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(*ORCINUS ORCA*) AND VESSEL TRAFFIC WITHIN A TRANSBOUNDARY

REGION: IMPLICATIONS FOR CONSERVATION MANAGEMENT

by

Courtney Elizabeth Smith

A Dissertation.
Submitted to the Graduate School,
the College of Education and Psychology.
and the Department of Psychology.
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy.

December 2017

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ABSTRACT

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The social lives of animals are defined by group dynamics based on the nature and strength of associations and movements between individuals, often resulting in highly complex and interconnected social networks. However, understanding of how environmental variables may shape this structure is poorly understood. Within the inland waters of Washington State and southern Vancouver Island, British Columbia, mammal-eating Bigg's (transient) killer whales occur in relatively small, but stable social groups. Group size and occurrence in recent years has increased, coinciding with a growing whale watching industry. Given the central importance of the social network within killer whale population dynamics, such as the maintenance of cooperation and cultural transmission of information, shifts in social network structure caused by environmental processes may have significant ecological and evolutionary consequences. Thus, it is reasonable to assume that the increased presence of Bigg's killer whales within the Salish Sea leaves them susceptible to the various and growing anthropogenic pressures within this area. Utilizing a long-term data set (1987-2015), the objectives of this doctoral study are to: (1) identify the level(s) of preferred associations and social differentiation within Bigg's societies relative to foraging specializations; (2) re-evaluate and compare historical measures and persistence of Bigg's sociality, including demographic influences

and dispersion patterns; and, (3) assess the extent to which individual sociality can predict received vessel traffic levels, as well as other variables driving targeted whale watching. The results of this work will better clarify the social dynamics and population structure of Bigg's killer whales and will thus inform on proper management of this conservation unit. Likewise, the combined evaluation of social dynamics and anthropogenic pressures (vessel traffic) experienced by this population can provide key information that may enable managers to implement proper measures to mitigate anthropogenic impacts. Finally, the results of this analysis will serve as a platform for further evaluating the predator-prey dynamics of Bigg's killer whale stocks that are central to the Salish Sea ecosystem.

ACKNOWLEDGMENTS

Darvis Taylor, Adam Ü, Kari Koski, Erin Heydenreich, Chris Teren, and Traci Walter deserve particular mention. Your friendship over the years helped to make San Juan Island a second home and you've given me an anchor there forever.

This dissertation would not have been completed without the daily accountability and moral support of my 'remote lab' writing group: Brandon Drescher, of the University of Southern Mississippi; Sara Johnson, of Purdue University; and Christina Toms, of the University of Central Florida. Your constant presence and encouragement were reminders that none of us are alone, giving me strength to forge ahead to completion. You are there with me even as I write this acknowledgement. I so look forward to helping each other through our next chapters in life.

Finally, I extend my sincere gratitude to my doctoral committee: Dr. Heidi Lyn, Dr. Deborah Giles, Dr. Donald Sacco, Dr. Alen Hajnal, and Dr. Nicole Phillips. Your support and guidance from afar were essential for keeping me on target with my doctoral work. Thank you for the many helpful comments and recommendations that shaped the entirety of this project. I especially thank my doctoral advisor, Dr. Heidi Lyn, for providing me with a student-advisor relationship I never thought I'd get to experience during my graduate career. Your acceptance, guidance and mentoring from the very beginning was everything I hoped for and I am so thrilled to continue our research partnership and friendship.

DEDICATION

This dissertation is dedicated to my husband, Doma. You've sacrificed as much as I have and this achievement would not have been possible without your being with me every step of this long journey. It's time for a new adventure.

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LIST OF ABBREVIATIONS

TWM	The Whale Museum
DFO	Department of Fisheries and Oceans Canada
CWR	Center for Whale Research
NMFS	National Marine Fisheries Service
MMPA	Marine Mammal Protection Act
ESA	Endangered Species Act
SARA	Species At Risk Act
SRKW	Southern Resident Killer Whale(s)
NOAA	National Oceanic and Atmospheric Administration
PCA	Principal Components Analysis

CHAPTER I - INTRODUCTION

Literature Review and Background

Animal Social Complexity and Network Analyses

Animal societies are founded upon a complex series of interactions within and

between individuals and their environment, with the resulting population structure

reflecting the quality and effects of such interactions (Farine & Whitehead, 2015; Hinde,

1976). The diversity of these interactions across and within a given species can vary

across local and population level scales, subsequently influencing fundamental ecological

and evolutionary processes (Leu, Farine, Wey, Sih, & Bull, 2016), such as gene flow and

frequency-dependent selection (e.g., Farine & Sheldon, 2015; McDonald, James, Krause,

& Pizzari, 2013); transmission of information and culture (e.g., Cantor, Shoemaker,

Cabral, Flores, Varga, & Whitehead, 2015), as well as parasites and diseases (Fenner,

Godfrey & Bull, 2011; Leu, Kappeler, & Bull, 2010; Guimarães, de Menezes, Baird,

Lusseau, Guimarães, & dos Reis, 2007). The social dynamics based on and driving these

processes are referred to as social networks.

The structures of social networks are spatiotemporally diverse (Hinde, 1976;

Pinter-Wolman et al., 2013), ranging from fission-fusion societies with short-term

associations of individuals which frequently form new groups (e.g., Lusseau et al., 2006,

de Silva Ranjeewa, & Kryazhimskiy, 2011), to those exhibiting strong membership

fidelity over time (e.g., Lusseau et al., 2003; Wittemyer, Douglas-Hamilton, & Getz,

2005) or even pair-bonded monogamy (Mock & Fujioka, 1990). Likewise, environmental

conditions themselves, such as habitat and resource availability can also shape individual

behavior and social structures through learning processes, with the ultimate balance of

maximizing individual – and in turn group – fitness within an ecosystem (Chapman & Rothman, 2009; Leu et al., 2016).

Past studies of animal social structures were limited to a seemingly two-dimensional approach that was largely descriptive in nature (e.g., with Dice's coefficient and cluster analyses), emphasizing dyadic relationships and associations rather than the processes driving them. Likewise, it was not until recently that statistics were even available to test the significance of those associations. However, the application of social network theory to these subjects has enabled researchers to expand the scale of these relationships, providing context as to how local processes can influence group-level properties by accounting for discrete social environments experienced by individuals (Bejder, Fletcher, & Bräger, 1998). Social network analysis is an analytical approach that evaluates the social connectivity and dynamics between individual members of a population through a quantitative framework (Croft et al., 2006; Krause et al., 2007; Farine & Whitehead, 2015; Wey, Blumstein, Shen, & Jordán, 2008). Social network analysis was first employed by sociologists and psychologists in the early 20th century (Wasserman & Faust 1994); however, it was not until very recently that biologists embraced this tool in earnest as a way to better evaluate the links between biological phenomena and animal social behavior (Farine & Whitehead, 2015; Scott, 2000; Wasserman & Faust, 1994). Social networks, graphically, are expressed in terms of nodes and edges; nodes can represent individuals or groups, with the edges between them reflecting their interactions or relationship – which can often reveal hierarchical social tiers nested within a population (see Figure 1).
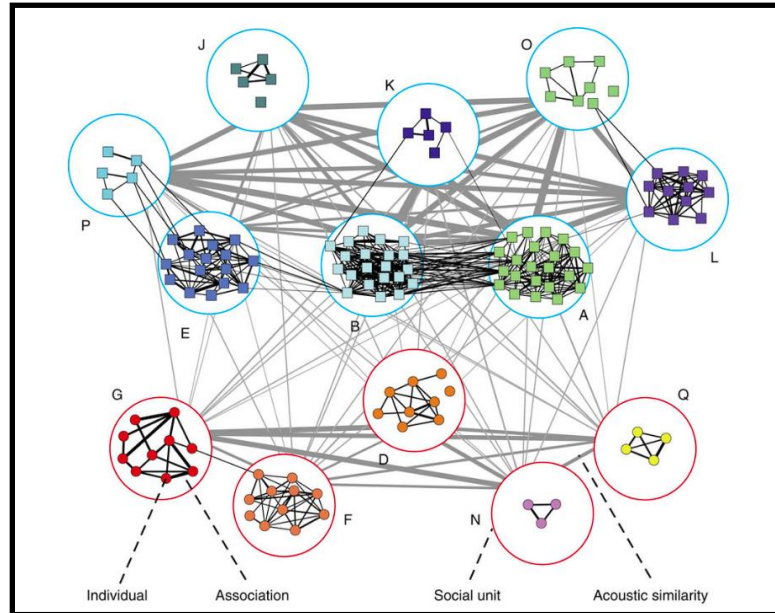
Figure 1. Example of a multi-tiered cetacean social network.

An example of a multilevel network depicting three nested social tiers within a sperm whale society off the Galápagos Islands: individuals (small colored nodes) connected by their relationships (black lines with proportional thickness reflecting how often individuals were observed together) within social units (red and blue circular borders) within vocal clans (as linked by the thick grey edges) (from Cantor et al. 2015).

In addition to the processes described above, early applications of network analyses in animal behavior and ecological studies in various ways to gain a better understanding of social organization through the evaluation of the roles of individuals on and within the network (Croft et al., 2006, 2009; Williams & Lusseau, 2006; Krause et al., 2007; Lusseau et al., 2006). Network analysis identifying group structure has been key in understanding population structuring and cultural transmission, leading to proposed differences of conservation units in management (Baird & Whitehead, 2000; Esteban et al., 2016a; Whitehead, Rendell, Osborne, & Würsig, 2004). However, it was just recently that network analyses have begun examining the roles that external factors play in shaping animal community structures, and in turn, how those network dynamics

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create a feedback loop to individuals and their environment (Farine & Whitehead, 2015).

Much remains unknown of how social networks are influenced by environmental

perturbations and the implications of such events for the social connectivity of a

population (Sih et al., 2009; Godfrey, Sih, & Bull, 2013). Longitudinal evaluation of a

population over time can identify those factors influencing network dynamics in terms of

temporal stability and robustness of a social network against change (Blonder, Wey,

Dornhaus, James, & Sih, 2012; Godfrey, Sih, & Bull, 2013).

Of all taxa, our understanding of marine mammal social structures is largely

limited due to the difficulties of identifying and monitoring interactions between

individuals, rather than the group, over time within the marine environment (Whitehead,

1995). Cetaceans, by nature, are difficult to observe, spending significant time under the

surface; therefore it is commonplace to record their associations rather than interactions

(Whitehead 2008). As a result, there is a general paucity of consistent, longitudinal data

for many species and populations. However, this uncertainty trend has shifted over the

past several decades, particularly in the case of coastal cetaceans (whales and dolphins),

which often form large, stable groups and spend significant time nearshore enabling

consistent monitoring of individuals and populations (Mann, 2000).

Cetaceans have attracted much attention through studies of their social

organization, group behavior, and cultural transmission of information (Cantor &

Whitehead, 2013), however network analyses have only recently been used to evaluate

patterns of individual interactions and social hierarchy. Key examples of species studied

include: common bottlenose dolphins, *Tursiops truncatus* (Lusseau et al., 2003, 2006),

sperm whales, *Physeter macrocephalus* (Gero, Bøttcher, Whitehead, & Madsen, 2016),

killer whales, *Orcinus orca* (Baird & Whitehead, 2000; Beck, Kuningas, Esteban, & Foote, 2012; Esteban et al., 2016a; Foster et al., 2012b), short-finned pilot whales, *Globicephala macrorhynchus* (Mahaffy, Baird, McSweeney, Webster, & Schorr, 2015), and humpback whales, *Megaptera novaeangliae* (Allen, Weinrich, Hoppitt, & Rendell, 2013; Lubansky, 2016).

As anthropogenic activities (human disturbance) continue to expand and impact the environment, it grows ever more important to evaluate and understand the extent of those effects so that mitigation measures can be taken to conserve and protect wildlife populations. In marine mammals, biologists generally assess disturbance effects by measuring the acute behavioral changes of animals in response to human activities (e.g., Southall, Moretti, Abraham, Calambokidis, DeRuiter, & Tyack, 2012). However, behavioral responses vary widely across species, locations, and context making it difficult to determine if such changes are even biologically meaningful; thus, this approach may not be the best metric to evaluate the significance of human disturbance (e.g., Goldenberg, Douglas-Hamilton, Daballen, & Wittemyer, 2016; Gomez, Lawson, Wright, Buren, Tollit, & Lesage, 2016). For the purposes of conservation management, the consequences of human disturbance of wildlife are only important if there is a significant, shift within the population and related vital rates (e.g., survival or fecundity) that can lead to population declines (Gill, Norris, & Sutherland, 2001). Therefore, an integrative approach accounting for behavior, physiology, ecology, and population dynamics, such as the PCoD (Population Consequences of Disturbance) framework (New et al., 2014), is the best way to identify severity of human disturbance. In this respect,

social network analyses can aid in better understanding the many factors involved in population shifts.

Disturbance Effects on Social Networks: Examples from Cetaceans

Few studies have investigated cetacean social networks relative to ecological disturbance conditions; those best described involve environmental pulse events or shifts in prey dynamics. For example, a resident common bottlenose dolphin community within the Bahamas split into two distinct social units following two major hurricanes, with members showing high levels of association within, but not between, units likely due to the lack of geographic isolation and choices of association between residents and immigrants (Elliser & Herzing, 2010). A common bottlenose dolphin community experienced a similar social structure fragmentation in Mississippi Sound following the passage of Hurricane Katrina, likely a result of decreased vessel presence and commercial and recreational fishing activities (Mackey, Solangi, & Kuczaj, 2013). Killer whales in the northeastern Pacific also exhibit plasticity in leadership, grouping behaviors and social fragmentation relative to prey abundance, forming smaller groups (with sparse network connections) led by older individuals (i.e., matriarchs) when prey availability is low (Brent et al., 2015; Parsons, Balcomb, Ford, & Durban, 2009; Foster et al., 2012b) and that seem to take place two years following a lower phase of the Pacific Decadal Oscillation (Lusseau et al., 2004).

Anthropogenic activities (human disturbance) can also influence or even shift ecological conditions creating both short- and long-term effects, which some species have acutely responded to through learning and behavioral plasticity. As an example of short-term effects, dolphins exploiting an artificial increase in prey availability from marine

aquaculture showed lower levels of associations, likely because cooperative foraging

behaviors were not as necessary (Lopez & Shirai, 2008). Similarly, a family group of

killer whales that uniquely depredated on long-line fisheries recently underwent fission,

perhaps as a means to accommodate a more efficient foraging strategy (Esteban et al.

2016b). Long-term influences and potential effects of anthropogenic activities on a

population's social structure are far less understood. One example may be the lingering

population depression resulting from the targeted removal of nearly seventy individuals

(mostly juvenile females) for dolphinariums, which likely altered the social structure of

the Southern Resident killer whale population within the northeastern Pacific (Bigg &

Wolman, 1975; Williams & Lusseau, 2006). Indeed, the demographics and social

dynamics of the Southern Resident population can serve as a proxy for understanding

dynamics within other killer whale populations within this region.

Killer whales have emerged as a keystone species for understanding the role of

anthropogenic and environmental influences on sociality and behavior (e.g., Bigg,

Olesiuk, Ellis, Ford, & Balcomb, 1990; Baird & Whitehead, 2000; Brent et al., 2015;

Esteban et al., 2016b; Parsons et al., 2009; Beck, Kuningas, Esteban, & Foote 2012;

Foster et al., 2012b). Their social structure has been broadly investigated around the

world and is typically characterized by strong natal philopatry and stable hierarchically

structured social units based on maternal lineages, with variation in sociality between and

within populations of killer whales (Ford & Ellis, 1999; Ford, Ellis, & Balcomb, 2000).

Likewise, killer whales are described as having culture, with behavioral traditions and

communication traits transmitted both vertically and horizontally amongst individuals

within a population through social learning mechanisms (Deecke, Spong, & Ford, 2000; Rendell & Whitehead, 2001).

Social learning and acquisition is an important mechanism to maintain uniformity within groups, as well as behavioral variability and sociality between groups (Laland & Galef, 2009). Thus, behavioral plasticity and transmission creates a cultural feedback that in turn shapes an individual's phenotype, including sociality across that individual's lifetime; altered social structuring may in turn perpetuate intergroup variation in phenotype (Pike, Samanta, Lindstrom, & Royle, 2008; Whiten & van Schaik, 2007). However, much of this information is derived from only a handful of studies throughout the globe. Given the known biological and cultural variability between killer whale populations, it is important to evaluate and understand these fine scale differences, particularly in areas where multiple populations may overlap, rather than apply generalizations. This is essential when it comes to implementing conservation measures that are often based regionally rather than nationally; that is, what may be good practice for one group may not be beneficial to another (e.g., Wallace et al. 2010).

Killer Whales of the Northeastern Pacific

Killer whales are a cosmopolitan species with distribution ranges throughout all oceans and seas of the world, but are most concentrated in colder, productive waters at higher latitudes (Forney & Wade, 2006; Leatherwood & Dahlheim, 1978). In the northeastern Pacific, seasonal and year-round occurrence has been noted for killer whales throughout Alaska, within intra-coastal waterways of British Columbia and Washington State, and as far south as California (Bigg et al., 1990; Balcomb, Boran, & Heimlich, 1988; Dahlheim et al., 2008). Assessment via photo-identification methods and

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assessment of morphology, ecology, genetics, and behavior, experts have identified three broad ecotypes, or forms, of killer whales inhabiting this region: *resident*, *transient*, and *offshore* (Ford, Ellis, & Balcomb, 2000).

Though these ecotypes live in sympatry – particularly residents and transients – they reflect deeply divergent evolutionary lineages; individuals from these groups do not interbreed or socialize, produce distinct communicative signals, and have exclusive prey niches (Ford, Ellis, & Balcomb, 2000; Baird, Abrams, & Dill, 1992; Dahlheim et al., 2008; Jefferson, Stacey, & Baird, 1991; Hoelzel, Dahlheim, & Stern, 1998; Morton, 1990; Riesch, Barrett-Lennard, Ellis, Ford, & Deecke, 2012). Resident killer whales forage almost exclusively upon fish, namely salmonids, while transients feed upon other marine mammals, and occasionally sea birds (Felleman, Heimlich-Boran, & Osborne, 1998; Ford et al., 1998).

Indeed, transient killer whales likely diverged from all other killer whale lineages ~700,000 years ago and may warrant assignment as a new species (Hoelzel, Natoli, Dahlheim, Olavarria, Baird, & Black, 2002; Morin et al., 2010). Likewise, the Society for Marine Mammalogy's Committee on Taxonomy (2016) currently denotes these northeastern Pacific ecotypes as un-named *Orcinus orca* subspecies. In recognition of it's status as an un-named subspecies or species, local researchers now refer to transient killer whales as Bigg's killer whales, in tribute to the late Dr. Michael Bigg – the pioneer of modern killer whale research (e.g., Ford, 2011; Riesch, Barrett-Lennard, Ellis, Ford, & Deecke, 2012; Committee on Taxonomy, 2016).

