Between a ship and a hard place: Inferring fin whale behaviours and vulnerability with acoustic localizations in a fjord system

by

Chenoah Shine
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With deep respect and gratitude, I acknowledge the historical and persistent stewarding relationships between the Gitga'at Nation and their territories, which I was so fortunate to experience, and learn from throughout the process of this thesis.

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Abstract

Large whales face increased threats from vessel traffic. Current threat mitigation strategies are difficult in constricted geographies, such as fjords, and direct observations of whales during nighttime, which can inform approaches, remains challenging. However, technological advances in whale research are also facilitating new methods to understand vulnerability during day and night. Passive acoustic monitoring, and specifically localization, provides spatial and behavioural information on species in continuous space and time. The objective of this thesis research is to examine how acoustic localizations might inform behaviour investigations of fin whale (*Balaenoptera physalus*) vulnerability throughout diurnal cycles. I first examined how passive acoustic localization data and species distribution modeling can be used to inform behavioural context of different fin whale calls. I then investigated the degree to which whales' vulnerability to different vessel traffic types (associated with different threats) varies among whale behaviours. This research focuses on two call types of fin whales sensed by a four-hydrophone array on a northern latitude foraging site within Gitga'at Territory in the Pacific Northwest. This site is characterized by a narrow channel at the entrance to a fjord system and serves as a particularly relevant point of study as it faces rapid expansion of large vessel traffic in the coming decade and its constricted geography limits traditional management solutions. I found selected habitat features varied among whale behaviours, which confirmed expected social and foraging partitioning of distinct whale calls. Results also suggested potential for nighttime foraging in this area. Social calling fin whales were more vulnerable to cruise ships during daytime, while foraging callers were more vulnerable to passenger, pleasure craft, tug/towing, and fishing vessels, especially at night. It is expected that nighttime foraging callers will likely be the most vulnerable to planned increases in large vessel traffic in this region.

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Chapter 1: Research Context

1. Introduction

The rise of human pressures in the world's oceans are increasingly putting marine wildlife at risk. Over-hunting has caused the near extinction of several marine species, legacies of which leave species vulnerable to new anthropogenic threats (Clapham et al., 1999; Thomas et al., 2016). Further, there are clear linkages between oceanic habitat degradation and species decline, as human-induced environmental change has been observed to alter the timing, quality, and distribution of species behaviours and their prey (Edwards & Richardson, 2004; Halpern et al., 2015). More recently, maritime trade networks have been shown to exert a range of negative consequence for marine species (Merchant et al., 2015; Pirotta et al., 2019). In the past century, global vessel density has increased over fourfold (Frisk, 2012), and commercial vessel tonnage continues to rise by about 4% annually (Erbe et al., 2019). This rise in vessel activity has not only altered oceanic soundscapes (McDonald et al., 2006), but also represents a direct threat to marine species through risk of collision (Schoeman et al., 2020). While vessel traffic impacts many marine species, whales are one of the most affected because their large size, and their need to breathe air at the surface puts them at risk to being hit by vessels (referred to hereafter as a vessel strike) (Pirotta et al., 2019). Further, their dependence on long-range acoustic communication means that disturbed soundscapes can have adverse consequences for maintaining the reproductive and foraging success of whales (Erbe, 2002).

Typically, whale vulnerability to vessel threats is assessed with spatially explicit modeling techniques (Calambokidis et al., 2019; Cates et al., 2017; Clapham et al., 1999; Conn & Silber, 2013; Keen, Scales, et al., 2019a; Lammers et al., 2013; Jessica V. Redfern et al., 2020; Rockwood et al., 2017a; Wiley et al., 2011). Such approaches involve the use of spatial data on whale and vessel distributions that require certain assumptions to be made across temporal scales given that most whale distribution data are either from daytime surveys or tag data from few individuals. However, whale activity is largely influenced by diurnal patterns (Calambokidis et al., 2019) that may produce distinct spatial distributions between day and night. In addition, previous models have traditionally treated both whales and vessels as homogenous entities, ignoring the potential that whales may be more vulnerable when engaged in certain behaviours or when exposed to vessels of different types. Previous research has shown that whales may be less aware of vessels while foraging (Laist et al., 2001a; Lima & Dill, 1990), while others have observed that vessel noise can cause whales to reduce foraging activities (Blair et al., 2016; Miller et al., 2022). Further, whales engaged in social calling activity (i.e., actively dispelling energy to communicate for a purpose) may alter their calls or cease their vocalizations altogether if vessel noise is too disruptive (Erbe et al., 2019; Guazzo et al., 2020; Varga et al., 2018).

Like whales engaged in different behaviours, vessel movement patterns (i.e., behaviours) can vary among vessel type. For instance, passenger and cruise ships travel notably faster than cargo and tanker vessels, and commercial vessel types follow set routes while recreational and private vessel types traveled in more dispersed patterns (Greig et al., 2020). Noise and strike threats produced by vessels also vary based on vessel properties, as faster boats make louder sounds and larger ships generally make the most noise at lower frequencies (Gabriele et al., 2018; Gervaise et al., 2012). Larger (>20m) and faster (>10knots) vessels are also known to produce largest lethal strike threats to cetaceans due to vessel mass and limited maneuverability (Vanderlaan & Taggart, 2007). Although smaller vessels present less lethal consequences, and their higher maneuverability may help limit collisions, they are still capable of producing lethal impacts to whales (Kelley et al., 2020; Vanderlaan & Taggart, 2007a). The management options and success of different strategies may also vary among vessel types, as vessel maneuverability and size could limit changes in operation speed and space, and existence of regulatory bodies vary across vessel types. For instance, previous research has found variable compliance with mandatory speed restrictions among passenger, tanker, and cargo vessels, where large passenger vessels (cruise ships) had lower compliance than cargo and tanker vessels (Silber et al., 2014). Others found fishing vessels were the least compliant type with spatial separation strategies (Guzman et al., 2020). As such, vessel behaviour and type is equally relevant when investigating vessel-whale interactions.

Combined, variations among human and whale behaviours may facilitate more varied patterns of vulnerability, and knowledge of such variation could inform management strategies, especially in places where management strategies are limited. For instance, in constricted coastal geographies such as fjords, traditional strike mitigation strategies of spatial separation are not always feasible. However, few analyses of whale vulnerability have explicitly investigated differences in spatial temporal vulnerability of whales engaged in different activity states to different vessel traffic types. This may be because behavioural perspectives on risk evaluation are more difficult to parse out given the inherent challenge of observing cetaceans and their behaviour, especially during darkness.

One approach that can facilitate observing whale behaviour is passive acoustic localization. Such data collection techniques allow for species and behaviourally-relevant location data to be collected over continuous space during daytime and darkness when traditional visual methods of cetacean study are impossible (Hendricks et al., 2019; Noad, et al., 2004; Nowacek et al., 2016). While acoustic data comes with the disadvantage of lost individual identification, for cetaceans such data offer unprecedented opportunities for advancing understanding of behaviour over continuous space and time.

The objective of this thesis research is to examine how acoustic localizations can inform behaviourally sensitive investigations of fin whale vulnerability throughout diurnal cycles. I specifically investigate how passive acoustic localization data can be used to understand the spatial and temporal nature of whale behaviours and the degree to which different behaviours might place whales at greater risk to varied vessel threats. This research focuses on two call types of fin whales sensed by a four-hydrophone array on a northern latitude foraging site within Gitga'at Territory in the Pacific Northwest. This site is a particularly important as it faces rapid expansion of large vessel traffic in the coming decade (Meisner, 2015a). Specifically, this research asks the following questions:

1. Do fin whales exhibit spatial and temporal partitioning of acoustic behaviours?
2. Are certain fin whale behaviours more at risk to specific types of vessels than others?

The subsequent chapters address these questions. Chapter 2 characterizes the environment at locations of distinct acoustic whale behaviours to investigate whether fine scale habitat relationships can be used to confirm differences among behaviour of acoustically active whales. Chapter 3 details a temporal and spatial analysis of overlap among whale behaviours and vessel types. I discuss the characteristics of different vessel types and the potentially distinct threats each type presents, and then identify vessel types representing greatest threat to different whale behaviours. Chapter 4 summarizes key findings of preceding chapters, discusses potential limitations, and identifies implications for policy and future research.

