AN ABSTRACT OF THE THESIS OF

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The desire to understand the spatial and temporal drivers of animal behavior and distribution relative to scale is central to movement ecology. Optimal foraging theory states that a predator should continue exploiting a patch until it is no longer profitable to do so. As human developments increasingly encroach on the marine environment, understanding how anthropogenic interactions affect predator searching and foraging behaviors is key to minimizing disturbance. In 2015 and 2016, two studies were conducted to assess how gray whale behavior state changes (1) relative to static and dynamic environmental cues, and (2) relative to vessel interactions. The first study was addressed through the non-invasive documentation of gray whale movements (n = 76 tracks) using shore-based theodolites for eight weeks from July-August 2016, in Port Orford, Oregon, USA. When conditions allowed, a research kayak was concurrently navigated to 18 sampling stations in two comparative study sites (Mill Rocks and Tichenor Cove) within the study area. Go-Pro cameras were used to record zooplankton relative density in the water column (n=198 casts), and zooplankton net tows (n=107) were used to assess community structure. Video stills were scored for quality and relative density of zooplankton, and averaged through the water column to provide a daily density estimate of zooplankton density for each station. Whale behaviors were categorized into search, forage, and transit using the Residence in Space and Time (RST) method; behavior state was then assessed relative to static and dynamic variables at multiple scales. Despite being only one kilometer apart, there were significant spatio-temporal differences in the community assemblages of zooplankton between the two study areas, and whales demonstrated scale-dependent habitat selection relative to predictable static features (kelp) and dynamic prey availability. In Tichenor Cove, mysids (*Holmesimysis sculpta*), a known regional gray whale prey item, dominated the community, yet whales spent little time foraging here. Whales preferentially foraged in Mill Rocks where a combination of mysids and gammarid amphipods, previously undocumented as gray whale prey in Oregon, were prevalent. The second study occurred in the summer of 2015, and tracked whales and vessels using non-invasive, shore based theodolite and photo ID techniques. Two sites with differing levels of vessel traffic, Boiler Bay and Port Orford, were monitored for 4 weeks each. Whale focal follows were again analyzed with RST to assess behavior state changes relative to location, individual, and vessel presence, type, and distance to whale. There were significant differences in population level gray whale activity budgets between control and impact conditions, and between study sites. No significant difference in individual response to vessels disturbance was found. Taken together, the results of these two studies show that gray whales maximize energy gain through predictable, successful foraging. In the absence of vessels, foraging gray whales use information from a static feature and prey availability at a fine scale (<0.5 km) and larger regional scale (1-2 km), but searching behavior may be influenced by these features in a scale-dependent manner. When a vessel is present, disturbance appears to be tolerated as long as the foraging is profitable. Multi-faceted studies such as these advance the knowledge of which factors inform fine scale predator decision making in an increasingly anthropogenically impacted environment and have the potential to inform local management and conservation efforts.

Fine Scale Foraging Behavior of Gray Whales in Relation to Prey Fields and Vessel Disturbance Along the Oregon Coast

by
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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Florence A. Sullivan, Author

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CHAPTER 1 – GENERAL INTRODUCTION

Gray whales, *Eschrichtius robustus*, are baleen whales that inhabit the coastal, nearshore waters of the North East Pacific Ocean. The population was decimated by commercial whaling, reaching a low of 1,000-2,000 individuals in the early 1900s (Rice and Wolman 1971). They were delisted from the US Endangered Species Act (1973) in 1994, and have now recovered to a population of approximately 20,000 individuals. With the shortest, toughest baleen of any of the great whales, gray whales are known to feed benthicly on ampeliscid amphipods in their principal Bering Sea foraging grounds. Yet, they are flexible foragers, and have also been documented feeding on mysids, amphipods, porcelain crab larvae, and ghost shrimp in other parts of their range (Oliver *et al*. 1984; Dunham and Duffus 2001; Newell 2009; Feyrer and Duffus 2011). Each year, the adult portion of the population migrates south from the Bering Sea to the lagoons of Baja California, Mexico where they calve and mate in December through February (Rice and Wolman 1971). By the time they return to the foraging grounds, individuals need to regain between 11-29% of their body mass due to the energetic costs of the journey (Villegas-Amtmann *et al*. 2017).

The Pacific Coast Feeding Group

The Pacific Coast Feeding Group (PCFG) of gray whales is a group of approximately 200 individuals that do not complete the full northern migration to the Bering Sea, but instead spend the foraging season along the Pacific Northwest Coast. The group is defined as individuals who have been re-sighted in multiple years, during the months of May to October, between Northern California and Southern British Columbia. Individuals demonstrate high inter- and intra-annual re-sight rates (Darling 1984), but also variable and often broad (110 km to 330 km) movement patterns across the PCFG region within one foraging season (Calambokidis *et al*. 2010; Mate *et al.* 2010). Although Lang *et al*. (2014), found evidence of mtDNA genetic differentiation between the PCFG and the Eastern North Pacific (ENP) stock of gray whales, with matrilineal fidelity as a potential driver for this structure, there is debate over whether the PCFG is a genetically distinct subpopulation (D'Intino *et al*. 2013), as other scenarios (*e.g.*, colonization history, number of founders, and immigration rates) could explain mtDNA differences. Yet, there is agreement that the PCFG should be managed separately from the ENP because ‘takes’ from this population will disproportionally affect certain matrilineal lines, potentially impacting the cultural memory of these feeding grounds and resulting in localized extirpation (Clapham *et al.* 2008; D'Intino *et al.* 2013). Therefore, anthropogenic impacts to this small sub-population should be monitored and evaluated.

In Clayquot Sound, British Columbia, D.A. Duffus and colleagues have been documenting patterns in local gray whale behavior since the late 1980s. They have found evidence of flexible foraging strategies (Nelson *et al*. 2008), threshold densities of prey needed for foraging to occur (Feyrer and Duffus 2014), potential vessel disturbance (Duffus 1996), and have defined some key differences in PCFG foraging strategies compared to those that summer in the Bering Sea (Stelle *et al*. 2008). Comparatively limited temporal and spatial sampling of the PCFG whales has occurred in Oregon Coastal waters. Newell and Cowles (2006) documented gray whales foraging on a singular species of mysid, *Holmesimysis sculpta*, during 2003-2005 in areas around Depoe Bay on the central Oregon Coast. Delayed upwelling and a reduction in surface chlorophyll-*a* caused unusually low mysid availability in 2005, and 80% of gray whales passing through the area did so without foraging (Newell and Cowles 2006).

Hazards of a Coastal Environment

A number of marine mammal populations spend part, or all, of their lives in the nearshore environment where they are often impacted by multiple anthropogenic activities including renewable energy development, pollution, fishing pressure, and vessel traffic (Halpern *et al*. 2008; Maxwell *et al*. 2013). Simultaneously, marine mammals living in such nearshore environments also provide easy viewing opportunities for tourists that form the base resource for lucrative businesses.

However, marine mammals are known to be sensitive to anthropogenic disturbance including behavior state changes (Lusseau 2003; Constantine *et al*. 2004), increased stress (Rolland *et al*. 2012), and altered habitat use patterns (Bejder *et al*. 2006; Hartel *et al*. 2014; Russell *et al*. 2014), reinforcing the need for caution and appropriate regulations concerning marine mammal ecotourism ventures. Additionally, marine mammals utilizing nearshore habitats may face a cumulative burden of repeated disruptions to their normal behavior patterns from these activities. In particular, evidence shows that cetacean populations are vulnerable to vessel disturbance with long-term consequences on the health of individuals and populations in areas of high vessel traffic (Lusseau and Bejder 2007). In the northeast Pacific, the preferred foraging habitat of the gray whale occur in the nearshore environment (1-4 km from coast; Sumich 1984), making them vulnerable to the cumulative effects of coastal anthropogenic impacts. Gray whales are popular attractions for ecotourism whale watching operations on their breeding grounds in Baja California (Sumich 2014), their migration route up the California coast, and their feeding grounds in Oregon, Washington, British Columbia, and Alaska.

Vessel Disturbance

Vessel disturbance to cetacean populations has been previously documented (Duffus 1996, Williams *et al*. 2002, Bejder *et al*. 2006a, Bejder *et al*. 2006b, Williams and Ashe 2007, Lusseau *et al*. 2009, Christiansen *et al*. 2013). For example, minke whales (*Balaenoptera acutorostrata*) near Iceland take shorter breaths, increase the sinuosity of their movements, and engage in fewer surface foraging behaviors in the presence of tour boats (Christiansen *et al*. 2013). Killer whales (*Orcinus orca*) in the Johnstone Strait, Canada, react differently to varying levels of boat traffic; when few vessels are present (1-3), the whale’s path is tortuous, but when the number of vessels increases (> 3) , the whale’s path becomes straighter (Williams and Ashe 2007). In areas of high vessel traffic, these sorts of repeated disruptions can have long-term consequences for the health of the individual.

From 1991-1994, gray whale foraging behavior and distribution patterns were recorded in the southern portion of Clayquot Sound, BC (Duffus 1996). This study noted a sequential shift of several kilometers away from the central commercial whale watch port of Tofino each year, although the mechanism for these changing spatial patterns was not identified (Duffus 1996). If this displacement is caused by vessel avoidance, the whales may be compromising their long-term health by avoiding a profitable foraging region, and the whale watching industry may be losing profit due to longer travel times, increased effort needed to find the whales, and decreased customer satisfaction (Duffus 1996). In Shark Bay, Australia, Bejder *et al*. (2006b) also documented a significant decline (about 1 in 7 individuals) in bottlenose dolphin (*Tursiops truncatus*) presence in an area with tour boat activity compared to no significant change in dolphin presence at a near-by control site with no tourist activity. Frid and Dill (2002) argue that human disturbance should be considered analogous to predation risk because of the behavioral choices (*i.e.*, vigilance, fleeing, habitat selection) and the accompanying energetic costs that it engenders. Significant impacts on the behavior of wild cetacean populations have been documented including a 49% reduction in bottlenose dolphin foraging activity when vessels were present (Pirotta *et al*. 2015) and a significant decrease in surfacing rate (P=0.01) by bottlenose dolphins already habituated to boat traffic when approached by a dolphin watching vessel (Janik and Thompson 1996). Tolerance and sensitization to anthropogenic disturbance is also a concern for commercially exploited marine mammal species (Bejder *et al*. 2009). Constantine (2001) demonstrated the importance of long-term monitoring studies concerning impacts of human disturbance by documenting an increase in bottlenose dolphin avoidance behaviors to swim-with-dolphin tours. Successful swim attempts by tour operators decreased from 48% in 1994-1995 to 34% in 1997-1998, and avoidance of swimmers increased from 22% to 31%. Younger animals were more likely to interact with swimmers, suggesting that sensitization to vessel disturbance increases with age and experience.

Vessel Operation Guidelines

Many successful whale watching industries in the USA and elsewhere around the globe have undertaken local action to create self-imposed ethical standards or vessel operation guidelines, which are tailored specifically to their businesses and the marine animals with which they interact (*e.g.*, Grand Manan Whale and Seabird Research Station 2006, International Whaling Commission 2014, Pacific Whale Watch Association 2014). Oregon whale watch operators currently have no such guidelines and are only obliged to comply with standards established by the Marine Mammal Protection Act (MMPA) of 1972, which prohibits the ‘harassment’ of marine mammals – defined as any “act of pursuit, torment or annoyance which has the potential to injure…or disturb a marine mammal”. The MMPA provides guidelines to boaters to maintain a distance of 100 yards or more from marine mammals (Office of Protected Resources 2013). While an excellent starting point, this statute is problematic in its implicit claim that all marine mammals, from harbor seals to blue whales, have equal disturbance thresholds and spatial needs regardless of location, time period, or vessel type. Programs such as ‘Be Whale Wise’ have arisen from community efforts to recognize that different species have different reactions to human disturbance, and should therefore have protective guidelines tailored to their ecological needs (NOAA-NMFS 2014). Common guideline approaches include efforts to minimize vessel disturbance to cetaceans by decreasing speed of approach and departure, creating ‘slow’, ‘no-wake’ and ‘no-go’ zones, limiting the number of boats within a given radius of cetaceans, limiting the amount of time any one vessel may spend near cetaceans, and interdictions against moving into a whale’s path or ‘herding’ it.

Foraging Ecology

The annual return of gray whales to Bering and Chukchi Sea mudflats is a top down control on infaunal benthic amphipod populations (Coyle *et al*. 2007; Brower *et al*. 2016). However, the same search tactics that are effective at locating these static mudflats may not be applicable to pelagic swarms of mysid that are a preferred prey target of the PCFG in their summer foraging region. On the coast of British Columbia, Feyrer and Duffus (2014) found a significant positive relationship between mysid density and gray whale foraging effort, with a threshold of 2,300 mysid/m^3 needed for foraging effort to be observed. Mysids are obligate aggregators that cluster at a scale of meters by species and sizes (Kaltenberg and Benoit-Bird 2013). Most swarms include multiple developmental stages and differ in shape, size and mobility depending on season, sexual maturity, and predation risk (Folt and Burns 1999). In a 2010 study of Depoe Bay, dense layers of mysids were about two meters thick and consistently found just above the seafloor (Kaltenberg and Benoit-Bird 2013). Gray whales have been observed foraging in and near kelp beds (*Nereocystis leutkeana*) - an association that may be a response to mysids swarming under the protective canopy during the day (Murison *et al*. 1984). PCGF gray whales may preferentially seek out kelp patches as potential foraging areas where they engage in area restricted search (Newell and Cowles 2006).

The different searching and foraging tactics required for infaunal versus epifaunal prey are reflected in the activity budgets from Alaskan waters versus the Pacific Northwest coast. Gray whales in the Arctic spent equal amounts of time foraging and traveling compared to gray whales on the coast of British Columbia who spent much less time (15% total) traveling (Stelle *et al* 2008). Optimal Foraging theory (OFT) posits that, with perfect knowledge of a patchy prey environment, a predator should maximize its encounter rate with the highest available densities of prey, and move on to new areas when the current patch has been depleted to background levels (Charnov 1976). Optimization of foraging effort requires complex tradeoffs between patch density, travel costs between foraging patches, levels of inter- and intra-specific competition, and disturbance. Threshold foraging, an aspect of OFT that characterizes the level of prey density when a predator should switch to a less energy expensive or non-feeding behavior, was documented in gray whales feeding on mysids (Feyrer and Duffus 2014). A successful predator will balance energy intake and loss by efficient use of predictable static and dynamic environmental cues to inform scale dependent patterns of search and forage behavior.

Currently, there is no unifying method for identification and classification of animal movement behavior states across spatial and temporal scales or between species (Ogburn *et al*. 2017). This can make direct comparison of the results of different studies difficult, even for case studies of the same species. Proposed newly developed behavioral classification method for movement data, termed Residence in Space and Time (RST; Torres *et al*. 2017) may bring consistency and objectivity to movement data analysis. RST is an extension of first passage time (Fauchald and Tveraa 2003) and residence time (Barraquand and Benhamou 2008). The method is scale dependent, and quantifies occupancy patterns in space and time within a circle of a given radius. RST identifies “time intensive”, “travel”, and “time and distance intensive” behaviors through the use of normalized residence time and residence distance metrics. Dynamic scaling of individual tracklines is possible to determine the appropriate radius of analysis for each track and assign behavior states accordingly. RST provides the ability not only to standardize data exploration across studies, but also overcome individual bias and observer inexperience within studies. The opportunity for direct comparisons of movement and behavior data across studies, ecosystems, and sampling methods opens the doors for greater understanding of the idiosyncrasies of varied locales, species-specific behavior patterns, and spatial and temporal scales.

Local Oregon Needs

Without economic incentive, it can be difficult to convert human behavior from an extractive business model to a conservation based economy. A well-developed whale watching industry has the potential to leave lasting social, economic, educational and conservation impressions on a community and its ecosystem. Furthermore, an effectively managed whale watching enterprise can create or revitalize a coastal economy (*i.e*., lodging, restaurants, shopping). In 2008, whale watching alone brought in over $29.8 million and > 645,000 visitors to the Oregon Coast (O'Connor *et al*. 2009). This successful whale watch industry in Oregon stimulates the local economy through job opportunities and tourism revenue. Therefore, it is critical that as the industry grows, it operates with sustainable protocols that protect whales from overexploitation by minimizing stress and displacement. The creation of vessel operation guidelines tailored to gray whales in Oregon will allow local operators to increase their revenue through eco-tourism and ensure the sustainability of the industry. In order to tailor the guidelines to Oregon coastal conditions, a robust understanding of the foraging ecology of local gray whales and their reaction to vessel disturbance is needed. The aim of this thesis is to fill knowledge gaps about gray whale foraging ecology in Oregon coastal waters that can inform the development of vessel operation guidelines.

