaps for reproductive reasons or due to their increased vulnerability to predation risk within the large group envelope. For example, large groups of dusky dolphins have been observed swimming at close to their maximum speed in response to killer whales. Presumably females with calves would have the greatest difficulty maintaining top swimming speeds for sustained periods, so forming smaller, less conspicuous nursery groups may serve as an alternative predator avoidance strategy (Srinivasan and Markowitz 2010).

The main predators of dusky dolphins in New Zealand are killer whales which frequent Kaikoura especially during the calving season (Constantine et al. 1998, Srinivasan and Markowitz 2010), and sharks which leave telltale scars on surviving dolphins and are at times attacked by groups of dolphins with calves (Markowitz 2004). Unlike their terrestrial cousins, the ungulates, dusky dolphins must defend against these predators in not only two dimensions but three. If anything, killer whales and sharks are more likely to attack from below than from the surface. Moving into shallow water presumably reduces this danger, and dusky dolphins at Kaikoura have been observed to flee to shallow water in the presence of killer whales (Würsig and Würsig 1980, Srinivasan and Markowitz 2010). The nearshore environment may also provide greater acoustic cover, in the form of ambient noise from waves crashing along the shore, and visual cover, in the form of increased turbidity (especially near river mouths), improving the chances for small, quiet groups to remain undetected by predators. Of course, even the best hiding places only work effectively if animals behave in a cryptic fashion (reviewed by Davies et al. 2012), so small groups of dolphins hiding nearshore should be expected to behave in such a manner as to be less detectable to a potential predator than dolphins in larger groups offshore. Based on this reasoning, I tested the following hypothesis and predictions.

Hypothesis: Dolphins in small groups will be found in relatively shallow, nearshore, tubid habitat where they behave in an inconspicuous manner and maintain tight groups.

Specifically, I predict that:

1. As group size decreases, dolphins will be found closer to shore, in shallower water, and closer to river-mouths.
2. Surface (splash) behaviours such as noisy-leaping and tail-slapping will occur less frequently as group size decreases.
3. Dolphins in smaller groups will show lower inter-individual distance than dolphins in larger groups.

Seasonal influence on social behaviour

Seasonal shifts in water temperature increase energetic demands for marine mammals during winter. Water temperatures at Kaikoura fluctuate from 18°C in summer to 8°C in winter (Cipriano and Webber 2010). Foraging time for dusky dolphins at Kaikoura feeding on the DSL also varies between seasons (12-13 h in winter and 7-9 h in summer) although primary productivity and vertical migration cues for dusky dolphin prey species are likely to be reduced in winter, limiting prey availability during the longer winter foraging hours (Sinclair and Zeppelin 2002, Beentjes et al. 2002, Benoit-Bird et al. 2004, 2008, Meynier et al. 2009). The high energetic demands of calving and lactation are best met by dusky dolphin females in spring and summer when primary productivity is high and warmer water temperatures reduce energetic demands for both females and developing calves (Whitehead and Mann 2000). High-energy mating activities and social behaviours are also supported by these seasonal shifts, with male social behaviour tied to the seasonal reproductive patterns of females.

Due to the seasonal variability in water temperature, prey availability and reproductive effort described above, I hypothesise that**:**

Dolphin habitat use and behaviour change seasonally, with highly mobile, coordinated groups found offshore in the winter and restful, social groups found inshore during the calving and breeding season.

Specifically, I predict that:

1. Dolphins will be found closer to shore in shallow water, resting in tighter groups (at slower swimming speeds) during the calving and breeding season (centering on summer) than in the non-breeding season (winter).
2. Dolphins in winter will exhibit greater group cohesion and lower fission/fusion rates than dolphins in summer.
3. Dolphins will show more organized and directional swimming with high speed behaviours in winter as travelling increases, and social behaviours (including play and leaping behaviours) will be more common during the reproductive season (summer).

Diurnal influences on social behaviour and habitat use

Diel vertical migration of zooplankton and their predators is cued primarily by shifts in light levels and is driven by risk from predators that use light to capture prey (Zaret and Suffern

1976, Hays 2003). This vertical migration of zooplankton and their associated predators is the largest migration of biomass on earth and profoundly influences the diel behavioural cycles of marine predators that feed on these vertically migrating prey (Hays 2003). Dusky dolphins at Kaikoura take advantage of the high productivity and prey biomass associated with the Kaikoura Canyon, foraging primarily at night on vertically migrating lanternfishes and squids associated with the deep scattering layer (Würsig et al. 1991, Cipriano 1992, Benoit-Bird et al. 2004, 2009). Nighttime foraging behaviour leaves daylight hours available for resting and socializing near shore (Markowitz 2004, Würsig et al. 2008, 2010). Dusky dolphins at Kaikoura rest primarily at midday, with increased activity and movement offshore later in the day as dolphins prepare to feed (Cipriano 1991, Markowitz 2004, Würsig et al. 2008). Social behaviour and interactions increase among dusky dolphins after successful foraging events (Würsig and Würsig 1980). Increases in social behaviour while entering into rest have also been noted for other delphinids which forage at night on vertically migrating prey (Norris and Johnson 1994, Notarbartolo-Di-Sciarai et al. 2009).

Hypothesis: Diurnal habitat use and behaviour patterns will reflect the dolphins' diel foraging schedule, with socialising occurring after feeding (morning), followed by rest (midday), and increased activity in preparation for the next night of foraging (afternoon).

Specifically, I predict that:

1. Social and play behaviours will peak during the morning as dolphins reinforce social bonds after feeding and prior to resting.
2. Dolphins will be closest to shore in shallow water while resting during midday, with reduced speed and reorientation rates.

3. Dolphins will be least dispersed with lower fission-fusion rates, high-speed activity and leaping behaviour while resting during midday.
4. Dolphins will move offshore, increase activity, and disperse late in the day in preparation for foraging.

METHODS

Data Collection

Field Effort

Boat based surveys for dolphin groups were conducted off Kaikoura from a 5.5 m research vessel. Research effort from January 2007 through March 2009 included 699 hours of vessel surveys on 140 days with 332 dolphin group encounters. Of these, there were 197 encounters with small groups and 135 with large groups (>50 dolphins). Focal group behavioural sampling was conducted with 81 small groups and 111 large groups.

For each encounter, sea surface temperature, depth, wind speed and Beaufort sea state were recorded, as well as other marine mammal and bird sightings including estimated number of individuals and behaviour. Boat-based surveys were used to locate small groups of dusky dolphins off Kaikoura and south of the Haumuri Bluffs. Surveys were conducted south along 22 km of coastline from Kaikoura to the Haumuri Bluffs. Surveys were run at a distance of 2 km from shore and speed of 10-13 knots (18.5-24 km/h, see Figure 2.1). If no dolphin groups were located, surveying continued back to the north 1 km from shore at the same speed. During surveys, two primary observers and a secondary observer were used. The secondary observer was the boat driver and was not able to concentrate fully on spotting dolphins. The primary observers each concentrated their effort on one side of the boat, from the track line to abeam of the vessel.

Systematic line-transect surveys were also used to document the presence of dolphin groups south of the Haumuri Bluffs to the Waiau River (Figure 2.1; see DuFresne and Markowitz 2010 for detailed survey methods). These surveys were only run in summer and so these data were not included in seasonal GIS analyses. Two primary observers and a secondary observer surveyed for dolphins as described above. Vessel speed was maintained at between 12 and 15 knots (depending on conditions). Surveys were carried out during January and February 2008; and January and March 2009. A zigzag survey design with respect to depth was used to maximize encounter rates. The inshore apexes of the zigzags were generally within 2.5 – 3.0 km of shore. During March, 2009, an additional zigzag survey was plotted in the inshore waters along the same section of coast.

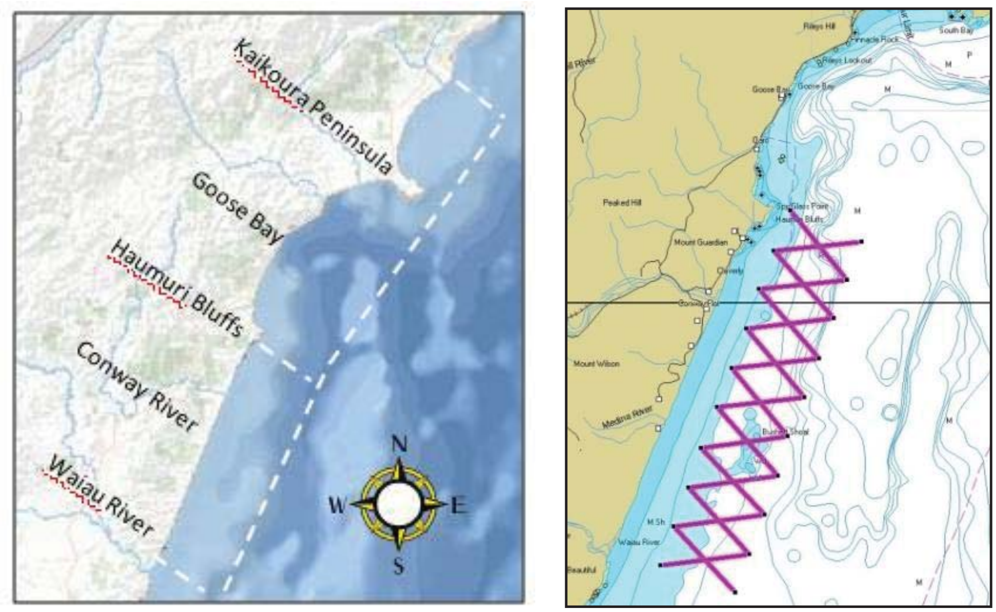


Figure 2.1. The primary (Haumuri Bluffs and north) and secondary (Haumuri Bluffs – Waiau River) research areas with river locations and bathymetry indicated in blue (left). In the secondary research area (right), purple lines show line transects along shore from the Haumuri Bluffs to the Waiau River. Blue lines indicate water depth isobaths, with shallower depths shaded. The black line at the Conway River indicates the approximate southern limit of operations for most research effort in the primary research area (from DuFresne and Markowitz 2009).

Due to the extent of the study areas surveyed, systematic line-transect surveys were an inefficient method for locating large groups of dolphins off Kaikoura, particularly for data collection with regard to tourism interactions (see Chapters 5 and 6). Large groups of dolphins (> 50 individuals) were located through communication with shore teams (Cipriano 1992, Würsig et al. 1997, Barr and Slooten 1998, Yin 1999), other vessels, and aircraft. Smaller groups encountered in the vicinity of large groups were sampled opportunistically. These data are included in the GIS analysis for this study. Surveys were conducted throughout the hours of daylight in all seasons.

Although use of a research vessel has the potential for disturbance of the dolphins, consistent and careful handling of the research vessel so as to reduce disturbance is likely to result in minimal and constant effects of the research vessel on dolphins (Bejder and Samuels 2003). Habituation to the research vessel (Mann 1999, 2000), combined with slow and steady vessel driving parallel to dolphin group movement (Würsig and Jefferson 1990), has been found to reduce effects of the researcher on dolphin group behaviour (Lusseau 2006a), but it is often difficult to obtain unbiased data on the level of habituation to the research vessel from the vessel itself. In an examination of responses by dolphins to vessels from a concurrent study conducted by a research team on shore, the research vessel was the only vessel type for which no significant changes in behaviour were found (Lundquist and Markowitz 2009). This suggests that the dolphins were reasonably well habituated to the research vessel when compared with tour vessels or recreational vessel traffic; however, there is no question that the dolphins were aware of the research vessel's presence.

Defining Groups and Subgroups

Dolphin groups were defined using the "10-m chain rule" that relies on spatial proximity of individuals (Smolker et al. 1992). Dolphins were considered part of a group if they were within 10 m of a nearest neighbour. This "distance measure" rather than a definition that includes a "coordinated activity" behavioural component was chosen as it does not rely upon assumptions about the behaviour of an individual to qualify it as a member of the group

(Mann 2000). Subgroups were defined as individuals <1 or 1-3 body lengths apart from each other and >3 body lengths from other dolphins in the group, moving in a coordinated fashion and surfacing synchronously.

Focal Group Behavioural Sampling and Tracking

Upon encounter of a dolphin group, data collected include group size, direction, behavioural state, group composition, and tour or recreational vessel presence or absence. Group size categories were recorded as <50, 50-99, 100-249, 250-500 and >500 individuals. Group age class composition was estimated by size of individuals present based on lengths of aged post-mortem specimens (Cipriano 1992), with age class categorized as: adult/subadult (> 2 years, 1.6-1.8m), juvenile (1-2 years, 1.3-1.5m), calf (< 1 year, 1-1.2m). Dolphins in groups of <50 individuals were counted and the number of juveniles, calves and adults present documented. For groups larger than 50 individuals, presence or absence of juveniles and calves was noted. After an initial group behavioural state was identified, the research vessel approached and paralleled the group at no-wake speed for photo-identification and behavioural observation (Würsig and Jefferson 1990). Groups were tracked using a Garmin GPS 60 to log latitude and longitude position each minute from a vessel driven parallel to, and matching speed with, the dolphins. Direction and speed of movement were calculated from these data (see below).

For behavioural data collection, I categorized behaviour as "states" that made up a majority of the behavioural time-budget and discrete behavioural "events". During focal group follows, predominant group activity was recorded as the behavioural state for the group (Mann 2000). These data were collected by scan sampling at 2-minute intervals for large groups and continuously for small groups throughout the observation period (Altman 1974, Martin and Bateson 1993, Lehner 1996). Group follows ended when the weather deteriorated, groups were lost from view, adequate sample duration was obtained (more than 20 min) or failing light made follows impracticable. When a ‘group split’ occurred (see definition below) the portion of the group that was closest to the research vessel was followed and designated with the original group number and ‘A’ (e.g., Group 1 becomes Group 1A). These groups were not treated as independent for analysis. Groups were treated as independent if they were encountered on different days or if they were encountered on the same day at such a distance apart that, given the time between group encounters, it was unlikely they were the same individuals.

Behavioural states (adapted from Shane 1990, Hanson and Defran 1993, Acevedo-Gutiérrez and Parker 2000) recorded were:

Resting – Dolphins stay close to the surface and each other, surfacing at regular intervals in a coordinated fashion; movement is very slow;

Milling – Non-directional weaving movements with group members oriented in varying directions; movement is moderate in speed;

Travelling – All individuals are oriented and moving in the same direction and movement is moderate to fast; this behavioural state may include group speed bursts (“slicing”) and porpoising behaviour;

Foraging – Dolphins are seen either capturing or pursuing fish. High numbers of re-entry leaps occur with rapid changes in direction and long dives.

Behavioural events were recorded using all-occurrence sampling (Lehner 1996, Mann 2000) during continuous data collection. Presence of the behaviour, number of times the behaviour was performed and number of individuals involved were recorded. As it was not always possible to view all dolphins simultaneously, particularly in large groups, a team of trained volunteers assisted by calling behaviours as they were observed. When continuous data were not being collected, intermittent and non-discrete behaviours, such as social or ‘play’ behaviours (including social rubbing, ventral presentation, intromission, spy-hops, and playing with kelp) were recorded using one-zero interval sampling (2-min intervals, Martin and Bateson 1993).

Individual behavioural events (adapted from Markowitz 2004) were recorded as:

Head/Chest slap – partial breach in which an animal clears its head or chest from the surface and slaps it down creating a loud splash;

Tail slap – the tail flukes are raised above the surface and lowered with force creating a noisy splash;

Noisy leap – jump in which the dolphin clears the surface and lands with its entire body on the surface creating a loud splash;

Re-entry leap – jump in which the dolphin re-enters the water head first in a clean, quiet manner;

Acrobatic Leap – jump in which the dolphin clears the surface, flips head to tail, and re-enters the water with a splash;

Wiggle – quick vibratory movement of the body with ripples that can be seen on the surface;

Synchronous surfacing – two or more individuals surface together simultaneously and in close proximity (<1 body length apart);

Speed burst (‘slice’) – rapid surfacing of individual with dorsal fin creating white-water splash;

Group speed burst – rapid surfacing of a majority of group members that is usually directional and occurring at the onset of travelling behaviour;

Chase conspecific – one dolphin rapidly pursuing another dolphin with many changes in direction;

Bow-ride – one or more dolphins riding on the bow of the research or tour vessel;

Fish toss – tossing of fish using head, pectoral flipper or fluke where fish is thrown clear of the surface;

Blow bubbles – the animal releases a large volume of air through its blowhole while submerged in one short burst;

Chuff – a brief, noisy, forceful exhalation;

Play with kelp – carrying seaweed in mouth or on dorsal fin or other body parts

Spyhop or Eye-out – a brief vertical surfacing of the head with the eye and rostrum clearly above the surface of the water

Inverted swimming – swimming with belly to the surface usually during a sexual pursuit of a conspecific that is at or near the surface;

Ventral presentation – rolling ventral surface toward conspecific such that white ventral surface 'flashes' usually in a quick motion before rolling back;

Contact ('social') rub – defined as any touching of the body (Connor *et al.* 2000) and includes biting, pectoral touch, body touch, or rolling together at the surface.

Ventral contact – swimming belly to belly in which intromission may or may not be seen;

Sexual approach – approaching another dolphin with the penis out usually while inverted swimming;

Confirmed intromission – confirmed observation of sexual approach with ventral contact and intromission of conspecific;

Nursing (rostro-genital contact) – confirmed observation of calf rostrum touching ventral surface of adult in area of mammary slits, with position held.

Like spinner dolphins (*Stenella longirostris*; Norris et al. 1994), dusky dolphins are, arguably, always social, although their social group sizes and interactions may change in different environments (Würsig et al. 1989). They perform behaviours usually described as 'social' for dolphins when they are foraging, resting, milling and travelling. Instead of describing a "social" behavioural state (which is common for dolphin behavioural studies), the amount and quality of social interactions (as behavioural events) were documented in real time during the behavioural states described above. In particular, dusky dolphins are prolific leapers. Leaping behaviour has been used in other studies to describe a 'social' behavioural state (e.g., bottlenose dolphins, *Tursiops truncatus*, Shane 1990). Describing detailed social behaviour as events rather than a social 'state' allowed for the dolphins' behaviour to be characterised as both ‘resting’ (state) and ‘social’ (events), which was particularly common for small groups with calves (i.e., nursery groups, see Chapter 3).

Group behavioural events recorded included:

Group split – One or more group members move more than 10 m away from any individual in the group, maintain distance for at least 2 min, and appear to be leaving area;

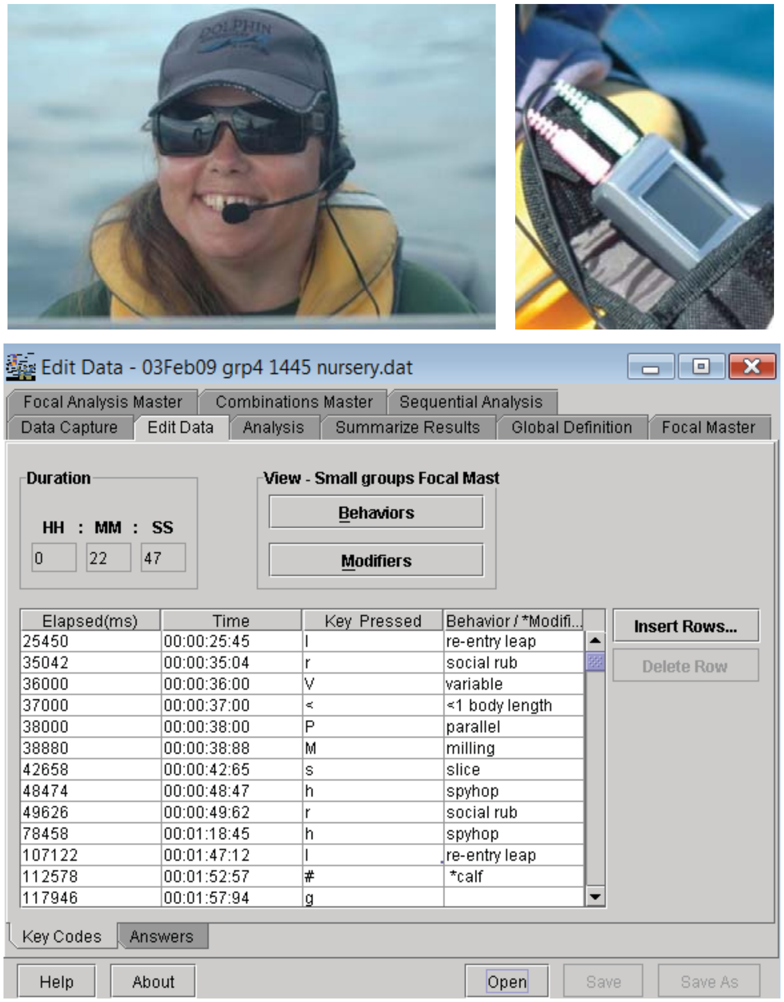
Group join – One or more dolphins is observed approaching the focal group from a distance of more than 10 m, merges with group members such that all members are within 10 m of each other and maintains this association for at least 2 minutes;

Birds feeding with dolphins – Seabirds are associated with the dolphin group flying above the group and diving into the water amongst group members.

Group dispersion and formation were recorded as individuals <1, 1-3 or >3 body lengths apart, with formation recorded as circular (equally spread from side to side and head to tail), linear (spread further from head to tail than side to side), echelon (triangular or ‘v’ formation with relatively few leaders and followers fanned out behind), or parallel (spread further from side to side than head to tail, Weaver 1987, Markowitz 2004). Small dolphin groups cycled rapidly between parallel and echelon formation and differentiating between the two was problematic during continuous sampling. Parallel and echelon formations were combined to form a single parallel/echelon category for behavioural scoring. Group size and number and size of subgroups were recorded continuously. Data were resampled in 2-min intervals for consistency with other studies (Pearson 2009).

Interval versus Continuous Sampling

During interval sampling (large group focal follows), a stop-watch with a timer was used to keep track of intervals, and data were recorded by 2-minute time block on a standardised data sheet. During continuous sampling (March 2008-February 2009), behavioural data were recorded continuously using an Olympus VN-2100PC digital voice recorder with noise reducing headset (Figure 2.2).



Duration

HH : MM : SS

0 : 22 : 47

Elapsed(ms)	Time	Key Pressed	Behavior / *Modifi...
25450	00:00:25:45	l	re-entry leap
35042	00:00:35:04	r	social rub
36000	00:00:36:00	V	variable
37000	00:00:37:00	<	<1 body length
38000	00:00:38:00	P	parallel
38880	00:00:38:88	M	milling
42658	00:00:42:65	s	slice
48474	00:00:48:47	h	spyhop
49626	00:00:49:62	r	social rub
78458	00:01:18:45	h	spyhop
107122	00:01:47:12	l	re-entry leap
112578	00:01:52:57	#	*calf
117946	00:01:57:94	g	

Figure 2.2. Continuous behavioural sampling of focal dolphin groups was accomplished with a digital voice recorder with noise reducing headset (top). Following data collection, digital recordings were reviewed and transcribed with JWatcher V1.0 (bottom).

Using this method, I documented behavioural state, group dispersion, heading and number of individuals associated with the research vessel (bow-riding) whenever these parameters changed. Behavioural events were documented in real time. For small groups, digital audio recordings were transcribed into JWatcher V1.0 (Blumstein et al. 2006) for detailed analysis of behaviour (Figure 2.2). Transcribing of audio recordings rather than direct entry into the JWatcher program in the field allowed for hands free observation of behaviour without having to look away from the subjects, the ability to review data collected as many times as necessary to obtain accurate input, and correction of any misentered keystrokes.

Data Analysis

Seasonal and Diurnal Patterns

For examination of seasonal patterns, seasons were defined as: winter = June-August, spring = September-November, summer = December-February and autumn = March-May (Markowitz 2004, after Cipriano 1992). For examination of diurnal patterns, the day was divided into “morning” = 6:00-11:29, “midday” = 11:30-13:29, and “afternoon” = 13:30-18:00.

Group Size and Composition

Mean group size and differences in group composition were compared for dusky dolphin large and small groups. Group size and age class composition were analyzed for variation with season, time of day and bathymetry. Interval data were entered into a Microsoft Access database for querying by time of day, season, and other relevant parameters. Continuous data were queried using JWatcher v1.0. Data were queried by day and group to ensure the independence of points, and subsequent statistical tests run in SPSS v.10. Data were tested for normality using the Kolmogorov-Smirnov test, and equality of variance using Levene’s statistic.

Group Locations and Movements

Group locations and tracks of group movements were estimated using longitude, latitude and time data recorded by the Garmin global positioning system (GPS) receiver from the vessel as it was positioned alongside the group. Time and location data were recorded at one-minute intervals and later downloaded to computers for analysis of focal dolphin group location, ranging, and movement patterns (e.g., surface speed). Longitude/latitude positions were imported into ArcGIS v. 10.0, and overlaid onto a shoreline base map and a bathymetric chart supplied courtesy of the National Institute of Water and Atmospheric Research, New Zealand (NIWA). All map features presented in this chapter were imported as Longitude/Latitude tables, and then projected using the WGS 84 coordinate system in ArcGIS 10.0.

To obtain more accurate estimates of distances and areas, the data frame was changed to the New Zealand national grid system NZ UTM 59S that centres on 171° East Longitude and all data layers exported to shape files matching this data frame. Track points and geographic reference data were uploaded and analyzed using ArcGis 10.0 for relation to bathymetry and distance from shore. Locations were plotted in WGS 1984 datum and re-projected to local Universal Transverse Mercator (UTM). Standard deviation ellipses (based on 1 SD) were calculated in ArcGIS v.10 to examine the geographic distribution of group encounters by season, time of day and group type.

To obtain estimates of water depth, data layer shape files (points) were joined by spatial proximity to the bathymetric shape file, such that each point was assigned a depth equal to the nearest isobath. Points closer to shore than to the nearest 10 m isobaths were assigned a depth value of 5m. This spatial joining analysis resulted in depth estimates for all GPS locations with depth binned as 5m (0-5m), 10m (6-14m), 20m (15-24m), 30m (25-34m), 40m (35-44m), 50m (45-54m), 60m (55-64m), 70m (65-74m), 80m (75-84m), 90m (85-94m), 100m (95-104m), 110m (105-114m), 120m (115-134m), and 150m (135-174m) , followed by 50m increments at greater depths. The resulting shape files were then joined by spatial proximity to the coastline shape file to obtain the estimated distance from shore of each location. All statistical analyses for significant differences between groups in behaviour, habitat use and grouping patterns with season and time of day were conducted using SPSS v. 10.

Leg speed (km/h) was calculated by dividing the distance between locations by the time between location records. A maximum swim speed filter of 24 km/h (13 knots, equal to the highest sustained speed of dolphin groups documented in previous field observations, Markowitz 2004) was applied to remove any inaccuracies due to oversampling. Reorientation rate (degrees per minute) was calculated by dividing the change in bearing by time between successive records (1 min apart) of dolphin group position.

Behaviour

Behaviour was analysed for variation with season, time of day and group size. Statistical analyses were conducted on values from samples of independent group encounters using SPSS v. 10.0. Data were tested for normality using the Kolgomorov-Smirnov test and heterogeneity of variance using Levene’s statistic, and compared across groups using appropriate parametric and non-parametric statistical analyses (Kruskal Wallis and ANOVA tests for season and time of day). The critical alpha value for all statistical tests in this dissertation was 5%.

RESULTS

Seasonal Patterns

Seasonal Habitat Use

Dusky dolphins were found in the study area in all seasons (Figure 2.3, 2.4). Large groups that were encountered varied in distribution of location by season, with groups found closest to shore during the summer. Distance from shore increased by season, with groups ranging further from shore in autumn. During winter large groups appeared to range furthest from shore and further south of the Kaikoura Canyon (Figure 2.3a).

Small groups of dusky dolphins were found throughout the Kaikoura Canyon area and to the north and south of the canyon in all seasons except summer (Figure 2.4). As with large groups, small groups were furthest from shore and north and south of the Kaikoura Canyon during winter and early spring (Figure 2.4 a, d).

Examination of areas used by dolphin groups in different seasons (standard deviation ellipses) showed similar patterns for large and small groups, with dolphins encountered in the narrowest range near shore in summer from Goose Bay to the Haumuri Bluffs, moving into deeper water over the Kaikoura Canyon in autumn, shifting offshore across a broader range in winter, and moving south in the spring (Figure 2.5). Small groups generally showed a smaller range than large groups.

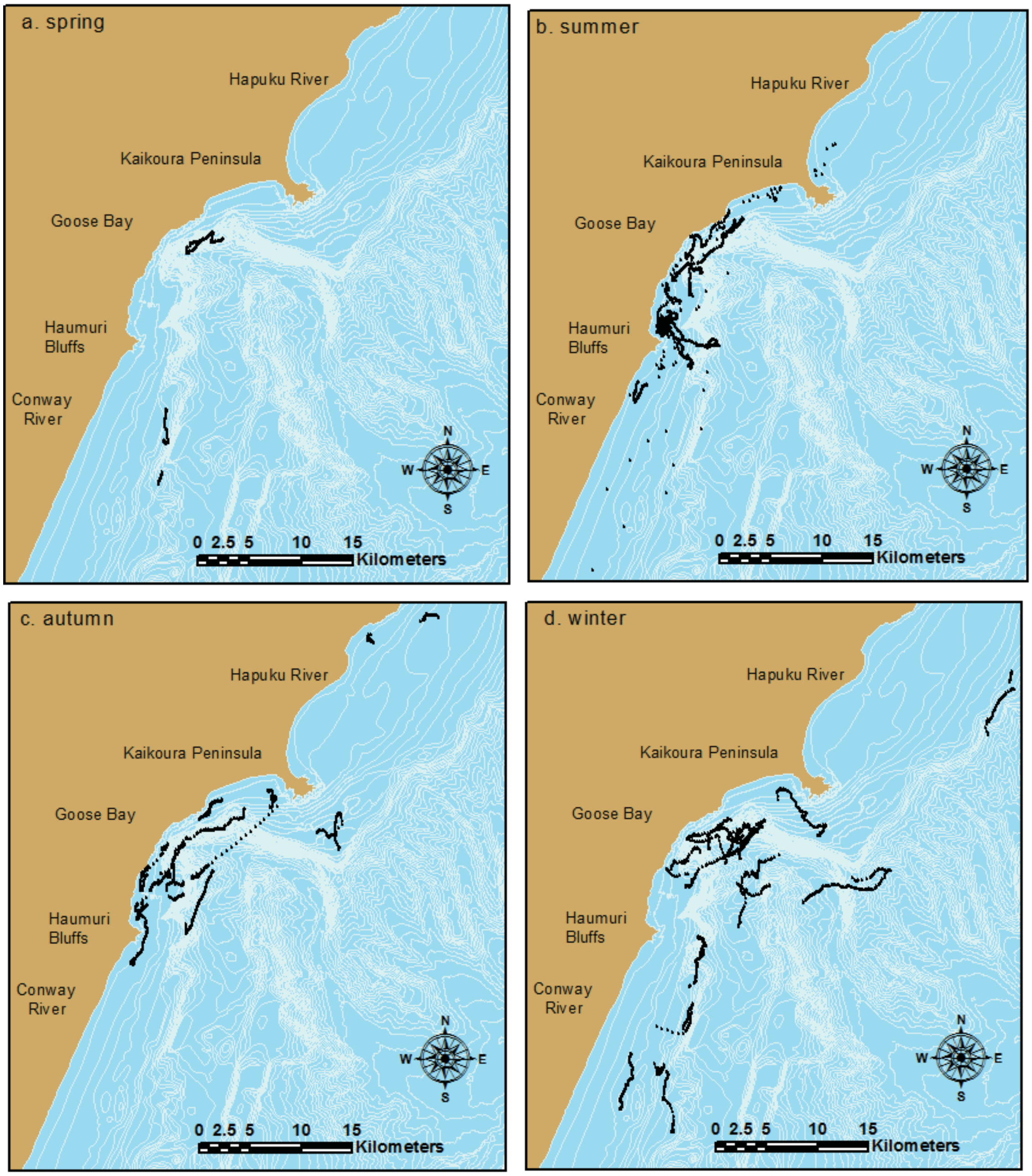


Figure 2.3 The distribution of large dusky dolphin groups encountered by season (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups). GPS tracks are shown with location collected in 1-min intervals. White lines represent isobaths at 50m intervals (bathymetric data courtesy of NIWA).

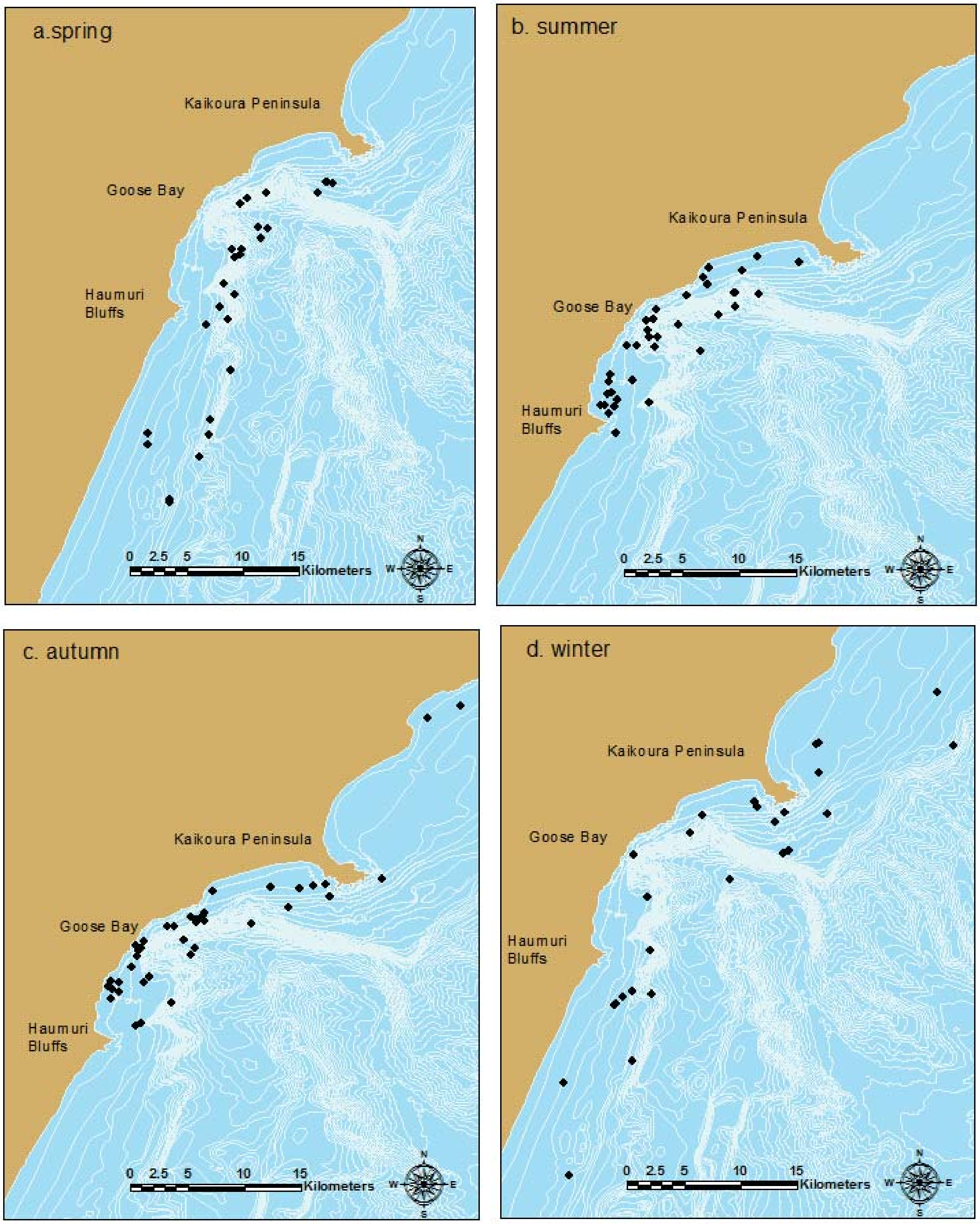


Figure 2.4 . Encounter locations for small dusky dolphin groups at Kaikoura by season (spring = September -November, summer = December -February, autumn = March -May, winter = June –August; n=30 spring, n=40 summer, n=44 autumn, and n=26 winter small groups).

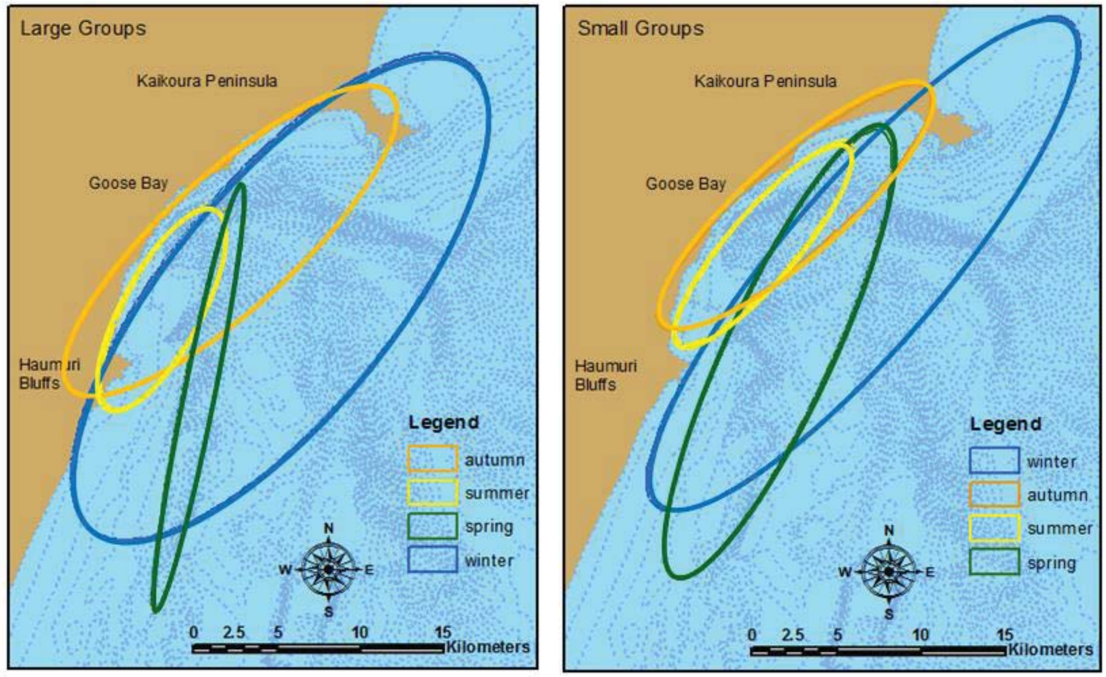


Figure 2.5. Areas where dusky dolphin groups were encountered are compared by group size (a. large groups ≥ 50 dolphins, b. small groups <50 dolphins) and by season (spring = September → November, summer = December → February, autumn = March → May, winter = June → August). Ovals show standard deviation ellipses based on GPS data (1 standard deviation). Data presented include n=30 spring, n=40 summer, n=44 autumn, and n=26 winter small groups, and n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups.

Large group distance from shore varied significantly by season (Kruskal Wallis, H=17.837, *p*<0.001). Large groups were closest to shore in summer and autumn (1-2 km), and tracked 4-6 km offshore in winter and spring (Figure 2.6). Estimated mean water depth based on dolphin group locations varied significantly between seasons (Kruskal Wallis, H=17.931, *p*<0.001), with dolphin groups typically found in water depths of 250-400m in winter and spring *versus* <200m in summer and autumn (Figure 2.6).

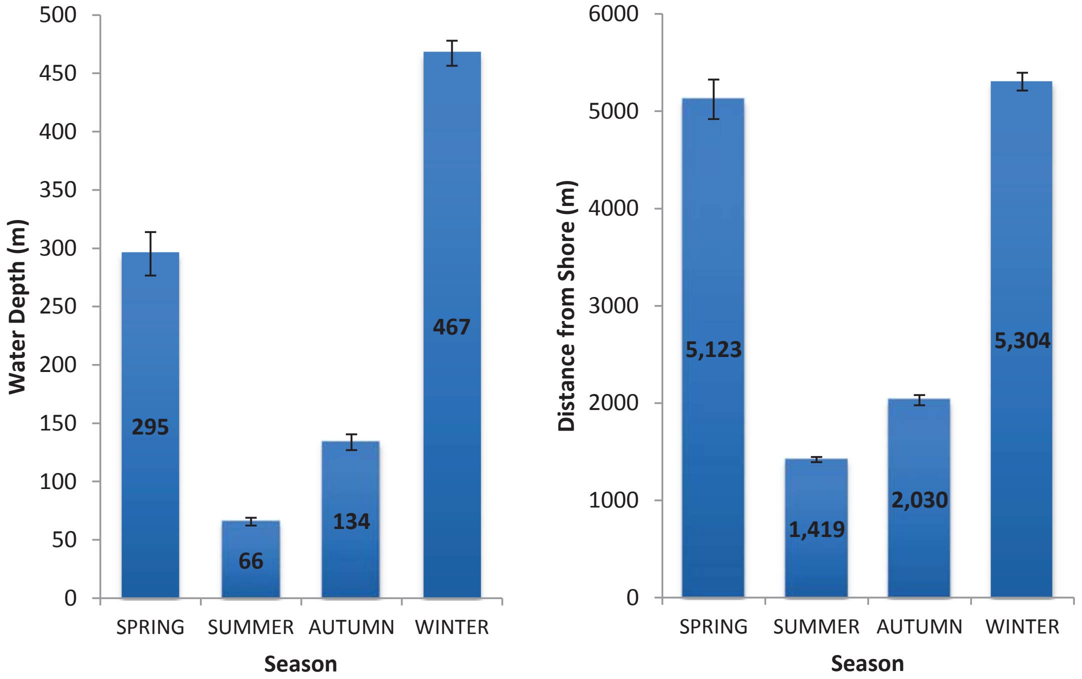


Figure 2.6. Distance from shore and water depth, estimated by GPS Longitude-Latitude position of dolphin groups, is compared by season for large groups. Bars represent mean values with standard error (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

Water depth and distance from shore (Figure 2.7) of small dusky dolphin groups varied significantly by season (Kruskal Wallis, depth: H= 28.654, P<0.001, distance H=55.709, P<0.001). While small groups of dolphins were found furthest from shore in spring and winter (Figure 2.7), the tendency to wander further alongshore outside the Kaikoura Canyon during these months caused them to enter shallower water (Figure 2.7, see GIS Figure 2.4). Large groups were generally found further offshore and in deeper water than small groups, but these differences were most pronounced in winter and spring, with little difference in summer (Figures 2.6, 2.7). In summer, dolphin groups encountered during line transect surveys from the Haumuri Bluffs to the Waiau River were further from shore in deeper water than dolphin groups encountered in the primary study area north of the Haumuri Bluffs (Figure 2.8).

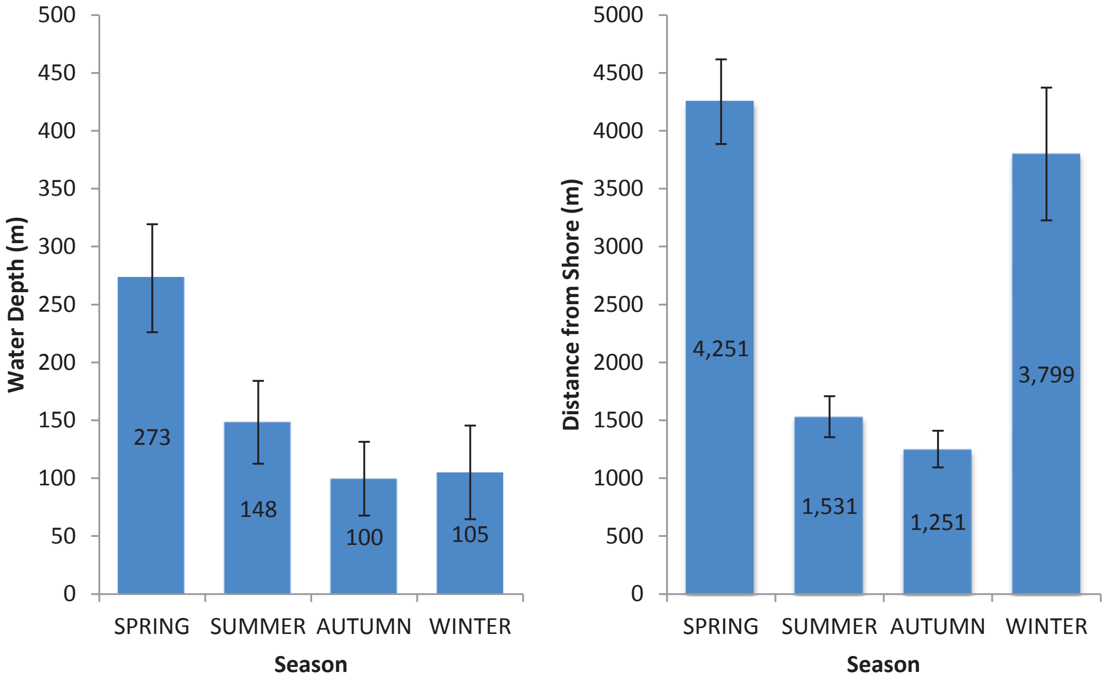


Figure 2.7. The water depth (left) and distance from shore (right) at which small groups of dusky dolphins (<50 dolphins) were encountered are compared by season. Bars represent mean depths and distances in meters with standard errors (n=30 spring, n=40 summer, n=44 autumn, and n=26 winter small groups).

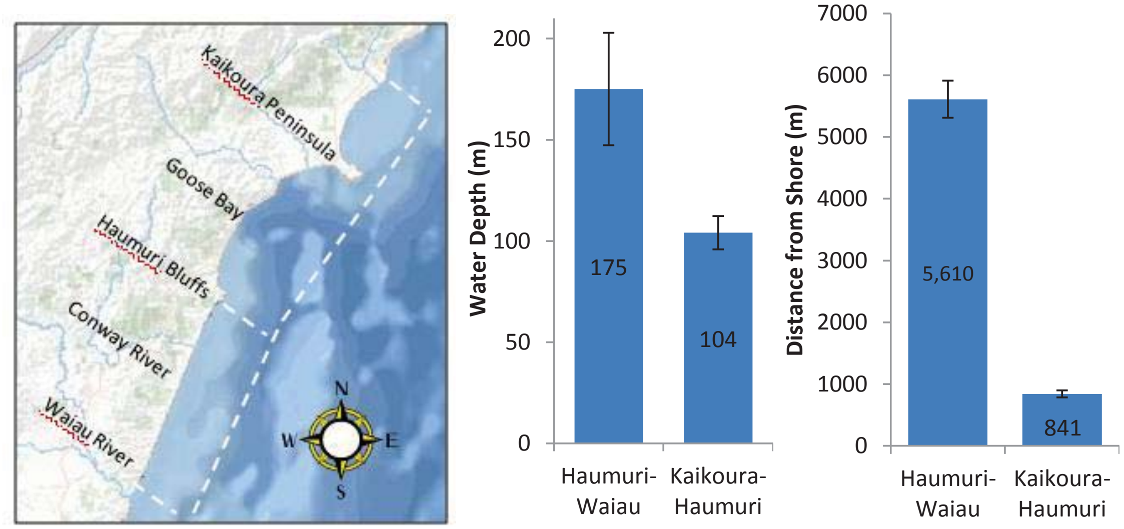


Figure 2.8. The estimated water depth (middle) and distance from shore (right) at which dusky dolphin groups were encountered during summer is compared for two areas (left): south of the Haumuri Bluffs (to the Waiau River, n=64) and areas north of the Haumuri Bluffs (n=97).

Estimated mean speed of movement for large groups varied significantly by season (Kruskal Wallis, H= 15.435, *p*=0.001), with the highest speed in winter (Figure 2.9). Reorientation rate for large groups did not vary significantly between seasons (Kruskal Wallis, H= 4.412, *ns*).

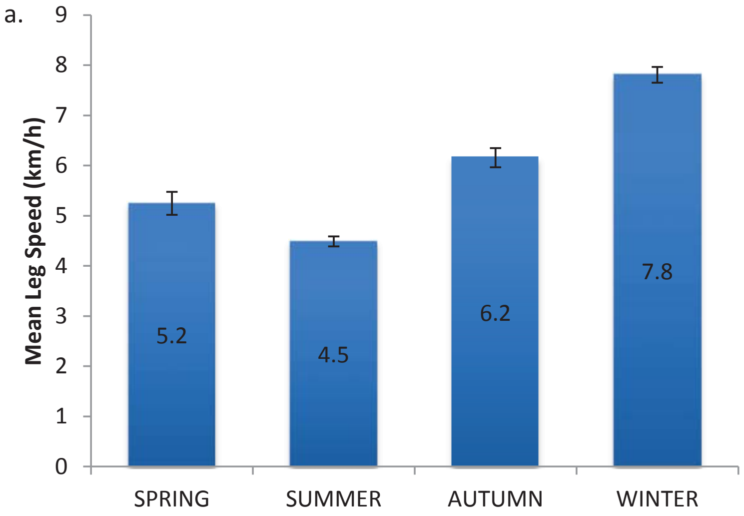


Figure 2.9. Mean leg speed of large dolphin group movements (calculated by dividing the distance between successive position fixes by the inter-fix interval) is compared by season. Bars represent mean values with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

Seasonal Behavioural Patterns

Behavioural State

Durations of behavioural states were examined for small groups of dusky dolphins. Mean duration for behavioural states including behaviour, dispersion, formation and direction were greater than the 2-min interval sampling protocol that was used for behavioural data collection. In particular, the mean duration for behavioural state was more than 4 min. These data support the 2-minute interval as adequate for capturing changes in behavioural state of dusky dolphin groups (Figure 2.10).

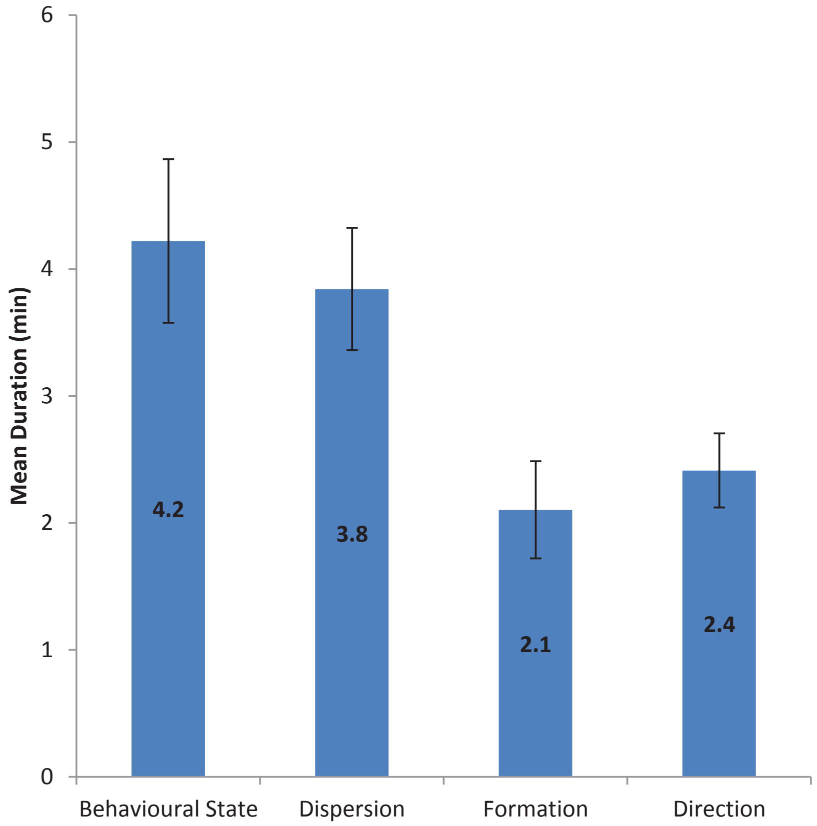


Figure 2.10. Mean durations of all behavioural states, dispersion, formations and directional headings were calculated for dusky dolphin small groups from continuous data (n=56 groups).

Seasonal variation in behaviour was exhibited by both large and small groups of dusky dolphins (Figures 2.11 and 2.12). There were significant seasonal differences for travelling (Kruskal Wallis, H=10.106, $p<0.05$) and milling (Kruskal Wallis, H=12.492, $p<0.01$) in large groups, with dolphins travelling most in winter and milling most in summer and autumn (Figure 2.11). Daytime foraging was rarely observed in either large or small groups (<1% of time observed).

Small group behavioural state duration varied significantly by season (Figure 2.12a). Dolphins rested for longer durations in winter (Kruskal Wallis, H=12.689, $p<0.01$) and milled for longer durations in summer (Kruskal Wallis, H=9.271, $p<0.05$). The proportion of time spent milling, resting and travelling varied by season for dusky dolphin small groups (Figure 2.12b). Dolphins rested more in spring and winter (Kruskal Wallis, H=14.024, $p<0.01$) and milled more in summer and autumn (Kruskal Wallis, H=14.906, $p<0.01$). Unlike large groups, small groups of dusky dolphins spent short durations (a few minutes) and a very small proportion of time travelling (<10%) in all seasons, including winter. In comparison, travelling for large groups in winter occurred 57% of the time.

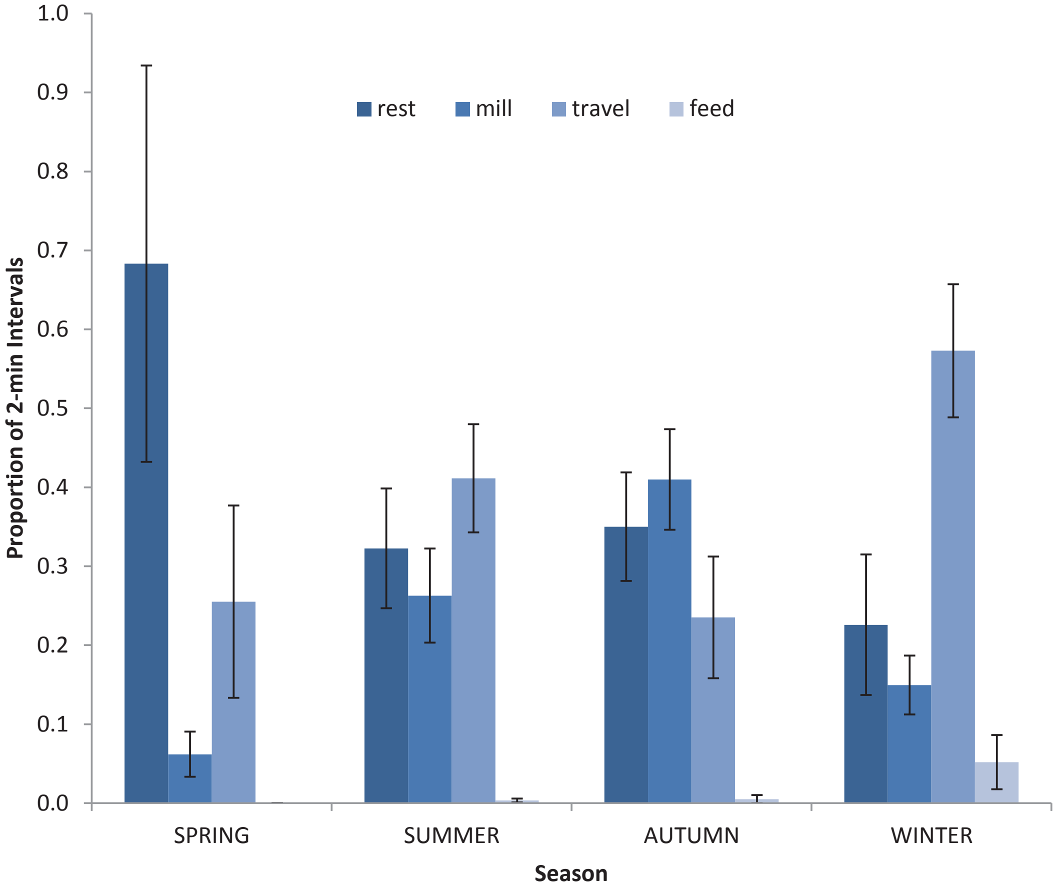


Figure 2.11. Proportion of 2-minute scan samples of large dusky dolphin groups (>50 dolphins) were observed in each behavioural state and compared by season. Bars represent mean values with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

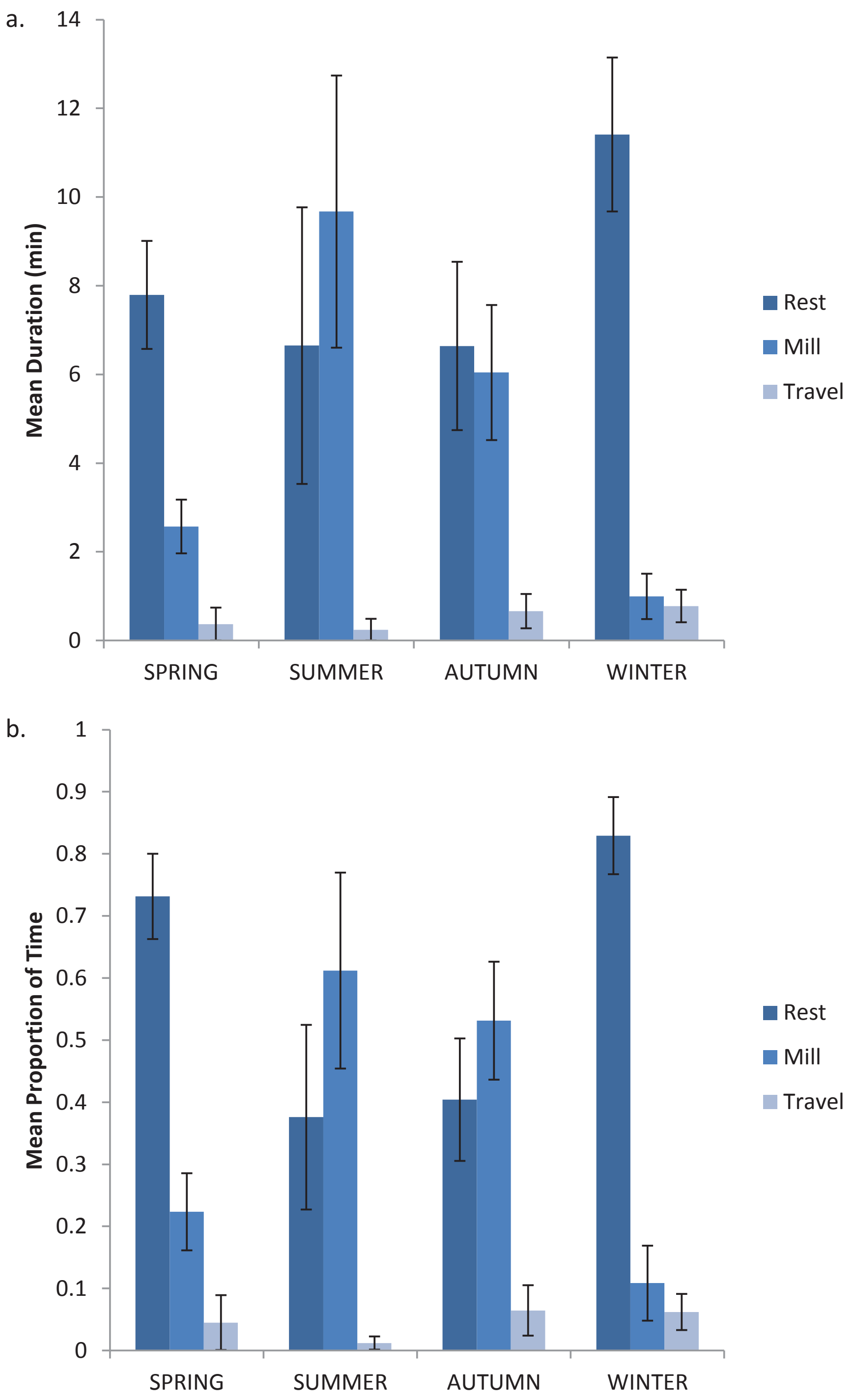


Figure 2.12. Duration (a) of behavioural states and proportion of time (b) spent in each behavioural state are examined by season for small groups. Y-error bars represent standard error of the mean (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups). Foraging was not included in the figures as it occurred rarely for dusky dolphin small groups off Kaikoura.

Inter-individual Distance (Dispersion)
Dispersion (mode inter-individual distance) averaged 2.7m in large groups, ranging from a mean of 2.1-4.6m (Figure 2.13). Dispersion did not vary significantly in large groups by season (Kruskal Wallis H=2.215, *ns*).

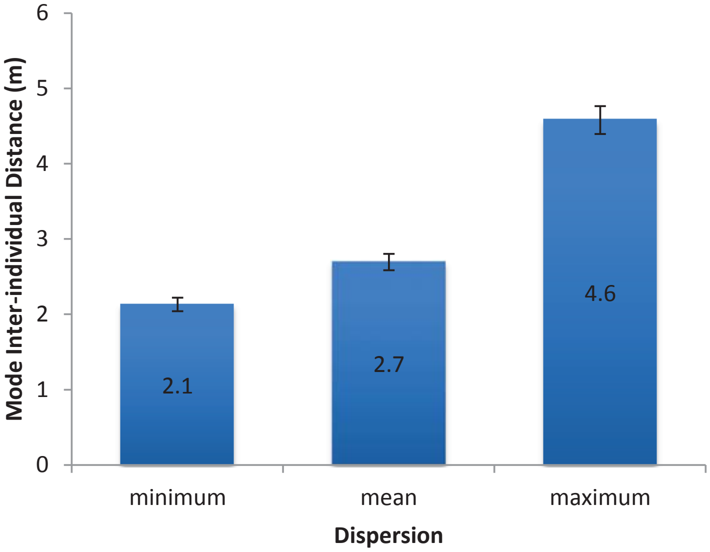


Figure 2.13. Estimated minimum, mean and maximum dispersion (mode inter-individual distance in meters) in large groups. Bars represent mean values with standard error (n=111 large groups).

Duration at varying dispersions was compared seasonally for dusky dolphin small groups (Figure 2.14a). Dusky dolphins in small groups spent longer durations 1-3 body lengths apart in winter than other seasons and were more tightly grouped for longer durations in summer (Kruskal Wallis, H=10.040, *p*<0.05). When proportion of time spent at varying dispersions was compared seasonally for dusky dolphin small groups, there were no significant differences among seasons (Kruskal Wallis, *ns*). Overall, small groups of dolphins were more tightly grouped than large groups, spending most of their time within a single body length (1.7m) of other group members.

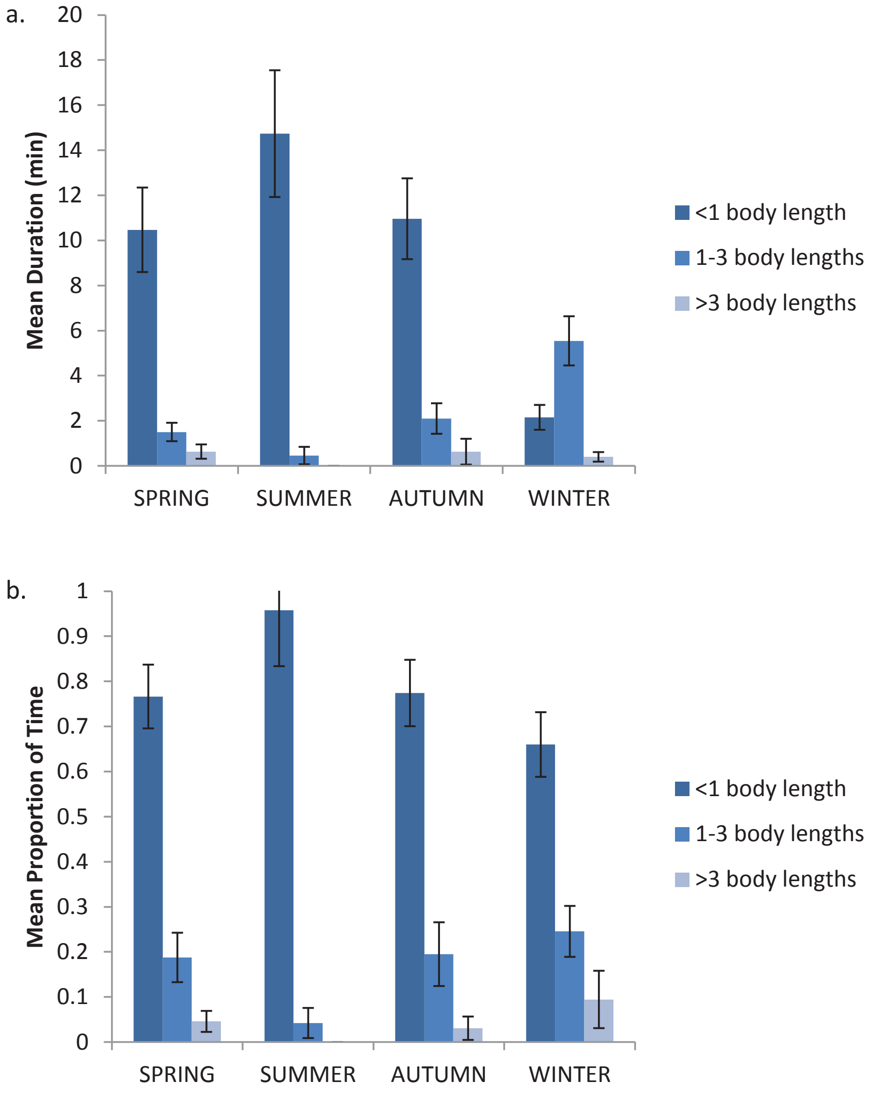


Figure 2.14 Duration (a) and proportion of time (b) at varying dispersions are compared seasonally for dusky dolphin small groups. Y-error bars represent standard deviation of the mean ((n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Swimming Formation

Swimming formation varied by season in large groups. The proportion of scan samples at which dolphins swam in no formation (H =23.602, P<0.001), parallel (H=13.138, P=0.004), and echelon formation (H=17.334, P=0.001) showed significant seasonal changes (Kruskal Wallis tests). Dolphins in large groups were most likely to swim in a formation during the summer, and that formation was more often parallel in summer than in other seasons (Figure 2.15). Large dolphin groups were more likely to swim out of formation in winter and spring, and echelon formation was most common in winter (Figure 2.15). Linear and circular formations did not vary significantly in large groups by season (Kruskal Wallis tests, *ns*).