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Chapter 2: Evaluating spatial and temporal partitioning among fin whale behaviours

Abstract

Cetaceans are soniferous species that inhabit dynamic marine systems governed by diurnal oscillations in prey availability. Fin whales produce different call types that have been associated with distinct behaviours, but uncertainty remains about the spatial and temporal context of different whale calls. Habitat association analyses may serve to clarify behavioural roles but require spatial information on whale calls. Hydrophone networks paired with localization techniques have been used to collect location-based information on whale calls, thus providing the required data on when and where whales are engaged in different behaviours. In this context, we developed species distribution models using acoustic localizations to investigate if two distinct whale behaviours exhibited spatial and temporal partitioning, and if so, whether habitat in those locations aligned with expected behavioural roles of those call types in a coastal fjord system. We found low habitat similarity (D statistic of niche similarity = 0.52 - 0.81) among vocalizations made by the same species, indicating divergent spatial use among behaviours. As expected, foraging calls were more associated with bathymetric features that facilitate primary productivity and upwelling (proxies for prey quality and accessibility). However, contrary to expectations, nighttime calls were also more associated with foraging habitat than daytime calls, suggesting nocturnal feeding activity at this site. We therefore propose that distinctive soundscapes and dynamic oceanography of nearshore habitats could promote nighttime foraging or encourage use of this call type. Such findings have implications for future acoustic monitoring of fin whales in coastal environments and emphasize the

importance of considering acoustic components of whale habitat as this historically depleted species recovers.

1. Introduction

Sound production is a meaningful component of animal behaviour. Terrestrial and marine species often produce different sounds in social, reproductive, and foraging contexts (Ladich & Winkler, 2017). Variation in sound production has been linked to diurnal cycles across taxa, including invertebrates (Lillis et al., 2017), birds (Catchpole & Slater, 2003), fish (Feng & Bass, 2016), and mammals (Stafford et al., 2005). In addition, sound production is often spatially variable because animal sounds can be constrained by characteristics of their environment (Bormpoudakis et al., 2013; Endler, 1993), so that habitat selection is informed by variable acoustic properties across space (Mullet et al., 2017). Understanding heterogeneity of sound production in space and time is important because animal communication can be impacted by anthropogenic noise, potentially inciting behavioural changes with evolutionary effects.

Sound production (and reception) is particularly important to marine species, owing to the higher efficiency of sound propagation than light underwater (Berta et al., 2005). Cetaceans, in particular, display marked acoustic variability that are both temporally and spatially partitioned (Edds-Walton, 1997); understanding this variability is critical for contextualizing activity patterns, habitat use, and associated behaviour which inform policy to mitigate human impacts on whales. Further, acoustic presence is an important aspect of whale research given that they spend most of their time submersed and are inherently difficult to study visually. Significant increases in vessel traffic and anthropogenic noise in the past century have altered the oceanic soundscapes that whales inhabit (Tyack, 2008); with known impacts on foraging efficiency (Nabi et al., 2018), stress hormones (Trumble et al., 2018), and communication ranges (Tyack, 2008). Furthermore, acoustic habitat needs (which vocalization variability can reveal) are recognized as essential for species' conservation and are becoming actionable components of habitat quality protection and spatial planning (Dumyahn & Pijanowski, 2011; Merchant et al., 2015; Williams et al., 2015).

The acoustic calls of cetaceans can vary over diurnal scales, such as odontocete foraging related calls (echolocation) that are primarily produced at night (Carlström, 2005; Johnston et al., 2008). For baleen whales, Matthews et al., (2001) found North Atlantic right whales (*Eubalaena glacialis*) made more moans and gunshot calls during the night than during the day. Prey-independent singing activity of Humpback whales (*Megaptera novaeangliae*) in Hawaii also peaked during night-time hours (Au et al., 2000), with greater relevance being attributed to acoustic social and reproductive song during darkness when visual cues were not feasible. Temporal separation between different call types of blue whales (*Balaenoptera musculus*) was identified off southern California (Oleson, Wiggins, et al., 2007); foraging-related calls were made primarily during the day (when feeding on krill at depth) and song-related calls were mainly produced during crepuscular hours (i.e., dawn and dusk). Much like blue whales, diurnal variability in different fin whale call-types has also been detected; in the eastern North Pacific, foraging and social calls are produced in different proportions between day and night (Širović et al., 2013). In several large baleen whale species, dive behaviour shifts between day and night with deeper dives performed during the day and shallower dives at night (Calambokidis et al., 2019; Stimpert et al., 2015). These cyclical patterns in calling and dive behaviours are likely driven by vertical diurnal migrations of krill (primary prey) which are tightly concentrated at depth during the day (thus more efficient to capture), but close to the surface, yet diffuse, and at night (thus more difficult to capture) (Keen et al., 2019). Diurnal patterns in calling activity offer insight into whales' behavioural roles during times of darkness when they cannot be visually observed. However, interpretation of such temporal patterns are often limited without specific spatial context.

Spatial separation of sound production is equally important and may be especially prevalent in marine systems where food is patchily distributed. Humpback whales, for example, display spatial acoustic variability as they forgo nutrient acquisition for breeding when migrating long distances between prey-rich summer foraging areas (where foraging calls are frequent) to prey-absent and warmer winter birthing and mating areas (where song is most frequent) (Hebblewhite & Merrill, 2009; Heithaus & Dill, 2009). Further, in several baleen whale species, mother-calf pairs preferentially occupy nearshore habitats and produce lower frequency calls to communicate with young, likely to avoid detection by predators (i.e., *Orcinus orca*) that generally communicate with high frequency calls (Nielsen et al., 2019). Mother-calf pairs even select nearshore environments likely as a predator avoidance strategy because of higher ambient noise levels here (i.e., breaking surf) that help to hide communication with young from predators (Nielsen et al., 2019; Pacheco et al., 2021). In fin whales, different patterns of song between regions has been suggested as a method to distinguish sub-populations, and a distinct coastal shelf sub-population along the pacific northwest has been theorized (Širović et al., 2017).

Investigating the temporal and spatial variability of cetacean calls requires spatially accurate observations of call types throughout day and night over a sufficiently large and diverse set of habitat characteristics. Historically, such data with concurrent spatial and behavioural observations over relevant temporal and spatial coverage was difficult, if not impossible, to acquire for naturally elusive diving marine mammals. This data limitation is responsible for the scarcity of behaviour-specific habitat selection analyses (Roever et al., 2014; Beyer et al., 2010).

However, such data have more recently become available with Passive Acoustic Monitoring (PAM) arrays with classification and localization capacity (Gervaise et al., 2021; Hendricks, et al., 2021; Mellinger et al., 2007). While PAM is not new and hydrophone installations recording underwater sounds are now widespread, the volume of data that these devices collect presents a data processing challenge to researchers interested in specific species. Recent developments have led to standardized algorithms of detection, classification, and localization. These enable automated extraction of relevant cetacean calls from large recordings that are otherwise time-intensive to manually review. Localization algorithms then match calls across hydrophones with timing differences revealing the caller's location in space.

Fin whales are an excellent balaenopterid candidate for data collected through PAM localization because they communicate with low frequency pulses at two generalized frequency peaks: 20Hz and 40Hz (Širović et al., 2013; Stimpert et al., 2015; Watkins, 1981). Fin whales engaged in foraging-like dive behaviour have been observed producing 40Hz pulses (Watkins, 1981). Recently, 40Hz pulses have been positively associated with direct comparisons to prey-type back-scatter (Romagosa et al., 2021). Additionally, whales have not been observed to use 40Hz calls in a counter-call fashion, suggesting there is not a strong social component to this call type (Wiggins & Hildebrand, 2020). Conversely, 20Hz calls, when produced in repetitive patterns, have been associated with breeding because only male fin whales have been documented to produce 20Hz calls in regular sequences (Stimpert et al., 2015; Watkins, 1981). These repetitive sequences have been associated with a winter breeding season (Croll et al., 2002; Širović et al., 2013). Consequently, 20Hz calls, especially in sequence, are generally interpreted to have social and reproductive function, while 20Hz calls in irregular sequences may be linked to intra-species communication or even navigation (Edds-Walton, 1997). Seasonal separation of these fin whale call types has been detected as consistent across regions of the North Pacific with general peaks in 40Hz calls in the spring to summer and peaks in the 20Hz calls in the fall and winter (Širović et al., 2013). This seasonal shift from feeding calls during peak summer prey productivity, to peaks in social calls several months later, strengthens expected behavioural distinction of these call types in foraging grounds. Fin whales also exhibit distinct movement and acoustic behaviours between day and night; in most regions of the Pacific during the day they perform deeper, longer dives associated with daytime foraging on euphausiid prey (Calambokidis et al., 2019; Keen et al., 2019; Stimpert et al., 2015). During the night, fin whales generally make shallower dives and engage in longer surface intervals with more near-surface travel that can put them at greater risk of ship-strike (Calambokidis et al., 2019; Stimpert et al., 2015). Interestingly, these diurnal call proportions differed between sites from Alaska to southern California despite common diel dive patterns among sites. Evidently, acoustic fin whale behaviours require further contextualization.

