

DUSKY DOLPHIN (*LAGENORHYNCHUS OBSCURUS*)
OCCURRENCE AND MOVEMENT PATTERNS
NEAR KAIKOURA, NEW ZEALAND

A Thesis

by

ADRIAN DANIELLE DAHOOD

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

May 2009

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Bernd Würsig
Committee Members,	Douglas C. Biggs
	Kirk O. Winemiller
Head of Department,	Thomas E. Lacher, Jr.

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ABSTRACT

Dusky Dolphin (*Lagenorhynchus obscurus*) Occurrence and Movement Patterns Near
Kaikoura, New Zealand. (May 2009)

Adrian Danielle Dahood, B.S.; B.S., University of Washington

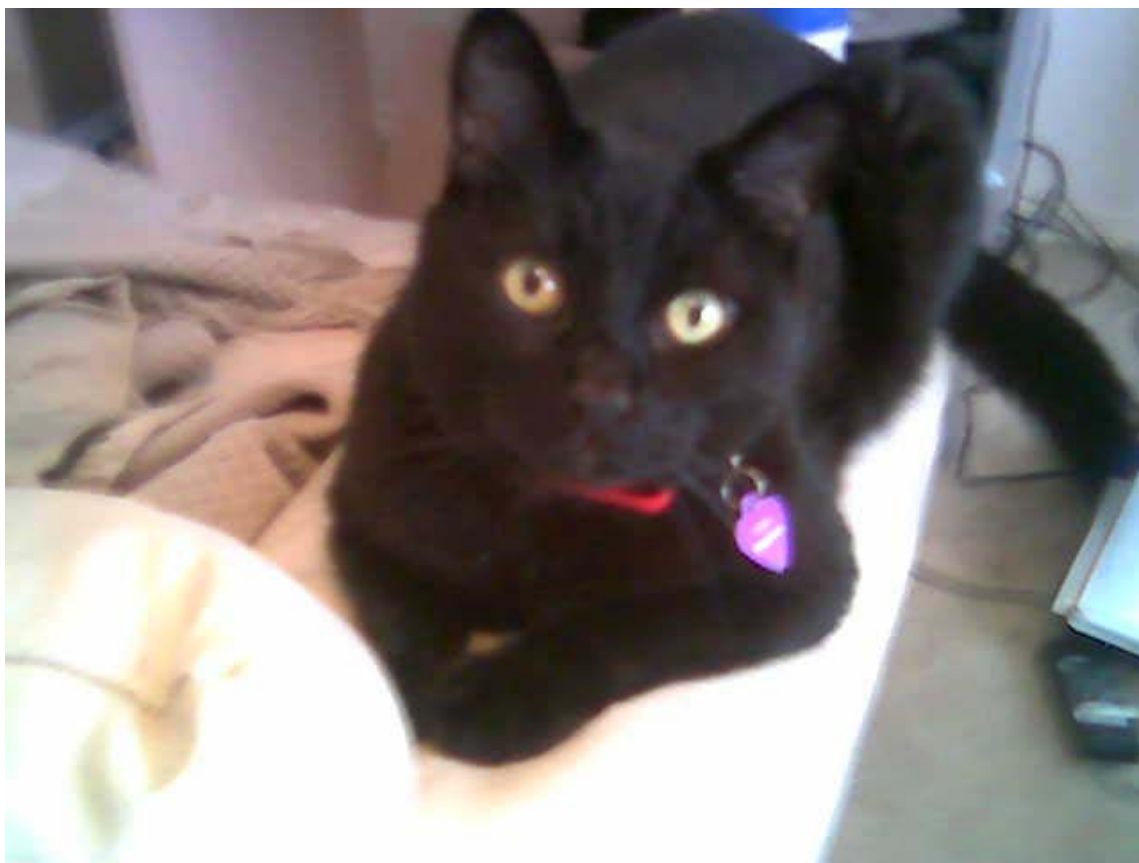
Chair of Advisory Committee: Dr. Bernd Würsig

In Kaikoura, New Zealand dusky dolphins (*Lagenorhynchus obscurus*) are economically and ecologically important. However, more information on key habitat requirements is needed to develop an effective management plan for them. I use systematic shore-based observations and tour operator gathered boat-based observations and review night-time foraging observations to explore dusky dolphin occurrence and movement patterns. I discuss possible influence of prey on these patterns. From January to December 2006, I conducted crepuscular observations from three cliff-top stations. With these geospatial data I examined occurrence, mean speed, and linearity over seasonal, diel, and tidal temporal scales. From October 1995 to November 2006 tour guides recorded GPS locations for over 5,000 dusky dolphin groups, allowing me to examine seasonal occurrence patterns. For both datasets I quantified occurrence patterns relative to depth, distance from the Kaikoura Canyon, and distance from shore. I reviewed the three studies conducted on dusky night foraging behavior in Kaikoura. I explore the effects of seasonal and lunar-scale changes in night-time light levels on dusky dolphin foraging behavior.

Duskies exhibited seasonal and diel, but not tidal occurrence and movement patterns. Dolphins were found farther offshore, in deeper water, and travelling faster in winter and approaching sunset. The areas of highest sightings density were associated with the Kaikoura Canyon, and shifted almost entirely into the canyon in winter and approaching sunset. Dolphins made sharper turns during summer. Dolphins were, on average, closer to the Kaikoura Canyon than to shore. Seasonal occurrence patterns described by tour operator data agreed with those described by geospatial data collected by shorebased observers. Duskies exhibited flexible foraging behavior and appeared to use both seasonal and lunar phase specific tactics. Night-time light levels appeared to influence dusky foraging behavior, possibly through changes in prey behavior. Prey availability and behavior patterns appeared to influence dusky occurrence and movement patterns. The dolphins' affinity for the Kaikoura Canyon may reflect a strategy to maximize access to prey.

DEDICATION

To Jake, and those who kissed his head while I was away working



July 31, 1998- July 14, 2008

ACKNOWLEDGEMENTS

Bernd and Melany Würsig provided advice and support throughout all stages of this project. Fieldwork in New Zealand would not have been possible without their local area knowledge and use of their research vehicles, equipment, and home, Muritai. I am particularly grateful to Bernd for editing draft after draft of my thesis and conference papers AND helping me to obtain funding for far flung conferences.

My committee members, Drs. Biggs and Winemiller, provided many helpful comments on my proposal and early drafts of this thesis. This thesis has improved greatly due to their efforts. Dr. Kelly Benoit-Bird patiently taught me what little I know about fisheries acoustics and was a tremendous help with Chapter IV.

Dennis Burman, Lynnette Burman, and Ian Bradshaw of Encounter Kaikoura provided in-field support, the dataset analyzed in Chapter III, and funding for conferences through the Encounter Kaikoura Research fund. Without their enthusiastic support, I would not have presented at CMT 2007 in Auckland, New Zealand or IWC 60 in Santiago, Chile.

The Trewin family graciously granted access to Haumuri Bluffs and a cabin to stay in while working there. The Prentice family kindly allowed me to park my truck on their lawn and drive through their farm to get to Haumuri Bluffs.

My “faithful field assistants”, Inna Annsman, Miriam Kunde, Danielle Greenhow, and Rónán Hickey, were invaluable in the field. I am grateful for their good humor, and excellent work ethic. Mridula Srivivasan, Emily Kane, Heidi Pearson, and

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No little paragraph could even begin to acknowledge and thank Andrew Fritz for his help. Andrew served as my very own IT department and got me through many “technical difficulties”. He wrote custom software to speed my data processing. Andrew was also an excellent cat-sitter, personal chef, and cheerleader. Without his help I would have taken another year to finish!

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CHAPTER I

INTRODUCTION

Dusky dolphins (*Lagenorhynchus obscurus*), or “duskies”, are small delphinids living along the continental shelf in the southern oceans. New Zealand dusky dolphin distribution is centered around 40°S to 45°S Latitude (Würsig *et al.* 1997) and seems closely tied to cool waters of the Subtropical Convergence (Gaskin 1968). Dusky distribution changes seasonally, but they are sighted near Kaikoura, New Zealand, year round (Würsig *et al.* 1997). There, duskies support a thriving dolphin watching industry (Barr and Slooten 1999, Duprey 2007, Würsig *et al.* 2007). As such, the ongoing status of the population is of concern to managers and dependent communities alike.

Successful conservation of a species relies on understanding how that species interacts with its environment and what factors affect those interactions (Karczmarski *et al.* 2000a), and more information on dusky key habitat requirements is needed to develop an effective management plan (Suisted and Neale 2004). Dolphin occurrence and movement patterns are frequently related to abiotic factors (Gaskin 1968, Neumann 2001, Bräger *et al.* 2003, Ballance *et al.* 2006, Redfern *et al.* 2006, Garaffo *et al.* 2007). Preferences for certain temperatures or depths may reflect the dolphins’ ability to detect and capture prey (Würsig and Würsig 1980, Harzen 1998, Neumann 2001) or avoid predators (Constantine *et al.* 1998, Heithaus and Dill 2006, Wirsing *et al.* 2008). Dusky dolphins near Kaikoura likely choose habitat to maximize access to prey while

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

minimizing vulnerability to predators and other disturbances. However, studies there have yet to systematically explore dusky habitat selection.

ABIOTIC FACTORS

Cetaceans appear to choose habitat at least in part based on bathymetry and distance from shore. On a large geographic scale, cetaceans in the northeast Pacific are strongly associated with continental shelf breaks and canyon systems (Yen *et al.* 2004). On a small scale, dolphins living in near-shore waters and shallow bays have distinct depth preferences. Bottlenose dolphins (*Tursiops truncatus*) in the Sado Estuary, Portugal (Harzen 1998) are more often found in water that is between 5-40 m deep. Water depth is important in predicting the presence of Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand, but preferences for deep and shallow waters can change by location (Bräger *et al.* 2003). Coastal dolphins are often associated with river mouths (Parra *et al.* 2006b) or show distinct onshore/offshore movement patterns (Norris and Dohl 1980). Cetaceans' depth and distance from shore preferences may change seasonally, perhaps more closely reflecting changing patterns of prey distribution rather than the dolphins' thermal needs (Wilson *et al.* 1997, Neumann 2001, Ballance *et al.* 2006, Redfern *et al.* 2006).

Recent studies of duskiies in Kaikoura have revealed correlations between habitat features and dolphin occurrence patterns. Duskiies most frequently occur near the head of the Kaikoura Canyon (Brown 2000) where they forage at night (Cipriano 1992, Benoit-Bird *et al.* 2004). They tend to move offshore into deeper waters in late afternoon and generally occur farther offshore in winter than summer (Cipriano 1992,

Markowitz 2004). The daily onshore/offshore movement pattern is often attributed to foraging in deep water at night (Cipriano 1992, Markowitz 2004). Seasonal onshore/offshore movement pattern may result from changing prey patterns (Cipriano 1992) or mothers with calves choosing shallow near-shore waters in summer (Weir *et al.* 2008). Chapters two and three describe seasonal dusky movement and occurrence patterns. Chapter two uses geospatial data gathered systematically from three shore-based observation stations for one year to explore how abiotic factors such as depth, distance from shore, and season influence occurrence and small scale movement patterns. Chapter three examines occurrence patterns described in a 12 year data set gathered by a tour operator.

PREY

The daily and seasonal occurrence patterns exhibited by dolphins may be strongly influenced by patterns of prey availability (Maze and Würsig 1999, Neumann 2001, Hastie *et al.* 2005, Ballance *et al.* 2006, Redfern *et al.* 2006). Feeding strategies, and the tactics dolphins use to capture prey, influence how dolphins use the water column. Because dolphins often feed on mobile fish that are largely invisible to surface observers, it is difficult to test prey influence directly (Wirsing *et al.* 2008), and even more difficult when dolphins forage in the dark.

In Kaikoura, duskies primarily feed at night on lanternfishes (family Myctophidae) and arrow squids (*Nototodarus spp.* and *Todaroides spp.*) that are part of the nocturnally rising deep scattering layer (DSL) (Cipriano 1992, Benoit-Bird *et al.* 2004). The DSL is a community of fish and invertebrates that rise towards the surface

each night; the organisms occur in sufficient density to scatter sounds wave and create the illusion of bottom for early depth sounding devices(Cushing 1973). Because of this density, the DSL serves as a food source for many marine predators (Cushing 1973).

An indirect way to examine duskies' interactions with their prey is through gut content analyses. Studies of stranded and incidentally caught duskies near Kaikoura indicate that summer diet is dominated by myctophids, while in winter, arrow squids and hoki (*Macruronus novaezelandiae*) gain importance (Cipriano 1992). In Golfo San Jorge Patagonia, Argentina, where duskies feed primarily on the non-migrating Patagonian stock of the Argentine anchovy (*Engraulis anchoita*) and squids, diet composition is stable year round (Alonso *et al.* 1998). This contrast indicates that duskies in Kaikoura may experience seasonal patterns of prey availability that influence their foraging tactics. Support for this possibility comes from studies of demersal fish communities in nearby Pegasus Bay and Canterbury Bight, roughly 150 km southwest of Kaikoura, which found that many species,including the arrow squid (*Nototodarus sloanii*), an important winter prey item for duskies, shift offshore into deeper waters in winter (Beentjes *et al.* 2002).

With the advent of active acoustic techniques it is now possible to simultaneously track dolphins and their prey (Benoit-Bird *et al.* in press), though it is still difficult to differentiate suitable prey items from other organisms in a sound scattering layer. One major advantage of active acoustic techniques is that the accuracy of observations is not affected by light levels, making this a useful tool for studying dolphin night-time foraging (Benoit-Bird *et al.* in press). Acoustic surveys conducted in

Kaikoura, New Zealand during the austral winter of 2002 illustrated that after the DSL moved into the upper 130 m of the water column, dusky dolphin dive depth was strongly correlated with DSL depth (Benoit-Bird *et al.* 2004). Dusky dolphins typically dove on the DSL in coordinated subgroups of 2-5 , and tracked the DSL such that dolphins were 1 m deeper than the shallowest part of the layer (Benoit-Bird *et al.* 2004). Because of seasonal diet changes and seasonal movement patterns exhibited by nearby demersal fish communities, it is suspected that summer foraging tactics are different from winter tactics.

Systematic night-time acoustic surveys were conducted in Kaikoura in austral summer/early fall of 2006. Chapter four discusses night-time foraging behavior, by comparing and contrasting findings of Cipriano's (1992) radio tracking work, and the winter 2002 (Benoit-Bird *et al.* 2004) and summer 2006 (Benoit-Bird *et al.* in press) acoustic surveys.

OBJECTIVES

The purpose of this project is to use three very different datasets to examine dusky dolphin movement and long-term occurrence patterns near Kaikoura, including less frequently studied southern areas, and to ascertain what factors are most important in determining these patterns. The first dataset represents a systematic effort to gather dolphin sightings from cliff-top stations throughout 2006. The second dataset represents dolphin sighting information gathered on dolphin tour boats during 1995-2006. For these two datasets I will (1) identify the regions within the study area that are most important to dusky dolphins based on density of sightings; (2) investigate the effects of

bathymetry, distance from shore, and sea surface temperature in influencing occurrence patterns; and (3) compare these patterns across tidal states, time of day, seasons, and years (for the tour operator's data). The third dataset describes systematic night-time acoustic surveys. For this dataset I will discuss dusky night-time foraging behavior and how it compares to other night foragers.

CHAPTER II
DUSKY DOLPHIN OCCURRENCE AND MOVEMENT PATTERNS ACROSS
SEASONAL, DIEL AND TIDAL SCALES

INTRODUCTION

Animals may respond to their environments by preferentially using certain regions within their range. These favored regions may represent areas of high food availability, provide shelter from predation or anthropogenic disturbances, or have other desirable traits. Typically, researchers examine marine animal habitat use patterns in relation to abiotic factors such as bottom depth, sea surface temperature, and distance from shore. These factors may directly influence habitat selection or, more likely, serve as a proxy for prey availability measures (reviewed in Ballance *et al.* 2006 and, Redfern *et al.* 2006). Successful management and conservation efforts rely upon understanding how animals chose habitat (Karczmarski *et al.* 2000a).

Dusky dolphins near Kaikoura, New Zealand, live in a complex, dynamic coastal area. The Kaikoura Canyon is the dominant bathymetric feature in the region. The canyon cuts deeply into the continental shelf at the 18 m depth contour. Near the canyon head, the seafloor depth can drop as much as 600 m over 1 km (Lewis and Barnes 1999). The topography of canyon systems creates complex currents that often interact to result in nearby prey aggregations (Genin 2004). In Kaikoura, duskie feed at night on such an aggregation, the nocturnally rising Deep Scattering Layer (DSL), a community of fish and invertebrates that occur in sufficiently high density to create the illusion of bottom

for early depth sounding devices (Cushing 1973). To understand how prey might influence habitat selection, it is important to study dusky occurrence and movement patterns during crepuscular periods, as they prepare to feed and finish feeding. Like all coastal environments, the area is affected by regular changes in sea surface temperature, currents and tides.

Bathymetry

Cetacean patterns of distribution and abundance are often significantly correlated with the underlying bathymetry (Reviewed in Ballance *et al.* 2006, Redfern *et al.* 2006). Cetaceans may concentrate near continental shelf breaks or submarine canyons (Yen *et al.* 2004). Dusky dolphins may be attracted to the Kaikoura area by the extensive and productive Kaikoura Canyon system (Lewis and Barnes 1999).

Cetacean movement and activity patterns also may be influenced by depth. Dolphins may choose specific depths to increase foraging efficiency (Harzen 1998, Karczmarski *et al.* 2000a, Bräger *et al.* 2003). Humpback dolphins (*Sousa chinensis*) in Algoa Bay, South Africa, are most often sighted near shallow-water rocky reefs where they have high feeding success (Karczmarski *et al.* 2000a). Bottlenose dolphins living in the Sado River estuary, Portugal, are most commonly found in water that is between 5-20 m deep where they are more likely to encounter and capture prey (Harzen 1998). Some species, such as the nocturnally foraging Hawaiian spinner dolphin (*Stenella longirostris*) show marked diel patterns in depth preference, resting in shallow waters during the day when prey are inaccessible, and moving into deep water each night as their prey rise to the surface (Norris and Dohl 1980). Dusky dolphins living near Kaikoura

might exhibit seasonal, diel, or tidal depth preferences in relation to patterns of prey availability.

