PREDATOR INFLUENCES ON THE BEHAVIORAL ECOLOGY OF DUSKY DOLPHINS

A Dissertation

by

MRIDULA SRINIVASAN

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

DOCTOR OF PHILOSOPHY

May 2009

Major Subject: Wildlife and Fisheries Sciences

PREDATOR INFLUENCES ON THE BEHAVIORAL ECOLOGY OF DUSKY DOLPHINS

A Dissertation

by

MRIDULA SRINIVASAN

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

DOCTOR OF PHILOSOPHY

Approved by:

Chair of Committee,	Bernd Würsig
Committee Members,	William Grant
	Jane Packard
	X. Ben Wu
Head of Department,	Tom Lacher

May 2009

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Predator Influences on the Behavioral Ecology of Dusky Dolphins.

(May 2009)

Mridula Srinivasan, B.Sc. (Honors), University of Delhi, India; M.Sc., University of Delhi, India; M.S., Florida Institute of Technology

Chair of Advisory Committee: Dr. Bernd Würsig

I developed a spatially explicit individual-based model (IBM) to capture the dynamic behavioral interaction between a fierce predator (killer whale, *Orcinus orca*) and a clever prey (dusky dolphin, *Lagenorhynchus obscurus*), and to answer the ultimate question of costs *vs.* benefits for dusky dolphins when making anti-predator decisions. Specifically, I was interested in calculating time/distance budgets for dusky dolphins in the presence/absence of killer whales and the presence/absence of movement and behavioral rules, which presumably evolved in response to spatial and temporal variations in predation risk. Results reveal that dusky dolphins rest less, travel more and have reduced foraging time when killer whales are present. These effects are more pronounced with increased presence of killer whales. The model suggests that a strong reason favoring the adoption of short and long-term anti-predator mechanisms is increased survival resulting from decreased encounters with killer whales. Further, a mother with calf rests less and travels more when killer whales are present relative to a dolphin without calf. However, a mother with calf on average, flee shorter distances and have fewer encounters with killer whales than a dolphin without calf. Thus, despite ecological costs, it makes evolutionary sense for dusky dolphins to adopt anti-predator rules. Bioenergetic consequences for dusky dolphins with and without calf were estimated as **total energetic costs** and **foraging calories** lost due to low/high presence of killer whales. I calculated total energy costs as: *Foraging costs (FC) + Locomotor costs (LC) (Travel) or LC (Travel) + LC (Flee)* based on the absence, as well as low/high presence of killer whales. Foraging costs contributed significantly to total energetic costs estimated. Travel costs are minimal owing to proximity to deep waters. The total energy costs were not significantly higher from low or high presence of killer whales for mother with calf, but increases by about 90 kcal/day for a dusky without calf. However, I estimate foraging calories lost due to increased killer whale presence is almost 5 times more for mother with calf. Therefore, it might be important to consider indirect predation risk effects by social type in future studies on animal bioenergetics.

DEDICATION

To the most important people in my life who made this happen…

Paati, Thatha, Amma, Appa, Chithi, Arvind,

and most specially Keiko and Jolly

...and

To Leonardo Da Vinci and Sir Isaac Newton

for inspiring me to be a student of science

ACKNOWLEDGMENTS

A dissertation results from the collaboration and support of many people. At the top of my list is my grandmother. Paati was there for me during trying times and was the voice of comfort and encouragement throughout my academic and personal pursuits. She is no longer with me today and I miss her very much at this crucial juncture in my life. I hope I can continue my life and learning with the resilience and temperament she has shown in hers.

This project would not have been possible without the quartet power of my doctoral committee. Thank you Dr. Jane Packard for challenging my thought process and research focus with probing questions and astute analyses. I am grateful for the research opportunity this past year and all the new skills I acquired when working on the USDA and NSF projects. Most of all, thank you for your unending support and for motivating me to be practical in achieving my academic and career goals.

Dr. Ben Wu introduced me to the world of landscape ecology and spatial analysis. His affable nature, insightful reasoning and problem-solving skills on issues beyond his technical expertise benefitted me immensely throughout the duration of my doctoral studies.

Dr. Bill Grant is a genius systems ecologist and I am so glad that I took his class. He opened my eyes to systems modeling and the wonderful possibilities it offers to address complex ecological questions. This project would not have been completed without his modeling, programming, and ecological expertise. I am inspired daily by his wit, wisdom, and passion for ecological modeling and grateful for his support and encouragement during my time at Texas A&M.

Dr. Bernd Würsig is not only my academic supervisor and doctoral committee chair, but also a great human being, friend, mentor, and a firm crutch to lean on in almost any trying circumstance. I am humbled by his intellectual prowess and vast experience in studying cetaceans and feel very fortunate to have been his student. He provided me the freedom and financial support to explore a challenging problem and negotiate the twists as I delved deeper into studying predator-prey interactions. He provided me direction and guidance, and most of all, kept my spirits up with those ‘sometimes bad’ jokes (smiles). He and his wonderful wife, Mel, have been a benefactor both off and on the field. I cherish all the good times at the Würsigs and always felt that it was a home away from home.

There are several individuals who have been instrumental in the success of my doctoral work. Hopefully, I have not left anyone out, but apologies if I do. I thank Dr. Bill Evans for his sage advice and for sharing his experiences working with marine mammals. I dearly cherish his friendship and support.

I especially thank Dennis Buurman at *Dolphin Encounter*, Kaikoura, New Zealand who went out of his way to support my research work in Kaikoura. He provided valuable data on dusky dolphins and killer whales. I am greatly indebted to him, Ian Bradshaw, Lynette Buurman and the crew for their friendship and support. Dennis Buurman and Gary Melville also provided shark data and shark chum for a short-term shark study. Also, Alex Thompson at *Dolphin Encounter* provided much help in getting

killer whale data sorted and organized. Needless to say, the unerring support and assistance provided by *Dolphin Encounter* staff and crew is greatly appreciated.

Special thanks to Victor and Colette Foster for letting me come on their fishing boat and helping me with the shark study. I am grateful for their generosity, shark expertise, and the support of their crew. Thanks also to Jodie West and Victor Foster for providing data from a previous shark study.

I thank Clinton Duffy for all New Zealand shark-related queries and for responding to my persistent emails. I thank Dr. Rochelle Constantine for her support and feedback on dusky dolphins-killer whale interactions as well as killer whale photos. Thanks to Dr. Ingrid Visser for accommodating me at her place and providing dusky dolphin and killer whale information.

Dr. Dave Ebert, Dr. Mike Heithaus, Gretchen Steiger, and Dr. John Van den Hoff helped sort and identify shark and killer whale-related dusky dolphin scars, and I am very grateful for their expertise and timely assistance.

National Institute of Atmospheric Research (NIWA) New Zealand provided bathymetry data for Kaikoura and Admiralty Bay regions. Special thanks to Dr. Michael Uddstrom at NIWA for long and short-term Sea Surface Temperature data for Kaikoura and Admiralty Bay. Thanks also to Murray Green and John Hocking for helping with boat maintenance and servicing.

A big thank you to Todd Swannack. Without his encouragement, I would not have finished my dissertation on time. His modeling assistance and all-round expertise with computers and statistics was much needed and welcomed. Dr. Mike Heithaus and

Dr. Tom Tinker provided valuable guidance that helped to improve the model during the initial development stages.

I am particularly grateful to all my fellow graduate students and research colleagues at the Marine Mammal Research Program in Galveston. I would like to especially mention Adrian Dahood who was always there to lend a helping hand regardless of the many pressing issues she faced. Thanks Adrian for making the Dolphin Encounter data electronic, for your humor, and for countless other favors you provided without asking. I also thank Sierra Deutsch for her immeasurable support and Jennifer Bennett who provided field assistance during the 2007 field season. Thanks also to Heidi Pearson for her photography tips and academic support.

This project would not be possible without the financial assistance provided by Earthwatch Research Institute and Earthwatch volunteers. Hats off to all Earthwatch volunteers. They roughed it out in the heat and cold to help collect valuable data. Their support of marine mammal work and the environment is gratifying and praise-worthy.

I thank Stacie Arms, Shirley Konecny, and Vicki Buckbee for handling all administrative issues and making my life easier, free of paperwork related headaches. Shirley's cheerful and gentle nature always made my day. She always had a solution to my innumerable questions and problems, and I will always think fondly of her.

Financial assistance for the project was provided through multiple sources, including Earthwatch, National Geographic, Wildlife and Fisheries Sciences at Texas A&M College Station, Department of Marine Biology, Texas A&M Galveston, Mooney Grants, Mini Grants, GPEF and Graduate Association Funds - Galveston and College

Station, Office of Graduate Studies, W.B. Davis Scholarship, Würsigs personal fund, and specifically, SWSS, USDA, and NSF for funding my research assistantships during my doctoral tenure at Texas A&M University.

I would like to thank my family who made all this worthwhile. Without the support of my parents, I could never imagine pursuing a seemingly unachievable dream to study marine mammals. Their faith in me inspires me every day, and I know, it was their prayers and well-wishes that has led me this far and will aid me in the future. Thanks for being the best parents in the world. I could not have done this without you. My brother, Arvind, was my voice of reason during my academic and career debacles, always there to comfort and encourage me. Chithi and Thatha, thanks for believing in me. Your prayers and blessings kept me going as I worked on my doctorate.

And to the most important man in my life, Jolly☺. Thanks for giving me the happiest moments of my life. I could not have accomplished this dissertation without your love, warmth, comfort, and sacrifice. You were my pillar of strength and inspiration as I negotiated every twist and turn in my quest for a doctorate. Thank you for being there for me every step of the way.

This acknowledgement would be incomplete if I did not thank the magnificent animals that are core to my research work. The ability of these sea mammals to effectively adapt to a challenging environment continually fascinates me. These mammals remain an inspiration to continue my study of their ecology and behavior.

TABLE OF CONTENTS

CHAPTER

LIST OF FIGURES

FIGURE Page

FIGURE Page

LIST OF TABLES

TABLE Page

TABLE Page

CHAPTER I

INTRODUCTION

> To explain all nature is too difficult a task for any one man or even for any one age. `Tis much better to do a little with certainty, and leave the rest for others that come after you, than to explain all things.
>
> Sir Isaac Newton (1642-1727)

Predation – an overview

In 2005, R.W Sussman and D.L. Hart came up with a fascinating theory that humans evolved in the manner they did, largely because they were prey to giant carnivores of several millions years ago (Hart and Sussman 2005). This claim challenged conventional wisdom that man was born a hunter. They suggested that to avoid getting killed by predators, both primates and humans developed strategies that eventually led to group living, greater mobility, and a larger brain. This notion remains controversial, but helped re-ignite discussion and debate on sociality and predation.

Is predation the only causative factor leading to sociality or are there other factors that have contributed independently to social living? While this debate continues, there are elementary aspects of predator effects that are still not fully understood, despite decades of research. So, there is much to learn about how predators influence prey behavioral ecology and ecological communities through consumptive and non-

---

This dissertation follows the style of Ecology.

consumptive ways. Also, when dealing with behaviorally responsive prey, considering both prey and predator behavior is necessary to make proper assessments of predator-prey interactions.

This chapter provides an overview of important predation concepts that are the foundation of most predator-prey studies today. The chapter also provides a lead-in to the rest of the chapters in the dissertation by focusing on the importance of non-lethal predation effects, predation risk in dolphins (Chapter II), and the use of modeling as an alternative to explain and evaluate predator roles in dolphin behavioral ecology (Chapter III).

The role of predators and predation first took center stage with Lotka-Volterra's predator-prey dynamics model, independently developed by both scientists (Lotka 1925, Volterra 1926). This classic model primarily focused on predator-prey population cycles in a virtually unlimited environment, where predators could eat as much prey as they wanted and prey populations kept growing, thus producing oscillating cycles with no asymptotic stability. Since then, their models have been improved to make them realistic (Abrams 2000, Krebs et al. 2001 (snowshoe hare and lynx 10-year cycle)). But it wasn't until Pulliam (1973), Alexander (1974), Jarman (1974), Wilson (1975), and Bertram (1978) that the role of predation was discussed in the context of social societies or group living. These authors synthesized information from their research on lions and antelopes, primates, social insects, and other sources to describe how predation risk could have contributed to group living by affecting prey behavior, social relationships, and habitat selection.

Some of the significant concepts that came forth from these early and later works include costs and benefits of grouping patterns (Bertram 1978, Pulliam and Caraco 1984), vigilance (Roberts 1996), predator-prey detection and encounter (Elgar 1989, Dehn 1990), 'selfish-herd' mentality (Hamilton 1971), dilution and confusion effects (e.g. Kruuk 1972, Landeau and Terborgh 1986), and finally the nature of social relationships involving kin selection, nepotism, and altruism (Hamilton 1972, Trivers 1972).

Early theories on predation also led to later attempts by other scientists to elaborate on non-lethal predation risk vs. lethal predation in a variety of taxa (Sih 1987, Lima 1990). What is prey to one, is predator to another, so an investigation of ecological interactions from predator and prey perspectives is necessary to acknowledge how behavioral plasticity has allowed animal societies to function.

Predation, however important, cannot solely determine spatial distribution and sex-specific behavior in some systems and species, for example in primates (van Schaik and van Hooff 1983). But by teasing apart concepts of group size, social structure and composition (as defined in Kappeler and van Schaik 2002) and behavioral variability, we can get a better idea of how predators have shaped prey societies and vice versa.

Predation concepts revisited

It was proposed first by Pulliam (1973), based on his observation on birds, that animals that forage in groups are more likely to detect a predator prior to an attack, and that such groups could afford to spend less time in vigilance without losing the ability to detect predators on time. Thus, the animal is able to allocate more time to other activities and still spend less time in vigilance. Studies on primates have also shown that larger parties are better able to detect predators than smaller parties (Van Schaik and Van Hooff 1983).

Fitzgibbon (1990), observed that cheetah preferentially kill more male gazelles, even though the sex-ratio of the gazelle population is tilted heavily in favor of females. The primary reason for this is that male gazelles tend to be more solitary than females, and most male gazelles situate themselves at the periphery of groups and maintain larger nearest neighbor distances compared to females in the center of the group.

Hamilton (1971) introduced the ‘selfish-herd’ concept, where certain individuals guard the periphery of the group, leaving them more vulnerable to attack, while other individuals position themselves at the center. These peripheral individuals are generally more vigilant than others in the group, because they are easy targets for attacking predators. But as group size becomes large, the proportion of individuals at the edge is reduced; this confounding ‘edge effect’ lowers the group-scanning rate for predators.

The idea that animals benefit by foraging in groups and therefore spending less time in predator surveillance has not been clearly substantiated, despite many avian and mammalian studies (Elgar 1989, Childress and Lung 2003). The negative correlation between increasing group size and decreased individual vigilance rates is confounded by not considering the density of the food resource, which can lead to competition of resources (Elgar 1989).

It has been suggested that perhaps there is an optimal group size (Bertram 1978, Alados 1985), beyond which vigilance effects is negated and competition for food and mates takes over. Bednekoff and Lima (1998) also called for re-assessment of the fundamental assumption of vigilance behavior and its functional consequences, based on differences in scanning rates in birds.

Joining groups can reduce the chances of encountering a predator, increased detection of predators, and in case of an attack prey can escape due to dilution-confusion effect because predators are unable to concentrate on a single prey (Jarman 1974, Bertram 1978, Norris and Dohl 1980, Norris and Schilt 1988, Elgar 1989, Connor 2000). Dilution effects result from the lower probability of an attack on the same individual in the group, and confusion effect results from the lower capture rate per attack (Connor 2000).

To reduce their probability of attack, animals may also associate with similar sized individuals (Krause 1994). Sometimes, predators may take advantage of this confusion effect and thus prefer attacking large groups – because in the ensuing chaos of an attack, animals may not be able to escape quickly enough and thus be isolated by their predators e.g. when impalas *Aepyceros melampus* are attacked (Jarman 1974). The skittering effect in schooling fishes is another example, when predators such as seals, dolphins, or killer whales (*Orcinus orca*) attack (Norris and Schilt 1988, Perryman and Foster 1980).

Wolf (1985) also observed that oddly colored parrotfish might abandon mixed-species groupings during an attack when threatened. Jackson et al. (2005), in a study on human subjects, observed that detection of cryptic prey increased asymptotically and leveled off with increasing group size, similar to lab observations on birds.

Animals may also resort to other predator avoidance measures such as fleeing (Ydenberg and Dill 1986) from predators, e.g. when spinner dolphins (*Stenella longirostris*) or bottlenose dolphins (*Tursiops aduncus)* are threatened by large sharks (Norris and Dohl 1980, Connor and Heithaus 1996), or when dusky dolphins are threatened by killer whales (Würsig and Würsig 1980, Würsig et al. 1997, Markowitz 2004). Dwarf sperm whales *Kogia sima,* release a plume of reddish excreta when threatened (Scott and Cordaro 1987), while cephalopods may eject ink from ink glands when threatened (Hanlon and Messenger 1996), such defense mechanisms may add to existing anti-predator tactics. Some prey may also rely on chemical cues from predators to assess the levels of predation risk, e.g. amphibian larvae respond to chemical cues from predatory fishes (Kats and Dill 1998).

What of the predator? Predators also have a tendency to increase group sizes to feed on large prey (Jarman 1974). Lions (*Panthera leo*) when attacking larger prey such as zebra or buffalo, associate with several individuals but when feeding on, for e.g. a warthog *Phacochoerus africanus*, might decide to go in alone (Scheel and Packer 1991). Similarly, Kruuk (1972) found that spotted hyenas had greater success in hunting wildebeest (*Connochaetes sp***.**) calves when hunting in pairs. Often, social carnivores will attack animals that are much larger than they are, e.g. lions, hyenas (*Crocuta crocuta*, Kruuk 1972), cheetahs (*Acinonyx jubatus*, Fitzgibbon 1990), and killer whales (Jefferson et al. 1991). Bertram (1978) suggested that two reasons for this: greater ability to bring down a larger animal through group effort and willingness to take higher risks despite personal injury, such that injured animals can still share a kill brought down by their companion animals. But Packer and Caro (1997) and Packer (1986) hypothesized that grouping in lions primarily resulted due to dispersal of resources and issues of resources defense (e.g. Lamprecht 1981), rather than to aid in cooperative hunting.

There can also be differences in who attacks. Male lions may often dissociate themselves from attacks on smaller animals, and sometimes in lions both females and males might ‘cheat’ and not participate in an attack (Scheel and Packer 1991). This has also been observed in male killer whales (Pitman et al. 2001).

Predators can typically track and follow their prey movements and migrations (Schaller 1972). Pacific white-sided dolphins (*Lagenorhynchus obliquidens,* Black 1994) and killer whales (Nichol and Shackleton 1996) are also known to track and follow prey. But do they choose areas where prey is abundant or where there is greater success in catching prey? Hopcraft et al. (2005) observed that even though lions followed their prey, they usually frequented areas where their success in capturing prey was greatest. Wolf (*Canis lupus*) kill sites and areas where they traveled were not found to be different, so they basically frequented areas where elk were most vulnerable (Bergman et al. 2006).

Unlike the numerous studies on prey behavior related to mate choice and finding food under the risk of predation, there are limited studies in recent years that investigate the other side of the interaction. Lima (2002) observed the dearth in data when it came to looking at predatory behavior and characteristics that influence prey behavior to change. He recommended that predator abundance and effects should not be assumed constant and unresponsive to prey behavior; instead, the interactive effect between the two should be acknowledged and incorporated in predation risk studies (discussed in Lima et al. 2003).

Sociality and predation risk

Observed prey behavior and spatial distribution often has been linked to social aspects of prey living. For example, Wrangham (1980) asserted that intraspecific competition for resources was an important factor in determining social behavior, and therefore should be considered along with predation pressure, resource abundance and distribution. Intraspecific competition can favor grouping or no grouping either due to habitat constraints or social constraints.

The basic feature differentiating males from females are that males will invest more in increasing fitness than avoiding predators and finding food (Trivers 1972), and thus their distribution will be governed by where females are distributed. Females on the other hand, equate reproductive success to finding food and avoiding predators and not by the number of mating opportunities. But in reality, the relationship is not that simple. Females can also increase fitness through mate choice. For example, females choose strong males who can enhance condition or survival of female and offspring (Bateson 1983). But other constraints also operate.

In females, phenotypic constraints such as differences in reproductive condition, affect dietary needs and susceptibility to predation. For example, non-lactating and non-pregnant females may prefer high quality vegetation and lactating females might need access to good food and safety from predators, but such differing choices may have energetic consequences. Female behavior can in turn affect male distribution and associations. In males, smaller males might resort to spending more effort in food acquisition rather than competing with larger, stronger adults, e.g. in sperm whales (*Physeter macrocephalus*, Whitehead and Weilgart 1999). Where female competition is low and food is abundant, females may aggregate near males either because of intense predation pressure or heightened male harassment or infanticide, e.g. in chimpanzees (van Schaik and Horstermann 1994) and bottlenose dolphins in Shark Bay (Connor et al. 2000). Alternatively, if food patches are rich but scarce, females may come together to reduce competition, e.g. in lions (Packer 1986).

The nature of prey habitat can also affect social relationships and spatial distribution. When predators are concentrated, grouping is favored (Bertram 1978, Pulliam 1973). Also, when food is concentrated in large patches, grouping is favored as it reduces competition (Jarman 1974). Frid et al. (2006) observed that predation rates in harbor seals (*Phoca vitulina*) were greater due to resource declines and lower energy states, making them susceptible to attacks by killer whales and sharks in Alaskan waters, and proposed it as one of the reasons for population declines in North Pacific harbor seals. Climate change and sea surface temperature (SST) may further affect large-scale seasonal and regional spatial distribution of animals (Simmonds and Issac 2007, Macleod et al. 2008)

Re-examination of predator effects

Animal societies are inherently complex — it is difficult to definitively dissociate predation risks from other social, ecological or environmental pressures. Nevertheless, it is clear that predation risk plays an important role in influencing group living. Since Lima and Dill (1990) provided a comprehensive account of the behavioral effects observed in a variety of prey resulting from predation risk, there has been a concerted approach and understanding towards considering non-lethal predation on an equal or greater scale than lethal predation (Peckarsky et al. 2008, Orrock et al. 2008).

Priesser et al. (2005) completed an extensive meta-analysis to demonstrate that the demographic effects from predation risk equaled or exceeded effects from predator consumption. They also showed that in aquatic realms, trophic cascades (indirect effects of predators on plants via herbivores) were more pronounced than in terrestrial systems (*see* Shurin et al. 2002, Werner and Peacor 2003 for details). Since then, numerous studies have provided strong evidence that non-lethal predation risk effects can have vast consequences for prey and for the ecological community (Luttbeg and Kerby 2005, Abrams 2007, Heithaus et al. 2008).

The concept of trophic cascade and its conservation implications has led to discussions on two important concepts based on Abrams (1995, 2007) – Density Mediated Indirect Effects (DMIE) and Trait Mediated Indirect Effects (TMIE, refer to Abrams 2007 for a terminology review). Density Mediated Indirect Effects and TMIE represent pathways that affect species interactions in ecological communities. These indirect effects that include *trait* changes (foraging behavior or predation risk) or population *density* and growth rates propagate from one species to another in a food web due to changes in an intermediate or transmitter species.

Ripple and Beschta (2004) described how the absence and reintroduction of wolves represented by trophic cascades, predation risk variations and prey optimal foraging reshaped the ecosystem structure in the Yellowstone National Park, United States. In essence, large carnivores, herbivores, and plants are linked in affecting the biodiversity of the ecosystem through trophic cascades, and wolves play a major part in the sustainability of such ecosystems. Other evidence from bottlenose dolphins (*Tursiops truncatus*) in Shark Bay, Australia, and the sea otter-sea urchin- kelp trophic system in the Aleutian Islands, Alaska (Dill et al. 2003) also described how predation risk, TMIEs, and trophic cascades are inextricably linked with conservation and maintenance of marine ecosystems.

Predation risk in dolphins

Dolphins are apex predators, but they can be prey too. Like all prey, they are affected by the presence of more powerful predators, such as killer whales and large sharks. While these predators may not choose dolphins as primary prey, they can scare dolphins into changing lifestyle decisions, i.e. where and when to feed, where and when to rest, etc. For the most part, the focus in marine mammal and dolphin research has been on lethal predation (see reviews by Jefferson et al. 1991, Bowen 1997, Norris 1994, Connor 2000, Trites 2002). However, it becomes difficult to explain seasonal preference for shallow or deep waters, rocky or sandy habitat, when there are no observations of dolphins being attacked. Food, reproductive needs, and environmental factors all play a small or large role in influencing dolphin patterns. But isolating the primary influencing factor/s from the rest remains an elusive objective in most ecological studies.

Evidence suggests that spatial distribution and behavior of terrestrial and marine organisms can be driven by fear (Sih and Wooster 1994, Creel and Winnie 2005, Wirsing et al. 2007). Similarly, dolphins may also modify their daily movement and distribution patterns in the face of fear, e.g. bottlenose dolphins (*Tursiops aduncus*) Heithaus and Dill (2002, 2006). But predation risk is a dynamic event and involves evolving and adapting prey and predators. Therefore, it is possible that in certain environments, predation risk from sharks may be minimal and killer whale threats may be higher, or there could be only seasonal threats from these predators. In such cases, it is therefore important to use a systems approach where several potential influencing variables are considered before legitimate conclusions can be reached (Chapter II).

Prey are affected by predator behavior, and accordingly prey exhibit different short-term tactics or long-term strategies to combat changing levels of predation risk (Chapter II). However, it is unclear what consequences the prey incurs by making these anti-predator decisions (Creel and Christianson 2008) — this is true for most taxa, including dolphins. First, we need to know if prey pays a price by adopting anti-predator mechanisms (see Chapter III, IV). Second, we need to determine the nature of these costs and quantify them (see Chapter III, IV). Third, we need to view these costs in a broader evolutionary context and elucidate the costs *vs.* benefits of using anti-predator rules to determine prey lifestyle choices (see Chapter III, IV).

Marine mammals, particularly whales and dolphins inhabit systems that preclude most types of experimental studies. For such systems, ignoring predation risk components, both lethal and non-lethal effects in behavioral ecology studies creates a myopic view of predator-prey interactions. This restricts the ability of scientists and managers to grasp the full influence of predators on prey habitat selection and population viability, especially for critical marine mammal species.

Models are substitutes for natural systems. They provide a simplified view of the ecosystem by incorporating important functional attributes, but are not meant to serve as 'real systems' (Hall and Day 1977). Modeling is especially applicable when empirical data is limited and field logistics and species concerns prevent elaborate hypothesis-driven studies. Models can be construed as a research strategy that aids in conceptualizing a system of interest and understanding how basic components function and interact (Jeffers 1978). The goal is to be able to manipulate systems components and address ecological questions that increase our understanding of how the players within the system function.

When dealing with clever prey and clever predators e.g. marine or land mammals that have a suite of strategies showcasing their behavioral and cognitive plasticity, dynamic or stochastic models provide an appropriate way to capture random variations and complex relationships within a network of interacting components. Dynamic simulation models provide the next level in modeling tools, where modeling processes and components are linked with computer software tools. Given system and individual complexities in dolphin societies and the need to ecologically assess the role of predators in influencing dolphin behavioral ecology, spatially explicit individual-based models, are ideally suited to address complex predator-prey behavioral interactions (Grimm and

Railsback 2005) where the focus is on individual behavior and is representative of the population.

In the following chapters (Chapters II – V), I narrow the scope of discussion on predation and social societies to include mainly non-lethal or indirect effects of predation risk, and how risk influences dolphin behavioral ecology. My focus is at the species level and does not extend to ecological communities. Indirect predation risk effects have been variously termed as fear effects, non-consumptive effects (NCE), non-lethal, non-consumptive predation, or risk effects. For purposes of the dissertation, I will use indirect predation risk effects or fear effects as the primary terms to describe predator effects on prey behavioral ecology.

Research objectives

In the present study, my species of interest is the dusky dolphin (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. At the basic level, I am interested in how fear drives changes in daily and long-term choices for dusky dolphins, i.e. habitat selection and foraging behavior. Ultimately, I am interested in the energetic, as well as ecological and evolutionary costs associated with dolphin decision-making within the context of fear. Specifically, my research objectives are to:

1) Identify and detail causal factors for observed dusky dolphin seasonal and daily patterns near Kaikoura, New Zealand, with emphasis on indirect predator effects and dusky dolphin anti-predator decisions;
2) Develop, describe, and evaluate an individual-based spatially explicit model (IBM) of a clever prey (dusky dolphin) and a clever predator

(killer whale) near Kaikoura, New Zealand to capture the dynamic relationship between predator and prey;

3) Determine quantitatively the potential consequences of anti-predator decisions using the IBM.

Overview of chapters

In Chapter II, I review current knowledge of predation risk in dusky dolphins and why indirect predation risk effects are an important facet of dolphin behavioral ecology. In Chapter III, I describe and evaluate a spatially explicit Individual-Based Model (IBM) developed to address indirect predation risk effects in dusky dolphins from both ecological and evolutionary perspectives, represented by dynamic dusky dolphin and killer whale behavioral interactions in a defined system off Kaikoura, New Zealand. In Chapter IV, I use the IBM to quantify the consequences of fear and to understand how anti-predator decisions can have lifestyle and bioenergetic consequences based on the representative dusky dolphin system near Kaikoura, New Zealand.

Importance of research

Predator-prey interactions deal with complex relationships that are difficult to generalize and much harder to document in the field, since most events go unobserved. This is particularly true of cetaceans that spend their entire lives at sea. Yet, it is difficult to disregard observational and anecdotal data that suggest that predators such as killer whales and large sharks play an important role in determining dolphin social dynamics, choice of feeding and rest areas. The challenge is to quantify the extent and nature of predator influence. In situations where field studies are not viable, lab experiments and modeling tools can serve as proxy for natural animal behavior and systems. The present study helps to overcome some of the limitations of previous predator-prey studies in several ways:

1. The spatially explicit, individual-based model proposed here provides potential to test a variety of hypothesis within a larger theoretical framework regardless of the species of interest. For example, we can test theoretical concepts of prey vigilance, predator-prey detection distance, flight initiation distance (FID), feeding-safety tradeoffs, and the consequences of group size variability, spatial distribution and social dispersion on predator-prey behavior.
2. The model is applicable to both direct and indirect predation risk effects. Thus, we can look at lethal effects of predators on population dynamics and demographics, as well as the effects of changing prey behavior in response to predation risk levels.
3. The study also provides strong evidence to consider indirect predation risk effects in bioenergetic models, previously ignored in behavioral ecology studies.
4. Unlike previous studies, the model lays emphasis on both predator and prey behavior, providing a more realistic representation of behaviorally responsive mobile prey and predators.
5. Developed with a systems modeling approach, it is possible to observe the interactions of several factors such as photoperiod effects, rainfall, or other environmental factors along with biotic factors on model outcomes.

6. The model allows visualization of simulated prey/predator movements and behavior. This simplifies verification of model rules and behavior, and provides an animated output of prey and predator behavior over a simulated time period of one or more days.
7. Data uncertainty and lack of empirical data are common problems associated with most marine mammal studies. In such circumstances, the model can be used as a testable tool to evaluate various possibilities and address parameter uncertainty, and therefore has important heuristic value.
8. Studies on several species have provided credible evidence that predators can have far-reaching effects that spread across spatial and temporal scales, and across one or more trophic levels. This has consequences for management and policy decisions related to species or resources management. Further, prey have evolved strategies that help them avoid predation or reduce encounters by making specific habitat choices. Habitat alterations or improper management practices could adversely affect these long-standing choices and therefore considering indirect predation risk effects may be necessary to manage critical as well as robust populations like dusky dolphins.
9. Dusky dolphins are categorized as *Data Deficient* by the International Union for Conservation of Natural Resources (IUCN, 2008), which means that there is insufficient information to assign them a conservation status. Further, a recent meta-analysis study (Schipper et al. 2008) evaluating the status of land and marine mammals worldwide, found that 38 % of marine mammals were *Data*

Deficient relative to 14% of land mammals that were *Data Deficient*. Moreover, nearly 36% of marine mammal species are threatened (range 23 – 61%). Thus, research on less studied species such as dusky dolphins will enable better assessment of conservation status and policy initiatives.

CHAPTER II

PREDATION RISK IN DUSKY DOLPHINS

Introduction

For decades, predator-prey interactions have been extensively discussed, debated, and described as the principal force driving group living in most taxa (Edmunds 1974, Alexander 1974, Wilson 1975, Bertram 1978, Sih 1980, 1987, Van Schaik and Van Hoof 1983). Over time, theoretical and empirical contributions have provided credible evidence that predators can affect prey behavior that have serious consequences on prey reproduction, habitat selection, mate and food choices (Lima and Dill 1990, Lima 1998).

Recently, the effects of predators scaring prey (Brown et al. 1999) have garnered considerable interest and study. Predator presence or behavior can create an environment of fear variously affecting prey behavior (Sih 1987, Lima and Dill 1990, Lima 1998, Laundre et al. 2001, Wirsing et al. 2008). Several studies also indicate that these predator effects can percolate down trophic levels, resulting in a trophic cascade (Estes and Duggins 1995, Pace et al. 1999, Ripple and Beschta 2004, 2006, Schmitz 2006, Otto et al. 2008).

Changes in prey behavior arising due to indirect predator effects can have impacts on lower trophic levels either through ‘trait-mediated’ or ‘density-mediated’ pathways (Abrams 1995, Dill et al. 2003, terminology reviewed in Abrams 2007). Further, there is strong evidence that these indirect predator effects can trigger resource declines or alter ecosystems with equal or greater consequence than changes in population dynamics from direct lethal predation, especially in aquatic systems (Kotler and Holt 1989, Werner and Peacor 2003, Preisser et al. 2005, Myers et al. 2007). Thus, there is an increasing focus on non-lethal or indirect predation risk effects on prey behavior.

This revised thinking allows us to explain evolutionarily and ecologically changing prey behavior and the (Luttbeg and Kerby 2005, Creel and Christianson 2008, Schmitz et al. 2008). Further, it provides scope to develop approaches to better understand upper trophic level predators in the marine ecosystem.