Study Design

Field work was conducted in two years; during the summer of 2015, data collection was focused on answering the question of gray whale reaction to vessel disturbance, while in 2016, data collection was focused on assessing predator-prey dynamics.

In 2015 (June – September), the research team synoptically recorded gray whale and vessel movements. Two sites along the Oregon coast were sequentially monitored for approximately 4 weeks total at each site to compare an area with relatively high vessel traffic and an active whale watch industry (Boiler Bay) to an area with low vessel traffic and minimal whale watch presence (Port Orford). Observers worked in teams of two or more to simultaneously track whales and vessels using non-invasive observational methods including binoculars and a theodolite, a surveyor's tool that provides precise geo-located positions of the targets (Bailey and Lusseau 2004). Behavioral impacts of vessel interactions on gray whale were investigated using Markov chains, chi-squared tests, and an analysis of variance (ANOVA). Involving stakeholders in the drafting of vessel operation guidelines from the beginning was an important way to ensure that these guidelines are implemented by the community. Throughout the project, community stakeholders were invited to a series of workshops held in the Depoe Bay and Port Orford communities to inform stakeholders of research efforts and preliminary results. Participants discussed ongoing research, global examples of issues with whale watching, examples of other communities' guidelines, and usefulness of guidelines. After final data analysis and stakeholder input, an informational brochure and website (watchoutforwhales.org) were created to distribute the new guidelines to all boaters on the Oregon Coast. Chapter 2 provides full details on this study.

In 2016 (June – August), the research team returned to the Port Orford study site and synoptically recorded gray whale movements and distribution of their zooplankton prey. A shore-based theodolite was again used to track whales, while a research kayak undertook prey sampling. Two study sites approximately one kilometer apart, Tichenor Cove and Mill Rocks, were designated for targeted prey sampling because these were areas of high use by whales. Zooplankton net tows and GoPro video methods were used to assess relative prey density in the water column. Zooplankton relative density was assessed through novel GoPro video analysis, and community composition was assessed through identification of net tow samples. Gray whale behavior relative to prey density was assessed at regional and fine scales through GAMs and ANOVAs. Chapter 3 provides full details on this study.

Literature Cited

Bailey H, Lusseau D. 2004. Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observation sites. Marine Mammal Science 20:880-885.

Barraquand F, Benhamou S. 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. Ecology 89:3336-3348.

Bejder L, Samuels A, Whitehead H, Finn H, Allen S. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395:177-185.

Bejder L, Samuels A, Whitehead H, Gales N. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour 72:1149-1158.

Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor RC, Heithaus MR, Watson-Capps J, Flaherty C, Krutzen M. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791-1798.

Brower AA, Ferguson M, Schonberg SV, Jewett SC, Clarke JT. 2016. Gray whale distribution relative to benthic invertebrate biomass and abundance: Northeastern Chukchi Sea 2009–2012. Deep Sea Research Part II: Topical Studies in Oceanography.

Calambokidis J, Laake JL, Klimeck A. 2010. Abundance and population structure of seasonal gray whales in the Pacific Northwest, 1998-2008. Paper SC/62/BRG32 presented to the IWC Scientific Committee, May 2010.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Christiansen F, Rasmussen M, Lusseau D. 2013. Whale watching disrupts feeding activities of minke whales on a feeding ground. Marine Ecology Progress Series 478:239-251.

Clapham PJ, Aguilar A, Hatch LT. 2008. Determining spatial and temporal scales for management: lessons from whaling. Marine Mammal Science 24:183-201.

Constantine R. 2001. Increased avoidance of swimmers by wild bottlenose dolphins (*Tursiops truncatus*) due to long-term exposure to swim-with-dolphin tourism. Marine Mammal Science 17:689-702.

Constantine R, Brunton DH, Dennis T. 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117:299-307.

Coyle KO, Bluhm B, Konar B, Blanchard A, Highsmith RC. 2007. Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002–2003. Deep Sea Research Part II: Topical Studies in Oceanography 54:2906–2918.

D'Intino AM, Darling JD, Urban J, Fraiser TR. 2013. Lack of nuclear differentiation suggests reproductive connectivity between the 'southern feeding group'and the larger population of eastern North Pacific gray whales, despite previous detection of mitochondrial differences. J. Cetacean Res. Manage 13:97-104.

Darling JD. 1984. Gray whales off Vancouver Island, British Columbia. The Gray Whale, Eschrichtius robustus. Academic Press, Orlando, Florida. Xxiv+ 600pp:267-287.

Duffus DA. 1996. The recreational use of grey whales in southern Clayoquot Sound, Canada. Applied Geography 16:179-190.

Dunham JS, Duffus DA. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine Ecology Progress Series 223:299-310.

Fauchald P, Tveraa T. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282-288.

Feyrer LJ, Duffus DA. 2011. Predatory disturbance and prey species diversity: the case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family Mysidae) community. Hydrobiologia 678:37-47.

Feyrer LJ, Duffus DA. 2014. Threshold foraging by gray whales in response to fine scale variations in mysid density. Marine Mammal Science. 31:560-578.

Folt CL, Burns CW. 1999. Biological drivers of zooplankton patchiness. Trends in Ecology and Evolution 14:300-305.

Grand Manan Whale and Seabird Research Station. 2006. Whale watching Code of Ethics, Available from (http://www.gmwsrs.org/watch.htm#Code 2014).

Halpern BS, et al. 2008. A Global Map of Human Impact on Marine Ecosystems.

Hartel EF, Constantine R, Torres LG. 2014. Changes in habitat use patterns by bottlenose dolphins over a 10-year period render static management boundaries ineffective. Aquatic Conservation: Marine and Freshwater Ecosystems 25:701-711.

International Whaling Commission. 2014. Whalewatching guidelines, Available from (http://iwc.int/wwguidelines#manage 2014).

Janik VM, Thompson PM. 1996. Changes in surfacing patterns of bottlenose dolphins in response to boat traffic. Marine mammal science 12:597-602.

Kaltenberg AM, Benoit-Bird KJ. 2013. Intra-patch clustering in mysid swarms revealed through multifrequency acoustics. ICES Journal of Marine Science: Journal du Conseil 70:883-891.

Lang AR, Calambokidis J, Scordino J, Pease VL, Klimek A, Burkanov VN, Gearin P, Litovka DI, Robertson KM, Mate BR. 2014. Assessment of genetic structure among eastern North Pacific gray whales on their feeding grounds. Marine Mammal Science. 30: 1473–1493.

Lusseau D. 2003. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology 17:1785-1793.

Lusseau D, Bain DE, Williams R, Smith JC. 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. Endangered Species Research 6:211-221.

Lusseau D, Bejder L. 2007. The Long-term Consequences of Short-term Responses to Disturbance Experiences from Whalewatching Impact Assessment. International Journal of Comparative Psychology 20:228-236.

Mate B, Lagerquist B, Irvine L. 2010. Feeding habitats, migration and winter reproductive range movements derived from satellite-monitored radio tags on North Pacific gray whales. IWC SC/62/BRG21.

Maxwell SM, et al. 2013. Cumulative human impacts on marine predators. Nature Communications.

Murison LD, Murie DJ, Morin KR, de Silva Curiel J. 1984. Foraging of the gray whale along the West coast of Vancouver Island, British Columbia in Jones ML, Swartz SL, and Leatherwood S, editors. The Gray Whale: Eschrichtius robustus. Academic Press Inc.

Nelson T, Duffus D, Robertson C, Feyrer L. 2008. Spatial-temporal patterns in intra-annual gray whale foraging: Characterizing interactions between predators and prey in Clayquot Sound, British Columbia, Canada. Marine mammal science 24:356-370.

Newell C. 2009. Ecological interrelationships between summer resident gray whales (*Eschrichtius robustus*) and their prey, mysid shrimp (*Holmesimysis sculpta* and *Neomysis rayi*) along the Central Oregon Coast.

Newell CL, Cowles TJ. 2006. Unusual gray whale Eschrichtius robustus feeding in the summer of 2005 off the central Oregon Coast. Geophysical Research Letters 33.

NOAA-NMFS. 2014. Be Whale Wise, Available from (http://www.bewhalewise.org/ 2014).

Office of Protected Resources. 2013. Feeding or harassing marine mammals in the wild is illegal and harmful to animals, Available from (http://www.nmfs.noaa.gov/pr/dontfeedorharass.htm).

Ogburn MB, Harrison A-L, Whoriskey FG, Cooke SJ, Flemming JEM, Torres LG. 2017. Addressing Challenges in the Application of Animal Movement Ecology to Aquatic Conservation and Management. Frontiers in Marine Science 4.

Oliver JS, Slattery PN, Silberstein MA, O'Connor EF. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Canadian Journal of Zoology 62:41-49.

O’Connor S, Campbell R, Cortez H, Knowles T. 2009. Whale Watching Worldwide: Tourism numbers, expenditures and economic benefits. Yarmouth MA, USA.

Pacific Whale Watch Association. 2014. Pacific Whale Watch Association, Available from (http://pacificwhalewatchassociation.org/ 2014).

Pirotta E, Merchant ND, Thompson PM, Barton TR, Lusseau D. 2015. Quantifying the effect of boat disturbance on bottlenose dolphin foraging activity. Biological Conservation 181:82-89.

Rice DW, Wolman AA 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalogists.

Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ, Nowacek DP, Wasser SK, Kraus SD. 2012. Evidence that ship noise increases stress in right whales. Proceedings of the Royal Society of London B: Biological Sciences. 279:2363-2368

Russell DJF, Brasseur S, Thompson D, Hastie GD, Janik VM, Aarts G, McClintock BT, Matthiopoulos J, Moss SEW, McConnell B. 2014. Marine mammals trace anthropogenic structures at sea. Current Biology 24:R638-R639.

Stelle LL, Megill WM, Kinzel MR. 2008. Activity budget and diving behavior of gray whales (*Eschrichtius robustus*) in feeding grounds off coastal British Columbia. Marine mammal science 24:462-478.

Sumich J 2014. E. robustus The biology and human history of gray whales. Whale Cove Marine Education, Corvallis, Oregon.

Sumich JL. 1984. Gray Whales along the Oregon Coast in Summer, 1977-1980. The Murrelet 65:33-40.

Torres LG, Orben RA, Tolkova I, Thompson DR. 2017. Classification of Animal Movement Behavior through Residence in Space and Time. PLoS ONE.

Villegas-Amtmann S, Schwarz LK, Sumich JL, Costa DP. 2017. A bioenergetics model to evaluate demographic consequences of disturbance in marine mammals applied to gray whales. Ecosphere **6**:1-19.

Williams R, Ashe E. 2007. Killer whale evasive tactics vary with boat number. Journal of Zoology 272:390-397.

Williams R, Trites AW, Bain DE. 2002. Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. Journal of Zoology 256:255-270.

CHAPTER 2 – GO-PROS, KAYAKS AND GRAY WHALES: LINKING FINE-SCALE WHALE BEHAVIOR WITH PREY DISTRIBUTIONS ON A SHOESTRING BUDGET

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Abstract

Linking predator-prey interactions is a favorite topic among ecologists, but can be expensive and challenging to accomplish at fine scales, particularly in shallow waters that limit traditional prey mapping methods. The Pacific Coast Feeding Group of gray whales forages in the near-shore environment, making them accessible for study with creative, low budget technology. This project aimed to link gray whale foraging behavior with fine-scale prey distributions. For eight weeks from July-August

2016, gray whale movements (n=76 tracks) were non-invasively recorded with shore-based theodolites in Port Orford, Oregon, USA. When conditions allowed, a research kayak was concurrently navigated to 18 sampling stations in two comparative study areas (Mill Rocks and Tichenor Cove). Go-Pro cameras were used to record zooplankton relative density in the water column (n=198 casts) and zooplankton net tows (n=107) were used to assess community structure. Video stills were scored for quality and relative density of zooplankton, and averaged through the water column to provide a daily density estimate for each station. Zooplankton community assemblage structure was derived from zooplankton net tows. Whale behaviors were categorized into search, forage, and transit behaviors using the Residence in Space and Time method. Despite being only one kilometer apart, there were significant spatio-temporal differences in the community assemblages of zooplankton between the two study areas, and whales demonstrated fine-scale habitat selection relative to this prey availability. In Tichenor Cove, mysids (*Holmesimysis sculpta*), a known regional gray whale prey item, dominated the community, yet whales spent little time foraging here. Whales preferentially foraged in Mill Rocks where a combination of mysids and gammarid amphipods, a previously undocumented as gray whale prey in Oregon, were prevalent. Such fine-scale predator-prey data, captured with inexpensive Go-Pro video and shallow net tows, has broad applications, and potential to inform local management efforts.

Introduction

Multiple studies have documented habitat use patterns by marine predators at meso-scales and large scales (Croll *et al*. 1998; Cotte *et al*. 2010), but exploration of marine predator habitat and resource use at smaller scales (< 1-5 km) remains limited (*e.g.*, Torres *et al*. 2008). The inherent challenges of synoptically recording predator and prey occurrence to assess tradeoffs in distribution and behavior patterns often force large scale models of predator distributions to assess the role of proxy variables for prey, such as temperature and chlorophyll-a (Tynan *et al*. 2005; Bluhm *et al*.

2007). These large-scale models successfully investigate the roles of static and dynamic proxy variables to inform predator choices, yet at finer scales the information capacity of static environmental features and dynamic prey availability to a foraging marine predator may differ due to rapidly changing predator behavior states and prey responses over shorter spatial and temporal scales. Therefore, a marine predator foraging at fine scales (< 1 km) in a heterogeneous coastal habitat may respond differently to information cues from static habitat features or dynamic resource availability, which relate to scale and behavior state (*i.e.*, search, forage, or travel). Increased predictability of resources in a system will increase the likelihood of successful patch exploitation by a predator.

Optimal foraging theory (OFT) posits that, with perfect knowledge of a patchy prey environment, a predator should maximize its encounter rate with the highest available densities of prey, and move on to new areas when the current patch has been depleted to background levels (Charnov 1976). While a useful theory, it quickly runs up against the reality that no predator has perfect knowledge of all the variables influencing the distribution of prey patches in its environment. Many predators focus their attention on areas near recent foraging success before moving on to new areas. This non-random foraging pattern is known as ‘area restricted search’ (ARS), a corollary of OFT which states that all other things being equal, a predator should spend more time in areas of high prey availability than areas of low availability (Kareiva and Odell 1987; Fauchald and Tveraa 2006).

Predators have a range of sensory systems that operate at multiple scales (Torres in press), and memory of seasonal and geographic foraging success may inform current decision making (Fagan *et al*. 2013). Both static and dynamic environmental variables can provide critical information for predators that must collate sensory information streams into effective area restricted search patterns to increase encounters with profitable resource availability; successful foraging relies on the predictability of resource distribution. However, the relevant cues may change with scale and behavior state (Mayor *et al*. 2009; Scales *et al*. 2014), particularly at fine-scales when predators rapidly switch between behavior states to increase search and capture success. Along the Pacific Northwest Coast, The Pacific Coast Feeding Group (PCFG) of gray whales (*Eschrichtius robustus*) forages in a heterogeneous coastal environment where their diet may switch between feeding on benthic amphipods, epibenthic mysids, ghost shrimp, and porcelain crab larvae (Oliver *et al*. 1984; Dunham and Duffus 2001; Newell and Cowles 2006; Feyrer and Duffus 2011). At fine scales this flexibility in foraging translates to increased decision making possibilities depending on the target prey and relevant sensory cues.

The PCFG is composed of approximately 200 individual gray whales that do not complete the full northern migration to the Bering Sea for the foraging season, but instead spend the summer foraging between northern California and southeast Alaska (Calambokidis *et al*. 2002). The group is defined as individuals who have been re-sighted in multiple years, during the months of May to October, between Northern California and Southern British Columbia (Calambokidis *et al*. 2002). PCFG individuals demonstrate high inter- and intra-annual re-sight rates (Darling 1984), but also variable and often broad (60 to 180 nm) movement patterns across the PCFG region within one foraging season (Calambokidis *et al*. 2010; Mate *et al*. 2010).