Distance from Shore

For many coastal cetacean species, distance from shore is nearly as important as depth in determining habitat use patterns (Karczmarski *et al.* 2000a, Bräger *et al.* 2003, Parra *et al.* 2006b). This may be because depth and distance from shore are typically closely related. Some cetaceans show preferences for near-shore waters because their prey base is dependent on river mouths or other coastal features (Karczmarski *et al.* 2000a, Bräger *et al.* 2003, Parra *et al.* 2006b). Other species appear to require sheltered near-shore waters to raise calves (Weir *et al.* 2008) or rest and reduce predation risk (Norris and Dohl 1980). Duskie may exhibit seasonal, diel, or tidal preferences for distance from shore based on the movement of prey, predation pressure, and the needs of calves.

Scales

Prey availability patterns may change across several temporal scales, and may result in varied cetacean habitat use patterns. Influences on cetacean occurrence and activity patterns are commonly examined across seasonal (e.g., Cipriano 1992, Nichol and Shackleton 1996, Ballance *et al.* 2006), diel (e.g., Bräger 1993, Harzen 1998), and tidal (e.g., Hanson and Defran 1993, Harzen 1998, Gregory and Rowden 2001, Ribeiro *et al.* 2007) scales.

OBJECTIVES AND HYPOTHESES

The objective of this chapter is to use systematic observations to examine dusky dolphin occurrence and movement patterns in relation to bathymetry and distance from shore. Further, I determine if there are trends across seasonal, diel and tidal temporal scales. To better capture potential effects of prey on habitat patterns, I use crepuscular observations, near sunrise and sunset, when dolphins are preparing for and finishing nightly foraging. I hypothesize that there are no differences in dolphin occurrence by 1) depth of water, 2) distance from shore, and 3) distance to the canyon for the three temporal scales. Additionally, the areas of highest sightings density are constant across seasons and time of day. I hypothesize that there are no differences in dolphin swim speed or linearity 1) across seasons, 2) between sunrise and sunset and, 3) across tidal states. I discuss the potential influence of prey on these patterns.

METHODS

Study Area

The study area (Fig. 1) encompasses approximately 30 km of coast stretching from the Kaikoura Peninsula (42.417 °S, 173. 700°E) south to 10 km past Haumuri Bluffs (42.567 °S, 173. 517°E). The Kaikoura Canyon head comes within 500 m of shore near Goose Bay (Lewis and Barnes 1999), in the central portion of the study area. The canyon cuts deeply into the continental shelf at the 18-m depth contour (Lewis and Barnes 1999). The South Bay harbor, where numerous commercial and recreational boats dock, is on the south side of the Kaikoura Peninsula

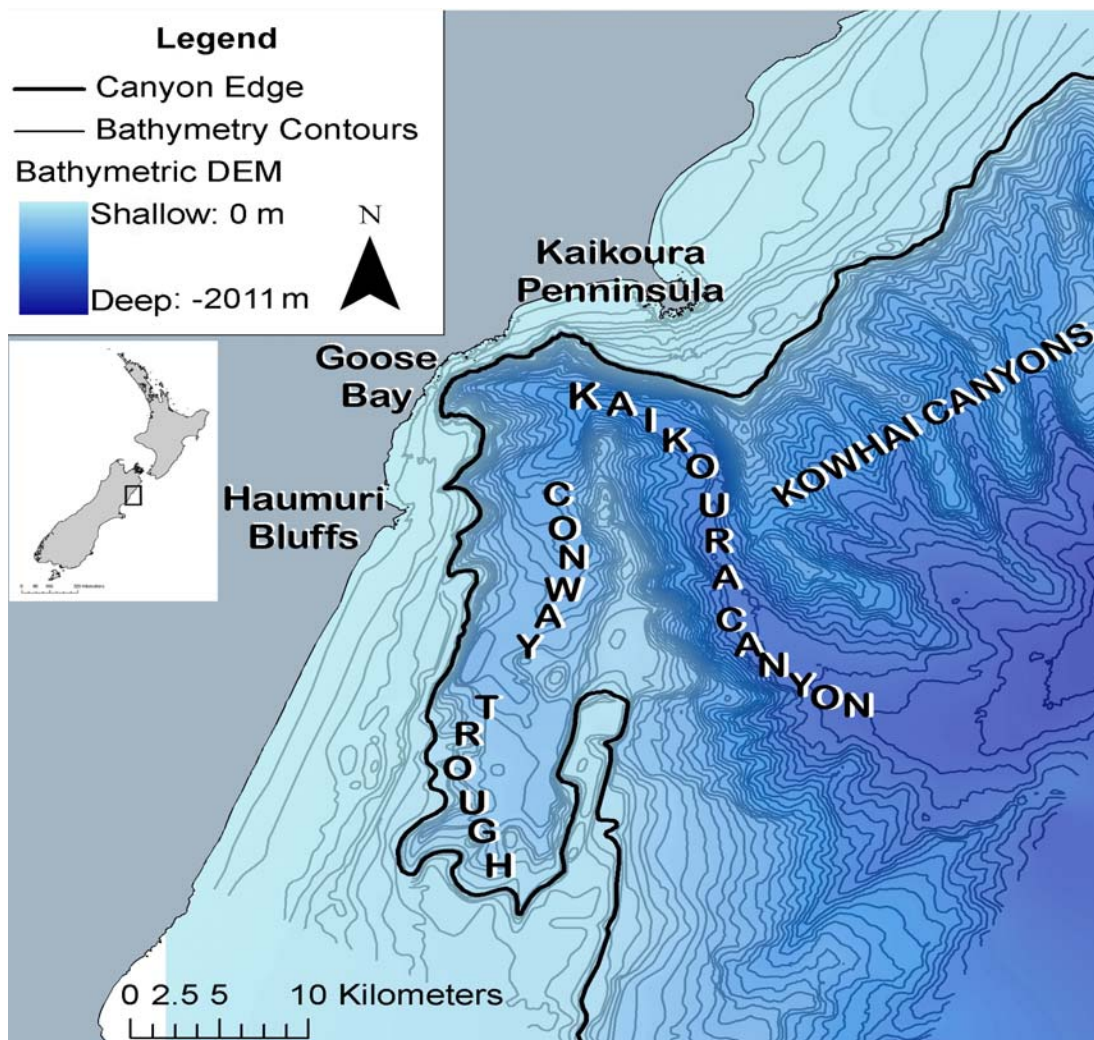


Figure. 1. Theodolite Study Area. Kaikoura is located on the north east corner of the South Island of New Zealand. The study area extends from 10 km north of the Kaikoura Peninsula to 10km south of Haumuri Bluffs. Theodolite stations were located on the Kaikoura Peninsula, above Goose Bay, and atop Haumuri Bluffs. The Kaikoura Canyon system, which includes the Conway Trough and the Kowhai Canyons, comes within 500 m of shore near Goose Bay. The bathymetric digital elevation model (DEM) displays depth as a continuous color gradient. Bathymetric data were provided by New Zealand's Institute of Water and Atmospheric Sciences (NIWA) and are discussed in detail in Lewis and Barnes (1999).

Theodolite Stations

I tracked large groups (>150 duskies) from three cliff-top stations using a Sokkia DT5 digital theodolite slaved to a laptop (Dell Inspiron 1100 or Dell Inspiron 8000). For each “fix”, or recording of dolphin position, the program *Pythagoras* (Gailey and Ortega-Oritz 2000) converted the theodolite’s vertical and horizontal angle measurements into geographic locations in real time.

I chose three elevated theodolite stations to ensure that all regions of the study area were visible from at least one station. The northernmost station, Peninsula Station, was near the meteorological station on the Kaikoura Peninsula (elevation 108.7 m; 42.417 °S, 173.700°E; reference azimuth 301.88°). The central station, Ota Matu, approximately 15 km south of the peninsula and overlooking Goose Bay (elevation 74.2 m; 42.4839 °S, 173.5282° E; reference azimuth 9.6°), has been used for theodolite work since 1984 (Cipriano 1992, Barr and Slooten 1999, Yin 1999, Brown 2000). The southernmost station, Haumuri, was on top of Haumuri Bluffs (elevation 152.3 m; Latitude 42.567 °S, Longitude 173.517°E; reference azimuth 351.61°).

I measured the height of all three stations with the help of published survey information and basic surveying techniques. I could not directly assess the error in my station height calculation, but at both Peninsula Station and Ota Matu Station I compared the accuracy of my position estimation calculations to GPS device position estimates (Peninsula n=3 and mean difference = 12m; Ota Matu n=3 mean difference = 9m).

Theodolite Tracking

I conducted observations during the 2.5 h following first light (sunrise sessions) and the 2.5 h leading up to last light (sunset sessions), on each possible weather-determined day. The stations were rotated such that I completed a sunset and following sunrise observation at the same station, then moved one station to the south.

Sea conditions of Beaufort three or higher, fog, rain, or winds in excess of approximately 15 km/h at the station were all considered unworkable. Whenever an entire day was unworkable, the rotation paused; if only half the day was unworkable, I continued with the rotation as if both halves had been workable. Excessive rain made the Haumuri Bluffs station unworkable for four to seven days after the rain stopped. This station was sometimes skipped in the rotation and is under-represented in the dataset.

I completed a scan of the study area before starting observations and after 2.5 h of tracking, or searching for, the large group. I randomized the starting point of the scan using the first boat, of any type, my assistant saw when we arrived on site. Boats were readily visible, even without binoculars and could therefore serve as a marker. I recorded all dolphin groups, regardless of size, within 10 km of the station. After completing the scan, I began tracking the first large group (> 150 duskie) encountered during the scan. I continued to track this group until it divided into two or more groups, or was no longer visible. If no large groups were encountered, my assistant and I searched continuously using binoculars (7x 35 and 10x40), for up to 2.5 h. A group was defined according to the 10 meter chain rule (Mann 1999): all individuals were within

approximately 10 m of at least one other individual in the group. This was typically manifest as an “unbroken and tight perimeter” encompassing all animals in the group (Würsig *et al.* 1989). I attempted to fix the center of the group and record group size every 90-120 s.

Analyses

Data were grouped by season, time of day, and tidal state. I defined winter as June 1- August 31, spring as September 1- November 30, summer as December 1- February 29 and fall as March 1- May 31. Sessions were designated as either sunrise or sunset. I used the “Tidal State” tool in *Theo Calc*, a suite of accessory calculations for theodolite data (Fritz Pers comm¹), to determine the tidal state when each fix was taken. The “Tidal State” tool determines rate of change (dh/dt) between successive tide heights on a smoothed sine wave of observed tide heights. I defined Ebb tide as $dh/dt < -0.0068$ m/s, flood tide as $dh/dt > 0.0068$ m/s, high tide as $-0.0068 \text{ m/s} < dh/dt < -0.0068 \text{ m/s}$ and the second derivative, or rate of change of the rate of change in tide height, was negative, and low tide as $-0.0068 \text{ m/s} < dh/dt < -0.0068 \text{ m/s}$ and the second derivative was positive; this divided the tidal cycles into 4 approximately equal phases of 190 min. I applied the “Tidal State” tool to a tide height data series gathered by New Zealand’s Institute of Water and Atmospheric Research (NIWA) Kaikoura monitoring station in 2 min intervals, for the entire study period; there was a data gap from March 20-March 30, 2006.

¹ Fritz, A., 1702 Cedar Dr., Richmond TX, Nov 2008, Theo Calc, custom designed software

Environmental Data

To test the effects of the environmental variables depth, distance from shore, and distance from the canyon, I used a suite of mapping tools to estimate and associate these variables with each fix. The Topogrid command in ArcInfo was applied to bathymetry lines, developed by Lewis and Barnes (1999) with an accuracy of ± 2 m and distributed by NIWA, to create a continuous model of depth at 30 m resolution. I used the “Intersect Points” tool in Hawth’s Tools (Beyer 2004) to associate each fix with its estimated underlying depth. I used the “Distance to Feature” tool in Theo Calc (Fritz 2008, Pers. comm².) to calculate the straight-line distance from each point to the nearest point of the shoreline (file of New Zealand coast courtesy of Eagle Technology, Wellington New Zealand) and Kaikoura Canyon edge. The 150 m isobath, the average depth of the continental shelf break (Garrison 1999), represented the canyon edge; when calculating distance to the canyon, all occurrences in waters deeper than 150 m were assigned a zero distance. The “Distance to Feature” tool uses a haversine function, which experiences relatively little rounding error at small distances, to calculate the angular displacement between the fix and all points in the feature (Sinnott 1984). The angular displacement is then multiplied by the number of meters per degree based on the radius of the earth (6.371×10^6 m) to determine the straight-line distance between each fix and all points of the feature (Gailey and Ortega-Ortiz 2000). The “Distance to Feature” tool recorded the smallest value.

² Fritz, A., 1702 Cedar Dr., Richmond, TX November , 2008, Theo Calc, custom designed software

First Sighting Properties

I investigated if there were significant seasonal, diel, or tidal state differences in occurrence patterns in relation to depth, distance from canyon, and distance from shore. To ensure independence, I used only the first sighting (first fix) for each large group. To increase accuracy, I excluded all first sightings greater than 10 km distant from the theodolite or taken during times that tide height data were absent.

I used the non-parametric Kruskal-Wallis test to compare the distributions because the data did not conform to a normal distribution for any of the tested variables. Seasonal sample sizes were approximately even. Tide state samples were biased toward flood tide. Diel samples were biased toward sunrise sessions due to frequent deterioration of afternoon weather (Table 1).

Table 1. Sample Sizes for First Sightings. Sample size is listed for each parameter used in determining mean depth, mean distance to canyon, and mean distance to shore.

Season	n	Session	n	Tide	n
Winter	28	Sunrise	82	Flood	35
Spring	28	Sunset	27	High	26
Summer	22			Ebb	16
Fall	31			Low	27

To examine potential effect of unequal diel and tidal state sample size, I used all sightings from the category with the smallest sample size and created three random subsets of equal sample size from the other categories. I calculated means and tested the three subsets as well as the full datasets. Means and Kruskal-Wallis results were similar

for the random sets and the full data sets; only results for the full data set are presented in 'Results'.

Kernel Home Range Analysis

I determined the parts of the study area where dolphins were most often seen by using sighting data gathered during each scan, with up to four scans recorded per day. I weighted sightings based on group size and search effort in the area. I assigned all areas within a 10-km radius of the station the amount of time I spent during the scans. Areas that were within 10 km of two stations were assigned the effort from both stations. I used the kernel density estimator in Hawth's Tools (Beyer 2004), which allows each observation to be assigned a weight, to create Kernel Home Range (KHR) maps for all dolphin sightings. Kernel methods do not have distributional assumptions, and can produce good estimates of home range when greater than 30 observations are used (Seaman *et al.* 1999). I used the default settings of bivariate normal kernel, smoothing factor (h) of 1000, and cell size 100. I then created KHR's for each season (winter= 51; spring = 389; summer= 47; fall= 109) and for sunrise (n= 517) and sunset (n= 79) sessions. I also generated 95% and 50% volume contours. KHR analysis is sensitive to sample size, making it difficult to compare KHR size between datasets with highly unequal sample sizes. Therefore, I compared locations of regions with highest density of sightings, rather than focusing on size of the KHR's.

Trackline Data

I tested for statistically significant effects of season, time of day, and tidal state on the speed and linearity of large groups. I measured linearity as absolute change in bearing between fixes. All trackline analyses assume straight-line travel between fixes. Following Yin (1999), I reduced error associated with this assumption by applying a conservative critical time interval of 120 s. Further, I analyzed only segments of tracks with a minimum of six consecutive fixes taken no more than 120 s apart. This restricted analyses to only those segments where I had high confidence in each fix.

Speed and linearity are measures of change and can not be determined from individual fixes. Within the high confidence segments, I created chains of three fixes, naming the central fix the “vertex”. I could then measure speed between each of the three fixes and the change in bearing required to move from the first fix to the third. For all described analyses, I randomly selected 10 vertices from high confidence segments. I calculated the speed across each vertex and the absolute change in bearing at each vertex. I used the mean value for each parameter to represent the track. By randomly selecting vertices instead of using continuous segments of the same length, I represent a larger portion of the total track length without giving extra weight to longer tracks. Because the data did not conform to a normal distribution, I used the non-parametric Kruskal-Wallis test to compare distributions.

I investigated the presence of tour boats with a group as a possible confounding factor. I selected 16 tracklines for which I had recorded the presence and/or absence of tour boats. Six of those tracks had segments in both boat states, and were divided into

subtracks. Similar to Yin's (1999) observations, mean speed when unaccompanied (1.88 m/s; $n=11$, $s = 0.82$) was faster than when the dolphins were accompanied by at least one tour boat (1.59 m/s; $n=11$, $s = 0.61$), but this difference was not statistically significant (Kruskal-Wallis: $\chi^2=0.786$, $p=0.375$, $df=1$). Mean change in bearing when unaccompanied (26.7° ; $n=11$, $s = 11.4^\circ$) and accompanied by at least one tour boat (38.8° ; $n=11$, $s = 19.6^\circ$) was not significantly different (Kruskal-Wallis: $\chi^2=2.804$, $p=0.094$, $df=1$). To reduce the effects of other confounding variables, I analyzed a subset of the data gathered only during January mornings when dolphins were in shallow waters, and obtained a similar result for both mean speed ($n=10$, $\chi^2=0.884$, $p=0.347$, $df=1$) and mean change in bearing ($n=10$, $\chi^2=2.455$, $p=0.117$, $df=1$). Therefore, the presence or absence of boats is not considered a significant factor in the following analyses. However, this study was not designed to investigate the effects of tour boats, and the methods may not have been able to capture such effects.

To investigate underlying depth as a possible confounding factor in determining seasonal, diel, and tidal movement patterns, I split the tracklines by depth. Segments that occurred in shallow waters (< 150 m) were separated from segments that occurred in deep canyon waters (≥ 150 m), resulting in 63 subtracks from 54 unique groups. Dolphins swam slightly faster when they were over deep canyon waters (2.37 m/s $n= 25$) than when they were in shallower water (2.03 m/s, $n= 39$). However, this difference was not significant (Kruskal-Wallis $\chi^2=2.842$, $p=0.092$, $df=1$). Dolphins made significantly (Kruskal-Wallis $\chi^2=6.538$, $p=0.011$, $df=1$) sharper turns when they were in canyon waters (54.3° , $n=25$) than when in shallower waters (37.8° , $n=39$). Therefore, underlying

depth was considered to confound linearity observations but not mean speed observations.