Predators can affect their prey's choice of habitat, movement patterns, social structure, and foraging behavior. Most dolphin studies attribute some of these lifestyle decisions to predation risk. For example, dolphins move to shallow waters to avoid deep-water sharks or increase group size to avoid predation (Würsig and Würsig 1979, Saayman and Taylor 1979, Norris and Dohl 1980, Shane et al. 1986, Norris and Schilt 1988, Wells et al. 1987, Connor 2000).

Studies of predator-prey interactions involving dolphins, including long-term investigations to date, have focused on consumptive or lethal predation (*see* Jefferson et al 1991 for killer whale interactions with marine mammals, Mann and Barnett 1999, Norris 1994; shark effects reviewed in Heithaus 2001). The indirect effects of tiger shark predation on multiple prey species including the bottlenose dolphin (*Tursiops aduncus*), in the Shark Bay ecosystem are well documented, but this research has not been replicated elsewhere (Heithaus and Dill 2002, 2006; Wirsing et al. 2007). When such field studies are not viable, alternative approaches, and a theoretical shift towards considering indirect predation risk effects, will revise our understanding of predator influences on dolphin lifestyle and the ecosystems they inhabit (Wirsing et al. 2008, Heithaus et al. 2008).

Objectives

In this chapter, my focus is on non-lethal/indirect predation risk effects that influence dusky dolphin (*Lagenorhynchus obscurus*) behavior. I review available data on their chief predators and the likely anti-predator decisions that these versatile dolphins make. While the research focuses on dusky dolphin interactions with predators in Kaikoura, New Zealand, I incorporate relevant details from other locations.

Methods

In synthesizing this review, I use opportunistic data from a dolphin tour operator (*Dolphin Encounter,* Kaikoura, New Zealand, data courtesy I. Bradshaw, L. Buurman, and D. Buurman) and systematic data collected from previous studies (Würsig et al. 1989, Cipriano 1992, Yin 1999, Markowitz 2004, Weir 2007, 2008) and from my own field season in 2007 (Jan – May).

During austral summer and fall 2007, I collected behavior and location information through systematic surveys across the Kaikoura Canyon. I modified pre-existing survey routes (Weir 2007) (Fig. 1) entered into a *Garmin*® *GPS 76S* device, visualized in *Garmin MapSource Ver. 6.12.4* and analyzed in ArcGIS *9.0*. The research vessel was a 5.5 m inflatable boat with an 80-Hp 4-stroke engine. The primary goal was to obtain information on dolphin habitat choices by social grouping, movement and swimming patterns that could be used to construct the dolphin's simulated environment. A second goal was to photograph dolphins for scarring, potentially attributable to sharks or killer whale attacks.

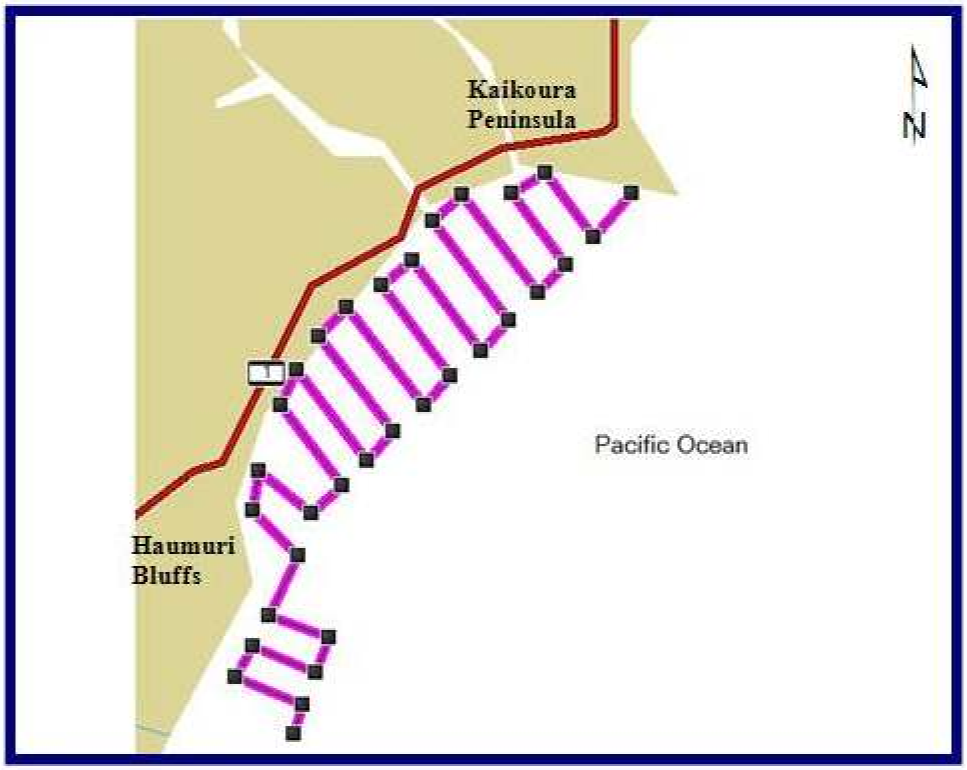

FIG. 1 Map of survey transects covering the study area near Kaikoura, New Zealand (Jan –May 2007).

The survey route was about 79.2 km long, covering an area of 80 sq km, and was covered at an average speed of 12 km/hr. Start locations were varied by beginning either from the start, middle, or at the end of the transect. Usually, I continued from the last completed transect route. On alternate days, a different survey route was used (Deutsch 2008) to record location and behavior of ‘nursery groups’ composed mainly of mothers with calves.

Once a dolphin group was encountered, at least within 200 meters of the route, termed an *initial encounter*, GPS location and behavior data (e.g. group structure, group behavior – rest, travel, forage/feed, and social) was recorded. If the dolphins were amenable to being followed closely by the boat, a 1-hour focal follow was initiated. This provided a good opportunity to photograph all the dolphins and look for marked individuals. During follows, data was collected at 2-min intervals and scan sampling techniques (Altmann 1974) was used to record group behavior.

Natural history of dusky dolphins, Kaikoura, New Zealand

Near Kaikoura (42°30’S 173°35’E), dusky dolphins exhibit a semi-pelagic lifestyle. They feed almost exclusively at night on mesopelagic organisms associated with a deep submarine canyon (Cipriano 1992, Würsig et al. 1989, Würsig et al. 1997, Benoit-Bird et al. 2004). Every afternoon, dolphins travel to offshore locations to feed and return to near shore locations in the morning to rest and socialize — a lifestyle comparable to Hawaiian spinner dolphins (*Stenella longirostris*, Norris and Dohl 1980).

These nocturnal foraging excursions tend to remain stable over the year, except in winter. However, daytime distance from shore varies by season and time of day (Cipriano 1992, Markowitz 2004, Dahood et al. 2008). In winter, dusky dolphins occur farthest from shore in the daytime and in deep waters (typically, > 200 meters, Dahood et al. 2008). Such trends were also observed during the summer/fall 2007 field season

(Fig. 2), where dolphins were typically found close to shore (< 5 kms). Some sightings > 5 kms were recorded during late afternoon hours when the animals were moving offshore to feed.

Patch density, composition, and locations where the visually sensitive organisms surface likely change between days and seasons. Foraging time also differs between seasons. In winter, dusky dolphins have a longer foraging window (12–13 hours) relative to summer (7-9 hours), a consequence of early sunset and late sunrise (Benoit-Bird et al. 2004, Benoit-Bird et al. in press). With a shorter summer feeding time, the dolphins would be expected to stay offshore throughout the day. This would presumably reduce food searching and increase foraging efficiency. But, dusky dolphins exhibit a strong diel nearshore-offshore movement, which suggests that other factors may apply.

Predation risk from deep water sharks and killer whales has been linked to observed dusky dolphin movement patterns (Würsig et al. 1989, Würsig et al. 1997, Cipriano 1992, Markowitz 2004, Weir 2007). However, our knowledge of their predators is limited.

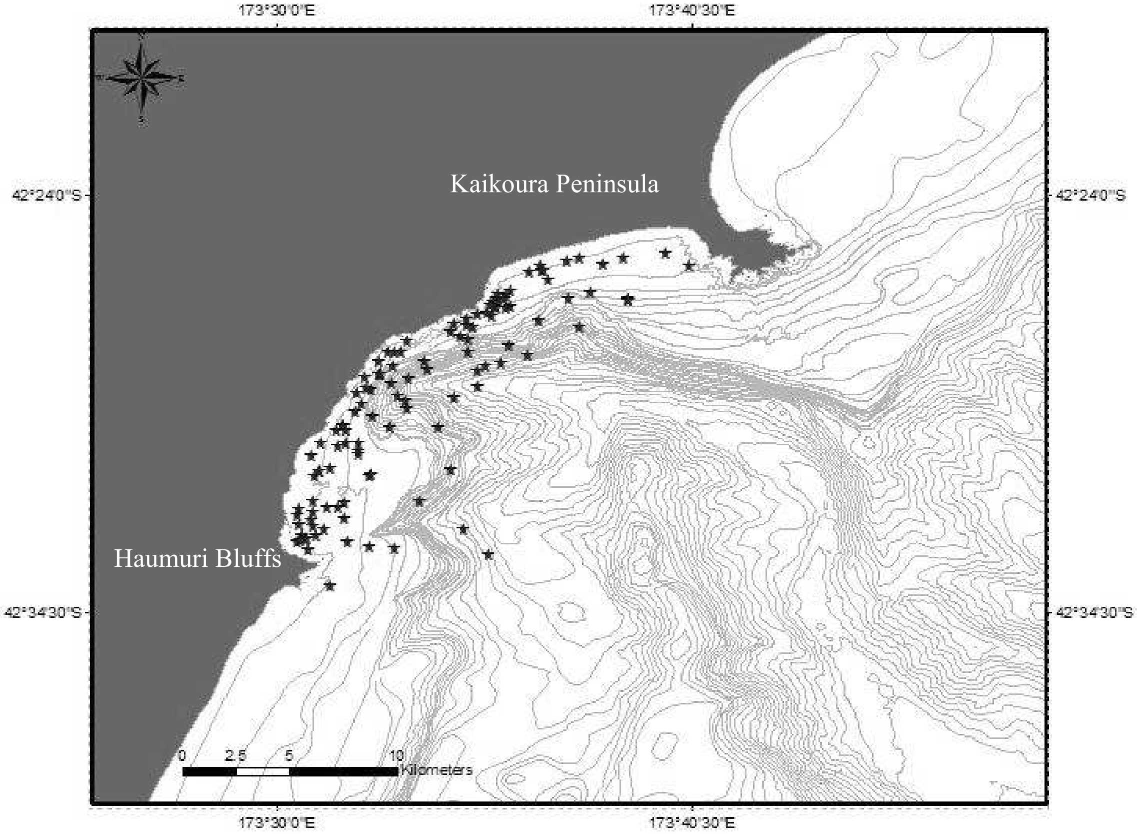

FIG. 2 Dusky dolphin sightings from surveys between January 22 and May 30 2007 over a period of 37 survey days (n = 118 sightings) near Kaikoura, New Zealand. Bathymetry data courtesy: National Institute of Atmospheric Research (NIWA), New Zealand.

Sea surface temperature and dusky dolphin seasonal trends

An alternative suggestion for dusky dolphin seasonal movement patterns off Kaikoura is sea surface temperature (SST). Gaskin (1968) noted that SST influences dusky distribution in New Zealand. However, within specific areas, localized SST fluctuations may have different influence on dolphin distribution.

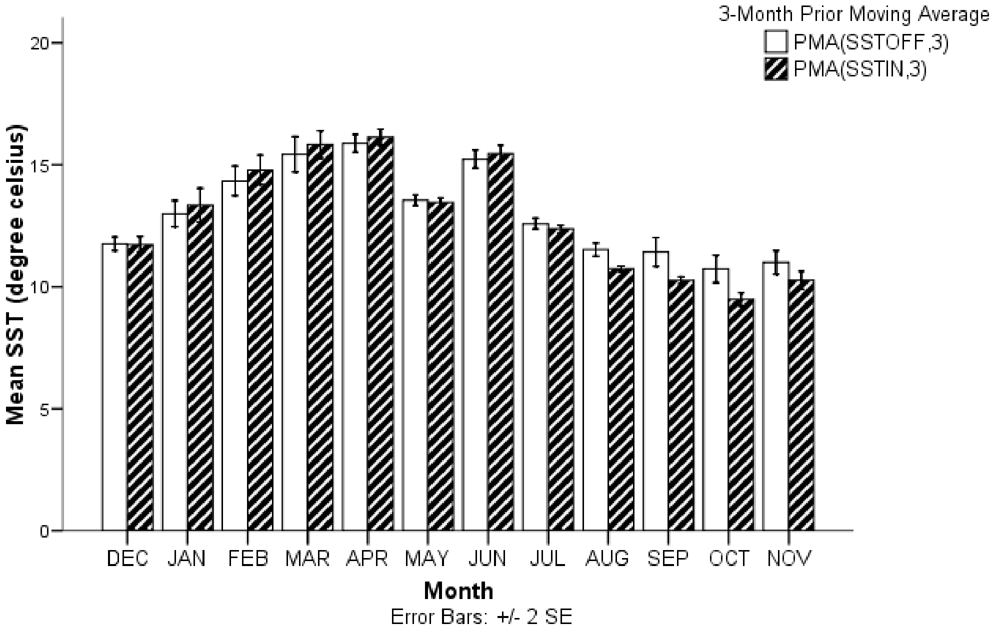

FIG. 3 Sea Surface Temperature (SST) variations between near shore (~ 5 km from shore) and offshore (~ 22 km from shore) locations off Kaikoura, New Zealand (2003-2007). (SST archival data courtesy: Michael Uddstrom, NIWA; Uddstrom and Oiens 1999).

Sea surface temperature from Kaikoura waters calculated from a long-term archival SST dataset (5 years) for inshore location (~ 5km from shore) versus offshore (~22 km from shore), provides some insight into the seasonal differences in dusky dolphin distribution in the area (Uddstrom and Oien 1999; NIWA SST Archive Data, Courtesy Michael Uddstrom).

Mean monthly SST for an area is calculated from per-pass values for the entire month i.e. (30 days x min of 3 satellites x 2 (1 day and 1 night pass over location)). For the offshore and near shore location, I averaged spatially to calculate the mean monthly SST along a 3 x 3 tile centered on the location of interest.

Monthly SST variations between inshore and offshore zones (2003-2007) are shown in Fig. 3. Seasonal and monthly mean SST between inshore and offshore areas were significantly different ($F_{seasonal} = 49.494$, df (7, 112) $n = 120$, $p < 0.0001$; $F_{monthly} = 41.962$, $n = 120$, df (22, 97), $p < 0.0001$). Pair-wise comparisons reveal that winter and summer water temperatures significantly differ ($p < 0.0001$) for both near and offshore areas. However, winter inshore SST is not significantly different from winter offshore; this is true for spring inshore/offshore, fall inshore/offshore and summer inshore/offshore SSTs as well.

A movement into warmer waters may have thermoregulatory value in preventing heat loss (Meagher et al. 2008). So while SST is cooler in winter than summer, the trend is pervasive through offshore and nearshore waters within a season. Thus based on current evidence, SST variations do not influence dusky choices for nearshore waters in summer or offshore in winter, but may have influence on their prey.

Killer whales – primary predator

The New Zealand killer whale population is estimated to be between 65-167 animals (Visser 2000). Also, it is believed that there are 3 sub-populations of killer whales with geographic affiliations to the South and North Island, or both. Stomach content data to guage New Zealand killer whales' diet diversity are scarce, with most information coming from direct observation of predation events (Visser 2000). Available data indicate that killer whales off New Zealand have a varied diet ranging from rays (frequently observed) and sharks (Fertl et al. 1996, Visser 1999, Visser et al. 2000) to cetaceans, including whales and dolphins (Visser 2000). It is possible that some pods specialize in dolphin hunting and frequent the region (Visser 2000).

They are no reported observations of killer whale attacks on New Zealand fur seals (*Arctocephalus forsteri*), despite known consumption of fur seals elsewhere (Matkin et al. 2007). On one occasion, when a small pod of killer whales was observed near the Kaikoura Peninsula, fur seals exhibited a threatened response by staying out of water and hauling out on a rock as the killer whales passed by. However, on a different day, a male killer whale swam past a fur seal with no apparent reaction from either animal (M. Srinivasan, *personal observation*).

After years of decline, fur seal populations are on the rise (Bradshaw et al. 2000), and with an increasing prey resource it is possible that killer whales may choose them as prey often. For example, Mamaev and Burkanov (2006) reported increasing killer whale attacks on northern fur seals (*Callorhinus ursinus*) off the Commander Islands since 2000, even though there was no evidence of attacks before that.

Near Kaikoura, killer whales are rarely observed to prey on dusky dolphins (Constantine et al. 1998, Visser 2000). Further, photographic analyses of scarred dolphins (n = 147: 70 with scars, 77 with rake marks) chosen from a database of over 1000 dolphins, showed no clear evidence of shark or killer whale potential attacks. In fact, nursery groups, composed of mothers with calves, showed little or no scarring (<< 1%). However, dusky dolphins are small dolphins (~ 2 m), more likely to be completely consumed by a killer whale or large shark rather than bear scars. A low scar rate does not imply that predation does not happen, since behavioral responses suggest that dusky dolphins are clearly fearful of killer whale presence.

Killer whales may also target calf humpback whales during their migration in New Zealand. A high scarring rate for humpback whales in New Zealand has been reported relative to other regions, though only 3 of 8 individuals showed rake marks (Mehta et al. 2007).

Visser (2000) reported a peak in austral summer for killer whale sightings near Kaikoura (1992-1997). Also, Markowitz (2004) observed killer whale sightings to vary by season (1997-2003) — spring (21%), summer (55%), autumn (21%), and winter (3%). Long-term killer whale sighting (1995-2006) from a dusky dolphin tour operator, *Dolphin Encounter,* confirm this seasonal trend (Dahood et al. 2008), with peaks in November (spring), austral summer and fall, and few sightings in winter (Fig. 4a). These sightings suggest that dolphins stay close to shore in response to peak killer whale attendance off Kaikoura (Fig. 4b).

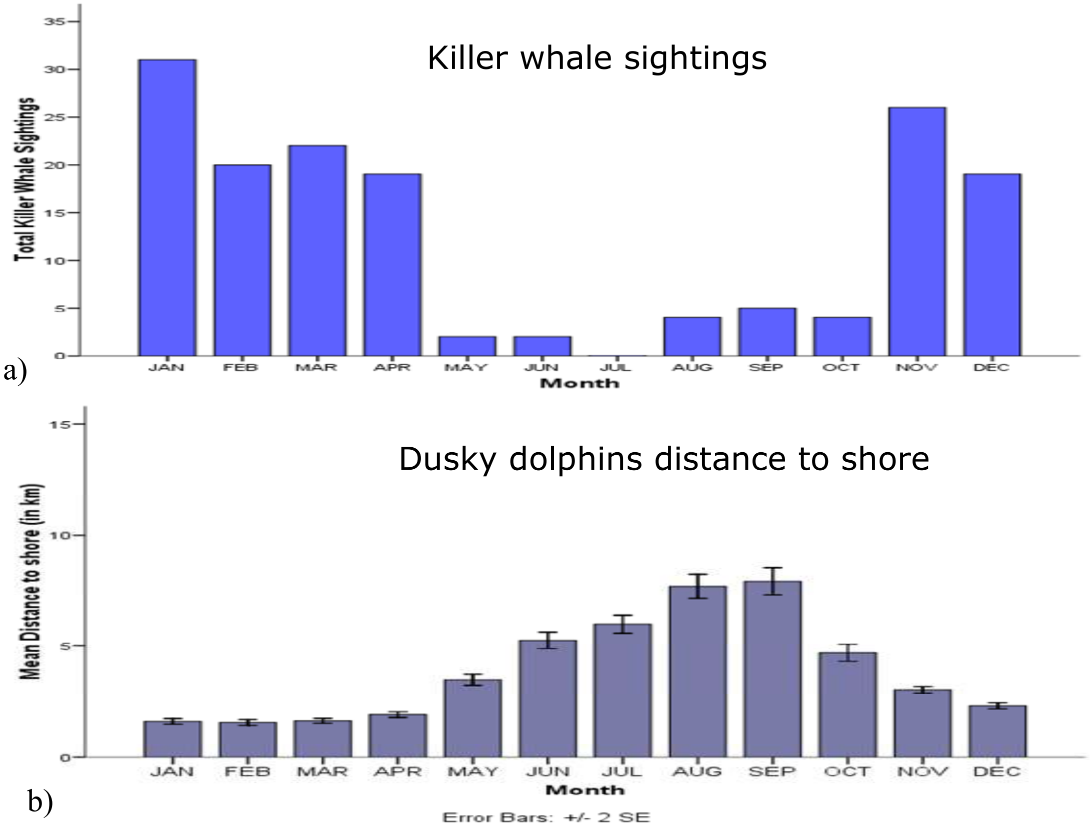

FIG. 4 a) Total killer whale sightings near Kaikoura recorded during dusky dolphin tours 1995-2007. There were no killer whale sightings in July, b) Dusky dolphin average distance to shore (km) between months (1995-2006) (Data Source: Dolphin Encounter, Kaikoura, New Zealand, courtesy: I. Bradshaw, L. Buurman, and D. Buurman).

Non-predatory reasons such as changes in social needs or prey could influence these seasonal patterns. Although, stomach content analysis of dusky dolphins suggest that they consume myctophid fishes and squid throughout the year (Cipriano 1992). We still need to learn more about food patterns before definitive conclusions can be drawn.

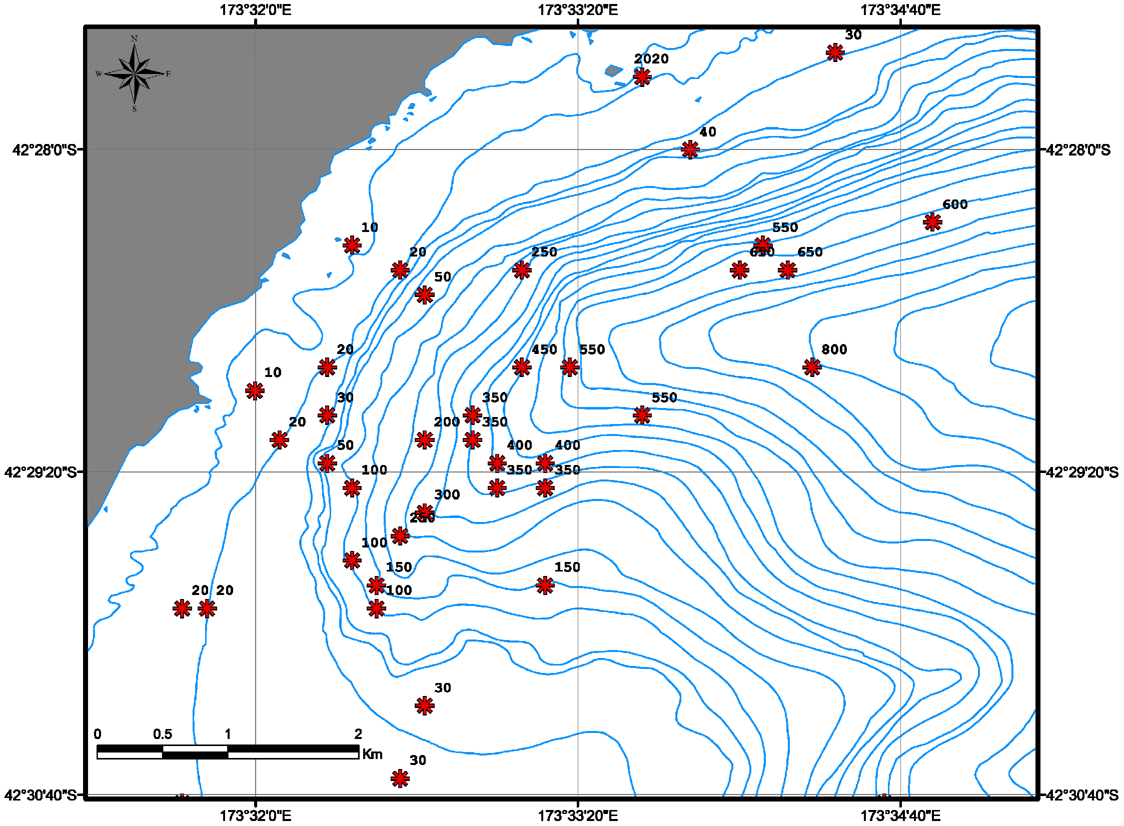

FIG. 5 Selected killer whale sightings to highlight depth choices (depth in meters) off Kaikoura, New Zealand (1995-2007). (Data Source: *Dolphin Encounter*, Kaikoura, New Zealand, courtesy: I. Bradshaw, L. Buurman, and D. Buurman). Bathymetry data, courtesy: National Institute of Water and Atmospheric Research (NIWA), New Zealand.

Markowitz (2004) reported 82% of observed dusky dolphin interactions with killer whales in > 50 m water depth, often where the Kaikoura canyon approaches closest to shore. Killer whales often travel parallel to the shore, generally displaying a directional movement. They may be sighted in shallow (< 20 meters) and deep waters (Fig. 5) and likely follow depth contours. Occasionally, they are stealthy and not easily followed.

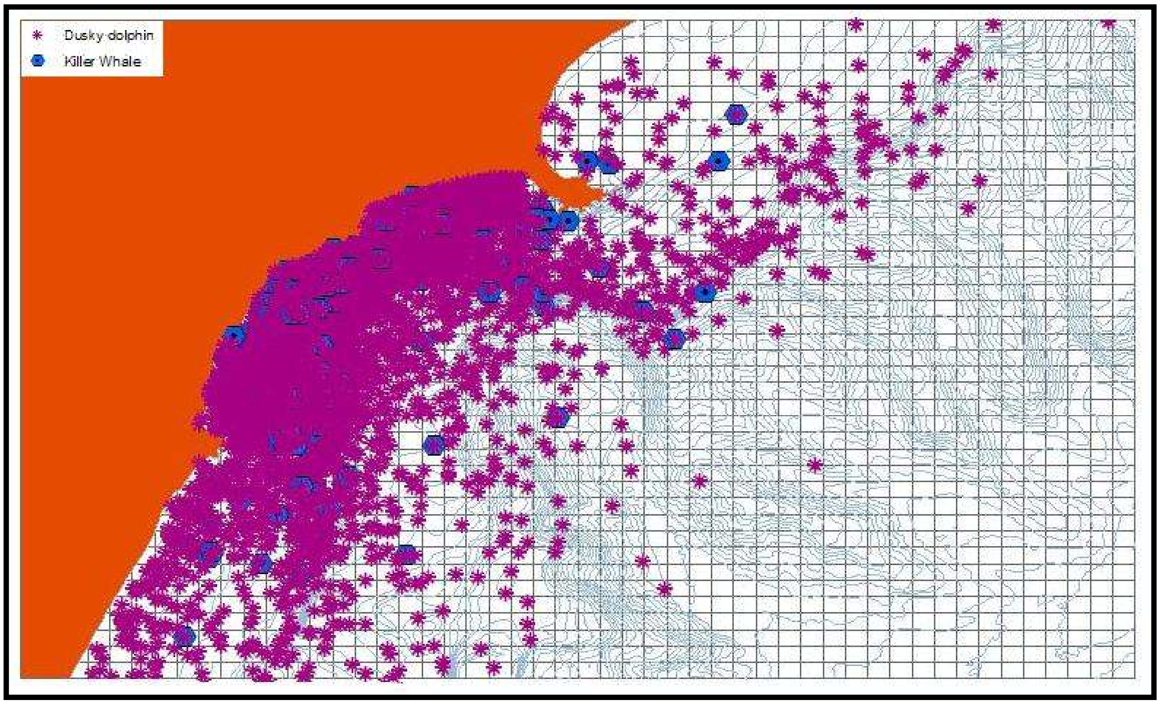

FIG. 6 Killer whale and dusky dolphin sightings off Kaikoura represented within a 50 x 40 grid and used to calculate density of occurrence and spatial correlation for the two species. (Data Source: *Dolphin Encounter*, Kaikoura, New Zealand, courtesy: I. Bradshaw, L. Buurman, and D. Buurman). Bathymetry data courtesy: National Institute of Water and Atmospheric Research (NIWA), New Zealand.

Some killer whale pods are composed of 3-5 individuals, while some are larger (5-30). However, we don't know if group size and depth preference dictate killer whale prey choice and hunting strategy.

I used dusky dolphin tour boat data (*Dolphin Encounter* 1995-2007) to perform a CRH-modified t-test to directly correlate killer whale and dusky counts or density of occurrence in a grid (50 x 40 cells with centroid X Y geographic coordinates) off Kaikoura (Fig. 6). The test assumes that variables may be spatially autocorrelated. Killer whale and dusky occurrence showed a 73% correlation (effective sample size $n = 122$). I also performed a cross Mantel test (Wu and Mitsch 1998, Kjelland et al. 2007) to test for spatial correlation of dusky dolphin and killer whale tour boat data variables measured at different times over the same area. All spatial analysis was conducted using *PASSAGE* software ver. 2.0 (Rosenberg 2001). There was significant spatial cross-correlation between killer whale and dusky dolphin distance matrices (2000 x 2000) ($t = 33.20$, $p = 0.001$, $\alpha = 0.05$). Thus, killer whale and dusky occurrence patterns appear to be interdependent, assuming all killer whales entering Kaikoura seek dolphins as prey.

There are suggestions that prey may respond to habitat differences as a measure of predation risk, rather than actual predator presence or abundance (Boinski et al. 2003, Verdolin 2006). So prey may choose habitats that allow them to escape easily, rather than simply avoid predation (Ydenberg and Dill 1986). Both factors may influence dolphin habitat use during peak killer whale season.

Nursery groups composed of females with young calves respond dramatically to predation risk from killer whales, and therefore are a good indicator of varying predation risk levels. Calving in dusky dolphins typically occurs in late spring to early summer, and vulnerable mothers and calves tend to stay in shallow water (≤ 20 meters, Markowitz 2004, Weir 2007, 2008). Nursery groups have not been reported in winter. Weir (2007) noted that nursery groups were harder to find on days when killer whales were reported in the area, a trend seen in the 2007 field season as well. She also described an incident of a lone calf, stressed and in shallow water, possibly due to an earlier sighting of killer whales in the area.

Dusky dolphins exhibit a few reliable responses to killer whales, which serve as short-term anti-predator strategies. They flee at a top speed of 16-22 km/hr (Markowitz 2004) or in extreme situations hide in waters less than 1 m deep, a response noted in Argentina (Würsig and Würsig 1980) as well. Off Kaikoura, Cipriano (1992) observed such ‘hiding’ dolphins to stay in this ‘stressful’ refuge for nearly 4 hours until the observation period ended.

Sharks

To associate shark effects with observed dolphin behavior, knowledge of shark characteristics and behavior is necessary (Lima 2002). For instance, some sharks can easily move between shallow and deep waters, e.g. white sharks (*Carcharadon carcharias*, Weng et al. 2007)*,* tiger sharks *(Galeocerdo cuvier*, Heithaus et al. 2002), and sevengill sharks (*Notorhynchus cepedianus*, Ebert 1991). The degree of risk posed by these sharks can differ by species, size, season, temperature, time period, abundance, and habitat — this in turn can affect observed dolphin behavior (Long and Jones 1996, Heithaus 2001, Ebert 2002, Heithaus 2004, Klimley et al. 2002, Lucifora et al. 2005, Wirsing et al. 2006).

There is strong evidence that great white and sevengill sharks exhibit an ontogenic shift towards marine mammal prey once they mature into adults (Ebert 2002, 2003, Long and Jones 1996), making them among the most lethal sharks for marine mammals.

There are five species of sharks that potentially pose a risk to dusky dolphins off Kaikoura. These include: the great white, shortfin mako (*Isurus oxyrinchus*) (suspected cetacean predator, Heithaus 2001), seven gills, sleeper sharks (*Somniosus pacificus*), and less likely, the blue shark (*Prionace gluca*). There are limited data on distribution and movement patterns of these shark species in New Zealand, but some species-specific general behavior is discussed below.

Sleeper sharks

Two species of *Somniosus* or sleeper sharks have been reported in New Zealand waters (Francis et al. 1988). Although small sleeper sharks (*S. rostrata*) have been identified near Oaro, Kaikoura, these pose no risk to dolphins. The other species, the Pacific sleeper shark, is a known marine mammal predator and scavenger (Crovetto et al. 1992, Taggart et al. 2005, Sigler et al. 2006). Pacific sleeper sharks typically rise to the surface at night and stay down at depths during the day, exhibiting continuous vertical movement (Taggart et al. 2005, Hulbert et al. 2006). They tend to stay in deep waters in low latitudes where they are believed to never come to the surface, whereas in high latitudes, they often come close to the surface (Compagno 1984). Their presence in

Kaikoura waters is unconfirmed and there is little information from elsewhere in New Zealand.

Sevengill sharks

These are nocturnal, venturing into deeper waters during the day and typically preferring turbid waters (Ebert 1991). They also engage in cooperative hunting, which facilitates attacking fast-moving and larger marine mammals, including dolphins. There is also evidence of habitat shift in La Plata river dolphins, *Pontoporia blainvillei*, in response to peak abundance of sevengill sharks (Lucifora et al. 2005). In Argentina, cetacean remains of possibly dusky dolphins in sevengill stomachs have been recorded (Crespi-Abril et al. 2003). Their habitat use and distribution patterns in Kaikoura are unknown.

Great white, blue and mako sharks

White sharks use shallow and deep waters (Weng et al. 2007), while blue and mako sharks are pelagic species. All three species exhibit vertically oscillating movements or 'yo-yo' swimming that aid in thermoregulation, travel and predatory behavior (Carey and Scharold 1990, Holts and Bedford 1993, Klimley et al. 2002). Blue sharks also feed on the vertical migrating layer off California (Tricas 1979). With their preference for cephalopods, blue sharks may feed at night near Kaikoura as well, where the potential for interaction with dusky dolphins increase. However, they probably pose no risk to adult dolphins, unless they are over 2 meters and encounter vulnerable or wounded ones.

