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## Distinct habitat use strategies of sympatric rorqual whales within a fjord system

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## ABSTRACT

We used ecosystem sampling during systematic surveys and opportunistic focal follows, comparison tests, and random forest models to evaluate fin whale (*Balaenoptera physalus*) and humpback whale (*Megaptera novaeangliae*) habitat associations within an inland feeding ground (Kitimat Fjord System, British Columbia, Canada). Though these species are sympatric and share a common prey source, they were attuned to different aspects of the local habitat. The fin whales were associated with habitat properties reminiscent of the open ocean. Humpback whales, in contrast, were associated with features more commonly associated with the inland waters of fjords. Fixed habitat features, such as seafloor depth and distance from the fjord mouth, were the most important predictors of fin whale presence, but fixed and dynamic variables, such as surface properties, predicted humpback whale presence with equal (moderate) success. With the exception of strong salinity gradients for humpback whales, habitat conditions were poor predictors of feeding state. Fin whales practiced a spatially confined, seasonally stable, and thus more predictable use of certain channels within the fjord system. These findings are compatible with site loyal behavior, which is interesting in light of the species' historical, unique use of this fjord system. The relatively lackluster performance of humpback-habitat models, coupled with the importance of oceanographic properties, makes the humpback's habitat use strategy more uncertain. The fact that two sympatric species sharing a common prey source exhibited different habitat use strategies suggests that at least one species was informed by something in addition to prey. Given that the two species are attuned to different aspects of the fjord habitat, their responses to habitat changes, including anthropogenic impacts, would likely be different in both nature and degree. Our findings highlight the value of comparative studies and the complexity of rorqual habitat use, which must be understood in order for critical habitat to be identified and protected.

### 1. Introduction

Strong associations are often found between features of marine habitat and the distribution of mobile predators such as whales and seabirds (Redfern et al., 2006; Ferguson et al., 2006; Panigada et al., 2008; Cotte et al., 2009; Dalla Rosa et al., 2012; Bombosch et al., 2014). The identification of such associations is a logical precursor to understanding how and why a given habitat is used, which informs whether that habitat is important relative to others (Cañadas et al., 2005). Such assessments are commonly an early requirement in legislation for protecting species (e.g., Endangered Species Act in the United States, Species At Risk Act in Canada, etc.).

The mechanistic or “process-based” inferences of many association studies are inherently limited by their basis in correlation modeling (Dormann et al., 2012). However, if invoked with care, associations can still advance mechanistic inquiries. One such approach is sequential modeling in which only certain variables are included at each stage of the exercise (Dormann et al., 2012). Variable selection is therefore of paramount importance, and a perennial issue in marine mammal habitat modeling is how to handle habitat and prey variables that, if not statistically correlated, are mechanistically coupled via ocean processes.

Both a predator and its prey associate with their shared habitat either directly or indirectly, intentionally or otherwise. For example,

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cetacean associations with oceanographic and physiographic features are often assumed to be the result of their planktonic prey, whose distributions are a strong function of water properties and ocean currents (Redfern et al., 2006). In models of predator distribution, therefore, prey and habitat data can be difficult if not impossible to disaggregate. Several studies have included both data types despite the potential redundancies (e.g., Friedlaender et al., 2006; Hazen et al., 2009; Benoit-Bird et al., 2013; Keen et al., 2017). But this simultaneous inclusion can be confounding within the context of conservation, in which we are seeking a mechanistic understanding of distributions in order to prioritize habitat protection.

It is worth noting that cetacean-habitat associations can be unrelated to foraging, particularly during the breeding and migration seasons where applicable. Even during periods of feeding, cetacean movements have been explained by needs other than nutrition (e.g., parasite mitigation, as hypothesized by Durban and Pitman, 2011; culturally transmitted behaviors at unique habitats, such as beach rubbing reported in Ford et al., 2000), and site-loyalty, which facilitates social cohesion and safety in addition to reliable access to prey. And, even if habitat use is motivated primarily by food, it may be that whales achieve sufficient associations with prey indirectly by relying instead upon habitat cues, such as property gradients, or upon previous experience, such as site loyalty. Such information may be more easily tracked than patchy, ephemeral, drifting swarms of prey. These possibilities, in addition to sampling limitations that prevent us from capturing the prey attributes most relevant to cetaceans, may explain why the inclusion of prey-related metrics in cetacean habitat models does not always increase model performance (Torres et al., 2008; Barlow et al., 2009; Anderwald et al., 2012; Keen et al., 2017).

Parsing the relationships among whales, their prey, a place, and its environmental features is important in understanding how habitat is used and how species might respond to its alteration. However, the synoptic and scale-appropriate collection of the necessary data may not be feasible for all species or habitats. Comparative studies of co-occurring species can be a valuable and efficient means of investigating habitat use. The strategies of one species can be used as context or foil for another, particularly within uncommon habitats where there are few precedents to guide our inferences. Studies of sympatric whale species are increasingly common (e.g., Friedlaender et al., 2009; Friedlaender et al., 2015; Witteveen et al., 2015; Witteveen and Wynne, 2016; Keen, 2017a). These efforts afford rare insights into cetacean ecology and competitive interactions, such as trophic niche partitioning, that are not possible in single-species studies.