To examine patterns in mean speed, I analyzed all data together, regardless of underlying depth. To examine patterns in linearity, I performed separate analyses in deep and shallow water for each variable. I was able to examine seasonal and tidal linearity patterns in shallow water and diel linearity patterns in deep water. Low sample sizes prevented other comparisons (Table 2).

Table 2. Sample Sizes for Movement Analyses. Because depth influenced mean change in bearing, data were split by depth before examining linearity in each category. Due to small sample size, only groups denoted by * were used in the final analysis.

	Speed n	Linearity	
		Shallow n	Deep n
Season	*	*	
Winter	22	8	15
Spring	11	6	5
Summer	8	6	2
Fall	20	19	3
Session	*		*
Sunrise	44	37	12
Sunset	17	2	13
Tide	*	*	
Flood	17	11	6
High	18	8	8
Ebb	7	8	1
Low	19	12	10

Sample sizes were not equal across categories in each parameter. I examined the possible effects of unequal sample size, by creating three random sets where each category was equally represented for each parameter. For all three parameters, means

and Kruskal-Wallis results were similar for the random sets and the full data set; only results for the full data set will be presented in ‘Results’.

Effort

I completed a pilot study from January 5th to January 25th, 2006, working only from Ota Matu Station. I spent approximately 60 hours familiarizing myself with the study area and study methods. At the end of this period, both Ota Matu Station and Peninsula Station were established. I was unable to access Haumuri Station until March, 2006.

From January 26 to December 5, 2006, I completed 188 full, two scans and 2.5h tracking period; or partial, 1 scan and at least 1-h tracking period, observation sessions on 143 separate days. I visited Peninsula Station 80 times (53 sunrise and 27 sunset), Ota Matu Station 82 times (49 sunrise and 33 sunset), and Haumuri Station 35 times (17 sunrise and 18 sunset). I spent 426.8 h tracking or searching with binoculars for large groups and 116.5 h scanning for small groups and boats. I observed 141 large groups and 649 small groups.

RESULTS

First Sightings Properties

Dolphins exhibited seasonal patterns in terms of all three tested abiotic variables (Fig. 2). Mean depth was deepest during winter (491 m) and spring (307 m, n=28), and shallowest during summer (244 m; n=22) and fall (138 m; n=31). Average distance to the canyon was greatest during fall (1.15 km) and summer (0.88 km), and smallest

during winter (0.15 km) and spring (0.15 km). Average distance to shore was greatest for winter (4.82 km) and spring (3.25 km), and shortest for fall (1.94 km) and summer (2.31 km). Kruskal-Wallis tests confirmed that seasonal occurrences differed significantly in terms of depth ($\chi^2=28.987$, $p<0.001$, $df=3$), distance to canyon ($\chi^2=31.267$, $p<0.001$, $df=3$), and distance to shore ($\chi^2=33.286$, $p<0.001$, $df=3$).

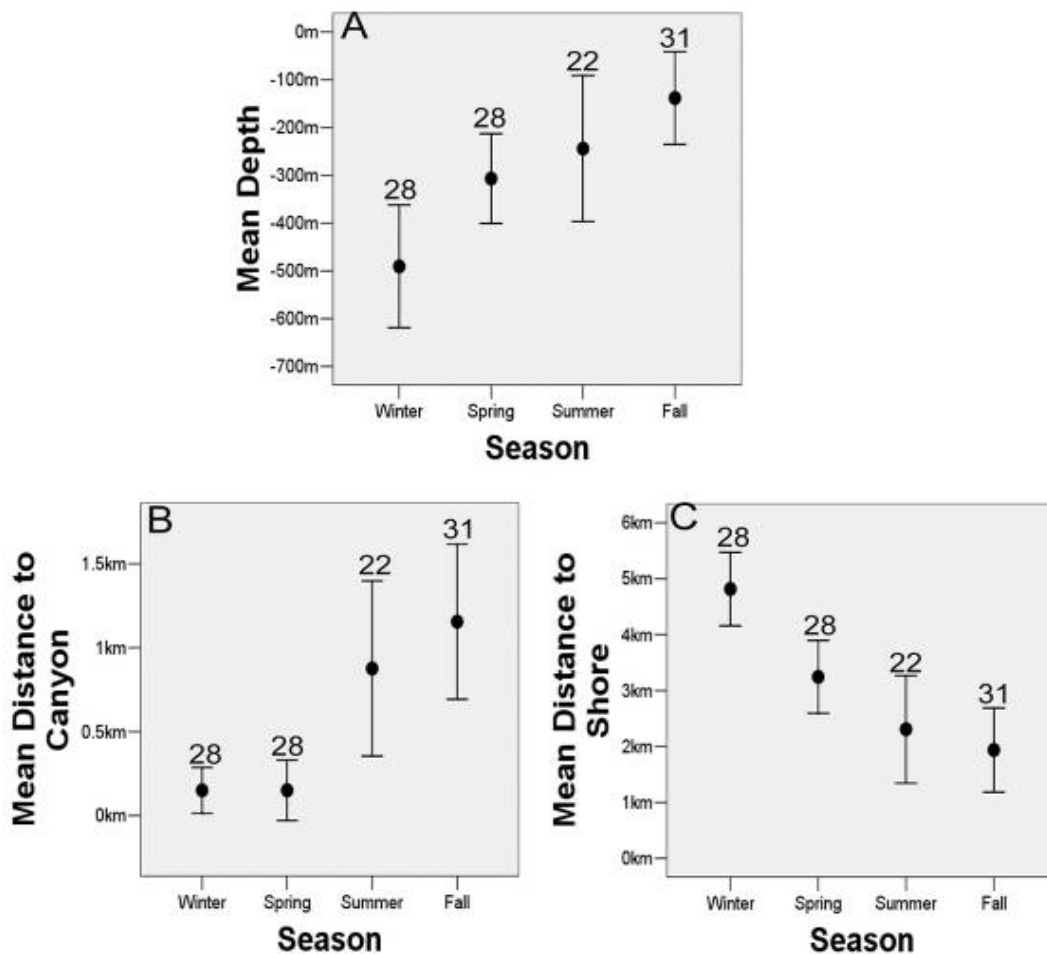


Figure 2. Effect of Season on Depth (A), Distance to Canyon (B) and Distance to Shore (C). Seasonal means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Seasonal dolphin occurrence patterns differed significantly in terms of all three variables.

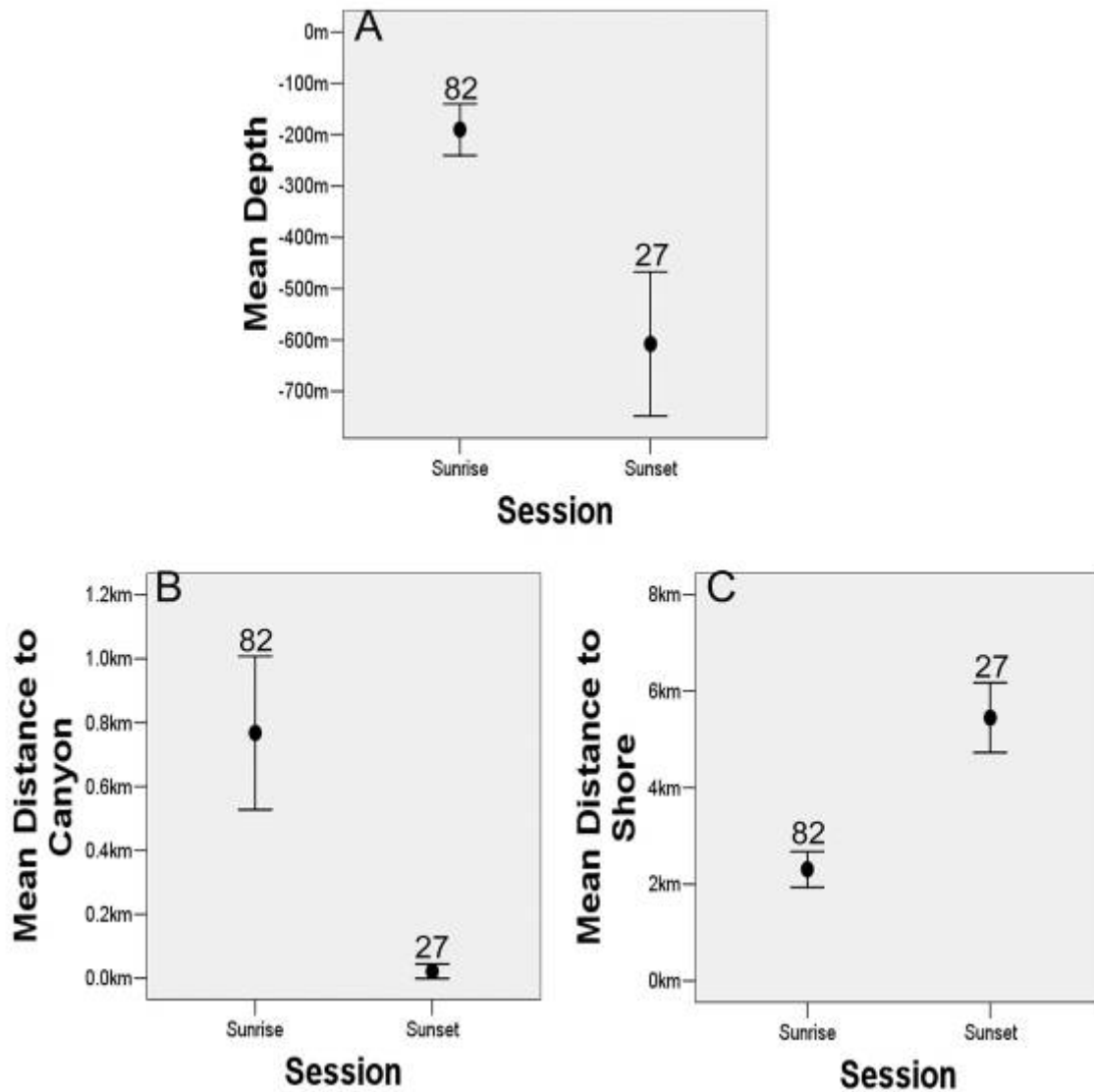


Figure 3. Effect of Diel Period on Depth (A), Distance to Canyon (B) and Distance to Shore (C). Means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Diel dolphin occurrence patterns differed significantly in terms of all three variables.

Dolphins exhibited obvious diel patterns in terms of the three tested variables

(Fig. 3). Mean depth was deeper approaching sunset (608 m) than near sunrise (190 m).

Dolphins were, on average, closer to the canyon approaching sunset (0.02 km) than near sunrise (0.77 km), and farther from shore approaching sunset (5.45 km) than near sunrise (2.31 km). Kruskal-Wallis tests confirmed that diel occurrence patterns differed significantly in terms of depth ($\chi^2=29.671$, $p<0.001$, $df=1$), distance to canyon ($\chi^2=19.275$, $p<0.001$, $df=1$), and distance to shore ($\chi^2=36.612$, $p<0.001$, $df=1$).

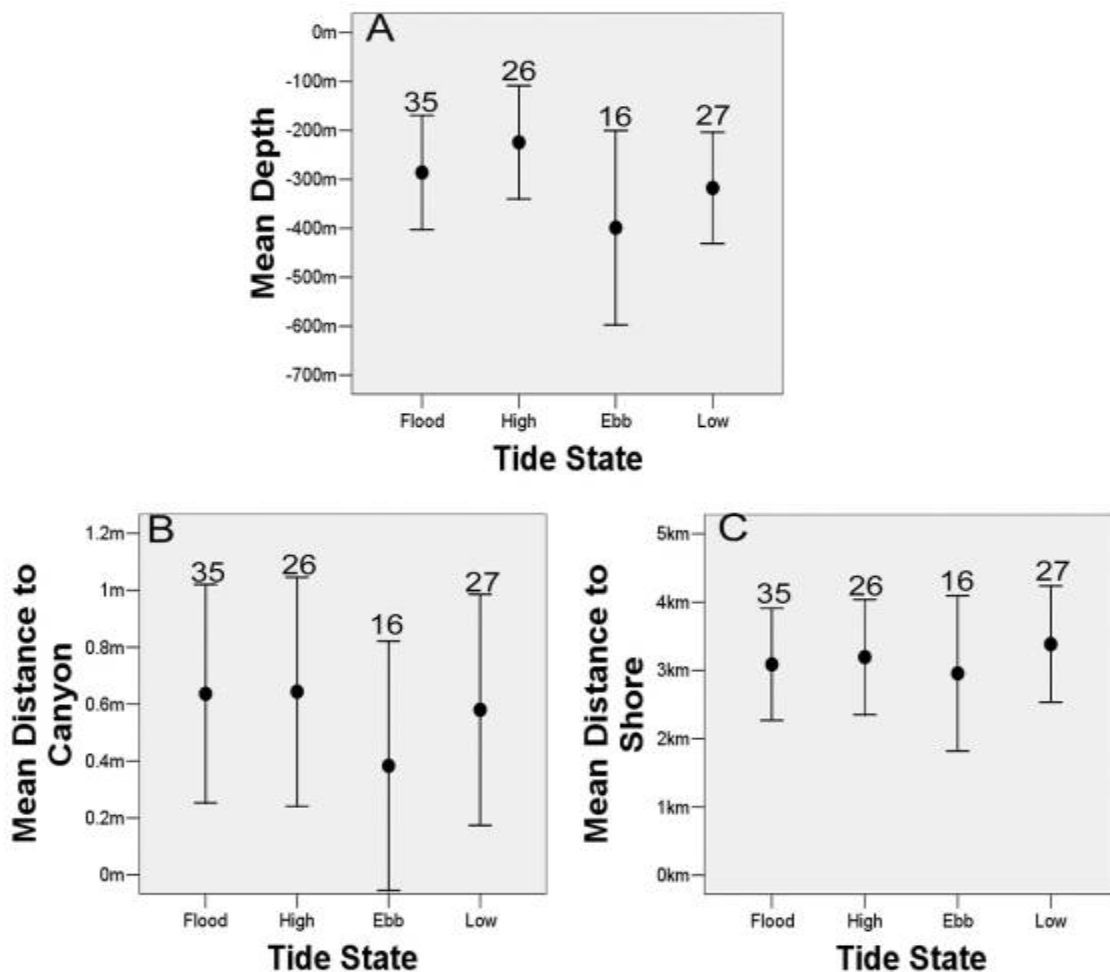


Figure 4. Effect of Tide on Depth (A), Distance to Canyon (B) and Distance to Shore (C). Means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Dolphin occurrence patterns did not differ significantly by tide state in terms of any of the three variables.

Dolphins exhibited seasonal and diel, but not tidal state occurrence patterns; dolphins were, on average, closer to the canyon than shore and in deeper water every season and each night (Fig 4). Kruskal-Wallis tests confirmed that tidal state occurrence patterns did not differ significantly in terms of depth ($\chi^2=2.522$, $p= 0.466$, $df=3$), distance to canyon ($\chi^2=1.701$, $p= 0.637$, $df=3$), and distance to shore ($\chi^2=0.663$, $p= 0.882$, $df=3$)

Kernel Home Range Analysis

Dolphins revealed seasonal (Fig. 5) patterns in the location of areas of highest sightings density. The summer and fall 95% volume contours, which encircle areas containing 95% of the sightings, included a large proportion of shallow near-shore waters. The 50% volume contours, or core areas, included almost equal proportions of shallow and canyon waters. In winter, the 95% volume contour included very little near-shore water and the core areas were almost entirely in canyon waters. The spring KHR was intermediate between summer and winter both in terms of the amount of near-shore water contained in the 95% volume contour and the location of the core areas.

Dolphins exhibited diel differences in location of KHR's (Fig. 6). The 95% volume contour for sunrise followed the coast line, and core areas included a significant portion of shallow waters. Near sunset, the 95% volume contour was located farther offshore, and core areas were located almost entirely in canyon waters.

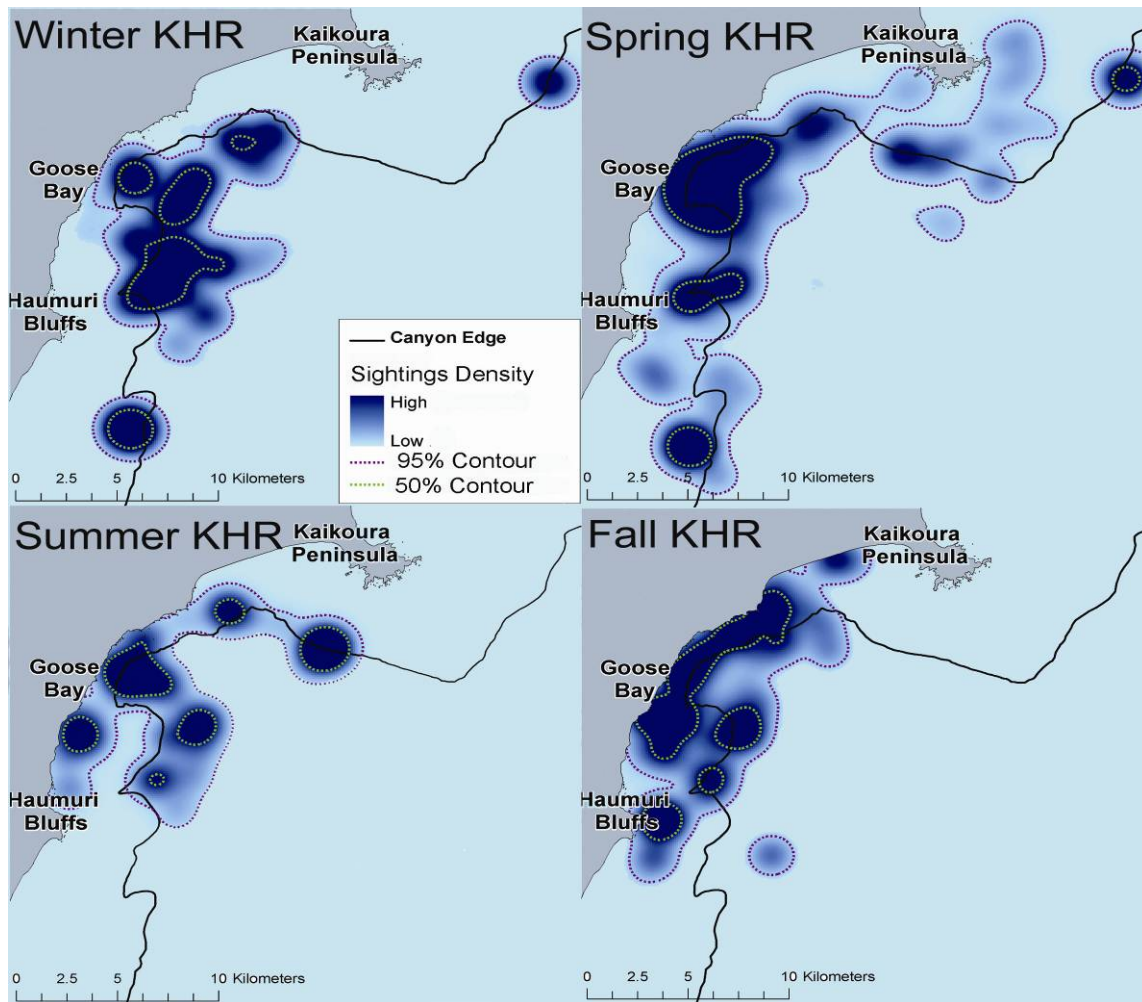


Figure 5. Systematic Seasonal Kernel Home Range (KHR). In summer and fall 95% KHR's include a large portion of shoreline and 50% KHR, or core areas, include both shallow and canyon waters. Winter 95% KHR includes very little shoreline and core area is overwhelmingly located in the canyon. Spring 95% and 50% KHR's are intermediate.