Mobbing of juvenile blue sharks has been reported in Kaikoura (Markowitz 2004, M. Srinivasan *personal observation*) — such behavior could serve as a predator deterrent, help sense predator motivation or be a learning tool against more dangerous predators such as killer whales. For example, Graw and Manser (2007) observed that meerkats (*Suricata suricatta*) mob both threatening and non-threatening animals, but adjust their mobbing behavior based on the degree of threat posed by the encountered animal. Also, mobbing behavior varied with age, with young meerkats mobbing squirrels more than adult meerkats, but exhibiting caution against the more dangerous snake.

Blues and makos have been recorded making the deepest dives during the day (Carey et al. 1981, Carey and Scharold 1990), possibly older and larger individuals (Graham 2004). However, blue, mako, and white sharks also spend a substantial amount of time at the surface or close to the surface (Klimley et al. 2002, Graham 2004). Preliminary results of a white shark satellite tagging project being conducted in New Zealand waters show no evidence of white shark tracks near Kaikoura, although this species occurs throughout the region (Clinton Duffy[†], *personal communication*).

Sharks in Kaikoura

In Kaikoura, local fishermen and tour operators report that shark abundance is low and apparently decreasing. Blues are the most commonly observed shark, followed by mako sharks. Shark sightings peak in austral summer and fall. Shark diving operations in Kaikoura closed in the late 1990s due to lack of regular shark sightings. However, no systematic studies have been initiated to monitor shark populations in the area.

In March 2007, I conducted a brief shark presence/absence study in Kaikoura from a fishing boat. The owner had previous experience with shark diving operations

---

[†] Clinton Duffy, Marine Conservation Unit, Department of Conservation, New Zealand

and was familiar with favored shark spots in the area, particularly a zone just north east of the Kaikoura Peninsula. Frozen bait (composed of ground up fish) released an oily residue, providing a chum line to attract sharks. Burley bags with cod and perch fish scraps were floated on the sides of the boat as additional bait. During 3 different days for about 13 hours, using 5 kilograms of frozen chum/hour — some small sharks, 2-3 porbeagle sharks *Lamna nasus* (1.5 meters), and one 2.5 meter mako shark took the bait. A similar study conducted in 2003 (Feb 5–March 13), for about 70 hours, off the same fishing boat resulted in a single sighting of a 3 meter mako shark (Victor Foster and Jodie West, unpublished data). Further, from 1999–2007, a seabird tour operator in Kaikoura, *Albatross Encounter*, recorded 51 blue and 7 mako with 31 sightings in fall, 17 in summer, 3 in spring, and none in winter.

It is possible that sharks are wary of fishing boats and avoid the bait, or shark abundance in Kaikoura waters is low. Current evidence points to a shrinking or low shark population off Kaikoura. So killer whales may be a more potent threat than sharks in Kaikoura waters. Other factors may contribute to the reduced shark presence e.g. shark finning and increasing longline tuna fishing bycatch (Ayers et al. 2004, Ministry of Fisheries 2007a, b).

Dusky dolphins – group living and vocal repertoire

Group living

Predation risk can lead to group living by affecting prey behavior, social relationships, and habitat selection, well described in several classic papers (Hamilton 1971, Pulliam 1973, Alexander 1974, Jarman 1974, Bertram 1978, Van Schaik and Van Hoof 1983, Trivers 1985, Elgar 1989, Dehn 1990). Over evolutionary time, prey developed strategies to find food, water, and potential mates, knowing that danger lurked close by.

Recent studies have shown that some fundamental assumptions on predation risk and how it correlates with group size and the consequent differences in vigilance, detection, dilution and encounter effects can vary between species, habitat, and predation pressures (Inman and Krebs 1987, Krause and Godin 1995, Bednekoff and Lima 1998, Creel and Winnie 2005, Liley and Creel 2007).

Thus, anti-predator strategies need to be evaluated in context. For example, Wolff and Horn (2003) in their study on wolf effects on elk (*Cervus elaphus*) behavior in Yellowstone (predators present) and Rocky Mountain National Parks and Mammoth Hot Springs (predator-free), reported no correlation between percentage of cows vigilant and group size in either locations. In Yellowstone, cows with calves spent more time vigilant than foraging relative to cows without calves. In the other two parks, there was no difference in levels of vigilance for cows with and without calves.

Their findings were consistent with results obtained by Laundre et al. (2001) who also found no correlation between predator vigilance levels and group size for elk in Yellowstone. Thus, levels of predation pressure can determine the degree of anti-predator behavior, and may or may not influence group size.

Dolphins have few refuges from predators in the marine environment (Connor et al. 2000). In dolphins, safety in numbers due to the ‘selfish herd’ effect (Hamilton 1971), and a tight social structure and organization with heightened sensory awareness (*reviewed* in Norris and Schilt 1988) are essential to predatory detection and avoidance.

Group size

Off Kaikoura, dusky dolphins exhibit larger group sizes in winter (often >1,000) when they are found further offshore, than in summer (generally < 1,000) when they are found inshore (Markowitz 2004). Group size also varies with social type/class. Mixed-age/sex groups form the largest groups comprised of > 50 individuals, (most often hundreds). Mother-calf nursery groups are typically comprised of fewer dolphins (median group size = 14, Weir 2007). Nursery groups are rarely observed in winter (Markowitz 2004). Other social groups also have smaller group sizes. For example, mating groups have a median group size of 6 and non-sexually active adult groups have a median group size of 8-10 (Markowitz 2004, Srinivasan (this study)).

For most dolphin species, correlating group size with predation risk is not straightforward, especially in open habitats (Gygax 2002, Gowans et al. 2008). In general, individuals in large groups may derive anti-predator benefits (Krause and Ruxton 2002).

However, larger dusky dolphin group sizes in winter may not necessarily correspond to higher predation risk, as killer whale and shark presence is minimal. Larger winter group sizes may instead reflect a large influx of new individuals (Markowitz 2004, Würsig et al. 2007) or may have foraging or social benefits. Creel and Winnie Jr. (2005) in their elk studies found that grouping is not always an anti-predator tactic, as elk herd size increased when wolves were absent. Instead, elk aggregation in areas away from cover in the absence of wolves was attributed primarily to foraging needs.

Also, Inman and Krebs (1987) explored the idea that even though the probability of detection increases with group size, group size does not increase linearly. After a certain stage detection becomes independent of group size. Krause and Godin (1995) found that cichlids preferentially attacked large shoals of guppies, even though percentage of success was relatively low. Other studies on birds and mammals also show preferential attack on larger groups (Brown and Brown 1996).

Nursery groups

The formation of mother-calf nursery groups, common among dolphins, can offer calves protection from predators by choosing low risk areas and also provide increased opportunities for social learning (Wells 1991). Isolation of nursery groups from large adult groups may serve a dual purpose — 1) reduce harassment from larger groups (Weir 2007), and 2) reduce vulnerability by choosing safer areas, and thereby increase ability to escape undetected prior to an imminent threat.

A female dolphin with a calf is both energy and speed handicapped (Noren 2008), and an easier target than a fast and independent adult dusky (Markowitz 2004). This may alter their decision to flee from a lethal shark or furtively move along the shallows to avoid killer whales. Similar to Markowitz (2004), I observed nursery groups and large mixed groups to maintain tight inter-individual proximity (< 2m) especially when resting and slow travel.

Group swimming formation and inter-individual distance

Dusky dolphins differ in group spread and swimming formation (shape) depending on season, time of day, activity and social grouping. In general, dolphins spread out further in winter than in summer or spring. Spacing increases from daytime to afternoon as the dolphins move offshore to forage. Also, dusky dolphins generally prefer circular or echelon positions when resting but switch to linear or staggered swimming formations when traveling (Markowitz 2004).

Norris and Schilt (1988) suggested that Hawaiian spinner dolphins are cautious against both killer whales and sharks, and therefore school both day and night. Dusky dolphins near Kaikoura may risk a tradeoff to maximize food searching. Alternatively, they could rely on acoustic contact to maintain group cohesion and predator detection, similar to dusky dolphins in Golfo San José, Argentina (Würsig et al. 1989).

As for their predators, killer whales may actively hunt at night (Volker Deecke, personal communication, Newman and Springer 2007) and may adopt special acoustic signals or tactics to attack dolphins. Thus, predation at night may go unnoticed. Though in summer, greater than 12 day light hours are available for killer whales on the hunt, and daytime preying might be more advantageous than hunting at night.

Vocalizations

Dusky dolphins rarely whistle, more often producing clicks and burst pulses (Yin 1999). When milling (resting) and traveling, whistles were rarely recorded (Yin 1999), and therefore may not be a significant component of their daytime communication. Could the lack of whistles be a killer whale avoidance mechanism, perhaps similar to what Morisaka and Connor (2007) hypothesized for non-whistling odontocetes? Further studies on dusky vocalizations during day and night, and in the presence/absence of killer whales, may clarify the importance of whistles and other calls in dusky communication as anti-predatory.

Conclusions

Dusky dolphins, like other prey, have adopted short and long-term strategies that appear effective against potential killer whale attacks. For example, they choose shallow water habitats during peak killer whale season, flee or make drastic maneuvers, change group formation, and form nursery groups, which have their own set of tactics. Much remains to be learned about the benefits versus costs of making such choices, as dusky dolphins seek to minimize predation risk while meeting food needs. Investigating this aspect forms the crux of my research and is discussed at length in the subsequent two chapters. Such research explorations allow us to question and understand the theoretical underpinnings of prey and predator strategies that have stood the test of time.

CHAPTER III

EXPLORING FEAR EFFECTS IN DUSKY DOLPHINS WITH A SPATIALLY EXPLICIT INDIVIDUAL-BASED MODEL

> Simplicity is the ultimate sophistication.
>
> Leonardo Da Vinci (1452-1519)

Introduction

Fear can drive spatial patterns and distribution of terrestrial and marine organisms (Lima and Dill 1990, Sih and Wooster 1994, Lima 1998, Wirsing et al. 2008). How this translates into prey lifestyle decisions and costs has led to many interesting studies (*reviewed in* Dill 1987, Sih 1987, Lima 1998, Verdolin 2006). But in most predator-prey studies, the chief participants are not treated as clever and dynamic interacting subjects that influence each other's behavior and spatial distribution (Mitchell and Lima 2002, Lima, 1998, 2002, Luttbeg and Sih, 2005, Brown and Kotler, 2004). Theoretical models proposed to represent these dynamic relationships have not been simulated (Lima 1998, Brown et al. 1999, 2001, Brown and Kotler, 2004). Further, most predator-prey models tend to focus on aggregated population dynamics, typically involving derivations of the Lotka and Volterra classic equations (Lotka 1925, Volterra 1926), not on individual behavior. Therefore, for most species, we do not know how changing prey and predator behavioral tactics affect their foraging moves and what costs are incurred by prey engaged in predator avoidance.

Among available modeling tools, individual-based models (IBM) are ideally suited to address movement and individual behavior in a heterogeneous environment (Adams and DeAngelis 1987, Grimm and Railsback 2005). Also, individual based models provide an excellent medium to simulate predator and prey behavior where the focus is on the individual. Previous IBM models on predator-prey interactions have concentrated on prey growth rates (e.g. Madenjian and Carpenter 1991), survival (e.g. Rice et al. 1993), marine mammal population dynamics (Chivers et al. 1999, Testa et al. 2007), and energy budgets and bioaccumulation (Klanjscek 2006, Hall et al. 2006).

The IBM framework can be used to represent larger processes and patterns based on field data (Grimm et al. 2005, Peterseni et al. 2008) that govern complex predator-prey interactions, such as indirect predation risk effects with emphasis on prey and predator behavior.

When both predator and prey reign at the top of the food chain and share similar sensory modalities, e.g. as in marine mammals, understanding indirect predation risk effects can be complicated due to behavioral and cognitive plasticity exhibited by predator and prey. However, exploring these relationships can provide new insights into the evolution and persistence of anti-predator mechanisms in clever prey facing clever and fiercer predators.

To my knowledge, there are currently no IBMs that simulate behavior and movement to describe and evaluate predation risk effects in dolphins. Thus, despite information suggestive of predator effects in dolphins and other marine mammals

(Jefferson et al. 1990, Connor 2000, Heithaus 2001), there are few studies that have explored the influence of predators on the behavioral ecology of dolphins.

To answer the ultimate question of fear-driven costs versus benefits for a clever prey dealing with a clever predator, I developed an IBM to represent the dynamic nature of dusky dolphin (*Lagenorhynchus obscurus*) and killer whale (*Orcinus orca*) interactions near Kaikoura, New Zealand. More specifically, I was interested in calculating time/distance budgets for dusky dolphins in the presence/absence of killer whales and the presence/absence of movement and behavioral rules, which presumably evolved in response to spatial and temporal variations in predation risk. The simulation results were used to estimate the costs *vs.* benefits of dusky dolphin anti-predator choices from both ecological (time/distance budgets) and evolutionary (survival) perspectives.

Background

Near Kaikoura, New Zealand (42°30’S 173°35’E), dusky dolphins are occasionally preyed upon by killer whales. Both predator and prey are large-brained social mammals (Marino 1998) that have an impressive repertoire of social, foraging, and survival skills in a demanding and largely refuge-free environment.

Despite the rarity of predation events observed, dusky dolphins are clearly fearful of killer whale presence in the area. They show an immediate and drastic response of hiding in shallow waters (10 m), sometimes <1 m waters, or fleeing when killer whales are in the area (*reviewed in* Chapter II). Additionally, they exhibit the chronic response of choosing to stay in near shore shallow waters (typically < 200 m deep for adults, < 20 m deep for mothers with calves) during peak killer whale season (late spring (November) and summer/fall)) (Dahood et al. 2008, Chapter II).

Killer whales are not a regular or predictable presence off Kaikoura. However, long-term killer whale sighting trends (1995-2007) correlate strongly with dusky dolphin choices for near shore shallow locations (Dahood et al. 2008, Chapter II).

Dusky dolphins feed at night in offshore deep waters on vertical migrating prey composed of mesopelagic organisms (Würsig et al. 1989, Cipriano 1992, Benoit-Bird et al. 2004). So they make near shore-offshore foraging trips during the year, except in winter. In winter, they are found farthest from the shore relative to other seasons and have easier access to their primary food source (Dahood et al. 2008).

Food abundance, location, and composition may change between seasons, but dusky dolphins appear to feed year round on the deep scattering layer (DSL) (Cipriano 1992). The foraging time available also varies by season, a result of the changing sunrise/sunset times. In austral winter, food is available longer (12 – 13 hours) versus summer/fall (7-9 hours) (Benoit-Bird et al. in press). November to early January is also the calving season for dusky dolphins (Cipriano 1992). So, for a major part of the year dusky dolphins have to contend with unpredictable predators, variable foraging time, and also successfully rear newborn calves. Conceptually, dusky dolphin movement and behavior off Kaikoura, New Zealand can be visualized in Fig. 7.

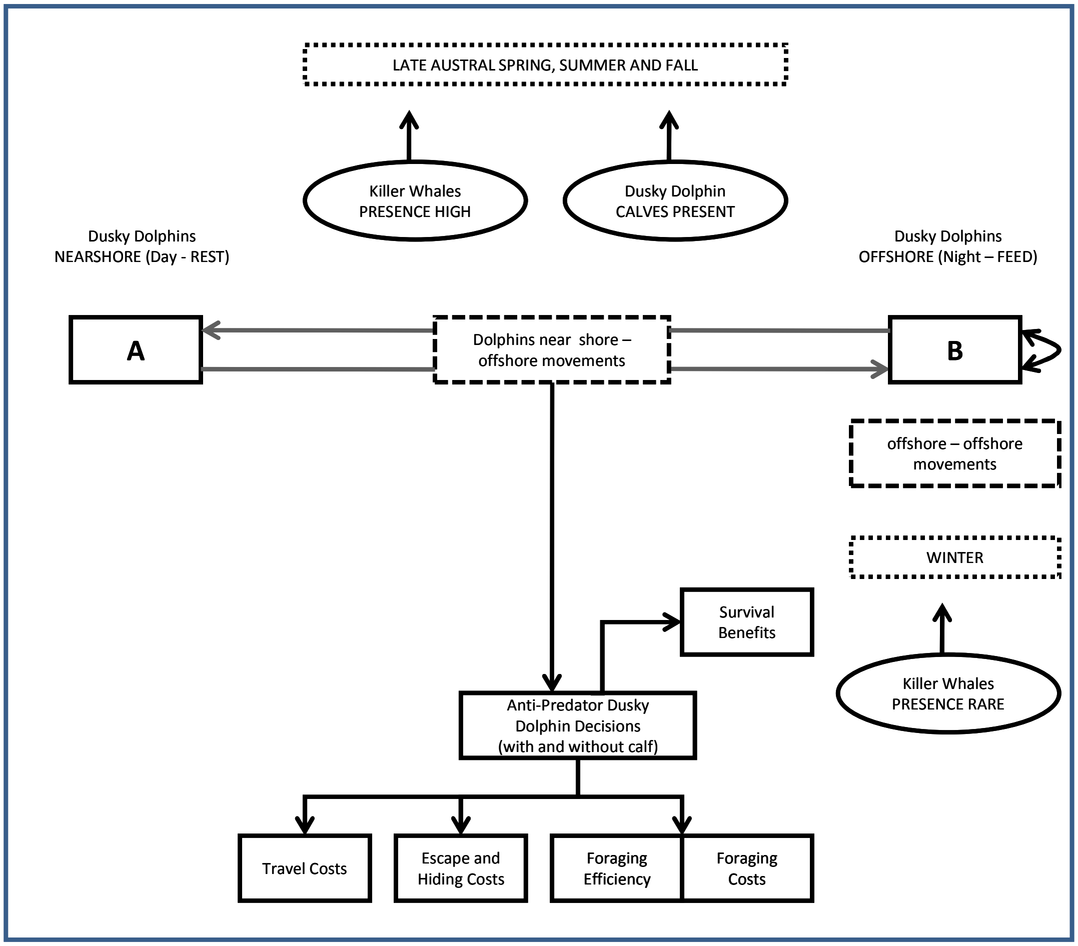

FIG. 7 A conceptual model of the dusky dolphin – killer whale system off Kaikoura, New Zealand, where A = nearshore shallow waters, B = offshore deep waters. In winter, dolphins are found in offshore deep waters B, and do not make near shore-offshore trips to feed and killer whale presence is rare.

So what are the consequences of dusky dolphin anti-predator decisions? Swimming costs are minimal for marine mammals relative to terrestrial organisms, but higher than fishes (Williams 2002). At sea however, marine mammals can be compromised by foraging time available, time available for other activities, travel (distance), and lactation costs.

In this chapter I describe and evaluate a spatially explicit IBM dealing with indirect predation risk effects using a representative dolphin system off Kaikoura, New Zealand. I also discuss model potential and future applications.

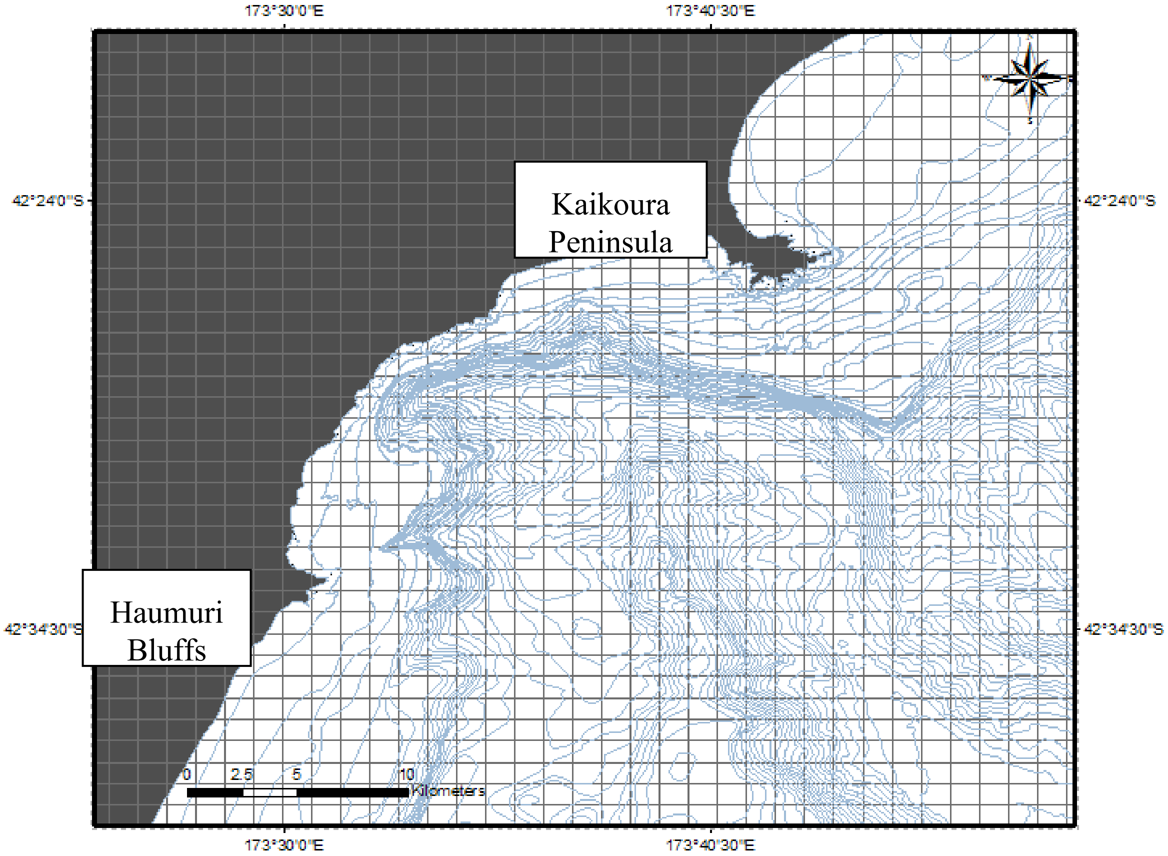

FIG. 8 Map of the system of interest off Kaikoura, New Zealand, indicating the coastline and offshore bathymetry, as well as the grid of 1468, 1 km x 1 km cells used to represent the habitat of the model. Bathymetry data courtesy NIWA, New Zealand.

Model structure

The system of interest near Kaikoura, New Zealand is characterized by the presence of a vast submarine canyon (Lewis and Barnes 1999) associated with a sub-tropical convergence of cold Antarctic and warm tropical waters producing a higher primary productivity than other locations north or south (Boyd et al. 1999). The Kaikoura Canyon is roughly 60 km^2 in length and about 1,200 m deep with a U-shaped profile. The canyon head begins within 500 meters from shore, bringing deep waters close to shore.

In the model, the Kaikoura habitat is represented by 1468, 1 km x 1 km cells (Fig. 8). This area was chosen based on observed dusky sightings from tour boat data (*Dolphin Encounter*, New Zealand 1995 – 2007, courtesy: I. Bradshaw, L. Buurman, and, D. Buurman) and dedicated surveys (Cipriano 1992, Markowitz 2004, Chapter II). Dusky dolphins have not been observed farther than 20 km from shore. Each habitat cell is linked to bathymetric features or contour lines. Where lines are absent, the closest bathy line depth value was used (Bathymetric Data Courtesy: National Institute of Water and Atmospheric Research (NIWA), New Zealand) (Fig. 8).

The model has 3 main components: 1. Dusky dolphins (prey), 2. Killer Whales (predator) and 3. Habitat (bathymetry and Deep Scattering Layer). Class attributes of the main model components are described in Table 1.

Table 1 Attributes of dusky dolphin, killer whale, and habitat modules of the dusky dolphin IBM representing the system of interest off Kaikoura, New Zealand

Dusky Dolphins	Killer Whales	Habitat
2 dolphin types - female w/calf and adult (male/female without a calf)	2 killer whale groups	Food is available between sunset and sunrise
Group size female with calf (20 - 75) adults (150 - 500)	Group size 1 - 30	Food composition not considered
Max number of animals in population 2,000 at any particular moment, system closed	Both groups add up to max 30 animals in the system at any particular moment	Food appears in random cells > 400 meters at night
Dolphins have an age and sex, randomly assigned. Individual calves are assigned a specific mom.	Groups can be composed of males or females, juveniles	Patch density in each food cell > 400 m varies through the night.
Behavioral states: rest, travel, search, feed, flee and hide	Behavioral state: cruise, search, stalk, wait, post hunt mode	Lunar cycle effects not considered
Exhibit variable speeds that vary with activity and between social classes.	Exhibit variable speeds that vary with activity	Food abundance unknown, assume more than enough food is available to eat
Individual dolphins have hunger levels, arbitrarily set at 0 and progressively increased with time and activity. Is calculated as: daily energy requirements (DEQ) – foraging costs (FC) + maintenance costs (MC), as well as group size.	Not Included	Each cell is linked to bathymetric contour lines. (Bathymetry data courtesy, NIWA, New Zealand)
Each dusky dolphin has an individual clock, keeping track of change in time with movement.	Each killer whale has an individual clock, keeping track of change in time with movement.	

Model process overview

The model is a grid-based, spatially explicit, stochastic individual-based model, programmed in VB.NET© (Microsoft Visual Studio 2003). Each grid cell is geo-referenced and represents a 1 km^2 area of the Kaikoura Canyon. Model simulates predator-prey dynamics over 210 days in 80,640 1/16th of an hour time steps. Model results were recorded as .CSV files, and were analyzed spatially in ArcGIS 9.0. The sequencing of the main process represented in model is shown in Fig. 9. The program cycles through this sequence of events each 1/16th hour. Unless stated in the text, supported by literature or data, behavioral and movement rules for dusky dolphins and killer whales can be assumed as model hypothesis.

Initial conditions

The first step in the model simulation is the initialization of the primary variables (Fig. 9): killer whale, dusky dolphins (initial cell), and habitat (bathymetry and initial DSL cell). Dolphins and killer whales move 16 steps in an hour. The idea was to use the smallest possible time step to capture the movement of dolphins and killer whales between cells as they switch between behaviors. Baseline values used in model simulations are listed in Table 2.

Update environment

I update clocks, calendars and photoperiod determined by sunrise and sunset times. Sunrise/sunset times were obtained from the United States Naval Observatory http://www.usno.navy.mil/

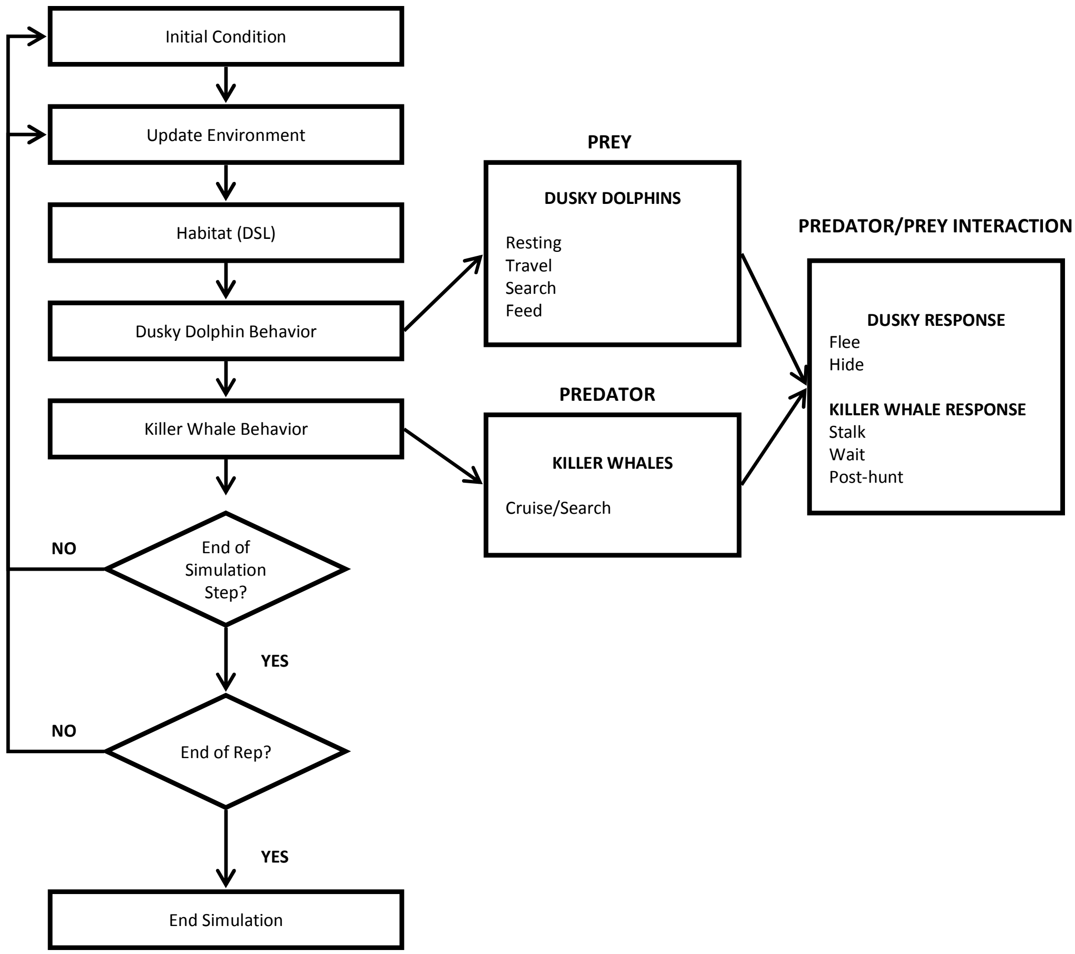

FIG. 9 Sequencing of the model process included in the IBM with a time step of 1/16th of an hour.

Table 2 Baseline values of parameters used in model simulations. Values are based on literature, available data, or from similar species. Where information was lacking, conservative estimates were used. KW = Killer whale, DSL = Deep Scattering Layer

Parameters	Values	Source
Simulation Begin (day of year)	306	(Nov - May) KW season and calf presence (Cipriano 1992, Markowitz 2004, Dahood et al. 2008, Chapter II)
Simulation Length (in days)	210	Model Simulation
Number of killer whale groups	2	Model Simulation
Number of dolphin groups	1	Model Simulation
Dolphin escape rules on = 1 off = 0	1	Model Simulation
Maximum time steps (km) per hour	16	Model Simulation
Killer whale detection distance (km)	5	Estimate
Dolphin detection distance (km)	4	Estimate
KW Return Time (days)	3	(Based on 1995-2007 *Dolphin Encounter* tour boat data, Kaikoura, NZ, Visser 2000)
KW Post-hunt time (hour)	1	Estimate
Dolphin Memory in refuge (hour)	1	(Estimate based on Cipriano 1992)
KW Wait time (hour)	1	Estimate
Mean DSL density (kcal/cu.m)	0-100	(Estimate based on Benoit-Bird 2004)
Giving up foraging threshold (proportion of max DSL)	0.67	Model Simulation
Rest (km/hr)	4.5	(Based on Markowitz 2004)
Feed (km/hr)	5	Estimate
Search for Food (km/hr)	5	Estimate
Travel (km/hr)	8	(Based on Markowitz 2004)
Flee (km/hr)	18	(Based on Markowitz 2004)
KWCruise(km/hr)	8	(Based on Williams 2002, Ford et al. 2005)
KWStalk(km/hr)	16	(Based on Williams 2002, Ford et al. 2005, Ford and Reeves 2008)

Habitat

Daylight hours differ between seasons, shorter in winter and longer in summer, thus, affecting the amount of time food is available for foraging dolphins. The DSL is also strongly affected by lunar cycles (Benoit-Bird et al. 2004, Benoit-Bird et al., in press). However, I do not consider lunar effects in the present IBM. Total DSL available is unknown for Kaikoura. I assume DSL available varies in density and occurs in randomized patches or cells (water depth >400 m) at night, which differs from day to day.

The deep scattering layer generally occurs in daytime depths of 400 – 700 m (Reid 1994), and at night can range between 400 meters to the surface. The daytime depth of the DSL makes it inaccessible to foraging dolphins. In Kaikoura, at night, the DSL rises to within 30 m off Kaikoura, (Benoit-Bird et al., in press), and becomes available to the foraging dusky dolphins (Benoit-Bird et al. 2004). I assume DSL movement from daytime depths to shallower accessible depths for dolphins, but this is not explicitly programmed in the model.

Acoustic studies on the DSL off the Hawaiian Islands show that the mean caloric density of the mesopelagic boundary (island-associated) community is 83 kcal/cu.meter with a maximum of 9,000 kcal/cu.meter (Benoit-Bird 2004). It is believed that the density of mesopelagic organisms off Kaikoura is lower than off Hawaii (1,800 individuals/cu.m off Hawaii, Benoit-Bird, 2004, Benoit-Bird et al., in press), but prey distribution is more uniform relative to Hawaii. In the model, I estimated the mean patch density of the DSL in each cell to vary between 0 and 100 kcal/cu.meter. I also assume that more than enough food is available for the foraging dolphins considering that dolphins feed exclusively at night and year round on the DSL. Dolphins are assumed to feed throughout the duration of DSL availability.

Food density can change due to mesopelagic organisms avoiding or fleeing dolphins, or falling below dolphin diving depths (> 150 m, Benoit-Bird et al. 2004), or due to a group of dolphins depleting a food source. While I consider group size depletion of food patch, I do not explicitly consider the other two mechanisms by which food becomes unavailable. Instead, I consider a threshold in giving up due to food density, so when food density falls below 2/3rds the total food units, dolphins move to a different patch or cell.

Dusky dolphin behavior

Dusky dolphins start in a random cell at the start of the simulation, but their position in the system is conditional on whether a calf is involved and depth rule specifications. Dolphins move because of a) photoperiod (sunrise/sunset) change, b) presence/absence of killer whales, c) food presence/absence. In the model, during peak killer whale presence (summer, fall, late spring), dolphins move from nearshore shallow (< 200 m deep) during the day and into offshore cells (> 400 m deep) during the afternoon and night to forage on the DSL.