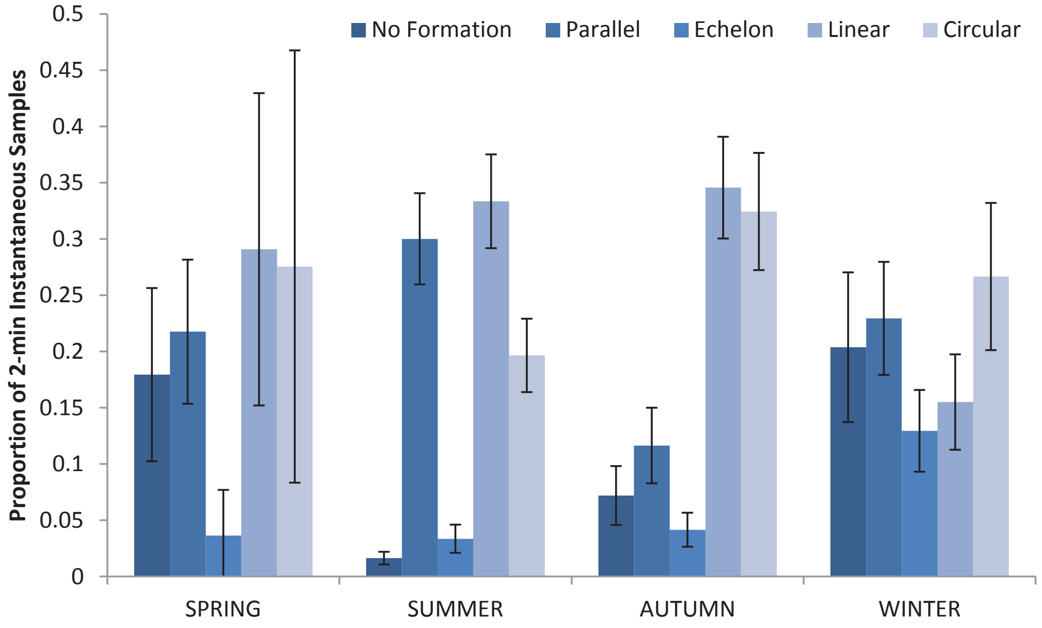


Figure 2.15. The proportion of 2-minute scan samples with large dusky dolphin groups (>50 dolphins) observed swimming in formation are compared by season. Bars represent mean values with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

Mean duration and proportion of time spent in swimming formations varied seasonally in small dusky dolphin groups (Figure 2.16). Dolphins in small groups spent longer durations with no formation in summer, and the shortest durations with no formation in winter and early spring (Figure 2.16a, Kruskal Wallis, H=9.987, *p*<0.05). Dolphins spent more time in parallel/echelon formation in the autumn (Kruskal Wallis, H=15.581, *p*<0.01) and most time in linear formation in the spring (Kruskal Wallis, H=13.244, *p*<0.01, Figure 2.16b).

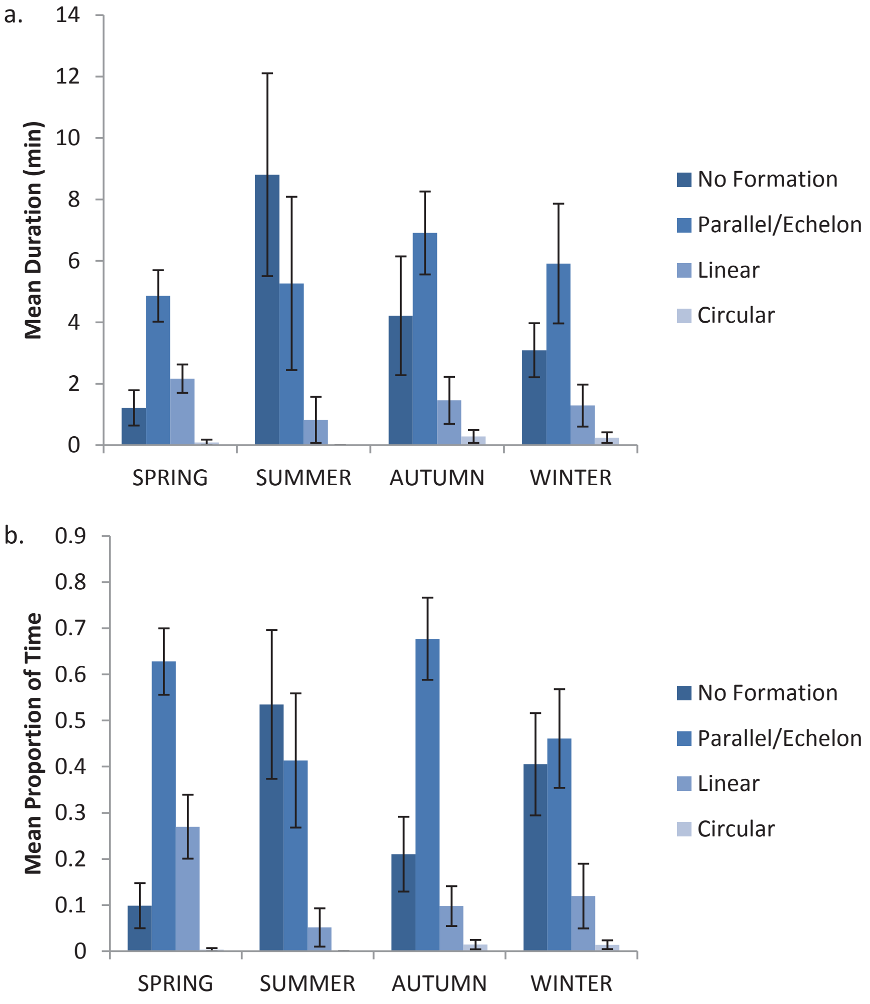


Figure 2.16. Mean duration (a) and proportion of time (b) spent in varying group formations are compared for dusky dolphin small groups by season. Y-error bars represent standard error of the mean (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Direction of Movement

Dolphins in small groups spent significantly longer durations moving in variable directions in summer and were most directional in their movements in winter (Figure 2.17a, Kruskal Wallis, H=7.947, $p<0.05$). Longer durations of directional movement by small groups of dolphins in the winter were primarily to the north (Figure 2.17b, Kruskal Wallis, H=7.947, $p<0.01$). Dolphins spent a greater proportion of their time in directional movement in the winter and least time in directional movement in summer (Figure 2.17c, Kruskal Wallis, H=9.660, $p<0.05$). There were no significant differences in direction of movement for large groups by season (Kruskal Wallis tests, *ns*).

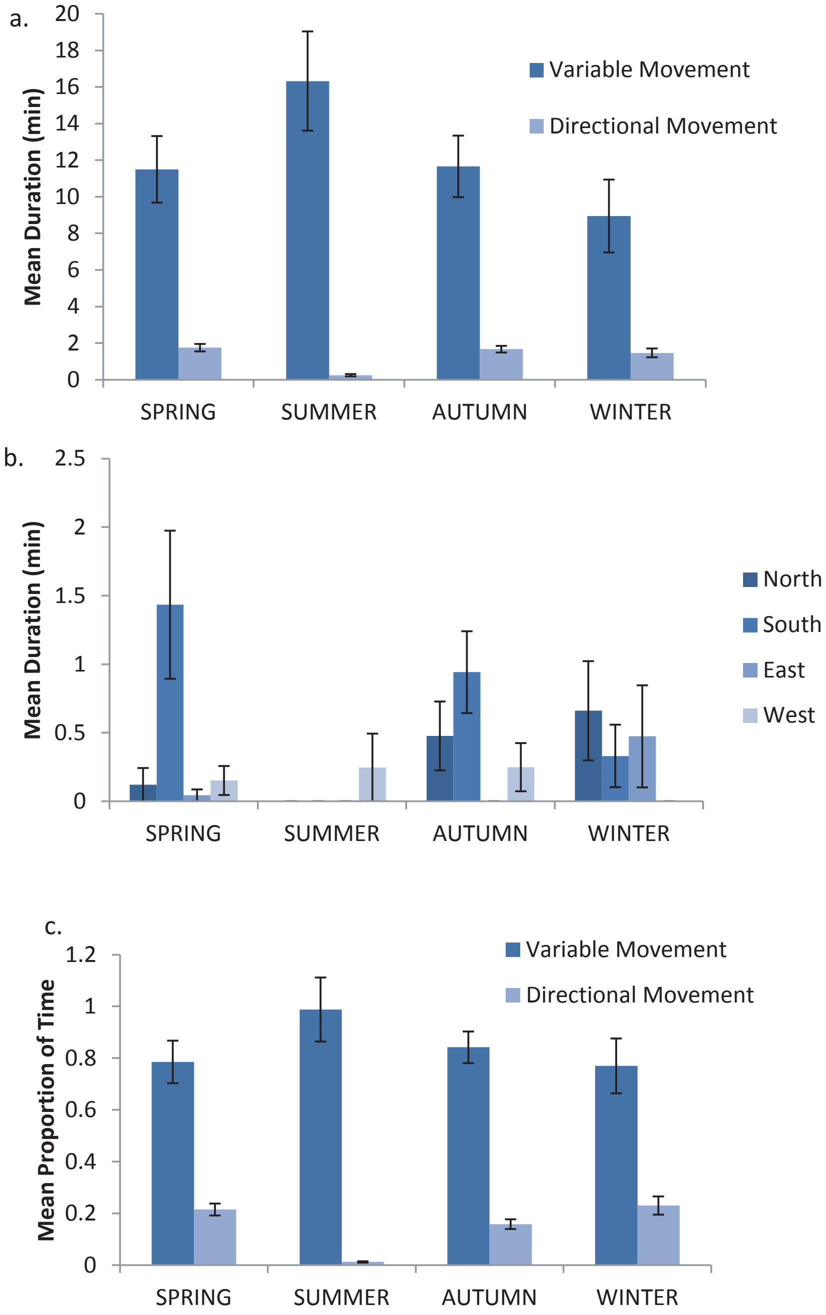


Figure 2.17. Duration (a and b) and proportion of time (c) for directional movement is compared for small groups of dolphins by season (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups). Y-error bars represent standard error of the mean.

Behavioural Events

During large group focal follows, behavioural events were scored in 2-minute intervals, using all occurrences sampling for leaping rate and one-zero sampling for high speed activities, interactive social behaviours and sexual activity. Behavioural event analysis was conducted by season for dusky dolphin small groups from continuous data. Mean number of events per individual per hour were compared for each type of behavioural event, and varied significantly by season.

High-Speed Activity

High speed activities varied significantly by season in large groups (Kruskal Wallis tests: speed burst H=30.963, P<0.001, porpoise H=17.110, P=0.001), and were more prevalent in winter than in other seasons (Figure 2.18).

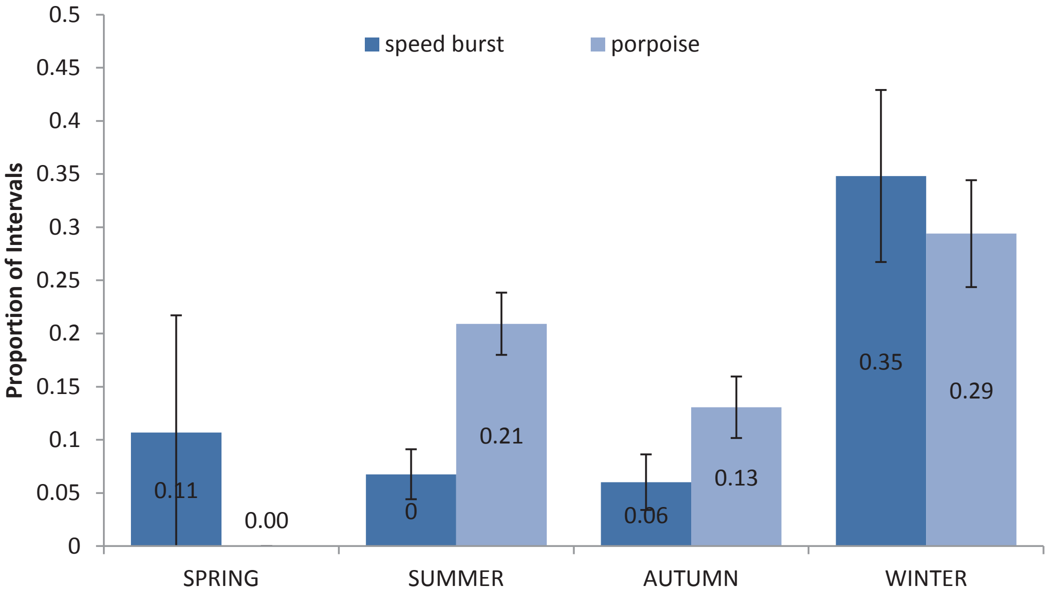


Figure 2.18. The proportion of two-minute intervals during which high-speed activities were documented in large groups (>50 dusky dolphins) is compared by season. Speed bursts indicate high-speed "slicing" through the water by the entire group. Porpoise is an outward, traveling leap. Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

High speed behaviours that significantly differed in expression by season in small groups included porpoising (Kruskal Wallis, H =14.806, *p* <0.01), speed bursts (‘slice’, Kruskal Wallis, H =17.326, *p* <0.01), and chasing conspecifics (Kruskal Wallis, H =19.327, P<0.001). High speed behaviours were most likely to occur in summer, with speed burst behaviour remaining prominent in autumn (Figure 2.19). Speed bursts were the most prolific behavioural event recorded for small groups; occurring a mean of 15.7±5.6 times per individual per hour in summer , as well as the most common event occurring in all seasons.

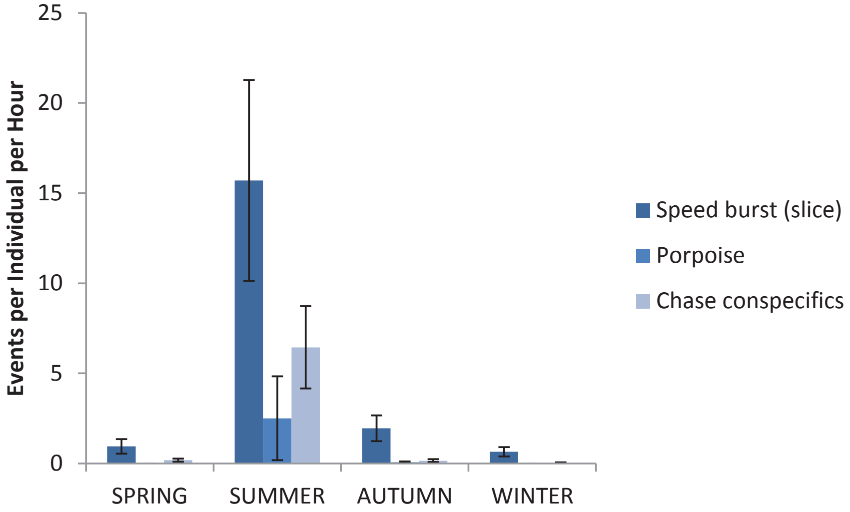


Figure 2.19. Frequency of high speed behaviours is compared by season for small groups. Bars represent mean values with standard error (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Play Behaviour

Play behaviour varied significantly by season in large groups (Kruskal Wallis tests: spyhop H=8.667, P<0.04, playing with kelp H =7.855, P<0.05), and were generally less prevalent in winter than in other seasons (Figure 2.20). Bubble blowing play did not vary significantly by season (Kruskal Wallis tests: H = 5.167, ns).

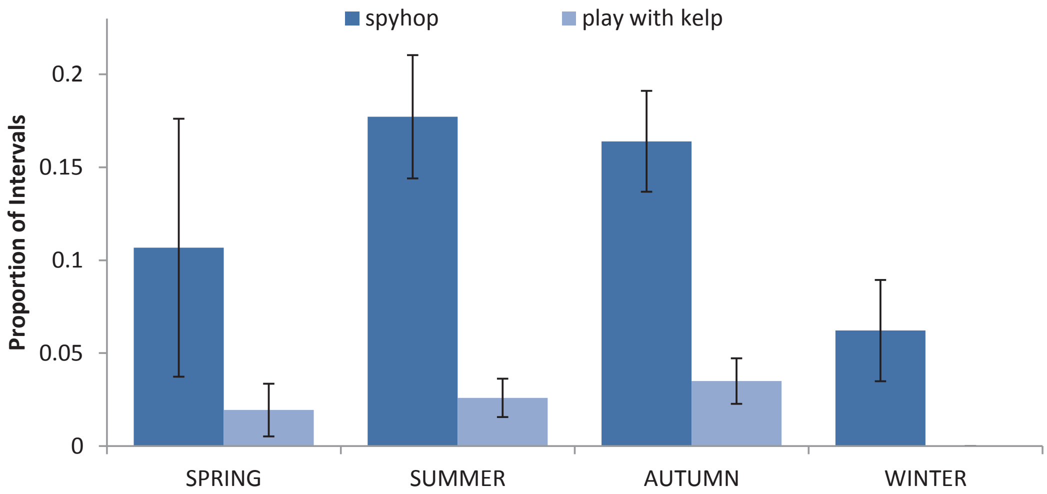


Figure 2.20. The proportion of two-minute intervals during which interactive play behaviours (spyhopping and playing with kelp) were documented in large groups (>50 dusky dolphins) is compared by season. Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

Interactive play behaviours that varied seasonally for small groups, included 'blow bubbles' (Kruskal Wallis, H =17.493, *p* <0.01), 'spyhop' (Kruskal Wallis, H =16.143, *p* =0.001), and 'play with kelp' (Kruskal Wallis, H =19.718, *p* <0.001). Play behaviours were exhibited most often by individuals during summer, with 'blow bubbles' occurring to some degree during spring and autumn (Figure 2.21). Bow-riding behaviour did not vary significantly by season in either large or small groups (Kruskal Wallis tests, *ns*).

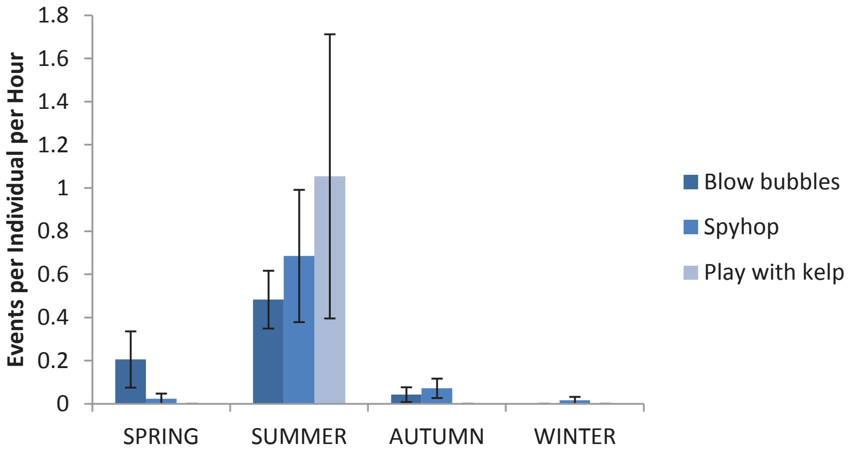


Figure 2.21 Frequency of interactive social play behaviours for small groups are compared by season. Bars represent mean values with standard error (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Social Behaviour

In large groups, social contact behaviour (social rubs) varied seasonally (Kruskal Wallis, H = 14.538, *p*=0.002), peaking in spring (Figure 2.22). The proportion of intervals during which social-sexual activity was recorded in large groups did not vary significantly by season (Kruskal Wallis tests, *ns*). However, this is likely due to the relatively rare occurrence (per unit time) of social-sexual behaviours in large groups (confirmed intromission once every 2.2 hours on average), as the total percent of groups in which social-sexual activity was documented varied seasonally, with the lowest values in all categories occurring in winter (Table 2.1).

Table 2.1. Incidence of social-sexual activity documented in large groups (>50 dolphins) is compared by season. Values represent the percentage of all large group focal follow samples (n =111) in which social-sexual behaviour was recorded.

Season	n	*Ventral Presentation*	*Sexual Approach*	*Ventral Contact*	*Confirmed Intromission*
Spring	*5*	80%	20%	60%	20%
Summer	*53*	64%	6%	36%	11%
Autumn	*33*	70%	12%	52%	21%
Winter	*20*	50%	5%	25%	10%

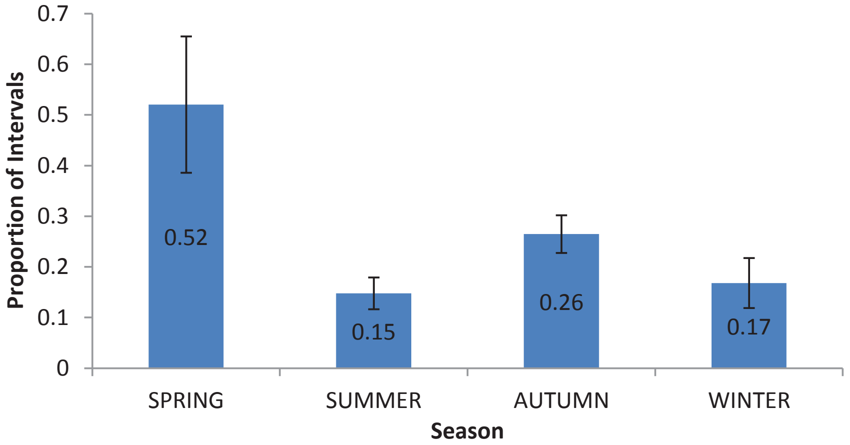


Figure 2.22. The proportion of two-minute intervals during which social contact behaviour was documented in large groups is compared by season. Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

Social behaviour varied seasonally in small groups, with social-sexual activity most prevalent in the summer (Figure 2.23). Behaviours that were significantly different by season included: ventral contact (Kruskal Wallis, H =38.870, *p* <0.001), confirmed intromission (Kruskal Wallis, H =35.416, *p* <0.001), social rub (Kruskal Wallis, H =27.753, *p* <0.001), tail slap (Kruskal Wallis, H =13.447, *p* <0.01), inverted swim (Kruskal Wallis, H =23.593, *p* <0.001), and sexual approach (Kruskal Wallis, H =19.718, *p* <0.001).

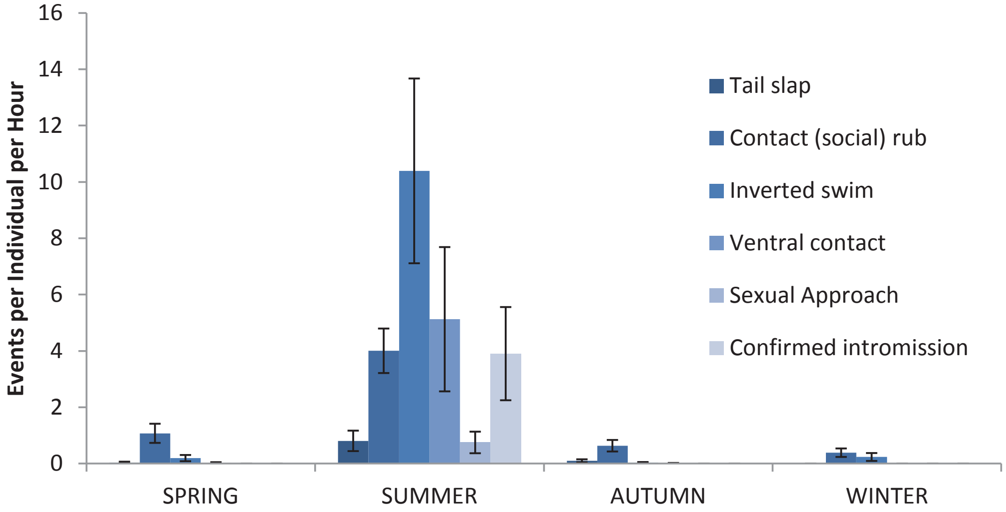


Figure 2.23 Social behavioural events are compared for dusky dolphins in small groups by season. Bars represent mean values with standard error (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Leaping Activity

Leaping activity varied by season in large and small groups. In large groups, leaping rates were compared overall per group, as it was not possible to get an accurate count of dolphins in groups of hundreds. Although group sizes were largest in winter (often estimated >1,000 dolphins), the rate of leaping within these especially large groups was not higher than in other seasons (Figure 2.24). Rather, re-entry leaps declined sharply in winter and did not peak in large groups during summer. Re-entry leaps varied by season in small groups (Kruskal Wallis, H =43.747, *p* <0.001). Re-entry leaping in small groups was primarily associated with the summer breeding season, suggesting a connection between this leap type and mating activity (Figure 2.25). Re-entry leaps occurred at a rate of 13.3±4.2 events per individual per hour, but primarily in summer.

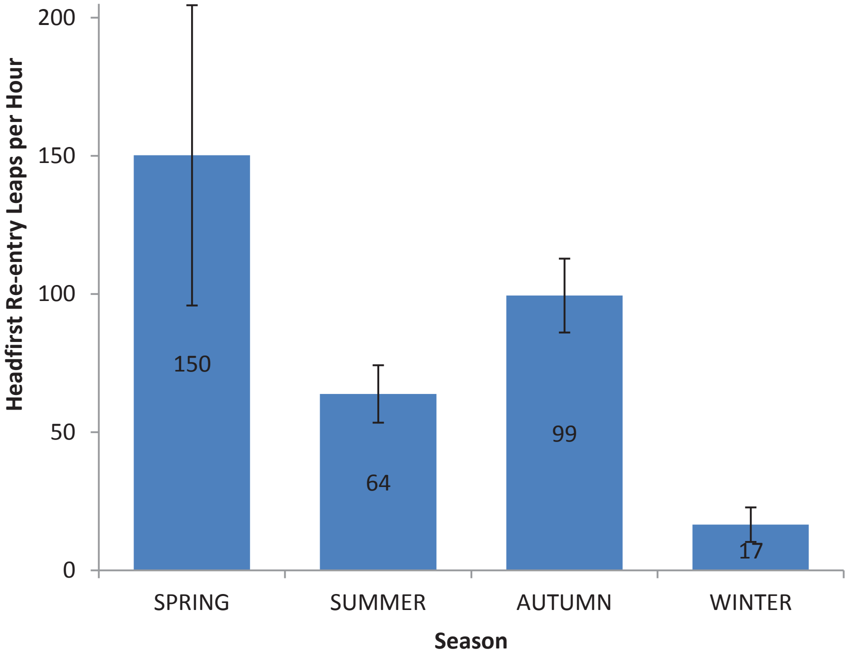


Figure 2.24. The number of clean headfirst re-entry leaps occurring in large groups is compared by season. Leaps shown are per group, not per individual (as it was impossible to count the number of individuals). Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

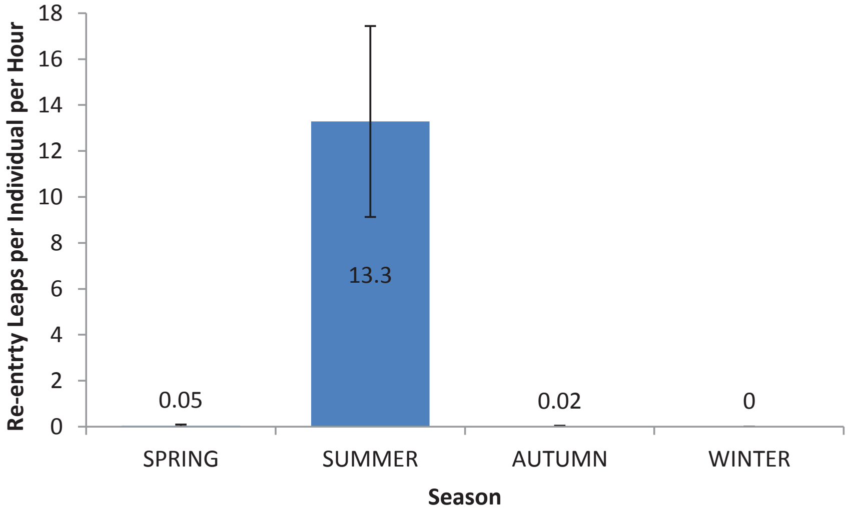


Figure 2.25. The rate of clean headfirst re-entry leaping (leaps per individual dolphin per hour) in small groups is compared by season. Bars represent means with standard errors (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

In large groups, long bouts of noisy leaps (>5) varied significantly by season (Kruskal Wallis H= 9.106, P <0.03), occurring at the lowest rate during summer (Figure 2.26). Short bouts of noisy leaps did not vary significantly by season (Kruskal Wallis H= 4.195, *ns*). The rate at which dolphins in large groups engaged in bouts of acrobatic leaps varied significantly by season (Kruskal Wallis, H=8.664, P<0.04), with the lowest leaping rate in summer (Figure 2.27). Noisy leaps varied significantly by season in small groups (Kruskal Wallis, H =17.683, *p* <0.001), but unlike large groups, leaping rate in small groups peaked in summer (Figure 2.28).

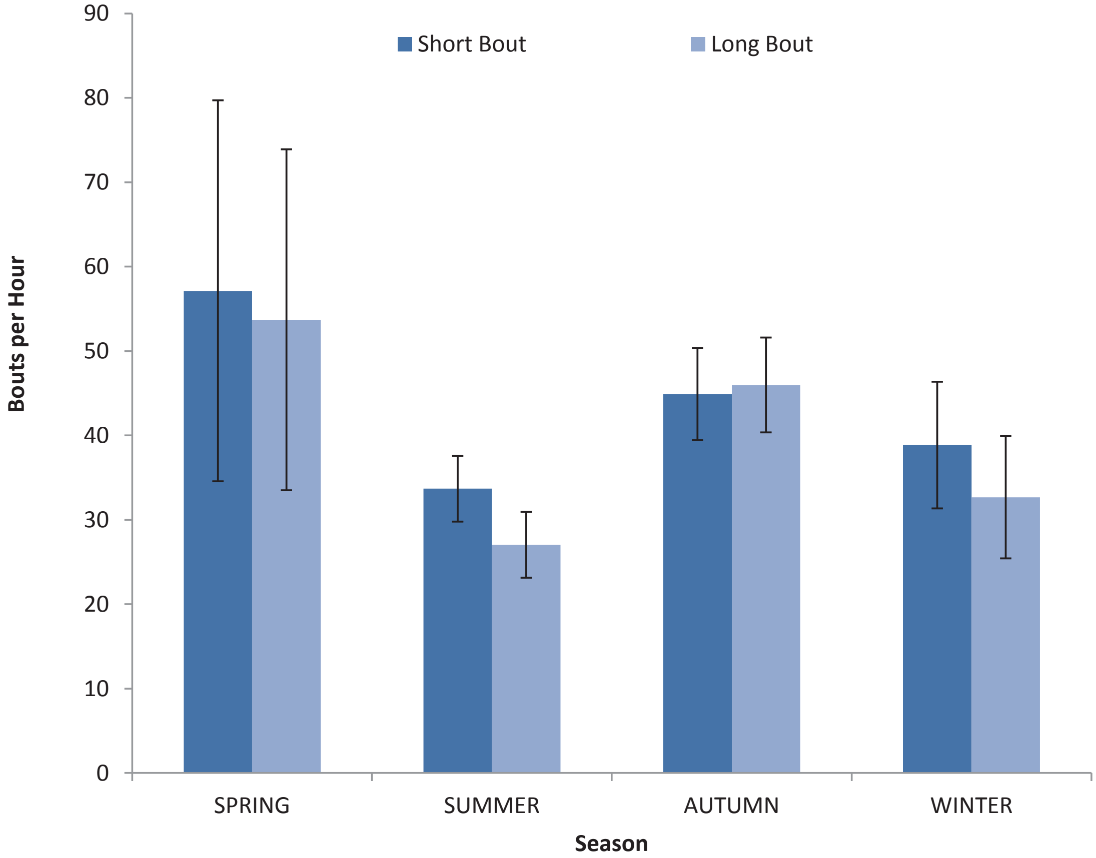


Figure 2.26. Noisy leaping rate in large groups is compared by season. Leaps are per group not per individual (as it was impossible to count the number of individuals). Bouts of noisy leaps were divided into short bouts (≤ 5 noisy leaps) and long bouts (>5 noisy leaps). Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

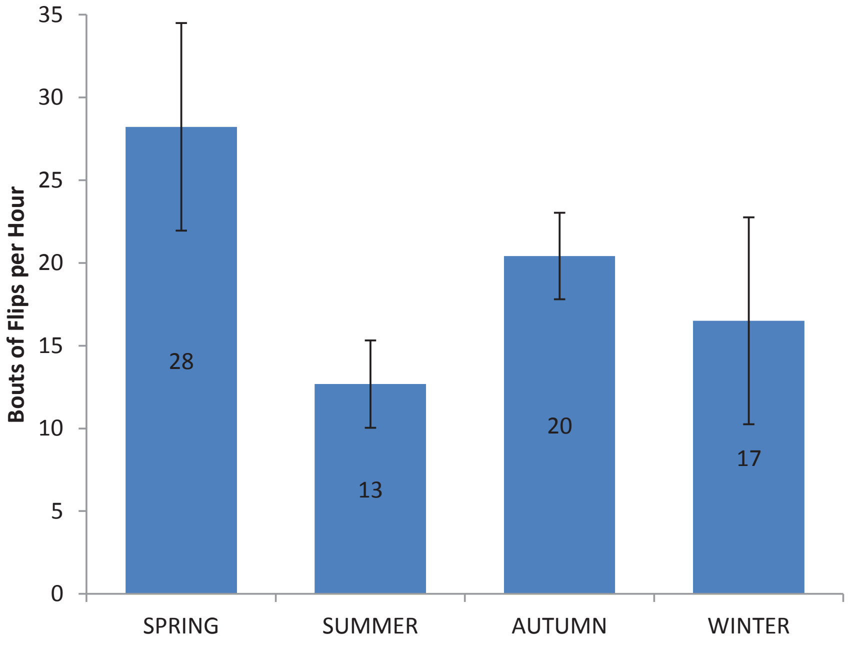


Figure 2.27. Acrobatic leaps in large groups are compared by season. Bouts of leaps shown are per group not per individual (as it was impossible to count the number of individuals). Bars represent means with standard errors (n=5 spring, n=53 summer, n=33 autumn and n=20 winter large groups).

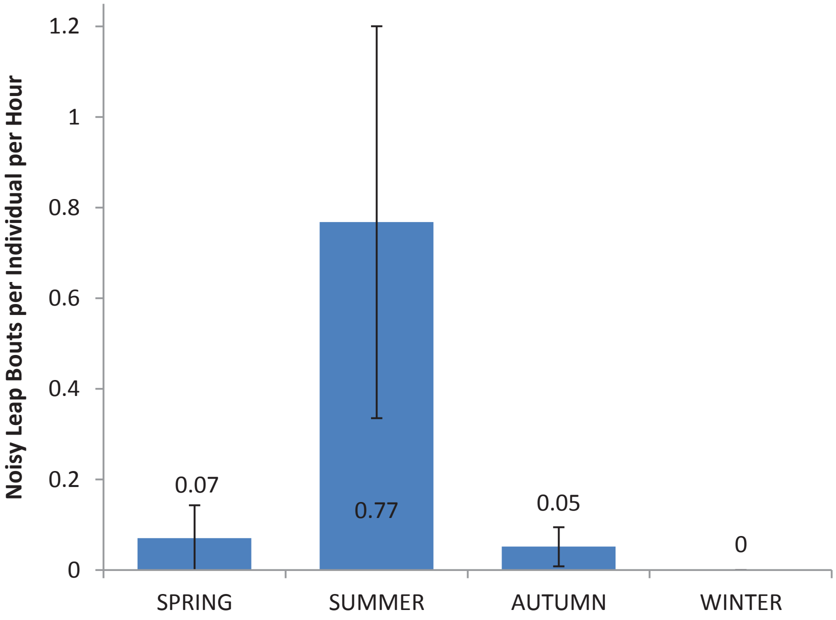


Figure 2.28. The number of bouts of noisy leaps per individual per hour in small dusky dolphin groups is compared by season. Bars represent mean values with standard errors (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Group Behavioural Events

Although there was no significant difference in group splits by season, there were more group join events in summer (Kruskal Wallis, H =13.467, *p* =0.004; Figure 2.29). There was no significant difference in birds feeding with dolphins by season, although for dusky dolphin small groups this event was only observed with any regularity in spring. There was no significant difference in dive duration by season for dusky dolphin small groups off Kaikoura (Kruskal Wallis, *ns*).

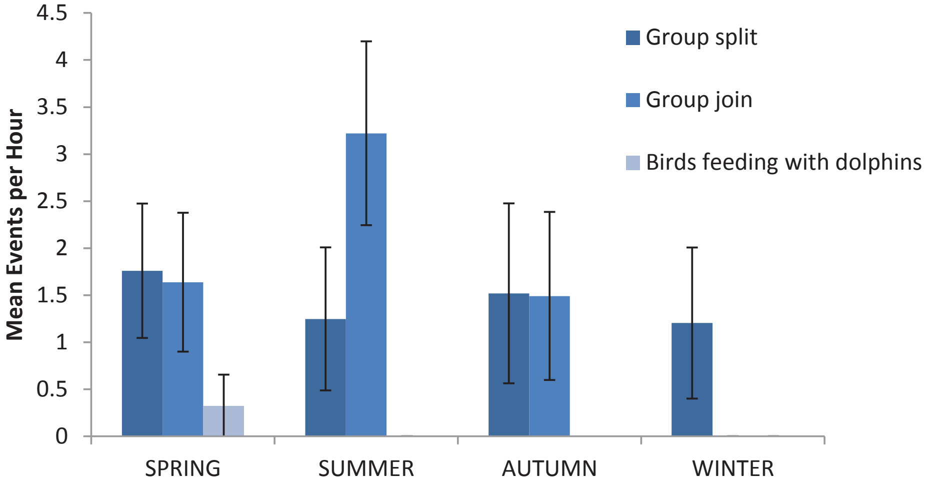


Figure 2.29. Group behavioural events for dusky small groups are shown by season. Bars represent mean with standard error (n=14 spring, n=12 summer, n=15 autumn and n=15 winter small groups).

Diurnal Patterns

Diurnal Habitat Use

Large dolphin groups occurred further north early in the day, moving to the south of the Kaikoura Canyon area and further offshore as the day progressed (Figure 2.30). In winter, large dolphin groups did not exhibit a strong trend in distance from shore with time of day and were as likely to be found north of the Kaikoura Canyon as to the south regardless of time of day.

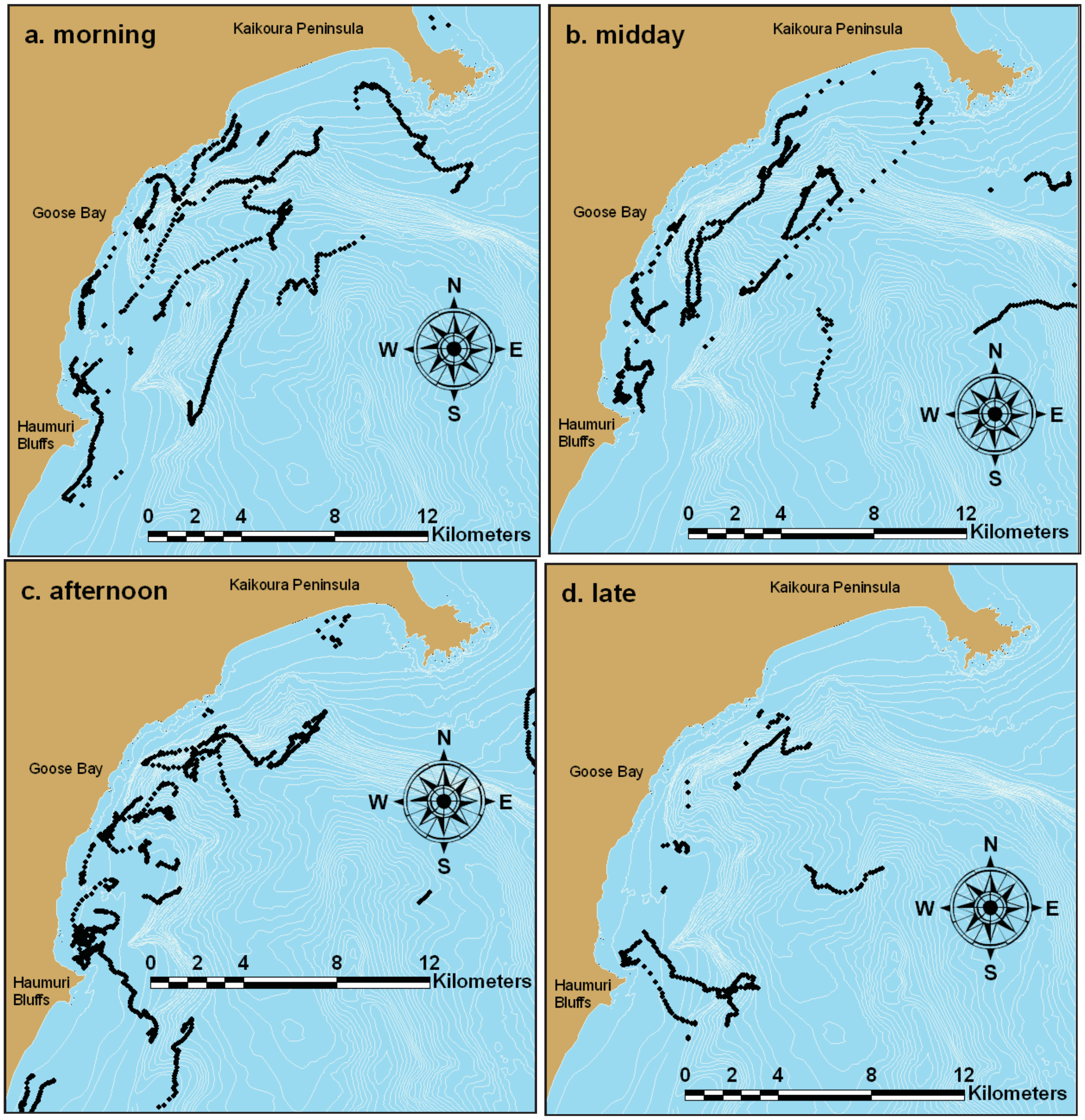


Figure 2.30: Large Group locations by time of day (morning <11:30 n=35, midday 11:30-13:29 n=35, afternoon 13:30-15:00 n=43, late >15:00 n=12).

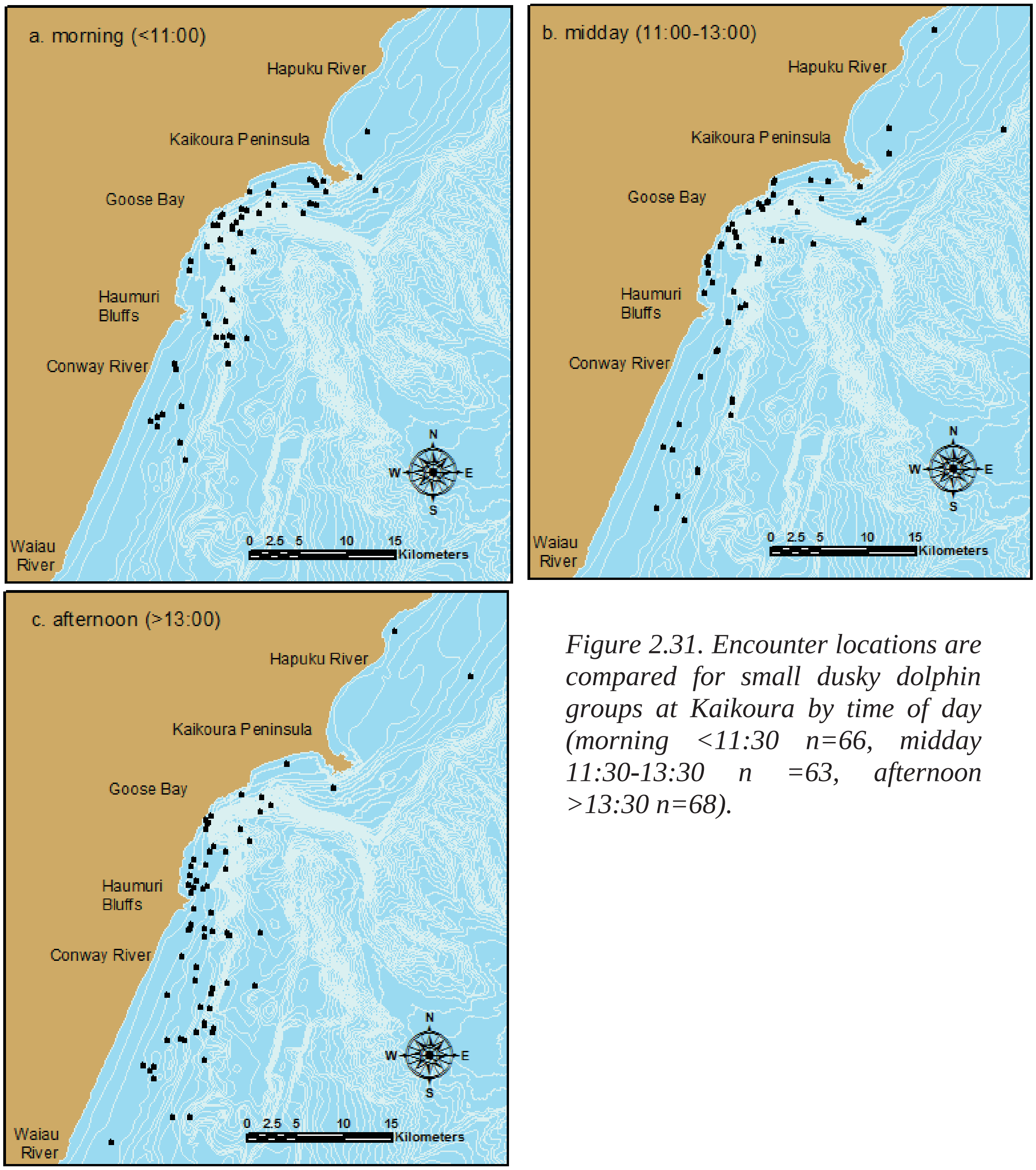


Figure 2.31. Encounter locations are compared for small dusky dolphin groups at Kaikoura by time of day (morning <11:30 n=66, midday 11:30-13:30 n =63, afternoon >13:30 n=68).

Analysis of areas in which small groups of dusky dolphins were encountered by time of day (standard deviation ellipses) showed dolphin groups closest to shore along the narrowest range centering on the Kaikoura Canyon in morning; spreading out, offshore and south midday; and shifting further south toward the Conway River in the afternoon (Figure 2.31, Figure 2.32).

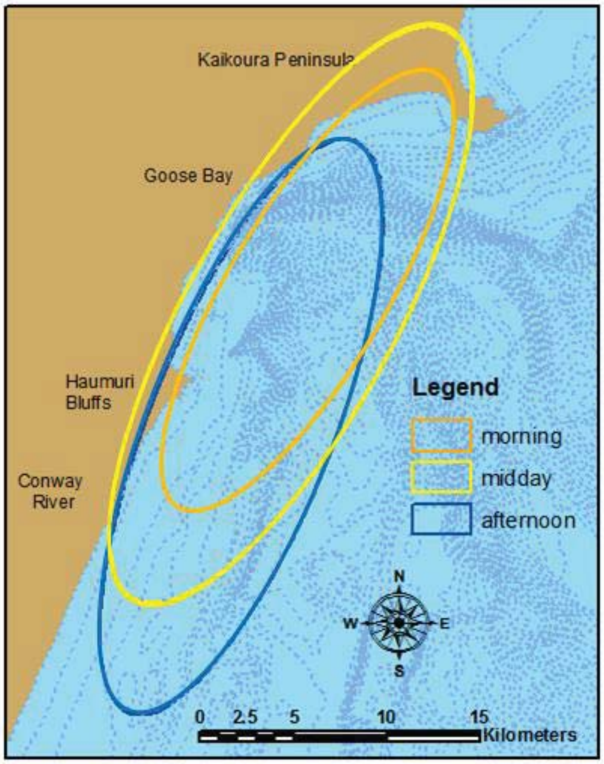


Figure 2.32. Areas that small groups of dusky dolphins were encountered are compared by time of day (morning <11:30 n= 66, midday 11:30-13:30 n=63, afternoon >13:30 n=68) using standard deviation ellipses (1 standard deviation).

Large group distance from shore varied significantly with time of day (Kruskal Wallis, H=7.802, *p*=0.02), with dolphin groups located closer to shore early in the day and moving offshore later in the day (Figure 2.33). Distance from shore at midday may be upwardly biased because large groups were not often tracked during midday. Mean water depth did not vary significantly by time of day for large groups (Kruskal Wallis, *ns*); perhaps due to the large amount of variability in the data set and limited sampling during the summer midday rest period. Dolphin groups were tracked moving through areas of greater water depth particularly in the afternoon, when water depth for large groups averaged 224±48.9 m (mean ± se).

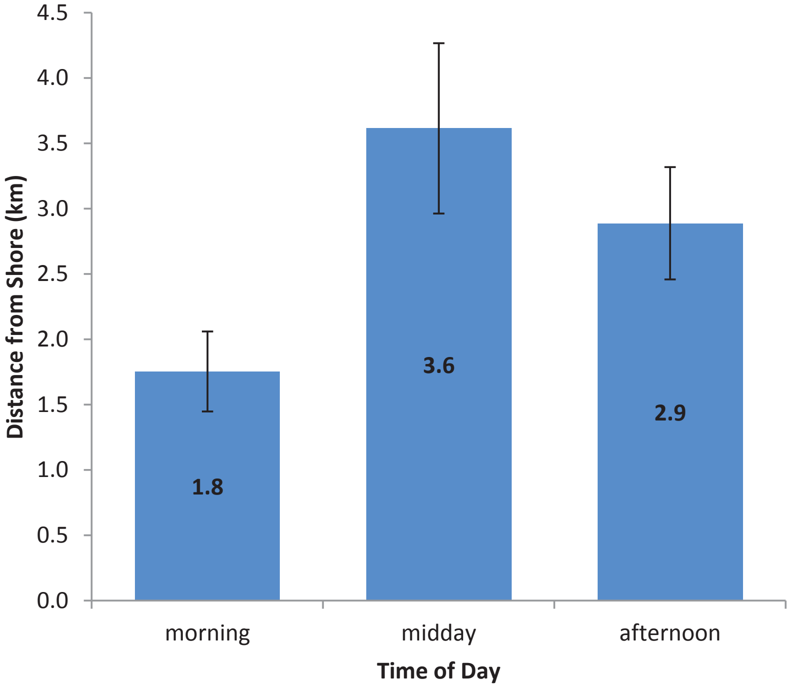


Figure 2.33. Distance from shore, estimated by longitude-latitude position of dolphin groups, is compared by time of day for large dolphin groups. Bars represent mean values with standard errors. Time of day was divided into morning (<11:30, n=35), midday (11:30-13:30, n=35), and afternoon (>13:30, n=55).

Water depth varied significantly by time of day for small groups of dusky dolphins (Kruskal Wallis, depth: H= 8.075, $p<0.02$); however, distance from shore did not vary significantly by time of day (Kruskal Wallis, depth: H= 1.677, *ns*). This finding is explained by dusky dolphin groups moving southward along the shore, out of the Kaikoura Canyon, where they were typically found in the morning, and up onto the continental shelf in the area between the Oaro River and Conway River later in the day (Figure 2.34, see also Figure 2.31).

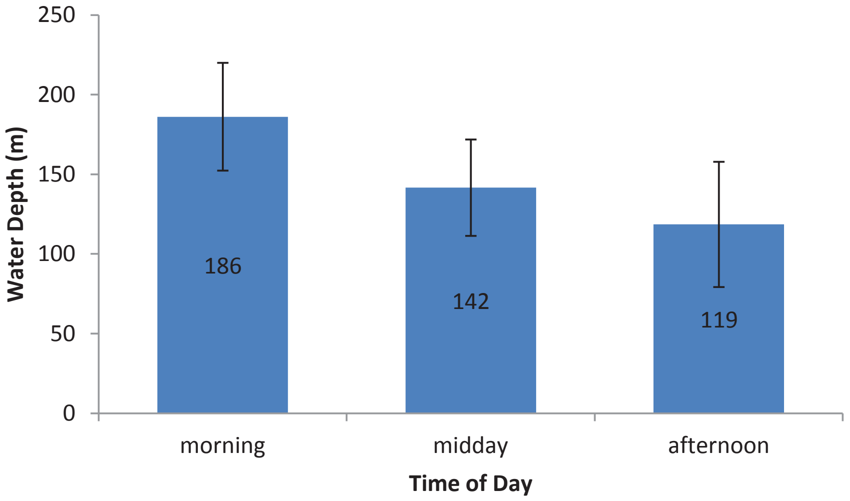


Figure 2.34. The water depth that small dusky dolphin groups (<50 dolphins) were encountered is compared by time of day (morning <11:30 n= 66, midday 11:30-13:30 n=63, afternoon >13:30 n=68). Bars represent mean depths and distances in meters with standard errors.

Leg Speed and Reorientation Rate by Time of Day

Differences in leg speed with time of day were not significant for large groups based on GPS tracks (Kruskal Wallis, H= 1.978, *ns*). This is likely because sampling from the research vessel was limited during the summer midday rest period, when leg speeds were particularly low. Reorientation rate of large groups did not vary significantly by time of day (Kruskal Wallis, H=0.613, *ns*).

Diurnal Behavioural Patterns

The proportion of time large groups spent resting varied significantly by time of day (Kruskal Wallis H=6.781, $p<0.05$), with resting peaking at midday (Figure 2.35). Travelling and milling did not differ significantly by time of day (Kruskal Wallis tests, *ns*), and daytime foraging was rarely observed (Figure 2.35). Dispersion (reported above) and swimming formation of large groups did not vary significantly by time of day (Kruskal Wallis tests, *ns*).

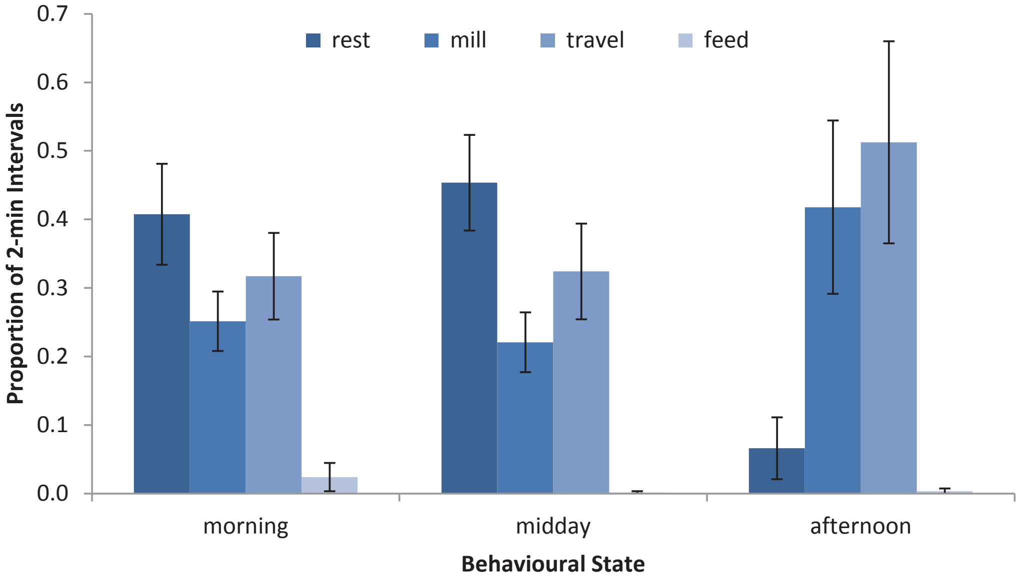


Figure 2.35. Proportion of 2-minute scan samples of large dusky dolphin groups (>50 dolphins) were observed in each behavioural state and compared by time of day (morning <11:30 n= 34, midday 11:30-13:30 n=32, afternoon >13:30 n=44). Bars represent mean values with standard errors.

In small groups, there were no significant differences by time of day in duration or proportion of behavioural states, dispersion, formation or direction of movement (Kruskal Wallis tests, *ns*). Dive duration varied significantly by time of day in small groups (ANOVA F=3.456, *df*=2, $p<0.05$), with groups followed in the morning having shorter dive durations than the other two times of day (Figure 2.36, Bonferonni post-hoc tests, $p<0.05$).

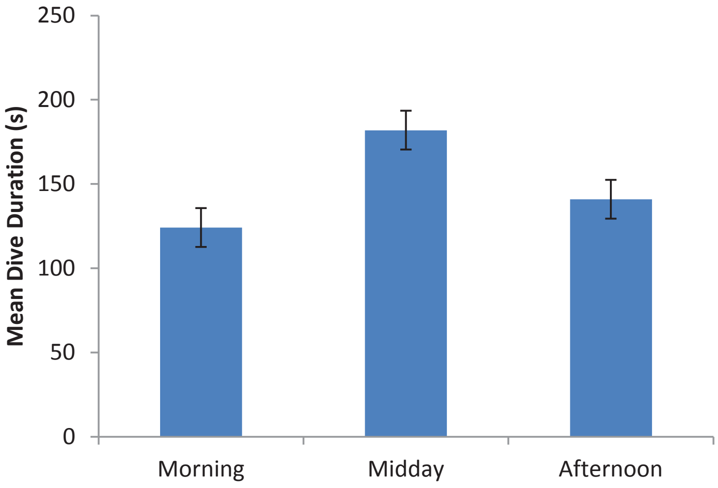


Figure 2.36. Dive duration is compared by time of day for small groups. Y-bars represent standard error of the mean (n=31 morning, n=17 midday and n=8 afternoon small groups).

High-speed activity in the form of bursts of speed (slicing through the water) by the entire group varied significantly in large groups by time of day (Kruskal Wallis H=7.289, *p*<0.03), peaking during morning hours when they occurred during an average of 20% of 2-minute intervals (Figure 2.37). Other high-speed activities (individual speed bursts and porpoising) did not vary significantly with time of day (Kruskal Wallis tests, *ns*).

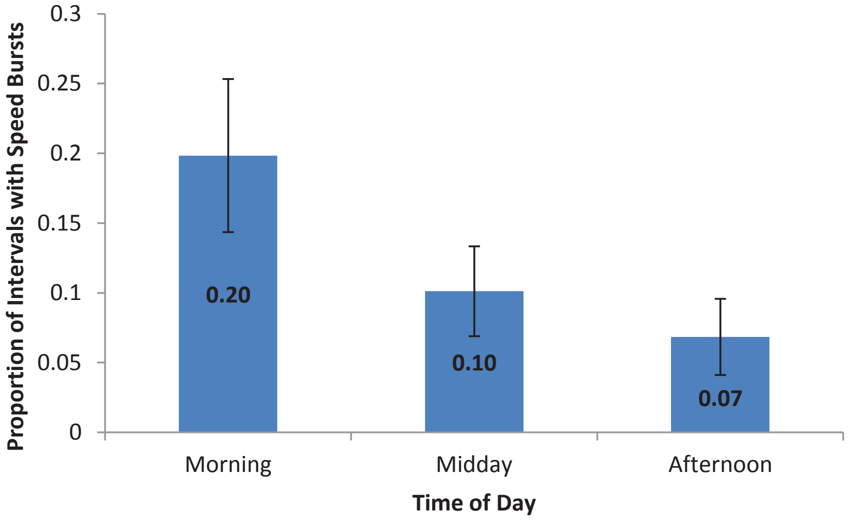


Figure 2.37. The proportion of two-minute intervals of high-speed activity in the form of speed bursts ("slicing" through the water by the entire group) were documented in large groups (>50 dusky dolphins, n = 111 groups) is compared by time of day (morning <11:30 n= 34, midday 11:30-13:30 n=32, afternoon >13:30 n=44). Bars represent means with standard errors.

Bubble blowing play varied significantly by time of day in large groups (Kruskal Wallis H=6.473, P<0.04), occurring during a greater proportion of 2-minute intervals in the morning hours than later in the day (Figure 2.38). Other interactive social behaviours and social sexual activity did not vary significantly by time of day in large groups (Kruskal Wallis tests, *ns*). Behavioural event analysis revealed no significant differences by time of day for small groups (Kruskal Wallis tests, *ns*).

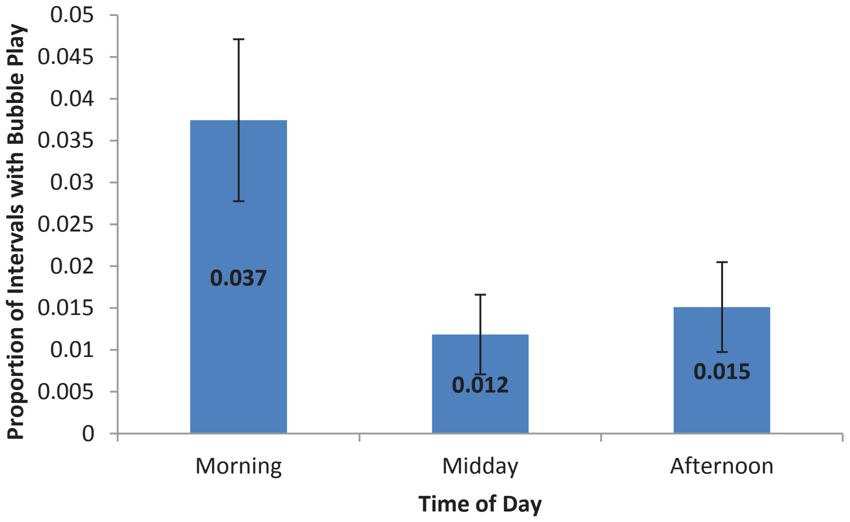


Figure 2.38. The proportion of two-minute intervals of bubble blowing play in large groups (>50 dusky dolphins, n = 111 groups) is compared by time of day (morning <11:30 n= 34, midday 11:30-13:30 n=32, afternoon >13:30 n=44). Bars represent means with standard errors.

Water depth and distance from shore did not vary significantly with the activity level of large dusky dolphin groups (Mann-Whitney depth: U=1994.0, *ns*, distance: U=1874.0, *ns*). In other words, groups were no more likely to rest in shallow water or closer to shore than deeper water further offshore.

DISCUSSION

Seasonal Distribution

The seasonal distribution of large groups follows patterns that have been reported for large groups of dolphins off Kaikoura in other studies (Cipriano 1992, Markowitz 2004, Würsig et al. 2007, Weir et al. 2008, Dahood 2009). Large dolphin groups ranged more widely and were encountered further from shore and in deeper waters in winter. This may be a response to variation in prey availability in the Kaikoura Canyon area by season (Cipriano 1992, Dahood 2009) and seasonal predation risk and calf rearing strategies (Weir et al. 2008, Srinivasan and Markowitz 2010).

The distribution of small groups varied seasonally with the same pattern of increasing distance from shore in winter. Small groups in winter were located further alongshore both north and south of the Kaikoura Canyon than small groups in summer. Small groups did not have similar distribution patterns as large groups in winter, and may have remained in shallow waters to continue to avoid predation risk when the large group envelope of safety was less available. The increased speed of large groups in winter has been reported in other studies of large dusky dolphin groups off Kaikoura (Markowitz 2004, Dahood 2009) and is likely a result of increased ranging patterns of dusky dolphins in winter.

Behavioural States and Season

Seasonal behaviour of large dusky dolphin groups is consistent with seasonal ranging patterns off Kaikoura. Large groups mill more in summer and travel more in winter. Behavioural variation by season for small groups differed from large groups. Small groups in winter rested more rather than travelling, and were more likely to mill in summer. Small groups spent 10% of time travelling. It may be an alternative strategy for dolphins off Kaikoura to remain in small groups near shore year-round to take advantage of the deep scattering layer prey in the canyon area, rather than ranging more widely in large groups. If this is the case, photo-identification data may reveal that dolphins found in small groups (particularly adult non-mating winter groups and winter nursery groups) are not often found in large groups in winter.

Dispersion data collected from small groups showed an increase in dispersion in winter. This result is similar to results from other studies of dispersion of dolphin groups by season off Kaikoura (Markowitz 2004). Dolphins may increase distance between group members in winter to increase search area for opportunistic prey encounters due to lower prey availability. Decreased distance between group members in summer may be due to reproductive patterns of behaviour in summer, such as mating and raising young calves (see Chapter 3).

Examination of seasonal variation in swimming formation showed dolphins in large groups rarely swimming out of formation in summer but dolphins in small groups often swimming with no clear formation in summer. Although dispersion was higher in winter than summer, small groups may be more organised in their grouping patterns as resting increases and milling decreases, or they maintain greater group coordination when under greater energetic constraints in winter. Direction of movement of small groups was more consistent in winter than in summer. This result has been found in other studies of large groups of dolphins off Kaikoura (Markowitz 2004, Dahood 2009). Although dolphins in small groups showed an increase in directional movement in other seasons than summer, overall less than 20% of their time was spent in directional movement in all seasons; this is reflected in the lack of travelling behaviour for small groups in this study.

Season and Behavioural Events

The increase in play activities noted for summer in small groups is likely due to a combination of increased prey availability (decreased energetic output for feeding), increased milling and the presence of calves and mating behaviour in summer. Play behaviours recorded in this study were more prevalent in mating groups than nursery or other small groups (see Chapter 3). High energy activities such as speed bursts (‘slicing’), re-entry leaps and porpoising were most common in summer and least common in winter, which is most likely due to energetic constraints in winter. In all seasons, the reduced noisy leaping in small groups (<0.5 per individual per hour for spring and autumn and not occurring in winter) may be adaptive in reducing detection of small groups by predators. Noisy leaps produce a percussive splash (Figure 2.39). While large groups off Kaikoura maintain a regular cacophony of burst pulse and click train vocalisations, small groups, and particularly nursery groups, are almost completely silent (W. Markowitz, unpublished data). Even the relatively noisy large groups maintain complete ‘radio silence’ when killer whales are present in the study area (W. Markowitz, unpublished data). Noisy leaps, which are more prevalent in large groups, may serve as a long-range signal to coordinate group movements across distances beyond the range of vocal communication (Markowitz 2004).

Figure 2.39. Noisy leap sequence is shown with leap (left) and then percussive splash of dorsal surface against the water (right).

Social behaviours were much more common in small groups in summer than other seasons. This reflects the particularly charged social interactions of dusky dolphins off Kaikoura in summer during the breeding and calving season. The highly social nature of small groups in summer is reflected in the number of group joining events recorded. In summer, dusky dolphin small groups were much more likely to be joined by other small groups, or to join large groups than in winter.

Diurnal Distribution

The movement of large groups offshore late in the day is consistent with findings of other studies for dusky dolphins off Kaikoura (Markowitz 2004, Dahood 2009), and is generally related to nocturnal foraging offshore on the deep scattering layer (DSL) associated with the Kaikoura Canyon. The lack of this diurnal pattern in winter has been described as a response to reduced prey availability in winter and a longer association with the submarine canyon habitat as the DSL layer is more available in winter (Dahood 2009). The movement of small groups away from the Kaikoura Canyon late in the day is opposite the general movement pattern for large groups. Dolphins in small groups later in the day are more closely associated with the shallow waters near the Oaro (Mikinui) River located inshore between Goose Bay and the Haumuri Bluffs. This area provides a shallow refuge against predation for small groups and is still close enough to the Kaikoura Canyon for easy travel to this foraging location as day turns into dusk. This is reflected in the lack of significant difference in distance from shore with time of day for small groups, although the depths they are encountered in are shallow. Tourism (Chapters 5 and 6) may be displacing large dusky dolphins groups south toward this area throughout the day. Small groups that are associated with the large group may be following this same pattern.

The lack of significant differences in leg speed and reorientation rate with time of day for large groups is largely due to a small sample size for large groups during the midday rest period, when large groups were not followed (see Chapter 5).

Diurnal Behaviour

As found previously in studies from a shore station and a research vessel (Würsig et al. 1997, Barr and Slooten 1998, Markowitz 2004), the proportion of time dolphins in large groups spent resting varied significantly by time of day, with resting peaking during the middle of the day. As in other studies, daytime foraging was rarely observed (Markowitz 2004). Small group behaviour did not vary much with time of day. The primary behaviour for small groups of dolphins off Kaikoura was resting (58% of time) with group members <1 body length apart (76% of the time, see chapter 4), regardless of time of day. This behaviour appears to supersede any effects of time of day. Dolphins were more likely to increase dive duration (defined as the duration between the last surfacing of any group member and the subsequent first surfacing of any group member) during the middle of the day. Although no significant differences were found for behavioural state with time of day, increased dive durations may be correlated with resting behaviour in dusky dolphin small groups (see Chapter 3) off Kaikoura.

