EFFECTS OF HUMAN ACTIVITIES ON COASTAL DOLPHIN BEHAVIOR

A Dissertation

by

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ABSTRACT

This dissertation contributes to our understanding of anthropogenic effects on wildlife, a central question in the growing field of conservation behavior. I present three case studies of coastal delphinid species in diverse ecosystems with varied human pressures. I examine how 1) common bottlenose dolphins (*Tursiops truncatus*) in a narrow congested waterway respond to heavy vessel traffic, 2) Indo-Pacific humpback dolphins (*Sousa chinensis*) respond to chronic maritime construction and associated vessel activity, and 3) dusky dolphins (*Lagenorhynchus obscurus*) use distinct patches within a bay that supports shellfish aquaculture.

In each study, group focal follows were conducted using non-invasive shore-based theodolite tracking. Data collection included behavioral states, movement patterns and habitat-use patterns. Metrics to evaluate alterations in movement patterns included swimming speed, reorientation rate, and linearity. Data to evaluate alterations in habitat-use included behavioral activity states and track duration among habitat patches. Multivariate generalized additive models identified significant explanatory variables.

Dolphin movement and habitat-use patterns were good indicators of response to human activity across diverse species and ecosystems. Bottlenose dolphins avoided tour boats and were attracted to commercial trawlers that may facilitate prey accessibility. Current voluntary dolphin-viewing recommendations do not protect dolphins from behavioral harassment, but dolphins did not abandon the area, which may reflect a lack of ecologically similar habitat nearby. Humpback dolphins avoided areas near chronic construction activity during the day, but some returned at night when human activity decreased. Dusky dolphins used defined patches within the bay in different ways. Mid-bay and nearshore patches reflect areas that may yield greater benefits

relative to prey ball herding opportunities, whereas patches near mussel farms reflect areas that may yield greater benefits relative to non-prey ball foraging opportunities.

Flexibility in foraging tactics occurred across study sites and species, and allows dolphins to adjust to fluctuating environments with ephemeral and patchily distributed prey. Behaviors are likely influenced by human activity, prey characteristics, and accessibility to alternate habitats that support prey. Integration of data on prey characteristics (e.g., fish species, abundance, and distribution) in future research will enhance our understanding of factors influencing dolphin behavior in these dynamic systems.

To my father, Thomas Victor Piwetz, who inspired my love of nature.

You are dearly missed.

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NOMENCLATURE

3RS	Third Runway System
AICc	Akaike Information Criterion with correction
CEDD	Civil Engineering and Development Department
DOC	Department of Conservation (New Zealand)
FSB	Foraging in Association with Shrimp Trawlers
GAM	Generalized Additive Model
GPS	Global Positioning System
GSC	Galveston Ship Channel
HKIA	Hong Kong International Airport
HKIA-N	Hong Kong International Airport - North
HKIA-NE	Hong Kong International Airport – Northeast
HKIA-W	Hong Kong International Airport – West
HKMZB	Hong Kong to Macau and Zhuhai Bridge
HSF	High Speed Ferry
IUCN	International Union for Conservation of Nature
LKC	Lung Kwu Chau
LKT	Lung Kwu Tan
MB	Mid-bay
MPA	Marine Protected Area
NMF	Near Mussel Farm
NMFS	National Marine Fisheries Service

NOAA	National Oceanic and Atmospheric Administration
NS	Nearshore
PAM	Passive Acoustic Monitoring
PCoD	Population Consequences of Disturbance
PRE	Pearl River Estuary
PTS	Permanent Threshold Shift
SC	Sha Chau
SCLKC	Sha Chau and Lung Kwu Chau
SHW	Siu Ho Wan
SSF	Slow Speed Ferry
TMCLKL	Tuen Mun-Chek Lap Kok Link
TTS	Temporary Threshold Shift
USCG	United States Coast Guard
VIF	Variance Inflation Factor

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CHAPTER I

INTRODUCTION

Human and dolphin habitat overlap[1]

Dolphins that inhabit coastal waters are exposed to human presence in the form of recreational and commercial activities (Jefferson et al., 2009; Würsig, 1989) where habitats and resources, such as prey items, are exploited (Fertl and Leatherwood, 1997). Coastal systems are among the most naturally productive areas, and are also among the most threatened by ecosystem alteration due to human activity and development (McGranahan et al., 2007). Human settlement has historically been concentrated in coastal areas that provide natural resources and trading opportunities (McGranahan et al., 2007), and approximately half of the worldwide population currently lives within 125 miles of a coastline. Activities in and near coastal waters include marine shipping and transportation, fisheries and aquaculture, construction and development, habitat alteration, new land formation, oil and gas exploration, boat-based tourism, and recreation. These activities have a physical presence, and also introduce noise into the environment, that can elicit shifts in dolphin behavior, displace prey species, and mask acoustics important in navigation, prey acquisition, and social organization (Jefferson et al., 2009; Jensen et al., 2009; Lesage et al., 1999; Richardson and Würsig, 1997). When human activities overlap with dolphins in coastal habitats, a number of outcomes are possible. In the best case scenario, no disturbance occurs. On the other end of the spectrum, a population or species risks extinction,

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[1] Portions of this chapter are reprinted with permission from Humpback dolphin (Gensu Sousa) behavioural responses to human activities, in: T. A. Jefferson and B. E. Curry (Eds.), *Advances in Marine Biology* by Piwetz S., Lundquist D., and Würsig B., 2015, Academic Press, Oxford.

as in the extreme case of the baiji (Lipotes vexillifer), and a range of potential responses fall between these limits. For example, human activity may influence dolphin vital rates, behavioral time budget, spatial distribution, or social structure, to varying degrees, with potential short-term effects or long-term impacts.

Population consequences of disturbance

To better understand how human activity can affect cetacean (whales, dolphins, and porpoises) behavior and physiology, which may ultimately lead to population-level effects, a U.S. National Research Council committee developed the Population Consequences of Disturbance (PCoD) model (NRC, 2005). The model was originally designed for cetacean responses to acoustic disturbance, later modified to a more general structure that includes all potential sources of human-generated disturbance, and has become a prevailing theoretical framework to assess disturbance to marine mammals (**Figure I-1**). The model distinguishes between responses that have an acute, immediate effect (e.g., a collision with a vessel), and effects that are more chronic in nature (e.g., repeated dolphin-based tourism). The central hypothesis of the PCoD is that small, repeated, non-lethal disturbances can result in changes in physiology and/or behavior that influence an individual's health over time.

Physiological changes may be triggered by the stress response to an extrinsic stimulus perceived as a risk (Moberg, 2000). The acute response to a stressor occurs via the autonomic nervous system, associated with the flight or fight response, by secretion of epinephrine (flight) and/or norepinephrine (fight) into the bloodstream. This response affects body physiology including changes in heart rate, respiratory rate, and blood pressure (Ewbank, 1985; Fair and Becker, 2000; Moberg, 2000). Response may also include a secretion of hormones from the hypothalamic-pituitary-adrenal axis that may have longer-lasting effects on the body by affectingimmune competence, reproduction, and metabolism (Moberg, 2000). Often the goal of studying disturbance of wildlife is to identify impacts that have health consequences (Beale, 2007; Nisbet, 2000). However, these physiological and neurochemical responses are not easily detectable (Stankowich, 2008), especially in free-ranging animals. In some cases, studying behavioral changes allows long-term impacts on animals to be inferred (Lusseau and Bejder, 2007). However, long-term impacts are inherently more difficult to study logistically than short-term changes in animal behavior, particularly for species with long life expectancy and long inter-birth intervals, and long-term datasets are limited in the relatively young field of marine mammalogy.

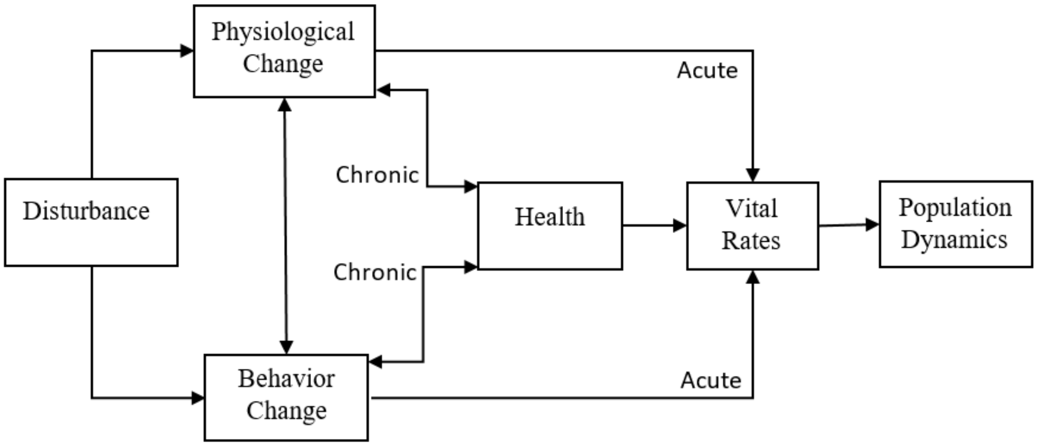

Figure I-1. Conceptual model of population consequences of disturbance. Model shows the relationships linking disturbance to changes in behavior and physiology, health, vital rates, and population dynamics. Adapted from New et al., 2014.

Behavior may change in response to human activity, which can affect the animals' life functions, inherently linked to vital rates, which can ultimately lead to population-level effects (Nowacek et al., 2016; NRC, 2005). Interpreting wildlife behavioral responses to human activity is complex and behaviors are influenced by a variety of natural and human-generated factors. Wildlife responses to extrinsic stimuli likely reflect a ratio of costs (e.g. expending energy or abandoning resources) and benefits (e.g. reducing capture probability) (Frid and Dill, 2002). Over time, repeated short-term behavioral responses may result in changes in activity state, movement patterns, and habitat selection (Fernández-Juricic and Tellería, 2000; Frid and Dill, 2002; Sirot, 2010; Srinivasan et al., 2010), in which time and energy are spent engaged in one biologically significant activity at the expense of another (Dugatkin, 2009; Frid and Dill, 2002). For example, defensive tactics such as increased vigilance may alter foraging patterns, including timing, rate, and location of feeding, which lead to reduced overall energy consumption (Brown, 1999; Christiansen and Lusseau, 2014; Dugatkin, 2009; Preisler et al., 2006). The function of behavior is shaped, in part, by an animal's immediate environment (Rands, 2011); therefore, direct observations in field settings are important to understand how animals use a given habitat, identify areas associated with fundamental biological processes (e.g. foraging, mating, calf-rearing) (Hastie et al., 2004; Stockin et al., 2009), and provide a basis to identify area-specific overlap of human activities that may disrupt behaviors. Such observations may be particularly useful in natural settings involving highly mobile animals where intensive human activity occurs and controlled experimental designs are not logistically feasible (Beale, 2007). In situ studies are important for assessing real-scenario human-wildlife encounters for informing wildlife conservation and management (Cooke et al., 2014; Mann and Würsig, 2014).

Conservation behavior framework

Conservation behavior is a relatively young, developing field that integrates the principles of behavioral ecology with conservation-based wildlife management practices. Two of the key areas of conservation behavior are the management of 1) anthropogenic impacts on wildlife and 2) wildlife in urbanizing environments (Blumstein and Fernández-Juricic, 2010). Studying behavioral responses of wildlife to human disturbance can provide insights into the underlying mechanisms of human-wildlife interactions that lead to the population consequences of disturbance and help reduce conflict through management of human activity. Furthermore, a better understanding of how urbanization contributes to wildlife habitat selection, dispersion, and avoidance-attraction to humans can reduce negative effects of urbanization through practical management.

The conservation behavior framework is a parsimonious conceptual model developed to standardize approaches to bridging the gap between the 2 core disciplines. Three key behavioral ecology domains identified as central to survival and thus to conservation issues, include: 1) movement and space-use patterns, 2) foraging and predator-prey related behaviors, and 3) social behavior and reproduction. The conservation behavior framework proposes that behavior-oriented conservation research focuses on: 1) human impacts on animal behavior (potential stressor stimuli), 2) behavioral indicators (responses to potential stressors), and 3) behavior-based management (Berger-Tal et al., 2011).

Behavioral responses to anthropogenic stimuli

To resolve human–wildlife conflicts, we must first understand how animals behaviorally respond to different types of activity (Beale, 2007). In broad terms, wildlife may find human-generated stimuli aversive (leading to avoidance), reinforcing (leading to attraction), or neutral (Whittaker and Knight, 1998).

Avoidance

Fleeing is a form of avoidance and is the most common short-term behavior observed by prey animals in response to predators (Humphries and Driver, 1970). Several delphinid species have been reported to flee in response to natural predators, including spinner, *Stenella longirostris*, and common bottlenose, *Tursiops truncatus*, dolphins from sharks (Connor and Heithaus, 1996), and dusky dolphins, *Lagenorhynchus obscurus*, from killer whales, *Orcinus orca* (Würsig and Würsig, 1980; Würsig et al., 1997). Examples of human-generated stimuli that might be perceived as threatening include unfamiliar movements or sounds not previously encountered at the individual level or in the phylogenetic history (Dill, 1974; Frid and Dill, 2002). From an evolutionary perspective, anthropogenic activities in the marine environment are a recent occurrence and cetaceans may instinctually respond in the same manner to human presence that they would to predators (Bejder et al., 2009; Frid and Dill, 2002; Lima and Dill, 1990). Short-term effects of human-generated activity on behavior have been demonstrated across a broad suite of odontocete, or toothed whale, taxa and, in some cases, resemble responses to potential predators. For example, some dolphins respond to vessel activity by fleeing, including diving for longer durations (Higham and Shelton, 2011), altering bearing (i.e. swimming direction), and altering swimming speed (Dans et al., 2008; Lundquist et al., 2012; Lusseau, 2006; Nowacek et al., 2001; Stensland and Berggren, 2007; Williams et al., 2002). Reduced or disrupted foraging, resting, and/or socializing bouts have also been documented relative to anthropogenic activity (Christiansen et al., 2010; Constantine et al., 2004; Dans et al., 2008; Lusseau et al., 2009; Stockin et al., 2008; Visser et al., 2011; Williams et al., 2006).

On a larger scale, wildlife may avoid select habitats based on human presence. Some dolphins avoid areas with vessel traffic all together (Higham and Shelton, 2011). Common bottlenose dolphins off Clearwater, Florida avoided important foraging areas when motorboat traffic was high (Allen and Read, 2000). If adjacent vessel-free areas are of equal quality and require minimal energetic costs for animal movement, displacement from a habitat might not be of concern (Nowacek et al., 2007). However, avoidance behavior in response to extrinsic stimuli (Beale, 2007) may prevent animals from exploiting a resource-rich environment or from utilizing their entire home range (Whittaker and Knight, 1998). Continued vessel activity may cause long-term displacement of some animals to a particular area, leading to a decrease in abundance in the local population (Lusseau, 2004). A large-scale avoidance of tourism vessels in Shark Bay, Australia, coincided with a decline in abundance of bottlenose dolphins (*T. cf. aduncus*) in a previously used habitat (Bejder et al., 2006b). The decline was partially attributed to displacement of those dolphins most sensitive to the vessel activity. Boat-based tourism was also implicated in long-term shifts in habitat use by common bottlenose dolphins off New Zealand (Lusseau, 2004). When boat frequency increased, dolphins switched from local avoidance to avoiding the area all together. However, this habitat shift may not have been due entirely to tourism. A decline in abundance may not always have a negative outcome for large and genetically diverse populations, but may have biologically significant consequences for smaller or resident cetacean populations (Bejder et al., 2006b).

High-energy sound source levels associated with modern human activities, such as construction pile driving, explosive detonations, industrial seismic exploration, and military active sonar, can also elicit behavioral responses by marine mammals such as changes in activity state or exposure avoidance (Southall et al., 2007). For example, Blainville’s beaked whales, *Mesoplodon densirostris,* have demonstrated behavioral responses including disrupted foraging bouts and avoidance of impact areas of up to tens of kilometers (Tyack et al., 2011). Lower-energy underwater sound (e.g. chronic engine noise, dredging, or seismic/sonar further from the source) may also elicit shifts in behavior.

The context in which threatening stimuli appear may also influence responses. For example, ungulates, terrestrial mammals related to dolphins, respond to stimuli in a less threatened manner when they occur in a predictable context (e.g. humans hiking on designated trails, rather than random movement off trails) (Stankowich, 2008). Furthermore, ungulates tend to flee at greater distances when stimuli approach rapidly or directly versus slowly or indirectly (Stankowich, 2008). A comparable example in the marine environment might be a slow-moving cargo ship along a predictable shipping lane versus a fast-moving and meandering non-commercial motorboat with a less restricted route.

Attraction

Attraction, the opposite of avoidance, is defined by the movement of an animal toward a particular stimulus that may result in acquiring food, shelter, or other positive reinforcements (Whittaker and Knight, 1998). Cetaceans are often attracted to fishing vessels where acquisition of concentrated prey sources may be facilitated (Fertl and Leatherwood, 1997). Many cetacean species exploit gillnets, commercial trawling nets, and fishing hooks that congregate food sources and make them easier to access than naturally occurring, patchily distributed prey (Fertl and Leatherwood, 1997; Gilman et al., 2007; Jefferson and Curry, 1994; Perrin et al., 1994).

Attraction behavior may seemingly benefit animals in the short term, yet close proximity to fisheries can be risky with potentially negative consequences for both dolphins and humans (Fertl, 2009; Garrison, 2007; Hung and Jefferson, 2004; Read, 2008). These risky attractants, in which prey acquisition may be facilitated, increase proximity to boat propellers and fishing gear that increase the risk of mortality due to vessel strike or incidental bycatch, or injury due to propeller lacerations or net entanglement (Dwyer et al., 2014; Parsons and Jefferson, 2000; Sutaria and Jefferson, 2004; Wade, 1995). Furthermore, dolphins may interfere with commercial fishing operations by taking fish from gear, disturbing prey, or damaging fishing equipment. In some cases, real or perceived damage caused by dolphins elicits hostile responses from fishers including lethal and non-lethal deterrence methods (Fertl, 2009).

In cases of wildlife food provisioning, animals may be attracted to easily obtained food sources. However, recipients may ultimately become dependent on food supplementation that can alter the quality of their natural diet. Animals may also become food-aggressive toward humans that do not offer food (Whittaker and Knight, 1998), creating negative interactions for both wildlife and humans. In Monkey Mia, Western Australia, calves of provisioned female bottlenose dolphins (*T. cf. aduncus*) received reduced maternal care and increased mortality compared to those of non-provisioned females (Mann and Kemps, 2003; Mann et al., 2000). Calf survivorship increased with improved tourism regulations, but calf behavioral development was affected and the long-term impacts of provisioning, in this case, remain unclear (Foroughirad and Mann, 2013).

Many species of dolphins have also been recorded approaching vessels and preferentially selecting to swim along pressure waves created by moving vessels, at both the bow and stern positions (Williams and Friedl, 1992). They have been described as riding the pressure waves of vessels in a manner similar to human surfers riding oceanic waves (Fish and Hui, 1991). Dolphin bow- and stern-riding may have adapted from a natural form of wave-riding, as seen on the lee slopes of large oceanic waves and nearshore surf (Würsig, 2018). Dolphins have also been observed riding pressure waves created by large baleen and sperm whales. Although the reasons for riding pressure waves is not fully understood, play is likely.

Neutral

In some cases, there may be no observable behavioral response to extrinsic stimuli. In these cases, there may truly be no disturbance. Alternatively, animals may be responding in discreet ways that are not easily detectable. Internal physiological responses, as represented in the PCoD model, may be occurring. For example, Humboldt penguins, *Spheniscus humboldti*, showed a significant increase in heart rate in the presence of humans, and a subsequent decrease in breeding success, with no observable behavioral reactions (Ellenberg et al., 2006). Furthermore, animals that respond most noticeably to extrinsic stimuli may actually be less affected than individuals that display little to no behavioral changes (Beale and Monaghan, 2004). Physically weaker individuals may lack the capacity to respond in the same way or at the same intensity as healthy animals. For example, ruddy turnstones, *Arenaria interpres*, in poor nutritional condition, showed reduced scanning, fled when threatening stimuli were closer, and decreased flight distance from threatening stimuli, when compared to those in better condition (Beale and Monaghan, 2004).

Management considerations

In many regions where dolphins and humans overlap, few behavior-sensitive regulatory or management frameworks exist, and especially lacking are plans with long-term management in mind (Higham et al., 2009). Even when regulations are in place, enforcement is often absent or ineffective, particularly in remote locations. Adaptive management is a process that evolves based on ongoing review of management goals and methods are adjusted as new information is obtained (Ban et al., 2012; Walters and Hilborn, 1978). This iterative process includes several steps: planning, implementing, monitoring, reviewing, learning, revising, and repeating (Ban et al., 2012), and may be especially important in dynamic environments with shifting environmental and anthropogenic input. Adaptive management benefits from rapid implementation of revised protocols, and may be more challenging in developed countries with structured top-down legislative systems (Ban et al., 2012).

One of the biggest challenges to coastal dolphin conservation is protecting and maintaining suitable high-quality habitat, particularly in developing and densely populated regions. One potentially effective tool for protecting portions of dolphin habitat is proper designation and management of Marine Protected Areas (MPAs) in known dolphin “hotspots”, especially where site fidelity has been described. Ideally, MPAs should be truly protected with effective enforcement and restriction of development, fisheries, and other vessel activity. MPA boundaries, as well as travel corridors between protected areas, should be developed and managed with knowledge of dolphin movement patterns and habitat use. Research should be ongoing, with adaptive management schemes in place, in order to modify boundaries according to shifts in dolphin occurrence and behavior. With this approach, past successes and shortcomings can be gleaned to inform future approaches.

In areas where MPA’s are not feasible, such as economically important shipping channels created for transportation, site-specific regulations can be introduced to reduce behavioral disruption of dolphins. The U.S. Fish and Wildlife Department applies the term ‘mitigation’ to natural resources, at the landscape-scale, as a means to “avoid and minimize damage to natural resources and to effectively offset remaining impacts”. In doing so, the overall goal is to compensate for loss, or achieve “a net gain in conservation outcomes, or at a minimum, no net loss of resources and their values, services, and functions” (Ashe, 2016). In the context of marine mammal conservation in many regions, mitigation also regularly includes monitoring and reducing behavioral changes of animals. Solutions used to mitigate behavioral disturbance are rooted in altering human behavior and may include designating and enforcing vessel speeds, regulating marine mammal tourism, and modifying commercial fishing practices. In many areas, voluntary codes of conduct have been established, particularly in the case of marine mammal tourism. Though well-intended, voluntary recommendations are often inadequate without practical hands-on operator training and enforceable regulations. A formal permitting requirement for commercial dolphin-based tour operators, including regulations and restrictions, may be the best way to improve commercial dolphin viewing to minimize disturbance to dolphins. The New Zealand Department of Conservation (DOC) serves as an example of how a formal permitting process aids in managing the rapidly growing commercial marine mammal tourism industry with an aim to minimize effects on marine mammal behavior. Research-based recommendations are often integrated to better inform regulatory and management decisions. For example, permits for viewing Hector’s dolphins (*Cephalorhynchus hectori*) off New Zealand, including restrictions on vessel number and operating time, were formally established by the DOC based largely on research findings (Bejder, 1997). Based on researcher recommendations from another study off Kaikoura, New Zealand, changes were made to operating practices around dusky dolphins including limits on the number, timing and duration of vessel interactions (Barr and Slooten, 1999; Markowitz et al., 2009).

Several mitigation efforts have been applied to fisheries practices within dolphin ranges, including gear modification and restricted fishing zones. Off Angola, commercial trawlers are required to operate several km from the coast, which may reduce interactions with humpback dolphins. Off Hong Kong, some humpback dolphins (*Sousa chinensis*) historically followed and fed behind active commercial fishing trawlers (Jefferson, 2000), including pair, stern, shrimp, and hang trawlers. These large-scale trawling activities were banned from Hong Kong waters in late 2012, in part to improve the local ecosystem that experienced declining fish stocks (Hung, 2015). However, illegal trawling may still occur sporadically (Hung, 2014), often times at night. Although enforcement can be an issue, these modifications highlight how management efforts can contribute, both directly and indirectly, to dolphin conservation.

A number of mitigation measures have been developed to minimize impacts of industrial noise in marine mammal environments. However, most approaches for acute sound sources include relatively small safety zones, warning signals, and acoustic decoupling aimed at minimizing risk of direct physical injury with less consideration of behavioral responses at varying distances (Jefferson, 2000). Creative techniques have been developed in humpback dolphin habitat aimed to reduce potential communication interference and behavior modification. For example, off Hong Kong, a large rubber hose that produced a screen of air bubbles was designed to reduce sound transmission during percussive pile driving activity in *S. chinensis* habitat. The bubble curtain attenuated some sounds in isolated areas, primarily in the single digit kHz frequency range that is within hearing sensitivities of some odontocetes. However, many humpback dolphins left the area immediately after pile driving activity occurred. It is not clear what other factors may have contributed to the shift in dolphin distribution or how behavior may have differed if the bubble curtain was not in use (Würsig et al., 2000). Real-time visual data collection during noise-intensive construction is an excellent example of future research needs.

Finally, stakeholder involvement in developing regulations may serve to increase the overall effectiveness of management efforts (Ban et al., 2012). Marine mammal regulation is handled at the national level in many countries, and stakeholders will vary in each specific region. Local stakeholder involvement serves to increase knowledge and conservation awareness, leading to improved compliance, and may include tour-boat operators, commercial fishers, shipping managers, marine mammal recovery organizations, researchers, and the local community at large. In this way, ecological, social, and economic systems can be simultaneously addressed.

Chapter overview - three case studies

The broad objective of this dissertation is to assess the effects of human-generated activities on free-ranging dolphin behavior and movement patterns, and provide science-based management recommendations. The focus is on one component of the PCoD model: short-term behavioral responses to chronic human activity at the individual level. The second key component, physiological changes, is important to the overall PCoD model, but it is beyond the scope of this fully non-invasive approach. The conservation behavior framework is applied to three different coastal delphinid species, inhabiting diverse ecosystems with varied human pressures, and findings are discussed and compared. The behavioral component of this research focuses on short-term findings, spanning months to several years of data collection. These short-term effects contribute to our understanding of animal behavior and lay the foundation on which long-term studies are built. Future work, spanning decades, can ultimately be incorporated to detect long-term impacts at the population level. This dissertation is organized into the following chapters:

Chapter II: Common bottlenose dolphin behavior in an active narrow seaport

This chapter examines how common bottlenose dolphins that forage in a narrow, congested waterway respond to heavy vessel traffic in a confined space. Variation in dolphin behavior and movement patterns are analyzed based on the presence and absence of specific vessel types, including dolphin-targeted tour boats, commercial shrimp trawlers, and private recreational boats. Management recommendations for reducing behavioral harassment are suggested.

Chapter III: Effects of coastal development on Indo-Pacific humpback dolphin habitat-use off Hong Kong

This chapter examines how Indo-Pacific humpback dolphin behavior and spatio-temporal occurrence vary based on vessel presence and proximity to maritime construction activities off Hong Kong, one of the most densely urbanized coastal communities in the world. Short-term changes across solar and oceanographic seasons, time of day, and location relative to proximate human activity are quantified and management suggestions are offered.

Chapter IV: Dusky dolphin behavior near mussel farms in New Zealand

This chapter examines how dusky dolphin behavioral activity states and movement patterns vary based on defined habitat patches within a bay that supports marine shellfish aquaculture. An understanding of habitat patch use and movement patterns in response to ecologically diverse and artificially altered environments gleaned from this research can be applied to other marine environments where dolphins and aquaculture overlap, and more broadly across diverse taxa where physical obstructions infringe on habitat.

Chapter V: Research synthesis and recommendations

This chapter summarizes findings from chapters II-IV, makes comparisons among case studies, including human-generated activity and behavioral indicators of disturbance, and discusses implications for long-term management.

CHAPTER II

COMMON BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) BEHAVIOR IN AN ACTIVE NARROW SEAPORT

Introduction

Marine mammals that inhabit near-shore waters are exposed to recreational and commercial activities (Jefferson et al., 2009; Würsig, 1989) where habitats and resources, such as prey items, are exploited by humans (Fertl and Leatherwood, 1997). Common bottlenose dolphins (*Tursiops truncatus*) and other coastal-living marine mammal species are often found in or near natural and artificially-dredged channels that may reflect areas of abundant and concentrated fish aggregation (Bailey and Thompson, 2006; Hastie et al., 2004; Parra, 2006; Wilson et al., 1997). The ability of dolphins to exploit features of channels, such as steep slopes, may increase their efficiency of prey detection and acquisition by providing barriers with which to herd prey (Allen et al., 2001). Natural and dredged channels created for large vessel passage may present increased feeding opportunities for dolphins. However, exposure to vessels is intensified in these channels, particularly in narrow channels (<1km wide) where space available for horizontal movement is limited. Accessible prey may be a risky attractant in seaports, where heavy vessel activity and dolphins overlap with potentially negative consequences. Dolphins may not avoid high risk areas that support key resources such as prey, particularly if adjacent habitats are not equivalent (Gill et al., 2001).

Common bottlenose dolphins (hereafter in this chapter ‘dolphins’) occur in the narrow and congested artificially-dredged Galveston Ship Channel (GSC), off the coast of Texas, year-round, yet little is known about their habitat use and behavior relative to diverse vessel activity.

Dolphin behavior has been studied extensively, but the behaviors of populations off Texas have received less attention than those in other areas such as Florida (Scott et al., 1990) and Australia (Foroughirad and Mann, 2013). Several studies have focused on habitat use of deep, narrow channels, but few have included dolphin responses to diverse vessels in these active seaports. Delphinids in other areas have been described as altering behavior in the presence of vessels. For example, common dolphins (*Delphinus sp*.) spend less time foraging in the presence of tour boats in open waters off New Zealand, which raises concerns about disruption of biologically important behaviors (Meissner et al., 2015). The GSC has been suggested as a major feeding area for dolphins in the Lower Galveston Bay region, where prey characteristics may be the most likely predictor of dolphin presence, given the deep channels where highly-saline waters and prey species flow in from the Gulf of Mexico (Moreno, 2005). Foraging is a critical component for predators, and the potential for disruption of this behavior for dolphins in the GSC is high.