Dusky dolphins have six different behavioral states

Rest: represents dusky day time movement into adjacent cells. Except in winter, dolphins move into adjacent cells parallel and along the shore, guided by depth restrictions (< 200 m for adult female/male, and < 20 m for female with calf (Weir et al.

2008, Dahood et al. 2008. Chapter II). In winter, there are no calves and all dolphins are in deeper water. Dolphins make more of a north-south movement (Cipriano 1992, Markowitz 2004). I assume that for female with calf, average cruising speed is 4 km/ hr, and for adult female/male, average speed is 4.5 km/hr, based on Cipriano (1992) and Markowitz (2004).

Travel: dolphins increase speed to 6-8 km/hr (Markowitz 2004). Dolphins switch from resting to travel mode as sunset approaches and desire to feed increases. They travel through every cell to the closest deepest cell (> 400 m) that may contain food.

Search: once the dolphins are in deeper water, they initiate food search and switch behaviors. They can move within a 5 km^2 area searching for food among adjacent cells.

Feed: if dolphins locate food they stop searching. Search and feeding speed are assumed to be same (~ 5 km/hr), exact values are not available. I do not consider dolphin diving speed and duration, which shortens the time spent at the surface. Dolphins feed on low or high density patches, but are dependent on depth of food layer (Benoit-Bird et al., in press). If food is inaccessible e.g. > 150 m they move to different food patch. This depth limiting aspect of the DSL is not programmed in the model explicitly. In the model, dolphins feed throughout the period food is available unless interrupted by a predator threat or they are in search mode.

Flee: when dolphins detect killer whales, they exhibit a flee response, which is not instantaneous, but within a time step. They switch to flee state from the previous behavioral state and increase speed (16-22 km/hr (Markowitz 2004)). Dolphins choose the shortest distance to the nearest shallow water zone (< 10 m) to escape an attack. The idea that dolphins will choose the shortest distance to safety or after feeding offshore is merely a hypothesis and not based on direct observations.

Hide: Post-fleeing, dolphins can hide in near shore shallow waters > 10 m deep to escape from a potential killer whale attack. They re-emerge from their refuge between 1-3 hours for adult dusky dolphins, 3-5 hours if a female with calf is present. Dolphins resume normal activity once killer whales are out of system or beyond detection range (> 5 km). They have a memory to return to normal activity that can be varied, but I use an average waiting time of 1 hour. It is not known how long a dolphin can stay in a refuge, but Cipriano (1992) observed that during one event after killer whales were sighted in the area, dolphins moved into shallow waters (> 1 m) and stayed for nearly 4 hours until his observation period ended.

Killer whale behavior

Killer whales are present in the system as groups, with a maximum of two groups present in the system at any particular time with a group size of 1 to 30. The groups can be affiliated to the same pod or different pods, but the combined group size of both groups is 30: this corresponds with the maximum number of animals observed in the Kaikoura area (*Dolphin Encounter* 1995-2007 tour boat data). Dolphin group sizes can easily be varied.

Killer whales are not in the system at the start of the simulation, but each group enters randomly with a defined realistic return probability and a random route (shallow or deep water contour) in the system. Killer whales enter the system randomly from any of the last row of north or south cells in the grid. If they enter from the north end they typically move out of the system through the south end and vice versa. Their entry into the system and the depth contour they follow are randomized. Killer whales (max of two groups) follow the depth contour lines, moving either through deep water > 200 m or in shallow water contour lines (>10 m < 200 m).

I assume that the killer whale groups encountering dusky dolphins are specifically on the hunt for dolphins, while other killer whales in the system are not motivated to hunt or are seeking other prey. Killer whales once out of the system can return the next day, 0.5 days, 3 days later, or a week later, characterizing the unpredictability of their visits to Kaikoura. Because of the random nature of entry, direction of movement, and choice of contour line, they can be in the system but have no effect on the dusky dolphins due to the limits of their prey detection range.

Killer whales exhibit the following behavioral states

Cruise/Search: When cruising and in search mode, killer whales travel 6 – 8 km/hr (Williams 2002) and follow bathymetric contour lines within a few hundred meters difference between the initial contour line they choose when entering into the system. During search mode, they search through adjacent cells around them and if a dusky dolphin is within detection range, they orient themselves towards that closest individual and take the straightest path to the dolphin.

Stalk: When stalking (hunting), killer whales travel faster, between 15 – 25 km/hr. Speed data are based on killer whale average speed estimates (Williams 2002, Ford et al. 2005, Ford and Reeves 2008). Here I assume an average stalk speed of 16 km/hr but do not account for diving speed or duration when they are on the hunt.

Wait: When killer whales are unsuccessful in capturing a dusky dolphin, they wait near hiding dolphins to see if another attack opportunity presents itself, approximately 1 hour, but can be varied. There is little information on predator behavior post-attack and this behavior is hypothesized in the model.

Post-hunt: Killer whales engage in a post-hunt mode where they temporarily suspend their predation attempts for a minimum of one hour or 16 time steps before they can revert to stalk mode again. Once killer whale presence is detected and dolphins engage in escape behavior, I assume that the killer whales lose an element of surprise to launch another attack and therefore, bide their time till another opportunity presents itself. If dolphins are out of detection range and in hiding mode, killer whales resume *cruise* mode.

Killer whale-dusky dolphin behavioral games

Both dolphins and killer whales detect each other at variable distances — 5 kms for killer whales and 2-5 kms for dolphins. Detection distance is kept constant for the model simulations, but detection distances for both species can be varied. The mechanisms of detection for vocalizing or active dolphins are not considered. Killer whales when in cruising mode switch to stalking mode when they detect dolphins in any of the 8 directions (NE, N, NW, S, SW, SE, W, E) and head straight towards the closest dolphin. In case killer whales follow the dolphins into shallows and are unable to launch a successful attack, they patrol or stalk for one hour, and then enter into a post-hunt mode.

If a dusky dolphin detects a killer whale, they enter into flee mode moving into nearest shallow waters but if killer whales are in the way to nearest shallow zone, they flee to maximize distance between them and the predator and then head to closest shallow cell (model hypothesis). An encounter index maintains the number of killer whale-dusky dolphin encounters in a cell. These encounters accrue and thus, the dolphin is immortal.

Both prey and predator maintain a short-term memory of the attack. I do not maintain long-term memory of attacks that may influence dusky dolphins to avoid certain high risk locations. Both dolphins and killer whales traverse through each of the cells that fall between their current position and their final desired destination. The movement through each cell enables greater encounter between predator and prey, and also provides time for prey to avoid predator, or for predator to catch up with prey. All behavioral states for dusky dolphins and killer whales are color-coded (Fig. 10) and can be visualized in ArcGIS using the animation tool.

Model evaluation

In the IBM, uncertainty over chosen parameter values could have the most influence on final model outcomes. To assess differences arising from using different parameter estimates, I conducted several short simulations (20 treatments, 5 reps, 210 days (Nov - May) to look at primarily the effect of killer whale return probabilities, dolphin detection distance of killer whales, and dolphin memory in refuge on time/distance budgets and encounter index (Table 3). For analysis, Time is displayed as a proportion of time spent by a dolphin in an activity and is calculated as simulated time (variable)/ (length of simulation i.e., 210 x 24 x 16).

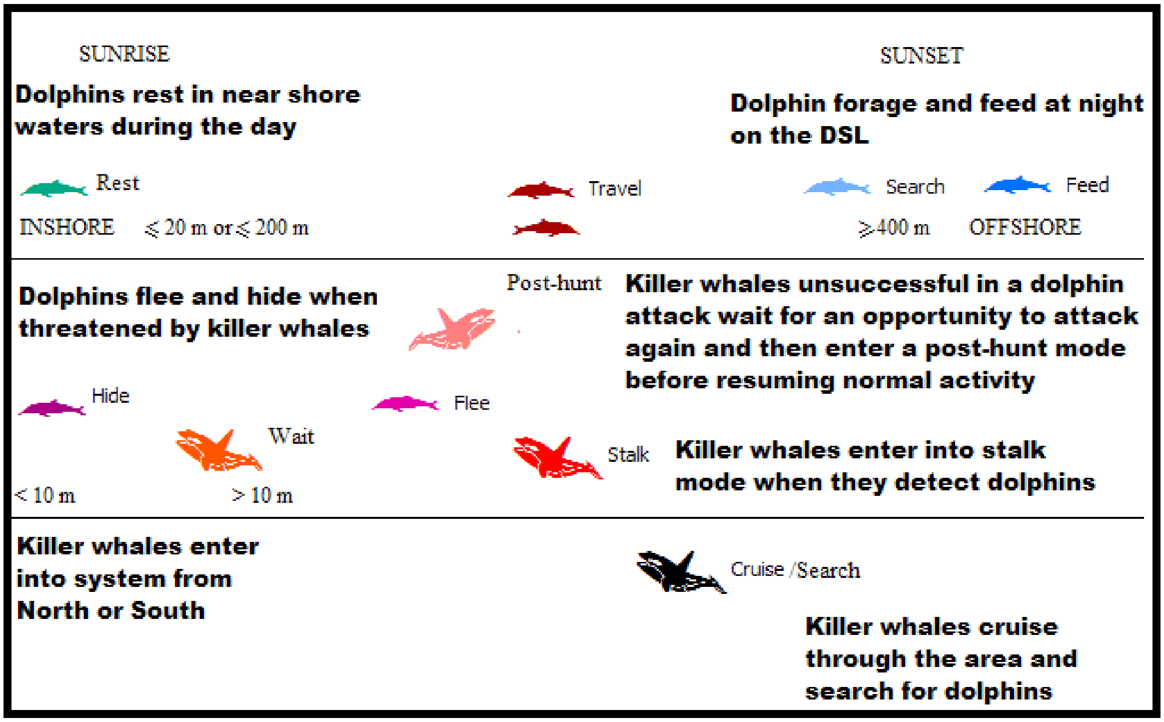

FIG. 10 A representation of the animated, color-coded movement and behavior of dusky dolphin and killer whale pre and post-encounter in the individual-based model (water depth indicated in meters).

Table 3 Set of parameter combinations used in model sensitivity analysis to look at effect on dusky dolphin time/distance budgets and encounter index (n = 20 treatments)

Treatment	Dolphin detection distance (km)	KW detection distance (km)	KW return time (days)	KW memory after dolphin escape (hr)	Dolphin memory in refuge (hr)	KW wait time (hr)
1	5	6	7	1	1	1
2	5	6	7	1	3	1
3	10	6	7	1	1	1
4	10	6	7	1	3	1
5	5	6	3	1	1	1
6	5	6	3	1	3	1
7	10	6	3	1	1	1
8	10	6	3	1	3	1
9	5	6	2	1	1	1
10	5	6	2	1	3	1
11	10	6	2	1	1	1
12	10	6	2	1	3	1
13	5	6	1	1	1	1
14	5	6	1	1	3	1
15	10	6	1	1	1	1
16	10	6	1	1	3	1
17	5	6	0.5	1	1	1
18	5	6	0.5	1	3	1
19	10	6	0.5	1	1	1
20	10	6	0.5	1	3	1

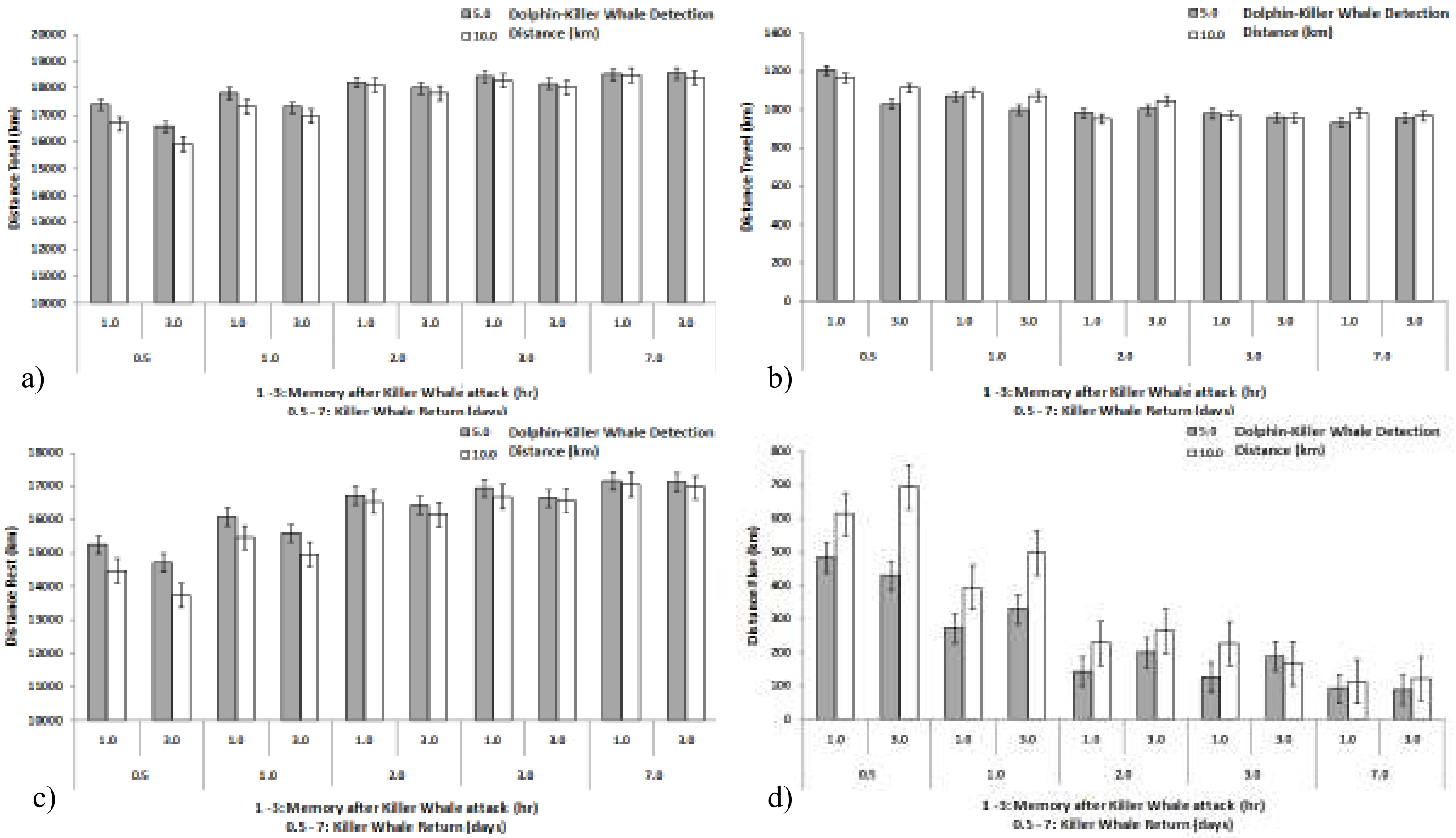

FIG. 11 Distance budgets (a-d) for a dusky dolphin exposed to variation in parameter levels and combinations with particular emphasis on killer whale return rates, dusky dolphin memory in refuge (memory after killer whale attack), and dusky dolphin detection distance of killer whales between Nov-May (20 treatments, 210 days, n = 5 reps). See Table 3 for parameter combinations used for all 20 treatments.

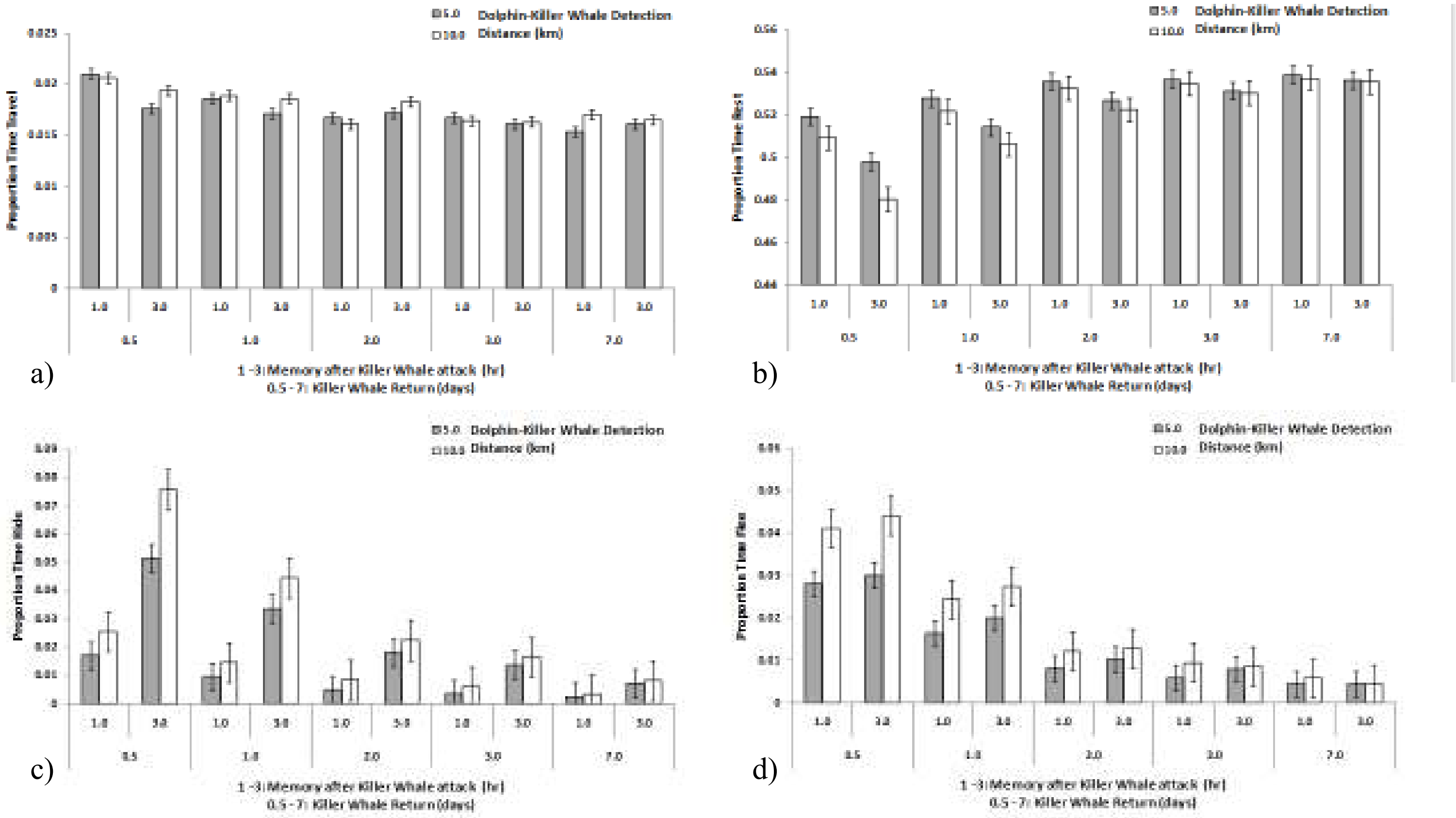

FIG. 12 Time budgets (a-d) for a dusky dolphin exposed to variation in parameter levels and combinations with emphasis on killer whale return rates, memory in refuge (memory after killer whale attack), and dolphin detection distance of killer whales (210 days, n = 5 reps).

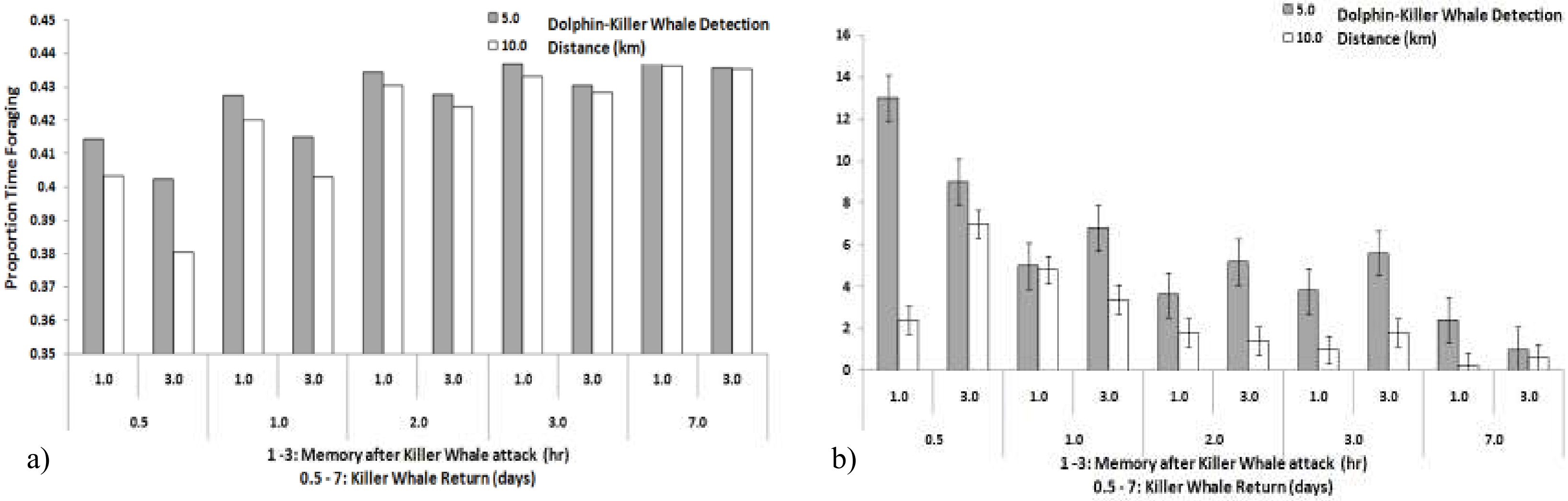

FIG. 13 Foraging time and encounter index for a dusky dolphin exposed to variation in parameter levels and combinations with emphasis on killer whale return rates, memory in refuge (memory after killer whale attack), and dolphin detection distance of killer whales (210 days, n = 5 reps).

When dusky dolphin detection distance was increased, hiding time for the dolphin was correspondingly increased. This I believe to be ecologically relevant since if the dolphins are detecting the killer whales sooner, they are likely to flee sooner and stay in the refuge longer until the threat passes. However, other combinations were tested as well.

Overall, there does not seem to be significant variation in time/distance budgets to account for the different parameter combinations. However, the time/distance budgets appear to be sensitive to killer whale return rates. This is reflected in distance flee, rest, travel, encounter index, proportion foraging time, and other variables considered (Figs. 11, 12, and 13). Based on these initial results, I believe the model is robust under most combinations of parameter values.

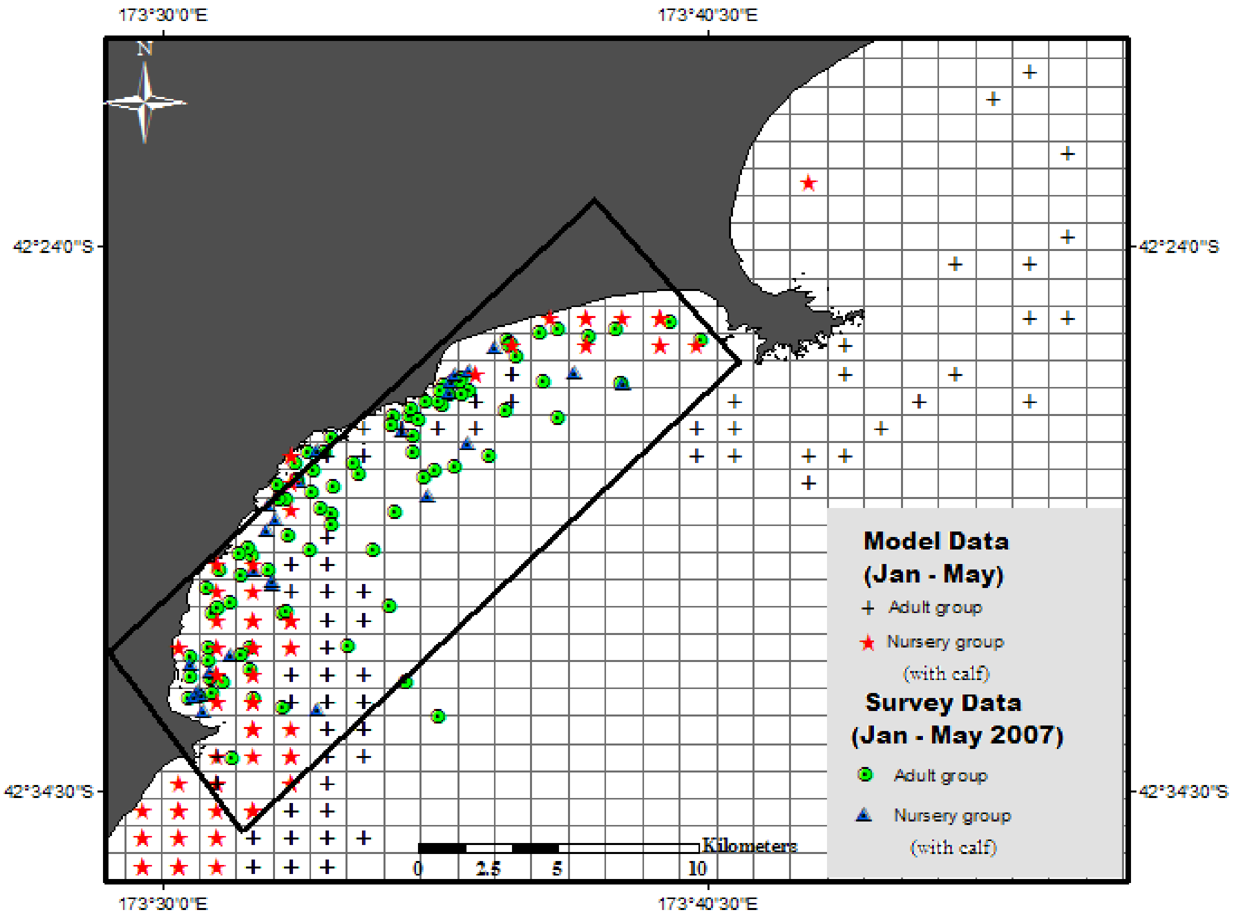

FIG. 14 Sightings data of dusky dolphins by social type (n = 118) (green circles and blue triangles) from systematic surveys between Jan-May 2007 (Chapter II) compared with simulated sightings (red stars and black crosses) obtained by sampling the model results at times and periods corresponding to systematic survey efforts (n = 118, 5 reps). Rectangular box represents systematic survey area covering 80 km^2. Grid represents model study area comprising1468 km^2.

Using baseline parameter values for the model (Table 2), I conducted a simple model evaluation of comparing observed data with simulated sightings of dusky dolphins (with and without calf, Fig. 14). I used data from systematic surveys conducted between Jan and May 2007 (Chapter II) (n = 118). These surveys involved instantaneous sampling of dolphin positions within 200 meters of a survey transect route (Chapter II). I sampled simulated dusky dolphin sightings for the same survey period (Jan – May) using similar social groupings observed mothers with calves (nursery group) and other adult groups, including mixed age/sex groupings). For sampling purposes, I used corresponding times as far as possible since model simulations run at 16 time steps/hour. To accommodate the stochastic nature of the model, I used 5 reps of 118 sightings each to compile likely dusky dolphin sightings in the system for the stipulated period.

The boat-based survey data (Chapter II) used here for evaluation covers a much smaller area (80 km^2) vs. the model habitat and also follows a different sampling protocol. The simulated sightings that are observed outside the survey area are consistent with long-term datasets from opportunistic dolphin tour boat data (1995-2007) from *Dolphin Encounter*, Kaikoura, New Zealand and from dedicated datasets (Markowitz 2004). More evaluations can involve simulating a boat or a researcher's survey route to record dolphin position and compare with model generated sightings.

Clever predator and clever prey model simulations

Based on the experimental design in Table 4, I conducted 4 treatments to obtain dusky dolphin time/distance budgets under the four prescribed scenarios. Only one dolphin (without calf) was simulated for the devised treatments. While dolphins are social animals, for purposes of developing and evaluating the model, I use a single dolphin that is representative of the dusky dolphin population in Kaikoura by virtue of its behavioral and movement rules. Also, the use of single dolphin simplifies model simulation and is adequate to address current study objectives.

Model simulation period was between November and May for about 210 days (NZ late spring, austral summer/fall) to coincide with peak killer whale season, calf presence, and food variability. I repeated the simulation 35 times (n = 35 reps). The number of reps was estimated based on sample size calculations (Zar 1999) from preliminary model runs. The index of measurement included time spent by dolphins in various behavioral states: Time Rest, Time Flee, Time Hide, Time Travel, Foraging Time (time search+ time feed). Similarly for distance, I calculated: Distance Total, Distance Travel, Distance Flee, Distance Rest, and Distance Search. For current purposes, I modeled only 1 adult dusky dolphin (male/female) and a total of 2 killer whale groups.

All baseline parameter values used are shown in Table 2. For model simulations, I used a higher detection distance for killer whales (5 km) *vs.* 4 km for dusky dolphins, assuming killer whales are intent on hunting dolphins. I used an 18 km/hr flee speed for dolphins, but maintained an average stalk speed of 16 km/hr for the killer whales since studies indicate that while killer whales may pursue fast prey such as dolphins at top speed (45 km/hr), their average speed may be lower (Fish 1998). Moreover, sensitivity analysis did not indicate a significant variation from changing detection distances alone on time/distance budgets.

Table 4 Experiment design of the IBM model simulations. Treatment acronyms indicate whether anti-predator rules (R) for dusky dolphins are ON or OFF and whether killer whales (KW) are present or absent. A theoretical interpretation of the ecological costs and evolutionary (survival) benefits from adopting anti-predator strategies is represented by a ratio, where 0 indicates no costs, 1 a minimum cost, 2 a higher cost due to travel plus anti-predator decisions, which in turn reduces survival costs, 3 represents a higher survival cost due to increased vulnerability to predator attacks and prey adopting no defensive strategies. R-KW represents current understanding of system off Kaikoura

Status	Killer Whales Present	Killer Whales Absent
Anti-predator RULES ON	***R-KW***	***R-NOKW***
Ecological Costs (Time/Distance budgets)	**2** (Travel plus Flee, Hide Costs)	**1** (Travel Costs)
/Evolutionary (survival) Benefits	**1** (reduced survival costs, fewer encounters)	**0** (No Encounter with KWs)
Anti-predator RULES OFF	***NOR-KW***	***NO-RKW***
Ecological Costs (Time/Distance budgets)	**0** (No Travel, Flee or Hide Costs)	**0** (No Travel, Flee, Hide Costs)
/Evolutionary (survival) Benefits	**3** (increased survival cost, more encounters)	**0** (No Encounters with KWs)

Return probability for a killer whale is calculated by the equation: Probability _(x) = 1 / (24hours*16 time steps* Killer whale (KW) return day = 3)_ = 0.0008. I used a 3 day KW return period and so, there can be 11-13 killer whale days/whale over a 210 day period — this is comparable to field recorded killer whale sighting records (_Dolphin Encounter_ tour boat data 1995-2007). Model evaluation of parameter combinations revealed sensitivity towards varying killer whale return probabilities. So for comparison, I conducted the same treatments with a higher killer whale return probability of 0.5 days. So, average number of killer whale days/whale over a 210 day period was ~55-56 days.

As a measure of killer whale-dusky dolphin encounters, I used an encounter instead of a mortality index. For testing treatment effects, baseline values for parameters are shown in Table 2. These values are within acceptable range estimates for the species and are based on available literature. Where information was lacking, I used conservative estimates. In Table 4, R-KW represents ‘system reality’ with both anti-predator rules and killer whales present. R-NOKW is a situation where there are no killer whales in the system, but travel rules operate. In NOR-KW, the anti-predator rules (travel as well as flee plus hide) rules are turned off, but killer whales are present in the system. This helps to measure if the rules make any difference in affecting overall time/distance budgets and encounter index. NO-RKW in a way corresponds to the ‘winter’ situation off Kaikoura, but represents the null model here where there are no rules and no killer whales in the system. I did not conduct any specific simulations for winter months.

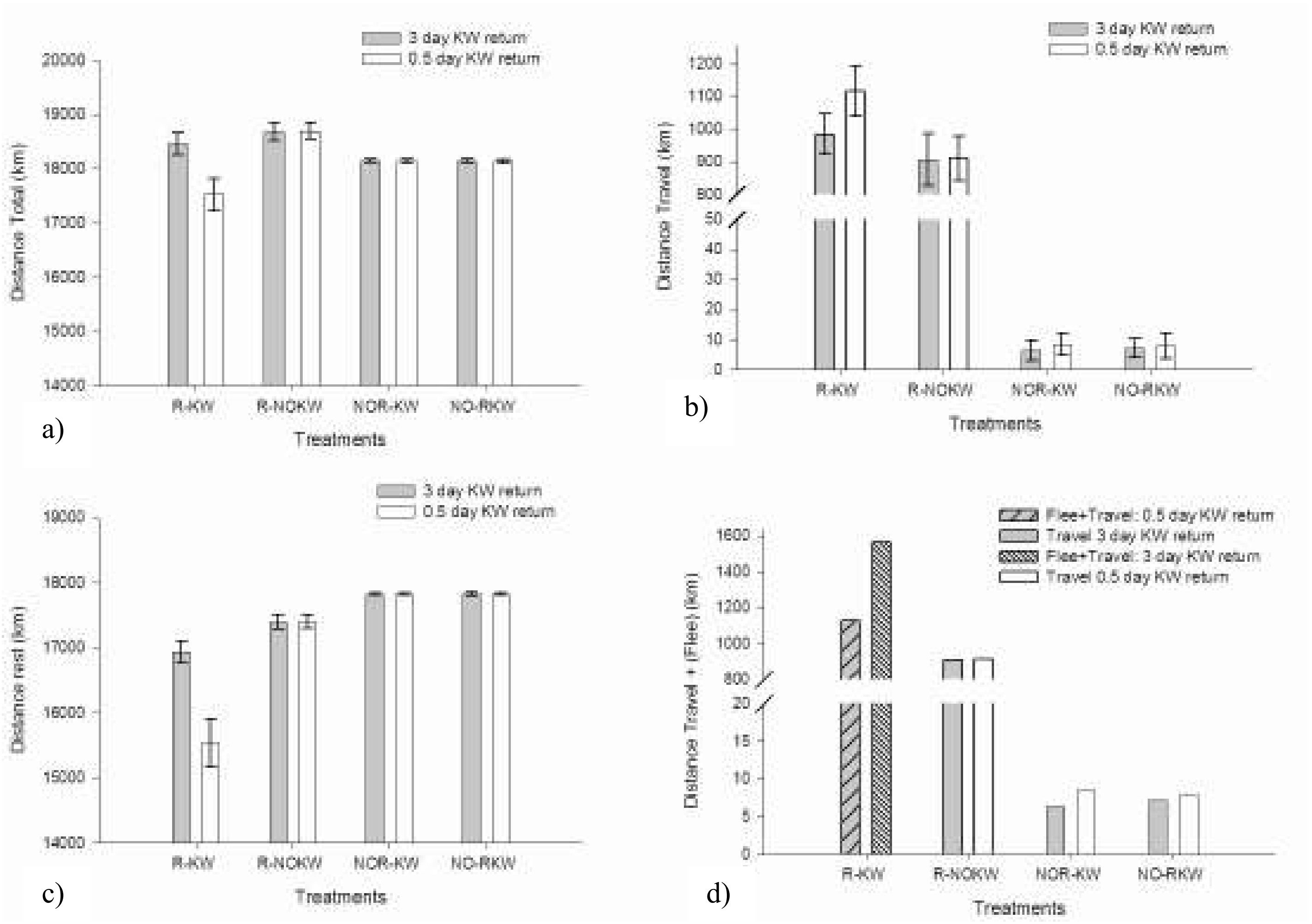

FIG. 15 Distance budgets for dusky dolphins exposed to 4 different treatments between November and May (1 rep = 210 days, n = 35 reps) during a killer whale (KW) return rate of 0.5 and 3 days.