The abundance and behavior of PCFG gray whales has been correlated with prey availability at larger spatial and temporal scales throughout their range. Gray whale abundance in the Northeastern Chukchi Sea has been linked with infaunal amphipod prey availability at a 40 km^2 scale (Brower *et al*. 2016), and in British Columbia, Canada, the intensity of gray whale predation on benthic amphipods depleted this prey resource, causing whales to progressively switch over 5 years to foraging on mysid swarms over rocky, inshore reefs (Burnham and Duffus 2016). Such prey switching between infaunal and epifaunal prey may impact the activity budgets of gray whales, as gray whales foraging on amphipods in Alaskan waters spend almost equal time foraging and traveling, while whales feeding on mysids spend much less time (15% total) traveling (Stelle *et al*. 2008). These changes in diet and behavior patterns illustrate their ability to adapt their foraging strategy across spatial scales and geographic locations. Furthermore, gray whale foraging behavior has been correlated with the density of mysid prey (Feyrer and Duffus 2014) and ARS (Newell and Cowles 2006), demonstrating their adaptive response to relative prey availability. However, the fine scale drivers and patterns of gray whale foraging have not been previously assessed in Oregon. Additionally, this project is unique for its inclusion of fine scale, inexpensively gathered prey data, rather than the use of proxy variables of prey in models describing whale behavior.

Understanding how marine predators such as cetaceans locate prey in a patchy environment often requires expensive and complex study designs in order to gather synoptic data about both predators and prey at multiple scales. Satellite tags (Block *et al*. 2011), Acoustic Doppler Current Profiler (ADCP) profilers (Hazen and Johnston 2010), and hydroacoustics can be effectively applied and combined (Kaltenberg *et al*. 2011), but these techniques can be expensive and invasive so that acquiring adequate replicates to address study questions can be difficult to obtain. Prey sampling is particularly difficult in shallow water environments due to discrete habitat features such as shallow bathymetric features and equipment-entangling vegetation (*i.e.* kelp beds), research vessel maneuverability, and limits of technology. For example, when ship mounted echosounders are used to assess prey, the first 5-10 meters of water depth are frequently omitted due to noise in the data in close proximity to the transducer (Benoit-Bird 2014). In order to assess the fine-scale response of foraging gray whales to static and dynamic features, budget limitations were overcome to collect synoptic data of predators and prey by combining three low cost technologies: (1) non-invasive, cliff based theodolite tracking of gray whales, (2) imagery of relative zooplankton prey density captured from GoPro cameras, and (3) a 100% renewable energy powered research kayak.

Foraging dynamics of gray whales on the Oregon Coast were explored at two scales to assess the importance of static and dynamic features influencing whale behavior patterns. A two scale sampling design was applied: (1) Study Region at a sub-meso-scale (1-2 km), and (2) Study Site at a fine scale (<0.5 km). Data collection and analysis at these two scales enabled me to test the hypotheses that (1) zooplankton community composition is heterogenous at fine scales, and stable over time, and (2) static variables inform gray whale searching behavior at regional scales, while dynamic prey variability predicts foraging behavior at fine scales.

Methods

Field methods

During the summer of 2016 (June – August) we synoptically recorded gray whale movements and relative distribution of their zooplankton prey in Port Orford, Oregon, USA (Fig. 1). The Port Orford region has rocky reefs, extensive kelp beds (Merems 2011), and sandy bottom areas within the area of ~12 km^2 visible from a cliff top (65 m elevation) observation post (Fig. 1A). Two designated study sites viewable from the cliff top were approximately one kilometer apart, Tichenor Cove and Mill Rocks, and were targeted for prey sampling due to high use by foraging whales. Zooplankton net tows and GoPro video methods were used to assess relative prey density in the water column. Two stochastic events during the study period impacted GoPro video zooplankton sampling. Between July 11 and July 23, 2016 the port of Port Orford underwent a dredging operation that caused increased turbidity in the region near the Tichenor Cove study site. Additionally, a diatom bloom occurred across the entire Port Orford study region between July 8- July 11 and July 27-July 31 that limited underwater visibility.

Prey sampling

Fifteen stations were repeatedly sampled throughout the study period to assess prey variation within each study site: Tichenor Cove: n = 10 stations spaced 120 m apart; Mill Rocks: n = 5 stations spaced 200 m apart (Fig. 1). GoPro video was used to assess relative density of zooplankton at each station, while a zooplankton net (8 inch diameter, 363µm mesh) was used to assess zooplankton community species structure. Both GoPro and zooplankton net casts were conducted from a research kayak. Increased spatial and temporal prey sampling was conducted in the Tichenor

Cove study site because the original study design focused solely on sampling within this site based on the distribution of whale foraging the previous summer (2015). However, over the course of the 2016 study season, gray whales spent a substantial amount of time in Mill Rocks, prompting adaptive sampling in this study site as well.

Stations were accessed and sampled using a tandem research kayak, guided by a pre-programmed handheld GPS unit (Garmin GPS72). Station habitat varied between substrate and distance to kelp, and depth varied between 4 and 12 meters (Table 1). Once on station, team members used a fishing outrigger to lower an instrument package of a horizontally aligned GoPro camera (GoPro Hero 3+ Black/Silver) and Time-Depth recorder (TDR; Solinst Levellogger 3001 F100/30) at a steady rate through the water column. The instrument package was held at bottom for approximately 10 seconds, and then retrieved. Before deployment, camera, computer, and TDR were time-synched with a digital watch to enable accurate time alignment between images and depth during the analysis phase. The GoPro camera was fitted with a magenta filter to optimize visibility and contrast. After the instrument package was retrieved, the zooplankton net was attached to the outrigger, lowered through the water column, held at depth for approximately 10 seconds, and rapidly retrieved to capture zooplankton. The cod end was then emptied into a small, sterilized jar until it could be refrigerated and processed in the lab on shore. Jars were labeled by site, and sterilized between each use. Kayak surveys began daily at sunrise, but effort was limited to Beaufort Sea State of 3 or less, and differences in site exposure to prevailing winds often precluded both sites from being sampled on the same day.

Whale tracking

A theodolite is a surveyor's tool that provides precise geo-located positions of the targets (Bailey and Lusseau 2004). A Sokkia model DT210 connected to a laptop computer running the tracking software Pythagoras (Gailey and Ortega-Oritz 2000) was used to non-invasively track gray whales from an elevated (65 m) vantage point above Tichenor Cove. Photo-identification images of each tracked whale were collected to determine re-sightings and replicate tracks of individual whales. Observers worked in teams of two or more to track whales and were aided by binoculars to spot whales, and record behavior state (forage, search, or travel) at each whale surfacing. Whale survey effort began daily at sunrise (barring fog) and continued until Beaufort Sea State of 4 or more compromised visibility and data collection. In addition, the theodolite was used to map surface kelp extent within the Port Orford region.

Analysis Methods

Prey sampling

GoPro video footage collected at each sampling station was processed using GoPro Studio (version 2.5). Time stamps were matched between video clips and TDR profiles in order to extract images at one meter depth intervals to assess the vertical distribution of zooplankton. Each still image was divided equally into a consistent 3x3 grid, and each grid square was scored according to relative zooplankton density on a scale of 0-5 where 0 was no zooplankton present, and 5 was highest density of zooplankton. A single image analyst scored all images and utilized representative example images of each score to maintain consistency. If any grid cell was obscured due to extreme turbidity or interference from rock or kelp, a score of NA was assigned. The nine grid cell scores were then averaged to provide a single relative density score for the whole image. These 1 m relative zooplankton density scores were associated with accurate TDR depth positions, and therefore used to assess temporal, spatial, and depth variation.

Patchiness of prey occurred at a finer scale than the 1 m interval used to assess spatio-temporal and distribution patterns of prey, as described above. Therefore, to accurately relate relative zooplankton density through the water column to whale behavior, still images were also extracted at 5 second intervals during the retrieval cast. Each 5 sec image was scored on a 0-5 scale like the 1 m images, but lacked associated depth positions; all 5 sec images from a cast were then averaged to calculate a daily relative density of zooplankton for each station. This method normalized the data between stations of varying depth and compensated for variation in camera retrieval speeds.

To assess zooplankton community composition at the site level and over time, net tows were performed at selected stations approximately every three days (stations 1, 4, 8 in Tichenor Cove; stations 14, 16, 18 in Mill Rocks). Captured zooplankton from the tows were pooled by site for community analysis. Samples were sieved through a coarse mesh, and a random representative subsample was placed in a scint vial and preserved in 70% ethanol for identification. In the lab, a dissection microscope was used to identify a total of 100 individuals per sample to the species level for mysids, and the suborder level for amphipods.

Spatial analysis of prey data

For each day of prey sampling, an interpolated layer of zooplankton density was created in ArcGIS (ESRI v10.3) to represent the spatial distribution of relative zooplankton availability at the site level. These layers were created using the averaged 5 sec GoPro image scores at each station. Site boundaries for each layer were defined as a 200 meter buffer around all sampling stations (Fig. 1). A resolution of 60 m cell size was applied for this spatial analysis because this was half the average distance between sampling stations within both sites.

Whale Behavior classification

All theodolite tracks were produced using the program Pythagoras (Gailey and Ortega-Oritz 2000), and corrected for height of station, tide, and azimuth. All tracklines were smoothed using a custom R (R Core Team 2015) script to identify gaps in whale location of greater than 8 minutes, and linearly interpolated at 4 minute intervals. Tracklines were then analyzed using Residence in Space and Time (RST; Torres *et al*. 2017) to assign behavior states to each location. This behavior classification method is scale dependent, and quantifies occupancy patterns in space and time within a circle of a given radius. RST identifies “time intensive”, “travel”, and “time and distance intensive” behaviors through the use of normalized residence time (RT) and residence distance (RD) metrics. Dynamic scaling of each trackline was used to determine the appropriate radius of analysis for each track and assign behavior states accordingly. Due to the fine scale analysis of this study and the lack of any observed resting behavior, ‘time intensive’ behaviors were interpreted as ‘foraging’ due to persistent presence in a small area (patch use), and ‘time and distance intensive’ behaviors were interpreted as ‘searching’. RST analysis produces residual values for each location, which were interpreted as follows: negative residuals (-1 to <0) = Forage (RT > RD); positive residuals (>0 to 1) = Search (RD > RT); zero residuals (0) = Travel.

Relating whale behavior to environment

Whale distribution and behavior was related to dynamic prey variability and an important static environmental feature, distance from kelp. Previous authors have noted a relationship between kelp beds, mysid aggregations and whale foraging activity, prompting the use of distance from kelp as a static metric (Newell and Cowles 2006; Feyrer and Duffus 2011). Depth was not related to whale behavior in this analysis because it was assumed that the small depth range (4 -14 m) across the study region would be unlikely to inform behavior patterns, but more likely physically limit whale distribution and behaviors. Therefore, the analysis focused on the integrative static environmental feature of distance from kelp. Using the kelp extent boundaries mapped by the theodolite from the cliff top, a distance from kelp layer was created in ArcGIS (Euclidean distance). All whale theodolite locations were then spatially associated with a ‘distance from kelp’ value and the corresponding daily value of relative zooplankton density extracted from interpolated layers of averaged 5 sec GoPro images. Furthermore, whale locations were classified by site as within Mill Rocks or Tichenor Cove, or outside of either boundary.

Statistical methods

Several statistical methods were used to address three ecological patterns: (1) describe the depth stratification of prey distribution, (2) characterize differences in site-level zooplankton communities, and (3) assess variation in whale behavior relative to scale, day, relative density of prey, and distance to kelp. To address pattern (1), a linear regression was used to establish the relationship between relative density of zooplankton and depth using results from the 1 m GoPro image analysis. A non-metric multidimensional scaling (NMDS) plot on a Bray-Curtis resemblance matrix was used to address pattern (2) and visualize patterns in the relative zooplankton species abundance and diversity between samples collected in Tichenor Cove and Mill Rocks. Zooplankton community data were standardized to 100% and square root transformed before the analysis. NMDS were performed using PRIMER v. 6.0 and PERMANOVA+ add on. A linear regression was also used to assess site level differences in daily average relative density of zooplankton. Pattern (3) was addressed through generalized additive models (GAM; Wood 2006) that were fit to the RST residual values of search (residuals > 0) and forage (residuals < 0). RST residuals are calculated on a continuous scale, allowing the intensity of the behavior to be assessed. These GAMs were used to determine if relative density of zooplankton prey, distance to kelp, and site affected whale behavior state. Site was excluded in the models of search and forage to examine the relative role of the dynamic and static variables at the Port Orford regional scale (1-2 km), yet site was included in the models to examine those same relationships at the fine site scale (<0.5 km). Day was included as a random factor in all models to account for stochastic variation in prey availability and whale presence. A Quasipoisson distribution was used to account for overdispersion in the data. The travel behavior state was not assessed because unquantified factors (*e.g.*, sociality, satiation, and large-scale resources) may significantly influence travel. Additionally, prey availability was not assessed outside the Tichenor Cove and Mill Rocks study sites where a majority of travel behavior occurred (see Results).

Results

Relative zooplankton density

Relative zooplankton density as assessed through the 1 m GoPro image analysis varied both spatially and temporally across sites and stations (Fig. 1). Zooplankton were stratified in the water column, and a linear regression model (relative density ~ depth) confirmed the prey to be more prevalent near the seafloor ($p < 0.01$). At a fine scale, a linear regression (average relative density ~ site + day) of average relative density (derived from 5 second image analysis), pooled at the site level by day found no significant difference in prey availability between Mill Rocks and Tichenor Cove by day ($p = 0.37$). However, temporal variation of zooplankton density within site is evident in Tichenor Cove where sampling was more consistent throughout the field season. For example, July 16-17 had high zooplankton density levels across all stations, including those in Mill Rocks, followed by a period of lower prey abundance, and another peak in relative density on August 2-3. Spatial variation in zooplankton density was also evident: stations 1, 4, 8 and 9 had consistently high relative densities of zooplankton compared to stations 2, 3, 5, 6, 10, and 13 (Fig. 1). This patchiness of prey may be related to habitat at each station, as sites 1, 4, 8, and 9 were all rocky bottom, and stations 2, 3, 5, 6, 10, and 13 had sandy bottoms (Table 1).

Zooplankton community structure

Significant differences in zooplankton community structure were evident across both space (site level) and time (date; Fig. 2). The most abundant species in both Mill Rocks and Tichenor Cove was the mysid *Holmesimysis sculpta*, followed by another mysid species *Neomysis rayi* in Tichenor Cove. However, the epibenthic amphipod Gammaridea (S) was the second most abundant type of zooplankton in Mill Rocks (Fig. 3b). SIMPER analysis of temporally pooled samples revealed that Tichenor Cove had a more homogenous species composition (Av. similarity = 82.02) than Mill Rocks (Av. similarity = 45.01). Simpson's diversity index (1-D) confirmed this result: Tichenor Cove (1-D = 0.318) was lower than Mill Rocks (1-D = 0.616).

Although other mysid species were captured (*Telacanthomysis columbiae*, *Columbiaemysis ignota*, *Exacanthomysis davisi,* Caprellidea (S)), the differences between sites were driven by *H. sculpta*, Gammaridea, and *N. rayi*. Temporal changes in community structure between the two sites are also evident: samples taken early in the season (17 – 25 July) had more similar zooplankton community compositions between sites than samples taken later in the season (6 - 9 August; Fig. 3). Over the season, Gammaridea became steadily more prevalent at Mill Rocks while in Tichenor Cove, *H. sculpta* and *N. rayi* continued to dominate the community (Fig. 3). This is the first study to document an association between gray whale foraging and the amphipod gammarid amphipods in Oregon.

Whale behavior (RST)

The presence of gray whales in the Port Orford region steadily increased over the course of the field season (Fig. 3A). Overall, gray whales spent 31.2% of their time foraging, 42.3% searching, and 26.3% traveling. However, there were differences in activity budgets between the two study sites, and the surrounding area (Table 2). Most notably, gray whales beyond the boundary of the Tichenor Cove and Mill Rocks sites (outside) spent more than twice as much time traveling as whales inside Mill Rocks. Whales spent 56% of their time inside Mill Rocks, 19% inside Tichenor Cove, and only 25% outside the study site boundaries despite being a much larger area (Table 2).

Using RST residuals as the response variable, quasipoisson GAMs were used to examine the role of distance to kelp (a static feature) and dynamic relative prey density on searching and foraging behaviors at the regional and fine scales. The GAM of search intensity that accounted for site did not find relative prey density to be an influential factor, but distance from kelp was significant in the model (Table 3). However, without site in the model, relative prey density was found to contribute significantly to search behavior (more so than distance from kelp). Hence, at the regional scale (1-2 km) gray whales appear to primarily search relative to prey availability, while at the finer site scale (<0.5 km), searching is more informed by the static distance from kelp feature. In contrast, the GAMs of foraging behavior intensity demonstrate that both the static feature distance from kelp and the dynamic patterns of relative prey density significantly influence the intensity of foraging behavior at both regional and site scales. The random factor Day was not significant in the search models, indicating that the whales searched equally across sampling days. Yet, Day was significant in both the foraging models, highlighting the temporal variability in foraging behavior relative to other factors such as prey community (Fig. 3).