Here we characterized environmental features at the location of different whale call categories for fin whales in a coastal fjord system in Gitga'at Territory along the Eastern North Pacific Coast. Using acoustic data derived from a local PAM network, we investigated whether habitat associations of acoustically localized social (20Hz) and foraging (40Hz) fin whale calls during night and day align with our expectations, given the emerging behavioural contexts of distinct fin whale calls over the diurnal cycle. Second, we applied species distribution models (SDM) to investigate if significant relationships between habitat and call types exist and tested the hypothesis that distinct habitat would be selected by different diurnal and call type groupings of fin whale activity that have already been associated with different behaviours. Given expected behavioural differences between fin whale 20Hz and 40Hz call types, and between day and nighttime calling (see discussion above), we investigated whether habitat selected by whales making calls in these different categories followed expected patterns. We predicted that 40Hz calls would be positively associated with greater seafloor roughness, or subsurface slopes with aspects perpendicular to large channels that - subjected to tidal flows - likely produce upwelling and concentrate prey in patterned ways. Conversely, we expected that 20Hz calls will have less directional associations with any particular habitat features because social communication is likely less constrained to prey presence. However, if certain significant habitat relationships were revealed for 20Hz calls, preferences would be expected to align with features that support effective communication and the dispersal of sound. We expected that day and night-time call comparisons would reveal similar patterns within each call type showing that the function of that call type is consistent throughout the diurnal cycle. If these patterns differ, then there may be different functional roles of call types between daytime and nighttime contexts. Our results will reveal what environmental characteristics of a coastal fjord are most relevant to different acoustic fin whale behaviours. This novel application of PAM localization data for acoustic habitat analysis could inform managers in developing relevant conservation strategies in complex geographies with competing social, ecological, and industrial interests.

2. Materials and Methods

2.1. Study Site

The study area is located within Squally Channel along the north coast of British Columbia (BC), Canada (53ºN), just south from the Gitga'at community of Hartley Bay (Figure 1). The Gitga'at Nation, North Coast Cetacean Society, and WWF Canada collaborated to install a time-synchronized four-hydrophone array in the channel. This array has the capacity to detect, classify, and localize fin whale (*Balaenoptera physalus*) 20Hz and 40Hz calls across a continuous area of approximately 200 km^2 to an average accuracy of 70.4m (max error 148.4 m; as determined by acoustic transmission experiments). For a complete description of this system and classification details, see Hendricks et. al. (2019). Specifically, our study site includes ocean area within a 4km buffer of the array's localization range (Figure 1). The study site is comprised of deep, steep sided channels at the entrance to coastal fjord system and serves as a summer foraging ground for fin whales.

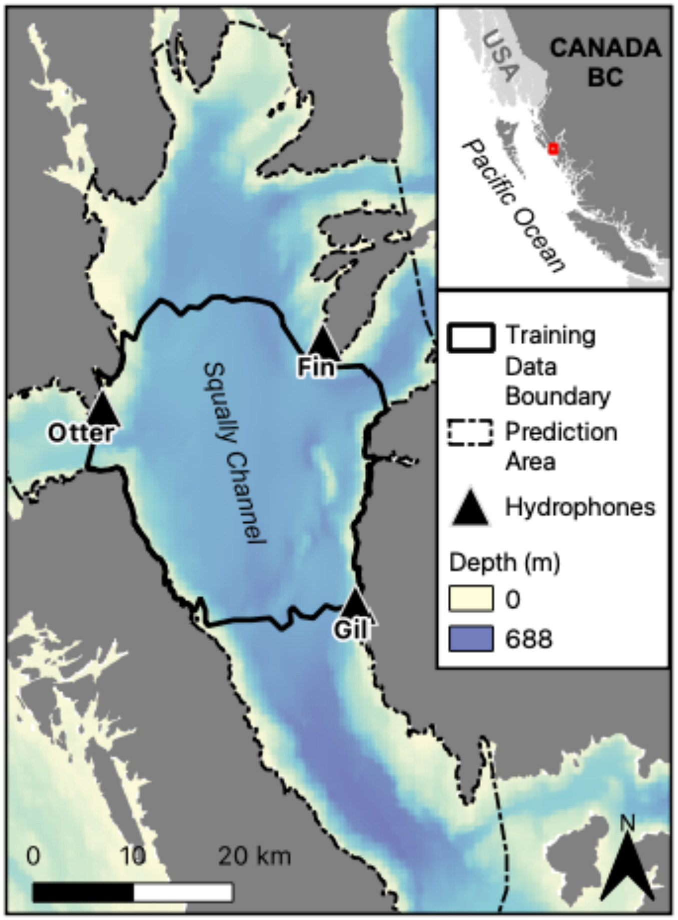

Figure 1. Study area and hydrophone array in Gitga'at First Nation Territory (GFNT) on the west coast of Canada. Training data boundary shown; area where acoustic localization accuracy is less than 200 meters. Prediction area also shown; boundary of a 4km buffer around maximum localization range of hydrophone network.

2.2. Data

2.2.1. Whale Locations

We used fin whale localizations (n = 4418) between July and October 2019 and confined our training data to points with modeled accuracy of < 200m by cropping data to this boundary (Figure 1), assuming that localization capacity and spatial accuracy is uniform within the boundary. This is a reasonable assumption given that fin whales produce low frequency calls that can travel long distances (> 50km; Širović et al., 2007) and thus are viable and efficient for localization at these scales.

2.2.2. Environment Variables

Six candidate environmental variables (Table 1; Figure 2) were selected based on potential ecological relevance to fin whales in a coastal fjord system: depth, slope, sub-surface roughness, distance to shore, aspect, and substrate composition. Depth, slope, and roughness of the sea floor are consistently recognized as important in whale distribution models because of their influence on prey occurrence and accessibility to whales (Breen et al., 2016; Díaz López & Methion, 2019; Panigada et al., 2008). Fin whale distributions (from visual and acoustic observations) have been associated with sub-marine canyons (Moors-Murphy, 2014), and regions of higher bathymetric relief (i.e., greater roughness, large changes in depth, steep slopes), which is largely explained by these areas interacting with ocean cycles (i.e., currents, wind) to become regions of high primary productivity that support prey. Fin whales are deep diving cetaceans (maximum observed dive depth = 365 meters; Irvine et al., 2019) that frequently select deep waters to pursue dense krill patches (Keen et al., 2019; Witteveen & Wynne, 2016). Distance to shore has also been a top predictor in other related research; fin whales often select further distances from shore (Panigada et al., 2008). Some studies found increasing probability towards deeper depths and constant probability of occurrence after ~175km from shore (study area = 24,000 km^2; Panigada et al., 2008); others found occurrence peaked around 30km offshore (study area = 400,000 km2 ; Irvine et al., 2019). While specific drivers of distance to shore patterns are rarely discussed, relationships between depth (i.e., profitable prey presence) and distance to shore could be relevant. In a fjord system with pronounced tidal currents, bathymetry perpendicular to predictable tidal flow could force water and krill (prey) closer to the surface and at more accessible depths in predictable ways (Johnston et al., 2005; Jones et al., 2019). Substrate composition was considered for its potential relevance to sub-marine noise and call propagation, as well as existing evidence of its role in habitat selection of singing rorquals (Oña et al., 2017). Ocean substrates can influence underwater sound propagation and may result in optimal locations for whales to produce sounds for the farthest propagation, and thus efficient communication. Accordingly, we used substrate data from a fine scale geomorphological analysis of the Kitimat fjord system that categorized bottom type based on a combination of bottom material type (i.e., mud, sand, gravel) as well as bathymetric properties (i.e., slope, roughness) (Shaw & Lintern, 2016; Natural Resources Canada, 2016).

Original habitat covariates were acquired from DataBC, NOAA, and Natural Resources Canada and other layers were also derived (see Table 1 for source and units). We then used a bathymetry layer at 100m resolution (finest resolution available) to compute slope, roughness, and aspect surfaces using the "terrain" function (R package "terra"; Hijmans, Bivand, et al., 2022). We also calculated distance to shore in relation to a shoreline polygon (see Table 1) using R package "sf" (Daniel & Anderson, 2018). Substrate was derived directly from classes in the source vector data and converted to raster format with QGis version 3.10.5-A Coruña (QGIS Development Team, 2022). Following preliminary investigations of resulting presence-absence proportions across environment data resolutions from 100m to 1km, analysis proceeded at a

500m resolution to balance proportions of presence and absence cells and, importantly, encompass potential localization error (200m). Prior to modeling we tested for collinearity and inspected variance inflation factors (VIF) to identify and remove collinear predictor variables one at a time (Pearson's R > 0.6 and VIF < 3) with R package "usdm" (Naimi et al., 2022; Nichol & Heaslip, 2018; Zuur et al., 2010).

Table 1. Candidate habitat variables, their units, and sources; the non-collinear covariates with VIF < 3 selected for final models are in bold.