Summary of Findings

As group size decreased, dolphins were found closer to shore and in shallower depths closer to river-mouths. This is likely an adaptive response to reduce predation risk, particularly for young calves in late spring and early summer. Milling in summer and travelling in winter were typical behavioural patterns for large groups in this and other studies (Markowitz 2004, Dahood 2009). Fish species migrate to depth as both hours and intensity of sunlight are reduced in winter, causing a decrease in both primary productivity and cues for initiation of vertical migrations (Springer 1992, Sinclair and Zeppelin 2002). Demersal fish species tend to increase depth during winter months on the east coast of the South Island (Beentjes et al. 2002). Arrowtooth squid (*Nototodarus sloanii*), a primary prey species for dusky dolphins (Cipriano 1992), and other South Island marine mammals (e.g., New Zealand fur seals *Arctocephalus forsteri*, New Zealand sea lions, *Phocarctos hookeri*) is relatively absent from pinniped diets in winter (Fea et al. 1999, Meynier et al. 2009) .

The tendency for small groups to rest in winter and mill in summer may be a response to reduced prey availability in winter in the Kaikoura Canyon area (Beentjes et al. 2002). As prey become less available, individuals are likely to increase nocturnal foraging efforts to locate and consume prey (Cornish and Mrosovsky 1965, Collier 1969). This increased energy expenditure could result in increased resting during the day to conserve energy until prey become available. Although dusky dolphins in large groups travel more in winter, presumably to increase prey encounter rates, dolphins in small groups may use this alternative resting strategy as fewer group members would limit the productivity of search efforts (Pitcher et al. 1982, Connor 2000). Instead, forming small groups that forage on more localized prey resources associated with the Kaikoura Canyon would reduce competition among group members for limited local resources (Kinsey and Cunningham 1994, Connor 2000, Gowans et al. 2008).

Increased resting in small groups in winter was concomitant with an increase in dispersion. Usually, cetaceans group more closely when resting (Wells 1991). Although small groups were more dispersed in winter, they were more organised with respect to swimming formation (i.e., dolphins swam in parallel or echelon formation rather than no formation). Increased dispersion and swimming in parallel or echelon formation during the day may increase opportunistic prey encounter rates for dolphins in small groups in winter.

Surface (splash) behaviours such as noisy-leaping and tail-slapping occurred less frequently as group size decreased. Reduced noisy leaping in small groups may be adaptive in reducing detection of small groups by predators. Noisy leaps, which are more prevalent in large groups, may serve as a long range signal to coordinate group movements across distances beyond the range of vocal communication (Norris et al. 1994, Markowitz 2004).

Dusky dolphins off Kaikoura respond to seasonal and diurnal variation in prey availability with changes in association patterns and behaviour. Dusky dolphins in small groups invest high energy in reproductive behaviours such as calf rearing and mating during the breeding season. The formation of large groups in all seasons and times of day is likely an anti-predator strategy for dusky dolphins in a highly productive habitat on the edge of the Kaikoura Canyon. It may be an alternative strategy for dolphins off Kaikoura to remain in small groups near shore year-round to take advantage of the DSL prey availability in the canyon area, rather than ranging more widely in large groups.

CHAPTER 3

SOCIAL COHESION AND REPRODUCTIVE EFFORT IN SMALL GROUPS OF DUSKY DOLPHINS OFF KAIKOURA, NEW ZEALAND

INTRODUCTION

Social organisation is strongly influenced by both social and ecological pressures. Male reproductive success is highly dependent on access to females whereas female reproductive success is influenced primarily by foraging efficiency (Emlen and Oring 1977). In fission-fusion societies subgroups will form depending on tradeoffs between costs and benefits of group formation (Chapman et al. 1995). These trade-offs allow group members to capitalise on the benefits of group formation without ensexing the costs associated with living in permanent social groupings (Kinsey and Cunningham 1994). Individuals may leave a group or join a smaller group when the costs associated with group formation (e.g., increased parasite loads, increased risk of predation, competition for food, and aggression of conspecifics) outweigh the benefits (Krebs and Davies 1993, Connor 2000).

Small Adult Groups

Although dusky dolphins (Lagenorhynchus obscurus) off Kaikoura are known to form large groups of hundreds to thousands of individuals, smaller groups of less than 50 individuals have been noted (Markowitz 2004, Weir et al. 2008). Dusky dolphin group sizes in South Africa generally ranged from 2-50, although groups of hundreds have been noted (mode group size=10; Elwen et al. 2009). In Argentina, dusky dolphins form groups of 6 to 15 individuals, with up to 300 dolphins in larger feeding aggregations reported during the 1970s (Würsig and Würsig 1980), although such large aggregations appear to no longer occur as often as before (Würsig 2010). In the Marlborough Sounds, New Zealand, group sizes are typically 1-50 individuals (Markowitz et al. 2004) and on the west and southeast coasts of the South Island group sizes range from 3 to 100 (usually <20) individuals (Markowitz 2004, Würsig et al. 2007). Small groups of <50 dusky dolphins appear to be common throughout the southern hemisphere and may be the most typical social group size for dusky dolphins in shallow coastal environments.

The formation of small, mixed sex groups is common for most mammals (Emlen 1995), and the norm for primates (van Hooff and van Schaik 1992, Snaith and Chapman 2007) and some cetaceans (Wells et al. 1999). Group size is usually related to the ecology of the areas in which they are found, although species may be constrained by their phylogenetic history in their ability to respond to local shifts in ecology (Henzi and Barrett 2005). The large groups formed by dusky dolphins resting throughout the day in the Kaikoura Canyon area are a rather unique social pattern for this species in coastal environments and are likely related to both the abundance of prey and the depths of the Kaikoura Canyon, which may increase the risk of predation in this area (Srinivasan and Markowitz 2010).

Calf-Rearing

In mammals, female grouping patterns are primarily related to rearing offspring. Group formation may consist of only one female and her offspring or may include additional females, often with offspring of similar ages (Figure 3.1, Wells 1991, Whitehead 1996, Sterck et al. 1997, Payne 1998, Whitehead and Mann 2000, Mann et al. 2000, Moss 2001, Archie et al. 2006). Competition between group members for resources (e.g., food, shelter) is weighed against the social benefits of group living for females with young including offspring survival (Silk et al. 2003) and protection against aggressive males (Hrdy 1979, Packer and Pusey 1983, Mann et al. 2000). Additional benefits to offspring may include increased opportunities for alliance formation, social experience and learning (Harcourt and

De Waal 1992, Connor 2000, Connor 2007) that are crucial for reproductive success in large-brained, social mammals.

Nursery groups are found off Kaikoura particularly in summer and usually in the vicinity of large groups of dolphins (Weir et al. 2008). These smaller satellite groups seek shallow water inshore to reduce risk of predation and harassment from conspecifics (Weir et al. 2008, Srinivasan and Markowitz 2010, Weir et al. 2010). Diurnal behaviour of nursery groups includes primarily resting with calves in infant or echelon position, with some social contact behaviours (e.g., contact 'social' rubs; Weir et al. 2010).

Genetic analyses indicate potentially high relatedness among females in nursery groups that form off Kaikoura (Shelton et al. 2010), but little evidence that kinship plays a role in the formation of mating groups or other small groups of adults. Female dusky dolphins may remain in their natal group, forming long-term associations with relatives. Much like the matriarchal fission-fusion patterns that have been described for African elephant (Archie et al. 2010) and sperm whale (*Physeter macrocephalus*; Whitehead and Christal 2001) societies, these 'core' family groups of 6 to 20 individuals may split and join in response to prey availability and predator threats. Off Kaikoura, mothers with calves may be seen in large or small groups and nursery groups sometimes join to form much larger associations of over 100 individuals consisting of adults with calves in almost a 1:1 ratio (Weir et al. 2010). Female dusky dolphins may stay with their natal group past weaning (approximately 1 yr), in order to raise their own young within matrilineal groups. Females reach sexual maturity at 7-8 years (*n*=21 female specimens, Cipriano 1992), and reproduce approximately every two years, with gestation lasting about one year (11.4 months at Kaikoura; Cipriano 1992, Van Waerebeek and Read 1994).

Figure 3.1 Dusky dolphin adult and calf encountered in a small group off Kaikoura, New Zealand.

Mating Associations

Males can either remain in their natal habitat or disperse. Natal philopatry may be common for male cetaceans (Connor et al. 2000) with dispersal usually a result of intense competition for mates (Eibl-Eibesfeldt 1961, Manson 1996, LeBoeuf and Kaza 1981, Modig 1996, Leslie and Jenkins 1985). Males develop social behaviour while in nursery groups, then disperse to join other groups (which may be all males or mixed sex and ages) or remain solitary. Males may form strong associations in species with male philopatry (e.g., chimpanzees, *Pan troglodytes*; Mitani et al. 2000), in species where related males disperse together (e.g., lions, *Panthera leo;* Packer and Pusey 1982), or in species where unrelated males cooperate in alliances (e.g., bottlenose dolphins, *Tursiops* sp., Connor et al. 1992). Male long-term alliances and short-term coalitions can improve male reproductive fitness by increasing access to mates (e.g., baboons, *Papio cynocephalus;* Noë 1992). Less stable male associations may form to increase access to foraging information, provide sparring partners or improved defence from predators (Mooring et al. 2003, MacFarlane and Coulson 2009), with some evidence for preference of relatives and the importance of adult males in all-male associations of African elephants (*Loxodonta Africana*, Chiyo et al. 2011).

Male alliance formation to improve access to mating opportunities has been well documented in bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia. Males in this location form two and possibly even three levels of distinct alliances within their social network (Connor 2007). Alliances, unlike short-term coalitions, are enduring cooperative relationships between two individuals (De Waal and Harcourt 1992). Alliances may also repeatedly cooperate with each other, forming second or third order alliances in aggressive or competitive contexts. Previous research indicates alliance formation among dusky dolphin males is likely, with the same partners forming mating associations in Kaikoura and foraging associations in Admiralty Bay, New Zealand (Markowitz et al. 2010a). Small dolphin groups in Admiralty Bay are primarily male (Shelton et al. 2010), suggesting that all male groups may form in the New Zealand dusky dolphin.

Although dusky dolphin reproduction is seasonal, mating is observed throughout the year, occurring for social as well as reproductive reasons (Cipriano 1992, Markowitz et al. 2010a). The reproductive season for dusky dolphins off Kaikoura ranges from late spring through summer, with a peak in calving in November (Markowitz et al. 2010a). Mating groups begin to form in November and are found in the vicinity of large groups through February and even into March (current study). They are observed to frequently join and split apart from larger groups (fission-fusion, Markowitz 2004). High levels of social-sexual interaction including chasing of conspecifics, ventral contact and intromission are often observed, with high incidences of leaping and high-speed behaviours (Markowitz et al. 2010a).

Males, like females, reach sexual maturity at age 7-8 years (Cipriano 1992); with testes mass accounting for as much as 5% of adult male body weight (4 kg) during the breeding season (Cipriano 1992). For dusky dolphin males, seasonal variability in testis mass and high testis mass to body mass ratios indicate high levels of sperm competition (Würsig and Würsig 1980, Cipriano 1992, Van Waerebeek 1992, Van Waerebeek and Read 1994).

Research Objectives and Predictions

Habitat near shore may serve as a refuge from predation for dusky dolphins at Kaikoura (Weir et al. 2008, Srinivasan and Markowitz 2010, Weir et al. 2010). Small dolphin groups with calves should be most likely to make use of this habitat feature as a refuge for young animals. Group sizes for nursery groups should be larger than mating or other small adult groups as females with young group together to reduce the risk of predation (Dunbar 1989, van Schaik 1989, Weir et al. 2010). Subgroups within nursery groups are likely to be larger to maintain this protective envelope. Genetic relatedness among individuals in nursery groups implies that these groups may be more stable than other small groups of dolphins (Shelton et al. 2010), with fewer changing partners than mating groups or other adult non-mating groups. In other mammals, groups of females with young tend to be more stable than other social groupings (Funston et al. 1998, Henzi and Barrett 2005, Wittemeyer et al. 2005), although in bottlenose dolphins male-male alliances appear to be very stable as well (Connor et al. 1992).

Lactation is costly, may double the energetic expenditure of pregnancy, and requires roughly 50% more prey intake for odontocetes (Whitehead and Mann 2000). Therefore, groups of mothers and their offspring can be expected to show decreased activity levels. Close association and high levels of social contact likely reinforce social bonds, maintaining cohesion within groups of females and offspring formed generally to reduce predation risk (van Hoof and van Schaik 1992).

Mating activity can result in dramatic behavioural displays for even the most sedentary of species. From the 'love' darts of land snails (e.g., *Helix aspersa*, Koene 2006) and mating dances of banana slugs (*Ariolimax dolichophallus*, Leonard et al. 2002, Reise and Hutchinson 2002) to the booming of prairie chickens (*Tympanuchus cupido*, Robel and Ballard 1974), mating activities can be some of the most costly and interactive behaviours individuals engage in. Cetacean mating behavioural displays can be just as dramatic. The signature breach of the humpback whale (*Megaptera novaeangliae*) as well as the tusk crossing and dominance displays of narwhal males (*Monodon monoceros*) occur in the context of mating and breeding behaviour (Clapham 2000, Heide-Jørgensen 2009). Dusky dolphin mating behaviour is characterised by high re-entry leaping, jostling for position and mating chases (Markowitz et al. 2010a). Mating groups are likely to have high levels of surface behaviours and behavioural activity as competition between males is highest and social interaction most intense in this type of small group at Kaikoura.

Fission-fusion social dynamics allow individuals to maximise fitness by leaving groups when the costs of competition with group members outweigh the benefits of group membership (Kinsey and Cunningham 1994). This fluid social system allows males to leave and enter groups in response to mating opportunities and to monitor reproductive females (Whitehead and Wielgart 2000, Chiyo et al. 2011, Lehman and Boesch 2004). The formation of mating 'subgroups' in the vicinity of large groups of dusky dolphins allows males to capitalise on this fission-fusion social structure to increase access to mating opportunities. These mating groups are likely to have high fission-fusion rates as males compete for access to females. High-speed activity may attract additional males to the chase as unsuccessful males leave to search for other mating opportunities nearby.

Even solitary species increase social contact and interactions with conspecifics in the context of courtship and mating (e.g., solitary felids, Kleiman 1973). Delphinid social interaction also increases during the breeding season with more contact behaviours and behavioural displays than at other times of year (reviewed by Mesnick and Ralls 2009). For dusky dolphins, inter-individual distance is likely to be reduced in mating groups as males chase and mate with females. These reproductive chases should result in longer dive durations in these groups as the chase continues at depth. Mating group sizes may be larger than non-mating adult groups but smaller than nursery group sizes as individuals balance the benefit of group participation (i.e., mating opportunities) with the risk of predation (high levels of surface behaviours and reduced vigilance among group members).

Group sizes for adult non-mating groups are likely to be the lowest, with the greatest dispersion between group members and lower fission-fusion rates than adult mating groups. Individuals do not have the added benefit of mating opportunities to increase group size or the need to maintain the group envelope for protection of offspring.

Mammals form small, mixed sex groups to reinforce social bonds, provide protection for young and increase mating opportunities (Emlen 1995, van Hooff and van Schaik 1992, Wells et al. 1999, Connor 2000). Group size is usually related to ecology but is also influenced by phylogenetic history (Henzi and Barrett 2005). The formation and stability of small group associations are driven by trade-offs between the benefits described above and the costs of group living such as increased risk of predation, competition for food and aggression of conspecifics (Kinsey and Cunningham 1994).

Females with young tend to group together to reduce the risk of predation (Dunbar 1989, van Schaik 1989, Weir et al. 2010) and protect offspring from aggressive males. These groups of females with young tend to be more stable and can form larger group sizes than other social groupings (Funston et al. 1998, Henzi and Barrett 2005, Wittemeyer et al. 2005). The high costs of laction and parturition require more prey intake as females balance the benefits of group membership with competition for resources between group members (Whitehead and Mann 2000). Close associations with consistent bond reinforcement likely help to maintain group cohesion as females join together in groups with young primarily to reduce predation risk (van Hoof and van Schaik 1992).

Based on this theoretical framework, one would expect groups with calves to select habitat and behave so as to minimize predation risk and energetic expenditure:

Hypothesis: Small social groups with calves will show greater social cohesion, inhabit more sheltered areas, and engage in fewer high energy behaviours than other small groups.

Specifically, I predicted small groups with calves would:

1. Form larger group and subgroup sizes, inhabiting shallower areas closer to river mouths than other small groups.

2. Have reduced fission/fusion rates and lower inter-individual distance between group members than other small groups.

3. Spend more time in parallel/echelon swimming formation than other groups.

4. Rest more with less high-speed and leaping behaviour than other small groups, and more social contact behaviour than adult groups not focused on mating activities.

Male reproductive success and social organization is driven by access to females (Emlen and Oring 1977). Fluid fission-fusion social systems allow males to leave and enter groups to maximise fitness in response to mating opportunities and to monitor reproductive females (Kinsey and Cunnhingham 1994, Whitehead and Wielgart 2000, Chiyo et al. 2011, Lehman and Boesch 2004). Behavioural displays in the context of mating and breeding can be costly for males as they balance increased access to mates with increased predation risk (Reviewed by Magnhagen, 1991). Like most cetaceans that increase behavioural displays and social interactions in the context of mating and breeding (Clapham 2000, Heide-Jørgensen 2009, Mesnick and Ralls 2009), dusky dolphins perform high re-entry leaping and jostling for position during mating chases (Markowitz et al. 2010a). These mating groups are likely to have high fission-fusion rates as males are attracted to mating chases, compete for access to females, and respond to the costs of mating group formation as reduced vigilance and increased behavioural displays increase predation risk.

Hypothesis: Dolphins in mating groups will engage in more high energy and social activity than other small social groups, while showing the least dispersion and social cohesion.

Specifically, I predicted that:

Small groups of adults focused primarily on mating behaviour would:

1. Form intermediate group sizes with less social stability and higher rates of fission/fusion than other small groups of adults and groups with calves.

2. Mill more and rest less with higher leaping rates and more high-speed behaviours, longer dive durations and less group dispersion than other small groups.

Social stress increases with increasing group size (Lehman et al. 2007). Although large groups are common off Kaikoura, the more typical coastal pattern of small group associations are found in all seasons throughout the Kaikoura Canyon area as well. Small mixed-sex adult groups may form consistent associations or could simply be temporary associations of individuals in the vicinity of the large group envelope. If the former, joining less wide ranging small groups with more stable associations may be an alternative strategy to associating in large wide ranging groups at Kaikoura for adults and sub-adults. It is possible that this alternative strategy lowers detection by predators and allows for reinforcement of social bonds away from the socially complex setting of large groups.

Hypothesis: Habitat use and behaviour of small groups of non-mating adults will be intermediate between the restful, socially stable, near shore pattern of groups with calves, and the high energy, socially dynamic mating groups.

Specifically, I predicted that small groups of adults would:

1. Form smaller groups and subgroups that range further from shore, further from river mouths and in deeper water than groups with calves.
2. Rest more with lower fission-fusion rates than groups focused on mating activites and rest less with higher fission-fusion rates than groups with calves.
3. Have the greatest dispersion among group members when compared with groups focused on mating behaviour or groups with calves.
4. Have fewer high-speed behaviours, surface behavioural displays, and social contact behaviours (e.g., contact ‘social’ rub, ventral contact) than groups with calves or mating groups.

METHODS

Defining groups

Dolphin groups were defined using the “10-m chain rule” which relies on spatial proximity of individuals (Smolker et al. 1992, Mann 1999). Dolphins are considered part of a group if they are within 10 m of a nearest neighbour. This “distance measure” rather than a definition that includes a behavioural component was chosen as it does not rely upon assumptions about the behaviour of a group’s members (Mann 1999). Subgroups were defined as individuals <1 or 1-3 body lengths apart and >3 body lengths from other dolphins in the group, moving in a coordinated fashion and surfacing synchronously. Group size, and subgroup number and size, was sub-sampled from the continuous data in 2-min intervals to compare with methods from other studies.

Small Group Definitions

A small group of dusky dolphins was defined as any group with <50 individuals. Small groups were further classified as mating groups if both sexual approach and ventral contact or confirmed intromission were observed (defined below). Group age class composition was estimated by size of individuals present based on lengths of aged post-mortem specimens (Cipriano 1992). Small groups of <50 individuals were defined as nursery groups if one-fourth to one-half of group members consisted of calves swimming primarily in echelon position (close, alongside the mother toward the head or alongside the dorsal fin) or infant position (in contact under the mother slightly behind and to the side near the mammary slits (Mann and Smutts 1999).

Behavioural Data Collection

Boat based surveys for dolphin groups were conducted off Kaikoura from a 5.5 m research vessel (see Chapter 2 for detailed survey methods). Surveys were conducted south along 22 km of coastline from Kaikoura to the Haumuri Bluffs and were run at a distance of 2 km from shore and speed of 10-13 knots. If no dolphin groups were located, surveying continued back to the north 1 km from shore at the same speed. Systematic line-transect surveys were used south of the Haumuri Bluffs (DuFresne and Markowitz 2009, see Chapter 4 methods) but were limited to the summer season due to logistical constraints. Small dusky dolphin groups were encountered opportunistically in the vicinity of large groups and during surveys for Hector's dolphins and these data were included for behavioural analysis.

Research effort from January 2007 through March 2009 included 699 hours of vessel surveys on 140 days with 197 small group encounters including 127 adult non-mating groups, 33 mating groups and 37 nursery groups. Focal group behavioural sampling was conducted for 46 adult non-mating groups, 16 mating groups and 19 nursery groups. Focal group approaches and follows were conducted following the protocols recommended by Würsig and Jefferson (1990). Group locations and movements were estimated using longitude/latitude and time data recorded by Garmin global positioning system (GPS) receivers from the vessel as it was positioned alongside the group. Time and location data were recorded at one-minute intervals and later downloaded to computers for analysis. Continuous behavioural observations were recorded using an Olympus VN-2100PC digital voice recorder with noise reducing headset combined with digital photography. These devices greatly increased the quantity and quality of data that could be collected per unit time while monitoring often rapid and fleeting behavioural events. Social contact behaviors were observed at a typical distance for small groups of roughly 20m, allowing for near surface social behaviour to be reliably recorded. Behavioural observations were only conducted in Beaufort Sea States of 1 or less.

Predominant group activity was recorded as the behavioural state for the group (Mann 2000). Behavioral state (rest, mill, travel, forage), group dispersion (<1, 1-3, >3 body lengths), heading (variable, north, south, east, or west), formation (no formation, parallel/echelon, linear, circular) and number of individuals associated with the research vessel (bow riding) were documented whenever these parameters changed (see Chapter 2 for detail; adapted from Shane 1990, Hanson and Defran 1993, Acevedo-Gutiérrez and Parker 2000). Small dolphin groups cycled rapidly between parallel and echelon formation and differentiating between the two was problematic during continuous sampling. Parallel and echelon formations were combined to form a single parallel/echelon category for behavioural scoring (see Chapter 2 methods for detailed definitions of behavioural states and events). Direction of travel for small groups was calculated by compass bearing and noted when changed. If groups changed direction repeatedly during observation, the direction was scored as ‘variable’. For mating groups, sex and position of individuals was recorded (if discernible).

Behavioural events (defined in Chapter 2) were documented in real time including noisy leap, acrobatic leap, re-entry leap, tail slap, synchronous surfacing, speed burst (‘slice’), group speed burst, chase conspecific, blow bubbles, play with kelp, spyhop, inverted swim, ventral presentation, contact (‘social’) rub, ventral contact, sexual approach, and intromission (see Figure 3.2). Incidence of birds feeding with dolphins was recorded. Social (contact) rubbing, inverted swimming and chases, ventral contact, and sexual approach often preceded mating. Copulation was noted only if intromission was confirmed (Figure 3.2). Behaviours recorded for nursery groups included all interactive behaviours such as contact (social) rubbing events and play behaviours (spyhop). Rostrum-genital contact between calves and adults (which may have been nursing behaviour) and other adult-calf interactions were documented in real time.

Figure 3.2. Social-sexual contact behaviors examined in this study were: (left, top) social rub, (right, top) inverted swimming (left, bottom) sexual approach with penis out, and (right, bottom) intromission (confirmed copulation).

The observation of an erect penis was the method most often used to sex males in the field. Group composition (including sexing of individuals) was conducted in real time as much as possible and confirmed post-hoc through analysis of digital photographs. Dolphins have an anal opening and genital groove on the ventral surface. The anogenital slit appears continuous in females with small slits on either side of the genital slit that contain mammary glands. The genital slit in males is located about 4 cm forward of the anal opening (Schroeder 1990, Figure 3.3).

Figure 3.3. Dolphins can be sexed using digital photographs. Females (top) were identified by the lack of separation between the genital slit and anus, and by mammary slits and (bottom) *males were identified by the distance between the genital slit and anus.*

Data Analysis

GIS Analysis

Group locations were estimated using data recorded by the Garmin global positioning system (GPS) receiver from the vessel as it was positioned alongside the group. Data were recorded at one-minute intervals and were plotted in Mapsource Bluechart Pacific 5.5 (Garmin International, Inc., Olathe, KS, U.S.A.). Longitude/latitude positions were imported into ArcGIS v. 10.0 and overlaid onto a shore line base map and a bathymetric chart supplied courtesy of the National Institute of Water and Atmospheric Research, New Zealand (NIWA).

All map features presented in this chapter were imported as Longitude/Latitude tables, and then projected using the WGS 84 coordinate system.

To obtain more accurate estimates of distances and areas, the data frame was changed to the New Zealand national grid system NZ UTM 59S that centres on 171° East Longitude and all data layers exported to shape files matching this data frame. Track points and geographic reference data were uploaded and analyzed using ArcGis 10.0 for relation to bathymetry, and distance from shore (ESRI, Inc. Redlands, CA, U.S.A.). Locations were plotted in WGS 1984 datum and re-projected to local Universal Transverse Mercator (UTM). Standard deviation ellipses (based on 1 SD) were calculated in ArcGIS v.10 to examine the geographic distribution of group encounters by season.

Data layer shape files (points) were joined by spatial proximity to the bathymetric shape file, such that each point was assigned a depth equal to the nearest isobath. Resulting shape files were then joined by spatial proximity to the coastline shape file to obtain the estimated distance from shore of each location. To calculate distance of dolphin groups from river mouths, an oceans and topography base map was downloaded from ArcGIS online with rivers indicated. River mouth locations were set as points on the base map and a shapefile of river mouths was created. All group encounter locations were then spatially joined to this shapefile to calculate distance from river mouths by group. The resulting attribute tables were exported to Microsoft Access databases for querying by season and time of day, with analyses blocked by independent dolphin groups (see Chapter 2 for detailed GIS analysis methods). All data were analysed using SPSS v.10 as described below.

Behavioural Data Analysis

Digital audio recordings were transcribed into JWatcher V1.0 (Blumstein et al. 2006) for detailed analysis of behaviour. Transcribing of audio recordings rather than direct entry into the JWatcher program in the field allowed for hands free observation of behaviour and the ability to review data for accurate input. Re-entry leaps, group dives (time from the last animal at the surface to the first animal re-surfacing), and social interactions were analyzed by group for frequency and duration. Using this technique, it was possible to assess durations of behavioural states and rates of behavioural events. In addition, duration of copulation, as well as inter-copulatory intervals and sequences of group behaviour could be documented. Sequences of mating group behaviour were analyzed from re-entry leaps through chase bouts to intromission(s).

Continuous data were queried using JWatcher (v1.0.) by day and group to ensure the independence of points, and subsequent statistical tests run in SPSS v.10. Data were tested for normality using the Kolmogorov-Smirnov test. As data were compared by group type, the non-parametric test most often used was a Kruskal Wallis test. Normally distributed data were tested for equality of variance using Levene’s statistic, and an ANOVA test was used. Mann-Whitney or t-tests were used to test for some differences between just two group types.

RESULTS

Habitat Use Patterns

Small adult groups of dusky dolphins (n=127) were encountered throughout the study area and were found well to the north and south of the Kaikoura Canyon, with two groups encountered north of the Hapuku River (Figure 3.4c). Mating groups (n=33) were encountered primarily in the Kaikoura Canyon area in deep water and to the south of the Haumuri Bluffs (Figure 3.4a). Nursery groups (n=37) were encountered in shallow water inshore of the Kaikoura Canyon and appear to associate closely with the southern edge of the Kaikoura Canyon isobath (Figure 3.4b). The concentration of nursery groups in the area of the Oaro River suggests this location may provide a shallow water refuge in easy travelling distance to evening foraging opportunities at the edge of the Kaikoura Canyon for mothers with calves.

Standard deviation ellipses show the general distribution of small dusky dolphin groups by group type (Figure 3.5). Adult non-mating groups have the widest distribution both offshore and to the north and south of the canyon. Mating and nursery groups are more closely associated with the Kaikoura Canyon. Mating group distribution is wider and further offshore and south of the Haumuri Bluffs. Nursery groups were distributed furthest inshore and focused on the shallow area just south of the Oaro River.

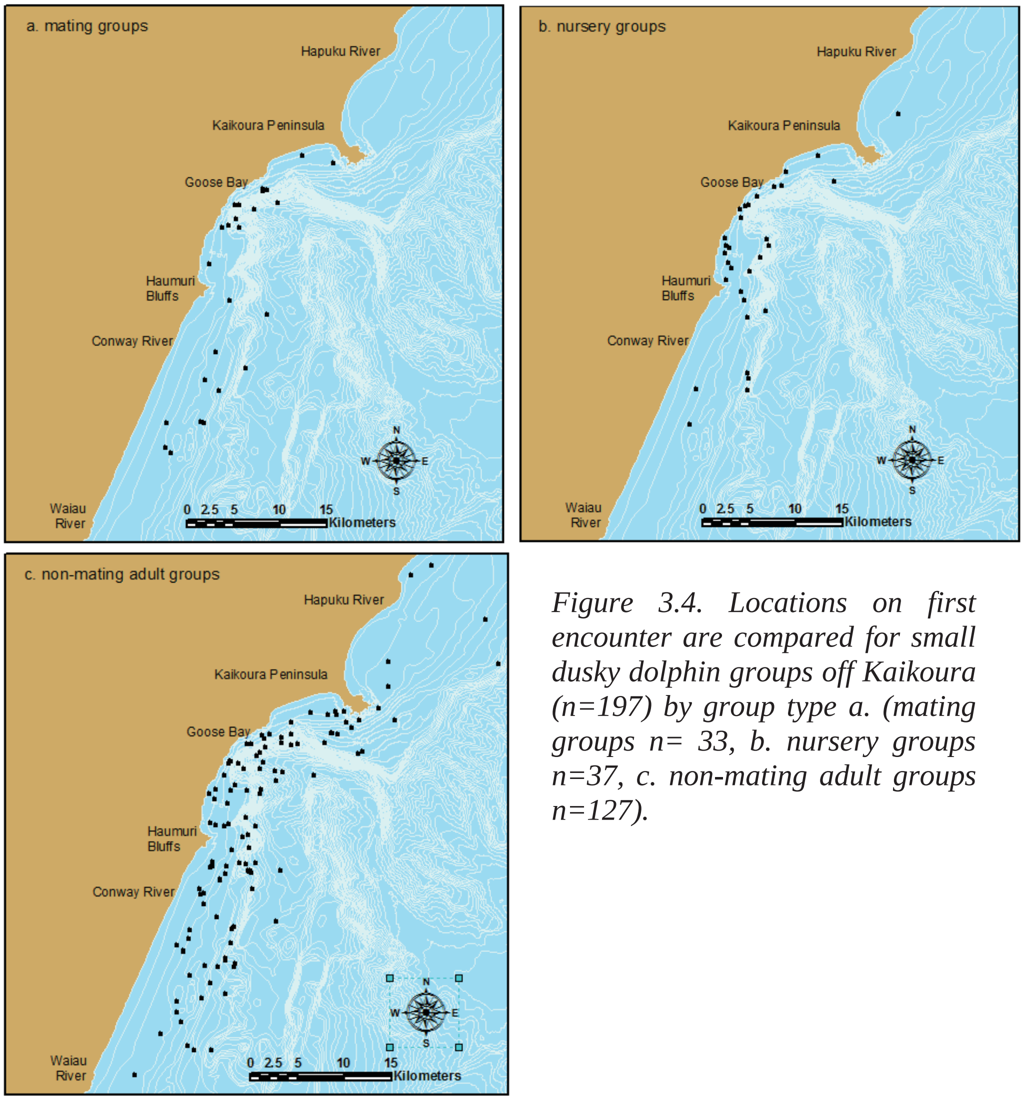


Figure 3.4. Locations on first encounter are compared for small dusky dolphin groups off Kaikoura (n=197) by group type a. (mating groups n= 33, b. nursery groups n=37, c. non-mating adult groups n=127).

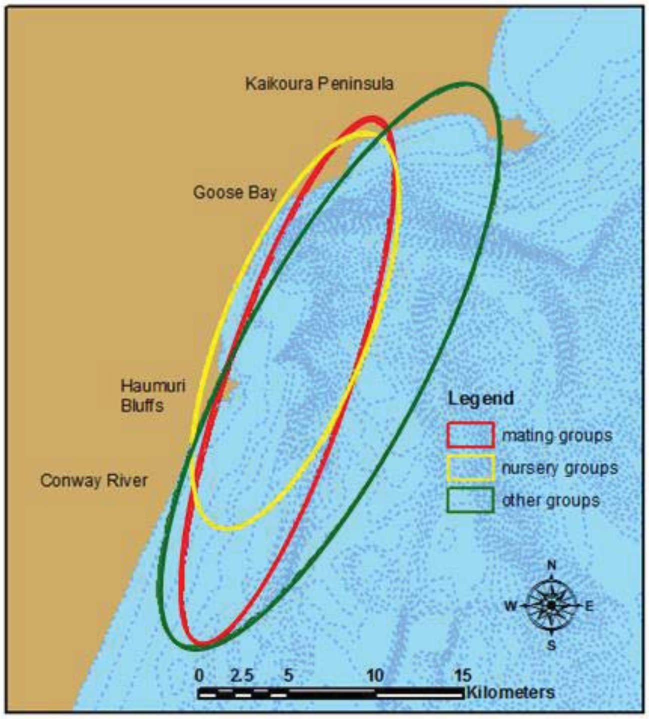


Figure 3.5. Standard deviation ellipses compare the area across which different types of dusky dolphin small groups were encountered (red line: mating groups n=33, yellow line: nursery groups n=37, green line: non-mating adult groups n=127).

Mean water depth was compared for different types of dusky dolphin small groups. Water depth varied between non-mating adult, mating groups, and nursery groups (Kruskal Wallis, H=14.208, *p*=0.001) with nursery groups found in the shallowest water (Figure 3.6). Distance from shore varied by group type (Kruskal Wallis, H=12.091, P=0.002). Non-mating adult groups of dolphins were encountered further from shore (Figure 3.6) than mating or nursery groups.

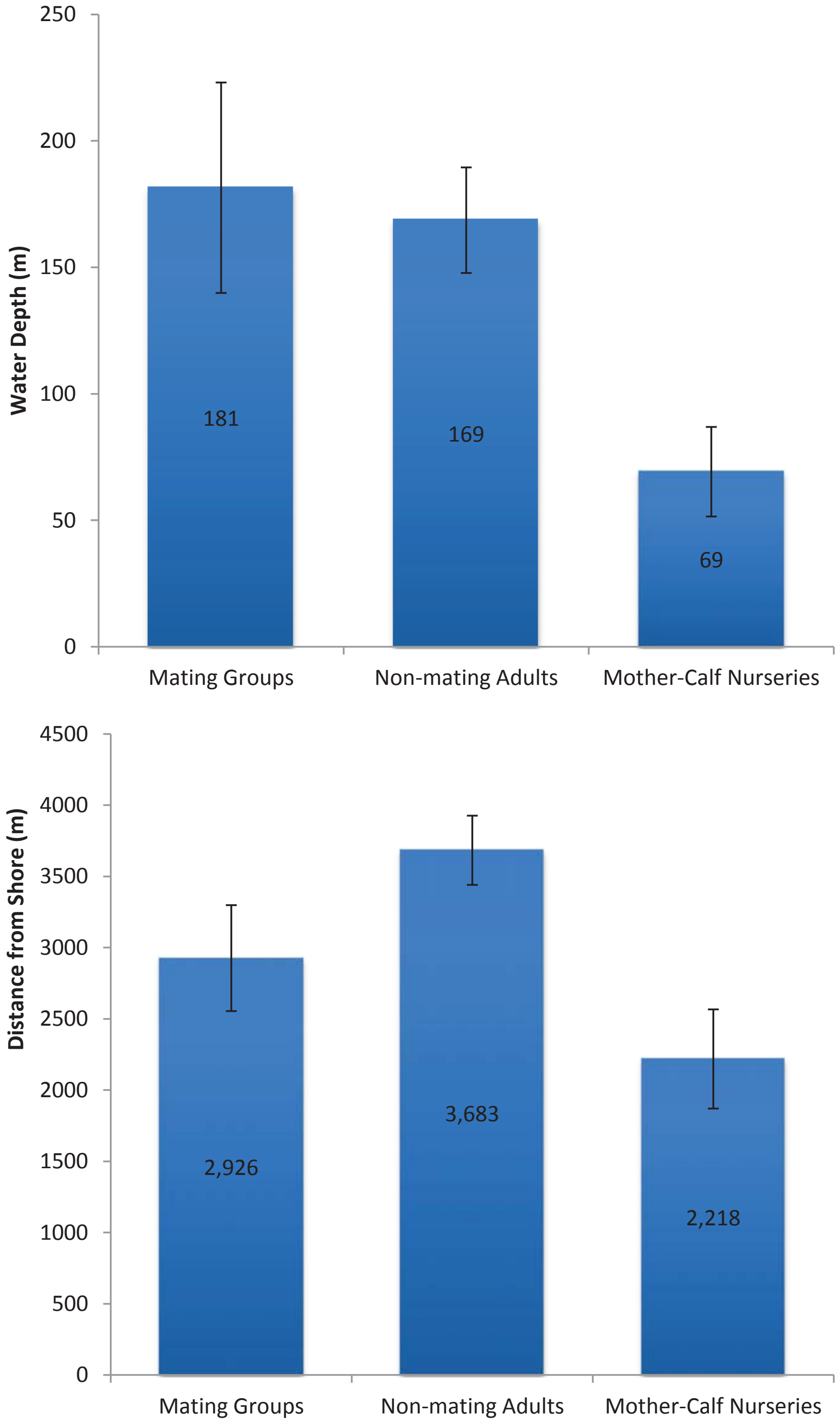


Figure 3.6. The water depth (top) and distance from shore (bottom) at which small groups of dusky dolphins were encountered are compared between mating groups (n=33), non-mating adult groups (n=127), and mother calf nursery groups (n=37). Bars represent mean depths and distances in meters with standard errors.

Distance to the nearest river mouth varied significantly between nursery groups, mating groups and non-mating adult groups (Kruskal Wallis, H=15.931, P<0.001), with nursery groups found closest to river mouths and small non-sexually active adult groups found furthest from river mouths (Figure 3.7).

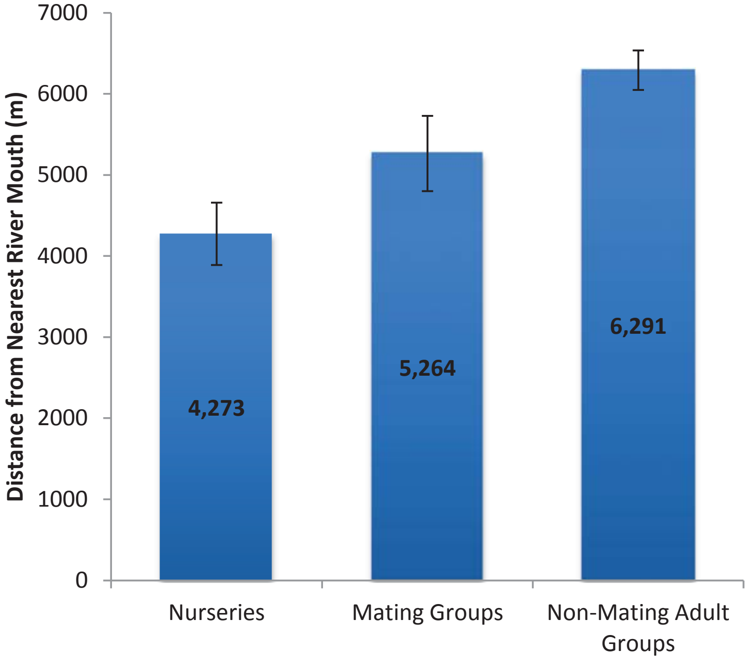


Figure 3.7. The distance to the nearest river mouth, estimated based on first encounter GPS position, is compared between small groups of dusky dolphins: nursery groups (n=37), mating groups (n=33), and non-sexually active adult groups (n=127). Bars represent means with standard errors.

Nursery groups were most closely associated with the Oaro River, while adult groups (both mating groups and other non-mating groups) associated more evenly with different rivers across the study area to the north and south (Figure 3.8).

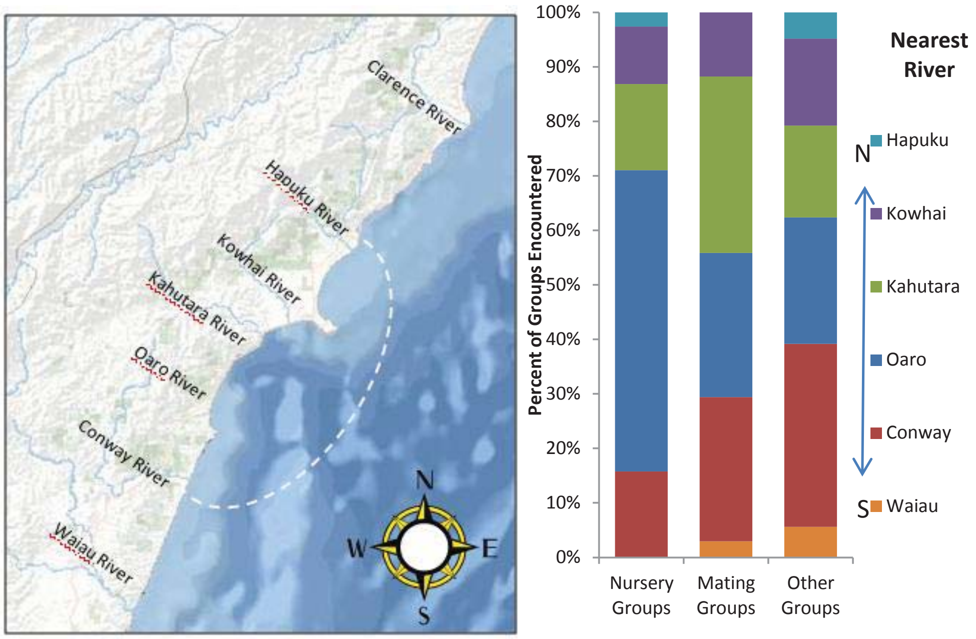


Figure 3.8. Association of dolphin groups encountered with rivers in the study area (left) is compared between different types of small dusky dolphin groups (n=197): mother-calf nursery groups (n=37), mating groups (n=33) and non-mating adult (n=127) groups (right). The white dashed line (left) indicates the primary study area, with five rivers. Surveys to the south in summer extended this area as far as the Waiau River. The stacked bars on the right show the percent of all groups encountered associated most closely by distance with each of the six rivers arranged north to south.

Group Size and Fission-Fusion Patterns

Group Size

Dusky dolphin small groups varied in mean group size per 2-min interval (Kruskal Wallis, H=9.144, p <0.05) with mean group size for nursery groups almost double that of mating or other adult groups (Figure 3.9).

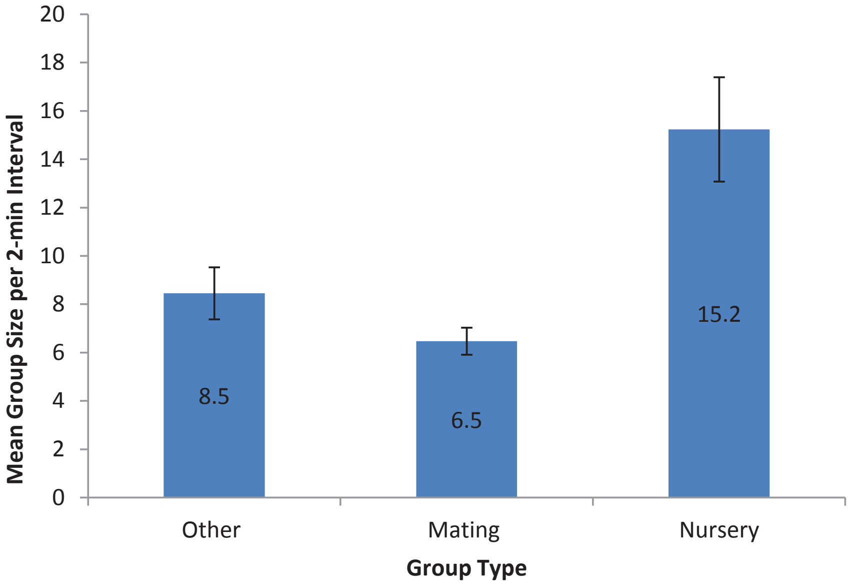


Figure 3.9 Mean group size per 2-min intervals compared by group type for dusky dolphin small groups. Bars represent mean values with standard error (n=33 other, n=11 mating and n=11 nursery groups).

Mean percent of intervals in which group size changed was 8.7±2.0% for other adult groups, 18.4±6.0% for mating groups and 11.1±4.7% for nursery groups (Figure 3.10). Although the percent of intervals with a change in group size was not significantly different among all group types (Kruskal Wallis H=2.773, *ns*), other adult mating groups had significantly fewer changes in group size than mating groups (Mann-Whitney U=126.5, $p<0.05$). The mean number of individuals leaving or entering the group during 2-min intervals was 1.9±0.5 individuals for mating groups, 6.5±2.7 individuals for nursery groups, and 4.4±0.7 individuals for other adult groups. The number of individuals leaving or entering a group per 2-min interval was significantly higher in adult non-mating groups when compared with mating groups (Mann-Whitney U=20.5, $p<0.05$).

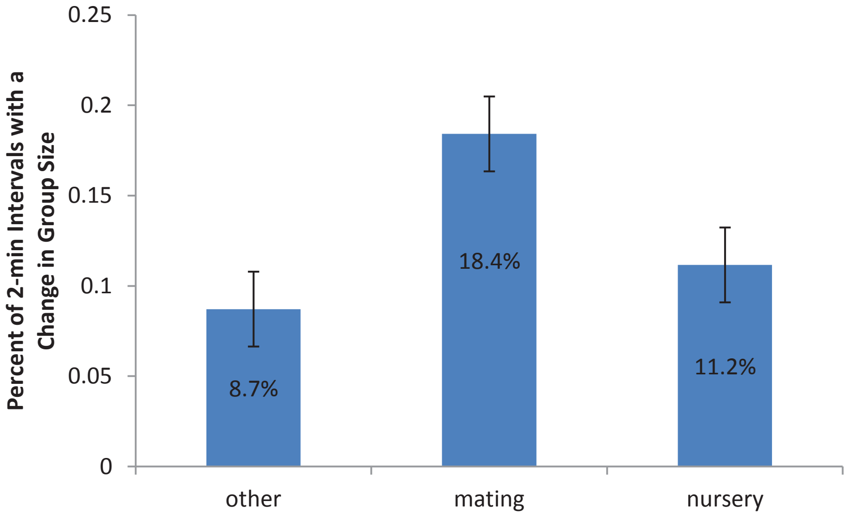


Figure 3.10. Percent of 2-min intervals with a change in group size is compared by group type. Bars represent mean values with standard error error (n=33 other, n=11 mating and n=11 nursery groups).

Group Size Duration

There were no significant differences in mean group size duration by group type. All groups had group size durations that were greater than 13 minutes, with mating group mean durations of 10.1±2.2 min and 12.1±1.0 min for other non-mating adult groups. Nursery groups had a mean group size duration of 14.8±2.3 min.

Subgroup Size

Mean subgroup size varied significantly by group type (Kruskal Wallis, H=8.141, p <0.05) with nursery groups forming larger subgroups than mating or other adult groups (Figure 3.11). Mean number of subgroups did not vary significantly by group type with similar numbers of subgroups for other adult groups (1.6±0.1), mating (1.7±0.2) and nursery (1.5±0.1) groups (Kruskal Wallis, *ns*), although subgroups were more likely to form in other adult non-mating groups (59% of groups) than in mating or nursery groups (each ~55% of groups).

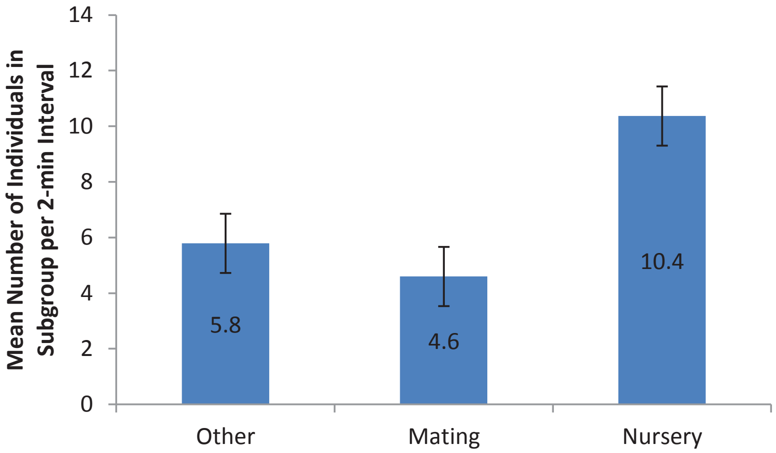


Figure 3.11 Mean subgroup size per 2-min interval is compared by group type. Bars represent mean values with standard error error (n=33 other, n=11 mating and n=11 nursery groups).

Behaviour

Behavioural States

When proportion of time spent in each behavioural state was compared by group type, nursery groups spent more time resting than other groups and mating groups spent very little time resting (Kruskal Wallis H =23.092, p <0.001). Mating groups spent the greatest amount of time milling, followed by other adult groups. Nursery groups spent only 10% of their time milling (Kruskal Wallis H =16.732, p <0.001; Figure 3.12a). Behavioural state duration varied among group types with mating groups resting for shorter durations and nursery groups resting for longer durations than other adult groups (Kruskal Wallis H=23.229, p<0.001). Dusky dolphin mating groups milled more than other adult groups and nursery groups milled less (Kruskal Wallis, H=13.742, p <0.01; Figure 3.12b).

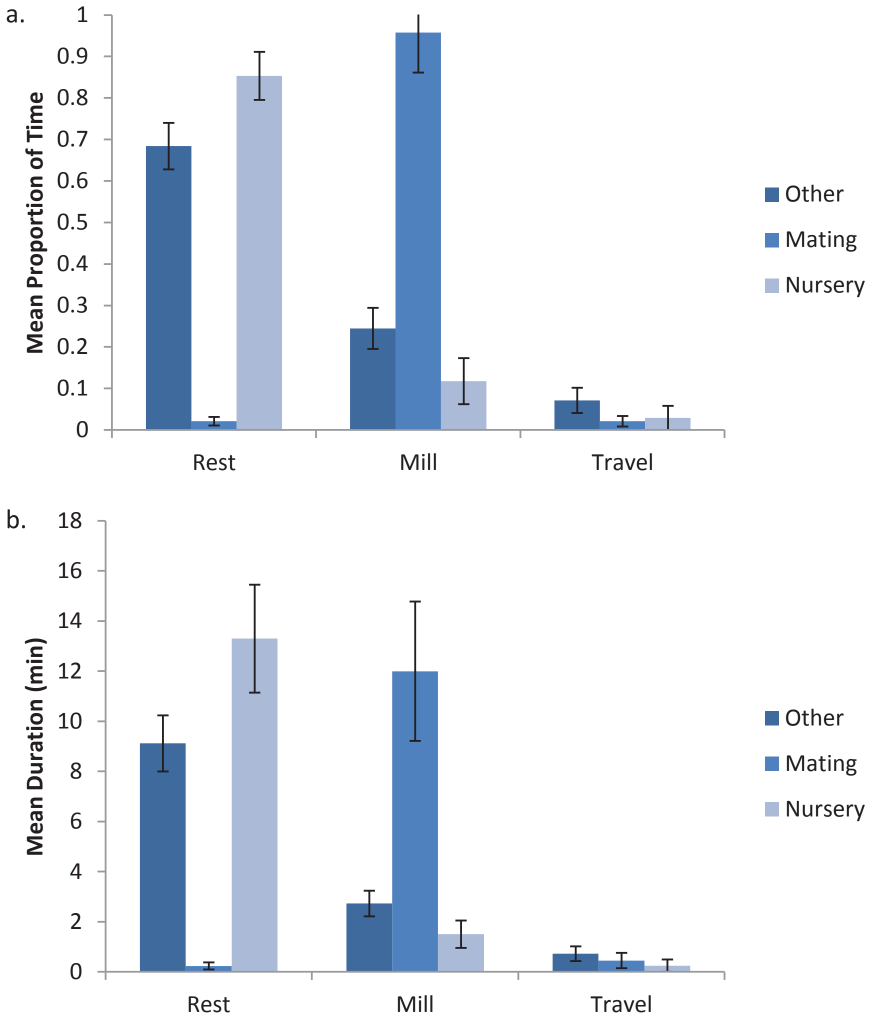


Figure 3.12 Proportion of time spent in each behavioural state (a) and duration of behavioural states (b) are compared for dusky dolphin small groups. Bars represent mean values with standard error. The behavioural state 'forage' was removed from analysis because it occurred very rarely in small groups error (n=33 other, n=11 mating and n=11 nursery groups).

Proportion of time spent at varying inter-individual distances was compared among small groups (Figure 3.13a). Groups varied in the time they spent at the tightest dispersion (< 1 body length) with nursery groups most closely grouped, followed by mating groups (Kruskal Wallis $H=7.148$, $p < 0.05$). Nursery groups spent only 5% of their time at 1-3 body lengths (medium dispersion) with mating groups slightly less dispersed than other groups

(Kruskal Wallis H=8.482, p <0.05). Only other adult groups spent any time with >3 body lengths between group members (Kruskal Wallis H=8.482, p <0.05).

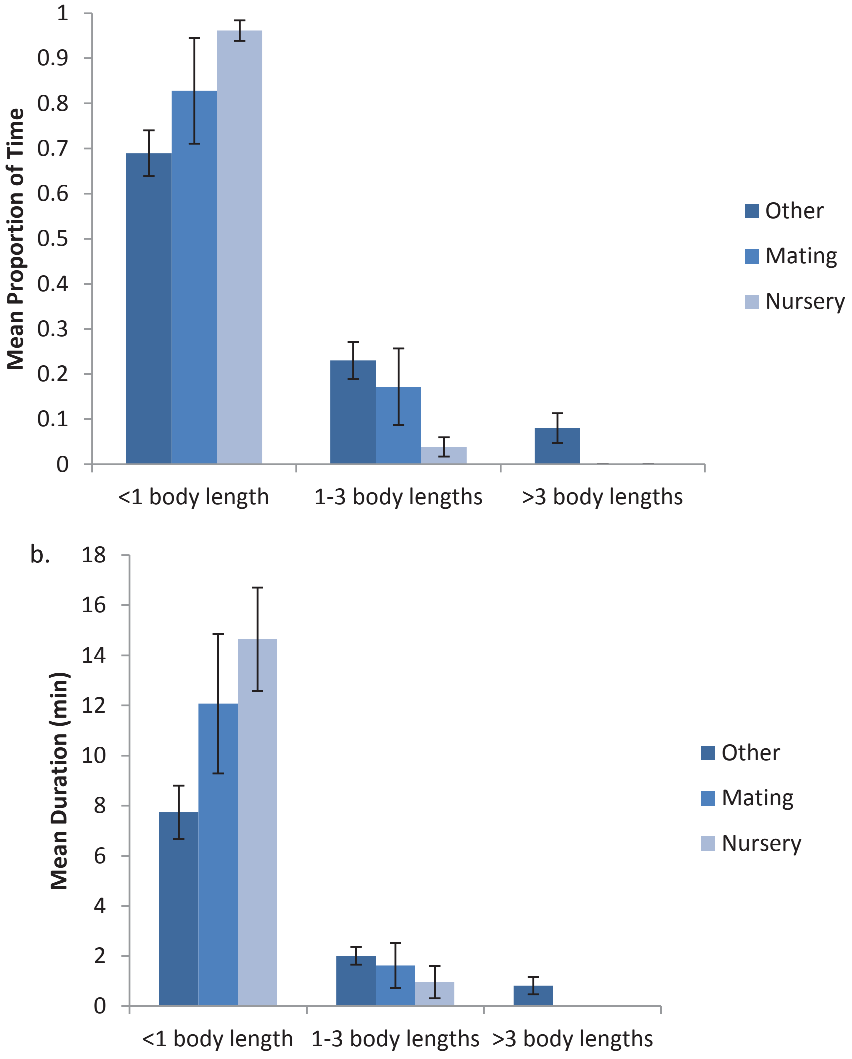


Figure 3.13 Mean proportion (a) and durations of time spent (b) at varying inter-individual distances are compared for dusky dolphin small group types. Bars represent mean values with standard error (n=33 other, n=11 mating and n=11 nursery groups).

Dusky dolphin small groups varied significantly in the duration of time spent at different dispersions, with mating and nursery groups spending longer durations with less than one body length distance between group members (Kruskal Wallis H =9.208, p <0.05). Mating and nursery groups had shorter durations than other adult groups with 1-3 body lengths distance between group members (Kruskal Wallis H =6.470, p <0.05; Figure 3.13b).

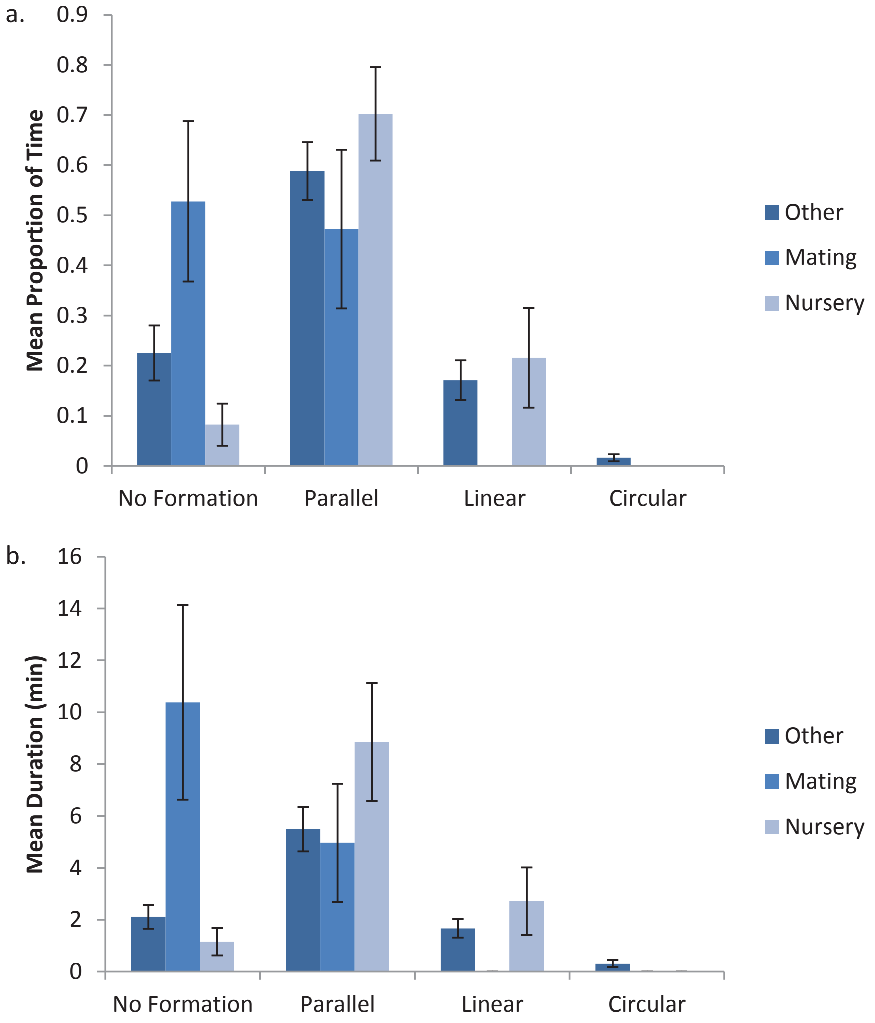


Figure 3.14 Mean proportion of time (a) and duration (b) in different formations for dusky dolphin small groups are compared by group type. Bars represent mean values with standard error error (n=33 other, n=11 mating and n=11 nursery groups).

When formation of group members was compared among small groups, mating groups spent almost no time in linear formation (Figure 3.14a; Kruskal Wallis, H=9.901, $p < 0.01$) consistent with the milling behaviour noted for these groups (above). Durations of time spent in linear formation (Kruskal Wallis, H=11.058, $p < 0.01$) and circular formation (Kruskal Wallis, H=6.112, $p < 0.05$) were significantly different by group type with mating groups the least likely to spend time in either linear or circular formation.

There were no significant differences in either mean duration or proportion of time by group type in the direction of movement (Kruskal Wallis tests, *ns*). All small groups tended to move in variable directions and did so for mean durations of more than 10 min (other adult groups=10.6±1.3, mating groups=12.9±2.5, nursery groups= 13.1±2.6). Nursery and other adult groups spent almost 80% of their time moving in variable directions (Figure 3.15). Mating groups that had very high reorientation rates (see analysis below) spent almost 95% of their time in non-directional movement.

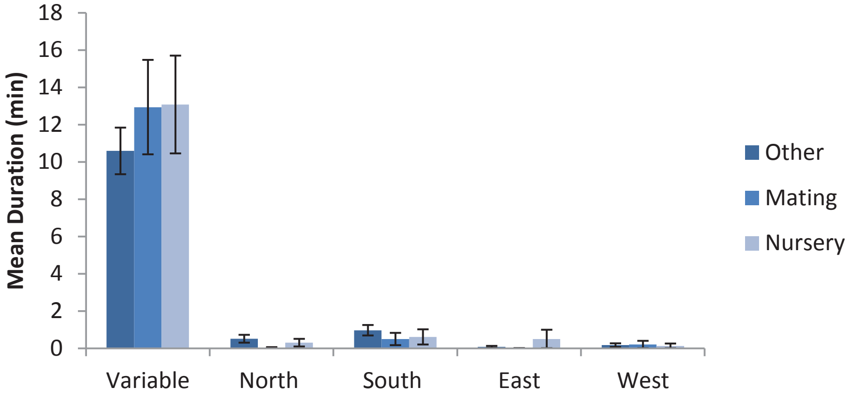


Figure 3.15. Most small dolphin groups spent a majority of their time in a variable directional heading. There were no significant differences among groups in heading (n=33 other, n=11 mating and n=11 nursery groups).

Behavioural Events

The frequency of events differed by small group type. Play behaviours were most common in mating groups with 'blow bubbles' occurring most often in mating groups followed by non-mating adult groups (Kruskal Wallis, H=24.065, p <0.001). Spyhopping occurred most often in mating groups and was likely related to female mating strategies (see below). This behaviour occurred more often in nursery groups (Kruskal Wallis, H=11.752, p <0.01) than other adult groups. In nursery groups, spyhopping by calves was noted in summer. Playing with kelp was scored only for mating groups during the current study (Figure 3.16).

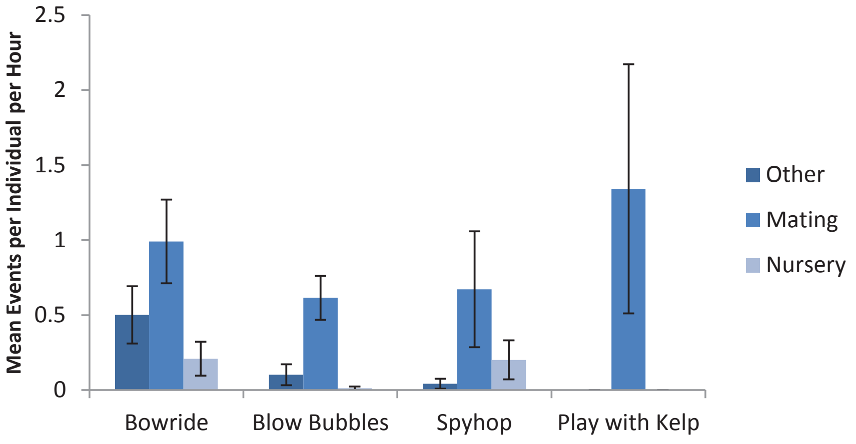


Figure 3.16. Frequency of play behaviours are compared by group type for dusky dolphin small groups. Bars represent mean frequencies with standard errors (n=33 other, n=11 mating and n=11 nursery groups).

High speed behaviours occurred most often in mating groups (Figure 3.17) with group speed bursts (Kruskal Wallis, H=6.136, p <0.05) and porpoising (Kruskal Wallis, H=19.301, p <0.001) occurring in nursery and other adult groups with less frequency. Leaping behaviour, such as re-entry (Kruskal Wallis, H=42.534, p <0.001) and noisy leaps (Kruskal Wallis, H=12.259, p <0.01) occurred most frequently in mating groups, with re-entry leaps least frequent in other groups and noisy leaps very rare for nursery groups (Figure 3.17).

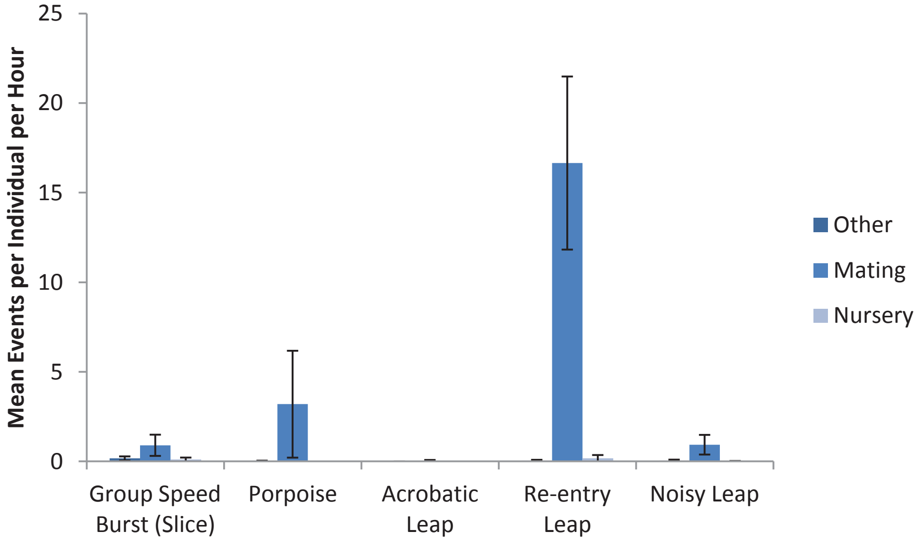


Figure 3.17 High speed behaviours are compared by group type. Bars represent mean frequencies per individual per hour with standard error (n=33 other, n=11 mating and n=11 nursery groups).