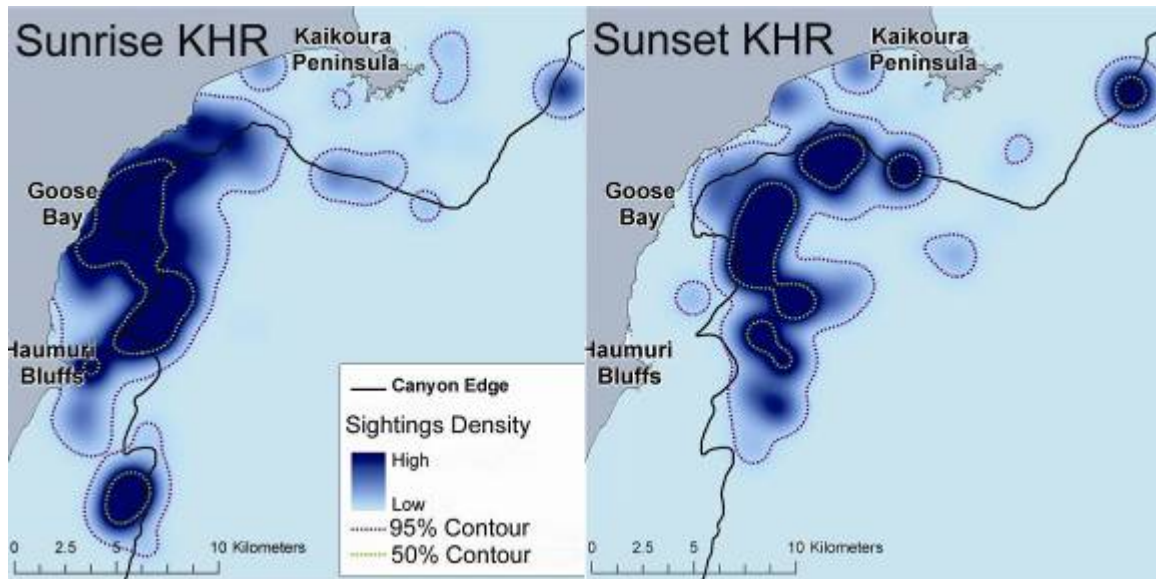


Figure 6. Systematic Diel Kernel Home Range (KHR). At sunrise 95% KHR's include a large portion of shoreline and 50% KHR, or core areas, include both shallow and canyon waters. Sunset 95% KHR includes little shore line and core area is primarily located in the canyon.

Trackline Data

Dolphins exhibited seasonal patterns in both mean speed and linearity (Fig. 7). Average speed was greatest during fall (2.35 m/s) and winter (2.29 m/s), and lowest during spring (1.63 m/s) and summer (2.02 m/s). In shallow water, dolphins made significantly sharper turns in summer (51.83°) than at other times of year (winter = 21.93° ; spring = 33.07° ; fall = 40.17°). Kruskal-Wallis tests confirmed that these were significant differences (speed: $\chi^2=9.496$, $p= 0.023$, $df=3$; linearity $\chi^2=11.613$, $p= 0.009$, $df=3$).

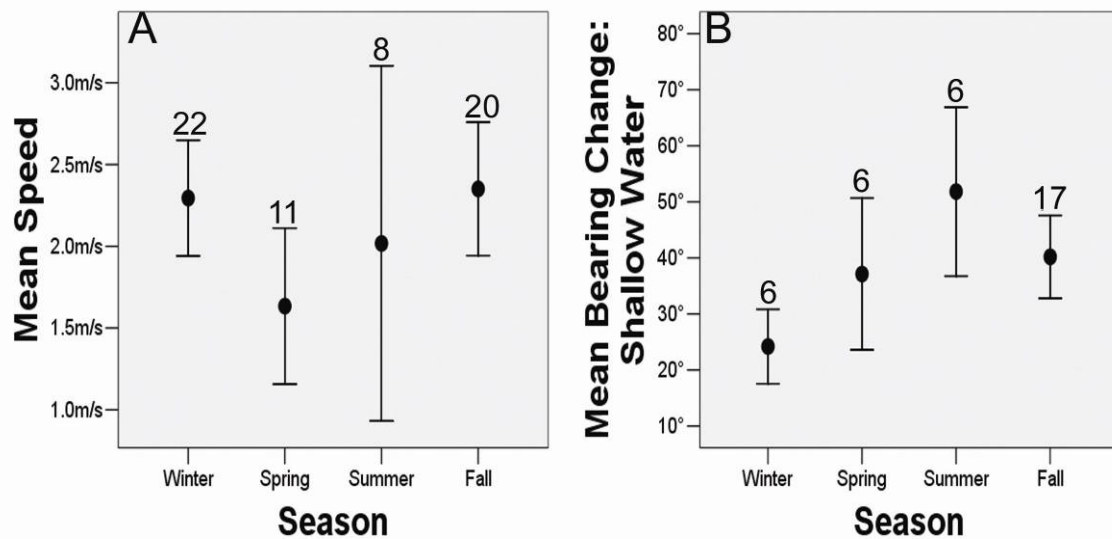


Figure 7. Effect of Season on Speed (A) and Linearity (B). Means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Seasonal dolphin movement patterns differed significantly in terms of both variables.

Time of day had a significant effect on dolphin speed, but not linearity (Fig. 8).

Dolphins travelled faster near sunset (3.00 m/s) than near sunrise (1.83 m/s). A Kruskal-

Wallis test confirmed that this was a significant difference ($\chi^2=17.898$, $p< 0.001$ $df=1$).

In deep water, the mean change in bearing was very similar at sunset (54.47°) and

sunrise (51.78°). Kruskal-Wallis tests confirmed that this difference was not significant

($\chi^2=0.068$, $p= 0.794$, $df=1$).

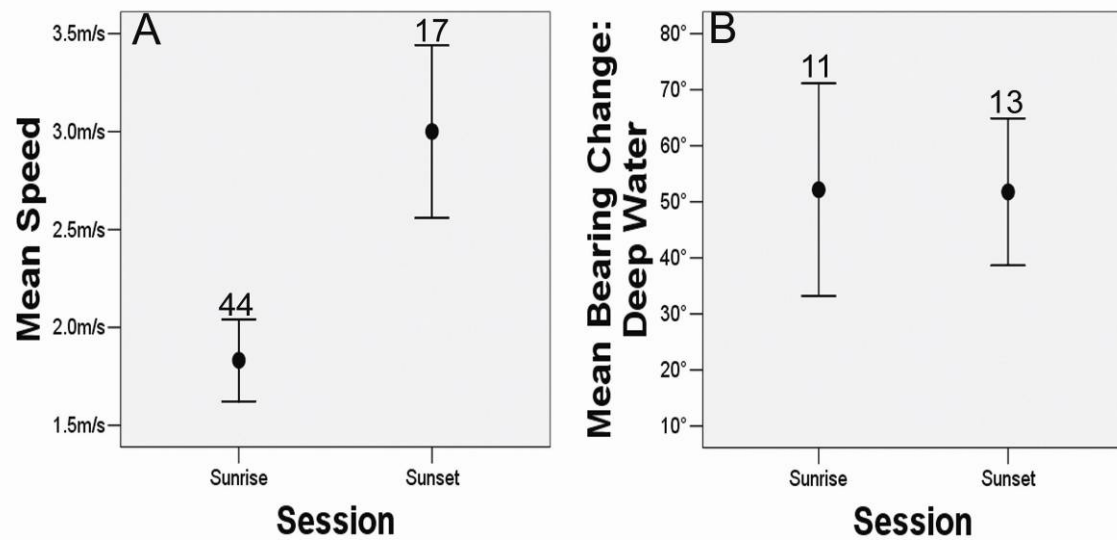


Figure 8. Effect of Diel Period on Speed (A) and Linearity (B). Means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Diel dolphin movement patterns differed significantly in terms of speed, but not linearity, as measured by mean absolute change in bearing.

Tidal state did not appear to influence either mean speed or linearity (Fig. 9).

Dolphins traveled at approximately the same speed across all tidal states (flood= 1.98 m/s; high= 2.45 m/s; ebb= 1.83 m/s; low= 2.16 m/s). In shallow water, the mean change in bearing was very similar across all tidal states (flood= 33.98°; high= 36.67°; ebb= 38.91°; low= 42.22°), and Kruskal-Wallis confirmed that there were no significant differences (Speed $\chi^2=3.073$, $p= 0.380$, $df=1$; Linearity $\chi^2=0.912$, $p= 0.823$, $df=3$).

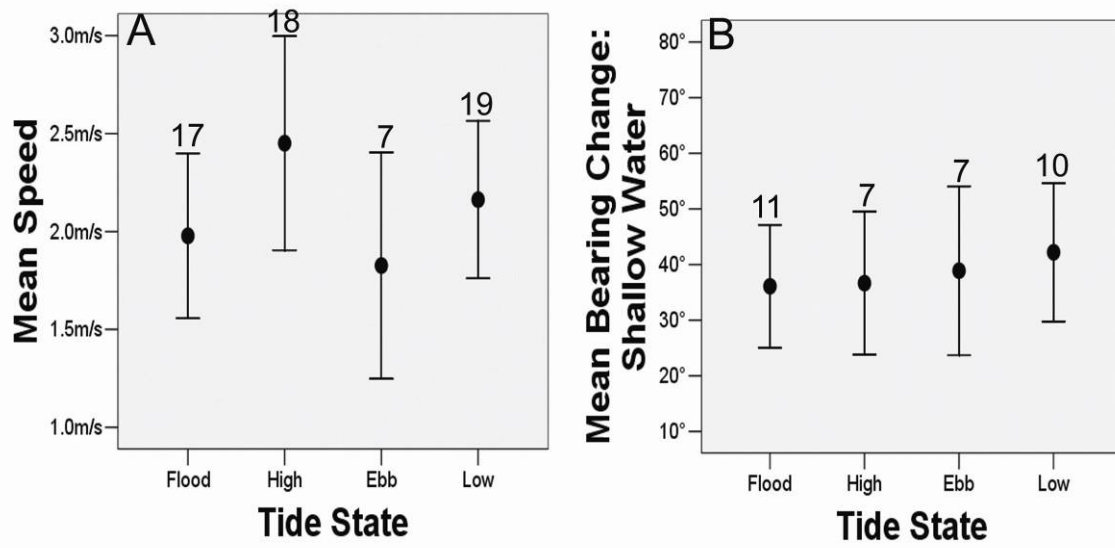


Figure 9. Effect of Tide on Speed (A) and Linearity (B). Means are depicted by points; the error bars illustrate the 95% confidence interval. Sample sizes are above the error bars. Tidal dolphin movement patterns did not differ significantly in terms of either variable.

DISCUSSION

Dusky dolphins off Kaikoura revealed strong seasonal and diel occurrence and movement patterns. These patterns were evident in depth, distance to the canyon, distance to shore, speed, linearity and in the 50% and 90% KHR's. In winter, fall, and approaching sunset, dolphins travelled faster than at other times and were more often sighted farther offshore in deeper canyon waters. Dolphins made sharper turns in summer than during other seasons. KHR analysis showed that core areas were focused near the canyon head and along the canyon axis, and shifted offshore for winter and approaching sunset. Occurrence and movement patterns did not appear to be affected by tidal state. Dusky dolphin occurrence and movement patterns are probably influenced,

at least in part, by prey availability patterns (Würsig and Würsig 1980, Cipriano 1992, Harzen 1998, Ballance *et al.* 2006, Redfern *et al.* 2006).

On large scales, cetaceans often choose habitat to exploit prey. Plankton and fish often form aggregations above large bathymetric features such as canyons, shelfbreaks and seamounts (Genin 2004). Cetaceans also aggregate above such features, most likely drawn by the abundant and reliable prey (Genin 2004, Yen *et al.* 2004, Ballance *et al.* 2006). Within the canyon system, diurnally migrating zooplankton may get caught in near surface currents and form dense accumulations near the downstream edge of the canyon (Genin 2004).

The Kaikoura Canyon supports a dense nocturnally rising DSL (Benoit-Bird *et al.* 2001), and may attract dolphins to the area. At all times of year, duskies tended to be closer to the Kaikoura Canyon than they were to shore (Fig. 2). All seasonal KHR's included a significant proportion of canyon waters; core areas typically straddled the canyon edge, except during winter when core areas were contained almost exclusively in canyon waters (Fig. 5). These observations are consistent with the hypothesis that at large scales, dolphins choose habitat with abundant prey. This study explored how dolphin occurrence and movement patterns within a presumably prey rich area change over smaller seasonal, diel, and tidal time scales in Kaikoura.

Seasonal Patterns

Many dolphin species seem to track their prey on seasonal time scales (e.g., Würsig and Würsig 1980, Bräger 1993, Nichol and Shackleton 1996, Neumann 2001, Bräger *et al.* 2003, Acevedo-Gutiérrez and Stienessen 2004, Ballance *et al.* 2006,

Redfern *et al.* 2006). The seasonal shift offshore in the winter has been noted previously for duskies living near Kaikoura, and was speculated to reflect changing prey patterns (see Cipriano 1992, Markowitz 2004). Little is known about seasonal migration of the DSL associated with the Kaikoura Canyon. Canyon systems can experience seasonal changes in biomass and species richness (reviewed in Genin 2004) and in the spatial distribution of resident species (Tudela *et al.* 2003); gut content analysis of duskies in Kaikoura implied that the composition of the prey assemblage changed seasonally (Cipriano 1992). Dusky dolphin diets showed decreasing diversity of prey taxa in winter and an increasing instance of squids, which provide fewer calories per gram than lanternfishes (Family Myctophidae), another key prey item (Cipriano 1992). Studies of demersal prey communities approximately 150 km southwest of Kaikoura demonstrated that many taxa, including the arrow squid (*Nototodarus sloanii*), an important dusky prey item, move offshore into deeper waters in the winter (Beentjes *et al.* 2002). The winter shift offshore into deeper waters by duskies (Fig. 2 and Fig. 5) might reflect an effort to match prey distribution patterns.

Prey species may exhibit seasonal changes in the amount of time that they are vulnerable to air breathing predators. Marine organisms that undergo diel vertical migration are affected by light levels (Enright 1979). Seasonal changes in lunar light levels can result in seasonal differences in the extent and timing of vertical migration (Koslow 1979, Haney *et al.* 1990, Balino and Aksnes 1993). In Kaikoura, the extent of vertical migration is nearly constant between summer and winter, with the layer reaching a minimum depth between 30 m and 40 m. However, the timing of migration changes

significantly between summer and winter; in winter the DSL is in the top 150 m of the water column, and therefore accessible to dolphins approximately four hours longer than it is in summer (Benoit-Bird *et al.* in press). At times of year when prey are most accessible (Benoit-Bird *et al.* in press) and dolphins capture a higher percentage of lower energy prey items (Cipriano 1992), dolphins may choose to stay longer in productive patches, thus maximizing overlap with prey and minimizing the energy required to reach the prey patch. Such a choice could result in the winter shift offshore into canyon waters (Fig. 5.)

In addition to showing seasonally specific core areas, dusky dolphins at Kaikoura also revealed seasonal patterns of movement. Speed was highest in winter and fall, and change in bearing was most gradual in winter; speed was lowest in summer and spring, and change in bearing was greatest in summer (Fig. 7). These seasonal movement patterns agree with earlier findings that duskies spend more time engaged in directional travel in winter, and spend more time “zig zag swimming”, and making complex sexual displays in summer (Cipriano 1992, Markowitz 2004). I would expect travelling duskies to have a higher speed and to travel in straighter lines than animals engaged in other activities. Cipriano (1992) suggests that “zig zag swimming” functions to increase foraging and predator detection efficiency. Both activities would be very important for mothers with calves who burn extra calories nursing and caring for their calves. Indeed, dolphins travelled slower and made more sharper turns at in summer when the DSL was accessible at night for four hours less than it is in winter (Benoit-Bird *et al.* in press), young calves were most common (Weir *et al.* 2008), and killer whale (*Orcinus orca*)

attendance was highest (Dahood *et al.* 2008). Perhaps this less directional travel helps duskies identify rare daytime foraging opportunities and more efficient detection of killer whales. Killer whales may effect both short-term and long-term behavior of dusky dolphins (Srinivasan and Markowitz in press). However with available information, it is not possible to evaluate the specific effects of prey searching and predator avoidance tactics on speed and linearity. I am currently collaborating on analyses with a colleague to investigate more directly the effects of killer whales on dusky dolphin occurrence and movement patterns.

Diel Patterns

Many dolphin species exhibit diel occurrence and movement patterns (e.g., Bräger 1993, Hanson and Defran 1993, Karczmarski *et al.* 2000b). An example of such patterns would be the Hawaiian spinner dolphin. Spinner dolphins spend daylight hours resting and socializing in shallow near-shore habitats, where they experience lower predation rates than in the open ocean; they move offshore into more dangerous deep water to forage at night on a rising scattering layer (Norris and Dohl 1980). Clearly, the night-time accessibility of dense prey patches influences spinner dolphins to leave the safety of near-shore habitats. The behavior of duskies is similar to that of Hawaiian spinner dolphins. During day-time both species forage at night on the DSL and typically rest and socialize in near-shore waters (Norris and Dohl 1980, Markowitz 2004), where they seem to experience lower risk from predators (reviewed in Srinivasan and Markowitz in press).