Variable	Description	Units	Source
aspect	azimuth of terrain surface faces	degrees (°)	depth layer *
DTS	distance to shore	meters	BC coastline shapefile ^ (Geo BC, 2002)
substr	substrate composition	categorical	(Shaw & Lintern, 2016)
depth	depth below mean sea level	metres	(NOAA, 2000)
slope	gradient of the sea floor	degrees (°)	depth layer *
roughness	difference between maximum and minimum value of a cell and its 8 surrounding cells	Δ meters	depth layer *

** calculated with R function "terra::terrain"*
^ calculated with R function "sf::st_distance "

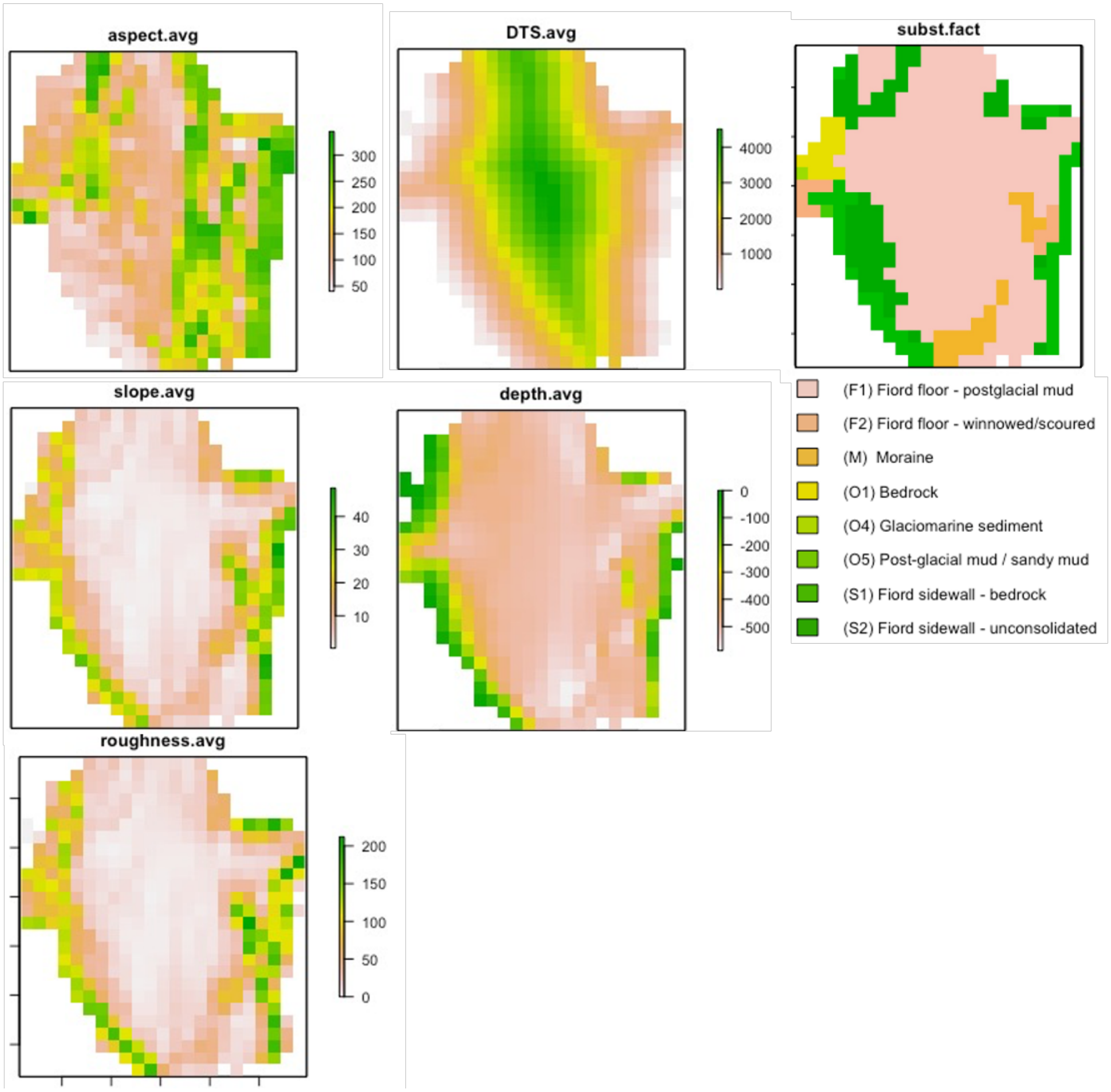

Figure 2. Habitat covariates at 500m resolution within study site and 200m accuracy boundaries overlayed. Substrate class definitions in Table S3.

2.3. Analysis

We used habitat modeling techniques to reveal environmental relationships among different fin whale call types. Within this framework we treat different call categories like different species. First, optimal modeling parameters were selected for, then used in the modeling of all behaviour categories. Outputs were compared between call categories to understand first which covariates were most important to different behaviours, and second to describe the specific shape and direction of environmental relationships among behaviours. Finally, we evaluated how much spatial use among behaviours differed.

2.3.1. Parameter Selection

The purpose of our models was to investigate what habitat features best explained the occurrence of different fin whale call types. Model parameters were chosen according to this explanatory goal. Acoustic localizations are best treated as presence-only data because whales can be present but not calling and therefore it is not possible to know when whales are truly absent (El-Gabbas et al., 2021; Hannay et al., 2013). Without true absence data, we chose to implement MaxEnt models, which are recognized as the most appropriate for presence only data (Elith et al., 2006). This machine learning model works by minimizing entropy between probability density curves across covariates sampled from (a) background available environmental variables and (b) known species presence locations. In our context, this means MaxEnt model predictions represent the probability of a certain call type occurring in a location (cell) based on the concurrent environmental variables (Merow, 2013). We also used the R package "ENMEval" to determine optimal predictor combinations, and model parameters (Muscarella et al., 2014). Feature selections were made using a sequential method in which models are first filtered to the lowest average test omission rate then the final model selected by the lowest Akaike's information criterion (AIC) (Radosavljevic et al., 2014, Kass et al. 2020).

Of the candidate covariates, aspect, distance to shore (DTS), and substrate type were retained because these were the non-correlated variables (Pearson's $R < 0.6$) with $VIF < 3$ (Nichol & Heaslip, 2018; Zuur et al., 2010). There were 598 cells in the study area at the 500m resolution and sample sizes in training sets per call category ranged from 93 to 396 (Table 3). Lowest AIC values after filtering in ENMEval investigations were achieved for the models with the following Maxent parameters; feature class "hinge", a regularization factor of 2.5, and the "cloglog" output were selected for output surfaces; which produces cell values that represent the probability of a certain call type occurring in a location (cell) based on covariates.

2.3.2. Model Implementation

We modeled habitat associations as a function of different acoustic whale behaviours (call types), adapting methods from Pacheco et al. (2021) who investigated habitat as a function of group composition. Selected models and criteria (discussed above) were applied across behaviour categories for comparability. Fin whale calls were split into eight categories distinguished by unique call type and time of day. Solar angles were calculated for each observation in R package oce (Kelley et al., 2022) and used to distinguish day (solar angle > -12) from night (solar angle < -12). Next, for each category a random sample of points (25%) was set aside as the independent test data for model validation, and remaining points (75%) were used to train the model. We then selected background points (or pseudo-absences) of equivalent point density per category from within the training data boundary, which represented the full environmental range calls within which calls were possibly localized (Webber et.al., 2011). Model replication was achieved with 5 cross validation runs per category. Acoustic habitat suitability models were implemented in R package "dismo" with the "maxent" function (Hijmans, Phillips, et al., 2022; R Core Team, 2022).

Models were evaluated with two measures. We used area under the curve (AUC) to describe how well the model distinguishes between presence and background data (Phillips et al., 2006), and point biserial correlation (COR) to describe how well aligned (correlated) predicted surfaces were with true presence pseudo-absence surfaces (Elith et al., 2006). Models were evaluated with area under the ROC curve (AUC) and point biserial correlation (COR) using “dismo::evaluate” in R. AUC represents how well the model can distinguish between presence and background points (AUC > 0.5 is better than random) and COR shows how correlated a predicted surface is within the actual distribution of points (higher correlation is better alignment) (Elith et al., 2006).

After modeling, habitat relationships were mapped and compared over space. Model prediction surfaces are 'cloglog outputs', representing the probability between 0 and 1 that if a calling whale was present, it would be in that cell based on the concurrent habitat features there. MaxEnt models predict habitat suitability on a scale from 0 (not suitable) to 1 (most suitable) (Mero et al, 2013). We report on the percent contribution by predictor variables to the model using relative variable importance. Response curves were also compared because they are useful for understanding the relationship with each environmental predictor among behaviours.