There are approximately 70 deep draft (>4.3m deep) human-altered commercial seaports in the U.S., many of which are onshore terminals linked to coastal regions (NRC, 2004) where diverse vessel activity may overlap with dolphins. These seaports are used by commercial vessels and are easily accessible for public recreational use, necessitating management of diverse vessel types by local and federal agencies. Galveston Bay is the largest estuary in Texas, the seventh largest in the United States, and supports three major shipping ports (Houston, Texas City, and Galveston) (Leatherwood, 2016). The GSC is narrow, carved out between two land masses, and ranks among the top 50 U.S. ports in terms of total tonnage. The GSC has the capacity to accommodate large, fully loaded ships and is an important contributor to the regional economy (Hegar, 2015). In addition to the transportation sector, for which it was developed, the GSC supports commercial fisheries (Galveston “Mosquito” Shrimp Fleet), dolphin-based tourism (BayWatch Dolphin Tours, Galveston Harbor Tours, Galveston Water Adventures), high-speed amusement boat rides (Galveston Water Adventures), and private recreational boating and fishing. The Ports and Waterways Safety Assessment listed the Galveston Channel as having heavy congestion and the most diverse mix of vessel types within the Houston-Galveston Port area where “no one follows a traffic scheme” (USCG, 2009). There is no formal speed limit in the area, with a suggested “no wake” speed. Dolphins that utilize this area may potentially tolerate vessel disturbance for concentrated prey assemblages (Henningsen and Würsig, 1991). However, the National Marine Fisheries Service threat assessment identified boat traffic and tourism among the top 4 of 19 potential threats to common bottlenose dolphins in Galveston Bay (including the GSC) (Phillips and Rosel, 2014).

Interpreting wildlife responses to human activity is complex and behaviors can be influenced by a variety of natural and human generated factors. Many conservation-based studies involving marine mammals and human activity focus on direct interactions that lead to injury or mortality, such as vessel strike, fisheries bycatch, and entanglement (Moore et al., 2009; Van Waerebeek et al., 2007; Weir and Pierce, 2013). Signs of direct injury are observed in the Galveston Bay region (e.g., fishing gear entanglement, propeller wounds), but it is unclear how these incidents relate to overall mortality (pers. comm. Heidi Whitehead, TMMSN). Anthropogenic activity also affects marine mammals in ways that are less obvious, such as altering behavior (Lima and Dill, 1990; Srinivasan et al., 2010), and can be detected using behavioral indicators of disturbance (Berger-Tal et al., 2011). Direct observations in field settings are important to understand how animals use a given habitat, identify areas associated with fundamental biological processes (e.g. foraging, mating, calf-rearing) (Hastie et al., 2004; Stockin et al., 2009), and provide a basis to identify overlapping human activities that may disrupt behaviors. Such observations may be particularly useful in natural settings involving highly mobile animals and intensive human activity, where controlled experimental designs are not logistically feasible (Beale, 2007), and are important for assessing real-scenario human-wildlife encounters for informing wildlife conservation and management (Cooke et al., 2014; Mann and Würsig, 2014). The conservation behavior framework, a parsimonious model that aims to link behavior and conservation, proposes that behavior-oriented conservation studies focus on: 1) human impacts on animal behavior (potential stressor stimuli), 2) behavioral indicators (responses to potential stressors), and 3) behavior-based management (Berger-Tal et al., 2011).

A variety of short-term behavioral responses by odontocetes, including horizontal and vertical movements, have been described relative to marine vessel traffic. Some dolphins respond to vessel activity by fleeing, including diving for longer durations, swimming away, or avoiding areas with vessel traffic altogether (Higham and Shelton, 2011). Dolphins have also been observed altering grouping patterns or inter-individual distances when vessels are present (Bejder et al., 2006a). Alterations in swimming direction and swimming speed, and reduced or disrupted foraging, resting, and socializing bouts have also been reported in response to vessels, including dolphin-based tourism (Christiansen et al., 2010; Constantine et al., 2004; Dans et al., 2008; Lundquist et al., 2012; Lusseau, 2006; Nowacek et al., 2001; Stensland and Berggren, 2007; Stockin et al., 2008; Williams et al., 2002). Metrics used to identify shifts in behavior include quantifying inter-breath intervals, distance to nearest neighbor, swimming speed, reorientation rate, and linearity. Not all behavioral responses are classified as avoidance, and dolphins may alter behavior to approach vessels. For example, dolphins may be attracted to discarded bycatch, or prey stirred up by, or caught in, the nets of commercial trawlers (Fertl and

Leatherwood, 1997). These risky attractants, in which prey acquisition may be facilitated, increase proximity to boat propellers and fishing gear that increase the risk of injury to dolphins via propeller lacerations or net entanglement. In the U.S., disturbing a marine mammal's behavior pattern is considered harassment, as defined by the US. Marine Mammal Protection Act of 1972 (MMC, 2007), and is a federal offense. Harassment in this context includes any act of pursuit that has the potential to disturb a wild dolphin by disrupting behavioral patterns, including, but not limited to, feeding (MMC, 2007).

In this study, dolphin behavior was investigated in the absence and presence of diverse vessel traffic in the narrow and deep-dredged seaport of Galveston, and provides evidence-based suggestions to balance marine mammal protection and maritime vessels. Specific objectives include: 1) determine how dolphin behavioral activity states vary based on natural (time of day, dolphin group size, and calf presence) and anthropogenic (vessel presence) factors 2) quantify movement patterns (swimming speed, reorientation rate, linearity) to assess dolphin behavioral responses to diverse vessel traffic, and 3) provide recommendations for behavior-based management to contribute to conservation efforts. Findings from this study can be broadly informative to areas where delphinids and vessels overlap, and more specifically, where delphinids occur in narrow, deep channels that support heavy vessel traffic.

Methods

Ethics Statement

Data collection was conducted from elevated, stationary, shore-based platforms in which no approaches to or harassment of animals or vessels were performed. No permits were required for this fully non-invasive method.

Study Area

The Galveston Ship Channel (29º N, 94º W) is located on the upper Texas Coast, at the mouth of the Galveston Bay Estuary, with adjacent access to the Gulf of Mexico via Bolivar Roads (**Figure II-1**). The channel is narrow, between 370m-980m wide, extends 6.8km in length, and has a steep U-shaped human-altered slope with maximum dredged depths of 14m (Sallese, 2013; USACE, 2014). Bottlenose dolphins are the only marine mammals that are regularly observed in the Galveston Bay area, although manatees (*Trichechus* spp.) are occasionally reported (pers. comm. Heidi Whitehead, TMMSN).

Sampling Methods

Elevated land-based theodolite tracking of bottlenose dolphins and vessels was conducted along the GSC in the summer season (June-August) of 2013. Field observations totaled 31 days and 158 hours on effort. Two observation areas were selected based on their close proximity to the water, elevation above sea level, and unobstructed views of the channel (**Figure II-1**). A digital theodolite (Sokkia/Sokkisha Model DT5) with 30-power magnification and ±5-second precision was used to obtain vertical and horizontal angles of bottlenose dolphin and vessel positions (Würsig et al., 1991). *Pythagoras* software (v 1.2) (Gailey and Ortega-Ortiz, 2002) was used to record and convert theodolite angles to geographic coordinates, record surface behavioral states, and facilitate data management for analyses. Hand held binoculars (7x50 magnification) were used to conduct systematic scans of the viewable area at the start of each tracking session to locate dolphins. Data collection involved three team members - a theodolite operator, an observer, and a data-entry computer operator. To minimize inter-individual variation in data gathering, theodolite tracking was conducted by one experienced operator at all times. To reduce

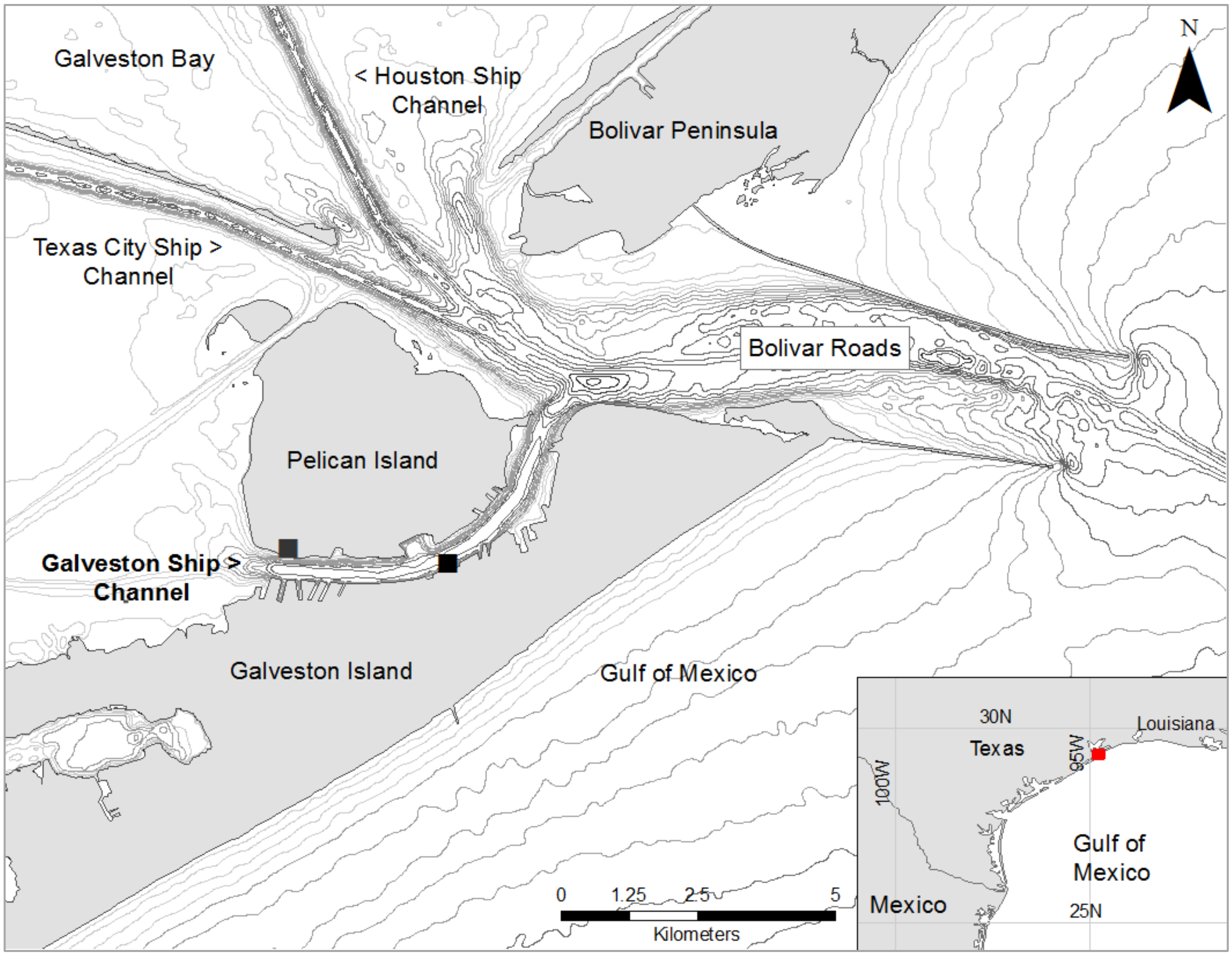

Figure II-1. Study area showing theodolite observation platforms (■) and isobaths at 5m intervals. Map created using ArcGIS® software and basemaps by Esri.

potential for visual fatigue associated with computer and binocular use, the observer and computer operator rotated positions every hour.

Dolphin groups were defined using a combination of the 10m chain rule (individuals within 10m of another individual are part of the same group) (Smolker et al., 1992) and coordinated activity (Mann et al., 2000). Focal follow (Altmann, 1974; Mann, 1999) sessions were initiated once dolphins were located. Often, only a single individual or group was present within the study area making focal group selection straightforward. If multiple groups were present during times of high vessel traffic, only one would be designated for the focal follow. To reduce bias in group selection, the larger group was selected for the first session, the smaller group for the subsequent session, and so on (Mann, 1999). When possible, multiple individuals or groups were followed simultaneously. If group members split during a follow, an attempt was made to alternate between following the smaller group the first time members split, the larger group if group members split up again, and so on.

Dolphin data were recorded continuously and subsampled at 60-second intervals *post hoc*. Focal dolphin data included geographic position, group size, calf presence/absence, and predominant group (≥50% of individuals) behavioral state. Age classification included adults and calves only, excluding juveniles given the difficulty in accurately distinguishing this class consistently. Calves were classified based on size (2/3 the length of an adult, or less) and swimming position (echelon position “beside and slightly behind an adult”; (Shane, 1990). Surface behavioral states were classified using a combination of definitions provided by Henderson (2004), Fertl (1994a), and Shane (1990) (**Table II-1**). Focal individuals were tracked by fixing theodolite crosshairs on the animals’ body at the water line. Groups were tracked by recording positions based on a central location within the group (Bejder, 2005; Lundquist et al., 2013). Focal follows continued until the individual or group was lost, moved beyond the range of reliable visibility (>3.5km), or environmental conditions obstructed visibility (e.g., intense haze or fog, Beaufort sea state >3, or sunset).

All vessels that moved within approximately 500 m of the focal individual/group were tracked via theodolite. Vessel data were recorded continuously, alternating with dolphin data, and included geographic position, vessel type, vessel name (if available), and activity (e.g., travelling, stationary, following dolphins). Due to small sample size, vessels were broadly categorized *post hoc* based on vessel type, vessel length and movement characteristics (**Appendix A Table 1**).

Table II-1. Bottlenose dolphin behavioral state definitions

Behavioral State	Definition	Source
Foraging	Variable direction of movement, generally remaining in the same area, high arching dives, fish chasing or tossing, little apparent interaction between individuals	(Henderson, 2004)
Foraging in association with shrimp trawlers (FSB)	Repeated dives in varying directions around the side or behind the stern of shrimp trawlers	(Fertl, 1994a)
Resting	Moving very slowly or drifting in one direction	(Shane, 1990)
Socializing	Variable direction of movement, individuals in close proximity or touching, often interacting, frequent surface active behavior	(Henderson, 2004)
Traveling	Moving steadily or rapidly in one direction Often synchronous and frequent surfacings	(Shane, 1990) (Henderson, 2004)

A Before-After-Control-Impact (BACI) experimental design is often used to monitor effects of variables over time by comparing responses in a treatment area with a control area. This design was not possible due to the lack of an ecologically similar adjacent site utilized by dolphins, with no vessel traffic, to that of the deep and narrow GSC. Likewise, a Before-During-After (BDA) experimental design, often used to monitor variables over time within the same site, was not logistically feasible. All vessels could not be experimentally controlled in this heavily saturated and economically important shipping port. A natural variation of the BDA design was used by collecting data in the presence (test) and absence (control) of the potential stressor (opportunistic vessel approaches) within the same area (Bejder and Samuels, 2003) and a sophisticated modelling framework was applied to control for confounding effects.

Dolphins were observed every day of data collection, totaling 278 groups tracked via theodolite, with nearly 6,000 data records. Data were filtered to exclude bottlenose dolphin tracks with fewer than 2 positional fixes, less than 10 minutes in duration, and/or erroneous positions with maximum swim times exceeding known values for bottlenose dolphins (Rohr et al., 2002). For standardization among observations that varied in duration, each focal follow was binned into multiple 10-minute segments (Bejder et al., 1999; Lundquist et al., 2012), comprising 11 interpolated positional fixes per segment, with associated data, based on 60 sec intervals. Of the 278 groups tracked, 167 10-minute segments met the criteria for analyses. The time interval was selected to avoid errors associated with non-linear travel. The number of segments per focal follow varied based on duration (e.g., a group followed for 30 minutes would have 3 segments, a group followed for 40 minutes would have 4 segments). Because successive observations of animal movements pose problems due to lack of independence, temporal autocorrelation was performed during preliminary analysis to identify potential pseudo-replication (i.e., not statistically independent) (Dray et al., 2010) for groups with more than one 10-minute segment. Issues of collinearity among potential explanatory variables were also assessed via augmented pairs plots and correlation coefficients >0.60 were considered to have potential masking effects. If collinearity was expressed among a pair of variables, the most interpretable variable was preserved, and the other variable was dropped.

Dolphin response variables that were calculated for each 10-minute segment included mean swimming speed, reorientation rate, and linearity. Response variables were transformed (Log10 for swimming speed, Square Root for reorientation rate, and Empirical Logit for linearity) to approximate a normal distribution. Candidate explanatory variables for each segment included time of day, dolphin group size, calf presence/absence, predominant dolphin behavioral state, number of vessels present, and type of vessels present. Sunrise and sunset varied throughout the summer season, so a time of day index was calculated to represent a percentile of daylight hours where sunrise =0 and sunset =1. Swimming speed (km/hr) was calculated by taking the distance travelled and dividing by the duration between two consecutive dolphin positions (Gailey et al., 2007). Reorientation rate (degrees/minute) was calculated by taking the sum of bearing changes within a segment and dividing by the total duration of that segment. Linearity is an index of net movement ranging from 0 to 1, with 0 representing no net movement and 1 representing moving in a straight line. Linearity was calculated by dividing the net distance between the first and last fix of a segment by the sum of all distances travelled between each of the 11 interpolated positional fixes within each segment. The 10-minute segments calculated for movement analysis were also used to analyze behavioral state data. However, all 11 data points within each segment were considered, totaling 1,837 records, due to potential fluctuating behavior within each segment.

It was necessary to analyze dolphin movement when no vessels were present with the focal individual/group to establish a control. The National Marine Fisheries Service (NMFS) Southeast Region suggests that vessels maintain a minimum distance of 45m from dolphins (NOAA, 2017). For this study, vessels were considered “present” when traveling within 100m of the focal individual/group. The distance threshold encompasses the NMFS suggested distance of at least 45m and extended to 100m (Williams and Ashe, 2007) to include dolphins that were actively following shrimp trawlers (hereafter in this chapter ‘trawlers’). A theodolite can determine the position of only one target at a time; therefore, to calculate accurate distances of vessels from dolphins, vessel positions were interpolated *post hoc* relative to binned dolphin positions and times. The “no vessel” category included dolphin tracks for which no moving vessels were present during and for at least 10 minutes prior to the focal follow to reduce the potential that dolphin movement was influenced by recent vessel presence.

Statistical Analysis

Univariate and multivariate statistical analyses were conducted, including log-likelihood ratio and Chi-square contingency tests to assess nominal categorical data (i.e., behavioral states), binomial *z* score and Freeman-Tukey Deviate (FTD) post hoc tests to assess which factors occurred more or less frequently than expected by chance, and generalized additive models (GAMs) to evaluate continuous numerical data (i.e., movement patterns). The FTD *z* score decision rule was based on the critical value 0.95, and the binomial *z* score decision rule was based on 1.96. Group size categories were pooled together to meet expected frequency requirements (minimum expected value >5). Linear mixed-effects modelling was run to detect autocorrelation, using the lme function (package nlme) in program R. The fully saturated linear mixed-effects model incorporated fixed effects of time of day and vessel category, and the random effect of successive segments from a single dolphin focal group. The best fitting model for swimming speed included the fixed factor of vessel category and no significant autocorrelation was found in the residuals. The models including both fixed factors did not show significant autocorrelation either. The best fitting model for reorientation rate and linearity included an interaction between both fixed factors and no significant autocorrelation was found in the residuals.

The GAM framework was applied to relate dolphin movement patterns (i.e., swimming speed, reorientation rate, linearity) to natural (time of day, group size, calf presence, predominant group behavioral state) and anthropogenic (vessel number, vessel category) candidate explanatory variables. The candidate explanatory variable ‘vessel number’ was dropped to address issues with multicollinearity. No significant collinearity was detected among remaining candidate explanatory variables, based on aug.pairs plots (i.e., no values >50%) and Variance Inflation Factor (VIF) values (i.e., no values >10). The fully saturated GAM incorporated the fixed effects of time of day, dolphin group size, calf presence, behavioral state, and vessel category, and the random effect of successive segments from a single dolphin focal group. Models were run using the multiple generalized cross-validation (mgcv) package in program R (Wood, 2006) appropriate for detecting trends in complex data that are multivariate and nonlinear (Hastie and Tibshirani, 1986). Generalized additive models incorporate smoothing terms, fitting data locally rather than globally (Quinn and Keough, 2002), with a penalty for excessive flexibility (Wood, 2006; Wood, 2008). Flexibility was determined by the number of knots for each smooth term. The default value of 10 knots, set by package mgcv, was used unless there were fewer than 10 categories per term, in which case the knot value was lowered. Models were tested with all combinations of the fixed factors and Akaike Information Criterion correction (AICc) values were calculated and compared. AICc is derived from AIC and is appropriate for smaller datasets where $n<40$ data records per parameter (Burnham and Anderson, 2004; Hurvich and Tsai, 1989). These models evaluate candidate explanatory variables simultaneously, reducing problems associated with many step-wise techniques. Model selection was based on adj-R^2 (high), GCV (low), and deviance explained (high).

Microsoft Excel 2013 was used to conduct computational analysis of swimming speed, reorientation rate, and linearity and to calculate log-likelihood and binomial *z* score statistics; R statistical software (2.14.1) was used to perform exploratory work, autocorrelation tests, and GAM analyses; and ArcMap (v 10.2.2) was used to produce maps.

Results

Behavioral Activity States

Observed dolphin behavioral states varied significantly from values expected by chance (Chi-square test, χ^2=1216.38, n=1,837, df=3, P<0.001). Foraging (57%, n=1052) and socializing (27%, n=501) were observed more than expected by chance, and travelling (5%, n=96) and resting (10%, n=188) were observed less than expected by chance (**Figure II-2**). Foraging in association with trawlers accounted for 30% and foraging without trawlers accounted for 27% of observed behavior.

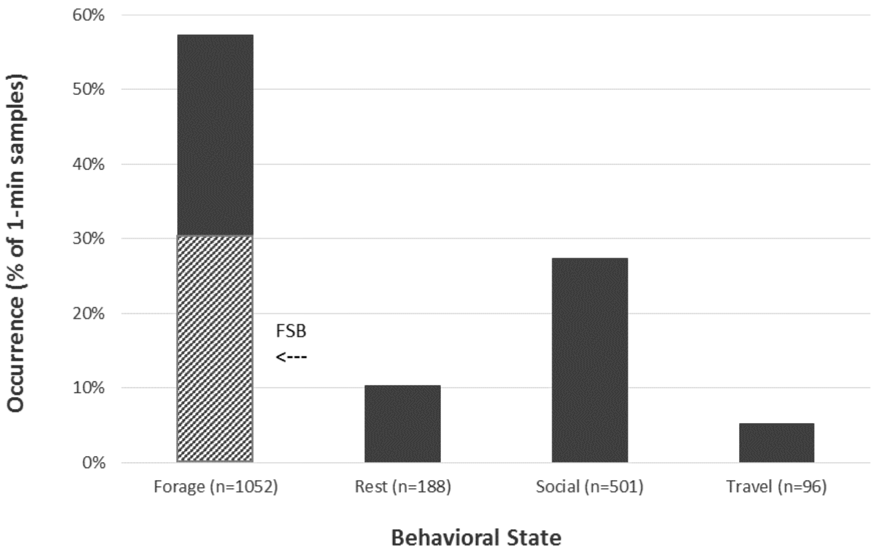

Figure II-2. Behavioral activity states of bottlenose dolphin groups in the Galveston Ship Channel. FSB indicates foraging in association with shrimp trawlers.

Dolphin behavior varied significantly by time of day (log-likelihood ratio test, G^2=328.13, n=1,837, df=8, P<0.001; **Figure II-3**). Post hoc tests showed that if a sample occurred during the morning, dolphins were more likely to be foraging in association with trawlers (*z*=8.84) than at other times of day. During mid-day, dolphins were more likely to be socializing (*z*=5.99) than at other times. During the afternoon, dolphins were more likely to be foraging (*z*=9.08) than during mid-day, and more likely to be resting (*z*=3.16) and traveling (*z*=3.36) than in the morning.

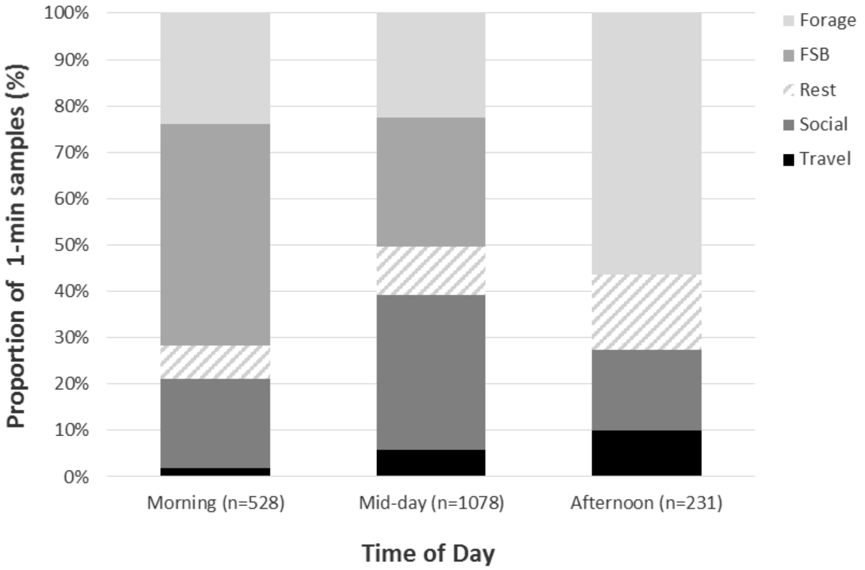

Figure II-3. Bottlenose dolphin behavioral activity states based on time of day, percentile from sunrise (0) to sunset (1). FSB indicates foraging in association with shrimp trawlers.

Dolphin behavior varied significantly with group size (G^2=888.49, n=1,837, df=16, P<0.001; **Figure II-4**). The mean group size was 3.85 dolphins (SD=±2.21) with a range of 1-12 dolphins, similar to prior findings from the early 1990’s with a range of 1-15 dolphins (Fertl, 1994a). Post hoc tests showed, in general, if a sample occurred in larger groups, dolphins were more likely to be foraging in association with trawlers (*z*=19.07, $\bar{x}$ =5.68±SD 2.45), or socializing (*z*=14.57, $\bar{x}$ =4.89±SD 1.80), than in smaller groups. If a sample occurred in smaller groups, dolphins were more likely to be foraging without trawlers (*z*=16.98, $\bar{x}$ =2.66±SD 2.02). If a sample occurred in groups of 2-4 individuals, dolphins were more likely to be resting (*z*=7.28, x̄ =2.89±SD 1.15), and if a sample occurred in groups of 2, dolphins were more likely to be traveling (*z*=5.02, x̄ =3.50±SD 2.40).

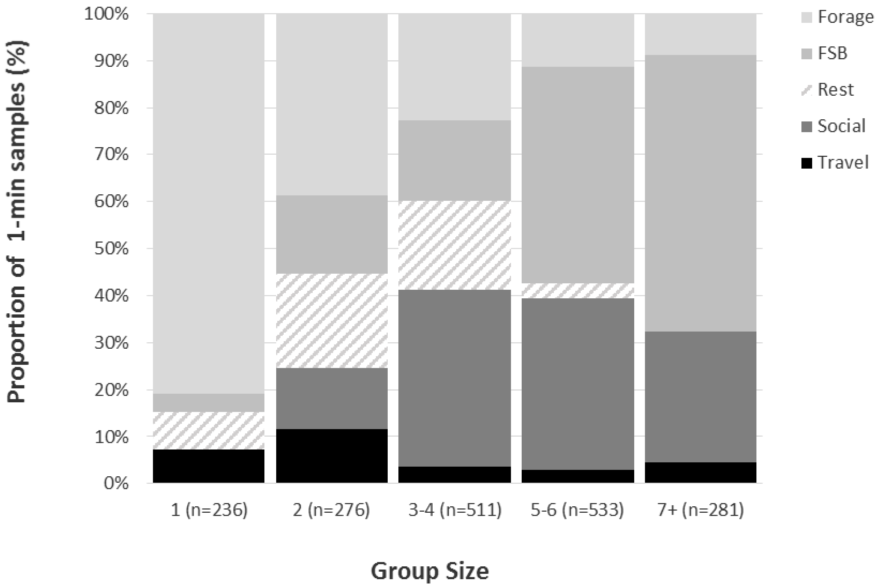

Figure II-4. Bottlenose dolphin behavioral activity states based on group size. FSB indicates foraging in association with shrimp trawlers.

Dolphin behavior varied significantly with calf presence (log-likelihood ratio test, G^2=93.162, n=1,837, df=4, P<0.001; **Figure II-5**). At least one calf was present in 20% (n=373) of the groups tracked. Post hoc tests showed that if calves were present in a sample, dolphins were more likely to be socializing (*z*=4.14) or foraging in association with trawlers (*z*=3.35) and less likely to be resting (*z*=-5.83) or foraging without trawlers (*z*=-4.04).

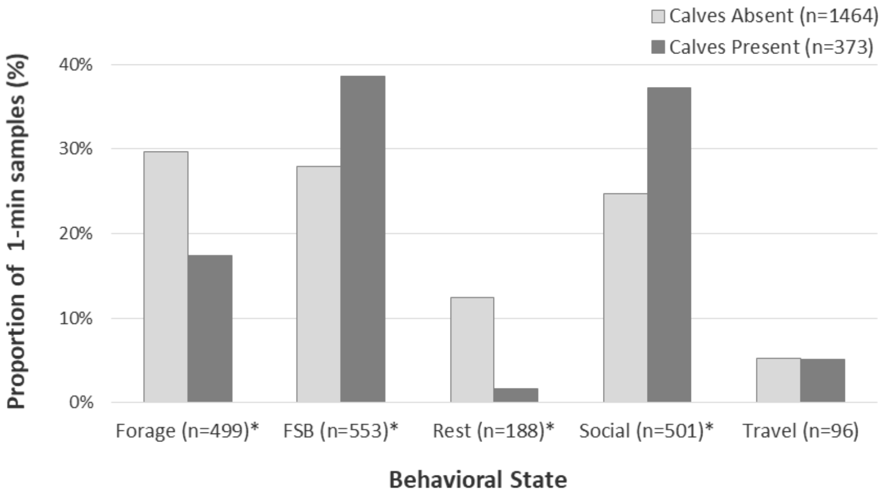

Figure II-5. Bottlenose dolphin behavioral activity states based on calf presence. FSB indicates foraging in association with shrimp trawlers. Asterisk indicates statistically significant difference.