Recent studies indicate that occurrence and movement patterns of dusky and Hawaiian spinner dolphin may be similar during foraging. In Hawaii, spinner dolphins track both the vertical and horizontal migration of their prey on through out the night; spinner dolphins do not remain offshore all night, but rather track areas of high prey density as their prey undergoes both vertical and horizontal migration (Benoit-Bird and Au 2003). In Kaikoura, duskies track the vertical migration of their prey, diving to interact with the layer when it is within 130 m of the surface (Benoit-Bird *et al.* 2004); in winter, duskies track the layer so closely that they dive 1m deeper than the shallowest area of high concentration (Benoit-Bird *et al.* 2004).

Dusky dolphin diel occurrence and movement patterns may partially reflect this close tracking of prey. Seemingly in anticipation of feeding, duskies moved offshore into deeper waters each night (Fig. 3), a trend that was also noted by Cipriano (1992). Their core areas shifted to almost entirely inside the canyon (Fig. 6), and mean speed increased significantly approaching sunset (Fig. 8). Würsig and Würsig (1980) note d that duskies in Argentina travel faster as they are preparing to feed, it possible that duskies in Kaikoura exhibit the same pattern, traveling faster at night in anticipation of night foraging. The DSL becomes inaccessible to dolphins several hours before sunrise (Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press), giving the dolphins ample time to move back to safer near-shore waters before first light.

Tidal Patterns

Unsurprisingly, tidal state did not appear to influence dusky dolphin occurrence (Fig. 4) or movement (Fig. 9) patterns. Dolphins that exhibited tidal patterns typically

live in shallow coastal areas, and their foraging success seems to be associated with tidal phase (e.g., Harzen 1998, Gregory and Rowden 2001, Ribeiro *et al.* 2007). While duskie living near Kaikoura inhabit near-shore waters, they forage in deep water at night on the rising DSL (Benoit-Bird *et al.* 2004). Thus daytime tidal changes likely would not affect foraging success.

Disturbance

Animal occurrence patterns are often correlated with prey distribution. Some examples include Mongolian gazelles (*Procapra gutturosa* Pallas) (Mueller *et al.* 2008), black-headed gulls (*Larus ridibundus*) (Schwemmer and Garthe 2008), stone flounder (*Platichthys bicoloratus*) and starry flounder (*P. stellatus*) (Tomiyama and Omori 2008) and grassland earless dragon (*Tympanocryptis pinguicolla*) (Starr and Leung 2006). However, to examine habitat use patterns without considering the effects of predators (reviewed in Schmitz *et al.* 2008 and, Wirsing *et al.* 2008) or anthropogenic disturbance, including tourism activities (Bejder *et al.* 2006, Thiel *et al.* 2008) oversimplifies the choices animals make. When predation pressure is high, marine and terrestrial animals will sometimes choose the safest, rather than the most productive, areas (Reviewed in Schmitz *et al.* 2008 and, Wirsing *et al.* 2008). Additionally, both marine and terrestrial animals will leave seemingly productive foraging grounds when they can no longer tolerate anthropogenic disturbance (e.g., dolphins: Bejder *et al.* 2006, birds: Thiel *et al.* 2008).

In Kaikoura, dusky dolphins' likely predators are large sharks and killer whales. Shark abundance near Kaikoura is low and seems to be declining, therefore killer whales

likely present a greater threat to dolphins than sharks (Srinivasan and Markowitz in press). Killer whales may visit Kaikoura throughout the year, but abundance is highest in summer. Over a 12 year period there were 138 sightings and, 70% of sightings occurred in summer and fall (Dahood *et al.* 2008). In the presence of killer whales, duskies often swim rapidly into shallow waters and continue swimming along the shore (Constantine *et al.* 1998). The summer preference for near-shore shallow waters may reflect an effort to remain close to predation refuges when predation risk is high, rather than an attempt to match prey patterns (Dahood *et al.* 2008).

Kaikoura supports a thriving marine tourism industry, and many tours visit the dolphins each day (Barr and Slooten 1999, Duprey 2007). There was concern in the late 1990's that increased tourism pressure was causing the dolphins to shift their preferred habitat south, away from town (Brown 2000). In the past seven years, tourism activities and two major companies adopted larger, faster vessels, yet the areas of highest dolphin density have shifted north, towards town (Dahood *et al.* 2008). At a large scale, tourism in Kaikoura does not seem to have affected the long-term habitat use patterns of large groups of duskies. However, it cannot be ruled out that similar to Shark Bay, Australia (Bejder *et al.* 2006) sensitive individuals left the area

CONCLUSIONS

This study used systematically gathered geospatial data to document occurrence and movement patterns for large groups of dusky dolphins living near Kaikoura. Duskies revealed strong seasonal and diel patterns, with dolphins moving offshore into deeper waters during winter and approaching sunset. Dolphins did not exhibit

occurrence or movement patterns on a tidal scale. Prey availability patterns probably influence dusky dolphin occurrence and movement patterns across all studied temporal scales. However, other factors such as predation and anthropogenic disturbance that were not considered in this study, could have an influence. Indeed, an increasing number of studies demonstrate that, at times of high predation risk, animals will choose the safest rather than the most productive habitat (reviewed in Schmitz *et al.* 2008 and, Wirsing *et al.* 2008).

CHAPTER III

TOUR OPERATOR DATA ILLUSTRATE LONG-TERM DUSKY DOLPHIN OCCURRENCE PATTERNS NEAR KAIKOURA, NEW ZEALAND

INTRODUCTION

In Kaikoura, New Zealand, duskies are both ecologically and economically important. As upper level predators capable of consuming large amounts of prey, dolphins may influence ecosystem processes (Kenney *et al.* 1997). Their year-round presence and acrobatic displays have allowed a dolphin tourism industry to develop and prosper (Barr and Slooten 1999, Duprey 2007).

New Zealand's Department of Conservation, the agency responsible for managing marine mammals in New Zealand waters, lists '...to better understand...key habitat requirements' as a key objective for dusky dolphin management (Suisted and Neale 2004). Cetacean habitat use patterns are commonly related to abiotic factors (reviewed in Chapter I and Chapter II). Cetacean habitat selection may be further influenced by attempts to avoid anthropogenic disturbance (Bejder *et al.* 2006b, Lusseau 2004, Lusseau 2005).

Cetaceans exhibit habitat preferences based at least in part on water depth and distance from shore (reviewed in Chapter I and Chapter II). In shallow areas, small differences in depth (on the order of 10 m) influence habitat selection by bottlenose dolphins in the Sado Estuary, Portugal (Harzen 1998) and Hector's dolphins inhabiting New Zealand's near-shore waters (Bräger *et al.* 2003). Bathymetric preferences may

reflect efforts to improve foraging success (Benoit-Bird and Au 2003, Elwen and Best 2004a, Yen *et al.* 2004) or avoid disturbances such as predation (Yen *et al.* 2004, Weir *et al.* 2008). Similarly, distance from shore influences habitat selection of coastal cetacean species (Bräger *et al.* 2003, Elwen and Best 2004a, Parra *et al.* 2006a). Near-shore waters may offer protection from predation (Norris and Dohl 1980, Constantine *et al.* 1998) or provide nursery habitat for cetaceans (Elwen and Best 2004b, Weir *et al.* 2008).

There is a growing concern that marine mammal behavior is affected by boat traffic (Barr and Slooten 1999, Yin 1999, Constantine *et al.* 2004). Several studies assessed immediate or short-term effects of boat activity on dolphin behavior (Bejder *et al.* 1999, Lusseau 2003, Constantine *et al.* 2004), but few have addressed long-term effects on cetacean habitat selection. In Shark Bay, Western Australia, over a 14 year period, Indian Ocean bottlenose dolphins living in an area exposed to tourism declined in abundance with increasing tourism activity; there was no decline in adjacent tourism-free areas (Bejder *et al.*, 2006b). Some individuals probably relocated to the tourism-free area (Bejder *et al.*, 2006b). Similarly, bottlenose dolphins off the north coast of New Zealand's South Island spent less time in Milford Sounds when boat traffic levels are high (Lusseau 2005). In the late 1990's there was speculation that increased tourism in Kaikoura might have caused duskies to shift their preferred habitat south, away from the busy commercial boat ramp (Yin 1999, Brown 2000).

OBJECTIVES AND HYPOTHESES

Research on duskies has been conducted sporadically near Kaikoura since 1984 (Würsig *et al.* 2007), but since October 1995, Encounter Kaikoura (<http://www.encounterkaikoura.co.nz>) skippers have been recording dusky locations on most good weather days. The Encounter Kaikoura dataset represents the longest continuous all-season record of duskies in the area. This record provides a unique opportunity to examine effects of abiotic factors on dusky dolphin long-term occurrence patterns and to explore how these patterns change over time. Because of the long-term collaboration between Texas A&M University and Encounter Kaikoura, the data collection process is standardized and researchers have access to a large dataset that would be difficult to build and maintain without tour operator support. I test the hypotheses that duskies have seasonally specific preferences for depth, distance to the Kaikoura Canyon edge, and distance to shore. Further, I test whether dusky dolphin occurrence patterns during summer, when tourist numbers are highest, were consistent between 1995-2000 and 2001-2006.

METHODS

Encounter Kaikoura vessels searched for dolphins in an approximately 2,800 km² area, which included about 90 km of coastline and some of the Kaikoura Canyon system (Fig. 10). Tours departed daily at 0530, 0830 and 1230 h; the early tour ran only when tourist numbers were high, between October and April. Boats typically left the South Bay Harbor (42°25'31" S, 173°40'53" E), in the middle of the permitted area, and headed south until dolphins were found. Skippers recorded GPS coordinates to the nearest one

tenth of a minute when they first approached the dolphin group. This dataset is therefore a measure of group closeness to the commercial on-shore boat harbor during tour times, and not a fair indication of location of all dolphin groups in the Kaikoura area. Skippers estimated group size with each GPS location. However, the definition of ‘group’ was not consistent between skippers or years; group size will not be discussed in this study. Skippers also recorded the presence of other cetaceans, such as killer whales, in the area.

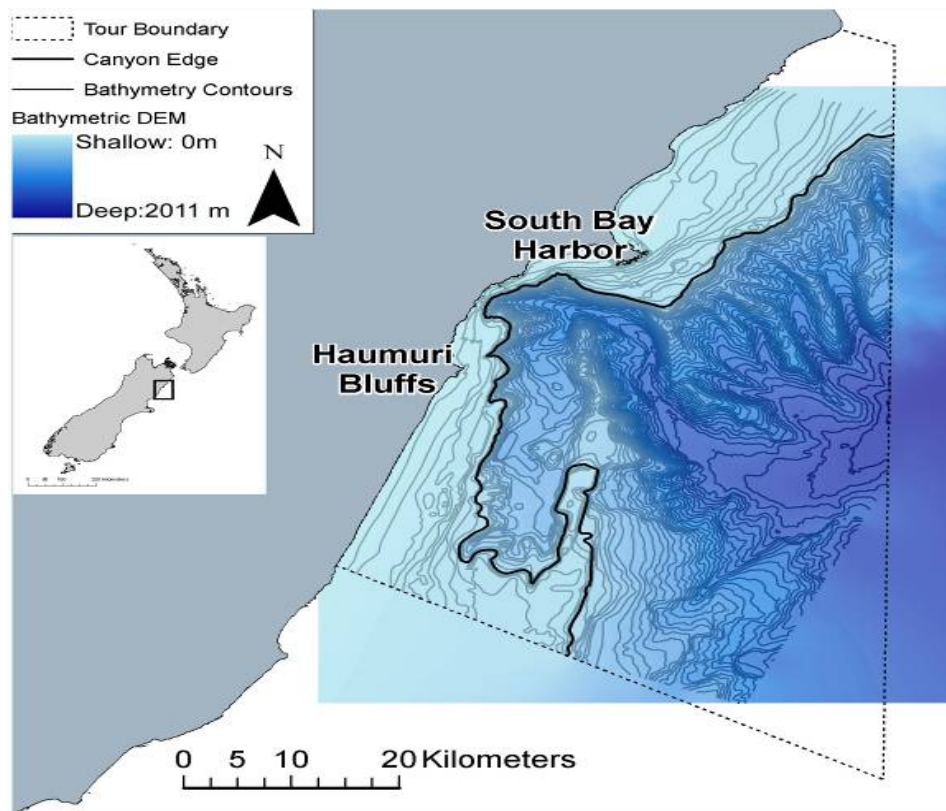


Figure 10. Tour Operator Study Area. The area in which tour boats focus their searches is outlined by a dotted line. The commercial dolphin watching permit sets the north and south boundaries, but does not define an offshore limit. The Canyon Edge is marked at 150 m depth contour. The South Bay Harbor, where all the dolphin tour boats launch, and Haumuri Bluffs, an important southern landmark for the skippers, are noted on the map.

From October 1995 to November 2006, there were more than 5,000 useable dusky sighting records spread unevenly across years and seasons, and 138 instances of killer whales in the permit area. Summer months, with better weather and higher tourist numbers, had 1,792 records. Winter months had only 755 records. The data were analyzed using ArcGIS 9.1, Arcview 3.3 and SPSS 13. All spatial data, including a shapefile of the NZ coastline (courtesy of Eagle Technology, Wellington, NZ) were projected to the New Zealand Transverse Mercator Projection 2000, to provide the most accurate spatial reference for the study area (Land Information New Zealand 2001). Data were grouped by season across the twelve year period, defining winter as June 1- August 31, spring as September 1- November 30, summer as December 1- February 29 and fall as March 1- May 31.

First Sightings Properties

Analyses proceeded in two different phases. First, depth and distance-to-feature measurements were associated with each point. The Topogrid command in Arcinfo was applied to bathymetry lines, developed by Lewis and Barnes (1999) with an accuracy of $\pm 2\text{m}$ and distributed by NIWA, to create a continuous model of depth at 30 m resolution. The Nearest Features extension for ArcView 3.3 (Jenness, 2004) was used to calculate distance-to-feature variables. The 150 m isobath poly line, the average depth of the continental shelf break (Garrison 1999), represented the canyon edge and access to deep-water prey preferred by duskies in Kaikoura (Cipriano 1992, Benoit-Bird *et al.* 2004). When calculating distance to the canyon, all occurrences in waters deeper than 150 m were assigned a zero distance. Seasonal means for each factor were calculated,

and the distributions compared using the non-parametric Kruskal-Wallis test in SPSS 13.0 (SPSS 2004). To examine potential effect of unequal samples sizes on the results (winter= 755, spring= 1175, summer= 1792, fall= 1647), all 755 winter points were used and five random subsets of 755 samples from each season other than winter were created. The five subsets as well as the full dataset were tested. Means were similar for the random sets and the full data set; only results for the full data set will be presented in 'Results'.

Kernel Home Range Analysis

In the second phase, I compared areas occupied by duskies using Kernel Home Range (KHR) probability polygons. The Animal Movement Extension 2.0 for Arcview 3.3 (Hooge and Eichenlaub 2000) and ad hoc smoothing parameters were used to create 50% and 95% KHR's for each season and for summers grouped by year, 1995-2000 and 2001-2006. The program did not recognize that land is not accessible to dolphins, and therefore the western edges of some KHR's overlapped land. The KHR's were clipped to eliminate this overlap. KHR analysis is sensitive to the numbers of points used to generate the polygons. Numbers of points used to generate seasonal KHR's were highly unequal, but numbers of points used to generate summer KHR's separated by year were similar (1995-2000= 830; 2001-2006 = 962). Because of clipping and dissimilarity in numbers of points, only general trends in north-south location and size, but not absolute areas of the KHR's, can be compared.

RESULTS

Mean depth was greatest during winter (411 m) and spring (386 m) and shallowest during summer (131 m) and fall (165 m). Distance to the canyon was greatest during summer (1.58 km) and fall (1.23 km), and shortest during spring (0.23 km) and winter (0.60 km). Distance to shore was greatest for winter (6.32 km) and spring (4.51 km), and shortest for summer (1.82 km) and fall (2.14 km). Kruskal-Wallis tests confirmed that seasonal occurrences differed significantly in terms of depth ($\chi^2=1379$, $p<0.001$, $df=3$), distance to shore ($\chi^2=1792$, $p<0.001$, $df=3$), and distance to canyon ($\chi^2=1039$, $p<0.001$, $df=3$). Dolphins revealed seasonal preferences for all three abiotic factors. On average, at all times of year, duskies were closer to the canyon than shore.

Killer whales were recorded 138 times in the Kaikoura area. Killer whales were seen in every season (winter $n=6$, spring $n=35$, summer $n=58$, fall $n=39$). Approximately half of the spring sightings occurred during the last two weeks of the springs of 1996, 2000, 2003, and 2004.

Seasonal differences in shape and size of the 95% KHR and 50%KHR probability polygons were evident. Winter had the largest 95% and 50% KHR (668.41km² and 109.59km² respectively), and summer sightings were concentrated in much smaller 95% and 50% KHR's (115.31 km² and 15.07 km², respectively) (Fig. 11). Spring and fall KHR's were intermediate in both size and location. Areas enclosed by 95% KHR's representing summers of 1995-2000 (129.99 km²) and 2001-2006 (114.69 km²) were very similar, but the 95% KHR for summers of 1995-2000 was farther south

than in later years (Fig. 12). However, 50% KHR's were in nearly identical locations and occupied similar amount of area (14.01 km² for 1995-2000 and 19.01 km² for 2001-2006). The Kaikoura Canyon head was included in all KHR'S.