Discussion

Successful foraging in the marine ecosystem requires adept predator response to environmental cues (Torres in press) and effective searching patterns, both of which are a function of scale. This study documents how gray whales depend on information from a static feature more while searching or foraging at a fine scale (<0.5 km) than when searching at a larger regional scale (1-2 km). At fine scales, the ‘distance from kelp’ static feature may offer gray whales searching for prey greater predictability than the more dynamic patterns of relative prey density. Yet, dynamic prey patterns inform foraging behavior at both regional and fine scales, likely because once a suitable prey patch is detected the animal switches behavior states from search to forage, regardless of scale.

Predictability of a resource is a function of previous success and failure associated with that feature. The knowledge of previous success near kelp could be an important part of a whale’s foraging strategy at multiple scales. While kelp extents shift between years, the general location and density of kelp within a summer foraging season is unlikely to change dramatically. Mysids are obligate aggregators that cluster at a scale of meters by species and sizes (Kaltenberg and Benoit-Bird 2013), and are known to swarm under the protective canopy of kelp during the day (Murison *et al.* 1984). The stochastic nature of zooplankton prey distribution and abundance likely drives searching gray whales to rely more significantly on kelp as a proxy for prey availability.

Such predictability of resources is also relevant at large scales. Many large-scale models focus on relating predator habitat use and distribution with dynamic oceanic processes, such as oceanic fronts (Bluhm *et al*. 2007; Bost *et al*. 2009). Despite high spatio-temporal variability at small scales, these oceanographic features are often characterized as static variables relative to predator movements in order to capture the predictability of prey in the system (Moore *et al*. 2003). Hence, despite the dynamic nature of oceanic features, these large scale models may also describe patterns between 'static' features and marine predators because they enhance resource predictability. The influence of a static or dynamic feature also appears to be related to whale behavior state, which is often ignored or reduced in large-scale models that use either presence/absence data (Tynan *et al*. 2005; Block *et al*. 2011) or search vs. travel behavior states (Fauchald and Tveraa 2006) as response variables. Similar to the regional scale results of this study, Torres *et al*. (2008) found that including prey data as a predictive variable did not improve model fit of fine scale dolphin habitat selection, and static environmental variables had higher predictive capacity. Yet, this dolphin study compiled all behavior states together, limiting the ability to detect variable correlations between dynamic prey density and foraging at regional scales, as documented for gray whales here. Furthermore, in this study, gray whale behavior was related to direct measures of prey instead of proxy variables. Our findings demonstrate that whale behavior is differentially mediated by spatial scale, temporal variation, static features of the environment, and dynamic prey availability.

Gray whales respond to a threshold prey density at regional scales (Feyrer and Duffus 2014). In Port Orford, the relationship between intensity of whale searching behaviors and relative prey density was also stronger at regional scales than at fine scales, corroborating what has been seen in the literature. Depending on the sensory cue informing whale perception of the prey-scape, the regional scale may be the finest resolution at which the dynamic cue is informative. Once searching at the sub-regional scale, it may be more efficient to locate prey using static cues, such as the location of kelp beds. Alternatively, at this fine scale, returning whales may have perfect knowledge of kelp bed locations, making this static variable key to the execution of OFT. However, a more likely explanation is that given the fluid nature of zooplankton swarm dynamics (Feyrer 2010), and the possibility of one whale depleting a patch before another whale moves through the same area (Feyrer and Duffus 2011), the sampling resolution of prey at this fine scale was not adequate to correlate with whale searching behavior.

Gray whale foraging studies in Oregon waters are limited, with one previous effort documenting predation of *H. sculpta* in the Depoe Bay region of the central Oregon coast (Newell and Cowles 2006). It has since been assumed that gray whales in Oregon primarily prey on this mysid species. However, our study documented a clear association between increased gray whale foraging behavior and increased relative abundance of gammarid amphipods. Despite the two study sites being less than 1 km apart, the zooplankton community structure was significantly different, driven by the presence of gammarids at Mill Rocks, and whales preferentially searched at this site more than Tichenor Cove (Fig. 3; Table 2). Gray whales are known to be flexible, and opportunistic foragers (Oliver *et al*. 1984; Dunham and Duffus 2001; Newell and Cowles 2006; Feyrer and Duffus 2011), and it is possible that gammarids have a greater energetic reward than mysids; spurring whales to take advantage of its abundance when available. There was no significant difference in daily average relative prey density between sites, so observed differences in distribution and behavior states could be driven by prey species composition of the zooplankton community, indicating that whales preferentially chose to use the site with increased occurrence of gammarids (Table 2, Fig. 3).

Gaps in the temporal prey sampling record, particularly at Mill Rocks, prevented full resolution of whale behavior relative to site and prey density at the sub-site scale (< 0.25 km). While the daily temporal prey sampling effort was adequate to resolve whale behaviors at the fine-scale site-level (<0.5 km), there is a mismatch between a daily prey evaluation and whale behavior resolved at a 4 min interval via theodolite tracks. In order to determine which combination of variables (site, prey relative density, prey community, distance to kelp, and day) most fully explain sub-site level whale behavior, a higher temporal and spatial prey sampling resolution is needed. Due to our daily temporal scale of prey density, it was not possible to account for potential prey patch depletion caused by foraging whales, nor for changes in prey distribution or density that may occur due to fine scale clustering dynamics of zooplankton swarms (Kaltenberg and Benoit-Bird 2013), tides, and other oceanographic factors.

GoPro sampling of relative prey density is limited to waters with clear visibility, but allows for increased spatial and temporal resolution sampling in shallow regions. Species identification of individual zooplankton remains elusive, and a synoptic net tow is recommended to characterize the zooplankton community. In conclusion, we found the GoPro can be a cheap, useful tool for assessing relative density when paired with net tows to identify species and an effective sampling design.

This work demonstrates that in a small, coastal area (12 km^2), predictability of resource distribution (*i.e.*, static variables such as kelp) is a key factor directing predator searching at fine scales (< 0.5 km). The hypothesis that static variables inform searching behavior at regional scales was rejected. Gray whales rely more heavily on the dynamic patterns of relative prey density when searching at the study region scale (1-2 km), but are dependent on both dynamic prey patterns and static kelp predictability to determine forage behavior. The hypothesis that zooplankton community composition would be heterogeneous at fine scales was upheld; there was significant variation in prey communities between the study sites. Furthermore, species composition may be a driver of increased foraging behavior rather than prey density alone. Through investigation of behavior patterns relative to prey availability at multiple spatio-temporal scales, we are able to gain a better understanding of predator decision making processes.

Tables

Table 1. Zooplankton sample station characteristics. Range of depth based on tidal variation.

Station	Site	Bottom Type	Depth (m)	Average Zooplankton relative density score	Within 5m of Kelp
1	Tichenor Cove	Rock	4.8 +/- 1.3	3.22 +/- 1.14	Yes
2	Tichenor Cove	Sand	10.4 +/- 0.9	2.33 +/- 0.33	No
3	Tichenor Cove	Sand	11.4 +/- 3.6	2.11 +/- 0.83	No
4	Tichenor Cove	Rock	8 +/- 1.2	3.00 +/- 1.12	Yes
5	Tichenor Cove	Sand	13.3 +/- 0.6	2.0	Yes
6	Tichenor Cove	Sand	12.3 +/- 0.5	2.0	No
8	Tichenor Cove	Rock	8.5 +/-1.2	3.45 +/- 0.86	Yes
9	Tichenor Cove	Rock	4.7 +/- 1.6	3.84 +/- 0.65	Yes
10	Tichenor Cove	Sand	11.3 +/- 0.6	1.5 +/- 0.71	No
13	Tichenor Cove	Sand	8.9 +/- 0.9	1.6 +/- 0.89	No
14	Mill Rocks	Rock	5.6 +/- 1.6	2.94 +/- 0.78	Yes
15	Mill Rocks	Rock	3.3 +/- 1.5	2.13 +/- 0.62	Yes
16	Mill Rocks	Rock	4	-	Yes
17	Mill Rocks	Rock	6	2.33	Yes
18	Mill Rocks	Rock	6 +/- 4.2	1.25	Yes

Table 2. Breakdown of gray whale activity budget in the Port Orford region by site.

Site	**Area (km^2)**	**Search**	**Forage**	**Travel**	**Number of theodolite locations**
Mill Rocks	0.19	45.3%	36.2%	18.4%	1374
Tichenor Cove	0.25	38.0%	30.3%	31.5%	478
Outside	11.56	38.9%	19.5%	41.4%	562
Overall	12.00	42.3%	31.2%	26.3%	2414

Table 3. Results of search and foraging behavior models where the response variable was the distribution of RST residuals of a given behavior, and predictors were site, relative prey density, distance from kelp, and the random factor day. *Statistically significant predictors (p-value <0.01) are in bold.*

Response	**Model family, type**	**Predictors (F,p-value)**	**Deviance explained**	**Scale of Analysis**
log (All negative (Search) RST values)	Quasipoisson GAM	**Site (T = 5.953 ,p < 0.001)** Relative prey density (F = 1.499, p =0.18) **Distance from kelp (F = 3.637,p < 0.01)** Day (F = 0.00,p = 0.928)	21.6%	Fine <0.25 km
	Quasipoisson GAM	**Relative prey density (F = 2.367 ,p = 0.013)** Distance from kelp (F = 2.154,p = 0.062) Day (F = 2.094,p = 0.0814)	14.7%	Regional ~1-2 km
log (All positive (Forage) RST values)	Quasipoisson GAM	Site (T = 0.817 ,p = 0.127) **Relative prey density (F = 7.476 ,p = 0.007)** **Distance from kelp (F = 4.771, p = 0.003)** **Day (F = 3.063, p = 0.04)**	16.9%	Fine <0.25 km
	Quasipoisson GAM	**Relative prey density (F = 10.05,p = 0.001)** **Distance from kelp (F = 4.31, p = 0.006)** **Day (F = 6.139, p = 0.007)**	15.9%	Regional ~1-2 km

Figures

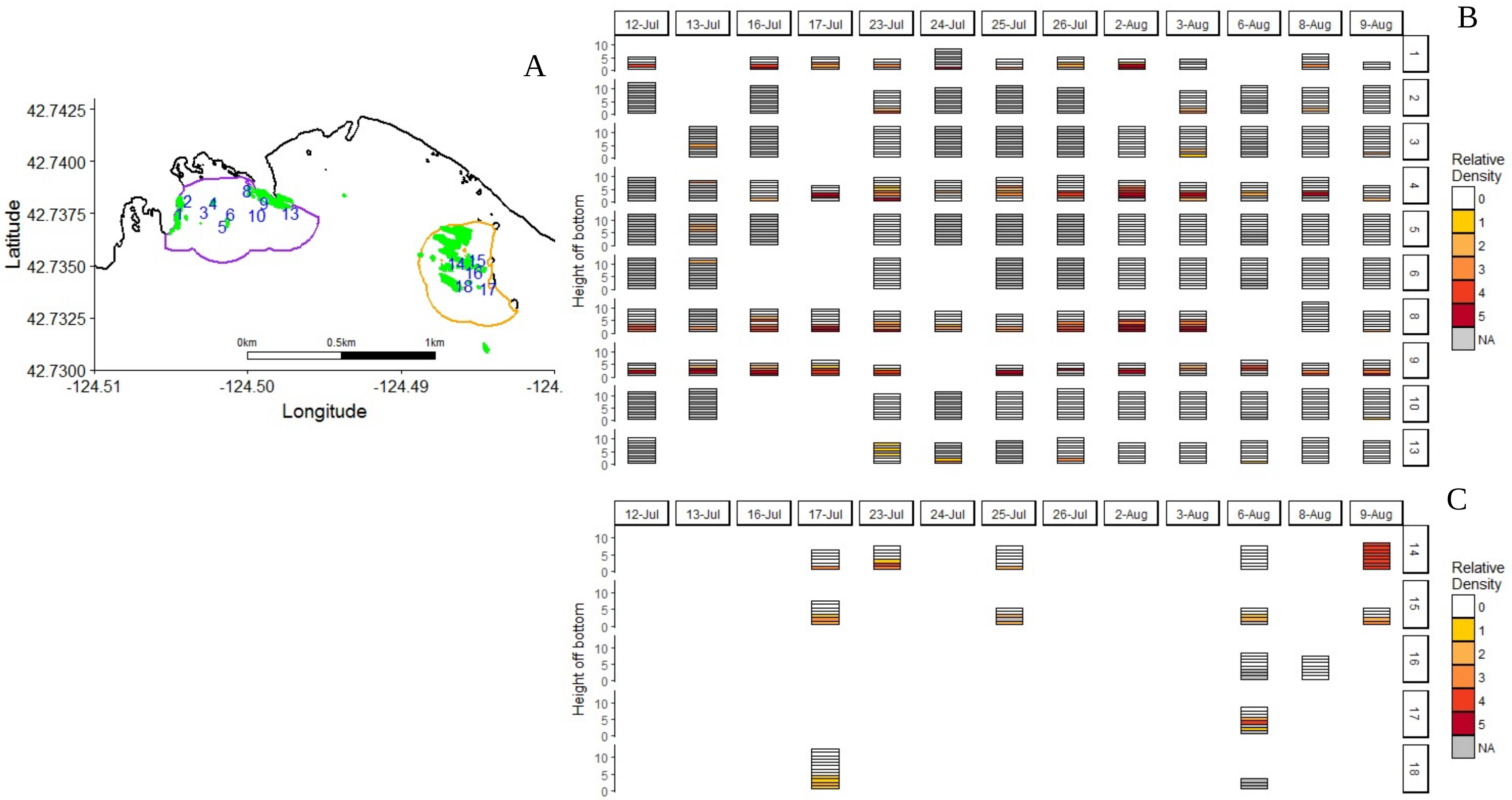

Figure 1. Location of study sites in the Port Orford region with temporal and spatial illustration of relative zooplankton density as discerned from 1 meter GoPro image analysis. Map of the Port Orford study region (a) with Tichenor Cove study site outlined in (purple) and Mill Rocks study site outlined in (orange). Surface kelp extent is shown in green. GoPro sampling effort and image analysis results at stations in Tichenor Cove (b) and Mill Rocks (c). Date of samples is on the x axis, and station numbers on the y axis correspond to locations on the map (a). Each box represents a GoPro sample. Each slice of a box correspond to height off bottom in meter increments, and are color-coded according to the relative density of zooplankton score derived from GoPro image analysis. The scale runs from no zooplankton present (white) to highest density of zooplankton (deep red). Gray indicates that no score was assigned, either due to poor visibility or obstruction by rock or kelp.

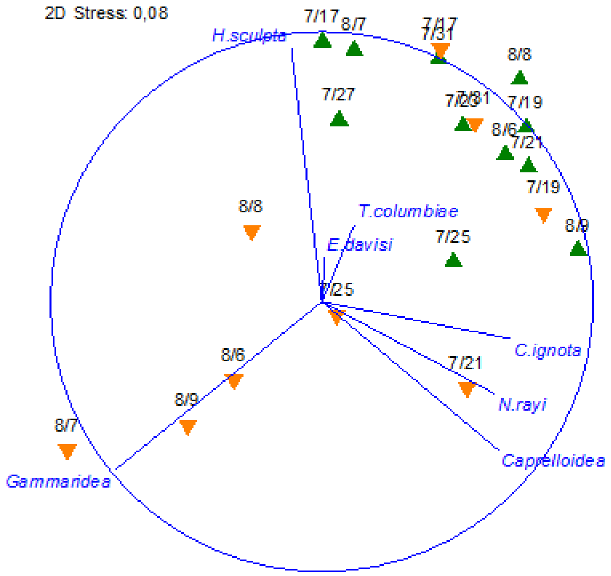

Figure 2. NMDS plot describing the zooplankton community at Tichenor Cove (green triangles) and Mill Rocks (upside-down orange triangles) sampling stations. Labels indicate date of collection (month/day 2016). Vectors of all mysid species and the two amphipod suborders found in the zooplankton samples are shown in the plot.