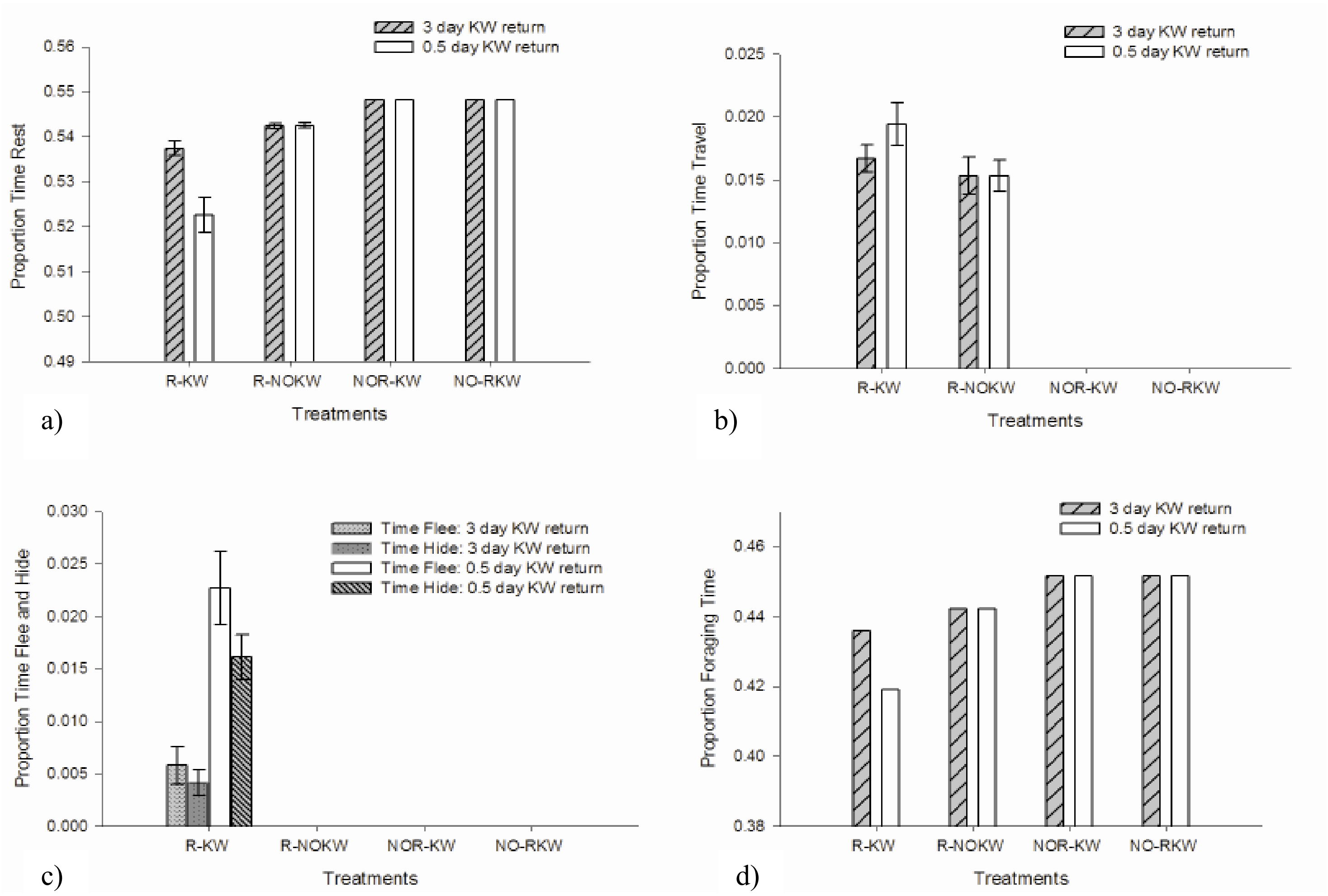

FIG. 16 Time budgets for dusky dolphins exposed to four treatments between November and May (1 rep = 210 days, n = 35 reps during a killer whale (KW) return rate of 0.5 and 3 days.

.

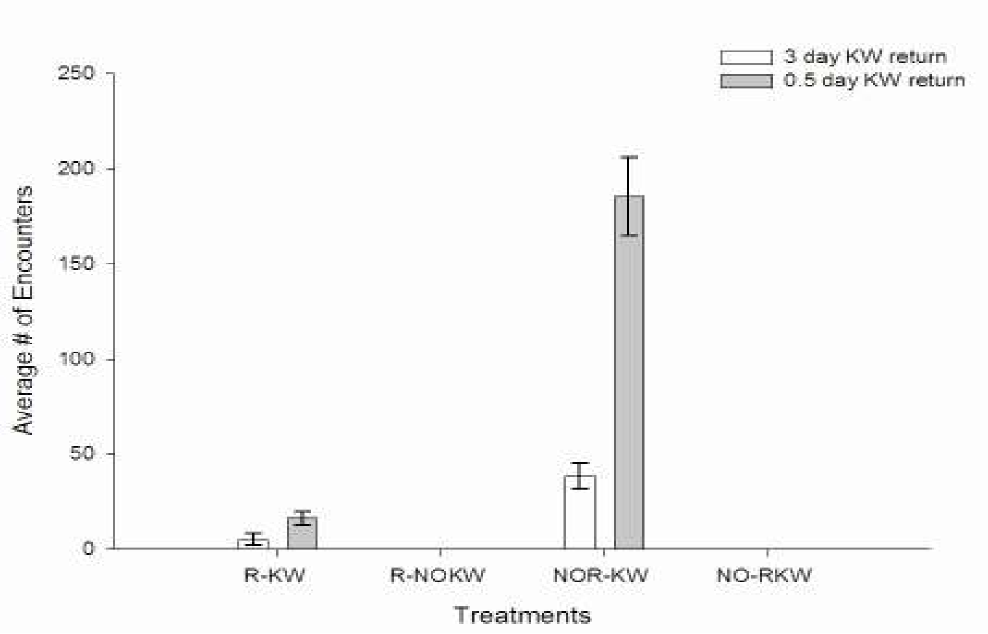

FIG. 17 Average number of killer whale-dusky dolphin encounters during high (0.5 days) and low (3 day) killer whale (KW) return rates. Encounter index is measured as during a single rep or 210 days of the model simulation (n = 35 reps). Treatment definitions are provided in Table 4.

Results

At a glance, dusky dolphins incur short-term costs of having to travel more and rest less as a result of their nearshore-offshore movements during peak killer whale season (R-KW, Fig. 15). Compensating for these short-term costs of travel and fleeing/hiding (Figs. 15 and 16) and decreased foraging time (Fig. 16) is the increased survivability of dolphins adopting these behavioral and movement rules represented by the encounter index (Fig. 17). The encounter index rapidly rises when dolphins switch off anti-predator rules.

MANOVA tests reveal statistically significant differences between treatment subjects for Distance (Total, Travel, Rest, Search) and Time variables (Rest, travel, Search, Feed) ($n = 35$, $df = 7$, $p < 0.0001$, $\alpha = 0.05$) at both killer whale return rates (0.5 and 3 days). Specifically, post-hoc Bonferroni tests reveal that Distance Total, Distance Rest, and Distance Travel are not significantly different for R-NOKW and NOR-KW and NO-RKW at both killer whale return times ($p > 0.05$). Distance Rest and Distance Travel are significantly different between the 3 day and 0.5 KW return times under R-KW ($p < 0.0001$). Statistical trends are similar for time budgets.

Travel costs for dolphins under R-KW is the sum of distance travel plus distance flee — this provides a true measure of killer whale effects on travel costs. For NOR-KW and NO-RKW, dolphins travel a minimal distance as they try to search for a suitable foraging cell.

In Fig. 16, for R-KW when rules operate, dolphins are compromised on proportion Foraging Time in the presence of killer whales. This effect is pronounced when the killer whale return rate is higher (0.5 days). Within treatment R-NOKW and in the absence of killer whales, dolphins can feed longer and are not hampered by escape rules such as fleeing and hiding, which can reduce Foraging Time available. R-NOKW may represent an ideal situation, but dolphins still incur travel costs as they move offshore to feed.

There were no differences in proportion Foraging Time for both killer whale return rates for NOR-KW and NO-RKW. Dolphins are not impacted by increased killer whale presence in NOR-KW since anti-predator rules are inoperable and therefore access to food is unlimited. Also, while the ‘immortal dolphin’ can have successive encounters with killer whales, it does not completely disrupt all activities such as foraging and resting. The effect of NOR-KW is best exemplified by the encounter index.

Discussion

In general, model results reveal that dusky dolphins incur short-term ecological costs of having to travel more, rest less, and have reduced foraging time when killer whales are present. The effect is pronounced with increased presence of killer whales. However, by adopting anti-predator rules, dusky dolphins have fewer encounters with killer whales and therefore increased survivability. Revisiting Table 4, dusky dolphins pay a price by adopting short and long-term anti-predator mechanisms. The cost is smaller when killer whales are absent, but increases with killer whale presence. However, without any anti-predator mechanisms dusky dolphins pay a higher price in terms of increased killer whale encounters and reduced survival. Thus, evolutionary benefits of staying alive far outweigh short-term ecological costs.

The minimal number of encounters during low killer whale return probabilities (3 days) is similar to observations of minimal scarring in real dusky dolphin population off Kaikoura (Chapter II). However, dusky dolphins are small dolphins (< 2 m in length), so it is expected that most attacks on them by adult killer whales (6-8 m in length) are likely to be fatal.

The return probability does not account for the number of actual killer whale-dusky close encounters. So, even if killer whale return rate is high (0.5 days, or twice per day), the probability of killer whale-dusky encounters (being in same cells) is still low owing to the random nature of their entry into the system, and the route that the killer whales takes (shallow *vs.* deep contour).

In real systems, every predator entering the system or detected by prey may not be deemed threatening. Also, every predator in the system may not have an ‘intent to hunt’ dolphins. This variation is captured to an extent in the model by killer whale return probabilities and detection distances between prey and predator, such that reaction to a predator occurs only at certain detection distances and not every time a predator enters the system. Future models can incorporate predator intention such that some killer whale groups entering the system and within detection distance pose no threat to nearby dolphins.

As gregarious animals, dusky dolphins rely on their social networks and may therefore detect killer whales much sooner and react much quicker than if they were alone. In the current model, I assume that the simulated lone dolphin receives this information. In other words, as far as detection probablility, the lone dolphin could also be a part of a group of dolphins. The mechanism of information transfer however is not stated explicitly in the IBM.

The model is stochastic and therefore tries to incorporate the uncertainty within the real system. Parameter uncertainty has been addressed to an extent during model evaluation. With increasing knowledge and more parameter permutations, complex aspects of detection and vigilance as related to species group size can be tackled. Also, knowledge of food distribution and composition is limited, and these parameters may further affect the way dusky dolphins use time and space independent of predator influence.

The model can be further refined to explore new questions and concepts. For example, an integral component of mammals such as killer whales and dolphins is their social system (Connor et al. 1998). Thus, prey detection of predator can be affected by an efficient dolphin communication network determined by social organization and spatial dispersion. This will provide a true measure of prey sophistication and predator hunting flexibility as determined by an effective social communication network.

The model also allows us to trace movement patterns of dusky dolphins and killer whales over defined time periods. Analysis and comparisons with field-based movement data can improve the model and help assess prey and predator movement patterns. Modeling predator behavior is vital as well. Future models can be improved to make the predator smarter by incorporating group composition, predator motivation and energetics.

The current model was developed using Kaikoura as the system of interest. However, I believe this does not limit the scope of the model. The goal was to develop a generalized model that would have applications to various systems regardless of the species.

Risk effects, miscellaneously defined as nonconsumptive, non-lethal, or indirect predation risk effects, deal with the ecological consequences of fear (Lima 1998, Luttbeg and Kirby 2005, Creel and Christianson 2008, Peckarsky et al. 2008). How prey responds to a fierce predator can be gauged through various ways, including habitat selection, activity variations, predator-prey spatial and temporal overlap, and foraging behavior (Lima and Dill 1990, Brown et al. 1999, Lima and Bednekoff 1999, Laundre et al. 2001, Creel et al. 2005, Fortin et al. 2005, Heithaus and Dill 2002, 2006, Winnie and Creel 2007).

There is strong evidence that these anti-predator decisions can produce risk effects with equal or greater influence on prey population dynamics than lethal predation (Abrams1990, Nelson et al. 2004, Preisser et al. 2005, Creel and Christianson 2008). Further, these effects can move down the food chain and structure ecological communities (Kotler 1984, Estes and Duggins 1995, Peacor and Werner 2001, Ripple and Beschta 2004, 2006, Myers et al. 2007, Heithaus et al. 2008, Cresswell 2008).

Fear-driven ‘costs’ have been explored briefly in previous studies (growth rates, and fecundity, life history traits, Peckarsky et al. 1993, 2002, Peckarsky and McIntosh 1998, Collier et al. 2008, prey stress, Boonstra et al. 1998, fitness framework, Ajie et al. 2007, reproductive physiology Creel et al. 2007), and direct effects on prey population dynamics have been indicated.

When dealing with complex systems and often inaccessible dolphin species, we do not have the means of getting adequate field data to measure indirect predation risk effects. Therefore, many simple questions are left unanswered. There is enough circumstantial evidence suggesting that predators play important roles in shaping dolphin behavior, just like other prey. But we know little about how risk effects can affect dolphin behavioral ecology.

Dusky dolphins are recognized as a *Data Deficient* species by the IUCN (IUCN 2008), which means that there is insufficient information to determine their conservation status. Further, a recently concluded global assessment of land and marine mammals (Schipper et al. 2008) calls for expanded research on *Data Deficient* marine mammal species, which are fairing poorly relative to land mammals, to establish proper conservation and management practices. Off New Zealand, current dusky dolphin populations appear to be robust (Würsig et al. 2007). To ensure that dusky dolphin populations remain robust, it is important to continue research on the behavioral ecology of this species. Currently, I do not believe that predator effects are likely to have a significant effect on population dynamics of dusky dolphins, but may have an important influence on their habitat selection and foraging practices.

The model is representative of a simple marine system, i.e., oceanographic and other environmental variables are excluded since they do not appear to have a strong influence on dusky distribution patterns off Kaikoura (see also Chapter II). This may not be the case in other systems. However, by incorporating new rules and environmental data, the model can be adapted for complex systems such as off Monterey Bay, California where oceanographic variables have important influence on dolphin prey and distributions (Keiper et al. 2005). In conclusion, while the current model provides much heuristic value, further model evaluations and enhancements can be achieved by applying the model to other dolphins systems with strong baseline knowledge of its ecological players and components.

CHAPTER IV

ECOLOGICAL CONSEQUENCES OF FEAR: BIOENERGETICS OF PREDATION RISK EFFECTS IN DUSKY DOLPHINS

Introduction

To feed or not to feed is a problem that many animals regularly face in a dangerous habitat. Often, they strive to maintain a balance between seeking food and safety (Sih 1980, Lima and Dill 1990). Only recently, dedicated studies on predation risk effects on marine mammals have shown that they also engage in energy-safety tradeoffs (Heithaus and Dill 2002, 2006, Frid et al. 2007, Wirsing et al. 2007).

Marine mammals live in a largely refuge free world, so when scared, they resort to trusted measures to identify predators and escape potential attacks (e.g. Deecke et al. 2002, Ford and Reeves 2008, Wirsing et al. 2008). They are an example of both a clever prey and a predator, relying on social organization, sensory modalities, behavioral flexibility, and diverse prey to survive and reproduce. However, just as finding and consuming prey bears costs and benefits, avoiding a predator can have ecological consequences or risk effects (Luttbeg and Kirby 2005, Brown and Kotler 2004, Preisser et al. 2005, Creel and Christianson 2008).

The extent and nature of these costs is still relatively unknown for most animals (Creel and Christianson 2008), including marine mammals. For example, we do not know what penalties dolphins pay by changing habitat use, movement patterns, foraging strategies, and spatial distribution out of fear.

There is evidence that prey may compromise on food quality to avoid predation (e.g. rodents, Brown 1988; Western sandpipers *Calidris mauri* Ydenberg et al. 2002; bottlenose dolphins *Tursiops aduncus*, Heithaus and Dill 2002; broad-headed skink *Eumeces laticeps*, Cooper 2000). However, there are other costs to pay, such as traveling further to feed on high quality food (e.g. Antarctic fur seals *Arctocephalus gazella*, Staniland et al. 2007) or blue whales (*Balenoptera musculus*) that vary dive duration and foraging time because of high feeding costs (Acevedo-Gutierrez et al. 2002).

Marine mammals can incur lower energetic costs than terrestrial animals (Williams and Yeates 2004), due to variations in environment, hunting strategies, and behavior. However, these differences plus the need to breathe air and maintenance costs can be energetically expensive for marine mammals at sea (Williams 2002). Mothers with calves can have additional locomotor (Noren 2008) and lactation costs (Reddy et al. 1994; Kastelein et al. 2002).

Previous bioenergetics models have focused on population dynamics and prey foraging costs without an explicit consideration of predation risk changes, and the dynamic nature of predator-prey relationships (Lima 2002, Brown and Kotler 2004, Ruzicka and Gallagher 2006). Studies on marine mammal bioenergetics usually have dealt with foraging behavior (e.g. Benoit-Bird 2004, Williams et al. 2004, Costa 2008) or life-history (*reviewed* Lockyer 2007) or physiological constraints (Rosen et al. 2007) within the context of marine mammals as predators, not prey.

Dolphins as prey can make anti-predator decisions that vary with predation risk levels (e.g. Heithaus and Dill 2002, 2006, Chapter II). The challenge is to quantify the costs associated with the decisions and the extent, in the absence and presence of predators.

Off Kaikoura, New Zealand (42°30'S 173°35'E), dusky dolphins make nearshore-offshore foraging trips to feed exclusively on mesopelagic organisms associated with the deep scattering layer (DSL) at night. The DSL is a year round available resource with some changes in food composition based on dusky dolphin stomach content analysis (Cipriano 1992). The day time choice of near shore habitats for dusky dolphins between late spring (Nov) and fall (Mar-May) (< 200 m) appears to be strongly influenced by the seasonal threat of killer whales (*Orcinus orca*) in the area (Chapter II). Killer whales are the principal dusky dolphin predator, and in early austral spring and winter, when risk from killer whales is rare, dolphins shift closer to their food source by moving farther from shore into deeper waters (> 200 m) (Dahood et al. 2008, Chapter II). Killer whales off New Zealand appear to be generalist predators feeding on diverse prey but may occasionally feed on dusky dolphins (Constantine et al. 1998, Visser 2000). Also, some killer whale sub-groups may specialize on hunting dolphins (Visser 2000).

Food availability is longer in winter relative to summer, a consequence of early sunset and late sunrise. Mothers with calves form nursery groups and prefer shallower waters (< 20 m deep) (Weir et al. 2008), but are expected to feed on the DSL at night. Daytime foraging by dusky dolphins is rarely observed (Cipriano 1992, Markowitz 2004).

Dolphin response to killer whale threats is both immediate and long-term (Chapter II). In brief, dusky dolphins use near shore shallower areas during peak killer whale season as a long-term strategy (Dahood et al. 2008, Chapter II). During pulses of high predation risk, they resort to measures such as fleeing at top speed away from danger or hiding in the shallows (< 10 m), in extreme cases in 1 m deep pools (Würsig and Würsig 1980, Cipriano 1992).

With spatial and temporal fluctuations in predation risk influencing dusky dolphin lifestyle choices, it would be interesting to assess the energetic consequences of (short and long-term) anti-predator decisions by social groupings (with and without calf) as driven by fear.

Using an individual-based model (IBM) of the dusky dolphin system near Kaikoura, New Zealand (Fig. 18, see also Chapter III), I predict energetic costs of dusky dolphin anti-predator decisions during temporal and spatial variations in predation risk, and the likely differences for lactating mothers with calf and an adult without a calf and discuss ecological and evolutionary implications.

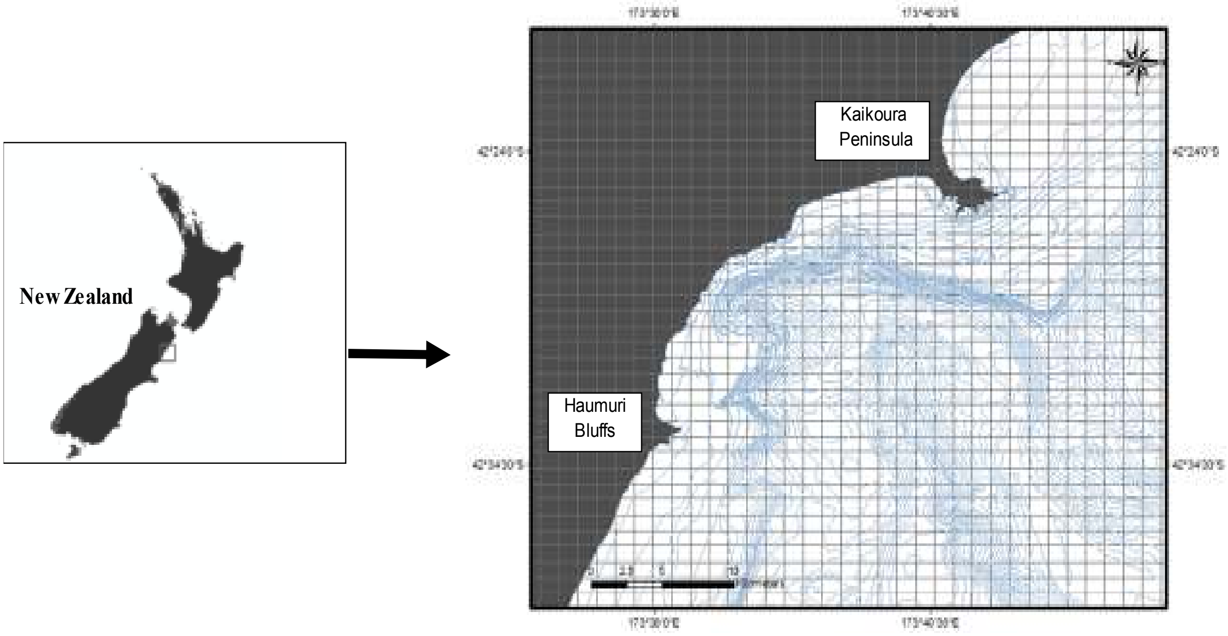

FIG. 18 Habitat map of system of interest off Kaikoura, New Zealand.

Methods

The IBM was created to represent the dynamic behavioral relationship between a clever prey and clever predator, in this case dusky dolphins and killer whales, respectively. Detailed model description as well as prey and predator behavioral rules are available in Chapter III). I describe the salient features of the IBM here.

Dusky dolphins are placed initially in a random cell as long as it meets their depth requirements and is apropos to their social class (with or without calf). Dusky dolphins have essentially 6 behavioral states (*travel, rest, search, feed, flee, and hide*); each of these states is characterized by changes in speed and depth restrictions based on literature values. During the day, dolphins are in *rest* mode and move into adjacent cells in a zig-zag fashion (Würsig et al. 1989), and cruise at slow speeds. They switch into travel mode when they make the afternoon trip to feed on the DSL, and increase travel speeds. Once in appropriate depths to feed (> 400 m) and in a 'DSL' cell, they engage in feeding, and switch between search and feed modes throughout the duration of the DSL availability.

Killer whale groups (maximum of 2 groups) are not present in the system initially and enter into the system based on a return probability $\mathbf{(x)} = 1 / (24\textit{hours} * 16\ \textit{time step} * \textit{Killer Whale (KW) return day} = 3) = 0.0008$. The three day killer whale return time corresponds well with the unpredictability and frequency of killer whale sightings off Kaikoura based on long-term datasets (Chapter II, Chapter III). Killer whales have 4 behavioral states (*cruise/search, stalk, wait, post-hunt*). Once killer whales enter the system, they can follow a shallow (> 10 < 200 m) or a deep (> 200 m) contour line with a difference of a few hundred meters. They can enter the system day or night but typically during peak killer whale season (Nov-May). The return probabilities and the choice of depth contour greatly control the number of possible close encounters with dusky dolphins.

When killer whales are in *cruise* mode they simultaneously *search* adjacent cells for presence of dusky dolphins. If dolphins are within their detection range, killer whales take the closest, straightest path towards the dolphins. Killer whales can be successful or unsuccessful in their predation attempts. Dusky dolphins also maintain detection ranges for killer whales. Upon detection of a killer whale, dusky dolphins can enter into *flee* mode and then *hide* in shallow water refuges (< 10 m) until killer whales are beyond detection range. Dusky dolphins can resume normal behavior within an hour of entering into the refuge or later as may be the case for mothers with calves, and thus maintain a short-term memory of the attack/encounter.

To monitor predator-prey encounters in a habitat cell, I use an encounter index instead of a mortality index. If killer whales are unsuccessful in their predation attempt, they typically wait one hour (*wait mode*) near the hiding dolphins to search for potential hunting opportunities. If unsuccessful, they enter into a *post-hunt* mode where they refrain from hunting for up to one hour since the element of surprise is lost and they wait to see if other opportunities become available.

Based on other studies, the mesopelagic layer is available only at night, assumed to be available in different cells (> 400 m, Reid 1994) and of varying density between days. Acoustic studies off Kaikoura and Hawaii (Benoit-Bird 2004, Benoit-Bird et al. in press) suggest that DSL distribution appears uniform off Kaikoura; though numerical prey density is lesser than off Hawaii, exact numbers are unavailable for Kaikoura. The amount of DSL available per day and density is unknown. Therefore, I allocated an index of 0 to 100 kcal/cu.m of food per habitat cell (see Chapter III). In the model I do not consider lunar effects (Benoit-Bird et al. in press), but consider solar changes using sunrise/sunset times available from the United States Naval Observatory.

A dolphin is restricted from feeding *ad libitum* in a cell by a giving up density (2/3rd of Total DSL available) beyond which it moves to another cell in search of food. Dusky dolphins in captivity consume roughly 10% of their body weight (for a 70 kg dolphin) (Kastelein et al. 2000). Food consumption is likely much higher in the wild, but food intake is generally smaller with increasing size of animal (Kleiber 1975). In the model, I assume that dolphins feed throughout the period the DSL is available, which is coupled with sunset/sunrise times, but interspersed with food searching or other activity, e.g. when interrupted by a predator.

Dolphin distance traveled and time spent during regular activities (travel, feed, search, rest) and during an attack (flee and hide) were calculated daily and cumulatively. Foraging time spent and encounter index were also calculated for adults with/without a calf and with varying killer whale presence in the system.

I devised four treatments to estimate time/distance budgets for dusky dolphins with and without a calf and in the presence/absence of killer whales (Table 5). The model was simulated for a 210 day period (Nov – May) coinciding with peak killer whale presence, food variability, and presence of calves. I ran 35 replicates of each simulation based on sample size estimates from early model runs (Zar 1999). Dusky with calf is assumed to be an adult lactating female. Each female is associated with a single calf and are given identity codes. Baseline parameter values used for model simulations are shown in Table 6. All model simulations are run with behavioral and movement rules operating, representing current understanding of system off Kaikoura.

Table 5 Experimental design for model simulations and calculation of dusky dolphin time/distance budgets. Acronyms indicate whether a calf is present (CA) or absent (NCA) and whether killer whales (KW) are present or absent from the system. R - implies that dusky dolphin movement and behavioral rules operate

Status	Killer Whales Present	Killer Whales Absent
Anti-predator RULES ON	*C- R-KW*	*C-R-NOKW*
	NC-R-KW	*NC-R-NOKW*

Changes in time/distance estimates appear sensitive to killer whale return probability (Chapter III), and therefore I used both a 0.5 day and 3 day KW return probability in estimating time/distance budgets and dusky dolphin bioenergetics.
For energetic calculations, I used available information from captive and field studies, and model simulation results (time/distance budgets). Where information was lacking, I used available data from other systems and similar species.

Daily energetic requirements (DER) for dusky dolphins to meet their maintenance needs was assumed at 50 kcal/ kg/ day for a 70 kg adult, roughly 3,500 kcal/day (based on Cipriano 1992), I assumed this DER for all calculations as the energy required to meet dusky dolphin maintenance needs.   I do not consider growth, reproductive, or thermoregulatory costs in the calculations.

Table 6 Baseline parameter values used in model simulations for dusky dolphins with and without calf. KW = Killer Whale, DSL = Deep Scattering Layer. Values are based on literature, available data, or are conservative estimates from similar species

Parameters	Values		Source
Simulation Begin (day of year)	306	306	(Nov - May) KW season and calf presence (Cipriano 1992, Markowitz 2004, Dahood et al. 2008, Chapter II, this volume)
Simulation Length (in days)	210	210	Model Simulation
Number of killer whale groups	2	2	Model Simulation
Number of dolphin groups	1	1	Model Simulation
Dolphin escape rules on = 1 off = 0	1	1	Model Simulation
Number of Reps	35	35	Model Simulation
Maximum time steps (km/hr)	16	16	Model Simulation
Calf = 1, No Calf = 0	0	1	Model Simulation
Dusky dolphin detection distance (km)	5	5	Estimate
Killer whale detection distance (km)	4	4	Estimate
KW Return Time (days)	3	3	(1995-2007 *Dolphin Encounter* tour boat data, Kaikoura, NZ, Visser 2000)
Post-hunt (hr)	1	1	Estimate
Dusky dolphin memory in refuge (hr)	1	3	(Estimate based on Cipriano 1992)
KW Wait time (hr)	1	1	Estimate
Mean DSL density (kcal/cu.m)	100	100	(Estimate based on Benoit-Bird 2004)
Giving up foraging threshold (proportion of max DSL)	0.67	0.67	Model Simulation
Dolphin energy requirement (DER) without calf (kcal/day)	3500	3500	(Cipriano 1992)
Dolphin energy requirement with calf (kcal/day)	7000	7000	(Based on Reddy et al.1994, Kastelein et al. 2002)
Mean estimated feeding rate (kcal/hr) to meet DER	330	675	Estimate
Rest (km/hr)	4.5	4	(Based on Cipriano 1992, Markowitz 2004)
Feed (km/hr)	5	5	Estimate
Search for Food (km/hr)	5	5	Estimate
Travel (km/hr)	8	6	(Markowitz 2004)
Flee (km/hr)	18	18	(Based on Markowitz 2004, (calf) Weihs 2004)
KW Cruise (km/hr)	8	8	(Based on Williams 2002, Ford et al. 2005)
KW Stalk (km/hr)	16	16	(Based on Williams 2002, Ford et al. 2005, Ford and Reeves 2008)

The DER used here are comparable to other dolphin species of similar size (e.g. spinner dolphins *Stenella longirostris*, Benoit-Bird 2004). Lactating mothers supporting a calf are expected to have higher energetic needs relative to other adult dolphins. For example, they can exhibit a 200% increase from normal energetic demands (Reddy et al. 1994) or between 52 % – 97% (Kastelein et al. 2002) based on captive bottlenose dolphin (*Tursiops truncatus*) studies. I decided to use a 100 % increase and therefore estimated DER for a lactating mother with calf to be 7,000 kcal/day.

Dusky dolphins off Kaikoura are known to consume primarily hoki (*Macruronus novaezelandiae*), squid, and myctophids (*Family Myctophidae*) throughout the year (Cipriano 1992). Cipriano (1992) provided a summary of stomach contents for dusky dolphins obtained from strandings, incidental and opportunistic captures for all seasons — summer, fall, spring, and winter (n = 26). From these data, he used 13 specimens to obtain estimates of prey energetic content for the 3 most common prey items identified above, based on literature values of the prey length range consumed by dusky dolphins. Estimated energy value for squid (size range 75-155 mm) is 38.6-424 kj/item; hoki (size range 250-500 mm) is 338-2460 kj/item; Myctophids (size range (40-70 mm) is 10.6 – 31.9 kj/item (from Cipriano 1992 and references therein). To estimate foraging costs for dusky dolphins, I used only 6 of 13 dolphin specimens, including only dolphins with full guts and disregarding outliers in terms of weight or length. The dolphin specimens considered for analysis weighed between 69 and 77 kg, with a total length 160-186 cm, and stomach contents were composed of fresh, intact prey parts (Table 7, Cipriano 1992).

