

BEHAVIORAL FLEXIBILITY OF FEEDING DUSKY DOLPHINS
***(Lagenorhynchus obscurus)* IN ADMIRALTY BAY, NEW ZEALAND**

A Thesis

by

CYNTHIA JOY MCFADDEN

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

December 2003

Major Subject: Wildlife and Fisheries Sciences

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ABSTRACT

Behavioral Flexibility of Feeding Dusky Dolphins (*Lagenorhynchus obscurus*) in

Admiralty Bay, New Zealand. (December 2003)

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Chair of Advisory Committee: Dr. Bernd Würsig

Foraging theory suggests that hungry animals balance a complex set of costs and benefits when determining what and how to eat. Prey distribution, patch size, and the presence of conspecifics are important factors influencing a predator's feeding tactics, including the decision to feed individually or socially. Dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand employ different feeding tactics in varying habitats and seasons. I used programmed survey routes and opportunistic sightings to examine the habitat use and feeding mechanics of dusky dolphins in Admiralty Bay, New Zealand, a protected shallow-water environment frequented by wintering dolphins. I encountered 253 dolphin groups, of which 58.5% were engaged in food-acquisition activities. Photographic efforts revealed a total of 177 individually-recognizable dolphins, 100 of which were returnees from previous seasons. Thirty-seven feeding groups and 70 bouts of feeding behavior were followed. Two-minute interval sampling as well as active acoustic sonar were used to test the hypothesis that diurnally-feeding dolphins would work in a coordinated manner to bring schooling fish to the surface. Feeding tactics observed in Admiralty Bay were then compared to foraging by some of the same

animals in the unprotected, deep-water environment off Kaikoura, where large numbers of dusky dolphins feed during the night on organisms associated with a vertically-migrating scattering layer. Evidence supporting coordinated surface feeding was not statistically significant, but indicative of behavioral flexibility in feeding styles as part of a larger feeding repertoire. A potential shift in prey distribution from previous years may also explain some observed patterns. Feeding groups were positively correlated with seabirds and New Zealand fur seals (*Arctocephalus forsteri*). Mean group size of 6.1 (\pm 8.23 S.D., n=253) in Admiralty Bay is dramatically less than groups observed off Kaikoura, a variation likely reflecting differences in prey number and distribution, as well as differences in predation risk by deep-water sharks and killer whales. Behavioral flexibility likely confers an adaptive advantage for species subject to environmental fluctuation, whether due to natural or anthropogenic sources. Further research is necessary to evaluate prey distribution in Admiralty Bay and its possible effects on feeding dusky dolphins.

DEDICATION

This thesis is dedicated to my parents, Mike and Pam McFadden, for supporting me throughout my financially insane decision to quit my job, sell my house, and pursue my dream. I love you both.

ACKNOWLEDGEMENTS

This work would not have been possible without the help of so many wonderful people. First of all, I thank my parents, Mike and Pam McFadden, for their unending support - financial, emotional, and physical (all those moves!!). My research assistants helped make my life so much easier when I was busy stressing out over the lack of dolphins in Admiralty Bay. Thank you so much Tim Markowitz for your unending good humor, patient advice, adept photographic skills, movie nights in Danny's basement, and really bad dancing skills (John Travolta medley on the boat trailer at dusk – in a Mustang suit, no less)!!! I will never look at floating cows or killer penguins in quite the same way! I also thank Kathy Young, Patrice Irvine, Brigid O'Leary, Laura Boren (go seals!), and Philippa Brakes for their capable assistance, keen eyesight, deft recording skills, and good humor. Danny and Lyn Boulton were most gracious hosts and kept us up to date on the latest political/environmental events in the Marlborough Sounds. The fresh scallops were fabulous, and thank you for allowing us to dig up your carpark to install the phone line! Rob and Annika Schuckard helped with fish and seabird information in Admiralty Bay and treated us to dinner at their own private beachfront paradise. Mel Würsig was an invaluable logistic aide and able “bunny driver”. Mr. B. Nose helped steady the GPS and provided much-needed moral support.

Our sonar work was aided by the expertise and generous assistance of Dr. Whitlow Au and Kelly Benoit-Bird of the University of Hawaii. Ron Peterson of Kaikoura donated the use of two heavy-duty batteries for our use in Admiralty Bay, and

was a great help to us with vehicular matters. Jon Jolly helped us negotiate the lease of the Imagenex 881a sonar unit from his private collection of marine archaeological equipment.

This work was generously supported by a grant from the Marlborough District Council, and I especially thank Hans Versteegh, Keith Heather, and Brian Dwyer for recognizing the value of basic research into dusky dolphin ecology. I was also supported by a grant from the Lee and Louis Kuhn Foundation, as well as assistance via a Regent's fellowship and Association of Former Students fellowship from Texas A&M University. A portion of my analysis was assisted by the Finscan grant through the National Science Foundation.

While I was away in New Zealand, my dear animals were capably cared for by Gigi and Alex Bormann and Tricia Hamilton. Your updates and news from the homefront helped me greatly when I missed my “furry kids”.

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CHAPTER I

INTRODUCTION

Animals are driven by their need for predator avoidance and suitable resources. Whether measured as food, water, suitable habitat, mates, appropriate nesting/nursery sites, or shelter; life and death revolve around the ability to find and utilize those resources necessary in a particular environment. Survival in all species requires feeding to maintain energy stores and permit the physical processes associated with growth and reproduction. Resources associated with feeding may include the type and size of prey patches and individual prey items, as well as their temporal and spatial distribution. Generalist species capable of locating and utilizing a wide variety of food sources should have an advantage over specialist species restricted in dietary preference or geographic locale, especially when food is scarce or patchily distributed (Krebs and McCleery 1984, Pianka 1978).

In the search for adequate nutrition, many species find group foraging profitable over feeding individually [antelope, Jarman 1974; wolves (*Canis lupus*), Mech 1970; cetaceans, Norris and Dohl 1980; lions (*Panthera leo*), Schaller 1972; birds, Ward and Zahavi 1973)]. The primary advantages for group foraging include increased vigilance against predators and improved detection of scarce, patchy resources (Caraco 1987,

This thesis follows the style and format of Behavioral Ecology and Sociobiology.

Clark and Mangel 1986, Galef and Giraldeau 2001, Hamilton 1971, Pulliam and Caraco 1984). Additionally, other advantages deemed important in specific cases include an increased ability to subdue large prey, more effective resource defense, and increased efficiency in exploiting depletable forage (Clark and Mangel 1986, Galef and Giraldeau 2001, Packer and Rutan 1988). In this paper, I use the terms “group foraging” and “social foraging” interchangeably, meaning multiple animals locating and feeding from the same resource, using information gleaned from conspecifics or associated species to make individual foraging/feeding decisions (Galef and Giraldeau 2001). Foraging theory suggests that animals will act to maximize their food intake, and this goal may be influenced by such factors as prey patch size, presence and numbers of conspecifics feeding on the same patch, distribution of prey patches, and shared information between group members (Clark and Mangel 1986, Galef and Giraldeau 2001, Iwasa et al. 1981, Krebs et al. 1974, Ward and Zahavi 1973). In some instances, species may show true cooperative hunting behavior, where group members work together, resulting in an overall increase in per capita food intake over individual foraging up to some optimal group size, as has been demonstrated in killer whales (*Orcinus orca*) (Baird and Dill 1996), wild dogs (*Lycaon pictus*) (Creel and Creel 1995), and lions (Schaller 1972). Demonstration of cooperative hunting (rather than “coordinated” efforts) requires knowledge of comparative prey intake rates and caloric values, often unavailable under natural, and especially marine, field conditions. Additionally, use of the term “cooperative” implies knowledge of the relative fitness of each player, information again unavailable in most marine field conditions. I therefore avoid use of the term

“cooperative” in this study except when referring to previous research that specifically uses that term, and instead describe behaviors observed as “coordinated” when warranted.

Several well-studied cetacean species are characterized by group feeding specializations and complex social systems, notably killer whales (Baird 2000, Hoezel 1993, Similä and Ugarte 1993), humpback whales (*Megaptera novaeangliae*) (Jurasz and Jurasz 1979, Weinrich et al. 1992), and bottlenose dolphins (*Tursiops truncatus* and *T. aduncus*) (Hoese 1971, Shane 1990b, Smolker et al. 1997). That these species are adaptable and capable of exploiting a variety of food resources may be related to some combination of social learning, environmental variation (habitat and seasonal), and prey diversity (Connor 2001, Rendell and Whitehead 2001).

The dusky dolphin (*Lagenorhynchus obscurus*, or dusky for short) is a small delphinid inhabiting select areas of coastal temperate waters in the Southern Hemisphere. Dusky dolphins occur frequently in the waters off southwestern Africa, South America, and New Zealand, and to a lesser degree in waters surrounding several South Atlantic and southern Indian Ocean islands (Gaskin 1968, Van Waerebeek et al. 1995). Most research on this species has centered in Argentina and New Zealand, where studies have made significant progress in describing dusky social behavior, movement, genetics, and foraging habits (Cipriano 1992, Harlin et al. 1999, Harlin et al. 2003, Würsig and Würsig 1980, Würsig et al. 1997).

Research efforts on the behavior of dusky dolphins have concentrated primarily in two locations: Kaikoura, on the eastern side of New Zealand’s South Island, and the

waters off Patagonia, southern Argentina (Cipriano 1992, Würsig and Würsig 1980, Würsig et al. 1997). Despite similar latitudes, habitats and corresponding feeding tactics vary widely in these two areas. Golfo San José, Argentina (42° 20' S, 64° 20' W) is a shallow-water bay (<60 m) where small schooling fish support numerous scattered groups of socially-foraging dolphins. In this location, small groups of 8-12 dolphins scout for schools of southern anchovy (*Engraulis anchoita*) during daylight hours, often recruiting additional dolphin groups upon locating prey. Coordinated surface feeding is widely evident, with dolphin groups surrounding and containing prey against the water's surface. Dolphin groups are joined by feeding seabirds, and large prey schools may attract up to 300 dolphins and over 1000 birds, with feeding lasting for several hours (Würsig and Würsig 1980).

This contrasts with the habitat and feeding tactics exhibited by dusky dolphins in the waters around Kaikoura (42° 25' S, 173° 42' E). Here, the Subtropical Convergence and the deep Kaikoura Canyon combine to create a highly productive region of upwelling (Lewis 1998) where pelagic fishes, squid, and other species associate with a vertically-migrating Deep Scattering Layer (DSL) that is found as close as several hundred meters from shore in the Canyon. Water depths exceeding 1,000 m just over 1,000 m from shore allow dolphins to remain close to shore during the day, where they travel, rest, socialize, and care for young in large groups that may number up to 1,000 animals or more, yet provide easy access to scattering layer organisms for night-time feeding. Kaikoura dolphins feed at night on myctophid fish and squid associated with the scattering layer, moving offshore during the evening and diving to meet the

ascending layer, then returning to near-shore waters as morning approaches and food descends beyond the dolphin's reach (Cipriano 1992, Würsig et al. 1997). These differences in prey availability, species, and habitat necessitate that dusky dolphins exhibit very different foraging techniques in these two widely-separated populations.

Recent work conducted in another area of New Zealand is illuminating further aspects of dusky behavior. The Marlborough Sounds region, located on the northeast portion of New Zealand's South Island, is characterized by hundreds of kilometers of convoluted shoreline, encompassing many shallow-water bays and protected inlets. Dusky dolphins do not appear to use the entire Marlborough region equally, instead concentrating consistently during winter in Admiralty Bay ($40^{\circ} 56' S$, $173^{\circ} 53' E$) (Harlin et al. 2001, Markowitz et al. in press). Why dolphins gather here is unknown, but may be related to prey availability and/or the hydrography of the area. Waters passing through adjacent French Pass, a narrow shortcut from Cook Strait into Tasman Bay, are subject to tidal currents of up to 7 knots, and may be responsible for increased water mixing, primary productivity, and prey concentration. Photographic identification of marked individuals demonstrates that some of the same dolphins that frequent Kaikoura waters during the summer, feeding on mesopelagic organisms at night, migrate to the warmer waters of Admiralty Bay during winter months, where they appear to feed on a variety of schooling bait fish during daylight hours, apparently altering their feeding techniques in accordance with changes in habitat and prey (Markowitz et al. in press).

The opportunity to study behavioral variability in one population of animals in two different habitats makes dusky dolphins good models for examination of feeding

flexibility. Studies of dusky dolphin feeding in both Kaikoura and Argentina have been limited to examination of stomach contents, with little information concerning the mechanics of foraging and site use (Alonso et al. 1998, Cipriano 1992, McKinnon 1994). The physical habitat and prey species available in Admiralty Bay are similar to those of Golfo San José, Argentina, and similar dolphin feeding habits might be expected in these two widely separated populations. Information from the New Zealand population in the differing environments of Kaikoura and Admiralty Bay can be compared to feeding behavior in the Argentine dusky population. Ecological pressures influencing differences in observed group sizes can also be examined. Understanding the breadth of dusky foraging behavior between and within populations is important to answering questions of behavioral plasticity in this social species.

This study describes the habitat use and feeding behavior of dusky dolphins in Admiralty Bay, New Zealand, during winter 2002. Chapter II addresses photo-identification of marked individual animals, dolphin numbers, locations, as well as intra-specific interactions and behavioral states. Details of specific feeding behavior, as well as observations enhanced by remote-sensing of predators and prey with a modified acoustic “fish-finding” sonar are examined in chapter III. Summary and conclusions follow in chapter IV. The purpose of the study is to examine the following questions: Is feeding behavior in Admiralty Bay comparable to that seen in similar shallow-water environments? How does the winter feeding behavior of duskies in Admiralty Bay compare with the foraging behavior of the same animals in the summer off Kaikoura? How do group sizes vary between New Zealand and Argentine dusky populations?

What does this tell us about the ability of marine mammals to alter foraging behavior with season and locale to better utilize available resources? How do theories of social foraging correspond with observations of dusky feeding habits in these environments? The work represents basic science, but is also building a data set of habitat use and foraging strategies that may be useful for management/conservation purposes in the Marlborough Sounds and other areas.

CHAPTER II

HABITAT USE AND ABUNDANCE

Dusky dolphins are not currently listed as an endangered species; in fact, insufficient data exist for any real classification (Baillie and Groombridge 1996). In some areas of their range off South America, however, pressures from by-catch and directed fisheries subject populations to unsustainable levels of harvest, practices which may ultimately negatively impact the viability of those populations (Dans et al. 1997, McKinnon 1994, Van Waerebeek 1992, Van Waerebeek and Reyes 1990). While the New Zealand dusky dolphin population currently appears healthy, ongoing monitoring is necessary to ensure continued robustness and spot trends that could have potentially deleterious effects. Characteristics influencing the vulnerability of cetacean species to exploitation include proximity to shore, vulnerability to by-catch, and size, with larger cetaceans increasingly vulnerable due to their higher commercial value (Whitehead et al. 2000).

Dusky dolphins reside in coastal and continental shelf waters (Crespo et al. 1997, Van Waerebeek 1992), rendering them vulnerable to impacts from nearshore fisheries, tourism, and other forms of habitat degradation. Some of the same dolphins that frequent Admiralty Bay during winter spend their summers off Kaikoura, where they become part of an established multi-million dollar ecotourism industry (Fairweather and Simmons 1998). Currently, the impacts of ecotourism on these dolphins appear minimal, and with continued careful management by New Zealand resource agencies,

this situation should remain favorable for both conservation and financial interests (Barr and Slooten 1998, Würsig et al. 1997). Migration of these animals into warmer, more northerly waters in winter makes them susceptible to other potential coastal threats, such as habitat modification and chemical run-off from nearby agriculture (Whitehead et al. 2000). As habitat modification via mussel farming in Admiralty Bay may impact wintering dusky dolphins, it is important to gather data on the importance of this area for the dolphins.