There are currently three stocks of Bigg's killer whales recognized within the northeastern Pacific: 1) the Gulf of Alaska, Aleutian Islands, and Bering Sea Transient

stock - occurring mainly from Prince William Sound through the Aleutian Islands and Bering Sea; 2) the depleted AT1 transient stock - occurring in Alaska from Prince William Sound through the Kenai Fjords; and 3) the West Coast transient (WCT) stock – considered transboundary, occurring from California through southeastern Alaska (Allen & Angliss, 2013; Figure 2).
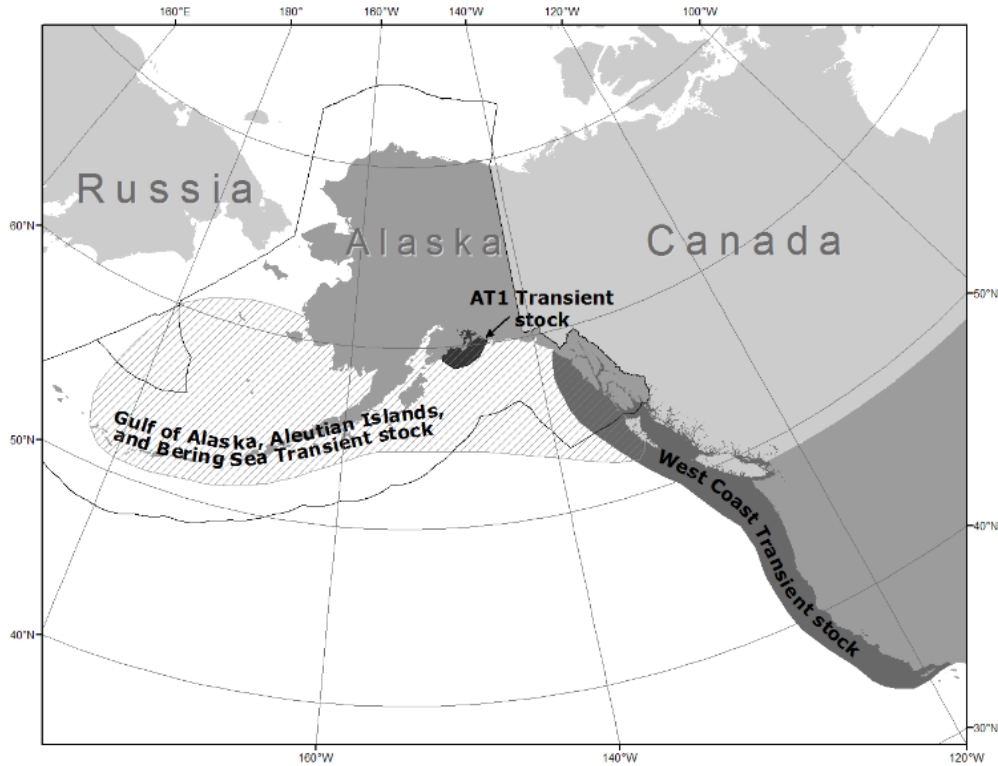
Figure 2. Approximate distribution of Bigg's (transient) killer whale stocks within the northeastern Pacific (Allen & Angliss, 2013).

The WCT stock of Bigg's killer whales is perhaps the best studied of this ecotype, with consistent encounters and direct counts of individuals taking place since 1975 (Ford & Ellis, 1999). Based on these records, the last assessment identified approximately[1] 521

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[1] The number of cataloged whales does not necessarily represent the number of live animals. Some animals may have died, but whales cannot be presumed dead if not resighted because long periods of time between sightings are common for some transient animals. Also, the given that the California transient numbers have not been updated since the publication of the catalogue in 1997 (Black et al., 1997), the total number of Bigg's killer whales reported above should be considered as a minimum count for the WCT stock.

individuals; of these, 217 are considered part of the poorly known outer coast WCT

subpopulation and 304 belong to the more well-known inner coast subpopulation (Allen

& Angliss, 2013; Ford, Stredulinsky, Towers, & Ellis, 2013). However, there is some

debate among researchers about the composition of the inner coast group; a recent mark-

recapture estimate excluded whales from California and resulted in an estimate of 243

inner coast individuals that occur within the coastal waters of southeastern Alaska,

British Columbia, and northern Washington (Fisheries and Oceans Canada, 2007, 2009;

Ford, Stredulinsky, Towers, & Ellis, 2013; Allen & Angliss, 2013). The WCT population

grew rapidly from the mid 1970's to the mid 1990's, likely a result from a pronounced

increase in prey abundance, but has since slowed (Fisheries and Oceans Canada, 2007,

2009; (Houghton, Baird, Emmons, & Hanson, 2015).

Given the relatively low abundance and the high levels of chemical contaminants

found in Bigg's killer whale tissue, which result from feeding at a high trophic level (see

below for further discussion), these whales in British Columbia have been classified as

Threatened under the Species at Risk Act (SARA) since 2001 (Fisheries and Oceans

Canada, 2007, 2009). General protections are afforded to Bigg's killer whales in the U.S.

under the Marine Mammal Protection Act (MMPA), however they are not designated as

Depleted (and thus, are not considered to be a strategic stock – which would trigger

additional management actions). Likewise, they also do not meet the criteria for

consideration of being listed as *Threatened* or *Endangered* under the Endangered Species

Act.

Studies across the various Bigg's killer whale stocks show that life-history

metrics (e.g., maturation, reproductive rates, and longevity) may be similar to those of the

sympatric resident populations (Ford, Ellis, & Durban, 2007; Olesiuk, Ellis, & Ford, 2005). Male killer whales have a mean life expectancy of ~ 30 years, with maximum longevities up to 60-70 years. Females have a mean life expectancy of ~45 years and a maximum longevity of about 80 years, and are known to experience periods of post-reproductive senescence (Brent, Franks, Foster, Balcomb, Cant, & Croft, 2015; Franks et al., 2016; Olesiuk et al., 2005; Foster et al., 2012a). The survival rates for Bigg's killer whales are high and relatively stable over time, though recruitment to the population has decreased in recent years.

The social organization and demographic independence of Bigg's killer whale populations, with the exception of the AT1 stock, remains relatively understudied; the most recent assessment took place nearly two decades ago (Baird & Whitehead, 2000; Baird & Dill, 1995, 1996). However, there is evidence that Bigg's social structure is comprised of various hierarchical social tiers. Like residents, Bigg's killer whale societies are centered upon semi-stable maternal lineages (*matrilines*), which typically consist of an adult female and her offspring (e.g., Figure 3).

In resident societies, individuals and matrilines with consistently high association levels (that associate more than 50% of the time with one another) are delineated as pods; groupings of related pods comprise acoustic "clans" that are based on their acoustic traditions (Bigg et al. 1990). However, unlike residents, dispersal from Bigg's matrilineal groups is generally a regular occurrence for adult males and for females that have offspring of their own; this dispersal may be temporary or permanent (Bigg, Ellis, Ford, & Balcomb, 1987, Ford & Ellis, 1999, Baird & Whitehead, 2000).

Figure 3. Example of a Bigg's killer whale matriline, comprised of three generations.

Matriarch T36, with her daughter T36B and her offspring. Individual scar patterns on the saddle patch and fin shape enables long-term monitoring of individuals, which are denoted by an arbitrary alphanumeric code. Class information for birth year and sex, if known, is also noted. Schematic courtesy of the Center for Whale Research.

Despite dispersal, past studies revealed that individual Bigg's killer whales do form stable, long-term associations, even to the point of being distinguished pods (Baird & Whitehead, 2000; Bigg et al. 1990). Notably, associations between Bigg's pods are non-random and reflect interpod foraging specializations (foraging 'clusters'), with some foraging close to shore ('nearshore foragers') and others foraging primarily in open water ('non-nearshore foragers'). The exception to these persistent relationships lies with "roving" males that generally spend much of their time alone, but will occasionally associate with groups comprised of potentially reproductive females (Baird & Whitehead, 2000; E.g., Figure 4). It is currently unknown how many social tiers comprise a Bigg's killer whale stock; how stable the composition of foraging clusters are and how they fit within Biggs' social structure; and whether or not each of the three transient killer whale stocks are uniform in their social structure. This study aims to address some of these unknowns.

Previous studies showed that Bigg's group sizes usually consist of 2–5 individuals within a matriline, an optimum group size for managing caloric expenditure during targeted foraging behaviors (Baird & Dill, 1995, 1996). However, larger groups (>20 animals) have become more common within the waters of lower British Columbia and adjacent inland waters of Washington State (hereafter referred to as the Salish Sea; see Figure 4) in recent years, likely in response to increased prey diversity, demographic recruitment, and local emigration (Houghton et al., 2015). Bigg's killer whales are cooperative hunters, and recent evidence suggests that an increase in prey abundance (i.e., more efficient foraging opportunities) could alleviate the need to forage in the smaller, optimum group size within this changing ecosystem (Baird & Dill, 1995;

Houghton, Baird, Emmons, & Hanson, 2015). In addition to changes in group size, Bigg's killer whales (particularly, non-nearshore foragers) are often occurring significantly more often in the Salish Sea as compared to twenty years ago, with some Bigg's matrilines exhibiting fine-scale site fidelity and seasonality within this ecosystem, particularly in the summer months (Houghton, Baird, Emmons, & Hanson, 2015). For example, the most commonly encountered matrilines from 1987-1993 (see Baird & Dill, 1995) also occurred more frequently in recent years (2004-2010); however, additional matrilines that were not documented in earlier years are now commonly encountered (Houghton, Baird, Emmons, & Hanson, 2015; CWR, unpublished data).

Killer Whale Management Issues within the Salish Sea

In addition to shifting predator-prey dynamics, killer whales of all ecotypes are facing many environmental shifts within the Salish Sea. As apex predators, the greatest known threats to killer whales have anthropogenic sources, including: human-induced mortality (e.g., shooting linked to commercial fishing activities (Keyes cited in Hoyt 1981; Matkin et al., 1986); contaminants (e.g., polychlorinated biphenyls, PCBs and polybrominated diphenyl ethers, PBDEs; Ross, Ellis, Ikonomou, Barrett-Lennard, & Addison, 2000); toxic spills (e.g., crude oil; see Matkin, Ellis, Olesiuk, & Saulitis, 1999; Matkin, Saulitis, Ellis, Olesiuk, & Rice, 2008); acoustic disturbance (e.g., Houghton et al., 2015a; Viers, Viers, & Wood, 2016) and increased interactions - physical disturbance and collision events - with vessels (J. Durban, NOAA Fisheries, pers. comm.; Fisheries and Oceans Canada, 2009). Each of these stressors can act independently and cumulatively, in which case possibly causing stronger negative, and event lethal effects.

The Salish Sea hosts one of the largest, most economically profitable whale watch industries in the world, due in large part to the transboundary location and collective vessel contribution to both U.S. and Canadian economies, along with related international trade and tribal treaty agreements. Established in the mid-1970s, commercial whale watching has rapidly increased in recent years. In 2015, the industry comprised of 96 active commercial vessels from both the U.S. and Canada – the highest number ever recorded – and generated over $100 million (Seely, 2015; S. Grace, pers. comm.). Whales within this area are also exposed to private and commercial fishing boats, recreational powerboats, sailboats, kayaks, research vessels, military vessels and freight carrying ships (Pynn, 2016; Seely, 2015).

The effects of vessel disturbance, particularly those from commercial whale watching, have long been a source of contention (Higham & Lusseau, 2007; New et al., 2015; Parsons, 2012). In general, the vessel impact hypothesis argues that chronic exposure to a high abundance of vessel traffic is associated with behavioral disruption, increased energy expenditure and/or foraging interference, which can thus result in psychological and/or nutritional stress, displacement and reduced population fitness (e.g., Bejder et al., 2006; Lusseau, 2003, 2004; Lusseau, Slooten, & Currey, 2006; Pirotta et al. 2015; Williams, Lusseau, & Hammond, 2006). A recent meta-analysis revealed that the most consistent responses cetaceans had towards whale watching vessels are disruptions of activity budget and of path directionality; animals are more likely to travel and less likely to rest and forage, and show a tendency to increase path sinuosity and decrease path linearity in the presence of vessels (Senigaglia et al., 2016).

In response to the growing body of evidence of vessel disturbance, the

International Whaling Commission (IWC) recently concluded that "there is compelling

evidence that the fitness of individual odontocetes repeatedly exposed to commercial

whale watching vessel traffic can be compromised and that this can lead to population-

level effects" (IWC, 2006; see also Fleishman et al., 2016). As a result, the sustainability

and management of this industry and exploitation of the resources (cetaceans) being

targeted is now considered to be an international priority (Higham, Bejder, Allen,

Corkeron, & Lusseau, 2016).

To address the concerns over increasing vessel traffic within the Salish Sea, in

2011, NOAA Fisheries implemented federal regulations restricting the approach of

vessels within 200 yards of all killer whales (despite ecotype) within inland waters of

Washington State, each of the entrances to the Strait of Juan de Fuca, and south of the

U.S./Canada border; parking a vessel in the path of traveling killer whales is also

prohibited (76 FR 20870; Giles & Koski, 2012). No such regulations exist in Canada.

Instead, voluntary approach prohibitions (up to 100 meters/yards) are in place

(www.behwhalewise.org) with various degrees of compliance (Seely, 2015).

Although no studies have yet focused on vessel impacts on Bigg's killer whales,

residents have been shown to alter their swimming behavior and cease feeding when

approached by boats (Noren, Johnson, Rehder, & Larson, 2009; Williams, Bain, Smith,

& Lusseau, 2009; Williams & Ashe, 2007; Williams & Noren, 2009); as well as increase

their call amplitude to compensate for acoustic masking from vessel noise (Holt, Noren,

Veirs, Emmons, & Veirs, 2008). A recent cumulative effects analysis showed that

resident killer whales secrete stress hormones primarily due to a decrease in prey

abundance, however it appears stress was exacerbated due to chronic exposure to vessels (Ayers et al., 2012).

Each of these factors may very well have the same effect, if not more so, on Bigg's killer whales. The increased intensity of whale watching activity within the Salish Sea coupled with the more frequent presence and larger group sizes of Bigg's killer whales in this area creates many scenarios for potential disturbance on this understudied group of whales. For example, the close approach of multiple vessels could potentially reduce overall foraging success. Transient attacks on marine mammals are cooperative, often prolonged and involve energetic, high-speed swimming. The close approach of multiple vessels could potentially reduce overall foraging success, by causing the whales to abandon their attack (as has been observed in residents, see Williams et al., 2009), or provide the prey item with a refuge to escape from the attacking whales (e.g., Schmunk, 2015). Likewise, a larger group size could also be a means to combat missed foraging opportunities as a result of increased interference from vessels.

Study Objectives

Although resident killer whales are broadly studied within the Salish Sea ecosystem, much about the social structure of the Bigg's ecotype remains unknown. Given the central importance of the social network within killer whale population dynamics, such as the maintenance of cooperation and cultural transmission of information, shifts in social network structure caused by environmental processes may have significant ecological and evolutionary consequences. Previous studies demonstrate that sociality in fish-eating killer whales is to some extent plastic and can be adapted to reflect the local ecological conditions (Esteban et al., 2016b; Foster et al., 2012b; Parsons

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et al., 2009). It is reasonable, then, to assume that the increased presence of Bigg's killer whales within the Salish Sea makes them susceptible to the various and growing anthropogenic pressures within this area.

In this doctoral study, I aimed to address two major objectives:

(1)   Explore the current social dynamics of Bigg's killer whales within the Salish Sea, and determine possible shifts from past assessments of their sociality; and

(2)   Evaluate the patterns and potential relationships of vessel exposure from whale watching activities relative to Bigg's individuals and social groups.

The bulk of this dissertation research will encompass the first objective, creating a foundation for future analyses. The second objective will serve as a case study for the utility of social network analyses as a means to evaluate killer whale social and grouping dynamics in response to anthropogenic activities. I will revisit and build upon the initial quantitative assessment of transient (Bigg's) killer whale ecology and association patterns first made by Baird (1994) two decades ago (Baird & Dill, 1995, 1996; Baird & Whitehead 2000) and will evaluate the matrilineal grouping dynamics recently described by Houghton and colleagues (2015) using network analyses.

The present chapter (Chapter I) provided a general introduction to the social and behavioral ecology of Bigg's killer whales and the conservation pressures they are experiencing within the transboundary waters of British Columbia, Canada and Washington, United States. The remainder of this thesis is organized into five chapters to explore three facets of Bigg's killer whale behavioral ecology: localized community social structure within transboundary waters (Chapter II), the roles of individuals within a

society (Chapter III), and targeted anthropogenic activities (whale watching) (Chapter IV). The final chapter (Chapter IV) provides a brief conclusion to this thesis, revisiting the results of each of the studies. Effective conservation management practices require accurate science on both local and global scales to inform decision-making. The three data chapters presented here were motivation for furthering the understanding of this dynamic science-management issue on a local scale, focusing on the transboundary waters of Haro and Juan de Fuca Straits shared by Canada and the United States (Figure 4).

General Field Methodology

The proposed study is a collaborative effort leveraging archival datasets from three collaborative researchers and organizations. The primary data is from vessel-based, photo-identification field surveys derived from the research efforts of Robin Baird (1994; see also Baird & Dill, 1995, 1996) and the Center for Whale Research (CWR), spanning from 1987-1993 (Baird; following wildlife viewing approach guidelines); and 2005-2016 (CWR). These data were collected in a comparable manner, following standard field protocol for killer whale research in this region (Balcomb, Boran, & Heimlich, 1982; Bigg et al., 1990), and were collected under local whale watching guidelines (Baird), or under NMFS permit #532-1822, #15569 and/or various DFO SARA licenses (CWR).

Information on vessel abundance and trend data are available from the Soundwatch Boater Education Program (of The Whale Museum) from 1993 onward, however only a subset (2011-2016) of the data, focusing on the years since will be used in this dissertation. Details on the methodology for this project are detailed in Chapter IV. It should be noted that due to the transboundary nature of the target species, the

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Department of Fisheries and Oceans (DFO) Canada maintains additional information on the target species, particularly in Canadian waters; the work derived from this proposed study will be shared with DFO and Canadian partners and may serve as a baseline for future collaborative projects.

Study Area

The study area is approximately 3000 km^2 of the Salish Sea, a small region of the Puget Sound ecosystem, centered around the southern tip of Vancouver Island, British Columbia, Canada, including the western San Juan Islands, Washington, USA (Figure 4).
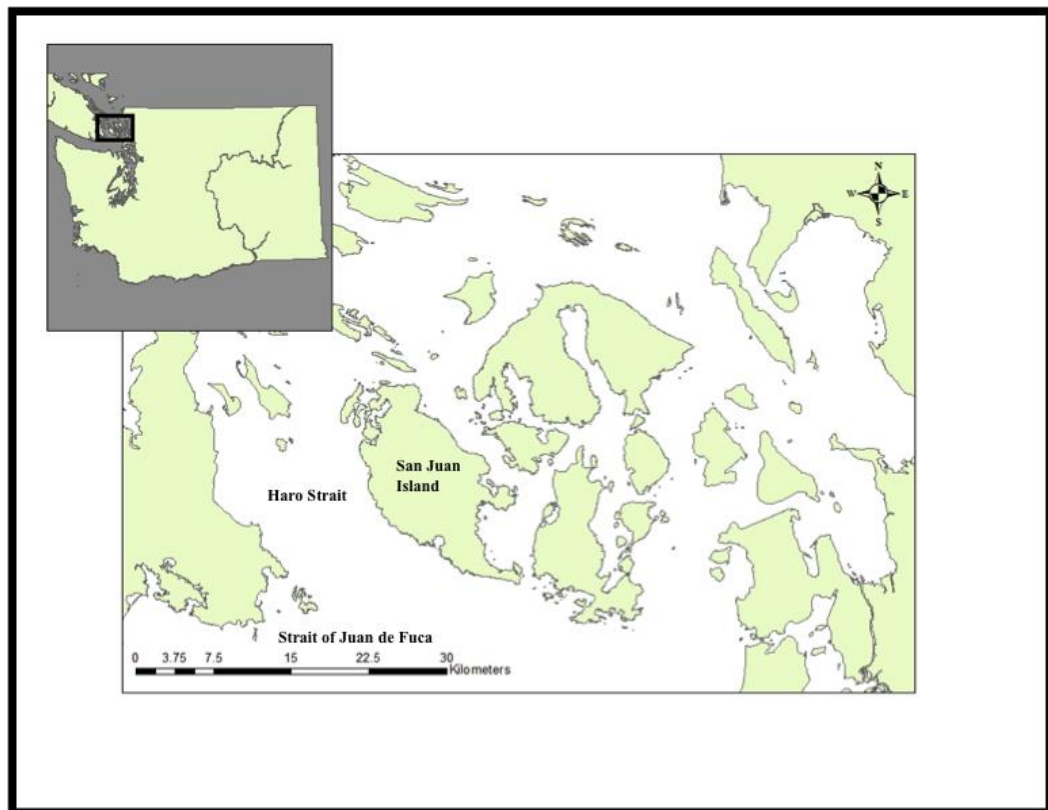
Figure 4. Map of the survey area, a subset of the Salish Sea, which encompasses Haro Strait, the Strait of Juan de Fuca, Puget Sound and adjacent waters.