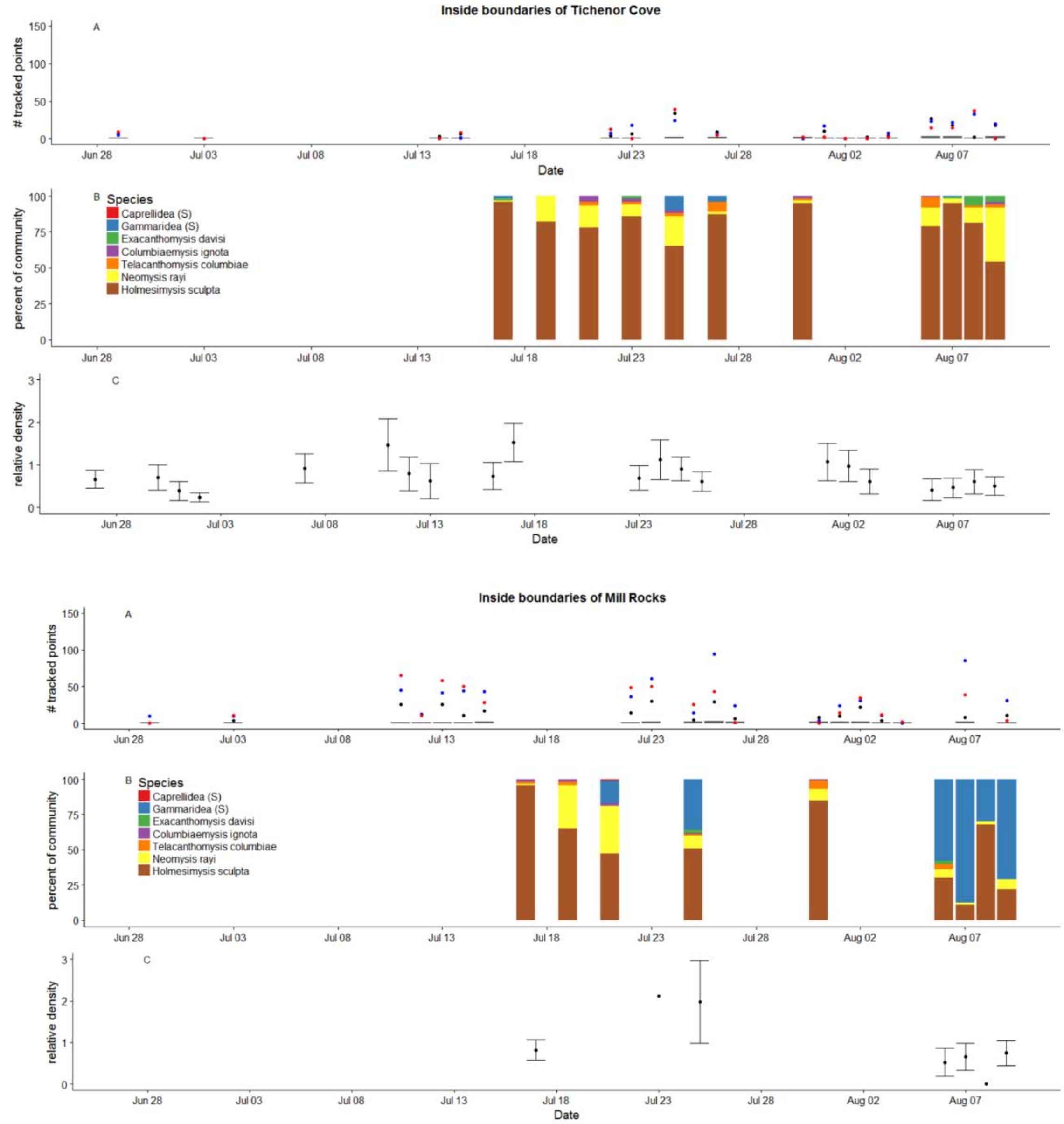

Figure 3. Temporal patterns of whale behavior states as determined through Residence in Space and Time (RST; A), zooplankton community structure (B), and relative zooplankton density as determined by GoPro image analysis (C). (A) The number of whale locations classified as forage (red), search (blue) and travel (black) by day. Gray bars indicate the number of whales tracked per day (thin = 1, medium = 2, thick = 3). (B) The structure of the zooplankton community each day. (C) The relative density of zooplankton averaged over the site by day. Top panel of plots represent results at Tichenor Cove; bottom panel are results from Mill Rocks.

Literature Cited

Bailey H, Lusseau D. 2004. Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observation sites. Marine Mammal Science 20:880-885.

Benoit-Bird K. 2014. Personal communication.

Block BA, et al. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475:86-90.

Bluhm BA, Coyle CO, Konar B, Highsmith R. 2007. High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea. Deep Sea Research Part II: Topical Studies in Oceanography 54:2919–2933.

Bost CA, Cotte C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H. 2009. The importance of oceanographic fronts to marine birds and mammals of the southern oceans. Journal of Marine Systems 78:363–376.

Brower AA, Ferguson M, Schonberg SV, Jewett SC, Clarke JT. 2016. Gray whale distribution relative to benthic invertebrate biomass and abundance: Northeastern Chukchi Sea 2009–2012. Deep Sea Research Part II: Topical Studies in Oceanography.

Burnham RE, Duffus DA. 2016. Gray Whale (*Eschrichtius robustus*) Predation and the Demise of Amphipod Prey Reserves in Clayoquot Sound, British Columbia. Aquatic Mammals 42:123-126.

Calambokidis J, Darling JD, Deeke V, Gearin P, Gosho M, Megill W, Tombach C, Goley D, Toropova C, Gisborne B. 2002. Abundance, range and movements of a feeding aggregation of gray whales (*Eschrictius robustus*) from California to southeastern Alaska in 1998. Journal of Cetacean Research and Management 4:267-276.

Calambokidis J, Laake JL, Klimeck A. 2010. Abundance and population structure of seasonal gray whales in the Pacific Northwest, 1998-2008. Paper SC/62/BRG32 presented to the IWC Scientific Committee, May 2010.

Charnov EL. 1976. Optimal foraging, the marginal value theorem. Theoretical Population Biology 9:129-136.

Cotte C, d'Ovidio F, Chaigneau A, Lèvy M, Taupier-Letage I, Mate B, Guinet C. 2010. Scale-dependent interactions of Mediterranean whales with marine dynamics. Limnology and Oceanography 56:219-232.

Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR. 1998. An integrated approch to the foraging ecology of marine birds and mammals. Deep Sea Research Part II: Topical Studies in Oceanography 45:1353-1371.

Darling JD. 1984. Gray whales off Vancouver Island, British Columbia. The Gray Whale, Eschrichtius robustus. Academic Press, Orlando, Flordia. Xxiv+ 600pp:267-287.

Dunham JS, Duffus DA. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine ecology. Progress series 223:299-310.

Fagan WF, et al. 2013. Spatial memory and animal movement. Ecology Letters 16:1316-1329.

Fauchald P, Tveraa T. 2006. Hierarchical patch dynamics and animal movement patterns. Oecologia 149:383-395.

Feyrer LJ. 2010. Differences in embryo production between sympatric species of mysids (family Mysidae) in the shallow coastal waters off Vancouver Island, BC. Marine biology 157:2461-2465.

Feyrer LJ, Duffus DA. 2011. Predatory disturbance and prey species diversity: the case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family Mysidae) community. Hydrobiologia 678:37-47.

Feyrer LJ, Duffus DA. 2014. Threshold foraging by gray whales in response to fine scale variations in mysid density. Marine Mammal Science. 31:560-578

Gailey G, Ortega-Oritz JG. 2000. Pythagoras.

Hazen EL, Johnston DW. 2010. Meridional patterns in the deep scattering layers and top predator distribution in the central equatorial Pacific. Fisheries Oceanography 19:427-433.

Kaltenberg AM, Benoit-Bird KJ. 2013. Intra-patch clustering in mysid swarms revealed through multifrequency acoustics. ICES Journal of Marine Science: Journal du Conseil 70:883-891.

Kaltenberg AM, Benoit-Bird KJ, Waluk CM. 2011. Spatial and temporal patch dynamics of mysid swarms using combined stationary and shipboard active acoustics. The Journal of the Acoustical Society of America 129:2370-2370.

Kareiva P, Odell G. 1987. Swarms of predators exhibit" preytaxis" if individual predators use area-restricted search. American Naturalist:130:233-270.

Mate B, Lagerquist B, Irvine L. 2010. Feeding habitats, migration and winter reproductive range movements derived from satellite-monitored radio tags on North Pacific gray whales. IWC SC/62/BRG21.

Mayor SJ, Schneider DC, Schaefer JA, Mahoney SP. 2009. Habitat Selection at Multiple Scales. Ecoscience. 16:238-247

Merems A. 2011. Kelp canopy and biomass survey.

Moore SE, Grebmeier JM, Davies JR. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81:734-742.

Murison LD, Murie DJ, Morin KR, de Silva Curiel J. 1984. Foraging of the gray whale along the West coast of Vancouver Island, British Columbia in Jones ML, Swartz SL, and Leatherwood S, editors. The Gray Whale: Eschrichtius robustus. Academic Press Inc.

Newell CL, Cowles TJ. 2006. Unusual gray whale *Eschrichtius robustus* feeding in the summer of 2005 off the central Oregon Coast. Geophysical Research Letters 33.

Oliver JS, Slattery PN, Silberstein MA, O'Connor EF. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Canadian Journal of Zoology 62:41-49.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC. 2014. REVIEW: On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. Journal of Applied Ecology 51:1575-1583.

Stelle LL, Megill WM, Kinzel MR. 2008. Activity budget and diving behavior of gray whales (*Eschrichtius robustus*) in feeding grounds off coastal British Columbia. Marine Mammal Science 24:462-478.

Torres LG. in press. A sense of scale: Foraging cetaceans use of scale-dependent multimodal sensory systems. Marine Mammal Science.

Torres LG, Orben RA, Tolkova I, Thompson DR. 2017. Classification of Animal Movement Behavior through Residence in Space and Time. PLoS ONE.

Torres LG, Read AJ, Halpin P. 2008. Fine-scale habitat modeling of a top marine predator: Do prey data improve predictive capacity? Ecological Applications 18:1702-1717.

Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB. 2005. Cetacean distributions relative to ocean processes in the northern California Current System. Deep Sea Research Part II: Topical Studies in Oceanography 52:145-167.

Wood SN. 2006. Generalized Additive Models: An Introduction with R. Chapman and Hall/CRC.

CHAPTER 3 – ASSESSMENT OF VESSEL DISTURBANCE TO FORAGING GRAY WHALES (*ESCHRICHTIUS ROBUSTUS*) ALONG THE OREGON COAST TO INFORM SUSTAINABLE ECOTOURISM

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Abstract

Ecotourism is movement which seeks to sustain local communities by uniting conservation, travel, and education. To minimize effects on critical animal behavior, ecotourism operations must be carefully managed. This integrative research and outreach project on the Oregon coast found significant differences in gray whale (*Eschrichtius robustus)* behavior when interacting with vessels, and translated results into vessel operation guidelines. A profitable and growing whale watch industry exists in Oregon, but prior to this project, no regional guidelines existed to protect animals and maintain sustainability of the industry. This study tracked whales and vessels in the summer 2015 using non-invasive, shore based theodolite and photo ID techniques. Two sites with differing levels of vessel traffic, Boiler Bay and Port Orford, were monitored for 4 weeks each. Whale focal follows were analyzed to assess behavior state changes relative to location, individual, and vessel presence, vessel type, and distance. There were significant differences in gray whale activity budgets between control and impact conditions, and between study sites. No significant difference in

individual response to vessels disturbance was found. Researchers and stakeholders collaboratively applied results to create scientifically informed vessel operation guidelines that balance the economic and education gains of a whale watch industry with adequate protection of the observed whale population.

Introduction

Charismatic megafauna and stunning landscapes have always attracted tourists and visitors eager to partake in the earth’s natural wonders. At its core, ecotourism is a strong and growing movement that advocates for responsible travel to natural areas that conserves the environment, sustains the wellbeing of the local people, and involves interpretation and education (Ross and Wall 1999; TIES 2015). When properly managed, such enterprises can bring monetary and educational benefits to the communities within which they are based (O’Connor *et al*. 2009). However, whenever and wherever anthropogenic activities occur, there are often environmental impacts. Communities and businesses that promote and engage in ecotourism opportunities must carefully plan for industry sustainability that maintains or improves animal and ecosystem welfare.

A number of marine mammal populations spend part, or all, of their lives in near-shore environments that provide easy viewing opportunities that form the base resource for lucrative businesses. Marine mammals also often act as an educational platform and gateway attraction to an appreciation of the marine environment. However, marine mammals are known to be sensitive to anthropogenic disturbance including behavior state changes (Lusseau 2003; Constantine *et al*. 2004), increased stress (Rolland *et al*. 2012), and altered habitat use patterns (Bejder *et al.* 2006b; Hartel *et al*. 2014; Russell *et al*. 2014), which reinforces the need for caution and appropriate regulations concerning marine mammal ecotourism ventures. Furthermore, the coastal environment is often impacted by multiple anthropogenic activities including renewable energy development, pollution, fishing pressure, and vessel traffic (Halpern *et al*. 2008; Maxwell *et al*. 2013). Marine mammals utilizing these habitats may face a cumulative burden of repeated disruptions to their normal behavior patterns from these activities. In particular, evidence shows that cetacean populations are vulnerable to vessel disturbance with long-term consequences on the health of individuals and populations in areas of high vessel traffic (Lusseau and Bejder 2007).

Despite many marine mammal species listed as threatened or endangered (IUCN 2016) protective measures vary widely by country, location and species. In the United States, the Marine Mammal Protection Act (MMPA 1972) prohibits harassment of marine species, and provides guidelines concerning approach distance (no closer than 100 yards), vessel behavior, time limits for viewing, and more. Similar strictures exist in New Zealand, Europe, South America and other countries and regions around the globe (Garrod and Fennell 2004; Carlson 2012). However, as anthropogenic seascape use increases in complexity, these large scale regulations cannot account for species, ecosystem, or industry specific disturbance thresholds, and can be difficult to enforce due to large numbers of uninformed vessel operators. To avoid disturbance while also balancing sustainable vessel-based ecotourism operations, many efforts around the world have found success with community and industry led vessel operation guidelines (Carlson 2012; NOAA-NMFS 2014) . By combining federal or regional regulations with smaller scale educational efforts tailored to species targeted by local ecotourism, conservation efforts can be more effective.

In the northeast Pacific, the preferred foraging habitat and migration routes of the gray whale (*Eschrichtius robustus*) occur in the nearshore environment (1-4 km from coast, (Sumich 1984; Green *et al*. 1995)), making them vulnerable to the cumulative effects of coastal anthropogenic impacts. Gray whales are popular attractions for ecotourism whale watching operations on their breeding grounds in Baja California, Mexico (Sumich 2014), along their migration route up the California coast, and on their feeding grounds in Oregon, Washington, British Columbia, and Alaska. The Pacific Coast Feeding Group (PCFG), a subset of the eastern North Pacific (ENP) gray whale population, is comprised of approximately 200 individuals that spend the summer months (May-October) foraging between northern California and northern British Columbia instead of migrating all the way to the Bering Sea from calving grounds in Baja California (Calambokidis *et al*. 2002). For all gray whales, the summer foraging period is a critical time to regain energy stores since individuals can lose between 11-29% of their body mass during the migrations (Villegas-Amtmann *et al*. 2017).

Gray whales are very flexible and opportunistic in their foraging strategies. Their most well-known foraging tactic is suction feeding in shallow mud flats, but they have also been documented foraging on mysids, amphipods, porcelain crab larvae, and ghost shrimp (Oliver *et al*. 1984; Dunham and Duffus 2001; Newell 2009; Feyrer and Duffus 2011). Though many uncertainties about the ecology of the PCFG remain, individuals demonstrate high inter- and intra-annual re-sight rates (Darling 1984), but also variable and often broad (110 km to 330 km) movement patterns across the PCFG region within one foraging season (Mate *et al*. 2010, Calambokidis *et al*. 2010). Although Lang *et al*. (2014) found evidence of mtDNA genetic differentiation between the PCFG and the ENP, with matrilineal fidelity as a potential driver for this structure, there is debate over whether the PCFG is a genetically distinct subpopulation (D'Intino *et al*. 2013), as other scenarios (*e.g.*, colonization history, number of founders, and immigration rates) could explain the observed mtDNA differences. Yet, there is agreement that the PCFG should be managed separately from the ENP because ‘takes’ from this population could disproportionally affect certain matrilineal lines, potentially impacting the cultural memory of these feeding grounds and resulting in localized extirpation (Clapham *et al*. 2008; D'Intino *et al*. 2013). Therefore, anthropogenic impacts to this small sub-population should be monitored and evaluated.