Table 7 Summary of stomach content of dusky dolphins (n = 6) with fresh prey used to determine prey energy content and dusky dolphin foraging costs with and without calf. Squid species included: *Nototodoras sp., Moroteuthopsis sp., Teuthowenia sp.,* and unidentified squids. Percentage contribution of prey meal to dusky dolphin daily energetic needs were based on power output/energetic efficiency estimates of Hui (1987). All stomach content data and energy values are based on Cipriano (1992)

Specimen No.	Dusky Length (cm)	Dusky Weight (kg)	Gut state	Prey (Fresh and intact prey)			Estimated Energy Value (kj)	Estimated % of dusky dolphin daily energy requirements
				#Squid	#Myctophids	#Hoki		
85FC02	186	77	Full	3		7	14750	29.9 - 100.4
85FC03	180	75	Full	3		1	2900	5.9-19.7
86FC01	175	77.5	Full	1		5	10250	20.8-69.8
87FC01	175	77	Full	4	206	2	11580	23.5-78.8
88FC02	167	69	Full	10	2	4	12060	24.4-82.1
88FC03	160	71	Full	5		1	3650	7.4-24.9

Refers to number of prey items represented by intact squid, squid head, intact fish or Hoki skulls

Similar to dusky dolphins, Hawaiian spinner dolphins also feed at night on mesopelagic organisms, traveling about 8 km back and forth between near shore rest areas and offshore waters (Benoit-Bird and Au 2003). Like dusky dolphins, they dive to at least 150 m to feed on the rising DSL (Benoit-Bird and Au 2003). Dusky dolphins may feed solitarily on the ascending DSL in austral summer/fall and both solitarily or in small subgroups (5 individuals) in winter based on prey density (Benoit-Bird et al. 2004, Benoit-Bird et al. in press). Therefore based on Benoit-Bird (2004), I calculated *foraging cost = 0.15 kcal fixed search cost per prey + capture cost expressed as a percentage caloric content of each prey (assumed at 5%, 10% , 20% of each prey)*, with the assumption that dolphins will preferentially seek larger prey regardless of prey capture costs, but if they do seek smaller prey their foraging costs will significantly increase as they will need more prey to meet their maintenance requirements. Like Benoit-Bird (2004), I assume dusky dolphin 'search costs' to include searching, diving, and feeding on prey and to be independent of prey size. A 0.15 kcal fixed search costs is a low estimate and corresponds to about an 8% increase over the animal's maintenance energy needs during active foraging (discussed in Benoit-Bird 2004).

Since the exact prey size/length from stomach contents is not known, to calculate net value of prey, I used both the high and low estimate for total prey energy value (based on prey size) percentage contribution to DER of dusky dolphin (3,500 kcal) (see Table 7). The average of percentage prey energy contribution was used to determine how much more dolphins have to eat to meet a DER of 3,500 kcal/day. The total foraging cost was then doubled for mother with calf, assuming a 100% increase in energy costs (Reid et al. 1994, Kastelein et al. 2002).

In addition to foraging costs, I estimated locomotor (swimming) costs for dusky dolphins in the presence/absence of killer whales, by incorporating dusky dolphin behavior and movement rules. Specifically, I calculated dusky dolphin travel costs in the absence of killer whales, and travel plus flee costs during high (0.5 day KW return) and low (3 day KW return) presence of killer whales.

Cost of Transport (COT) is typically defined as the metabolic costs of moving one unit mass one unit distance (Schmidt-Nielsen 1972). $COT_{TOTAL} = LC + MC$ (Williams 2002), LC is Locomotor Costs or energy expended by animals when swimming, analogous to COT_{NET} (Schmidt-Nielsen 1972) for running mammals, and MC refers to maintenance costs for animals in a resting state. Since I was interested in calculating LC, I used Rosen and Trites (2002) allometric equation $LC = 1.651M^{1.01}$, where M is mass in kg and the absolute energy costs is measured in joules/m. The exponent in the equation suggests that cost of swimming is proportional to body mass. The equation is suitable for determining locomotor costs in bioenergetic models for animals with limited empirical data (Rosen and Trites 2002). For consistency, all units were converted into kcal/day in the calculations.

Using time/distance budgets from the simulated model from treatments C-RKW, C-R-NOKW (baseline), NC-RKW and NC-R-NOKW (baseline) and based on speed parameters specified in Table 6, I estimated total bioenergetic costs for a dusky dolphin with and without predators as *Foraging costs (FC) + LC for (Travel) or FC + LC (Travel)+LC (Flee).*

Results

In general, time and distance budgets for with calf treatments are significantly different than without calf treatments for Distance (Total, Travel, Rest, and Flee) and Time (Rest, Travel, Flee, and Hide) [t-tests, $p < 0.0001$, Table 8], but insignificant for Distance and Time Search [$p > 0.05$, Table 8]. Dusky dolphins in general travel more and rest less during increased threat from killer whales (Figs. 18 and 19).

ANOVA and post-hoc Bonferroni tests between the 8 treatments at both levels of killer whale return rates confirm graphical trends in Figs. 19 and 20. Overall, total distance covered is different for with calf (C-R-NOKW & C-R-KW) than without calf treatments (NC-R-NOKW & NC-R-KW) for the 3 day KW return period. (Post-hoc Bonferroni tests, $p > 0.05$). Whereas, with a higher KW presence, all 4 treatments were significantly different (Post-hoc Bonferroni tests, $p < 0.0001$).

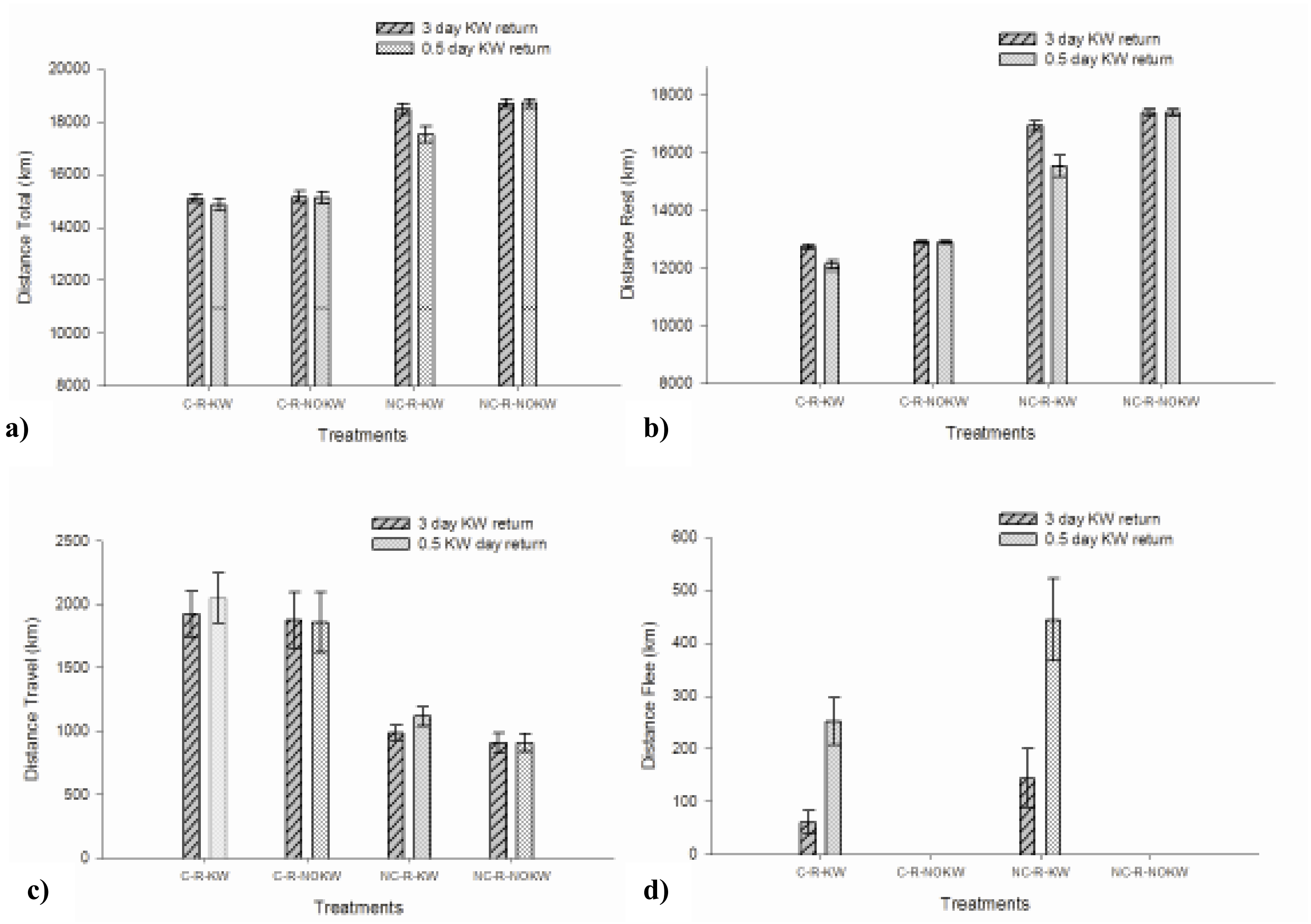

FIG. 19 Distance budgets (a-d) for dusky dolphins during low (3 day KW return) and high (0.5 day KW return) killer whale presence. Treatment acronyms indicate whether the dusky dolphin has calf (C) or no calf (NC), and whether killer whales (KW) are present or absent from the system of interest off Kaikoura. All model runs involve behavioral and movement rules (R).

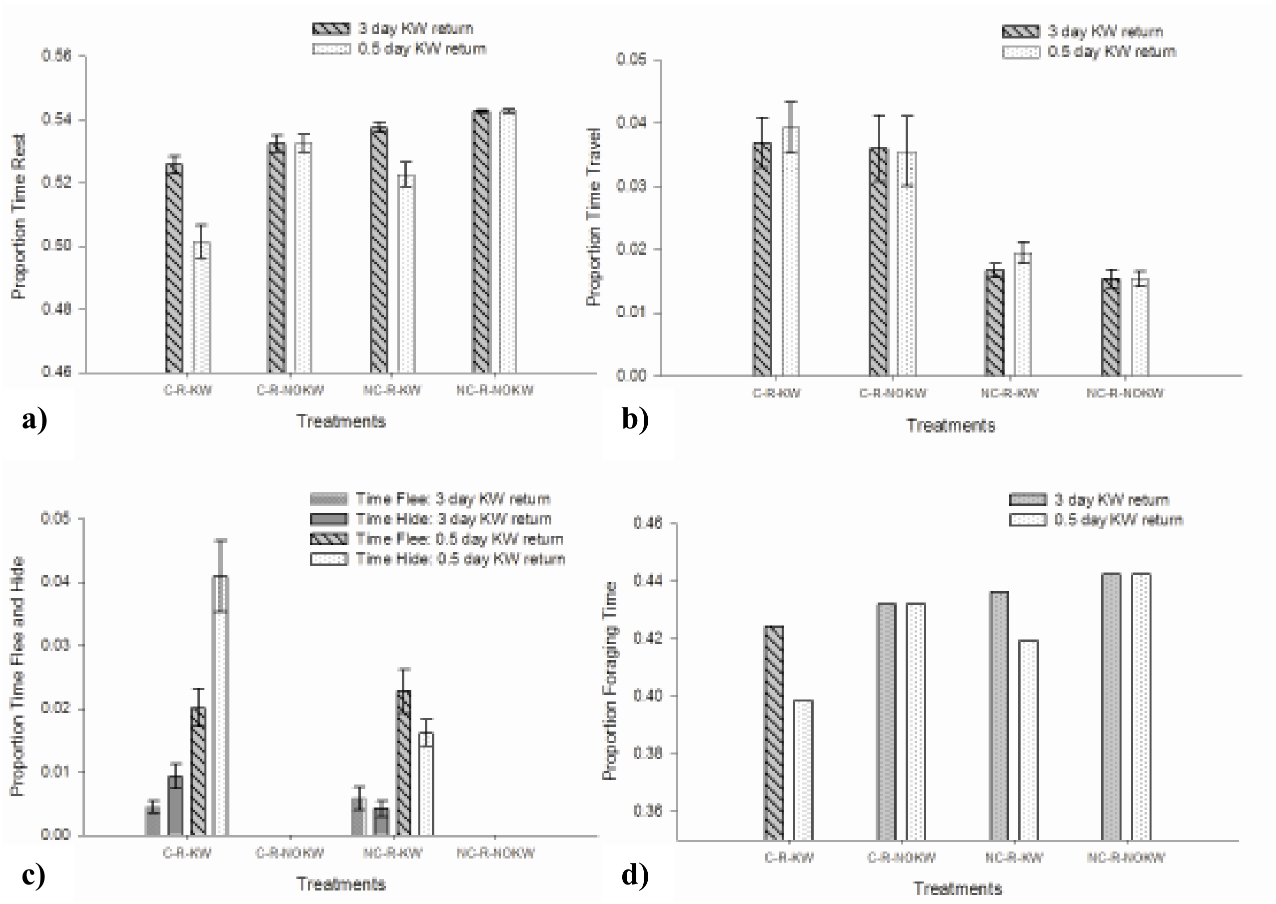

FIG. 20 Time budgets (a-d) for dusky dolphins during low (3 day KW return) and high (0.5 day KW return) killer whale presence, n = 35 reps. Treatment acronyms indicate whether the dusky dolphin has calf (C) or no calf (NC), and whether killer whales (KW) are present or absent from the system of interest off Kaikoura. All model runs involve behavioral and movement rules (R). Time is displayed as a proportion of time spent on an activity and is calculated as simulated time (variable)/ (length of simulation i.e., 210 x 24 x 16 or 80,640) (Nov-May).

Table 8 Independent sample t-tests for distance and time budget variables obtained from model simulations

	t	df	Sig. (2-tailed)
Distance Total	66.589	194.29	0.000
Distance Rest	57.266	183.74	0.000
Distance Travel	-45.375	205.43	0.000
Distance Flee	3.767	219.82	0.000
Distance Search	-0.876	278.00	0.382
Encounter Index	3.805	216.50	0.000
Time Rest	-3.633	162.29	0.000
Time Travel	-42.915	235.05	0.000
Time Feed	-6.074	140.84	0.000
Time Search	-6.421	168.61	0.000
Time Flee	2.796	202.75	0.006
Time Hide	-3.615	195.25	0.000

For Distance Travel, NC-R-KW was significantly different than NC-R-NOKW for both high and low killer whale presence (Post-hoc Bonferroni tests, $p < 0.0001$), whereas there were no significant differences between C-R-KW and C-R-NOKW at both levels of killer whale presence (Post-hoc Bonferroni tests, $p > 0.05$). However, distance Rest was significantly different for dusky with and without calf at both levels of predation risk (Post-hoc Bonferroni tests, $p < 0.05$).

For treatments C- R-KW and NC-R-KW, based on the parameters specified (Table 6) and as expected, distance traveled for a dusky dolphin with calf was more than one without (Fig. 19). These distances were larger (~ 100 km) for both dolphin types when killer whales were present at higher levels. I penalized the mother with calf by reducing her mean travel speed (6 km/hr, instead of 8 km/hr). Recent evidence from captive bottlenose dolphins (Noren 2008) suggests that mother can be speed and energy handicapped when dragging a calf in her slipstream or echelon position. In the model, I taxed her on the mean speed rather than energy she spends. Thus, her travel time also increases (Fig.20).

Fleeing distance for a female with calf upon detecting a killer whale is less than that of a dolphin without a calf, reflecting the proximity of female with calf to shallow water environments. I did not change her flee speed as mothers with calf are capable of attaining these speeds and higher (Weihs 2004). Instead, I penalize her with higher hiding costs in the refuge, i.e. memory of 3 hours instead of 1 hour (Table 6). The distances estimated are realistic based on the mean speed and simulation period considered.

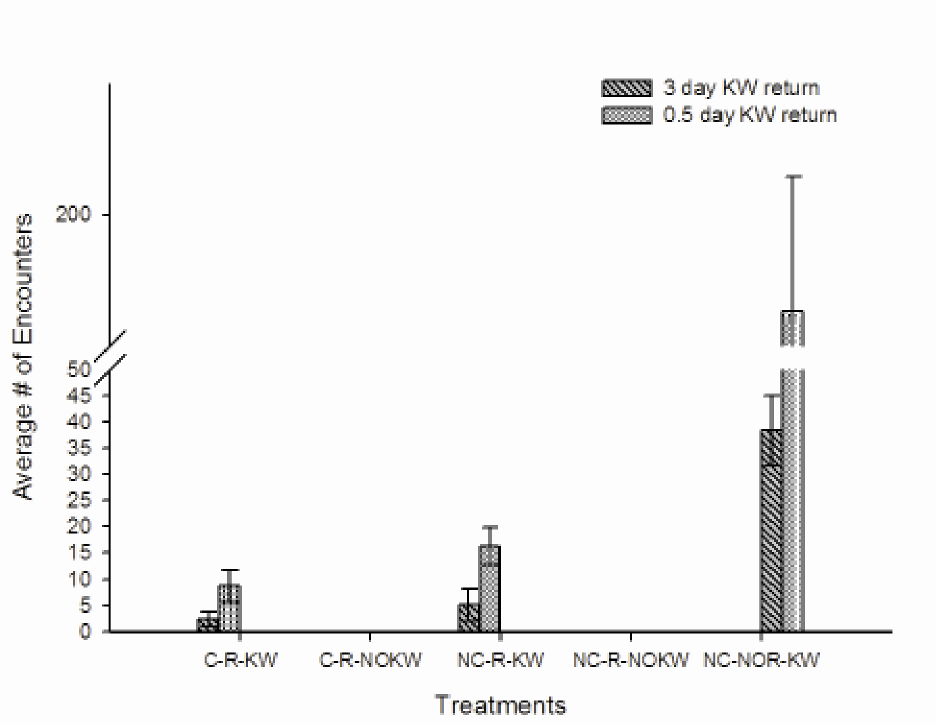

FIG. 21 Average number of encounters accumulated by a dusky dolphin with a calf (C) and without (NC) during low (3 day KW return) and high (0.5 day KW return) presence of killer whales (KW) in the system of interest off Kaikoura. All (R) movement and behavioral rules were operational during model simulations.

Short-term ecological (time/distance) costs incurred by females with calf relative to adults without calf seem justified when encounter rates are considered (Fig. 21). Females with calf have fewer encounters relative to adults without calf. The encounter rate measured here is comparable to real time observations of scarring in dusky dolphins by social type (Chapter II). Though scarring rate among all dusky dolphin social groups was minimal, nursery groups had << 1 % scars relative to other adult groups (Chapter

II). Dusky dolphins are small dolphins (< 2 m) and therefore may be consumed by the larger killer whale, leaving no evidence of potential attacks by killer whales.

Bioenergetics of scared prey

Dusky dolphins spend approximately 629-1,502 kcal/ day (with calf) and 310-747 kcal/day (without calf) considering a 5 % prey capture cost of prey in foraging and travel costs in the absence of killer whales, based on high and low prey energy value estimates (Table 9). This number rises to approximately 1,683-5,035 kcal/day (with calf) and 837-2,500 kcal/day (without calf) at a 20% capture cost (i.e. 20% of prey energy value is lost in capture) (Table 9). The values are not significantly higher from low or high presence of killer whales for dusky with calf, but increase to about 90 kcal/day for an adult without calf. For a mother with calf, regardless of killer whale presence levels, the expense is not much higher due to fleeing. In essence, her maximum expense is sustained during traveling, which is twice that of an adult without calf.

The energy expense incurred in the absence of killer whales still represents a cost for the animals, as it reflects their anti-predator choice of traveling between near shore and offshore waters.

Based on foraging times calculated in the absence of killer whales (NC-R-NOKW and C-R-NOKW) approximating 10.6 hours over a 210 day period (Nov-May), average foraging rate is estimated at 330 kcal / hour for adult dusky dolphins without calf, and about 675 kcal/ hour for females with calf, assuming a DER of 3,500 kcal/day and 7,000 kcal/day respectively. These feeding rates and foraging times calculated in the absence of killer whales were used to determine lost foraging time due to low/high presence of killer whales.

I estimate that foraging calories lost due to increased killer whale presence are almost 5 times more for mother with than without calf. However, under conditions of low predation risk (3 day KW return), for a dusky dolphin with calf, foraging calories lost is about 129 kcal/day while a dolphin without a calf loses only 50 kcal/day (Table 9). Feeding rates and duration will vary considerably based on dolphin feeding rates driven by hunger, number of dolphins feeding, DSL density, and the fact that dolphins may consume far more than their energy needs (Kastelein et al. 2002).

Prior to using baseline values for model simulations, I conducted a sensitivity analysis of parameter values and combinations to address parametric uncertainty (Chapter III). Here, I summarize sensitivity analysis results comparing with/without calf treatments (n = 40) with an emphasis on killer whale return times, memory of dusky dolphin in refuge, and dusky dolphin detection distance of killer whales. Parameter combinations and levels used in the analysis are shown in Table 10.

Table 9 Bioenergetic summary for dusky dolphins facing high (0.5 day KW return) and low (3 day KW return) predation risk levels, and in the absence of killer whales (KW) but with dusky dolphin anti-predator behavioral and movement rules. Summary of foraging and locomotor costs for dusky dolphins with and without calf are shown below, where Foraging costs = 0.15 kcal fixed search cost per prey + capture cost expressed as a percentage caloric content of prey (assumed at 5%, 10%, 20%) based on Benoit-Bird 2004 and dusky dolphin stomach content data from Cipriano (1992) (Table 7), Locomotor costs (LC, joules/m) = 1.651M$^{1.01}$, where M = body mass in kg (from Rosen and Trites 2002)

Foraging Costs (FC)				
Prey capture costs	**5%**	**10%**	**20%**	
Average # of prey items based on dusky dolphin full gut contents (n = 6 dolphin specimens)	42.3			
Fixed search cost	0.15			kcal
Low prey energy value contribution to DER (Table 7)				
Dolphins have to feed x times to be full based on low percentage prey energy value contribution to DER, where x =	5.36			
Total estimated foraging cost for an adult dolphin	622.805	1211.601	2389.193	kcal/day
Total estimated foraging cost for a lactating mom with a calf with a DER of 7,000 kcal/day	1245.610	2423.202	4778.386	kcal/day
High prey energy value contribution to DER (Table 7)				
Dolphins have to feed x times to be full based on high percentage prey energy value of DER of 3,500 kcal/day, where x =	1.6			
Total estimated foraging cost for an adult dolphin	185.912	361.672	713.192	kcal/day
Total estimated foraging cost for a lactating mom with a calf with a DER of 7,000 kcal/day	371.824	723.344	1426.384	kcal/day
Locomotor Costs (LC): Killer whales absent				
LC mom with calf (Travel costs)	257.205	kcal/day		
LC for adult dusky (Travel costs)	124.532	kcal/day		

Table 9 continued

Total Estimated Energetic Costs = FC + LC				
Prey capture costs	**5%**	**10%**	**20%**	
Low prey energy value contribution to DER (from Table 3)				
Absence of killer whales but with dusky dolphin behavioral and movement rules				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel)	1502.816	2680.408	5035.592	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel)	747.337	1336.133	2513.725	kcal/day
Presence of killer whales and with dusky dolphin behavioral and movement rules (3 day KW return)				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel) + LC (Flee)	1517.871	2695.463	5050.647	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel) + LC (Flee)	777.702	1366.498	2544.090	kcal/day
Presence of killer whales and with dusky dolphin behavioral and movement rules (0.5 day KW return)				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel) + LC (Flee)	1561.381	2738.973	5094.157	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel) + LC (Flee)	837.039	1425.835	2603.427	kcal/day
High prey energy value contribution to DER (from Table 7)				
Absence of killer whales but with dusky dolphin behavioral and movement rules				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel)	629.029	980.549	1683.589	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel)	310.444	486.204	837.724	kcal/day
Presence of killer whales and with dusky dolphin behavioral and movement rules (3 day KW return)				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel) + LC (Flee)	644.085	995.605	1698.645	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel) + LC (Flee)	340.809	516.569	868.089	kcal/day
Presence of killer whales and with dusky dolphin behavioral and movement rules (0.5 day KW return)				
Energy Expense for adult lactating dusky dolphin with calf : (FC) + LC(Travel) + LC (Flee)	687.594	1039.114	1742.154	kcal/day
Energy Expense for adult dusky dolphin: (FC) + LC (Travel) + LC (Flee)	400.145	575.905	927.425	kcal/day

Table 9 continued

Foraging calories lost in low-high killer whale presence		
Presence of killer whales and with dusky dolphin behavioral and movement rules (3 day KW return)		
Foraging calories lost by a dusky dolphin with calf	128.988	kcal/day
Foraging calories lost by a dusky dolphin without calf	49.979	kcal/day
Presence of killer whales and with dusky dolphin behavioral and movement rules (0.5 day KW return)		
Foraging calories lost by a dusky dolphin with calf	543.661	kcal/day
Foraging calories lost by a dusky dolphin without calf	182.351	kcal/day

Note: Foraging calories lost during high and low presence of killer whales. Values are calculated based on dusky dolphin with and without calf feeding rates of 330 kcal/hour and 675 kcal/hour, respectively. Daily energetic requirement (DER) is assumed at 3,500 kcal/day (without calf) and 7,000 kcal/day (with calf) with dusky dolphins foraging throughout duration of DSL availability over a 210 day period (Nov-May).

Table 10 Parameters used in 40 different combinations for model sensitivity analysis to look at effect on dusky dolphin time/distance budgets and encounter index. Total treatments n = 40 (with calf = 20 and without calf = 20 treatments). KW = Killer whale. Each treatment was run for 5 reps. Note: For each dolphin detection distance value both values of memory in refuge were tested for with and without calf treatments. [Memory in refuge = memory after killer whale attack]

Variables	Values
Dolphin detection distance (km)	5, 10
KW detection distance (km)	6
KW return time (days)	0.5, 1, 2, 3, 7
KW memory after dolphin escape (hr)	1
Dolphin memory in refuge (hr)	1, 3 (without calf); 3, 5 (with calf)
KW wait time (hr)	1

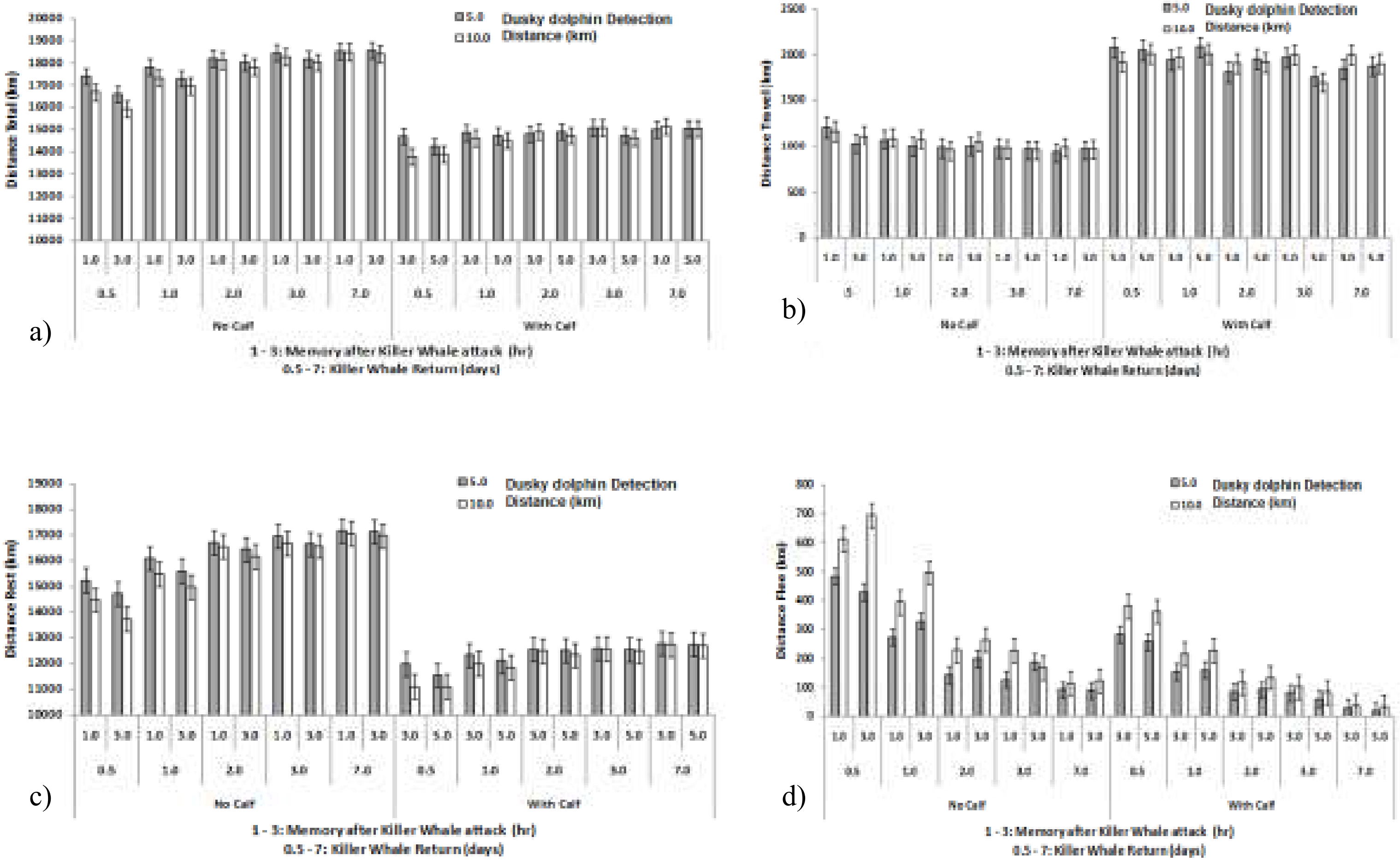

FIG. 22 Distance budgets (a-d) resulting from different parameter combinations (Table 10) in model simulation for with and without calf treatments (n = 40, 5 reps) over a 210 day period (Nov-May).

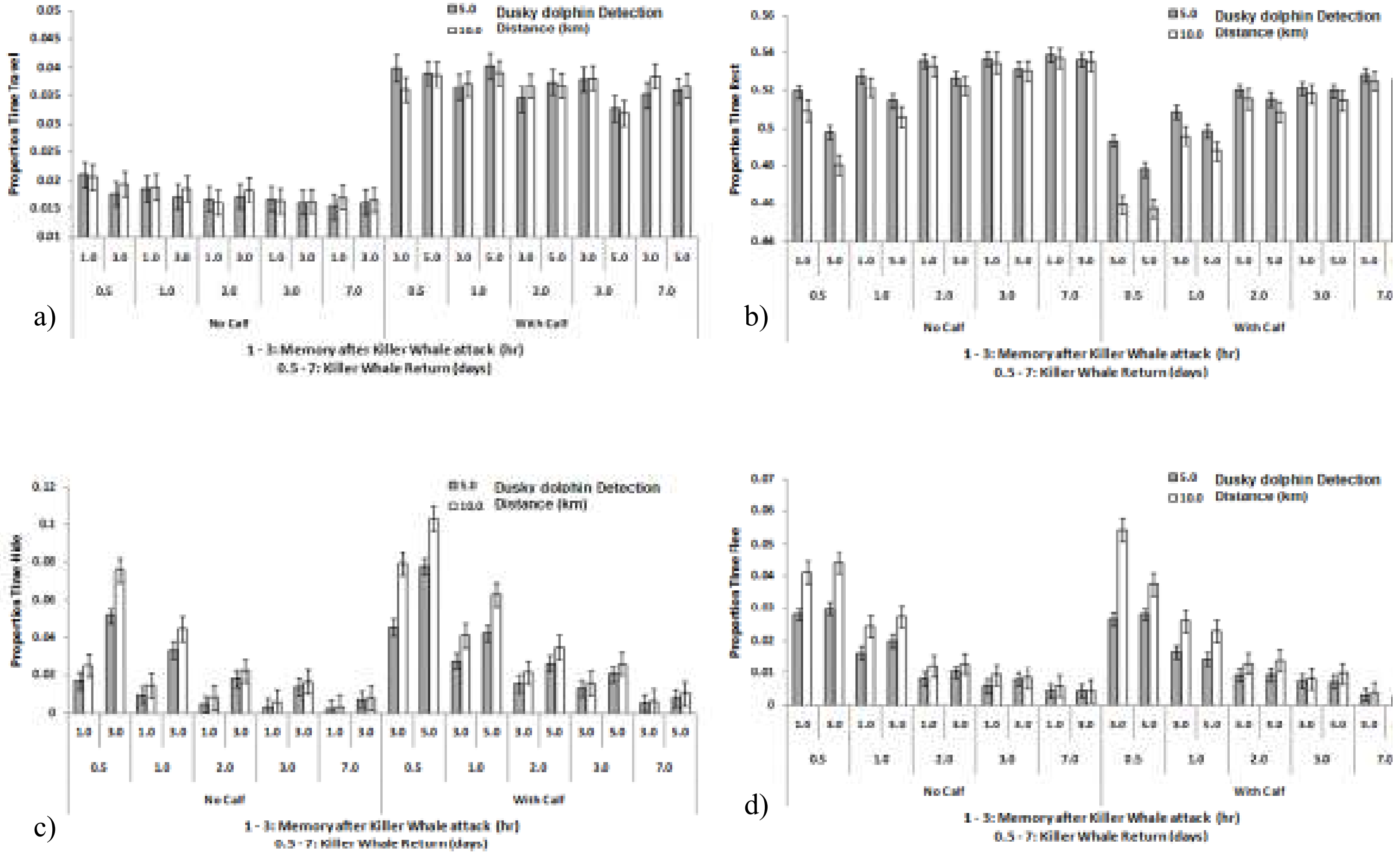

FIG. 23 Time budgets based on different parameter combinations (Table 10) in model simulation for with and without calf treatments (n = 40, 5 reps) over a 210 day period (Nov-May).