Field Efforts and Data Collection

The Salish Sea is a unique study area where, especially in the last few decades, it is difficult to quantify search effort in locating whales due to the many 'eyes' (individual spotters) and 'ears' (passive acoustic monitoring for whale vocal activity) available as part of an extensive sightings network (Smith & Giles, 2015) comprised of commercial whale watch operators, fishermen, lighthouse keepers, the general public, an extensive hydrophone network, and by researchers scanning from shore or traversing the study area by boat. When whales are sighted or heard, information such as ecotype, group identity, location, and direction of movement is rapidly relayed to the research community in real time, enabling the research teams (Baird and CWR) to intercept the whales.

Because different researchers (pursuing various research objectives) contributed to the pooled dataset, there were minor differences in how groups were characterized. For example, Baird (1994; Baird & Dill, 1995, 1996) defined a group as all whales acting in a coordinated manner (e.g., all traveling in the same direction at the same speed, often surfacing within 5–10 s of each other) and within visual range of the observers; individuals were considered associated if they were within the same group. Similar to Baird, CWR also considers coordinated movements and proximity to individuals as group membership criteria; however, they also recognize that individuals within acoustic proximity (~10 km) have the opportunity to interact (Parsons et al., 2009; Miller, 2006). Thus, individuals identified within this range were considered to be part of the same group. These criteria have been used in other killer whale social network analyses (e.g., Beck, Kuningas, Esteban, & Foote 2012; Esteban et al., 2016b). However, both studies considered all group members to be within a few hundred meters of each other (i.e., within communicative range or within close physical proximity). These differences in the

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data will be controlled by only using encounters from which all individuals within a group were identified and thus can be used for comparative analyses.

Encounters took place from small (< 8 m) vessels, manned by one to four observers, during ideal sampling conditions: no rain and relatively calm sea state (i.e., less than Beaufort 4; Figure 5). Behavioral data for all individuals were collected using focal-group sampling, documenting all occurrences of all behaviors (Altmann, 1974). Typical information collected from both research teams included: direction of travel, orientation and distance between individuals (group spread), relative travel speed, dive durations, synchronization of respirations, and occurrence of discrete behavior events (Baird & Dill, 1995; Jacobsen, 1986).

Figure 5. Example of a close approach for photo-identification of individual whales. Bigg's killer whale T20 (male) pictured. Photo credit: Adam U.

Individual killer whales were identified photographically and/or visually[2] based on distinctive characteristics of the dorsal fin (e.g., notching) and the saddle patch (e.g., scar patterns) and sexed using dorsal fin shape and pigmentation patterns around the genital slits (Bigg, Ellis, Ford, & Balcomb, 1987; Baird & Stacey, 1988; Figure 6).

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[2] Visual identifications, particularly in early years, were only made by expert researchers that know the individuals and were usually relied upon only when a particular individual or small group of individuals was seen several days in a row and were distinctively marked.

Encounters occurred year-round, but were concentrated during the summer season

(loosely defined as May-October). Given the extensive sightings network and that

encounters were distributed both near shore and offshore throughout the study area,

sightings (and thus, encounters) were not considered biased towards larger groups.
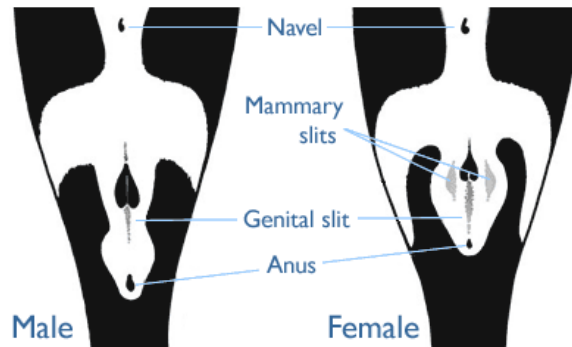
Figure 6. Markings to denote sex of animals encountered. Graphic compiled by Kelley Balcomb-Bartok, Center for Whale Research.

CHAPTER II – THE ROLE OF FORAGING BEHAVIOR IN SOCIAL

DIFFERENTIATION OF BIGG'S KILLER WHALES IN THE SALISH SEA

Introduction

Background

Gregariousness plays a vital role in the behavioral ecology of many animal

societies, with a balance of costs and benefits that should facilitate maximum fitness for

the group and the individuals within (Alexander, 1974). For vertebrates, group living

offers reproductive access, robustness to predators, and increased foraging success.

Alternatively, these benefits can cycle into a negative feedback loop reducing fitness;

uninhibited mating can lead to rapid population growth, subsequently increasing

competition for mates and resources, while an increase in conspecifics can enhance the

propagation of disease (Chapman & Valenta, 2015; Macdonald, 1983). This may, in

turn, prompt behavioral changes among individuals to ensure a fitness advantage. One

way this may manifest is the preferential affiliation among conspecifics within groups,

which presents potentially beneficial cooperative opportunities (Ranta, Rita, &

Lindstrom, 1993).

It is well demonstrated in both terrestrial and marine mammals that predator-prey

dynamics influence population dynamics; when prey is abundant, predators typically

thrive (Sinclair & Krebs, 2002). Which subsequently may allow for increases in group

size. This currently is the case with Bigg's killer whales within the Salish Sea, which

have become more common at different times of the year, particularly during summer

months, and have also increased in their occurrence and group size, most likely in

response to an increase in species they predate upon: seals, sea lions, porpoises and

occasionally other cetaceans throughout their range (Houghton et al., 2015). Optimal foraging theory implies that for individuals to maximize fitness, the benefits of foraging (i.e., caloric input) must outweigh the efforts of the behavior itself (energy spent). Thus, optimum group size for associated prey, as well as cooperation and communication with conspecifics can help to alleviate costs during foraging behavior (Clark & Mangel, 1986; Baird & Dill, 1995).

Alternatively, prey sources of low diversity and/or abundance can quickly become exhausted due to intraspecific competition. However, this can be mitigated by niche partitioning and divergent foraging strategies (Kie & Boyer, 1999). For example, a discrete group of Indo-Pacific bottlenose dolphins in Shark Bay, Australia employ tool-use by wearing basket sponges on their beaks to protect themselves while foraging on the seafloor (Mann, Stanton, Patterson, Bienenstock, & Singh, 2012. Common bottlenose dolphins off of Georgia (U.S.A.) exhibit social differentiation reflective of foraging activities related to commercial and recreational fishing activities (Kovacs, Perrtree, & Cox, 2017). Similar social divisions, also linked with kinship, related to commercial fisheries are also present in killer whales in the Strait of Gibraltar (Esteban, Verborgh, Gauffier, Giménez, & Foote, 2015). Over time, this can eventually lead to social and genetic segregation. The emergence of sympatric killer whale ecotypes within a shared habitat, as described in Chapter 1, is the prime example of how foraging specialization over time can evolve into social, and species, differentiation.

Bigg's killer whales have been shown to employ two diverse foraging strategies: nearshore foraging, which involves hunting and predating small pinnipeds along shorelines, and non-nearshore foraging, which requires more coordinated efforts targeting

larger and more agile prey species (Baird & Dill, 1995, 1996; Baird, 2000). This same

population was later described as having social differentiation, defined by measures

historically used to designate Resident killer whale 'pods': individuals observed more

often together (50% >) than apart (Bigg et al. 1990; Baird & Whitehead, 2000).

However, no study to date has explored the links between foraging class and social

differentiation within the Bigg's killer whale population. The increase in Bigg's killer

whales and their various prey species, as well as the observed shifts in occurrence and

grouping behaviors proves a unique opportunity to quantitatively define the social

structure of Bigg's killer whales using social network measures in the context of

observed prey preferences. Thus, the objectives of this chapter are to (1) assess foraging

strategies of individuals based on preferred prey type and (2) determine the level of social

differentiation Bigg's killer whales exhibit in transboundary waters, and (3) determine

whether social differentiation is linked to perceived diet. Associations will be based on

the Half-weight index (HWI), described below. The hypotheses I will be testing in this

chapter are:

H_{01}: Social differentiation occurs at the pod level (HWI=0.50).

H_{a1}: Social differentiation does not occur at the pod level (HWI $\neq$ 0.50).

H_{02}: Social differentiation is reflective of foraging class.

H_{a2}: Social differentiation is not reflective of foraging class.

Methodology

Field Encounters

Whale encounters occurred within the study area and followed the field protocol

as described in Chapter I. For the purposes of this chapter's analyses, only CWR

encounters (2006-2015) were evaluated. The CWR dataset yielded 263 encounters over 223 days spanning a decade (2006-2015), with 1802 total whales comprised of 207 unique individuals. Encounters occurred throughout the year, within all months.

Following the "gambit of the group" approach (Whitehead & Dufault, 1999), all individuals within a few hundred meters of each other (i.e., within close physical proximity) that were moving in the same direction and engaged in the same behavioral state were considered associated within a group. Consistent with most other killer whale studies, groups are generally easily qualified based on their spatio-temporal discreteness. Sampling periods were set as calendar days, which assumes animals were associated the entire day if they were observed together on that day. Individuals sighted in two or more groups within the same day were considered associated with each of the respective groups.

Foraging Strategies

Discrete predation events of identifiable prey species were obtained from the behavioral data collected during field surveys (see Chapter 1). Observed prey included harbor seals (*Phoca vitulina*), Steller sea lions (*Eumetopias jubatus*), and both Dall's and harbor porpoises (of the *Phocoenidae* family). Baird and Dill (1995) previously assigned foraging strategy classes to individuals; harbor seal hunters were considered nearshore foragers, while those hunting large pinnipeds (e.g., sea lions, Elephant seals (*Mirounga angustirostris*)) and porpoises were identified as non-nearshore foragers. These delineations reflect foraging tactics given that non-nearshore prey is more agile in open waters further from shore, thus requiring more maneuverability and/or group members for a successful kill (Baird & Dill, 1996).

As it was not always possible to discern which specific individuals were directly involved with a predation event (i.e., those individuals responsible for chasing and capturing prey, as observed with prey in mouth), all individuals aggregated during a predation event were considered associated with that particular prey. However, some predation events occurred among rather large group sizes and it is possible that not all individuals within the group participated in the foraging event. Therefore, only those individuals that were observed associated with a prey class three or more times had the highest levels of confidence to be classified as a nearshore (i.e., primarily harbor seal feeders) or non-nearshore forager (i.e., foragers targeting larger, agile species farther offshore). Percentages were extrapolated to those individuals and parsed into nearshore prey and non-nearshore prey. If the proportion of the prey type was 60% or higher, the individual was classified as being either a nearshore or non-nearshore forager, while individuals with proportions between 40-60% were considered as being both. The percentages by individuals were then averaged within the clusters defined by modularity to generate a qualitative description of predation type by cluster. The data were not normally distributed, so a Kruskal-Wallis test analysis was used to test for significance of foraging class differences among social clusters (see below).

Social Analyses

Social analyses were run on the entire CWR data set. To reduce biases associated with small sample sizes, restrictions were set to only include individuals observed in five or more encounters. Half-weight indices (HWI) of association were calculated for each dyad (pair of individuals) using SOCPROG 2.7 (Whitehead, 2009), a program run

through MATLAB R2015a (The MathWorks, Inc.). The Half-Weight index is expressed below:

$$HWI = \frac{x}{(x + yab + 0.5(ya + yb))}$$

where x is the number of times both individual a and individual b are seen together, ya and yb represent when either individual a/b were seen alone, and yab where each individual was seen at the same time separately. The HWI reduces the inherent bias in situations where not all associates of an individual are identified within a sampling period (Cairns and Schwager 1987, Whitehead 2008a). Although this study only utilizes encounters where 100% of the individuals were identified, the HWI accounts for potential bias if the sampling period was set too narrowly. Additionally, the HWI is most commonly used in cetacean social network studies, thus allowing for future comparisons across taxa (Whitehead 2008a).

To gauge the extent of Bigg's killer whale social structure, social differentiation (*S*) was estimated using a maximum likelihood approximation of the correlation based on the variability (coefficient of variation; CV) between true and estimated HWI values to determine accuracy of the association indices. Follow-up tests using Newman's (2006) eigenvector-based algorithm for maximizing modularity (*Q*) was used to further identify community division of clusters of individuals that are more highly associated with each other than with others in the community. This involved permutations of the data to determine the difference between the observed and expected associations within the cluster as compared to overall associations. Finally, the mean HWIs for each dyad were compared within and between matriline, social cluster, and foraging classes, while a Mantel matrix correlation test was used to determine significance.

A cumulative bifurcation analysis will be used to identify potential social tiers within the Bigg's community. This analysis involves graphing of the number of bifurcations (branches) occurring within cluster analysis tree, increasing up the tree as the degree of association between individuals decreases. When plotted, points (or 'knots') emerge where rates of bifurcations significantly change indicating structural changes in the cluster analysis (i.e., social tier delineations).

Results

The CWR dataset yielded 110 unique individuals, representing roughly 33% of the entire inner coast subpopulation of the WCT stock, that were observed five or more times, during 217 encounters, and used in subsequent analyses. The mean group size was 6.9 ± 4.3 for all sightings, although group sizes of four individuals were most frequently observed (Figure 7). While summer groups (6.4 ± 3.8) were only slightly smaller than winter groups (7.6 ± 4.9), this difference was significant ($t = -2.28443$, $p = 0.023$). Total number of whales encountered peaked in both April and August (Figure 8), which generally aligns with the harbor seal pupping seasons for the outer coastal and inland water areas that comprise and border the study area (Huber, Jeffries, Brown, DeLong, & VanBlaricom, 2001; Huber, Dickerson, Jeffries, & Lambourn, 2012).
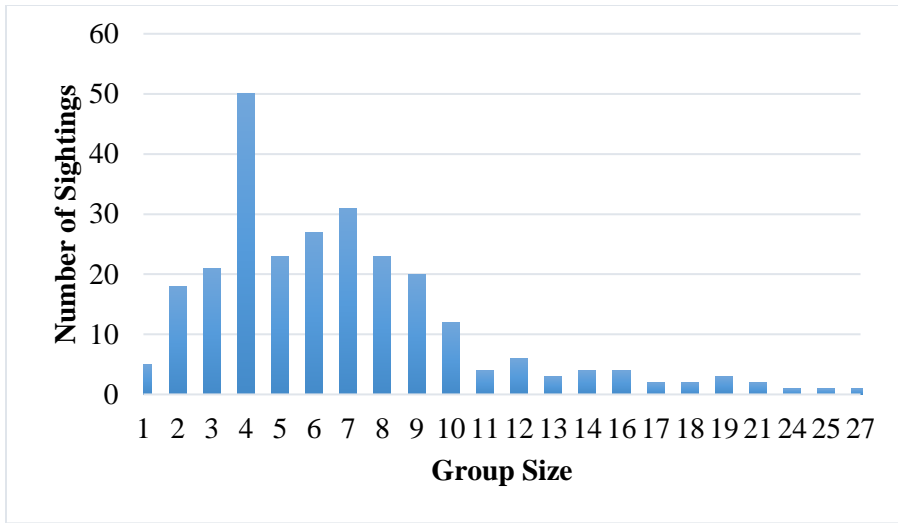
Figure 7. Frequency distribution of Bigg's killer whale group sizes observed within the study area.
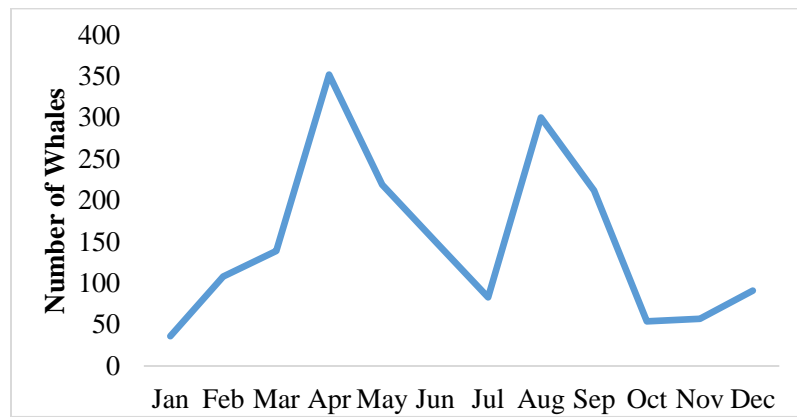
Figure 8. Distribution of total number of whales seen monthly.

Note: These numbers are raw counts of encountered whales, rather than that of unique individuals.

Overall, the likelihood approximation showed that the estimate of the correlation coefficient between the true and estimated association indices was 0.498 (S.E. 0.025), suggesting that the calculated HWIs were only somewhat representative of the true associations and that association indices between specific dyads should only be generalized. The overall mean half-weight index (HWI) was 0.07 ± 0.03, with a mean maximum HWI of 0.87 ± 0.18.

Significant social differentiation within the Bigg's killer whale community was evident ($S = 1.203 \pm$ SE .017). Community division using maximum modularity (based on gregariousness) identified ten distinct social clusters ($Q = 0.523$ at mean HWI = 0.071; see Table 1). The cluster sizes varied broadly, with a range 2–31 individuals each (Table 1). Cluster membership was generally segregated by matriline, with the exception of individuals from T36 matriline; sisters T36A and T137 both dispersed from their mother, T36, and were assigned to Clusters 8 and 9, respectively. Every cluster except one (Cluster 10) had at least one mature female, while Cluster 4 happened to have more sexually mature females (n = 8) than any of the others. Lone (roving) males factored prominently in cluster divisions; Cluster 4 comprised more than half of the 11 known lone males within the study area (T14, T40, T87, T93, T97, and T124C). Similarly, T49C and T77A, also two roving males, were the only individuals assigned to Cluster 10. Average within-cluster associations were significantly greater than those between clusters (HWI = 0.36 ± 0.19 and $.03 \pm .02$, respectively; t = 41.627; p = 0.0000, r = 0.5922). Only three clusters had mean HWIs greater than 0.50 (Clusters 3, 6, and 10; Figure 9), indicating that meaningful community division does occur at association rates lower than the 50% rule. Thus, the null hypothesis is rejected in favor of the alternative.
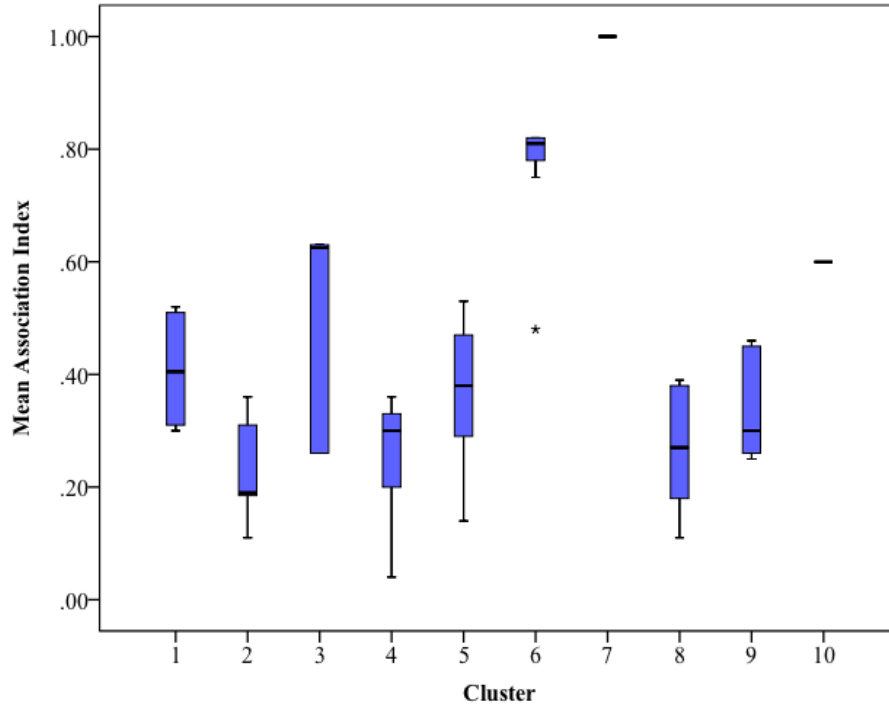
Figure 9. Mean association (Half-weight) indices for individuals associating within social clusters.