Dolphin behavior varied significantly with vessel presence (G^2=257.97, n=1,837, df=4, P<0.001; **Figure II-6**). Post hoc tests showed that if vessels were present, dolphins were more likely to be foraging in association with trawlers (*z*=10.55). If vessels were present, dolphins were less likely to be socializing (*z*=-7.06) or foraging without trawlers (*z*=-3.52). The National Marine Fisheries Service suggests that boats maintain a minimum viewing distance of 45m from dolphins to reduce the chance of injury and behavioral harassment. Vessels were closer than 45m from dolphins during 42% of unfiltered tracks, including 21 accounts of boats transiting directly through dolphin groups.

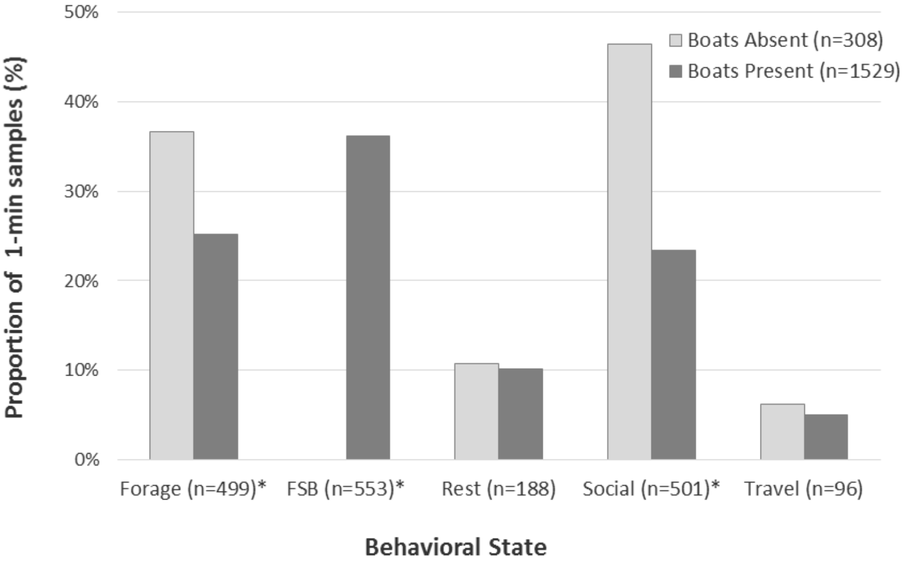

Figure II-6. Bottlenose dolphin behavioral activity states based on vessel presence. Asterisks indicates statistically significant differences.

Fine-scale Movement Patterns

Swimming Speed

The GAM described significant variation in swimming speed, at the 0.05 alpha level, explaining 45.3% of the deviance (adj-R^2=0.390, GCV=0.054, n=167). The best fitting model included all five candidate explanatory variables with a smooth term for both time of day and dolphin group size, and linear terms for predominant group behavior, and vessel category:

[*Log10(Speed) ~ s(TimeOfDay) + s(GrpSize) + Calf + BehavState + VesselCat*]

Swimming speed was significantly higher in the presence of tour boats, trawlers, and highest when both tour boats and trawlers were present during the same sampling interval (i.e., tour boats follow dolphins that are following trawlers). Travelling behavior was associated with significantly higher swimming speed along the horizontal plane than foraging and socializing. At the 0.1 alpha level, swimming speed was significantly higher in the presence of small recreational boats and travelling was associated with significantly higher speed than resting. Time of day, dolphin group size and calf presence had no significant effect on swimming speed, though there was variation based on these factors (**Table II-2**; **Figure II-7**).

Table II-2. Summary of output for best fitting model for bottlenose dolphin swimming speed. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Absent (calf), Travelling (behavioral state), and None (vessel category). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	Std. Error	t	*P*-value
(Intercept)	0.327	0.117	2.789	0.006
Calf - Present	-0.058	0.047	-1.253	0.212
BehavState - Foraging	-0.250	0.108	-2.318	0.022*
BehavState - FSB	-0.055	0.145	-0.383	0.703
BehavState - Resting	-0.211	0.119	-1.781	0.077 •
BehavState - Socializing	-0.231	0.112	-2.062	0.041*
VesselCat – Large	0.052	0.091	0.570	0.570
VesselCat - Mid	0.033	0.072	0.454	0.651
VesselCat - Small	0.121	0.064	1.882	0.062 •
VesselCat - Tour	0.173	0.075	2.325	0.021*
VesselCat - Trawler	0.228	0.102	2.235	0.027*
VesselCat - Tour&Trawler	0.280	0.113	2.477	0.014*
	Edf		F	*P*-value
s(TimeOfDay)	4.314		0.534	0.776
s(GrpSize)	1.879		1.131	0.281

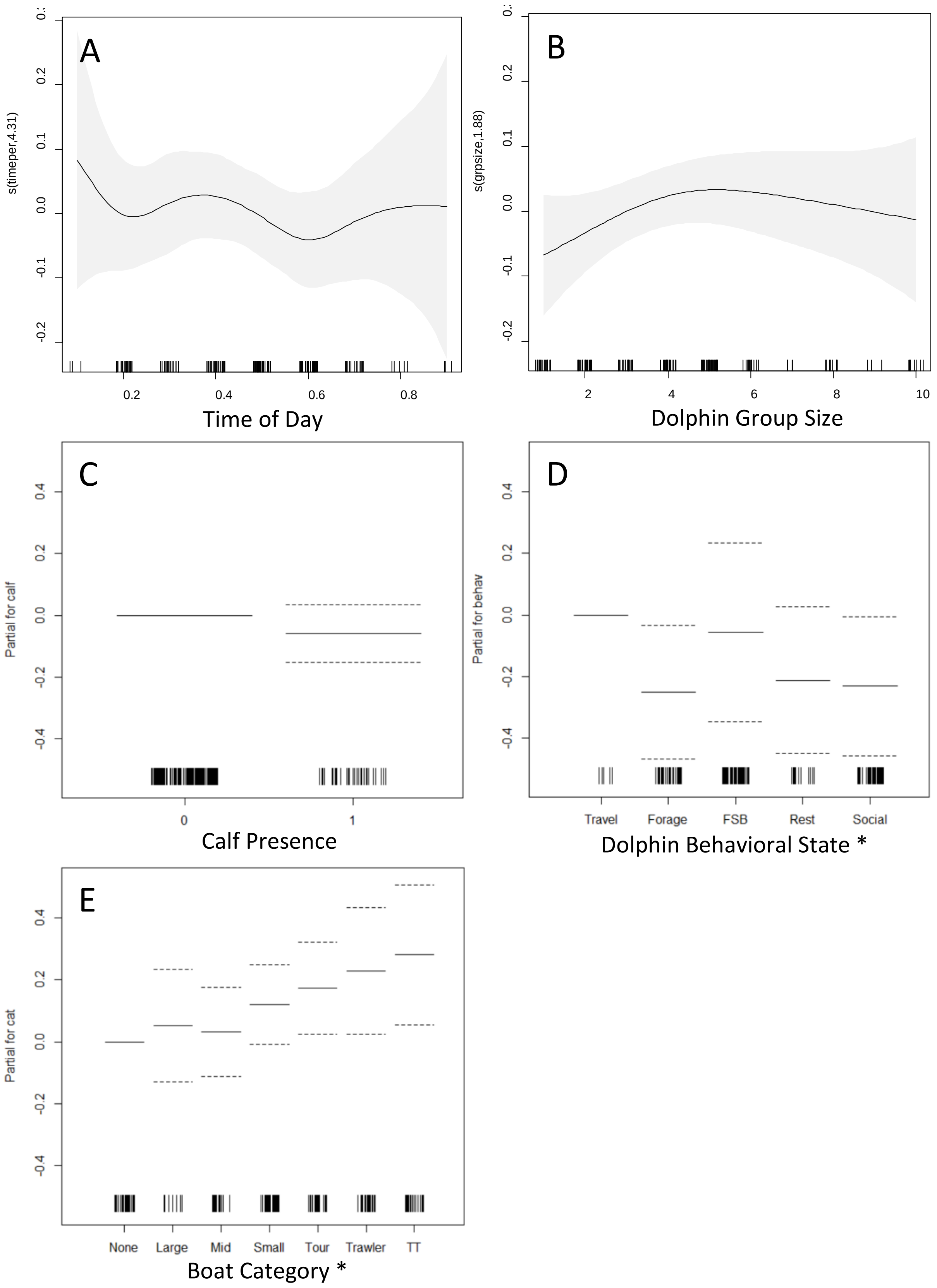

Figure II-7. Charts for the partial contribution of individual explanatory variables in the fitted GAM for swimming speed. Includes A) time of day, B) dolphin group size, C) calf presence, D) dolphin behavioral state, and E) vessel category. The rugplot along the x-axis indicates the number of observations for each factor. The gray shading for smooth terms, and the dotted lines for linear terms, indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with swimming speed, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Reorientation Rate

The GAM described significant variation in reorientation rate, at the 0.05 alpha level, explaining 42.4% of the deviance (adj-R^2=0.361, GCV=3.440, n=167). The best fitting model included all five candidate explanatory variables with a smooth term for both time of day and dolphin group size, and linear terms for predominant group behavior, and vessel category:

[Sqrt(*ReorientationRate) ~ s(TimeOfDay) + s(GrpSize) + Calf + BehavState + VesselCat*]

The non-linear relationship between reorientation rate and time of day was significant, with the lowest reorientation rates occurring from late morning to mid-day and the highest reorientation rates occurring from the afternoon to early evening. Travelling behavior was associated with significantly lower reorientation rates than foraging behavior. At the 0.1 alpha level, travelling was associated with lower reorientation rates than socializing, and dolphins reoriented significantly more in the presence of tour boats and trawlers. Dolphin group size and calf presence had no significant effect on reorientation rate (**Table II-3**; **Figure II-8**).

Table II-3. Summary of output for best fitting model for bottlenose dolphin reorientation rate. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Absent (calf), Travelling (behavioral state), and None (vessel category). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	Std. Error	t	*P*-value
(Intercept)	4.825	0.916	5.267	4.69e-07
Calf - Present	0.524	0.365	1.434	0.154
BehavState - Foraging	1.840	0.862	2.134	0.035 *
BehavState - FSB	-1.443	1.123	-1.285	0.201
BehavState - Resting	0.672	0.944	0.711	0.478
BehavState - Socializing	1.474	0.873	1.687	0.094 •
VesselCat – Large	0.326	0.725	0.449	0.654
VesselCat - Mid	0.713	0.569	1.254	0.212
VesselCat - Small	-0.197	0.503	-0.392	0.695
VesselCat - Tour	0.989	0.590	1.677	0.096 •
VesselCat - Trawler	1.397	0.814	1.716	0.088 •
VesselCat - Tour&Trawler	0.877	0.892	0.983	0.327
	Edf		F	*P*-value
s(TimeOfDay)	3.407		3.669	0.006 *
s(GrpSize)	0.572		0.518	0.490

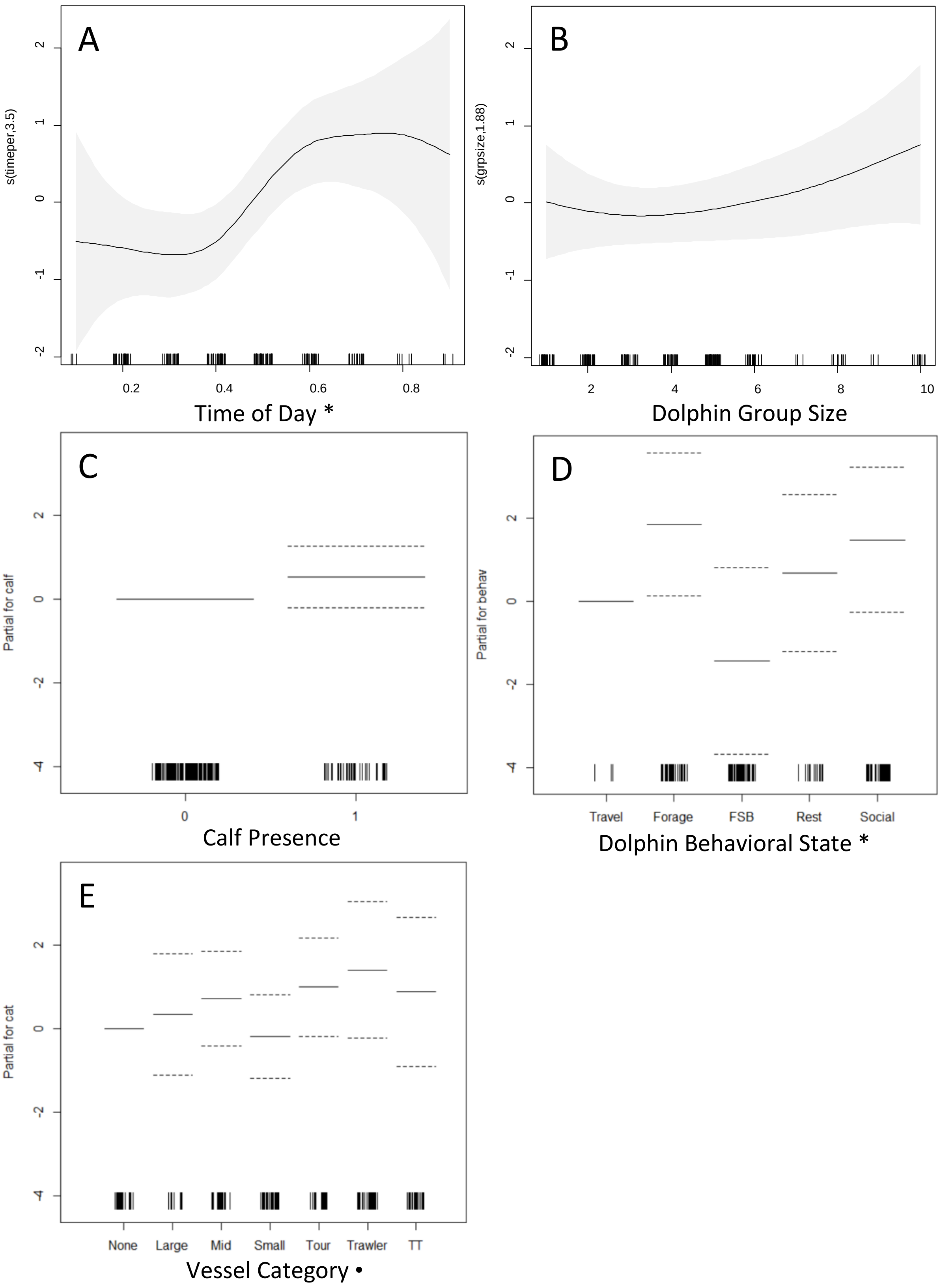

Figure II-8. Charts for the partial contribution of individual explanatory variables in the fitted GAM for reorientation rate. Includes A) time of day, B) dolphin group size, C) calf presence, D) dolphin behavioral state, and E) vessel category. The rugplot along the x-axis indicates the number of observations for each factor. The gray shading for smooth terms, and the dotted lines for linear terms, indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with reorientation rate, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Linearity

The GAM described significant variation in linearity, at the 0.05 alpha level, explaining 31.5% of the deviance (adj-R^2=0.230, GCV=4.058, n=167). The best fitting model included all five candidate explanatory variables with a smooth term for both time of day and dolphin group size, and linear terms for predominant group behavior, and vessel category:

[*EmpLogit(Linearity) ~ s(TimeOfDay) + s(GrpSize) + Calf + BehavState + VesselCat*]

The non-linear relationship between linearity and time of day indicated more linear movement from late morning to mid-day and less linear movement from afternoon to early evening, which is congruent with reorientation rate patterns. The non-linear relationship between linearity and dolphin group size indicated more linear movement in groups of three to eight dolphins, and less linear movement in smaller and larger groups. Vessel category, calf presence, and dolphin behavior had no significant effect on linearity (**Table II-4**; **Figure II-9**).

Table II-4. Summary of output for best fitting model for bottlenose dolphin linearity. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Absent (calf), Travelling (behavioral state), and None (vessel category). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	Std. Error	t	*P*-value
(Intercept)	1.133	0.965	1.174	0.242
Calf – Present	-0.523	0.405	-1.292	0.198
BehavState - Foraging	-1.289	0.923	-1.397	0.165
BehavState - FSB	0.780	1.212	0.643	0.521
BehavState - Resting	-0.437	1.022	-0.428	0.670
BehavState - Socializing	-0.941	0.942	-0.999	0.319
VesselCat – Large	-0.367	0.780	-0.471	0.638
VesselCat - Mid	-0.262	0.618	-0.424	0.672
VesselCat - Small	0.280	0.541	0.517	0.606
VesselCat - Tour	-0.172	0.647	-0.266	0.791
VesselCat - Trawler	-0.429	0.874	-0.491	0.624
VesselCat - Tour&Trawler	0.144	0.981	0.147	0.883
	Edf		F	*P*-value
s(TimeOfDay)	3.067		1.070	0.043 *
s(GrpSize)	4.253		1.399	0.080 •

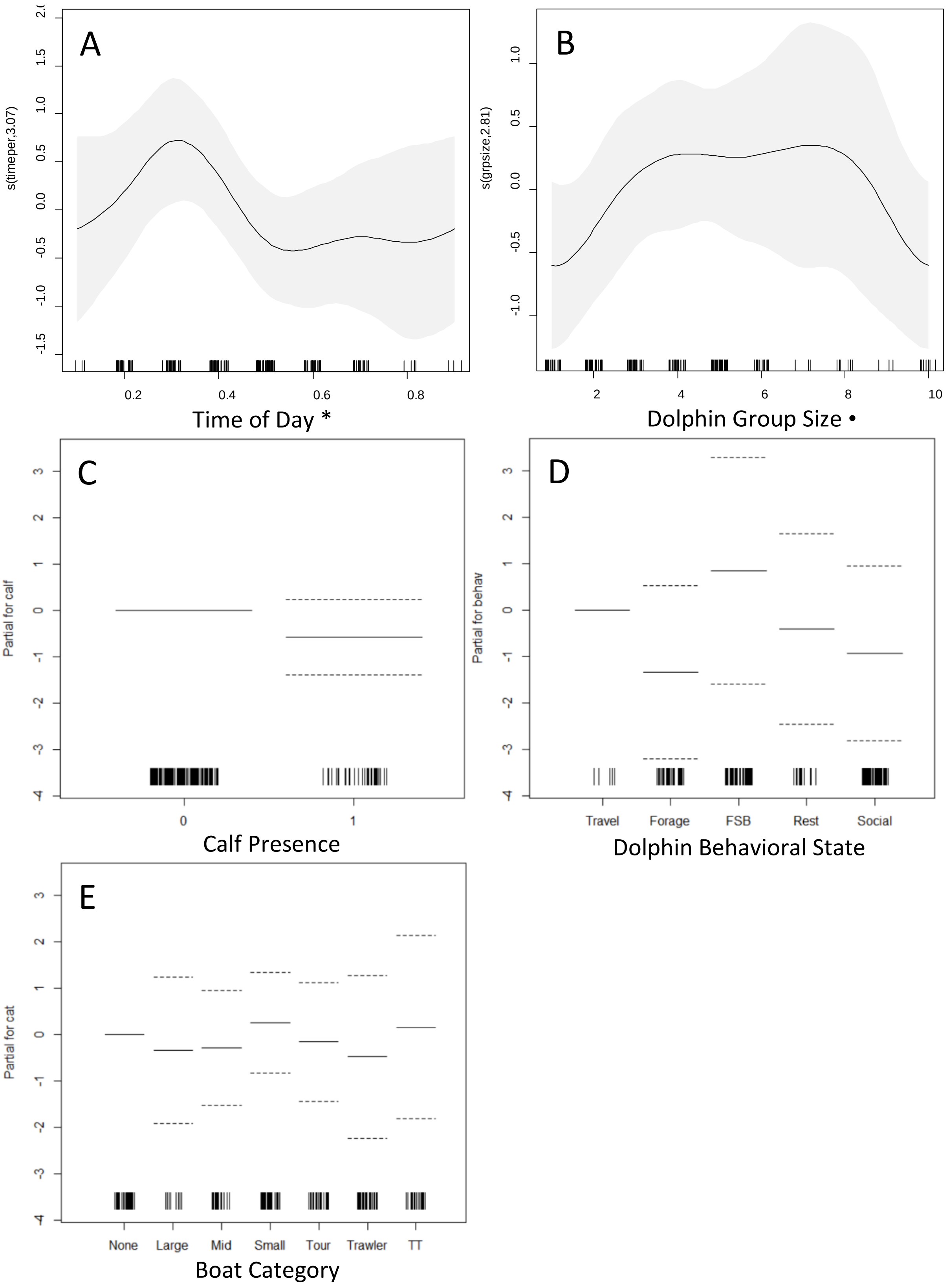

Figure II-9. Charts for the partial contribution of individual explanatory variables in the fitted GAM for linearity. Includes A) time of day, B) dolphin group size, C) calf presence, D) dolphin behavioral state, and E) vessel category. The rugplot along the x-axis indicates the number of observations for each factor. The gray shading for smooth terms, and the dotted lines for linear terms, indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with linearity, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Discussion

This study highlights variability in dolphin behavior and movement patterns relative to natural and anthropogenic factors in a narrow, congested seaport. Common bottlenose dolphins occur regularly in the Galveston Ship Channel during summer months. They were observed every sampled day, during all hours of daylight and during periods of low and high vessel traffic. The GSC is an important habitat for foraging and socializing, and not simply a travel corridor for bottlenose dolphins to access other favorable sites. Calves also occur regularly in the GSC, suggesting the area is important for calf-rearing and early life development.

Behavioral activity states and movement patterns varied significantly based on several natural factors including time of day and dolphin group size. Behavioral activity state also varied based on calf presence, though movement patterns did not. A diurnal pattern emerged, with foraging peaking in the morning (in association with trawlers) and afternoon (without trawlers), and dropping in general at mid-day. This is congruent with a 1990's study of dolphins in the adjacent Galveston Bay system and coastal Gulf of Mexico waters, although a distinction was not made between foraging with and without trawlers (Bräger, 1993). Traveling behavior peaked in the afternoon, which is also congruent with the prior study in which dolphins presumably travelled in the afternoon to return to the bay from gulf waters. Socializing peaked during mid-day, as foraging decreased. Guiana dolphins, *Sotalia guianensis*, have the same post-foraging peak in socializing, in which socializing was initiated after foraging concluded in areas with elevated prey availability (Guilherme-Silveira and Silva, 2009).

In terms of group size, dolphins that foraged in association with trawlers were in larger groups than those foraging without trawlers. This is incongruent with results of prior research in the GSC from the early 1990's in which the smallest groups foraged behind trawlers ($\bar{x}$

=2.70±SD 1.78) (Fertl, 1994b). During the present study, a higher proportion of foraging in association with trawlers was observed with larger groups of dolphins and when at least one calf was present in a focal group. Increased numbers of dolphins, and groups with calves, engaging in this tactic over time may reflect social learning. Socializing was observed significantly more in larger groups. Socializing encompasses a variety of events, including active socio-sexual displays at the water's surface and less obvious interactions, such as pectoral fin rubbing between two individuals. It is possible that there was a sighting bias towards more obvious displays that included larger numbers of active individuals. Resting and travelling were observed significantly more in smaller groups. In open ocean environments, large group formation may reduce susceptibility to predation and enhance detection and capture of prey that are patchily distributed. However, the conceptual framework presented by Gowans et al. (2007) predicts that when resources are predictable and found in complex inshore environments where predator density is low, there are few benefits to large group formation. This might shed light on why dolphins in the GSC form smaller groups when engaged in resting, travelling, and foraging independent of trawlers.

Vessel Activity

Dolphins were not displaced from the GSC due to vessel presence, but behavioral states varied significantly when vessels were in close proximity (<100m). Two biologically important activities, foraging independent of trawlers and socializing, decreased in the general presence of vessels. However, foraging in association with trawlers increased in the presence of vessels. Reduced foraging and socializing behavior due to human activity has been described in other studies. Indo-Pacific bottlenose dolphins, *T. aduncus*, off Zanzibar (Christiansen et al., 2010), and *T. truncatus* off Western Australia (Arcangeli et al., 2009), showed reduced foraging, socializing and resting behaviors, and increased travelling behavior in the presence of tour boats, indicating that less time was spent engaged in biologically important activities. These behavioral responses to vessels may result in increased energy expenditure (e.g., increased swimming speed) and decreased energy consumption (e.g., disrupted foraging activity) that may result in overall reduced energy acquisition (Williams et al., 2006). This is important when considering lactating females and dependent calves, given that lactation is one of the most energetically expensive periods for female mammals (Gittleman and Thompson, 1988). The dolphin population in the Galveston Bay and GSC area occurs in relatively small numbers and shows site fidelity, increasing the likelihood of repeated exposure of individual dolphins to vessels.

Distinct vessel type affected dolphin movement patterns in different ways. Movement patterns did not vary significantly in the presence of vessels categorized as large, including cargo container and cruise ships, or vessels categorized as mid-sized, including pilot boats and U.S. Coast Guard (USCG) boats. The sample size for the large category was low and it’s likely that these slow, predictable linear-moving vessels were relatively easy for dolphins to avoid. Wave-riding at the bows of large ships in the GSC was only occasionally observed. Vessels categorized as mid-sized were also relatively slow and linear in movement, compared to vessels categorized as small that moved quickly and unpredictably, at times. Movement patterns varied significantly in the presence of vessels categorized as small, including personal recreational boats and a commercial jet-boat, dolphin-based tour boats, shrimp trawlers, and most significantly, when tour boats and trawlers were both present during the same sampling period. Small boats were the fastest moving and least predictable in terms of linear movement. Field observations suggest that dolphins may alter behavior along the vertical water column, as inter-surfacing intervals appear to increase in the presence of small boats. This behavior was difficult to quantify while tracking groups of dolphins from land using a theodolite that tracks movements along the horizontal water surface. Several other studies have shown an increase in breathing synchrony and longer inter-breath intervals of dolphins in response to vessel traffic (Hastie et al., 2003; Lusseau, 2003; Nowacek et al., 2001).

The narrow, active GSC may restrict opportunities for lateral movement and dolphins may not have adequate time to avoid small, fast moving boats, as indicated by encounters of small boats operating directly through focal groups. Although obvious signs of external injury from propeller strike were not observed during this study, potential internal injury from blunt trauma from other parts of boats (e.g., the hull) may not be easily detected directly following an incident. Mother-calf pairs may be especially vulnerable to this type of boat activity because calves are not fully developed and are physiologically limited in their ability to swim and dive (Mann and Smuts, 1999; Noren et al., 2002), which may hinder maneuverability of both mother and calf. Additional data collection on individual surfacing intervals in the presence of small, fast-moving boats is suggested to address this stressor. There is currently a recommended “no wake” speed (no more than approximately 8 km/hr) in the GSC, but few adhere to it (small private recreation boats were recorded travelling up to 78.94 km/hr). Establishing a formal speed limit in the GSC may help reduce disturbance.

More than half of the recorded foraging activity was in association with trawlers. Dolphins significantly altered their patterns of movement and behavior to more closely match the movement patterns of trawlers, highlighting alternative tactics for hunting prey in response to human activity. Dolphins followed operating trawl nets, likely feeding on prey stirred up by, or caught in, the nets. They also surrounded trawlers as nets were lifted and by-catch was discarded.

Odontocetes are often oriented around fishing vessels where acquisition of concentrated prey sources, and prey that are disoriented or injured, may be facilitated (Fertl and Leatherwood, 1997). For example, at least some Australian humpback dolphins (*Sousa sahulensis*) feed in association with fishing trawlers as a major source of food (Parra and Ross, 2009), and Indo-Pacific humpback dolphins (*S. chinensis*) off Hong Kong fed near commercial trawlers for hours at a time when trawling operations there were still active (Hung, 2008; Jefferson, 2000). There appeared to be inter-individual selection for this type of feeding off Hong Kong, where some dolphins associated with trawlers more than others (Jefferson, 2000). Likewise, in Moreton Bay, Australia, two distinct sympatric communities of Indo-Pacific bottlenose dolphins (*T. aduncus*) have been identified, one that engages in trawler foraging, and one that does not (Chilvers and Corkeron, 2001). Although dolphins were observed in the GSC foraging without trawlers, at times while shrimp boats were actively trawling in the area, it is unclear if a similar individual or community preference exists in this population. Shrimp trawling in the Galveston Bay system is seasonal and dolphins do not have the opportunity to forage in association with boats year-round. Delineating community structure and foraging tactics in this population will offer additional information on this specialized form of foraging.

Groups with calves foraged in association with trawlers significantly more than foraging without trawlers, which may reflect the high energetic needs of breeding females (Fertl and Leatherwood, 1997). Off Hong Kong, humpback dolphin groups with calves were more likely to feed near fishing vessels than those without calves (Hung, 2008). Dolphin groups that foraged in association with trawlers were significantly larger than those foraging without trawlers. More than 20 years ago, the opposite was observed in the GSC (Fertl, 1994a). Social learning over the years may contribute to this shift, especially considering a higher percentage of groups with calves engage in this type of foraging than those foraging without trawlers. The same pattern has been observed in other populations. Off Hong Kong, humpback dolphins actively approached and followed trawlers, in significantly larger schools than those not pursuing trawlers, likely to access prey that were concentrated into a small area or stirred up by fishing nets (Hung and Jefferson, 2004; Jefferson and Hung, 2004; Ng and Leung, 2003).