The frequency of social and contact behaviours varied significantly by group type (Figure 3.18). Contact (social) rubs (Kruskal Wallis, H=20.384, *p* <0.001), speed bursts (slice) (Kruskal Wallis, H=19.915, *p* <0.001), and tail slaps (Kruskal Wallis, H=10.521, *p* <0.01) were all much more common in mating groups than other small groups. Chasing of conspecifics (Kruskal Wallis, H=28.310, P<0.001), inverted swimming (Kruskal Wallis, H=19.022, *p* <0.001) and ventral contact (Kruskal Wallis, H=44.347, *p* <0.001) were most common in mating groups, with reduced frequencies for these events in nursery and other adult groups. Although synchronous surfacing was not significantly different among group types (Kruskal Wallis, *ns*), when this behaviour was compared between mating groups and other adult non-mating groups, synchrony was higher for adults in mating groups (Mann Whitney U=117, *p*<0.05). Social-sexual behaviours such as sexual approach (Kruskal Wallis, H=26.888, *p* <0.001) and confirmed intromission (Kruskal Wallis, H=48.294, *p* <0.001) were only scored for mating groups, consistent with the methods for defining mating groups in this study. Birds feeding with dolphins did not occur at greater frequency with any specific small group type (Kruskal Wallis tests, *ns*).

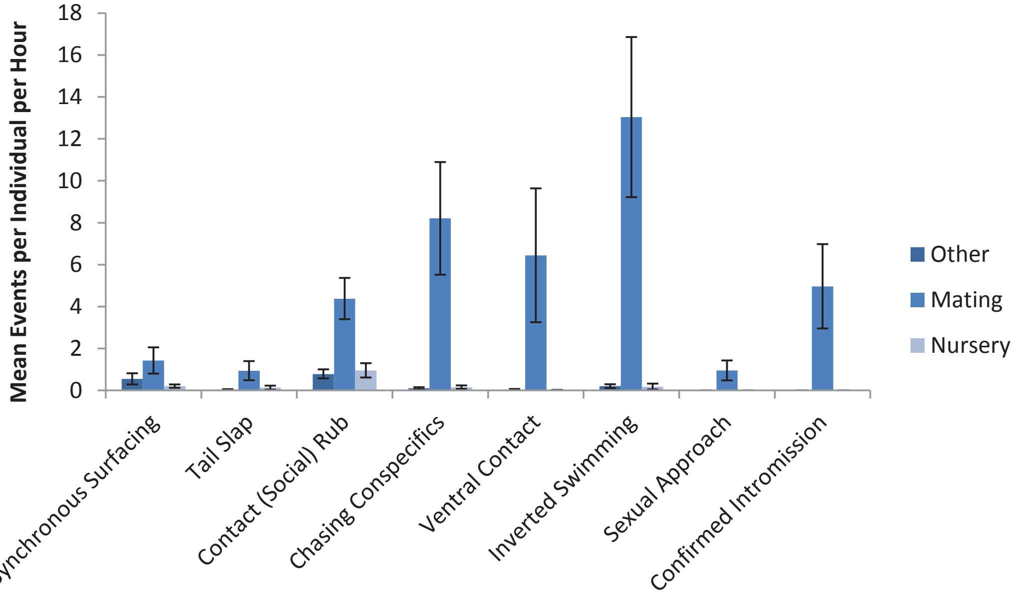


Figure 3.18 Social events are compared by group type for small groups. Bars represent mean frequencies with standard error (n=33 other, n=11 mating and n=11 nursery groups).

Both the number and type of behavioural events displayed varied significantly with group type. Mating groups had the greatest number of behavioural events per individual per hour (Figure 3.19; Kruskal Wallis H=26.072, p <0.001). Mating groups had a greater variety of behavioural events displayed (Kruskal Wallis H=26.217, p <0.001).

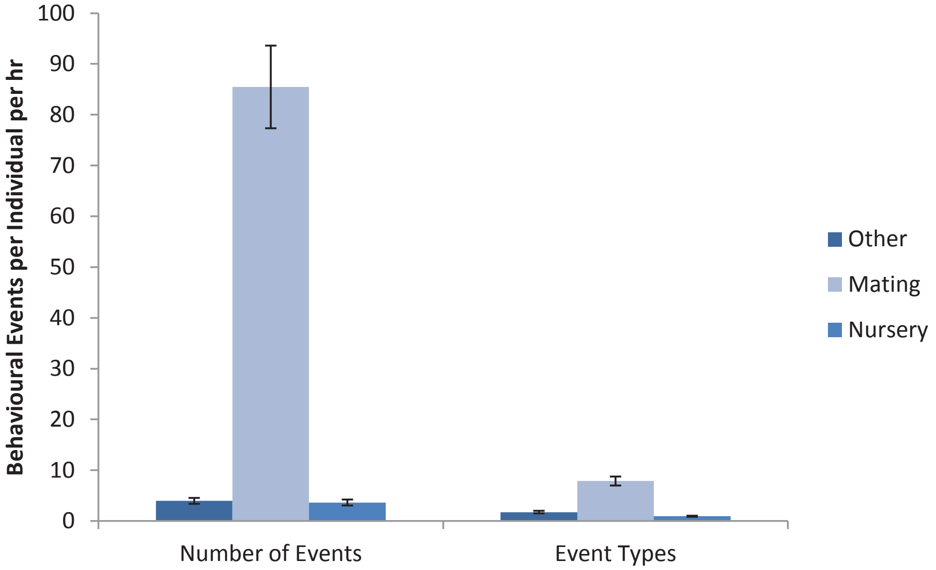


Figure 3.19 Behavioural events per individual per hour are compared by dusky dolphin small group type. Bars represent mean values with standard error (n=33 other, n=11 mating and n=11 nursery groups).

Dive Duration

Dive duration varied significantly for adult non-mating, mating and nursery groups (Kruskal Wallis, H= 9.212, p =0.01), with durations about half as long in mating groups as in nursery or other adult groups (Kruskal Wallis, H= 9.212, p =0.01; Figure 3.20).

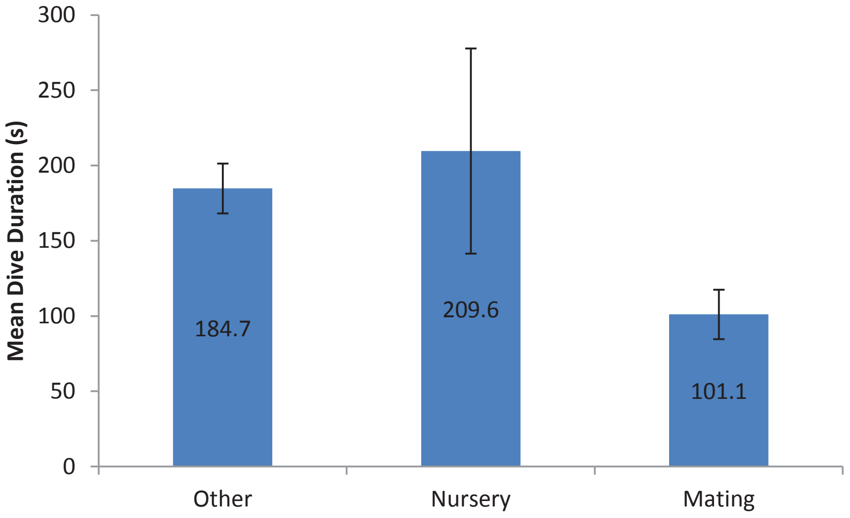


Figure 3.20. Mean dive duration in seconds is shown by group type. Bars represent mean values with standard errors (n=33 other, n=11 mating and n=11 nursery groups).

Behaviour of Dolphins in Adult Non-Mating Groups

Although seasonal changes were less pronounced in non-reproductive adult groups than in those groups engaged in reproductive effort and parental care (mating groups and mother-calf nurseries), they did show a seasonal shift in habitat use. Mean water depth and distance from shore varied seasonally for small groups of adult dolphins (Kruskal Wallis tests, depth: $H = 24.906$, $P<0.001$, distance: $H = 36.737$, $P<0.001$). Small adult dolphin groups were found closer to shore in summer and autumn, moving offshore in winter and spring, and into the deepest water in spring (Figure 3.21).

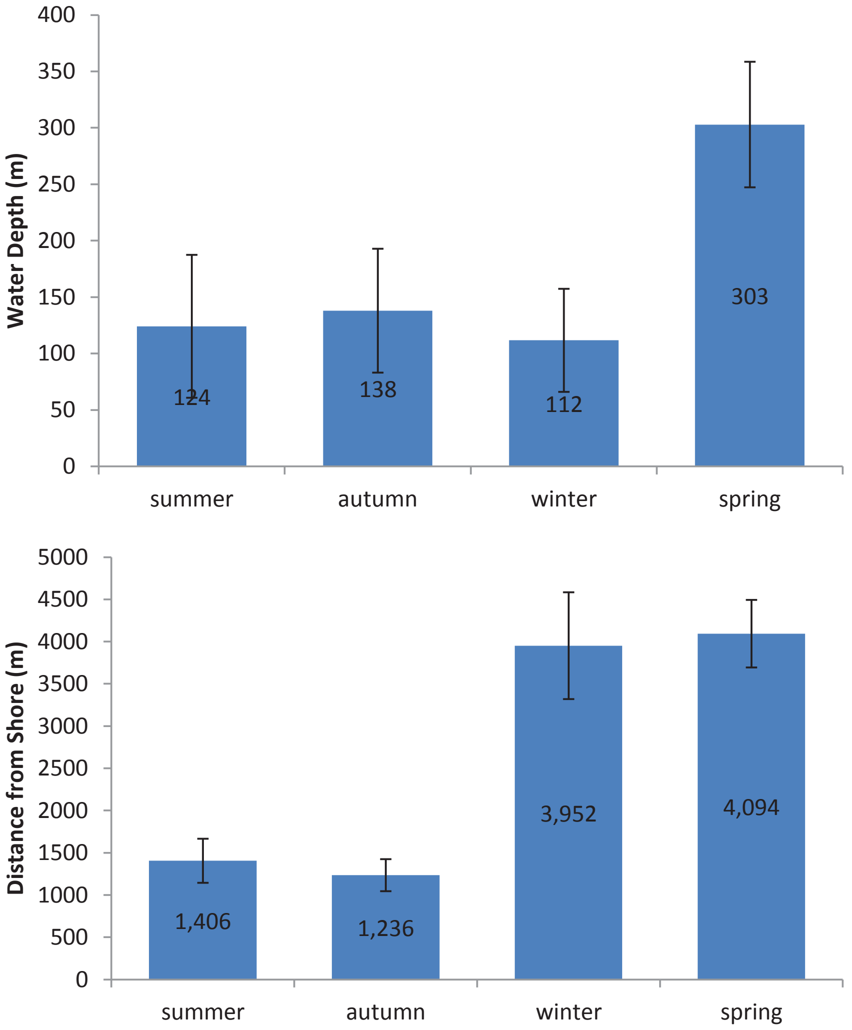


Figure 3.21 Depth and distance from shore are shown by season. Bars represent mean values with standard error (n=3 summer, n=7 autumn, n=11 winter and n=12 spring).

Behavioural state, group dispersion, swimming formation, and directional heading did not vary significantly by season in small non-mating adult groups (Kruskal Wallis tests, *ns*).

Swimming formation of small non-mating adult groups varied by time of day, with dolphins swimming in linear formation significantly more often in the morning (Mann-Whitney, U=83.5, $P<0.05$) and swimming out of formation significantly more often in the afternoon (Mann-Whitney, U=81, $P<0.05$; Figure 3.22).

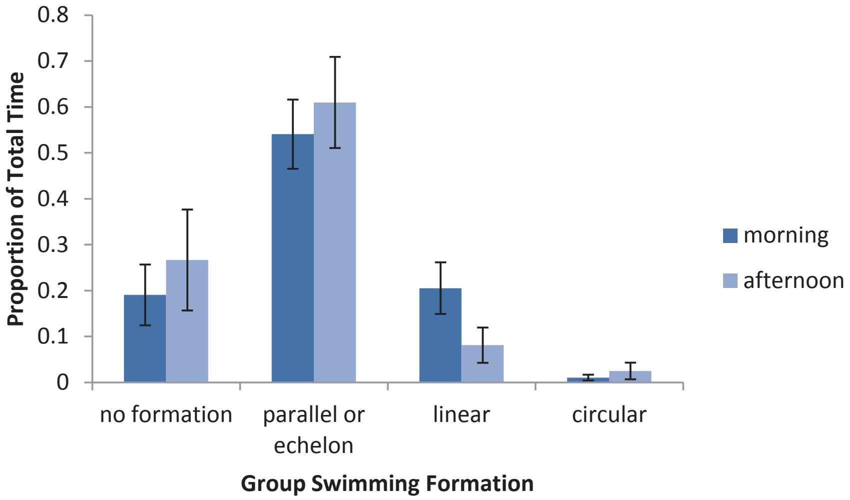


Figure 3.22. The swimming formation of small, non-reproductively active adult groups is compared by time of day. Bars indicate means with standard errors (dark bars = a.m., light bars = p.m., n=23 morning, n=10 afternoon).

Water depth and distance from shore did not vary by time of day in small non-mating adult groups (Kruskal Wallis tests, *ns*).

Behaviour of Dolphins in Mating Groups

Copulation rate was negatively correlated with reorientation rate (Kendall's tau, $R^2 = 1.0$, $p = 0.04$) suggesting that as dolphins' rate of reorientation increased, the rate of intromission decreased. Rapid chases of a single female by multiple males with frequent changes in direction may extend copulatory chases and increase the inter-copulatory interval in mating groups. Calculated mean values for linearity, leg speed and reorientation rate for mating groups are shown in Table 3.1. These values likely underestimate actual swimming speeds and overestimate linearity due to the limited maneuverability of the vessel relative to the dolphins. Mean inter-copulatory interval for dusky dolphins in this study was 78 s (min 40 s, max 353 s).

*Table 3.1. Movement patterns of small mating groups off Kaikoura**

Group	**% Linearity** (total/net km)	**Reorientation Rate** (degrees/minute)	**Leg Speed (km/h)** Mean	Top	Variance
min	**10%**	**10.8**	**1.7**	**2.6**	**0.4**
mean	**55%**	**35.9**	**3.8**	**11.5**	**8.3**
max	**89%**	**72.3**	**7.2**	**27.0**	**22.7**

*The data related to linearity, reorientation rate and leg speed presented in this table and the above text for mating groups are adapted from *Markowitz et al. 2010a*. These results include data I collected during the current study, as well as data collected previously by T.M. Markowitz and L.M. Morton.

Mean (± se) duration of surface chases (include group speed bursts and travelling at the surface) in mating groups was 20.6 ± 3.6 seconds. The longest surface chases (55s, 29s) occurred in smaller groups (3 individuals) coinciding with higher intromission rates (1.2 per min).

Apparent agonistic behaviours documented included jostling for position, biting (on one occasion), open mouth threats (on two occasions), and a "rolling over" behaviour in which one male rolled over the top of a copulating pair of dolphins, forcing the coupled pair to split apart (on six occasions; Figure 3.23).

Figure 3.23 Dolphin social contact in the context of mating is shown. One dolphin is performing a 'rollover manoeuvre' in an attempt to break up a mating pair. A fourth dolphin is approaching from behind the group.

When sex could be determined, individuals performing inverted swims, chases and sexual approaches were always male. Individuals at the surface during copulations were always female. These results are consistent with sex of individuals confirmed in other studies of mating off Kaikoura (Markowitz et al. 2010a). The (presumed) female at the surface during copulation maintains a body position with both the head and tail stock at the surface or even held above the water resulting in an unusual ‘U-shaped’ dorsal surface (Figure 3.24). Most confirmed copulations for mating groups resulted in the individual on top maintaining this characteristic position for the duration of copulation. As this behaviour can be seen from some distance, it may be used to help indicate copulation and duration of copulation in dusky dolphins.

Figure 3.24. A characteristic ‘U-shaped’ position is held by the individual at the surface during copulation.

The mean (± se) duration of intromission was 6.8 ± 4.59 seconds. The highest intromission rate (1.5 per minute) and maximum intromission duration (22 seconds) both occurred in a small group consisting of two males and a single female. Synchronous ventral chases with copulations by both males in quick succession occurred repeatedly. Longer copulations were performed by the first male in the sequence, which may indicate sperm competition in what appeared otherwise to be a relatively non-competitive interaction.

Synchronous surfacing and re-entry leaping occurred in all groups with a mean of 2.5±0.2 individuals surfacing synchronously and 2.5±0.3 re-entry leaping synchronously. In 13 cases where more than two individuals performed synchronous re-entry leaps only one led to subsequent intromission, suggesting that when competition between males is greater (with two or more leaping after the female at once) successful intromission is less likely to immediately follow. Most intromissions were scored after re-entry leaping by just 1 or 2 individuals.

The mean (± se) duration of below surface chases following re-entry leaps in mating groups was 11.5±2.6 seconds while the highest number of intromissions between re-entry leap events was 8. These longer sequences of intromission were observed in a small group of three dolphins. The female in this group was observed playing with kelp (which was a play behaviour observed most often in mating groups, see Figure 3.25).

Figure 3.25. Re-entry leaping is shown. Re-entry leaping is common in mating groups with most intromissions scored after re-entry leaping of two individuals at the beginning of a chase sequence.

The depth and distance from shore at which small mother-calf nursery groups were encountered varied significantly by season (Kruskal Wallis, depth H= 12.805, P=0.005, distance H=11.491, P=0.003), with nursery groups encountered in deeper water, further offshore as calves matured (Figure 3.26). Approximate age of calves in this study was: summer 0-3 months, autumn 3-6 months, winter 7-9 months, spring 10-12 months. Due to the nature of the sampling times in this study (early spring), no neonatal calves were observed during the spring. Water depth and distance from shore of nursery groups did not vary significantly by time of day (Kruskal Wallis, depth H= 2.289, *ns*, distance H=1.676, *ns*).

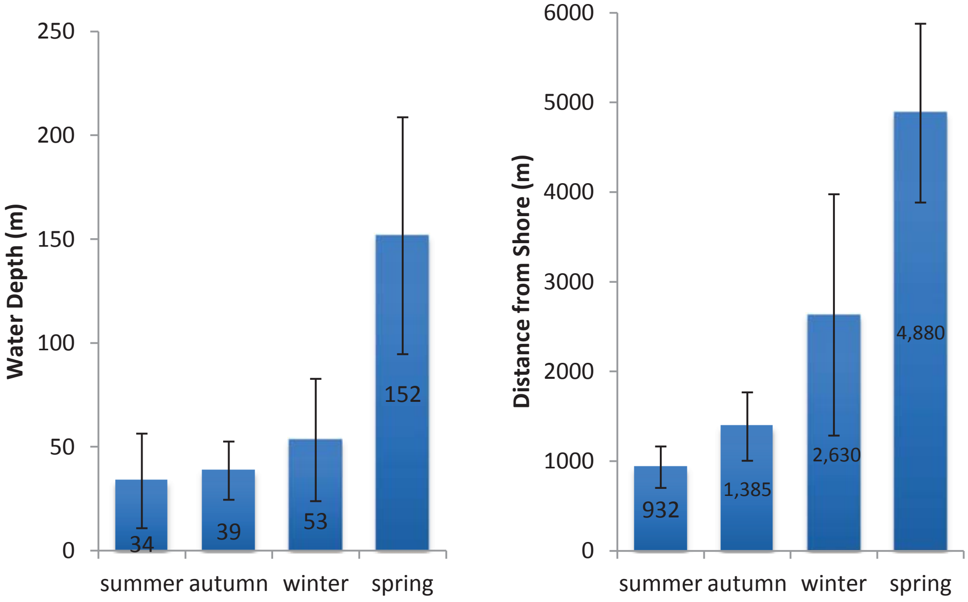


Figure 3.26. The water depth (left) and distance from shore (right) at which nursery groups comprised of dusky dolphin mothers and calves were encountered are compared by season (seasons are arranged according to the approximate age of the calves). Bars represent mean depths and distances in meters with standard errors (n=10 summer, n=12 autumn, n=6 winter, n=12 spring).

Examination of the areas nursery groups were encountered by season (standard deviation ellipses, Figure 3.27) showed that mothers with calves were found across a relatively small area near shore when the calves were youngest (summer and autumn) and across a broader area as the calves approached the age of one year (winter and spring). In summer, nursery groups occurred in a tight band alongshore in the shallow, sheltered waters from Goose Bay to the Haumuri Bluffs. In autumn nursery groups moved closer to deeper waters of the Kaikoura Canyon, but remained near shore in the Goose Bay region. By winter, the nursery groups ranged more widely, further offshore and in deeper water. In early spring (September to mid-October), nursery groups were found further offshore and to the south of the Haumuri Bluffs (Figure 3.27)

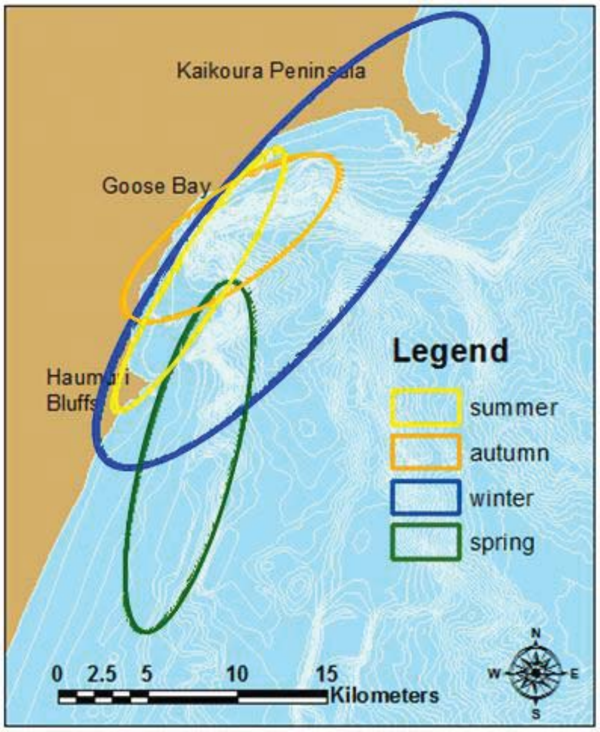


Figure 3.27. Standard deviation ellipses are used to compare the areas in which mother-calf nursery groups were encountered off Kaikoura (n=37) by season (spring = September-November, summer = December-February, autumn = March-May, winter = June-August, n=10 summer, n=12 autumn, n=6 winter, n=12 spring).

High speed behaviours by calves occurred in all seasons with most speed burst (‘slicing’) behavioural events (16) scored in summer. Calves spyhopped in summer and autumn with 5 events in summer and 3 in autumn. Re-entry leaping and tail slapping were both sequences of behaviour among mother calf pairs that were initiated by an adult and copied by a calf (within 15 s) during focal follows in autumn.

Social rubs were initiated by calves in all seasons, with the highest percent of social rubs initiated by calves in nursery groups encountered in late autumn (33%) and in winter when calves were generally >6 months old (100%). Belly presents from adult to calf occurred in summer and autumn, with most occurring in summer (19 events) when calves were youngest. Calves presented to adults at a lower rate with most occurring in summer (5 events). In one sequence of behaviour in late autumn, a calf performed ‘ventral present’ behaviour to an adult, then chased the adult and made ventral contact. This sequence of behaviour was observed 4 minutes before the only incidence of a calf making rostrum-genital contact with an adult (possibly nursing) was observed for the group. Calf chases of adults were scored primarily in autumn.

DISCUSSION

Adult Non-Mating Groups

Habitat Use

Non-mating adult groups were encountered year-round throughout the Kaikoura Canyon habitat. Unlike nursery and mating groups that were located in the immediate vicinity of the Kaikoura Canyon, other adult groups were more dispersed and located further to the north and south of the canyon, with groups south of the Haumuri Bluffs further from shore and in deeper water. They showed a seasonal shift in distribution, generally remaining within 2 km of shore in summer and autumn, and moving offshore in winter and into deeper water in the spring. They were generally further offshore than groups engaged in parental and reproductive effort, especially during the summer, when calves were youngest and mating groups most active. This wider distribution and distance from the productive canyon habitat may indicate reduced energetic stress for adult non-mating groups when compared with individuals in calf-rearing or mating groups. Adult and subadult mixed-sex groups form commonly in animals (Wells 1991, Ruckstuhl and Neuhaus 2002), with groups tending to range more widely in search of resources, particularly in the less productive winter (Avery 1994). Non-mating adult groups were found further from shore, and further from river mouths than nursery or mating groups, but in shallower water than mating groups. Formation of small mixed-sex groups may allow individuals of similar age and size to synchronise their movement and behaviour patterns at Kaikoura.

Group Size

Group size of non-mating adult groups was less than nursery group size, but similar to the group size of mating groups (8 individuals). Although group size was similar between non-mating and mating groups, the pattern of fission-fusion varied between the two group types. Fission-fusion events were rarer in non-mating groups than in mating groups. However, when such events occurred in non-mating adult groups, they involved a greater number of individuals either joining or leaving the group at one time than in mating groups. Overall, non-mating adult groups had intermediate fission-fusion rates between mating groups (high) and nursery groups (low).

The sex-class composition of non-mating adult groups is unknown, but there is no reason to suspect that it does not reflect the 1:1 sex ratio of males to females found for large groups of dusky dolphins off Kaikoura (Harlin 2004). Group sizes for non-mating groups are likely driven by the particular needs of sub-adult and adult group members in response to both the distance from the relative safety of the large group and fine-scale changes in habitat such as depth and distance from shore (Bednekoff and Lima 1998, Beecham and Fransworth 1999). Social interactions with group members may also influence the fission-fusion patterns of these groups (Boehm 1992, van Hoof and van Schaik 1992). Adult groups may form stable associations over time as has been suggested by Markowitz (2004) or could simply be fluid associations of individuals that seek nearby partners for resting throughout the day (Shelton et al. 2010).

Behaviour

Other adult groups maintained intermediate behavioural state patterns between the two extremes of almost continuous resting for nursery groups and very active milling for mating groups, providing a sort of ‘control’ of behaviour for dusky dolphin small groups without the demands of lactation and parental care or rigorous mating competition. Travelling was rarely observed among small groups in this study compared with large groups (Chapter 2).

Distance between group members was greatest for other adult non-mating groups that were not raising calves, resting as much or performing such coordinated activities as occur in mating groups. This finding, along with lack of surfacing synchrony among group members when compared with mating groups, suggests that these groups may be less stable and coordinated than other groups.

Small, non-mating adult groups were more likely to swim in linear formation during morning hours and lack a clear swimming formation in the afternoon. This finding could be related to the dolphins' diel feeding schedule, with small groups more likely to return from a night of foraging swimming in formation, then becoming less coordinated in their movements following the period of greatest rest in the middle of the day (Würsig et al. 2007). Relatively few observations were made during this study of small adult groups very late in the day, when the dolphins typically move offshore to feed (Dahood and Benoit-Bird 2010).

The lack of significant difference by group type in directional heading is not surprising. Most small groups were non-directional in movement patterns, particularly when compared with movement patterns of dolphins in larger groups (Chapter 2). Dolphins may prefer to range directionally in larger groups to avoid the risk of predation when encountering new habitat and then break off from the main group when they arrive to strengthen social bonds and capitalise on the benefits of associating in smaller groups (Chapman et al. 1993, Kinsey and Cunningham 1994).

High speed behaviours were rare for non-mating adult groups. Reduced frequencies for these behaviours may be an anti-predator strategy (reducing conspicuousness and chance of detection). Contact (social) rubs occurred in all group types with almost one social rub per individual per hour in both nursery and adult non-mating groups. The comparable rates of social rubs for adult non-mating groups and nursery groups suggest that non-mating groups, although more dispersed, are still maintaining contact with group members through the delphinid version of grooming behaviour. Dive durations for non-adult mating groups were similar to durations for nursery groups.

Mating Groups

Habitat Use

Mating groups were only encountered in summer and early autumn, whereas nursery and other groups were encountered year round. Although mating groups were relatively close to shore (compared with non-mating adult groups), they were much more likely to be found in deep water. It is possible that females maintain locations for mating groups in deep water to increase manoeuvrability for three-dimensional chases (described below); however, a more parsimonious explanation may be that the depth is simply a function of proximity to large groups in deeper water rather than intentional habitat selection by group members.

Mating groups were encountered closer to river mouths than non-mating adult groups. As these groups have similar sizes, the behaviour of the groups may be related to group locations. Mating group activity is particularly ‘loud’ and is likely audible from a distance. Mating groups could maintain proximity to river mouths to reduce the risk of predation. Males in mating groups seek out females in nursery groups for mating opportunities. On occasion in this (and other) studies, males were seen to enter and begin mating chases in the midst of nursery groups (Markowitz 2004, Weir et al. 2010). Access to females in nursery groups may keep mating groups closer to females and therefore closer to river mouths.

Group Size

Mating groups had significantly more changes in group size than adult non-mating groups. This reflects the dynamic nature of mating groups involving chases, high speed activities and leaping behaviour. The mean duration of group size for mating groups was over 10 minutes. This duration is almost twice that of group size durations for dusky dolphins foraging in Admiralty Bay, New Zealand (5.2 min, Pearson 2009). As predicted, mean group size was smaller for mating groups than other small groups. Reduced group size would allow for less competition among group members for access to females. Although rates of fission-fusion were high for mating groups, the mean number of individuals leaving and joining groups were relatively low (1.9±0.5) when compared with other group types. The competitive nature of mating groups may limit the number of individuals joining mating groups and the motivation level of male dolphins in these groups could cause fewer to leave at any one time.

Behaviour

The behavioural state most often scored for mating groups was milling, with very high frequencies of social behavioural events. This is consistent with predictions for these groups and is a result of the tremendous activity, reorientation and leg speed (see below) for dusky dolphin mating groups off Kaikoura. These parameters reflect the sperm competition (dusky dolphins have the largest testes for their body size among odontocetes, 8.0%, van Waerebeek and Read 1994, Pabst et al., 1999, Connor et al. 2000) and perhaps also the 'mating of the quickest' promiscuous mating system for dusky dolphins (Markowitz et al. 2010a). Mating activity in bottlenose dolphin groups that sequester females is much more an aggressive contest for dominance, and mating sequences are likely to be quite different. Other cetaceans with sperm competition (e.g., right whales, *Eubalaena australis*) share some of the characteristics of multiple males competing for access to females through agility. Like dusky dolphins, groups of male right whales that have the largest testes on earth (900 kg, Pabst et al. 1999), attend single females with copulations or attempted copulations by different males in the group (Boyd et al. 1999). In the case of the right whales, contests of agility are less about speed than about manoeuvrability as males engage in relatively slow motion bouts of "jousting" with penises >14% of their body length compared to 7.5-11% for other mysticetes (Wells et al. 1999). Female right whales have been observed to copulate with multiple partners in a relatively short amount of time (Connor et al. 2000), with simultaneous intromission by more than one male with a single female reported (Brownell and Ralls 1986, Würsig 2000a, Mate et al. 2005), a feat not yet observed in dusky dolphins.

Participating in mating behaviour while in or very near the Kaikoura Canyon habitat and in the vicinity of large groups for protection from predators may provide males with the best trade-off for participating in competitive small groups. Males maintain the ability to rejoin the large group and access to productive foraging grounds during the breeding season for the additional energetic input to meet the demands of these high-energy chases. Although direct aggression between males does not occur often in these mating interactions, there is some evidence for male-male competition in the form of chasing contests of quickness and agility (Markowitz et al. 2010a).

The lack of consistent group formation patterns for mating groups reflects the high speed activity and movement patterns for these groups. Swimming in formation suggests coordination while swimming without formation indicates every dolphin for himself, as might be expected in a case of "mating of the quickest" (Markowitz et al. 2010a).

The prevalence of play behaviours in mating groups, particularly when compared with nursery groups, may indicate the importance of play in the context of mating for dusky dolphins. Play behaviour has been well-documented for dusky dolphins and other delphinids in the context of social and reproductive mating (reviewed by Würsig 2009). The social context for play behaviour has been documented for a number of species, but particularly for primates (Bekoff 2001). Primates use play behaviour to socialize young, to reinforce social bonds and learn about their environment. Bubble blowing in cetaceans is a common behaviour used in the contexts of both foraging (Clapham 2000), and social 'play' behaviour (Slooten 1994). It has been described for captive beluga whales (*Delphinapterus leucas*) as both a social signalling ('alert') behaviour and play behaviour (Hill et al. 2011), and for Hector's dolphins (*Cephalorhynchus hectori*) in both social 'play' and agonistic contexts (Slooten 1994). In the context of dusky dolphin mating group interactions, bubble blowing may be agonistic (toward conspecifics), may add a level of confusion to the chase, or may simply be a play behaviour used to reinforce bonds during competition.

The most common play behaviour for mating groups was 'playing with kelp'. This behaviour is a form of 'object play' that can be used to learn from peers (Fedigan 1972), particularly when the object is associated with a 'tug-of-war' or when the object passes among group members and is used in similar ways by each member of the group. Dusky dolphins pass kelp among group members and carry kelp on dorsal fins, pectoral fins and the tail stock. These interactions with play objects require skill and manoeuvrability (Norris and Johnson 1994). In the current study, playing with kelp was most noticeably witnessed in female dolphins associated with mating groups. These females maintained the piece of kelp as a 'play object' throughout mating group chases and during intromission. However, play behaviour in dolphins is not well understood.

Social and contact behaviours were most prevalent in mating groups, with most behaviour produced at reduced frequencies for nursing and other adult non-mating groups. Chasing conspecifics, ventral contact and inverted swimming took place at the greatest rates among mating group members, although these behaviours occurred in non-mating adults and nursery groups at lower rates (<0.25 per individual per hour). Social rubbing behaviours may be akin to social grooming behaviour in primates, and could be used to strengthen and develop social bonds among dolphins. This would explain the highest rate of contact rubbing in mating groups as these groups probably have the highest levels of competition among group members. Contact rubbing may serve to reinforce social relationships that are stressed by competition in mating groups. In primates, social grooming has been found to influence the rate at which males support one another in agonistic contests (Silk 1992).

Synchronous surfacing was significantly higher for mating groups than other adult non-mating groups. Synchronous surface activities have been reported in bottlenose dolphin groups with first, second and possibly third order alliances (Connor et al. 2006). The synchronicity of these behavioural patterns is highest between males in first order alliances when they are chasing a female for mating purposes. Synchronous behaviour among males may be used to strengthen social bonds as males compete for access to females (Connor et al. 2006).

Mating groups had the shortest dive durations when compared with nursery and other groups. I predicted that mating groups, which use dives for female evasive tactics, would have the longest dive times. Energy expenditure in mating groups may explain this result. Rapid underwater chases with males chasing females against the surface may require increased respiration rates. However, when group dive times from mating groups are compared to dive times from dusky dolphin small groups foraging in Admiralty Bay, they are quite long in duration (101.1±16.4 s for mating groups and 35±1.9 s for foraging groups in Admiralty Bay; Markowitz et al. 2004).

Spyhopping was most common in mating groups. This behaviour generally occurred during surface mating chases when a female raised her head and lowered her body down through the water, stopping suddenly. This resulted in males swimming past the female as she turns quickly heading in the opposite direction (first described in McComber 1999). Reproductive chases were extremely rapid, involving frequent changes in direction, male chasing strategies and female "escaping" strategies. With females apparently always on top during copulation, males had to chase from an inverted position, a “handicap” in the context of the chase that could help facilitate female choice of the most vigorous males (Zahavi and Zahavi 1997). Females utilized a number of apparently effective strategies, including rapid changes in direction and head-up braking manoeuvres, to evade males and prolong the chase.

Relatively few males (usually two per mating sequence) appeared to successfully copulate with the female (although all the males may eventually be successful), suggesting that behavioural contests may play an important role in reproductive success for males. Agonistic interactions among males during mating chases were rare, and males appeared unable to either dominate mating contests or sequester females. Synchronous surfacing and chases performed by two individuals with usually two copulations by two different males at the end of the chase suggests cooperation by males to obtain access to females, indicating male alliance formation as is found for bottlenose dolphins (Connor et al. 2002). High intromission rates and long intromission durations for a mating group consisting of just two males and one female suggest that when more males are present, competition for mating opportunities is more intense. The mating of two males with a single female has also been described for spinner dolphins (*Stenella longirostris*, Norris and Johnson 1994). The idea that competition increases with the number of males is further supported by reduced copulations after more than two dolphins perform re-entry leaps at the initiation of a three-dimensional mating chase.

The fact that acrobatic leaps occurred so rarely in small groups suggests they are not a fitness display. Otherwise they would occur in mating groups and in small groups where the individual displaying would be quite noticeable by group members. They, along with noisy leaps, must function in some way specific to large groups of dolphins, perhaps as signalling behaviours to direct group movements (Markowitz 2004) or delineate the edges of large groups (Norris et al. 1994). Social mating behaviour (rather than breeding) did not appear to be very common in small groups but occurs with some frequency when individuals are in large groups (Chapter 2). Social mating, like grooming, functions to strengthen social bonds in primates (De Waal 1992). Possibly social mating is most necessary in large groups where the content and quality of social interactions would involve many more individuals, requiring an increase in bond reinforcement (Dunbar 1991, Würsig and Würsig 1980, Würsig 1984, Würsig et al. 1989).

Photo-identification records have suggested it is possible that alliances among males are maintained to aid in the pursuit of mating opportunities (Markowitz et al. 2004, Markowitz et al. 2010a). It would be quite an intellectual feat for dusky dolphins to remember interactions among all their potential partners in an area with such a large population (2,000 individuals at any one time, Markowitz 2004), although it has been reported to occur for bottlenose dolphins in the Indian Ocean with population sizes of over 600 identified individuals (Connor 2007). Social complexity has been proposed to be a driving force in the evolution of large brain size (Harcourt 1992). Odontocetes have some of the largest brains on earth for their body size, and dolphins of the *Lagenorhynchus* genus have one of the highest brain to body mass ratios of all (E.Q.=4.55; Marino 2009), which is only slightly less than that of human beings and double or more that of all other primates (Marino 1998). High levels of folding in the cerebral cortex result in a greater cerebral surface area when compared with humans (Ridgway and Brownson 1984, Pabst et al. 1999). It stands to reason that dusky dolphins use large brains to improve foraging, predator avoidance, and reproductive success. Females presumably use their large brains in parental contexts, but also in the mating arena with tactics to ensure their offspring get the best genes for success in a rich and varied socioecological setting.

Mother-Calf Nursery Groups

Habitat Use

Nursery groups were found close to shore, in shallow water and near river mouths when compared with other groups of similar size (< 50 individuals) off Kaikoura. These results are consistent with the use of near shore, shallow habitat to reduce the risk of predation and avoid aggressive conspecifics. Nursery groups with young calves are likely to use the turbid water of river mouths as a haven against predators. River mouths may be more productive areas for opportunistic foraging (although foraging was rarely seen by small groups in this study). Spinner dolphins move into shallow water to rest (Norris 1994, Karczmarski 2005, Notarbartolo-Di-Sciarai 2007).

During this study, a nursery group moved very near shore and near to the Kahutara River when killer whales were present in the area. These responses to predation have been found in other studies of dusky dolphins at Kaikoura (Würsig 1989, Weir et al. 2010) and are similar to beluga whales (*Delphinapterus leucas*) seeking river mouths and inlets in the presence of killer whales in Turnagain Arm, Alaska (Shelden et al. 2003). Female gray whales (*Eschrichtius robustus*) with young calves maintain a very close distance to shore on their return trip north from calving grounds in Baja Mexico ostensibly to reduce encounter rates with killer whales (Barrett-Lenard et al. 2011). Although nursery groups were located in shallow water, location data indicated that they were more likely to be located near the edge of the Kaikoura Canyon, which allowed them to remain close to foraging opportunities and the safety of the large groups.

The difference in ranging patterns between nursery and other adult groups may indicate that nursery groups remain closer to the canyon to reduce the travel distance to evening foraging opportunities on the DSL (Dahood and Benoit-Bird 2010). The depth and distance to shore at which mother-calf nursery groups are located shifts seasonally with groups encountered in deeper water further from shore as calves age.

Group Size

As predicted, nursery groups were significantly larger than mating or other adult groups. Larger groups may allow for more protection for calves in nursery groups and were found in other studies to be larger when calves were younger (Weir et al. 2010). Mean group size per 2-min interval reflected the larger grouping patterns for nursery groups, with nursery group size remaining almost double that of mating or other adult groups.

The differences in mean group size when compared with subgroup size suggest that when dolphins temporarily split from the group they did so as individuals for mating and adult groups but in subgroups of approximately 6 individuals for nursery groups. Subgroup sizes for small groups reflect a minimum group size of 5 or 6 individuals, with nursery groups again maintaining larger subgroup sizes (likely with 5 or 6 adults and 5 associated calves). This social unit of 5 or 6 individuals may be a significant one for dusky dolphins off Kaikoura (see discussion, Chapter 4).

Behaviour

As has been noted in other studies (Markowitz 2004, Weir et al. 2010), nursery groups rested more than other small groups. Continuous sampling in this study confirmed nursery groups had a longer duration of resting as well as a greater proportion of total time spent resting than other groups. Resting behaviour is common for cetaceans with young (Mann 2000). Dolphins are known to rest in parallel formation with other group members. In small and large groups of dolphins, this can function to allow group members hemispheric sleep, keeping 'one eye open' to conspecifics (Goley 1999). Long dives are usually associated with foraging in cetaceans (Wells 1999, Würsig 2000b). Nursery groups make long dives while resting when compared with mating groups that are actively diving and interacting in chase sequences.

The Kaikoura Canyon habitat provides abundant foraging opportunities (dusky dolphins congregate here in large numbers), allowing dolphins in nursery groups to feed at night and spend many hours resting during the day (Würsig. et al 2007). This use of habitat may increase the reproductive success of dusky dolphin females when compared with groups of dolphins with calves that must both feed and rest during the day on more patchy resources. A comparison of calving intervals between nursery groups off Kaikoura and nursery groups in Argentina, perhaps through the use of long term photo-identification information, would make an interesting future study for these different strategies.

As expected, inter-individual distance was lowest among nursery group members. It appeared that affiliative interactions between calves and adults were most often initiated by mothers when calves were newborn (summer) and by calves in autumn and winter when calves were older, but more data are needed to confirm this behavioural pattern. Contact (social) rubs occurred in nursery groups at a frequency of one social rub per individual per hour. This was similar to rates for this behaviour in adult non-mating groups.

High-speed behaviours were very rare for nursery groups compared to all other groups. This reduction in high-speed activity likely functions to conserve energy for females, already strained by the demands of lactation, and calves, limited by maturational constraints (Mann 2000). Less high-speed behaviour may also decrease conspicuousness and, therefore, the chance of detection by predators and/or male conspecifics in mating groups.

The high percentage of social rubs initiated by calves in autumn and winter may indicate calf reinforcement of social bonds as they approach weaning. Most chases of adults by calves were observed in autumn, when calves were older. The ventral presentation of adults to calves in all seasons indicates that this behavioural signal is important to mother-calf social interaction. The sudden ‘flash’ of the white ventral surface is quite striking, even when viewed from the water surface, and may function as an affiliative signal to reinforce adult-calf synchrony. Calves were observed to seek out the vessel to bow-ride with each calf accompanied by an adult some distance away. Adults made repeated forays toward calves in what appeared to be efforts to ‘entice’ them away from the vessel with ventral presentation. Calves responded by swimming synchronously with adults for a short length of time and then returned to bow-riding. The behavioural sequence of ventral presentation, chase and ventral contact initiated by a calf toward an adult during this study suggests that these behaviours may be used to indicate a desire to nurse.

Detailed behavioural observations of sequences of adult-calf interactions and events recorded by age-class were conducted for only a few nursery groups. Small sample size did not allow for a statistical analysis of questions related to initiation of social contact during development and nursing conflict. The data presented here allow us a ‘peak through the window’ at the possibility for detailed observations and analysis of behavioural sequences for dusky dolphin nursery groups. Continuous behavioural sampling allowed for this detail to be collected and certainly warrants use in the future. If nothing else, these ‘tidbits’ suggest that it is quite possible to collect information on dusky dolphin adult-calf interactions and behavioural sequences in real time. Data such as these could help us understand such interactions as nursing conflict and social development of calves off Kaikoura.

The mother-calf nursery is likely the core social unit for dusky dolphins in the first year of life. In these groups, young dolphins develop the intelligence and social skills to navigate the intricate social and ecological environments they will eventually master. The recent evidence for kin associations in female-calf nursery groups suggests that this core society is matrilineal, much like elephant or sperm whale societies (Whitehead 1996, Moss 2001) although dusky dolphin societies may be more complex with regard to the number of individuals interacting.

Summary of Findings

Most predictions for mating groups were substantiated by the findings presented here; however, dive durations were longest in nursery groups which contradicted the prediction for this behaviour. Nursery groups were more complex than predicted, or at least individuals in nursery groups were as complex in their behavioural expression as individuals in non-mating adult groups. Other adult non-mating groups appeared to serve as a ‘control’ for nursery and mating groups, often having intermediate behaviour to these two extremes. Social contact behaviours were least common for this group type, as was predicted.

Small groups of dolphins off Kaikoura appear to be employing an alternative grouping strategy to that of most dolphins off Kaikoura, which form large groups. For nursery and mating groups, the trade-offs of reduced competition in smaller groups, reduced aggressive interactions with conspecifics, and lower visibility to predators may explain this alternative grouping strategy. For other adult non-mating groups, the purpose of splitting into small groups rather than joining with the large group usually in the vicinity of the animals is not so easily explained. Clearly there must be a benefit to these group members for this alternative grouping strategy. Overall, the behaviour and ranging patterns of small groups of dusky dolphins off Kaikoura allow us a closer look at the complex social and ecological lives of dusky dolphins living in and around this submarine canyon habitat.

CHAPTER 4

COMPARATIVE SOCIOECOLOGY OF SYMPATRIC DUSKY AND HECTOR'S DOLPHINS AT KAIKOURA, NEW ZEALAND

INTRODUCTION

Species evolve in intricate interaction with their environments. Resource distribution and predation risk influences the biology, morphology and behaviour of a species, as well as the plasticity of all three factors. Organisms are 'decision makers' that evaluate their behavioural options and select those behaviours that will maximise fitness (Emlen 1995). Behavioural flexibility allows advanced organisms, such as large brained mammals, to increase their reproductive success by improved accuracy and precision in their behavioural responses to a variety of environmental cues. When similar species co-occur in a region they are likely to compete for resources unless they occupy different physical locations or ecological niches (Gause1934, Hutchinson 1957, Hardin 1960, Connell 1980).

Both dolphins and great apes form sympatric associations with closely related species (e.g., bottlenose dolphins, *Tursiops* sp., with common dolphins, *Delphinis delphis*, Bearzi et al. 2005*;* chimpanzees, *Pan troglodytes,* with gorillas, *Gorilla gorilla*, Yamigawa and Basibose 2006). Resource partitioning and flexibility in foraging patterns and prey selection may have evolved in these large-brained mammals as a response to repeated competitive encounters with sympatric species. The formation of fission-fusion societies that allow individuals to respond with changes in group size and structure as resource distribution and interaction with sympatric species varies may be a result of competition (Bearzi and Stanford 2007).

Socioecological models developed for terrestrial species suggest a tendency for small-bodied species in closed habitats to show limited ranging patterns with small social groups (Estes 1974). Species in open habitats tend to be larger-bodied, range more widely and form larger social groupings. Habitat structure can also influence the nature of associations such as mixed *versus* same sex grouping patterns (Funston et al. 1998). Like terrestrial species, cetaceans generally follow the same pattern of small, less widely ranging species with few social partners in coastal habitats when compared with more neritic species, like the dusky dolphin (Wells et al. 1999, Gowans et al. 2008). Neritic species are expected to be larger, range more widely and have larger social groups. Indeed, likely due to their phylogenetic history, members of the genus *Cephalorhynchus* are found in coastal habitats close to shore and in smaller groups than dusky dolphins throughout their shared ranges (Heinrich et al. 2010). Recent genetic studies indicate that the genera *Cephalorhynchus* and four species in the genera *Lagenorhynchus* (including dusky dolphins) should be placed in the same sub-family (Lissodelphininae; Pichler et al. 2001, Harlin-Cognato and Honeycutt 2006). It has been suggested that speciation and population subdivision has occurred more rapidly among *Cephalorhynchus* than *Lagenorhynchus* due to the relatively limited ranging patterns and gene flow of the former (Harlin-Cognato et al. 2007).

The dusky dolphin (*Lagenorhynchus obscurus*) is found in habitats that are shared by the genus *Cephalorhynchus* throughout the southern hemisphere (reviewed by Heinrich et al. 2010) with apparent habitat partitioning and differences in prey selection for Heavisides (*C. heavisidii*) and dusky dolphins in South Africa (Sekiguchi et al. 1992, Elwen et al. 2009a and b). Studies in South America indicate habitat partitioning between Chilean dolphins (*C. eutropa*) and Peale's dolphins (*L. australis*) as well as between Commerson's dolphins (*C.comersonii*) and dusky dolphins (Garaffo et al. 2011, Viddi et al. 2011). While these other studies shed some light on differences between the genera *Lagenorhynchus* and

Cephalorhynchus, I report here findings from the first direct comparison of habitat use, social grouping patterns and behaviour of dusky dolphins and Hector's dolphins (*Cephalorhynchus hectori*). Although Hector's and dusky dolphin ranging patterns in New Zealand often put them in the same locations, fine scale habitat selection and possibly prey size distributions differ for the two species (Dawson and Slooten 1988, Würsig et al. 1997). These sympatric species have carved out niches for themselves, reducing the extent to which they overlap and minimizing competition for resources.

The Hector's dolphin is an endemic coastal New Zealand species found primarily on the South Island of New Zealand. This small-bodied cetacean forms small groups in near shore waters with higher population concentrations near river mouths and harbours (Table 4.1, Figure 4.1, Dawson and Slooten 1988). Hector's dolphins have small home ranges with little migration along shore, although offshore migration in winter is likely (Slooten and Dawson 1995, Bräger 1998). Small populations and reduced gene flow for Hector's dolphins, as well as their preference for habitat near shore, put them at greater risk for extinction than more widely ranging species (Pichler et al. 1998, Pichler and Baker 2000). Past fisheries by-catch estimates were reported as unsustainable for this species, and new protection measures are likely to result in recovery for only some populations (Slooten and Dawson 2010). Currently the Hector's dolphin is listed as endangered and the North Island Hector's dolphin subspecies (*Cephalorhynchus hectori maui*) as critically endangered (Baker et al. 2010). Tourism interactions have expanded on the east coast of the South Island of New Zealand with some documented responses by Hector's dolphins to tourism (Bejder et al. 1999, Martinez et al. 2010).

Table 4.1. Life history parameters of dusky and Hector's dolphins are compared (Estimates from Leatherwood and Reeves 1983, Cipriano 1992, Würsig et al. 1997, Slooten 1991, Dawson 2009).

Parameter	**Dusky Dolphin**	**Hector's Dolphin**
Gestation length	11.4 months	10-11 months
Lactation duration	18 months	12-24 months
Calving season	Early summer	Spring to late summer
Age at first reproduction	7-8 years	7-9 years
Size at birth	0.97-1.02 m	0.6-0.8 m
Size of adults	1.65 to 1.86 m	1.2 to 1.4 m
Maximum Age	≥ 35-36 years	20 years

The diet of Hector's dolphins in New Zealand consists of small benthic and epi-benthic fish and squid, with lantern fish possibly also forming a large part of the diet. The preference of Hector's dolphins for turbid, near shore, waters has been attributed to increased prey availability and predator avoidance, although predation events on Hector's dolphins have rarely been observed (Bräger 1998).

In contrast to Hector's dolphins, dusky dolphins are relatively abundant and wide ranging. However, direct harvest for human consumption and bait in Peruvian fisheries (Read et al. 1988, Van Waerebeek and Reyes 1990, Vidal 1993, Van Waerebeek and Reyes 1994, Van Waerebeek and Würsig 2009) as well as incidental by-catch (Sekiguchi et al. 1992, Dans et al. 1997, 2003, Mangel et al. 2010) and direct competition with fisheries in Argentina (Trites et al. 1997) all affect the health and current population status of dusky dolphin populations worldwide (reviewed by Markowitz et al. 2010b). Tourism interactions with dusky dolphins are also increasing, with behavioural responses to tourism documented in some populations (Turpie et al. 2005, Coscarella et al. 2003, Würsig et al. 2007, see also

Chapters 5 and 6). Although dusky dolphin populations are described as ‘robust’ and doing quite well off the east coast of the South Island of New Zealand, human impacts including ‘top-down’ effects of global climate change, may be affecting the health and well-being of some populations (Würsig 2010).

Dusky dolphins adopt different foraging strategies in different habitats (Würsig et al. 1989). In the shallow bays of Golfo San José, Argentina, and Admiralty Bay, New Zealand, dusky dolphins hunt small schooling fishes in a coordinated fashion during the day (Würsig and Würsig 1980, Markowitz et al. 2004). In the deep submarine canyon off Kaikoura, dusky dolphins gather in large groups to rest and socialise during the day, feeding mainly at night on lantern fish (Myctophidae) and squid (*Nototodarus sp.* and *Todaroides sp.* Cipriano 1992, Würsig et al. 1997, Benoit-Bird et al. 2004) associated with the deep scattering layer.

Figure 4.1 Hector’s dolphin surfacing off the Hapuku River mouth.

Research Objectives and Predictions

Hector's dolphins form small groups near shore presumably to avoid predation and reduce competition among group members for limited local resources (Dawson and Slooten 1988, Gowans et al. 2008). Dusky dolphins at Kaikoura form larger groups and are more wide-ranging (Cipriano 1992, Markowitz 2004, Würsig et al. 2007), although small groups of dusky dolphins, particularly groups with calves, are found near shore (Weir et al. 2008). Hector's and dusky dolphin small groups are similar in size and therefore under similar threat of predation. However, dusky dolphins in small groups may range further from shore and river mouths in deeper water due to their phylogenetic history and prey preferences.

Differences in prey species for dusky and Hector's dolphins may result in increased foraging behaviour and longer dives as Hector's dolphins search for food during the day while dusky dolphins rest. The diurnal foraging behaviour of Hector's dolphins should also result in less time for behavioural displays and resting during the day. As Hector's dolphins have much smaller home ranges than dusky dolphins (Dawson and Slooten 1988, Markowitz 2004), dusky dolphins in small groups should travel more than Hector's dolphins.

Associating in small groups that compete for limited resources should reduce the need for social mating and other social behaviours that serve to reinforce bonds in larger groups (Dunbar 1993). Although Hector's and dusky dolphin small group sizes are similar, the fewer and more consistent social partners for Hector's dolphins at Kaikoura may require less social interaction to reinforce relationships.

Increased competition among group members for limited local resources may also increase fission-fusion rates for Hector's dolphins as individuals leave or join groups to increase fitness (Kinsey and Cunningham 1994). Duration of group size is shorter (i.e., fission-fusion rates are higher) for small groups of dusky dolphins that forage during the day on presumably more limited resources in Admiralty Bay, New Zealand when compared with dusky dolphin small groups at Kaikoura that primarily rest (Pearson 2009, Chapter 2).

Hypothesis: Habitat use, group dynamics and behaviour of Hector's dolphins at Kaikoura will be consistent with daytime benthic foraging that minimizes predation risk, while dusky dolphins in small groups primarily rest and socialise.

Specifically, I predicted Hector's dolphins would:

1. Be found closer to shore, in shallower water, and closer to river-mouths with longer dive durations and higher foraging rates than small groups of dusky dolphins.

2. Rest and travel less than dusky dolphins with less noisy leaping and social behaviours (including social mating) as the need for bond reinforcement decreases with group size.

3. Have more behavioural state transitions than dusky dolphins.

4. Form smaller groups and subgroups with less consistent social partners (higher fission-fusion rates) than dusky dolphins.

METHODS

Boat based surveys for dolphin groups were conducted off Kaikoura from a 5.5 m research vessel (see Chapter 2 for detailed survey methods for dusky dolphin groups). Hector's dolphin groups were located using boat-based surveys off Kaikoura as well as systematic line-transect surveys south of the Haumuri Bluffs to the Waiau River (DuFresne and Markowitz 2009; Figure 4.2). Line-transect surveys were limited to the summer season due to logistical constraints (e.g., cost, sea conditions).

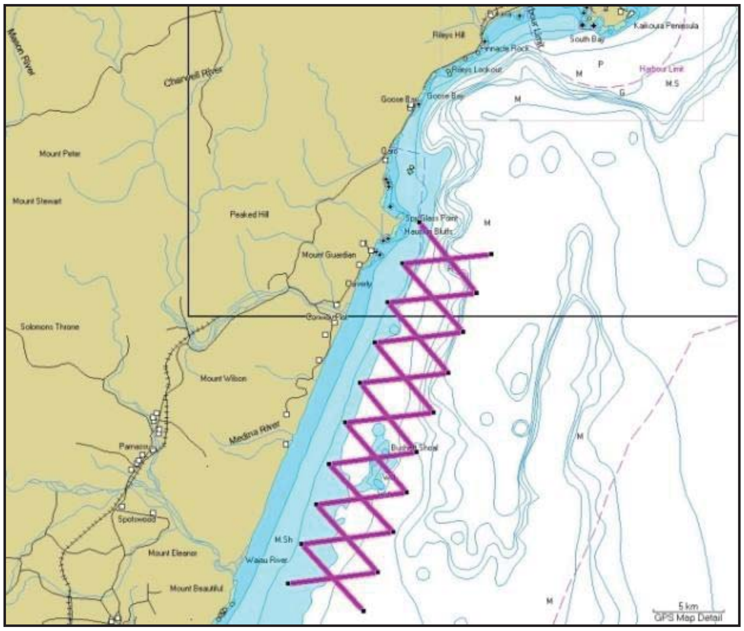


Figure 4.2. Purple lines show the line transects surveyed using the zigzag design along the near shore area from the Haumuri Bluffs to the Waiau River. Blue lines indicate water depth isobaths, with shallower depths shaded (from DuFresne and Markowitz 2009).

Surveys for Hector's dolphin groups were conducted from the Haumuri Bluffs south along the coast 1 km from shore at a speed of 10-12 knots. During surveys, two primary observers and a secondary observer were used. The secondary observer was the boat driver and was not able to concentrate fully on spotting dolphins. The primary observers each concentrated their effort on one side of the boat, from the trackline to slightly abeam of the boat.

Surveys for Hector's dolphin groups north of the Kaikoura Peninsula began 2 km northeast of the peninsula in a straight line to the Hapuku River mouth at 10-12 knots. Surveys were continued north and south alongshore 1 km from the coastline. Hector's dolphin groups were also encountered opportunistically during line-transect surveys south of the Haumuri Bluffs and in the vicinity of small and large groups of dusky dolphins. Data from opportunistic encounters were included in analyses. Research effort from January 2007 through March 2009 included 699 hours of vessel surveys on 140 days with 399 dolphin group encounters. Small dusky dolphin groups encountered included 197 groups. Hector's dolphin groups encountered included 67 groups with 49 groups encountered between the Haumuri Bluffs and the Hapuku River mouth and 18 groups encountered south of the Haumuri Bluffs off the Conway and Waiau River mouths. Focal group behavioural sampling was conducted for 79 dusky dolphin small groups and 25 Hector's dolphin groups.

Upon encounter of a dolphin group, data collected included group size, direction, behavioural state, group composition, and tour or recreational vessel presence or absence. Dolphins in groups of <50 individuals were counted and the number of juveniles, calves and adults present estimated. After an initial group behavioural state was identified, the research vessel approached and paralleled the group at no-wake speed for photo-identification and behavioural observation (Würsig and Jefferson 1990). Groups were tracked by paralleling the group using a Garmin GPS 60 to log latitude and longitude position each minute. Group follows ended when the weather deteriorated, groups were lost from view, adequate sample duration was obtained (more than 20 min) or failing light made follows impracticable. Group and subgroup definitions are shown in Table 4.2. The continuous data collected for group and subgroup size and number of subgroups were re-sampled in two minute intervals to be consistent with other studies of group size and dolphins (e.g., Pearson 2009).

Table 4.2. Terms related to social grouping patterns examined in the current study are defined.

Term	**Definition**
Group Size	Estimated number of individuals present at any given time during the focal behavioural sampling period based on the '10-m chain rule' (Smolker et al. 1992, Mann 1999). Group size was sub-sampled from the continuous data in 2-min intervals to compare with methods from other studies.
Subgroup Size	Dolphins in subgroups <1 body length or 1-3 body lengths from each other and >3 body lengths from other group members moving in a coordinated fashion and surfacing synchronously.

During continuous sampling (March 2008-February 2009), behavioural data were recorded continuously using an Olympus VN-2100PC digital voice recorder with noise reducing headset. During focal group follows, predominant group activity (Mann 2000) was used to document behavioural state (rest, mill, travel, forage), group dispersion (<1, 1-3, >3 body lengths), heading (variable, north, south, east, or west), swimming formation (no formation, parallel/echelon, linear, circular) and number of individuals associated with the research vessel (bow-riding) whenever these parameters changed (adapted from Shane 1990, Hanson and Defran 1993, Acevedo-Gutiérrez and Parker 2000). During continuous data collection small dolphin groups were observed to cycle rapidly between parallel and echelon formation and differentiating between the two was problematic. For this reason, parallel and echelon formations were combined to form a single parallel/echelon category for behavioural scoring (see Chapter 2 methods for detailed definitions of behavioural states and events).

Behavioural events documented in real time included noisy leaps, acrobatic leaps, re-entry leaps, tail slaps, synchronous surfacing, individual speed bursts (‘slice’), group speed bursts, chasing conspecifics, blowing bubbles, playing with kelp, spyhopping, inverted swimming, ventral presentation, contact (‘social’) rubs, ventral contact, sexual approach, and intromission. Incidence of birds feeding with dolphins was also recorded.

Digital audio recordings were transcribed into JWatcher V1.0 (Blumstein et al. 2006) for detailed analyses of behaviour. Transcribing of audio recordings rather than direct entry into the JWatcher program in the field allowed for hands free observation of behaviour without having to look away from the subject as well as the ability to review data collected as many times as necessary for accurate input, and correction of mis-entered keystrokes. All data were collected in the same manner for dusky dolphin and Hector’s dolphin groups during this study. The behaviours recorded were only scored in Beaufort Sea States of 1 or less. Turbidity usually made it possible to score behaviour to minimum depths of 2-5 m. These depths are similar to depths from other studies in which similar Hector’s dolphin behaviour was scored (Slooten 1994, Bräger 1998, Martinez et al. 2010) and all behaviours in this study occurred either at or very near the surface.

Data Analysis

Group locations and movements

Group encounter location data were analysed for distance from shore/river mouth and water depth (see Chapter 2 methods for detailed GIS analysis methods). Groups were treated as independent if they were encountered on different days or if they were encountered on the same day at such a distance apart that, given the time between group encounters, it was unlikely they were the same individuals. Data were queried by day and group and subsequent statistical tests run in SPSS v.10. Group locations and tracks of group movements were estimated using longitude, latitude and time data recorded by the Garmin global positioning system (GPS) receiver in 1-min intervals from the vessel as it was positioned alongside the group. GIS data were plotted in Mapsource Bluechart Pacific 5.5 (Garmin International, Inc., Olathe, KS, U.S.A.) and longitude/latitude positions were imported into ArcGIS v. 10.0, and overlaid onto a shore line base map and a bathymetric chart supplied courtesy of the National Institute of Water and Atmospheric Research, New Zealand (NIWA). All map features were projected using the WGS 84 coordinate system in ArcGIS 10.0 and converted to NZ UTM 59S (New Zealand National Grid System). Data layer shape files were joined by spatial proximity to the bathymetric shape file, such that each point was assigned a depth equal to the nearest isobath with resulting shape files joined by spatial proximity to the coastline shape file to obtain the estimated distance from shore of each location. All group encounter locations were spatially joined to a river mouths shapefile created in ArcGIS to calculate distance from river mouths by group. Resulting attribute tables were exported to Microsoft Access databases for querying by group type with analyses blocked by independent dolphin groups. Statistical tests of the resulting data were run in SPSS v. 10.

Behaviour

All statistical tests were conducted in SPSS v.10. Behavioural analyses were initially conducted using JWatcher v1.0 with data exported to Microsoft Excel v. 7.0 for data manipulation and production of tables and graphs. Behavioural analyses included comparisons of changing group size and differences in social behaviours and leaping rates. Data were tested for normality using the Kolgomorov-Smirnov test and for equality of variance using Levene’s statistic. For most comparisons between independent samples of Hector’s and dusky dolphin groups, the Mann-Whitney or student’s t tests were used.

RESULTS

Distribution and Ranging Patterns

Location on first encounter and ranging patterns for groups that were followed were compared for Hector's dolphin groups (n=67) and dusky dolphin small groups (n=197). Hector's dolphin groups were noticeably absent from the Kaikoura Canyon, although some groups were encountered in the vicinity of the canyon. Dusky dolphin groups were found throughout the Kaikoura Canyon and ranged to the north and south of the Haumuri Bluffs (Figure 4.3). Hector's dolphin groups that were located from the Kaikoura Peninsula to the Hapuku River were on the survey route for this area. Hector's and dusky dolphins may range closer to shore from the Kaikoura Peninsula north to the Hapuku River; however, this area was not surveyed. During line-transect surveys south of the Haumuri Bluffs to the Waiau River, Hector's dolphin groups were consistently located inshore of dusky dolphin groups of similar size. Hector's dolphin groups were also noticeably absent from areas used by dusky dolphin nursery and mating groups in the vicinity of Goose Bay and the Oaro River (Figure 4.3).

Hector's dolphin groups were encountered in significantly shallower water (Mann-Whitney U=3136.5, P<0.001; Figure 4.4) and closer to shore (Mann-Whitney U=1401.0, P<0.001) than small groups of dusky dolphins. Although large groups of dusky dolphins would be expected to range further from shore and in deeper waters than the smaller groups of Hector's dolphins (Chapter 2), small dusky dolphin groups of similar size to Hector's dolphin groups also inhabited deeper waters further from shore.

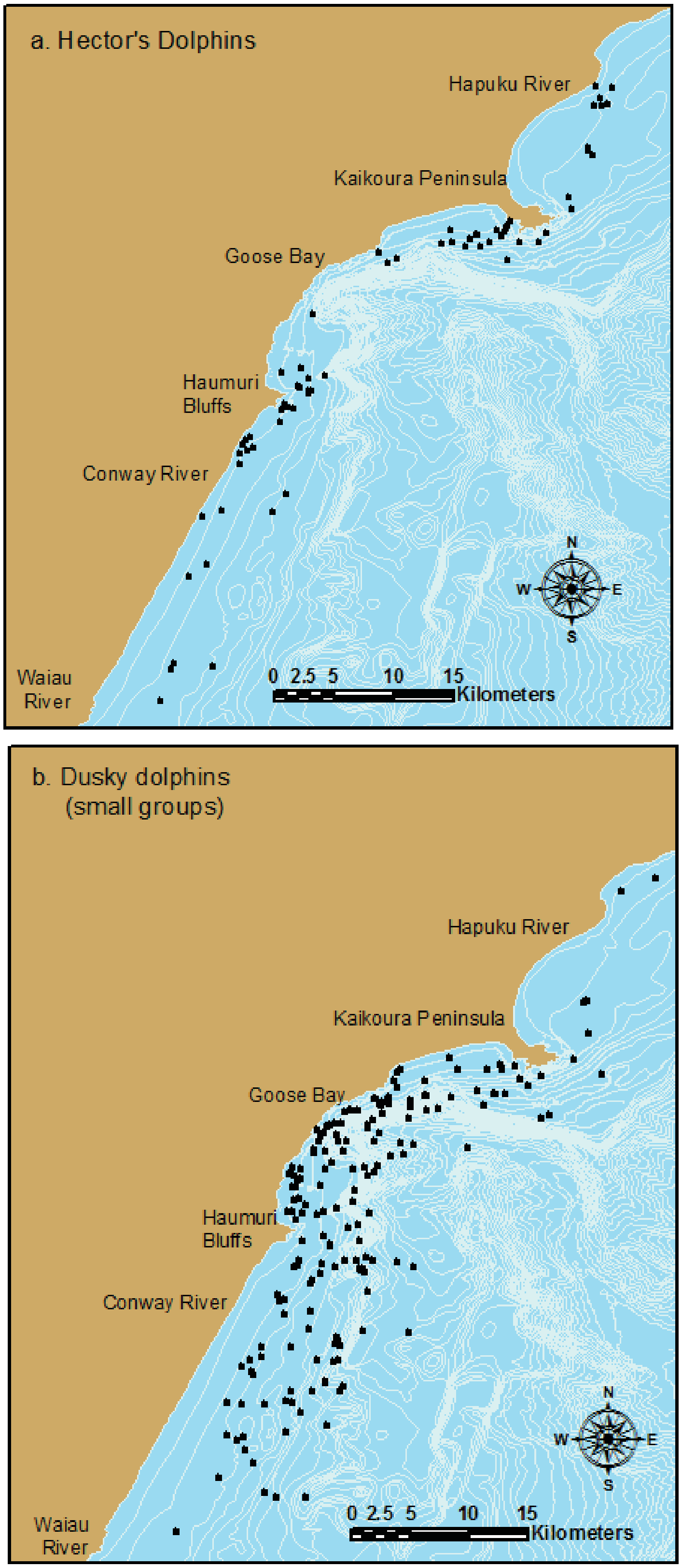


Figure 4.3. Encounter locations of Hector's dolphin (n=67) groups (a) and small dusky dolphin (n=197) groups (b) are compared.