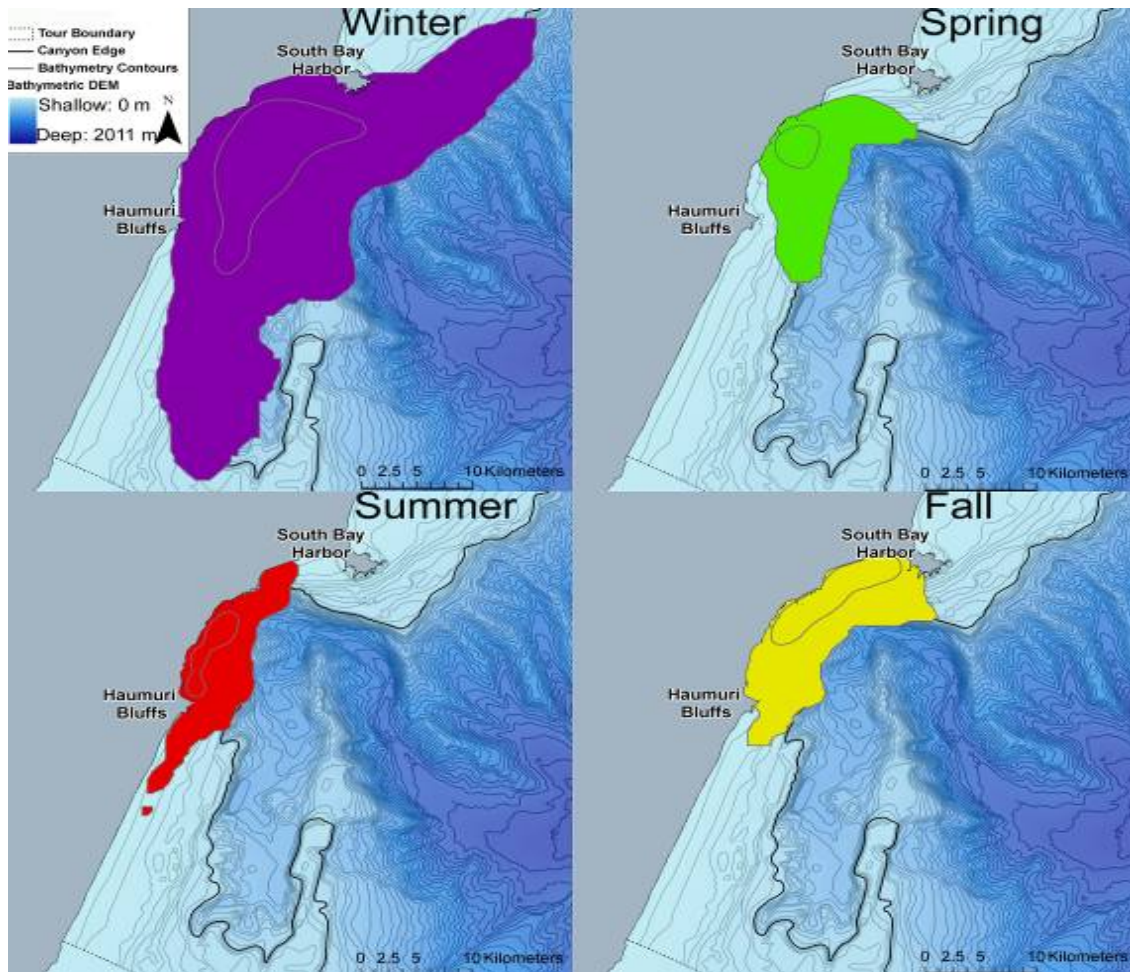


Figure 11. Tour Operator Seasonal Kernel Home Range. The outer edge of the KHR represents the 95% KHR, the outline nested inside illustrates the the 50% KHR. In winter, duskyies are not often in similar areas from day to day. This variability is reflected in the largest 50% and 95% KHR's. In summer, duskyies are highly predictable, often occurring close to shore between the South Bay Harbor and Haumuri bluffs. This is reflected by the smallest 50% and 95% KHR's.

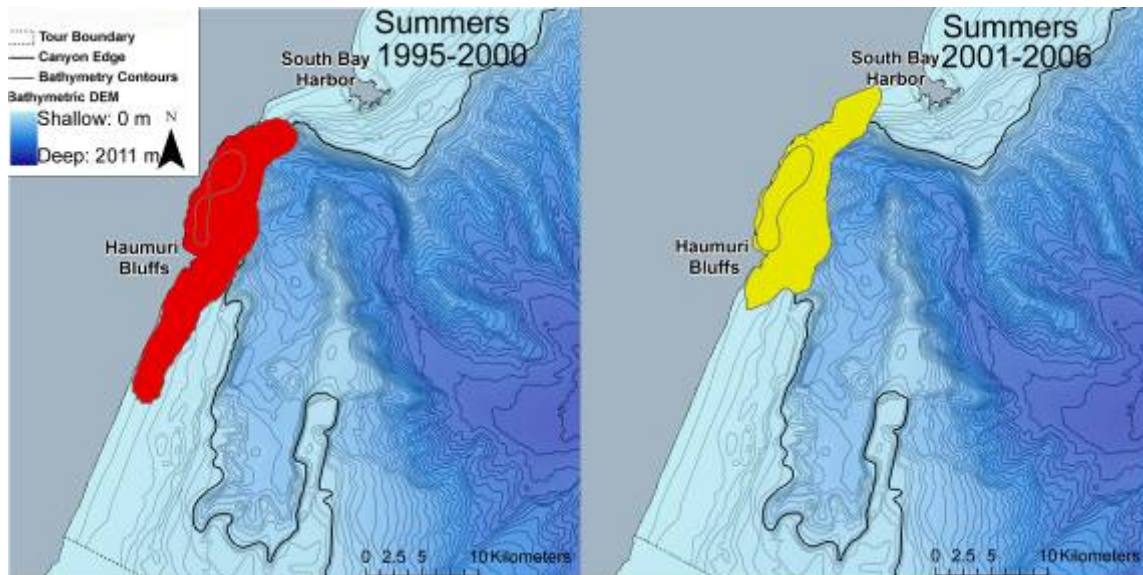


Figure 12. Tour Operator Summer Kernel Home Ranges. 95% KHR's illustrate that the boats had to make more trips in the southernmost part of the tour area to see dolphins in the late 1990's than in later years. However, 50% KHR's are comparable in area and location between the first and second half of the dataset, indicating that for the most part, the summer tours have been focusing on the same core areas since the 1990's.

DISCUSSION

Despite some annual variability, dusky dolphins exhibit clear seasonal occurrence patterns. These patterns are evident in depth, distance from shore, distance to canyon and location of 95% and 50% KHR's. In summer, sightings occurred in a relatively small area near-shore and were closely associated with the Kaikoura Canyon head; in winter, sightings were spread throughout a larger portion of the study area, were further offshore, and were frequently associated with the canyon axis (Fig. 11). Fall and spring showed intermediate patterns. Seasonal distribution patterns could be influenced by prey availability (Würsig and Würsig 1980, Cipriano 1992), predator attendance patterns

(Heithaus and Dill 2006), anthropogenic disturbance (Lusseau, 2005), or factors not considered in this dataset.

Prey

Dolphins often choose habitat to match prey patterns (Bearzi *et al.* 1999, Wilson *et al.* 1997). Bathymetric and distance-to-shore preferences of duskies may reflect a strategy to maximize access to prey. In Kaikoura, duskies feed at night on the Deep Scattering Layer, a community of fish and invertebrates that rises towards the surface at night (Benoit-Bird *et al.* 2004, Cipriano 1992). If prey availability influences dusky occurrence patterns, duskies should have a strong association with deep waters on a year-round basis. During all seasons, on average, duskies were found closer to deep water than to shore, and all 50% and 95% KHR's overlapped with the Kaikoura Canyon head (Fig.11). Further, dusky dolphins' shifted offshore in winter may reflect changing patterns of prey availability (Cipriano 1992). Studies of fish communities about 150 km southwest of Kaikoura reveal a winter shift offshore into deeper water for many species, including the arrow squid, *Nototodarus sloanii* (Beentjes *et al.* 2002), an important dusky prey item (Cipriano 1992). In winter, duskies may be following squid and other prey offshore.

Predators

As discussed in Chapter II, the level of predation risk from killer whales may influence dusky dolphin occurrence patterns. Dusky dolphins seem to use shallow waters as a predation refuge from killer whale attacks (Würsig and Würsig 1980,

Cipriano 1992, Constantine *et al.* 1998, Weir *et al.* 2008). Of 138 killer whale sightings recorded by Encounter Kaikoura skippers, 97 were reported in summer and fall (December-May), when duskies were found closest to shore. This same seasonal preference for shallow near-shore waters was revealed by the systematically gathered shore based data. During times of year when killer whale attendance is typically high, duskies may choose habitat to minimize detection or capture by predators rather than solely matching patterns of prey availability, a pattern which has been documented in Indian Ocean bottlenose dolphins and dugongs (*Dugong dugong*) in Western Australia (reviewed in Wirsing, 2008).

Demographics

Seasonal changes in occurrence patterns also may be influenced by changes in dolphin demographics not captured in these data. Summer groups contain calves and show predictable daily activity and onshore/offshore movement patterns. The sheltered waters of Goose Bay, near the Kaikoura Canyon head, are favored by nursery groups (Weir, 2007). Mothers may balance the need for protected waters for their calves (Elwen and Best, 2004b) and access to deep-water food for themselves by moving between these habitats on a daily basis. Winter groups contain few infants and may exploit habitats differently.

Additionally, duskies in Kaikoura may exhibit seasonal residency patterns. Photo ID databases reveal that some individuals are photographed only during winter months, while others are seen only during summer months (Markowitz 2004). This pattern hints at the possibility of “summer” and “winter” populations of duskies in

Kaikoura (Markowitz 2004). Kaikoura appears to function as a gathering location for dusky dolphins from around New Zealand's South Island (Harlin *et al.* 2003). Winter residents may prefer deeper habitats further offshore year round (Markowitz 2004).

Anthropogenic Disturbance

Across the 12 year study period, duskies occurred in approximately the same core areas (50% KHRs) (Fig. 12). However, the 95% KHR's reflect that the tour boats made significantly more trips to the southernmost portion of the study area during the summers of 1995-2000 than in later years (Fig. 12). During the late 1990's there was speculation that increased tourism pressure 1990's might cause the dolphins to shift their preferred habitat south, away from port (Yin 1999, Brown 2000). Since that time, tourism has not decreased, but the boats no longer make as many trips to the southernmost extent of the study area to find dolphins. Currently, there is no explanation for these changes. Inter-annual variation, potentially related to changes in prey occurrence and abundance, may have been largely responsible for the alongshore shifts.

The Encounter Kaikoura dataset does not include information regarding number of boats and boat maneuvering near dolphins, so the effects of tourism on duskies in Kaikoura cannot be directly examined. In several near-shore areas where dolphins number in the hundreds, groups exposed to tourism activity have relocated out of high traffic areas (Bejder *et al.* 2006, Lusseau 2005), and significant changes in activity budget have been observed (Constantine 2004, Lusseau 2003, Lusseau 2004). However, duskies in Kaikoura may be buffered against these negative effects. Approximately 1,900 duskies of a population of over 12,000 individuals are present in Kaikoura at any

one time (Markowitz, 2004), and the tour boats preferentially target large groups (this dataset, unpublished), thus effectively diluting tourism interaction experienced by individual dolphins. Duskie primarily rest and socialize during the day (Barr and Slooten 1999, Markowitz 2004), the two activity states that have been shown to be most vulnerable to disturbance in bottlenose dolphins (Constantine *et al.* 2004, Lusseau 2003). However, Encounter Kaikoura observes a voluntary midday rest period from 1130- 1330 h from December 1 to March 31, and does not visit dolphins when they are most likely to be resting (Barr and Slooten 1999, Duprey 2007), thus minimizing the extent of disturbance. It is encouraging that after nearly 20 years of dolphin tourism in Kaikoura, duskie still seem to be thriving. Duskie have maintained preferred habitat close to the commercial boat ramp, summer core habitat has not greatly changed over the past 12 years, and dolphins are still present in large numbers year round.

CONCLUSIONS

The Encounter Kaikoura dataset describes strong seasonal patterns that are consistent across years, despite some interannual variation in the location of areas of highest sightings densities. Seasonal preferences for water depth and distance to shore may reflect a strategy to maximize access to deepwater prey while balancing the need for near-shore predation refuges. Further investigations of prey patterns, predator patterns, human disturbance and other factors are needed to clarify inter-annual and seasonal patterns. Encounter Kaikoura skippers are continuing to collect data and develop the dataset in collaboration with researchers from Texas A&M University. These efforts will enhance understanding long-term dusky dolphin occurrence patterns.

CHAPTER IV

NIGHT FORAGING

INTRODUCTION

Foraging at night requires that predators locate and capture prey in low light or near total darkness. For many animals, vision is fundamental both in the detection and capture of prey and in the detection and avoidance of predators (Beauchamp 2007). Social foragers use vision to identify group members at a distance and maintain group cohesion (Beauchamp 2007). These abilities are limited at night. Despite this, animals choose to forage in the dark either to reduce predation risk or gain access to a food resource that is not available during the day (Benoit-Bird *et al.* 2004, Beauchamp 2007). Night foraging animals must adapt their foraging tactics to compensate for decreased visibility.

To forage successfully at night, some species develop specialized morphological adaptations. Nocturnal foragers tend to have large eyes and large pupils to let in maximum amounts of light; additionally, their eyes have significantly more rods, the photoreceptors that allow vision in dim light, than color sensitive cones (Warrant 2004). The eyes of nocturnal monkeys are significantly larger than those of diurnal monkeys, and also lack the ability to detect color (Bicca-Marques and Garber 2004). Many nocturnal mammals and fishes also have a *tapetum lucidum*, a reflective surface behind the retina that enhances the absorption of scarce light (Warrant 2004). Some nocturnal animals such as bats (Griffin *et al.* 1960), oil birds (Konishi and Knudsen 1979) and

odontocetes (Au 2004), evolved high frequency echolocation systems and rely mostly on sound, rather than vision, to locate prey in the dark.

In addition to morphological adaptations, animals also adjust their behavioral regimes to allow for night foraging. Some animals feed both day and night (Donati *et al.* 2007, Stimpert *et al.* 2007), but others switch feeding from diurnal to nocturnal based on perceived predation risk (Shimek 1977) or prey availability patterns (Mougeot and Bretagnolle 2000). Species that primarily use senses other than vision to forage might more readily switch to night foraging. Greater flamingos (*Phoenicopterus ruber ruber*) (Beauchamp and Mcneil 2003) and sea otters (*Enhydra lutris*) (Shimek 1977, Ribic 1982) are both tactile foragers and often forage at night to supplement low caloric intake during the day. Dusky dolphins rely on echolocation and switch between day and night foraging depending on habitat and available prey (Würsig *et al.* 1989, Benoit-Bird *et al.* 2004, Markowitz *et al.* 2004).

In aquatic environments, low light conditions regularly occur in the middle of the day at depth or in turbid, shallow waters (Lalli and Parsons 1995). Animals foraging in these conditions often have adaptations more commonly associated with night foragers (Warrant 2004). Elephant seals (*Mirounga sp.*) (Heithaus and Dill 2002) and king penguins (*Aptenodytes patagonicus*) (Wilson *et al.* 2002) feed during the day hundreds of meters below the surface and have large eyes, suggesting that at these foraging depths there is a source of light for visual predation (often by bioluminescence of prey). King penguins choose to forage at depth during the day rather than waiting for their preferred prey, lanternfishes, to rise to the surface at night, perhaps to take advantage of the small

amount of daylight visible at foraging depths and the decreased daytime speed of their prey (Wilson *et al.* 2002). In contrast, Indian river dolphins (*Platanista gangetica*) which live in shallow and turbid waters of the Indus and Ganges Rivers, are especially active during the day but have small, poorly developed eyes (Mass and Supin 2002, Smith 2002). They presumably forage using well-developed echolocation.

When there is insufficient light, animals may rely on sound to sense their environment using active echolocation and/ or passive listening. Echolocating animals can detect and identify prey, predators, and obstacles at a distance based on the characteristics of returning sound waves (Au 2002). Because of their ability to echolocate, odontocetes are well suited to foraging at night and several species commonly do so. Night foraging dolphins include Hawaiian spinner (Norris and Dohl 1980), pan tropical spotted (*Stenella attenuata*, Baird *et al.* 2001), dusky (Benoit-Bird *et al.* 2004), striped (*Stenella coeruleoalba*, Ringelstein *et al.* 2006) bottlenose (Klatsky *et al.* 2007), and common dolphins (*Delphinus delphis*, Pusineri *et al.* 2007).

Resting in protected near-shore waters during the day and foraging in deeper waters at night may reduce predation risk to small dolphins, including duskies (Norris and Dohl 1980, Würsig *et al.* 1997). Major predators of dolphins are killer whales (Constantine *et al.* 1998) and several species of large sharks (Norris and Dohl 1980, Heithaus and Dill 2006). Mammal-eating killer whales seem to hunt using combinations listening, vision, and to a lesser extent, echolocation (Baird 2000); low night-time light levels would impede their ability to see their prey. Little is known about mammal-eating killer whale diel dive cycles. Until recently, it had been assumed that like fish-eating

killer whales, they are most active during the day (Baird 2000, Baird *et al.* 2005).

However, new evidence suggests that mammal-eating killer whales in southeast Alaska hunt as much during crepuscular periods or at night as they do during the day³. To detect prey at a distance, sharks appear to rely on scent and pressure changes sensed by their lateral lines; the final strike is directed by changes in electromagnetic fields sensed by head-based ampullae of Lorenzini (Gardiner and Atema 2007). Because sharks do not highly depend on vision for prey detection or capture, they would be almost equally able to detect prey in the dark as in daylight. Many shark species, including some that may prey on marine mammals, are active during the night (Hulbert *et al.* 2006). Recent tagging studies have shown that some large sharks migrate to the surface at night and are presumably foraging (Hulbert *et al.* 2006, Chapman *et al.* 2007, Weng *et al.* 2007). Therefore, night-time foraging may be no less dangerous than day-time foraging, and may be even more so in areas where shark abundance is high.

For marine mammals and birds, an advantage to night foraging is the predictable nightly ascent of food associated with the diely migrating Deep Scattering Layer (DSL), a community of fish and invertebrate mesozooplankton and micronekton that serves as a rich food source for many marine predators (Johnson 1948, Cushing 1973, Pearcy *et al.* 1977, Pieper and Bargo 1980). The animals in the DSL occur in sufficiently dense concentrations to scatter sound waves, giving the illusion of bottom to early depth-sounding devices (Johnson 1948, Cushing 1973). The DSL is too deep for most air-breathing marine predators to access easily in daytime. However, the Diel Vertical

³ Volker Deecke, Sea Mammal Research Unit, University of St. Andrews, St. Andrews Fife KY16 8LB, Scotland, UK; July 3, 2008

Migration (DVM) of the DSL typically brings this abundant prey base from depths of hundreds of meters to within tens of meters of the surface (Enright 1979)

Duskies living near Kaikoura, New Zealand, are able to track the DSL at night as it approaches the surface (Benoit-Bird *et al.* 2004) and preferentially capture lanternfishes and squids within it (Cipriano 1992). Duskies foraging at night likely rely on echolocation and passive listening to detect and localize individual prey (Au and Würsig 2004), but at very close range, duskies may be able to see their prey, aided perhaps by moonlight or bioluminescence of lanternfishes (Gago and Ricord 2005). This differs from typical day-time feeding tactics, in which duskies rely on vision and light to capture schooling fishes (Würsig and Würsig 1980, Würsig *et al.* 1990).