2.3.3. Spatial Comparison Among Behaviours

Next, we compared niche spaces among acoustic behaviours spatially. Models were used to generate predictions of occurrence for each whale behaviour across the study region. Predictions were constrained to a 400m buffer around the network's localization range (Figure 1); beyond this buffer covariate values began to diverge from those within the model training area. We further reclassified each behaviour surface by the "maximum test sensitivity plus specificity" threshold (mTSS), which provides transformation from continuous to binary outputs, and is recommended for presence only data (Chou et al., 2020; Jorge et al., 2013). These binary outputs can simplify visual interpretation of differences among whale behaviours because they represent where the relative occurrence of a species is predicted to be above a certain proportion (threshold).

Finally, we calculated correlation and niche overlap among prediction surfaces for each behaviour to determine how much acoustic habit among call types was shared. Following Reino et al. (2017), we used a modified t-test that checks for correlation between two spatial processes to compare similarity among behaviour surfaces using the "modified.ttest" function supplied by the "SpatialPack" R package (Osorio et.al., 2022). Niche overlap among behaviour's binary surfaces were then described with the traditional Schoener's D statistic of niche overlap that ranges from 0 (no overlap) to 1 (complete overlap). Niche overlap calculations were made with the "calc.niche.overlap" function from the "ENMeval" R package (Muscarella et al., 2014) .

3. Results

3.1. Data

More localizations were made during the day (66.8%) than night (33.2%), and there were more 20Hz (88.3%) than 40Hz (11.6%) calls localized (Table 2).

Table 2. Summary of acoustic localization counts.

	Diurnal Distinction		
Call Type	**Day**	**Night**	**Total**
20Hz	2756 (62.4%)	1146 (25.9%)	3902 (88.3%)
40Hz	195 (0.4%)	321 (0.7%)	516 (11.6%)
Total	2951 (66.8%)	1467 (33.2%)	4418

3.2. Analysis

3.2.1. Model Implementation

Using AUC evaluations we found different model performance among behaviours. In our study AUC values were useful (AUC > 0.7; Swets, 1988) for all call categories (Table 3).

Models for day 40Hz (AUC = 0.77) and day 20Hz (AUC = 0.75) categories were best at distinguishing presence points from background points (Table 3). COR values were > 0.3 for all groups and highest for day 40Hz (COR = 0.45) and day 20Hz (COR = 0.40) (Table 3).

Covariate percent contributions and response curves varied among pooled and independent call categories. Higher contribution percentages indicate greater importance of that environmental covariate to the occurrence of that call type. Pooled models for temporal (day-night) and call-type (20Hz-40Hz) categories showed DTS was the most important predictor variable (> 48.2%) (Table 3). Among independent categories, substrate was the most important covariate to daytime and nighttime 40Hz calls (60.4% and 54.8% respectively; Table 3). Response curves across categories generally showed increased occurrence towards the largest distances from shore, and substrate type 'Moraine' (M) was more important to 20Hz than 40Hz calls (Figure 3). Fjord floor 'Winnowed/Scoured' (F2) was used more during nighttime and when whales used 40Hz calls. The 40Hz calls were more frequently localized over the 'Post glacial mud/Sandy mud' (O5) category at night (Figure 3). Occurrence peaked over aspects facing East-Southeast (~100º) for most categories. However, 40Hz calls were least likely to be found over seafloor facing north (aspect of < 40º and > 340), where 20Hz calls still had high probability (Figure 3). Among independent categories, nighttime 40Hz calls were the only category to show a drop in occurrence probability at the farthest distances (4.5km) from shore. Occurrence rates across aspect were more varied for 20Hz calls than for 40Hz calls (Figure 3).

Table 3. Tabulate per call category; number of points, training sample sizes, percent contribution of each variable to the model, area under the curve (AUC), and point biserial correlation (COR) values. Bold text represents the most important variable to the data grouping; italics represents the least important variable.

Call Category	Total No. Points	No. Training Samples	DTS (m)	Substrate (classes)	Aspect (direction º slope faces)	AUC	COR
Day 20	2756	281	**73.6**	14.3	*12.1*	0.751	0.403
Night 20	1146	224	**57.6**	23.0	19.3	0.734	0.398
Day 40	195	93	32.1	**60.4**	*7.5*	0.772	0.445
Night 40	321	145	31.2	**54.8**	*14.0*	0.743	0.386
Day Calls	2591	293	**64.4**	*15.7*	19.9	0.737	0.381
Night Calls	1075	257	**48.9**	*12.2*	38.8	0.698	0.342
All 20hz	3902	326	**50.7**	*11.2*	38.1	0.726	0.354
All 40hz	516	187	**48.2**	32.4	*19.4*	0.723	0.365

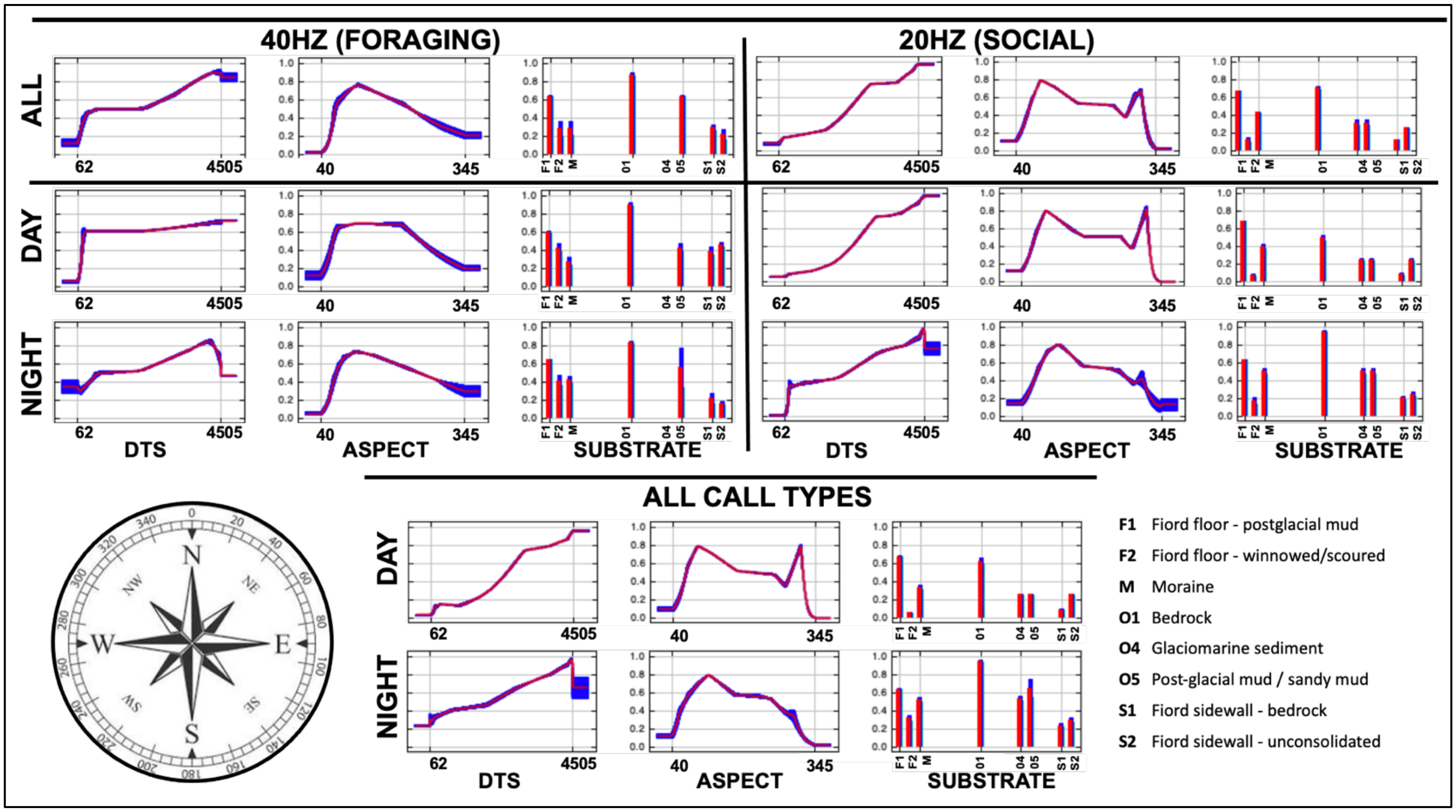

Figure 3. Response curves for each call category showing probability of occurrence from 0 to 1 (y-axes) along the range of available values for each environmental predictor variable (x-axes). Blue area shows the range in response amongst cross-validation runs.