Gray whales along the Oregon coast support a small, but lucrative whale watch industry that thrives in various communities along the Oregon coast. In 2008, whale watching alone brought in over $29.8million and >645,000 visitors to the Oregon Coast (O’Connor *et al*. 2009). Many of these whale watch operations occur in small coastal communities with lower economic standing, where declines in natural resource extraction and natural resource based manufacturing jobs have created a need for alternative revenue streams (Swedeen *et al*. 2008). Whale watching, and the tourists it attracts, has become an important component to the coastal economy. Reliance on a single resource necessitates a plan for sustainable use in order to ensure viability of any industry. It is crucial that gray whale health is prioritized as whale watching operations grow on the Oregon Coast to ensure the whales return in perpetuity and can sustain the industry. Additionally, whale watch vessels are not the only boats that come in close contact with whales. The Oregon coast supports a large commercial and recreational fishing industry, as well as pleasure boaters (kayak, sailboats) and transiting cargo and barge vessels. It is unknown how many vessel operators are aware of, or abide by, the recommendations of the MMPA guideline threshold approach distance of 100 yards. Prior to this work, no regional vessel operation guidelines were available to users of the marine environment in Oregon.

The aim of this study is to document gray whale behavioral response to vessels in Oregon coastal waters and use these data to collaboratively develop industry approved guidelines to reduce the impact of all vessels on whales in Oregon waters. Whales and vessels were tracked simultaneously to assess and monitor whale behavior changes due to vessel presence. Conservation science is only as good as its outreach; therefore, over the course of the project, public meetings were used to interface with a diverse group of community stakeholders. These forums were designed to build community engagement, report project activities and results, explain the need for and benefits of guidelines, generate local guidelines, and encourage the industry to lead by example.

Methods

Field operations

During the 2015 summer period (June – September) gray whale and vessel movements were synoptically recorded using a shore-based theodolite. Two sites along the Oregon coast were sequentially monitored for approximately 4 weeks total at each site to compare an area with relatively high vessel traffic and an active whale watch industry (Boiler Bay) to an area with low vessel traffic and minimal whale watch presence (Port Orford; Fig. 4). Boiler Bay is a small, rugged, basalt rimmed bay with a near-shore rocky reef and associated kelp beds; a small gully provides excellent fishing and gray whale foraging habitat. The survey area was limited by cliff height (18 m) and covered ~8 km^2. Nearby Depoe Bay, just 2.4 kilometers south, provides ocean access for the whale watching community, charter and recreational fishers, and personal watercraft. There are four companies that offer whale watching, charter fishing, or both in Depoe Bay. Together, they field a fleet of 19 vessels, many of which make multiple fishing or sightseeing trips a day. In contrast, the Port Orford region has both rocky reefs, extensive kelp beds (Merems 2011), and sandy bottom areas within the study area of ~12 km^2 visible from a cliff top (65 m). Local water access is restricted to a shallow harbor serviced by boat crane, resulting in a small commercial offshore fishing industry, but little other vessel traffic. There is one kayak-based wildlife-watching tour company operating in Port Orford.

Survey effort at both locations began daily at sunrise (barring fog) and continued until Beaufort sea-state of 4 or more compromised visibility and data collection. Observers worked in teams of three or more to simultaneously track whales and vessels using non-invasive observational methods including binoculars and a theodolite, a surveyor’s tool that provides precise geo-located positions of the targets (Bailey and Lusseau 2004). In addition to whale location data at each surfacing, the following data was collected: photo-identification images, group composition (with calf, solitary), behavior state (forage, rest, social, travel, sharking), and number of whales in a 100 m vicinity. Data on vessel characteristics was also recorded including vessel size, engine type, vessel type (fishing, tourist, recreational, kayak), speed of travel, and orientation to whale(s).

Community workshops

Throughout the two year research project, community stakeholders were invited to a series of workshops through email, phone and personal invitations. Four workshops were held in the Depoe Bay and Port Orford communities to inform stakeholders of research efforts and preliminary results. Meetings began with a short presentation of project updates and relevant information for the open forum question and answer session that followed. Participants discussed ongoing research, global examples of issues with whale watching, examples of other communities' guidelines, and potential for guidelines in Oregon. Guidelines were collaboratively drafted, and methods of brochure and information distribution were deliberated. A written feedback period culminated workshops. Finally, meeting minutes were typed and disseminated to stakeholders after workshops via email.

Data Analysis

Behavior classification

All theodolite tracks were made using the program Pythagoras (Gailey and Ortega-Oritz 2000), and corrected for height of station, tide, and azimuth. All tracklines were smoothed using an R (R Core Team 2015) script to identify gaps of greater than 8 minutes, and linearly interpolated at 4 minute intervals. Tracklines were then analyzed using Residence in Space and Time (RST; Torres *et al*. 2017) to assign behavior states to each point. Focal follows of less than 1 hour were discarded for this analysis to ensure accurate classification of behavior states by the RST analysis. The RST behavior classification method is scale dependent, and quantifies occupancy patterns in space and time within a circle of a given radius. RST identifies “time intensive”, “travel”, and “time and distance intensive” behaviors through the use of normalized residence time and residence distance metrics. Dynamic scaling of each trackline was used to determine the appropriate radius for analysis to each track and assign behavior states. Due to the fine scale of analysis and the lack of any observed resting behavior, ‘time intensive’ behaviors were interpreted as ‘foraging’ due to persistent presence in a small area (patch use), and 'time and distance intensive' behaviors were interpreted as 'searching'.

Vessel interactions

Using the R package wildlifeDI (Long 2014), whale and vessel tracklines were analyzed to identify instances of overlap within temporal (10 minutes) and spatial limits. Distance bins of 100 m, 150 m, 250 m, and 400 m were used to investigate distance mediated variations in vessel impact. Whale track locations where a vessel interaction occurred were classified as "impact", while locations without vessel interaction were considered "control". Vessels were classified into four categories: Fishing, Tour, Personal, and Kayak. Fishing boats tended to set up on a fishing hole and remained stationary for extended periods of time. Tour boats, ranging in size from 8 m (26 ft) zodiacs to 15 m (50 ft) charter vessels, were explicit whale and wildlife watching expeditions that often followed individual whales. Personal vessels were unpredictable in their fishing or wildlife watching behavior. Kayaks were non-motorized paddle craft that were typically closer to shore than motorized vessels that were constrained by size to stay further offshore.

Behavioral impacts of vessel interactions on gray whales were investigated using Markov chains. Markov chains quantify the dependence of a succeeding event on a preceding event while accounting for the inherent temporal autocorrelation (Guttorp 1995; Caswell 2001; Lusseau 2003). The dependence between events can be affected by any extrinsic element, allowing the effect of outside factors to be evaluated. Impact and control contingency tables were constructed and the three behavior states derived from the RST analysis (search, travel, and forage) were assessed. Transition probabilities (*e.g.*, likelihood of switching from search to forage, or to continue searching) were calculated according to Lusseau (2003):

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}} , \qquad \sum_{j=1}^{n} p_{ij} = 1$$

where j is the current behavior state, i is the previous behavior state, a_{ij} is the number of transitions observed from behavior state i to j, n is the total number of behavior states, and p_{ij} is the transition probability from i to j in the Markov chain. The impact and control activity budgets were compared using a Z test for proportions (Newcombe 1998; R Core Team 2015) and calculated 95% confidence intervals where p -values < 0.05 were considered statistically significant. Behavioral transition probabilities were investigated between impact and control, and between motorized and non-motorized vessels.

Several whale tracklines were repeat tracks of the same individual, as determined through photo-identification. To investigate the possibility of individual bias in responses to vessel interactions, a one way, between subjects ANOVA was performed on the output behavior change probabilities from the Markov chain analysis. These probabilities take into account the inherent track specific behavior transition probabilities during control periods (no vessel present), and hence describe the likelihood of whale behavior state change under impact conditions. Multiple tracklines were used as replicates to calculate average probabilities of behavior state change per individual, and each category of behavior transition was tested independently of the others.

Results

During the study period, the research team spent 52 days (245.5 h) observing whales and vessels. One hundred and eighty-one gray whale focal follows were conducted spanning 168.6 hours, and vessels were present in the study area during 90.8 hours (Table 4). Once the dataset was limited to only tracks longer than 1 hour, a total of 48 tracks from 28 individuals were available for analysis, including 4,146 behavior transitions. RST analysis radii per individual track were calculated with the dynamic scaling option and varied between 17-125 m, with an average of 48 m ± 27 m.

Activity budgets

There was no significant difference in gray whale activity budgets between the two different study sites ($\chi 2 = 0.662$, df = 2, p-value = 0.718; Fig. 5). On average, gray whales spent 62% of their time searching for food, 20% foraging, and 17% traveling. Slightly more searching behavior was observed at the Port Orford site, likely because the higher observation post allowed for a large observation area.

Gray whale activity budgets were affected by the presence of vessels, and there were differences between the two sites in how these impacts manifested (Table 5). Impact activity budgets presented here were calculated at a vessel distance bin of 250 m because sample size was too low in smaller bins (100 m, 150 m), and trends of significance were similar at 400 m.

When vessels were present within 250 m, whales in Port Orford spent 17% more time searching for food, while whales in Boiler Bay spent 17% less time searching for food. Whales in Boiler Bay spent more than twice as much time traveling when vessels were present than whales in Port Orford. Intriguingly, time spent foraging remained similar between impact and control situations in Boiler Bay, but decreased by 11% in Port Orford. The difference between Boiler Bay and Port Orford behavioral budgets when vessels were present was statistically significant ($\chi 2 = 30.38$, df = 2, p-value = <0.001), so the Markov chain analysis was split by site.

Markov Chains and Behavioral Transitions

Boiler Bay tests were run on 19 tracklines and 1732 behavioral transitions. Port Orford tests were run on 29 tracklines and 2409 behavioral transitions. Results from the Markov chain analysis and Pearson's chi-squared test demonstrated that vessel interactions had a non-homogenous effect on gray whale behavioral transitions (Fig. 6). In Boiler Bay, two behavior transitions showed statistically significant differences between impact and control situations. Under impact conditions with a vessel within 250 m, the likelihood of a gray whale transition from Searching → Traveling increased ($\chi 2 = 10.83$, p-value <0.001), while the likelihood of transition from Searching → Searching decreased ($\chi 2 = 12.89$, p-value <0.001). These results indicate that when gray whales in the Boiler Bay region encounter a vessel, they are up to 23% more likely to begin travelling and between 14 - 40% less likely to continue searching for food.

In Port Orford, three transitions were statistically different between impact and control situations. Under impact conditions two behavioral transitions decreased: traveling → traveling ($\chi 2 = 4.29$, p-value = 0.03) and foraging → foraging ($\chi 2 = 5.57$, p-value = 0.01). However, the likelihood of continuing to search (searching → searching; $\chi 2 = 6.02$, p-value = 0.01) increased. Contrasting with whale behavioral transitions in Boiler Bay, these results show that whales in Port Orford were 4 – 28% more likely to continue searching for food when under vessel impact conditions, 5-14% less likely to continue foraging, and 4-10% less likely to continue traveling. These trends held true for all distance bins investigated (100 m, 150 m, 250 m, and 400 m).

Kayaks vs vessels with motors

Investigations of whale behavioral transitions mediated by vessel type were limited by sample size of single vessel type interactions. Therefore, all motor vessels were pooled together and compared to the kayak group. The majority of kayak - whale interactions occurred in Port Orford, while the majority of motored vessel (tour, fishing and personal) interactions occurred in Boiler Bay. Two behavior transitions, searching → searching and foraging → foraging, showed statistically significant differences between kayak and motorized vessel - whale interactions. Whales were 27-63% less likely to continue searching in the presence of motor boats compared to kayaks ($\chi 2 = 19.45$, p-value <0.001). In contrast, whales were up to 26% more likely to continue foraging within 250 m of motor boats compared to kayaks ($\chi 2 = 6.17$, p-value = 0.01). While not statistically significant, it is interesting to note that whales were more likely to continue traveling ($\chi 2 = 1.96$, p-value = 0.16), or switch from searching to traveling ($\chi 2 = 2.69$, p-value = 0.10) in the presence of motor boats.

Individual whale vessel response

Tracklines used in this analysis came from three individuals that were tracked three times each under impact conditions, and eight individuals that were tracked multiple times, but only had one track under impact conditions. Results from the ANOVA show no significant difference in individual response to vessel presence except in the forage → forage transition (Table 5). However, post-hoc analysis showed this difference to be driven almost entirely by one individual, who exhibited a range of behaviors under control conditions, but foraged exclusively while under impact conditions.

Community workshops

Community workshop participants included representatives from the whale watch industry, commercial and recreational fisheries, local NGOs and conservation groups, The Oregon Department of Fish and Wildlife, Oregon Parks and Recreation, and local community members. Preliminary results were presented to stakeholders at meetings shortly after the 2015 field season (November), and follow up meetings were hosted approximately six months later to give progress updates on data analysis and brochure development.

Stakeholder meetings were cordial but some participants approached the process with skepticism regarding our intent and expected outcome. Throughout the stakeholder meetings, participants often repeated a desire for data concerning vessel impacts on whales before they would consider changing operating practices. Other common reactions from industry included (1) suspicion that community led guidelines would become legislation, (2) agreement that whales should be protected, (3) disinclination to change current practices since industry has been profitable for 30 years and whales have not left area, (4) dislike of time limits with individual whales, and (5) irritation with shore-based incident reporters. All these concerns were addressed by gathering, analyzing, and presenting the data presented above. It was also repeatedly emphasized that the intention of this effort was to increase sustainability of the industry, promote this sustainability through the website (watchoutforwhales.org) and brochure distribution, and highlight that the authors know of no precedent where ecotourism industry guidelines became laws. Furthermore, “Watch Out for Whales” guidelines are intended for all boaters in Oregon waters, and industry operators, who already adhere to MMPA rules, are well placed to act as advocates and lead by example in their implementation. Guidelines were written in conjunction with stakeholders, and built off the baseline provided by the MMPA (1972). The Oregon “Watch Out for Whales” vessel operation guidelines are as follows:

- Stay at least 100 yards away from whales. If a calf is present, stay 150 yards away.
- Do not fly drones within 300 yards (vertical or horizontal distance) of a whale.
- Do not spend more than 30 minutes with an individual whale.
- Let the animals decide where to go. Do not corral a whale between boats, or pin it against shore.
- Do not approach fast. Do not leave fast.
- Keep noise to a minimum (do not bang on the side of your boat).
- Do not feed or attempt to swim with whales.

An engaging information brochure (Fig. 7) was developed to bridge the gap between scientific results and public understanding. Eight thousand copies will be distributed along the Oregon coast to disseminate these guidelines, provide information on gray whale ecology, and explain why adherence to the guidelines is important for all vessels to follow. A website (watchoutforwhales.org) was also created where the brochure is freely downloadable, information is available on the scientific methods and results behind these guidelines, and links to project partners and other information on marine mammal guidelines are provided.

Discussion

This study demonstrates that gray whale behavior on the coast of Oregon was significantly affected by interactions with vessels. There were significant, site specific, differences between control and impact activity budgets, indicating that whales are more likely to abandon searching behavior when approached by vessels. These research efforts were communicated through outreach events targeted to the local stakeholders to enhance engagement in the guideline development process. This two year process of data collection, communication, and stakeholder engagement resulted in Oregon’s first vessel operation guidelines around whales and the dissemination of these guidelines through an informational brochure and website aimed at all vessel operators. Analyses indicated that individual whales reacted similarly to vessel disturbance, indicating that developed guidelines should be effective for management at the population level.

The Markov chain analysis revealed that, much like Newton’s law of inertia, whales were always more likely to remain in a given behavior state than to transition into a different one. Yet, the probability of gray whale behavior state switching varied by site. In Boiler Bay, where vessels were much more common, whales were significantly more likely to stop searching and switch to traveling when they encountered a vessel, but did not transition away from foraging behavior, indicating that the whales may tolerate vessel disturbance if foraging. Gill *et al*. (2001) argued that behavior changes due to anthropogenic disturbance varies both spatially and temporally based on local conditions, and Beale and Monaghan (2004) found that shorebirds with the most to lose from a reduction in feeding showed the least response to disturbance. For the PCFG whales at Boiler Bay, it appears that the opportunity to forage takes precedence over potential disturbance from vessel presence. However, if an energy rich foraging patch had not yet been found, whales were more likely to abandon searching behavior and begin traveling to avoid vessels. In contrast, whales in Port Orford were more likely to switch to searching from any other behavior when they encounter a vessel, possibly because searching is more common due to the larger area surveyed. Additionally, whales in Port Orford did not tolerate disturbance to foraging like in Boiler Bay, and were more likely to abandon a foraging bout. One explanation for this disparity between sites could be that individuals who exhibit site fidelity to Boiler Bay have become habituated to vessel disturbance over time, whereas individuals in Port Orford have not habituated. Some individuals have been documented returning to the Depoe Bay region for more than 20 years (Newell 2009), consequently, the tolerance to disturbance shown in this study, could be a learned response over time.