Before exploring the foraging tactics of dusky dolphins, it is important to understand their habitat use and abundance patterns. Comparisons of data from previous field seasons can provide useful information on demographic shifts, or alterations in environmental conditions. Photo-identification is a useful method of following individually-marked animals over multiple field seasons, allowing seasonal abundance estimates and insight into social relationships. Group movements of predators can reveal prey distribution, and behavioral budgets can demonstrate the importance of certain habitats for specific functions, such as mating or feeding. An understanding of basic biology can then lead to more detailed questions and hypothesis-driven behavioral inquiry. This chapter explores the behavioral biology and abundance of dusky dolphins in Admiralty Bay, New Zealand.

MATERIALS AND METHODS

Study location and survey procedures

Admiralty Bay is located in the Marlborough Sounds region of New Zealand's South Island, bounded to the northwest by D'Urville Island (Fig. 1. Maps modified using ArcGIS ArcMap v. 8.2, base map courtesy of Eagle Technology, Wellington, NZ). It is oriented primarily north-south, with the mouth opening north-northeast into Cook Strait. For purposes of analysis, I divided Admiralty Bay (AB) into two adjacent areas: Inner AB and Greater AB, with the headlands of Clayface Point and Whangapoto Point indicating the demarcation line between the two areas. Inner AB is approximately 7 kilometers long and between 3 and 6 kilometers wide. Greater AB encompasses that area outside Inner AB, up to Bonne Point on D'Urville Island in the north, French Pass to the west, and extending to Clay Point in the east (Fig. 2).

Depths in Admiralty Bay are uniformly shallow, never reaching more than 46 m in the Inner Bay (NZ 6152, Land Information New Zealand). A maximum depth of 105 m occurs in a very limited area immediately east of French Pass, where daily tidal flows through this narrow passage have created a scoured bowl of turbulent rips. Water flow through Inner AB moves in an approximate counter-clockwise direction, regardless of tide (Kuku Mara Partnership 2000). The substrate is primarily mud. As of winter, 2002, 44 mussel farms were positioned around the periphery of Inner AB within 200 m of shore.

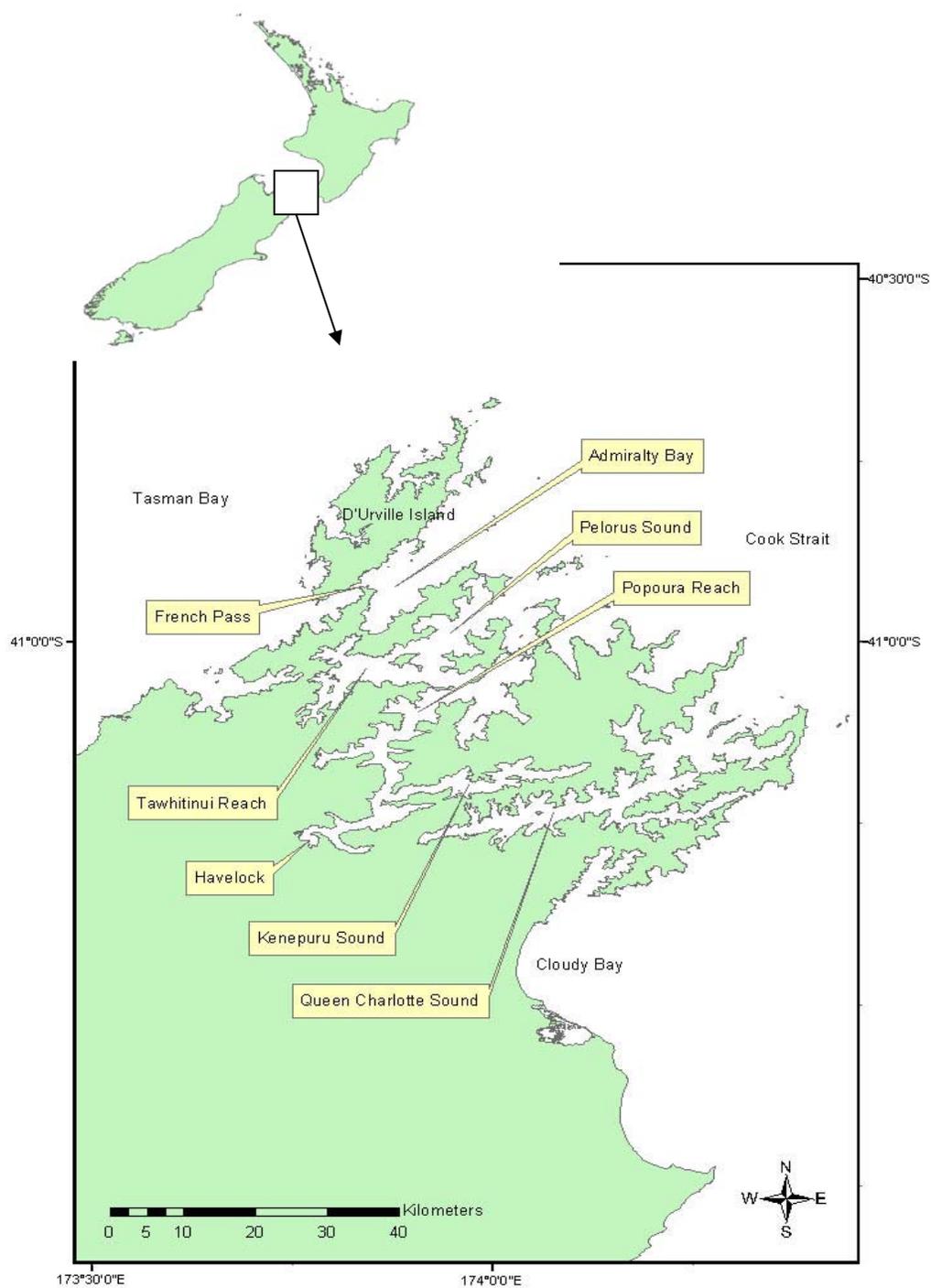


Fig. 1 Marlborough Sounds region of New Zealand's South Island.

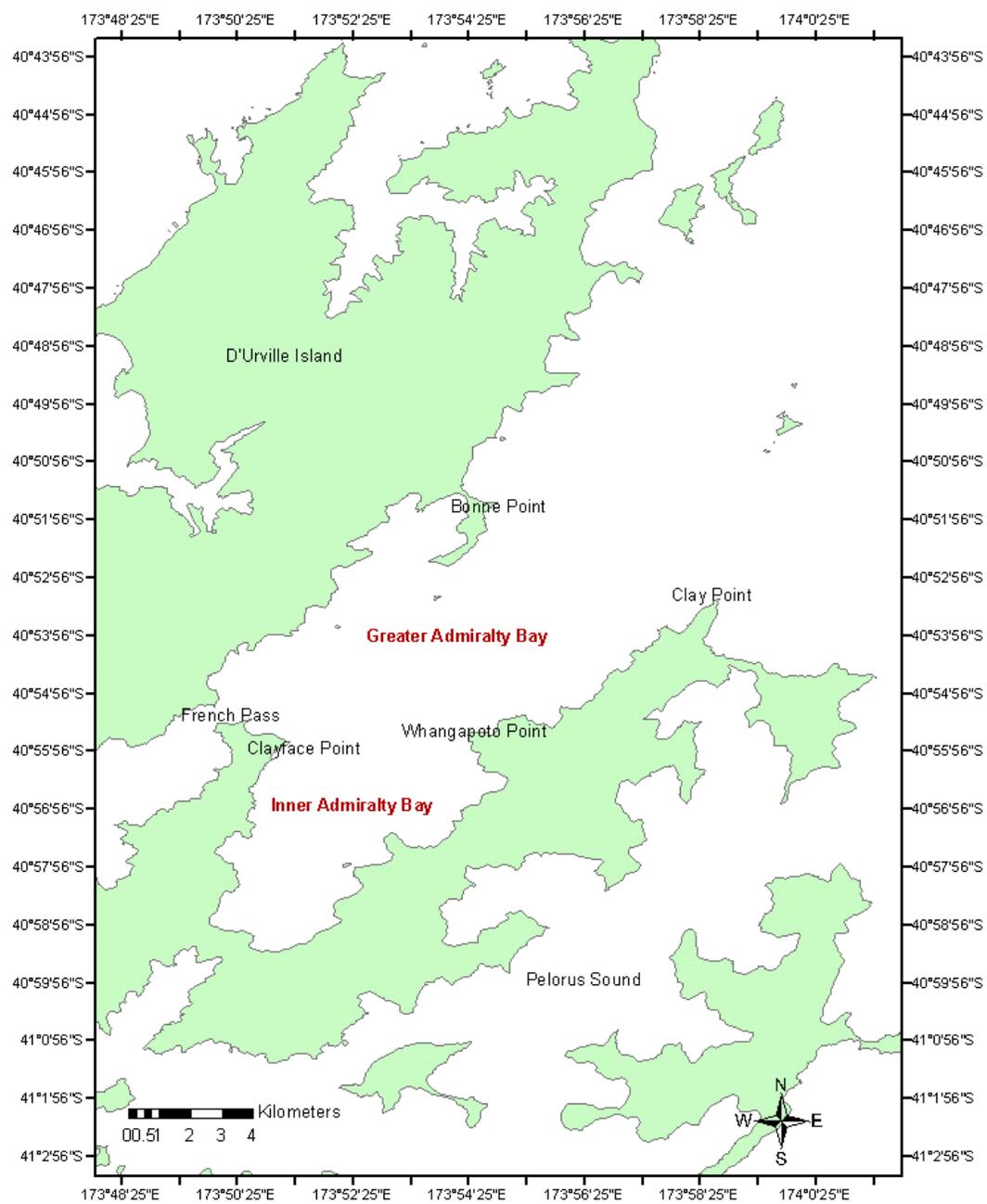


Fig. 2 Inner and Greater Admiralty Bay study areas.

Based on previous research (Markowitz et al. in press), I focused efforts on Inner AB, with occasional forays into Greater AB if no dolphins could be located otherwise. Sightings of dolphin groups were made both opportunistically and by use of systematic survey routes pre-programmed into a Garmin 12XL global positioning device, which automatically recorded my location every 2 minutes. A 5.5 m rigid inflatable boat (Better Boats, Christchurch, NZ) with Yamaha 85 horsepower two-stroke outboard motor was used to survey first Inner AB, then Greater AB as necessary to find dolphins. Two or three observers were present at all times. I searched for dolphins on all days weather permitting, from approximately 30 minutes after dawn until darkness or adverse weather ended efforts. Weather was considered appropriate for sighting dolphins if less than Beaufort 4 (many whitecaps). Survey track lines were set approximately 0.5 nautical miles (nm, 0.9 km) apart, providing observers with a search area of approximately 400 m on either side of the boat, and extended to within 500 m of shore. Survey lines used for the 2002 field season were modified slightly from those used by Markowitz et al. (in press), extending north approximately 0.25 nm (0.46 km) beyond the previous route to enhance Inner Bay coverage (Fig. 3).

Surveys were conducted at speeds of 10-12 knots (19-22 km/hr). Environmental data were collected at waypoints stationed on each line at opposite ends of the bay. Environmental parameters measured (and instruments used) were water temperature (thermometer), wind speed (anemometer), wind direction (compass), sea state (Beaufort scale), salinity (refractometer), and turbidity (Secchi disk). Visibility was estimated subjectively, based on sun glare, fog, haze, cloud cover, sea state, rain, and any other

conditions possibly affecting our ability to sight dolphins. Visibility was rated as excellent, good, fair, poor, or unacceptable. Surveys were terminated in unacceptable conditions, and speeds were reduced in poor conditions to minimize the risk of missing dolphin groups. To reduce the risk of surveying the same part of the bay at the same

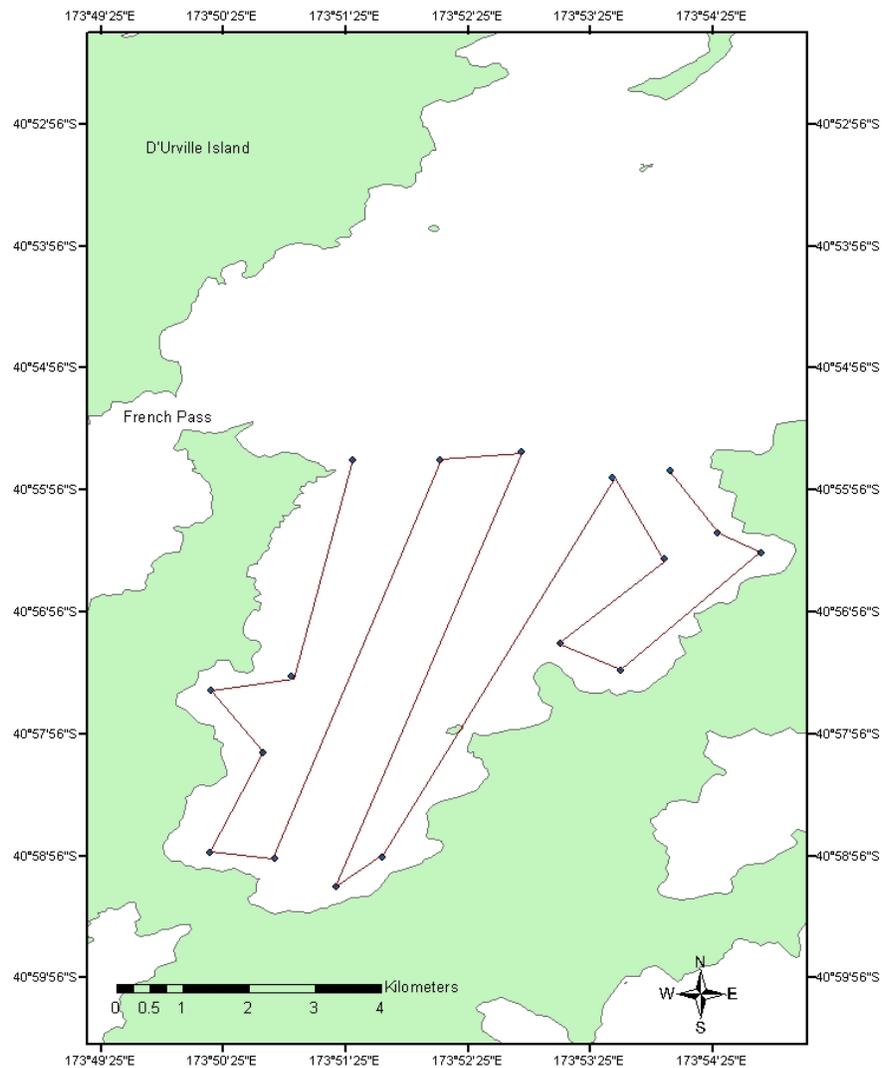


Fig. 3 Inner Admiralty Bay survey route, with waypoints indicated by dots.

time each day, I varied start locations between three different waypoints, and reversed survey directions on alternate days.

Upon sighting a group of dolphins, I marked my location with the Global Positioning System (GPS) before deviating from the track line toward the animals. This allowed me to resume surveying from the same spot on the track after an encounter ended. Information collected upon reaching a dolphin group consisted of encounter number, encounter time, location, estimated group size, bird species and numbers by category, and dolphin behavior. A dolphin group was defined by both proximity and behavioral components (Acevedo-Gutierrez 1997, Mann 1999a). Animals in apparent association with each other engaged in the same behavior might be spread over 30 m or more, but animals not engaged in the same behavior were required to be within approximately 10 m of at least one other animal to be considered part of a group. Behavioral states were modeled after Shane (1990a), and consisted of travel (purposeful movement in one direction), mill (directionless travel), rest (slow travel close to the surface, with little socializing and low activity levels), forage/feed (searching for or consuming prey), and social (interacting with each other or inanimate objects, including sexual activity). Forage/feed were combined into a single category of “food acquisition activities” for surveys, but were separated during focal feeding studies.