Note: The asterisk in Cluster 6 represents T37A1, an 8 year-old individual of unknown sex that has dispersed from its matriline.

Fifty-four predation events with identifiable prey were observed over 43 days during the study period, of which 93 individuals (which were observed five or more times) participated in, with a range of 1-9 events per individual (*M* = 3.26; Figure 9). Prey consisted of porpoises (*N*=13 porpoise, or 24%: 9 harbor porpoise, 1 Dall's porpoise, 1 harbor-Dall's hybrid, and 2 unidentified porpoise species); harbor seals (*N*=32, or 59%); and Steller sea lions (*N*=9, 17%). Fifty-two individuals met the criteria to be assigned to a foraging class; however, it should be noted that, with the exception of two individuals (T40, n=4 and T36A, n=3), all individuals were associated with predation events involving both nearshore and non-nearshore prey (Table 2).

Table 1

Composition of Social Cluster Divisions as Determined by Modularity

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Red labels indicate females; blue: males, bolded text: sexually mature individuals, italics: known lone, dispersed individuals.

Cluster ID	Cluster Size	Individuals	Matrilines
1	9	**T10**, **T10B**, T10C, **T30**, T30A, **T30B**, T30B1, T30C, T46B1	T10, T30, T46
2	12	**T2C**, T2C1, T2C2, T2C3, **T34**, T34A, **T37**, **T37A**, T37A2, T37A3, **T37B**, T37B1	T2, T34, T37
3	6	**T18**, **T19**, **T19B**, T19C, **T20**, **T21**	T18, T21
4	31	**T100**, **T100B**, T100C, T100D, T100E, **T101**, T101A, T101B, **T102**, **T124**, **T124A**, **T124A1**, T124A2, T124A2A, T124A3, T124A4, *T124C*, **T124D**, T124E, *T14*, *T40*, **T86A**, T86A1, T86A3, *T87*, **T88**, **T90**, T90B, T90C, *T93*, *T97*	T86, T90, T100, T101, T124
5	12	**T123**, T123A, T123B, T123C, **T49A**, T49A1, T49A2, T49A3, T49A4, **T49B**, T49B1, T49B2	T46, T49
6	8	**T36**, **T36B**, T36B1, T37A1, **T99**, T99A, T99B, T99C	T36, T37
7	2	**T65B**, T65B1	T65
8	15	**T36A**, T36A1, T36A2, T38C, **T65A**, T65A2, T65A3, T65A4, T65A5, **T75**, **T75A**, **T75B**, T75B1, T75B2, **T75C**	T36, T65, T75
9	13	**T137**, T137A, T137B, T137D, **T185**, T185A, T186, *T2B*, **T60**, T60C, T60D, T60E, T60F	T2, T36, T60, T185
10	2	*T49C*, *T77A*	T49, T77
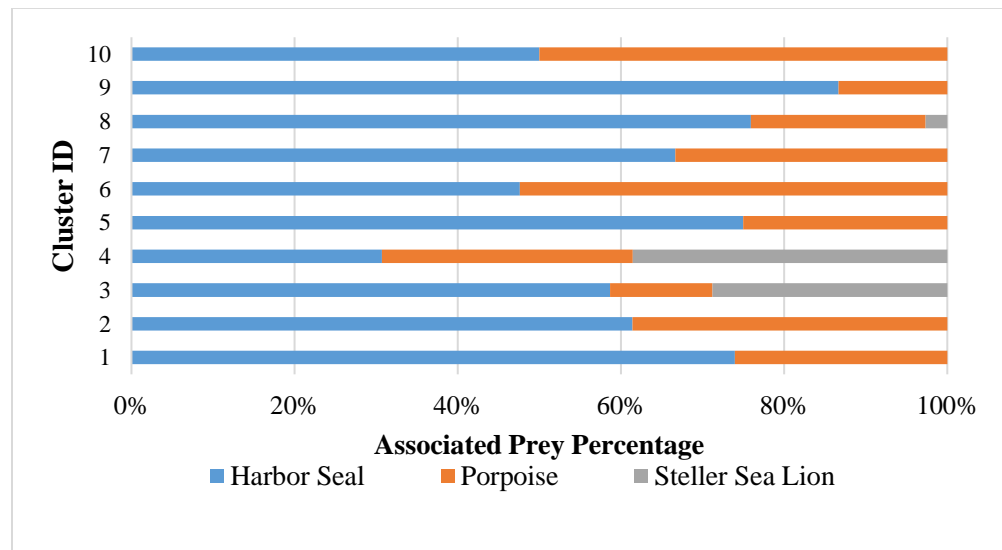
Figure 10. Percentage of prey types associated with individuals within Bigg's killer whale social clusters.

Table 2

Percentages of Prey Types Associated with Bigg's Killer Whale Social Clusters

Percentages and proportions within the second column from the left represent the number of individuals within a social cluster that had predation data.

Cluster ID	Individual Representation in Cluster	% Harbor Seal	% Porpoise	% Steller Sea Lion
		Nearshore Prey	Non-Nearshore Prey	
1	89% (8/9)	74%	26%	0%
2	92% (11/12)	59%	41%	0%
3	100% (6/6)	59%	13%	29%
4	87% (27/31)	31%	31%	39%
5	83% (10/12)	75%	25%	0%
6	88% (7/8)	48%	52%	0%
7	100% (2/2)	67%	33%	0%
8	73% (11/15)	76%	21%	3%
9	77% (10/13)	87%	13%	0%
10	50% (1/2)	50%	50%	0%

Twelve individuals from the T40, T86, T101, and T124 matrilines were considered non-nearshore (NNS) foragers, of which Steller sea lions comprised the majority (41%) of associated prey. Nearshore (NS) foragers were comprised of 33 individuals from the T10, T30, T37, T46, T49, T65, T75, and T100 matrilines, with harbor seals comprising 61% of associated prey. Seven members of the T18 and T124 matrilines were designated as specializing in both foraging strategies (Both). Notably, four members of the T18 matriline (T18, T19, T19B, and T19C) were observed more frequently during predation events than any other individuals, and were not ever observed during porpoise predation events.

Significant differences in foraging class by cluster were found (H=45.24, df=8, p<0.01): six of the ten clusters (Clusters 1, 2, 5, 7, 8, and 9) had a higher proportion of individuals present during harbor seal capture events (nearshore foragers), while Clusters 3, 4 and 6 had significantly more non-nearshore foraging events. Mean HWI values were roughly the same for individuals assigned to all three foraging classes: NS: 0.07 ± 0.02; NNS: 0.08 ± 0.03; and Both: 0.07 ± 0.02 (Table 3). However, associations within respective foraging classes (mean: 0.11 ± 0.10, max: 0.81 ± 0.26) were significantly greater than those between (mean: 0.06 ± 0.03, max: 0.53 ± 0.31), particularly with individuals considered to be Both (two-sided Mantel test, r =0.588, t = 4.049; p =0.001) (Table 3; Figure 11).

Finally, the cumulative bifurcation analysis revealed only one significant point of deflection (or "knot"), with community division occurring at a HWI of 0.91 (Figure 12). This level of association generally reflects associations at the matrilineal level, between females and their offspring, and is greater than that previously reported for this population. Utilizing the Baird data set (1987-1993), Beck and colleagues also indicated

Table 3

Summary of Association Indices Within and Between Foraging Classes

Relationships	Mean HWI	Max HWI
Both	0.07 (0.02)	0.99 (0.01)
NNS	0.08 (0.03)	0.83 (0.18)
NS	0.07 (0.02)	0.94 (0.12)
Both-Both	0.42 (0.08)	0.99 (0.01)
NNS-NNS	0.28 (0.07)	0.81 (0.19)
NS-NS	0.12 (0.05)	0.90 (0.17)
NS-Both[a]	0.03 (0.05)	0.06 (0.08)
NS-NNS[a]	0.04 (0.08)	0.13 (0.18)
NNS-NS[a]	0.04 (0.03)	0.30 (0.22)
NNS-Both[a]	0.19 (0.09)	0.39 (0.24)

Table 3 (Continued)

Both-NNS[a]	0.19 (0.18)	0.42 (0.42)
Both-NS[a]	0.04 (0.01)	0.18 (0.09)
NS-NNS[a]	0.06 (0.03)	0.45 (0.25)
Within	0.11 (0.10)	0.81 (0.26)
Between	0.06 (0.03)	0.53 (0.31)
Overall	0.07 (0.03)	0.87 (0.18)

[a] The duplicate comparisons between foraging classes are a remnant of the calculations and are not considered biologically significant.

Standard deviations are in parentheses.
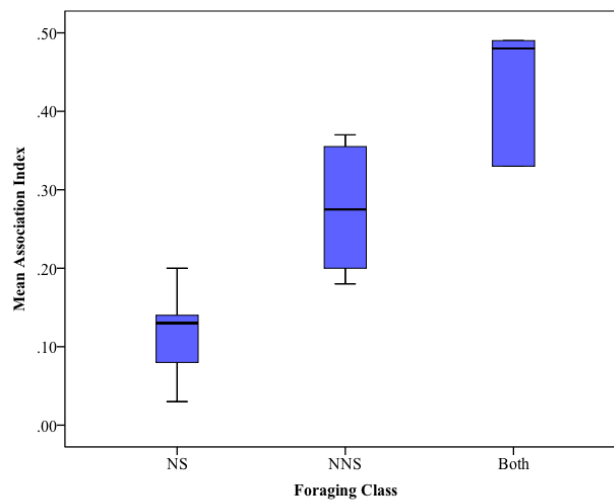
Figure 11. Mean within-class association indices for nearshore (NS), non-nearshore (NNS), and both (Both) foragers.

a lack of social hierarchy within this population, with a bifurcation cutoff of 0.84 (see

Figure 5 in Beck, Kuningas, Esteban, & Foote, 2011). This is somewhat expected, given

population growth and matrilineal recruitment. Indeed, associations were greater within

matrilines than between them (mean: 0.75 ± 0.23 and 0.04 ± 0.02, respectively; two-sided

Mantel test: $t = 31.291$, $p < 0.01$).
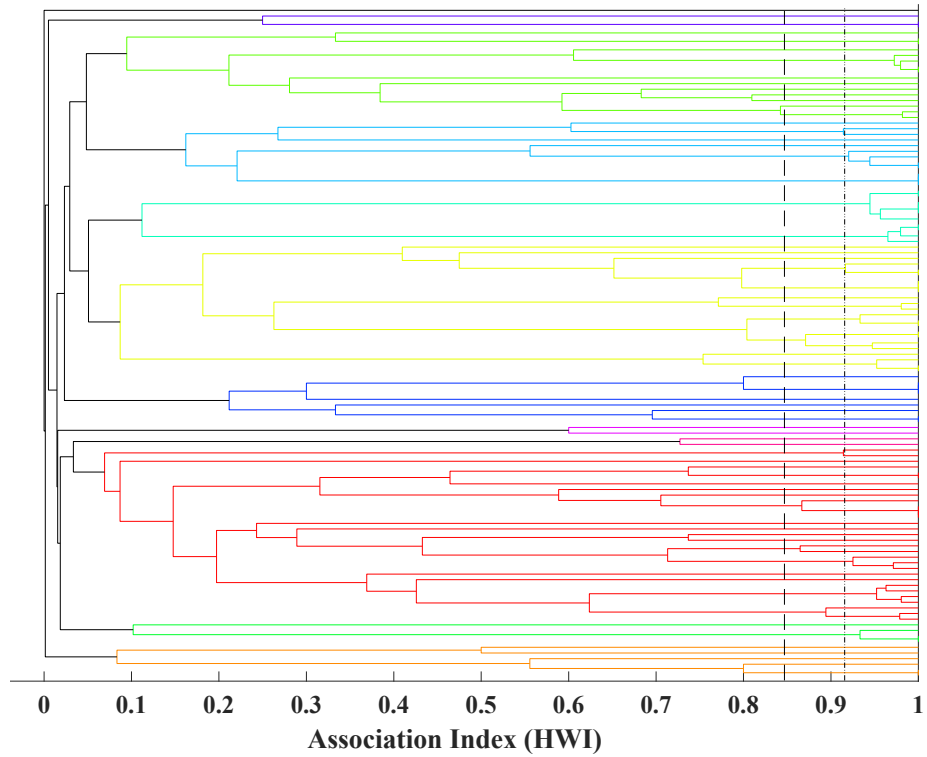
Figure 12. Dendrogram reflecting community social differentiation of Bigg's killer whales.

Average linkage cluster analysis of individuals identified within the transboundary study area that were observed at least five times. Maximum modularity (Q =0.523, HWI=0.071) denoting the ten social clusters are represented in the color variants. The cophenetic correlation coefficient = 0.93202 indicating this is an accurate visual representation of community divisions. The black dashed line reflects the cumulative bifurcations knot cutoff at HWI=0.91, while the grey dashed line represents the cutoff from data derived from 1987-1993 (as cited by Beck, Kuningas, Esteban, & Foote, 2011).

Discussion

The Bigg's killer whale population exhibits clear social division at association levels different from those historically used to delineate social units (e.g., pods) for killer whales within this region. Modularity-based community detection algortihms identified ten social units (clusters) for this population, with high levels of association within, rather than between, clusters –indicating that Bigg's killer whales continue to demonstrate having preferred associations and these associations are, at least in part, driving community division.

The social clusters varied in size and composition, with larger social clusters now (2-31 individuals) than what was previously reported as pods within this community. Whereas Baird and Whitehead (2000) determined that transient (Bigg's) pods in the past were comprised of a single matriline, the current social clustering suggests otherwise with nine of the ten clusters comprised of individuals from more than one matriline. Comparable findings were noted in a mammal-eating population of killer whales found off the sub-Antarctic Marion Island, where only approximately half of the individuals within social clusters were related, thus suggesting clusters are based on permanent or temporary (fission-fusion) dispersal (Reisinger, Beukes, Hoelzel, and de Bruyn, 2017).

Whereas lone males (rovers) were previously reported as never being seen associating together, even temporarily, several of the designated rovers have been observed together in the current dataset. Likewise, one of the clusters (Cluster 10) is solely comprised of a roving male dyad (T49A and T77A), with a significant association (based on permutation tests) index of 0.60. Notably six of the eleven designated roving males were assigned to the same cluster (Cluster 4); however, this cluster is also the

largest and has the lowest within-cluster mean association rate (HWI = 0.26). It is likely these associations are reflecting reproductive opportunity, as ten sexually mature females are also assigned to this cluster. With the exception of Cluster 10, each cluster is comprised of a mature female and at least one of her offspring. However, it is noteworthy that female dispersal is apparent in several of the clusters, with female offspring splitting into unique clusters, whereas male offspring either stay with their mother or fully disperse, evolving into roving males. These sex differences in associations and dispersal patterns will be further explored and discussed in Chapter III.

There does appear to be some level of fission-fusion dynamics occurring among Bigg's killer whales. Observed group size was not analogous to social cluster size, and not all individuals within a cluster were observed at the same time. Furthermore, although within-cluster associations were significantly greater than those between clusters, several cluster members had low HWI values between them. The highest levels of associations were between related individuals within matrilines, consistent with both transient and resident killer whale ecotypes found within the northeastern Pacific Ocean (Bigg et al., 1990; Ford, Ellis, & Balcomb, 2000). While clusters comprising of dyads with such contrasting association values is indicative of a multi-level community structure, the polarizing association values derived from the cumulative bifurcation analysis (HWI = 0.910, denoting matrilines) and the social modularity algorithm (HWI = 0.071) indicates that Bigg's killer whale communities do not resemble other tiered mammalian societies (e.g., primates [geladas], Snyder-Mackler, Bechner, & Bergman, 2012; African elephants, Wittemyer, Douglas-Hamilton, & Getz, 2005; Atlantic killer whales, Beck, Kuningas, Esteban, & Foote, 2011).

The differentiation of nearshore and non-nearshore foragers into separate social clusters suggests that foraging homophily may be driving community division; that is, individuals associated with a particular prey type tend to be associated with each other. In general, the size and stability of killer whale groups found throughout the world are reflective of dietary choice (Hoelzel 1991, 1993, Baird & Dill 1996; Beck, Kuningas, Esteban, & Foote 2011; Reisinger, Beukes, Hoelzel, and de Bruyn, 2017; Ford et al., 1998) and prey abundance (Foster et al. 2012). This is supported by the significant differences in mean proportion of foraging types across social clusters, as well as the higher levels of association within the two foraging classes rather than between. Some clusters, and most individuals, were overwhelmingly considered to be nearshore foragers. This is likely due to the density of harbor seals (nearshore prey) being greater than that of non-nearshore prey species. Recent analyses utilizing passive acoustic monitoring of the outer coast of Washington State supports Bigg's killer whale social differentiation based on prey preference. Different acoustic dialect groups (likely representing unique social groups; e.g., Smith et al., in press; Miller & Bain, 2000) were heard at significantly different rates along the continental shelf as opposed to areas farther offshore. Such spatial and temporal variability of transient social groups very likely follow the distributions of select prey (Rice et al., 2017).

Non-nearshore foragers had higher association values amongst each other (0.28 ± 0.07) than nearshore foragers (0.12 ± 0.05). Given that non-nearshore foraging involves larger, more agile prey and typically requires more individuals, energy and space to ensure a successful prey capture event, the higher association levels within this prey class is indicative of cooperative efforts among preferred associates (e.g., Pitman & Durban,

2012; Baird & Dill, 1996; Ford & Ellis, 2006). The lower association levels within

nearshore foragers was expected, given that harbor seals are so prevalent within the area

and the optimum group size needed for a successful capture event is three individuals

(Baird & Dill, 1995). Those individuals denoted as specializing in both foraging types

had the highest within-group association indices. While this could be an artifact of the

analysis to determine foraging class, it may also be indicative of foraging efficiency and

optimization. That is, individuals that are more versatile in foraging tactics and prey

diversity likely learned these behaviors from a more diverse pool of conspecifics, and are

therefore able to maximize food intake more quickly by being a prey generalist, rather

than a specialist (Giraldeau, 1984).

The increase in group sizes in the current dataset as opposed to past observations

could be attributed to a number of factors. It is possible that Bigg's killer whales can

now afford to be in larger aggregations because there is more prey; individuals can now

spend less time foraging and more time socializing. Historically, Bigg's killer whales

had a behavioral budget of 88.5-94.5% of their time travelling and foraging (Bearzi &

Stanford, 2007; Baird & Dill, 1995). With more prey and more conspecific to facilitate

successful foraging, shifts in behavior budgets would allow for increased opportunities

for socializing. Indeed, the opposite effect is true for Resident killer whales within the

study area, where a severely depleted prey resource (chinook salmon) has led them to

spend less time socializing and more effort (and reduced success) searching for food

(Foster et al., 2012b).