The vessel community composition between study sites also provides a plausible explanation for the contrasts in behavioral responses. Boiler Bay vessel traffic is dominated by motorized water craft whereas the majority of vessel interactions in Port Orford occurred with kayaks. When whale behaviors near kayaks are juxtaposed with those near motorized vessels, the same (non-significant) trends determined by the site comparison analysis are seen: whales were more likely to forage near motor boats (*i.e.*, more foraging in Boiler Bay than in Port Orford) and more likely to search near kayaks (*i.e.*, more searching in Port Orford than Boiler Bay). The trend for travelling, or switching to travel, more frequently in the presence of motor boats may be due to the fact that travelling behavior in Port Orford usually occurs further offshore, in deeper waters than most kayaks that stay closer to shore. Gray whales are also known to be acoustically sensitive (Moore and Clarke 2002, Dahlheim and Castellote 2016), thus the sound of vessel motors may forewarn individuals of a vessel's arrival and allow for risk assessment and a decision to continue its behavior or not. Since kayaks are acoustically cryptic, whales may be surprised by an encounter, perceive a risk, and abandon a forage patch (Frid and Dill 2002). This acoustic distinction could be an explanation for the decrease in foraging near kayaks, compared to near motor vessels.

Individual response to vessel interactions was only significant for one type of behavior transition: forage → forage, which was driven by one individual that only foraged while interacting with vessels. While ecologically interesting, this one significant behavior change is unlikely to be relevant for management purposes aimed at population-level patterns. The behavior transitions of PCFG whales exemplify how within niche variation falls within the curve of the total niche width (Bolinick *et al.*

2003). This ecological pattern is appropriate for management because population variability can be captured by broad recommendations and protective measures.

The marine environment is complex, making direct links between whale behavior and vessel presence difficult to conclusively ascertain. Animal behavior classification can be subjective and scale-dependent (Ogburn *et al*. 2017), yet the application of RST (Torres *et al*. 2017) here allowed each track to be assessed at an appropriate scale and assigned behavior states objectively. Confidence in behavior class assignment is gained from the dichotomous distribution of foraging and searching locations across the study areas (per obs.). Additionally, vessel impact analysis was constrained by a low sample size of single vessel-type interactions with whales (multiple vessel interactions were more common). With industry partnerships now established, collaborative controlled exposure experiments using individual vessel types and variable numbers of vessels could be conducted to more closely examine whale response patterns (*e.g.*, Williams and Ashe, 2007). Furthermore, only surface behaviors were monitored as metrics of disturbance, yet whales may exhibit responses through physiological traits or subsurface behaviors. Persistent occupancy of a habitat without measurable difference in surface behavior, does not imply an absence of impact from vessel interactions and other anthropogenic stressors (Gill *et al*. 2001; Bejder *et al*. 2006a). While gray whales appear to tolerate short-term disturbance to foraging behavior, future work could examine the stress hormone response of whales to vessel disturbance at multiple time scales. Additionally, future work should investigate whether demographic groups, such as sex, age, and health (body condition), are more or less susceptible to vessel disturbance.

Outreach efforts were directly informed by project results that found significant differences in whale behavior state change probabilities at all distance bins investigated (100 – 400 m). While the “Watch Out for Whales” guidelines are derived from federal guidelines and common sense, the addition of a specific local fact to guidelines (Fig. 7; upper right corner) helped to build a sense of regional specificity, and strengthened buy-in from some stakeholders. The stipulation that guidelines apply to all water craft was important in two ways: (1) Results show some divergence in how whales react to different types of vessels, and (2) no single group of vessel operators (*i.e.*, recreational, commercial, kayak) felt unduly targeted. A challenge to outreach efforts was convincing skeptic tour operators that local vessel operation guidelines would not be cumbersome or detrimentally impact their business. As long term monitoring of the PCFG continues, these community relationships will continue to develop, and the research team believes that skeptics will benefit from the publicity and sustainability offered by the guidelines.

Previous studies have cast doubt on the efficacy of voluntary codes of conduct in conserving natural resources (Duprey *et al*. 2008; Wiley *et al*. 2008; Parsons 2012). Wiley *et al*. (2008) found high levels (74-88%) of non-compliance with speed restrictions to voluntary vessel operation guidelines for whale watching on Stellwagen Bank, MA, USA. Furthermore, when informed of results, operators argued that due to fewer whales in the study area during the years of the study, operators were under increased time pressure to fulfill customer expectations while keeping to their commercial schedule. This willingness to ignore guideline programs when they impede business or otherwise become inconvenient is problematic. Distance limits are a common metric for vessel operation guidelines. However, distance estimation on the water takes practice, and overeager passengers, or inexperienced captains, can either willfully or unintentionally find themselves in breach of the MMPA’s 100 yard regulation. For this reason, the “Watch Out for Whales” brochure was designed to be posted in wheel houses and on marina information boards that are areas of high visibility to ecotourists and casual boaters. Retention of information in the brochure is encouraged through the use of infographics (and a touch of humor) for the guidelines. Partner stakeholders were supplied with brochures for distribution to customers to educate them about the guidelines and why they are needed. It is hoped that with increased visibility and education, customers may put less pressure on captains to bend the rules. Creation of the website (watchoutforwhales.org) had three goals: (1) to complement the brochure with additional information, and (2) to promote whale watch partners as sustainably conscious companies, and (3) to attract more business.

Marine mammal ecotourists who speak to a docent are more likely to believe that their actions affect the marine environment than visitors who do not speak to a docent (Christensen *et al*. 2007). Furthermore, marine mammal tourists that participated in targeted environmental education are more likely to be aware of the consequences of their actions and behave in an environmentally responsible manner (Christensen *et al*. 2008). These studies demonstrate that repeated encounters with information about the guidelines' value can lead to awareness of the consequences of human actions and hopefully, individual behavior change. Encouraging whale watch operators to educate passengers about the importance of the guidelines, as well as posting guidelines broadly will help the Oregon Coast grow as a sustainable, scientifically informed ecotourism destination.

This study adds to the growing body of literature concerning mitigation efforts for marine ecotourism impacts on marine mammals. Although vessel operation guidelines may not address all aspects of marine mammal health, collaborative, community efforts of education and outreach at multiple scales can be an effective tool to start discussions concerning marine conservation. Deliberate planning of joint research and outreach projects gives strength and credibility to translate results into action for sustainable growth of the marine ecotourism industry. Intentional design of vessel operation guideline media to be easily understandable and attractive to a wide audience also expands the potential reach of this project. As communities around the globe strive for more compliance with local and federal regulations, reaching out to the uninformed, and inspiring conservation of the marine environment through educational ecotourism opportunities are excellent strategies to recruit new conservationists. We hope that the combination of dedicated scientific investigation with targeted outreach and education will benefit all involved: whales, industry and community.

Tables

Table 4. Summary of vessel tracking effort.

	Fishing Boat	Personal Boat	Kayak	Tour Boat
Number of vessels tracked	173	142	73	26
Total time with whales (hh:mm)	41:41	20:09	16:30	12:33

Table 5. Behavioral budgets change with presence and absence of vessels by site. Cell values are the percent of time spent in behavior state.

	Boiler Bay		Port Orford	
	Vessels within 250 m	No Vessels	Vessels within 250 m	No Vessels
Search	43.2%	60.1%	81.0%	64.1%
Forage	25.0%	22.7%	7.9%	18.7%
Travel	31.8%	17.2%	11.1%	17.2%
Number of Transitions (n =)	44	1689	63	2333

Table 6. Pooled sample size of gray whale and vessel interactions by distance bin.

Distance bin	100m	150m	250m	400m
Impact (n=)	31	55	107	1663
Control (n=)	4105	4079	4022	3956

Table 7. Results from one way between groups ANOVA performed on probability of individual behavior state change in the presence of vessels. Bold type indicates a significant result.

Behavior transition	degrees freedom (within groups/ between groups)	F-stat	P-value
Search → Search	10/6	1.85	0.2333
Search → Forage	10/6	2.8	0.1103
Search → Travel	10/6	0.86	0.6056
Forage → Search	10/6	0.89	0.5886
Forage → Forage	**10/6**	**21.16**	**0.0007**
Forage → Travel	10/6	0.34	0.9354
Travel → Search	10/6	1.55	0.306
Travel → Forage	10/6	0.32	0.9451
Travel → Travel	10/6	2.28	0.1631

Figures

Figure 4. Locations of study sites along the Oregon Coast: Boiler Bay to the north, and Port Orford 240 km to the south.

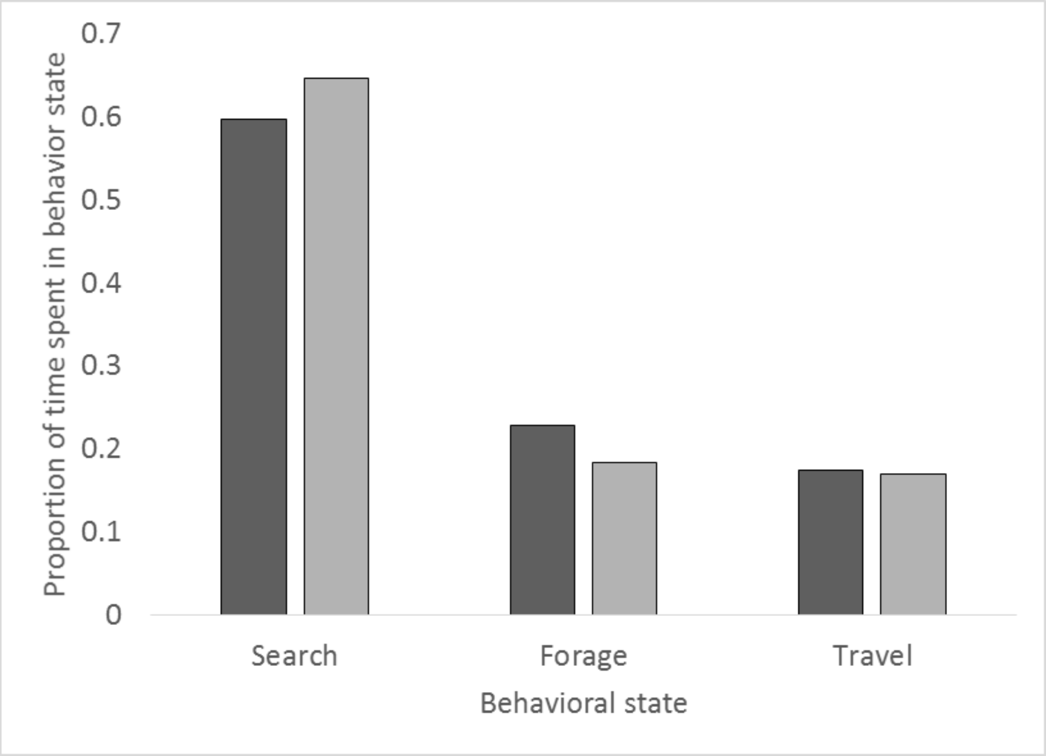


Figure 5. Behavioral activity budget for gray whales at two study sites along the Oregon Coast, indicating no significant difference between the two sites. Dark gray bars are Boiler Bay, light gray bars are Port Orford.

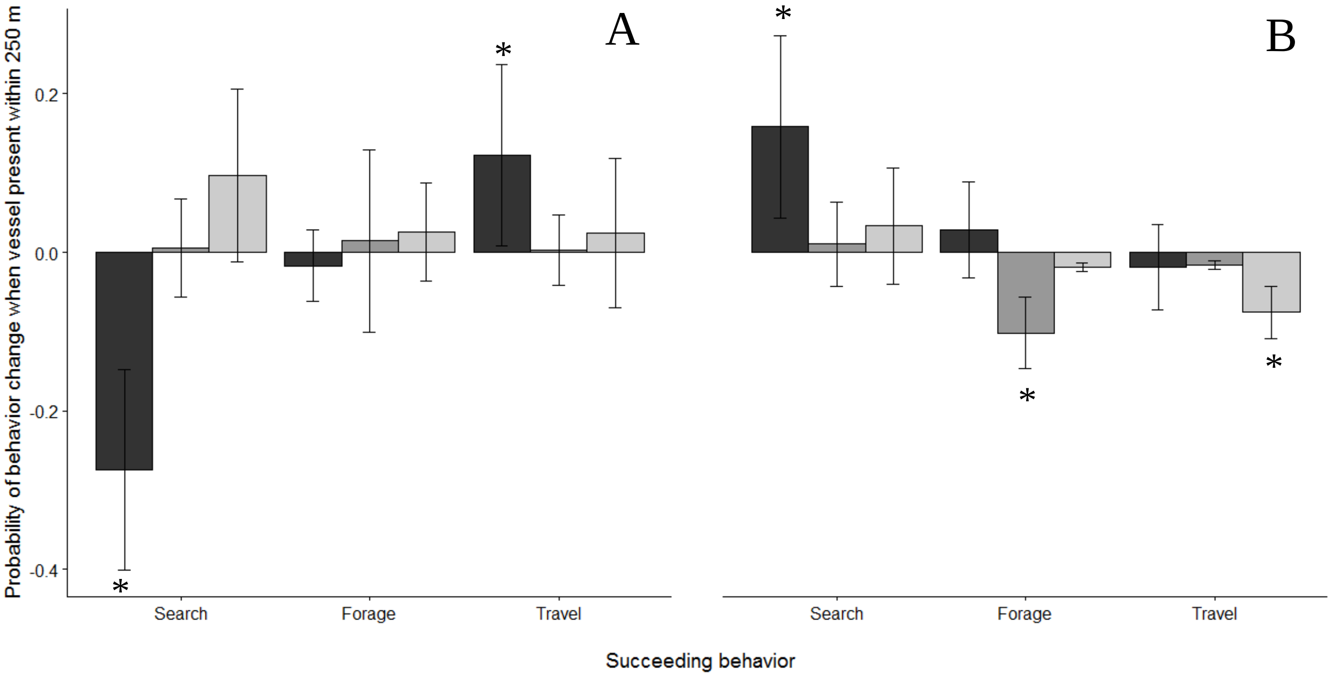
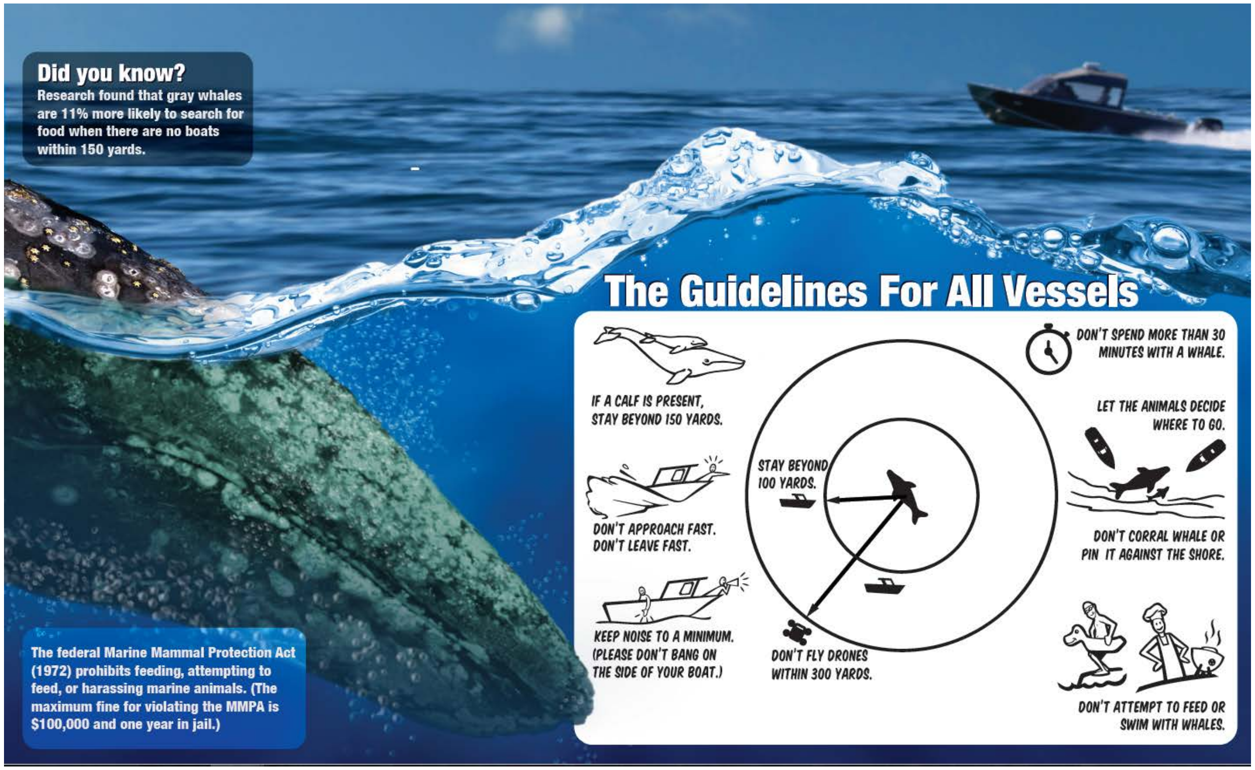


Figure 6. Difference in transition probabilities between impact (vessels within 250 m) and control (no vessels within 250 m) states at (A) Boiler Bay and (B) Port Orford. Bar shading depicts preceding behavior state: search (black), forage (gray), or travel (light gray). Error bars show 95% confidence interval. Asterisk denotes significance at $p < 0.05$, yet transitions with $p < 0.05$ where the confidence interval crossed zero were not considered significant.