Dolphin-based tourism in the GSC can lead to harassment. Horizontal avoidance of tour boats was expressed by increased swimming speed and increased reorientation rate. Commercial marine mammal tourism has often been considered a benign and sustainable activity, especially as an alternative to directed hunting. However, the proliferation of the industry on a global scale in recent decades raises questions about potential effects on target populations (Christiansen and Lusseau, 2014; O'Connor et al., 2009). Short-term behavioral responses to vessels can cause shifts in behavior and habitat use (e.g., reduced foraging and socializing and increased travelling), reduced energy consumption (lost foraging time), and interference with communication. These short-term changes do not necessarily affect long-term individual health and survival or population viability. However, dolphins that express repeated responses to a stimulus over time may experience increased energetic expenditure and chronic stress with broader biological, physiological and/or ecological consequences (Beale, 2007; Bejder et al., 2006a). For example, boat-based tourism was negatively correlated with female bottlenose dolphin reproductive success off Australia in an area of long-term tourism disturbance (Bejder, 2005). Females have been described moving between boats and their calves in other areas, which may be energetically costly to females with offspring. Off New Zealand, boat-based tourism was implicated in long-term shifts in habitat use by common bottlenose dolphins (Lusseau, 2004). When boat frequency increased, dolphins switched from local avoidance to avoiding the area altogether. In Galveston, there are currently three tour operations that formally involve dolphin viewing (other boat-based businesses view dolphins opportunistically), one of which began after this research concluded, and two additional entities have expressed interest in launching dolphin tour operations in the area. The three current operations all launch from the GSC and target the same population of dolphins, with no regulatory or management framework in place. Without proper management, short-term changes may lead to long-term consequences not only to individuals, but entire populations (Bejder et al., 2006a).

A central objective of this study is to apply the conservation behavior framework that aims to strengthen the connection between the fields of animal behavior and conservation biology, to identify dolphin behavioral responses to potential stressor stimuli (e.g., human activity) (Berger-Tal et al., 2011). Dolphin behavioral changes were detected in response to diverse human activity in the GSC. Proximity to vessel activity, specifically dolphin-targeted tourism, commercial trawlers, and small recreational boats, significantly affected dolphin behavior. Dolphin tourism vessels, which actively pursue dolphins, fall under the MMPA definition of behavioral harassment. The final component of the conservation behavior framework aims to connect these findings to management practice, which are discussed in the following section.

Management Implications

In many regions where dolphin-based tourism is conducted, no regulatory frameworks exist. Especially lacking are plans with long-term sustainable management in mind (Higham et al., 2009). There are currently no permit requirements for dolphin-based tourism in the U.S. Southeast Region (Anderson et al., 2011). The National Oceanic and Atmospheric

Administration (NOAA) has a voluntary code of guidelines for viewing dolphins in the Southeast Region which aim to reduce the potential for harassment. Additionally, a formal partner-based program, Dolphin SMART, was launched in Florida in 2007 that promotes responsible stewardship of wild dolphins in coastal waterways. The program has expanded to several other states in which tour operators can join to gain theoretical education in operating boats around dolphins, receive adherence evaluations, and actively promote conservation. However, the program has not expanded to Texas and none of the Galveston tour operators are currently members. Unfortunately, voluntary codes of conduct for dolphin watching, though well-intended, are often inadequate without hands-on practical operator training and supervision. For example, during this study, tour boats were observed operating contrary to NOAA recommendations, including breaching the minimum viewing distance of 45m, encircling/entrapping dolphins between their boat and another boat, making sudden changes in speed and direction in the vicinity of dolphins, approaching dolphins head-on, and approaching dolphins when another vessel was near. In the GSC, tour boats do not always adhere to recommended viewing guidelines, and voluntary codes of conduct for minimizing behavioral harassment are ineffective.

In the U.S., Marine Mammal Protection Act permits are required to conduct boat- and air-based research and education and require descriptions of operator experience around marine mammals, adherence to regulations, and annual reports, including number of dolphins approached. This is an excellent way to manage the number of researchers/educators in a given area, and to limit the number of animals that are approached with potential for harassment. A similar mandatory permitting requirement, including regulations and restrictions, for commercial tour operations may be the best way to minimize disturbance to dolphins. The New Zealand

Department of Conservation (DOC) serves as an example of how a formal permitting process aids in managing the rapidly growing commercial marine mammal tourism industry. Permits are required for tour operators and aim to minimize effects on marine mammal behavior. Furthermore, research-based recommendations are often integrated to better inform regulatory and management decisions. For example, permits for viewing Hector's dolphins (*Cephalorhynchus hectori*) off New Zealand, including restrictions on vessel number and operating time, were formally established by the DOC based largely on research findings (Bejder, 1997). Based on researcher recommendations off Kaikoura, New Zealand, changes were made to operating regulations around dusky dolphins (*Lagenorhynchus obscurus*) to reduce the number and duration of vessel interactions (Markowitz et al., 2009). In Texas, some regions include a secret-shopper style of monitoring that, though well-intended, is infrequent and inconsistent and does not provide the robust sampling and rigorous statistical analysis that science-based research can deliver.

In the GSC, tour boats that followed dolphins foraging in association with trawlers yielded the most significant findings in terms of altered movement patterns. This scenario places dolphins between at least two vessels while dolphins are actively feeding. Although trawlers may serve as an easy identification of dolphin location for tour operators, the potential for harassment during a critically important activity is high. Dolphin groups with calves frequently foraged in association with trawlers, with implications for these vulnerable members of the population. To reduce harassment, tour boats should be restricted from targeting dolphins that are foraging in association with trawlers, especially groups of dolphins with calves.

Conclusions and recommendations

Findings from this research show that some human activity in the GSC affects dolphin behavior. Large and mid-sized vessels do not appear to be a stressor to dolphins. No behavioral responses were detected in the presence of these vessel types. However, data were lacking for physiological changes and internal responses may have gone undetected. Based on dolphin behavioral responses, small boats, commercial trawlers, and dolphin-based tourism boats do appear to be stressors to dolphins. Trawlers are a risky attractant that dolphins forage in association with, and dolphins are aversive to tour boats.

Current legislation and recommended viewing guidelines do not protect dolphins in the GSC from behavioral harassment by tour boats. Behavioral harassment in this biologically important habitat may be detrimental to the short-term functioning of members of this federally protected population. Responsible wildlife viewing can stimulate local economies and promote public interest in dolphin conservation in positive ways, but operations should be conducted with appropriate knowledge of dolphin behavior and adherence to codes of conduct to reduce disturbance. According to one conceptual model, very strong ecotourism differs from very weak ecotourism in that it has an educational dimension (e.g., interpretation and training), and a sustainable dimension (e.g., emphasis on socio-cultural elements rather than only economic gains) (Diamantis and Westlake, 2001). Regulating and monitoring dolphin-based tourism would help to ensure that it is sustainable and operating within the principles of the MMPA. In narrow seaports, like the GSC, dolphins regularly occur very close to shore and land-based viewing is an excellent non-invasive alternative to boat-based viewing.

Bottlenose dolphins showed behavioral flexibility in exploiting food resources in which prey acquisition is facilitated by commercial trawlers. It is unclear if this risky attractant has positive or negative consequences to the overall population. Risk may be elevated when tour vessels follow dolphins that feed in association with trawlers, at which point dolphins become entrapped between at least two vessels. This added pressure during a risky form of foraging may alter behavior during a biologically important activity. Behavioral harassment was detected in the presence of tour boats and trawlers. However, dolphins do not appear to abandon the area, even during periods of consistent and intensive vessel presence in which boats actively follow dolphins. This may be due, in part, to lack of ecologically similar habitat, with similar prey characteristics, proximate to the GSC. Recommendations include permit requirements for dolphin tour operators, including restrictions on following dolphins that are actively foraging in association with trawlers.

Future research, including passive acoustic monitoring, is recommended to shed light on nighttime habitat-use when vessel activity is greatly reduced. Published data indicate that dolphin presence peaks in the GSC during spring and fall months (Fertl, 1994a) that may reflect periods of decreased recreational boating, commercial shrimping practices, and/or shifts in prey characteristics. Year-round behavioral research is suggested for a better understanding of present day seasonal shifts in habitat use and potential vessel-based disturbance. Research in other coastal areas off Texas is also needed to better understand discrete population dynamics relative to human activities.

CHAPTER III

EFFECTS OF COASTAL DEVELOPMENT ON INDO-PACIFIC HUMPBACK DOLPHIN (*SOUSA CHINENSIS*) HABITAT-USE OFF HONG KONG

Introduction

Ecosystem disturbance may be problematic for small populations of cetaceans (whales, dolphins, and porpoises) that show high site fidelity to biologically important areas used for foraging, mating, resting, or calf rearing, particularly where multiple industrial projects overlap (Bejder et al., 2009; Würsig, 1989). Construction-related noise (e.g., pile driving), direct loss of habitat (e.g., artificial land formation, port development), degradation of existing habitat (e.g., dredging), and an increase in construction-related vessel activity alter natural seascapes which can influence the distribution and behavior of marine mammals (Brandt et al., 2011; Pirotta et al., 2013; Thompson et al., 2013). These activities are growing threats for humpback dolphins (genus *Sousa*) that typically occur in shallow (<20 m deep), near-shore, brackish waters associated with estuarine systems, and display limited habitat flexibility relative to water depths and distances to shore (Jefferson and Curry, 2015; Jefferson and Smith, 2016; Parra and Ross, 2009). These waters are among the most productive aquatic systems for primary and secondary production (Beck et al., 2001). However, this distribution exposes *Sousa* to recreational and commercial maritime activities, particularly those living near densely populated urban cities and industrialized coastal areas (e.g., Hong Kong, Goa, India, and Queensland, Australia).

Hong Kong is one of the most densely urbanized coastal communities in the world (Schmitt, 1963), and ongoing development contributes to anthropogenic noise and activity in the habitats of Indo-Pacific humpback dolphin (*S. chinensis*; herein ‘dolphins’) (Jefferson et al., 2009; Karczmarski et al., 2016). The distribution of dolphins off Hong Kong is influenced by freshwater flowing from the Pearl River, where dolphins occur in higher densities in areas with steeper benthic slopes, often along natural island shores and rocky coastlines (Hung, 2008; Jefferson and Smith, 2016). Research concentrating on the Pearl River Estuary (PRE) population of dolphins began in the early 1990's (Jefferson, 2000; Parsons, 1997), and data show that the waters around Lantau Island (**Figure III-1**) have historically been an important habitat for dolphins (Jefferson and Hung, 2004; Marcotte et al., 2015). In the PRE, prey availability is one of the most important factors for predicting dolphin density (Hung, 2008). Alterations to inshore habitats are among the greatest potential threats to *Sousa* because energetic opportunities may be impacted when foraging grounds of prey species are degraded.

Although the PRE population of *Sousa* appear to be somewhat resilient to habitat alterations (Jefferson and Rosenbaum, 2014), dolphin abundance has significantly declined in the waters around Lantau Island over the past decade (Hung, 2017). The International Union for Conservation of Nature (IUCN) Red List of Threatened Species currently designates *S. chinensis* as Near Threatened (Reeves et al., 2008). However, this designation does not reflect the newly suggested and widely recognized taxonomic reclassification, which separates humpback dolphins into four species: *S. chinensis, S. plumbea*, *S. sahulensis,* and *S. teuzii* (Jefferson and Rosenbaum, 2014). Under this taxonomic restructuring, *S. chinensis* should meet the IUCN Red List requirements for Vulnerable status (Jefferson and Smith, 2016). Populations of *Sousa* spp. are regionally endemic with small geographic ranges, some of which show evidence of restricted gene flow (Mendez et al., 2011). Thus, research, conservation, and management efforts should focus not only on separate species, but on separate populations (Reeves, 2009).

Several large-scale development projects are currently underway, or planned for the near future, in the waters north of and adjacent to Lantau Island, Hong Kong, with unknown consequences to humpback dolphins. Construction of a massive bridge and tunnel system, which connects Hong Kong to Macau and Zhuhai (HKMZB), has been in progress since 2009 and extends directly through dolphin habitat from Macau through mainland China waters and to the west of the Hong Kong International Airport (HKIA) on Chek Lap Kok Island (Chen et al., 2010). One-hundred and fifty hectares of artificial land was formed to the east of Chek Lap Kok to support border crossing facilities associated with the HKMZB, and the southern landfall associated with the Tuen Mun-Chek Lap Kok Link (TMCLKL). Artificial land (16.5 ha) for the northern landfall for TMCLKL was also formed just off Tuen Mun, which will connect with the southern landfall via subsea tunnel. In addition to these projects, the HKIA is constructing a third runway to meet the needs of future air traffic growth. Construction for the third runway system officially commenced in August 2016 and will add 640 ha of artificial land north of Chek Lap Kok. In association with construction activity, marine vessel traffic used to transport people, equipment, and supplies has increased to facilitate these projects. Hong Kong waters also support ferries, including high speed hydrofoils, commercial fishing vessels, dolphin targeted tour boats, government boats, and private recreational boats. Escalating marine development and associated vessel traffic in Hong Kong has the potential to alter dolphin occurrence and behavior with unknown long-term consequences.

The effects of persistent marine construction and associated vessel activity on small odontocetes (toothed whales) have been described but are confounded when multiple industrial activities co-occur with varying methods and intensity (Todd et al., 2014). **S**everal studies have shown significant variation in odontocete behavior and habitat-use relative to construction. For

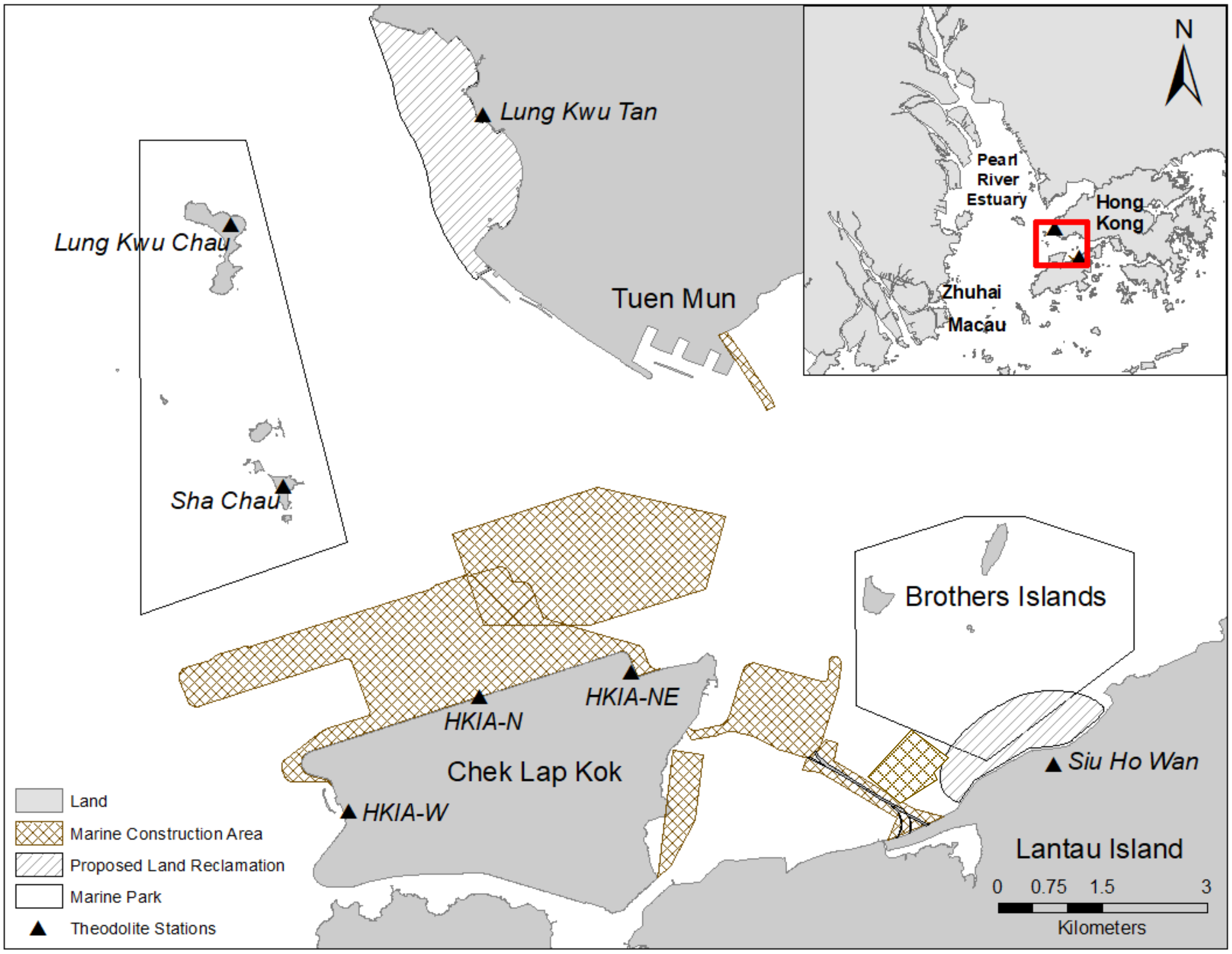

Figure III-1. Study area off Lantau Island, Hong Kong. Map shows land-based theodolite observation locations, marine construction areas, proposed land reclamation areas, and marine park boundaries. Map created using ArcGIS (Version 10.2.2, http://www.esri.com/software/arcgis).

example, construction of a gas pipeline reduced harbor porpoise presence in a historically important area off Ireland (Culloch et al., 2016). In another study off Europe, common bottlenose dolphins (*Tursiops truncatus*) spent significantly less time in a known foraging patch when local dredging activity intensified (Pirotta et al., 2013). In Chinese waters, dolphin swimming speed increased significantly during industrial pile-driving and overall presence declined directly following pile-driving activity (Würsig et al., 2000). In contrast, the population of Australian humpback dolphins (*S. sahulensis*) in Moreton Bay, Australia are abundant and appear to coexist with extensive coastal development. However, a proactive management approach has been recommended to provide protection to the endemic species (Chilvers et al., 2005). Based on these examples, the effects of construction activity can be measured by assessing shifts in animal behavioral activity states, and spatio-temporal presence and distribution patterns proximate to construction and related vessel activity.

Short-term behavioral responses by odontocetes to marine vessel traffic have also been described and often elicit a change in movement patterns. Some odontocetes respond to vessel activity by fleeing, including diving for longer durations, swimming away, or avoiding areas with vessel traffic altogether (Higham and Shelton, 2011). Alterations in swimming direction and speed, in addition to reduced or disrupted foraging, resting, and socializing bouts, have also been reported in response to vessels (Christiansen et al., 2010; Constantine et al., 2004; Dans et al., 2008; Lundquist et al., 2012; Lusseau, 2006; Nowacek et al., 2001; Stensland and Berggren, 2007; Stockin et al., 2008; Williams et al., 2002; Williams et al., 2006). Off South Africa, Indian humpback dolphins (*S. plumbea*) actively avoid fast-moving boats and have longer dive durations, changes in swimming direction, and extended underwater movements away from vessels (Karczmarski et al., 1997). Indian humpback dolphins in the Arabian Gulf show similar avoidance behaviors, including deep diving, group dispersal, and movement away from vessels (Pilleri and Gihr, 1974). Off Hong Kong, Indo-Pacific humpback dolphins have been described as fleeing in response to vessels moving at high speeds (e.g., high speed ferries), and as diving for longer durations during periods of heavy vessel traffic (Ng and Leung, 2003). Historical data comparisons from 1996 to 2013 showed a significant decline in localized dolphin density around the Brothers Islands and northeast of Chek Lap Kok (**Figure III-1**), which correlated with the implementation of two adjacent high speed ferry routes (Marcotte et al., 2015).

The conservation behavior framework, introduced in chapters I and II, proposes that behavior-oriented conservation studies focus on: 1) human impacts on animal behavior (potential stressor stimuli), 2) behavioral indicators (responses to potential stressors), and 3) behavior-based management (Berger-Tal et al., 2011). This framework was followed in chapter II to determine the effects of vessel activity in a confined area in the GSC on common bottlenose dolphin behavior. Ongoing, large-scale construction was absent in the GSC during the study period and there is a gap in knowledge about the additive effects of vessel and construction activity that is addressed in chapter III. In this study, the occurrence and behaviors of *S. chinensis* were investigated in the presence and absence of diverse vessel traffic and in proximity to maritime construction activities in the waters to the north of Lantau Island, Hong Kong. Specific objectives were to: 1) determine how dolphin track duration (i.e., amount of time dolphins are observed and tracked) varies with natural (time of day, solar season, oceanographic season, and discrete location) and anthropogenic (proximity to marine construction and vessel activity) factors, to better understand when and where dolphins are more likely to be sighted, 2) quantify dolphin movement patterns (swimming speed, reorientation rate, linearity) to assess dolphin behavioral responses to human activity, and 3) provide recommendations for behavior-based management to contribute to conservation efforts. Findings from this study can be broadly informative to areas where delphinids and human activity overlap, and more specifically, where delphinids with small near-shore ranges overlap with heavily populated urbanized coasts where development is diverse and continues to grow.

Methods

Ethics Statement

Data were collected from elevated, land-based positions in which no approaches to or harassment of animals or vessels were conducted. Permits were not needed for this fully non-invasive, observational method.

Sampling Methods

Data collection was part of large-scale assessments of two coastal urban development projects in the waters to the north of Lantau Island, Hong Kong including: 1) the Hong Kong International Airport third runway system (3RS) coordinated by the Hong Kong Airport Authority in partnership with Mott MacDonald, Inc., and 2) a land reclamation feasibility study coordinated by the Hong Kong Civil Engineering and Development Department (CEDD) in partnership with Arup, Inc. Land-based observations and theodolite tracking were conducted from seven locations to the north of Lantau Island (22º N, 113º E; **Table III-1**, **Figure III-1**). Five of these sites were established for the 3RS study, and two were established for the CEDD land reclamation feasibility study (**Table III-1**). Research was conducted discontinuously between October 2012 and December 2016, excluding most of 2015, with varying effort at individual sites. A total of 405 days, including 2301.55 hours, of survey effort were conducted. During this time, 636 groups of dolphins were recorded totaling 150.91 hours of dolphin tracks (**Figure III-2**). Only 32 groups (5%) contained calves. Position coordinates, heights of observation locations, and data collection periods are detailed in **Table III-1**.

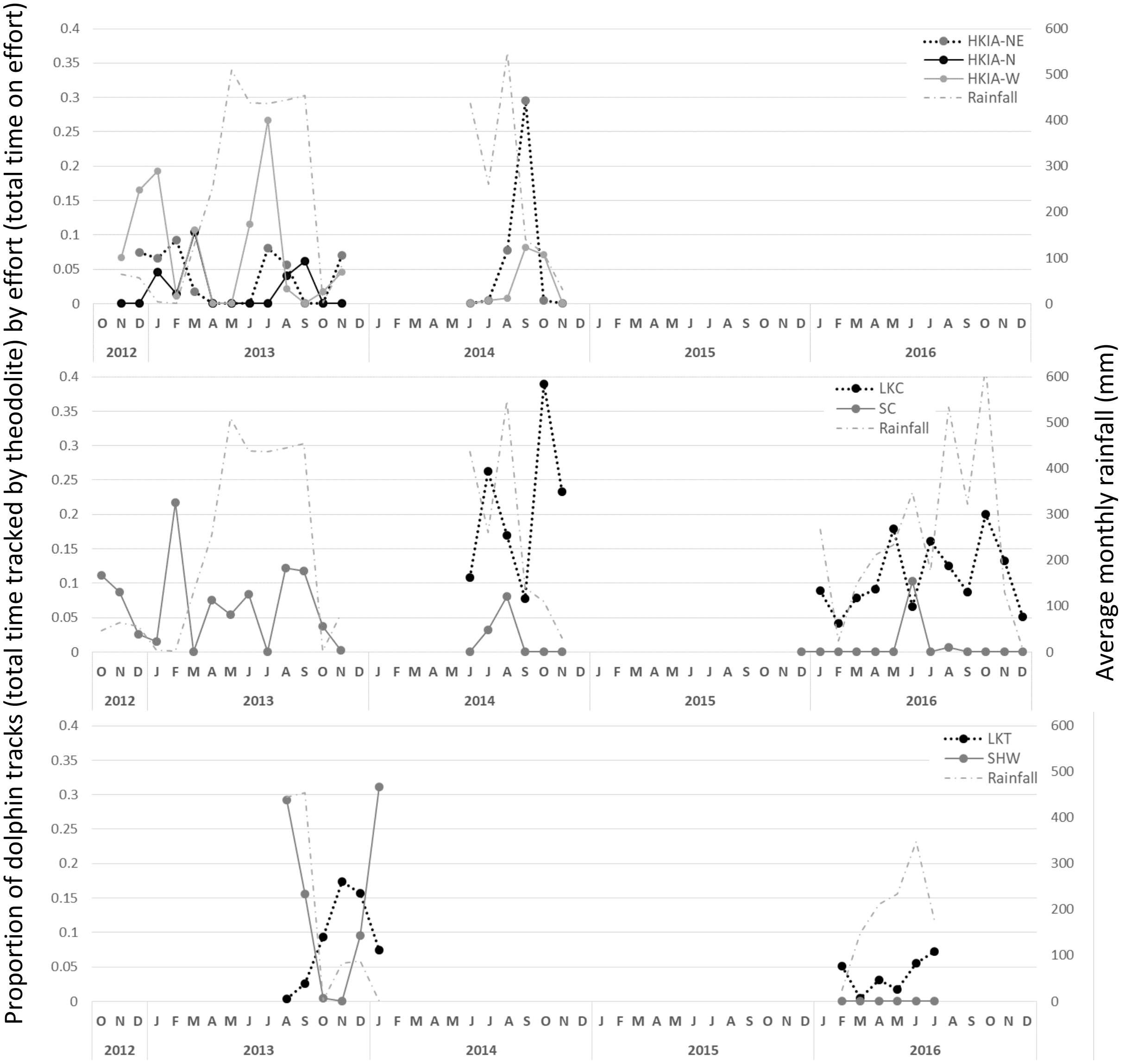

Figure III-2. Proportion of Indo-Pacific humpback dolphin track duration standardized by on-effort survey time. Figure includes year, month, and rainfall for each land-based location. Months with no points indicate zero effort.

Each daily survey comprised approximately 6 hours of effort unless inclement weather delayed or ended a session. Data collection involved a theodolite operator, an observer, and a data-entry computer operator. A systematic scan for dolphins was conducted once per hour. Observers searched for dolphins using handheld binoculars (7x50 magnification) for approximately 15-20 minutes followed by continuous non-systematic searching by unaided eye and binoculars until the next hourly systematic scan. Theodolite focal follow sessions were initiated when an individual dolphin or a group of dolphins was located. Digital theodolites (Sokkia/Sokkisha Model DT5) with 30-power magnification and ±5-second precision were used to obtain the vertical and horizontal angle of each dolphin and vessel position (Würsig et al., 1991). Data were recorded and angles were converted to geographic coordinates (latitude and longitude) using Pythagoras software, Version1.2 (Gailey and Ortega-Ortiz, 2002).

Table III-1. Land-based theodolite tracking sites. Details include associated project, geographic coordinates, observation height, and survey dates (see also **Figure III-1** for position information).

Project	Location	Acronym	Geographic Coordinates	Location Height (m)	Survey Dates (mm/yyyy)
Hong Kong International Airport 3rd Runway System (3RS)	Hong Kong International Airport Northeast	HKIA-NE	22° 19’ N 113° 56’ E	11.74	12/2012-11/2013 6/2014-11/2014
	Hong Kong International Airport North	HKIA-N	22° 19’ N 113° 54’ E	6.06	11/2012-11/2013
	Hong Kong International Airport West	HKIA-W	22° 18’ N 113° 53’ E	17.20	11/2012-11/2013 6/2014-11/2014
	Lung Kwu Chau	LKC	22° 22’ N 113° 53’ E	70.40	6/2014-11/2014 12/2015-12/2016
	Sha Chau	SC	22° 20’ N 113° 53’ E	45.66	10/2012-11/2013 6/2014-11/2014 12/2015-12/2016
Land Reclamation Feasibility Study (CEDD)	Lung Kwu Tan	LKT	22° 23’ N 113° 54’ E	51.40	8/2013-1/2014 2/2016-7/2016
	Siu Ho Wan	SHW	22° 18’ N 113° 59’ E	28.61	8/2013-1/2014 2/2016-7/2016

When possible, a distinguishable individual dolphin, based on coloration, was selected for a focal follow session. The focal individual (Altmann, 1974; Mann, 1999) was continuously tracked via theodolite with a position recorded (when possible) each time the dolphin surfaced. If an individual could not be positively distinguished from other members, the group was tracked by recording a position based on a central point within the group whenever the animals surfaced (Bejder, 2005; Martinez, 2010). Dolphins were considered part of a group if they were within 10 m of another individual (Smolker et al., 1992) or within 100 m and engaged in coordinated activity (Mann et al., 2000). Focal follow sessions continued until animals were lost from view, moved beyond the range of reliable visibility, or environmental conditions obstructed visibility (e.g., intense haze, Beaufort sea state >4). Dolphin data were recorded continuously in the field and later subsampled at 60-second intervals. For each positional fix of focal dolphins, data collection included geographic position, group size, calf presence/absence, and predominant group (≥50% of individuals) behavioral activity state. Surface behavioral activity states were based on definitions from Karczmarski and Cockcroft (1999) (**Table III-2**).

Table III-2. Indo-Pacific humpback dolphin behavioral activity state descriptions. Broad behavioral states modified from Karczmarski and Cockcroft (1999).

Behavioral State	Description
Foraging	Asynchronous diving in varying directions in one location. May observe dolphins visibly pursuing or capturing fish.
Milling	Individuals simultaneously moving in different directions with no overall clear direction of travel.
Resting	Low level of activity, dolphins close to surface of water and each other. At times apparently floating stationary and motionless at surface, with occasional slow forward movement.
Socializing	Vigorous activities including chasing, leaping out of water, high speed movement with frequent direction changes, and prolonged body contact with other dolphins
Traveling	All animals oriented and moving in the same direction with group members diving and surfacing synchronously, includes higher speed forward movement.