Alternatively, given the increase in Bigg's population size, it is possible that the

optimum group size previously described for foraging killer whales (3 individuals) is no

longer optimum. Smaller marine mammals have learned to distinguish between the

benign presence of fish-eating Resident killer whales as opposed to the mammal-eating

transient ecotype (Deecke, Slater, & Ford, 2002). It is possible that the increased and

widespread presence of Bigg's killer whales has triggered an increased vigilance amongst

prey; therefore, prey capture attempts may now require more individuals and more effort

to maximize caloric intake (Houghton et al., 2015; Giraldeau, 1984). Additionally,

anthropogenic influences could also be a factor. For example, Biggs killer whales are

silent hunters, relying on passive acoustic signaling from prey during capture events. The

sharp increase in ambient noise levels from vessel traffic within the study area (Viers,

Viers, & Wood, 2016) may be masking important acoustic cues from prey and hindering

successful prey capture events. Vessel traffic noise has been shown to disrupt foraging

behavior in a variety of cetacean species (Weilgart, 2007), including Resident killer

whales found in the study area (Lusseau, Bain, Williams, & Smith, 2009).

Individual variation and cooperative behaviors during niche exploitation can

influence conspecific interaction rates that, over time, can lead to population and species

level effects (Bolnick, Svanbäck, Fordyce, Yang, Davis, Hulsey, & Forister, 2002),

which is evident in killer whale populations (Foote et al., 2016). Bigg's killer whales

may be exhibiting social differentiation based on foraging preferences amidst shifting

prey in order to maximize fitness for the entire population. Alternatively, specialists that

emerge from social differentiation are more likely to be adversely impacted by

environmental perturbations, thus creating a fitness cost to the overall population.

It is important to understand the behavioral ecology of individuals in the context

of ecological shifts in order to employ successful resource management schemes. There

is increasing evidence of cetacean social differentiation aligned with human-interaction

behaviors, which compounded with social learning mechanisms, can create negative

impacts for both humans and cetaceans. For example, common bottlenose dolphins off

of Georgia have distinct social clusters of individuals that depredate off commercial fish

trawlers, which also include individuals that exhibit begging behaviors from commercial

and recreational fishers (Kovacs, Perrtree, & Cox, 2017). Learned provisioning

behaviors from human prey sources can lead to increased risk for injury and mortality

(Donaldson, Finn, & Calver, 2010). Similar impacts could be predicted in killer whales,

which are increasingly depredating on commercial long-line vessels (NOAA,

unpublished data), as also observed in the Sea of Gibraltar (Esteban, Verbough,

Gauffier, Giménez, Guinet, & De Stephanis (2016).

This chapter demonstrates that social differentiation in Bigg's killer whales today

is not consistent with prior assessments of this community's social structure, suggesting

that the shifts in abundance and occurrence by this population over the last decade are

reflected in their social behavior. This is supported by the higher association indices for

foraging groups that require greater coordination to maximize, and ensure, prey capture

foraging success. These prey-based differences are likely indicative of cooperative

behavior between individuals. In the following chapter, I will explore the social roles of

individuals within the Bigg's killer whale community using social network analysis,

paying special care to the levels of demographic (age and sex) influence on social

measures. Likewise, Chapter IV will discuss the context and implications of vessel

exposure on the social clusters defined here.

CHAPTER III - EXPLORING THE LONG-TERM TRENDS OF BIGG'S KILLER

WHALE SOCIAL NETWORK DYNAMICS: INDIVIDUAL SOCIALITY AND

DISPERSAL PATTERNS

Introduction

Chapter II discussed the aspects of group identity and definition within an animal

society - namely, Bigg's killer whales. However, the complexity of a community's social

structure is only as strong as it's parts; to understand social structure, one must first

consider the extent of connectedness between individuals within a society (also referred

to as network position, or centrality). Social network analysis can do just this by

quantifying the number, connectivity, and strength of relationships between individuals

(Wasserman & Faust, 1994; Croft et al., 2008; Whitehead, 2008).

There is strong evidence that network position is a predictor of fitness in both

humans and non-humans (Stanton & Mann, 2012; Formica, Wood, Larsen, Butterfield,

Augat, Hougen, & Brodie, 2012; Cameron, Setsass, & Linklater, 2009; McFarland,

Murphy, Lusseau, Henzi, Parker, Pollet, & Barrett, 2017). Behavioral attributes of

network position may be linked to optimum foraging potential. With reference to

Chapter II, individuals more versatile in multiple foraging strategies (e.g., 'Both'

animals) may have learned this skill by having more contact and/or stronger connectivity

(i.e., high betweenness) to other individuals; thus, these individuals may not be

compromised if one of their prey sources becomes depleted. Demographic influences

(age and sex) on association patterns and network position are also important factors. For

example, in matrilineal societies, older females hold leadership positions and are

responsible for finding food sources and promoting antipredator behaviors (McComb,

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Shannon, Durant, Sayialel, Slowtow, Poole, & Moss, 2011; Brent, Franks, Foster, Balcomb, Cant, & Croft, 2015). Additionally, sex differences in mammalian dispersal patterns are posited to incur advantages for both sexes, for example by eliminating reproductive competition in procuring mates or by offsetting energy and fecundity costs (Dobson 1982; Johnson 1986; Pusey 1987). Therefore, network position can be a useful measure in evaluating dispersed individuals and their role within a society.

The application of network analysis in the study of animal social behavior is comparatively recent. However, it provides a unique opportunity to evaluate broad scale social changes within a population when coupled with robust, longitudinal data sets. The sociality of Resident killer whales of the northeastern Pacific has been studied extensively. We know that preferential mating generally occurs between, rather than within, matrilines to avoid inbreeding and that the oldest males have the greatest reproductive success (Ford et al., 2011, Pilot et al., 2010). Furthermore, these older males hold a more central network position with more associates than younger males (Foster, 2012).

While it is true that killer whales are matriarchal across ecotypes (Foote, Morin, Durban, Willerslev, Orlando, & Gilbert, 2011), and older females act as leaders for the community (Parsons et al. 2009; Ivkovich, Filatova, Burdin, Sato, & Hoyt, 2010), other female roles within social networks are not as clear. Juvenile whales, particularly females, within the Northern Resident community were shown to have the highest betweenness (i.e., central connectivity) levels, indicating this demographic holds a more central role to their community than the older matriarchs; although, it was not significant (Williams & Lusseasu, 2006). Comparable findings were concluded for Southern

Residents, where neither older nor younger females had more associates or a significantly different central network position (Foster, 2012).

Very little is known about the social dynamics and roles of individual mammal-eating killer whales (Beck et al., 2011; Reisinger, Beukes, Hoelzel, and de Bruyn, 2017; Baird & Whitehead, 2000). There is only one assessment to date of the sociality and grouping characteristics of individual Bigg's killer whales within the Salish Sea (Baird & Whitehead, 2000). However, this study was largely qualitative and focused on sex differences and stability of dyadic associations and dispersion patterns, and did not involve social network statistics. Given the recent significant shifts in the Bigg's killer whale population, grouping, and occurrence observed in the nearly two decades since this publication (Houghton et al., 2015), there is now a unique opportunity to reevaluate and compare shifts in the sociality of individuals over time.

The objectives of this chapter are threefold: (1) to assess the present sociality of individual Bigg's killer whales, including the influences that sex and age may have on social network position; and (2) examine sex differences in dispersion patterns, by comparing sociality measures within roving males and evaluating the role of birth order on female dispersion. In addition, we will briefly compare current (2006-2015) associations and network measures of individuals to those of the past (1987-1993; see Baird & Whitehead, 2000), including temporal persistence in dyadic relationships. Much of this will involve qualitative comparisons; however, these hypotheses will be tested:

H_{01}: Females and males do not differ in their preferred/avoided associations.

H_{a1}: Females and males differ in their preferred/avoided associations.

H_{02}: Females and males do not differ in their central network positions.

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H$_{a2}$: Females and males differ in their central network positions.

Methodology

Field Surveys

Photo-identification research surveys for Bigg's killer whales were conducted within the transboundary coastal waters bordering Washington State, U.S. and British Columbia, Canada by both Robin Baird and the Center for Whale Research; details on the field methods were outlined in Chapter I. Period 1 is comprised of the Baird surveys spanning 1987-1993, while those surveys conducted by the Center for Whale Research (2006-2015) are denoted as Period 2. Surveys occurred year-round, with a pulse in encounters occurring during the summer months (May-October; see Chapter II).

For the purposes of social network analysis and statistical comparisons of the population between two time periods, data were restricted to individuals observed five or more times within each of the respective time periods. This yielded data on 41 unique individuals from 97 days in Period 1 and 110 individuals over 217 days in Period 2. Unfortunately, the general lack of understanding of Transient population dynamics make it difficult to get an accurate estimate of the population over time. However, the population has grown substantially; roughly180 individuals comprised the WCT (Bigg's) population of killer whales from 1987-1993 (Baird & Whitehead), while the best minimum estimate for the current population is 304 individuals (Allen & Anglis, 2013). Thus, the data from each time period was representative of ~25 and 30% of the population, respectively.

Temporal Shifts in Sociality (Persistence of Associations)

Lagged association rates determine the extent of temporal changes in average dyadic relationships and have become an important component in describing long-term trends in social dynamics (Karczmarski et al. 2005). To investigate the persistence of Bigg's killer whale associations over time, all available data (1987-2015) were pooled and all individuals were used, regardless of the frequency with which an individual was encountered, to avoid positively skewing the rates. Standardized lagged association rates (SLARs) were calculated, which reflect the probability that when individuals *a* and *b* are associated at some point in time, a random associate of *a* after some time lag will be *b* (Whitehead, 1995, Whitehead & Dufault 1998). Plots of all individuals, as well as associations between and within sexes and non-calf individuals, were generated and compared to a standardized null association rate. Finally, exponential decay models were fitted to the pooled data following the quasi-Akaike information criterion (QAIC) for selection of the best fitting model (Whitehead, 2007). Confidence level estimates were determined using the jackknife method (Efron & Stein, 1981).

Demographic Factors in Sociality

An association matrix based on the HWI was generated for each time period using SOCPROG 2.7 (Whitehead 2009; see Chapter II for detailed methods). I then tested for differences in preferred and avoided associations between males and females using permutation tests, which compares and calculates significance of the observed (real) data against a random null model while controlling for autocorrelations within the data. This was achieved by running 1,000 randomizations of the data by flipping individuals

observed within the same sampling period 100 times for each randomization while preserving group size.

Several weighted social network measures were calculated and tested for significance using permutations of real data against that randomized (see above): strength, reach, eigenvector centrality, clustering coefficient, and affinity. Only three network measures held overall significance in any time period: strength, clustering coefficient, and affinity (Whitehead, 2008). Strength is a direct measure of an individual's gregariousness, defined as the sum of the weights of all edges connecting two nodes (individuals), thus reflecting the amount of time individuals spend with one another (Barthélemy, Barrat, Pastor-Satorras, & Vespignani, 2005). The clustering coefficient represents the density of a network, or how well connected associates of individuals are to others (Newman, 2003). Affinity is the average weighted strength of an individual's associates (Barthélemy, Barrat, Pastor-Satorras, & Vespignani, 2005; Whitehead, 2008).

Each of these measures was qualitatively compared between time periods to determine the extent of social network dynamics changes over time. Given the various dispersal trends that occur within Bigg's killer whale societies, differences in centrality between age and sex classes were compared within and between the two time periods. To evaluate age effects in network centrality measures, individual whale ages were calculated based on the central date for each of the two respective time periods (1990 for Period 1, and 2010 in Period 2) and tested against network measures using a Spearman's rank correlation. Finally, various visual representations of the Bigg's killer whale social

network were created using the program Gephi 0.9.1 following the ForceAtlas2 layout algorithm (Jacomy, Venturini, Heymann, & Bastian, 2014).

Sex differences in dispersal patterns

Currently, there are eleven documented adult roving males that frequent the transboundary waters of the study area (see Chapter 1). Following the methods of Baird & Whitehead (2000), I explored the grouping and social characteristics of all adult males (age ≥ 15; see Olesiuk et al., 1995) observed on five or more times during the study to identify if roving males and other adult males have anything in common. Variables examined include: typical group size experienced for each individual, and social network statistics. Finally, additional mention of Cluster membership (from Chapter 1) is briefly discussed to shed qualitative light on possible functions of roving males.

Based on the findings of Chapter II, it appears female siblings will disperse to different social clusters. Thus, female dispersion was examined with attention to birth order of these siblings. A 'mother ratio' was calculated for each individual within a time period, based on the number of times she was observed within a group with her mother. Mean mother ratios were plotted against age to identify a dispersion cutoff value. An initial steep drop off occurred at a mother ratio of 0.8, or age 15, which coincides with the typical age of mean sexual maturity for female killer whales (Olesiuk et al., 1990). Therefore, if an individual had a mother ratio of .8 or lower, it was considered to be dispersed. A Fisher's exact test was used to determine if significance of birth order (first-born vs. non-first born) influenced dispersion patterns.

Results

As indicated in Chapter II, the network analysis revealed that Bigg's killer whales currently have a loosely connected social network of casual acquaintances (clustering coefficient $C = 0.28 \pm 0.10$; Figure 13) where individuals largely associated with other individuals within their matrilines and social cluster. For reference, a clustering coefficient of one indicates that all of individuals' associates are also associates with each other, and zero indicates that none of an individual's associates associate with each other (Newman, 2003).
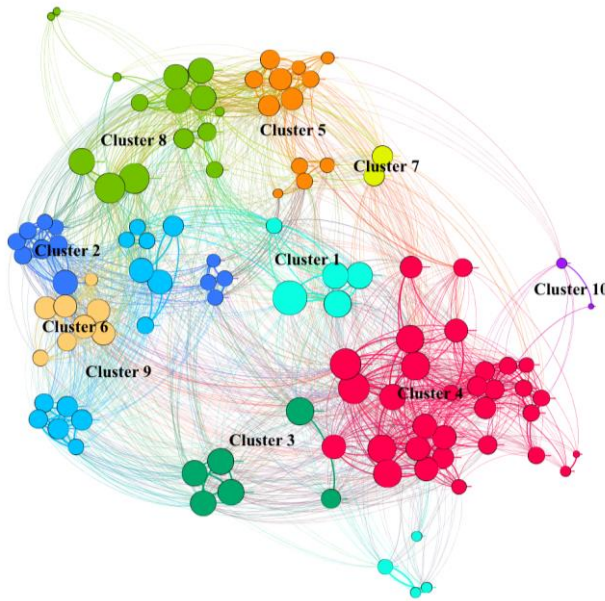
Figure 13. Visual social network representation of Bigg's killer whales.

Colors denote each of the ten social clusters identified, and labeled accordingly. Node size reflects individual strength.
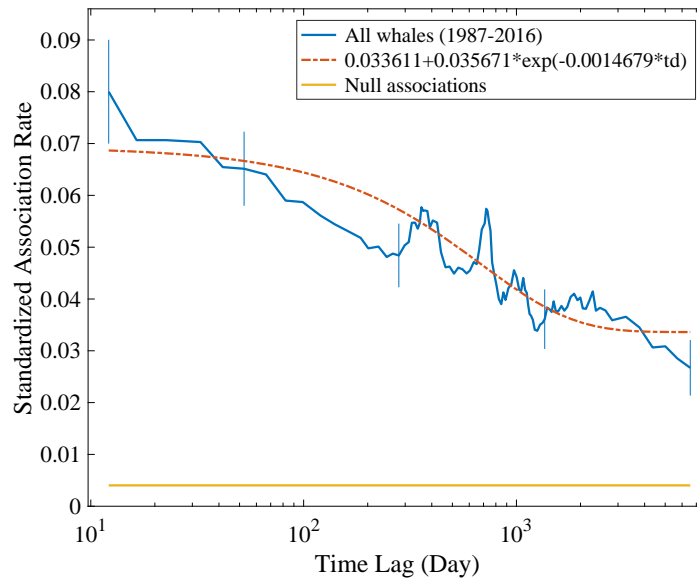
Figure 14. Standardized lagged association rates for Bigg's killer whales (1987-2016)

Includes all individuals of all ages and all sexes, regardless of number of encounters. All associations were above the null (randomized) association rate. The model fit indicates that Bigg's killer whales comprise a society of casual acquaintances, who associate for some time, disassociate, and may associate again in the future (Whitehead, 2008).

Temporal Associations

The pooled data for both periods demonstrate that preferred associations between some individuals can be stable over multiple years (Figure 14). Considering only adult and subadult (ages 10-14) associations, comparisons show that the temporal patterns of standardized lagged association rates (SLARs) between the two time periods did not generally change over time (Figure 15). For both time periods, association rates rapidly decreased between ~800 and ~1000 days, and then more slowly up to ~1400 days; association rates always remained above the calculated null expected to occur randomly.

Multiple models were fitted against the SLARs for adult and subadult associations within each time period; the model type with the lowest quasi-Akaike information criterion (QAIC = 8319.3879 for 1987-1993; QAIC = 18858.4072 for 2006-2015) and

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the best fit (Whitehead, 2007) was: a3 * exp(a1 * td) + (1 a3) * exp(a2 * td); where, a1

is the damping factor; a2 is the relative seasonal change between the mean seasonal

value, and maximal seasonal value; a3 is the cyclic period in days; a4 is the inverse of the

typical group size; and, td is the time lag (see Smith, Frere, Kobryn, & Bejder, 2016).

The SLAR model fit indicates that for both time periods there are two levels of

associations, with fission-fusion movements of fixed social units (matrilines) into/out of

groups (social clusters) in the short term, and near permanent transfers between units

(dispersal) in the long-term (Whitehead, 2008); thus, consistent with findings in Chapter

II.

The temporal stability of associations between and within males and females

varied, with the expected rates of random associations between all individuals being low

and relatively constant (Figure 16). Eliminating temporal biases between mothers and

dependent and young offspring, I focused on relationships between adults and subadults.