However, previous work has been primarily limited in scope to whale-prey interactions, highlighting the need for efforts that compare whale associations with aspects of their environment other than prey (hereafter referred to as their habitat). Comparative studies of cetacean-habitat association that exclude prey data are more common on the larger scale (e.g., the California Current, Becker et al., 2010 and references therein; eastern Pacific Ocean, Forney et al., 2012 and references therein). These explore habitat partitioning on the population-level but cannot speak to the dynamics of sympatry on the level of individual interactions or at the scale of a single discrete habitat. Data on relatively fine-scale habitat associations are sparse, but they could prove useful as we try to understand how whales interact with their habitat.

The recent return of recovering humpback whale (*Megaptera novaeangliae*) and fin whale (*Balaenoptera physalus*) populations to the Kitimat Fjord System (KFS) of British Columbia (Ashe et al., 2013; Ford, 2014) provides an opportunity to conduct a scale-appropriate comparative study of whale-habitat associations within a relatively compartmentalized and oceanographically dynamic habitat (Fig. 1). The KFS is the only fjord system in British Columbia (BC) used heavily by fin whales both before whaling and in the decades since the end of whaling (Ford, 2014). During the commercial whaling era more fin whales were caught per unit effort in the KFS than in other BC fjord systems (Gregg et al. 2000), suggesting that fin whales historically foraged in the KFS

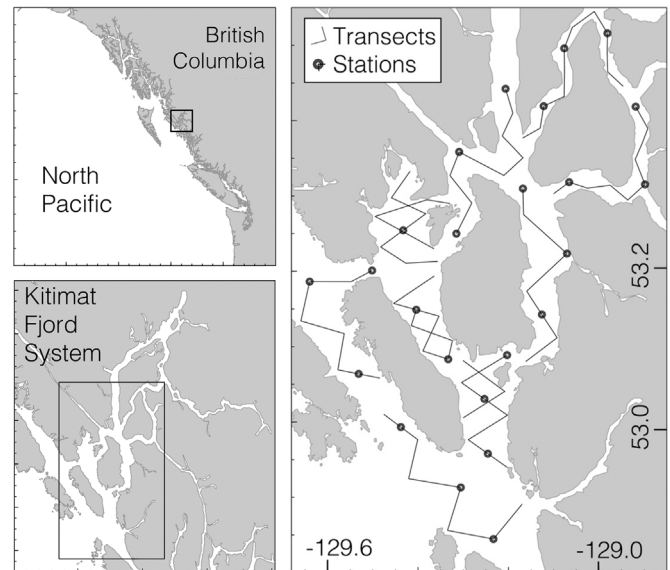


Fig. 1. Study area and study plan. Study area and study plan within the Kitimat Fjord System, Gitga'at First Nation territory, British Columbia, Canada.

more than other fjords on the BC coast. Since the end of whaling, fin whales were not seen regularly within the KFS until 2006 (authors, unpublished data). Since 2006, the number of individuals identified here has increased annually, possibly reflecting the recovery of the BC population (Nichol et al., 2017). As of 2005 the northeast Pacific fin whale population was an estimated 50% of numbers 60–90 years ago, and has been assessed as “Threatened” by COSEWIC (2005) and under the Species at Risk Act (SARA) (Gregg et al., 2006). This protected status requires critical habitat to be designated; the outer channels of the KFS have been identified as a potential site (Nichol and Ford, 2011; Nichol et al., 2017), but detailed data on the area's habitat and fin whale associations with it are required to make serious consideration possible. The co-occurrence of a second species in this habitat presents the opportunity for even richer insights.

Keen (2017a) reported on the prey types and patch characteristics that govern the distributions and feeding state of these two rorquals (f. Balaenopteridae) within this fjord system. Both species were found to be primarily euphausiivorous, observed feeding in large krill patches. The distributions of the two species were correlated with areas of high krill density. Humpback whales also fed opportunistically upon schooling fish, but their distribution was associated with the distribution of backscatter attributed to krill, not fish. The fact that these two species appear to be sharing a common prey source lends further intrigue to the question of how their habitat associations differ, if at all.

The field effort from Keen (2017a) also involved oceanographic sampling, enabling us here to compare the two species' habitat use strategies using both systematic surveys and close behavioral observations. Our intent was to carry out this analysis with particular attention to the relative importance of fixed physiographic characteristics (e.g., bathymetry, distance from fjord mouth, etc.) and dynamic oceanographic features of the fjord system (e.g., salinity, temperature, turbidity, and phytoplankton). We then aimed to develop hypotheses that may explain the differences we find, if any, between the habitat strategies of the two species.

## 2. Materials & methods

### 2.1. Study area

The study area (1961 km<sup>2</sup> of water) is located within the Kitimat Fjord System (KFS) of northern mainland BC, centered at 53°N and

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