Vessels that moved within approximately 1 km of the focal individual/group were also tracked via theodolite. Vessel data were recorded continuously and included geographic position, vessel type, and activity (e.g., travelling, stationary, following dolphins). Vessels were broadly categorized *post hoc* based on vessel type. Data on proximate marine construction projects underway during the sampling periods were obtained from the Government of the Hong Kong Special Administrative Region, Marine Department.

Statistical Analysis

Univariate log-likelihood ratio and binomial *z* score post hoc tests were used to assess nominal categorical data (i.e., behavioral states). The binomial *z* score decision rule was based on the critical value 1.96. Regression modeling and multivariate generalized additive models (GAMs) were used to evaluate continuous numerical data (i.e., dolphin swimming speed, reorientation rate, linearity, and track duration). Computational analyses of swimming speeds, reorientation rates, and linearity were calculated in Microsoft Excel 2013, as were log-likelihood ratio and binomial *z* score statistics. R statistical software (Version 3.2.2) was used to perform exploratory work, regression modeling and GAM analyses. Linear mixed-effect modelling was run to detect autocorrelation, using the lme function (package nlme) in R. ArcMap (Version 10.2.2) was used to calculate distances of construction-related activity and for map production.

Dolphin track duration was based on the total duration of dolphin focal follows (hh:mm:ss) at each location, with the exposure variable of survey time on-effort. Potential explanatory variables included year, solar season (spring, summer, autumn, or winter), oceanographic season (wet or dry), time of day, location, and construction activity. The potential explanatory variables of location and year were dropped from the fully saturated model due to model output errors likely associated with collinearity. Oceanographic season was based on total monthly rainfall (wet season defined as a month with average rainfall ≥60 mm, generally late spring through early autumn; dry season defined as a month with average rainfall <60 mm, generally late autumn through early spring). Variation in track duration was assessed using regression models with time converted to count data (i.e., each second equates to an integer of 1). Zero-inflated negative binomial hurdle models were fit and evaluated using the Akaike Information Criterion with correction (AICc). Hurdle models use a two-stage approach in which one model predicts the probability of an observation to be zero or not, and one model predicts amounts for positive counts (Hu et al., 2011). AICc is derived from AIC and is appropriate for smaller datasets where n<40 data records per parameter (Burnham and Anderson, 2004; Hurvich and Tsai, 1989).

Over the course of this research, eight major marine construction areas were identified in the waters north of Lantau Island, proximate to dolphin viewing locations. Activities included dredging, backfilling, capping of contaminated mud pits, non-dredge land reclamation, seawall construction, and stone column installation. Information on geographic coordinates of working boundaries and start/end dates of individual projects are included in **Appendix B Table 1**. General details were available, but fine-scale information on daily construction activities was not accessible. It was necessary to establish a distance threshold to classify the presence or absence of construction activity in a given habitat. One study predicted that dredging noise could be detected by unspecified “marine fauna” up to 6 km from the sound source, depending on local conditions (Thomsen et al., 2009). A study in the PRE estimated that sounds produced by the OCTA-KONG, the world’s largest vibration hammer, may be detectable by dolphins up to 3.5 km from the sound source (Wang et al., 2014). Another study described behavioral changes by harbor porpoises up to 15 km from sound-intensive pile-driving activity (Madsen et al., 2006). In the absence of data clearly relating the effects of chronic low-intensity marine construction activity on dolphin responses based on distance, a 5 km diameter threshold from each theodolite location was selected as a moderate metric. Construction boundaries were plotted in ArcMap and distances from each of the seven theodolite locations were calculated (**Figure III-1**).

For movement analysis, data were filtered to omit dolphin tracks with only 1 positional fix, less than 10 minutes in total track time, and/or erroneous positions. To standardize across observations that varied in duration, individual focal follows were separated into 10-minute segments (Bejder et al., 1999; Lundquist et al., 2012), comprising 11 interpolated data records per segment, based on 60 sec intervals. The selected time interval reduces issues associated with non-linear travel observed by dolphins. The total number of segments varied based on focal follow duration (e.g., a group followed for 30 minutes would have 3 segments, a group followed for 40 minutes would have 4 segments). Successive records from the same focal group pose problems due to lack of independence; therefore, temporal autocorrelation was performed to identify potential pseudo-replication (Dray et al., 2010) for groups with multiple segments. Tracks were filtered as needed, based on the temporal lag at which two samples from the same group were no longer autocorrelated. From the 636 dolphin groups tracked, 417 10-minute segments were appropriate for movement pattern analyses. The 10-minute segments were also used to analyze behavioral state data. However, each of the 11 data points within each segment were included in analysis due to the potential for behavioral activity state to fluctuate over the course of 10 minutes. Behavioral data totaled 4,587 records (i.e., 11 records per 417 filtered segments). Unknown behavioral states (n=1,854) were excluded from behavioral activity state analysis. Collinearity among potential explanatory variables was evaluated using augmented pairs plots (i.e., correlation coefficients >0.50 indicated potential masking effects) and Variance Inflation Factor (VIF) values (i.e., values >5 indicated potential masking effects). If collinearity was expressed among potential explanatory variables, the most interpretable variable was retained, and the masking variable was dropped.

Dolphin response variables calculated for every 10-minute segment were mean swimming speed, reorientation rate, and linearity. To approximate normal distribution, response variables were transformed (Log10 for swimming speed, Square Root for reorientation rate, and Empirical Logit for linearity). Candidate explanatory variables for each 10-minute segment included time of day, solar season, dolphin group size, predominant dolphin behavioral state, number of vessels present, and type of vessels present. Sunrise and sunset times fluctuated throughout the study period; therefore, a time of day index was calculated to standardize the percentile of daylight hours where sunrise =0 and sunset =1. Swimming speed (km/hr) was calculated by dividing the distance travelled by the duration between two consecutive positions (Gailey et al., 2007). Reorientation rate is the degrees per minute of change in direction of a tracked individual or group of dolphins. Reorientation rate was calculated by dividing the sum of bearing changes within a segment by the total duration of that segment. Linearity is an index of net movement, or distance made good, represented by a range from 0 to 1, where 0 represents no net movement by dolphins (i.e., a circular path) and 1 represents movement in a straight line. Linearity was calculated by dividing the net distance (i.e., distance between the first and last fix of a segment) by the sum of all distances travelled between each of the 11 interpolated positional fixes within each segment.

Dolphin movement was evaluated based on vessel presence/absence. Several vessel distance thresholds (i.e., distance in which vessels were considered “present”) were evaluated during the exploratory analysis phase, including 500 m, 300 m, and 100 m, to select an appropriate threshold. Variation emerged for the 100 m threshold only, and this distance has been established in other odontocete literature involving effects of human activity (Constantine, 2001; Weir et al., 2010; Williams and Ashe, 2007) and is the same threshold used in **Chapter II** of this dissertation. The “no vessel” control category included segments in which no moving vessels were within 100 m during, and for at least 10 minutes prior to, the dolphin focal follow. Vessels were recorded in proximity of only 13% (n=54) of dolphin groups. A positional record, with associated data, can be collected for only one dolphin or vessel at a time; therefore, to calculate accurate distances, vessel positions with two or more positional fixes were interpolated *post hoc* relative to dolphin locations.

The GAM framework, appropriate for evaluating complex data that are multivariate and nonlinear (Hastie and Tibshirani, 1986), was used to evaluate numerical dolphin movement patterns in response to natural (time of day, solar season, group size, predominant group behavioral state) and anthropogenic (vessel number, vessel type) candidate explanatory variables. These models evaluate candidate explanatory variables simultaneously, reducing problems associated with many step-wise techniques. The fully saturated GAM included the fixed effects of time of day, solar season, dolphin group size, behavioral state, and vessel number, and the random effect of successive segments from a single dolphin focal group. The candidate explanatory variable ‘vessel type’ was dropped from the fully saturated model due to issues with multicollinearity with number of ‘vessel number’. Models were tested with all combinations of the fixed factors and model selection was based on adj-R^2 (high), GCV (low), and deviance explained (high).The multiple generalized cross-validation (mgcv) package in program R (Wood, 2006) was used to run models.

Generalized additive models were also applied to assess variation in movement patterns in response to specific vessel type. Vessels were categorized as large fishing, small fishing, high speed ferry (≥18.5 km/hr), large, mid-size, dolphin research, small, slow speed ferry (<18.5 km/hr), and dolphin-targeted tourism. Individual GAMs were run for swimming speed, reorientation rate, and linearity. Potential explanatory variables were the same as above, with the exception of replacing the variable of ‘vessel number’ with ‘vessel type’. Data preparation was comparable to statistics run for ‘vessel number’, including transformations of response variables, corrections for autocorrelation and collinearity, and selection of best fitting model for each movement parameter. Significance for all naturally occurring variables (i.e., time of day, dolphin group size, predominant group behavior, and solar season) were the same as output for models with ‘vessel number’.

Results

Dolphin Track Duration

Dolphin track duration (i.e., the amount of time dolphins were observed and tracked) varied among study locations. The highest percentage of dolphin tracks was collected from LKC, twice the amount as any other station (**Table III-3**). The model described solar season, time of day, and construction activity as important factors for predicting presence/absence of dolphins. The selected hurdle model fit the data well, provided plausible estimates, and included four potential explanatory variables and an offset variable for on-effort search time:

[*DolphTrack* ~ *offset*(*log*(*Effort*)) + *OcnSeason* + *SolarSeason* + *TimeBlock* + *ConstructionActivity*]

Dolphin track duration was significantly lower during the spring season than any other season, and significantly lower in areas within 5 km of chronic construction activity (ϴ=1.19, p<0.001;Table III-4). Variation was also expressed based on time of day, with higher overall track duration during mid-morning hours between 9:00 AM and 12:00 PM (**Figure III-3**). However, variation exists among stations. For example, track duration off SC was highest during late afternoon hours between 3:00 PM and 5:00 PM.

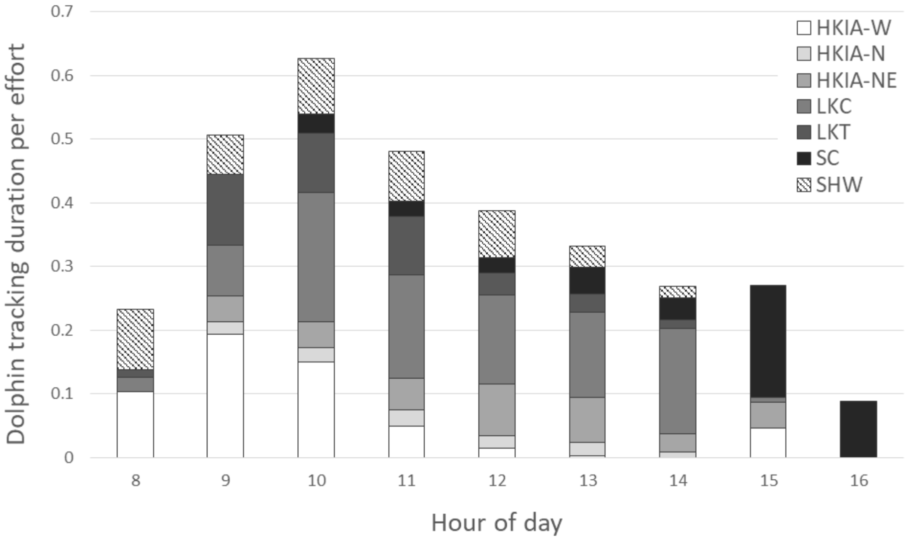

Figure III-3. Indo-Pacific humpback dolphin track duration per effort based on hour of day.

Behavioral Activity States

Behavioral activity states varied significantly based on discrete location (log-likelihood ratio test, G^2=458.98, n=2,642, df=24, P<0.001). Overall, foraging (32%, n=881) and travelling (32%, n=877) were the most frequently observed behavioral states, followed by milling (22%, n=597), socializing (11%, n=287), and resting (3%, n=80). Resting was only observed off LKC and was excluded from univariate analysis due to inadequate minimum expected value. Post hoc tests showed that dolphins were more likely to be foraging off HKIA-NE (*z*=9.14) and LKC (*z*=6.10), and less likely to be foraging off HKIA-N/W (*z*=-6.43/-3.76), LKT (*z*=-1.98) and SHW (*z*=-3.11). Dolphins were more likely to be travelling off LKT (*z*=2.29) and SHW (*z*=4.46), and less likely to be travelling off HKIA-NE (*z*=-3.39) and SC (*z*=-3.93). Dolphins were more likely to be milling off HKIA-W (*z*=4.57), LKT (*z*=4.98), and SHW (*z*=2.10), and less likely to be milling off HKIA-N (*z*=-5.19) and LKC (*z*=-4.94). Dolphins were more likely to be socializing off HKIA-N (*z*=10.91) and SC (*z*=4.29), and less likely to be socializing off HKIA-NE (*z*=-5.11), LKT (*z*=-5.15), and SHW (*z*=-3.41). Resting was observed only off LKC (**Figure III-4**).

Table III-3. Survey effort and Indo-Pacific humpback dolphin track duration. Total number of 1) on-effort survey days and hours, 2) number of days that Indo-Pacific humpback dolphins were tracked, total number of Indo-Pacific humpback dolphin groups and track duration, and 3) percentage of Indo-Pacific humpback dolphin track duration per on-effort survey time per station.

Location	Effort (days)	Days with dolphins	Dolphin groups (w/ calves)	Effort duration (hh:mm)	Dolphin track duration (hh:mm:ss)	Dolphin duration/effort	% dolphin duration/effort
HKIA-NE	51	20	54 (2)	289:10	15:02:55	0.052	5%
HKIA-N	29	7	11 (2)	159:36	2:55:32	0.018	2%
	55	24	64 (2)	307:14	21:45:58	0.071	7%
LKC	54	47	260 (9)	323:21	45:14:53	0.140	14%
LKT	72	38	114 (8)	413:22	25:44:39	0.062	6%
SC	71	27	78 (3)	389:04	12:19:38	0.032	3%
SHW	73	16	55 (6)	419:46	27:51:16	0.066	7%
Total	405	179	636 (32)	2301:33	150:54:51	0.063	6%

Table III-4. Summary of output for the plausible zero-inflated negative binomial hurdle model.

Zero hurdle model coefficients (binomial with logit link):

	Estimate	Std. Error	*z* value	Pr(>|z|)	
(Intercept)	-9.65321	0.36597	-26.377	<2e-16	***
ocnseasonLow	0.04465	0.16145	0.277	0.782126	
solarseasonSummer	0.81752	0.18159	4.502	6.73E-06	***
solarseasonAutumn	0.94774	0.18385	5.155	2.54E-07	***
solarseasonWinter	0.76696	0.22524	3.405	0.000661	***
Timeblock	-0.10055	0.02915	-3.449	0.000563	***
constructionNone	1.11035	0.10809	10.272	<2e-16	***

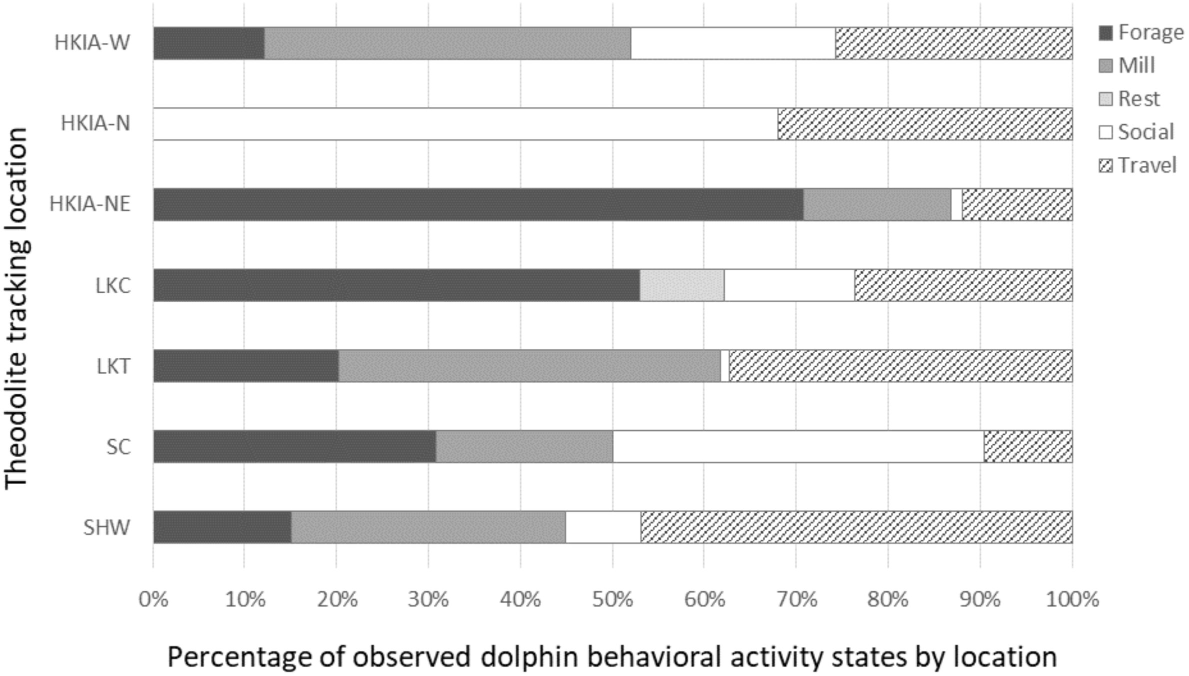

Figure III-4. Stacked bar graph showing behavioral activity state percentages of Indo-Pacific humpback dolphins off Hong Kong, based on theodolite tracking locations.

Fine-scale Movement Patterns

Swimming Speed

The GAM described significant variation in swimming speed, at the 0.05 alpha level, explaining 14% of the deviance (adj-R^2=0.098, GCV=0.061, n=417). The best fitting model included all five candidate explanatory variables, with a smooth term for both time of day and dolphin group size, and linear terms for predominant group behavior, solar season, and vessel number present:

$$[Log10(Speed) \sim s(TimeOfDay) + s(GrpSize) + BehavState + Season + VesselNum]$$

Travelling behavior was associated with significantly higher swimming speed along the horizontal plane than foraging and milling. Swimming speed was significantly higher in the spring season than in all other seasons. Swimming speed increased significantly as vessel number increased. Time of day and group size had no significant effect on swimming speed, though there was variation based on these factors (**Table III-5**, **Figure III-5**).

Table III-5. Summary of output for best fitting model for Indo-Pacific humpback dolphin swimming speed. Summary includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Spring (season), Travelling (behavioral state). An asterisk (*) indicates a statistically significant effect at alpha level 0.05.

Term	Estimate	Std. Error	t	*P*-value
(Intercept)	0.539	0.049	11.097	<2e-16*
BehavState - Forage	-0.145	0.037	-3.920	1.04e-04*
BehavState - Mill	-0.106	0.043	-2.487	0.013*
BehavState - Rest	-0.128	0.084	-1.531	0.127
BehavState - Social	-0.066	0.045	-1.466	0.143
Season - Autumn	-0.125	0.049	-2.577	0.010*
Season - Summer	-0.096	0.049	-1.969	0.050*
Season - Winter	-0.140	0.049	-2.877	0.004*
VesselNumber	0.075	0.033	2.303	0.022*
	Edf		F	*P*-value
s(TimeOfDay)	3.209	3.898	1.664	0.198
s(GroupSize)	5.107	8.000	1.042	0.131

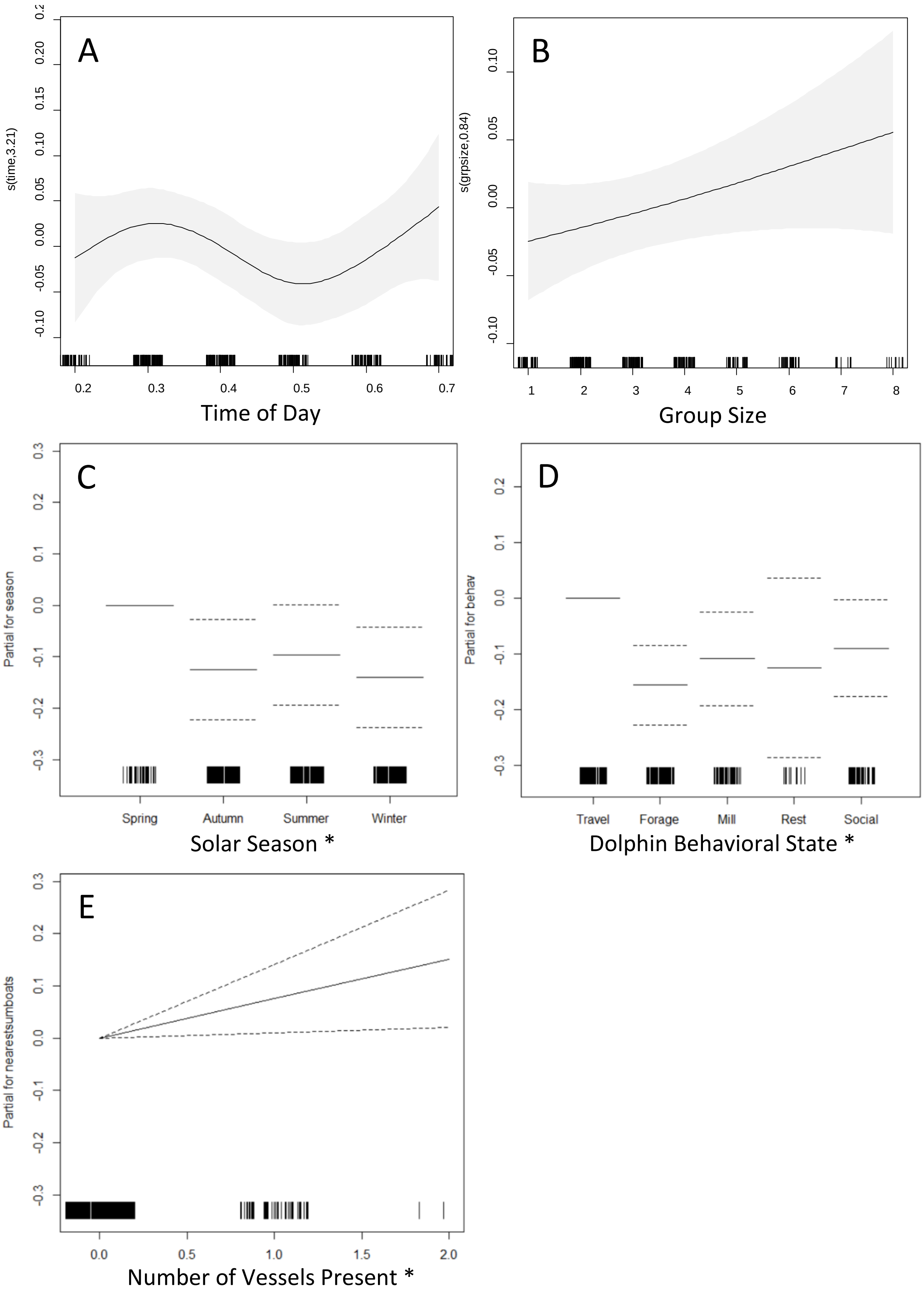

Figure III-5. Charts for the partial contribution of individual explanatory variables in the fitted GAM for swimming speed. Charts include: A) time of day, B) dolphin group size, C) solar season, D) dolphin behavioral state, and E) number of vessels present. The rugplot along the x-axis indicates the density of observations for each factor. On the y-axis, values >0 indicate a positive correlation with swimming speed, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Reorientation Rate

The GAM described significant variation in reorientation rate, at the 0.05 alpha level, explaining 8% of the deviance (adj-R^2=0.055, GCV=3.484, n=417). The best fitting model included all five candidate explanatory variables, with a smooth term for time of day and linear terms for dolphin group size, predominant group behavior, solar season, and vessel number present:

[*Sqrt(ReorientationRate) ~ s(TimeOfDay) + GrpSize + BehavState + Season + VesselNum*]

Travelling behavior was associated with significantly lower reorientation rate along the horizontal plane than foraging, milling, and socializing. At the alpha 0.1 level, reorientation rate increased as dolphin group size increased. Season, time of day, and number of vessels had no significant effect on reorientation rate, though there was variation based on these factors (**Table III-6**, **Figure III-6**).

Table III-6. Summary of output for best fitting model for Indo-Pacific humpback dolphin reorientation rate. Summary includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Spring (season), Travelling (behavioral state). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	Std. Error	T	*P*-value
(Intercept)	4.061	0.388	10.470	<2e-16*
BehavState - Forage	0.928	0.276	3.361	8.5e-04*
BehavState – Mill	1.442	0.320	4.504	8.7e-06*
BehavState - Rest	0.445	0.629	0.707	0.480
BehavState - Social	1.197	0.341	3.512	4.9e-04*
GroupSize	0.074	0.042	1.796	0.073 •
Season - Autumn	0.092	0.367	0.250	0.803
Season - Summer	0.047	0.367	0.127	0.899
Season - Winter	-0.193	0.370	-0.522	0.602
VesselNumber	0.175	0.248	0.705	0.481
	Edf		F	*P*-value
s(TimeOfDay)	1.366	1.648	0.672	0.363

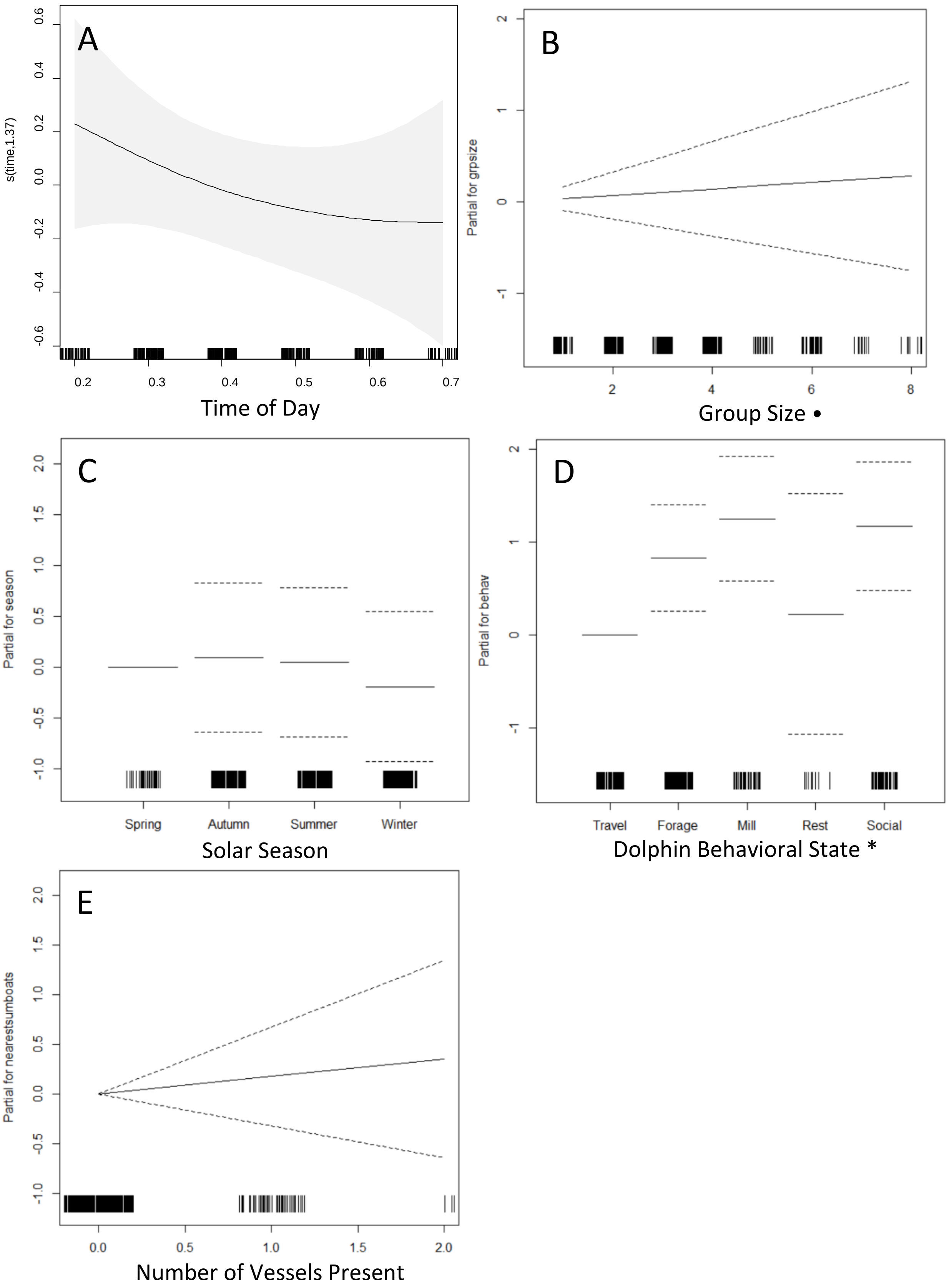

Figure III-6. Charts for the partial contribution of individual explanatory variables in the fitted GAM for reorientation rate. Charts include: A) time of day, B) dolphin group size, C) solar season, D) dolphin behavioral state, and E) number of vessels present. The rugplot along the x-axis indicates the density of observations for each factor. On the y-axis, values >0 indicate a positive correlation with reorientation rate, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Linearity

The GAM described significant variation in linearity, at the 0.05 alpha level, explaining 4% of the deviance (adj-R^2=0.014, GCV=3.292, n=417). The best fitting model included all five candidate explanatory variables, with a smooth term for time of day, and linear terms for and dolphin group size, predominant group behavior, solar season, and vessel number present:

[*EmpLogit(Linearity) ~ s(TimeOfDay) + s(GrpSize) + BehavState + Season + VesselNum*]

Travelling behavior was associated with significantly higher linearity along the horizontal plane than foraging and milling. Season, time of day, dolphin group size, and number of vessels had no significant effect on linearity, though there was variation based on these factors (**Table III-7**, **Figure III-7**).