3.2.2. Spatial Comparison Among Behaviours

Continuous surfaces showed smoother occurrence probabilities across the site for pooled categories and especially for 20Hz Calls (Figure 4). Across categories, highest occurrence was predicted mid-channel, with the exception of a nearshore patch to the west of Squally Channel (Figure 4). Binary surfaces produced from reclassification to the mTSS threshold (0.5 for all categories) showed variation among behaviours. These surfaces emphasize the higher mid-channel occurrence of all call categories and clarify differences among them, especially the disparity between 20Hz and 40Hz occurrence in nearshore waters off the southwest shoreline of our study site (Figure 4).

We found that all layers compared were significantly (p-value <0.001) positively correlated (pearson's R value > 0; Table 4). However, call type categories (20Hz vs. 40Hz) were less similar than temporal categories (day vs. night), and this pattern was pronounced between call types during the day (Table 4).

Table 4. Correlation and niche similarity results among behaviour categories. *p-value < 0.001.

Call Categories Compared		Correlation	D Statistic
All40hz	All20hz	0.70*	0.52
Day 40	Day 20	0.58*	0.57
Night 40	Night 20	0.82*	0.52
Night Calls	Day Calls	0.83*	0.81
Night 20	Day 20	0.80*	0.75
Night 40	Day 40	0.73*	0.73

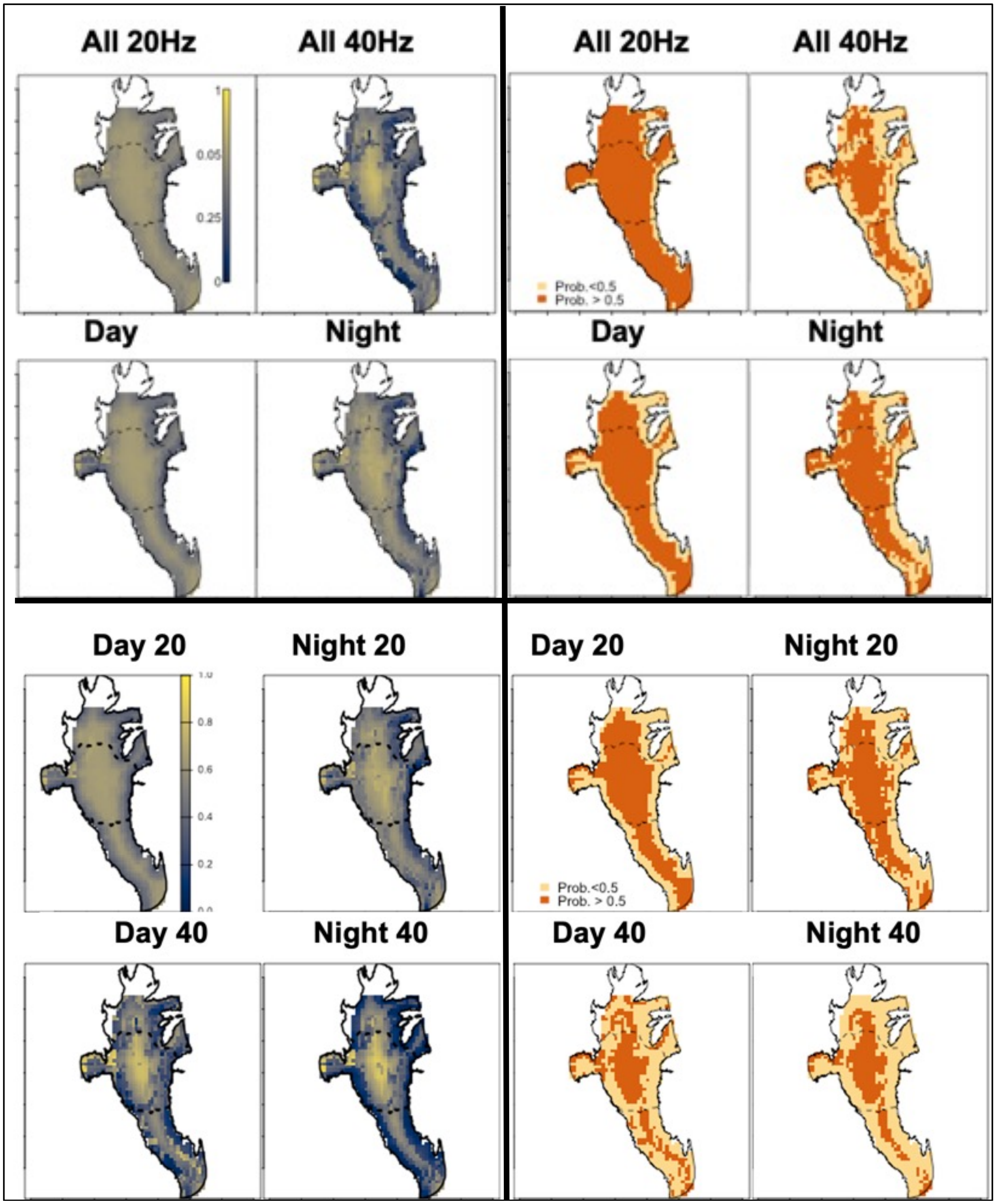

Figure 4. Predicted cloglog surfaces (left) and binary threshold (mTSS) filtered surfaces (right) from best MAXENT models run across pooled (top) and independent (bottom) call categories.

4. Discussion

We characterized spatial habitat of acoustically localized fin whales across behaviour and temporal call categories and identified differences between them. These data provide a unique opportunity for fine scale spatial and temporal analysis of acoustic habitat selection. The SDMs identified that there were differences in selected habitat features between call type categories and results generally aligned with our hypotheses that distinct behaviours occurred in distinct habitats. Below we explain how acoustically active fin whales used our study site, describe the tenets of acoustic habitat selection, and explore how acoustic properties of a coastal site could affect fin whale call use and acoustic habitat selection.

4.1. Behavioral Habitat Use

We found 40Hz call localizations were associated with habitat features expected for foraging fin whales (i.e., those which promote vertical water mixing and prey productivity). First, substrate was the most important predictor to daytime and nighttime 40Hz calls (60.4% and 54.6 % respectively; Table 3). Substrate was classified based on seafloor components including seafloor composition (e.g., sand, mud, gravel, rock) as well as structural form (i.e., slope and rugosity). Greater association of foraging calls (40Hz) with this variable supports the association of 40Hz calls and foraging behaviour in our site as these bottom characteristics relate to prey habitat and foraging efficiency. These subsurface characteristics for which our substrate covariates (i.e., seafloor slope, rugosity, and depth) served as proxies likely influence euphausiid distribution and their accessibility to whales. For instance, steep underwater slopes with strong upwelling can promote dense krill aggregations at multiple depths (Cotté & Simard, 2005; Moors-Murphy, 2014). We also found 40Hz callers consistently selected slopes with specific aspects regardless of the time of day as indicated by consistent occurrence peaks towards East-

Southeast facing aspects (~100°) for independent and pooled 40Hz categories (Figure 3). In our site, sea-floor oriented East-Southeast faced perpendicular to the eastern passage leading into Squally Channel from fjord headwaters (Figure 1), which could be delivering nutrient rich waters forced by freshwater outflow from higher up in the fjord system (Johannessen et al., 2015). Krill aggregations have also been strongly associated with tidal interactions related to bathymetry; indeed, fin whales have been observed to take advantage of current sheer and eddies to trap prey and conserve energy (Johnston et al., 2005; Sourisseau et al., 2006). Further in a constricted system such as Squally Channel, vertically migrating krill may travel into the upper water column at night where stronger current flows could flush krill into Squally Channel through the narrow western entrance. As such, this specific "corner" could become an important current-driven krill aggregation feature (Cotté & Simard, 2005; Sourisseau et al., 2006). The consistency of this selection for specific aspects aligned with our hypothesis that foraging fin whales would select seafloor areas facing specific directions in a fjord with tidal influence because these locations would facilitate more consistent access to prey. Spatial prediction surfaces further reflected these patterns with 40Hz calls having a high probability of occurrence at the mouth of the western entrance to Squally channel (Figure 4).

In contrast to foraging related calls, social-related 20Hz calls showed reduced association with foraging related features and showed less consistent feature selection. For categories containing 20Hz calls, DTS was invariably the most important covariate with a contribution of 50% or more (Table 3). Relative to substrate and aspect, DTS is not as direct a driver of fin whale prey distribution (Friedlaender et al., 2011), suggesting 20Hz calls are less associated with foraging habitat. Response curves also showed that 20Hz call occurrence was less consistently associated to specific aspects than 40Hz calls. In fact, this variable response across aspects suggests that 20Hz callers in fjords are not guided by habitat features that likely concentrate prey. Divergence from foraging-related habitat features supports our hypotheses that 20Hz calling in this fjord serves a social purpose as suggested by previous studies (Romagosa et al., 2021; Širović et al., 2013; Stimpert et al., 2015). The increased specificity of foraging related habitat suggests as expected that that foraging whales are more selective in space for foraging related features compared to social callers.