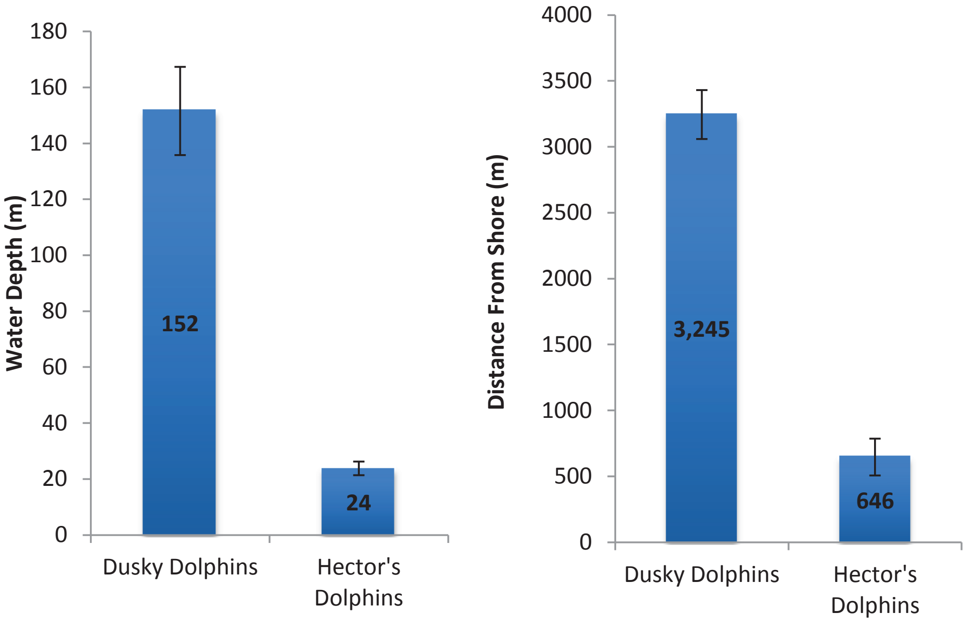


Figure 4.4. The water depth (left) and distance from shore (right) at which small groups of dusky (n=67) and Hector's (n=197) dolphins were encountered are compared. Bars represent mean depths and distances in meters with standard deviation.

Hector's dolphin groups were encountered closer to river mouths than dusky dolphins (Mann-Whitney U = 4736, P<0.001). These groups were encountered on average 1.4 km closer to the nearest river mouth (Figure 4.5). A more striking difference was observed in the particular river areas frequented by the two species. Hector's dolphin groups appeared to be associated preferentially with rivers further from the Kaikoura Canyon. Dusky dolphin groups were more evenly associated with rivers across the study area, frequenting all six river areas, but most particularly those between the Kaikoura Peninsula and the Conway (Figure 4.6).

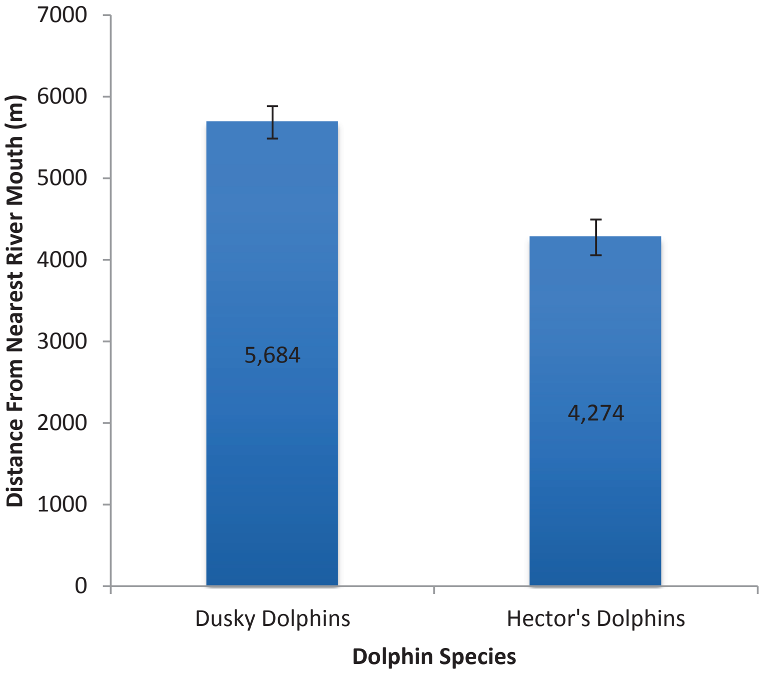


Figure 4.5. The distance to the nearest river mouth, estimated based on first encounter GPS position, is compared between small groups of dusky dolphins (n=197) and Hector's dolphins (n=67). Bars represent means with standard errors.

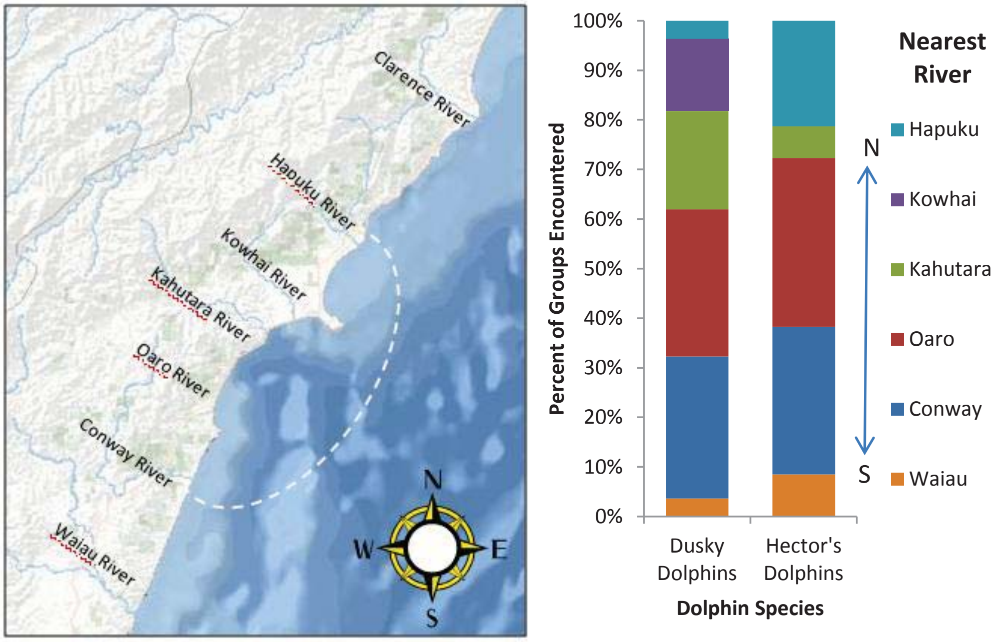


Figure 4.6. Association of dolphin groups encountered with rivers in the study area (left) is compared between small groups of dusky dolphins and Hector's dolphins (right). The white dashed line (left) indicates the primary study area, with five rivers. Surveys to the south in summer extended this area as far as the Waiau River. The stacked bars on the right show the percent of all groups encountered associated most closely by distance with each of the six rivers arranged north to south (dusky dolphin small groups n =197, Hector's dolphin groups n = 67).

Dive Duration

Hector's dolphin dive durations were significantly shorter than dusky dolphin dive durations (Mann-Whitney U= 44, *p* <0.001). Dusky dolphin small groups had dive durations nearly four times longer than Hector's dolphin dive durations (Figure 4.7).

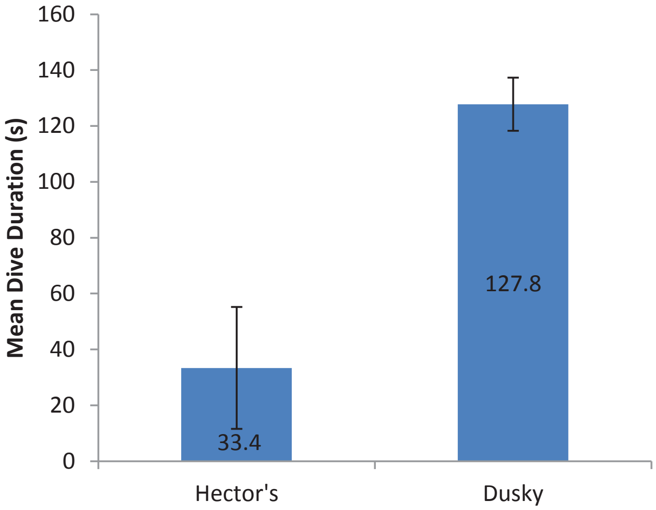


Figure 4.7. A comparison of the mean dive duration for Hector's (n=22) and dusky dolphin (n=56) groups is shown. Bars represent mean values with standard error.

Mean Duration of Behavioural States

Mean duration of time spent in a behavioural state was calculated for Hector's and dusky dolphins. There were no significant differences between Hector's and dusky dolphins in the mean duration (min) of all behavioural states including (travel, mill, rest, and forage; Table 4.3). There were, however, significant differences in the durations of specific behavioural states (Figure 4.8).

Table 4.3: Mean durations ± SE (min) of behavioural state, dispersion, formation and directional heading are compared for Hector's dolphin (n=22) and dusky dolphin (n=56) small groups.

Species	Behavioural State	Dispersion	Formation	Direction
Hector's dolphin	3.5±0.9	3.8± 1.4	2.3± 0.9	3.1±0.6
Dusky dolphin	4.2±0.6	3.8±0.5	2.1±0.4	2.4±0.3

Dusky dolphins rested for longer durations (Mann-Whitney U=457, $p < 0.05$) and milled for shorter durations (Mann-Whitney U=426, $p < 0.05$) than Hector's dolphins (Figure 4.8a). No foraging behaviour was scored for dusky dolphin small groups during continuous data collection sampling. Mean ± se duration of time Hector's dolphins spent foraging was 2.2±1.8 min and the mean proportion of time dolphins were engaged in foraging was 6.0±4.4% (Figure 4.8b). Dusky dolphins spent a greater proportion of time resting (Mann-Whitney U=422, $p < 0.05$) and a lesser proportion of time milling (Mann-Whitney U=0.027, $p < 0.05$) than Hector's dolphins (Figure 4.8b).

There was a significant difference in birds feeding with dolphins between Hector's and dusky dolphin groups (Figure 4.9), that may be a further indication of dolphin foraging activity. Birds were found to feed with Hector's dolphin groups significantly more often than with dusky dolphin groups (Mann-Whitney U=391, $p < 0.001$).

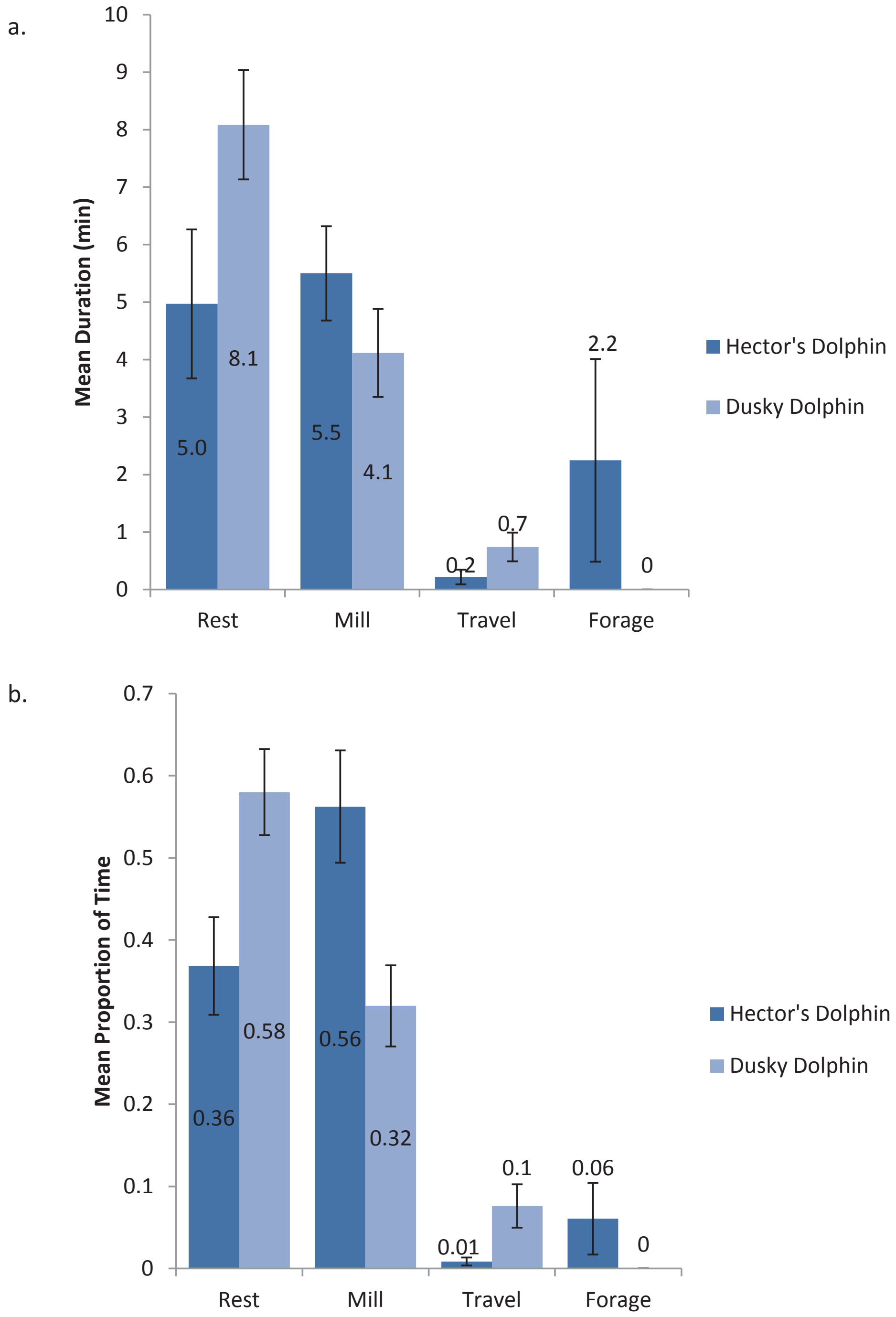


Figure 4.8 Duration (a) of behavioural state for Hector's (n=22) and dusky dolphin (n=56) groups scored using continuous behavioural monitoring and (b) mean proportion of time in each behavioural state are compared for Hector's and dusky dolphins. Bars represent mean values with standard error.

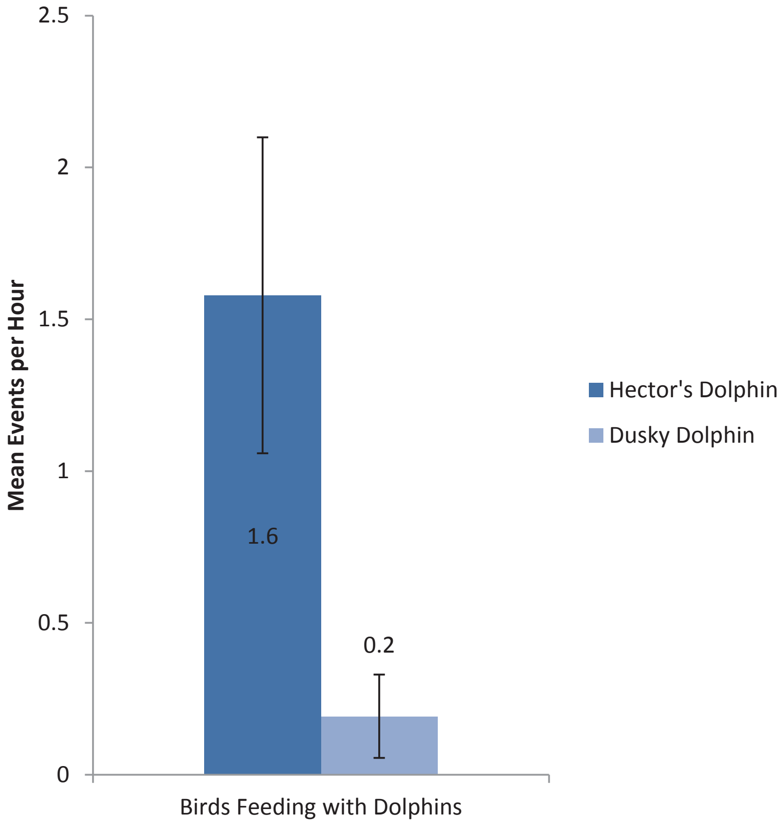
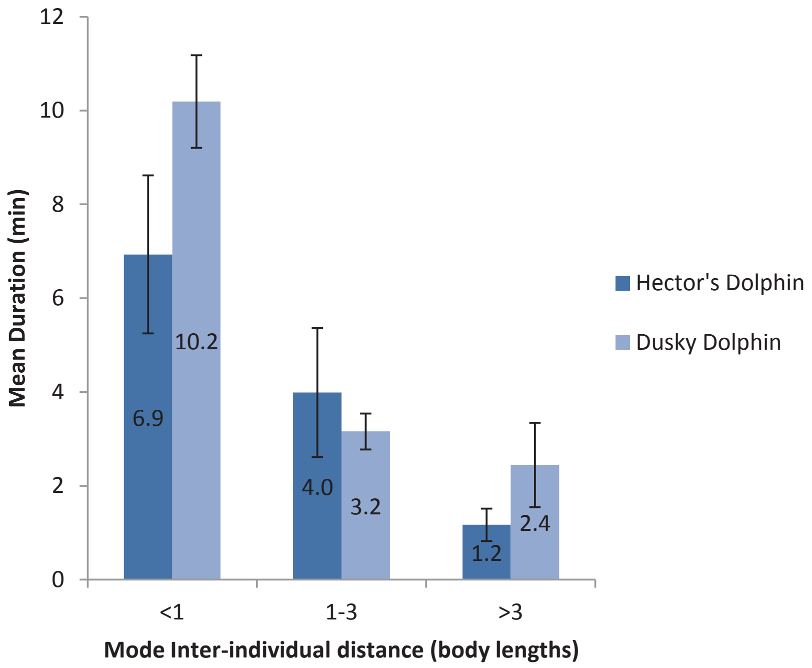


Figure 4.9 Mean occurrences per hour of seabirds feeding in and around groups of Hector's (n=22) and dusky dolphins (n=56) are compared. Bars represent mean values with standard error.

Hector's dolphins had significantly greater inter-individual distance between group members than dusky dolphins. Dusky dolphins were grouped close together (within one body length) for longer durations than Hector's dolphins (Mann-Whitney U=387, $p < 0.05$). Mean proportion of time Hector's dolphins spent at <1 body length was significantly lower than dusky dolphins in small groups (Mann-Whitney U=378, $p<0.05$). Hector's dolphins spent a significantly greater proportion of time with >3 body lengths between individuals than dusky dolphins (Mann-Whitney U= 408, $p = 0.01$, Figure 4.10).

a.



b.

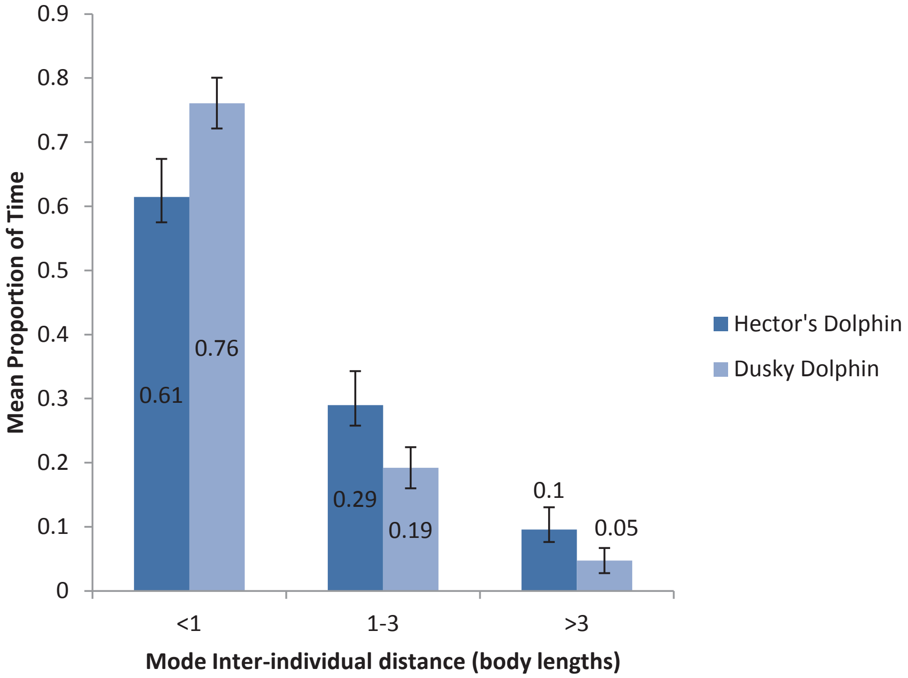
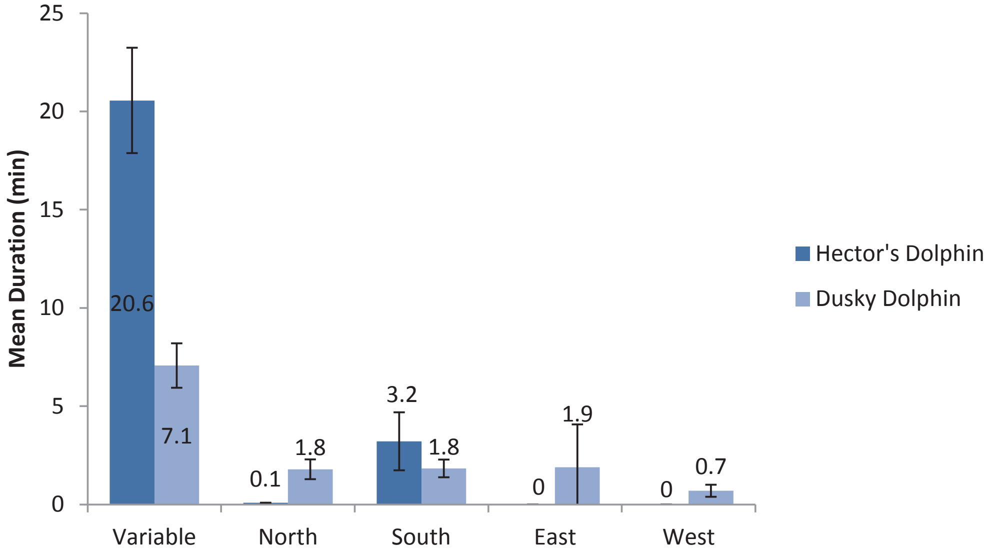


Fig 4.10 Mean duration (a) and proportion of time (b) of different categories for inter-individual distance among group members is compared for Hector's (n=22) and dusky dolphin (n=56) groups. Bars represent mean values with standard error.

Hector's dolphins were more likely to remain variable in the direction of movement than dusky dolphins (Mann-Whitney U=189, $p<0.001$). Dusky dolphins spent more time in directional movement consistent with the reduced milling behaviour for dusky dolphins (Mann-Whitney U=427.5 $p<0.05$, Figure 4.11 a and b).

a.



b.

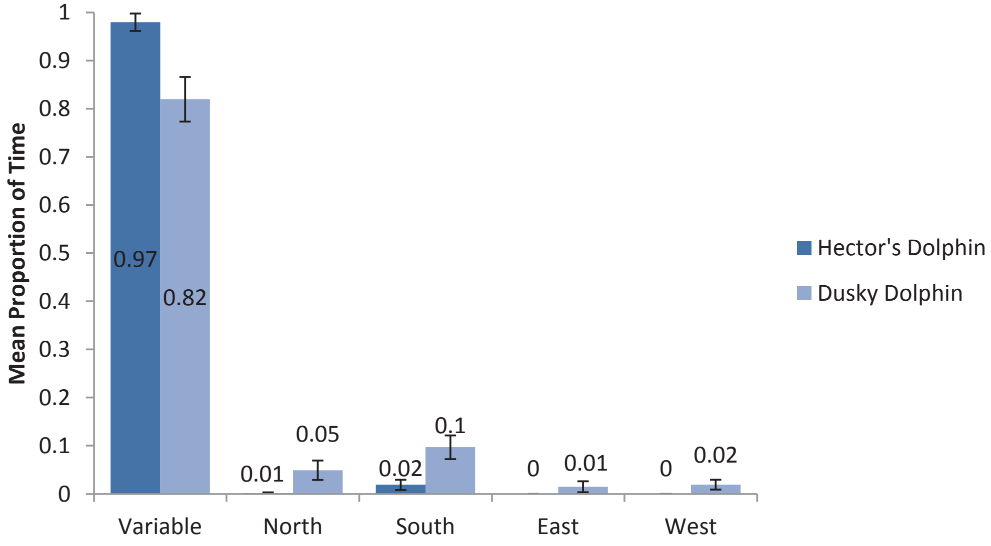


Figure 4.11. Mean durations (a) and proportions (b) for direction of travel are compared for dusky (n=56) and Hector's (n=22) dolphin groups. Bars represent mean values with standard error.

There were no significant differences between dusky and Hector's dolphin groups in duration of formation (Mann-Whitney test, *ns*). However, dusky dolphin groups were more organised with regard to formation of group members and spent more time in parallel, linear or circular formation than Hector's dolphin groups (Mann-Whitney U=368, $p<0.05$; Figure 4.12).

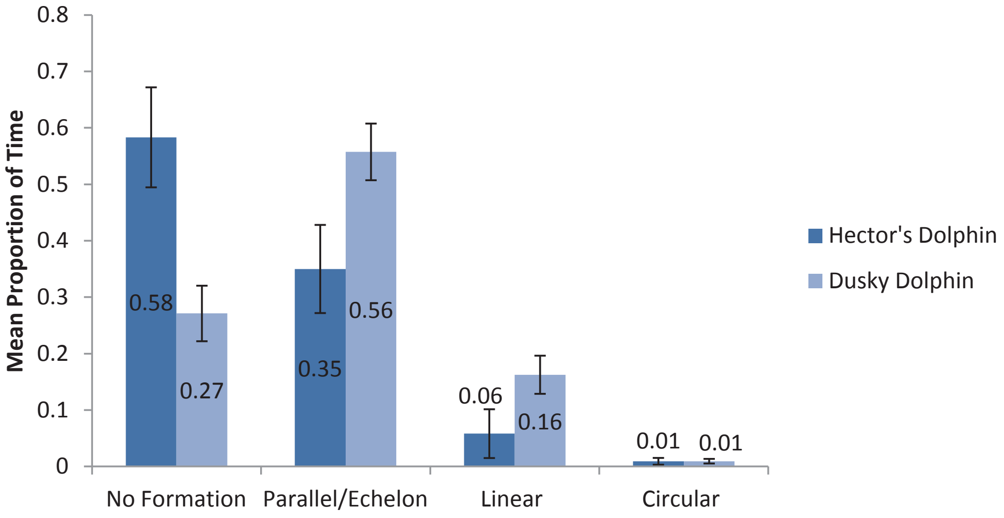


Figure 4.12 Mean proportion of time spent for dusky (n=56) and Hector's (n=22) dolphins in various group formations are compared. Bars represent mean values with standard error.

Behavioural Events

Some social behavioural events that were recorded in dusky dolphin groups were rarely seen in Hector's dolphin groups. These included sexual approach (inverted swimming with penis out; 0.01 per individual per h) and ventral contact (0.01 per individual per h). These events were characteristic of dusky dolphin mating groups (see Chapter 3). Intromission was scored only in dusky dolphin mating groups and was not seen in Hector's dolphin groups. Nursing was seen in dusky dolphin nursery groups, although very rarely, and was not seen in Hector's dolphin groups. Other behavioural events that occurred in dusky dolphin nursery and other small groups, and were seen on a more consistent basis in Hector's dolphin groups, included contact social rubs, chasing of one conspecific by another, ventral presentation (one conspecific to another) and inverted swimming (ventral presentation to the surface). Although these behaviours occurred in both dusky and Hector's dolphin groups, most were more prevalent in dusky dolphins (Mann-Whitney tests; chase U=475, *p*<0.05, contact social rub U=396, *p* <0.01, inverted swim U=415, *p* <0.01), although ventral presentation occurred in both dusky and Hector's dolphin groups at almost equal rates (Figure 4.13).

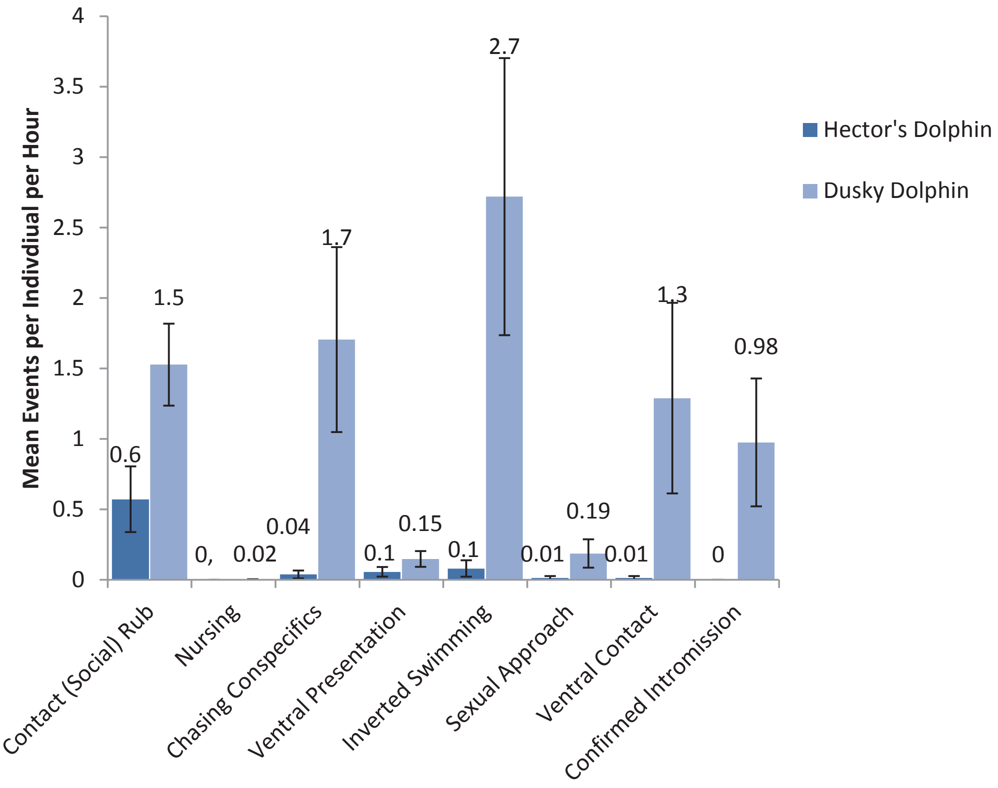


Figure 4.13. Frequency of behavioural social events is compared for dusky dolphin (n=56) and Hector's dolphin (n=22) small groups. Mean rate of occurrence is shown with Y-error bars representing standard error.

Hector's dolphins were more likely to surface synchronously than dusky dolphins (Mann-Whitney U=376, *p*<0.01). The rate of tail slapping was similar between both Hector's and dusky dolphins (Mann-Whitney U=600.5, *ns*). In groups where speed bursts or 'slicing' behavioural events occurred, the rate of slicing was higher for dusky dolphin small groups than Hector's dolphins (t-test, t= -2.522, *p* <0.05, *df*=39; Figure 4.14). Despite morphological differences between the two species (e.g., body size, dorsal fin shape) it was noted that when Hector's dolphins did perform speed bursts at the surface with surface splashes, this behaviour was quite obvious and comparable to dusky dolphin surface splashes.

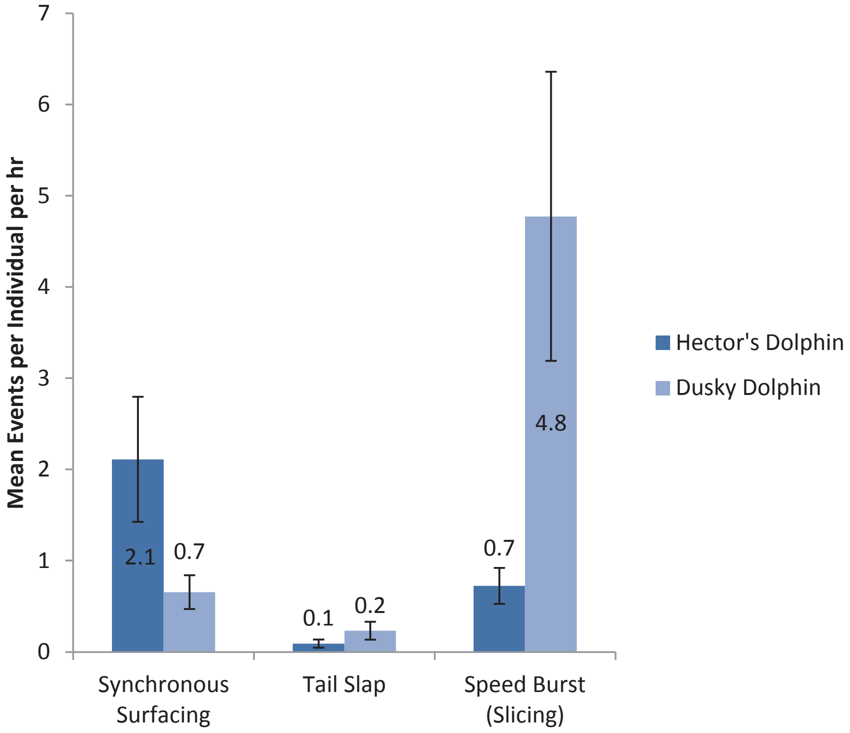


Figure 4.14. Mean rates of occurrence of surface social behavioural events are compared for dusky (n=56) and Hector's dolphins (n=22). Y-error bars represent standard error of the mean.

Leaping behaviour did not occur often in small groups of dusky dolphins (when compared with large groups, see Chapters 2 and 3) and in Hector's dolphin groups. When leaping did occur, it was more common for dusky dolphin groups. Particularly, head-first re-entry leaps occurred more often in dusky dolphin groups than in Hector's dolphin groups (t-test, t=-3.197, *p*<0.01, *df*=14; Figure 4.15).

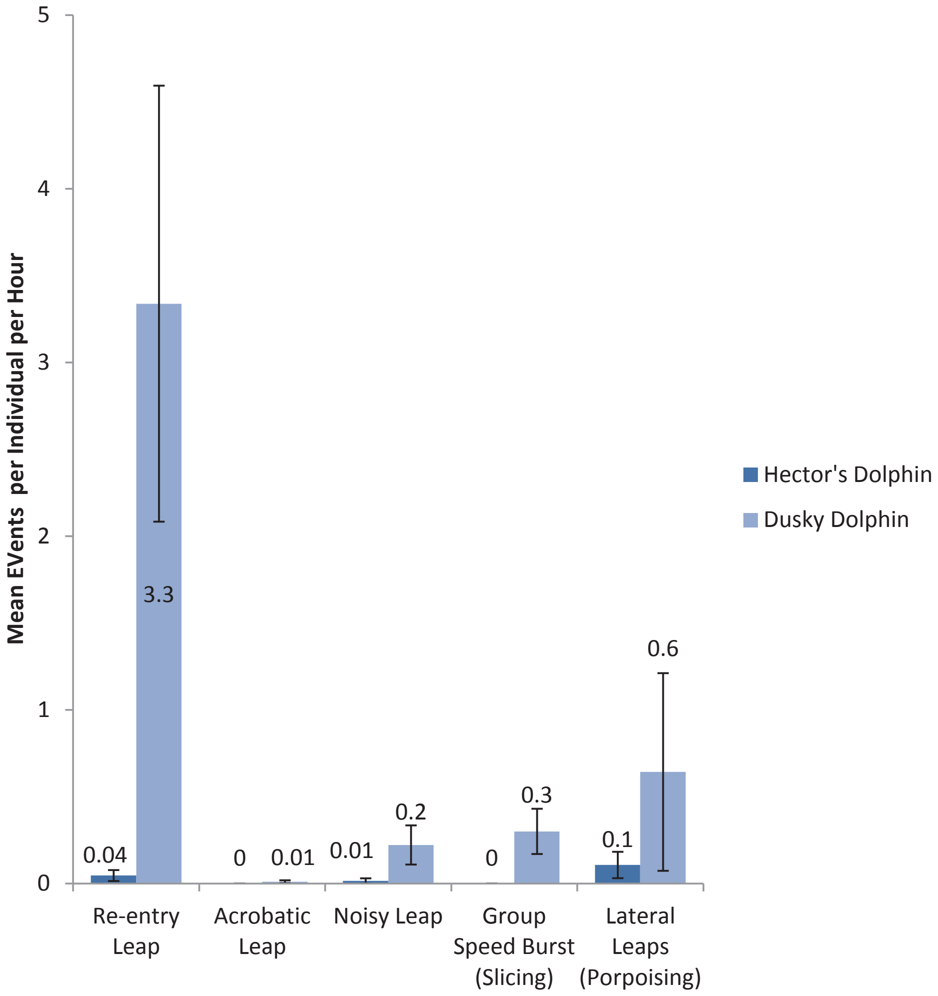


Figure 4.15. Mean rates of leaping behaviour are compared for Hector's (n=22) and dusky (n=56) dolphins. Y-bars represent standard error of the mean.

Play behaviours such as blowing bubbles, spyhopping or playing with kelp occurred at similar low rates for the two species (Figure 4.16) and at fairly low rates overall for dusky dolphins when compared with other behaviours such as social rubs and speed bursts (slicing). There were no significant differences found between dusky and Hector's dolphins with regard to play behaviours, which is most likely due to the sporadic nature of these events and the high variability in rates of occurrence.

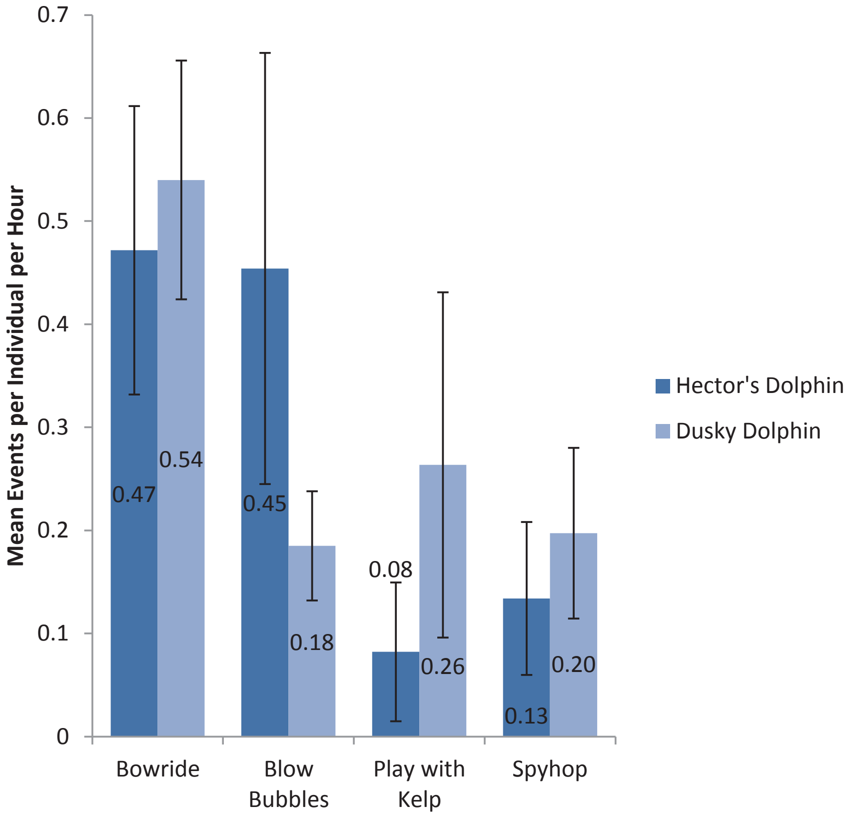


Figure 4.16. *Play behaviour is compared for dusky (n=56) and Hector's (n=22) dolphins. Mean occurrence of events with y-error bars representing standard error of the mean are shown.*

Mean number of behavioural events per hour per individual were compared as well as types of behavioural events per hour per individual. Although the types of events displayed were similar for the two species, the frequency of behavioural events per individual per hour was much greater for dusky dolphins when compared with Hector's dolphins (t-test, t=-2.586, p<0.05, df=76; Figure 4.17).

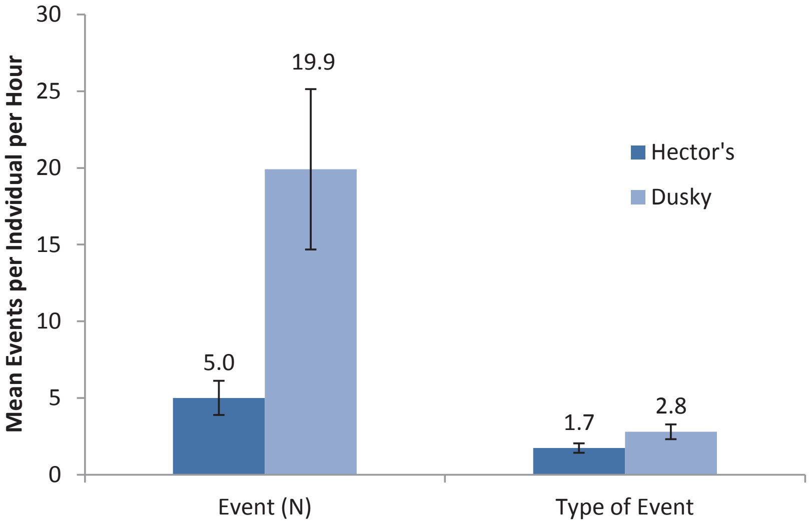


Figure 4.17. Behavioural event frequency and type for Hector's (n=22) and dusky (n=56) dolphins. Bars represent mean values with standard error.

Subgroup Structure and Group Fission-Fusion

Hector's and Dusky Dolphin Group Structure

Number and composition of subgroups (<1 or 1-3 body lengths between subgroup members and >3 body lengths between subgroup members and the rest of the group; see Table 4.1) was assessed for Hector's and dusky dolphin groups with all changes continually noted (Figure 4.18).

Figure 4.18. A typical subgroup of Hector's dolphins during the current study.

The mean number of subgroups was significantly fewer for dusky dolphins when compared with Hector's dolphins (Mann-Whitney U=304, p<0.001; Figure 4.19).

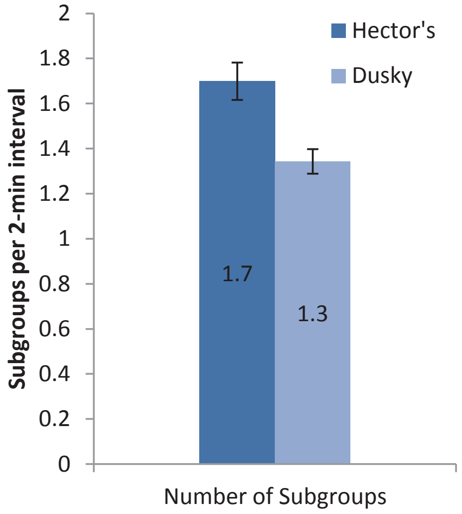


Figure 4.19. Number of dusky (n=56) and Hector's (n=22) dolphin subgroups. Bars represent mean values with standard error.

Group Size and Subgroup Structure

On average, the group size for Hector's dolphin groups changed every 6.8 ±1.4 min and dusky dolphin groups every 12.2±1.0 min. Mean group size was 4.5±0.9 individuals per interval for Hector's dolphins and 9.4±0.8 individuals for dusky dolphin small groups. In Hector's dolphin groups, mean group size per interval was significantly smaller (Mann-Whitney U=269, p<0.001), and mean group size duration was significantly shorter (Mann-Whitney U=269, p=0.001) than in dusky dolphin groups (Figure 4.20). Subgroup size was significantly smaller for Hector's dolphins than dusky dolphins (Mann-Whitney U=142.5, p<0.001).

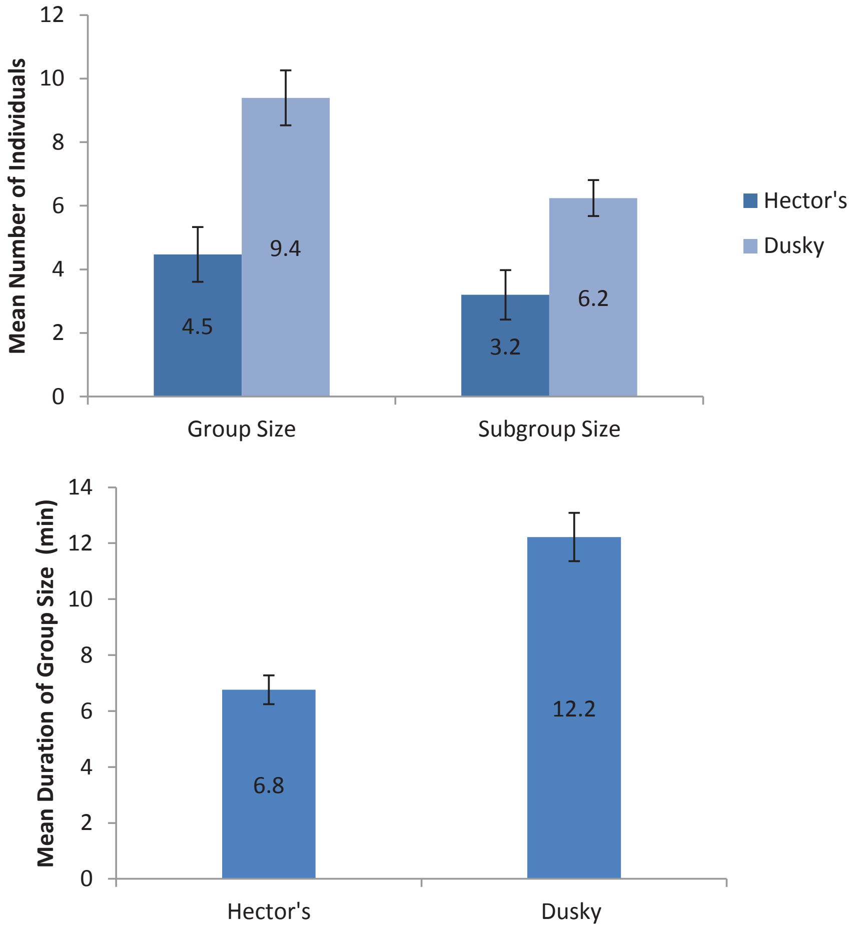


Figure 4.20 Mean group size and subgroup size per 2-min interval are compared for Hector's (n=22) and dusky dolphin (n=56) small groups (above) with mean duration of group size (below). Bars represent mean values with standard error.

A change in group size occurred in a mean of 11.1±1.9% of intervals for dusky dolphins small groups with a mean change in group size of 4.2±0.7 individuals. Mean group size changed in 24.8±3.4% of intervals for Hector's dolphins with a mean change of 2.7±0.6 individuals when group size did change. The percent of intervals in which group size changed was greater for Hector's dolphins than dusky dolphins (Mann-Whitney U=306.5, *p*<0.001).

DISCUSSION

Habitat Use

The distribution and ranging patterns of Hector's dolphins in the vicinity of the Kaikoura submarine canyon area are consistent with ranging patterns reported for dolphins of the genus *Cephalorhynchus* elsewhere in the southern hemisphere (reviewed by Heinrich et al. 2010). Hector's dolphins were found in shallow water, closer to shore, and closer to river mouths than dusky dolphins. This is particularly noteworthy since the group sizes for Hector's and dusky dolphins in this comparison of ranging patterns were similar. Larger dusky dolphin groups were encountered further from shore in deeper water (Chapter 2).

Small dusky dolphin nursery groups were most comparable to Hector's dolphins in their ranging patterns. Although dusky dolphins with calves generally form larger group sizes than Hector's dolphins, the locations of dusky dolphin nursery groups near shore, river mouths and in shallow water may be the greatest overlap between habitat use for dusky and Hector's dolphins off Kaikoura. However, even these similarities in ranging patterns do not reflect the fine-scale habitat selection for dusky dolphin nursery groups and Hector's dolphin small groups. Dusky dolphin nursery groups (see Chapter 3) are most closely associated with rivers and near shore areas adjacent to the Kaikoura Canyon whereas Hector's dolphins prefer river habitat to the north and south of Kaikoura (i.e., The Hapuku and Conway River mouths). This variability in habitat preference may be illustrated best by the greater distances from shore and water depths for dusky dolphin small groups when compared with Hector's dolphin groups encountered south of the Haumuri Bluffs. Smaller social groups have less competition among group members but there is probably a trade-off of reduced predator detection. Similar to smaller groups of primates that range higher in the forest canopy to counteract this increase in predation risk (van Schaik et al. 1983), Hector's dolphins probably range closer to shore to avoid encountering predators.

Although mixed groups of dusky and Hector's dolphins occur in the Kaikoura Canyon area (Markowitz 2004, current study), these associations are fleeting and likely occur as dusky dolphin groups pass through Hector's dolphin preferred habitat. In particular, associations of Hector's dolphins with dusky dolphin nursery groups have been observed, with neonates for both species present (Markowitz 2004). Although dusky and Hector's dolphins probably interact on a regular basis throughout their ranges, and may at times compete for resources, antagonistic interactions between the two species have not been observed off Kaikoura.

Dive Duration

Mean dive durations of Hector's dolphins were shorter than those of dusky dolphins in small groups off Kaikoura. Dive times for Hector's dolphins were predicted to be longer than dives for dusky dolphins, as diurnal foraging for Hector's dolphins was thought to increase dive times. It is possible that increased energy expenditure as dolphins search for prey resulted in reduced dive times. The mean dive duration for Hector's dolphins (33.4±21.8 s) is similar to dive durations documented for dusky dolphin small groups foraging in Admiralty Bay (35±1.9 s; Markowitz 2004), although variability is higher in dive duration for Hector's dolphins. Longer dive durations for dusky dolphin small groups off Kaikoura may be related to resting behaviour, particularly in nursery groups (see Chapter 3).

Behavioural States

Increased resting in dusky dolphin small groups and milling in Hector's dolphin groups likely reflect the differences in diurnal behavioural patterns for the two species. Dusky dolphins off

Kaikoura forage nocturnally on the deep scattering layer (DSL), and Hector's dolphins are thought to forage diurnally on coastal schooling fishes. Although foraging behaviour was never scored for dusky dolphin groups and rarely noted for Hector's dolphins, this may be a result of my strict definition for foraging behaviour. Foraging behaviour was only scored if dolphins were seen chasing fish or with fish in their mouths (after Acevedo-Gutiérrez and Parker 2000). Observations of Hector's dolphins doing long dives combined with milling behaviour and synchrony in surfacing may have been foraging behaviour. Social behaviours were not as common for Hector's dolphins as they were for members of dusky dolphin small groups. Birds feeding with Hector's dolphin groups are described elsewhere in detail (Bräger 1998). Feeding on fish stirred up by Hector's dolphins is an important feeding strategy for white-fronted terns (*Sterna striata*) that breed on the Kaikoura Peninsula. Associations of birds with foraging dusky dolphins have been noted in other studies (McFadden 2003, Vaughn et al. 2008) and are usually an indication of dolphin foraging behaviour. Terns also appear to feed on very small prey items that may be disturbed by the rapid movement of Hector's dolphins at the surface of the water in coastal habitats (W. Markowitz, personal observation).

The greater inter-individual distance of Hector's than dusky dolphins in this study may be related to Hector's dolphins more active behavioural states. Mammals tend to have lower group dispersion to maintain group cohesion while resting, and foraging mammals increase their encounter rate with prey by spreading out (Wu 1993, Norris and Dohl 1980). However, this increase in inter-individual distance may also reflect an evolutionary adaptation for this species and its current habitat use pattern. Hector's dolphins associated with river mouths are less likely to require close associations with group members for predator confusion effects and, due to their stable association with these habitats and assumed greater knowledge of prey resources and predator danger may not require such close affiliations among group members. Dusky dolphins must maintain social groupings in the context of hundreds of dolphins when in large groups. It is possible that dusky dolphins associate with conspecifics with less distance between group members as a result of this variation in social grouping patterns and social history of the species in relation to their ecology.

The direction and formation of Hector's dolphins when compared with dusky dolphin small groups is consistent with reduced ranging and less social cohesion for Hector's dolphins resident in the Kaikoura Canyon area. Dusky dolphins, even in small groups, were more likely to have consistent group formations and move directionally than Hector's dolphins based on the widely ranging, large group size formations for this species. This is the case even though they use quite similar habitats (compared with large groups) and their group sizes are similar.

Behavioural Events

Social-sexual behavioural events such as sexual approach and ventral contact were rarely seen in Hector's dolphin groups. Intromission was never observed in Hector's dolphin groups. This was strikingly different from observations of dusky dolphin small groups (particularly mating groups) and dusky dolphins in large groups that regularly engage in social mating activities (Chapter 2). Slooten, (1994), reports that Hector's dolphins do not perform leaps or other affiliative behaviours unless joined in larger groups of 11 or 15 animals. Group sizes for Hector's dolphins on encounter averaged 6 individuals with mean group size of 4.5±0.9 individuals per 2-min interval. It is possible that social-sexual activity was reduced in Hector's dolphins for this study because group sizes were small. The Hector's dolphins in this study were encountered in more turbid water closer to river mouths than dusky dolphin groups. However, water clarity was adequate to score behaviour to minimum depths of 2-5 m and all behaviours could be scored accurately for Hector's dolphin groups.

Other affiliative behaviours not necessarily related to sexual interactions including contact (social) rubs, chasing conspecifics, and ventral presentation, were all much more common in dusky dolphin small groups than in Hector's dolphins. The lack of affiliative interactions between Hector's dolphins is consistent with observations of grooming behaviour in primates. Grooming behaviour usually decreases with decreasing group size as individuals require less reinforcement of bonds in a less socially stressful environment (Dunbar 1993). The prevalence of synchronous surfacing for Hector's dolphins when compared with dusky dolphins may be related to diurnal foraging behaviour and prey searching in Hector's dolphin groups. Synchronous surfacing was more common in small mating groups of dusky dolphins than adult non-mating groups (Chapter 3). Synchronous surfacing may also indicate synchrony of above and underwater movements that allow group members to strengthen affiliations among individuals for a species that likely has increased competition among group members for food and mating opportunities (Connor 2007, Gowans et al. 2008).

Although noisy leaping did occur, the most common leaping behaviour in small groups of dolphins was head-first re-entry leaps. In small groups of dusky dolphins in Admiralty Bay, these sorts of leaps are associated with herding fish (McFadden 2003, Markowitz et al. 2004, Pearson 2009). Off Kaikoura, these leaps are most often associated with chasing conspecifics in the context of mating (see Chapter 3). The reduced rate of head first re-entry leaping in Hector's dolphin groups may indicate that Hector's dolphins, if foraging or looking for prey, do not herd prey in as coordinated a fashion as dusky dolphins in Admiralty Bay (Vaughn et al. 2010). In another study of Hector's dolphin behaviour, re-entry leaping was associated with social and sexual behaviour rather than foraging behaviour

(Slooten 1994). The frequency of behavioural events was much greater in dusky dolphin groups than in Hector's dolphin groups, occurring at a rate of almost four times that of Hector's dolphins.

Group Fission-Fusion

Possibly the best measure for group fission-fusion rate was changes in group size per 2-min interval. These changes are reported here in 2-min intervals for consistency with other studies (e.g., Pearson 2009) although they were collected in real time. The mean duration that groups maintained the same group size (without fission or fusion events) was much shorter for Hector's dolphins than dusky dolphins, which is consistent with my prediction that Hector's dolphins would have higher rates of fission-fusion than dusky dolphins. This may be a result of reduced social bonds for the less widely ranging and more resident Hector's dolphins as group members compete for resources . Mean group size was lower for Hector's dolphins than dusky dolphins, and group size for small groups of dusky dolphins was higher than group size reported for dusky dolphins in Admiralty Bay (7.0±6.0 individuals). The fission-fusion rates for Hector's dolphins were most similar to dusky dolphins in Admiralty Bay (24.8 *versus* 19.7% of intervals, respectively). Group size duration was longer for both Hector's (6.8±0.5 min) and dusky dolphins (12.2±0.9 min) in this study when compared with dusky dolphins in Admiralty Bay (5.2 min; Pearson 2009).

The mean group size for Hector's dolphins of 6.0±1.2 individuals compared with the subgroup size for dusky dolphins small groups of 6.2± 0.6 individuals. This basic social unit size has been reported for other dolphin species (e.g., Risso's dolphin, *Grampus griseus*; Hartman et al. 2008) and may be a trait conserved among delphinids. Both the group size for Hector's dolphins and the subgroup size for dusky dolphin small groups is similar to a 'base' social unit (or subgroup) described by Norris (1994a) for spinner dolphins (*Stenella* *longirostris*). Wild and captive spinner dolphins encircled by nets during experimental trials were unwilling to escape through small openings that would fit only one or a few individuals (Perrin and Hunter 1972, Norris 1991). Only when holes in the net were 5.5 to 6 m across (roughly the size for 6 individuals to pass easily) did captive dolphins move freely through the opening, and wild dolphins only when severely crowded. Norris proposed a minimum social unit size or 'basic reaction unit' for spinner dolphins (Norris and Schilt 1988, Norris 1994a) and suggested that dolphins under stress are unwilling to leave this social unit when in a state of 'predator defense' (K.S. Norris pers.comm. 1992[1]). There are likely to be 'exceptions to the rule' of sociality for dolphins, like coastal species such as the bottlenose dolphins that are observed to forage alone at times (Sargeant and Mann 2009) and especially river dolphins (Platanistidae, Iniidae, Pontoporiidae; Reeves and Martin 2009). Nevertheless, this similarity in basic social unit size among Hector's and dusky dolphins relates not only to the importance of schoolmates for dolphins but also the observation that a dolphin without its group is "much less than a complete animal" (Norris 1994b).

Summary of Findings

Hector's dolphins were found closer to shore, in shallower water and closer to river mouths than dusky dolphins in small groups. Use of river mouth habitat was further defined by Hector's dolphin associations with the Hapuku and Conway River mouths that are to the north and south of the Kaikoura Canyon. Because they are resident year round, Hector's dolphins are likely to have more detailed knowledge of predation risk and resource distribution of various micro-habitats in the vicinity of the Kaikoura Canyon than dusky dolphins that remain in Kaikoura for a few months at a time. Dusky dolphins may capitalise

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[1] K.S. Norris, personal communication, April 1992. University of California, Santa Cruz

on prey items associated with the DSL and remain closer to the Kaikoura Canyon to make use of this feature.

Dive durations were not longer for Hector’s dolphins than for dusky dolphins. In fact, dusky dolphin dive durations were quite long when compared with Hector’s dolphins. Hector’s dolphin dive durations were similar to dive durations for dusky dolphins foraging in Admiralty Bay as well as mating groups of dusky dolphins off Kaikoura. Increased energetic expenditure in the pursuit of prey may reduce dive durations for Hector’s dolphins. Diurnal foraging behaviour did occur more often in Hector’s dolphins than dusky dolphins; however, foraging rates were quite low for Hector’s dolphins during this study. This finding is consistent with previous work (Bräger 1998) that assessed Hector’s dolphin behaviour year-round off Kaikoura. Hector’s dolphin foraging was not as obvious outside spring and summer when dolphins fed on small schooling fishes, likely due to seasonal variation in prey availability. Hector’s dolphins rested less and milled more than dusky dolphins and travelling behaviour occurred at very low rates in both species.

Noisy leaps occurred at very low rates in Hector’s and dusky dolphin small groups, likely to reduce predator detection of small groups or as a response to smaller group sizes. Hector’s dolphins engaged in less social behaviour than dusky dolphins, although surfacing was more synchronous for Hector’s dolphins. Synchronous surfacing has been described as an indication of both foraging and social bond reinforcement in the context of competition for other delphinids (Connor et al. 2006).

Hector’s dolphins formed smaller groups than dusky dolphins. This may be adaptive for this resident species to reduce competition among group members. Group fission-fusion rates were higher for Hector’s dolphins than dusky dolphins, possibly due to increased competition for resources in the less wide-ranging Hector’s dolphin.

Socioecological models

Hector’s and dusky dolphins conform to socioecological models proposed for coastal *versus* neritic dolphin species (Gowans et al. 2008). Hector’s dolphin behaviour and fission-fusion rates generally follow the predicted pattern of small, less widely ranging species with few social partners in coastal habitats. Dusky dolphins form larger groups in similar habitats, with behaviour and fission-fusion rates that compare with more neritic species (Wells *et al.* 1999, Gowans *et al.* 2008). Neritic species are expected to be larger, range more widely and have larger social groups. Although dusky and Hector’s dolphins form groups of similar size off Kaikoura, as compared in this study, differences in behaviour and grouping patterns reported here suggest the factors influencing group formation and group membership are quite different for the two species.

The formation of smaller groups with higher fission-fusion rates for Hector’s dolphins is consistent with the proposed model for coastal species of increased competition among group members for limited local resources. Reduced social behaviour for Hector’s dolphins in these smaller groups also supports this trend of reduced sociality in species in more complex habitats (Estes 1974). Although dusky and Hector’s dolphins formed groups of similar size, habitat selection by Hector’s dolphins was consistently closer to shore, river mouths and shallow waters. This fine-scale habitat selection by Hector’s dolphins is consistent with predictions for coastal species, or species in complex habitats, relying on habitat features rather than social partners for protection from predators (Estes 1974, Wells *et al.* 1999, Gowans *et al.* 2008).

The phylogenetic history of each species likely contributes to the differences in fine-scale habitat selection, social grouping patterns, and behaviour reported here. The predictions based on socioecological models for each species hold true even when associations of similar group sizes are compared. Competition between these sympatric species is mediated by differences in fine-scale habitat and prey selection.

CHAPTER 5

INTERACTIONS OF DUSKY DOLPHINS WITH TOUR AND RECREATIONAL VESSELS OFF KAIKOURA, NEW ZEALAND

INTRODUCTION[2]

Tourism and wildlife viewing support economies of local communities, particularly those with accessible populations of large mammals (Okello et al. 2008). These activities allow participants to experience and reconnect with the natural environment, and can promote conservation and wilderness preservation (Tapper 2006, Orr 2009). However, tourism interactions can also affect the behaviour, physiology and movement patterns of animals (Dyck and Badack 2004, Nowacek et al. 2004, Amo et al. 2006, Mathews et al. 2007, Semeniuk et al. 2009), with associated impacts on distribution, habitat use or breeding success in some populations (Mann et al. 2000, Bejder et al. 2006a, b, Ellenberg et al. 2007, Thiel et al. 2008).

Cetacean tourism is a multi-billion dollar industry with 13 million viewers annually (O'Connor et al. 2009), focused mainly on large whales and small groups of resident coastal dolphin species (Hoyt 2009). This alternative to consumptive uses and unsustainable exploitation provides economic incentive for conservation of dolphin populations (Markowitz et al. 2010b). Nevertheless, concerns remain regarding the effects of tour activities on wild dolphin populations (Constantine 1999, Bejder and Samuels 2003). In one of the best-studied cases, tourism was shown to potentially impact a bottlenose dolphin (*Tursiops aduncus*) population off Western Australia, changing dolphin distribution (Bejder et al. 2006a) and apparently increasing calf mortality (Mann and Barnett 1999, Mann et al. 2000, Mann and Kemps 2003).

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[2] This chapter contains findings and text with modifications that were originally reported to the New Zealand Department of Conservation in a contract report (Markowitz and Markowitz 2009a).

In New Zealand, as elsewhere, dolphin behavioural responses to vessels have been found in a number of studies focused primarily on small groups of resident species. Responses to tourism activities included reduced resting, avoidance of vessels through changes in dive rates, and long-term sensitization to swim-tourism resulting in bottlenose dolphins (*Tursiops truncatus*) avoiding swimmers (Constantine 2001, Constantine et al. 2004, Lusseau 2003, 2004, 2005, 2006). Tour vessel avoidance was also found for Hectors' dolphins (*Cephalorhynchus hectori*, Bejder et al. 1999). Behavioural changes and reduced foraging in the presence of tour vessels has been documented in common dolphins (*Delphinus delphis*, Neumann and Orams 2005, Constantine and Baker 1997, Stockin et al. 2008) and sperm whales (*Physeter macrocephalus*, Richter et al. 2006).

Behavioural responses of dolphin groups to the presence of vessel traffic include short- term and long-term avoidance of vessels or areas in which vessel traffic occurs (Allen and Read 2000, Nowaceck et al. 2001, Williams et al. 2002, Bejder et al. 2006a). Behavioural state, events and sequences of behaviour can also be altered in the presence of boats, specifically tour vessels that target dolphins (Constantine and Baker 1997, Barr and Slooten 1998, Constantine et al. 2004, Lusseau 2006b). Lack of complexity in dive behaviour in response to interactions with tourism has been used as an indicator of stress in Indo-Pacific bottlenose dolphins (Seuront and Cribb 2011)

It has been hypothesized that tourism activities can result in a breakdown in social structure of dolphin groups, and this breakdown may have long-term impacts on development and survival of individuals (Bejder et al. 2006b).

Tourism and recreational vessel activity have increased dramatically at Kaikoura over the past 10 years (Te Korowai 2008). The closing of recreational fisheries in other areas of the South Island has also increased fishing pressure off Kaikoura, resulting in an increase in recreational fishing vessels. Other recreational activities that occur at Kaikoura regularly and often interact with dolphin groups include kayaking tours, jet-skiing vehicles, and aircraft.

Dolphin behavioural responses to tour vessels have been examined from a small research vessel for bottlenose (Constantine et al. 2004, Lusseau 2003, 2004, 2005, 2006) and common dolphins (Neumann and Orams 2005, Constantine and Baker 1997, Stockin et al. 2008) in New Zealand, and dusky dolphins in Argentina (Dans et al. 2008, Markowitz et al. 2010b). Advantages of this data collection platform include fine-scale measurements of changes in behavioural state, behavioural events, direction and grouping patterns of dolphins (Bejder and Samuels 2003).