Foraging dolphin groups are often associated with seabirds, who may attempt to benefit from dolphin feeding efforts by scavenging prey remains or taking whole prey (Bräger 1998, Evans 1982, Martin 1986, Ridoux 1987). Whether dolphins benefit from the presence of seabirds is not currently clear; however, it is possible that dolphins, like

researchers, use massed seabirds as a visible surface indicator of subsurface prey (Würsig and Würsig 1980). In order to estimate the relative overlap of feeding dolphins with seabirds, I counted all incidences of birds feeding in association with dolphins, logging bird species and categorizing abundance on a scale of 1-4. Bird counts were designated as follows: category 1 = 1-5 animals (corresponding to “a few”), category 2 = 6-20 (“some”), category 3 = 21-50 (“lots”), and category 4 = 51+ (“a whole bunch”). Additionally, bird groups noted to be feeding without dolphins were recorded with a time, location, and species/category. Unless otherwise stated, all statistical analyses were conducted using SPSS for Windows v. 11.0.1.

I noted all instances of dolphins entering mussel farms, and calculated elapsed times inside farms. Mussel farms, with their parallel rows of seed lines hanging vertically in the water column, may present a physical obstruction to dolphin foraging efforts (Markowitz et al. in press, Würsig and Gailey 2002). To assess the relative importance of areas immediately adjacent to mussel farms, I also tallied all observed instances of dolphins within 200 m of a mussel farm, corresponding to areas approved for future expansion of existing farms (Marlborough District Council - Marine Farm Resource Consent Applications poster, July 30, 2002). As I did not begin collection of 200 m proximity data until some two weeks into the season, these results should be considered underestimates.

To assess the possible influence of environmental factors on dolphin behavior, I examined behavioral data and reduced categories into feeding or not feeding. Continuous environmental parameters were also reduced into categories and compared

pairwise to behavior using binomial test Z-scores. This non-parametric test determines significant effects in each cell of a matrix when data are not independent and/or sample sizes are small (Gottman and Roy 1990). Descriptive statistics were used to evaluate all other environmental and behavioral data.

Photo-identification

In dusky dolphins, as in several cetacean species, persistent natural markings such as nicks and gouges in the dorsal fin present a useful method for recognizing individual animals repeatedly over time (Würsig and Jefferson 1990, Fig. 4). Animals possessing markings can be “captured” photographically, then “recaptured” throughout a field season upon successive photographic encounters, providing a relatively non-invasive method for collection of data on group composition, movements, and numbers.

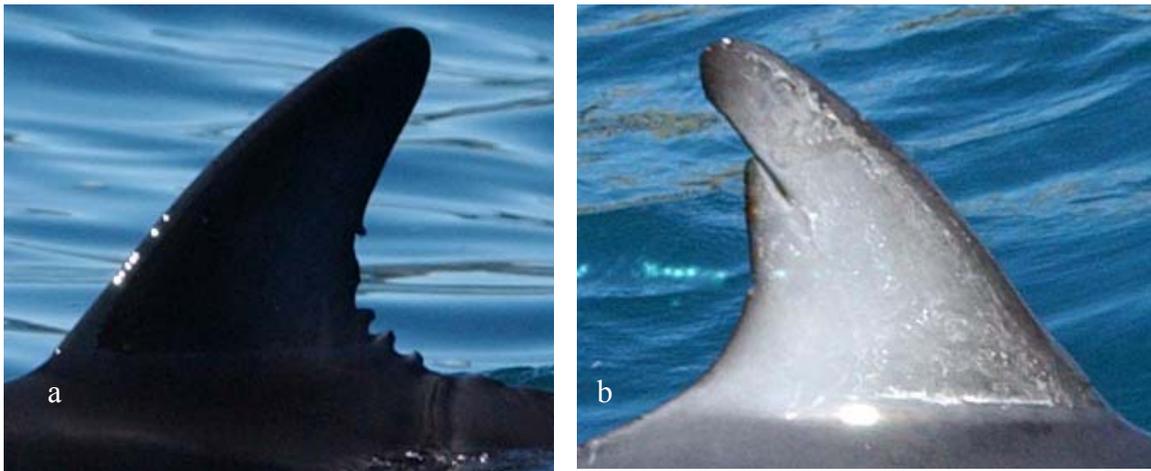


Fig. 4a, b. Individually-recognizable dusky dolphins. **a** Raggedy 065a, sighted in 2000-2002.
b Cleft 440a, new in 2002.

Upon finding a dolphin group, I attempted to photograph all individuals present. After marking my location with the GPS, I deviated from the track line to intercept the animals, approaching the group slowly from the rear, traveling parallel and approximately 5-10 m from group members. The boat driver maneuvered such that dolphin dorsal fins were parallel to the long axis of the boat, and perpendicular to the camera as per Würsig and Jefferson (1990). Animals were photographed randomly using a Nikon N80 SLR camera and Kodak TMAX 400 black and white slide film, or Nikon D1H digital camera. Digital images were stored on Compact Flash media and downloaded to a laptop at the end of each day. Both cameras were used with a Nikon 80-400 mm vibration-reduction zoom lens.

Mark rate, or the percentage of individuals with distinctive markings, was estimated by taking photographs of all dolphins at random and counting the number of photographs with marked versus unmarked individuals. Marked individuals were catalogued according to the number and location of notches and scars, using the Finscan v.1.5.4 Computer Assisted Dolphin Photo-Identification System, software that employs string and curve-based matching methods to present most likely identification matches in decreasing order of likelihood (Araabi et al. 2000, Hillman et al. 2003). All final assessments of individual identity were confirmed by eye.

Mark-recapture population estimates were calculated using the POPAN module of SOCPROG v. 1.3 (developed in MATLAB by H. Whitehead). Using a 1-week sampling interval, a population estimate was calculated for the 5-year period 1998-2002 with additional estimates of average abundance per week ("re-immigration" model,

Whitehead 1990). Single-season population estimates (“mortality” model, Gowans et al. 2000) were also generated for the 2001 and 2002 field seasons, as these years had the most comprehensive photographic records.

RESULTS

Surveys

This study was conducted between June 21 and August 17, 2002, corresponding to the Austral winter. I collected data during 42 days, spending 218.25 hours on the water (mean duration = 5.20 hrs/day \pm 2.245 S.D.). I attempted 31 surveys, completing 18, with 13 partial surveys. Additional data were obtained during 11 non-survey days. Poor weather was the most frequent reason for aborting a survey (n=8), followed by darkness (n=5). Mean survey speed was 7.9 knots \pm 2.83 S.D. (14.6 km/hr \pm 5.24 S.D., n=187). Water temperature during winter 2002 averaged 12.42°C \pm 0.486 S.D. (n=247), mean wind speed = 5.47 knots \pm 4.503 S.D. (10.13 km/hr \pm 8.339 S.D., n=253), and wind direction was primarily west or southwest (combined = 66.5%). Mean water clarity (turbidity) was 7.64 m \pm 1.822 S.D. (n=217), and salinity averaged 37.4 ‰ \pm 1.15 S.D. (n=242). Mode Beaufort level (measure of sea state) was 3, representing scattered whitecaps (n=254). Visibility was excellent 31.7% of occasions measured (n=73), good = 34.8% (n=80), fair = 23.5% (n=54), poor = 7.8% (n=18), and unacceptable = 2.2% (n=5). Unacceptable numbers do not include situations where I did not attempt a survey due to inclement weather at dawn.

I encountered 253 dusky groups, 173 (68.0%) while on survey, and 81 (32.0%) during non-survey effort (Fig. 5). Survey and non-survey groups were separated as the sighting methodologies and locations differed, i.e., surveys were conducted systematically via set transect lines, while non-survey search patterns were not set up along specific transect lines and were primarily opportunistic. While groups encountered on survey were restricted by definition to Inner AB, non-survey groups might be encountered in either Inner or Greater Admiralty Bay. I spent 4,180 minutes with dusky groups (mean time per group = 16.52 min \pm 16.592 S.D., n=253) and traveled 1,116.7 km (survey distance = 801.7 km, non-survey distance = 315.0 km). Mean group size = 6.1 \pm 8.23 S.D. (n=253). Sighting information and encounter rates are described in Table 1. Groups considered feeding/foraging accounted for 58.5% of all encounters (n=148), and 50.5% of all behaviors observed (Fig. 6). Feeding/foraging groups were encountered throughout the day (0800-1000 hours = 16.2%, n= 24; 1000-1200 hours = 31.1%, n=46; 1200-1400 hours = 22.3%, n=33; 1400-1600 hours = 23.0%, n=34; 1600-1800 hours = 7.4%, n=11). Due to day length and weather constraints, effort was not equal across all time blocks.

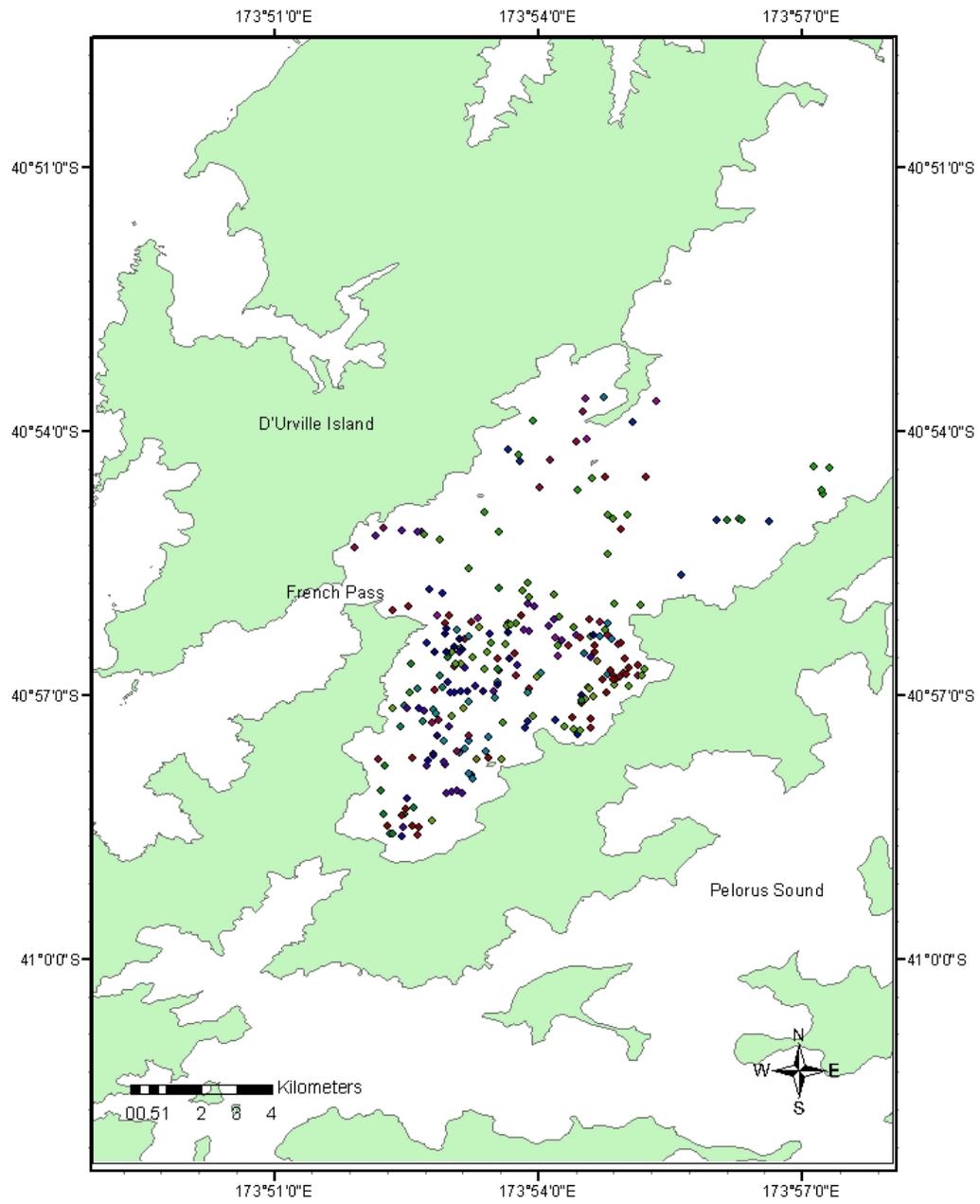


Fig. 5 Admiralty Bay 2002 dusky group sightings. Colors represent sightings on different days.

Sightings 2002	No. groups	Dolphins/grp.	Groups/hour	Groups/km	Inter-group distance
Survey	172	6.1	3.3	0.21	4.7 km
Non-survey	81	6.1	3.7	0.26	3.9 km
Total	253		3.5	0.23	4.3 km

Table 1 Dolphin sightings, Admiralty Bay 2002.

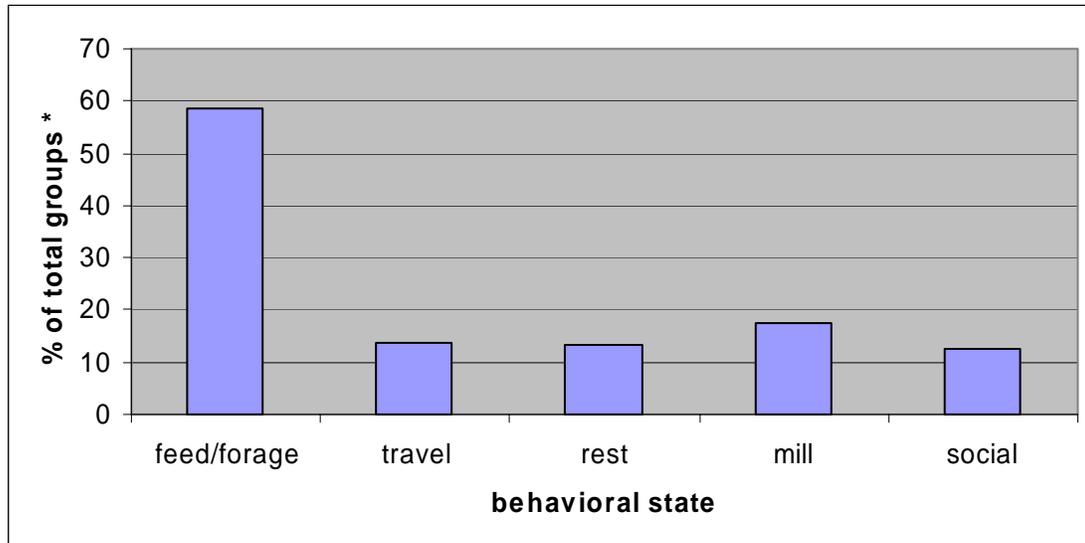


Fig. 6 Dusky dolphin behavioral states, winter 2002. (* Note: behavioral states not mutually exclusive, therefore percentages total >100%).

Seabird species observed in association with dolphins consisted of the Australasian gannet (*Sula serrator*), spotted shag (*Stictocarbo punctatus*), fluttering shearwater (*Puffinus gavia*), red-billed gull (*Larus novaehollandiae*), black-billed gull (*L. bulleri*), black-backed gull (*L. dominicanus*), and white-fronted tern (*Sterna striata*) (Fig. 7). Additionally, little blue penguins (*Eudyptula minor*) and endangered king shags (*Leucocarbo carunculatus*) were occasionally sighted in the same area as duskies, although not associated with dolphin groups (n=30, n=29, respectively). Seabirds were

tallied by number of sightings and category, and all gull species were combined (Table 2).



Fig. 7a-c Seabirds associated with feeding dolphins. **a** Fluttering shearwater; **b** Australasian gannet; **c** Spotted shag in breeding plumage

Seabirds associated with dolphins			
Species	no. sightings	% total sightings	mode category
Fluttering shearwater	253	44.5	2
White-fronted tern	113	20.1	1
Australasian gannet	96	16.9	1
Spotted shag	65	11.4	1
Gull spp.	40	7	1
Total	568	99.9	

Table 2 Seabird frequencies.