Lagged association rates between males and females (M-F) had moderate values

compared to those observed within the two gender classes. Female-female (F-F)

relationships had the lowest association rates of any of the gender class comparisons,

though the rates had a more gradual decrease over time and were the most stable over

time. Lagged rates for male–male (M-M) associations had the sharpest decline over time

compared to other gender combinations; however, male-male associations were also

higher and more persistent than those found with females.
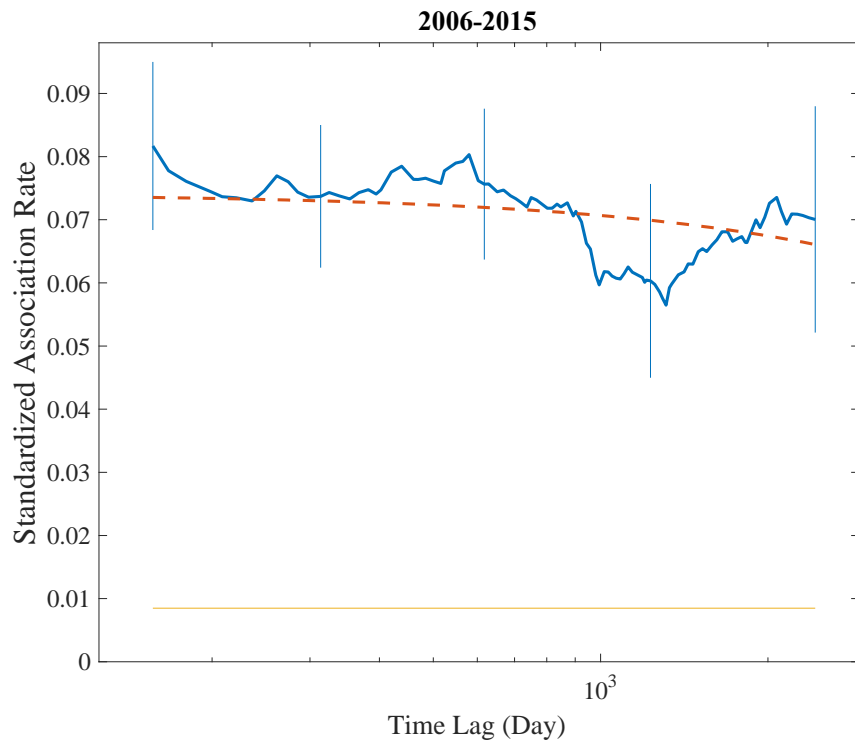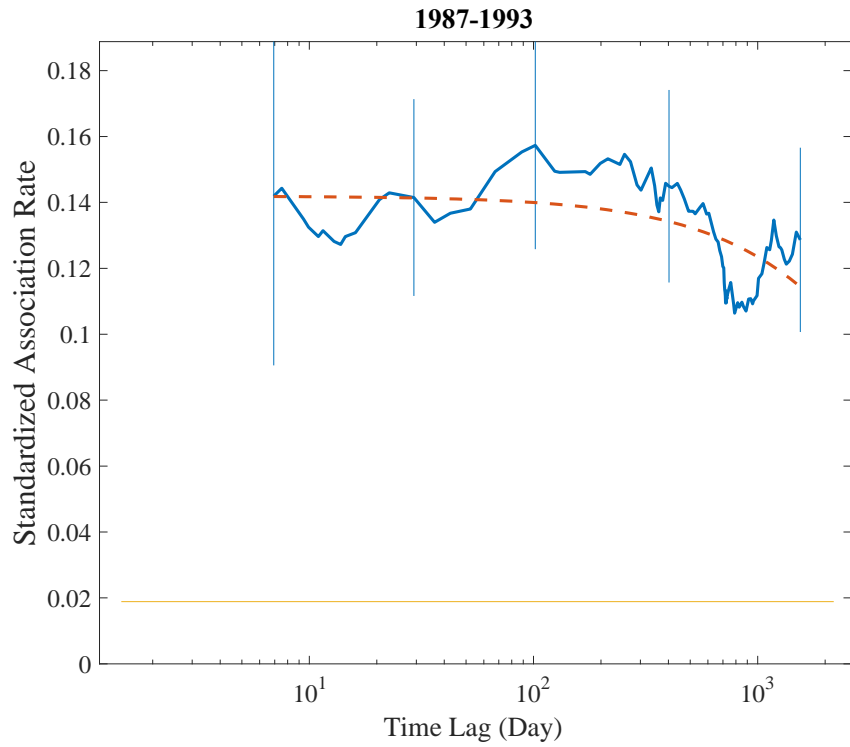
Figure 15. Standardized association rates of individuals of adults and subadults (ten years of age or older) between the two study periods.
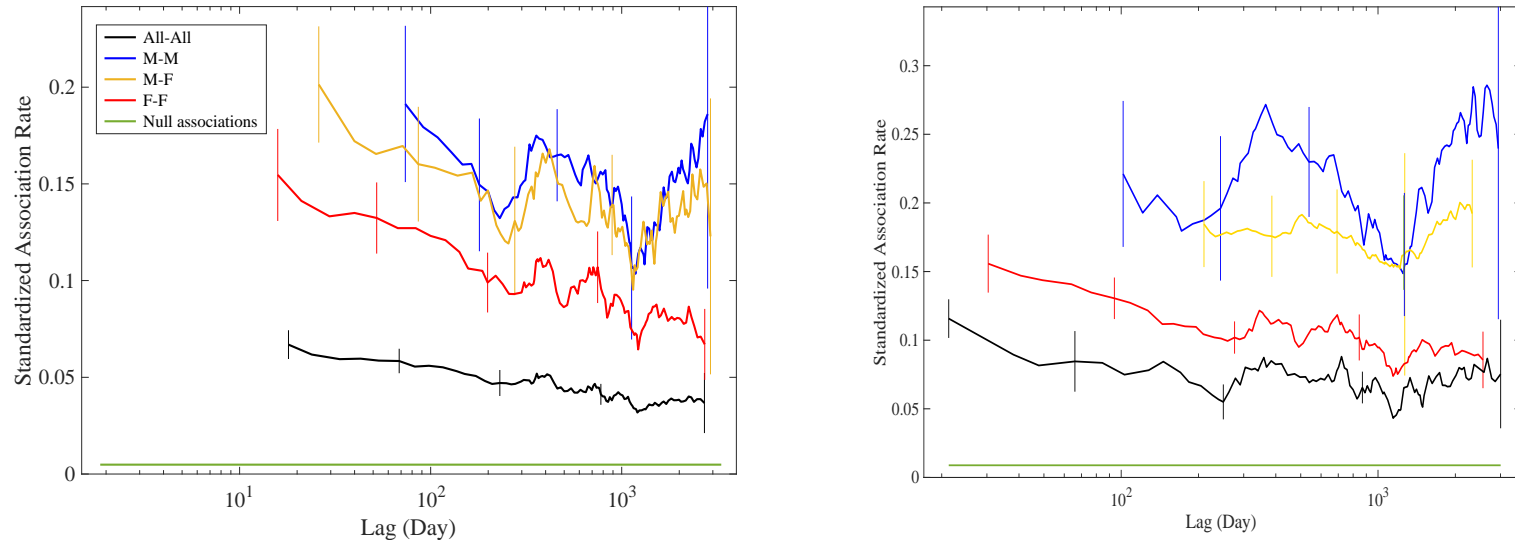
Figure 16. Standardized lagged association rates between all individuals of all ages (2006-2015).

Plots showing standardized lagged association rates (SLAR) for gender class associations within the Bigg's killer whale population. On the left, SLARs for all individuals of all ages. On the right, SLARs for adults and subadults only. Note that while male-male associations show a steeper decline over time, they generally have higher and more persistent associations than the other gender combinations.

Demographic Factors in Sociality

Bigg's killer whales have no preferred associations for individuals based on sex, with no significant differences in preferred associations between or within adult males and females (age $\geq$ 15) in either time period (Period 1: two-sided Mantel test: $t = -1.116$, $p = 0.2220$, $r = -0.082$; Period 2: two-sided Mantel test, $t = 0.165$, $p = 0.7880$; $r = 0.005$). However, the extent of these relationships changed between 1987 and 2015. Mean associations within and between sex classes decreased over time, with the exception of male-male (M-M) associations, which slightly increased in Period 2 (Table 4). However, focusing on the current dataset (Period 2), M-M associations are lower than F-F associations, with mean HWI values for pairs of males (0.05 ± 0.03) being slightly lower than the mean HWI for pairs of females (0.06 ± 0.03), and those of mixed pairs (0.06 ± 0.03). Mean HWI values both between (mean: 0.05 ± 0.04, max: 0.51 ± 0.36) and within (mean: 0.05 ± 0.03; max: 0.50 ± 0.35) the two sex classes were roughly the same.

Table 4 *Summary of Association Indices Between and Within Sex Classes.*

Relationships between	Mean HWI	Max HWI	Mean HWI	Max HWI
	Period 1 (1987-1993)		Period 2 (2006-2015)	
F-F	0.10 (0.06)	0.43 (0.28)	0.05 (0.03)	0.60 (0.32)
F-M[*]	0.12 (0.07)	0.61 (0.37)	0.05 (0.03)	0.45 (0.35)
M-F[*]	0.12 (0.08)	0.78 (0.36)	0.06 (0.03)	0.63 (0.36)
M-M	0.04 (0.03)	0.17 (0.15)	0.05 (0.04)	0.29 (0.32)
Within	0.08 (0.06)	0.34 (0.27)	0.05 (0.03)	0.50 (0.35)
Between	0.12 (0.07)	0.67 (0.36)	0.05 (0.04)	0.51 (0.36)
Overall	0.10 (0.05)	0.70 (0.33)	0.05 (0.03)	0.72 (0.28)

[*] The duplicate comparisons between foraging classes are a remnant of the calculations and are not considered biologically significant.

Table 5 *Mean Social Network Measures for Bigg's Killer Whales Over Time (1987-2015)*

	Strength (Degree)			Eigenvector Centrality			Reach			Clustering Coefficient			Affinity		
	Period 1	Period 2	△	Period 1	Period 2	△	Period 1	Period 2	△	Period 1	Period 2	△	Period 1	Period 2	△
Overall	3.93 (1.53) SE = 0.29 *p* >0.999	6.83 (3.14) SE = 0.38 ***p* =0.00**	↑	0.13 (0.08) SE = 0.01 *p* =0.97	0.07 (0.05) SE = 0.01 *p* >0.999	↓	17.76 (8.73) SE = 2.92 *p* >0.999	56.41 (32.12) SE = 6.78 *p* >0.999	↑	0.38 (0.20) SE = 0.02 ***p* =0.00**	0.28 (0.10) SE = 0.02 *p* =0.80	↓	4.22 (1.13) SE = 0.33 ***p* =0.07**	7.62 (1.85) SE = 0.45 *p* >0.999	↑
Classes															
M-All	3.67 (1.65) SE = 0.26	6.17 (3.31) SE = 0.37	↑	0.13 (0.09) SE = 0.01	0.07 (0.06) SE = 0.01	↓	16.46 (9.66) SE = 2.62	49.08 (33.17) SE = 6.11	↑	0.40 (0.21) SE = 0.02	0.24 (0.10) SE = 0.02	↓	3.99 (1.46) SE = 0.30	7.15 (1.92) SE = 0.45	↑
F-All	4.19 (1.48) SE = 0.34	7.33 (3.39) SE = 0.41	↑	0.14 (0.08) SE = 0.01	0.08 (0.06) SE = 0.01	↓	18.92 (8.45) SE = 3.30	60.90 (35.47) SE = 7.51	↑	0.38 (0.21) SE = 0.02	0.29 (0.12) SE = 0.3	↓	4.31 (0.90) SE =0.35	7.53 (2.11) SE = 0.46	↑
M-M	0.91 (0.63)	1.77 (1.20)	↑	0.17 (0.20)	0.11 (0.13)	↓	1.20 (1.09)	4.53 (4.13)	↑	0.19 (0.12)	0.15 (0.09)	↓	1.13 (0.38)	2.31 (0.61)	↑
M-F	2.60 (1.30)	3.01 (1.69)		-	-		-	-		-	-		-	-	
F-M	1.63 (0.65)	2.28 (1.22)		-	-		-	-		-	-		-	-	
F-F	2.43 (0.98)	2.92 (1.62)	↑	0.17 (0.12)	0.11 (0.09)	↓	6.85 (3.47)	11.06 (8.00)	↑	0.29 (0.09)	0.25 (0.16)	↓	2.67 (0.60)	3.38 (1.05)	↑

Values calculated on Half-Weight association indices for individuals seen on 5 or more days during each respective time period. Overall significance of social network measures within each time period were calculated using permutation tests; values in bold denote significance. The shifts in values between the two time periods are represented by the up and down arrows within the delta columns. Standard deviations are in parentheses, with standard errors of the means below. Period 1: 1987-1993, Period 2: 2006-2015.

Social network measure shifts are evident between the two time periods (Table 5). Eigenvector centrality and clustering coefficient decreased over time, while strength, reach, and affinity increased. However, only clustering coefficient and affinity were significant in Period 1, while only strength was significant in Period 2. Bigg's killer whales had a more densely connected social network in the past, but as the population has increased, individuals now have significantly more associates but associate with fewer members of the population; thus supporting the findings of social differentiation as described in Chapter II. Strength and clustering coefficient were significantly, but negatively correlated ($r =$-0.0271, $p < 0.001$). Focusing on the present population (2006-2015), females have more and stronger associates within the community than males (Figure 15). Weighted strength between males and females is significantly different, with higher values for females (7.33 ± 3.39) than males (6.17 ± 3.31). Significant differences in the relationships between strength and age are also apparent between males and females.
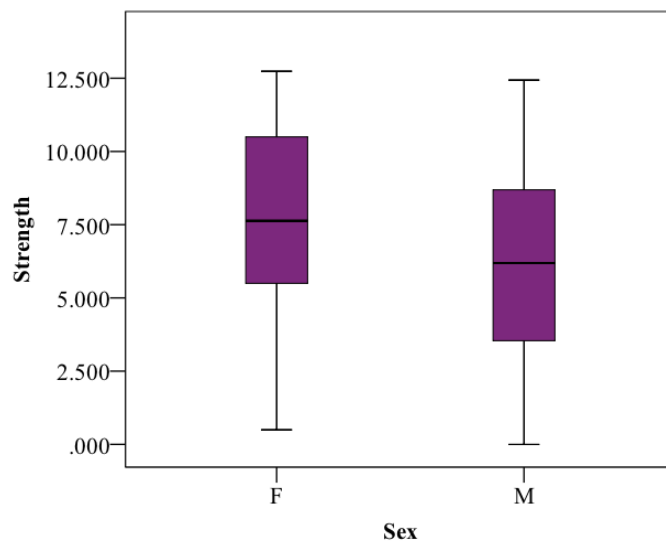
Figure 17. Differences in strength values among male and female Bigg's killer whales.

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There are no differences in the central position of the social network for females across all ages, with negative, non-significant correlations between female strength and age (r_S= -0.223, p=0.132; Figure 17). Alternatively, males exhibit slight differences in sociality measures, with a negative, significant relationship between strength and age (r_S=-0.506, p=0.002; Figure 18) indicating that overall, as males age, they have fewer and weaker associations with other individuals. However, given the long-term temporal stability of some male-male relationships (Figure 16), these results most likely reflect the sociality of roving males (Baird & Whitehead, 2000).
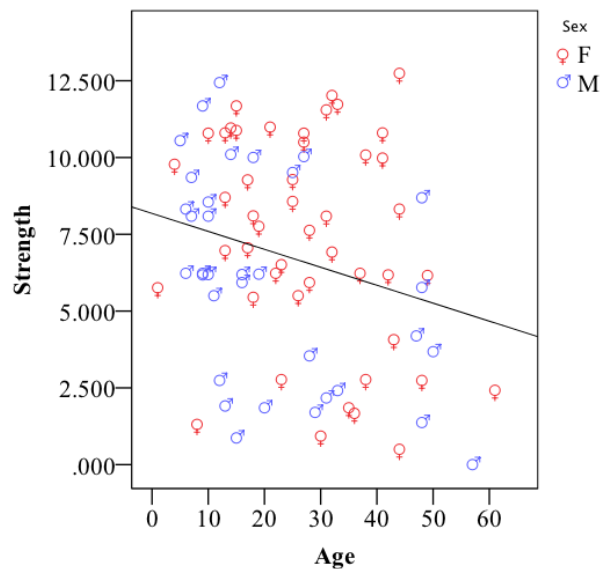
Figure 18. The relationship between age and strength for Bigg's killer whales.

Sex differences in dispersal patterns

Localized social network measures of roving males seen five or more times in Period 2 are summarized in Table 6, focusing on the statistic network measures identified above. Five of the eight males were also documented (five or more times) in Period 1, enabling for comparisons over time. Shifts in social network measures have clear

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patterns over time: typical group size, strength and affinity increased for all five roving

males seen in both periods. Clustering coefficient decreased over time for roving males,

excepting for T93 and T97, which were considered isolates (connected to only one other

individual – each other) in Period 1 but were more connected to conspecifics in Period 2.

Given the persistence, and higher than expected association values, for male-male

associations determined by the SLAR in Period 2, I used permutation tests (1,000

randomizations and 100 trials) to further identify significant dyads among roving males;

three were identified: T93-T87 (HWI = 0.12, p =0.9876), T97-T87 (HWI = 0.22, p

=0.9862), and T93-T97 (HWI = 0.73, p =0.9902).

Finally, differences between first born and non-first born siblings was not a

significant factor in the dispersion patterns of female siblings (p =0.148), indicating other

factors may be driving female dispersion to other social clusters.

Table 6 *Grouping characteristics of adult roving males (2006-2015)*

Whale ID	Birth Year	Typical Group Size		Strength		Clustering Coefficient		Affinity	
		Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
T14	1964	3.98	5.19	2.91	4.19	0.19	0.16	4.01	7.8
T40	1961	4.58	4.68	3.58	3.68	0.58	0.25	4.95	2.68
T49C	1998	-	2.91	-	1.91	-	0.15	-	4.74
T77A	1996	-	1.87	-	0.87	-	0.00	-	3.38
T87	1963	3.85	9.69	2.84	8.69	0.46	0.23	3.42	6.41
T93	1963	2.00	2.37	1.00	1.37	und	0.14	1.00	1.38
T97	1980	2.00	3.17	1.00	2.17	und	0.19	1.00	1.95
T124C	1992	-	7.20	-	6.19	-	0.24	-	7.3

Note: Local clustering coefficients for T93 and T97 in period is undefined (und) because they are isolates within the network and only

connected to one other individual (each other).

Discussion

The social dynamics of Bigg's killer whales within the Salish Sea has notably

changed over the last three decades. From 1987-2016 the overall measures of association

were halved, with half-weight association indices of 0.10 ± 0.05 in Period 1 (1987-1993) and 0.05 ± 0.03 in Period 2 (2006-2015). Additionally, both strength and affinity of these associations increased over time. This coupled with the lower overall mean HWI suggests that individuals share more associates now than in the past, but that these conspecifics are not highly associated with any others within the community. However, the overall clustering coefficient decreased over time, indicating that individuals within the community in the past were more significantly connected to other individuals than they are now. However, the significance of these changes warrants further testing.

The results presented here, with a lower clustering coefficient over time corresponding with a growing population and supposed abundant prey, suggest somewhat contrary results to comparative studies. As evidenced by the social differentiation and matrilineal differences in association indices, along with the changes in social network measures, there appears to be some level of fission-fusion dynamics occurring among matrilines within social clusters (Chapter II) which is consistent with other cetacean populations relative to prey abundance – though, with varying effects. For example, Indo-Pacific bottlenose dolphins, *Tursiops aduncus,* in Moreton Bay, Australia became less socially differentiated, forging stronger associations through their population following a reduction in trawler fisheries (Ansmann, Parra, Chilvers, & Lanyon, 2012). Likewise, Resident killer whales fragment into smaller, less clustered groups in years when their preferred prey, chinook salmon, is lacking (Foster et al., 2012b). Similar social-resource dynamics have been observed in primates (e.g., baboons). When food was abundant, the strong, preferred associations forged during periods of limited resources disappeared and were replaced by casual acquaintanceships representative of

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the increase in overall individual gregariousness (Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009).

Despite observed shifts in association and network measures over time, the overall temporal stability of associations were relatively unchanged between the two time periods, with generally stable SLARs for all individuals. Plots of lagged association rates for both transient killer whales of all ages (Fig. 3) and just for adults and subadults (Fig. 4) show that associations between individuals are quite stable over time. However, there are clear differences in adult association patterns and longevity of associations between males and females over the two time periods. In the current dataset (2006-2015), female-female relationships held the lowest, but most persistently stable association values over time. This sharply contrasts with associations in the past, where it was male-male relationships that had the lowest associations and rates over time, with relationship persistence declining to random null levels after two to three years (Baird & Whitehead, 2000). Currently, relationships between males have the highest levels of association with some level of decline as previously described, but also evidence for the most long-lasting relationships. These within-gender association trends generally reflect differences in dispersion pattern differences between sexes.

Previous studies opined that female offspring disperse from their natal group at some point close to the time when they become sexually mature (Baird & Whitehead, 2000). However, the results in the current study suggest this is not the case, with no significant differences in the co-occurrence of sexually mature females and their mothers, regardless of sibling birth order, within the same group during an encounter. Female siblings do have significant dissociations, which resulted in their assignment to different

social clusters, while others continue to have high associations with their mothers and reside within the same cluster (see Chapter II). For example, matriarch T37 and her two adult daughters (T37A and T37B) co-occur in Cluster 2, whereas T36 and her daughter T36B co-occur in Cluster 5, but two other daughters (T36A and T137) had low levels of associations with their mother that warranted social differentiation to separate, respective clusters. There was a previous account of a single case of a female dispersing from it's maternal pod around the age 12, which generally coincided with the birth of a third sibling into the matriline. This female eventually rejoined the matriline after the death of one sibling, but it is noteworthy that she also did not successfully produce offspring herself thus indicating that reproductive success, rather than age, is driving female dispersal (Baird & Whitehead, 2000).