Did you know?
Research found that gray whales are 11% more likely to search for food when there are no boats within 150 yards.

The federal Marine Mammal Protection Act (1972) prohibits feeding, attempting to feed, or harassing marine animals. (The maximum fine for violating the MMPA is $100,000 and one year in jail.)

The Guidelines For All Vessels

IF A CALF IS PRESENT, STAY BEYOND 150 YARDS.

DON'T APPROACH FAST. DON'T LEAVE FAST.

KEEP NOISE TO A MINIMUM. (PLEASE DON'T BANG ON THE SIDE OF YOUR BOAT.)

STAY BEYOND 100 YARDS.

DON'T FLY DRONES WITHIN 300 YARDS.

DON'T SPEND MORE THAN 30 MINUTES WITH A WHALE.

LET THE ANIMALS DECIDE WHERE TO GO.

DON'T CORRAL WHALE OR PIN IT AGAINST THE SHORE.

DON'T ATTEMPT TO FEED OR SWIM WITH WHALES.

Figure 7. Vessel operation guideline brochure interior. Design intentionally places viewer in the whale’s perspective to enhance empathy with the whale at the interface of underwater and surface habitats with vessel nearby. Layout also encourages use as a poster in vessel wheelhouses and marine notice boards. Humor was used in infographics to help readers remember guidelines.

Literature Cited

Bailey H, Lusseau D. 2004. Increasing the precision of theodolite tracking: modified technique to calculate the altitude of land-based observation sites. Marine Mammal Science 20:880-885.

Beale CM, Monaghan P. 2004. Behavioural responses to human disturbance: a matter of choice? Animal Behaviour 68:1065-1069.

Bejder L, Samuels A, Whitehead H, Gales N. 2006a. Interpreting short-term behavioural responses to disturbance within a longitudinal perspective. Animal Behaviour **72**:1149-1158.

Bejder L, Samuels A, Whitehead H, Gales N, Mann J, Connor RC, Heithaus MR, Watson-Capps J, Flaherty C, Krutzen M. 2006b. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20:1791-1798.

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003. The Ecology of Individuals: Incidence and Implications of Individual Specialization. The American Naturalist 161:1-28.

Calambokidis J, Darling JD, Deeke V, Gearin P, Gosho M, Megill W, Tombach C, Goley D, Toropova C, Gisborne B. 2002. Abundance, range and movements of a feeding aggregation of gray whales (*Eschrictius robustus*) from California to southeastern Alaska in 1998. Journal of Cetacean Research and Management 4:267-276.

Carlson C. 2012. A review of whale watch guidelines and regulations around the world version 2012, International Whaling Commission.

Caswell H. 2001. Matrix population models. Sinauer Associates, Boston, Massachusetts.

Christensen A, Needham MD, Rowe S. 2008. Whale Watchers' Past Experience, Value Orientations, and Awareness of Consequences of Actions on the Marine Environment. Tourism in Marine Environments 5:271-285.

Christensen A, Rowe S, Needham MD. 2007. Value orientations, awareness of consequences, and participation in a whale watching education program in Oregon. Human Dimensions of Wildlife. 289-293.

Clapham PJ, Aguilar A, Hatch LT. 2008. Determining spatial and temporal scales for management: lessons from whaling. Marine Mammal Science 24:183-201.

Constantine R, Brunton DH, Dennis T. 2004. Dolphin-watching tour boats change bottlenose dolphin (Tursiops truncatus) behaviour. Biological Conservation 117:299-307.

D'Intino AM, Darling JD, Urban J, Fraiser TR. 2013. Lack of nuclear differentiation suggests reproductive connectivity between the ‘southern feeding group’and the larger population of eastern North Pacific gray whales, despite previous detection of mitochondrial differences. J. Cetacean Res. Manage 13:97-104.

Dahlheim M, Castellote M. 2016. Changes in the acoustic behavior of gray whales Eschrichtius robustus in response to noise. Endangered Species Research 31:227-242.

Darling JD. 1984. Gray whales off Vancouver Island, British Columbia. The Gray Whale, Eschrichtius robustus. Academic Press, Orlando, Flordia. Xxiv+ 600pp:267-287.

Dunham JS, Duffus DA. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine Ecology Progress Series 223:299-310.

Duprey NMT, Weir JS, Wursig B. 2008. Effectiveness of a voluntary code of conduct in reducing vessel traffic around dolphins. Ocean and Coastal Management 51:632–637.

Feyrer LJ, Duffus DA. 2011. Predatory disturbance and prey species diversity: the case of gray whale (*Eschrichtius robustus*) foraging on a multi-species mysid (family Mysidae) community. Hydrobiologia 678:37-47.

Frid A, Dill LM. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11.

Gailey G, Ortega-Oritz JG. 2000. Pythagoras.

Garrod B, Fennell DA. 2004. An analysis of whale watching codes of conduct. Annals of Tourism Research 31:334–352.

Gill JA, Norris K, Sutherland WJ. 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265-268.

Green GA, Brueggeman JJ, Grotefendt RA, Bowlby CE. 1995. Offshore distances of gray whales migrating along the Oregon and Washington Coasts, 1990. Oceanographic Literature Review. 69:711.

Guttorp P 1995. Stochastic modeling of scientific data. Chapman & Hall, New York.

Halpern BS, et al. 2008. A Global Map of Human Impact on Marine Ecosystems.

Hartel EF, Constantine R, Torres LG. 2014. Changes in habitat use patterns by bottlenose dolphins over a 10-year period render static management boundaries ineffective. Aquatic Conservation: Marine and Freshwater Ecosystems 25:701-711.

IUCN. 2016. The IUCN Red List of Threatened Species Available from http://www.iucnredlist.org (accessed 21 December 2016).

Lang AR, Calambokidis J, Scordino J, Pease VL, Klimek A, Burkanov VN, Gearin P, Litovka DI, Robertson KM, Mate BR. 2014. Assessment of genetic structure among eastern North Pacific gray whales on their feeding grounds. Marine Mammal Science.30:1473-1493.

Long J. 2014. wildlifeDI: Calculate Indices of Dynamic Interaction for Wildlife Telemetry Data.

Lusseau D. 2003. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. Conservation Biology **17**:1785-1793.

Lusseau D, Bejder L. 2007. The Long-term Consequences of Short-term Responses to Disturbance Experiences from Whalewatching Impact Assessment. International Journal of Comparative Psychology 20:228-236.

Maxwell SM, et al. 2013. Cumulative human impacts on marine predators. Nature Communications. 4.

Merems A. 2011. Kelp canopy and biomass survey.

Moore S, Clarke JT. 2002. Potential impact of offshore human activities on gray whales(*Eschrichtius robustus*). Journal of Cetacean Research and Management 4:19-25.

Newcombe RG. 1998. Interval Estimation for the Difference Between Independent Proportions: Comparison of Eleven Methods. Statistics in Medicine 17:873–890.

Newell C. 2009. Ecological interrelationships between summer resident gray whales (*Eschrichtius robustus*) and their prey, mysid shrimp (*Holmesimysis sculpta* and *Neomysis rayi*) along the Central Oregon Coast.

NOAA-NMFS. 2014. Be Whale Wise, Available from (http://www.bewhalewise.org/ 2014).

Oliver JS, Slattery PN, Silberstein MA, O'Connor EF. 1984. Gray whale feeding on dense ampeliscid amphipod communities near Bamfield, British Columbia. Canadian Journal of Zoology 62:41-49.

O’Connor S, Campbell R, Cortez H, Knowles T. 2009. Whale Watching Worldwide: Tourism numbers, expenditures and economic benefits. Yarmouth MA, USA.

Ogburn MB, Harrison A-L, Whoriskey FG, Cooke SJ, Flemming JEM, Torres LG. 2017. Addressing Challenges in the Application of Animal Movement Ecology to Aquatic Conservation and Management. Frontiers in Marine Science 4.

Parsons E. 2012. The negative impacts of whale-watching. Journal of Marine Biology 2012.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice DW, Wolman AA 1971. The life history and ecology of the gray whale (*Eschrichtius robustus).* American Society of Mammalogists.

Rolland RM, Parks SE, Hunt KE, Castellote M, Corkeron PJ, Nowacek DP, Wasser SK, Kraus SD. 2012. Evidence that ship noise increases stress in right whales. Proceedings of the Royal Society of London B: Biological Sciences. 279:2363-2368

Ross S, Wall G. 1999. Ecotourism: towards congruence between theory and practice. Tourism management 20:123-132.

Russell DJF, Brasseur S, Thompson D, Hastie GD, Janik VM, Aarts G, McClintock BT, Matthiopoulos J, Moss SEW, McConnell B. 2014. Marine mammals trace anthropogenic structures at sea. Current Biology 24:R638-R639.

Sumich J 2014. E. robustus The biology and human history of gray whales. Whale Cove Marine Education, Corvallis, Oregon.

Sumich JL. 1984. Gray Whales along the Oregon Coast in Summer, 1977-1980. The Murrelet 65:33-40.

Swedeen P, Batker D, Radtke H, Boumans R, C. W. 2008. An Ecological Economics Approach to Understanding Oregon's Coastal Economy and Environment. Earth Economics. Portland, OR.

TIES. 2015. TIES announces ecotourism principles revision. The International Ecotourism Society. Available from https://www.ecotourism.org/news/ties-announces-ecotourism-principles-revision (accessed December 12, 2016).

Torres LG, Orben RA, Tolkova I, Thompson DR. 2017. Classification of Animal Movement Behavior through Residence in Space and Time. PLoS ONE.

Wiley DN, Moller JC, PACE RM, Carlson C. 2008. Effectiveness of voluntary conservation agreements: case study of endangered whales and commercial whale watching. Conservation Biology 22:450-457.

Williams R, Ashe E. 2007. Killer whale evasive tactics vary with boat number. Journal of Zoology 272:390-397.

CHAPTER 4 – GENERAL CONCLUSION

Marine predators operate in a heterogeneous seascape of prey availability, and must respond to environmental cues at multiple scales in order to forage effectively (Torres in press). Due to the tendency of prey to aggregate at all scales (Fauchald and Tveraa 2006), there is a cumulative burden of lost opportunity cost when a predator does not search at an appropriate scale compared to prey availability. Optimization of foraging effort requires complex tradeoffs between patch density, travel costs between foraging patches, levels of inter- and intra-specific competition, disturbance, predation threat and more. In particular, the predictability of resources, learned as a function of previous success and failure associated with a given feature, is an important part of a predator's foraging strategy at multiple scales (Scales *et al*. 2014). However, stable productive oceanic fronts, upwelling zones, and coastal areas are often areas of spatial and temporal overlap between foraging marine predators and humans engaged in resource extraction (*e.g.*, fishing, mining, renewable energy developments; Halpern *et al.* 2008; Maxwell *et al.* 2013). Anthropogenic disturbance from these and other industries can inhibit a predator's ability to forage effectively (Christiansen *et al.* 2013).

In Port Orford, gray whales depend on information from a static feature more while searching or foraging at a fine scale (<0.5 km) than when searching at a larger regional scale (1-2 km). At fine scales, the 'distance from kelp' static feature may offer gray whales searching for prey greater predictability than the more dynamic patterns of relative prey density. Depending on the sensory cue informing whale perception of the prey-scape, the regional scale may be the finest resolution at which the dynamic cue is informative. Once searching at the sub-regional scale, it may be more efficient to locate prey using static cues, such as the location of kelp beds. Alternatively, at this fine scale, returning whales may have perfect knowledge of kelp bed locations, making this static variable key to the execution of OFT. However, another explanation for this result is that given the fluid nature of zooplankton swarm dynamics (Feyrer 2010), and the possibility of a whale depleting a patch before another whale moves through the same area (Feyrer and Duffus 2011), the sampling resolution of prey at this fine scale was not adequate to correlate with whale searching behavior. Yet, dynamic prey patterns inform foraging behavior at both regional and fine scales, likely because once a suitable prey patch is detected the animal switches behavior states from search to forage, regardless of scale. There was significant variation in prey communities at fine scales, and community species composition may be a stronger driver of increased foraging behavior rather than simple presence of high prey density.

Gray whale behavior on the coast of Oregon was significantly affected by interactions with vessels. There were significant, site specific, differences between control and impact activity budgets, indicating that whales are more likely to abandon searching behavior when approached by vessels. Our analyses indicated that individual whales reacted similarly to vessel disturbance, indicating that management efforts should be effective for the population as a whole.

Taken together, the results of these two studies show that whales attempt to maximize energy gain through predictable, successful foraging. As they work to optimize foraging effort on the Oregon coast, whales face several decisions. In the absence of vessels, the question becomes when and where is the higher quality or higher density prey located? Conversely, when a vessel is present, the whale must also consider whether the current foraging conditions are worth tolerating the disturbance.

Our study adds to the growing body of literature concerning predator – prey interactions at fine scales and mitigation efforts for anthropogenic impacts on marine mammals. The marine seascape is a shifting environment with complex interactions between environment, cetaceans, commercial interests, pleasure boaters, tourists, and local communities. Although vessel operation guidelines may not address all aspects of marine mammal health, collaborative, community efforts of education and outreach at multiple scales can be an effective tool to start discussions concerning marine conservation. Deliberate planning of joint research and outreach projects gives strength and credibility to translate results into action for sustainable management and conservation.

Future work should focus on resolving questions of predator and prey behavior cues at finer spatial and temporal resolution. Assessing the energy content of variable zooplankton communities could determine if species composition is a significant driver of whale distribution. An effort to synoptically sample prey, whale behavior and vessel disturbance would clarify the conditions in which whales tolerate disturbance. Additionally, greater effort should be made to document whale behavior change relative to single vessel types, as well as by individual whale. From a management perspective, social scientists should be invited to collaborate on an evaluation of the “Watch Out For Whales” brochure and website messaging, and measure efficacy of targeted messaging. This low cost and ecologically interesting project has the potential to develop into a fascinating long term monitoring study of fine scale predator prey interactions.

Literature Cited

Christiansen F, Rasmussen M, Lusseau D. 2013. Whale watching disrupts feeding activities of minke whales on a feeding ground. Marine Ecology Progress Series 478:239-251.

Fauchald P, Tveraa T. 2006. Hierarchical patch dynamics and animal movement patterns. Oecologia 149:383-395.

Feyrer LJ. 2010. Differences in embryo production between sympatric species of mysids (family Mysidae) in the shallow coastal waters off Vancouver Island, BC. Marine biology 157:2461-2465.

Feyrer LJ, Duffus DA. 2011. Predatory disturbance and prey species diversity: the case of gray whale (Eschrichtius robustus) foraging on a multi-species mysid (family Mysidae) community. Hydrobiologia 678:37-47.

Halpern BS, et al. 2008. A Global Map of Human Impact on Marine Ecosystems.

Maxwell SM, et al. 2013. Cumulative human impacts on marine predators. Nature Communications.

Scales KL, Miller PI, Hawkes LA, Ingram SN, Sims DW, Votier SC. 2014. REVIEW: On the Front Line: frontal zones as priority at-sea conservation areas for mobile marine vertebrates. Journal of Applied Ecology 51:1575-1583.

Torres LG. in press. A sense of scale: Foraging cetaceans use of scale-dependent multimodal sensory systems. Marine Mammal Science.