Bird species were combined when looking for evidence of feeding with dolphins. Overall, I observed 99 instances of birds feeding without dolphins (including survey and non-survey effort), and 142 instances of birds feeding with dolphins. Of all dolphin feeding groups (n=148), 95.9% contained seabirds (n=142). When dolphins were not feeding (n=105), birds were present only 57.1% of the time. This suggests that seabirds may be using the presence of feeding dolphins as an indicator of available prey. This suggestion is strengthened by numerous anecdotal occasions, when I watched

shearwaters sit quietly on the water surface until a foraging group of dolphins surfaced, at which point the shearwaters immediately flew to the dolphins' location and dove. The shearwaters clearly followed the movements of the dolphins, most likely using the dolphin locations as indicators of potential prey.

Dusky dolphins rarely entered mussel farms, and were only sighted within the boundary of a farm on 4 occasions, for a total of 8.1 minutes (mean = 1.6 min \pm 1.52 S.D.). Dolphins were observed on 28 occasions lingering within 200 m of an existing mussel farm, totaling 336 minutes (mean = 12.6 min \pm 16.20 S.D.). Of total time spent with dolphin groups (n=4,180 min), 8.1% occurred within 200 m of a mussel farm, while dolphins were sighted within farms only 0.19% of the time. Dolphins were never first encountered in a farm, and only moved into the farm after my arrival. On two occasions, dolphin groups were observed to travel rapidly down the lanes of the farm from one end to the other. On another occasion I recorded dolphins traveling under harvested lines to cross between lanes (harvested farms contain no vertical lines, instead consisting only of anchor buoys linked by surface support ropes, see Fig. 8), and on one notable occasion I watched a dolphin apparently pursuing fish within a farm.

The incident of a dolphin within a farm, as well as the behavior of associated group members, warrants attention as an unusual case study in dusky behavior. In that particular location (40° 57.318' S, 173° 50.970' E), the water within the mussel farm and shoreward was unusually turbid, with virtually no subsurface visibility. Three dolphins were observed chasing fish, although only one actually entered the mussel farm to pursue its prey, the other dolphins apparently attempting to contain prey against the

shoreline in a manner more closely resembling that of bottlenose dolphins (Shane 1990). Photographs confirmed the dolphins as duskies, and revealed at least one prey species to be piperfish (*Hyporhamphus ihi*), the only time during the 2002 season that I recorded this particular prey item. Thus, individual foraging on non-schooling prey may at times occur within mussel farms. Additionally, dusky dolphins may use continuous physical barriers such as the shoreline to attempt to herd or confine individual prey.

Binomial tests of comparisons of behavioral state with environmental data yielded no significant interactions between pairs (group size vs. behavior, n=51, NS for all cells; wind speed vs. behavior, n=52, NS for all cells; water temperature vs. behavior, n=51, NS for all cells; Beaufort vs. behavior, n=52, NS for all cells; salinity vs. behavior, n=52, NS for all cells; turbidity vs. behavior, n=38, NS for all cells; wind direction vs. behavior, n=43, NS for all cells).



Fig. 8 Dusky dolphin travels through harvested mussel farm. Note buoys connected to harvested lines sitting high in water column, and lack of vertical lines. The first and third rows have been harvested in this image, while the second row, next to the dolphin, contains mussels (note lines dragging in water and buoy sitting low due to weight of mussels). See discussion.

Photo-identification

A total of 6,461 photographic records were obtained during the 2002 field season (1,941 film images; 4,520 digital images). Of these, 75.3% were suitable for analysis. Mark rate, or percentage of animals with natural identifiable markings based on random photography, was determined by dividing the number of marked images by the total marked and clean images (mark rate = 69.2%). Based on estimated number of animals per group compared with actual number of individuals photographed, I photographed an average of 87.5% of animals present. Of interest was the observation that despite spending an average of 16.52 min per group, and attempting to observe all animals from close range, photographic analysis revealed that I underestimated group size 39% of the time (i.e., more individual animals were photographed than counted).

A total of 177 individually recognizable dolphins were photographed during the 2002 season (Fig. 9). When combined with a 69.2% mark rate, this indicates that at least 256 dolphins passed through Admiralty Bay during winter 2002. Of marked animals, 77 (43.5%) were new this season, and 100 (56.5%) were animals that had been sighted and photographed in previous study years (returnees). A total of 66 animals (37.3%) photographed during the 2001 season returned in 2002. Fifteen animals (8.5%) sighted in 2000, but not 2001, returned in 2002. Eight animals (4.5%) were returnees from more than one, but not all previous years (1998-2001), and 9 animals present in more than one previous year were not sighted in Admiralty Bay during winter 2002.

Total number of marked individuals photographed from 1998-2002 was 421, with an average mark rate of 76% (S.E. 2%). Using a one-week sampling interval

(n=28), the estimated total population size of dusky dolphins in Admiralty Bay over the 5 consecutive winter seasons was 1,013 (Jackknife S.E. = 186.7), with an estimated mean population size of 220 (Jackknife S.E. = 25.9) for any given week (“re-immigration” model, Markowitz et al. in press, Whitehead 1990). Single-season estimates (“mortality” model, Gowans 2000) indicate fewer dusky dolphins in Admiralty Bay in 2002 than 2001 winter season, with a mean of 272 (S.E. = 17.3, 95% C.I. = 249-300) in 2001 (n=13 weeks), and 179 (S.E. = 18.0, 95% C.I. = 164-198) in 2002 (n=9 weeks).

For all identified animals (n=177), dolphins were sighted an average of 3.6 days in AB (S.D. = 3.10), and were photographed in an average of 4.8 groups over the entire study season (S.D. = 4.32). Dolphins were photographed in an average of 1.3 groups per day (S.D. = 0.50). Interestingly, returning dolphins were encountered and photographed on significantly more days than new animals (mean 4.2 days \pm 3.45 S.D. days for returning animals versus 2.7 days \pm 2.40 S.D. for new animals. Mann-Whitney U; Z = -2.227, p=.015).

All animals sighted were large juvenile or adult size, with no calves observed. In addition, of multiple instances when the sex of the animal could be determined visually (usually while swimming inverted next to the boat), all dolphins except one were male. Previous genetic research has demonstrated an overwhelming male bias in Admiralty Bay dusky dolphins, the cause of which is not currently understood (Harlin et al. 2003).

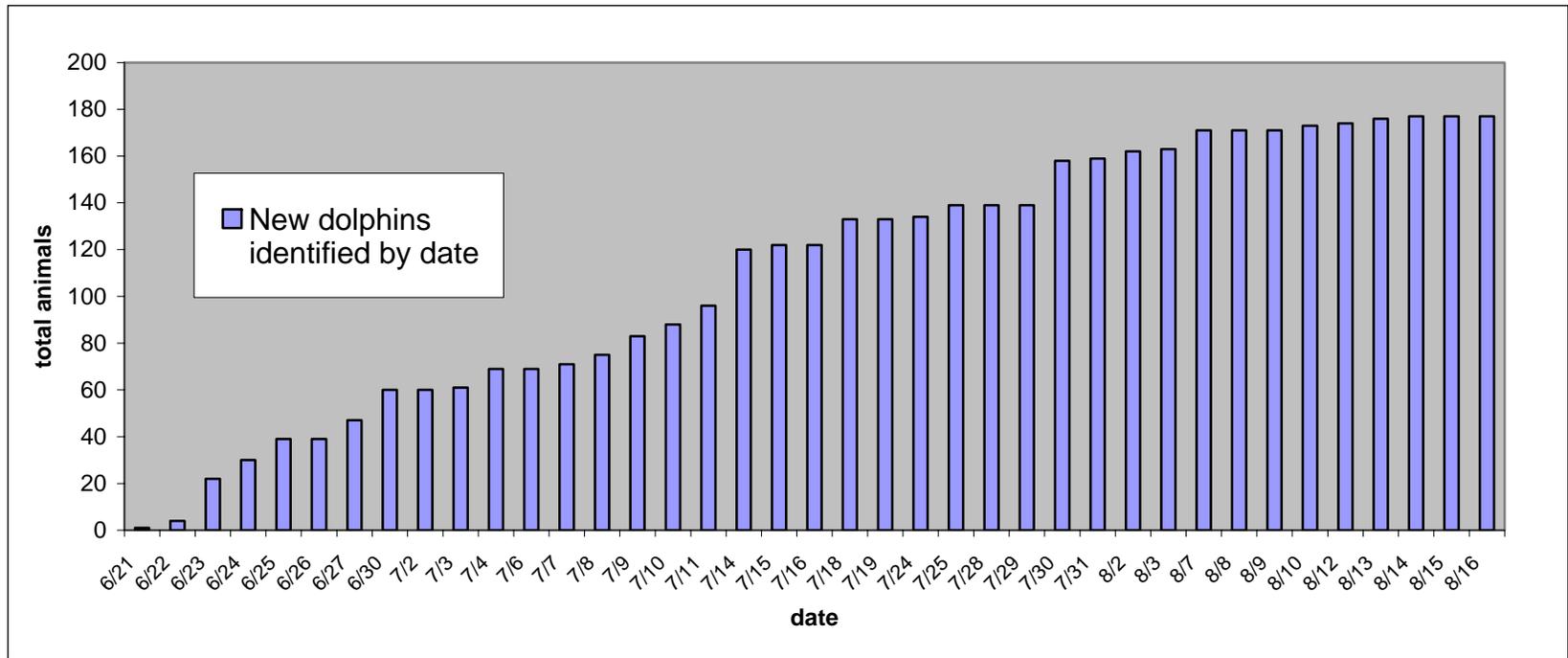


Fig. 9 Discovery curve for Admiralty Bay 2002 photo-identification catalog.

DISCUSSION

Dusky dolphins were sighted in all areas of Inner Admiralty Bay, scattered approximately randomly throughout the Inner Bay (Fig. 5). On days when dolphins could not be located within Inner AB, they were generally present in Outer AB, albeit in fewer numbers. Sighting rates and abundance were less than those reported by Markowitz et al. (in press) for the 2001 season. Comparisons of sighting rates for both years demonstrate differences in mean groups encountered per hour effort, as well as inter-group distances and total identified animals (Table 3). Encounter rates for 2002 were similar to those for Greater Admiralty Bay during 2001. Several potential reasons could explain the observed differences.

2001	No. groups	Mean grp. Size	Groups/hr.	Inter-group distance	No. individuals ID'ed
Inner AB	213	5	7.5	2.2 km	total = 235
Greater AB	90	5	3.3	5.7 km	
2002	172	6.1	3.3	4.7 km	total = 177
Inner AB (survey only)					

Table 3 Comparison of dolphin group sightings during 2001 and 2002.

The most compelling reason for decreased dolphin sightings in 2002 likely relates to prey availability. During the 2001 field season, 83% of groups followed demonstrated feeding activity (Markowitz et al. in press), compared to 59% of 2002 groups, supporting the idea of reduced prey abundance in 2002. A shift in prey distribution from Inner Admiralty Bay would likely cause a corresponding shift in predator distributions. The major prey species of dusky dolphins in this area consist of

pilchard (*Sardinops neopilchardus*), sprat (*Sprattus antipodum*), yellow-eye mullet (*Aldrichetta forsteri*), and anchovy (*Engraulis australis*). While identification of prey species in the field was problematic, photographic records support the presence of pilchard, sprat, and mullet in association with feeding dolphin groups. Pilchard, sprat, and anchovy were introduced into the New Zealand Ministry of Fisheries Quota Management System in October 2002, and although insufficient pilchard biomass estimates exist in the region encompassing Admiralty Bay (PIL 7), it is acknowledged that this area likely contains all three species in similar proportions (Ministry of Fisheries, *Initial decisions on introduction of pilchard to QMS*). Winter migration of prey animals out of the area as a regular seasonal occurrence is not a likely explanation for decreased dolphin numbers in 2002, as research conducted in 4 previous seasons demonstrated a high degree of feeding activity, and therefore prey presence, throughout winter (Harlin et al. 2001, Markowitz et al. in press). Although pilchard are thought to migrate to warmer winter waters in other parts of the world (Culley 1971), the protected, shallow waters of Marlborough Sounds represent warmer habitat than the open ocean waters surrounding this region, making Marlborough Sounds a more likely, rather than less likely, destination for wintering prey (Garner 1959). It is possible that prey movements out of Admiralty Bay into other areas of Marlborough Sounds would explain my observations. Despite the reduction in animals during winter 2002, population estimates nonetheless suggest that on average, over 200 dolphins visited Admiralty Bay each week over the last 5 winter field seasons (1998-2002), supporting the importance of Admiralty Bay as a wintering site for dusky dolphins.

Alternate reasons for decreased dusky numbers could relate to changes in environmental conditions or normal cyclic fluctuations that vary on a time scale greater than the 5-year research effort. Unfortunately, there is little evidence to support or deny these suggestions, and further research is warranted to examine these possibilities.

In winter 2002, dolphins returning to Admiralty Bay were sighted significantly more than new animals. This suggests that returning animals had expectations of resource availability based on previous experience, and remained in an area that had previously proven profitable. On the other hand, new animals, lacking previous knowledge of prey availability in the new location, may have been less likely to remain in the area when faced with uncertain prey stocks.

Environmental factors did not appear to influence whether a dolphin group was engaged in feeding activities. However, this result should not be interpreted as failsafe, as any possible effects may have been lost due to clustering of environmental data to increase categorical sample size. This process may result in potential loss of resolution when examining possible effects.

Mussel farming is New Zealand's most significant aquaculture industry, with 90 percent of farms occurring in Marlborough Sounds (Gall et al. 2000). The most common species farmed is the green-lipped mussel (*Perna canaliculus*). In July 1999 a marine farming moratorium was removed, allowing consideration of new resource consent applications; consequently, approximately 180 applications were received in the nearby Nelson region alone (Hartstein 2001). The Marlborough Sounds currently boasts 455 established farms (Gall et al. 2000) with 44 in Admiralty Bay, and little detailed

research has yet been done to examine the effects of mussel farming on marine mammal habitat. One study conducted in Shark Bay, Australia, demonstrated the displacement of Indian Ocean bottlenose dolphin (*Tursiops aduncus*) mothers and calves by illegal oyster farming activities. Dolphins subsequently returned to the area when the farms were removed (Mann 1999b).

Dusky dolphins surveyed during winter 2001 significantly avoided areas occupied by mussel farms, while utilizing immediately adjacent areas (Harlin et al. 2001, Markowitz et al. in press). My results again indicated that dusky dolphins use the areas immediately around mussel farms, while largely avoiding the farms themselves (Fig. 10).



Fig. 10 Dusky dolphins travel adjacent to mussel farm.

It is probable that the vertical arrangement of parallel seeded lines interferes with the dolphins' ability to maneuver and forage in their usual manner, and may interfere with their ultrasonic visualization of the area (Fig. 11). Sonar images obtained using an Imagenex 881a pole-mounted digital sonar transducer (Imagenex Technology, Port Coquitlam, British Columbia, Canada; see CHAPTER III) show mussel farms' vertical lines extending downward into the water, which to human eyes subjectively appear to resemble bars (Fig. 12). To dolphins, these lines may represent a barrier the animals are reluctant to pass through or under. Harvested farms may present less of a hindrance to dolphin movement, as vertical lines are absent in harvested rows, removing a source of obstruction (Fig. 8). Despite this, dolphins rarely enter mussel farms, whether harvested or seeded.