The most prominent shift in temporal stability of associations was that of male-male relationships, which is likely a function of philopatry. In terms of position within the society, Bigg's males either remain closely associated with their mother their entire lives or disperse (Baird & Dill, 1996). However, the inferred abundance in prey, population growth, and larger group sizes (Houghton et al., 2015) suggests there is less pressure for dispersion. The SLARs for Period 2 likely largely reflect persistent associations between undispersed male siblings within their matriline. Indeed, every social cluster identified in Chapter II held a known or likely (e.g., Cluster 6) adult and/or subadult male offspring of a matriarch with several significant, preferred associations between sibling dyads (not reported). However, there was also evidence of persistent, strong associations between adult, roving males, which was not previously documented;

Baird and Whitehead (2000) reported that that adult, dispersed males rarely associated with each other.

The pooled dataset from 1987-2015 reflects 8 of the 11 known roving males within the population; 5 of the males were observed in both time periods (Table 6). Of those individuals seen in both time periods, three (T87, T93, and T97) were part of significant dyads: T93-T87 (HWI = 0.12), T97-T87 (HWI = 0.22), and T93-T97 (HWI = 0.73). The genetic relationship of these individuals is currently unknown, but it is probable that T93 and T97 are close kin (Center for Whale Research, unpublished data; David Ellifrit, personal communication), which may explain the high association index relative to the other dyads. Interestingly, the roving male dyad T49A and T77A had a relatively high association index (HWI = 0.60) and were solely differentiated to Cluster 10, but this was not considered significant and likely an artifact of the moderate correlation coefficient (indicating that calculated association indices are only generally representative of the dataset). The high HWI value between these two may also be a function of age, however, as they both became physically mature toward the end of Period 2.

Strengthened bonds between older males are evident in several cetacean species. For example, strong bonds between lone, dispersed male sperm whales (*Physeter macrocephalus*) are now being observed in higher latitudes, and are thought to be linked to cooperative foraging while depredating on long-line fisheries (Straley et al., 2015). In bottlenose dolphin fission-fusion societies, males will form long-term alliances, of dyads and trios that can be stable over decades, that aid in mating and reproductive success (Connor, Heithaus, & Barre, 2001; Wiszniewski, Brown, & Möller, 2012).

Age and sex differences in social network metrics may help inform dispersion patterns. In general, the grouping characteristics and network measures of adult roving males are consistent with the overall trends of the community. Typical group size, strength, and affinity values generally increased for roving males between the two time periods, while clustering coefficient decreased – a consistent trend for individuals to continue to have preferred associations within a growing population. Roving male social network measures are largely lower than the overall means for the entire population. This was expected, as these individuals were rarely, if ever, observed with conspecifics. However, the older roving males hold a more central position in the current network, being connected to more individuals than the younger whales. For example, in Period 2, T87 has higher strength values than the overall mean (9.69), while T14 had a higher affinity than the overall mean (7.80). This could be a function of age, with more time to develop relationships. Alternatively, the older males may be serving as breeding brokers between social clusters within the community (Sih, Hanser, & McHugh, 2009; Lusseau & Newman, 2004). In Resident killer whales, the oldest males within the community had the greatest reproductive success, fathering nearly all of the offspring (Ford et al., 2011). It is unknown if Bigg's killer whales follow this paradigm, however genetic testing is currently planned.

The social dispersal of individuals to new clusters indicates mating likely occurs between social clusters as a means to prevent inbreeding (Reisinger, Beukes, Hoelzel, and de Bruyn, 2017; Clutton-Brock, 1989). Breeding in Resident killer whales occurs between lesser-related social units, typically between pods and then matrilines. A notable case study of a newly dispersed individual is T37A1, an 8 year old individual of unknown

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sex that has dispersed from it's natal matriline (T37; Cluster 2) and no longer travels with them, typically traveling with the T36 matrilines in Cluster 6. If a male, it is unlikely he would contribute to the genetic pool, while if female, she would be approaching sexual maturity. As suggested for males, the dispersal of females between clusters as an indicator of breeding may also be reflected in social network measures. Focusing on the present population (2006-2015), females had significantly higher weighted strength values than males (7.33 ± 3.39 and 6.17 ± 3.31, respectively), thus indicating that females have more and/or stronger associates within the community than males (Figure 15). While this is somewhat expected for a matriarchal species, with high values reflecting the relationships between females and their offspring, it may also be representative of new associates gained when dispersing to a new social cluster. Indeed, this latter point is supported by the negative, non-significant correlation between Bigg's female strength and age. Alternatively, strength and age were significantly, but negatively, correlated in males indicating that as males age they have fewer associates and/or associations with other individuals. However, given the long-term temporal stability of some male-male relationships, these results most likely reflect the sociality of roving males (Baird & Whitehead, 2000).

The findings discussed in this chapter demonstrate the Bigg's killer whale social dynamics have changed over time, which in turn influenced the behavior and network position of individuals. Individuals in the past were more connected to the entirety of the community than they are now, which has incurred stronger, localized affiliations within socially differentiated clusters which are, in part, created by dispersion. However, the significance of these differences warrants future testing. There is diverse social

heterogeneity of individual positions within the current Bigg's killer whale network, with various levels of demographic (age and sex) influence on sociality measures, which apparently contribute to dispersion patterns. These individual differences are important factors to consider when evaluating external impact factors and subsequent ecological shifts; some individuals and social units may receive differing levels of adverse exposure based on local sociality measure and, in turn, may respond differently than others. This may affect individual, and population level, fitness. This leads to difficult questions for scientists and resource managers: how does individual sociality fit in the context of impact assessments and conservation decision-making? I further explore this topic in the next chapter, within the context of a highly lucrative and rapidly expanding international whale watching industry.

CHAPTER IV – THE RELATIONSHIP BETWEEN VESSEL TRAFFIC AND

SOCIALITY IN BIGG'S KILLER WHALES WITHIN A TRANSBOUNDARY

MANAGEMENT AREA

Introduction

Evaluating the patterns of associations between individuals presents a key opportunity to investigate the relationship between animal social organization and extrinsic (ecological or anthropogenic) factors. Over the last two decades, numerous studies have examined the nature and extent of whale watching activities on marine mammals. As the industry continues to grow, concerns have mounted over it's sustainability and the animals they are targeting (Higham & Lusseau, 2007). It is well documented that whale watching activities can have adverse impacts on cetaceans (Parsons, 2012; Christiansen & Lusseau, 2014; New et al., 2015): behavioral disruptions (Lusseau & Bejder, 2007), spatial displacement or habitat shifts (Bejder et al., 2006), communication loss (masking) (Holt et al. 2013; Jensen, Bejder, Wahlberg, Soto, Johnson, & Madsen, 2009), decrease in fitness or fecundity (Weinrich & Corbelli, 2009; or direct injury and mortality (Carrillo & Ritter, 2010; Jensen, Silber, & Calambokidis, 2004). However, while there is extensive evidence related to the extrinsic factors driving impacts, the intrinsic factors of whale-vessel interactions are less understood. For example, passengers of whale watching vessels are more satisfied during trips when they encounter large numbers of whales or those that are engaged in active behaviors (e.g., socializing) (e.g., Andersen & Miller, 2006). Therefore, it seems practical that the more gregarious an individual is, the more exposure to whale watching activities it would receive. Given what we know of the importance of group size as it relates to foraging

success in Bigg's killer whales, it is key to determine the extent of vessel traffic individuals and groups receive.

Within the Salish Sea region, organized, binational commercial whale watching has steadily increased since the 1970's. While whale watching activities occur year round, the peak season for whale occurrence and tourism is during the summer season (roughly May through October). The total active fleet peaked in 1997 with 78 commercial vessels originating from ports in both the U.S. & Canada, and was stable over the next several year until it hit an all-time high with 98 active vessels in 2016 (Seely, 2015). There are general differences between Canadian and U.S. fleets: Canadian vessels are mostly smaller, rigid hull inflatable (RHIB) style vessels, with high powered – and sometimes multiple – engines, while the U.S. fleet is comprised of larger passenger- style vessels and a growing number of smaller 6 - 8 person fiberglass vessels.

While this particular international fleet originated and is largely centered on the well-known, iconic Southern Resident killer whales, in recent years, the overall rate of Resident killer whales sightings has been low due to prey (chinook salmon) shortages in this area. Additionally, when Residents are in the area, they occur in smaller, more spread out formations than in previous years, reflecting prey scarcity. In the absence of Resident killer whales, the whale watching fleet is now capitalizing on the increasing numbers of Bigg's killer whales as a surrogate focus of whale watching activities; though the extent of the whale watching activities targeting this ecotype in this region is poorly understood.

The objectives of this chapter are threefold: (1) to determine how many (and what kinds of) vessels are interacting with Bigg's killer whales; (2) to identify the extent of

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vessel traffic (i.e., the typical (median) number of boats accompanying a group of whales at any given point in the day) experienced by individual whales, social clusters, and foraging classes; and (3) determine if sociality is a factor in predicting vessel traffic levels targeting individual whales. Specific hypotheses of this study that will be tested are:

H_{01}: There are no differences in vessel traffic levels between social clusters and foraging class.

H_{a1}: There are differences in vessel traffic levels between social clusters and foraging class.

H_{02}: There is no relationship between vessel traffic levels and extrinsic (observed) group size.

H_{a2}: There is a relationship between vessel traffic levels and extrinsic (observed) group size.

H_{03}: Sociality is not a factor contributing to vessel traffic levels targeting individuals.

H_{a3}: Sociality is a factor contributing to vessel traffic levels targeting individuals.

Given passenger expectations during whale watching activities and industry needs to have satisfied customers, I predict that the individuals with the higher values of sociality (e.g., those that are more gregarious) will have higher vessel traffic levels. In turn, I expect nearshore foragers to have lower vessel traffic levels than non-nearshore foragers because they occur in smaller observed groups.

Methodology

Field Surveys

In 2011, National Oceanic Atmospheric Administration (NOAA) Fisheries implemented new vessel approach regulations around all killer whales, regardless of ecotype, within inland waters of Washington State (NMFS, 2011). This includes two prohibitions: not approaching killer whales within 200 yards and not positioning a vessel within 400 yards of the path of killer whales. This study utilizes a subset of the CWR photo-identification dataset; specifically, the summer months (May-October) from 2011-2015 (see Chapter I). Bigg's killer whales (n=164) were encountered by CWR 160 times spanning 84 distinct days, of which 105 unique individuals were encountered five or more times.

Data from vessel surveys conducted by the Soundwatch Boater Education Program (Seely, 2015; Seely et al., *submitted;*NMFS permit no. 16160) were used to quantify vessel traffic. Unlike other whale researchers in the area, Soundwatch aims to reduce vessel disturbance to killer whales and other marine wildlife by educating boaters of regional guidelines and regulations as well as to provide systematic monitoring of vessel activities around all cetaceans; that is, the Soundwatch research vessel targets boaters engaged in whale watching, rather than the whales directly. Soundwatch researchers utilized the same sightings network as described in Chapter I to determine when whales were in the area. Once the Soundwatch vessel was on a focal group of whales, counts of all vessels within one half-mile (880 yards; 'A' count) of whales are collected every half-hour. Range finding tools (e.g., laser range finders, electronic radar, chart plotters, and high-power binoculars) were used to gauge distances; in all cases, on-

water vessel counts are derived from most conservative estimates when determining distances.

Calculating Vessel Traffic

Five specific categories of vessels are exempt from Federal approach vessel regulations based on the likelihood of such vessels having impacts on the whales and the potential adverse effects involved in regulating certain vessels or activities, and were not included in median vessel counts (NMFS, 2011; 76 FR 20870): (1) government vessels, (2) cargo vessels transiting in the shipping lanes, (3) permitted research vessels, (4) fishing vessels actively engaged in fishing, and (5) vessels limited in their ability to maneuver safely (e.g., towed vessels, commercial cruise ships). The remaining categories which were included in counts targeting whales were: commercial whale watching vessels, private vessels (both sail- and motor-powered), and miscellaneous vessels that were oriented toward whales and not listed in the above categories. For example, if a private charter fishing vessel was whale oriented and not fishing, it was counted as a private vessel. Non-permitted research vessels (e.g., citizen science efforts) that were whale oriented were included in the private vessel count. Although the Soundwatch vessel was permitted from 2012 onward, it was included in the private vessel totals to account for observer presence.

Vessel data were not normally distributed, thus a median vessel count was calculated for each day as being the best representation of the typical amount of vessel traffic accompanying a group of whales throughout the day. Because Soundwatch and CWR were not always on the water on the same day, I derived vessel count data from Soundwatch surveys from the closest survey within 3 days (before and after) of the CWR

encounter. A custom loop code programmed in R was used to sum the median daily

vessel counts to each individual whale encountered by CWR; these counts were then

corrected for the number of days for which Soundwatch counts were made of an

individual whale, yielding a mean vessel traffic value comprised of the number of vessels

typically focused on an individual.

Sociality Network Measures

The same centrality measures described in Chapter III – strength, eigenvector

centrality, reach, clustering coefficient, and affinity – were calculated for each individual

in SOCPROG 2.7 (Whitehead, 2009) and tested for significance using permutation tests

of 1,000 randomizations and 100 trials per randomization, while controlling for group

size within a sampling period (day). The mean HWI for each individual was also

calculated to provide a local measure of the mean strength of associations for individuals.

In addition to observed group size, the typical group size (Jarman, 1974) was calculated

to evaluate grouping behavior from an intrinsic point of view for individual whales.

Statistical Analyses

A Kruskal-Wallis test was used to test the hypothesis of whether particular social

clusters and foraging class have a higher vessel traffic level than others; post-hoc tests

were used to determine further significance. A Spearman's rank correlation test was used

to determine the relationship between mean vessel count and observed group size. Due

to the lack of independence in nodal network measures used to describe individual

sociality on a local scale, I first reduced the aforementioned variables using a principal

components analysis (PCA). Following the Kaiser-Guttman criterion, only components

of the PCA with eigenvalues greater than 1 were extracted and used for further testing.

Stratified bootstrapping methods at 1,000 iterations within clusters were used to further account for autocorrelation within the data. A stepwise, linear regression analysis was used to determine if sociality measures, as reflected in the PCA factor scores, could predict the mean vessel traffic experienced by an individual. All statistical analyses were conducted using SPSS.

<div align="center">Results</div>

There were 81 CWR encounters spanning 70 days from 2011-2015, which had corresponding vessel count data from the Soundwatch surveys. Consistent with trends described by Soundwatch (Seely, 2015), I found that significantly more commercial vessels targeted Bigg's killer whales than private vessels ($H= 6.163$, $p = 0.013$). Mean boat counts differed significantly both between social clusters ($F=22.490$, $df=9$, $p <0.001$; Figure 19) and foraging classes ($F=8.389$, $df=2$, $p=0.001$). Cluster 2 individuals (n = 12) had the highest vessel traffic levels, followed by Clusters 9 (n = 13) and 6 (n = 8), respectively; Cluster 10 (two lone males) had the lowest vessel traffic. Nearshore foragers had a higher mean traffic boat count than non-nearshore foragers (M=9.60 and M=7.75, respectively), though this difference was only slight. A significant, positive relationship was found between mean exposure boat counts and observed group size (r=0.236, p=.034; Figure 20). The mean group size was M = 6.47 ± 0.93 (see Chapter II).
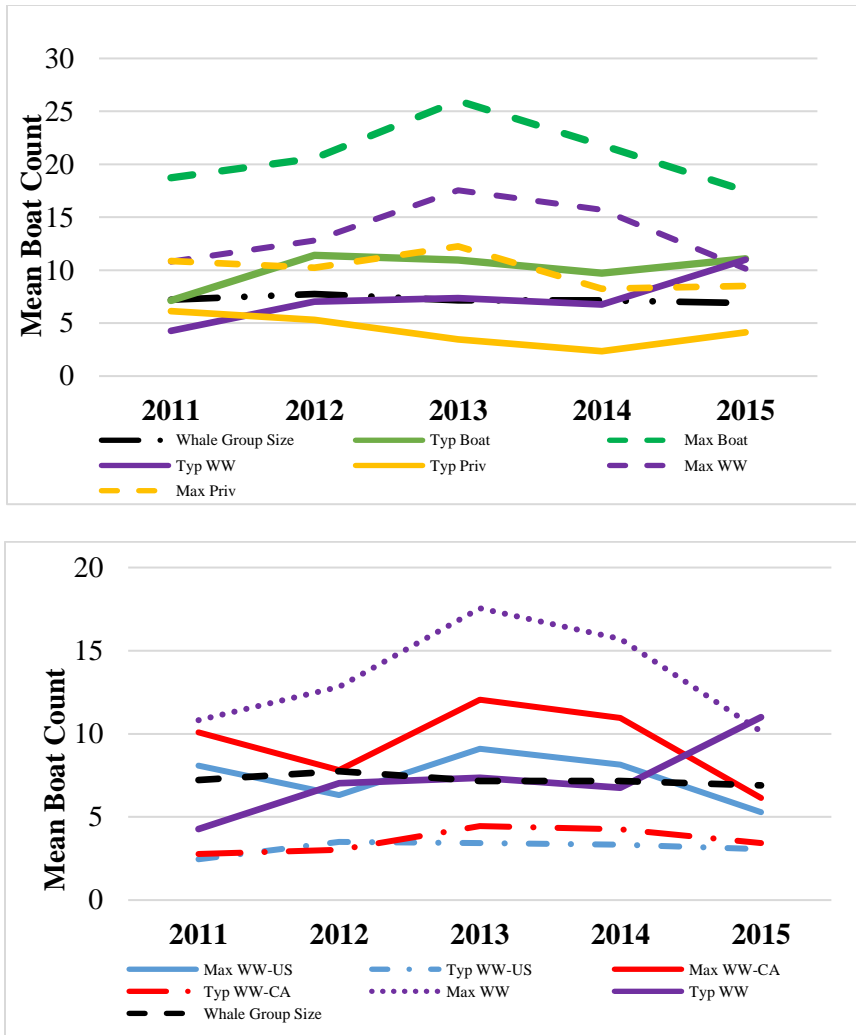
Figure 19. Vessel count data involved in Bigg's killer whale watching activities.

The top figure denotes counts for the typical (Typ) (median) and maximum (Max) boat counts that Bigg's killer whales are exposed

to. The bottom figure breaks down trends in the commercial whale-watching (WW) fleet for the United States (US) and Canada (CA).