Objectives of the Study

Dusky dolphin behaviour was quantitatively examined in response to different types of commercial and private vessel traffic off Kaikoura, New Zealand. The research vessel platform cannot be used to provide data on dolphin behaviour without the presence of vessels, as the research vessel itself was always present during the observations. However, it could be used to examine dolphin behaviour with respect to the type and the activity of other vessels interacting with the dolphins.

The specific objectives of this study were to assess the effects of:

1. swim-with-dolphins tours
2. non-swim, ocean-based dolphin watching tours
3. recreational vessels, and
4. aircraft tours

on predominant behavioural state, movements, distribution, dispersion, leaping rate and incidence of high-speed behaviours of dusky dolphins found in large groups at Kaikoura, New Zealand.

Based on the findings of previous research investigating the effects of tourism on dolphins, the following hypothesis and predictions were tested.

Hypothesis: If dusky dolphins at Kaikoura are disturbed by tour activity, they will respond with changes in behaviour, social organization and grouping patterns similar to dolphin responses to predators.

Specifically, I predicted that dolphins would:

1. Rest less and travel more in the presence of tour vessels with higher leaping rates and high-speed behaviours.
2. Change direction more often in the presence of tours, moving away from approaching vessels with reduced group dispersion.

METHODS

Data Collection

As most tour vessels focus on large groups comprised of hundreds of dolphins (Markowitz 2004), behavioural data from large groups were the primary focus for analyses reported in this chapter. It is impractical to conduct focal individual follows within such large groups. Therefore, focal group sampling was used to document behaviours exhibited within the group (Martin and Bateson 1993, Mann 2000). Because of the inherent difficulty in accurately counting dolphins within the large groups most frequently visited by tour operators in the Kaikoura area, group size was categorized as 50-99, 100-249, 250-499, 500-1,000 or >1,000 (Markowitz 2004). These data cannot be used to estimate the frequency of behaviours exhibited by individuals, but can be used as a measure of group activity and responses to tour vessels (Bejder and Samuels 2003). These data were blocked by time of day and timing with respect to visitation by swim-with-dolphins tours (Table 5.1).

Table 5.1. Research Effort by Time of Day and Dolphin Swim Tour Activity (# and % of 2-minute intervals).

Time of Day	**Morning**		**Afternoon**		**Combined**	
Dolphin Tour	#	%	#	%	#	%
Before	191	22%	195	20%	386	21%
During	325	37%	300	32%	625	34%
After	275	31%	223	23%	498	27%
Control	96	11%	234	25%	330	18%
Total	887	48%	952	52%	1839	

I utilised a small 5.5 m vessel with an 85 hp outboard motor. Focal group approaches and follows were conducted following the protocols recommended by Würsig and Jefferson (1990), with the vessel positioned alongside the dolphins, matching dolphin group heading and speed in parallel so as to minimize disturbance. Simultaneous monitoring from a shore station during a concurrent study did not find any significant effects of the research vessel on dolphin group behaviour (Lundquist and Markowitz 2009). Dolphin groups were located with the assistance of these shore-based monitoring teams engaged in theodolite tracking (Würsig et al. 1989). Dolphin groups were defined by spatial proximity according to the "10-m chain rule" (Smolker et al. 1992). Group age class composition was estimated from sizes of individuals present based on lengths of aged post-mortem specimens (Cipriano 1992), with age class categorized as: adult/subadult (> 2 years, 1.6-1.8m), juvenile (1-2 years, 1.3-1.5m), calf (< 1 year, 1-1.2m). Group locations and tracks of group movements were estimated using longitude, latitude and time data recorded by Garmin global positioning system (GPS) receiver from the vessel as it was positioned alongside the group. Time and location data were recorded at one-minute intervals and later downloaded to computers for analysis of focal dolphin group location, ranging, and movement patterns (e.g., surface speed). GPS tracks were plotted and analysed using GIS, Mapsource and GPS Utility software.

Upon group encounter, a time and GPS position was noted along with the estimated group size, group composition and behavioural state. The presence of vessels within 300 m of the dolphin group was also noted, including vessel type (swim-with dolphin, dolphin watch, recreational/fishing, fixed-wing aircraft tour, helicopter tour, or other aircraft). Vessels were documented within 300 m of the group and all vessel approaches and departures within 50 m of the dolphin group were noted, including a categorical speed (no wake, slow wake, at speed) measure, a direction of approach (front, side or rear of group) and angle of approach (0-180 °). Behavioural data were collected using scan sampling of behavioural state, heading, mode nearest neighbour distance, and group swimming formation at 2-minute intervals (Martin and Bateson 1993, Lehner 1996, Markowitz 2004). All occurrences of leaping (categorized as noisy, clean re-entry, or acrobatic leap) were recorded during each interval (Markowitz 2004). Intermittent and non-discrete behaviours such as social or 'play' behaviours (including social rubbing, ventral presentation, intromission, spy-hops, and playing with kelp; Markowitz 2004) were recorded using one-zero interval sampling (Martin and Bateson 1993).

Continuous behavioural data were recorded using an Olympus VN-2100PC digital voice recorder with noise reducing headset. Using this method, I documented behavioural state, group dispersion, heading and number of individuals associated with the research vessel (bow riding) whenever these parameters changed (Martin and Bateson 1993). Other indicators of potential disturbance or excitement, including sudden bursts of speed ("slicing" by individuals or the entire group) and tail slapping, were documented in real time. Intermittent and non-discrete behaviours such as social or 'play' behaviours (including social rubbing, ventral presentation, intromission, spy-hops, and playing with kelp; Markowitz 2004) were recorded continuously. Continuous digital audio recordings of behaviour were transcribed onto datasheets and re-sampled in accordance with scan and one-zero sampling techniques to improve sample size. Bow riding behaviour was documented in the manner described by Markowitz (2004) as an indication of vessel approach by dolphins.

For examination of seasonal patterns, seasons were defined as: winter = June-August, spring = September-November, summer = December-February and autumn = March-May (Markowitz 2004, after Cipriano 1992). For examination of diurnal patterns, the day was divided into "morning" = 6:00-11:29, "midday" = 11:30-13:29, "afternoon" = 13:30-18:00.

Data Analysis

Data were entered into a Microsoft Access database for querying by vessel type, time of day, season, and other relevant parameters. Statistical tests were conducted in SPSS v. 11. Data were tested for normality using the Kolmogorov-Smirnov test, and parametric or non-parametric statistical tests run as appropriate.

For analyses of responses to swim-with-dolphin tour boats, a before-during-after analytical approach was employed (Bejder and Samuels 2003, Bejder et al. 2006a). Markov-chain analysis was used to assess changes in focal group behavioural state before, during and after swim-with-dolphin tour vessel encounters, with chi-square and z-tests used to test for significant changes in transition proportions (Lehner 1996, Lusseau 2003, Lundquist and Markowitz 2009). Freidman tests were used to assess significant differences for samples that included all three conditions (before, during and after). Continuous samples of all three conditions were difficult to collect because the research vessel left the focal dolphin group whenever more than two other vessels approached the group. To increase sample size, I separated before and during from during and after conditions. These analyses were conducted using matched pairs t-tests or Wilcoxon signed rank tests. As interactions with other vessels were relatively intermittent and short, dolphin behaviour was compared in the presence *versus* absence of dolphin watching tour boats, recreational boats and aircraft. Matched-pairs tests (t-tests, Wilcoxon) were used to compare behaviour of dolphin groups during vessel interactions and other times when vessels were not present on the same day. Tests of independent control (no tour vessel visits) *versus* treatment (tour vessel visits) groups were conducted using Mann-Whitney U tests and t-tests.

Initial plotting of GPS locations and calculations of movement patterns were performed in Mapsource Blue Chart Pacific v.8. Longitude/latitude positions from all stations were imported into ArcGIS v. 10.0, and overlaid onto a shore line base map and a bathymetric chart supplied courtesy of the National Institute of Water and Atmospheric Research, New Zealand (NIWA). All map features presented in this chapter were imported as Longitude/Latitude tables, and then projected using the WGS 84 coordinate system in ArcGIS 9.3. To obtain more accurate estimates of distances and areas, the data frame was changed to the New Zealand national grid system NZ UTM 59S that centres on 171° East Longitude and all data layers exported to shape files matching this data frame.

North-south variation in bearing was calculated from the bearing relative to true north (0-360°). North-south bearing deviation was subtracted from 90° (true east or true west). The resulting north-south bearing deviations ranged from -90° (true south) to 90° (true north), with bearings of true east and west = 0°. Data were tested for north-south variation by one-sample t-test relative to 0° (no significant north-south variation).

RESULTS

Before, During and After Swim-with-dolphin Tour Interactions

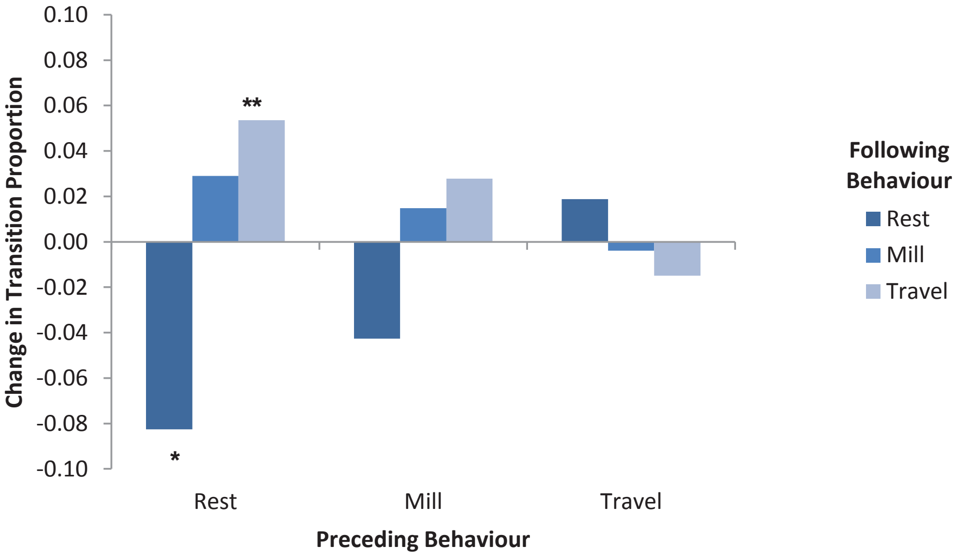
Swim-with-dolphin tour boats (operated by Encounter Kaikoura) were present 34% of the time large dolphin groups were monitored from the research vessel. This probably underestimates the actual proportion of time tour vessels were present because, as a matter of courtesy, the research vessel left dolphin groups when an approaching tour boat would be the fourth vessel. Swim-with-dolphin tour vessels generally approached and left dolphin groups from the side at an angle parallel or near-parallel to the dolphins' heading (Table 5.2). Although most approaches were estimated to be at either no wake (< 5 knots) or slow wake (~ 5 knots) speed, many also occurred at wake speeds apparently exceeding 5 knots (27%).

Changes in Behavioural State

Dolphin group behavioural transition proportions based on Markov chain analysis changed from before to during to after visitation by swim-with-dolphin tour boats ($\chi^2 = 67.707$, df=16, $p<0.001$). Dolphin groups were less likely to remain at rest during swim-with-dolphin tour interactions than before tour interactions, with an increase in transitions from rest to travelling (Figure 5.1a.). After departure of swim-with-dolphin tour vessels, dolphin groups were more likely to continue either resting or travelling (transitions from resting to milling decreased and transitions from travelling to milling decreased), and less likely to continue milling (milling was more likely to change to rest), than during tour interactions (Figure 5.1b).

These changes in behavioural state transitions resulted in differences in the estimated bout durations for resting, milling and travelling (Figure 5.2a). Bouts of resting decreased in duration during swim-with-dolphin tour interactions. Duration of travelling bouts increased after swim-with-dolphin tour vessels left. Overall, dolphin groups engaged in less resting after interacting with dolphin swim tours than before interacting with the tours (*t*= 1.678, *p*=0.05, Figure 5.2b).

a. From Before to During Swim-with-dolphin tour interaction



b. From During to After Swim-with-dolphins tour interaction

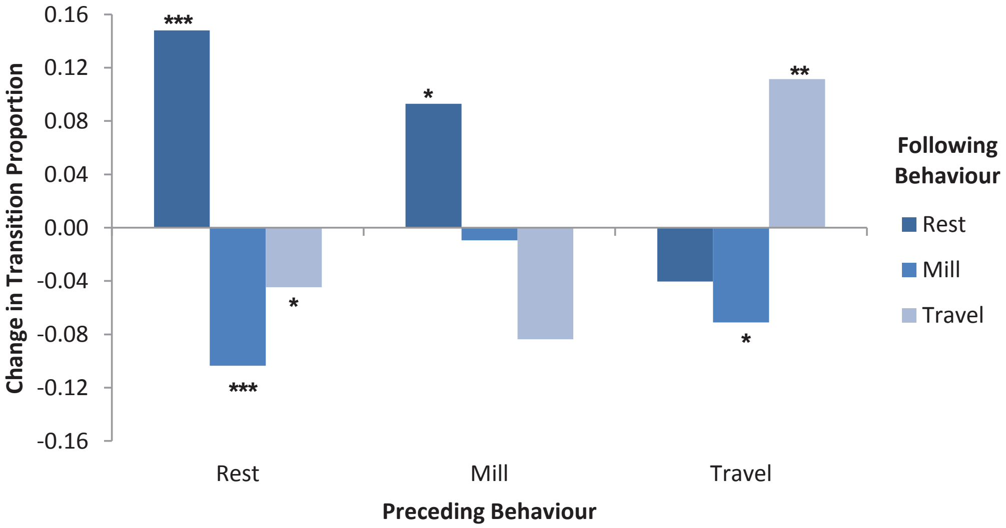
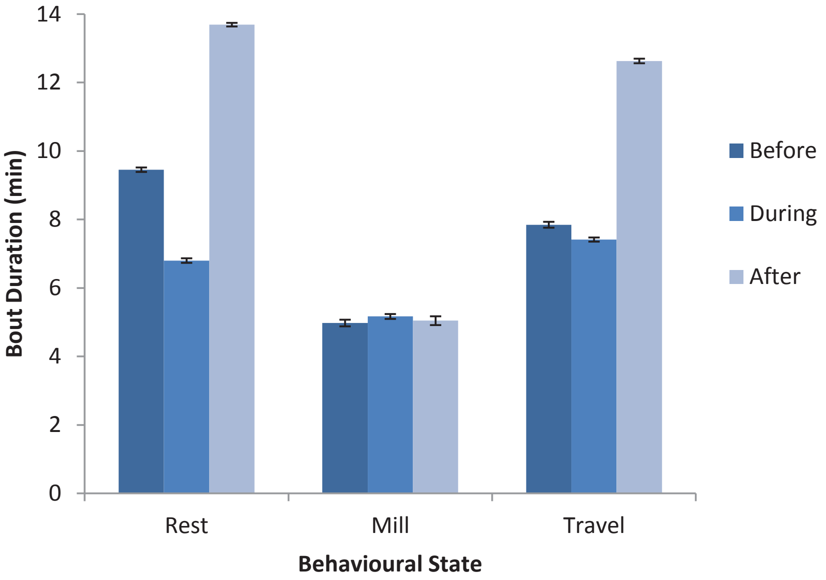


*Figure 5.1. Changes in behavioural state transition proportions based on Markov chain analysis are compared for dusky dolphin groups (a) before versus during and (b) during versus after swim-with-dolphins tour boat interactions (n= 386 before, 625 during, 498 after). Significant differences are indicated by * p<0.08, ** p<0.05, ***p<0.01 (z-tests).*

a. Bout durations before, during and after tour interactions



b. Behavioural budget before, during and after tour interactions

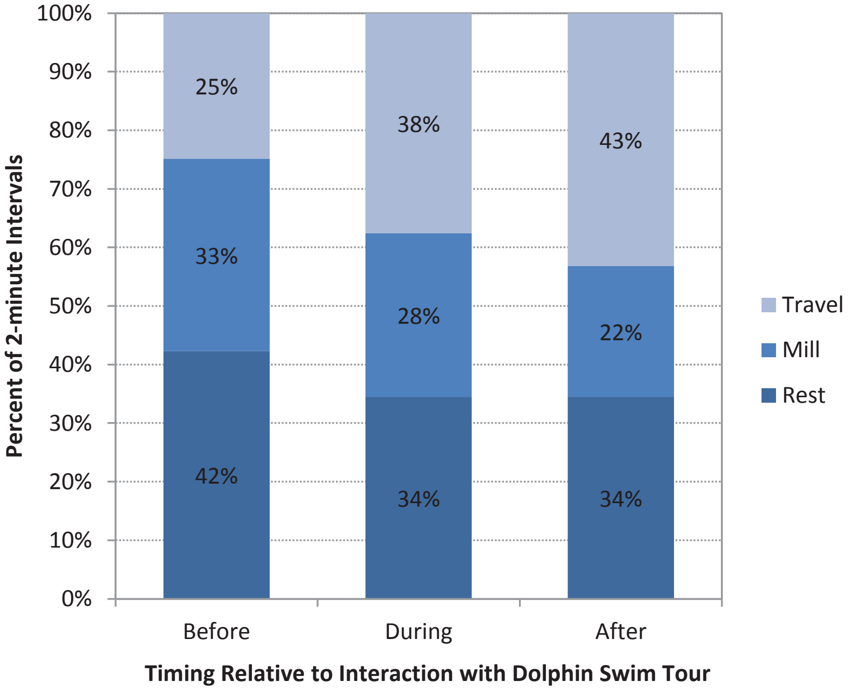
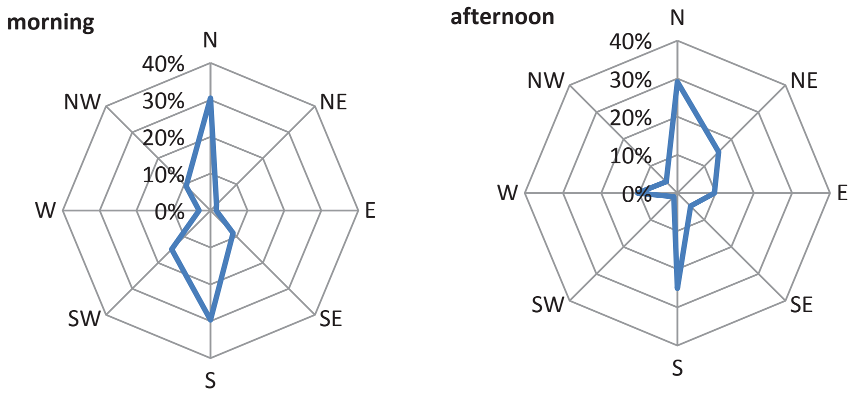


Figure 5.2. Behavioural state of dusky dolphins is compared before, during and after visits by swim-with-dolphins tour vessels by examining (a) mean estimated bout durations (n= 386 before, 625 during, 498 after).and (b) mean proportion of 2-minute scan samples during which dolphin group predominant activity was resting, milling and travelling (n=50 groups).

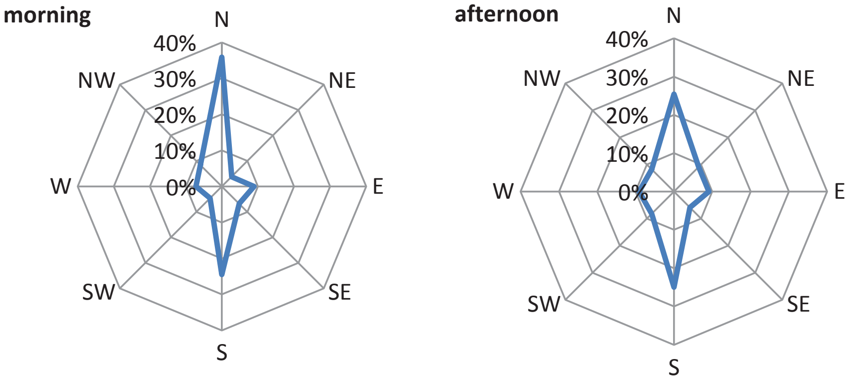
Changes in Group Heading

In the morning, dolphin group headings were predominantly northward or southward (alongshore) before, during, and after swim-with-dolphins tour interactions (Figure 5.3).

a. Before Tour Interaction



b. During Tour Interaction



c. After Tour Interaction

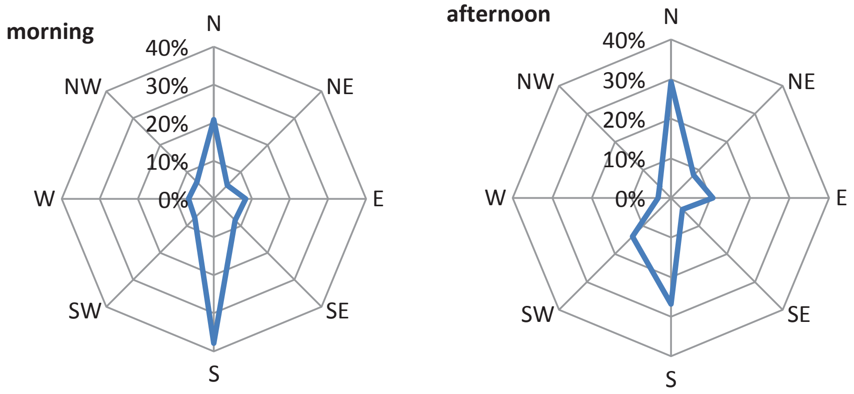


Figure 5.3. Directional heading of dolphin groups is compared (a) before, (b) during, and (c) after swim-with-dolphins tour interactions in the morning (left, n=22 groups) and afternoon (right, n=28 groups).

Table 5.2. Estimated speeds and angles (relative to dolphin group heading) of swim-with-dolphin tour vessels approaching and leaving dusky dolphin groups (n=142 approaches).

Speed	Approach	Depart	From		Bearing	
no wake	30%	46%	front	20%	0 - 45°	50%
slow wake	43%	50%	side	48%	90°	32%
at speed	27%	4%	rear	32%	180°	18%

Dolphin group bearing was significantly more southward during than before interactions with swim-with-dolphin tour vessels during the morning (matched pairs $t = 1.878$, $p<0.05$). This change appeared to last for some time because after the tour vessels left the bearing of the dolphins became significantly more southerly than during the interactions with the tour vessels (matched pairs $t = 2.636$, $p<0.05$). Before and during tour interactions, dolphin group bearing alongshore was as likely to be north as south (one-sample t-tests, *ns*, Figures 3.3 and 3.4). Bearing of dolphin groups after swim-with-dolphin tour interactions in the morning was significantly more likely to be southerly than northerly (one sample t-test, $t=2.539$, $p<0.05$, Figure 5.4). Independent of tour vessel interactions, bearing of dolphin groups during early morning (before 10:00), mid-morning (10:00-11:00), and late morning (after 11:00) did not show significant north-south variation (1 sample t-tests, *ns*). In the afternoon, dolphin group bearing was slightly more often eastward or westward (offshore or inshore) than in the morning although still predominantly alongshore (Figure 5.3). Dolphin group bearing did not vary significantly east-west or north-south before, during, and after swim-with-dolphins tour interactions in the afternoon, (one sample t-tests, *ns*).

Dolphin groups changed heading by 45° or more during a significantly greater proportion of 2-minute sampling intervals during interactions with dolphin swim tour boats than either before (Wilcoxon $z= 2.624$, $p<0.05$) or after (Wilcoxon $z=1.790$, $p<0.05$) interacting with the tour boats (Figure 5.5).

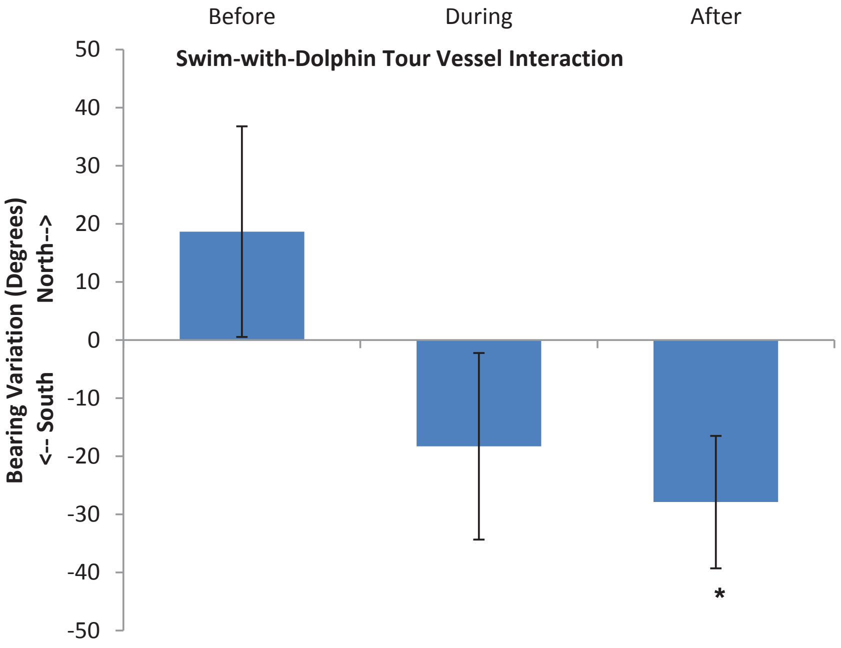


*Figure 5.4. Dolphin group bearing is compared before, during and after interacting with swim-with-dolphin tour vessels (n=50 groups). Positive bearings indicate a northward heading; negative bearings indicate a southward heading. Bars represent mean values with standard errors (significant variation from 0°is indicated by *, 1-sample t-test p<0.05).*

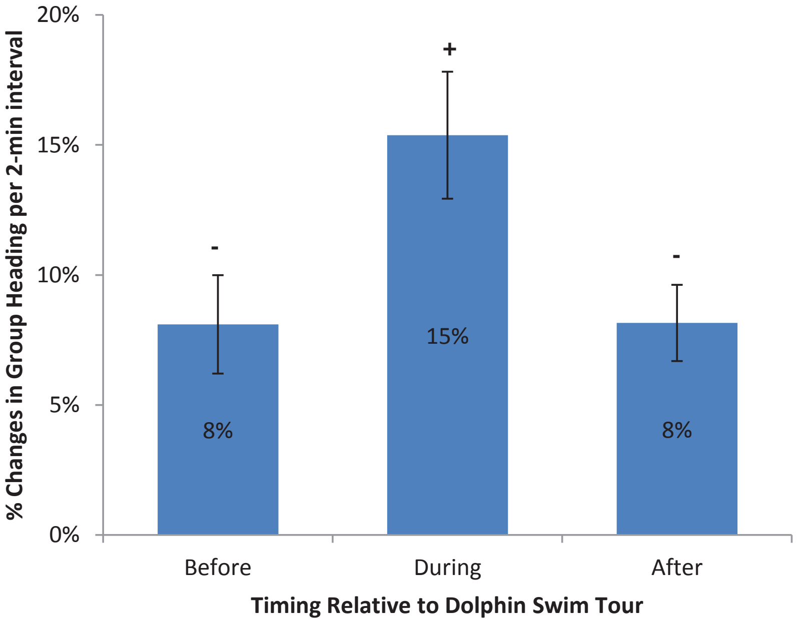


Figure 5.5. Changes in dolphin group heading of 45°or more are compared before, during and after swim-with-dolphins tour boat interactions (n=50 groups). Bars represent mean values with standard errors. Significant differences (p<0.05) are indicated by + and – signs.

Changes in Group Dispersion

Dispersion (mode nearest neighbour distance) did not vary between before, during and after swim-with-dolphins tours in either the morning (means ± se: before=2.5±0.28m, during=2.7±0.20m, after=2.4±0.21m, Wilcoxon tests, *ns*) or the afternoon (means ± se: before= 2.4±0.20, during= 2.5±0.17, after=2 .6±0.29, Wilcoxon tests, *ns*). Dispersion also did not vary between dolphin groups visited in the morning by swim-with-dolphins tours and control groups that were not visited by tours (Mann-Whitney, U = 68, *ns*, Figure 5.6). However, dolphins were more tightly grouped on afternoons when interacting with dolphin swim tour vessels than on afternoons when they did not interact with the tour vessels (Mann-Whitney, U = 101, $p<0.05$, Figure 5.6). Afternoon samples were evenly distributed with respect to season (both samples with tour vessels and controls = 64% summer *versus* 36% winter) and time of day, so this finding does not appear to be a sampling artefact.

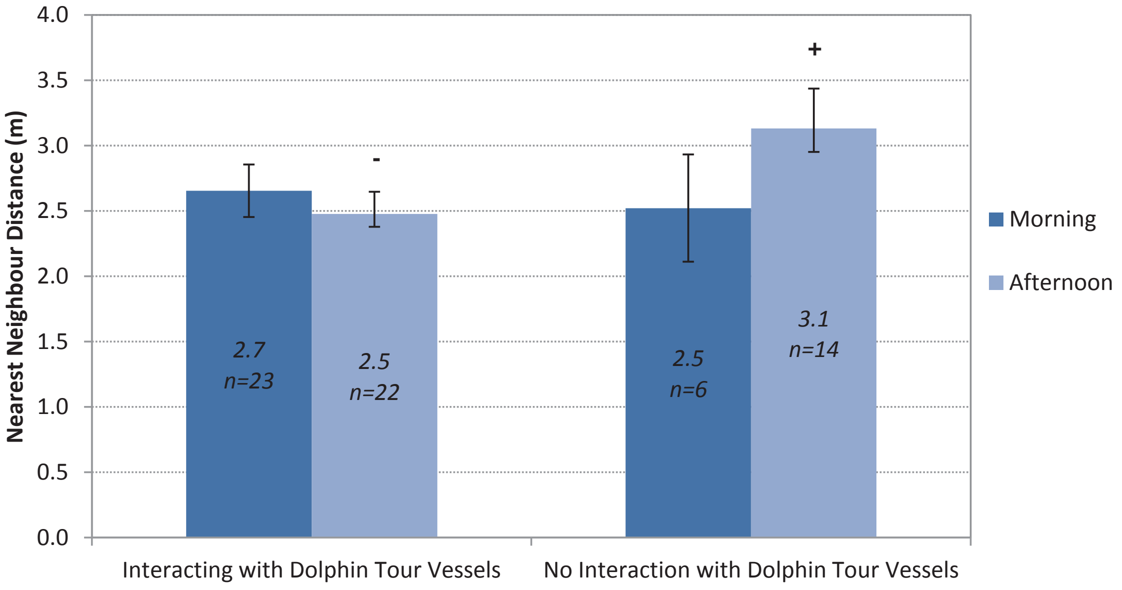


Figure 5.6. Dispersion of dolphin groups interacting with dolphin swim tour vessels and groups not visited by dolphin swim tour vessels is compared by time of day. Mode nearest neighbour distance was estimated by number of body lengths between individuals (1 body length =1.7m). Bars represent means with standard errors (Significant differences are indicated by + and – signs).

Changes in Leaping Rate

Noisy leaping increased in the presence of swim-with-dolphins tour vessels (matched pairs t-test: *t*=-2.053, *df*=26, *p*<0.05, Figure 5.7). Noisy leaping after the tour boats left was not different from noisy leaping activity before or during the tour (t-test, *ns*).

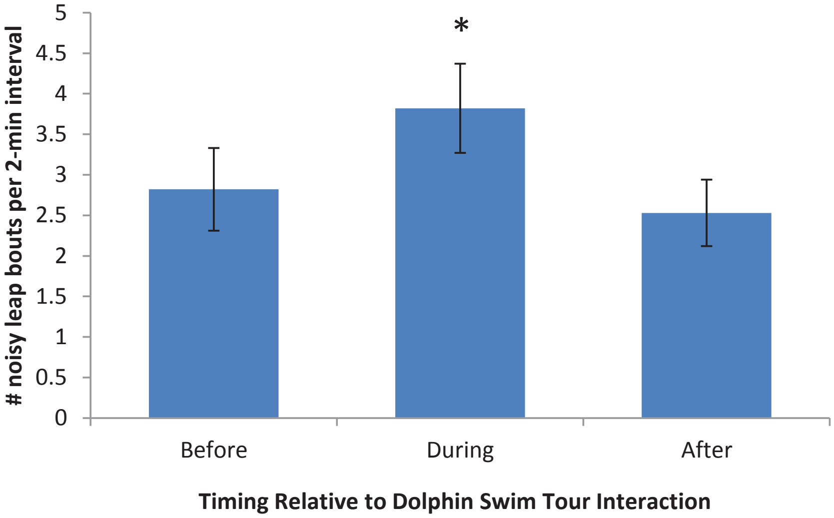
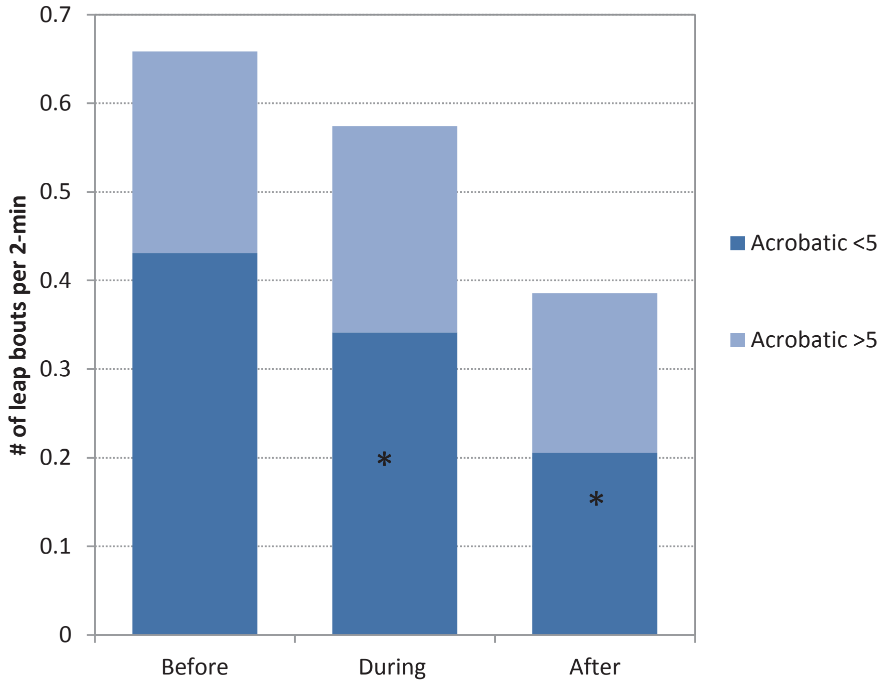


Figure 5.7. The number of bouts of noisy leaps is compared before, during and after swim-with-dolphins tour boat interactions (n=50). Bars represent means with standard errors (p<0.05).*

The increase in noisy leaping during the tour was a result of an increase in non-acrobatic leaping behaviour. Dolphins performed more bouts of non-acrobatic leaps in the presence of dolphin swim tour vessels regardless of bout duration (n=26, paired samples t=-1.984, *df*=25, *p*<0.05; Figure 5.8b). However, dolphins engaged in fewer short bouts of acrobatic leaps during and after the tour than before the tour (Freidman χ^2 =4.919, *df*=2, *p*<0.05; Figure 5.8a). There were no differences in clean re-entry leaping behaviour between dolphin groups before, during or after interactions with swim-with-dolphin tour vessels. Clean re-entry leaping also did not vary between dolphin groups interacting with swim-with-dolphin tour vessels and dolphin groups that did not interact with the tours.

a. Acrobatic Noisy Leaping



b. Non-Acrobatic Noisy Leaping

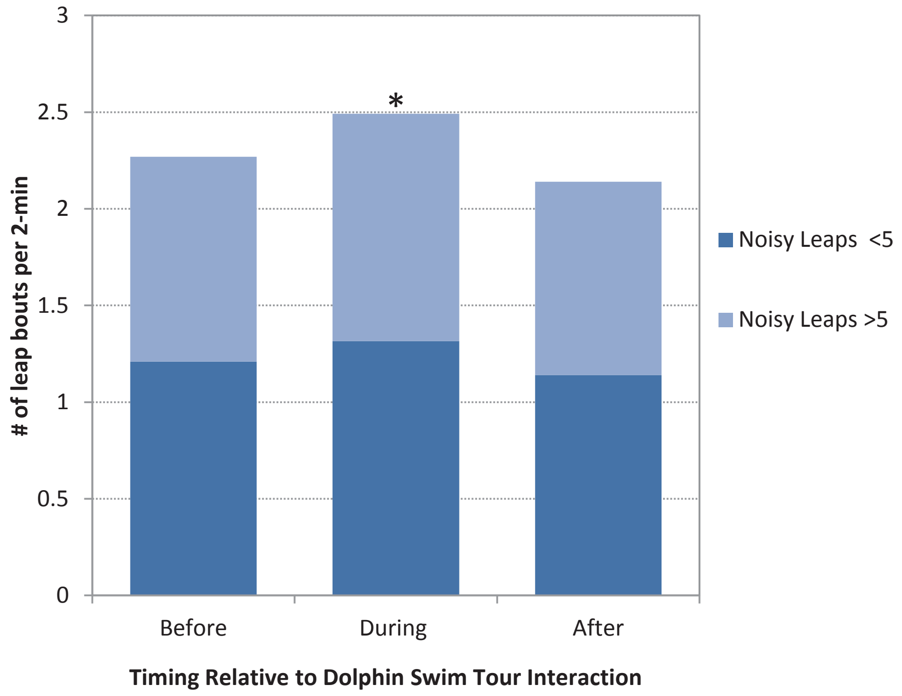


Figure 5.8. (a) Acrobatic leaps and (b) non-acrobatic noisy leaping behaviour are compared before, during and after swim-with-dolphin tour vessel interactions (n=50 groups). Stacked bars represent mean number of short bouts (<5 leaps) and long bouts (>5 leaps) of aerial behaviour per 2-minute interval (p<0.05).*

Incidence of porpoising (horizontal, travelling leaps without a splash) also increased during interactions with dolphin swim tour vessels (Figure 5.9). The proportion of intervals during which dolphins engaged in porpoising increased in the presence of the swim-with-dolphin tour vessels when compared with porpoising behaviour before the encounter (Wilcoxon Signed Ranks Test; Z=-2.214, $p<0.05$), and decreased again after the vessels left the dolphins (Wilcoxon Signed Ranks Test; Z=-1.608, $p<0.05$). Other high speed activity such as bursts of high-speed travel at the surface ("slicing") did not vary from before or after swim-with-dolphin tour vessel interactions (Wilcoxon signed rank tests, *ns*).

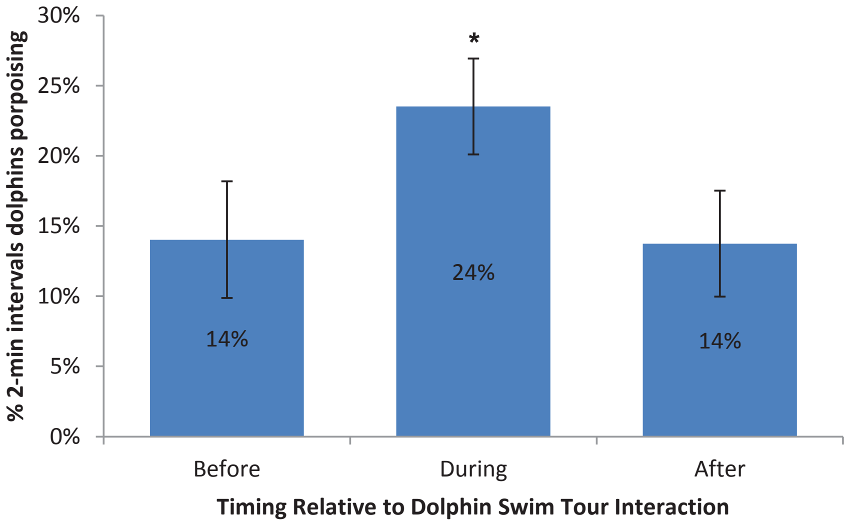


Figure 5.9. Proportion of 2-minute intervals during which dolphins engaged in porpoising is compared before, during and after swim-with-dolphin tour vessel interactions (n=50 groups). Bars represent means with standard errors (p<0.05).*

Bow-riding Behaviour

The number of dolphins riding the bow of the research vessel (Figure 5.10) was significantly higher after interactions with swim-with-dolphins tour vessels than before interactions (non-matched samples, Mann-Whitney, U=234.5, $p<0.05$). The number of dolphins riding the bow of the research vessel during tour interactions was not analysed as dolphins were more likely to ride the bow waves of other vessels during the tour.

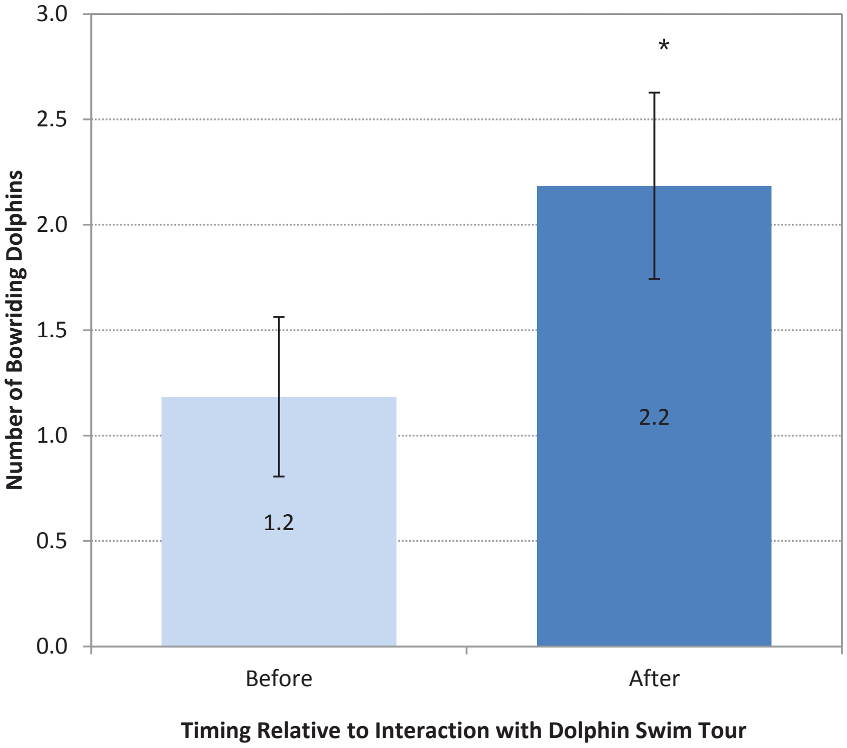


Figure 5.10. Number of dolphins riding the bow of the research vessel increased after swim-with-dolphin tour vessel interactions when compared with bow-riding before tour vessel interactions (p<0.05, n=50 groups).*

Non-swim Dolphin Watching Tour Interactions

Dolphin watching tour boats that did not include a swim-with-dolphins component as part of the tour (operated by Whale Watch Kaikoura) generally visited dolphin groups for brief periods. A total 30.1% of large dolphin groups monitored from the research vessel were visited by dolphin watching only tour boats, and these interactions lasted for 7.8% of the time that dolphin groups were monitored. Approaches by non-swim tour vessels toward dolphin groups were most often at slow wake speed (~5 knots) and departures at no wake speed (<5 knots, Table 5.3). Dolphin groups were generally approached from the rear at a bearing parallel or near-parallel to the heading of the group.

Table 5.3. Estimated speeds and angles (relative to dolphin group heading) of non-swim dolphin watching tour boats approaching and leaving dusky dolphin groups (n=38).

Speed	Approach	Depart	From		Bearing	
no wake	29%	59%	front	21%	0 - 45°	48%
slow wake	45%	12%	side	33%	90°	33%
at speed	26%	29%	rear	45%	180°	21%

The activity level of dolphin groups did not vary significantly in the presence *versus* in the absence of non-swim dolphin watching tour boats (Wilcoxon z=-1.552, *ns*). Activity level of dolphin groups also did not vary between groups visited by dolphin watching tour boats (Whale Watch Kaikoura) and those that were not visited by dolphin watching tour boats (unmatched samples, Mann-Whitney U=376.5, *ns*). Dolphin groups visited by dolphin watching tour boats did not vary in the proportion of time spent resting (36%±6.0%), milling (31%±4.5%), and travelling (33%±5.6%) when dolphin watching tour boats were present and absent (Wilcoxon, z=0.369, 0.710, 1.335, *ns*). Dolphin group bearing did not vary from random in the presence of non-swim dolphin watching tour boats (1-sample t-tests, *ns*). The percent of 2-min intervals during which dolphin groups changed heading did not differ significantly when non-swimming dolphin tour boats were present compared to when they were absent (Wilcoxon Z=-0.26, *ns*).

Dispersion of dolphin groups increased slightly during visits by non-swim tour boats (Figure 5.11). Mode nearest neighbour distance was less than one body length (<1.7 m) less often (Wilcoxon, z=-1.977, $p<0.05$) and between one and three body lengths (1.7-5 m) more often (Wilcoxon, z=-2.102, $p<0.05$) than when non-swim tour boats were not present.

Dusky dolphin groups visited by non-swim dolphin watching tour boats engaged in less acrobatic leaping during these interactions than dolphin groups not visited by non-swim dolphin watching tour boats (Figure 5.12). The number of long bouts of acrobatic leaps (Figure 5.12a) and the mean number of acrobatic leaps counted (Figure 5.12b) per 2-minute interval was lower in the presence than in the absence of non-swim dolphin watching tour boats (Mann Whitney tests, U=401, 439, *p*<0.05). Non-acrobatic noisy leaping and re-entry leaping did not vary with visitation by non-swim dolphin watching tour boats.

High-speed activities, including high-speed bursts in which some or all dolphins in the group "sliced" along the surface throwing up spray and porpoising, were less frequently noted during 2-minute intervals when non-swim dolphin watching tour boats were visiting dolphin groups than when the groups were not being visited by the boats (sign tests, *p*<0.05, Figure 5.13).

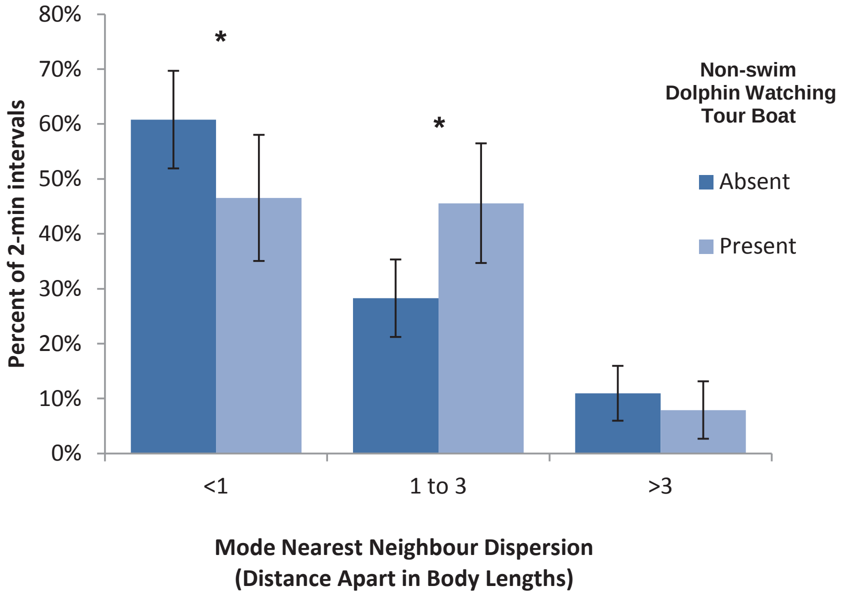


Figure 5.11. Dispersion of dolphin groups during interactions with dolphin watching tour vessels is compared to times when the vessels were not present (n=19 groups). Mode nearest neighbour distance was estimated by number of body lengths between individuals (1 body length =1.7m). Bars represent mean percent of 2-minute intervals with standard errors (p<0.05).*

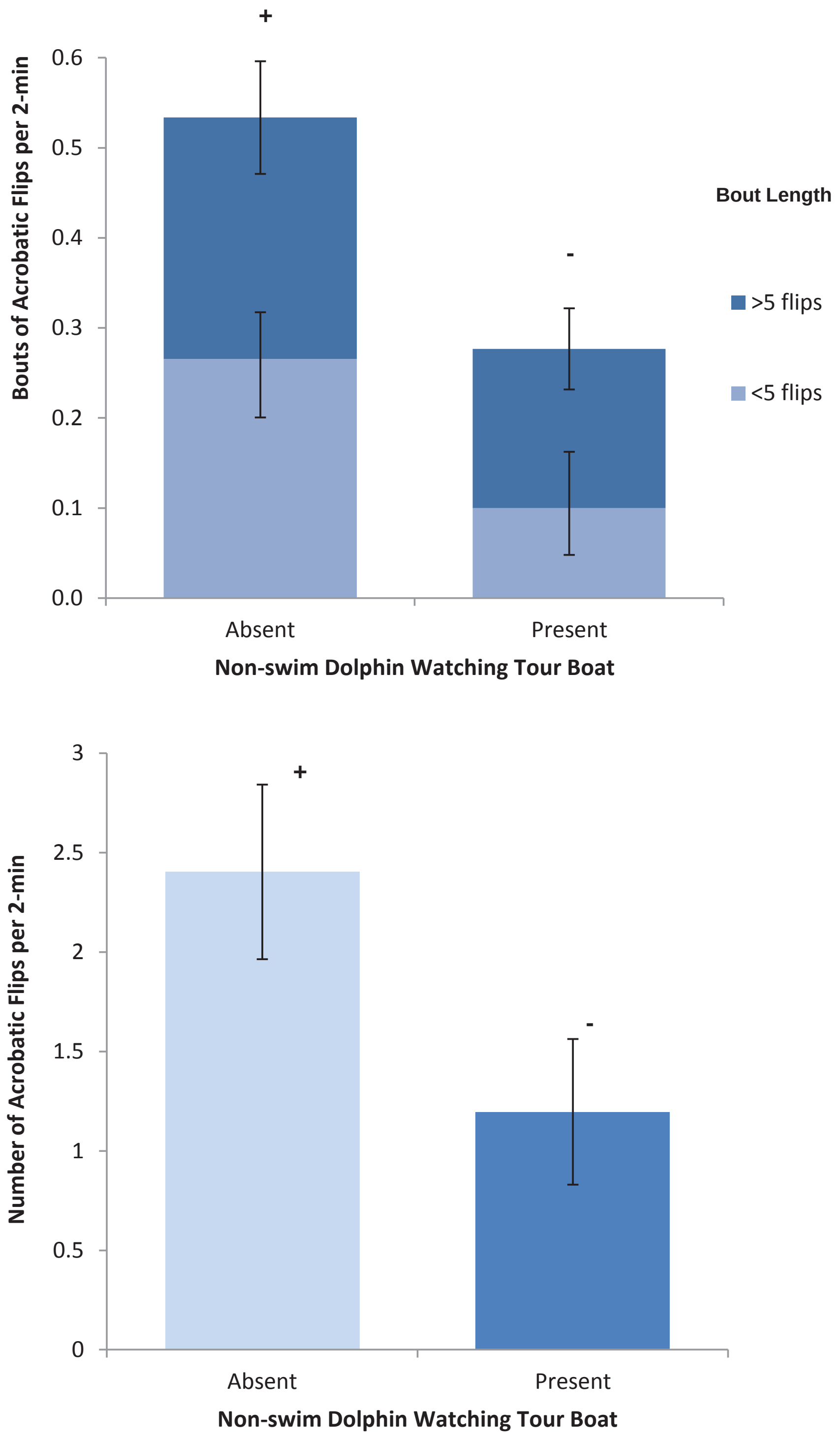


Figure 5.12. Number of bouts of acrobatic leaps (top) and total number of flips (bottom) per 2-minute sampling interval are compared when non-swim dolphin watching tour boats are present and absent (n=19 groups). Bars represent mean values with standard errors. Significant differences are noted by + and – labels (Mann Whitney U tests, p<0.05).

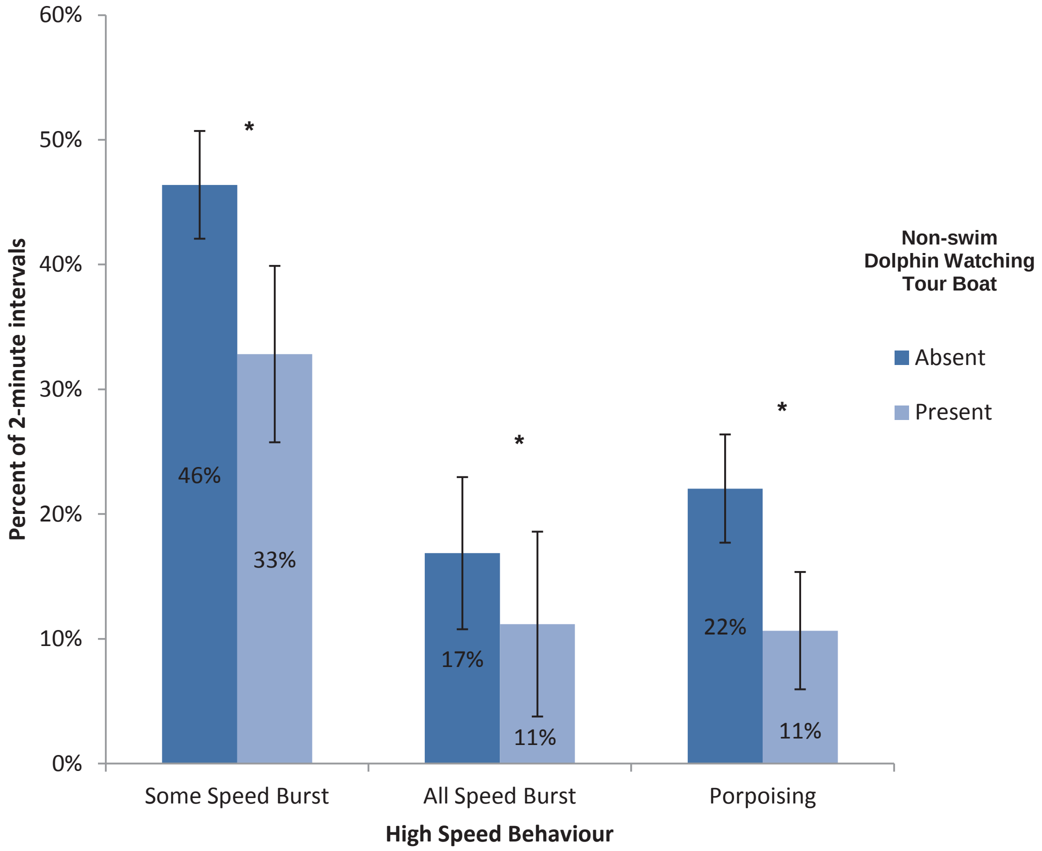


*Figure 5.13. The percent of 2-minute intervals during which high speed behaviours (speed bursts by some dolphins, speed bursts by all dolphins, and porpoising) were observed is compared in the absence and presence of non-swim dolphin watching tour boats (n=19 groups). Bars represent mean values with standard errors for matched comparisons. Significant differences are noted by * labels (sign tests, p<0.05).*

Interactions with Recreational Boats

Recreational boats were observed with dolphin groups 3.6% of the time, although as described above this likely underestimates the actual proportion of time dolphins in the Kaikoura area interact with recreational boaters. Table 5.4 summarises approach and departure speed and angle by recreational boaters relative to dolphin group bearing. At least for this limited sample, recreational boaters appeared more likely to approach and depart at speed, toward or from the front of the dolphin group, and on a bearing at odds with the dolphins' movement (perpendicular or opposite the dolphin group heading) than tour boat operators.

Table 5.4. Estimated speeds and angles (relative to dolphin group heading) of private recreational boats approaching and leaving dusky dolphin groups (n=16 approaches).

Speed	Approach	Depart	From		Bearing	
no wake	36%	50%	front	44%	0 - 45°	0%
slow wake	27%	17%	side	12%	90°	43%
at speed	36%	33%	rear	44%	180°	57%

The activity level, dispersion, leaping rate, and incidence of high speed behaviours of dolphin groups did not vary significantly by presence/absence of recreational boats (Mann-Whitney U tests, *ns*), although this may be due to low sample size limiting statistical power. Samples of recreational vessel-dolphin interactions were limited from the research boat (n=10 dolphin groups), as the research team maintained a policy of departing immediately whenever an approaching recreational boat would be the fourth vessel, restricting the number of observations of such interactions from this platform.

Dolphin groups changed heading by 45° or more significantly more often during visits by recreational boats than when the recreational boats were absent (Wilcoxon, z=-2.142, $p<0.05$, n= 10 groups visited by recreational boats). On average, dolphin groups changed directional heading more than three times as often when recreational boats were present as when they were absent, although there was considerable variability around the mean (Figure 5.14).

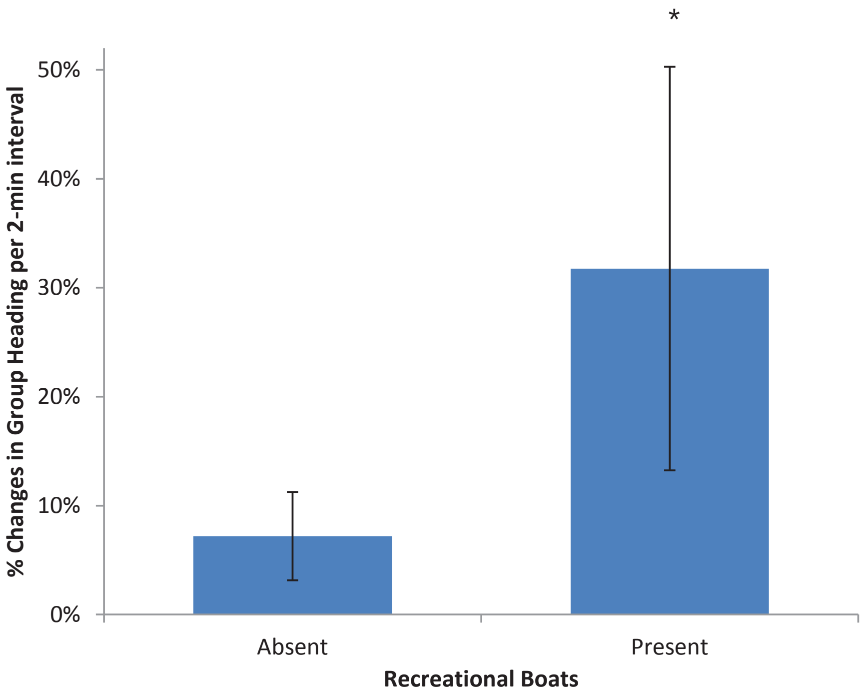


*Figure 5.14. Changes in dolphin group heading of 45˚ or more are compared in the presence versus in the absence of recreational boats (n=10 groups visited by recreational boats). Bars represent mean values with standard errors (*p<0.05)*

Visits by Aircraft

Visits by aircraft occurred at some point during 32% of focal dolphin group behavioural monitoring sessions. The duration of aircraft visits to the dolphins was generally brief, averaging 3.6±0.44 minutes for fixed-wing planes and 2.5±0.58 minutes for helicopters (mean ± se). In total, aircraft were overhead during 1.7% of the time dolphin groups were monitored from the research vessel (1.4% fixed wing planes, 0.3% helicopters). These brief, sporadic visits by aircraft had little to no measurable effect on the behaviour of dusky dolphins. The activity level, dispersion, leaping rate, incidence of high-speed activities, and changes in heading of dolphin groups did not vary significantly when either fixed wing aircraft or helicopters were circling overhead compared to when they were not present (Wilcoxon tests, *ns*, n=16).

DISCUSSION

Swim-with-Dolphin Tour Interactions

It is evident from the findings of this study that swim-with-dolphin tourism at current levels is having short-term effects on the behavioural state, direction of movement, dispersion, and leaping rate of dusky dolphin groups off Kaikoura, New Zealand. Use of a before, during and after (BDA) approach allowed an examination of effects of interactions with swim-with-dolphin tour vessels on large dusky dolphin groups. This approach provides comparisons of dolphin group changes when groups interact with tour or other vessels (Bejder and Samuels 2003, Bejder et al. 2006a). Although large dolphin group behaviour measured before interactions with swim-with-dolphins tour vessels was not completely undisturbed by all types of vessel activity, I focused on the BDA approach for swim-with-dolphin vessels to assess affects of these types of vessel interactions as they are the most prolonged, with the greatest number of vessel approaches (Markowitz et al. 2010b). When examining dolphin groups using the BDA approach, it is important to note that effects found after tour vessels left were most likely not simply carry-over behaviour from tour vessel interactions, but prolonged behavioural changes, as these 'after' behavioural samples were often of long duration (46.5 ± 4.33 min, n=32). I controlled for the effects of natural variation in dusky dolphin behaviour by time of day (Cipriano 1992, Barr and Slooten 1998, Barr and Slooten 1999, Yin 1999, Markowitz 2004, Würsig et al. 2007) related to the diel pattern of nocturnal foraging (Benoit-Bird et al. 2004) by blocking BDA analyses by morning and afternoon. The matched-pairs approach controlled for the effect of seasonal variation in dusky dolphin behaviour (Würsig et al. 1997, Markowitz 2004). Behavioural changes due to boats may also have cumulative daily effects, with dolphins reacting differently during the third drop of one boat or the afternoon drops after a day of activity.

Cumulative effects of multiple vessel approaches are examined in chapter 6. Dolphin responses to tourism by time of day are discussed below and in chapter 6.

The results of my study indicate that large dusky dolphin groups at Kaikoura rest less during and after swim-with-dolphin tour interactions and travel more after interacting with tour vessels. These changes in behavioural state transitions, bout duration and behavioural budget of dusky dolphins are important because dolphin groups off Kaikoura typically use this habitat for resting during the day (Würsig et al. 1997, 2007, Barr and Slooten 1999, Weir et al. 2008). A reduction in resting and increase in travelling behaviour may disrupt this habitat use pattern. Other dolphin species that rest during the day in near-shore environments (e.g., spinner dolphins) use this rest period to nurse calves during the breeding season and to strengthen social bonds (Norris 1994, Silva and Silva Jr., 2009). Off the coast of Egypt, tour interactions with spinner dolphins are managed such that tour activities are limited to areas that do not constitute the ‘core’ habitat of resting dolphins (Notarbartolo-Di-Sciarai 2007). As nursery groups are known to rest in near-shore areas off Kaikoura, New Zealand (Weir et al. 2008), it is advisable to restrict dolphin tourism, and possibly all vessel approaches, to dolphin groups in near shore areas during mid-day, given that a voluntary rest-period is not always adhered to by tour vessel operators (Duprey et al. 2008, Lundquist and Markowitz 2009). Due to the findings presented here and in Chapter 6, this voluntary rest period is now mandatory.

As I found for resting in large dusky dolphin groups in this study, foraging in both New Zealand common dolphin groups (Stockin et al. 2008) and Argentina dusky dolphin groups (Dans et al. 2008) was disrupted by tour vessel activity, and the dolphins took longer to transition back to foraging after interactions with tour vessels ceased. Similar behavioural changes have also been found in several studies on interactions between vessels and dolphins in New Zealand and elsewhere (Constantine et al. 2004, Bejder et al. 1999, Bejder and Samuels 2003, Stensland and

Berggrend 2007). Reductions in resting duration during tour vessel interactions with resulting increases in changes in direction and porpoising behaviour indicate that dolphin group behaviour is changed by the presence of dolphin swim tour vessels over the short term. Unlike some locations where behavioural short-term disruption has been linked to long-term displacement or biologically significant impacts such as infant or adult mortality in a reportedly closed population (Bejder et al. 2006b, Lusseau 2004, 2005, 2006), I found no strong indication of biologically significant population impacts such as these or habitat displacement of dusky dolphins in relation to tourism (Sapolsky 1994, Orams 2004).

The finding that dolphin groups are more likely to travel for longer periods after tour vessels depart, primarily in a southerly direction, suggests movement of groups away from swim-with-dolphin tour vessels (that arrive from the north). Previous shore-based research (Brown 1999, Cipriano 1992) indicated that dusky dolphins to the south of Kaikoura appeared to move southward more as the day progresses since the advent of tourism (in the late 1990s) than prior to tourism (in the 1980s), although data collected by tour vessels from the 90's onward refutes this reported trend (Dahood et al. 2008). It is noteworthy that I found changes in direction to the south more often in the morning than in the afternoon. Typically, dusky dolphins off Kaikoura increase group dispersion and move offshore in the afternoon in preparation for foraging. The movement of dolphin groups 'away' from Kaikoura while resting or preparing to rest in the morning may be a direct response to interactions with tour vessels. Other examinations of dusky dolphin abundance and behaviour to the south of Kaikoura confirm this finding (Du Fresne and Markowitz 2009).

The increase in changes in direction during interactions with swim-with-dolphin tour vessels could be related to the behavioural state changes noted above. Increases in changes in direction were also found in killer whales (*Orcinus orca*, Williams and Ashe 2007), and in other dolphin species (Bejder et al. 1999, Bejder and Samuels 2003, Bejder et al. 2006a) interacting with tour vessels. This behavioural response has been characterised as 'avoidance' behaviour in predator-prey interactions that occur in open habitats (Frid and Dill 2002, Williams et al. 2002), and could be employed by dusky dolphin groups to avoid swim-with-dolphin tour vessels.

Like many social herding animals (e.g., antelope , Berger et al. 1983; schooling fish, Pitcher and Parrish 1993), dusky dolphin groups tighten in response to disturbance by potential predators (e.g., killer whales, Würsig et al. 1997, Constantine et al. 1998). Dusky dolphins off Kaikoura also group more tightly at times when they might be most vulnerable. Previous research found dusky dolphin groups off Kaikoura tighten diurnally around midday, when the dolphins are resting, and seasonally during summer, when young calves are present in greatest numbers, with especially tight proximity maintained in small nursery groups of mothers and calves (Barr and Slooten 1999, Markowitz 2004). Although group dispersion did not change when dolphins interacted with tour vessels in the morning, it is likely that the tendency for reduced group dispersion as dolphin groups enter into rest (deepest resting at midday and coinciding with tightest group dispersion, Barr and Slooten 1999, Markowitz 2004) may supersede any effects of the tour vessel. The reduced dispersion in the afternoon of groups interacting with swim-with-dolphin tour vessels differs from the normal pattern of increasing dispersion late in the day (Markowitz 2004) in preparation for nocturnal foraging (Benoit-Bird et al. 2004). Reductions in inter-individual distance at this time could limit information gathering by individuals (and thus groups) as they proceed offshore to begin foraging. Reductions in inter-individual distance in response to vessels have been found in studies of Hector's and bottlenose dolphins (Bejder et al. 1999, Nowacek et al. 2001, Bejder et al. 2006a).

Increased noisy leaping by dusky dolphins in response to tour vessels in this study agrees with the results of previous shore-based research (Barr and Slooten 1998, Barr and Slooten 1999, Lundquist and Markowitz 2009). Humpback whales (*Megaptera novaeangliae*) sing longer songs in the presence of vessels (Miller et al. 2000). If noisy leaping functions as a form of loud, long-range communication in dusky dolphin groups as has been proposed previously (Markowitz 2004), increases in noisy leaping may represent an increasing need to 'shout' in the presence of noisy vessels (Miller et al. 2000). Alternatively, increased noisy leaping in the presence of tour vessels might simply indicate a higher level of activity of dolphins during interactions independent of communicative function. Increases in porpoising behaviour also represent increases in aerial behaviour during tour vessel interactions. Porpoising, which can allow dolphins to move more rapidly for brief periods of time because drag is reduced in air compared to water, occurs during short bursts of high-speed travel by dolphin groups off Kaikoura (Markowitz 2004).