Applications on file would expand Admiralty Bay mussel farms to include an additional 36 extensions to existing farms and new mid-bay farms, all of which would encroach into the open-water areas of the Inner Bay (Marlborough District Council Marine Farm Resource Consent Applications, 30 July, 2002). Proposed expansion of farming efforts to include the majority of Admiralty Bay could have potentially drastic effects on dusky habitat use by exclusion of dolphins from the area and restriction of normal movement patterns. Additional research is necessary to determine the possible consequences of shellfish aquaculture on marine mammal habitat.

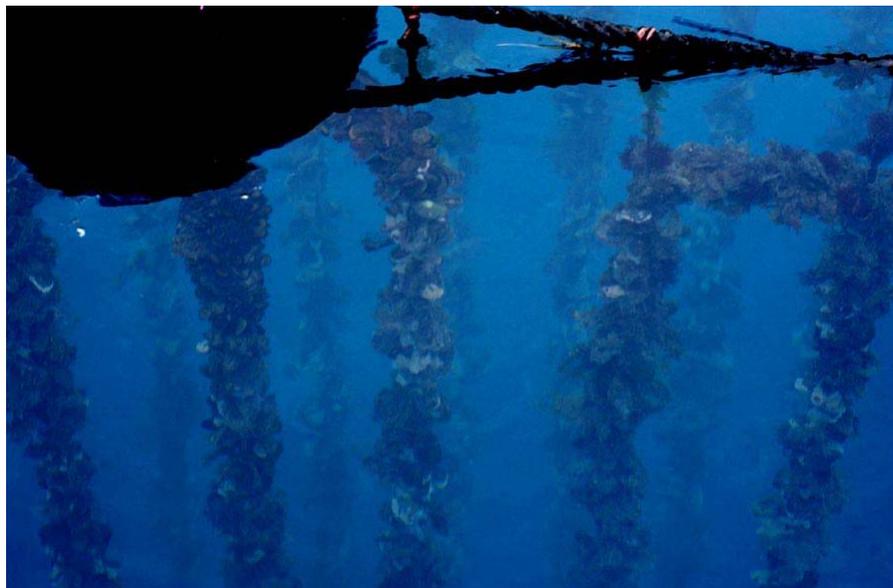


Fig. 11 Vertical arrangement of mussel farm lines, showing accumulations of mussels. Black shape at top left is surface anchor buoy.

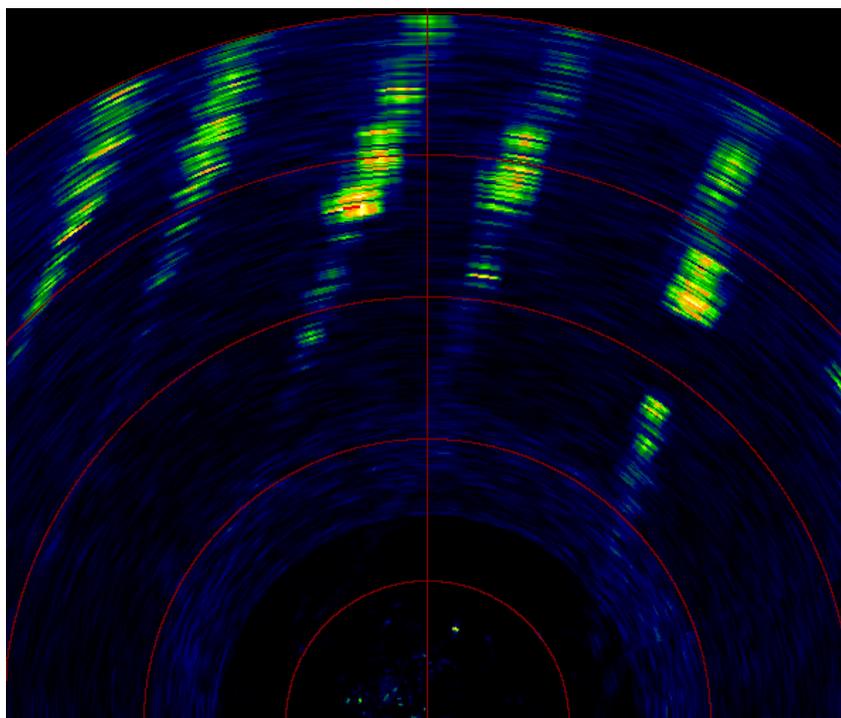


Fig. 12 Sonar image of vertical mussel farm lines.

CHAPTER III

DUSKY DOLPHIN FEEDING BEHAVIOR

Predator-prey relationships in the marine environment occur in a 3-dimensional world of measures and countermeasures. Tactics evolved by prey to find their own food and escape predation are countered by a predator's ability to overcome prey defenses and secure a meal. Schooling fish and piscivorous predators use a variety of tactics in their quests to eat and avoid being eaten.

Schooling fish such as herring, sardines, and anchovies provide an important food source for many marine animals. Fish schools are comprised of highly synchronized groups of individual animals that move together in a polarized manner, each responding precisely and rapidly to the movements of its neighbor via input from vision as well as water movements detected by the lateral line system (Partridge 1982, Pitcher 1983). Fish schools provide defense against predation through increased numbers (and decreased chance of any one individual being consumed in an attack, known as the dilution effect), as well as increased foraging efficiency through increased food encounter rates (Norris and Schilt 1988, Partridge 1982, Shaw 1978). If attacked, fish schools exhibit a variety of escape mechanisms, with individual animals attempting to minimize actions that isolate or distinguish them from the larger school body. In addition to conformity and dilution, prey may evade predators using a confusion effect, where masses of identical bodies impair the ability of a predator to cue in on any one

specific individual through visual disruption, allowing the majority of the school to escape unharmed (Fréon and Misund 1999, Norris and Schilt 1988, Partridge 1982).

Predators of schooling fish have developed their own methods for overcoming the escape methods used by prey. Grouping of predators provides significant prey capture success over individual hunting. Experimental studies of predatory jacks (*Caranx ignobilis*) found that predators gained a significant advantage by hunting in groups when pursuing Hawaiian anchovy (*Stolephorus purpureus*) (Major 1978). Moreover, coordinated foraging efforts appeared to overcome prey defenses by using the confusion effect against the prey themselves, rendering prey incapable of polarization through attack from multiple locations (Potts 1983). Predators readily take advantage of non-conforming individual prey, picking them out of a school based on aberrant behavior or distinctive appearance, and will often charge through a packed prey ball in an attempt to flush out and isolate individuals for easier capture (Partridge 1982, Potts 1983, Shaw 1978).

Prey patch sizes and their spatial and temporal distributions are also important factors that influence a predator's foraging decisions (Caraco 1987, Iwasa et al. 1981, Krebs and McCleery 1984). Group foraging provides an advantage over individual feeding in that the presence of conspecifics may improve the detection of scarce or patchy prey resources, as well as provide increased defense against predators (Caraco 1987, Clark and Mangel 1986, Galef and Giraldeau 2001, Hamilton 1971, Pulliam and Caraco 1984). Aggregation of individuals into feeding groups is warranted in many areas of the marine environment, as patchy, ephemeral prey are not uncommon. An

elevated per capita food intake may stimulate increased predator numbers up to and beyond some optimal group size, as long as the benefit of foraging socially outweighs that of individual foraging (Clark and Mangel 1984, Packer and Ruttan 1988). Uniform prey distribution should not promote increased aggregations of predators, as resource information is presumably equally available to all individuals. Nonetheless, in these situations, predation pressure or social mechanisms may serve to preserve group foraging (Clark and Mangel 1984, Hamilton 1971).

Group hunting marine mammals use a variety of methods to concentrate prey. Black Sea bottlenose dolphins are known to herd prey balls using a “carousel” or “kettle” formation (Bel’kovich et al. 1991), where animals swim around concentrated prey, making excursions through the middle to isolate and feed on individual prey items. Shane (1990b) summarized 27 different feeding behaviors exhibited by bottlenose dolphins, including using flukes to kick fish through the air, partially stranding while chasing fish against the shore, herding fish against shore or into a fishing net, and feeding behind shrimp trawlers. Alaskan humpback whales use bubble nets to encircle and concentrate prey fish, rising through the middle of the “net” to feed on the packed prey (Jurasz and Jurasz 1979), while western Atlantic humpbacks developed a novel “lobtailing” method to concentrate prey (Weinrich et al. 1992). Norwegian killer whales also use a carousel formation to herd herring to the surface, with individual predators swiping at fish balls with their tail flukes, then feeding individually on stunned and injured prey (Similä and Ugarte 1993). The variety of tactics used by feeding marine mammals likely represent differences in prey species, distribution, habitat, and season, in

addition to differences in social learning opportunities by predators (Connor 2001, Rendell and Whitehead 2001).

Studies of dusky dolphin foraging behavior have been limited largely to stomach content analyses, revealing little of the mechanics associated with foraging and site use (Alonso et al. 1998, Cipriano 1992, McKinnon 1994; but see also Würsig and Würsig 1980). New Zealand dusky dolphins occur in both shallow and deep-water habitats, and differing foraging techniques would be expected. This chapter examines the foraging behavior of dusky dolphins in the shallow-water environment of Admiralty Bay. These results will then be contrasted with feeding behavior of some of the same animals in the deep-water habitat off Kaikoura, as well as with foraging by duskies in the shallow-water habitat off Patagonia, Argentina. The ability of the same animals to change foraging tactics with alterations in habitat and prey is important to answering questions of behavioral plasticity in social species. Equally important is a thorough understanding of the breadth of foraging behavior between and within dusky dolphin populations.

MATERIALS AND METHODS

Focal feeding groups

On non-survey days and opportunistically during surveys, I collected data on focal groups of feeding dolphins. Feeding groups were located by looking for dolphin dorsal fins and/or diving seabirds. Upon sighting a feeding group, I slowly approached to within approximately 100 m, attempting to stay outside the immediate area of activity and minimize disturbance. Group number, time, and GPS location were noted. For

focal group follows, feeding and foraging behaviors were separated and defined individually as follows (also see Acevedo-Gutierrez 1997):

Forage: Animals generally moving parallel, often spread, at low to moderate speed. Dives are common, and more distance is likely covered in the vertical than the horizontal plane. Animals may change direction periodically, but movement is generally maintained in a forward direction. Dolphins frequently accompanied by birds.

Feed: Increased activity level over foraging. Forward movement largely ceases, and becomes focused in a particular area. Dolphins may dive and surface in synchrony. Leaping activity may commence, especially clean leaps. May include chasing or sudden bursts of speed at the surface. Bird diving activity increases in same area as dolphin activity, and birds may be seen swallowing or with fish in beaks. May also be accompanied by fur seals. Fish may be visible at surface.

As visualization of subsurface feeding behaviors was not possible beyond approximately 3 m depth, readily visible surface behaviors were used as proxies for subsurface activities and position in the water column. Acevedo-Gutiérrez (2000) found that bottlenose dolphin surface behaviors could be used to reliably determine subsurface prey spatial arrangement. I used several prominent surface activities as behavioral indicators for dusky dolphins feeding below visible depth. Indicator behaviors included leaping activity, especially those leaps where the dolphin exits the water vertically, turns 180°, and reenters the water without making an appreciable splash or noise. These “clean leaps” are theorized to assist an air-breathing mammal working below the surface to stop what it’s doing, rise rapidly to breathe, then return to depth in the most efficient manner (Würsig and Würsig 1980). The dolphin overshoots the surface on ascent, allowing it to breathe, then use its body weight to return to subsurface activities. Especially high (>2 m) and vertical leaps most likely indicate dolphins working at

deeper depths, while relatively lower leaps indicate activities less deep in the water column. For the purposes of this study, I defined a clean leap to be any noiseless leap where the dolphin's belly was visible, accompanied by an upwards flip of the flukes at the top of the leap. On occasion this meant that the animal was not oriented vertically upon leaving the water, but as long as the movement was directed toward an area of feeding activity, I considered it a clean leap. Another indicator behavior used was synchronous dives by all or most of a group. These were measured in seconds from the disappearance of the last animal to the reappearance of the first animal, and were used as a proxy for depth of activity. Longer synchronous dives indicate deeper activities, while shorter (or fewer) synchronous dives indicate behaviors closer to the water's surface. The presence of sudden bursts of speed at the surface by dolphins was used as an indicator of prey chasing, when not directed at another dolphin. The presence of seabirds that feed at the surface indicates prey available at the surface, as does the presence of visible surface fish.

For analysis purposes, only dolphin groups considered feeding were used in data collection. Two-minute interval sampling (Altmann 1974) was used to collect information during focal group observations of feeding bouts. Group size, formation (linear, parallel, echelon, circular, or none), cohesion (mode inter-individual distance; tight = 0-1 body length, open = 2-5 body lengths, dispersed = 6-10 body lengths, and widely dispersed = 10+ body lengths), and visible fish at surface (yes/no) were recorded by instantaneous sample. All occurrences were recorded of leaping by type ["clean" reentry leaps; noisy leaps – dolphin exits water and twists or bends such that the body

makes a loud percussive noise upon reentry, often repeated multiple times in succession by the same animal; and acrobatic leaps – end over end somersault, sometimes accompanied by loud noise upon reentry depending on angle of body, sometimes repeated (Würsig and Würsig 1980)], synchronous dives and durations, sudden bursts of speed by a group or individual, and New Zealand fur seal (*Arctocephalus forsteri*) presence and numbers. Records of bird species were documented by recording the highest category per species per 2-minute interval.

These data were acquired every 2 minutes until feeding apparently ceased, generally indicated by a return to foraging activities or initiation of another behavioral state. I noted the end time for the feeding bout, and waited 10 minutes. If feeding recommenced within 10 minutes, I stayed with that group and continued collecting data until I had information for 3 bouts. This method ensured data collection for at least 2 full bouts, 1 partial bout, and 2 inter-bout intervals. Encounter times were compared to feeding start times. If the group encounter time was within 2 minutes of the noted start time for the feeding bout, the bout was considered to have already begun before I reached the group, was listed as “not true start time”, and excluded from statistical calculations of behavioral trends over bout length. If the encounter time was separated from the feeding bout start time by 3 minutes or more, the feeding bout start time was considered to represent the true start time for that bout. After 3 bouts, I left that group and resumed searching. For analysis purposes, feeding groups were considered independent, but bouts were not independent.

During focal follows of feeding groups, 1 observer acted as recorder, and 1 or 2 additional trained observers dictated behaviors as they occurred. To prevent bias, the author was the only individual to make determinations of group size, formation, and cohesion. The author and primary research assistant were the only people to determine leap type, fish seen, seals seen, bird categories, and sudden bursts of speed (SBOS), after discussion and agreement on terms. Behavioral data were tallied on standardized data sheets and entered into a computerized database upon return to shore each evening. Statistical tests were conducted using the working hypothesis that dolphins would operate in a coordinated manner to bring prey balls to the surface (Nøttestad 2001, Würsig and Würsig 1980). Expectations for this behavior come from previous research conducted on dusky dolphins feeding in the shallow water habitat of Golfo San José, Argentina, where coordinated surface feeding is common (Würsig and Würsig 1980). Although coordinated surface feeding is but one possible feeding strategy employed by dusky dolphins, the hypotheses generated provide a convenient point at which to start analyzing behavioral trends.

To examine the relationship between feeding dolphins and seabirds, I collected data on seabird species associated with dolphins, as well as on bird groups seen feeding when no dolphins were present. Bird species were further separated into diving birds and surface birds, to distinguish feeding behavior and serve as proxies for relative depth of prey. Diving birds were defined as those that submerge their entire body when feeding, whether from a plunge dive or surface dive, and include gannets, shags, and shearwaters. Surface birds were defined as those species that do not submerge

completely when feeding, and include gulls and terns. For diving birds, prey should remain largely accessible regardless of its vertical position in the water column (independent of visibility in deeper waters). Surface and diving birds, however, should be attracted to areas with large quantities of fish concentrated near the air/water interface. I tested the possibility of increasing numbers of surface birds with increased bout length by summing categories of diving bird species (gannets, shags, shearwaters), and dividing this number by the sum of categories for all birds. This created a proportion of diving/total birds that was compared to bout duration. I would expect this ratio to decrease if dolphins were bringing prey to the surface. This shift should occur if fish prey is available at depth early in a feeding bout, therefore only accessible to diving birds, and is later driven to the surface, where it then becomes additionally available to surface birds. I plotted the proportion value against bout duration for all bouts with more than 1 interval (n=55) and added a fit line. Kendall's tau non-parametric correlations were obtained and trends noted for each. Non-parametric statistics are appropriate in situations where the data do not meet assumptions of independence and/or sample sizes are small.