The black dashed line in both figures represents the mean extrinsic (observed) group size for each year relative to the vessels

interacting with them as a reference point indicating that on most occasions, there are more boats on scene than there are whales

themselves.
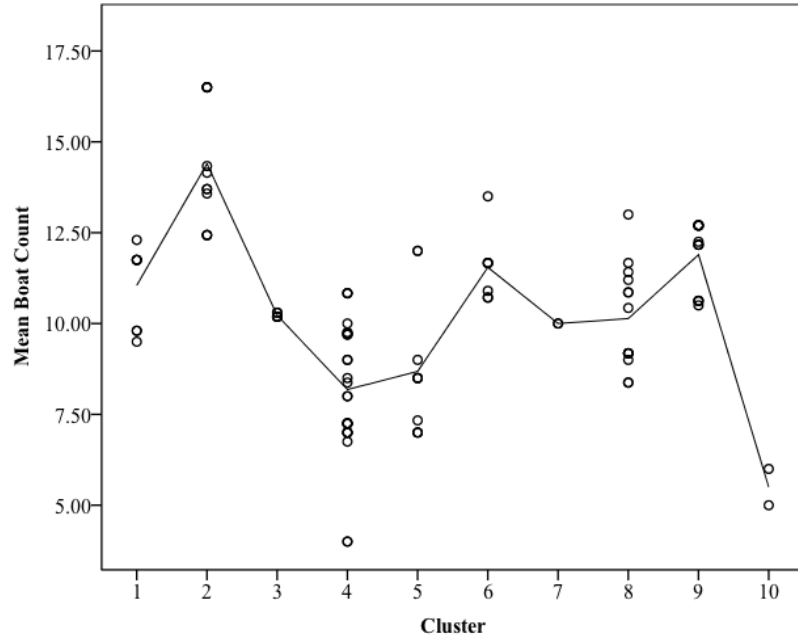
Figure 20. Mean exposure boat counts experienced by individuals within Clusters.
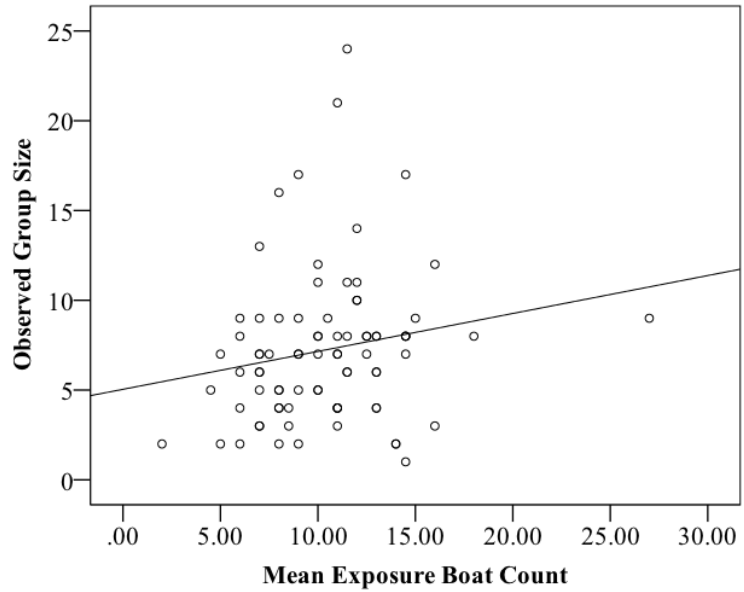
Figure 21. Positive relationship between mean vessel exposure and observed group size.
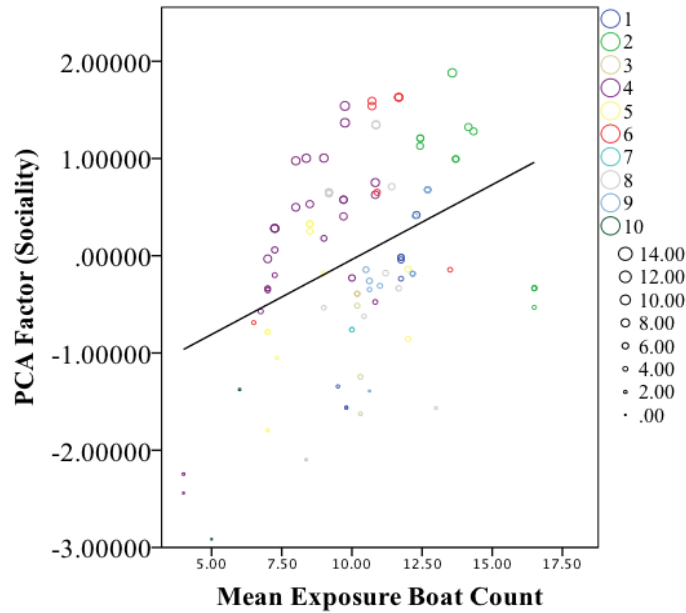
Figure 22. Regression results showing relationship between mean vessel exposure counts and sociality measures reflected in the PCA factor. Data points are weighted by strength of the individual. Colors denote social clusters.

Bigg's killer whales tend to associate with their closest neighbors, with few individuals associating with large numbers of individuals within the community; this is reflected in the Cluster assignments as described in Chapter II. Only two of the five social network measures were significant following the permutation tests: strength (6.24 $\pm$ 3.25; p <0.001) and clustering coefficient (0.36 $\pm$ 0.18 p <0.001), which were negatively correlated with one another (r =-0.3772, p <0.001). These measures, along with HWI and typical group size, were included in the PCA. Only one component from the PCA had an eigenvalue greater than 1 (2.591), which accounted for 64.79% of the variance within the data. Strength, mean HWI, typical group size, and clustering coefficient all loaded positively onto the component of the PCA (0.916, 0.882, 0.897, and

0.412, respectively), indicating that a high PCA score reflects high strength, HWI, typical

group size, and clustering coefficient. Results from the linear regression analysis

determined that sociality metrics (PCA score) significantly predicted the vessel exposure

levels received by individuals (ß = 0.269, p =0.006), but it only accounts for 7.2% of the

variance (R^2 = 0.072, F =7.893, p =0.006).

Discussion

The results of this study reflect somewhat intuitive information; whale watching

vessels go where the whales are. Tourists engaged in wildlife viewing activities prefer to

observe charismatic megafauna to other species that constitute a diverse ecosystem

(Goodwin & Leader-Williams, 2000; Kerley, Geach & Vial, 2003; Krüger, 2005).

Although megafauna biodiversity has significantly increased over the years within the

Salish Sea -- Minke whales, Humpback whales, Fin whales, Pacific white-sided dolphins,

Common dolphins, Steller sea lions and sea otters have also begun frequenting the region

(personal observation; Houghton et al., 2015), tourists visiting this region by far engage

in commercial whale watching with the primary goal of observing killer whales (Finkler

& Higham, 2004).

Clusters 2, 6 and 9 had the highest levels of vessel exposure than the other social

clusters. Interestingly, none of these social clusters had an adult male which are

generally sought out by tourists targeting Resident killer whales due to ease of

identification (personal observation). Rather, these clusters were comprised of 2-3

generations (e.g., the T37 matriline in Cluster 2) of females and their young offspring

(CWR, 2016). Notably, more than half of these individuals have distinct notching in

their dorsal fins, and young T2C2 (Male, b. 2005) has scoliosis; thus, the high vessel

exposure levels for these individuals and clusters may be attributed to easy recognition by whale-watching personnel. This would also explain the low, but significant variance attributed to the regression analysis; sociality is but one of several factors driving vessel exposure levels.

Individuals with high association indices, typical group size, and clustering coefficient had a higher level of vessel exposure. Most of the whales identified in the summer were classified as nearshore foragers, which corresponds to the harbor seal pupping seasons within and near the study area (Huber et al., 2001; 2012). While the optimum group size for this foraging class is three individuals, the disproportionate number of calf and juvenile whales within some groups may not be suitable for comparison with the energy maximizing group size (Baird & Dill, 1996). Thus, both nearshore and nonnearshore foraging is likely occurring in the now standard larger groups sizes.

The increased intensity of whale watching activity within the Salish Sea coupled with the more frequent presence and larger group sizes of Bigg's killer whales in this area creates many scenarios for potential disturbance on this understudied group of whales. Mammal-eating killer whale attacks on marine mammals are cooperative, often prolonged, and involve energetic, high-speed swimming (Baird & Dill, 1995; Pitman & Durban, 2015). The close approach of multiple vessels could reduce overall foraging success by causing the whales to abandon their attack (Williams et al., 2009). Although this study did not outwardly test foraging success rates compared with vessel exposure levels, the present results can be generalized with respect to positive relationship between larger groups and more gregarious individuals attracting more whale watching vessels.

Nearshore foragers are targeting prey that can easily escape predators. Harbor seal predation events occur close to rocky shorelines, where seals can haul out on, or hide in, rocky crevices. This issue is confounded when boats on site during a predation event can serve as a safe harbor for escape from feeding whales (e.g., Schmunk, 2015), which is happening more frequently within the study area. Indeed, the vessel data used in this analysis very likely underscores the potential effect of this occurring as stationary vessels that were not actively engaged in (oriented to) whales for viewing purposes were not included in the vessel counts.

Vessel traffic noise has been shown to disrupt foraging behavior in a variety of cetacean species (Weilgart, 2007), including Resident killer whales found in the study area (Lusseau, Bain, Williams, & Smith, 2009). This is especially concerning given that Bigg's killer whales are silent hunters, emitting irregular, and quieter, echolocation clicks to locate food and rarely emitting vocalization. The sharp increase in ambient noise levels from vessel traffic within the study area may be masking important acoustic cues from prey and hindering successful prey capture events (Viers, Viers, & Wood, 2016). This may be especially confounded given that larger Bigg's groups likely trigger increased vigilance among their prey (Deecke, Slater, & Ford, 2002).

Alternatively, smaller groups amidst a growing whale watching industry may be an indirect reason why Bigg's are thriving in this area. Of the individuals that had three or more prey capture events and were thus assigned to a foraging class, all but one (T40, lone male, non-nearshore forager) was present during a harbor seal prey capture event – suggesting it is likely all Bigg's whales are able to participate in nearshore foraging strategies to successfully hunt and capture harbor seals. Given that smaller groups had

lower vessel exposure levels, the interference of whale-watching vessels during Bigg's foraging activities may be negligible.

On the other hand, larger group sizes during nearshore prey capture events could also be a means to combat missed foraging opportunities as a result of increased interference from vessels. Likewise, the apparent boost in prey abundance coupled with the increase in typical (intrinsic) and observed group sizes is likely relaxing the need for a strict activity budget required for foraging (Baird & Dill, 1995; Houghton et al., 2015). The formation of larger groups may thus function to provide opportunities for mating, alloparenting, strengthening social bonds, and learning foraging and other social and cooperative skills (e.g., Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006; Guinet, 1991; Connor, 2000; Thornton & Clutton-Brock, 2011). The opportunity for learning cooperative behaviors is key for species exhibiting homophily, particularly for foraging strategies (Stanton & Mann, 2012). Indeed, the high clustering coefficient, strength, and association index as expressed in the PCA score, as well as high-within cluster association indices (Chapter II) indicate this is likely occurring with this community of whales. As demonstrated in Chapter II and here, younger individuals are disproportionately represented in large groups and certain social clusters (e.g., Clusters 2, 6, and 9). However, if transients are part of larger groups for social purposes, an increase in vessel exposure can tribute to masking social signals used for identifying individuals with whom they are cooperating (Holt, Noren, Veirs, Emmons, & Veirs, 2008) or mask important echolocation clicks used to detect prey (Viers, Viers, & Wood, 2017). In Resident killer whales, these have significant functions as they denote group identify, which offsets the risk of inbreeding (Ford, 1991; Deecke et al., 2000).

It is worth noting that this is one of the few studies to consider sociality in the context of human activities. Individuals that are more connected and associated within the community in this study area are more frequently targeted by whale watching vessels. Thus, the use of social network metrics such as those presented here can be used to evaluate population effects of disturbance. For example, sociality network measures in Resident killer whales reflects adverse ecological conditions, with lower clustering and association values in times when prey abundance is low (Foster et al., 2012b). Periods of low prey abundance lead to periods of stress (Ayres et al., 2012) and low levels of survival and fecundity (Wasser et al., 2017). For the purposes of conservation management, an integrative approach utilizing traditional ecological metrics (e.g., behavior, physiology, survival, fecundity) to evaluate the extent of human disturbance, such as the PCoD (Population Consequences of Disturbance) framework (New et al., 2014) should also incorporate social metrics. For example, some scientists are encouraging managers to incorporate the use of sociality metrics when estimating limits (Potential Biological Removal) of marine mammals that may be seriously injured or killed as a result of human-interactions (Ashe et al., in prep). Likewise, others have long been a proponent of considering learned, cultural patterns of a species when setting management schemes (in cetaceans: Higham, 2012; Whitehead, Rendell, Osborne, & Würsig, 2004; Whitehead, 2010). In this respect, social network analyses can aid in better understanding the many factors involved in population shifts.

The results shown here demonstrate that the number of boats and whales co-occurring is positively correlated, and that there are potential adverse impacts related to vessel exposure which have the potential to interfere with foraging behaviors and cause

adverse impacts to the animals (e.g., masking of acoustic signals). Thus, vessel behaviors

around these whales have significant conservation implications that transboundary

resources managers should consider. While the U.S. has included Bigg's killer whales

within it's federal regulations for close approach, Canada has none. Additionally,

Canada has developed a recovery plan for the WCT killer whale population, with plans to

designate critical habitat while the U.S. has not. It is also noteworthy, however, that

targeted whale watching activity was not considered by Canadian managers to be a

significant risk factor for Bigg's killer whales by which to design mitigation measures.

The typical number of vessels targeting Bigg's killer whales is lower than that

focusing on Residents (see Results; and unpublished Soundwatch data). Though this is

likely not because the industry prefers Resident killer whales, but rather the shifting

ecosystem and the new occurrences of additional cetacean species in the study area. That

is, there are more things to see during a whale watching trip. As a result, commercial

whale watching vessels will often 'trade off' groups in a seeming effort to self-regulate

time spent on any focal group of whales (personal observation). Indeed, implementing a

time limit for vessels with whales was considered in the approach regulations, however it

would be difficult to monitor and enforce and, therefore, was not considered further

(NMFS, 2011). While the staggering of vessels with whales certainly restricts the

number of vessel co-occurring with whales, the constant approach and departure of the

vessels has been shown to cause more of an acoustic impact to the animals than

consistent motoring (Erbe, 2002; Houghton et al., 2015). This is exacerbated by the lack

of guidance and regulations capping the number of vessels allowed to target any group at

one time.

While vessel approach regulations and viewing guidelines were developed for the benefit of the endangered Southern residents within U.S. waters, Bigg's killer whales are now the target of vessel approach within this region; thus their social dynamics and behavior should also be considered when developing conservation measures. A novel factor to now consider is the behavior and presence of stationary vessels. Many missed prey attempts occur with smaller, recreational boats engaged in fishing or that have moved to the side and turned their engine off (personal observation; e.g., Schmunk, 2015), following current wildlife viewing protocol (i.e., BeWhaleWise guidelines). Their vessel, in turn, serves as a static, predictable object by which prey can formulate an escape plan. Thus, it is worth noting that individuals mitigating their actions in compliance with the wildlife viewing guidelines may still impact the animals they are passively observing. It would be worthwhile if viewing best practices be amended in consideration of the needs of the mammal-eating killer whales.

It would also benefit resource managers to further embrace social science and economic studies to better understand tourist motivations and behavior which is driving the actions of the commercial whale-watch industry. The key factor driving tourist decision making and satisfaction is the potential interaction with and viewing of charismatic species, particularly those publicized in the media with notable physical features - and those linked with conservation issues are sought after even further (Krüger, 2005; Reynolds & Braithwaite, 2001). In this respect, killer whales are iconic (Ford, 2011). Indeed, it is likely that localized economic factors indirectly influence the vessel exposure experienced by individual whales. For example, studies evaluating big game tourism impacts noted that wealthier customers prefer to view more prominent

individuals, e.g., larger adult males, while tourists with lower income levels are generally

more interested in viewing breeding groups with young animals (Di Minin, Fraser,

Slotow, & MacMillan, 2013). Given the diversity of vessel types within the commercial

whale-watching fleet, ranging from large, multi-passenger luxury cruises to smaller,

economical six-packers (i.e., holding six passengers; Seely, 2015) – with equally diverse

acoustic output (Erbe, 2002) – it is possible that Bigg's individuals and social clusters are

receiving various acoustic impacts driven by passenger choice. This would explain why

sociality could only predict a small amount of the vessel exposure levels. However, this

would require further testing considering calf-to-adult ratios within groups. The local

stakeholders within this transboundary region all acknowledge that the Salish Sea

ecosystem is changing. Thus, fixed conservation measures must embrace an adaptive

management approach to remain effective. Current whale watching regulations in the

U.S. limit prohibit close approach of vessels within 200 yards with voluntary speed

restrictions of 7 knots within 400 yards of whales, while Canadian regulations do not

exist and suggest a voluntary, minimum approach distance of 100 m. The first, and most

important, step for conserving all killer whales within transboundary waters would be for

Canada to implement vessel approach regulations that are consistent with existing U.S.

measures. This would enable an enforcement mechanism that would encourage

compliance from all vessels in all waters.

Tourists engaged in whale-watching activities from both the shore and aboard

vessels in this area are concerned that boat presence disturbs whales; and, when viewing

from vessels, are understanding of compliance to guidelines and regulations – which does

not detract from their satisfaction of the experience (Finkler & Higham, 2004). By

embracing a more conservative approach to wildlife viewing in transboundary waters, both

whales and viewers alike will benefit, thus promoting better balance and sustainability within

the Salish Sea ecosystem.

CHAPTER V – CONCLUSIONS

The increased prevalence of Bigg's killer whales within the Salish Sea leaves this killer whale ecotype susceptible to the various and growing anthropogenic pressures within the transboundary waters of Haro and Juan de Fuca Straits shared by Canada and the United States. For conservation management practices to be effective, accurate science on both local and global scales is needed to inform decision-making. This dissertation revisited and built upon the initial quantitative assessment of Bigg's killer whale ecology and association patterns first described two decades ago, and explored the relationship between sociality and the emerging conservation concern of whale exposure to vessels during whale watching activities. Three major objectives were met: (1) identify the level(s) of preferred associations and social differentiation within Bigg's societies relative to foraging specializations; (2) re-evaluate and compare historical measures and persistence of Bigg's sociality, including demographic influences and dispersion patterns; and, (3) assess the extent to which individual sociality can predict received vessel traffic levels, as well as other variables driving targeted whale watching. Given the central importance of the social network within killer whale population dynamics, such as the maintenance of cooperation and cultural transmission of information, shifts in social behavior caused by human activities may have significant ecological and evolutionary consequences.

The three data chapters presented in this dissertation explored each objective, furthering the understanding of this dynamic science-management issue on a local scale. Chapter II examined the current social differentiation and structure of the local Bigg's killer whale community based on the association patterns of individual whales and links

to their observed diet. Results suggest that Bigg's killer whales continue to have preferred associations, which form distinct social clusters that are loosely based on foraging classes. Furthermore, unlike their sympatric counterparts – Resident killer whales, Bigg's killer whales do not appear to have a hierarchical, nested society.

Chapter III further explored the preferred associations noted in Chapter II by evaluating and comparing social factors within and between individuals. Here, I assessed the strength and extent of these associations, while considering demographic variables including sex, age, and foraging class. Additionally, temporal persistence of associations and dispersal patterns were briefly evaluated and compared to historical knowledge derived from the works of Baird & Whitehead (2000). Results show that as the Bigg's population increased (in Period 2), individuals forged stronger, localized preferences for individuals, and fewer connections with the overall population. To an extent, these associations reflect foraging homophily, with nearshore and non-nearshore foragers associating somewhat exclusively. However, nearshore foragers have lower association values than non-nearshore foragers. Over time, male-male relationships increased and became more persistent than historically reported, while the opposite is true for female-female relationships.

Chapter IV integrated management concerns with the understanding of social differentiation by quantifying vessel exposure levels experienced by individual Bigg's killer whales and social groups (i.e., clusters defined in Chapter I), and evaluating the relationships between vessels, grouping patterns, and sociality. Results show that some social clusters, and individuals, are more vulnerable to targeted whale watching activities than others. Additionally, there is a small, but significant relationship between individual

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sociality and vessel exposure; individuals with higher levels of sociality occurred in larger extrinsic group sizes, which attracted a greater level of whale watching activities.

The increased intensity of whale watching activity within the Salish Sea coupled with the more frequent presence and larger group sizes of Bigg's killer whales in this area creates many scenarios for potential disturbance on this understudied group of whales. The results of this study better clarify the social dynamics and population structure of Bigg's killer whales and will thus inform proper management of this under-studied conservation unit. Likewise, the combined evaluation of social dynamics and anthropogenic pressures (vessel traffic) experienced by this population provides key information that may enable managers to implement proper measures to mitigate anthropogenic impacts, such as improving wildlife viewing guidelines and regulations.

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