Similar to our findings, other studies have found that fin whales prefer further distances from shore using visual and acoustic detection methods (Storrie et al., 2018; Irvine et al., 2019). However, our scale of investigation differs from other published works where distances ranged from 0 - 100's or 1000's of kilometers, while our maximum DTS was about four kilometers. Still, DTS (or distance to coast) remains a principal predictor in fin whale models despite inclusion of dynamic variables and backscatter metrics directly influencing and predicting prey distributions (Friedlaender et al., 2011). Even in this system, past habitat association studies found that bathymetric features contributed more to explaining distributions than dynamic variables (Keen, 2017). In fact, Keen et al. (2018) found visual fin whale observations concentrated over minimal slopes and depths around 300 and 500 meters, which aligns with our observations of acoustic habitat preference. Even if correlation between depth and DTS is not driving this distinction between spatial occurrence of 20Hz and 40Hz calls, it remains important to vocal fin whales across spatial scales and warrants further investigation to identify potential drivers of this pattern.

Spatial comparisons among behavioural use provided further evidence of acoustic behavioural partitioning of habitat use. We found that all behaviours were significantly positively correlated and had niche overlap greater than 50%, implying a large degree of spatial use similarity among whale behaviours (Table 4). However, considering this was a niche overlap analyses for different behaviours of the same species, overlap proportions as low as 52% are surprising. In fact, a study of niche overlap among distinct marine mammal taxa (e.g., seals and cetaceans) feeding on krill was as high as 56% (Friedlaender et al., 2011). We also observed the lowest niche overlap among call type categories (D-statistic = 0.52; Table 4), which supports other findings that 20Hz and 40Hz calls are associated with distinct behaviours and that whales engaged in those behaviours have different habitat preferences. Further, spatial use differed (less positively correlated) among call types more during daytime than nighttime, indicating that the behavioural distinction of these calls is more pronounced during daylight hours. Ecological processes that differ between day and night are less important to spatial selection by fin whales than processes driving the use of different call types. Binary prediction surfaces were also useful in emphasizing the more selective range of foraging activity (Figure 4).

4.2. Temporal components of behavioural habitat selection

Distinct habitat was not only observed between call-type categories, but also between temporal call-type categories. Covariate importance differed between pooled and diurnal categories for both 20Hz and 40Hz calls. For instance, substrate was the most important predictor for day and night 40Hz calls, but not for the pooled 40Hz category (Table 3). Substrate was the least important predictor to the pooled category of 20Hz calls while aspect was least important to the 20Hz day and night categories. These misalignments of habitat relationships amongst pooled and independent call categories shows that 20Hz and 40Hz calls could have different functions during different times of the day.

Our investigation of differences in habitat between day and night found nighttime call habitat was more associated with foraging than daytime calls. Nighttime calls (especially nighttime 40Hz) occurred with greater probabilities over substrate type F2 - "Fjord floor -

winnowed/scoured" (Figure 3). This substrate class is described as an area with strong bottom current (Shaw & Lintern, 2016; Table S3) and is likely associated with higher productivity and ease of prey capture because areas of greater current flow typically produce more upwelling and concentrate prey (Crawford et al., 1995). We also found that, although DTS remained the most important predictor to both day and night 20Hz categories, 20Hz nighttime calls were associated with substrate and aspect (predictors related to upwelling and prey productivity) more than 20Hz daytime calls (Table 3). This finding supplements previous research findings within the same study site that showed significantly different movement patterns in fin whales engaged in repetitive 20Hz calling (only one call type investigated) between nighttime and daytime; where they observed nighttime 20Hz callers moved faster with greater track directionality than daytime callers (Hendricks et al., 2021). They found greater track directionality (more straight, less directional change), and higher speed at night which usually indicate a traveling state of behaviour as opposed to a foraging state, at least at larger scales which might suggest daytime foraging for this species. That conclusion also aligns with a tagging study that found fin whales in Squally Channel performed longer, deeper dives during the day, indicating daytime foraging on krill patches in this site (Nichol & Heaslip, 2018). Authors have suggested that speed differences may be due to energetic availability following daytime foraging (and energetically costly deep dives), or non-directional movement (i.e., diving) at un-resolvable scales (<200m) that impeded forward travel during daytime; however the specific reasons remain unclear (Hendricks et al., 2021). However, Hendricks et al., (2021) focused on 20Hz calls only, a call type that fin whales usually only produce in the top 15 meters of the water column (Stimpert et al., 2015). Our results suggest that the different track characteristics of repetitive 20Hz callers between day and night defined by Hendricks et.al., (2021) might instead be reflective of distinct foraging behaviours on prey at different depths requiring unique foraging strategies with different horizontal movement characteristics; alternatively, their focus on 20Hz calls alone prevented resolving foraging activity at this scale of investigation. More continuous scales of temporal investigation involving multiple call types may be able to address these uncertainties.

Relatedly, the dynamic nature of unique semi-enclosed coastal sites could promote fin whale foraging at more sporadic intervals than the clear patterns identified in other regions. Coastal and inland marine habitats are inherently dynamic; high primary productivity via ocean mixing and nutrient inflows and capture provide opportunities for fin whales to forage, which may influence observed acoustic behaviour. Such dynamic ecosystems are not only immensely productive but also likely provide dependable (if not temporally consistent) resources for fin whales (Bianchi et al., 2020). While researchers often prioritize identification of temporal peaks in important animal behaviour (i.e., foraging), in certain places and at some scales of observation, peaks are not always evident. Despite exhibiting activity peaks, large marine predators will still take advantage of accessible prey when available (Irvine et al., 2019; Piatt & Methven, 1992). Although baleen whale peaks in foraging intensity are supported by multiple streams of evidence such as stomach content (Víkingsson, 1997), call rates (Širović et al., 2013; Stimpert et al., 2015), visual observations (Oleson, Calambokidis, et al., 2007), and GPS depth tagging (Keen et al., 2019), this is not to the exclusion of foraging activity throughout the 24-hour cycle. Each of these methods also found evidence that fin whales likely feed throughout the 24-hour cycle, but efforts intensify in alignment with peaks in prey availability, or capture efficiency produced by their environment. In Squally Channel, nighttime krill patches (while more dispersed) may be closer to the surface and more easily captured, allowing foraging to continue at night (Burrows et al., 2016; ; Doniol-Valcroze et al., 2011; Kaartvedt, 2010; Stafford et al., 2005).

There could also be common threads between inshore habitats that connect nocturnal and 40Hz call activity with foraging features. For example, Squally Channel is similar in morphology to other Pacific fin whale habitats like the Gulf of California (GOC). Both Squally Channel and the GOC are enclosed by land with entrances to the open ocean via narrow channels (<15km wide), both are at the terminus of oceanic canyons, and both are fed by river systems. During a temporal comparison of fin whale calling (both 20Hz and 40Hz), the GOC stood out from two other Pacific sites for having higher proportion of 40Hz calling during nighttime, despite observations of physical daytime foraging behaviours across all sites (Širović et al., 2013). Like the GOC, 40Hz calls were detected more at night in Squally Channel. Nighttime calls also aligned more with foraging-type habitat features. The presence of disjointed acoustic and physical behaviour expectations among similar geographies suggests that combined site characteristics of semi-enclosed oceanic sites with freshwater contributions, as well as tidal circulation could provide the ideal conditions for nocturnal foraging. Alternatively, other factors may motivate the use of foraging-like habitat and 40Hz call production at night, such as marine acoustics.

4.3. Acoustic Habitat Selection

We found some evidence that fin whales tailor call type according to habitat covariates that potentially influence the efficacy of their acoustic communication. The acoustic habitat hypothesis states that acoustic species select habitat for properties of sound propagation that are relevant for communication (Mullet et al., 2017); thus, animals will select habitat and perform acoustic behaviours (calls) that maximize the fitness benefits of the energy expended to produce those sounds. Habitat characteristics (that vary with space) can influence sound, both in how far it travels and in the quality (signal clarity) it retains, so that acoustics can play a role in habitat selection.