If dolphins are working in a coordinated manner to herd fish schools to the surface, I would expect to see the number of clean leaps decrease with increasing bout length, as dolphins would have less need to return rapidly to depth if prey is contained near the surface. Similarly, I also expected to note a decrease in duration and number of synchronous dives with increasing bout length, as well as increasing frequency of speed bursts with bout length. Sudden bursts of speed would indicate surface prey chased by

dolphins. Also, if successful feeding groups attract the attention of nearby dolphins, I would expect to see group sizes increase with increasing bout length.

I encountered 2 potential confounds upon examining behavioral data. When observing a bout to detect the end of feeding activity, I looked for a general decrease in activity, so by definition, a bout that exhibited many leaps or speed bursts would be determined to be ongoing. To account for this factor, which might artificially decrease the number of leaps or speed bursts observed at the end of a bout, demonstrating a questionable negative trend, I examined all bouts with more than 1 interval duration (n=55). For leaping activity, since my expectation was that data would show a negative trend, I additionally limited examination to those bouts with a true start time, to ensure collection of data from the true beginning of the bout (n=36). I then individually summed all incidences of leaps or speed bursts for the first half of each bout, then compared this result to the sum of leaps or speed bursts for the last half of each bout. I disregarded the median interval in bouts with an odd number of intervals, ensuring an equivalent number of intervals in each hemi-bout. Speed bursts for groups were weighted the same as individual speed bursts (n=337), and Wilcoxon rank sign tests were performed to determine significant trends. While this method is not definitive, it provides a better estimation of activity trends over bout length than merely comparing the first and last intervals for each bout.

Lastly, to examine the incidence of visible fish at the surface, I determined the percent of bouts in which fish were visualized by dividing the number of bouts with fish by the number of available bouts for that time interval.

Sonar data

In addition to interval sampling of focal feeding groups, I conducted active acoustic surveys of Admiralty Bay during winter 2002 using 2 different methodologies. Opportunistic sightings of feeding groups were observed sonically using a pole-mounted Imagenex 881a high-resolution digital sonar (Imagenex Technology, Port Coquitlam, British Columbia, Canada; range: 1-200 m, frequency: 675 kHz, pulse length sector/sidescan mode: 10-530 μ s) connected to a laptop computer. The transducer signal was a 30-degree fan-shaped beam directed laterally toward the area of highest activity. Feeding groups were approached slowly, and the boat motor turned off when approximately 200 m from the group. A Mercury T4800 electric thruster was then used to quietly maneuver close to the feeding activity, minimizing disturbance, and the pole-mounted sonar transducer placed in the water. Digital sonar images were transmitted to the laptop, and select behavioral sequences saved for later analysis. Acoustic behavioral sequences were time-matched with above-water video/audio recordings to allow correlation between surface and sub-surface behaviors. Raw acoustic image data were not available for analysis with this method.

During analysis, feeding bouts were divided into 30 second increments ($n=197$), and the diameter of the largest return signal (fish ball) was determined in meters, from the scale provided on the sonar image for each interval. Approximate fish ball size was categorized as follows: category 1 = 0 m (no fish), category 2 = 2-5 m diameter (small fish ball), category 3 = 6-10 m diameter (medium fish ball), category 4 = 11+ m diameter (large fish ball). Surface dolphin behaviors, as recorded on video/audio tape,

were listed as feeding or not feeding for each 30 second interval. Cavitation artifact from propeller wash was apparent on 92.9% of all recordings, generally within 2 m of the boat hull. Fish balls less than 2 m diameter were not included in analysis, as they could not be distinguished reliably from prop wash if under the boat. Signals representing dolphins were recognized by their apparent size on the sonar image as well as the presence of a bright echo (presumably representing air-filled lungs) in the mid-portion of the signal. Dolphins within or behind dense fish balls were not distinguishable.

Additionally, a Computrol, Tournament Master Fishfinder NCC 5300, modified to read directly into a laptop computer, was used to collect acoustic data from dusky dolphins and their potential prey during transect surveys on August 7-8, 2002. The echosounder gave a 130 μ s long, 200 kHz pulse, and its returning echoes were digitized at a sampling rate of 10 kHz with a Computer Board PC DAS16/12-AO. The transducer's signal was a downward pointing, 10-degree cone (Benoit-Bird et al. 2001). The transducer was transom-mounted and towed at up to 8 knots (14.8 km/hr) in Admiralty Bay. Programmed survey routes were followed until a feeding group was encountered. At that point I deviated from the transect line and acoustically recorded dolphin feeding behaviors while moving parallel to the dolphin group, returning to the survey line at the end of a feeding bout. Standard survey information as described in Chapter II was also collected for each group. Whitlow Au and Kelly Benoit-Bird (University of Hawaii) generously provided sonar equipment and expertise for this portion of the study.

During feeding encounters, dusky dolphins were observed swimming beneath the transducer. This information was used to determine the individual scattering characteristics for large targets via an indirect calibration procedure (Benoit-Bird and Au 2001). As with spinner dolphins in Hawaii, the unique scattering characteristics of dusky dolphins make it possible to distinguish them from non-dolphins, and this relationship is consistent with the depth of the animal. Strong lung echoes were observed at one end of the animal, which was designated the front, allowing a determination of the orientation of swimming dolphins. I calculated the total calibrated scattering intensity of prey for each cubic meter sampled. As identification of prey species causing the scattering was not possible, I was unable to determine numerical density and prey abundance estimates. I used regression analysis to investigate the relationship between volume scattering of prey and dolphin relative abundance. Using average volume scattering of prey in 0.25, 0.50, and 1 km increments along the entire survey route, I compared these values to the relative abundance of dusky dolphins (Benoit-Bird et al. submitted).

RESULTS

Focal feeding groups

Thirty-seven focal feeding groups were examined for a total of 70 feeding bouts (mean 1.9 bouts/group \pm 0.94 S.D.) (Fig. 13), with an average feeding time per bout of 8.4 min (\pm 7.33 S.D.). Mean inter-bout interval was 6.4 min \pm 5.83 S.D. (n=33). Bout times decreased significantly over the course of the field season (Spearman's rho = -.558, p = .000, n=70) (Fig. 14). Dolphins did not have a consistent formation (mode formation = "none"), and mode cohesion was "open" (2-5 body lengths inter-individual distance, n=291) over all bouts. Mean feeding group size was 7.94 \pm 5.51 S.D., n=70.

I compared group size for the first interval to the last interval to test whether group size increased with advancing bout duration. In Admiralty Bay, group size increased significantly over bout duration when examining all bouts with true start times and at least 2 intervals duration (Wilcoxon sign rank test, Z = -2.001, n=36, p = 0.045); however, this result was not significant when only independent groups were examined (Wilcoxon sign rank test, Z = -1.275, n=12, p = 0.202, NS). This indicates that dolphins in Admiralty Bay usually required longer than the length of one feeding bout to accumulate additional animals.

To examine the possibility that dolphins were bringing prey balls to the surface, I looked at leap type and frequency, number and duration of synchronous dives, number of speed bursts, visualization of surface fish, and mixed-species associations for each 2 minute interval. Only bouts with true start times and at least 2 intervals duration were used for comparison of clean, head-first reentry leaps (n=36). I expected that if dolphins

move fish from depth to the surface that the number of clean leaps should decrease as bout length increased.

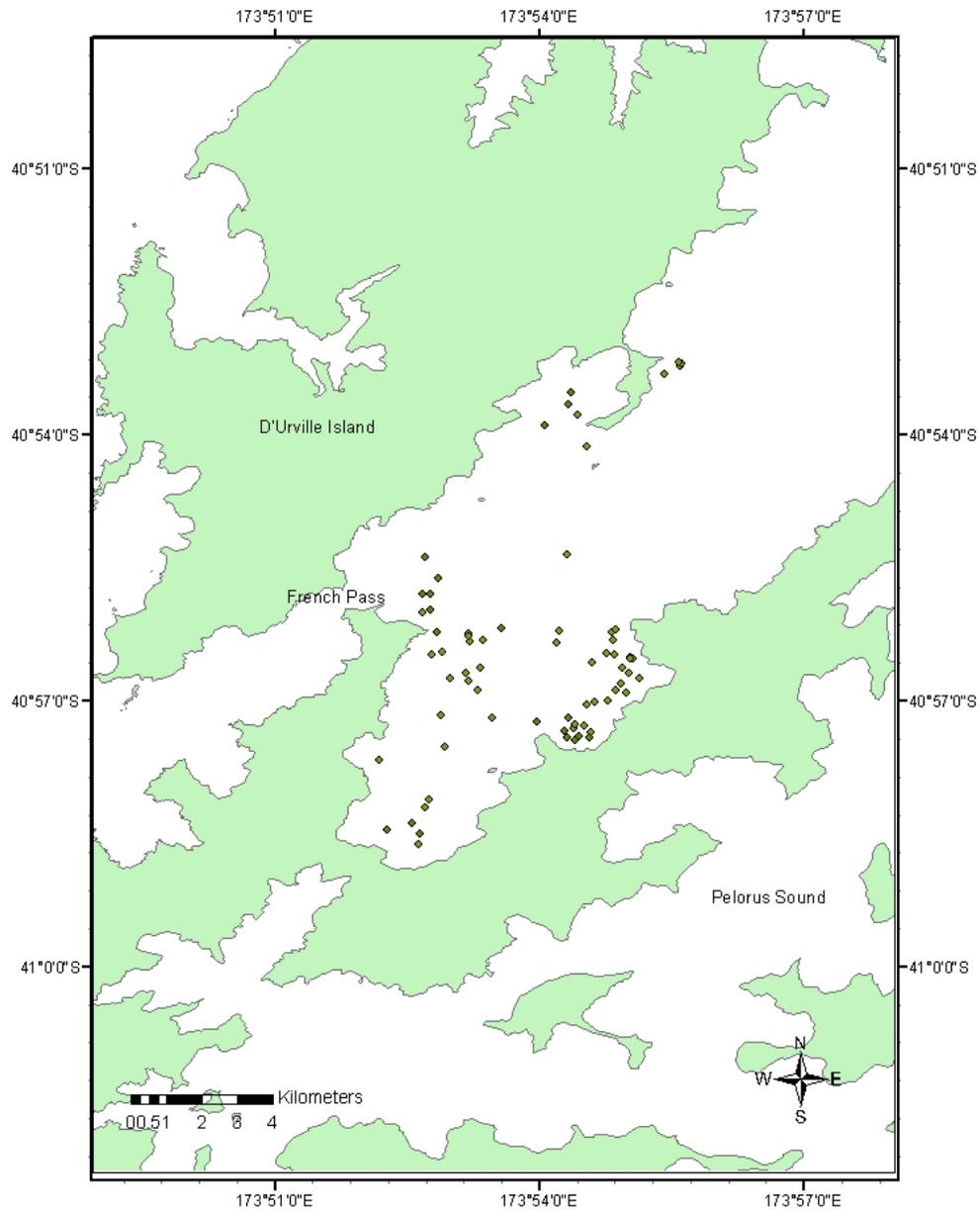


Fig. 13 Dusky dolphin feeding bout locations.

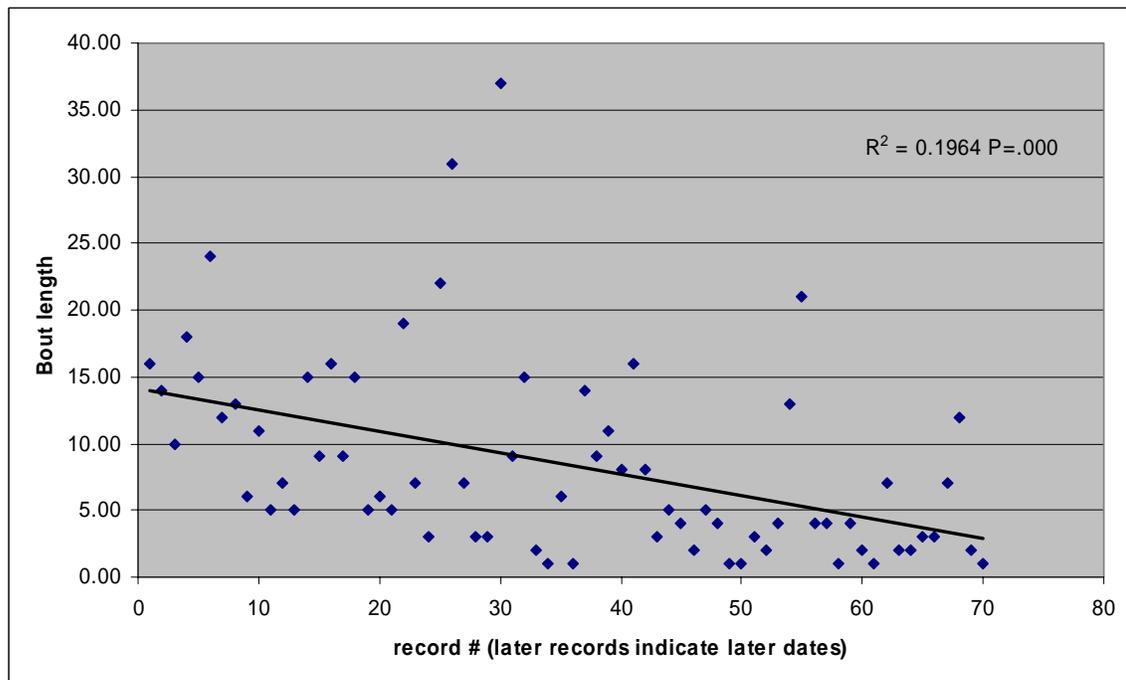


Fig. 14 Bout durations from beginning to end of season.

This was supported by a significant decrease in clean leaps over bout duration (Wilcoxon sign rank test, $Z = -2.322$, $n=36$, $p = 0.020$). I noted no acrobatic leaps, and only 2 instances of noisy leaping in 219 intervals.

I expected that synchronous dives should decrease in frequency and duration with increasing bout length if fish were being brought to the surface. To examine synchronous dive frequency, I computed a ratio by dividing the number of synchronous dives per interval by the number of bouts that lasted that long (for example, during the first 2 minute interval there were 37 synchronous dives out of a possible 70 bouts, for a ratio of 0.53). There was no significant decrease in the ratio of synchronous dives as bout length increased (Kendall's tau = -0.157, $n=17$, $p = 0.385$, NS) (Fig. 15). To

examine dive durations, I then analyzed bouts with synchronous dives in the first interval, and at least 2 intervals duration (n=17), and computed mean dive duration for the first and last intervals. There was a significant decrease in mean duration of synchronous dives when comparing first and last intervals for these bouts (Wilcoxon sign rank test, $Z = -3.575$, $p = 0.000$).