Table III-7. Summary of output for best fitting model for Indo-Pacific humpback dolphin linearity. Summary includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Spring (season), Travelling (behavioral state). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Term	Estimate	Std. Error	t	*P*-value
(Intercept)	1.806	0.377	4.790	2.4e-06*
BehavState - Forage	-0.721	0.268	-2.687	0.008*
BehavState - Mill	-0.899	0.311	-2.892	0.004*
BehavState - Rest	-0.352	0.611	-0.576	0.565
BehavState - Social	-0.463	0.332	-1.398	0.163
GroupSize	-0.002	0.040	-0.058	0.954
Season - Autumn	-0.239	0.356	-0.671	0.503
Season - Summer	-0.425	0.357	-1.192	0.234
Season - Winter	-0.109	0.359	-0.303	0.762
VesselNumber	-0.328	0.241	-1.363	0.174
	Edf		F	*P*-value
s(TimeOfDay)	1	1.001	1.213	0.271

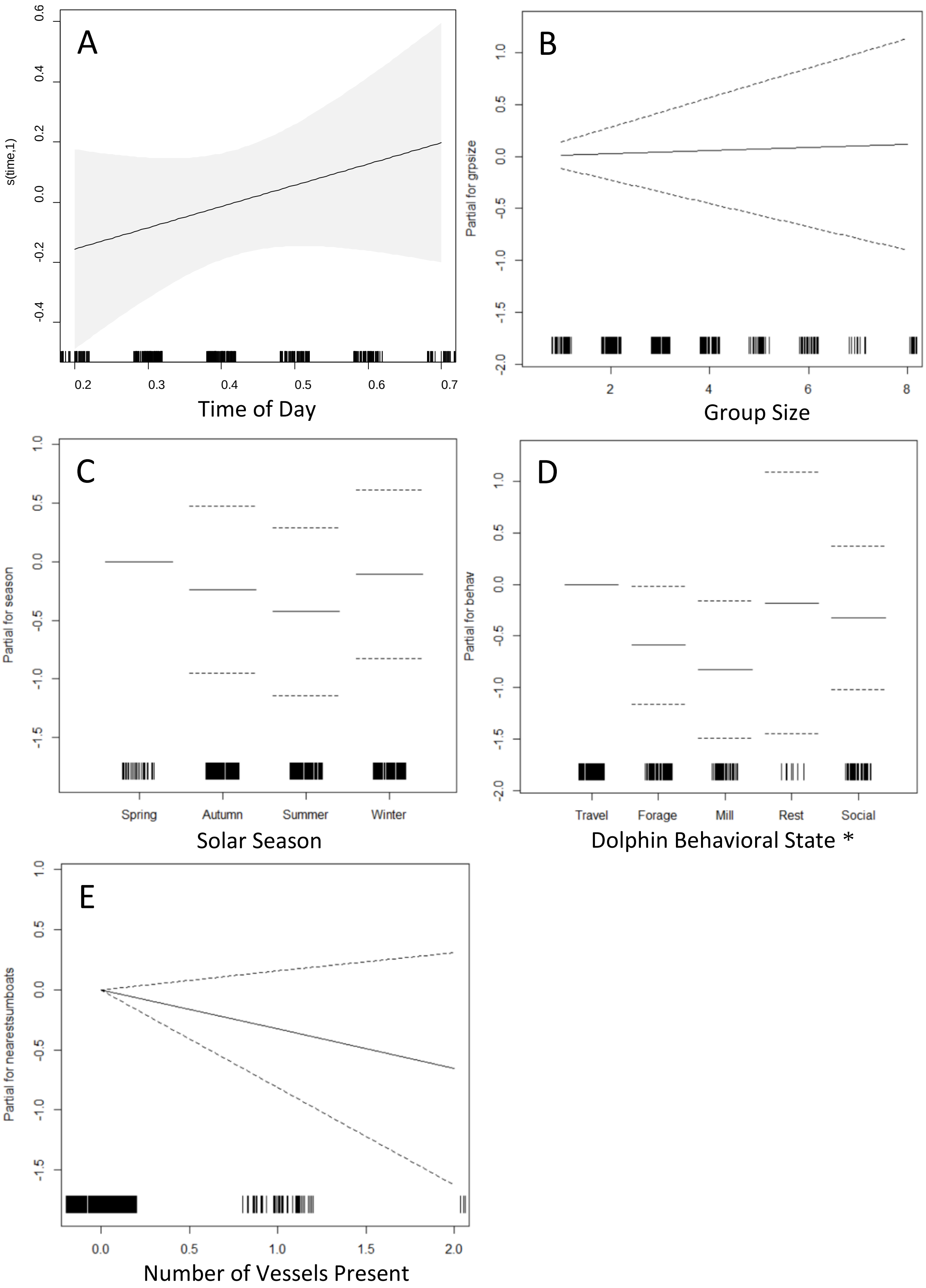

Figure III-7. Charts for the partial contribution of individual explanatory variables in the fitted GAM for linearity. Charts include: A) time of day, B) dolphin group size, C) solar season, D) dolphin behavioral state, and E) number of vessels present. The rugplot along the x-axis indicates the density of observations for each factor. On the y-axis, values >0 indicate a positive correlation with linearity, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Vessel Type

Movement patterns varied significantly based on vessel type. However, sample sizes for individual vessel types were low and unbalanced and should be treated as preliminary findings

Appendix B Table 2). Dolphin swimming speed was significantly faster in the presence of large, research, and small vessels. Reorientation rate did not vary significantly in the presence of any specific vessel type. Linearity was significantly lower in the presence of large and mid-sized vessels (**Figure III-8**,

Appendix B Table 3).

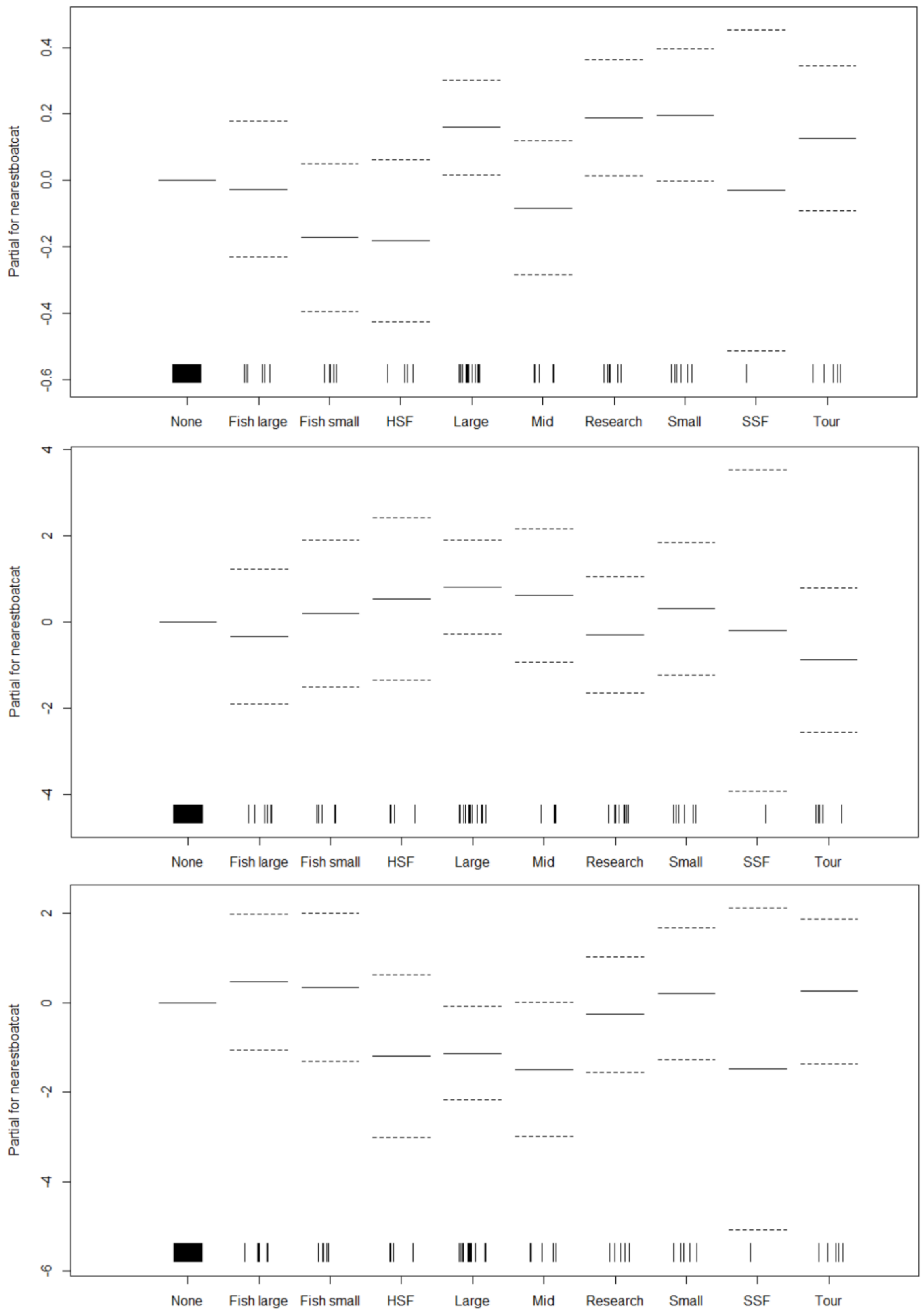

Figure III-8. Charts for the partial contribution of vessel category variable in the fitted GAM. Response variables include swimming speed (top), reorientation rate (middle), and linearity (bottom). The rugplot along the x-axis indicates the density of observations for each factor. On the y-axis, values >0 indicate an increase relative to the reference of no vessels present, values <0 indicate a decrease, and a value of 0 indicates no effect. See **Appendix B Table 3** for statistical significance.

Discussion

Dolphin day-time track duration and movement patterns varied in response to human activity. Track duration was significantly lower in areas within 5 km of long-term, low-intensity construction activity. One trend that was not captured in the analysis is that dolphin duration off SHW, which was relatively high in 2013-2014, dropped to zero in 2016, concurrent with an increase in the number of proximate construction projects. The area off SHW is historically important for dolphin foraging and socializing activity (Hung, 2008), making the total lack of dolphins as seen from visual surveys (on land and from vessels) during 2016 concerning. Likewise, track duration declined to zero off SC in all but two months of 2016, also concurrent with an increase in the number of proximate construction projects. Localized avoidance relative to construction activity has been documented in several other marine mammal studies. For example, construction of a gas pipeline reduced harbor porpoise and minke whale (*Balaenoptera acutorostrata*) presence off northwest Ireland (Culloch et al., 2016). Off Europe, common bottlenose dolphins spent significantly less time in a known foraging patch as local dredging activity intensified (Pirotta et al., 2013). During this study, multiple marine construction projects occurred simultaneously, and fine-scale temporal information was lacking. Therefore, the effect of specific activities could not be determined. Incorporating details, such as daily start/end time of specific construction activities, is suggested for future work.

Findings of high track duration off northern LKC via theodolite tracking are congruent with the acoustic recordings off southern LKC that had the highest number of days with dolphin vocalization detections (Munger et al., 2016). Dolphin track duration varied spatially, with the highest percentage off LKC. Passive acoustic monitoring was simultaneously conducted off all sites between 2012-2014, excluding northern LKC due to a logistically unsuitable environment

(Munger et al., 2016). An additional Passive Acoustic Monitoring (PAM) recorder was deployed off southern LKC. Findings from theodolite tracking were also congruent with the highest overall percentages of acoustic files with dolphin detections recorded from LKC, HKIA-NE, and SHW. Dolphin track duration also varied seasonally, with significantly lower duration during the spring season than any other season, which is also congruent with passive acoustic recorder findings. Dolphins have been reported to occur south of Lantau Island, particularly during the wet season (Hung, 2008), which may reflect an overall shift southward during the spring. Shifts in distribution off Hong Kong may potentially relate to calving season that peaks in the spring and early summer (Jefferson and Curry, 2015), or more likely to seasonal changes in river discharge related to prey distribution. Seasonal shifts in distribution patterns have also been described by *Sousa* off South Africa where dolphins inhabit Plettenberg Bay for significantly shorter periods in the spring than in the winter (Parsons, 2004). Variation in track duration was also identified based on time of day, with generally higher duration between mid-morning and mid-day and lower duration during early morning and afternoon hours. However, temporal patterns also varied based on location. For example, track duration off SHW peaking during late afternoon hours. Passive acoustic monitoring described significantly higher dolphin click detection rates at night than during daylight hours (Munger et al., 2016). Dolphins may be foraging more at night and/or using the monitored sites less during the day, possibly due to heightened vessel traffic and construction activity during daylight hours (Munger et al., 2016).

Lung Kwu Chau lies within the Sha Chau and Lung Kwu Chau (SCLKC) Marine Park and important foraging area for dolphins, and also supports other biologically important activities such as resting. Marine Parks in Hong Kong are protected areas that prohibit fishing, collection of animals or plants, operating vessels at greater than 10 knots, and damaging shoreline features, among other restrictions. The area off HKIA-NE currently includes a marine park around Brothers Islands and to the coast, but was not protected during this research was also an important foraging area for dolphins. Waters off SC and HKIA-N, which are in close proximity to one another, appear to be important for social behavior. Although SC lies within the bounds of the SCLKC Marine Park, both SC and HKIA-N overlapped directly with construction activity. The waters off LKT (near vessel activity) and HKIA-N (near construction and vessel activity) are important areas for travelling, which may serve as pathways for moving among other locations. Travelling was observed more than any other behavior off SHW (near construction and vessel activity), a historically important area for dolphin foraging and social activity.

An increase in swimming speed was the only movement pattern that varied significantly based on vessel presence. Increases in swimming speed in response to boats have been reported in other odontocetes, including beluga (*Delphinapterus leucas*) and killer whales (*Orcinus orca*) (Blane and Jaakson, 1994; Williams et al., 2002). In this study, dolphins appear to increase speed in the presence of small, research, and large vessels and exhibit less linear movement in the presence of mid-sized and large vessels. However, more data on dolphin responses in proximity to individual vessel types are needed to support robust statistical analysis. Small vessels included personal watercraft and government boats less than 10 m in length and large vessels included container shipping vessels, barges, and construction vessels. These large vessels generally move more slowly and in a more linear path than smaller vessels, and are considered more predictable in terms of movement. Two previous studies on *Sousa* behavior and vessel traffic show no reactions by dolphins to slow-moving vessels. Dolphins off Hong Kong and Indian humpback dolphins in the Indus Delta Region, Pakistan displayed no observable behavioral changes when vessels operated in the vicinity at slow speeds (Ng and Leung, 2003; Pilleri and Gihr, 1974). However, dolphin responses off Hong Kong were nominal (e.g., categorized as positive, negative, neutral) and vessel type and vessel distance (estimated by visual observation) were tested separately (Ng and Leung, 2003). Currently, high speed ferries off Hong Kong are of great concern in terms of potential vessel collision and acoustic disturbance (Hung, 2015; Marcotte et al., 2015). Considering the heavy traffic off Hong Kong, the low sample size of vessels in proximity to dolphin groups likely reflects avoidance of vessels in general. Avoidance of vessels has been observed in other species, for example common bottlenose dolphins off Clearwater, Florida (Gulf of Mexico), avoided important foraging areas when motorboat traffic was high (Allen and Read, 2000). In December 2015, speed control mitigation measures were placed on high speed ferries rerouted to travel around the northern portion of the SCLKC Marine Park off LKC, where dolphin presence is historically high. Vessels in this context may be more predictable, easier to move away from, and therefore perceived as less threatening.

In addition to human activity, dolphin movement patterns varied significantly based on natural factors. Swimming speed was highest during the spring season. This is counterintuitive as calving season peaks in the spring and early summer (Jefferson and Curry, 2015), and slower speeds are expected in the presence of newborn and young calves. However, few calves were identified from shore locations (too few to isolate for statistical analysis). Travelling behavior was associated with significantly higher swimming speed, lower reorientation rate, and increased linearity, along the horizontal plane, than foraging and milling behavior. Reorientation rate was also significantly lower during travelling than during socializing. This is not surprising as foraging, milling, and socializing behaviors include asynchronous movements in various directions, in which dolphins change bearing more frequently.

In addition to physical presence, vessels and construction activity introduce a great deal of sound into the marine environment. Noise emitted during construction activities off Hong Kong during this study, including drilling and dredging, were likely persistent at lower frequencies than noise produced by acute high-intensity sound energy with higher peak frequency levels, such as seismic airgun blasts and pile driving. Dredging can be a strong source of continuous noise in nearshore regions, strongest at low frequencies (< 1,000 Hz) but can exceed 6,000 Hz (Richardson et al., 1995; Todd et al., 2014). Large vessels, such as cargo and tanker ships, emit primarily low frequency sounds (10-500 Hz) and general vessel sounds examined off Hong Kong in 2010-2011 ranged from 315-45,000 Hz, well within the audible range of dolphins (Sims et al., 2012). Vessel levels can exceed that of dredging, however, unlike construction activities, may not remain in one area for prolonged periods (Richardson et al., 1995). These chronic, low-intensity sounds may affect dolphins directly (e.g., hearing loss, masking communication via noise pollution), where noise reflected off the seabed and steep benthic slopes in shallow systems can result in multiple transmission paths (Reine et al., 2014), or indirectly (e.g., shift in prey distribution).

Hearing is considered the most important sensory modality for odontocetes (Thewissen, 2009), compulsory for hunting prey, navigating the environment, and maintaining social contact with conspecifics. Human-generated sounds have the potential to alter marine mammal hearing on a temporary (TTS, temporary threshold shift) or permanent (PTS, permanent threshold shift) basis. A TTS is a temporary loss of hearing sensitivity, and long or repeated TTS events have the potential to induce PTS (Wartzok and Ketten, 1999). Trauma is dependent on frequency sensitivity of the subject, as well as the intensity and duration of the sound source, and is therefore species-specific (Ketten, 2004). Odontocetes possess good functional hearing generally between 200 Hz and 100,000 Hz and above, depending on species (Ketten, 2004). However, there are currently insufficient data on species-specific hearing ranges to establish exposure guidelines for all. The lower hearing sensitivity of *S. chinensis* is not known, with hearing only recently tested and with no useful data at low frequencies (<5,600 Hz) where much of the noise from industrial and vessel activities occurs (Li et al., 2012). The few odontocete species that have been tested at low frequencies hear strong sounds down to 40-75 Hz (Richardson and Würsig, 1997), well within the range of many chronic industrial activities. Although high-frequency echolocation clicks are not likely masked by most chronic industrial noise, *S. chinensis* may use passive listening to detect soniferous prey species, such as croakers (Family Sciaenidae), which are the most numerically important prey found in *S. chinensis* stomach contents (Barros and Cockcroft, 1999; Barros et al., 2004; Parsons, 2004). Sciaenids produce sounds at dominant frequencies between 100-1,000 Hz (Ramcharitar et al., 2006), and low frequency anthropogenic noise may mask sounds that they produce. The ability to detect prey via passive sonar tracking may be particularly important for dolphins off Hong Kong that live in a naturally turbid, estuarine environment, further agitated by construction activity, in which visibility is limited. Additionally, hearing sensitivities of fishes are variable, but general teleost fishes are sensitive to low frequencies (30-1000 Hz and above). This hearing range falls within frequencies produced by chronic construction and large vessel activity (Slabbekoorn et al., 2010), and some fishes have been described as avoiding vessels with low-frequency output (Todd et al., 2014).

Habitat modification may result in habitat loss (e.g., new land formation) or damage to existing habitat (e.g., dredging and boring tunnels in the seabed) that can cause shifts in prey distribution and abundance (Reine et al., 2014; Todd et al., 2014). Marine mammals may compensate for small–scale changes in prey distribution by moving to alternate foraging areas, switching prey species, or devoting more time to foraging. Habitat destruction and degradation are described as a threat to other species of *Sousa*, including *S. teuszii* off West Africa, in Senegal (Van Waerebeek et al., 2004) and Angola (Weir et al., 2010). *Sousa sahulensis* off western Australia are vulnerable to habitat degradation, particularly relating to environmental change (Brown et al., 2012), which has also been suggested as one potential factor in the absence of *S. teuszii* off Ghana (Van Waerebeek et al., 2009). *Sousa chinensis* of the eastern Taiwan Strait is another example of a small population that uses shallow near-shore habitat, wherein heavy and rapid coastal degradation is a serious conservation concern, listed as one of the top five major threats (Wang et al., 2007a; Wang et al., 2007b). Long term impacts of habitat displacement are dependent on the duration of the disturbance, the quality and proximity of alternate available habitat, and the potential for the historically used habitat to recover. Populations with small home ranges and strong site fidelity are especially vulnerable to habitat displacement in highly disturbed areas because they may have few suitable alternatives (Forney et al., 2017; Todd et al., 2014).

The general increase in human activity and associated low-frequency noise due to industrial construction and vessel traffic off Hong Kong seems to relate to reduced dolphin track duration and shifts in behavior that are presently occurring off SHW and SC. The consequences of displacement are poorly understood, but may include increased stress responses, and reduced foraging opportunities. Prior research in other areas has shown optimistic trends of marine mammals returning to previously abandoned areas. For example, harbor porpoises returned to Puget Sound after decades of being absent from the area (Jefferson et al., 2016). Causes for the initial decline are not fully understood, but potentially relate to large-scale human-induced changes (e.g., pollution, fisheries bycatch, habitat loss and degradation) (Jefferson et al., 2016). A similar situation for harbor porpoises in the southern North Sea was reported, wherein porpoises have returned after a significant decline in the mid-twentieth century (Thomsen et al., 2006). Gray whales (*Eschrichtius robustus*) were displaced from a breeding area for more than 5 years in response to industrial sounds, returning years after activities ceased (Jones et al., 1994). Bottlenose dolphins avoided northern portions of Galveston Bay, during a time of intensely poor water quality. Present-day studies indicate that bottlenose dolphins are returning to northern portions of Galveston Bay and we have seen the same behavior in humpback dolphins that returned to areas off Chek Lap Kok once intensive development activities stopped. These are encouraging outcomes, but habitats must recover and be protected for re-establishment to be possible. Alternatively, the outcome can be devastating for populations in areas that continue to degrade and where research and mitigation measures are absent or insufficient. An extreme example of a habitat alteration impact on a marine mammal species is the baiji (*Lipotes vexillifer*) that was recently declared extinct, due largely to intensive habitat degradation (Turvey et al., 2007).

One of the biggest challenges to *Sousa* conservation is protecting and maintaining suitable high-quality habitat (Parra and Ross, 2009), especially considering the cumulative nature of human activities in developing and densely populated regions. One important management tool for protecting portions of *S. chinensis* habitat is proper designation and enforcement of Marine Protected Areas (MPAs) in known dolphin “hotspots”, particularly where site fidelity has been described. These areas aim to reduce human disturbance in important habitats and may give refuge to dolphins displaced from highly-disturbed adjacent waters. Furthermore, if previously disturbed areas become designated MPAs once activity, such as construction, ceases, dolphins may return. Ideally, for MPAs to serve their intended purpose, they should be truly protected with effective enforcement and restriction of development, fisheries, dolphin-based tourism, vessel speed, and other vessel activity. Marine Protected Area boundaries, as well as travel corridors between locations, should be developed and managed with knowledge of humpback dolphin movement patterns and habitat use. Research should be ongoing, with adaptive management schemes in place in order to modify boundaries according to shifts in habitat. Currently, MPAs make up only 2% (3,400 ha) of the Hong Kong Special Administrative Region (165,000 ha), and only 1% (2,170) were designated with dolphins in mind. Recent arguments have been made for larger biosphere reserve-type areas worldwide that include core areas of known marine mammal critical habitat and are regularly reviewed and adjusted as needed (Hoyt, 2011). Off Hong Kong, a multi-organizational approach is encouraged to better understand cumulative impacts with a considerable number of overlapping and logistically complex projects that affect the same population of dolphins.

Conclusions

Indo-Pacific humpback dolphins off Hong Kong avoided historically important foraging areas during periods of chronic construction activity. Dolphins avoided these areas during the day but may return at night when construction and related vessel activities are reduced. Prior research in other areas shows that some odontocetes do return to previously abandoned habitats once intensive human activity ceases (Jefferson et al., 2016; Thomsen et al., 2006). Off Hong Kong, spatio-temporal overlap in development projects may displace animals for extended periods and/or from large areas that historically support prey species. In these cases, ecologically similar habitats should be identified and designated as marine protected areas to mitigate effects of disturbance. The overall impact to the dolphin population depends, in part, on alternative habitats with suitable prey accessibility. Therefore, future research should incorporate dolphin prey characteristics (e.g., species, distribution, and abundance) on a large spatio-temporal scale. This is especially important for species, such as Indo-Pacific humpback dolphins, with small population sizes and restricted distribution based on ecological features that reduce alternative habitat options to compensate for human disturbance.

CHAPTER IV

DUSKY DOLPHIN (*LAGENORHYNCHUS OBSCURUS*) BEHAVIOR NEAR MUSSEL FARMS IN NEW ZEALAND

Introduction

Marine-based aquaculture, defined as human cultivation of plants and animals in the sea, is one of the world's fastest growing food production technologies (Asche, 2008; FAO, 2016) and often overlaps with near-shore habitats used by marine mammals. Many delphinids have been documented selectively foraging near finfish farms that attract wild dolphin prey due to supplemental feed that disperses from cages (Tuya et al., 2006; Würsig and Gailey, 2002). Shellfish farms do not require supplementary feeding like their finfish counterparts and do not attract wild fishes in the same manner. Unlike finfish farms that have been described as an attractant to dolphins (Würsig and Gailey, 2002), shellfish farms have been described as a repellent. Shellfish farming is an expanding sector of the industry generally established in inland bays or waterways (Asche, 2008; FAO, 2016) where dolphins often occur. Several potential direct and indirect effects of shellfish farms on dolphins include habitat loss, habitat degradation, biodeposition accumulation, and shifts in foodweb ecosystems (Würsig and Gailey, 2002). When food resources change spatially or temporally, consumers are expected to shift between patches within habitats, or to change habitats altogether. Common bottlenose dolphins (*Tursiops* spp.) avoided portions of Red Cliff Bay, Australia when oyster (*Pinctada* spp.) farming was introduced (Watsoncapps and Mann, 2005), Chilean dolphins (*Cephalorhynchus eutropia*) largely avoid patches where shellfish farms exist (Ribeiro et al., 2007), and Indo-Pacific humpback dolphins in the Pearl River Delta avoided preferred habitat due to oyster farm development (Karczmarski et al., 2016).

Admiralty Bay, New Zealand is a historically important foraging habitat for dusky dolphins (*Lagenorhynchus obscurus*), where a large proportion of time is spent actively searching for food (Markowitz et al., 2004). One foraging technique of dusky dolphins in Admiralty Bay involves using open space to herd prey balls of schooling fish, whereby dolphins move in a coordinated manner to encircle, contain, and ingest prey (Vaughn et al., 2011). Maintaining a cohesive unit when herding dynamic prey balls involves a high degree of organization and the ability to move freely in open space. Obstructions in water can disperse tightly organized prey balls and reduce available space for dolphins to forage in this manner (Pearson et al., 2012). Another foraging technique observed in Admiralty Bay involves using the shoreline, a continuous natural barrier, during prey acquisition; dolphins drive non-schooling fish toward the shore in an apparent attempt to capture them (McFadden, 2003). Prey distribution, abundance, and other characteristics may affect patch choice (Guillemain et al., 2000), and dusky dolphins appear to use distinct habitat patch types within Admiralty Bay in diverse ways.

In addition to foraging in distinct patch types within a habitat, at least some dusky dolphins commute seasonally and forage in broadly diverse marine systems. Some dolphins commute approximately 275 km between the ecologically diverse habitats of Kaikoura’s deep water canyon system and Admiralty Bay’s partially enclosed shallow bay system within the Marlborough Sounds (Markowitz, 2004). These individuals demonstrate seasonal movement to Admiralty Bay during the austral winter and early spring, and some return in subsequent years (Markowitz, 2004; Pearson, 2009). Diverse ecological features and differences in prey distribution appear to facilitate the shift from foraging on nighttime mesopelagic prey off

Kaikoura to daytime schooling and non-schooling fishes in Admiralty Bay (Benoit-Bird et al., 2004).

In Admiralty Bay, New Zealand, shellfish aquaculture overlaps with dusky dolphin habitat, with potentially negative consequences. Green lipped mussel (*Perna canaliculus*) farming is an economically important industry in Admiralty Bay, introduced into the Marlborough Sounds in the 1970's (Dawber, 2004). Farms extend vertically in the water column, at a maximum depth of 15 m, horizontally from 50 m to 200 m off the coastline, and occupy nearly 1.2 km^2 of near-shore water (Childerhouse and Baxter, 2010; Duprey, 2007). Artificial structures, such as ropes, that occupy space in the water column may impede dusky dolphin movement, reducing space needed to herd schooling prey, with implications for habitat patch use. Studies in Admiralty Bay in the late 1990's and early- to mid-2000's show that dusky dolphins rarely enter the lines of mussel farms, avoiding space with farms already in position (Markowitz et al., 2004; Pearson et al., 2012).

Dusky dolphin behavior and movement patterns were investigated within three distinct patch types: 1) nearshore in proximity to mussel farms, 2) nearshore without mussel farms, and 3) mid-bay areas with open space. Dusky dolphin regional encounter rate and individual resighting rate were also determined for inter-annual comparison to prior research, conducted between 1998 and 2006, to evaluate changes in broad habitat use over time (Markowitz et al., 2004; Pearson et al., 2012). Specific objectives are to determine present day regional habitat use, determine how dolphin behavioral activity states vary based on defined habitat patches, and quantify movement patterns (i.e., swimming speed, reorientation rate, and linearity) within each distinct habitat patch.

Methods

Ethics Statement

Data collection from land was fully non-invasive and boat-based methods were minimally invasive (no physical contact with animals). Approval to conduct boat-based photo-identification was granted by the New Zealand Department of Conservation, no formal permitting process was required.