Increased bow-riding behaviour of dusky dolphins after interacting with dolphin swim tour vessels compared to before the tour interactions suggests that dolphin affinity for vessels was not decreased by swim-with-dolphins tours, and may even have increased as a result of tour interactions. However, I cannot rule out the possibility that the observed increase in bow-riding behaviour occurred mainly because the dolphins travelled more and rested less following the tour interactions, since bow-riding has been demonstrated to increase travelling efficiency in dolphins (Williams et al. 1992, W. Markowitz unpublished data).

Non-swim Dolphin Watching Tour Interactions

I found relatively few effects of the brief visits by non-swim dolphin watching tour boats on the behaviour of the dolphins. The increase in inter-individual distance of dolphins in the presence of non-swim tour vessels is opposite the tightening of groups expected in response to predators or other disturbances (Bejder et al. 2006a). The finding that most dolphins remained within three body lengths (~5m) suggests that the cohesion of dolphin groups as a whole was not disrupted by the greater dispersion exhibited during brief encounters with non-swim dolphin watching boats. Lower rates of acrobatic leaps in the presence of these vessels were consistent with findings for dolphin swim vessels. Such acrobatic leaps have been found among dusky dolphin groups in Argentina to occur most often following a successful feeding episode, which led to their being characterised as a form of "celebration" perhaps useful for re-affirming social and sexual bonds after having fed, and while aggregated in groups of up to 300 dolphins (Würsig 1984). Reduced incidence of high speed activities in the presence of these tours were counter to what one would expect in the event of a "fight-or-flight" stress response (Selye 1937, Orams 2004). These results may be due to fewer approaches, most approaches occurring from the rear of the group, less time spent with dolphins overall, and/or quieter engines when compared with swim-with-dolphins tours.

Interactions with Recreational Boats

A relatively small sample size of interactions between dolphins and recreational vessels restricted my ability to discern many effects. This sample was limited, as mentioned previously, because the research vessel left on approach of a fourth vessel. Even with such a limited sample, it was evident that recreational boaters were least likely to follow DOC approach guidelines, often approaching from the front of the group, at speeds exceeding 5 knots, and at a bearing opposite that of the dolphins' movement. These interactions apparently resulted in more frequent changes in dolphin group heading than interactions with commercial tour vessels, generally operated in a manner more consistent with DOC approach guidelines.

Visits by Aircraft

Visits by aircraft tours were generally very brief (<4 minutes) and had no measurable significant short-term effects on dolphin behaviour. While apparent responses of dusky dolphins to particularly low flying aircraft have been noted anecdotally on rare occasions in the past (T.M. Markowitz, personal observations), these findings generally support the interpretation that aircraft tours as currently operated and managed along the Kaikoura coast are relatively benign with respect to their effects on dusky dolphins.

Seasonal and Diurnal Patterns

The distribution of large groups of dusky dolphins followed with season and time of day show a trend in movement to the south of the Kaikoura Canyon later in the day in summer (Chapter 2). This movement south and offshore throughout the day may be a response to tour vessel activity that often approaches the dolphin group from the north. Large dolphin groups during the summer breeding season often consist of large numbers of adults with calves. The distribution of large dolphin groups followed does not necessarily reflect the location and movement patterns of all dolphin groups in the area, as these groups were not located using line-transect surveys. However, at any given time there are usually only one to two large dolphin groups in the Kaikoura Canyon area (Markowitz 2004, Würsig et al. 2007, Dahood 2009).

Summary of Findings

Similar short-term effects of tourism on small groups of marine mammals have been shown to those I report here, with long-term implications for some resident species (Bejder et al. 2006b, Lusseau and Bejder 2007). Tourism impacts on larger groups of animals have not been well-studied and this research provides new insight into the effects of tourism on large (>50 individuals) groups of dolphins. Interactions with tourism are likely to produce fewer long-term biologically significant impacts in large groups than in smaller resident groups of dolphins. Tourism interactions with dusky dolphins off Kaikoura may be sustainable at current levels, but increasing tourism beyond current levels combined with effects of increasing recreational and fishing vessel traffic, could have long-term consequences for this currently robust dolphin population.

Off the coast of Egypt, tour interactions with spinner dolphins are managed to limit tour activities to areas that do not constitute the ‘core’ habitat of resting dolphins (Notarbartolo-Di-Sciarai 2007). Smaller dusky dolphin nursery groups are known to rest in near-shore areas off Kaikoura, New Zealand (Weir et al. 2008). Restricting dolphin tourism, and possibly all vessel approaches, to dolphin groups in near shore areas during midday, particularly during the calving and breeding season, is necessary given that a voluntary rest period is not always adhered to by tour vessel operators (Duprey et al. 2008, Lundquist and Markowitz 2009). Due to the results of this study, the rest period is now mandatory and extended into spring with a five year moratorium (with four years remaining) on new dolphin watching permits. The identification of both critical habitat and times of day for resting, breeding or social bonding for social mammals is necessary for proper management of tourism interactions with these species (Bejder and Samuels 2003).

CHAPTER 6

REACTIONS OF DUSKY DOLPHINS TO TOUR VESSELS AND SWIMMERS OFF KAIKOURA, NEW ZEALAND

INTRODUCTION[3]

Dusky Dolphin Tours off Kaikoura

Effects of tourism on dolphin groups have been examined in many contexts, with changes noted in group behavioural state, movement patterns, fission-fusion events and breathing rates (reviewed by Markowitz et al. 2010b). In order to obtain detailed information on dolphin interactions with swim tours, a "focal tour" examination was undertaken from onboard swim-with-dolphin tour vessels, documenting tour vessel movements, speeds, and encounters with dolphin groups. Because the observations are performed from the tour vessel, these behavioural observations cannot provide dolphin information before the vessel arrived and after it left. However, since other vessels can be viewed from this platform, some before and after data can nevertheless be gathered.

Dusky dolphin tours began in Kaikoura in the late 1980s and have grown considerably since that time (Te Korowai 2008). Tour vessels that regularly interact with dolphin groups include swim-with-dolphin tour vessels (3) operated by Encounter Kaikoura, Whale Watch tour vessels (4), and aircraft operated by Wings Over Whales and Kaikoura Helicopters. Although swim-with-dolphin tourism permits are issued to both Encounter Kaikoura and Whale Watch Kaikoura, Whale Watch Kaikoura does not currently use its

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[3] This chapter contains findings and text with modifications that were originally reported to the New Zealand Department of Conservation in a contract report (Markowitz et al. 2009b).

permit to swim with dolphins and instead focuses their tourism on viewing sperm whales (*Physeter macrocephalus*) and dolphins.

The three swim-with-dolphin vessels operated by Encounter Kaikoura (Figure 6.1) included a 14 m mono hull Stabi-craft with a 680 hp Volvo inboard diesel motor (Delphinidae), a 13m catamaran with twin 315 hp Volvo inboard diesel motors (Lissodelphis) and a smaller 9 m Stabi-craft with twin 200 hp Yamaha petrol outboard engines (Kotuku). The two larger vessels, Delphinidae and Lissodelphis, were used most frequently on the dolphin swim tours.

Two tours per day were operated from April through November (each with up to three vessels). Tours usually departed about 09:00 and 13:00, returning at approximately 11:30 and 15:30. During the summer, an additional early morning tour departed at approximately 06:00, returning at about 08:30. Tours consisted of 1, 2 or 3 vessels depending on the tourist sign-ups for each day, resulting in a maximum total of 50 individual boat trips per week. Three vessels were usually used during the shoulder seasons (spring and autumn) and particularly in summer.

On the way to the dolphins, vessel crews provided passengers interpretive information, including a nature talk focusing on the unique coastal ecology and oceanography of Kaikoura. Once a suitable dolphin group was encountered, the vessel approached usually within 50-100 m of the group and then remained stationary while swimmers prepared to enter the water. When swimmers were suited up for the swim, they were advised to be seated on the back deck of the vessel as the vessel approached the dolphin group. Under existing permits at the time of the study, a maximum of 13 swimmers per vessel were allowed in the water at one time. Swimmers were outfitted with a wetsuit, fins, mask and snorkel for underwater viewing.

Once the dolphin group was approached (usually within <5 m of the group), a horn was sounded and the swimmers entered the water. The skipper moved to the rear of the vessel to monitor the swimmers and dolphins, operating the vessel from a rear control panel.

a. Lissodelphis

b. Delphinidae

c. Kotuku

Figure 6.1. Dolphin Encounter vessels used during swim-with-dolphin tours.

One to two additional crew members were onboard to monitor swimmers, including conducting regular counts of swimmers, helping swimmers out of the water, and monitoring for any swimmer distress. Both skippers and additional personnel also kept track of dolphins immediately adjacent to the swimmers, directing swimmers toward dolphins that were present. When most dolphins left the area, the swim was terminated by another horn blast and swimmers were required to return to the vessel. A pause in swim operations occurred as all swimmers were counted and confirmed returned to the vessel. Once the count was cleared by the skipper, the skipper returned to the front of the vessel and once again approached the dolphin group for another swim. This process was repeated until either the dolphins did not leave the swimmers or the time for the swim tour was depleted.

After swimming finished, the tour vessel approached the dolphin group while swimmers removed wetsuits and snorkel gear. When the swimmers were ready, they moved to the front of the vessel for pictures and a short talk about dusky dolphins that included biology, ecology and conservation of this species and other dolphin species in New Zealand (Duprey *et al.* 2008). This portion of the tour usually lasted for 15-30 minutes until the time for the tour ran out. At that time the tour vessel left the dolphin group to return to port.

Whale Watch tour vessels that approached the dolphins during both the swim portion and follow portion of the tour generally interacted with the dolphins by following alongside or behind the group while conducting a nature talk. Aircraft also circled the dolphins during the tour. Recreational vessels followed the group, drove around the group, or drove through the group depending on the disposition of the skipper and the distribution of the dolphins. On occasion, private recreational boaters also swam with the dolphins.

Use of Tour Vessels as a Research Platform

The use of a tour vessel as a research platform from which to measure the effects of the same tour vessel inherently introduces confounding factors in studies of dolphin responses to tourism (Bejder and Samuels 2003). Nevertheless, such a platform has been used with some success by researchers examining dolphin responses to tourism (e.g., Constantine 2001, Dans et al. 2008). An advantage of the use of tour vessels is that it allows systematic sampling of details related to vessel operation and swim activity (Bejder and Samuels 2003, Markowitz 2004, Würsig et al. 2007). I found it most effective for what might best be described as “focal tour boat” observations, rather than detailed “focal dolphin group” observations.

Tour Vessel Research Objectives

Vessel approach methods can affect dolphin group behavioural responses (Constantine et al. 2004, Bejder et al. 2006a) and guidelines for approaching dolphin groups have been introduced for both research and tour vessels (Würsig and Jefferson 1990, Childerhouse and Baxter 2010). Approaching groups from the side and paralleling the group at slow speeds is recommended. In addition, reducing the total number of tour vessels interacting with dolphins, or number of vessels interacting at any one time, is thought to reduce disturbance. Tourism interactions with delphinids sometimes include more direct human/dolphin interactions such as hand feeding or swimming with dolphins. Tours that offer a swim component are usually managed to limit the number of swimmers interacting with dolphins (Constantine et al. 2004, Martinez 2010, Childerhouse and Baxter 2010).

Hypothesis: Dolphins will show greater responses and spend less time interacting with swimmers as vessel traffic and assertive vessel approaches increase.

Specifically, I predicted dolphins would:

1. Mill more and rest less with cumulative effects of number of vessel approaches and number of vessels present increasing the likelihood of this behavioural response.
2. Reduce group dispersion in response to cumulative vessel approaches or number of vessels present.
3. Reduce duration of associations with swimmers with more vessel approaches.
4. Reduce duration of associations with swimmers with more assertive vessel approach methods (e.g. high speeds, dropping swimmers in front of the group, head-on approaches).

METHODS

Data Collection

Observations were made from the tour vessel platform during 424 hours on 145 days from January 2007 through February 2009. During 174 swim tours monitored, 192 hours were spent with dolphins, with 615 swim drops observed from onboard tour vessels. Time of departure, skipper, crew and number of tour passengers (including observers and swimmers) were recorded upon departure of the tour, and return time was recorded upon completion of the tour. All observations of dolphin group size and composition, behaviour, formation, and dispersion were made by experienced observers. Equipment used to collect data included a handheld Garmin GPS 60 and data sheets. Vessel positions and speeds were logged at 1-min intervals on a Garmin 60 GPS, and noted by researchers on datasheets for each vessel approach of dolphins. Smaller dolphin groups visited en route to the group chosen for the swim portion of the tour were noted, with encounter time, position, group composition (number of adults, juveniles and calves), and predominant group activity documented. Upon encounter of the swim group, time and position were recorded. The size of large dolphin groups (most swims were with large groups) was categorised as 50-99, 100-249, 250-499, 500-1000, and presence of juveniles or calves (Markowitz 2004). When there were large numbers of calves present, this was also noted. When dolphin groups were comprised of fewer than 50 individuals, the number of adults, juveniles and calves were counted. When the vessel departed the group, the time and GPS position were noted.

Vessel Activity

Approach speed, orientation (from the front, side, or rear of group), and bearing relative to the dolphin group movement (0° = parallel, 90°= perpendicular, and 180°= opposite) were recorded when the vessel approached within 50 m of the dolphin group. All approaches in which skippers manoeuvred the vessel in front of the group in such a manner as to stop and place swimmers in the path of the dolphins were documented. During each swim drop it was noted whether the motor was on or off. If the motor was on, the primary movement of the vessel was categorized as stationary (no movement), forward (slight adjustment of vessels in primarily forward direction), backward (slight adjustment of vessels aft, usually to pick up swimmers) or mobile (movement in all directions, includes circling swimmers). If primary movement included both forward and backing, the primary movement was recorded as mobile. Other sources of noise, such as use of a horn to signal swimmers, were documented in real time. These same parameters were recorded when the vessel approached the dolphin group for the final ‘follow’ portion of the tour.

Dolphin Behaviour

Dolphin behaviour was monitored by focal group sampling (Martin and Bateson 1993, Lehner 1996). Behavioural state, mode nearest neighbour distance, heading, number of leaping dolphins, and number of bow-riding dolphins were collected upon each approach to place swimmers in the water, as well as upon approach to conduct the ‘follow’ portion of the tour. Behavioural state was logged as resting, milling, socialising, travelling or foraging (Shane 1990, Markowitz et al. 2004) based on the predominant activity in the group (Mann 1999, 2000). Mode nearest neighbour distance (in adult body lengths) was used as a measure of group dispersion (Markowitz 2004). Mode nearest neighbour distance was classified as either <1 body length (<1.7 m), 1 to 3 body lengths (1.7 to 5.4 m), or >3 body lengths (>5.4 m). These data were collected as a point sample as soon as the vessel approached within 50 m of the dolphin group.

Swimmer deployment and swim activity

Times and positions of swimmer deployment, number of "swim drops," duration of swim, and number of swimmers in the water per drop were documented in real time. On each swim drop, the time at which the first swimmer entered the water and the time at which the last swimmer returned to the vessel were recorded to the nearest second. The number of swimmers logged for each swim drop was the maximum number in the water during that drop. For example, if 13 swimmers were placed in the water and two left the water earlier than others, the number of swimmers recorded was 13. Dolphin interactions with the vessel and swimmers were also documented, including the time at which the main group moved >50m away from swimmers, the number of dolphins (subgroup) remaining within 50m of the swimmers when the main group had moved away, and the distance from the main group to the swimmers at the end of a swim drop.

Other Vessels

The presence of other vessels, including other swim-with-dolphin tour vessels (Encounter Kaikoura), dolphin watching tour boats (Whale Watch Kaikoura), fixed-wing aircraft tours (Wings over Whales), helicopters (Kaikoura Helicopters), and recreational/fishing vessels was documented with approach time (when vessels approached within 300 m), departure time and primary activity (e.g., swimming, following, driving through).

Data Analysis

Data were entered and queried in a Microsoft Access database with linked record forms for dolphin tour headers, other vessel interactions, and swim drop data. Descriptive statistics (e.g., means ± standard errors, ranges, medians, percentages) were calculated and figures produced in Microsoft Excel 2007. For analysis of trends in continuous data, best fit regression lines were drawn. Statistical tests were conducted in SPSS v. 10, using non-parametric techniques for both ordinal and nominal data due to lack of normality or homogeneity of variance in the nominal data set (Lehner 1996). Wilcoxon signed rank tests, Friedman's tests, and chi-square tests were used to examine changes by approach number. Mann-Whitney U tests and Kruskal Wallis tests were used to test for significant differences between unpaired/ungrouped data sets.

I used durations of swim interactions as a measure of dolphin affinity for the tour vessel and swimmers. Swim durations were calculated by subtracting the time the first swimmer entered the water from the time the last swimmer exited the water. To assess the effect of tour vessels on dolphin activity level, predominant behavioural states were ranked from least to most active: rest=1, mill=2, social=3, travel=4. The rate of change in dolphin group behavioural state was calculated as the proportion of changes in behavioural state measured to behavioural state transitions recorded, which averaged 3 transitions (four approaches) per trip. Behavioural state was measured for this analysis each time the tour vessel approached within 50 m of the dolphin group. These measurements were taken, on average, every 10 minutes during the swim portion of the tour. Behavioural state transitions from the last approach to the follow portion of the tour were not included in the analysis. For statistical comparisons, dispersion was ranked by mode nearest neighbour distance from tightest to most spread out: within a body length=1, between one and three body lengths apart=2, more than three body lengths apart=3.

RESULTS

Characteristics of Swim-with-Dolphins Tours

Swim-with-dolphin tours were conducted with large groups of dolphins (>50 individuals) on 87% of tours monitored. The most common estimated group size approached by tour vessels was 100-250 dolphins (35% of tours, Figure 6.2). Large groups of dolphins off Kaikoura often consist of adults, juveniles and calves. Of all dolphin groups approached by tour vessels, 117 (67%) contained juveniles and 91 (52%) contained calves. Small groups (<50 individuals) were approached by tour vessels for swims on 13% of trips monitored (n=22). These small groups averaged 20 ± 3 individuals (range = 4 to 49). Juveniles were present in 6 of these small groups (27%) and a single calf was present on just two occasions (9% see methods, Chapter 2, for definition of juvenile and calf).

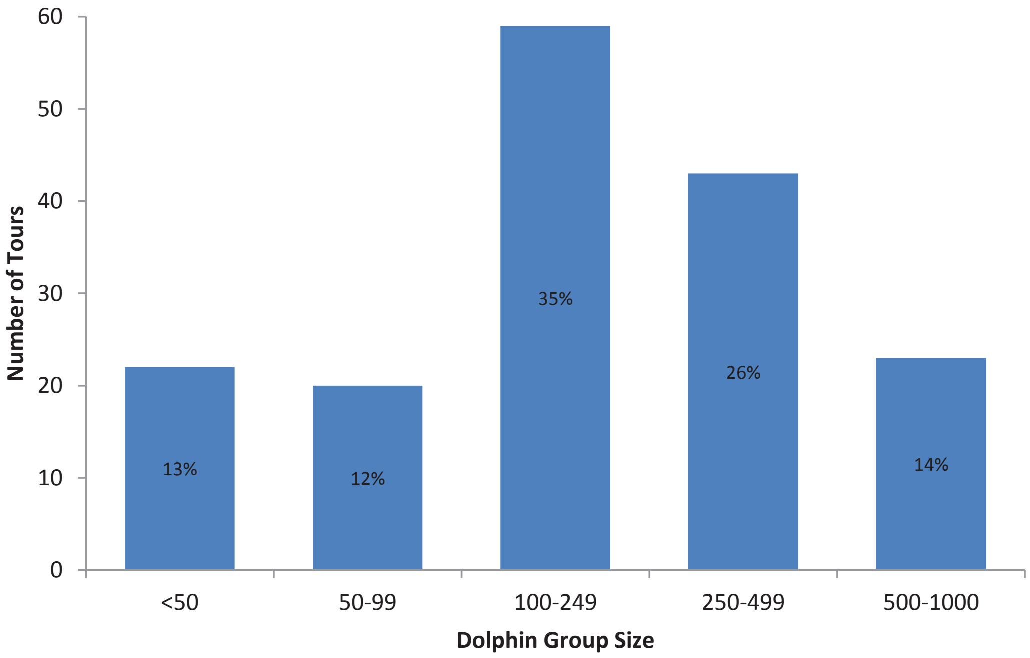


Figure 6.2. Size of dolphin groups approached by tour vessels during swim-with-dolphin tour operations, January 2007-February 2009 (n=174 tours).

The characteristics of swim-with-dolphin tours monitored are presented in Table 6.1. Time spent with dolphins averaged 52% of total tour duration. Dolphin groups that were evaluated as suitable for swimming were encountered on 95% of tours monitored. Of the 1.2 h spent with dolphins during a tour, the total time spent swimming averaged 26.2±0.83 min. During 68% of swim drops, the large group of dolphins moved >50 m away during the swim. On average this occurred within 4.2 ± 0.23 min of the swimmers entering the water (*n*=419 swim drops). The resulting total time spent swimming with the large dolphin group per tour averaged 11.2 min.

Table 6.1. Characteristics of Swim-with-Dolphin Tours off Kaikoura, New Zealand (mean values are presented with standard error, n = 174 tours).

Parameter	Mean ± se
Tour Duration	2.3 ± 0.04 h
Time with Dolphins	1.2 ± 0.03 h
Swimmers per Tour	13 (range = 1 to 23)
Observers per Tour	3 (range = 0 to 15)
Approaches per Tour	4.0 ± 0.16
Duration of Swim Drops	9.1 ± 0.60 min
Swimmers per Swim Drop	9 ± 0.3

Before and after the swim, dolphin tours sometimes approached other small groups of dolphins (mean = 9 ± 1.5 individuals) for brief periods of observation. This occurred during roughly half of tours (*n* = 91), and rarely were more than three groups approached (Table 6.2).

Table 6.2. Dolphin groups encountered by tour vessels before and after the swim (n=174).

# Groups	**1**	**2**	**3**	**4**	**5**	**6**	**Total**
# Tours	31	27	17	6	5	5	91
% Tours	17%	15%	9%	3%	3%	3%	49%

During most tours, swim-with-dolphin tour vessels interacted with the same large group for the duration of the tour. Just one swim-with-dolphin vessel was present during 35% of tours, and two were present during 43% of tours monitored (Figure 6.3). Most tours operated using the two larger dolphin vessels (Delphinidae and Lissodelphis). During 22% of tours, a third, smaller tour vessel was used (Kotuku).

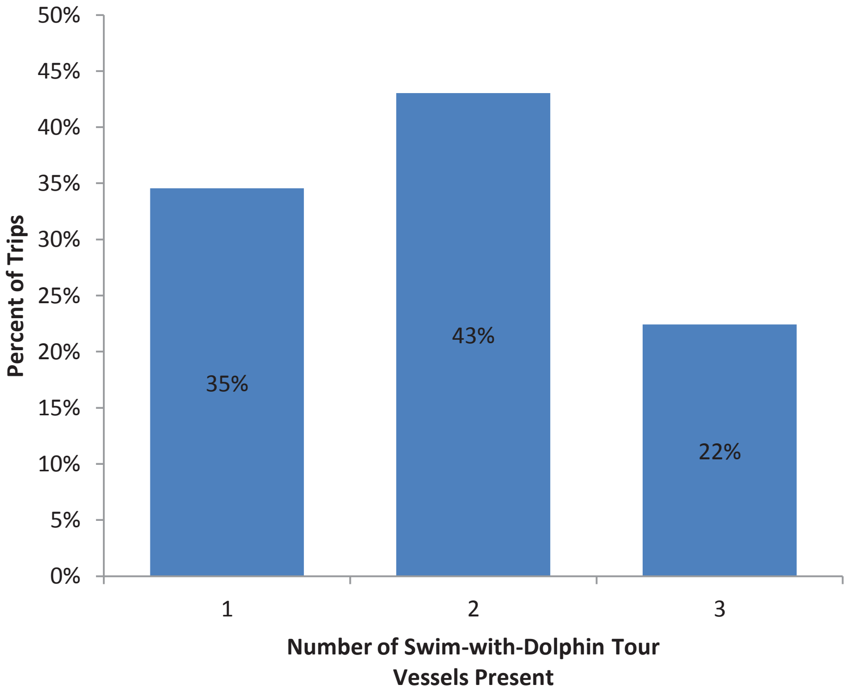


Figure 6.3. Percent of tours with number of swim-with-dolphin tour vessels present are shown (n=174 tours).

During 90% of tours, swim-with-dolphin tour vessels repeatedly approached the dolphin group to place swimmers in the water. The mean number of approaches by the tour vessel was 4.0 ± 0.16 (*n*=165) per tour, with six or fewer approaches on >90% of tours (Figure 6.4).

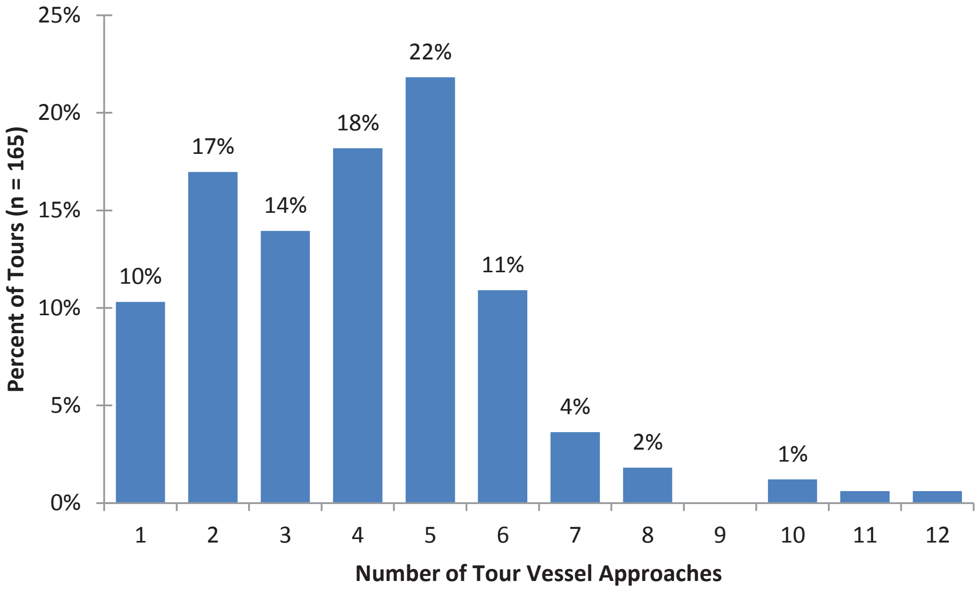


Figure 6.4. The frequency distribution of total number of swim approaches by the tour vessel per tour is shown (n=165 tours with swimming).

Vessel Activity

Swim-with-Dolphin Tour Vessels

The mean speed of approach was 11.7 ± 0.50 km/h (6.3 ± 0.27 knots) and did not vary significantly between vessel skippers. On average, swim tours approached dolphin groups roughly 3-4 km/h faster prior to a swim drop than the speed at which they followed groups after the swimming portion of the tour was completed (Figure 6.5). Vessel speed varied significantly between approaches 1-6 and the subsequent follow (Friedman, χ^2= 19.7, *df*=6, *p*<0.01), with approach speeds increasing following the first approach (1st approach < 2nd approach, Wilcoxon, z=1.983, p <0.05) and decreasing during the follow (1st approach > follow, Wilcoxon z = -.417, p <0.001).

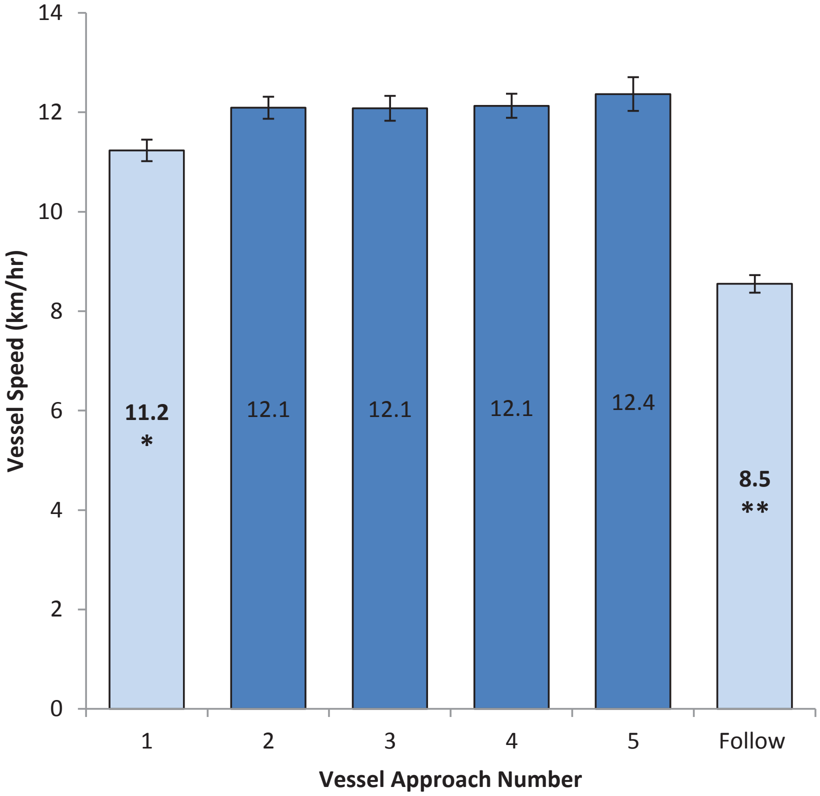


*Figure 6.5. Speed of swim-with-dolphin vessels during approaches of the dolphin group in preparation for a swim drop is shown (bars represent mean approach speeds with standard errors, n=165 tours with swimming). Approaches 1-5 are shown, with approach speed of the 'group follow' portion of the tour (end of tour) shown for comparison (*p<0.05, **p<0.001).*

Swim-with-dolphin tour vessels were primarily stationary with the motor on during swims (45% of swim drops). Skippers turned the motor off during a swim on only 3% of drops. On the 39% of swims when backing of the vessel occurred, the swim tour vessels were backing primarily to pick up swimmers. Swim vessels were highly mobile during only 9% of the swims (Figure 6.6).

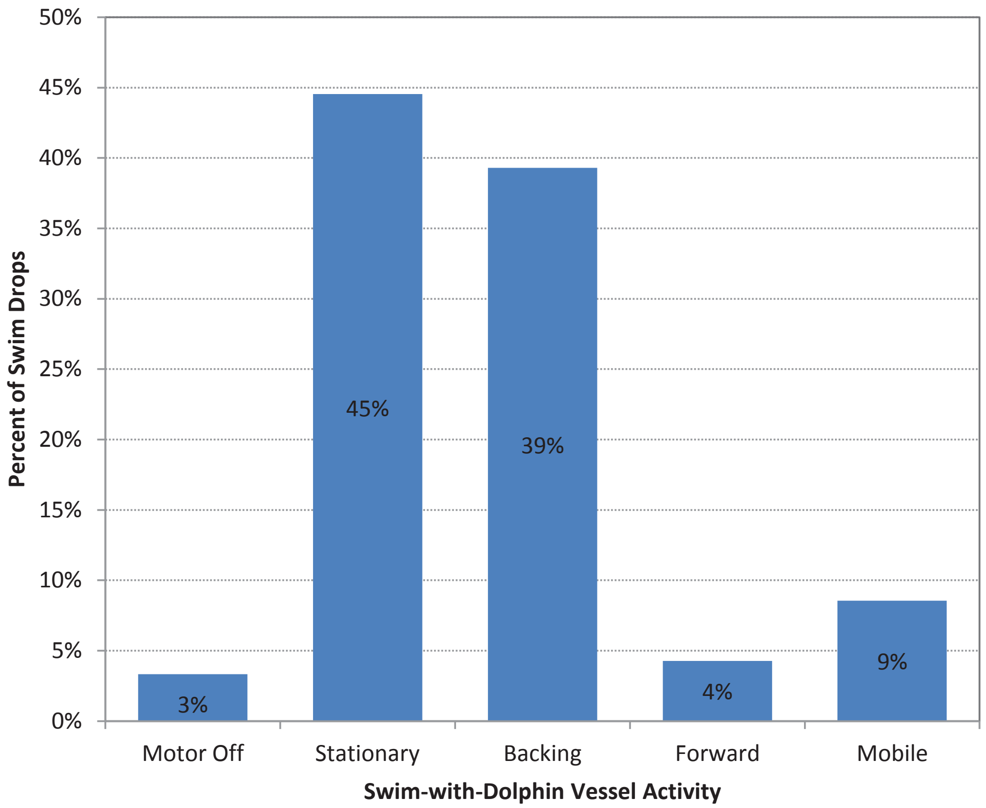


Figure 6.6. Swim-with-dolphin tour vessel activity during swims is shown with percent of swim drops in which activity occurred (n=165 tours with swimming).

Of the swim-with-dolphin tours monitored, 58 trips (33%) had more than 13 swimmers onboard (13 was the maximum number permitted to swim at any one time). Total time spent with dolphins, swim duration, and number of approaches by the tour vessel did not vary when only 1 or 2 additional ("swap") swimmers were onboard the tour (i.e., 14 or 15 swimmers). When 16 or more swimmers were present, time spent with dolphins was significantly longer than tours with 13 swimmers or fewer (1.5 ± 0.06 h *versus* 1.2 ± 0.03 h, Mann Whitney U=345.5, $p<0.01$). The number of swimmers per drop decreased (Mann Whitney U = 553.5, $p<0.05$) and number of approaches per trip increased (Mann-Whitney U=524.5, $p=0.01$) when there were 16 or more swimmers per trip (Figure 6.7).

Although duration of individual swim drops did not vary significantly with number of swimmers, trips with 16 or more swimmers averaged two more approaches and 0.3 h (18 min) more time spent with the dolphins than tours with fewer swimmers. These additional approaches with resulting swim drops averaged 9.2 min more time spent swimming with dolphins than trips with 16 or fewer swimmers. Only 8% of trips observed had 16 or more swimmers, although trips with large tour groups were often not available for researchers to monitor from the tour vessel.

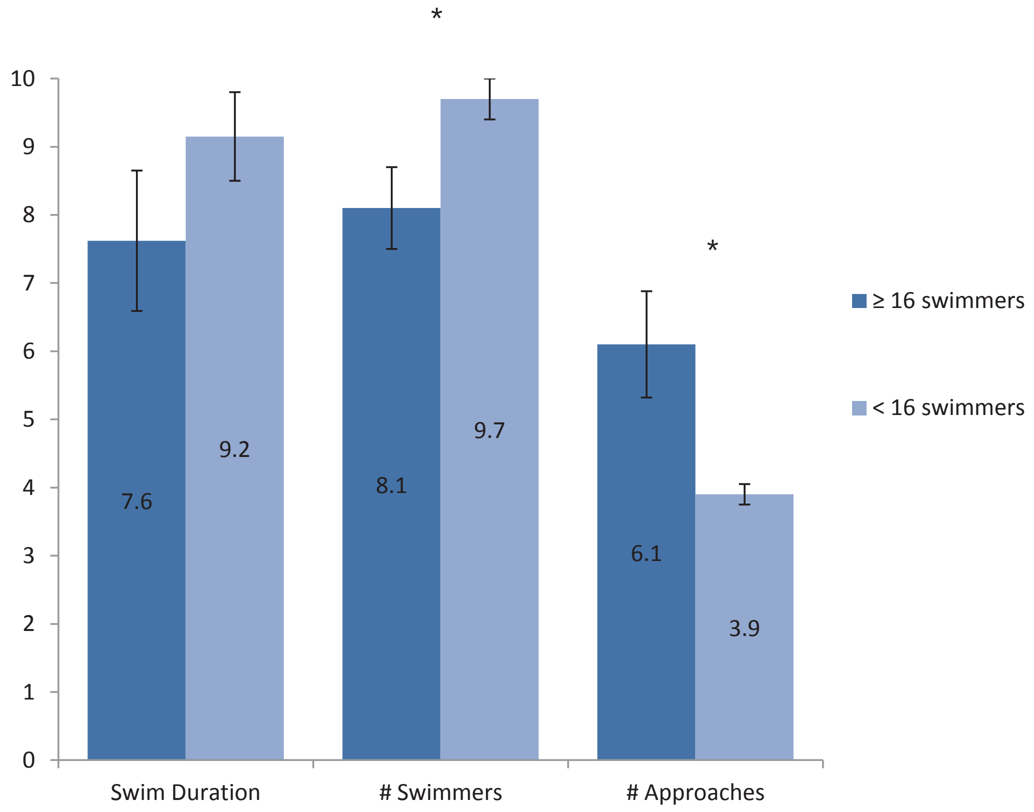


*Figure 6.7. Mean swim duration (min), number of swimmers and number of approaches per tour (n=165 tours with swimming) were compared for trips with 16 swimmers or more and less than 16 swimmers. Mean values are shown with standard error bars (*p<0.05).*

Swim duration decreased with the number of approaches to the dolphin group during a tour (Figure 6.8). The duration of the swim after first encounter was longest at nearly 9 minutes. By the sixth approach, duration of swims averaged less than 4 minutes.

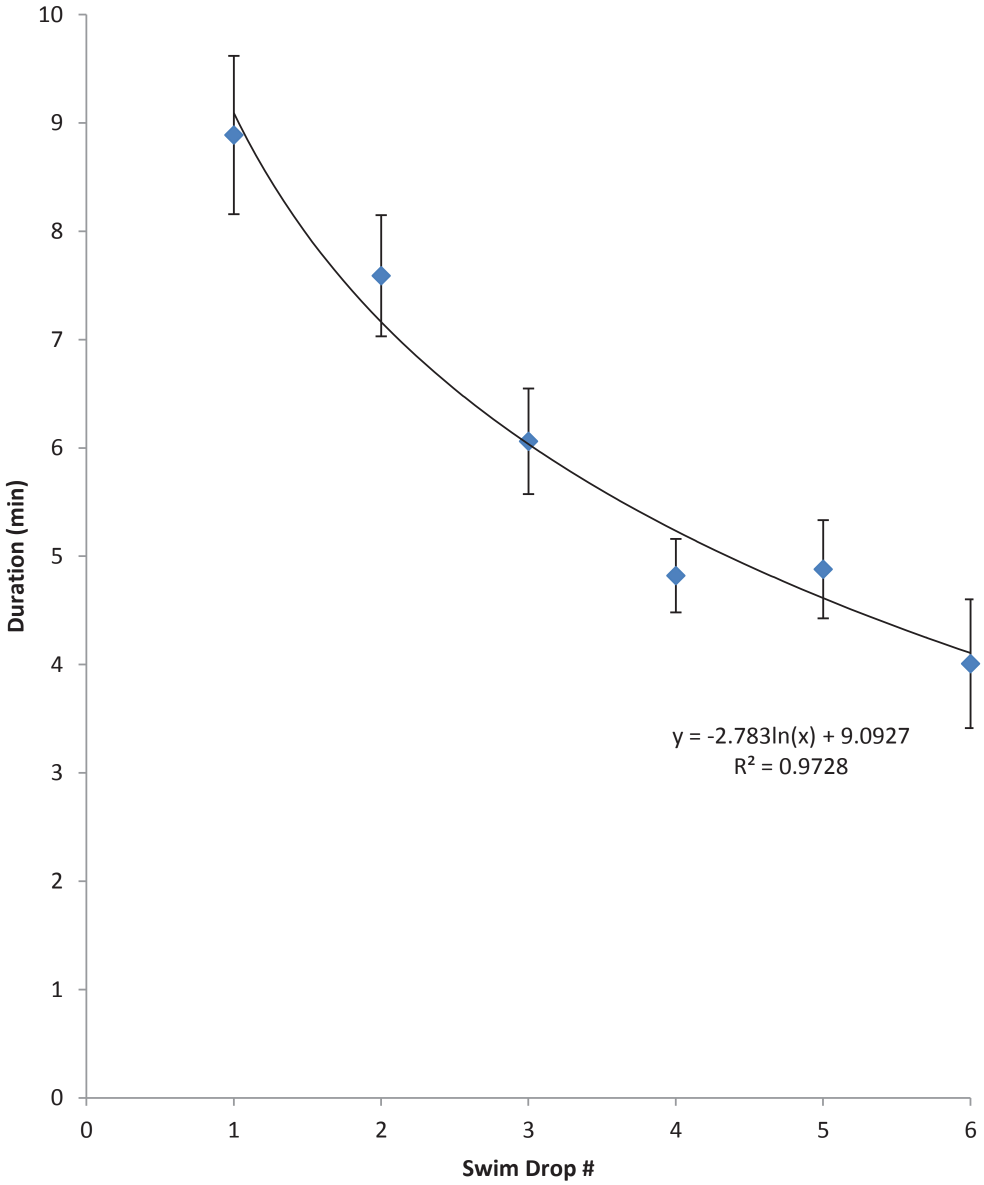


Figure 6.8. Swim drop duration decreased with increasing number of approaches. Mean values with Y-error bars representing standard error are shown (n=165 tours with swimming).

Other Vessels

Vessels documented within 300 m of the dolphin group during tour operations included other tour vessels and recreational or fishing vessels. Tours that approached dolphin groups for tourism interactions included other boats, fixed wing aircraft, and helicopters. Whale Watch tour vessels and fixed-wing aircraft tours were the most common visitors during the swim-with-dolphin tour. Whale Watch vessels visited the dolphin group on 19% of tours, and fixed-wing aircraft on 20% of tours. The percent of tours visited by recreational or fishing vessels was 12% (Fig. 6.9).

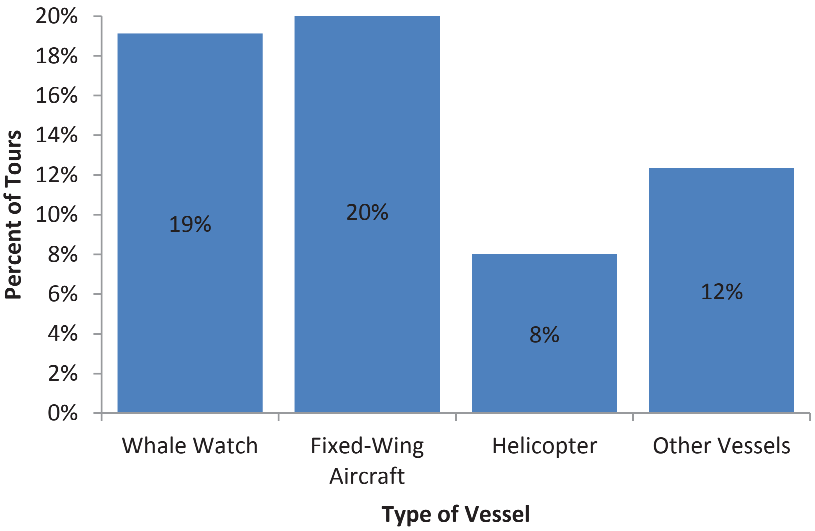


Figure 6.9. The percent of tours during which other vessels visited the dolphin group during swim-with-dolphin tours (n=174 tours).

Although recreational or fishing vessels were less frequent visitors during tours, the mean number of recreational/fishing vessels visiting per tour was higher than for other vessels, averaging almost two vessels per tour (Fig 6.10). The number of Whale Watch vessels visiting the dolphins during swim-with-dolphin tours averaged more than one vessel per trip (Fig. 6.11). The duration of visits was longer for private vessels than non-swim tour vessels. Although aircraft visited the tours regularly, the mean duration of these visits was much less than visits by other vessels, averaging just 2-3 minutes (Fig 6.10).

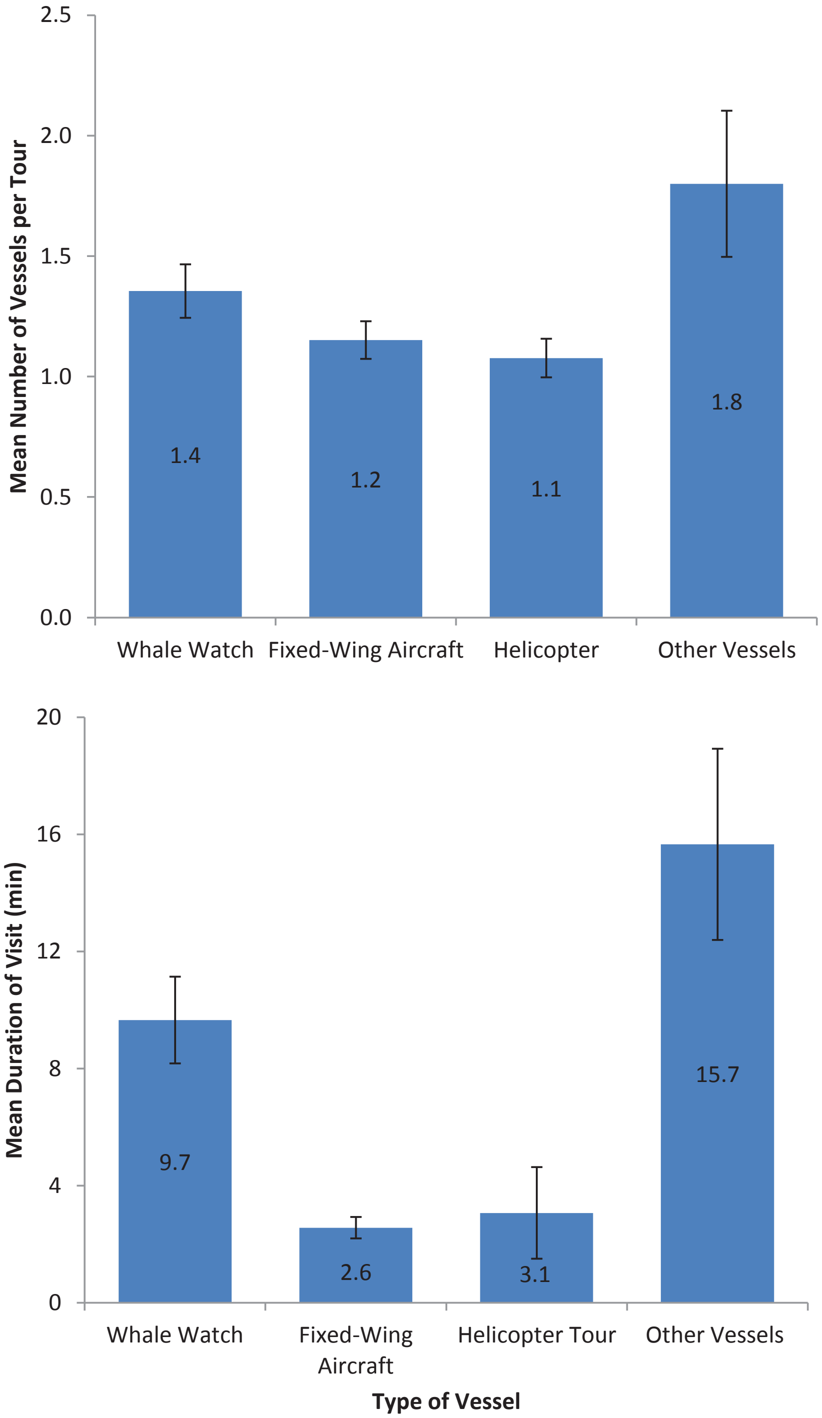


Figure 6.10. The mean number of vessels (top) and duration of visits (bottom) are shown for other vessels observed within 300 m of the dolphins during a tour (n=174 tours). Y-error bars represent standard error from mean values.

Effects of Tours on Dolphin Behaviour

The behaviour of dolphin groups changed from the beginning to the end of tours. Group behavioural state during the follow was significantly different from group behavioural state upon first encounter (Freidman test, χ^2= 57.47053, *df*=3, *p*<0.001), with a decrease in resting and increase in milling during the follow portion of the tour (Figure 6.11).

Variation in Dolphin Behaviour with Approach Number

Activity level of dolphins varied significantly between tour vessel approaches (Friedman, χ^2= 11.6, *df*=5, $p < 0.05$), with dolphins becoming more active (travelling more and resting less) as the swim progressed (Figure 6.12). At the 5th approach, milling fell dramatically, corresponding with a sharp rise in travelling. The mean number of approaches per trip did not vary significantly with behavioural state upon first encounter (travel=4.0±0.28, n=59, rest=4.5±0.28, n=42, mill=4.0±0.33, n=43, social=2.9±0.44, n=11, ANOVA, F=1.939, *ns*).

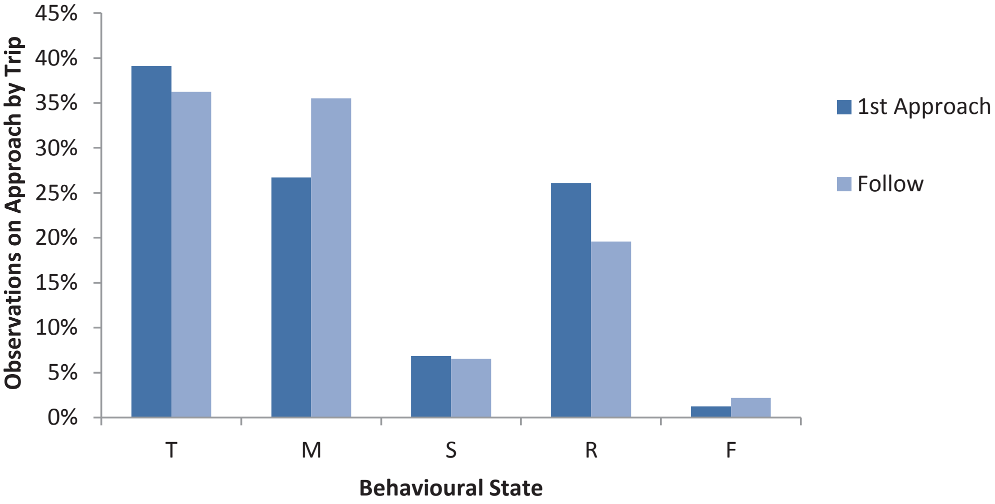


Figure 6.11. The behaviour of dolphin groups varied significantly from first encounter to final group follow. Group behavioural state on 1st approach and during the follow portion of the tour is shown (n=165 tours).

Mode nearest neighbour distance showed a tightening of groups with increasing number of approaches (Figure 6.13). The percent of approaches with dolphins <1 body length (<1.7 m) apart increased from 33% to 59% between the first and fifth approach. Dolphins were grouped more tightly during the follow at the end of the tour (60% <1 body length) than on group encounter (Approach 1, 33% <1 body length).

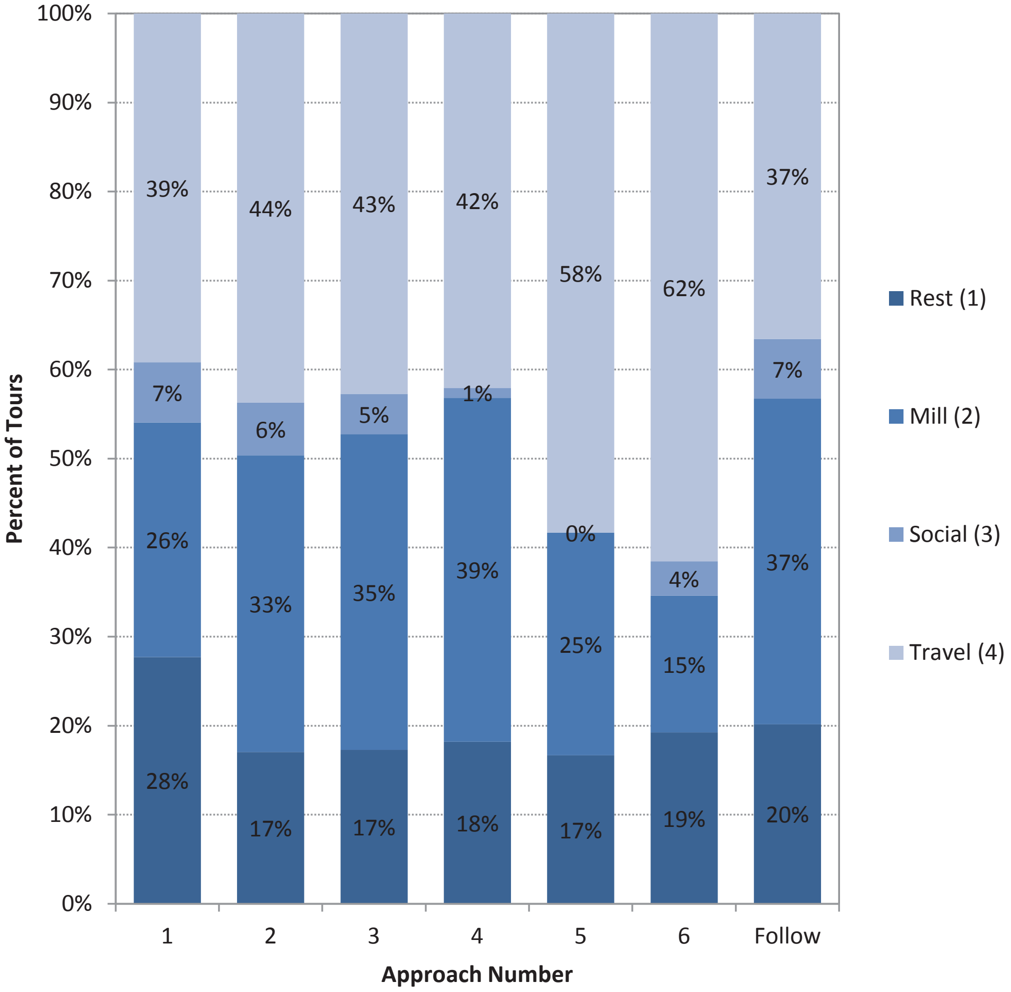


Figure 6.12. Activity level is shown by approach number. Behaviour is shown from least active (darker) to more active (lighter) shades (n=165 tours).

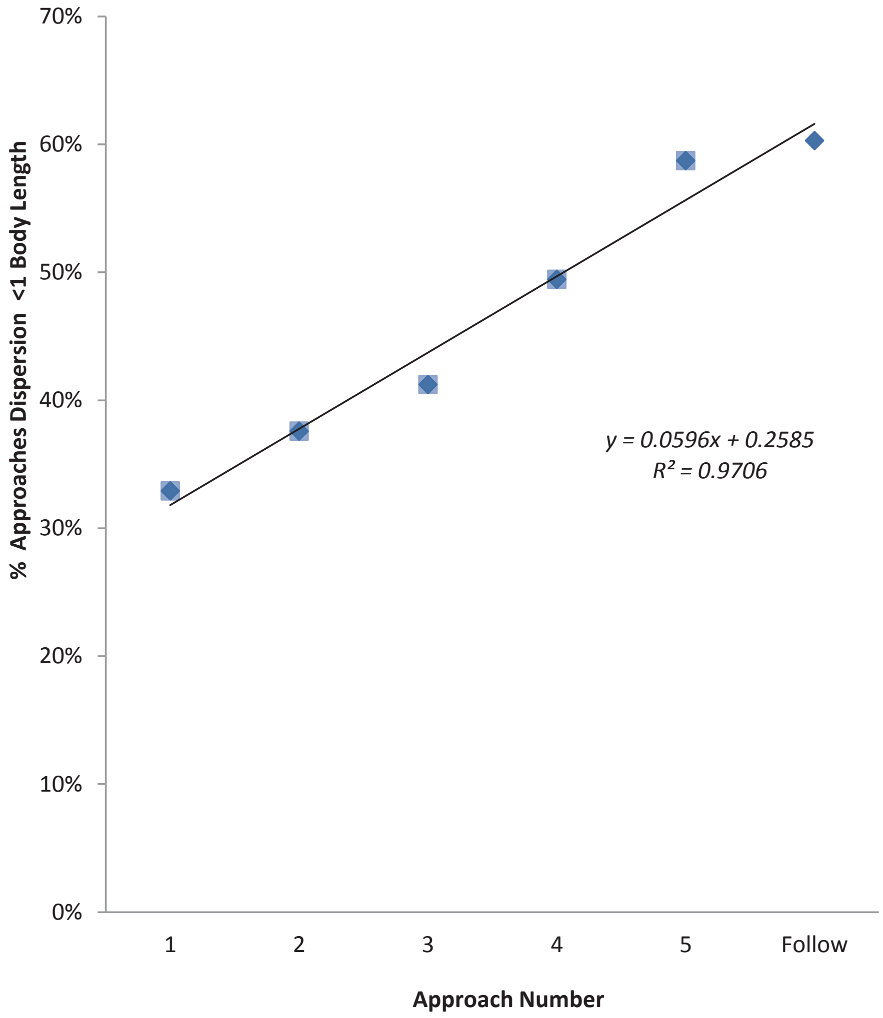


Figure 6.13. The percent of cases when dolphins were tightly grouped (mode nearest neighbour distance <1 body length) is shown by approach number (n=165 tours). Approach 1 represents group dispersion on first encounter with the end of the tour represented by the measurement during the follow.

The number of leaping dolphins was steady during the first four approaches (Friedman, χ^2=2.4, *df* =3, *ns*), but decreased when the number of swim drop approaches exceeded a mean of four (Figure 6.14). Number of leaping dolphins decreased significantly after the fourth approach (approaches 1-4 compared to approaches 5 and 6+, Friedman, χ^2=9.4, *df*=2, $p<0.01$). Number of leaping dolphins did not change significantly between the first approach and follow (Wilcoxon, z=-1.2, *ns*).

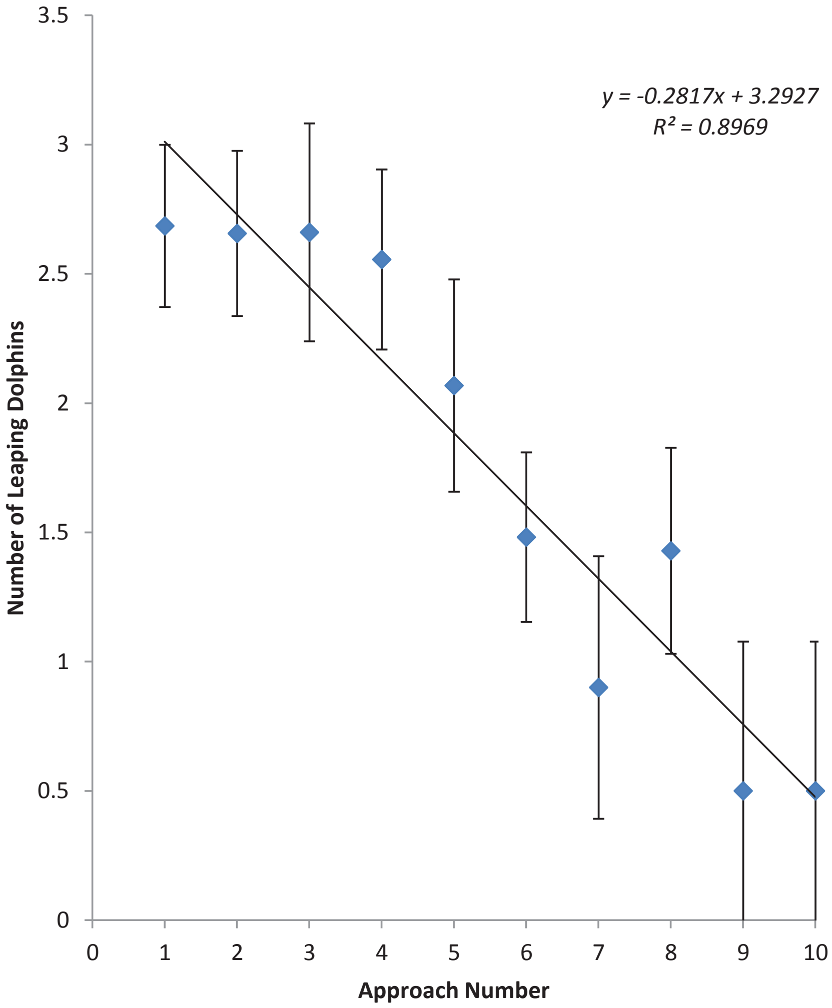
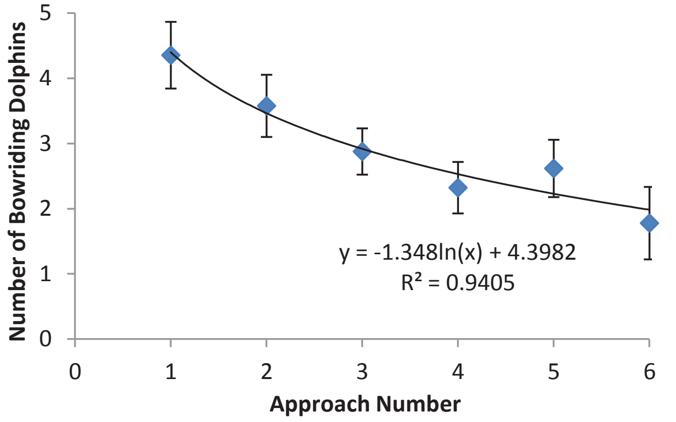


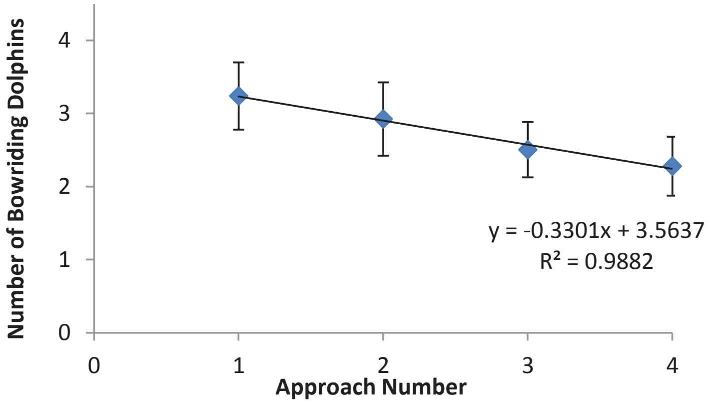
Figure 6.14. The number of leaping dolphins upon tour vessel approach is compared by approach number (n = 165 dolphin tours). Values plotted are means with standard error bars, with a linear trend line (R^2 = 0.90).

The number of bow-riding dolphins decreased significantly (Friedman, χ^2= 11.4, *df*=5, *p*<0.05) as the number of vessel approaches increased (Figure 6.15a). This relationship held true for tours with the average of four approaches (Figure 6.15b) and also for those with >4 approaches (Figure 6.15c).

a. *All Tours*



b. *Tours with 4 swim drops*



c. *Tours with >4 swim drops*

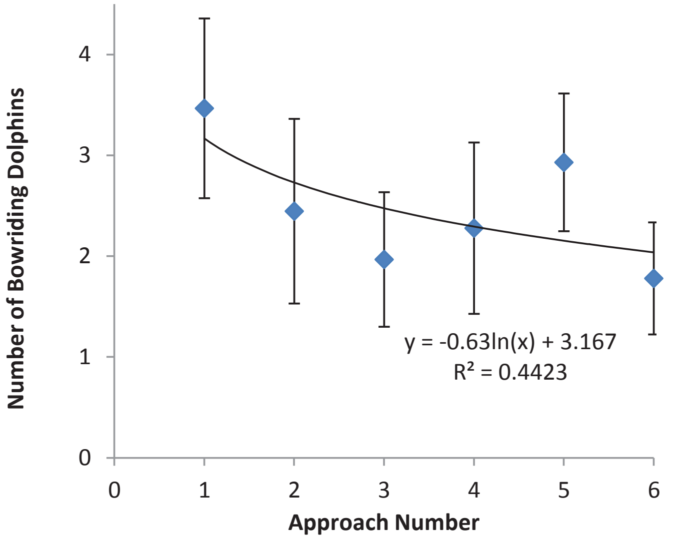


Figure 6.15. The number of bow-riding dolphins decreased with increasing approach number for (a) all tours (n=165 tours), (b) tours with 4 swim drops (n=85 tours), and (c) tours with >4 swim drops (n=29 tours). Mean values per tour with y-error bars representing standard error are shown.

Variation in Dolphin Behaviour with Approach Method

Types of approach by swim-with-dolphin tour vessels included approaches from the front, side and rear of the group. The primary approach method used was an approach alongside the dolphin group (57% of approaches, Figure 6.16). Approaches from the front included approaches in which tour vessels dropped swimmers in the path of dolphins.

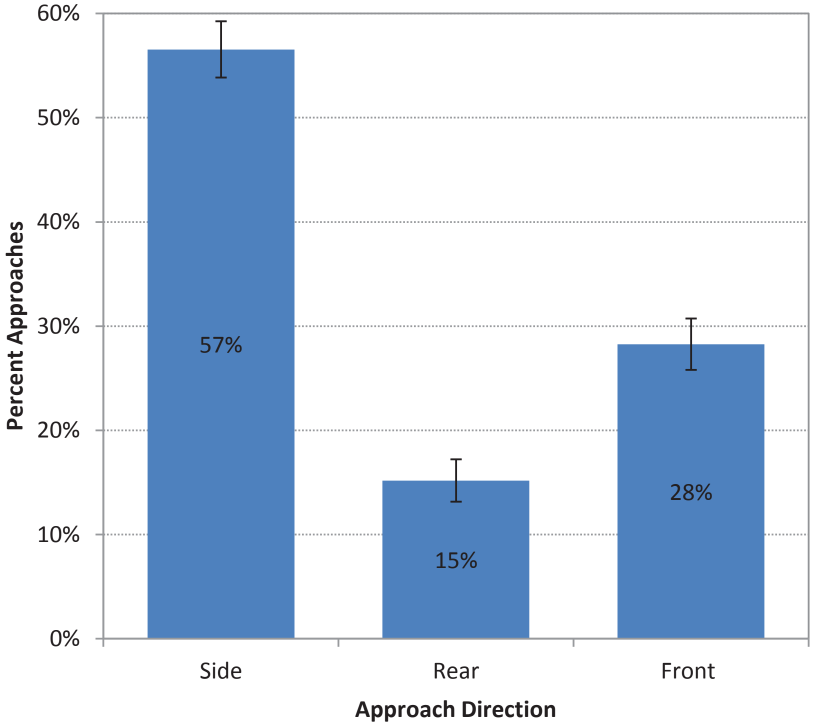


Figure 6.16. Mean percent of approaches by swim-with-dolphin tour vessels by approach type, with y-error bars representing standard error of the mean (n=165 tours).

The percent change in dolphin group behavioural state varied with the bearing of approach by swim-with-dolphin tours, with higher rates of change in behavioural state with increased bearing of approach from 0 or parallel (Median Test χ^2=7.3, *df*=2, *p*<0.05, Figure 6.17).