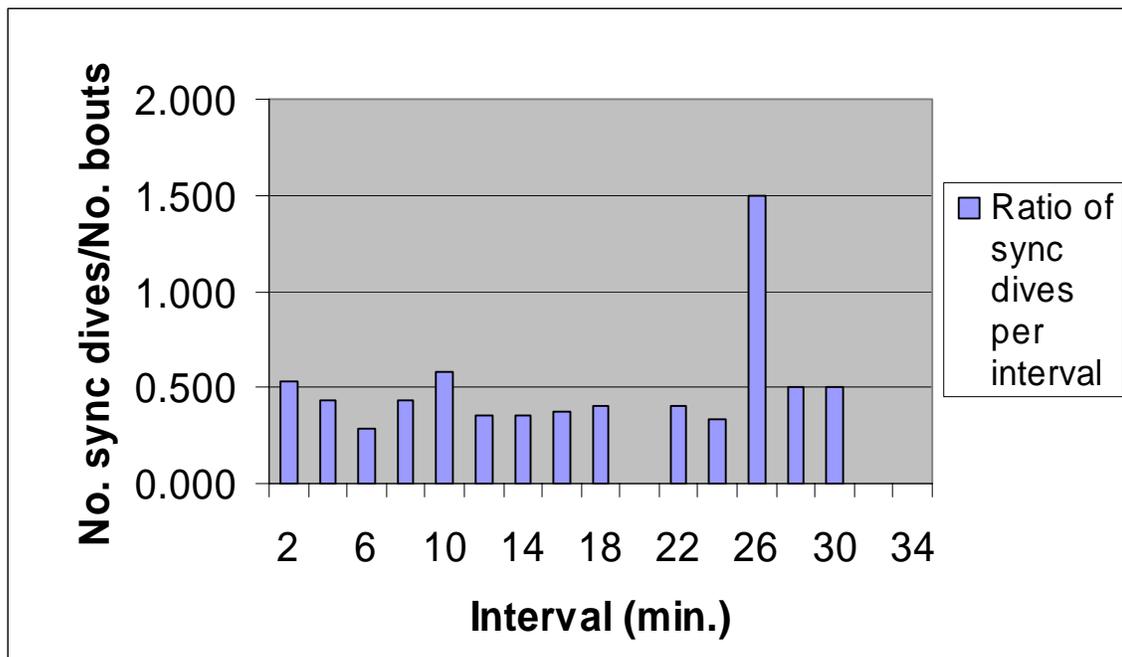


Fig. 15 Ratio of synchronous dives per interval.

I examined the incidence of sudden bursts of speed by dolphins across bout lengths. Speed bursts indicate probable chasing of prey at the surface, so I expected an increase in this behavior with increasing bout length, if dolphins are bringing prey balls to the surface. Contrary to expectations, there was in fact a significant decreasing trend to the mean number of speed bursts over bout length (Wilcoxon sign rank test, $Z = -2.311$, $n=55$, $p = 0.021$).

If dolphins are bringing fish to the surface, I expect to see visible prey at some point in a feeding bout. Of 291 intervals, I observed fish at the surface only 14 times (4.8%). Of possible bouts, 1.4% contained visible fish during interval 1 (n=1), 9.1% during interval 2 (n=5), 4.8% during interval 3 (n=2), 6.3% during interval 4 (n=2), 8.3% during interval 5 (n=2), none during interval 6, 7.1% during interval 7 (n=1), and no more until interval 15, in which 1 sighting of surface fish was present in 2 possible bouts (50%). These results indicate that dolphins are most likely consuming prey at depth, as visible fish were rare during my observations.

Another indicator that dolphins are bringing prey to the surface might be an increase in surface bird species as bout length increases. Comparisons using Kendall's tau correlation showed only 1 significant decrease in the ratio of diving birds to total birds from start to end of a feeding bout in all bouts with more than one interval (n=55), a result which fails to support my hypothesis.

In addition to seabirds, New Zealand fur seals were occasionally spotted in association with feeding dusky dolphins. Sixty-seven seals were sighted during 50 focal feeding intervals (17% of intervals), and seals were most commonly sighted during the first 12 minutes of a bout (n=63). Seals were never seen in bouts lasting longer than 18 minutes (Fig. 16). Seals were observed feeding on small schooling fish, presumably the same prey species targeted by dolphins. Additionally, seals were seen to consume larger prey such as barracouta (*Thyrsites atun*), most likely also drawn to the site by dolphin feeding activities. In one case, dogfish sharks (possibly *Squalus* or *Centroscymnus* sp.) were also observed feeding in the same area as dolphins and seals. Dolphins, seabirds,

seals, sharks, and other predatory fish species therefore all represent distinct components of a complex feeding web spanning multiple trophic levels (Fig. 17).

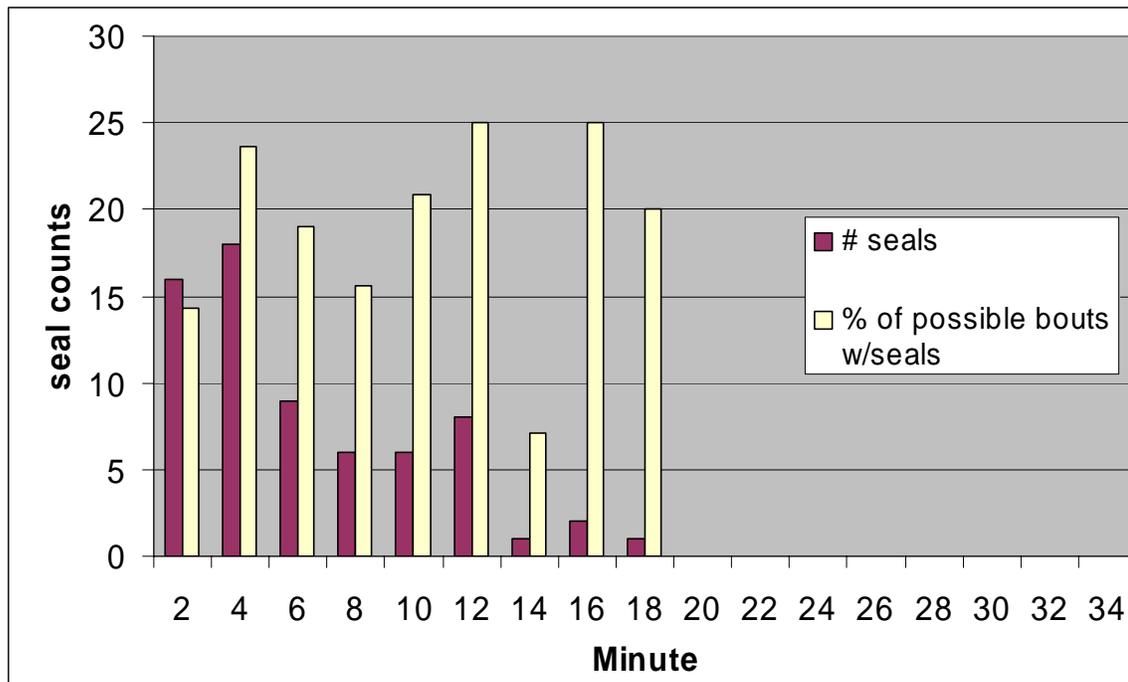


Fig. 16 Fur seal foraging with dolphins by number and percentage.



Fig. 17a-c Predator/prey relations in Admiralty Bay. **a** Fur seal flings a barracouta; **b** fish flee from feeding dusky while shearwaters watch; **c** a gannet displays his catch.

Sonar data

Using the Imagenex 881a, 20 episodes of feeding behavior were observed and recorded acoustically. A total of 98.5 minutes of sonar data were analyzed. There was a direct significant correlation between increasing fish category and the probability of dolphin feeding (Log-likelihood ratio for 4x2 matrix; G-square = 67.16, $n=197$, $df = 3$, $p = .001$), as well as significant differences from expected values in all individual matrix cells except those associated with fish category 2 (Binomial test Z score, $p = .05$) (Fig. 18). This indicates that my estimations of dolphin feeding activity as observed from the surface were accurate by confirmation of available prey. It also confirms that in instances where dolphin behavior was listed as “not feeding”, there was little available prey.

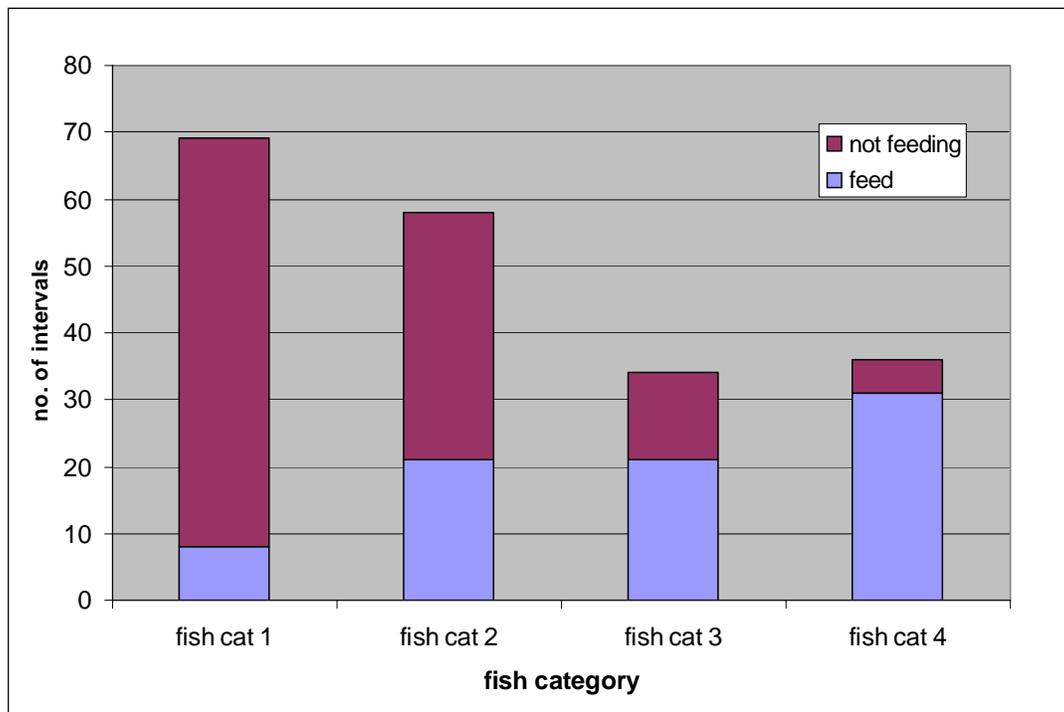


Fig. 18 Sonar summary: Fish presence vs. dolphin feeding.

Using the Computrol, I collected acoustic data during 2 days of surveys (August 7-8, 2002), covering 122 km of transects between the hours of 0930 and 1800. Dolphins were sighted visually every time they were detected with the sonar. All acoustic signals of dolphins were of solitary animals moving at least 4 m from other dolphins and not necessarily oriented in the same swimming direction. Dusky dolphin relative abundance was correlated with average volume scattering of potential prey over 0.25 km transect intervals. In all of the 17 occasions when mean volume scattering density reached $2 \cdot 10^{-6} \sigma/m^3$, dolphins were encountered, while dolphins were only sighted in 15 of 474 instances when mean volume scattering density was less than this (Benoit-Bird et al. submitted). This may indicate a general threshold for volume scattering density beneath which dolphins do not spatially overlap with prey.

DISCUSSION

Würsig and Würsig (1980) found that dusky dolphins in Argentina live in a fission/fusion society. Small groups of 8-12 dolphins tend to forage during daylight hours, spreading out parallel while foraging to maximize the chance of prey encounter, then combining with other small groups to form larger feeding aggregations upon locating prey. Würsig and Würsig noted an apparent threshold effect: a feeding group that failed to recruit at least one other small group to an area of feeding activity was generally unable to maintain prolonged surface feeding, presumably from an inability to adequately move and manage a prey ball with fewer than some critical number of predators. This does not mean, however, that feeding ceased, and feeding may have

continued at a low level beneath the surface. The most visible (and presumably successful) feeding aggregations might contain hundreds of dolphins and over 1,000 seabirds, and most likely represent successful recruitment of additional animals to aid in adequate restraint of prey. Dolphins appear to cooperatively herd southern anchovies (*Engraulis anchoita*), exhibiting restraint while herding and waiting their turn to dive through the middle of the tightly concentrated fish ball, exiting with up to 5 fish per pass. Prey balls are moved by dolphins to the surface, which may act as a barrier preventing fish escape. Feeding times positively correlate with dolphin group size; larger groups tend to feed for longer periods of time. Fissioning of large groups presumably occurs after post-feeding socialization, as by morning, small groups are again apparent (Würsig and Würsig 1980). Dolphins typically remain within 5 kilometers of shore, in water less than 60 m deep. This cooperative surface feeding pattern represent just one highly visible option for dusky dolphins, who likely vary their feeding behavior in Argentina in accordance with variation in prey distribution, numbers, and environmental conditions. Cooperative feeding strategies are not uncommon in dolphins, and occur as well in several terrestrial predator species [bottlenose dolphins, Acevedo-Gutiérrez 2000; African wild dogs (*Lycaon pictus*), Creel and Creel 1995; chimpanzees (*Pan troglodytes*), Goodall 1990; killer whales (*Orcinus orca*) Hoelzel 1993; lions (*Panthera leo*), Schaller 1972; for an overview see Packer and Rutan 1988].

The behaviors exhibited by Argentine dusky dolphins contrast with feeding behaviors exhibited by dusky dolphins off Kaikoura, New Zealand. Dolphins there

demonstrate little daylight feeding activity, and instead travel, rest, and socialize during the day in very large groups numbering up to 1,000 or more (Cipriano 1992, Würsig et al. 1997) (Fig. 19). In summer, dolphins typically spend the day close to shore, moving farther offshore at night, when subgroups of dolphins synchronously dive to feed on mesopelagic organisms associated with the rising Deep Scattering Layer (DSL). The presence of the Kaikoura Canyon, a deep submarine trench extending to within 200 m of shore at Goose Bay (just south of the Kaikoura Peninsula) results in a rich upwelling of nutrients from abyssal depths (Lewis 1998). The deep waters support the dense DSL and allow it to sink below a level accessible to dolphins during the day. Active acoustic sonar data collected during winter 2002 off Kaikoura revealed small subgroups of dusky dolphins following the progression of the DSL as it rose in the evening to a minimum depth of between 29 and 49 m from 2300 to 0100 hours. Dolphins were never recorded below 130 m, even though portions of the DSL were deeper than this for all but 1 hour each night (Benoit-Bird et al. submitted). Dolphins appear to minimize energy expenditures by not consistently diving deeper than the shallowest level necessary to satisfy their nutritional requirements. Dolphins fed either individually or in subgroups ranging in size from 1-5, with larger subgroups encountered during times when the prey layer was closest to the surface (Benoit-Bird et al. submitted).



Fig. 19 A portion of a large dusky dolphin group off Kaikoura.

Many duskies frequenting Kaikoura during summer head out of the area in winter, some moving north into warmer waters (Markowitz et al. in press). At about the same time, dolphins that have summered elsewhere move into the Kaikoura area for winter. “Winter” dolphins typically remain farther from shore, and mean group size increases over that of summer groups (Cipriano 1992, Würsig et al. 1997). Photographic identification of naturally marked individuals supports the suggestion of different winter and summer Kaikoura dusky populations (Markowitz et al. in press).

Admiralty Bay duskies would be expected to feed in a manner similar to that of dusky dolphins in Golfo San José, Argentina, where the analogous shallow water, protected habitat supports similar types of clupeid prey species (anchovy in Argentina

and primarily pilchard in Admiralty Bay). If this is the case, I expect to see decreased clean leaps, increased surface birds, increased surface fish, decreased synchronous dives, increased speed bursts, and increased dolphin group size as bout length progresses and fish are herded to the surface from deeper waters (Würsig and Würsig 1980). While I do see limited evidence of similarities in feeding styles, some of this support may be the artifact of a logistical tautology (i.e., definition of a feeding bout using activity level, clean leaps, and speed bursts, which sets up a situation whereby I defined my behavior by the presence of the behaviors I observed). The general lack of support for the hypothesis of coordinated surface feeding might also be due to a failure to collect the types of behavioral data appropriate to demonstrate a true effect. However, the most compelling reason for my lack of support for surface feeding most likely relates to the true diversity of behavior evidenced by feeding dusky dolphins, of which coordinated surface feeding was but one component. As this particular feeding strategy was apparently not the dominant tactic for these animals in the situations encountered in Admiralty Bay during winter 2002, it failed to appear with statistical significance in my tests. There are several alternate feeding strategies possible which would explain my results.