Study Area

Admiralty Bay (40^{o} S, 173^{o} E) is a small, shallow inlet located within the Marlborough Sounds near the northeast tip of the South Island of New Zealand. The total area of Admiralty Bay is approximately 117 km^2 with a muddy substrate (**Figure IV-1**) (McFadden, 2003). The bay has a relatively uniform water depth under 50 m, and a maximum depth of 105 m in an isolated area near French Pass. As of 2012, 54 mussel farms were distributed within 200 m of shore at the low-water mark, occupying a total area of 1.2 km^2. Three habitat patches were classified to distinguish between areas of interest: the nearshore (NS) patch encompasses area within 1 km of shore, where no mussel farms are in place, the near mussel farm (NMF) patch encompasses areas within 1 km of shore, where mussel farms are in place, and the mid-bay (MB) patch encompasses area greater than 1 km from shore. Previous research considered the nearshore zones that include areas with and without mussel farms to be within 500 m (Markowitz et al., 2004) and 400 m (Pearson et al., 2012) of shore. However, for movement data analysis, this research encompasses a greater area to determine how dusky dolphins behave not only within mussel farms, but also in close proximity to farms.

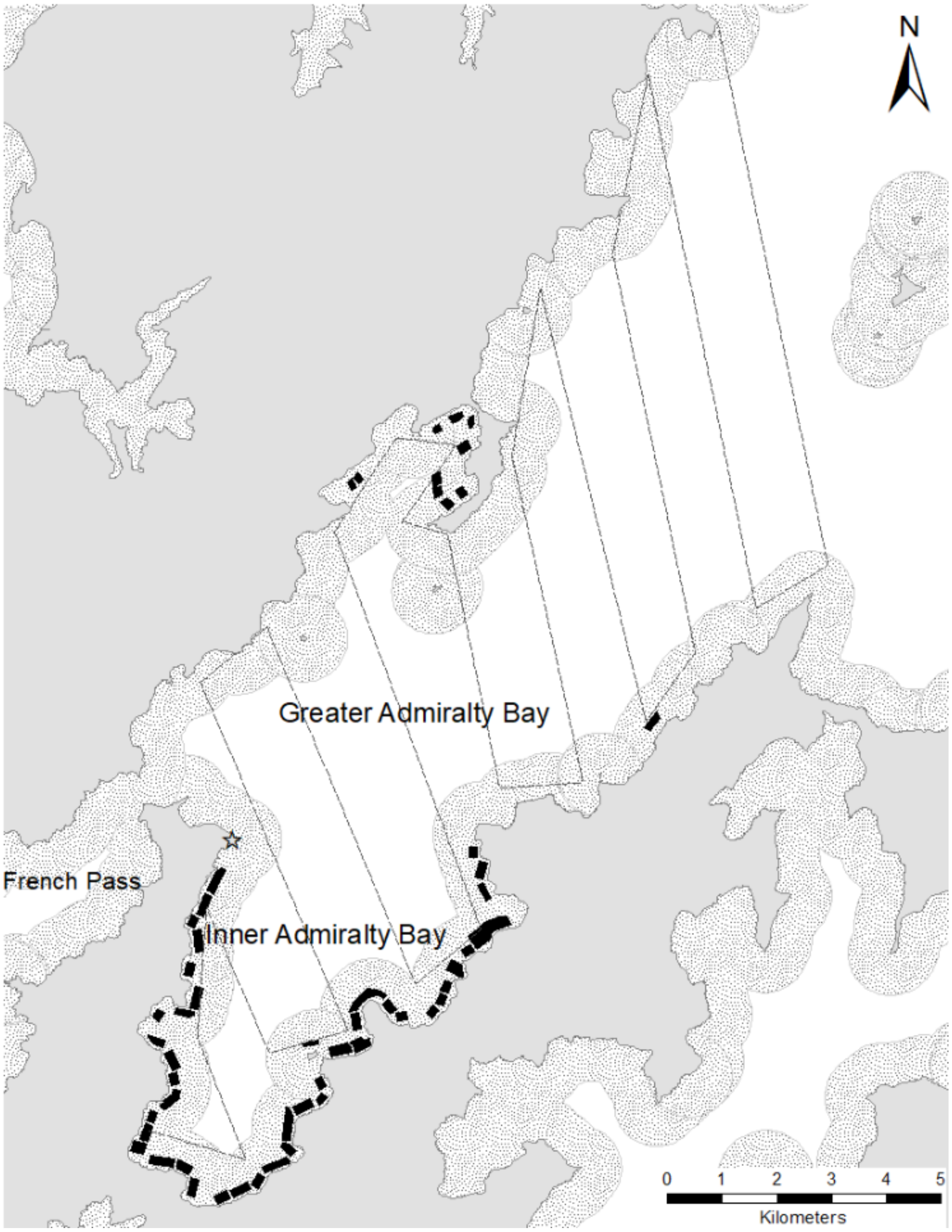

Figure IV-1. Study site in Admiralty Bay, New Zealand during 2011-2012. The star indicates the land-based theodolite station, the solid black polygons represent green-lipped mussel farms, dotted dark gray lines represent boat-based survey transect lines, and the gray dotted contour pattern represents 1 km distance from shore.

In addition to dusky dolphins, common dolphins (*Delphinus delphis*) and New Zealand fur seals (*Arctocephalus forsteri*) regularly occurred in Admiralty Bay during this study period. Mixed-species aggregations of dusky and common dolphins were occasionally observed.

Common bottlenose dolphins (*Tursiops truncatus)* and killer whales (*Orcinus orca*) are also occasionally observed in the bay, but were rare during this study. Data containing mixed-species groups were eliminated from analyses of dusky dolphins to minimize confounding effects.

A combination of land- and boat-based platforms were used to collect data during the Austral winter season (June-August) of 2011 and 2012, alternating between platforms every other data collection day. Field observations totaled 74 days, including 35 from land and 39 from boat, and 135 hours on effort, including 66 from land and 69 from boat (**Table IV-1**). An additional 92 hours were spent travelling to/from transect lines via boat where dolphin groups were observed opportunistically off-effort. Research was conducted during daylight hours between 0800 and 1800 and dusky dolphins were observed a total of 69% of survey days (n=51), totaling 217 focal follow groups and 74 focal follow hours (**Table IV-1**). Data were collected in sea conditions of Beaufort 0-3 with no rain. During data collection periods, records were made of all cetaceans encountered, and extended focal follows were conducted with dusky dolphins.

Table IV-1. Summary of research effort based on data collection platform in Admiralty Bay.

Platform	Survey Days	Days with Dolphins	% Days with Dolphins	On-effort Survey Hours	Focal Follow Hours	# Focal Follow Groups
Land	35	27	77%	66	37	132
Boat	39	24	62%	69	37	85
Total	**74**	**52**	**69%**	**135**	**74**	**217**

Land-based Data Collection

Land-based theodolite tracking of dusky dolphins was conducted from an elevated position, selected based on close proximity to the water (within 100 m), height above sea level (59 m), and unobstructed views of Inner and Outer Admiralty Bay (**Figure IV-1**). A digital theodolite (Sokkia/Sokkisha Model DT5) with 30-power magnification and ±5-second precision was used to obtain vertical and horizontal angles of dolphin positions (Würsig et al., 1991). *Pythagoras* software (v 1.2) (Gailey and Ortega-Ortiz, 2002) was used facilitate data management and convert theodolite angles to latitude and longitude for analyses. Handheld binoculars (7x50 magnification) were used to systematically scan the study area to locate dolphins at the beginning of each tracking session. Three team members collected data, including a theodolite operator, an observer, and a data-entry computer operator. One experienced theodolite operator collected positional fixes to minimize inter-individual variation in data gathering. The observer and computer operator rotated duties each hour to reduce the potential for visual fatigue.

A combination of the 10 m chain rule (individuals within 10m of another individual are considered part of the same group) (Smolker et al., 1992) and coordinated activity (Mann et al., 2000) were used to define a dolphin group. Focal follow (Altmann, 1974; Mann, 1999) tracking sessions began once dolphins were located. If multiple groups were present at the same time, an attempt was made to follow several simultaneously; otherwise selection rotated between following the larger group until the session ended, and then the smaller group for the subsequent session, and so on (Mann, 1999). A similar selection criteria was used if group members split during a follow (i.e., follow the smaller group if members split, then the larger group if members split again, and so on).

Dolphin data were recorded instantaneously every two minutes and included geographic position, group size, calf presence/absence, and predominant group (≥50% of individuals) behavioral state. The juvenile age classification was excluded given the difficulty in distinguishing this class consistently and correctly. Calves were identified based on small size

(≤2/3 adult length) and echelon swimming position ("beside and slightly behind an adult"; (Shane, 1990). Surface behavioral states were classified using definitions by Pearson (2008) (**Table IV-2**). All vessels that moved within approximately 1 km of the focal individual/group were documented. To track focal individuals, theodolite crosshairs were positioned on the animals' body at the water line. To track focal groups, theodolite crosshairs were positioned based on a central location within the entire group (Bejder, 2005; Lundquist et al., 2013). Focal follows were conducted for approximately 60 minutes unless the individual or group was lost or environmental conditions obstructed visibility (e.g., intense haze or fog, Beaufort sea state >3, or sunset).

Table IV-2. Dusky dolphin behavioral state definitions. Modified from Pearson (2008)

Behavioral State	Definition
Forage	Long dives followed by loud forceful exhalations ("chuffs"), and directionless movement; prey-ball foraging may include coordinated "burst swims" (rapid bursts of speed), "clean" noiseless headfirst re-entry leaps, coordinated clean leaps, and tail slaps. Fish prey balls may also be observed at the surface of the water. Diving gannets, shags and petrels may also be present
Rest	Slow, at times directionless, movement at speeds of < 3 knots close to the surface with low activity level; often includes slow surfacings and floating near the surface
Social	Interacting with conspecifics or inanimate objects; usually directionless movement and may include body and pectoral fin rubbing, rolling, belly-up swimming, spyhops (projection of the head above water), splashing at the surface, chasing, leaping, mating, and playing with seaweed
Travel	Steady movement in one direction at speeds of ≥ 3 knots

Boat-based Data Collection

For consistency in inter-annual comparisons, boat-based data collection closely followed Pearson (2008). Data were collected from a 5.5 m rigid-hull, semi-inflatable boat with an 80 Hp 4-stroke engine. Systematic surveys were conducted along pre-determined transect lines, programmed into a handheld Garmin 76 global positioning system (GPS), moving at speeds of 18-25 km/hr. To avoid sampling the same areas at the same time of day, survey start positions varied each day. The boat-based team consisted of three members, including a boat operator, data recorder, and photographer. While traveling along the survey route, the two team members that were not operating the boat scanned assigned zones for dolphins to the side and forward of the boat, totaling 240 degrees of viewing area. The boat operator scanned the entire 240 degree area opportunistically.

Once a group of dolphins was located, geographic coordinates and time were recorded prior to leaving the transect line. These data were recorded again once dolphins were approached within 50 m by the research vessel, adhering to New Zealand Department of Conservation vessel approach guidelines and travelling at matching speeds parallel to the group when possible. If dolphins were not dusky dolphins, data (species, group size, initial behavioral state, dorsal fin photographs) were recorded quickly and then the research boat returned to the transect line from where it departed. If the dolphins were dusky dolphins, a focal follow session was initiated. Dolphin data were recorded every two minutes and included geographic coordinates, time of day, number of individuals present, calf presence/absence, and predominant group (≥50% of individuals) behavioral state. Group, behavioral state, and age class were defined as above in the land-based data collection section. Focal follows continued for approximately 60 minutes unless the focal individual/group was lost prior.

Photo-identification was used to establish individual dolphin resighting rate. An attempt was made to photograph each individual dusky dolphin dorsal fin within a group, using a Nikon D7000 digital SLR with an 80-400 mm lens. The ability to capture all or most individuals for most groups was possible given the small group sizes of dusky dolphins in Admiralty Bay.

Photographs were used to identify individuals based on distinct nicks and notches in the dorsal fin (Würsig and Jefferson, 1990). Image selection for photo-identification analysis was based on the following criteria, following Pearson (2008) for inter-annual comparison: 1) the image was in focus, 2) with suitable light exposure, 3) the entire dorsal fin was in the frame and was not obscured by objects such as water splashes or other animals, 4) the dorsal fin was parallel to the camera, and 5) the individual possessed distinguishing notches. All images that did not fit these criteria, including clean dorsal fins that lacked notches, were not included in analysis (aside from calculating mark rate). The highest quality image for each individual per group encounter was selected manually and then processed and matched using Finscan v.1.5.4 semi-automated photo-identification software (Hillman et al., 2002). All images were matched by 2 individuals trained in photo-identification and confirmed by an experienced examiner.

Data Filtering

Dolphin focal follow data were removed if they contained only 1 positional fix, were less than 10 minutes in duration, and/or maximum swim times exceeded known values for dusky dolphins (Markowitz, 2004). Focal follow data were binned into 10-minute segments (Bejder et al., 1999; Lundquist et al., 2012), comprising 6 interpolated positional fixes per segment with associated data, based on 120 sec intervals, to standardize observations that varied in duration. Of the 217 focal follow groups, 235 10-minute segments met the criteria for analyses. Each focal follow varied slightly in duration; therefore, the number of segments also varied (e.g., a group followed for 50 minutes would have 5 segments, a group followed for 60 minutes would have 6 segments). Other than the research vessel, few vessels traveled through the bay during sampling times, and dolphin segments that included vessel transits during, or up to 10 minutes prior, were removed from analysis. Successive observations from the same individual/group of individuals poses problems due to lack of independence; therefore, temporal autocorrelation was performed to identify potential pseudo-replication (i.e., not statistically independent) (Dray et al., 2010) for groups with > one 10-minute segment. Issues of collinearity among potential explanatory variables were assessed via augmented pairs plots and correlation coefficients >0.50 were considered to have potential masking effects.

Each 10-minute segment included the dolphin response variable of mean swimming speed, reorientation rate, and linearity. Variables were transformed (Log10 for swimming speed, Square Root for reorientation rate, and Empirical Logit for linearity) to approximate normal distribution. Candidate explanatory variables for each segment included time of day, dolphin group size, calf presence/absence, predominant dolphin behavioral state, and patch type. To account for changing sunrise/sunset times throughout the season, a time of day index was calculated to represent a percentile of daylight hours (sunrise =0 and sunset =1). Swimming speed (km/hr) was calculated by dividing the distance travelled by the duration between two consecutive positions (Gailey et al., 2007). Reorientation rate is the degrees per minute of change in direction of a tracked individual or group of dolphins and was calculated by dividing the sum of bearing changes within a segment by the total duration of that segment. Linearity is an index of net movement, or displacement, ranging from 0 to 1, with 0 equating to no net movement (i.e., a circular path) and 1 equating to straight line movement. Linearity was calculated by taking the net distance between the first and last fix of a segment and dividing by the sum of all distances travelled between each of the 11 interpolated positional fixes within each segment.

Statistical Analysis

Univariate analyses included Chi-square contingency tests and log-likelihood ratio tests to assess nominal categorical data (i.e., behavioral states), with Freeman-Tukey Deviate and binomial *z* score post hoc tests (respectively) to assess which factors occurred more or less frequently than expected by chance. The FTD *z* score decision rule was based on the critical value 0.95, and the binomial *z* score decision rule was based on 1.96. For Chi-square and log-likelihood ratio tests, foraging and prey ball foraging categories were pooled together to meet minimum expected frequency requirements (value >5). Kruskal-Wallis rank sum and Dunn post-hoc tests (p-values adjusted with the Benjamini-Hochberg method) were run to assess non-parametric numerical data (i.e., mean group size relative to behavioral state; FSA package in program R). The *z* score decision rule was based on the critical value 1.96, the Kruskal-Wallis test was set at $p<0.001$, and Dunn tests were set at $p<0.05$. Z-tests were used to compare behavioral activity state proportions between studies.

Multivariate generalized additive models (GAMs) were applied to evaluate continuous numerical data (i.e., swimming speed, reorientation rate, linearity) with multiple potential explanatory factors. No significant collinearity was detected among candidate explanatory variables. Linear mixed-effect modelling, using the lme function (package nlme) in program R, indicated that autocorrelation was evident for speed and linearity at lag 2 and lag 1, respectively, and disappeared at lag 3. All tracks were filtered so that 30 minutes separated any two segments from the same focal group. The best fitting models for filtered data showed no significant autocorrelation in the residuals. Filtered data totaled 105 10-minute segments that were used for movement pattern and behavioral state analyses. However, all 6 data points within each segment were used for behavioral data due to potential fluctuating behavior within each segment.

Behavioral data totaled 630 2-min sampling interval records (i.e., 6 records per 105 filtered segments).

The GAM framework was applied to relate dolphin movement patterns to natural (time of day, dolphin group size, predominant group behavioral state) and anthropogenic (patch type) candidate explanatory variables. Models were run using the multiple generalized cross-validation (mgcv) package in program R (Wood, 2006) that is appropriate for detecting trends in complex data that are multivariate and nonlinear (Hastie and Tibshirani, 1986). Generalized additive models incorporate smoothing terms, fitting data locally rather than globally (Quinn and Keough, 2002), with a penalty for excessive flexibility (Wood, 2006; Wood, 2008). Flexibility was determined by the number of knots for each smooth term. The default value of 10 knots, set by package mgcv, was used unless there were fewer than 10 categories per term, in which case the knot value was lowered. Models were tested with all combinations of the fixed factors and Akaike Information Criterion correction (AICc) values were calculated and compared. AICc is derived from AIC and is appropriate for smaller datasets where $n<40$ data records per parameter (Burnham and Anderson, 2004; Hurvich and Tsai, 1989). These models evaluate candidate explanatory variables simultaneously, reducing problems associated with many step-wise techniques. Model selection was based on adj-R^2 (high), GCV (low), and deviance explained (high) values. Microsoft Excel 2013 was used to conduct computational analysis of swimming speed, reorientation rate, and linearity and to calculate Chi-square and log-likelihood statistics, including associated post-hoc tests; R statistical software (2.14.1) was used to perform exploratory work, Kruskal-Wallis and Dunn tests, and GAM analyses; and ArcMap (v 10.2.2) was used to produce maps. Positions of marine farms were obtained from Cawthron Institute and checked manually via handheld global positioning system (gps) in situ.

Results

Behavioral Activity States

Behavioral states varied significantly from values expected by chance (χ^2=145.17, n=620, df=3, p=0.001; **Figure IV-2**). Overall, foraging (39%, n=241) was the most frequently observed behavioral state, observed significantly more than expected by chance (*z*=6.16; prey-ball foraging accounted for just over 1% of total observed behaviors). Travelling (29%, n=180) was observed significantly more than expected by chance (*z*=1.95), and socializing (6%, n=35) was observed significantly less than expected by chance (*z*=-13.00). Resting accounted for 26% (n=164) of observed behavioral states. Compared to 2005-2006 results, dolphins spent more time foraging (z-test, *z*=12.169, p<0.001) and less time socializing (z-test, *z*=-6.077, p<0.001) and resting (z-test, *z*=-5.369, p<0.001) during the current study.

Mean group size did not vary significantly based on behavioral state. Mean group size, based on filtered data, was 3.35 dolphins (SD=1.85; range = 1-13). One group of 50 and one group of 30 dolphins were observed from land, but these outliers did not meet criteria for inclusion in statistical analysis.

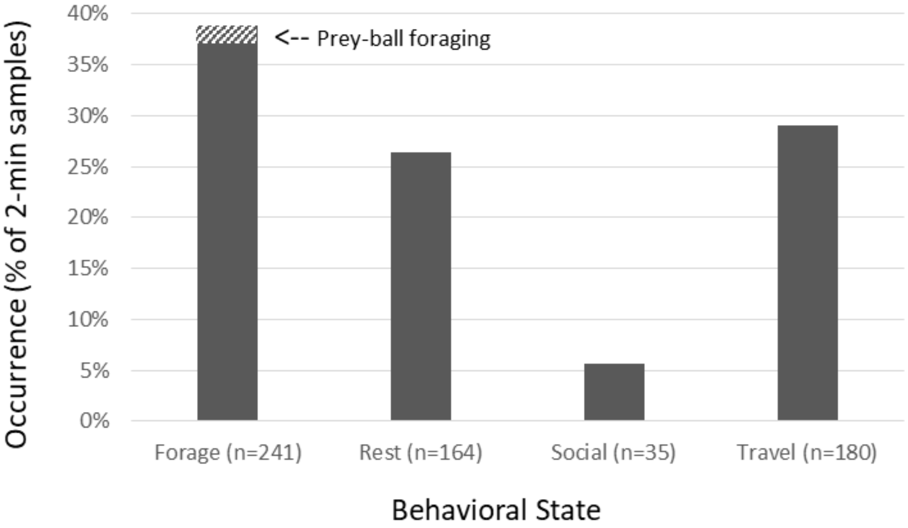

Figure IV-2: Behavioral activity states of dusky dolphin groups in Admiralty Bay.

Dolphin behavior varied significantly based on defined patches within the bay (G^2=18.70, n=620, p=0.05; **Figure IV-3**). Post hoc tests showed that if a sample occurred within the NMF patch, dolphins were more likely to be foraging (*z*=2.33), within the NS patch, dolphins were less likely to be foraging (*z*=-2.22), and within the NS patch, dolphins were more likely to be travelling (*z*=2.40). No prey-ball foraging was observed in the NMF patch. Dusky dolphins were recorded entering the actual bounds of mussel farms during only 1% (n=8) of filtered records, generally swimming parallel to buoys, down the open lanes of mussel farms, rather than transiting through the looped lines.

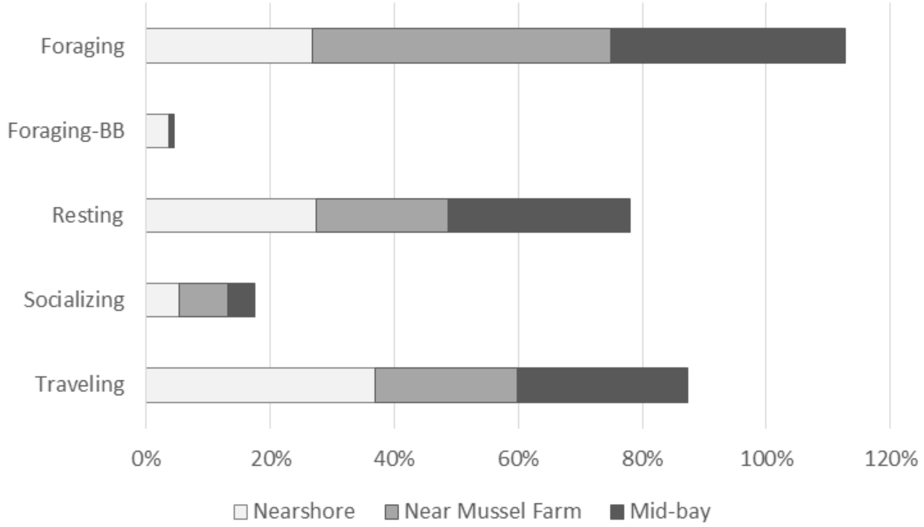

Figure IV-3. Stacked bar graph representing the total proportion of behavioral states observed in each habitat patch type.

Dolphin Encounter Rate

There is a negative trend in dolphin encounter rate compared to prior research in Admiralty Bay. The boat-based encounter rate (i.e., number of groups encountered per hour of survey effort) of dusky dolphins was 1.44 groups per hour in 2011 and 1.03 groups per hour in 2012, for a combined mean of 1.23 groups per hour (**Table IV-3**). The encounter rate dropped from 2.4 in 1998-2000, to 1.76 in 2005-2006, and 1.23 in 2011-2012 (**Table IV-3**).

The individual resighting rate (i.e., mean number of sightings per individual) also declined from the 2001-2006 study period to the 2011-2012 study period (z-test, *z*=-11.322, p<0.001, **Table IV-3**). A total of 186 individual dusky dolphins were identified from boat-based photo-identification during the 2011-2012 study period. The mean number of sightings per individual was 1.3±0.6 (n=186), and 80% (n=149) of individuals were encountered only once.

The mean number of sightings per individual during 2001-2006 was 4.4±4.68 (n=741), and 34% (n=251) of individuals were seen only once (Pearson, 2008).

Table IV-3. Summary of dusky dolphin encounter rate, mean group size, and individual resighting rate. Boat-based data collected in Admiralty Bay from 1998-2002 *(Markowitz, 2004; Markowitz et al., 2004)*, 2005-2006 (Pearson, 2008; Pearson et al., 2012), and 2011-2012.

Study Period	Encounter Rate (groups/hour)	Mean Group Size	Individual Resighting Rate	Proportion of time spent foraging
1998-2002 (winter months)	2.40 (1998-2000)	5 (1998-2000)	4.4 ± 4.68 SD 34% sighted once (2001-2006)	Roughly 25%
2005-2006 (late autumn/winter/spring)	1.76 ↓ (winter months)	7 ± 6 SD ↑ (n=4,632 2-min intervals)		18±18.2% (834 of 4,632 samples)
2011 (winter months)	1.44 ↓	3.47 ± 1.97 SD ↓ (n=324 2-min intervals)	1.3 ± 0.60 SD ↓ 80% sighted once (2011-2012)	38.87% ↑ (241 of 620 samples)
2012 (winter months)	1.03 ↓	3.20 ± 1.71 SD ↓ (n=294 2-min intervals)		

↑↓ = indicates the direction of trend from the previous study period

Movement Patterns

Swimming Speed

The GAM described significant variation in swimming speed, at the 0.05 alpha level, explaining 26.4% of the deviance (adj-R^2=0.171, GCV=0.217, n=105). The best fitting model included all four candidate explanatory variables with smooth terms for time of day and group size, and linear terms for predominant group behavior and patch type:

$$[\mathit{Log10}(\mathit{Speed}) \sim s(\mathit{TimeOfDay}) + s(\mathit{GrpSize}) + \mathit{BehavState} + \mathit{Patch}]$$

Swimming speed was significantly lower within the NMF patch than within the NS patch. Travelling behavior was associated with higher swimming speed along the horizontal plane than foraging. At the 0.1 alpha level, travelling behavior was associated with higher swimming speed than resting. Time of day and dolphin group size had no significant effect on swimming speed, though there was variation based on these factors (**Figure IV-4**, **Error! Not a valid bookmark self-reference.**).

Table IV-4. Summary of output for best fitting model for dusky dolphin swimming speed. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Nearshore patch and travelling (behavioral state). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	St. Error	t	*P*-value
(Intercept)	2.296	0.109	21.13	< 2e-16*
BehavState - Foraging	-0.308	0.111	-2.783	0.007*
BehavState - Resting	-0.212	0.127	-1.722	0.088 •
BehavState - Socializing	-0.147	0.215	-0.684	0.496
Patch – Mid-bay	-0.139	0.110	-1.266	0.209
Patch –Near Mussel Farm	-0.269	0.119	-2.262	0.026*
	Edf	Ref. df	F	*P*-value
s(TimeOfDay)	5.069	5.648	1.745	0.170
s(GroupSize)	0.562	7.000	0.168	0.142

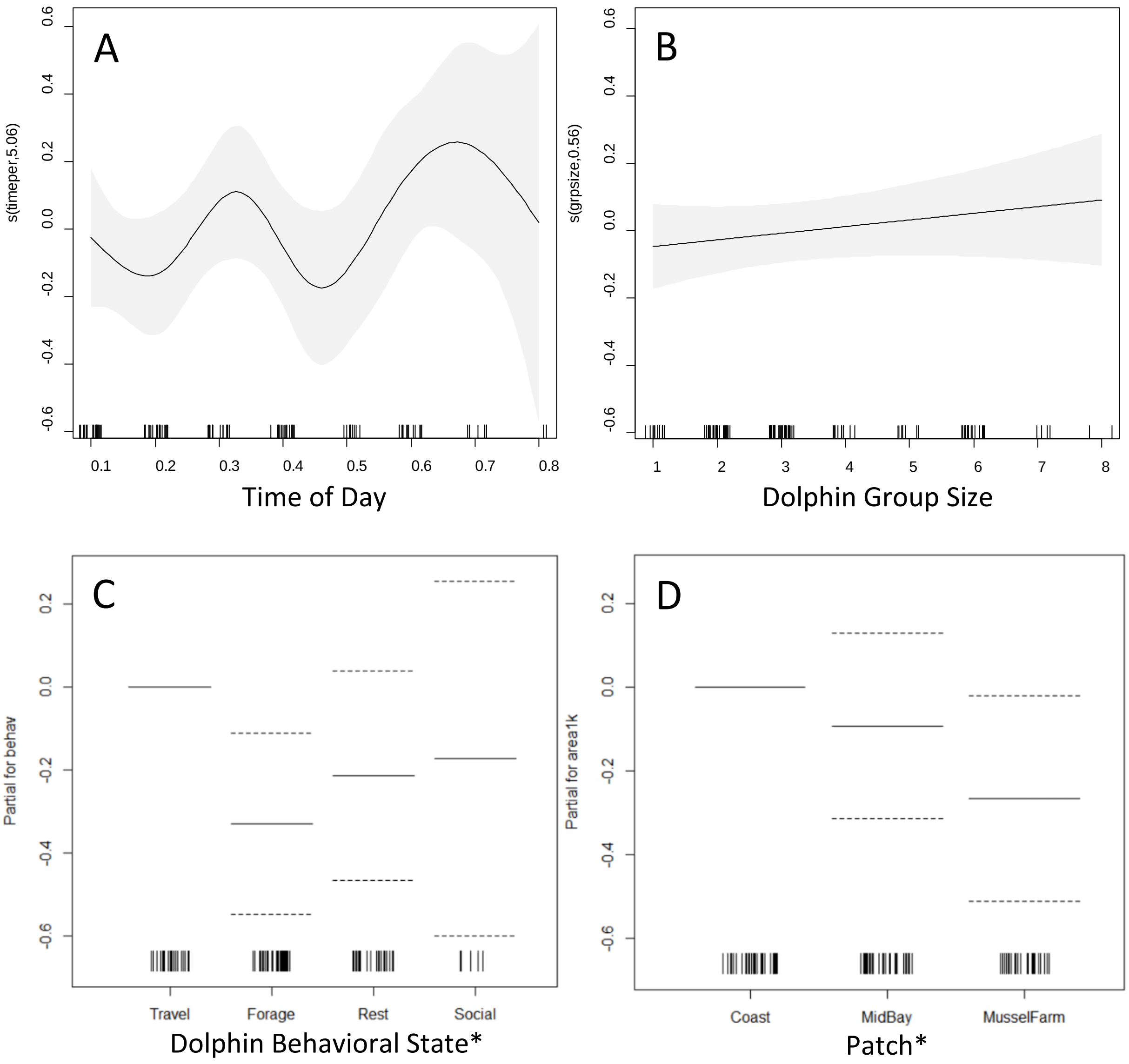

Figure IV-4. Charts for the partial contribution of individual explanatory variables in the fitted GAM for swimming speed. Charts include: A) time of day, B) dolphin group size, C) dolphin behavioral state, and D) patch type. The rugplot along the x-axis indicates the number of observations for each factor. The gray shading for smooth terms, and the dotted lines for linear terms, indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with swimming speed, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Reorientation Rate

The GAM described significant variation in reorientation rate, at the 0.05 alpha level, explaining 12.6% of the deviance (adj-R^2=0.072, GCV=2.023, n=105). The best fitting model included two candidate explanatory variables with linear terms for predominant group behavior and patch type:

[*ReorientationRate* ~ *BehavState* + *Patch*]

Reorientation rate was significantly higher within the NMF patch than within the NS patch. Travelling behavior was associated with significantly lower reorientation rate than foraging at the 0.1 alpha level (**Figure IV-5**, **Table IV-5**).