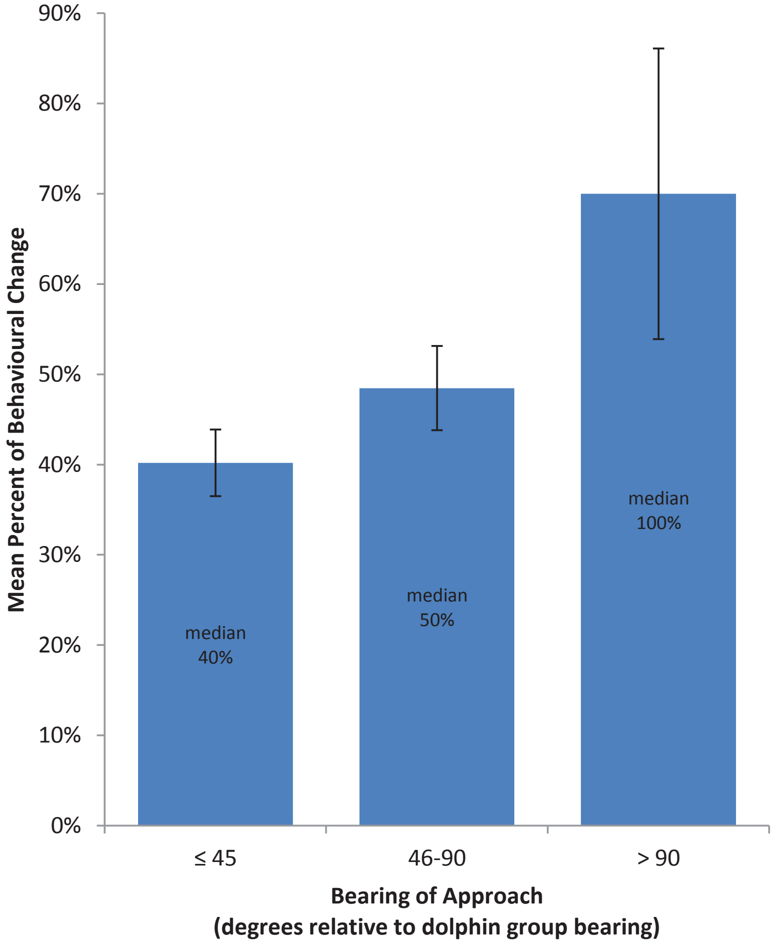


Figure 6.17. Percent change in behaviour is shown with increased deviation from a path parallel to the dolphin group (parallel = 0°, perpendicular = 90°). Bars are mean values with standard errors. Data labels show median percent change in behaviour by vessel approach bearing (n=165 tours).

Percent change in behaviour also varied significantly with median speed of tour vessel approach (Kruskal Wallis H =8.895, *df*=2, $p<0.05$, Figure 6.18). Median approach speeds of 10 or more knots were rare (14 cases) and corresponded with trips when the dolphins were primarily travelling for the duration of the tour (>70% of 14 cases). Median approach speeds were most often 4 to 9 knots (10-18 km/h, >70% of cases). These elicited a higher proportion of changes in behaviour than approaches at either slower (0-4 knots) or faster speeds (>10 knots).

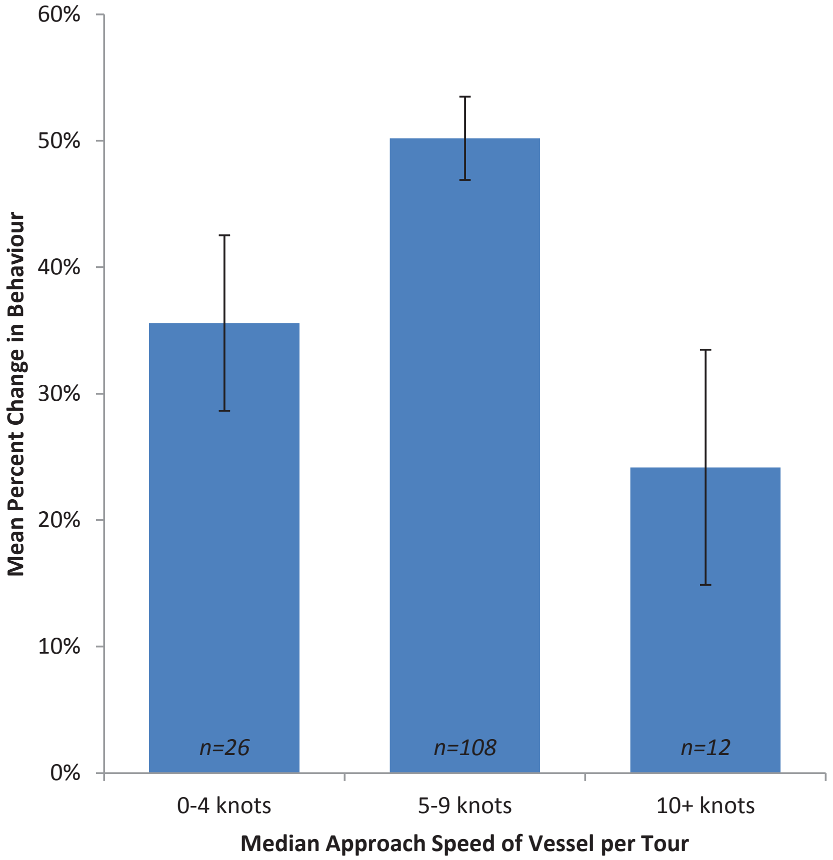


Figure 6.18. Percent change in dolphin group behaviour is compared by median speed of vessel approaches per tour. Bars represent mean percent change with y-error bars equal to 1 standard error of the mean.

Dropping swimmers in the path of the dolphin group affected the behaviour of dolphins. Median activity level of dolphin groups was significantly higher on trips when vessels dropped swimmers in the path of the groups than when another approach method (e.g., approaching alongside) was employed (Mann-Whitney, U =2350.5, $p < 0.05$). Dolphin groups engaged in travelling more, and all other activities less, during tours in which tour vessels approached and dropped swimmers in the path of the dolphin group (Figure 6.20).

Approach method varied among skippers, with a significant difference in rate of dropping swimmers in the path of dolphin groups (Kruskal Wallis H=13.258, df=6, p<0.05).

The mean number of approaches in which skippers dropped swimmers in the path of dolphin groups varied from 0 for one skipper to 1.2 approaches per trip for another (Figure 6.19). The percent of trips in which dropping in front occurred also varied significantly by skipper, from 0% to 28% of approaches (Kruskal Wallis H=15.334, *df*=6, *p*<0.05).

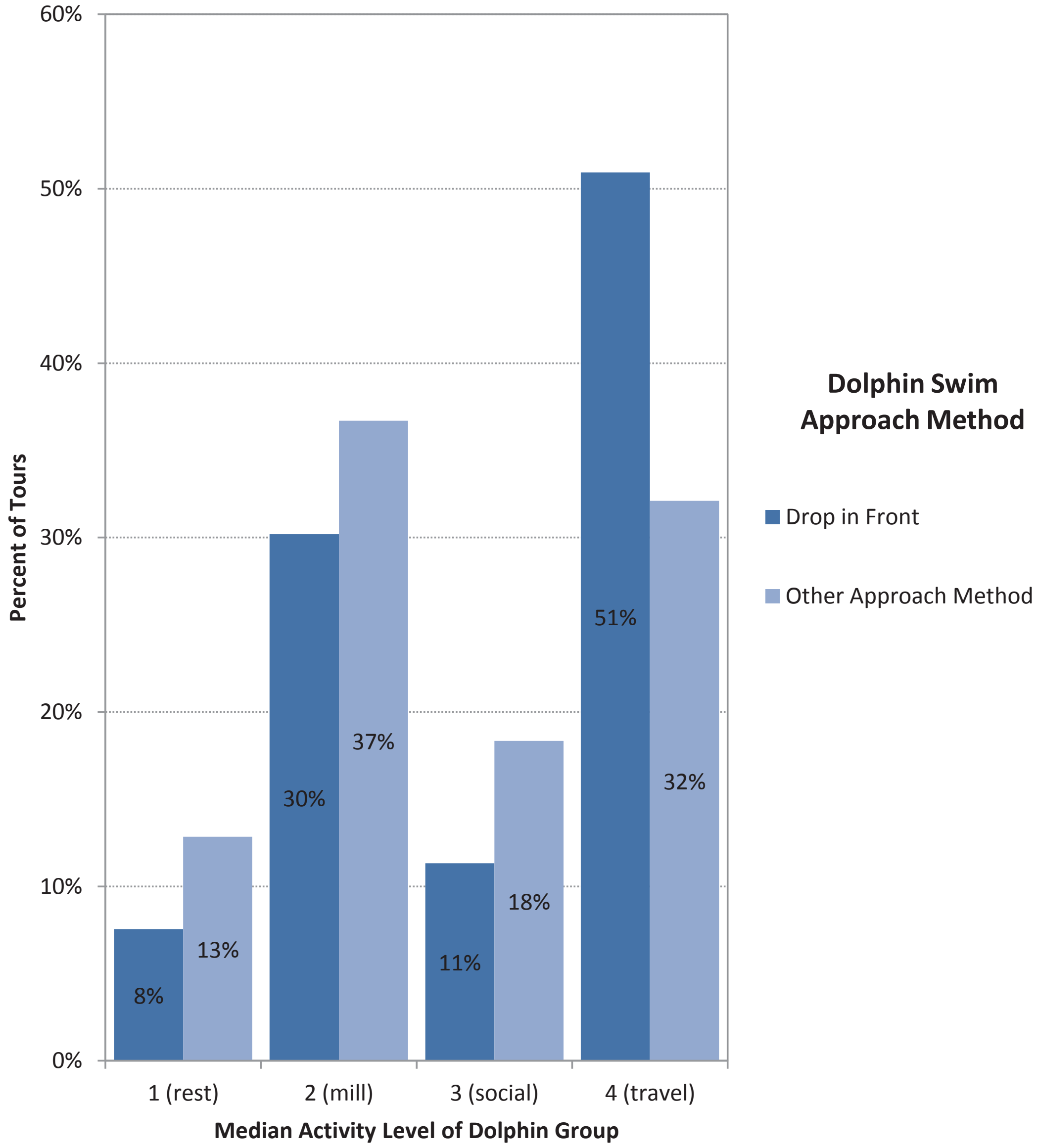


Figure 6.19. Median activity level of dolphin groups is shown with type of approach (n=165 tours).

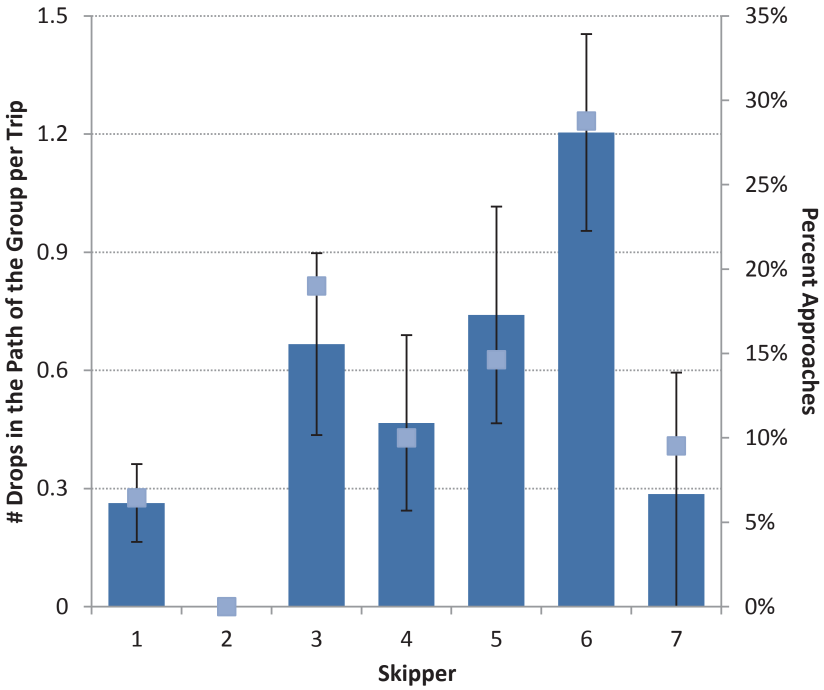


Figure 6.20. Mean number of drops in the path of the group is shown by skipper (gray bars) with y-error bars representing standard error. Percent of approaches in which skippers dropped swimmers in the path of the dolphin group (squares) is also shown (n = 38, 6, 8, 15, 26. 48, and 8 days for skippers 1-7).

Swim drop duration was significantly shorter when swimmers were dropped in the path of the dolphin group than when swimmers were dropped alongside the group (4.8±0.48 *versus* 8.7± 0.58 min, Mann-Whitney $U = 2847$, $p<0.001$). Approach type did not appear to influence the number of group behavioural changes per trip. Swim duration on the first drop was reduced by dropping in the path of the dolphins, regardless of behavioural state upon encounter (Figure 6.21). When dolphins were travelling and vessels dropped swimmers in the path of the dolphin group, subsequent swim duration was reduced by an average of 5.1 min (Mann Whitney U=99, $p<0.05$). The duration of swims also varied significantly when dolphins were not travelling (milling, resting, socializing or foraging) and swimmers were dropped in the path of the group (Mann Whitney U=276.5, $p<0.05$). Duration of swims when dolphins were not travelling was reduced by an average of 4.9 min when vessels dropped swimmers in the path of the dolphin group (Figure 6.21).

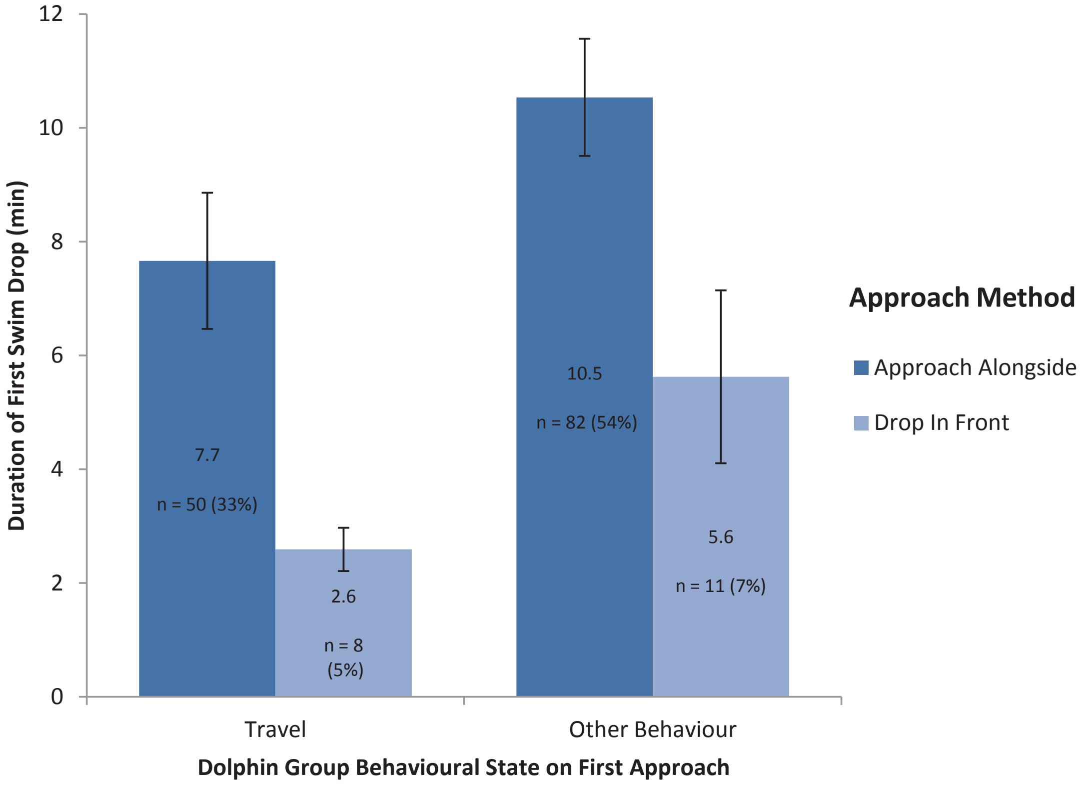


Figure 6.21. Duration of first swim encounters by approach method on first approach. Y-error bars represent standard error of the mean.

Dropping in the path of the dolphin group did not appear to be related to median activity level of dolphin groups upon first encounter (Mann-Whitney U=2506, *ns*). This approach method was as likely to be used by skippers when dolphins were primarily resting as when dolphins were travelling (Figure 6.22a). Activity level of dolphin groups changed when swimmers were placed in the path of the dolphins. Although activity level did not vary significantly on encounter and during the first approach (pre-tour vessel interaction), activity level varied significantly during subsequent approaches when this approach method was used (Mann Whitney U=1838, p<0.01). For these trips, increased travelling and decreased resting were observed (Figure 6.22b).

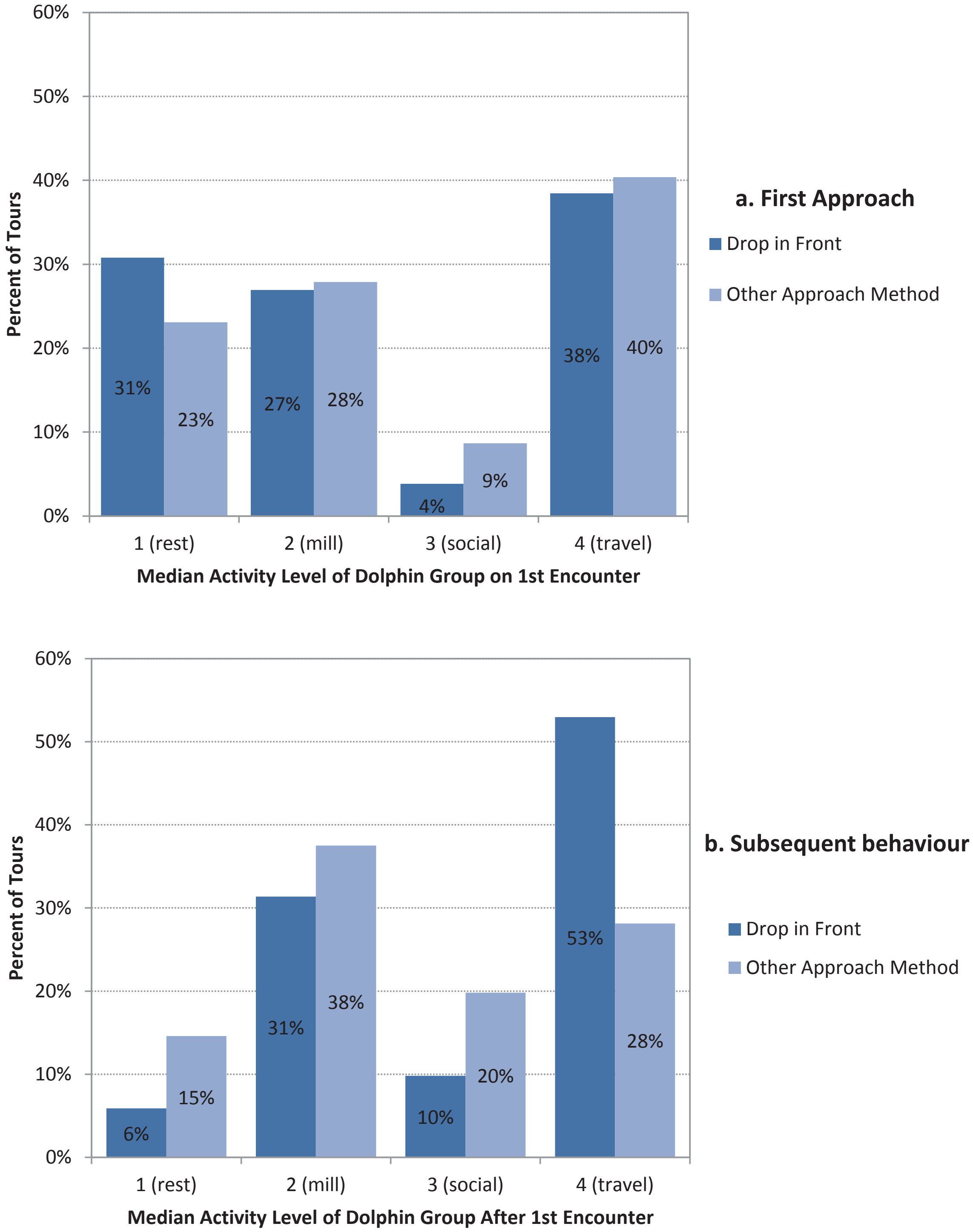


Figure 6.22. Median activity level (a) upon group encounter and (b) subsequent approaches for dolphin groups in which skippers chose to drop swimmers in the path of the dolphin group versus using another method (n=165 tours).

Swim duration varied significantly by season (Kruskal Wallis H=13.159, *df*=3, *p*<0.01), with the lowest mean swim duration in summer (Figure 6.23), coinciding with peak tourism season.

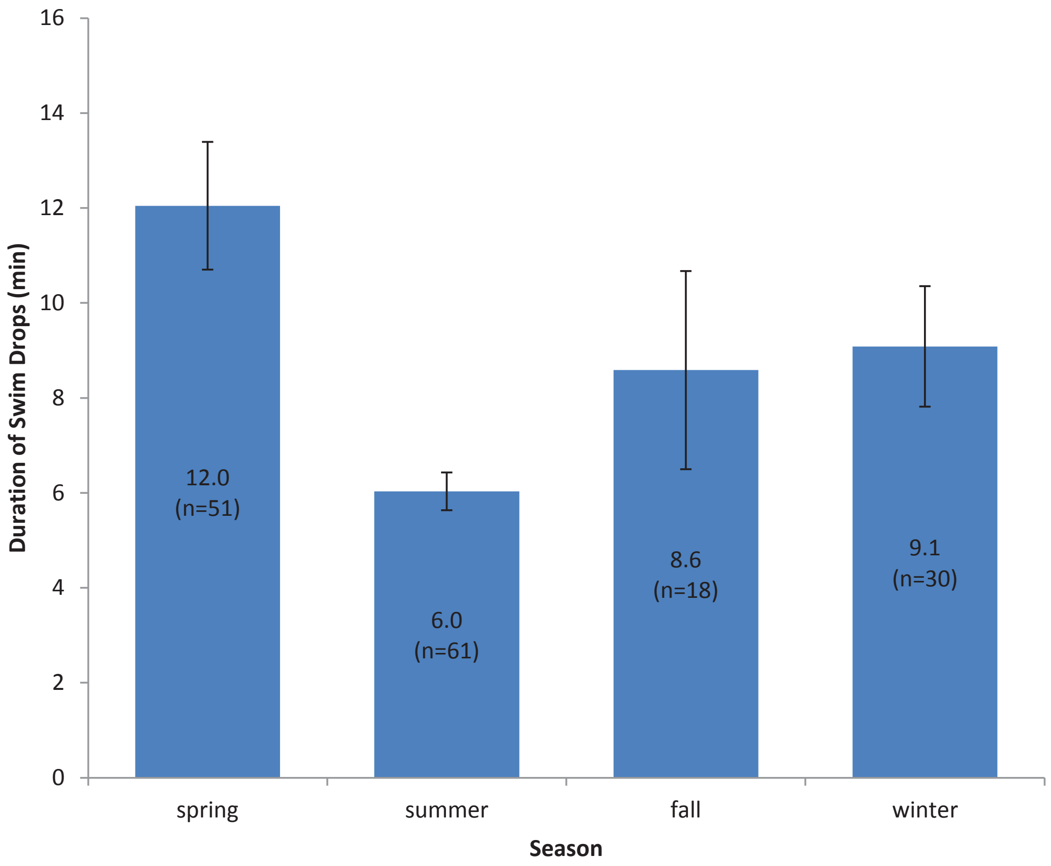


Figure 6.23. Mean swim encounter duration by season is shown. Y-error bars represent standard error of the mean

Swim duration varied significantly depending on the predominant behavioural state of the dolphin group on approach (Kruskal Wallis H=42.789, *df*=4, *p*<0.001). Swim durations were longest when dolphins were socializing prior to a swim drop (11.0±1.80 min) and shortest when dolphins were travelling prior to a swim drop (5.5±0.33 min, Figure 6.24).

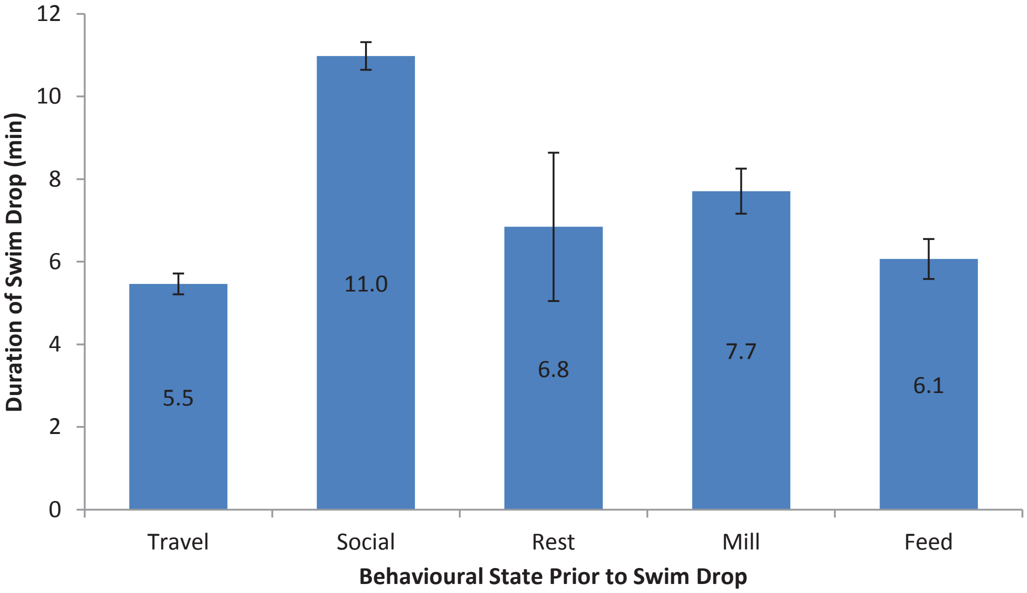


Figure 6.24. Behavioural state of dolphin groups prior to dropping swimmers in the water during tour vessel interactions with subsequent swim duration (bars represent mean durations with standard errors, (n=165 tours, 409 swim drops).

Swim drops generally ended when the dolphins moved away from the swimmers. The distance of the large group from swimmers at the end of the swim was estimated to be >100 m in 64% of cases. The large group remained near the swimmers (<50 m away) in 20% of cases (Figure 6.25).

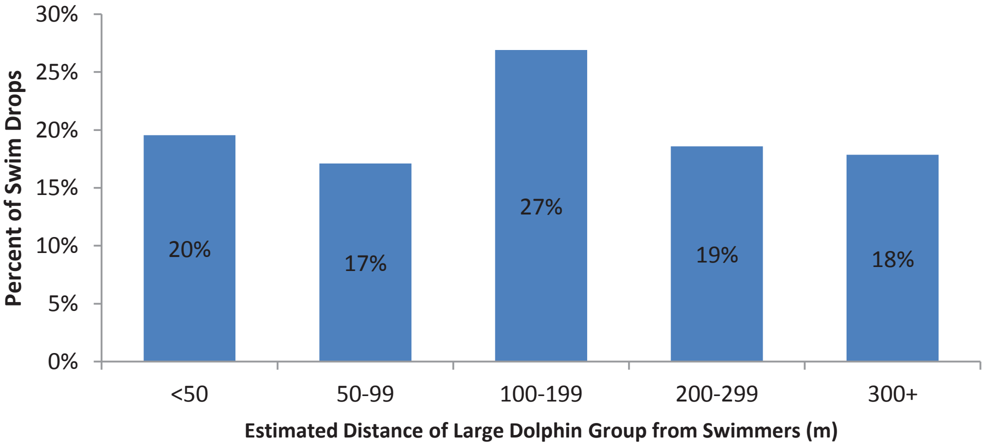


Figure 6.25. The estimated distance of the large group from the swim-with-dolphin tour vessel, at the end of the swim by percent of swim drops (n=165 tours, 409 swim drops).

Small subgroups of dolphins, averaging 6 adults and 1 juvenile, maintained an association with swimmers after departure of the large group during 42% of swim drops. Calves were rarely present in these smaller subgroups (just 2 instances, 1.5%). These associations often continued well after the large pod had moved >50m away from the swimmers. Consequently, swim duration significantly increased (Mann Whitney U= 2726, p<0.001) in the presence of these dolphin subgroups (Figure 6.26). Subgroup association with swimmers increased length of swim drops by an average of 3.5 min (53 %).

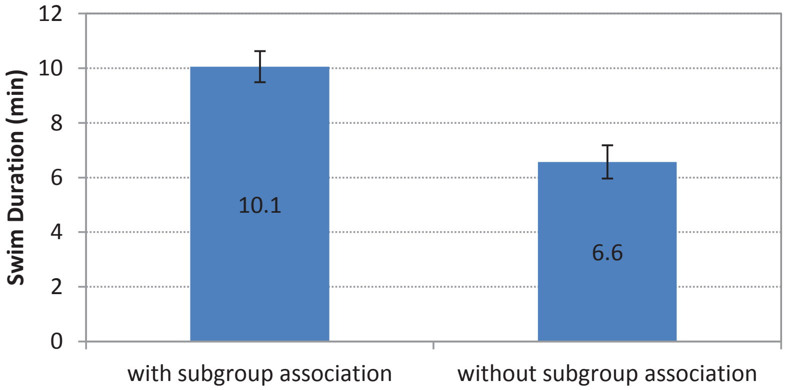


Figure 6.26. Swim duration is shown with and without the presence of dolphin subgroups. Y-error bars represent standard error of the mean (n=165 tours).

Swim duration did not vary by time of day (Kruskal Wallis χ^2=2.476, *df*=2, ns). No relationship was found between duration of swims and number of swimmers, bow-riding or leaping activity.

Variation in Dolphin Behaviour With Number of Vessels

Group dispersion (mode nearest neighbour distance) was reduced during the follow portion (end of tour) when more swim-with-dolphin tour vessels were present (χ^2= 15.295, df=4, p<0.01). Dolphins were tightly grouped (mode nearest neighbour distance <1 body length) during 19% of follows when just one swim-with-dolphin tour vessel was present, 46% of follows when two tour vessels were present, and 54% of follows when three vessels were present (Figure 6.27).

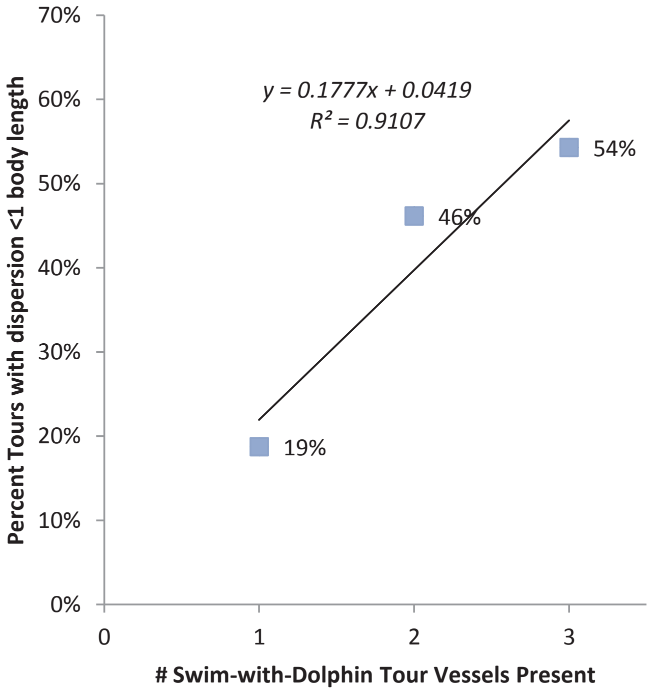


Figure 6.27. Mode nearest neighbour distance is shown with increasing number of swim-with-dolphin tour vessels (n=165 tours).

No significant difference was found in behavioural state during the 'follow' portion of the tour with increasing number of swim-with-dolphin tour vessels. Activity level of dolphin groups during swim drops did not vary with number of swim-with-dolphin tour vessels nor mean total number of vessels visiting the tour. The numbers of leaping and bow-riding dolphins during the follow also did not vary with total number of vessels visiting the group during the tour.

Dolphin group dispersion during the follow was reduced when a greater number of additional swim and non-swim vessels visited the dolphin group during the tour (Kruskal

Wallis H= 19.633, *df*=8, *p*<0.02). Dolphins were tightly grouped by the end of the tour 64% of the time when four or more vessels approached, compared with just 15% of the time when only one tour vessel visited the group (Figure 6.28, darkest bars – mode nearest neighbour distance < 1 body length). Additional vessels (including other swim-with-dolphin tours, non-swim dolphin watching tours, aircraft tours, and recreational boats) visited dolphin groups during 85% of tours monitored, with one additional vessel during 16%, two additional vessels during 30%, three additional vessels during 20%, and four or more additional vessels during 19% of dolphin swim tours.

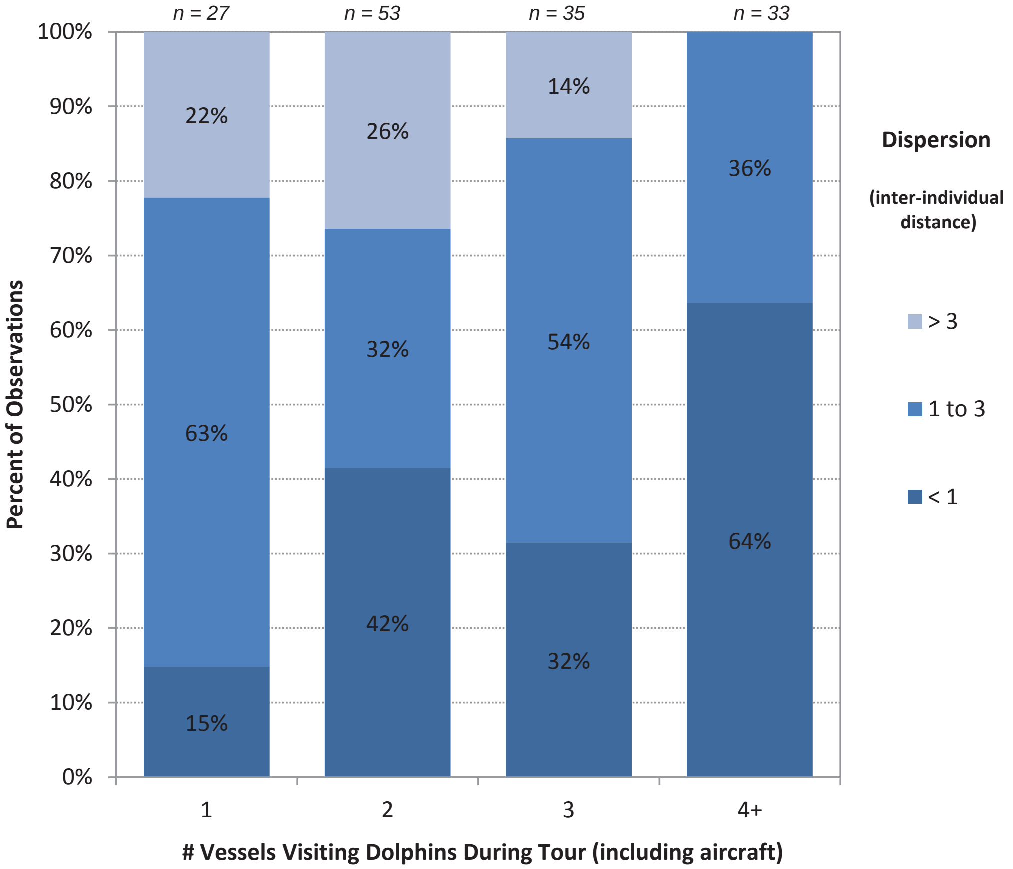


Figure 6.28. Dispersion of dolphin groups during the follow is compared for dolphin groups visited by 1, 2, 3, or 4 or more vessels (including swim-with-dolphin tours, whale watching tours, aircraft, and recreational vessels) during the swim-with-dolphin tour. Stacked bars show the proportion of groups with mode nearest neighbour distance <1, 1 to 3, and >3 body lengths (1 body length = 1.7m). Sample sizes above each bar indicate the number of tours monitored during which 1, 2, 3 or 4 or more vessels visited the group.

Neither the activity nor the dispersion of the dolphin groups at the end of the tour varied significantly with visitation by whale watch boats (Mann-Whitney: Activity U = 1822.5, Dispersion U = 2035, *ns*), fixed-wing aircraft tours (Mann-Whitney: Activity U = 1640.5, Dispersion U = 1985.5, *ns*), or helicopter tours (Mann-Whitney: Activity U = 546.5, Dispersion U = 750.5, *ns*) during the swim-with-dolphin tour.

Activity of dolphin groups at the end of the tour also did not vary significantly with the number of recreational vessels visiting the groups during the tour (Kruskal Wallis χ^2= 1.731, *df*=2, *ns*). However, dispersion of dolphin groups did vary with visitation by recreational vessels (Kruskal Wallis χ^2= 11.715, *df*=2, $p<0.01$), with dolphin groups more tightly grouped following an interaction with one or more recreational boats during a swim tour (Figure 6.29). Visits by recreational boats were relatively rare, noted on 20 out of 174 tours (12%).

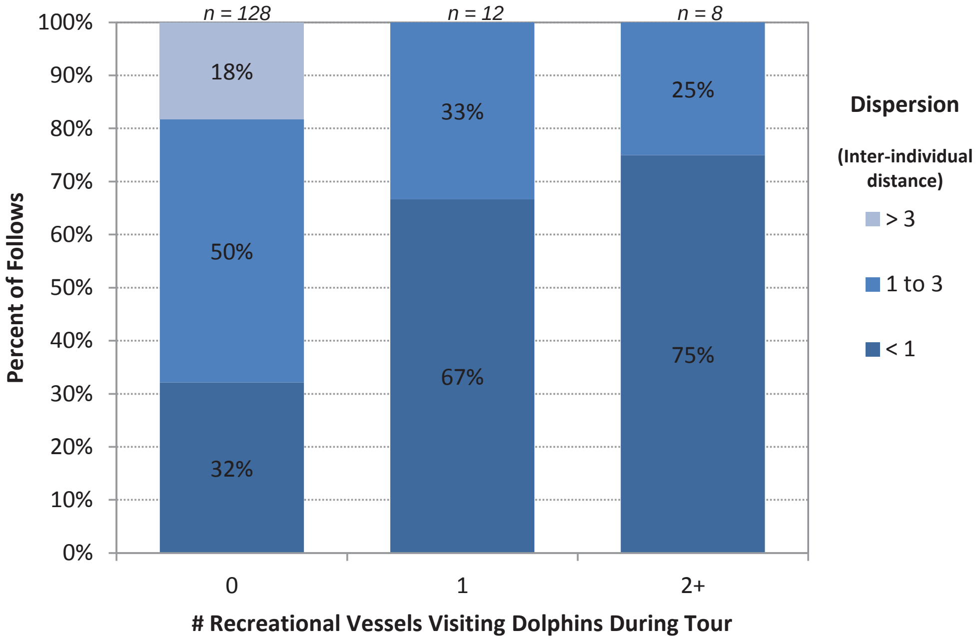


Figure 6.29. Dispersion of dolphin groups during the follow is compared for dolphin groups visited by 0, 1 and 2+ recreational boats during the swim-with-dolphin tour. Stacked bars show the proportion of groups with mode nearest neighbour distance <1, 1 to 3, and >3 body lengths (1 body length = 1.7m). Sample sizes above each bar indicate the number of tours monitored during which 0, 1, or 2 or more recreational vessels visited the group.

On average, dolphin groups moved southwest alongshore from the beginning to the end of the tour (Figure 6.30). One exception was autumn, when dolphin groups moved inshore between the beginning and end of the tour. On average, dolphin-tour interactions occurred closest to shore in summer and furthest from shore in winter (Figure 6.30).

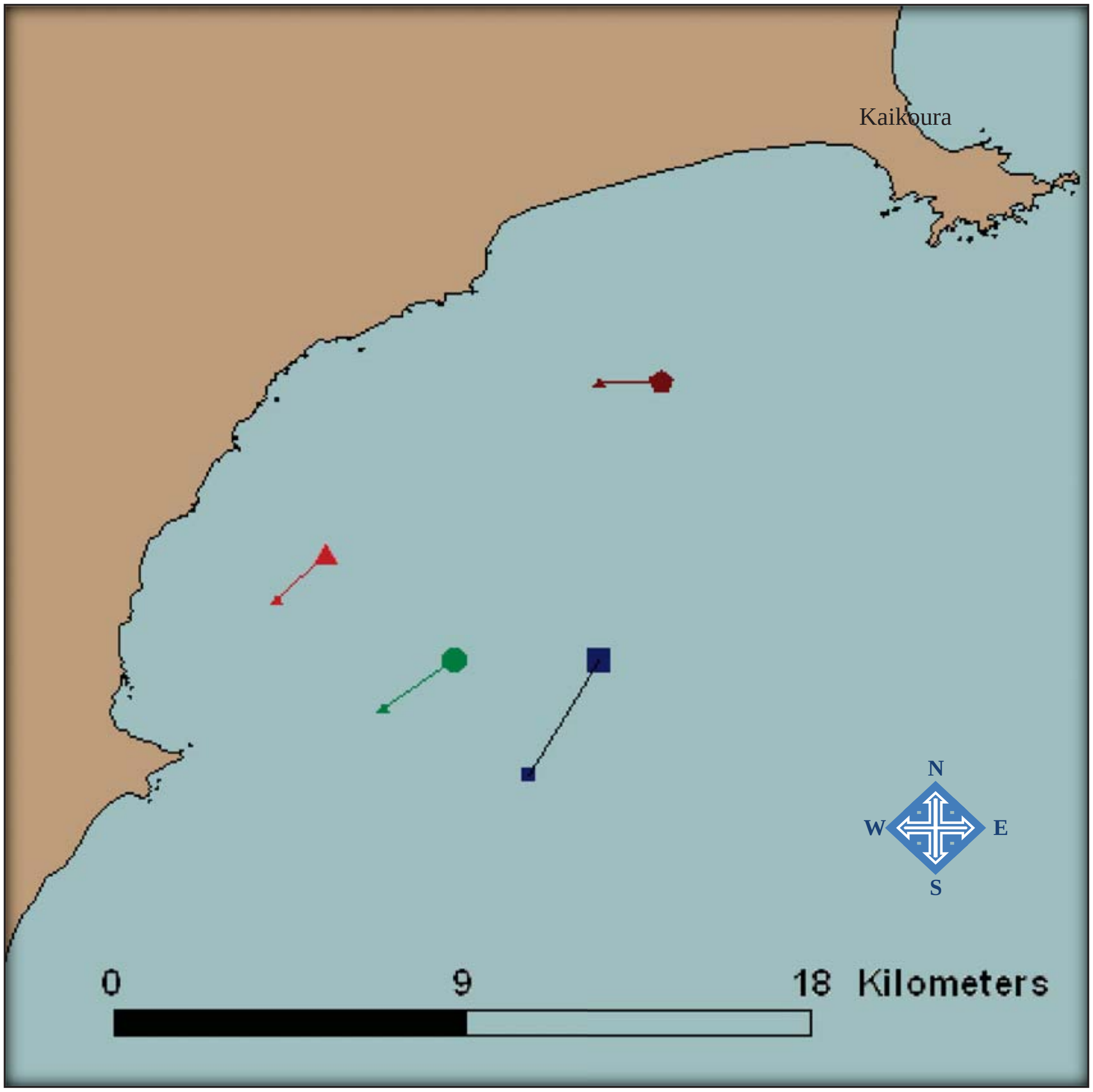


Figure 6.30. The average encounter and departure positions of swim-with-dolphin tours are shown by season. Large symbols indicate encounter position and smaller symbols indicate departure position,(●=spring n=51, △=summer n=61, ⬟=autumn n=18, ■=winter n=30).

DISCUSSION

Characteristics of Swim-with-Dolphin Tours

The focus of the tour on large groups of dolphins is consistent with previous observations of tourism off Kaikoura, New Zealand. Large groups of dolphins are easier to locate and provide a higher dolphin-to-swimmer ratio. Although large groups of dolphins often contain calves, particularly in summer, tour vessels consistently avoided swims with smaller nursery groups. Calves were rarely present in dolphin subgroups that formed an association with swimmers during the tour. Although calves were present in the large group, the lack of calves in these smaller subgroups effectively halved the time swimmers spent interacting with calves.

When compared with other studies from previous years, the mean number of approaches to the dolphin group by swim-with-dolphin tour vessels has increased by 19% while the duration of each swim increased by roughly 1 min (Table 6.3). Less than one-half of tours (41%) approached the group 1-3 times, while more than one-half (51%) approached the group 4-6 times to drop swimmers with the dolphins. Few tours (8%) approached the dolphin group > 6 times.

Table 6.3. Comparison of current study (bold) with previous data collected onboard swim-with-dolphin tours off Kaikoura, New Zealand.*

Year	Source	Tour Length	Swim Drops/ Tour	Swim Drop Duration
1997–1999	Markowitz 2004	2.1 h	3.4	8.3 min
2005	Duprey 2007	2.0 h	3.3	8.1 min
2007-2009	**This study***	**2.3 h**	**4.0**	**9.1 min**

Dolphins spend more time interacting with the tour vessels than the swimmers. The lack of any direct relationship between number of swimmers and dolphin behavioural changes further suggests that vessel activity and number of vessels, rather than swimmers, is the primary influence on changes in dolphin group behaviour. The number of swim-with-dolphin tour vessels present during a tour was lower than the maximum permitted number of vessels during 78% of tours.

Vessel Activity

Tour vessel speed on swim drop approaches was 32% - 46% faster than mean speeds when vessels were following the dolphin groups after the swims. The reduction in mean speed during the follow likely reflects skippers following behind and to the side of the dolphin groups more than ‘catching-up’ to place swimmers toward the front of the group. This is particularly noteworthy as dolphin groups travelled more and rested less during the ‘follow’ than during other portions of the tour. Therefore, a vessel just matching speed with the dolphins would be expected to move faster during the follow than during swim drop approaches.

Compared to tours monitored 10 years ago (1997-1999, Markowitz 2004), tour vessels monitored in the current study were less often stationary (45% compared to 60%) and more often left the motor running (97% *versus* 52%) during dolphin swims than in the past. This may be due to changes in the size and specifications of vessels, swimmer safety concerns, changes in swim-with-dolphin tour operator policies/protocols, or changes in vessel crews over the past decade. Keeping vessels stationary when swimmers are in the water is likely the best practice for minimizing disturbance of dolphins during swimming. Turning vessel engines off when stationary would likely further reduce the effects of engine noise on dolphins, so long as the engine is not suddenly turned back on with dolphins in the immediate vicinity of the vessel. Backing, a practice noted on more than one-third of swim drops, likely introduces different noises in the water than either idling in neutral or moving slowly forward. Vessels were mobile during swim drops a surprising 9% of the time. Among other movements of the vessels, circling was noted on seven tours (4%), apparently an effort by the skipper to attract bow-riding dolphins to the swimmers.

The significant increase in time spent with dolphins when 16 or more swimmers were onboard is likely due to a practice by tour operators of splitting the tour into two distinct swim groups. Although this practice does not double the duration of the tour or number of approaches, it does increase both parameters. Ironically, in this relatively rare situation, the 13 swimmer limit apparently resulted in an increased number of vessel approaches. When 14 or 15 swimmers were present, tour operators were more likely to use a ‘swap-swim’ practice of allowing a few additional swimmers to enter the water when some swimmers leave (maintaining a swimmer count of 13 individuals at all times). As the number of swimmers had no measurable effect while the number of approaches had a significant effect on the behaviour of the dolphins, the 13 swimmer limit in this situation resulted in increased disturbance of the dolphins.

When >1 swim-with-dolphin tour vessels were focused on the same group during a tour, the average number of approaches per vessel can be estimated as 4.0 based on the results presented above. This yields an estimated total of 8 approaches during tours with two vessels present and 12 approaches during tours with 3 vessels present. Increasing the number of swimmers per swim drop while decreasing the total number of approaches (either decreasing the number of approaches per vessel or the number of vessels) would presumably decrease the effects of vessel activity on dusky dolphins (see below). The decrease in duration of swims with swim drop number suggests a case of “diminishing returns,” particularly from the fourth drop on.

The number and variety of other tour vessels and recreational vessels visiting the dolphins during the tours indicates quite a high visitation rate throughout the day, with non-swim tours and fixed-wing aircraft each visiting about 20%, helicopters 8%, and recreational vessels 12% of the time. Aircraft tours, although numerous, spent the least amount of time with the dolphin group. Recreational vessels were often noted to be highly active in the presence of dolphin groups, suggesting that education of recreational vessel users on how to interact with dolphin groups is very important. Recreational vessels spent more time on average (mean = 3.4 min/tour) with the dolphins than other types of vessels (non-swim tours = 2.6 min/tour, fixed-wing aircraft tours = 0.6 min/tour, helicopter tours = 0.3 min/tour) during the swim-with-dolphin tours, and were most likely to break the three boat rule.

Effects on Dolphin Behaviour

Dolphins became more active by the end of the swim-with-dolphin tour interaction than they were at the beginning, with an increase in milling and decrease in resting behaviour. Dusky dolphins interacting with tour vessels in Argentina also increased milling in response to tour vessels (Dans et al. 2008, Markowitz et al. 2010b). In Argentina, foraging of dusky dolphins was reduced, while foraging was not affected in Kaikoura because dolphins in Kaikoura feed mainly at night and rest during the day (Cipriano 1992, Benoit-Bird et al. 2004). The increased activity level of groups in response to tour vessels is particularly noteworthy since most tours occur in the morning when dolphin groups are more likely to be heading into a resting state regardless of tour vessel activity (Markowitz 2004). The increase in activity level of dolphin groups during the swim portion of the tour bears this result out and further supports the interpretation that swim-with-dolphin tours are changing the behaviour of dolphin groups, reducing resting behaviour. Increased activity of dolphins was particularly apparent following the fourth swim approach, as dolphin behaviour changed to mainly travelling. Vessel approaches have also been found to disrupt resting by Hawaiian spinner dolphins (*Stenella longirostris*) at Kealakekua Bay, Island of Hawaii (Timmel 2005) and common dolphins in the Hauraki Gulf, New Zealand (Stockin et al. 2008).

Dolphins became more tightly grouped as the number of vessel approaches increased, with nearest neighbours most often swimming within one body length of each other after the fourth swim approach. Research conducted prior to the ten-year moratorium on dolphin tour permits found that dusky dolphin groups tightened during the middle of the day when vessels were present, a time of day when the dolphins also rest most heavily (Barr and Slooten 1998, Yin 1999, Markowitz 2004). These findings led to the adoption of a voluntary code of conduct, in which tour operators agreed to not approach dolphin groups during a “midday rest period” in the peak summer season (Duprey et al. 2008). This voluntary code of conduct is now mandatory based on the results of this study (see below).

Decreasing numbers of bow-riding dolphins with increasing swim approaches may reflect reduced interest on the part of the dolphins in the tour vessel later in the tour, an interpretation further supported by the shorter swim durations on later swim drops. The consistent reduction in inter-individual distance with increasing number of tour vessels indicates that tourism is affecting dolphin behaviour at current levels. This suggests that the number of permitted tour vessels should continue to be limited if the effects on dolphin groups are to be minimised.

Research prior to the ten-year moratorium on changes to dolphin tour permits showed that number of dolphins leaping increased with vessels (Barr and Slooten 1998), and observations from a shore station (Lundquist and Markowitz 2009) and research vessel during the current study confirm that this has not changed (see Chapter 5). Noisy leaps apparently can function in large groups as signals directing group movement (Markowitz 2004), but may also serve other functions (Würsig et al. 1997, 2007, Markowitz et al. 2010b). Leaping rates of bottlenose dolphins have also been documented to increase in the presence of tour vessels (Lusseau 2006). Observations from swim-with-dolphin tour vessels off Kaikoura in this study indicate that the number of leaping dolphins decreases after the fourth swim approach. This could be due to increased travelling of the dolphins, habituation to tour vessels, or some combination of these and other factors when the number of vessel approaches exceeded the average of four.

The changes in both behaviour and duration of swim associations with approach method indicate that the method skippers use to approach dolphins affects the way in which dolphins respond to the tour. Approaching at 90°, or basically perpendicular to the group, had the greatest effect, with 30% more changes in behaviour observed than when dolphin groups were approached from the rear of their movement at an angle of parallel to 45°.

Approaching and dropping swimmers in front of the group affected the behaviour of the group, increasing the dolphins' activity level, and decreasing the duration of the swim interaction. Bottlenose dolphins in the Bay of Islands also changed behaviour in response to vessels placing swimmers in the path of the group, avoiding vessels more when this approach method was used (Constantine 2001, Constantine et al. 2004). The preferences of different skippers for use of this method, as well as the lack of variation in prior behavioural activity when skippers use this method on first approach *versus* when they do not, indicated that this approach method is driven less by the behaviour of the dolphins and more by the preference of skippers. The increase in travelling and decreases in resting, milling, and social behaviour following use of this method, along with the reduction in subsequent swim duration, likely results in a less successful tour and suggests dolphin groups are more likely to be disturbed by this type of approach than others.

Subgroup associations with swimmers increased the length of the swim interaction by >50%. Such associations likely also result in the least amount of disruption for dolphins in the larger group, as the larger group moves on and continues “about its daily business” during the swim, while particularly interested dolphins remain interacting with the tour. Subgroup associations with swimmers were less likely to occur when swimmers were dropped in the path of the dolphin group.

The reduction in group dispersion during the ‘follow’ portion of the tour, with both increased number of swim-with-dolphin tours and increased number of other vessels visiting the tour, suggests that number of vessels influences the behavioural response of dolphin groups in a cumulative fashion. Tightening of groups (reduced dispersion) may indicate dolphin groups assuming a more defensive posture in response to a greater total number of vessels in the vicinity and cumulative number of vessel approaches over time. For many social animals, including dolphins, tightening of groups is often a response to a threat such as a predator (Hamilton 1971).

The consistent movement of dolphin groups from north to south during swim-with-dolphin tours suggests that dolphins may be moving south in response to tour vessels (away from the direction of tour vessel approach). This is particularly significant since this result was found regardless of season. However, these movements must be described as ‘short-term' changes in direction, as movements of dolphins before and after swim-with-dolphin tour vessel interactions were not observed from the tour vessel (but see Chapter 5).

Swim-with-dolphin tourism off Kaikoura, New Zealand, although not necessarily impacting the animals biologically, is shifting activity levels of large dolphin groups. The findings of decreased resting and increased milling and travelling are consistent with previous research showing increased activity of dusky dolphins in response to tour vessels off Kaikoura (Yin 1999).

As the peak tourism season coincides with the mating and nursing portion of the dolphins' annual cycle (Cipriano 1992, Markowitz et al. 2010b, Weir et al. 2010), the reduction in resting and increase in travelling and milling could affect the ability of mothers and calves in large groups to rest. Small nursery groups were never approached for swims by tour vessels, so nursery groups are not likely to be affected by swim-with-dolphin tours. The inclusion of mothers and calves in large groups off Kaikoura may be a response to predation pressure, with mothers and calves trading the increased potential for disturbance by conspecifics in large groups for the "safety in numbers" and increased vigilance provided by the large group. Given the physiological demands of lactation on mothers and rapid growth on calves, reduced resting of mothers and calves could be a concern (Weir et al. 2010). Therefore, it may be important that tour operators adhere to the midday rest period policy, where dolphin groups are given a break without visits from tours during the middle of the day in summer (and recently extended to spring as a result of this work; New Zealand Department of Conservation 2011). Recent research (Duprey 2007, Duprey et al. 2008, Lundquist and Markowitz 2009) showed that tour operators did not always follow the voluntary code of practice. As mating behaviour during the breeding season occurs most often in small groups rarely approached by swim-with-dolphin tours or other vessels (Markowitz et al. 2010b), it is unlikely that mating is significantly disrupted by tour vessel interactions.

It should be stressed that increased activity and tightening of dolphin groups in response to vessels generally does not appear to indicate a “fight-or-flight” stress response (Selye 1937) that could lead to chronic stress with impacts on dolphin health and reproduction as has been hypothesized for other dolphin populations (Orams 2004). High-speed evasive manoeuvres, such as group “slicing” (or “running”), often observed when killer whales are nearby (Markowitz 2004), appear to be a relatively infrequent response to tour vessels (see Chapter 5).

In particular, two actions on the part of swim-with-dolphin tour vessel operators elicited a behavioural response from the dolphins: (1) engaging in a higher number of approaches, and (2) dropping swimmers in the path of the dolphin group. Both of these actions resulted in increased activity levels of the dolphins. Neither of these actions enhanced the tour experience for the swimmers, as the durations of swims decreased in later approaches and approaches in front of the group. The observation that the mean number of approaches per trip increased from 3.4 during the 1990s to 4.0 in the current study indicates that this higher number of approaches may not be necessary for an effective tour. Two additional findings indicate that tour operators rather than dolphin behaviour influence the number of vessel approaches: (1) number of approaches was not related to dolphin behavioural activity on first encounter (i.e., dolphin groups that were travelling were not approached more during a tour than groups that were resting), and (2) approach numbers varied by skipper, with more experienced skippers approaching less often. As dolphins are repeatedly approached, avoidance behaviours may develop that may in turn cause skippers to continue approaching. However, the lack of relationship between dolphin behaviour on first encounter and either number of approaches or aggressiveness of approach method (see below) indicates that these characteristics of the tour are driven primarily by tour operators.

The observation that some skippers drop swimmers in the path of the dolphin group rarely or never indicates this method is not necessary. This approach method was used less often by the most experienced swim-with-dolphin tour skippers, and in total only during 19% of all approaches monitored. Dolphin group behaviour changed more frequently when approaches were perpendicular to the path of the group. Therefore, vessel activity and motor noise appear to be key elements in these dolphin-tour vessel interactions. Studies of tour vessel interactions with bottlenose dolphins in Doubtful Sound and Milford Sound, New Zealand showed that effects of vessels on dolphins were less pronounced if vessels were driven carefully in accordance with New Zealand Department of Conservation (DOC) guidelines (Lusseau 2006).

While brief visits by other tour companies (both ocean vessels and aircraft) did not, by themselves, appear to change the behaviour of dolphin groups at the end of the tour, short-term effects with and without swim-with-dolphin tour vessels present are still possible (see Chapter 5). The cumulative number of visits by other vessels did result in increased tightening of groups, with four or more vessel visits eliciting the greatest response by the dolphins. Fortunately, it was relatively rare that four or more additional vessels visited the dolphin group during a swim tour (19% of tours) under the current management regime. However, the fact that this high visitation rate already occurs with some regularity, and that dolphin groups responded by tightening, suggests that issuing additional dolphin watching permits would likely increase already high visitation rates and dolphin responses.

Recommendations and Summary of Findings

The changes in dolphin behaviour with number of approaches (particularly > 4) and number of vessels indicates the necessity of the three vessel rule and that it continue to be employed. In addition, a limit to the number of approaches (either per vessel or per tour) is recommended. Because the number of swimmers did not appear to influence behaviour of the large group (certainly not as much as number of vessels and approaches) it may make more sense to increase the number of swimmers per tour vessel (and per swim) while reducing the number of vessels and/or approaches per vessel. Increasing the number of permitted swimmers per vessel would decrease the number of vessels necessary to conduct a tour (e.g., the practice of sending out an additional vessel for a few additional swimmers, or conversely, increasing the number of approaches for a vessel with >16 swimmers). Additional permitted swim-with-dolphin tour operators would increase the number and rate of approaches and is not advisable. As a result of these findings, the number of approaches has been limited and the number of permitted swimmers per vessel has been increased (see below).

The duration of swims may be a good measure for assessing dolphin associations with swimmers and tours. This finding is supported by the reduction in swim duration with number of approaches, which corresponded to an increase in activity level of dolphin groups. Although activity level increased, social behaviour (considered a more active behaviour than milling) did not increase with approach number. This lack of increase in social behaviour, along with a reduction in swim duration, further supports the interpretation that increased number of approaches reduces dolphin associations with swimmers or swim tours, also indicated by the reduction in bow-riding behaviour with increasing approaches. Research on dusky dolphin interactions with tour vessels in Argentina found that dolphins reduced social behaviour in response to vessels (Dans et al. 2008, Markowitz et al. 2010b). The influence of prior group behavioural state and tour vessel approaches on dusky dolphin associations with swimmers suggests these interactions may be social in nature and disturbed by assertive tour vessel activity.

The low swim duration in summer, coinciding with the peak tourism season, indicates that dolphins are less associated with tours when tourism activity is highest. This is not what would be expected based on the general seasonal behavioural pattern of the dolphins, with groups generally less mobile (more likely to remain in a limited area) with more social behaviour in summer than in other seasons (Markowitz 2004, see Chapter 2). In the Bay of Islands, New Zealand, resident bottlenose dolphins showed long-term sensitisation to swim-with-dolphin tour activity, with avoidance increasing over time (Constantine 2001). Photo-identification data indicate dusky dolphins are seasonally resident in Kaikoura (Markowitz 2004), and lower swim durations in summer could indicate some level of sensitisation to seasonally high levels of vessel interaction.

Following submission of these research findings to the Department of Conservation, the Director-General of Conservation declared that no new dolphin viewing permits off the Kaikoura coast would be issued for a period of 5 years with the exceptions of kayaks and aircraft. Further, a preliminary view was issued to amend existing dolphin watching permits at Kaikoura to increase the maximum number of swimmers from 13 to 18 per vessel, limit the number of swim attempts per trip to a maximum of 4, extend and make mandatory the 11:30-13:30 midday rest period from October to March, and prohibit boats dropping swimmers off in the front of dolphin groups (Department of Conservation 2011). Based on the findings presented here, each of the proposed actions by the Director-General of Conservation will probably reduce the effect of swim-with-dolphin tourism on large dolphin groups off Kaikoura, New Zealand, and promote a sustainable dolphin tourism industry at Kaikoura.

CHAPTER 7

CONCLUSIONS

The social grouping patterns of dusky dolphins at Kaikoura conformed to socioecological models proposed for terrestrial species (Estes 1974) and for delphinids (Gowans et al. 2008). These models predict small-bodied species in closed habitats will show limited ranging patterns with small social groups. Large-bodied species in open habitats range more widely and form larger social groupings. Gowans et al. (2008) predict that delphinids generally follow the same pattern of small, less widely ranging species with few social partners in coastal habitats when compared with more neritic species. Dusky dolphins formed smaller groups with lower fission-fusion rates near shore, in shallower depths and closer to river mouths. This was particularly apparent during the reproductive season. Dolphins ranged more widely and further from shore in large groups, especially in winter, likely as a response to reduced prey availability. Although small groups also ranged in more open waters during winter, the consistent preference of these groups for near shore habitat when compared with large groups is likely an anti-predator strategy.

Increased resting behaviour and movement offshore in the afternoon for night-time foraging on DSL prey for large groups of dolphins is consistent with findings from other studies for dolphins at Kaikoura (Würsig 1997, Barr and Slooten 1998, Markowitz 2004, Dahood 2009). Small group behaviour varied primarily by season with small groups resting more in winter when compared with active mating and calf-rearing behaviour in summer. Noisy leaps were less prevalent in small groups which may reduce detection of these groups by predators or conspecifics. Small groups of dusky dolphins formed for mating and calf-rearing activities, but also as groups of adults and subadults that primarily rested. Dispersion was highest in non-mating adult groups. However, the frequency of social contact behaviour was similar to nursery groups. The formation of small groups of dolphins at Kaikoura may be an alternative strategy to associating in large groups, with trade-offs of reduced competition for mates, fewer interactions with aggressive conspecifics, and lower visibility to predators. Formation of small mixed-sex groups may allow individuals of similar age and size to synchronise their movement and behaviour patterns.

Rapid reproductive chases with decreased intromission rates as competition among group members increased substantiate the ‘mating of the quickest’ hypothesis for this polygynandrous species (Markowitz et al. 2010a). Females exercised mate choice by prolonging chases and using ‘escape’ strategies in the context of mating. As two males appeared to successively copulate for each chase sequence, coordination of males into alliances, as has been found for bottlenose dolphins (Connor 2000) is likely for dusky dolphins. Synchronous surfacing behaviour in these groups further substantiates this finding. Agonistic interactions among males, although not as prevalent as for bottlenose dolphins, included biting and ‘rolling over’ a copulating pair to interrupt copulation.

The mother-calf nursery is likely the core social unit for dusky dolphins with recent evidence for kin associations (Shelton et al. 2010) suggesting these social groups are matrilineal. These small groups had the lowest fission-fusion rates with individuals leaving and joining in the largest groups (6.5±2.7 individuals) and were found closest to shore and river mouths in shallow water. Nursery groups were also found closest to the canyon and evening foraging opportunities on the DSL. Affiliative interactions appear to be initiated primarily by mothers when calves are newborn, and by calves as they approach the age of weaning, but these indications from continuous focal mother-calf monitoring remain to be tested.

As socioecological models predict (Gowans et al. 2008), Hector's and dusky dolphins, although sympatric, appear to use different niches in the Kaikoura Canyon area. Resident Hector's dolphins, with detailed knowledge of prey availability and predator threats, use river mouths and habitats near shore to the north and south of the Kaikoura Canyon. The more widely-ranging and seasonally resident dusky dolphin capitalises on prey associated with the deep scattering layer, forming larger groups further from shore. Hector's dolphins were more active but engaged in less social behaviour than dusky dolphins, although surfacing was more synchronous for Hector's dolphins which may indicate foraging or solidifying social bonds in the context of competition.

Mean group sizes for Hector's dolphins were similar to subgroup sizes for dusky dolphins in small groups and the mean number of individuals that left and joined nursery groups during focal follows. This basic social unit size of approximately 6 individuals has been reported for other dolphin species (e.g., Risso's dolphin; Hartman et al. 2008, Spinner dolphin; Norris 1994a) and may be a trait conserved among delphinids. Behaviour of Hector's dolphins was more complex than dusky dolphins, which may facilitate information gathering and predator detection in small Hector's dolphin groups. The higher fission-fusion rates for Hector's dolphins also suggest more fluid grouping patterns and social bonds for this resident species as individuals compete for resources. These sympatric species avoid possible conflict with differences in fine-scale habitat selection and grouping patterns.

Short-term effects of tourism on large groups of dusky dolphins at Kaikoura included decreased resting behaviour. While such effects apparently have long-term implications for resident species (Bejder et al. 2006b, Lusseau and Bejder 2007), there are likely fewer long-term biologically significant impacts for large, seasonally migrating groups of dusky dolphins. Nevertheless, the identification of both critical habitat and times of day for resting, breeding or bonding is necessary for proper management of tourism interactions with social mammals (Bejder and Samuels 2003).

The duration of swimmer-dolphin associations may be a good measure for assessing dolphin responses to swimmers and tours. This finding is supported by the reduction in swim duration with number of vessel approaches, which corresponded to an increase in activity level but decrease in social behaviour of dolphins. The influence of behavioural state and approach methods on swimmer-dolphin interactions suggests they may be social in nature and disturbed by assertive tour vessel activity. Low swim durations in summer coincided with the peak tourism season and may indicate some level of sensitisation to seasonally high levels of vessel interaction. The proposed changes by the General-Director of Conservation to the management of dusky dolphin tourism at Kaikoura in response to these findings should promote a sustainable dolphin tourism industry in this unique canyon habitat.

Dusky dolphins are apparently abundant in New Zealand (Markowitz 2004). However, dusky dolphin populations in South America may be threatened by direct harvest for food and bait in Peru (Van Waerebeek 1992) and by high levels of by-catch in Argentina (Dans et al. 1997). The comparative investigation of social organization and behavioural ecology of dolphins at Kaikoura can inform management agencies as to the susceptibility of dusky and Hector's dolphin populations to potential anthropogenic impacts. Findings in this study regarding social grouping patterns and behaviour of dusky dolphins and sympatric Hector's dolphins support socioecological models proposed for dolphins. These large-brained, highly social mammals form intricate societies that are responsive to changes in habitat, predation pressure and resource distribution. Elucidating these responses at a time of rapid human social and environmental change is crucial for protection of these species and their societies.

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