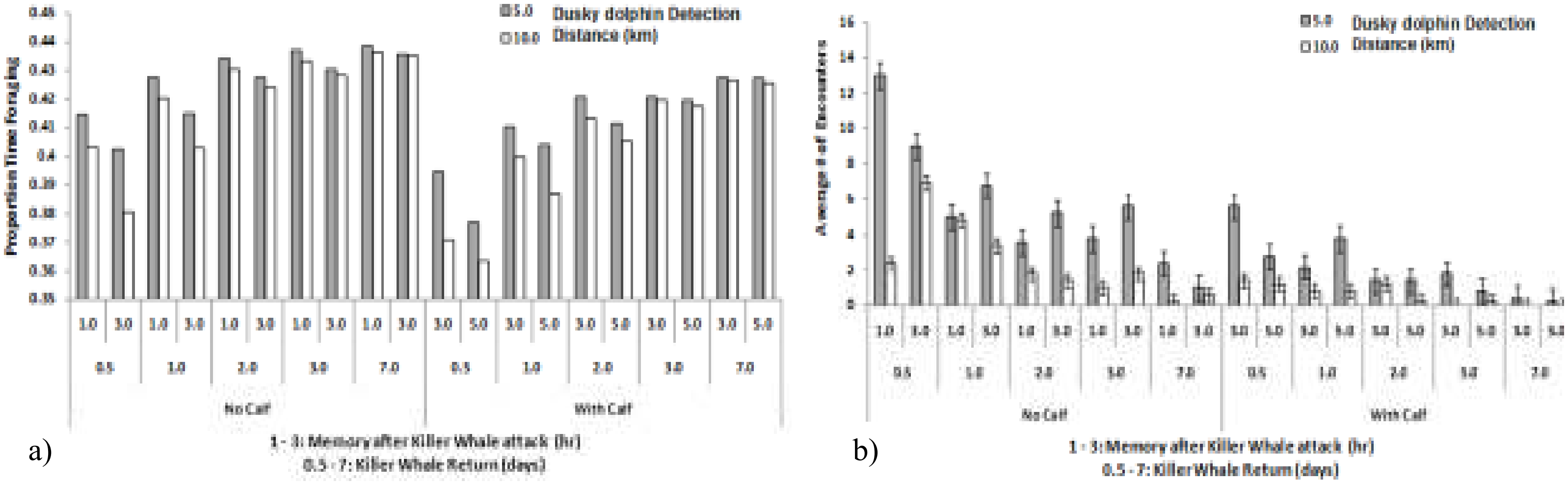

FIG. 24 Proportion foraging time and encounter index for dusky dolphins based on different parameter combinations (Table 10) in model simulation for with and without calf treatments (n = 40, 5 reps) over a 210 day period (Nov-May).

The graphs reveal sensitivity to changing killer whale return rates, particularly to higher killer whale presence (0.5 days) (Figs. 22, 23, 24). Independent sample t-tests for with and without calf treatments were found to be significantly different ($p < 0.0001$) for all variables considered Distance (Total, Travel, Rest, Flee) and Time (Rest, Travel, Hide), except for Distance and Time Search, and Time Flee (t-tests, $p > 0.05$). Distance/Time Search variables are insignificant as dolphins as there is little competition for food resources and food is abundant.

GLM MANOVA for with calf ($n = 20$) and without calf ($n = 20$) treatments were performed to assess the influence of Killer whale return times, dolphin memory in refuge, and detection distance of dusky dolphins on Distance and Time dependent variables. Results suggest that KW return times have the strongest influence on all time/distance variables considered (Table 11a, b), particularly for without calf treatments (also supported by Wilks Lambda multivariate tests for distance budgets, where Wilks lambda value = 0.066, $F = 21.1$, $df = 16$, $p < 0.0001$, relative to detection distance and memory in refuge). KW return in separate combinations with dolphin detection distance and memory in refuge also produce significant results for without calf treatments. Other interaction terms are not significant, also reflected in the test power (Table 11 a, b). For with calf treatments (Table 12a, b), killer whale return times still have the strongest effect on time/distance budgets relative to all other interaction terms (Wilks Lamda, multivariate tests for distance budgets, Wilks Lamda = 0.02, $F = 33.9$, $df = 16$, $p < 0.0001$), though time/distance travel do not appear to be as strongly affected by KW return relative to without calf treatments (Table 12 a, b).

Table 11 GLM MANOVA results for effect of parameter changes on a)distance budgets and b) time budgets without calf treatments (n = 20). See Table 10 for parameter combinations used in model simulations.

a) Distance budgets (without calf treatments)

Source	Dependent Variable	df	F	Sig.	Observed Power
Memory in refuge	DTot	1	49.796	0.000	1.0
	DLoaf	1	37.495	0.000	1.0
	DTravel	1	1.725	0.193	0.3
	DFlee	1	2.994	0.087	0.4
KWReturn	DTot	4	196.438	0.000	1.0
	DLoaf	4	263.880	0.000	1.0
	DTravel	4	20.096	0.000	1.0
	DFlee	4	122.870	0.000	1.0
Dolphin detection distance	DTot	1	35.211	0.000	1.0
	DLoaf	1	51.614	0.000	1.0
	DTravel	1	2.696	0.105	0.4
	DFlee	1	40.037	0.000	1.0
Memory in refuge * KWReturn	DTot	4	7.219	0.000	1.0
	DLoaf	4	3.677	0.008	0.9
	DTravel	4	4.254	0.004	0.9
	DFlee	4	1.366	0.253	0.4
KWReturn * Dolphin detection distance	DTot	4	5.606	0.000	1.0
	DLoaf	4	6.910	0.000	1.0
	DTravel	4	0.223	0.925	0.1
	DFlee	4	5.469	0.001	1.0
Memory in refuge * Dolphin detection distance	DTot	1	0.035	0.853	0.1
	DLoaf	1	0.089	0.766	0.1
	DTravel	1	3.288	0.074	0.4
	DFlee	1	0.018	0.893	0.1
Memory in refuge * KWReturn * Dolphin detection distance	DTot	4	0.254	0.906	0.1
	DLoaf	4	0.273	0.895	0.1
	DTravel	4	1.468	0.220	0.4
	DFlee	4	1.861	0.125	0.5

Table 11 continued. b) Time budgets (without calf treatments)

Source	Dependent Variable	df	F	Sig.	Observed Power
Memory in refuge	TRest	1	201.720	0.000	1.0
	TTravel	1	1.273	0.263	0.2
	TFeed	1	120.496	0.000	1.0
	THide	1	765.515	0.000	1.0
KWReturn	TRest	4	256.833	0.000	1.0
	TTravel	4	17.196	0.000	1.0
	TFeed	4	261.369	0.000	1.0
	THide	4	356.654	0.000	1.0
Dolphin detection distance	TRest	1	48.907	0.000	1.0
	TTravel	1	4.158	0.045	0.5
	TFeed	1	67.653	0.000	1.0
	THide	1	80.222	0.000	1.0
Memory in refuge * KWReturn	TRest	4	25.748	0.000	1.0
	TTravel	4	3.894	0.006	0.9
	TFeed	4	10.519	0.000	1.0
	THide	4	92.170	0.000	1.0
KWReturn * Dolphin detection distance	TRest	4	8.821	0.000	1.0
	TTravel	4	0.111	0.978	0.1
	TFeed	4	10.094	0.000	1.0
	THide	4	15.639	0.000	1.0
Memory in refuge * Dolphin detection distance	TRest	1	1.621	0.207	0.2
	TTravel	1	2.606	0.110	0.4
	TFeed	1	1.988	0.162	0.3
	THide	1	10.094	0.002	0.9
Memory in refuge * KWReturn * Dolphin detection distance	TRest	4	1.225	0.307	0.4
	TTravel	4	1.457	0.223	0.4
	TFeed	4	3.083	0.021	0.8
	THide	4	4.468	0.003	0.9

Table 12 GLM MANOVA results for effect of parameter changes on a) distance budgets and b) time budgets with calf treatments (n = 20). See Table 10 for parameter combinations used in model simulations.

a) Distance budgets (with calf treatments)

Source	Dependent Variable	df	F	Sig.	Observed Power
KWReturn	DTot	4	30.781	0.000	1.0
	DRest	4	225.671	0.000	1.0
	DTravel	4	2.578	0.044	0.7
	DFlee	4	278.505	0.000	1.0
Memory in refuge	DTot	1	8.441	0.005	0.8
	DRest	1	18.289	0.000	1.0
	DTravel	1	0.457	0.501	0.1
	DFlee	1	0.208	0.650	0.1
Dolphin detection distance	DTot	1	11.299	0.001	0.9
	DRest	1	65.024	0.000	1.0
	DTravel	1	0.083	0.775	0.1
	DFlee	1	66.370	0.000	1.0
KWReturn* Memory in refuge	DTot	4	0.948	0.441	0.3
	DRest	4	0.981	0.423	0.3
	DTravel	4	2.249	0.071	0.6
	DFlee	4	1.245	0.298	0.4
KWReturn * Dolphin detection distance	DTot	4	3.910	0.006	0.9
	DRest	4	12.394	0.000	1.0
	DTravel	4	0.315	0.867	0.1
	DFlee	4	6.252	0.000	1.0
Memory in refuge * Dolphin detection distance	DTot	1	0.390	0.534	0.1
	DRest	1	0.993	0.322	0.2
	DTravel	1	0.005	0.946	0.1
	DFlee	1	0.448	0.505	0.1
KWReturn * Memory in refuge * Dolphin detection distance	DTot	4	1.534	0.200	0.5
	DRest	4	2.373	0.059	0.7
	DTravel	4	0.775	0.545	0.2
	DFlee	4	0.122	0.974	0.1

Table 12 continued. b) Time budgets (with calf treatments)

Source	Dependent Variable	df	F	Sig.	Observed Power
KWReturn	TTravel	4	2.5	0.050	0.7
	TFeed	4	326.0	0.000	1.0
	THide	4	457.4	0.000	1.0
Memory in refuge	TRest	1	24.5	0.000	1.0
	TTravel	1	0.3	0.580	0.1
	TFeed	1	42.7	0.000	1.0
	THide	1	165.9	0.000	1.0
Dolphin detection distance	TRest	1	81.8	0.000	1.0
	TTravel	1	0.1	0.793	0.1
	TFeed	1	85.0	0.000	1.0
	THide	1	118.7	0.000	1.0
KWReturn* Memory in refuge	TRest	4	1.3	0.269	0.4
	TTravel	4	2.8	0.032	0.7
	TFeed	4	7.5	0.000	1.0
	THide	4	12.7	0.000	1.0
KWReturn * Dolphin detection distance	TRest	4	14.5	0.000	1.0
	TTravel	4	0.3	0.875	0.1
	TFeed	4	13.4	0.000	1.0
	THide	4	19.5	0.000	1.0
Memory in refuge * Dolphin detection distance	TRest	1	0.6	0.455	0.1
	TTravel	1	0.1	0.733	0.1
	TFeed	1	0.2	0.638	0.1
	THide	1	0.3	0.604	0.1
KWReturn * Memory in refuge * Dolphin detection distance	TRest	4	1.6	0.195	0.5
	TTravel	4	0.9	0.470	0.3
	TFeed	4	2.6	0.039	0.7
	THide	4	1.3	0.290	0.4

Discussion

Model simulation results and predicted energetic costs suggest the importance of considering indirect predation risk effects in bioenergetic models. A mother with calf has a higher price to pay by making short and long-term anti-predator choices in terms of greater distance traveled, less time to rest, higher foraging costs, and foraging calories lost due to perceived killer whale threats. However, they have fewer encounters with killer whales and flee shorter distances relative to an adult dusky for the same time period simulated. The distinction between the costs incurred and the benefits gained for dusky dolphins are clearly represented by the encounter index. Higher killer whale presence leads to more frequent encounters for adult *vs.* a mother with calf. When all anti-predator rules are switched off, the encounter index rises sharply to 10 times the encounters expected when rules operate. Therefore, it makes evolutionary sense to adopt anti-predator mechanisms and pay short-term ecological costs rather than become an unsuspecting prey to a powerful predator. Seeking shallower waters may allow them to escape a potential killer whale attack rather than preventing an encounter with killer whales (Verdolin 2006).

Quantifying ecological costs in terms of bioenergetics, reveal that dusky dolphins pay a minimal price in travel costs but have higher foraging costs — a function of dolphin prey energy values and foraging time. Proximity to deep food-laden waters allows foraging dusky dolphins to make shorter near shore-offshore trips. However, when considered in terms of foraging calories lost in the presence of killer whales, the foraging calories lost are 5 times more with increased killer whale presence. In fact, with a 10 km dusky dolphin detection distance and a 0.5 day killer whale return rate, total foraging time available for a dusky dolphin is reduced by > 10% over the 210-day simulated period. Further, nursery groups are likely paying a higher price due to physiological and maternal constraints, as well as due to safety options they may choose.

I do not cover the full range of bioenergetic consequences due to changes in food distribution/abundance, dusky dolphin group size variations, hunger and satiation requirements, and the propensity for dusky dolphins to consume food higher than their energetic requirements. Inclusion of these factors can produce variable results on the predicted bioenergetic costs from avoiding predators. For example, the foraging time used here is conservative, and in reality will differ due to: a) more dolphins feeding on a patch, thus increasing the need to search for rich patches through the night, b) lunar phase changes affecting the timing of the vertical migration of prey. In fact, dolphins could lose almost 2 hours of foraging time due to the delayed rising of the vertical layer and earlier downward migration during full moon periods (Benoit-Bird et al. in press), c) increased flight distance/hiding time post-killer whale encounter/detection preventing or delaying dolphin resumption of normal activity.

In the model, killer whales are simulated to enter the system day or night. So, while longer daylight hours available in austral summer/fall may favor day hunting, marine mammal seeking killer whales may hunt at night as well (Volker Deecke, personal communication, Newman and Springer 2007). If interrupted by potential threats, feeding dusky dolphins may have to increase feeding rates (Houston et al. 1993, Lima and Bedenkoff 2002), or become unsuspecting prey to killer whale attacks, if prey vigilance is reduced dictated by their hunger/energy states (McNamara and Houston 1990). On the other hand, if dusky dolphins detect killer whales, escape to a refuge and stay for an indeterminate time, they could lose valuable foraging time. Dusky dolphins on occasions have been observed to stay in shallow refuges for ~ 4 hours (Cipriano 1992), but the timing could vary based on threat levels (Lima 1998).

In the model, both social classes of dusky dolphins resume feeding after a memory lapse. However, to my knowledge, we know little about post-encounter refuge emergence times and resumption of normal activity for most prey species, including about differences by age/sex groupings (but see Sih 1992, Lima 1998 for reviews).

Nursery groups may choose safety over traveling offshore to feed or returning to feed when under threat. Off Kaikoura, when killer whales are sighted in the area, it often becomes difficult to observe nursery groups for several hours (Weir 2007, Chapter II). It is unclear whether nursery groups avoid costs of fleeing due to incompatible speeds with attacking killer whales (Chapter II), or the stress of potential separation from calf, by seeking refuge sooner or leaving the area? Perhaps it is both. Considering the DER of a lactating mother and locomotion costs, this may prove further expensive with consecutive days of killer whale presence and no feeding opportunities.

From theoretical perspectives, the model provides a testable tool on prey and predator detection distances, group vigilance and flight initiation distance (FID) as it relates to group size, species behavior, and risk level. Future investigation of these aspects may identify quantifiable consequences for prey investing in anti-predator mechanisms.

Currently, dolphins initiate flight within a time step. This could be varied to determine prey decisions to flee depending on risk level and predator motivation. Results from model simulations suggest that dusky with calf flee less distance relative to dusky without a calf. This may reflect the proximity of nursery groups being found in very shallow water (< 20 m), and therefore are closer to a refuge, whereas adult groups are found further from shore (< 200 m) during peak killer whale season. In the model, if a killer whale is in the way of a fleeing dusky dolphin, the dolphin maximizes distance to avoid the predator and takes a lengthier track to a shallow water refuge, instead of taking the shortest, straightest path, this adds to distance fled. I do not know whether this route of travel represents what duskies actually do, and data are needed.

The dusky dolphin system off Kaikoura could represent a prey with 'imperfect predator information' (see Fig. 5 in Brown et al. 1999). Predator presence though variable and unpredictable, can prove to be quite lethal for unsuspecting or 'ignorant prey' (Brown et al. 1999), as evidenced for the treatment without dusky dolphin anti-predator rules but with high/low killer whale presence. Thus, dusky dolphins maintain a background level of apprehension that is much higher for mothers with calves routinely displayed by their depth choices during high predation risk and social affiliations. But following the entry of a predator into the system, the anti-predator response is heightened and the curve rises gradually with increasing risk, but is predicted to be much steeper for a mother with calf.

Predation pressures off Kaikoura are highly variable from day to day and between years, yet dusky dolphins appear to follow a fixed response of choosing shallow waters during peak season over a 13-year period. This is not atypical, as evidenced in other prey studies (Sih 1987).

The choice of anti-predator strategy may vary by social groupings and the nature of immediate risk, but the responses are consistent over time. Long-term observations of dusky dolphins off Kaikoura (Chapter II) and model simulation results indicate that dusky dolphin strategies and tactics are effective against an unpredictable but powerful predator. This may well change if killer whale presence increases, as reflected in the current simulation studies.

As far as predator perspectives are concerned, we still lack sufficient knowledge about killer whale prey preference, motivation, and behavioral strategies that may enable them to be effective hunters when targeting difficult prey such as dolphins (Jefferson et al. 1991). Elucidation of these variables will enhance our understanding of clever predator tactics as they stalk behaviorally responsive prey (Lima et al. 2003).

In subsequent models, it is possible to include specific energetic considerations such as dusky dolphin hunger, DSL density, feeding rates, variable group size, as well as killer whale energetic requirements, motivation, prey search and handling to improve bioenergetic estimates and possible influence on dolphin population dynamics.

Recent articles (Schmitz et al. 2008, Peckarsky et al., 2008, Orrock et al., 2008 in Vol. 89, Issue 9 of *Ecology*) provide credible evidence on the nature and effects of non-consumptive effects (NCE) of predation risk in different systems and ecological communities. However, for most marine mammal species, studies continue to focus on lethal or consumptive predation (e.g. Trites 2002, Williams et al. 2004). Recent marine mammal articles (Springer et al. 2003, 2008, Wade et al. 2007, Steiger et al. 2008) have debated killer whale lethal effects on historic great whale and pinniped (sea lions, seals, and fur seal) populations, without analyzing sub-lethal effects on behavioral ecology of killer whale marine mammal prey, which may be more consequential.

Other studies by Heithaus and Dill (2002, 2006), Frid et al. (2006, 2007), Wirsing et al. (2007) on dolphins and other marine mammals, have shown that marine mammals, like other prey (Lima 1998), make important foraging and habitat use decisions borne out of fear. Future research on costs *vs.* benefits of marine mammal anti-predator mechanisms could greatly expand our understanding of direct and indirect effects of predation risk on population dynamics, bioenergetics, demographics, and ecological communities. Such knowledge would provide invaluable resources for managing critical marine mammal populations and habitats.

CHAPTER V

SUMMARY

I reviewed potential predator threats for dusky dolphins in the Kaikoura New Zealand area, and provided evidence that killer whales are the dominant threat, with little effect from deep water sharks. Killer whale sightings off Kaikoura appear to be strongly directly and spatially correlated with dusky dolphin preference for near shore shallow waters, regardless of social affiliation i.e. mixed age/sex, adult, or nursery groups (mothers with calves). Based on both systematic and opportunistic tour boat data, this trend is stable over a 13-year period. Killer whale and dusky dolphin density of occurrence show a 73% positive correlation (CRH modified t-test) in the Kaikoura area, as determined from long-term dolphin tour boat data (*Dolphin Encounter* 1995-2007). Also, killer whale and dusky dolphin sightings during the same time period and for the same dataset show significant spatial cross-correlation (cross Mantel tests, $p < 0.001$), suggesting that killer whale and dusky dolphin sightings may be interdependent (Chapter II).

Killer whale presence in Kaikoura waters is unpredictable, and attacks on dusky dolphins are rarely witnessed (Constantine et al. 1998). However, regardless of predation pressures, dusky dolphins appear to rely on consistent long-term stable strategies of choosing near shore waters during peak killer whale season (Nov-Apr) (Chapter II).

Peak killer whale season also coincides with reduced food availability governed by photoperiod changes and the presence of dusky dolphin calves (Markowitz 2004).

Variations in deep scattering layer (DSL) density, location, or composition on dusky dolphin distribution patterns are unknown. However, dusky dolphins feed on the DSL throughout the year, and thus may not be strongly affected by possible changes in food composition or location. Furthermore, environmental factors such as sea surface temperature (SST) may not have significant effects on dolphin near shore - offshore shifts between seasons (Chapter II), but rather may influence dolphin prey. Thus, based on current evidence, dusky dolphin long-term and seasonal patterns of habitat choice appear primarily influenced by killer whale occurrence patterns. Furthermore, dusky dolphins behaviorally respond with ‘fight or flight’ tactics besides a general response of seeking shallow near shore waters (Cipriano 1992, Markowitz 2004).

Dusky dolphins have several short-term and long-term survival strategies to avoid potential predator encounters. These strategies are represented by changes in group size, social affiliations, swimming patterns, and inter-individual distances that vary with activity (Chapter II). Mother with calf groups or nursery groups have a different set of tactics compared to adult groups. This includes choosing shallower waters (< 20 m), isolation from other social groups, and possibly a different exit strategy such as leaving the area entirely or hiding in the shallows when confronted with potential danger.

Overall, dusky dolphin anti-predator strategies are effective against the intermittent threat from killer whales, with the social groups of adults and nursery groups showing little evidence of scarring either from sharks or killer whales. However, since most predation events may go unnoticed, and dolphins may more often be consumed than scarred, predation risk assessments based on scars are inaccurate.

A spatially explicit individual-based model (IBM) was developed to attempt to answer why dusky dolphins make near shore-offshore trips in terms of costs *vs.* benefits from both ecological and evolutionary perspectives. My model attempts to capture the dynamic behavioral interactions between a clever prey (the dusky dolphin) and a clever predator (the killer whale).

The model was evaluated by comparing observed dusky dolphin sighting data with model-simulated sightings. Sightings from the model were sampled by time and month corresponding to observed dusky dolphin sightings from Jan-May 2007 field data (see Chapter II). The sightings were correlated within the survey area and were representative of social type depth preferences. Baseline parameter values for model simulations were determined from available data. Where information was lacking, best guess estimates from similar species were used. A sensitivity analysis of parameter levels and combinations revealed a significant influence of killer whale return times on time/distance budgets. Thus, for model simulations, low (3 day) and high (0.5 day) killer whale predation risk levels were assumed. Results reveal that dusky dolphins rest less and travel more during presence of killer whales (3 day killer whale return probability). Time/distance budget variability are more pronounced with increased killer whale presence (0.5 days return probability).

The model suggests that a strong reason to favor the adoption of short and long-term anti-predator mechanisms may be increased survival resulting from decreased encounters with killer whales. This is particularly evident when anti-predator rules are turned off, but killer whales are present in the system. Under this latter scenario, dolphins are allowed to freely move in the system and interact with cruising predators. Future versions of the model may include freely moving predators as well (e.g. *see* Hammond et al. 2007).

In Chapter IV, model simulations were extended to include dusky dolphins with calves. Baseline parameter values were changed to account for a dusky mother with calf, and concomitant increase in energetic demands for the lactating mother. Parameter sensitivity analysis revealed a strong influence of killer whale return times for with and without calf treatments on time/distance variables. A GLM MANOVA model was used to assess the influence of individual predictor variables: Killer Whale return times, dusky dolphin memory in refuge, and dolphin detection distance on dusky dolphin time/distance budgets. Results indicate that killer whale return times have the strongest influence on time/distance variables for both with and without calf treatments. However, separate combinations of killer whale return time and dolphin detection distance variables and killer whale return time and dolphin memory in refuge variables also have a significant influence on time/distance budgets for without calf treatments.

For bioenergetic calculations, model simulations included treatments with/without calf and with/without killer whales with all behavioral rules present. With calf and without calf treatments significantly differed for most time/distance variables, excluding time/distance search. Since all model simulations were conducted with one individual.

Simulation results reveal that dusky dolphins with calves rest less and travel more when killer whales are present, relative to dolphins without calves. However, dusky dolphins with calves have fewer encounters with killer whales regardless of levels of predation risk and have shorter distances to flee. The shorter distance fled by a dusky dolphin with calf is indicative of their proximity to near shore shallow waters (< 20 m) compared to adult dusky groups preferring deeper waters (< 200 m). Thus, dusky dolphins may incur short-term ecological costs resulting from killer whale presence, but may benefit from adopting anti-predator rules by having fewer lethal encounters. Such strategies appear to be stable despite varying predation pressures off Kaikoura.

Bioenergetic consequences for dusky dolphins faced with varying killer whale predation risk levels was determined by estimating total energy expended in foraging and locomotion (travel, and travel plus flee) as well as from variable dusky dolphin foraging times. Total energy expended for dusky dolphins (with and without calf) was estimated as: Foraging costs (FC) + Locomotor costs (LC) (Travel) or LC (Travel) + LC (Flee) based on the absence of killer whales, as well as low/high presence of killer whales. Travel and flee distance estimates were obtained from model simulations involving with and without calf treatments in the presence and absence of killer whales (Chapter IV). Dolphin daily energetic requirements were assumed at 3,500 kcal/day for an adult dusky dolphin (Cipriano 1992), which is comparable to other dolphins of similar size (Benoit-Bird 2004, Kastelein et al. 2002), and 7,000 kcal/day for a lactating mother with calf (Reid et al. 1994, Kastelein et al. 2002).

Dusky dolphins spend approximately 629-1,502 kcal/ day (with calf) and 310-747 kcal/day (without calf) in foraging and travel costs in the absence of killer whales, considering a 5 % prey capture cost of prey (Benoit-Bird 2004), and based on high and low prey energy value contribution to dusky dolphin daily energetic requirements (Cipriano 1992, Chapter IV), since exact prey size is unknown from dusky dolphin stomach content data. This number rises to approximately 1,683-5,035 kcal/day (with calf) and 837-2,500 kcal/day (without calf) at a 20% capture cost (i.e. 20% of prey energy value is lost in capture). The total energy costs calculated here is largely attributable to foraging costs (Chapter IV). Foraging costs calculated here are estimates and therefore, may need further verification as more accurate information becomes available.

The values are not significantly higher from low or high presence of killer whales for mother with calf, but increase by ~90 kcal/day for adult without calf. Thus, costs incurred from travel and fleeing appear minimal relative to foraging costs. Low travel costs for dusky dolphins with and without calf in part reflect the proximity of dolphins to deep water and having to cover shorter distances to feed. However, a suitable measure of killer whale effects is evident from reduced foraging time for with and without calf treatments. I estimate that foraging calories lost due to increased killer whale presence are almost 5 times more for mother with than without calf. However, maximum foraging time available can be reduced significantly with an increase in dolphin group size, inclusion of dolphin hunger, lunar phase and DSL density changes.

An increase in dolphin detection distance and hiding time due to presence of killer whales may further reduce feeding time. In fact, with a 10 km dolphin detection distance and a 0.5 day killer whale return rate, total foraging time available is reduced by > 10% over the 210-day simulated period. Therefore, I believe that future bioenergetic analysis should consider indirect predation risk effects as prey anti-predator mechanisms may result in significant energetic costs independent of physiological, growth, and reproductive costs. Also, bioenergetic analysis should incorporate differences due to social types, such as a lactating mother, to better understand the energy constraints within which different animals operate within the 'ecology of fear'(Brown et al. 1999) — This may have important consequences for prey population demographics and dynamics.

By evaluating costs *vs.* benefits for dusky dolphin anti-predator decisions, it appears that despite incurring short-term ecological costs, dusky dolphin strategies are effective against killer whale threats that vary spatially and temporally. Also, the long-term benefits of adopting anti-predator behaviors and rules pay dividends in terms of increasing dusky dolphin survival by reducing potential encounters with killer whales.

Concluding remarks

A male killer whale flinging a sea lion in the air, a breaching great white with a fur seal in its mouth, a pride of lionesses chasing a lone buffalo — all conjure up fantastic visuals, yet, there is more to this stark spectacle of predator consuming prey. In actuality, there is an entire series of intricate mechanisms involving subtle body language and repertoires of stable and flexible strategies that complicate the dynamic relationship between predator and prey.

For decades, predation effects have been about prey mortality and regulating prey populations (*reviewed in* Lima and Dill 1990, Peckarsky et al. 2008). As a result of revised thinking and approaches (Lima 1998, Brown et al. 1999), the effects of predators have expanded to include indirect predation risk effects to provide a more holistic perspective of predator influences on prey beyond the concept of consumption effects. This altered thinking has enabled scientists to better understand how predators can shape prey behavioral ecology, as well as ecological communities (Heithaus et al. 2008, Schmidt et al. 2008).

There is, however, much to learn at the species level, with regard to anti-predator decisions and evolving predator strategies. The current model is not a perfect recipe to address all aspects of predator-prey relationships. But the model has the capability to increase the veracity of findings, and test ecological questions within a broader theoretical framework. The IBM developed here is a start-up tool that can be refined to include species and systems that fit within the continuum of simple to complex. Behavior and movement rules and system components can be modified depending on species or system of interest. The better the baseline knowledge, the more significant will be the application to management or policy decisions.

There is, of course, no substitute to field-based information. After all, models are based on field-gained knowledge. However, especially when empirical data are limited, IBM's can provide a testable platform to ask ecological questions that result from the interplay of abiotic and biotic factors. Furthermore, the model helps to visualize the interconnectedness of different modules. Through sensitivity analysis and model evaluation procedures, new versions of the model can be generated that fit within our understanding of a realistic framework. However, inclusion of every influencing variable and generating a complicated model may not necessarily improve our understanding of a system, nor address every ecological question. Instead, the focus has to be on developing parsimonious models that address basic questions first, and incorporate complexity in a stepwise fashion.

Predator-prey relationships are fascinating, simply because they involve two animals matching skill, strength, strategy, and stamina — there is no expected victorious outcome each time. The inherent unpredictability of these events provide indication that regardless of where the animals are on the food chain, all prey are equipped with survival instincts that have saved them on various occasions from motivated predators. To unravel the games that predator and prey play with each other is not an easily achieved task. However, we can build on previous work and test the basic tenets governing most predator-prey interactions by beginning at the species level and expanding it to ecological levels. The focus though has to be on both predator and prey perspectives.

LITERATURE CITED

Abrams, P. A. 1990. The effects of adaptive behavior on the type-2 functional response. Ecology 71:877–995.

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. American Naturalist 146:112–134.

Abrams, P. A. 2000. The evolution of predator–prey interactions: theory and evidence. Annual Review of Ecology and Systematics 31:79–105.

Abrams, P. A. 2007. Defining and measuring the impact of dynamic traits on interspecific interactions. Ecology 88:255–2562.

Acevedo-Gutierrez, A., D. A. Croll, and B. R. Tershy. 2002. High feeding costs limit dive time in the largest whales. Journal of Experimental Biology 205:1747–1753.

Adams, S. M., and L. D. DeAngelis.1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. Pages 103–117 *in* W. C. Kerfoot and A. Sih, editors. Predation in aquatic communities. University Press of New England, Hanover, New Hampshire.

Ajie, B. C., L. M. Pintor, J. Watters, J. L. Kerby, J. I. Hammond, and A. Sih. 2007. A framework for determining the fitness consequences of antipredator behavior. Behavioral Ecology 18:267–270.

Alados, C. L. 1985. An analysis of vigilance in the Spanish ibex (*Capra pyrenaica*). Zeitschrift Für Tierpsychiologie 68:58–64.

Alexander, R. D. 1974. The evolution of social behavior. Annual Review Ecological Systems 5:325–383.

Altmann, J., 1974. Observational study of behavior - sampling methods. Behaviour, 49:227–267.

Ayers, D., M. P. Francis, L. H. Griggs, and S. J. Baird. 2004. Fish bycatch in New Zealand tuna longline fisheries, 2000-01 and 2001-02. New Zealand Fisheries Assessment Report 2004/46.

Bateson, P.P.G. 1983. Mate choice. Cambridge University Press, UK.

Bednekoff, P. A., and S. L. Lima. 1998. Randomness, chaos and confusion in the study of antipredator vigilance. Trends in Ecology & Evolution 13:284–287.

Benoit-Bird, K. J. 2004. Prey caloric value and predator energy needs: foraging predictions for wild spinner dolphins. Marine Biology 145:435–444.

Benoit-Bird, K. J. and W. W. L. Au. 2003. Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behavioral Ecology and Sociobiology 53:364–373.

Benoit-Bird, K. J., A. D. Dahood, and B. Würsig. 2008. Using active acoustics to compare predator-prey behavior in two marine mammal species. Marine Ecology Progress Series: In Press.

Benoit-Bird, K.J., B. Würsig, and C.J. McFadden. 2004. Dusky dolphin (*Lagenorhynchus obscurus*) foraging in two different habitats: Active acoustic detection of dolphins and their prey. Marine Mammal Science 20:215–231.

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and E. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. Ecological Applications 16:273–284.

Bertram, B. C. R. 1978. Living in groups: predators and prey. Fourth Edition. Blackwell, Oxford, UK

Black, N. 1994. Behavior and ecology of pacific white sided dolphins (*Lagenorhynchus obliquidens*) in Monterey Bay, California. Masters Thesis. San Francisco State University.

Boinski, S., L. Kauffman, A. Westoll, C. M. Stickler, S. Cropp, and E. Ehmke. 2003. Are vigilance, risk from avian predators and group size consequences of habitat structure? A comparison of three species of squirrel monkey (*Saimiri oerstedii*, *S. boliviensis*, and *S. sciureus*). Behavior 140:1421–1467.

Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs 68:371–394.

Bowen, W. D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology-Progress Series 158:267–274.

Bradshaw, C. J. A., C. Lalas, and C. M. Thompson. 2000. Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). Journal of Zoology 250:105–112.

Brown, C. R., and M. B. Brown, 1996. Coloniality in the Cliff swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Brown, J. S., B. P. Kotler, and A. Bouskila. 2001. Ecology of fear: foraging games between predators and prey with pulsed resources. Annales Zoologici Fennici 38:71–87.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Carey, F. G., and J.V. Scharold. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. Marine Biology 106:329–342.