Table IV-5. Summary of output for best fitting model for dusky dolphin reorientation rate. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Nearshore patch and travelling (behavioral state). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	St. Error	t	*P*-value
(Intercept)	3.480	0.323	10.775	<2e-16*
BehavState - Foraging	0.647	0.342	1.895	0.061 •
BehavState - Resting	0.209	0.383	0.547	0.585
BehavState - Socializing	0.435	0.670	0.650	0.517
Patch – Mid-bay	-0.028	0.323	-0.085	0.932
Patch – Near Mussel Farm	0.848	0.362	2.343	0.021*

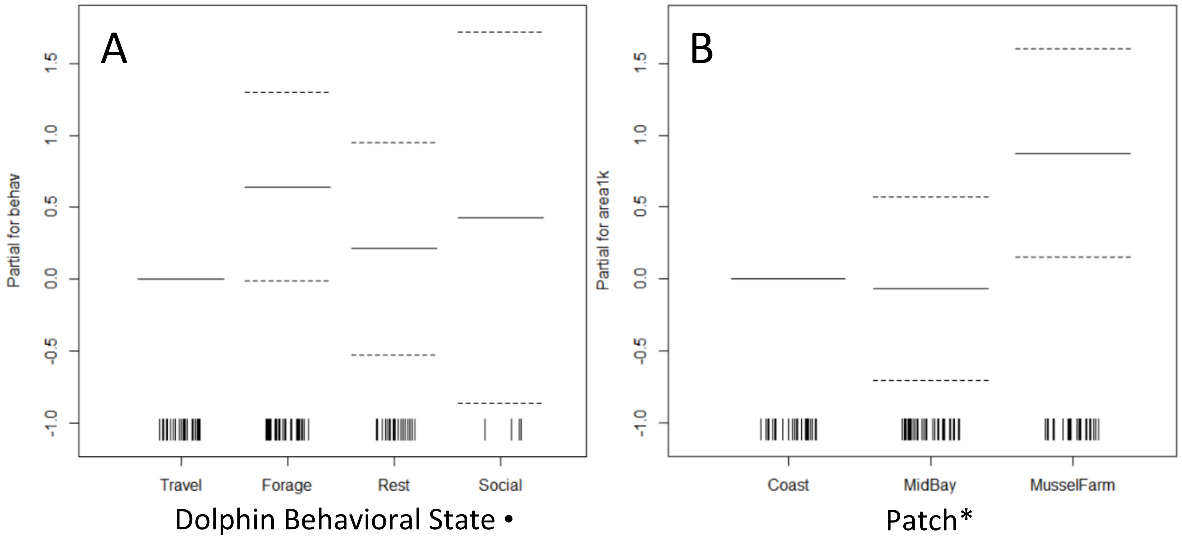

Figure IV-5. Charts for the partial contribution of individual explanatory variables in the fitted GAM for reorientation rate. Charts include: A) dolphin behavioral state and B) patch type. The rugplot along the x-axis indicates the number of observations for each factor. The dotted lines for linear terms indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with reorientation rate, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Linearity

The GAM described significant variation in swimming speed, at the 0.05 alpha level, explaining 20.2% of the deviance (adj-R^2=0.135, GCV=2.996, n=105). The best fitting model included all four candidate explanatory variables with a smooth term for time of day, and linear terms for group size, predominant group behavior, and patch type:

[*EmpLogit(Linearity) ~ s(TimeOfDay) + GrpSize + BehavState + Patch*]

Movement was significantly less linear within the NMF patch than within the NS patch. At the 0.1 alpha level, linearity increased throughout the day. Dolphin group size and behavioral state had no significant effect on linearity, though there was variation based on these factors (**Figure IV-6**, Error! Not a valid bookmark self-reference.).

Table IV-6. Summary of output for best fitting model for dusky dolphin linearity. Includes linear (top) and smooth (bottom) terms. Linear categorical terms are estimated relative to the reference value for that term: Nearshore patch and travelling (behavioral state). An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Term	Estimate	St. Error	t	*P*-value
(Intercept)	1.487	0.585	2.543	0.013*
Group Size	0.170	0.096	1.782	0.078 •
BehavState - Foraging	-0.226	0.422	-0.537	0.593
BehavState - Resting	0.102	0.476	0.215	0.830
BehavState - Socializing	-1.105	0.812	-1.360	0.177
Patch – Mid-bay	0.178	0.404	0.439	0.661
Patch – Near Mussel Farm	-1.163	0.445	-2.613	0.010*
	Edf	Ref. df	F	*P*-value
s(TimeOfDay)	1	1	3.506	0.064 •

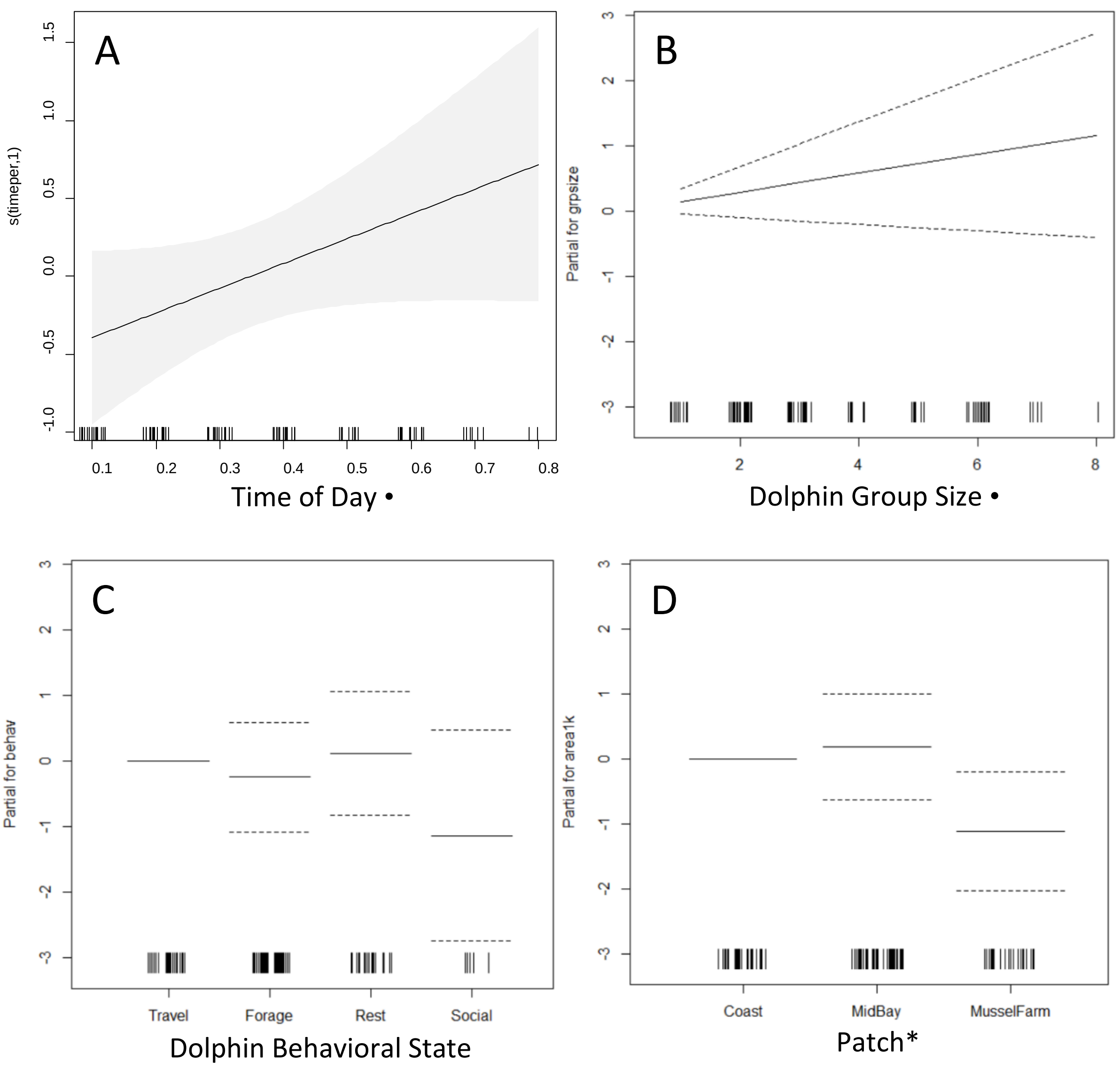

Figure IV-6. Charts for the partial contribution of individual explanatory variables in the fitted GAM for linearity. Charts include: A) time of day, B) dolphin group size, C) dolphin behavioral state, and D) patch type. The rugplot along the x-axis indicates the number of observations for each factor. The gray shading for smooth terms, and the dotted lines for linear terms, indicate the 95% confidence intervals. On the y-axis, values >0 indicate a positive correlation with linearity, values <0 indicate a negative correlation, and a value of 0 indicates no effect. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05. A closed circle (•) indicates a variable with a statistically significant effect at alpha level 0.1.

Discussion

Dolphins utilized defined patches within Admiralty in different ways. Within the NMF patch, foraging behavior increased, swimming speed and linearity decreased, and reorientation rate increased. Reduced swimming speed along the horizontal plane of the water is likely related to the increased foraging and diving activity in the vertical plane. Increased reorientation rate may also relate to foraging activity as well as movement around obstacles suspended in the water column (i.e., mussel farm ropes within the NMF patch). Within the NS patch, foraging behavior decreased and traveling behavior increased. Prey herding was observed only in MB and NS patches, and not within the NMF patch. In this scenario, MB and NS patches appear to be areas that yield greater benefits relative to prey ball herding opportunities; whereas, the NMF patch appears to be an area that yields greater benefits relative to non-prey ball foraging opportunities. These differences in patch use may be driven by a multitude of factors. In 2005-2006, dolphins were described as ceasing to feed on prey balls that moved within bounds of marine farms, indicating that the rope obstructions directly interfered with the dolphins' ability to maintain a prey ball. This supports the lack of prey ball foraging observed in the NMF patch during the current study.

It is not clear why non prey herding foraging behaviors occurred significantly more near the NMF patches. Artificial structures used in shellfish aquaculture often accumulate fouling organisms, such as seaweed, which may attract and aggregate non-schooling fishes. This aggregation may be advantageous to predators in the short-term, but intensive aquaculture has the potential to alter local food webs in ways that are not ecologically sustainable (Davenport et al., 2009). Long-standing applications for extensions to existing mussel farms in Admiralty Bay, which were modified over the years since first submitted in 1999, were formally declined in

2016 by the Environment Court of New Zealand (Thompson, 2016). The decision was based largely on accumulated dusky dolphin research findings over the years, and for concern over the New Zealand king shag (*Leucocarbo carunculatus*) that is endemic to the area.

The percentage of foraging was higher during this study than in previous years (Markowitz et al., 2004; Pearson, 2008). Dusky dolphin prey ball herding events were rarely observed during the present study (n=9). In 2005-2006, prey ball herding events were not distinguished from non-herding foraging events (Pearson, 2008). However, at least 52 herding events were described based on underwater video recordings. During the present study, a decrease in prey herding events, coupled with an overall increase in foraging behavior, may indicate that more time is allocated to searching for and acquiring prey when engaged in non-herding foraging tactics. Observations of other biologically important behaviors, including resting and socializing, decreased from previous years.

The decrease in prey herding events observed in the present study may relate to a shift in prey characteristics potentially relating to climate variation (Srinivasan et al., 2012), dusky dolphin grouping patterns, or possibly an underestimation of prey ball foraging events. In 2002, dusky dolphin groups joined together to form larger feeding aggregations once schooling prey were located (McFadden, 2003). A similar pattern, on a much larger scale, was described for dusky dolphins off Argentina. When a feeding group of dusky dolphins failed to recruit at least one other group during feeding activity, they were less likely to maintain a prolonged surface feeding event, presumably unable to herd a prey ball effectively with too few dolphins (Würsig and Würsig, 1980). Fewer dusky dolphins overall, with a smaller mean group size, in the present study may reduce opportunities to corral and maintain active prey balls. A trend of a larger mean dusky dolphin group size during prey ball foraging events during this study support the idea that larger aggregations of dolphins engage in this coordinated behavior. However, prey ball foraging sample size was low and additional data are needed to increase statistical power. Alternatively, it is possible that prey herding activity was simply underestimated in 2011-2012, given that prey balls are not always herded to the surface of the water and, therefore, not easily detected by observers above water. Research in 2005-2006 included underwater recording, giving researchers a better view of activity occurring below the surface.

This research builds upon previous findings in Admiralty Bay and results show that dusky dolphin encounter rate, mean group size and individual re-sighting rate have declined from previous years. These results indicate that fewer dolphins, with fewer individuals per group, are transiting through Admiralty Bay and staying for shorter durations than in the decade prior. A reduced encounter rate was identified from 2001 to 2006, and this study shows that the negative trend continues. One potential contributor to the shift in dusky dolphin habitat use may relate to inter-species overlap. During the current study, common dolphins were frequently observed, at times in large groups (up to approximately 100 individuals). They were encountered more often than dusky dolphins, 93 times during on-effort boat-based surveys (1.35 groups/on-effort hour), compared to 85 encounters of dusky dolphins (1.23 groups/on-effort hour). Previously published manuscripts have not quantified common dolphin presence. One study conducted in the winter of 2005 stated that common dolphins were “sporadically seen in the Admiralty Bay region” (Duprey, 2007). Researchers that conducted studies in 2005-2006 recall that common dolphins were not seen often, occurred in small groups, and generally were associated with dusky dolphin groups (pers. comm. Heidi Pearson, University of Alaska Southeast). Dusky and common dolphin inter-specific groupings have also been described off Kaikoura, where common dolphins were always present in smaller numbers than dusky dolphins. Interactions between these species do not appear aggressive, generally observed in foraging (including coordinated prey herding foraging) or socio-sexual contexts (Markowitz, 2004). Off Kaikoura, it has been suggested that common dolphins may use large dusky dolphin groups for enhanced predator detection, and dusky dolphins may tolerate common dolphins because they are not a threat for resources (Markowitz, 2004). It is unclear how the inter-species dynamics compare in Admiralty Bay, and more research is needed to better understand common dolphin habitat use, and how this apparent increase affects dusky dolphins in the area.

Conclusions

Dusky dolphin movement patterns and behavioral states varied significantly among defined habitat zones within Admiralty Bay. Mid-bay and nearshore zones yield greater prey-ball herding, whereas, near mussel farm zone foraging occurs on fishes that have not formed prey-balls. Prior research indicates that dusky dolphins avoid shellfish aquaculture farms that may interfere with coordinated prey-ball feeding tactics. During the 2011-2012 study, habitat patches in proximity to mussel farms appear to be an attractant for foraging dusky dolphins. However, few prey-balling events were identified, which is inconsistent with prior research, and mussel farms may represent an alternative resource when schooling fishes that form prey-balls are scarce in the bay. Dusky dolphins exhibit flexible foraging behavior that may allow dolphins to adjust to an inconsistent and fluctuating environment in terms of prey characteristics. Flexibility in foraging has also been described on a larger scale for dusky dolphins that migrate between Kaikoura, New Zealand and Admiralty Bay. Dolphins shift from foraging on nighttime mesopelagic prey off Kaikoura to daytime schooling and non-schooling fishes in Admiralty Bay. While the number of dusky dolphins that utilize Admiralty Bay has declined over the past decade, common dolphin presence appears to have increased. Potential contributing factors affecting local dusky dolphin habitat-use include prey characteristics, human activity, inter-species competition, and localized climate-ecosystem dynamics. An understanding of animal habitat patch use and movement patterns in response to an artificially altered environment gleaned from this research can be applied to other marine environments where dolphins and aquaculture overlap.

CHAPTER V

CONCLUSIONS

This dissertation contributes to our understanding of anthropogenic effects on wildlife, central to the growing field of conservation behavior. The conservation behavior framework served to address one of the key steps in the Population Consequences of Disturbance (PCoD) model, showing that dolphin habitat-use and movement patterns were good indicators of human-generated disturbance across diverse species and ecosystems. Generalized additive modeling was an important tool appropriate for addressing multiple additive factors in ecologically complex and fluctuating systems. Flexibility in foraging was also observed among all species, though tactics varied, and statistically significant shifts in behavior in response to human input were detected across species and included alterations in swimming speed, reorientation rate, linearity, and habitat use of historically important foraging sites.

Common bottlenose dolphins in the Galveston Ship Channel (GSC) showed behavioral flexibility in exploiting attractive food resources in which prey acquisition is facilitated by commercial trawlers. It is unclear if this risky attractant has positive or negative consequences to the overall population. Salvage records indicate that direct negative interactions with vessels have occurred, though it is unclear if they have contributed to population-level effects. Although the common bottlenose dolphin is listed as of Least Concern (Hammond et al., 2012), proactive and ongoing monitoring can serve to detect early signs of potential decline in any one population. Risk may be elevated when tour vessels take advantage of following dolphins that feed in association with trawlers, at which point dolphins become entrapped between several vessels. This added pressure during a risky form of foraging can alter behavior during a biologically important activity. Although behavioral harassment was detected in the presence of tour boats and trawlers in the GSC, dolphins do not appear to abandon the area, even during periods of consistent and intensive vessel presence when boats actively follow dolphins. This may be due, in part, to lack of comparable habitat, with similar prey characteristics, proximate to the GSC. Current voluntary codes of conduct do not protect dolphins in the GSC from tour-based behavioral harassment. Recommendations include regulating marine mammal tourism, including restrictions on following dolphins that are actively foraging in association with trawlers.

Indo-Pacific humpback dolphins off Hong Kong avoided historically important foraging areas that are presently associated with chronic construction activity. Displacement from these areas occurred during the day but may not necessarily exclude animals from resources at night when construction and related vessel activities are reduced. Research shows that some dolphins return to previously abandoned habitats once human-induced disturbances cease. Off Hong Kong, development projects that overlap in space and time complicate the situation and may displace animals for extended periods from large areas that support prey. In these cases, nearby ecologically similar habitats should be designated as marine parks or reserves, with proper regulations and enforcement in place, to mitigate effects of disturbance. The overall impact to the dolphin population depends, in part, on alternative habitats with prey accessibility. Therefore, a better understanding of dolphin prey characteristics (e.g., distribution and abundance) on a large spatio-temporal scale is needed. This is especially important for species, such as Indo-Pacific humpback dolphins, with small population sizes that occupy localized areas. Humpback dolphin distribution is restricted by ecological features, reducing alternative habitat options to compensate for human disturbance. Ongoing research should continue throughout and after construction activities to contribute to adaptive management schemes, as prey distribution and abundance may shift over time.

Dusky dolphins used defined patches within Admiralty Bay in significantly different ways. Mid-bay and nearshore zones may reflect areas that yield greater benefits relative to prey ball herding opportunities, whereas the near mussel farm zone may reflect an area that yields greater benefits relative to non-prey ball foraging opportunities. Prior research shows that dusky dolphins regularly herded prey in Admiralty Bay and avoided mussel farms that likely disrupt coordinated prey-ball feeding tactics. During the present study few prey-balling events were observed and patches containing, and in proximity to, mussel farms appear to be an attractant for foraging dusky dolphins. Perhaps mussel farms may serve as a sustaining alternative resource when prey, particularly schooling fishes that form prey-balls, are scarce in the bay. Flexible foraging behavior may allow dolphins to adjust to a fluctuating environment in which prey are ephemeral and patchily distributed. Flexibility in foraging has also been described on a larger scale for dusky dolphins that migrate between Kaikoura, New Zealand and Admiralty Bay. While the number of dusky dolphins that visit Admiralty Bay has declined over the past decade, common dolphin presence appears to have increased. Potential contributing factors affecting local dusky dolphin habitat-use include prey characteristics, human activity, inter-species competition, and localized climate-ecosystem dynamics. Findings from this study illustrate the need for research with a long-term perspective that incorporates local fisheries data.

Dolphin behavioral responses to human activities varied across the three case studies and were likely shaped not only by anthropogenic factors, but also by local prey accessibility and proximity to ecologically similar habitats. Indo-Pacific humpback dolphins avoided localized patches, appearing somewhat less resilient to heavy human activity and associated noise than common bottlenose dolphins that remain in areas even when directly pursued by vessels. This may reflect the proximity of suitable alternative habitat patches with comparable prey resources. Animals may be more likely to remain in a disturbed area to forage, if comparable alternatives are farther away. Population-level effects may be more likely when individuals have small home ranges, like the Indo-Pacific humpback dolphins off Hong Kong, or have high site fidelity to areas with heavy human activity, like the bottlenose dolphins in the Galveston Ship Channel. Dusky dolphins that visit Admiralty Bay likely have a large home range, with potentially more alternatives for prey. Fewer dolphins are presently using the bay, concurrent with fewer observations of prey-ball foraging events, and dolphins that use the bay appear to alter foraging tactics in response to changes in prey characteristics.

Human-wildlife conflict management is often directed at modifying human behavior. Involving stakeholders (i.e., any individual or group who has interest in, or is potentially affected by, management decisions) in the planning process of policy design has the potential to engage participants, which leads to better informed decision-making. Reaching a consensus among diverse stakeholders with different perspectives may be challenging, particularly in cases where the wildlife is a resource that has economic value (e.g., bottlenose dolphin tourism in the Galveston Ship Channel), or conflicts involve human population development pressures (e.g., humpback dolphins off Hong Kong) (White and Ward, 2011). However, a recent example involving MPA design and implementation off the northern coast of California demonstrates that, with specific guidelines in place, scientific information and stakeholder knowledge can be integrated for an outcome that meets legislative criteria, follows science guidelines, and garners diverse stakeholder support. The planning process for the northern California case study was structured to be science-based and stakeholder-driven, with a transparent decision-making process, defined roles, clear goals consistent with legislation, and accessibility to available scientific information and local knowledge (Gleason et al., 2010).

The three case studies presented here represent important foraging areas for dolphins, where intensive human activity contributed to shifts in dolphin behavior and movement patterns. Behaviors are likely influenced not only by human activity, but by prey characteristics and accessibility to habitats that support prey. Integrating data on dolphin prey characteristics (e.g., fish species, abundance, and distribution) will enhance our understanding of factors influencing dolphin behavior in these dynamic systems. Marine ecosystem-based management is an emerging approach to managing whole ecosystems, rather than isolated areas or a single species, designed to protect and maintain habitat integrity while minimizing anthropogenic impacts (Aburto et al., 2012). Ecosystem-based management in coastal areas may serve to regulate human activity, while aiming to protect the habitat on which dolphins and dolphin prey depend.

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APPENDIX A

Appendix A Table 1. Vessel categories based on size and movement characteristics

Category	Vessel types	Vessel length	Mean speed, km/hr (SD; Max)	Mean rr, deg/min (SD; Max)
Small	Personal recreational watercraft Commercial amusement ride	<10m	35.31 (18.57;78.94)	34.10 (42.09; 178.19)
Mid	Government boat (e.g., USCG) Harbor pilot boats University research vessel Tug boat (single, unattached) Yacht	10-30m	14.34 (7.44; 42.85)	18.96 (29.68; 133.01)
Large (Transport)	Barge (including tug boat attached) Cargo ship Cruise ship	>30m	9.19 (4.58; 21.68)	19.82 (33.83; 166.17)
Tour Boat	Baywatch dolphin tour Harbor tour & dolphin watch	9-16m	9.42 (5.74; 49.01)	41.38 (48.50; 178.19)
Trawler	Galveston shrimp trawler fleet	Variable	3.99 (3.01;42.14)	37.75 (45.09; 178.45)

APPENDIX B

Appendix B Table 1. List of large-scale marine construction projects. Information includes proximate dolphin survey sites and project start/end dates. Information obtained from various public resources including the Civil Engineering and Development Department (CEDD) and the Highways Department of the Government of the Hong Kong Special Administrative Region.

		2012			2013												2014												2015												2016											
Project	Proximate to	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
HKBCF	HKIA-W/NE/N, SC, SHW	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
TM-CLKL South	HKIA-NE/N, SHW									▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
TM-CLKL North	HKIA-NE														▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨										
CLK-NLH	HKIA-N/NE, SHW									▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
ESC Mud Pits	HKIA-W/N/NE, SC	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
SBI Mud Pits	HKIA-NE, SHW		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨
HKIA 3RS	HKIA-W/N/NE, SC																																															▨	▨	▨	▨	▨
CLK SE	HKIA-W/NE/N, SHW	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

Appendix B Table 2. Sample sizes

Location (n)		Time of day (n)		Season (n)		Group Size (n)		Behavior (n)		Sum Boats (n)		Boat Category (n)	
HKIA-W	(65)	≤0.2	(42)	Winter	(124)	1	(56)	Forage	(101)	0	(363)	Fishing large	(6)
HKIA-N	(10)	0.3	(111)	Spring	(34)	2	(105)	Mill	(57)	1	(50)	Fishing small	(5)
HKIA-NE	(40)	0.4	(105)	Summer	(112)	3	(75)	Rest	(10)	2	(4)	High speed ferry	(4)
LKC	(121)	0.5	(68)	Autumn	(147)	4	(68)	Social	(46)			Slow speed ferry	(1)
LKT	(72)	0.6	(61)			5	(36)	Travel	(93)			Large	(13)
SC	(30)	≥0.7	(30)			6	(27)	Unk	(110)			Mid	(6)
SHW	(79)					7	(9)					None	(363)
						8	(11)					Research	(8)
						Unk	(30)					Small	(6)
												Tour	(5)

Appendix B Table 3. Summary of output for best fitting models for vessel category. Summary includes linear term for vessel category for swimming speed (top), reorientation rate (middle), and linearity (bottom). Vessel types are estimated relative to the control of 'No Vessels Present'. An asterisk (*) indicates a variable with a statistically significant effect at alpha level 0.05.

Term	Estimate	Std. Error	t	*P*-value
Swimming Speed (Intercept)	0.563	0.049	11.504	2e-16*
Fishing - Large	-0.026	0.102	-0.257	0.797
Fishing - Small	-0.172	0.111	-1.546	0.123
High Speed Ferry (HSF)	-0.182	0.122	-1.490	0.137
Large	0.159	0.071	2.235	0.026*
Mid	-0.083	0.101	-0.824	0.411
Research	0.188	0.087	2.156	0.032*
Small	0.197	0.099	1.977	0.049*
Slow Speed Ferry (SSF)	-0.029	0.242	-0.120	0.904
Tour	0.126	0.109	1.159	0.247
Reorientation Rate (Intercept)	4.043	0.396	10.207	< 2e-16*
Fishing - Large	-0.335	0.786	-0.426	0.670
Fishing - Small	0.200	0.857	0.234	0.815
High Speed Ferry (HSF)	0.537	0.942	0.570	0.569
Large	0.816	0.545	1.499	0.135
Mid	0.622	0.775	0.803	0.423
Research	-0.289	0.672	-0.430	0.667
Small	0.312	0.767	0.406	0.685
Slow Speed Ferry (SSF)	-0.188	1.864	-0.101	0.920
Tour	-0.879	0.839	-1.048	0.295
Linearity (Intercept)	1.770	0.357	4.956	1.06e-06*
Fishing - Large	0.460	0.757	0.608	0.543
Fishing - Small	0.343	0.827	0.415	0.678
High Speed Ferry (HSF)	-1.195	0.909	-1.316	0.189
Large	-1.129	0.525	-2.149	0.032*
Mid	-1.495	0.748	-2.000	0.046*
Research	-0.263	0.648	-0.406	0.685
Small	0.204	0.739	0.277	0.782
Slow Speed Ferry (SSF)	-1.474	1.798	-0.820	0.413
Tour	0.250	0.808	0.310	0.757

APPENDIX C

Appendix C Table 1. Output for Dunn post-hoc test for mean group size relative to behavioral state.

Comparison	Z	P.unadj	P.adj
Foraging - Foraging-BB	-4.1963	2.71E-05	0.0003*
Foraging - Resting	-2.6968	7.00E-03	0.0117
Foraging-BB - Resting	3.3518	8.03E-04	0.0027*
Foraging - Socializing	-1.9309	5.35E-02	0.0764
Foraging-BB - Socializing	2.8780	4.00E-03	0.0100*
Resting - Socializing	-0.3885	6.98E-01	0.7751
Foraging - Traveling	-2.7024	6.88E-03	0.0138*
Foraging-BB - Traveling	3.3657	7.64E-04	0.0038*
Resting - Traveling	0.0299	9.76E-01	0.9761
Socializing - Traveling	0.4079	6.83E-01	0.8542