Dolphins should bring fish to the surface (as opposed to feeding at depth) if the energetic benefits of moving and maintaining prey at the top of the water column outweigh the costs. The surface may act as a wall through which prey cannot escape (Würsig and Würsig 1980), making it beneficial for dolphins to use the surface as one aspect of restraint. Feeding at depth requires air-breathing mammals to stop their

activities to breathe, reducing the time available for feeding while ascending and descending for breaths. Also, light levels are reduced with increasing depth, so visual predators would have more difficulty spotting deep prey (Boyd 1997, Nøttestad 2001). By this reasoning, it should be beneficial for dolphins to move prey to the surface. However, this is but one possible feeding strategy, and in situations where habitat, prey distribution, or predator numbers do not support this type of feeding, alternate strategies would be expected.

The evidence that seabird ratios did not significantly change during bouts, and surface fish did not become more apparent with bout length, support the idea that dusky dolphins do not always bring fish to the surface, but instead consume prey at depth. While I never observed fish in a dolphin's mouth in 2002 (although this was seen in previous seasons), I commonly saw gannets and shags swallowing upon surfacing, or surfacing with fish in their beaks, indicating the presence of prey below. Dolphins may have elected in many cases to not bring prey to the surface in an attempt (albeit somewhat unsuccessful) to avoid further kleptoparasitism by seabirds. This also supports the idea that seabird species benefit from the feeding activities of dolphins. In some instances, dolphins fed at the surface, and these situations were accompanied by visible fish and large numbers of surface birds, in addition to the usual contingent of diving birds (Fig. 20).



Fig. 20 Dusky dolphins surface feeding in Admiralty Bay. Note numerous surface and diving birds, and fur seal at far right.

Again differing from the pattern demonstrated in Argentina, group size in Admiralty Bay did not increase significantly with single bout length. Würsig and Würsig (1980) reliably used group size to indicate a “successful” feeding bout, with longer bouts sometimes consisting of hundreds of animals. I did not see this pattern in Admiralty Bay, and group size remained generally small (mean group size for all feeding bouts = 7.94 ± 5.51 S.D., $n=70$). Reasons for this discrepancy may be related to the overall number of dolphins in Admiralty Bay at any one time. Larger prey balls require more dolphins to successfully contain and manage them (Würsig and Würsig 1980). It is possible that there were not enough dolphins in AB to manage large prey balls, or not enough prey to create large aggregations of fish. A lack of available animals to manage a large prey ball may result in the fish scattering and escaping into the bay. Würsig and Würsig (1980) noted a threshold effect when examining dusky dolphin foraging in Argentina. If a small foraging group of 8-12 animals was unable to recruit at

least one other small group, surface feeding was not maintained, and activities died out rapidly. It is possible also that small-scale individual feeding in these cases continued at depth, but was not readily visible at the surface. Using this threshold approach, it is possible that dusky dolphins feeding in Admiralty Bay in 2002 were unable to recruit enough additional dolphins to maintain high levels of surface feeding behavior, and that this situation will vary with the numbers of dolphins in the bay at any one time and the size of the prey ball encountered.

Predator group sizes should increase for the same reasons prey schools aggregate, namely, increased foraging success through elevated prey encounter and capture rates, and increased detection of and protection against other predators (Caraco 1987, Clark and Mangel 1984, Partridge 1982). However, at some point group sizes will become large enough so as to render the benefit of group foraging as measured by prey capture success equal to that of individual foraging, and group sizes will fail to accumulate additional members (Caraco 1987, Clark and Mangel 1984). In the marine environment as in the terrestrial environment, the point at which this occurs depends on the size, type, and spatial distribution of prey. If the benefit of foraging individually is greater than that of foraging in a group, social foraging will not be a stable strategy (Caraco 1987). In areas with abundant prey, information about prey location should be equally available to all predators, and group formation is not expected. However, even in areas with abundant food resources, predation and social pressures may serve to maintain large groupings of animals. Jarman (1974) found a correlation between group size, predation pressure, and patchiness of forage when examining several species of

African antelope. In areas with abundant forage, large groups persisted due to increased predation risk and the benefits of increased predator detection. In areas with less predation risk and patchier resources, smaller group sizes were observed. In marine mammals, social influences as well as predation pressures are probably strong motivating factors in maintenance of large groups in areas with abundant food (Connor 2000). For Admiralty Bay, the relative patchiness of food resources, along with decreased relative predation risk when compared with Kaikoura, should result in smaller dusky dolphin group sizes than those observed off Kaikoura. This is consistent with observations.

An alternate hypothesis to explain the observed patterns is that dolphins in Admiralty Bay are not feeding in a coordinated manner, but instead feed largely independently of each other. Independent feeding would not require large numbers of animals, which may end up competing for limited resources. “Resident” killer whales in the Pacific Northwest forage together in family groups for salmonid (*Oncorhynchus* spp.) prey, but feeding itself appears to be an individual effort (Baird 2000). Independent feeding would be expected if prey were scarce or if the benefit to each individual animal did not increase with increasing group size. Prey encounter rate may increase with larger groups, but once a prey ball is encountered, if each predator’s behavior has no influence on its neighbor, cooperative hunting is not beneficial (Packer and Rutten 1988).

I subjectively noticed a difference in the “quality” of feeding bouts as the winter 2002 field season progressed. During the first 2 weeks, I noted many instances of bouts

that I subsequently labeled “high-level”. These were characterized by an apparent high degree of coordinated effort, many clean leaps, large numbers of diving gannets, and a high level of overall activity (Fig. 21). On several occasions, I recorded data on 1 feeding group, and noted the presence of multiple other “high-level” feeding groups simultaneously occurring across Admiralty Bay. This situation decreased after the first 2 weeks, and I noted that feeding bouts became increasingly “low-level”, with less apparent coordination, more appearance of independent feeding, lower activity levels, and fewer gannets. This trend is reflected in the significant decrease in bout length over the field season, as “high-level” bouts were generally longer duration than “low-level” bouts. “High-level” bouts continued to be observed occasionally in Admiralty Bay throughout the winter 2002 season, but not to the same degree as previously documented. These observations support the hypothesis that prey species altered distribution during winter 2002 (see Chapter II), moving out of Admiralty Bay and leaving relatively little for dolphins to consume. Another possible explanation is that “high-level” feeding bouts targeted larger prey balls, composed of larger, more energetic prey, while “low-level” bouts targeted smaller, slower prey species. Further work is necessary to assess the temporal components of feeding groups, and to better determine prey distribution throughout Admiralty Bay.



Fig. 21a-b “High-level” feeding bout. **a** Coordinated group leap. **b** Diving gannets target subsurface prey next to feeding dusky dolphin.

When taken in combination, these differing feeding situations all present evidence for exceptional behavioral flexibility in dusky dolphins. During the winter 2002 field season, I witnessed large feeding aggregations of apparently coordinated dolphins herding fish to the surface. I also observed large groups of dolphins apparently feeding at depth, large groups feeding individually at the surface, small groups feeding in a coordinated manner at depth, and small groups feeding independently. I also observed dolphins apparently using the shoreline and near-shore obstacles to contain

individual prey (see Chapter II). That feeding in a coordinated manner at the surface did not significantly stand out in my data series should not come as a surprise. It is merely indicative of the rich behavioral repertoire seen in dusky dolphins in situations of varying environmental conditions. Behavioral flexibility and large brain size were identified as possible causative factors in the invasion success of non-native New Zealand bird species (Sol et al. 2002), suggesting that the ability to vary behavior with varying environmental pressures has adaptive value.

This rich repertoire is again exhibited when observing dusky dolphins off Kaikoura. Some of the same animals documented in Admiralty Bay in winter have been photographed off Kaikoura during summer months (Markowitz et al. in press), where their feeding behavior again takes a dramatic twist, reflecting differences in prey availability and habitat. The deep oceanic waters off Kaikoura support a vertically-migrating scattering layer, a phenomenon not encountered in the shallow waters of Admiralty Bay. Instead, dusky dolphins off Kaikoura wait to feed until nightfall, when decreasing light levels cause mesopelagic organisms to ascend from depth. Dolphins then dive to meet the rising prey layer, choosing to consume primarily small squid (*Nototodarus* and *Todaroides* spp.) and lanternfish (*Myctophid* spp.), along with hoki (*Macruronus novaezelandiae*), red cod (*Physiculus bacchus*), and hake (*Merluccius australis*) (Cipriano 1992).

This pattern of moving offshore at night to meet the rising scattering layer, then returning to near-shore waters during daylight hours, closely resembles that of the Hawaiian spinner dolphin (*Stenella longirostris*) (Benoit-Bird and Au 2003, Norris et al.

1994). This tropical species typically splits into small groups to rest in shallow-water bays during the day, aggregating into larger groups that move rapidly offshore at night to feed on scattering layer organisms. It is theorized that spinner dolphins utilize the sandy shallow-water environment to avoid surprise attacks by deep-water shark species known to prey on dolphins (Norris et al. 1994). Dusky dolphins may also use the near-shore areas as protection against predation events by killer whales and sharks (Cipriano 1992, Constantine 1998, Würsig and Würsig 1980; for a review of shark predation on dolphins, see Heithaus 2001).

The relative wealth of food available off Kaikoura makes it possible for groups of up to 1,000 animals to exist in a limited physical area (Cipriano 1992). There, opportunities to observe other animals and develop alternate feeding strategies through imitative learning may assist dolphins in optimal exploitation of available resources. Some of these same animals then migrate to the warmer waters of the Marlborough Sounds in winter, where the physical situation does not permit the existence of similarly large dolphin groups. Changing resource availability might select for alternative levels of sociality, whereby fission-fusion societies meld and diverge depending on habitat and prey. Antelope species in Africa vary in sociality and group size depending on food patch quality, distribution, and predation risk (Jarman 1974). Patchy, ephemeral resources require alternate foraging strategies to those necessary with uniform resources, influencing group size and composition (Jarman 1974, Pianka 1978).

Group foraging theory suggests that animals should aggregate to exploit available food resources and maximize individual intake. Information gleaned from

conspecifics may be used to gauge patch location and quality, and aggregating is deemed a stable strategy when food is scarce and patchy, as demonstrated in many areas of the marine environment (Clark and Mangel 1984, Packer and Ruttan 1988). This pattern, however, becomes unstable when group numbers rise too high and per capita intake is reduced as patches are exhausted. Also, in areas with abundant food resources, there is no real advantage to group feeding, as information about food should be available to all individuals equally. In these situations, group foraging is not profitable; however, predation pressures or social mechanisms may serve to preserve aggregations (Connor 2000, Hamilton 1971). It is probable that uniformity of prey distribution, predation risk, and social facilitators are all causative factors in the maintenance of large dolphin groups seen off Kaikoura. Alternately, limited, patchy prey resources, a relative lack of predation risk, and alternate social factors are likely variables influencing smaller group sizes seen in Admiralty Bay.

The variability of feeding behaviors observed in dusky dolphins most likely confers an adaptive advantage over those species less able to adjust behavior. Natural variations and perturbations in prey distribution and habitat should favor those species able to compensate and adjust their behavior accordingly to maximize use of available resources. This does not mean, however, that the observed behaviors are the result of an evolutionarily stable strategy, as currently no evidence exists for the heritability of these behaviors. Rather, a more parsimonious explanation is that the feeding tactics themselves are not heritable, but that a heritable conditional strategy exists, whereby the ability to adjust behavior has a heritable component. This ability to change would confer

an adaptive advantage over more behaviorally rigid species such as koalas (*Phascolarctos cinereus*), giant pandas (*Ailuropodinae melonoleuca*), or Hector's dolphins (*Cephalorhynchus hectori*) (Dawson and Sooten 1993) in which behavioral constraints and a narrow environmental niche have endangered species survival in some areas. The variability evident in dusky dolphin feeding behavior should provide them with the ability to weather fluctuations in natural conditions and survive in a changing environment.

CHAPTER IV

SUMMARY AND CONCLUSIONS

A total of 253 dolphin groups were encountered in Admiralty Bay during 42 days of data collection in winter 2002. Dusky dolphin groups were small (6 animals), and most often engaged in food acquisition activities, which comprised the majority of behavioral states recorded (58.5%). Animals returning from previous years constituted 100 of 177 individually-recognized animals photographed in Admiralty Bay, with returning animals sighted significantly more often than new animals. Seabirds and fur seals were commonly observed competitors for dolphin prey. Pending aquaculture expansions pose a potential threat to dolphin movements and foraging ability, based on limited use of areas inside existing mussel farms. Reduced dolphin numbers compared with previous years suggests a shift in prey distribution for 2002, and this hypothesis should be tested via additional research efforts in Admiralty Bay in coming seasons.

Focal data on 37 groups and 70 bouts of feeding behavior revealed a lack of statistical support for the hypothesis that dolphins should work in a coordinated manner to bring fish prey to the surface. This suggests the alternate hypothesis that the variety of dusky feeding behaviors encountered was actually responsible for the results observed, and not the overwhelming significance of any one feeding tactic. Large and small groups of dolphins were observed to work in coordinated groups as well as individually to feed on surface fish and prey at depth. Dolphins were also observed using the shoreline to confine fish. This behavioral flexibility demonstrates the

adaptable and generalist nature of dusky dolphin foraging, which is capable of exploiting a variety of prey species in varying environments. Some of the same individual dusky dolphins observed feeding in Admiralty Bay again alter foraging strategies when feeding in the deep-water habitat off Kaikoura. There, sonar data revealed small subgroups of dolphins diving at night to meet rising DSL organisms, choosing to utilize that portion of the abundant prey layer closest to the surface, and therefore least energetically taxing. Although inhabiting similar habitats, dusky dolphins in Admiralty Bay do not strictly follow the most visible surface feeding patterns exhibited by those dolphins in the shallow bays of Argentina, but demonstrate a mixed behavioral repertoire appropriate to the variation and predation risk in their environment. Dolphins in Argentina likely also adjust feeding behavior with prey distribution and number, and evidence from Würsig and Würsig (1980) presents just one of many possible feeding strategies used as a basis for comparison with that of dusky dolphins in Admiralty Bay.

Dusky dolphins enjoy a rich and varied social life, and their social complexity may facilitate learning and adaptive behavior in an unpredictable environment. Predation risk also likely plays a part in the social makeup of these dolphins, especially in the area of group size. The deep-water habitat off Kaikoura poses increased predation risk from large sharks and killer whales, and this combined with a relatively abundant food source, should select for the exhibited large group sizes. Alternately, the shallow-water environment of Admiralty Bay poses less threat of predation for dolphins, and the ephemeral, patchy prey resources contribute to smaller observed group sizes.

The variety of feeding behaviors observed in dusky dolphins should not, however, be interpreted as an evolutionarily stable strategy, as there is currently no information on the relative fitness of animals displaying these behaviors, nor the heritability of behaviors. What is more likely is that heritability exists for a conditional strategy, or the ability to adjust feeding behavior dependent upon prey and environmental conditions and learned behavior. The behaviors themselves are not heritable, but the ability to vary behavior likely has a heritable component. This ability to vary behavior likely provides an adaptive advantage over more behaviorally rigid species such as koalas or giant pandas, which may be unable to adjust to perturbations in their habitat, whether from natural disasters or man-made alterations. Dusky dolphins should be better able to ride out environmental fluctuations and survive periodic hardships than less flexible species. Ultimately, dusky dolphins' behavioral flexibility and social acumen provide them with an adaptive advantage allowing them to successfully navigate and exploit the nuances and subtleties of their unpredictable world.

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