Dusky dolphins can drastically change their feeding tactics in relation to bathymetry and prey availability. In shallow habitats, typically areas shallower than 60 m (*e.g.* Admiralty Bay, New Zealand and Golfo San José, Argentina) duskies forage during daylight and coordinate movements to herd schooling fish into tightly packed balls near the surface (Würsig and Würsig 1980, Vaughn *et al.* 2007). When capturing fish from these prey balls, duskies typically orient their ventral surfaces towards the fish (Vaughn *et al.* in press). They may use the light reflecting off their white bellies to help control prey (Würsig *et al.* 1990), a behavior that has been recorded in fish-eating killer whales (Similä and Ugarte 1993). The same individuals that have been documented balling prey in Admiralty Bay, New Zealand, during winter migrate south and feed at night in deep waters of the Kaikoura Canyon during summer (Benoit-Bird *et al.* 2004, Markowitz 2004). When foraging at night on the DSL near Kaikoura, they can no

longer rely on vision to coordinate activities. Thus, when foraging at night in deep-water habitats, prey detection, containment and capture techniques must change from daytime tactics.

Foraging strategies and choices about when to use specific tactics affect individual and population level fitness (Krebs *et al.* 1974). To understand these choices, it is important to study both the temporal and spatial patterns of predators and prey. Dolphins feed on highly mobile prey out of sight of researchers, making it difficult to quantify both the available prey base and dolphin foraging behaviors. These difficulties are compounded when dolphins forage at night in deep waters. However, even in the dark, tagging can provide information on the diving behavior of individual dolphins, and active acoustic techniques make it possible to simultaneously track dolphins and their prey base (Benoit-Bird *et al.* in press). Using these tools, we are recently beginning to understand the night-time component of dusky dolphin flexible foraging strategy.

METHODS

Three studies have been conducted on night foraging in duskies. These studies were conducted near Kaikoura, New Zealand, between 1984 and 2006, and employed a variety of methods (Fig. 13 depicts the study area). I briefly summarize the methods used in each study.

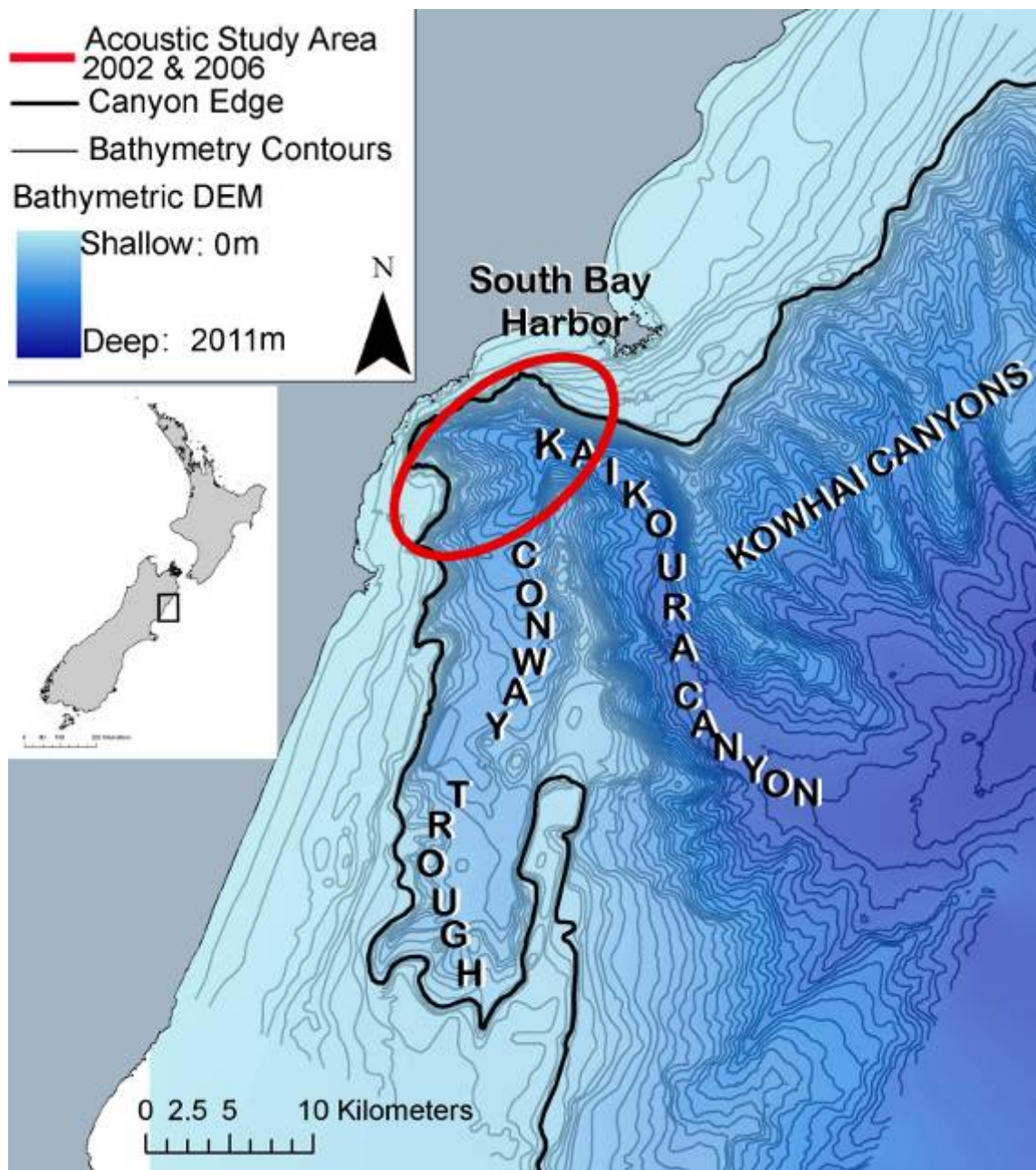


Figure 13. Night Foraging Study Area. Kaikoura is located on the northeast coast of the South Island of New Zealand. The Kaikoura Canyon head comes within 500 m of shore, in the center of the acoustics study area. Radio tags were monitored from the clifftops near South Bay Harbor. Bathymetric data were provided by NIWA and are discussed in detail in Lewis and Barnes (1999)(From Dahood and Benoit-Bird In press)

Cipriano 1992 and Würsig et al. 1991

As part of the initial studies of duskies in New Zealand, researchers radio tagged live duskies (Würsig *et al.* 1991, Cipriano 1992) and studied the gut contents of incidentally caught or beachcast duskies (Cipriano 1992) between January 1984 and February 1988. This approach allowed them to quantify both individual night foraging behavior and diet composition. Ten duskies near Kaikoura were outfitted with radio tags. The tags were monitored day and night from elevated shore stations, providing the first glimpse of night-time behavior. Dive duration was quantified by timing signal silences caused by dolphins diving below the surface. Dives less than 30 seconds were assumed to be part of the respiration pattern, and those greater than 59 seconds were considered feeding dives (Würsig *et al.* 1991, Cipriano 1992). The stomach and guts of 26 individuals were removed and opened. All hard parts, otoliths, squid beaks, eye lenses, intact crustaceans, and mandibles/jaws were sorted, counted and preserved separately. Prey were identified to species, when possible, and the minimum number of individuals consumed was estimated for each species or group (Cipriano 1992).

Benoit-Bird et al. 2004

Over the course of four nights during one week of the austral winter of 2002, researchers towed an echosounder along transect lines that crossed the Kaikoura Canyon (Fig. 14 illustrates the towing arrangement). The echosounder used a 130 μ s, 200 kHz pulse, and transmitted its signal downward in a 10° cone. The echosounder could detect dolphins and prey as deep as 156 m. The echosounder was connected directly to an onboard laptop computer, and returning echoes were displayed in real time as a series of

calibrated colored dots. Additionally, onboard observers scanned for dolphins and recorded dolphin surface behavior.

Benoit-Bird et al. In Press

In the late austral summer of 2006, a team set out to examine the effects of nighttime light patterns on DVM and dusky foraging behavior. On seven nights, spread unevenly across two lunar cycles, the team towed a newer-generation three echosounder array along transects that crossed the Kaikoura Canyon. The transects were located in the same general area, but were not the same, as those used in the previous study. A 38-kHz echosounder used a pulse length of 512 μ s, projected its signal in a 12° conical beam, and could detect targets down to depths of 1000 m. The 120- and 200-kHz echosounders each used a pulse length of 256 μ s, projected signals in a 7° conical beam, and could detect targets up to 300 and 200 m, respectively. At the conclusion of this study, the team was able to compare both dusky and DSL behavior between summer 2006 and winter 2002, and, in limited fashion, across lunar periods.

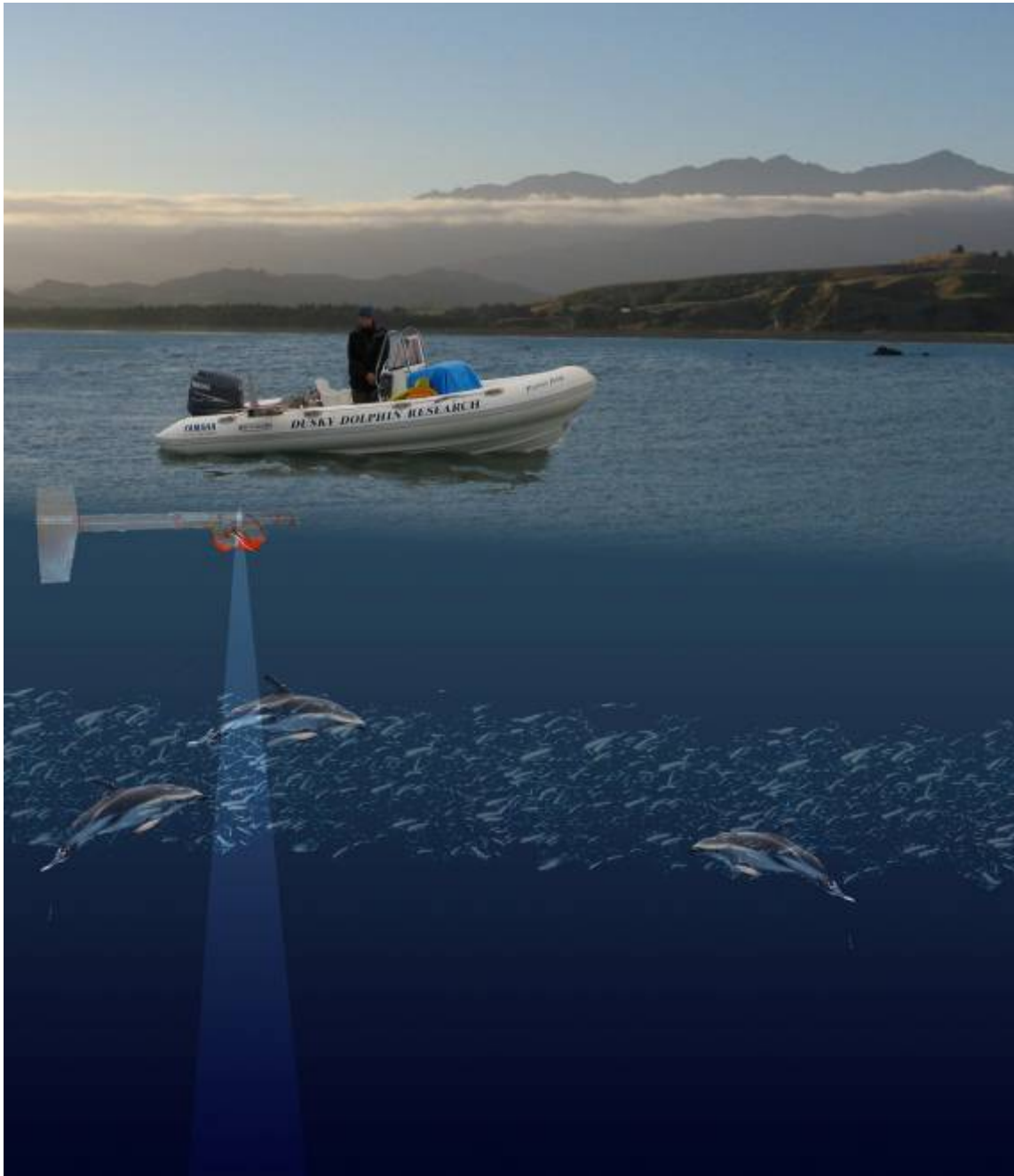


Figure 14. Towing Arrangement. This cartoon depicts the typical arrangement of the boat, the towfish, and the targets during acoustic surveys. The towfish was lowered to approximately 1m below the surface, and towed slightly behind the boat at 3-5 knots. The echosounders use conical sound beams pointed downwards, towards the bottom. The sound bounces off objects in its path, such as dolphins or fish, and returns to the echosounders (From Dahood and Benoit-Bird In press).

RESULTS

Each study was the first to describe a particular aspect of dusky night foraging, and as a result generated questions for future research. The first study quantified dive times of individuals, and, paired with gut content analyses, indicated that duskies were carrying out deep foraging dives at night (Cipriano 1992). The second study confirmed that duskies were diving at night on the rising DSL and explored how duskies interacted with the DSL during dives (Benoit-Bird *et al.* 2004). The third study examined how night-time light regimes, which influence DVM, might affect dusky dolphin interactions with the DSL (Benoit-Bird *et al.* in press). I briefly discuss the major findings from the studies below.

Cipriano 1992 and Würsig et al. 1991

Tracking confirmed that dolphins moved offshore, into deeper waters, at night. The frequency of both short and long dives increased at night and was interpreted as an increase in deep foraging dives coupled with more “recovery” respirations. Based on dive times alone, Cipriano hypothesized that, at night, duskies dove to 75-200 m, depths consistent with foraging on the rising DSL (Würsig *et al.* 1991, Cipriano 1992). Gut contents analysis of stranded dolphins confirmed that duskies were primarily eating lanternfishes and squids, species commonly associated with the DSL, and illustrated that diet composition changed seasonally. The diversity of lanternfish species was greatest in summer and the proportion of squid eaten increased in winter (Cipriano 1992). This work supported the hypothesis that duskies feed at night on the DSL, but provided no direct observations of foraging behavior. However, this study could not determine when

and at what depths duskies interacted with the DSL, and if they did so individually or in coordinated groups.

Benoit-Bird et al. 2004

This study provided the first observations of duskies overlapping spatially and temporally with the DSL. Dusky dolphins and the DSL were readily distinguished from each other and the background by unique characteristics of the returning echoes (Fig. 15). The simultaneous acoustic and surface visual observations showed that dusky dolphin surface behavior was not a good indicator of night-time foraging. Surface behaviors commonly associated with foraging began 2 hours before duskies overlapped with the DSL or other possible prey concentrations in the upper 130 m of the water column. Once the DSL crossed this threshold, duskies tracked it, diving about 1 m deeper than the shallowest area of high prey concentration, until the high concentration region sunk below 130 m. The DSL was accessible to dusky dolphins for about 12-13 h and attained a minimum depth between 29-49 m during the winter study period (four days sampled during one week).

As the DSL changed depth, foraging tactics changed. Dolphins dove individually when the layer was deep and formed coordinated subgroups of up to 5 animals when the layer was near the top 40m of the water column. Group size increased as the DSL approached the surface, and declined when the DSL started its descent after midnight. When dolphins were interacting with the DSL, they were most often detected in small subgroups; when dolphins were detected outside of the DSL, they most often swam alone. Of approximately 960 dolphin detections, including non-foraging animals,

approximately 300 were individual dolphins, 240 were pairs, 200 were groups of three, 160 were groups of four, and 60 detections were of groups of five (from Fig 4 in Benoit-Bird *et al.* 2004). The remote echosounding technique could not determine whether prey herding was taking place (Benoit-Bird *et al.* 2004).

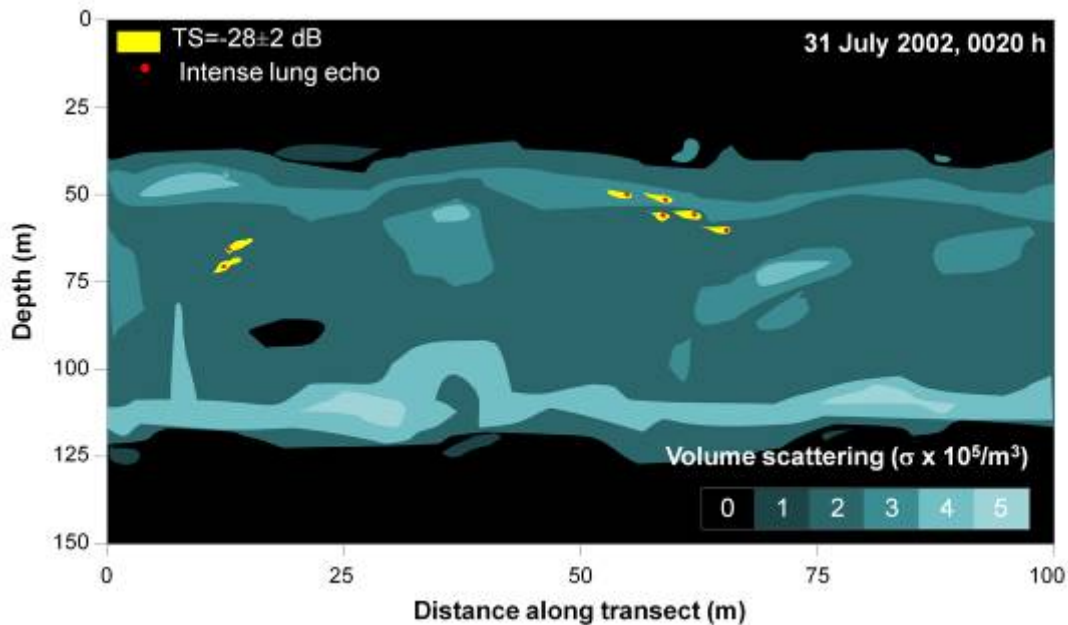


Figure 15. Processed Echoes from 2002. Echoes returning from the DSL, dolphins, and other objects are received by the echosounders and plotted in real time by a shipboard computer. These data were collected during the winter of 2002. The DSL is shown in blue-green as sound scattering isosurfaces. Echoes from dusky dolphins are indicated by the yellow points consistent with a narrow range in target strength (TS) values. These values surround a single extremely strong echo that is likely from the lungs of each dolphin. The coordinated dolphin subgroups that characterized the 2002 study are clearly visible. This “snapshot” was chosen because of its exceptional clarity (Figure redrawn from Benoit-Bird *et al.* 2004).