Carey, F. G., J. M. Teal, and J. W. Kanwisher. 1981. The visceral temperatures of mackerel sharks (Lamnidae). Physiological Zoology 54:334–344.

Chivers, S. J. 1999. Biological indices for monitoring population status of walrus evaluated with an individual-based model. Pages 239-247 *in* Garner, G.W., S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald, and D.G. Robertson, editors. Marine mammal survey and assessment methods. A.A. Balkema, Rotterdam.

Cipriano, F. 1992. Behavior and occurrence patterns, feeding ecology, and life history of dusky dolphins (*Lagenorhynchus obscurus*) off Kaikoura, New Zealand. Dissertation, University of Arizona, Tucson, AZ.

Collier, A., C. C. Bronk, B. Larson, and S. Taylor. 2008. The impact of predation stress by largemouth bass (*Micropterus salmoides*) on the growth and development of leopard frog tadpoles (*Rana sphenocephala*). Journal of Fish Ecology 23:281–289.

Compagno, L. J. V. 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date, Part 1. FAO Fisheries Synopsis 125.

Connor, R. C. 2000. Group living in whales and dolphins. Pages 199–218, Chapter 8 *in* J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead, editors. Cetacean societies. University of Chicago Press, Chicago, Illinois.

Connor, R. C., and M. R. Heithaus. 1996. Approach by great white shark elicits flight response in bottlenose dolphins. Marine Mammal Science 12:602–606.

Connor, R. C., J. Mann, P. L. Tyack, and H. Whitehead. 1998. Social evolution in toothed whales. Trends in Ecology & Evolution 13:228–232.

Connor, R. C., R. S. Wells, J. Mann, and A. Read. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. University of Chicago Press. Chicago & London.

Constantine, R., I. Visser, D. Buurman, R. Buurman, and B. McFadden. 1998. Killer whale (*Orcinus orca)* predation on dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. Marine Mammal Science 14:324–330.

Cooper, W. E. 2000. Tradeoffs between predation risk and feeding in a lizard, the broad-headed skink (*Eumeces laticeps*). Behaviour 137:1175–1189.

Costa, D. P. 2008. A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. Aquatic Conservation: Marine and Freshwater Ecosystems 17:S44–S52.

Cowlishaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. Animal Behavior, 53:667–686.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology & Evolution 23:194–201.

Creel, S., and J. A. Winnie. 2005. Responses of elk herd size to fine–scale spatial and temporal variation in the risk of predation by wolves. Animal Behaviour 69:1181–1189.

Creel, S., D. Christianson, S. Liley, and J. A.Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. Science 315:960–960.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

Crespi-Abril, A. C., N. A. García, E. A. Crespo, and M. A. Coscarella. 2003. Consumption of marine mammals by broadnose sevengill shark *Notorynchus cepedianus* in the northern and central Patagonian Shelf. Latin American Journal of Aquatic Mammals 2:101–107.

Cresswell, W. 2008. Non-lethal effects of predation in birds. Ibis, 150:3–17.

Crovetto, A., J. Lamilla, and G. Pequeno. 1992. *Lissodelphis peronii*, Lacepede 1804 (Delphinidae, Cetacea) within the stomach contents of a sleeping shark, *Somniosus cf pacificus*, Bigelow and Schroeder 1944, in Chilean waters. Marine Mammal Science 8:312–314.

Dahood, A. D., B. Würsig, Z. Vernon, I. Bradshaw, D. Buurman, and L. Buurman. 2008. Tour operator data illustrate long term dusky dolphin (*Lagenorhynchus obscurus*) occurrence patterns near Kaikoura, New Zealand. IWC/ SC 60/ WW2. Presented to the Scientific Committee of the International Whaling Commission June 2008.

Deecke, V. B., P. J. B. Slater, and J. K. B. Ford. 2002. Selective habituation shapes acoustic predator recognition in harbour seals. Nature 420:171–173.

Dehn, M. M. 1990. Vigilance for predators – detection and dilution effects. Behavioral Ecology and Sociobiology 26:337–342.

Deutsch, S. M. 2008. Behavioral development of dusky dolphins. MS Thesis, Texas A&M University, Galveston.

Dill, L. M. 1987. Animal decision-making and its ecological consequences - The future of aquatic ecology and behavior. Canadian Journal of Zoology 65:803–811.

Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151–1157.

Ebert, D. A. 1991. Diet of the sevengill shark *Notorynchus cepedianus* in the temperate coastal waters of southern Africa. South African Journal of Marine Science 11:565–572.

Ebert, D. A. 2002. Ontogenetic changes in the diet of the sevengill shark (*Notorynchus cepedianus*). Marine and Freshwater Research 53:517–523.

Edmunds. 1974. Defence in animals. Longman, New York, NY.

Elgar, M. A. 1989. Predator vigilance and group size in mammals and birds - a critical review of the empirical evidence. Biological Reviews of the Cambridge Philosophical Society 64:13–33.

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska - generality and variation in a community ecological paradigm. Ecological Monographs 65:75–100.

Fertl, D., A. Acevedo-Gutierrez, and F. L. Darby. 1996. A report of killer whales (*Orcinus orca*) feeding on a carcharhinid shark in Costa Rica. Marine Mammal Science 12:606–611.

Fischhoff, I. R., S. R. Sundaresan, J. Cordingley, and D. I. Rubenstein. 2007. Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation in danger from lions. Behavior Ecology 18:725–729.

Fitzgibbon, C. D. 1990. Why do hunting cheetahs prefer male gazelles. Animal Behaviour 40:837–845.

Ford, J. K. B. and R. R. Reeves. 2008. Fight or flight: antipredator strategies of baleen whales. Mammal Review 38:50–86.

Fortin, D., H. L. Beyer, M. S. Boyce, D.W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Francis, M. P., J. D. Stevens, and P. R. Last. 1988. New records of *Somniosus* (Elasmobranchii, Squalidae) from Australasia, with comments on the taxonomy of the genus. New Zealand Journal of Marine and Freshwater Research 22:401–409.

Frid, A., G. G. Baker, and L. M. Dill. 2006. Do resource declines increase predation rates on North Pacific harbor seals? A behavior-based plausibility model. Marine Ecology Progress Series 312:265–275.

Gaskin, D. E. 1968. Distribution of delphinidae (Cetacea) in relation to sea surface temperatures off eastern and southern New Zealand. New Zealand Journal of Marine Freshwater Research 2:527–534.

Gowans, S., B. Würsig, and L. Karczmarski. 2008. The social structure and strategies of delphinids: Predictions based on an ecological framework. Advances in Marine Biology 53:195–294. Elsevier Academic Press Inc, San Diego, CA.

Graham, J. 2004. Movement patterns and bioenergetics of the shortfin mako shark. California Sea Grant College Program. Research Profiles. Paper PPFisheries04_03. 4pp http://repositories.cdlib.org/csgc/rp/PPFisheries04_03. Accessed March 2008.

Graw, B., and M. Manser. 2007. The function of mobbing in cooperative meerkats. Animal Behavior 74:507–517.

Grimm V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton University Press, Princeton, NJ.

Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H. H.Thulke, J. Weiner, T. Wiegand, D. L. DeAngelis. 2005. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. Science 310:987–991.

Gygax, L. 2002. Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. Behavioral Ecology 13:583–590.

Hall, A. J., B. J. McConnell, T. K. Rowles, A. Aguilar, A. Borrell, L. Schwacke, P. J. H. Reijnders, R. S. Wells. 2006. Individual-based model framework to assess population consequences of polychlorinated biphenyl exposure in bottlenose dolphins. Environmental Health Perspectives. 114:60–64.

Hall, C. A. S. and J. W. Day, Jr. 1977. Ecosystem modeling in theory and practice. John Wiley & Sons, New York.

Hamilton, W. D. 1971. Geometry for selfish herd. Journal of Theoretical Biology 31:295–311.

Hamilton, W. D. 1972. Altruism and related phenomena, mainly in social insects. Annual Reviews of Ecological Systems 3:193–232

Hanlon, R. T. and J. B. Messenger. 1996. Cephalopod behaviour, Cambridge University Press, Cambridge, UK.

Hart, D.L., and R.W. Sussman. 2005. Man the hunted: primates, predators, and human. Westview Press, Boulder, CO.

Heithaus, M. R. 2001. Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. Journal of Zoology 253: 53–68.

Heithaus, M. R. 2004. Predator-prey interactions. Pages 487521 *in* J.C. Carrier, J. Musick, and M.R Heithaus, editors. The biology of sharks and their relatives. CRC Press, Boca Raton, Fl.

Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology & Evolution 23:202–210.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

Heithaus, M. R., L. M. Dill, G. J. Marshall, and B. Buhleier. 2002. Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem. Marine Biology 140:237–248.

Heithaus, M. R., and L. M. Dill. 2006. Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257–264.

Holomuzki, J. R., and J. D. Hoyle. 1990. Effect of predatory fish presence on habitat use and diel movement of the stream amphipod, *Gammrarus minus*. Freshwater Biology 24:509–517.

Holts, D.B., and D.W. Bedford. 1993. Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the southern California bight. Australian Journal of Marine and Freshwater Research 44:901–909.

Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. Journal of Animal Ecology 74:559–566.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation.

Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 341:375–397.

Hui, C. A. 1987. Power and speed of swimming dolphins. Journal of Mammalogy 68:126–132.

Hulbert, L. B., M. F. Sigler, and C. R. Lunsford. 2006. Depth and movement behavior of the Pacific sleeper shark in the north-east Pacific Ocean. Journal of Fish Biology 69:406–425.

Inman, A. J., and J. Krebs. 1987. Predation and group living. Trends in Ecology and Evolution 2:31–32.

International Union for the Conservation of Nature and Natural Resources (IUCN). 2008. 2008 IUCN Red List of Threatened Species. www.iucnredlist.org Accessed Feb 2008.

Jackson, A. L., S. Brown, T. N. Sherratt, and G. D. Ruxton. 2005. The effects of group size, shape and composition on ease of detection of cryptic prey. Behaviour 142:811–826.

Jarman, P. J. 1974. The social organization of antelope in relation to their ecology. Behavior 48:215–267.

Jeffers, J. N. R. 1978. An introduction to systems analysis with ecological applications. University Park Press, Baltimore, MD.

Jefferson, T. A., P. J. Stacey, and R. W. Baird. 1991. A review of killer whale interactions with other marine mammals - predation to coexistence. Mammal Review 21:151–180.

Kappeler, P. M., and C. P. Van Schaik. 2002. Evolution of primate social systems. International Journal of Primatology 23:707–740.

Kastelein, R. A., C. A. van der Elst, H. K. Tennant, and P. R. Wiepkema. 2000. Food consumption and growth of a female dusky dolphin (*Lagenorhynchus obscurus*). Zoo Biology 19:131–142.

Kastelein, R. A., N. Vaughan, S. Walton, and P. R. Wiepkema. 2002. Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity. Marine Environmental Research 53:199–218.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals Ecoscience 5:569–569.

Keiper, C. A., D. G. Ainley, S. G. Allen, and J. T. Harvey. 2005. Marine mammal occurrence and ocean climate off central California, 1986 to 1994 and 1997 to 1999. Marine Ecology Progress Series 289:285–306.

Kjelland, M. E., U. P. Kreuter, G. A. Clendenin, R. N. Wilkins, X. Ben Wu, E. G. Afanador, and W. E. Grant. 2007. Factors related to spatial patterns of rural land fragmentation in Texas. Environmental Management 40:231–244.

Klanjscek, T. 2006. Dynamic energy budgets and bioaccumulation : a model for marine mammals and marine mammal populations. Dissertation, Woods Hole Oceanography Institute (WHOI), Massachusetts Institute of Technology.

Kleiber M. 1975. The fire of life: an introduction to animal energetics. Krieger, Huntington, NY.

Klimley, A. P., S. C. Beavers, T. H. Curtis, and S. J. Jorgensen. 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environmental Biology of Fishes 63:117–135.

Kotler, B.P. 1984. Risk of predation and the structure of desert rodent communities. Ecology 65:689–701.

Kotler, B. P., and R. D. Holt. 1989. Predation and competition - The interaction of 2 types of species interactions. Oikos 54:256-260.

Krause, J. 1994. The influence of food competition and predation risk on size – assortative shoaling in juvenile chub (*Leuciscus cephalus*). Ethology 96:105–116.

Krause, J., and J. G. J. Godin. 1995. Predator preferences for attacking particular prey group sizes – consequences for predator hunting success and prey predation risk. Animal Behaviour 50:465–473.

Krause , J., and G. Ruxton. 2002. Living in groups. Oxford University Press, London.

Krebs, C.J., R. Boonstra, S. Boutin, and A.R.E. Sinclair. 2001. What drives the 10–year cycle of the snowshoe hare? BioScience 51(1):25–35

Kruuk, H. 1972. The spotted hyena: a study of predation and social behavior. University of Chicago Press, Chicago, IL.

Lamprecht, J. 1981. The function of social hunting in larger terrestrial carnivores. Mammal Review 11:169–179.

Landeau, L. and J. Terborgh. 1986. Oddity and the confusion effect in predation. Animal Behaviour 34:1372–1380.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

Liley, S., and S. Creel. 2007. What best explains vigilance in elk: characteristics of prey, predators, or the environment? Behavioral Ecology 19:245–254.

Lima, S. L. 1998. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. Trends in Ecology & Evolution 17:70–75.

Lima, S. L., and P. A. Bednekoff. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. American Naturalist 153:649–659.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation – a review and prospectus. Canadian Journal of Zoology–Revue Canadienne de Zoologie 68:619–640.

Lima, S. L., W. A. Mitchell, and T. C. Roth. 2003. Predators feeding on behaviourally responsive prey: some implications for classical models of optimal diet choice. Evolutionary Ecology Research 5:1083–1102.

Lockyer, C. 2007. All creatures great and smaller: a study in cetacean life history energetics. Journal of the Marine Biological Association of the United Kingdom 87:1035–1045.

Long, D. J., and R. E. Jones. 1996. White shark predation and scavenging on cetaceans in the eastern North Pacific Ocean. Pages 293–307 *in* A. P. Klimley and D. G. Ainley, editors. Great white sharks: the biology of *Carcharodon carcharias* Academic Press, New York, NY.

Lotka, A. J. 1925. Elements of physical biology. Williams & Wilkins Company, Baltimore, MD.

Lucifora, L. O., R. C. Menni, and A. H. Escalante. 2005. Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. Marine Ecology Progress Series 289:237–244.

Luttbeg, B., and J. L. Kerby. 2005. Are scared prey as good as dead? Trends in Ecology & Evolution 20:416-418.

Luttbeg, B., and A. Sih. 2004. Predator and prey habitat selection games: the effects of how prey balance foraging and predation risk. Israel Journal of Zoology. 50:233–254.

Macleod, C. D., C. R. Weir, M. B. Santos, and T. E. Dunn. 2008. Temperature-based summer habitat partitioning between white-beaked and common dolphins around the United Kingdom and Republic of Ireland. Journal of the Marine Biological Association of the United Kingdom 88:1193–1198.

Madenjian, C. P., and S. R. Carpenter. 1991. Individual-based model for growth of young-of-the-year walleye - A piece of the recruitment puzzle. Ecological Applications 1:268–279.

Mamaev, E. G., and V. N. Burkanov. 2006. Killer whales (*Orcinus orca*) and northern fur seals of the Commander Islands: is it feeding specialization development? Pages 347–351 *in* Marine mammals of the Holarctic, Fourth International Conference, St. Petersburg, Russia.

Mann, J. and H. Barnett. 1999. Lethal tiger shark (*Galeocerdo cuvier*) attack on bottlenose dolphin (*Tursiops sp*.) calf: defense and reactions by the mother. Marine Mammal Science 15:568–575.

Marino, L. 1998. A comparison of encephalization between odontocete cetaceans and anthropoid primates. Brain Behavior and Evolution 51:230–238.

Markowitz, T.M., 2004. Social organization of the New Zealand dusky dolphin. Dissertation Texas A&M University, Galveston, TX.

Matkin, C. O., L. G. Barrett-Lennard, H. Yurk, D. Ellifrit, and A. Trites. 2007. Ecotypic variation and predatory behavior among killer whales (*Orcinus orca*) off the eastern Aleutian Islands, Alaska. Fishery Bulletin 105:74–87.

McNamara, J. M., and A. I. Houston. 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheoretica 38:37–61.

Meagher, E. M., W. A. Mclellan, A. J. Westgate, R. S. Wells, J. E. Blum, and D. A. Pabst. 2008. Seasonal patterns of heat loss in wild bottlenose dolphins (*Tursiops truncatus*). Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology 178:529–543.

Mehta, A. V., J. M. Allen, R. Constantine, C. Garrigue, B. Jann, C. Jenner, M. K. Marx, C. O. Matkin, D. K. Mattila, G. Minton, S. A. Mizroch, C. Olavarria, J. Robbins,

K. G. Russell, R. E. Seton, G. H. Steiger, G. A. Vikingsson, P. R. Wade, B. H. Witteveen, and P. J. Clapham. 2007. Baleen whales are not important as prey for killer whales *Orcinus orca* in high-latitude regions. Marine Ecology Progress Series 348:297–307.

Ministry of Fisheries. 2007a. Blue Sharks (BWS) Fisheries Summary. Ministry of Fisheries Plenary Report. http://services.fish.govt.nz/fishresourcespublic/Plenary2006/BWS_06.pdf. Accessed March 2008.

Ministry of Fisheries. 2007b. Mako Shark (MAK) Fisheries Summary. Ministry of Fisheries Plenary Report. http://services.fish.govt.nz/fishresourcespublic/Plenary2007/MAK_07.pdf. Accessed March 2008.

Mitchell, W. A., and S. L. Lima. 2002. Predator-prey shell games: large-scale movement and its implications for decision-making by prey. Oikos 99:249–259.

Morisaka, T., and R. C. Connor. 2007. Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. Journal of Evolutionary Biology 20:1439–1458.

Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846–1850.

Newman, K., and A. M. Springer. 2007. Killer whales do it in the dark: nocturnal activity by transients at St. Paul Island. Abstract, Marine Science in Alaska: 2007 Symposium, Anchorage, AK.

Nichol, L. M., and D. M. Shackleton. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus spp*) in British Columbia. Canadian Journal of Zoology-Revue Canadienne De Zoologie 74:983–991.

Noren, S. R. 2008. Infant carrying behavior in dolphins: costly parental care in an aquatic environment. Functional Ecology 22:284–288.

Norris, K. S. 1994. Predators, parasites, and multispecies aggregations. Pages 287-300 *in* K.S. Norris, B. Würsig, R.S. Wells, M. Würsig, editors. The Hawaiian spinner dolphin. University of California Press, Berkeley.

Norris, K. S., and T. P. Dohl. 1980. Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. Fishery Bulletin 77:821–849.

Norris, K. S., and C. R. Schilt. 1988. Cooperative societies in 3-dimensional space – on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. Ethology and Sociobiology 9:149–179.

Orrock, J. L., J. H. Grabowski, J. H. Pantel, S. D. Peacor, B. L. Peckarsky, A. Sih, and E. E. Werner. 2008. Consumptive and non-consumptive effects of predators on metacommunities of competing prey. Ecology 89:2426–2435.

Otto, S. B., E. L. Berlow, N. E. Rank, J. Smiley, and U. Brose. 2008. Predator diversity and identity drive interaction strength and trophic cascades in a food web. Ecology 89:134–144.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology & Evolution 14:483–488.

Packer, C. 1986. The ecology of sociality in felids, pages 429–451 *in* D. I. Rubenstein and R.W. Wrangham, editors. Ecological aspects of social evolution: birds and mammals. Princeton University Press, Princeton, NJ.

Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences of the United States of America, 98:3904–3908.

Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. J. Schmitz, and G. C. Trussell. 2008. Revisiting the classics: considering non-consumptive effects in textbook examples of predator-prey interactions. Ecology 89:2416–2425.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836-1846.

Peckarsky, B. L., and A. R. McIntosh.1998. Fitness and community consequences of avoiding multiple predators. Oecologia 113:565–576.

Peckarsky, B. L., A. R. McIntosh, B. W. Taylor, and J. Dahl. 2002. Predator chemicals induce changes in mayfly life history traits: a whole-stream manipulation. Ecology 83:612–618.

Perryman, W. L., and T. C Foster. 1980. Preliminary report on predation by small whales, mainly the false killer whale, *Pseudorca crassidens*, on dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. Admin Rep LJ–80–05, Southwest Fisheries Science Center, La Jolla, CA.

Peterseni, J. H., D. L. Deangelas, and C. P. Paukert. 2008. An overview of methods for developing bioenergetic and life history models for rare and endangered species. Transactions of the American Fish Society 137:244–253.

Pitman, R. L., L. T. Ballance, S. I. Mesnick, and S. J. Chivers. 2001. Killer whale predation on sperm whales: observations and implications. Marine Mammal Science 17:494–507.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509.

Pulliam, H. R. 1973. Advantages of flocking. Journal of Theoretical Biology 38:419–422.

Pulliam, H. R. and T. Caraco. 1984. Living in groups: is there an optimal group size? Pages 122–157 *in* Chapter 5 J.R. Krebs and N.B. Davies, editors. Behavioural ecology: an evolutionary approach, 2nd Edition. Blackwell Scientific, Oxford, UK.

Reddy, M., T. Kamolnick, T., C. Curry, C., D. Skaar, D., and S. Ridgway. 1994. Energy requirements for the bottlenose dolphin (*Tursiops truncatus*) in relation to sex, age and reproductive status. Marine Mammals: Public Display and Research, 1, 26–31.

Rice, J. A., T. J. Miller, K. A. Rose, L. B. Crowder, E. A. Marschall, A. S. Trebitz, and D. L. Deangelis. 1993. Growth-rate variation and larval survival - inferences from an individual-based size-dependent predation model. Canadian Journal of Fish and Aquatic Sciences 50:133–142.

Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? Bioscience 54:755–766.

Ripple, W. J., and R. L. Beschta. 2006. Linking a cougar decline, trophic cascade, and catastrophic regime shift in Zion National Park. Biological Conservation 133:397–408.

Roberts, G. 1996. Why individual vigilance declines as group size increases. Animal Behaviour 51:1077–1086.

Rodriguez, A., H. Andren, and G. Jansson. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. Oikos 95:383–396.

Rosen, D. A. S., and A. W. Trites. 2002. Cost of transport in Steller sea lions, *Eumetopias jubatus*. Marine Mammal Science 18:513–524.

Rosen, D. A. S., A. J. Winship, and L. A. Hoopes. 2007. Thermal and digestive constraints to foraging behaviour in marine mammals. Philosophical Transactions of the Royal Society B-Biological Sciences 362:2151–2168.

Rosenberg M. S. 2001. PASSAGE. Pattern analysis, spatial statistics, and geographic exegesis. Version 2.0 beta Department of Biology, Arizona State University, Tempe, Arizona

Ruzicka, J. J., and S. M. Gallager. 2006. The importance of the cost of swimming to the foraging behavior and ecology of larval cod (*Gadus morhua*) on Georges Bank. Deep-Sea Research Part I -Topical Studies in Oceanography 53:2708–2734.

Saayman, G. S., and C. K. Tayler. 1979. The socioecology of humpback dolphins (*Sousa sp.).* Pages 165-226 *in* H.E. Winn and B.L. Olla, editors. The behavior of marine animals, Volume 3: Cetaceans, Plenum Press, New York.

Schaller, G. 1972. The Serengeti lion. The University of Chicago Press, Chicago, IL.

Scheel, D., and C. Packer. 1991. Group hunting behavior of lions – a search for cooperation. Animal Behaviour 41:697–709.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, et al. 2008. The status of the world's land and marine mammals: Diversity, threat, and knowledge. Science 322:225–230.

Schmidt-Nielsen, K. 1972. Locomotion - energy cost of swimming, flying, and running. Science 177:222–228.

Schmitz, O. J. 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87:1432–1437.

Schmitz, O. J., J. H. Grabowski, B. L. Peckarsky, E. L. Preisser, G. C. Trussell, and J. R. Vonesh. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. Ecology 89:2436–2445.

Scott, M. D., and J. G. Cordaro. 1987. Behavioral observations of the dwarf sperm whale, *Kogia simus*. Marine Mammal Science 3:353–354.

Shane, S. H., R. S. Wells, and B. Würsig. 1986. Ecology, behavior and social-organization of the bottle-nosed-dolphin - a review. Marine Mammal Science 2:34–63.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross–ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Sigler, M. F., L. B. Hulbert, C. R. Lunsford, N. H. Thompson, K. Burek, G. O'Corry-Crowe, and A. C. Hirons. 2006. Diet of Pacific sleeper shark, a potential Steller sea lion predator, in the north-east Pacific Ocean. Journal of Fish Biology 69:392–405.

Sih, A. 1980. Optimal behavior - can foragers balance 2 conflicting demands? Science 210:1041–1043.

Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, NH.

Sih, A., and D. E. Wooster. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. Ecology 75:1199–1207.

Simmonds, M. P., and S. J. Isaac. 2007. The impacts of climate change on marine mammals: early signs of significant problems. Oryx 41:19–26.

Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences of the United States of America 100:12223–12228.

Staniland, I. J., I. L. Boyd, and K. Reid. 2007. An energy-distance trade-off in a central place forager, the Antarctic fur seal (*Arctocephalus gazella*). Marine Biology 152:233–241.

Steiger, G.H., J. Calambokidis, J.M. Straley, L.M. Herman, S. Cerchio, D.R. Salden, J. Urbán-R, J.K. Jacobsen, O. von Ziegesar, K.C. Balcomb, C.M. Gabriele, M.E. Dahlheim, S. Uchida, J.K.B. Ford, P. Ladron de Guevara-P, M. Yamaguchi, and J. Barlow. 2008. Geographic variation in killer whale attacks on humpback whales in the North Pacific: implications for predation pressure. Endangered Species Research 4:247–256.

Taggart, S. J., A. G. Andrews, J. Mondragon, and E. A. Mathews. 2005. Co-occurrence of Pacific sleeper sharks *Somniosus pacificus* and harbor seals *Phoca vitulina* in Glacier Bay. Alaska Fishery Research Bulletin 11:113–117.

Testa, J. W., K. Mock, C. Taylor, H. Koyuk, J. Coyle, R. Waggoner, and K. Newman, , 2007. An agent-based model of predator-prey relationships between transient killer whales and other marine mammals. Final report for the Marine Mammal Commission, Washington DC.

Tricas, T.C. 1979. Relationships of the blue shark, *Prionace glauca*, and its prey species near Santa Catalina Island, California. Fishery Bulletin 77:175–182.

Trites, A. W. 2002. Predator-prey relationships. Pages 994-997 *in* W. F. Perrin, B. Würsig and H.G.M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press, San Diego, CA.

Trivers, R. L. 1972. Mother–offspring conflict. American Zoologist 12:648–648.

Trivers, R. L. 1985. Social evolution. Benjamin Cummings, Menlo Park. CA.

Uddstrom, M. J., and N. A. Oien. 1999. On the use of high-resolution satellite data to describe the spatial and temporal variability of sea surface temperatures in the New Zealand region. Journal of Geophysical Research-Oceans 104:20729–20751.

Van Schaik, C.P., and Hörstermann. 1994. Predation risk and the number of adult males in a primate group: a comparative test. Behavioral Ecology and Sociobiology. 35: 261–272.

Van Schaik, C. P., and J. Van Hooff. 1983. On the ultimate causes of primate social systems. Behavior 85:91–117.

Verdolin, J. L. 2006. Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. Behavioral Ecology and Sociobiology 60:457–464.

Visser, I. N. 1999. Benthic foraging on sting rays by killer whales (*Orcinus orca*) in New Zealand waters. Marine Mammal Science 15:220–227.

Visser, I. N. 2000. Orca (*Orcinus orca*) in New Zealand waters. Dissertation, University of Auckland, New Zealand.

Visser, I. N., D. Fertl, J. Berghan, and R. Van Meurs. 2000. Killer whale (*Orcinus orca*) predation on a shortfin mako shark (*Isurus oxyrinchus*), in New Zealand waters. Aquatic Mammals 26:229–231.

Volterra, V. 1926. Pages 409–448 (Appendix) *in* R. N. Chapman. Animal ecology. McGraw–Hill, NY.

Wade, P. R., V. N. Burkanov, M. E. Dahlheim, N. A. Friday, L. W. Fritz, T. R. Loughlin, S. A. Mizroch, M. M. Muto, D. W. Rice, L. G. Barrett-Lennard, N. A. Black, A. M. Burdin, J. Calambokidis, S. Cerchio, J. K. B. Ford, J. K. Jacobsen, C. O. Matkin, D. R. Matkin, A. V. Mehta, R. J. Small, J. M. Straley, S. M. McCluskey, G. R. VanBlaricom, and P. J. Clapham. 2007. Killer whales and marine mammal trends in the North Pacific - a re-examination of evidence for sequential megafauna collapse and the prey-switching hypothesis. Marine Mammal Science 23:766–802.

Walters, C.J. 1986. Adaptive management of renewable resources. Blackburn Press, Caldwell, NJ.

Weir, J. S. 2007. Dusky dolphin nursery groups off Kaikoura, New Zealand. Masters Thesis, Texas A&M University, Galveston, TX.

Weir, J. S., N. M. T. Duprey, and B. Würsig. 2008. Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: are shallow waters a refuge for nursery groups? Canadian Journal of Zoology 86:1225–1234.

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-226 *in* K. Pryor and K.S. Norris, editors. Dolphin societies: discoveries and puzzles. University of California Press, Berkeley, CA.

Wells, R. S., M. D. Scott, and A. B. Irvine. 1987. The social structure of free-ranging bottlenose dolphins. Current Mammalogy 1:247–305.

Weng, K. C., A. M. Boustany, P. Pyle, S.D. Anderson, A. Brown, and B. A. Block. 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. Marine Biology 152:877–894.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84:1083–1100.

Whitehead, H. and Weilgart, L. 2000. The Sperm Whale: social females and roving males. Pages 154–172 *in* J. Mann, R.C. Connor, P.L. Tyack and H. Whitehead, editors. Cetacean Societies: field studies of dolphins and whales. University of Chicago Press, Chicago.

Williams, T. M. 2002. Swimming. Pages 1213–1222 *in* W. F. Perrin, B. Würsig, and J.G.M. Thewissen, editors. Encyclopedia of marine mammals. Academic Press, San Diego, CA.

Williams, T. M., J. A. Estes, D. F. Doak, and A. M. Springer. 2004. Killer appetites: Assessing the role of predators in ecological communities. Ecology 85:3373–3384.

Williams, T. M., and L. Yeates. 2004. The energetics of foraging in large mammals: a comparison of marine and terrestrial predators. Pages 351–358 *in* Animals and Environments. Proceedings of the Third International Conference of

Comparative Physiology and Biochemistry. International Congress Series. Dec 2004.

Wilson, E.O. 1975. Sociobiology. Harvard University Press, Cambridge, MA.

Winnie, J., and S. Creel. 2007. Sex-specific behavioural responses of elk to spatial and temporal variation in the threat of wolf predation. Animal Behaviour 73:215–225.

Wirsing, A. J., M. R. Heithaus, and L. M. Dill. 2006. Tiger shark (*Galeocerdo cuvier*) abundance and growth in a subtropical embayment: evidence from 7 years of standardized fishing effort. Marine Biology 149:961–968.

Wirsing, A. J., M. R. Heithaus, and L. M. Dill. 2007. Fear factor: do dugongs (*Dugong dugon*) trade food for safety from tiger sharks (*Galeocerdo cuvier*)? Oecologia 153:1031–1040.

Wirsing, A. J., M. R. Heithaus, A. Frid, and L. M. Dill. 2008. Seascapes of fear: evaluating sublethal predator effects experienced and generated by marine mammals. Marine Mammal Science 24:1–15.

Wolf, N. G. 1985. Odd fish abandon mixed–species groups when threatened. Behavioral Ecology and Sociobiology 17:47–52.

Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology 81:266–271.

Wrangham, R. W. 1980. An ecological model of female–bonded primate groups. Behavior 75:262–300.

Wu, X. Y. and W. J. Mitsch. 1998. Spatial and temporal patterns of algae in newly constructed freshwater wetlands. Wetlands 18:9–20.

Würsig, B., and M. Würsig. 1979. Day and night of the dolphin. Natural History 88: 60-67.

Würsig, B., and M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fishery Bulletin 77:871–890.

Würsig, B., F. Cipriano, E. Slooten, R. Constantine, K. Barr, and S. Yin. 1997. Dusky dolphins (*Lagenorhynchus obscurus)* off New Zealand: status of present knowledge. Reports of the International Whaling Commission 47:715–722.

Würsig, B., M. Würsig, and F. Cipriano. 1989. Dolphins in different worlds. Oceanus 32:71-75.

Würsig, B., N. Duprey, and J.Weir. 2007. Dusky dolphins (*Lagenorhynchus obscurus*) in New Zealand waters: present knowledge and research goals. DOC Research and Development Series 270. Department of Conservation, Wellington, NZ.

Ydenberg, R. C., R. W. Butler, D. B. Lank, C. G. Guglielmo, M. Lemon, and N. Wolf. 2002. Trade-offs, condition dependence and stopover site selection by migrating sandpipers. Journal of Avian Biology 33:47–55.

Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Behavior 16:229–249.

Yin, S.E. 1999. Movement patterns, behaviors, and whistle sounds of dolphin groups off Kaikoura, New Zealand. MS Thesis, Texas A&M University, Galveston, TX.

Zar, J. H. 1999. Biostatistical analysis. Prentice-Hall, Inc., Upper Saddle River, NJ.

VITA

Name: Mridula Srinivasan

Address: Department of Wildlife and Fisheries Sciences, Nagle Hall,
Texas A&M University, College Station 77843-2258

Email: smridula@neo.tamu.edu

Education: B.Sc. (Honors), Zoology, University of Delhi, India, 1997
M.Sc., Zoology/Molecular Biology, University of Delhi, India, 1999
M.S., Environmental Management, Florida Tech, 2001