Dolphin diving behavior in this brief winter study was closely tied to the movements of the DSL and foraging tactics were flexible on the scale of one night. However, the diel vertical migration of the DSL in other regions is known to change

with season, and lunar phases (Clarke 1970, Blaxter 1974, Koslow 1979, Haney *et al.* 1990, Balino and Aksnes 1993), and it is still unknown how these changes would affect dusky diving behavior.

Benoit-Bird et al. In press

By sampling on seven nights across two lunar cycles, this study was the first to investigate lunar-scale changes in light levels on the DSL and dusky behavior. Comparison with the data collected in the winter of 2002 offered insight into potential seasonal patterns. Night-time light appeared to affect DSL behavior and the amount of time dusky forage. The general characteristics of the summer DSL, including relative abundance and minimum depth of approximately 35 m, were similar to the winter DSL, but in summer the layer was shallower than 150 m for only 7-9 h. As in winter, dusky tracked the DSL, diving within the layer, though they were not consistently 1m deeper than the shallowest area of high concentration. No other significant seasonal differences were discernable in the DSL (Benoit-Bird *et al.* in press), although it is possible that the layer composition or distribution of preferred prey changed seasonally and went undetected. Such changes could influence seasonal changes in dusky movement patterns and behavior.

Unlike winter 2002, summer 2006 surveys did not detect coordinated subgroups. Rather, dusky appeared to be part of larger and loosely organized groups (Benoit-Bird *et al.* in press). The time the layer is accessible, and the amount of dive time required to reach the DSL, may influence subgroup formation; however, we do not yet understand the mechanism of this complex relationship. Distribution of prey items within the DSL

may influence the effectiveness of subgroups, but it has not been possible to assess the distribution of specific prey types within the Kaikoura DSL.

Despite limited sampling, lunar cycle trends were evident in both DSL behavior and dusky dolphin relative abundance. Maximum and mean backscatter, measures of the density of animals detected, both decreased with decreasing lunar illumination, *i.e.* approaching the new moon (Fig. 16). Additionally, the number of larger animals, on the scale of 10 cm, present in the DSL increased with decreasing lunar illumination. Finally, the amount of time the DSL was accessible to duskies increased with decreasing lunar illumination; the layer was in the top 150 m of the water column for approximately 9 h during the new moon and 7 during the full moon. There was a general trend of dusky dolphin relative abundance decreasing with decreasing lunar illumination, and no dolphins were observed during the one new moon night sampled.

DISCUSSION

Over the past 20 years of dusky research, it has been speculated (Cipriano 1992) and confirmed (Benoit-Bird *et al.* 2004) that duskies interact with the DSL as it rises at night. Based on seasonal diet change Cipriano (1992) speculated, and Benoit-Bird *et al.* (in press) confirmed by active acoustic techniques that duskies employ seasonally specific foraging tactics. Seasonal and monthly changes in night-time light seem to affect the DVM of the DSL in Kaikoura (Benoit-Bird *et al.* in press). There may be a minimum time the DSL must be accessible for duskies to form coordinated subgroups, or the choice between coordinated and solo feeding may be more strongly influenced by changing prey patterns within the DSL. More questions are raised by the lack of dolphin

sightings during the new moon when the DSL is available for the longest period during summer. It is highly unlikely that duskies simply do not forage during the new moon. They must either finish foraging quickly and move on to other activities or forage outside of the study area (Benoit-Bird *et al.* in press). To better understand dusky nighttime foraging choices, future work will need to more closely examine changes in DSL composition and the effects of light on both the DSL and dusky behavior.

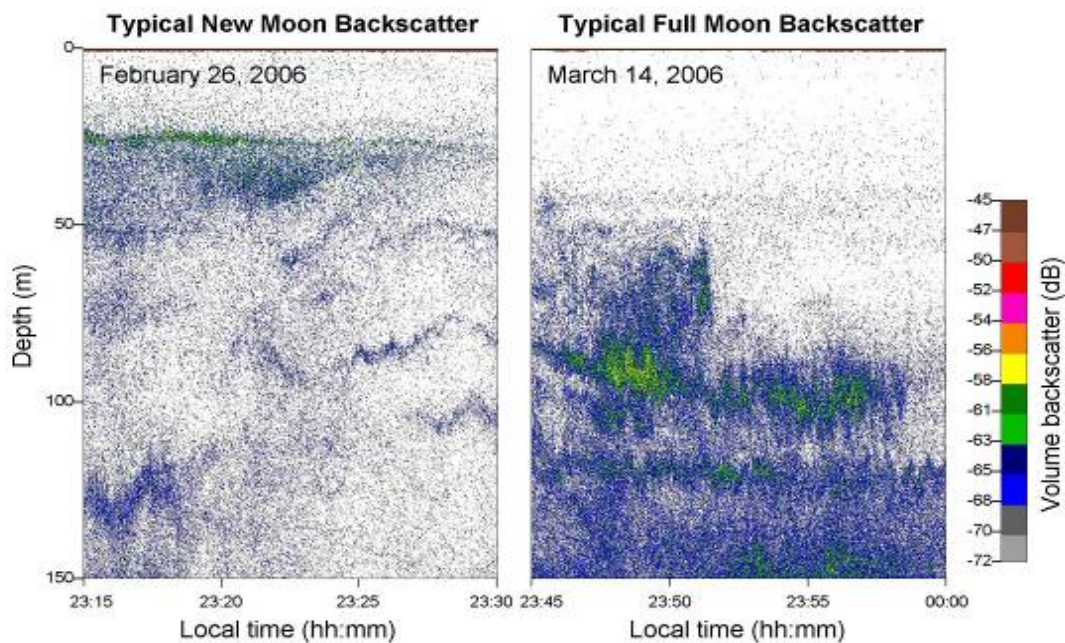


Figure 16. Raw Echoes from the 120kHz Echosounder. Depth is on the y axis; the top 150m of the water column are displayed. The x axis shows local time. Fifteen minutes of data are shown for each night. The color of the dots represents the intensity (dB) of the echoes and is a rough indication of the density of scatterers. These “snap shots” illustrate the trend of more scattering, and therefore more organisms, with increasing lunar illumination. There is also a clear trend of decreased scattering in the upper 50m of the water column with increasing lunar illumination. At 11:30 at night during the new moon, there is a concentration of organisms in the upper 50m. During the full moon, the area of concentration is deeper than 50m at midnight (From Dahood and Benoit-Bird In press).

Observations of feeding dolphins have shown duskies to be highly flexible in their foraging tactics (Cipriano 1992, Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press). Their ability to echolocate likely allows them to forage more easily in the dark than exclusively visual predators. Some duskies in New Zealand switch between shallow-water prey herding and individual foraging in Admiralty Bay in the winter to deep-water night foraging when in Kaikoura (Markowitz 2004, Benoit-Bird *et al.* in press). When night foraging, duskies can forage in a coordinated manner or in loosely organized groups (Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press). The decreasing abundance of foraging dolphins approaching the new moon (Benoit-Bird *et al.* in press) hints that duskies may use lunar phase specific foraging tactics. Additionally, seasonal change in diet (Cipriano 1992) suggests that duskies may use seasonally specific foraging tactics to accommodate a changing prey base. The decision to forage at night in Kaikoura is likely influenced by the predictability and abundance of prey in the DSL. The mechanisms for choosing the particular night foraging tactics are unknown, though the choice may be influenced by night-time light levels (Benoit-Bird *et al.* in press).

According to optimality models, animals choose foraging tactics to maximize net caloric gain and thereby improve fitness (Pyke *et al.* 1977). Duskies rarely forage during the day in Kaikoura (Cipriano 1992, Markowitz 2004) but commonly forage at night on the shallowest area of high prey concentration (Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press). Day foraging by herding prey is likely unprofitable in this area; the Kaikoura Canyon dominates the bathymetry (Lewis and Barnes 1999), making shallow water habitats favored by schooling prey scarce. Deep-water fishes and invertebrates

associated with the canyon form an abundant prey base for duskies (Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press), but they are out of the dolphins' diving range until the DSL enters the top 150 m of the water column at night (Benoit-Bird *et al.* 2004). Deep dives are energetically expensive (Williams *et al.* 1999); duskies experience a higher net gain per prey item when the DSL is closest to the surface. Therefore, shallow foraging dives at night are likely the most energetically profitable foraging tactic in Kaikoura.

In the patchy open ocean environment, duskies may forage in groups to improve foraging efficiency (Eklov 1992) or prey detection capabilities (Baird *et al.* 2001), or to reduce their individual risk of predation (Hamilton 1971). Off Kaikoura, duskies were detected foraging in groups both during the winter (coordinated subgroups: Benoit-Bird *et al.* 2004) and summer (loosely organized larger groups: Benoit-Bird *et al.* in press). In winter, formation of coordinated subgroups increased with patchiness within the DSL; there was no evidence of active concentration of prey by dolphins (Benoit-Bird *et al.* 2004), although it is possible that such efforts or resulting prey concentrations went undetected. The size of dolphin subgroups increased as the DSL approached the surface, implying that groups become more effective as prey density decreases and as dolphins spend less time travelling to and from the surface to the prey (Benoit-Bird *et al.* 2004).

Predation pressure may influence the type of groups formed. Larger coordinated groups may be detected more easily by predators (Ioannou and Krause 2008). In summer, when killer whale sightings (Dahood *et al.* 2008) and large black shark and seal

shark (Family Dalatiidae) catches are highest⁴, duskies forage in larger loosely organized groups (Benoit-Bird *et al.* in press). These dispersed groups may allow duskies to detect their predators more readily while not drawing the predators' attention as much as a closely coordinated subgroup. Because there is little evidence of prey herding in Kaikoura at night, it is likely that the advantage of group foraging lies in increased prey detection capabilities, increased safety from predators or both.

Night-time light regimes appear to influence foraging tactics employed by duskies (Benoit-Bird *et al.* in press), likely through changes in DSL composition and the timing and extent of diel vertical migration (Clarke 1970, Blaxter 1974, Balino and Aksnes 1993). Most studies of duskies in New Zealand have focused on seasonal changes in behavior or diet (see Cipriano 1992, Markowitz *et al.* 2004 and, Dahood *et al.* 2008), and acoustic studies confirm that there are significant seasonal differences in the timing of DVM (Benoit-Bird *et al.* in press). Recent studies indicate that changes in DVM and dusky behavior over the lunar cycle may be equally dramatic as seasonal changes (Benoit-Bird *et al.* in press). As lunar illumination decreases, the time the DSL is in the upper 150m of the water column increases, the proportion of larger animals in the DSL increases, and dusky relative abundance decreases (Benoit-Bird *et al.* in press). Together, these findings imply that duskies use lunar phase specific foraging tactics, which has been noted for juvenile Galápagos fur seals (*Arctocephalus galpagoensis*; Horning and Trillmich 1999) .

⁴ Peter Bradshaw, Encounter Kaikoura, 96 Esplanade, Kaikoura New Zealand; July 10, 2006

Although data on dolphin abundance over lunar phase were limited, there was a trend of decreasing dolphin relative abundance with decreasing lunar illumination. There are several potential explanations for the scarcity of dolphin sightings approaching the new moon. While night-time light levels are low, at times there may be sufficient illumination to allow effective vision. In low lunar illumination conditions, foraging efficiency may be improved by limiting the prey's ability to detect dolphins, the decreased depth of the prey, or by the greater availability of larger prey items with higher number of calories per item, or all of these. Under such conditions, dolphins may satiate quickly and move out of the area to pursue other activities. Conversely, foraging efficiency in low light conditions may be inefficient if the dolphins rely on moonlight to detect prey. Under such conditions, dolphins may choose to give up potentially inefficient night foraging in dangerous canyon waters to remain in safer or more profitable areas.

Night-time light levels seem to affect both duskiess and their prey. However, the relationships between night-time light levels, DVM, and dusky behavior are complicated. The dolphins' ability to detect and capture prey may be affected directly by changing light levels to or duskiess may respond to light induced changes in DSL behavior and composition. This uncertainty raises tantalizing questions about the flexibility of dusky dolphin foraging tactics, particularly at relatively short time scales.

CONCLUSIONS

At every temporal scale studied (nightly, seasonal and now lunar), duskiess show great flexibility in foraging behavior. Duskiess are able to switch between day and night

foraging (Benoit-Bird *et al.* 2004, Markowitz 2004), an ability that has been noted in other non-visual foragers (Beauchamp and McNeil 2003, Shimek 1997, Ribic 1982). Light appears to be important to night foraging dolphins and influences the tactics they use (Benoit-Bird *et al.* in press). Unlike day foraging, where it is well established that light is essential for prey detection and capture (Würsig *et al.* 1990, Beauchamp 2007, Vaughn *et al.* 2007) and the maintenance of social groups of land animals (Beauchamp 2007), studies are only just beginning to unravel the complicated relationship between duskie, their DSL prey, and night-time light.

CHAPTER V

SUMMARY AND CONCLUSIONS

INTRODUCTION

Abiotic factors are easily measurable and therefore often serve as proxies for less easily measured biological factors, such as access to prey or refuge from predation. For example, in terrestrial systems, landscape characteristics such as slope, aspect, elevation, and distance to roads mediate interactions between wolves and elk, and are measured to represent predation risk (Hebblewhite *et al.* 2005). In aquatic systems, measurements of sea surface temperature, salinity, and underlying bathymetry all serve as proxies for cetacean access to prey (reviewed in Ballance *et al.* 2006). The current study explored dusky dolphin occurrence and movement patterns relative to the abiotic factors of depth, distance from shore, and distance from the Kaikoura Canyon across three temporal scales. Further, I reviewed all studies conducted on night foraging dusky dolphins in Kaikoura and explored patterns across seasonal and lunar scales.

SUMMARY OF FINDINGS

Across all three data sets, dusky dolphins exhibited strong seasonal patterns. Both the systematically gathered shore-based data and the tour operator data illustrated that, in winter and spring, dolphins were found farther offshore, in deeper waters, with core areas contained almost entirely inside the canyon. The tour operator data further illustrate that while summer 95% Kernel Home Range (KHR) has shifted north since

2000, the location and size of summer core areas has remained relatively stable since 1995. The systematically gathered shore-based data show that dolphins travelled faster and made more gradual turns in winter than in summer. Studies of night foraging behavior indicate that dolphins use seasonally specific foraging tactics. In winter, when prey are available approximately four hours longer than summer, dolphins foraged in coordinated subgroups, while in summer dolphins foraged in loosely organized groups (Benoit-Bird *et al.* in press).

Dolphins exhibited strong diel, but not tidal, occurrence and movement patterns. Dolphins were found travelling faster, farther offshore, in deeper waters with core areas contained almost entirely within the canyon approaching sunset.

COMPARISON TO PREVIOUS STUDIES

The current work agrees with earlier studies conducted in both Argentina and New Zealand that dusky dolphins are found closer to shore, in shallower waters, in summer (Würsig and Würsig 1980, Cipriano 1992, Brown 2000, Markowitz 2004, Garaffo *et al.* 2007) and in the morning (Würsig and Würsig 1980, Cipriano 1992, Markowitz 2004). Similar to duskies living in Golfo San Jose, Argentina (Würsig and Würsig 1980), duskies living near Kaikoura move farther offshore, into deeper water, and travel faster approaching sunset. The dolphins' affinity for the canyon and their diel shift offshore were noted previously (Cipriano 1992, Brown 2000, Markowitz 2004). The current study adds that dolphins also travelled faster approaching sunset. The observation that dolphins make sharper turns in summer is consistent with a higher

prevalence of “zig zag swimming” (Cipriano 1992) and sexual displays (Markowitz 2004) during summer.

This study agrees with Brown (2000) that the areas of highest density of dolphin sightings were south of the Kaikoura Canyon head during the late 1990’s. Comparing the findings to Cipriano’s (1992) sightings records from the 1980’s, Brown (2000) concluded that dolphins shifted south to avoid disturbance from tour boats. However, the tour-operator data presented in Chapter III do not agree with this conclusion. KHR analysis revealed that dolphin core areas were of comparable size and location from 1995 to 2006. With increasing tourism activities, the 95% KHR shifted significantly north, closer to the commercial boat ramp, over the same time period. This implies that some factor, other than the number of boats visiting dolphins, was likely responsible for the more southerly location of dolphin sightings during the late 1990’s.

With the exception of Markowitz (2004) and Brown (2000), authors of earlier studies concluded that dusky seasonal and diel occurrence and movement patterns are likely influenced by both prey availability patterns and predation risk (Würsig and Würsig 1980, Cipriano 1992). Observations of night foraging duskies (Cipriano 1992, Benoit-Bird *et al.* 2004, Benoit-Bird *et al.* in press) indicated that the deep scattering layer (DSL) experienced seasonal and lunar scale changes in the timing of migration and in layer composition. Off Kaikoura, dolphin seasonal occurrence patterns seem correlated with killer whale (*Orcinus orca*) attendance patterns; at times of year when killer whales were most commonly seen, dolphins were found in near-shore shallow waters. Therefore, this study agrees with these earlier studies: dusky dolphin occurrence

and movement patterns likely reflect an effort to maximize access to prey while minimizing predation risk. However demographic factors such as the presence of newborn calves in summer or the existence of seasonally specific resident dolphins (Markowitz 2004) may also influence seasonal patterns.

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VITA

Name: Adrian Danielle Dahood

Address: Marine Mammal Research Program
Texas A&M University
5007 Ave U
Galveston, TX 77551

E-mail Address: adahood@gmail.com

Education: B.S., Zoology, and B.S., Fisheries
University of Washington, Seattle, 2001

M.S., Wildlife and Fisheries Sciences, Texas A&M University
College Station, 2009