We found that 20Hz calls were more probable over substrate types; M, O4, and S2 compared to 40Hz calls (Figure 3). These substrate types generally contain gravelly sandy mud and glaciomarine mud, which are more porous substrates that have been found to facilitate the furthest propagation ranges for lower frequency sounds (Jensen & Kuperman, 1983). Modelers determined that optimum frequencies (those which travels furthest with the least attenuation) exist and vary with water depth, whereby lower frequencies are more optimal in deeper water. Jensen and Kuperman (1983) also found that although optimal frequency was more dependent on water depth than substrate type, the propagation distance of sounds was significantly affected by substrate type with greater attenuation (loss) over harder less porous substrates (like bedrock). Given the expected sociality of 20Hz calls, maximizing communication range could be especially important to this call-type and habitat relationships we observed align with our expectation that social callers (20Hz - lower frequency call) in Squally Channel would be more likely to call over more porous substrates, and towards deeper depths, which would maximize propagation range and reach of this call type. Acoustic habitat selection has also been observed in other baleen species. Mercado and Frazer (1999) modeled optimal habitat for singing whales based on factors that affect sound transmission, and then observed humpback whales in the field using sites with similar characteristics across space to those that their models predicted. They found singing whales producing calls at frequencies between 50 and 800Hz often selected habitat with optimal characteristics for sound propagation at those frequencies (i.e., sandy/silty substrate, in water depths between 30 and 300m) (Mercado & Frazer, 1999). This alignment suggests that cetaceans can select habitats for properties of acoustic propagation.

We suggest that, like humpback whales, fin whales could also tailor calling activity as a function of the acoustic properties of their physical environment. They may even choose to alter calling activity to use higher frequency calls more often in nearshore environments where shallower water acoustics become important. In Squally Channel, 40Hz calls (higher frequency fin whale call type) were more probable than 20Hz calls over the dense bedrock substrate type (O1; Table S3). Higher frequency calls attenuate less than lower frequency ones over these denser substrates (Jensen & Kuperman, 1983), thus 40Hz calls would be more efficient in this habitat type. Marine acoustic propagation is affected by many factors but becomes particularly complicated in shallow waters (<200m) where sound waves interact with the bottom, and bathymetric shape, and substrate composition become relevant to how marine sounds travel (Mercado & Frazer, 1999; Richardson et al., 2013). Fin whales are generally thought of as open-ocean species, and their evolution to make single frequency pulses that transmit best over long distances reflects that they generally communicate in the open ocean (Richardson et al., 2013). Tagging studies have also determined that fin whales usually call at specific depths between 10-15m (Stimpert et al., 2015). This may show fin whales behaviourally select environmental cues (such as reaching neutral buoyancy, or swimming at a thermocline) that allow them to exploit depths that amplify their calls, maximizing communication range, and minimizing energy expenditure of calling (Stimpert et al., 2015). Given evidence that fin whales select optimal spaces for communication, and that different frequencies could be more advantageous in different locations (with different depths and substrates), it could follow that sometimes call type (use of higher or lower frequencies) might be adjusted spatially based on the acoustic habitat characteristics. In other words, acoustic fin whale acoustic behaviour may vary spatially as a function of habitat characteristics affecting sound propagation, not activity motivation alone.

5. Conclusions & Implications

We investigated acoustic habitat associations of different fin whale calls in a fjord within Gitga’at territory to understand whether habitat relationships aligned with the expected behavioural roles of these call types. This study has contributed fine scale habitat association knowledge to a growing understanding of fin whales' acoustic use of fjord systems. These patterns largely align with existing literature, as 40Hz foraging related calls were associated with features expected to promote prey availability. We showed that acoustically active fin whales selected distinct habitat in a coastal fjord during different calling activity (as defined by call type and time of day). Further, we found habitats differed between day and night expressions of the same call type and propose that 20Hz and 40Hz calls could serve different purposes between day and night for fin whales and suggest that unique features of this semi-enclosed coastal site might facilitate more diverse foraging patterns than in the open ocean. We also suggest that the shallower waters encountered here may encourage acoustic behavioural adaptations. We approached habitat associations from the perspective of the acoustic habitat selection hypothesis and found modest evidence that a nearshore stratification between call types could suggest that lower frequency signals offer advantages to fin whales in coastal environments. Finding these divergent spatial requirements among behavioural and temporal fin whale calling activities suggests that distinct acoustic whale behaviours could be more vulnerable than others to various anthropogenic impacts. Further, understanding behavioural variability (not just identifying peaks in activity) can be equally important information to a species' conservation as evidence for a lack of predictable behaviour requires more generous application of precautionary measures.

Environmental stochasticity may be further exacerbated by effects of human induced rapid environmental change. Thus, behavioural knowledge and vulnerability assessment techniques are urgently needed.

The Kitimat fjord system is unusual habitat for fin whales (Keen et al., 2021) but behavioural plasticity of social creatures can assist in their rapid adaptation to novel or changing environments. Recovering fin whale populations have been recently observed to increase their use of coastal and nearshore habitats (Herr et al., 2022). Whether this is driven by animals returning to ancestral habitats following precipitous declines during the commercial whaling era, or due to other global habitat trends, fin whales may interact more with shallow water environments than modern researchers have previously observed them doing. The soundscapes of these habitats fundamentally differ from the open ocean environments in which fin whales have been more traditionally studied. Thus, researchers must consider how acoustic components of habitat could shape fin whale communication as it could have implications for interpreting differences in observed calling patterns among distinct geographies.

6. Supplementary Information

Table S3. Substrate class code, full name, and detailed descriptions of how each class was defined by Shaw & Lintern, (2016).

Class	Name	Description
F1	Fiord floor - postglacial mud	Gentle relief (slopes <10º) deposits of postglacial mud and sandy mud; commonly located in banks to either side of channel thalwegs; acoustically transparent or with moderate internal reflections; low backscatter; formed primarily by deposition of fluvial sediments, but also by reworking of glaciogenic sediments.
F2	Fiord floor - winnowed/scoured	Low-relief (<2º) areas of non-deposition or erosion with glaciomarine mud exposed at the seafloor; some areas have scalloped appearance with relief of 0.5 to 2.0m; surgical lag of muddy sandy gravel overlies acoustically stratified glaciomarine sediments; high backscatter; formed where bottom currents are relatively strong.
M	Moraine	High-relief (>100m) transverse ridges; gullied in places; acoustically incoherent glacial dialect draped by acoustically stratified glaciomarine mud; surface veneer of muddy gravel; high backscatter; formed at former ice margins during the retreat of grounded ice.
O1	Bedrock	Bedrock ridges and knoll with relief up to 30 m, separated by depressions containing glacial and postglacial sediments; high backscatter in depressions.
O4	Glaciomarine sediment	Areas of low relief imprinted by iceberg furrows and pits; surface lag of sandy gravel overlies draped, acoustically stratified, gravelly sandy mud; high backscatter; formed by deposition from glacial meltwater plumes.
O5	Post-glacial mud / sandy mud	Low relief banks with weak acoustic stratification in a semi-ponded style; mud and sandy mud; low backscatter; formed by deposition of reworked glacial sediments and fluvial sediments.
S1	Fiord sidewall - bedrock	Steeply sloping (>40º) with bedrock outcrops separated by depressions containing gravelly sands mud; attached fauna on exposed rocks and infauna in depressions; high backscatter.
S2	Fiord sidewall - unconsolidated	Slopes >10º, smooth surfaces or incised by gullies up to 10 m deep; consist of glaciomarine sediment both surface lag or a veneer of postglacial mud; generally gravelly sandy mud (low backscatter).

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Chapter 3: Using Acoustic Localizations to Assess Spatial and Temporal Vulnerability of Fin Whale (*Balaenoptera physalus*) Behaviours to Vessel Traffic Types

Abstract

Whales are vulnerable to vessel traffic. Boats remain the leading source of mortality for several populations, and global shipping fleets have fundamentally changed oceanic soundscapes in which soniferous whales evolved. Previous research has focussed on identifying when and where whales are most vulnerable to vessel traffic, generally using spatially explicit risk assessments that inform spatial and temporal separation strategies. This body of work, however, frequently depends on assumptions of consistent spatial distributions of whales between day and night. Such an approach potentially obscures the detailed patterns of spatial and temporal interactions among specific whale behaviours and vessel traffic. To that end, we used acoustic localization data on fin whale behaviours and ship location data to quantify temporal and spatial vulnerability of whales to varying types of vessel traffic. We show that recreational, passenger, and cruise vessels exhibited daytime activity and commercial ships were more active at night along specific routes. We also found that whales' diurnal activity patterns were distinct among foraging and social calling, whereby foraging calls occurred more during darker crepuscular hours than social calls, which peaked in the afternoon. Further, the central locations in which these two call types occurred were distinct. These results demonstrate that during foraging related calling, whales may be more vulnerable to tanker/cargo vessels at night, while social callers had greater activity in daylight hours and are therefore more vulnerable to cruise ships. These findings can serve as important insights for informing management strategies, especially in constricted coastal geographies facing rapid vessel traffic increase.

1. Introduction

Vessel operations are the most pervasive, direct, and impactful way that whales and people interact. In the past century, global vessel density has increased over four times (Frisk, 2012), and ship gross tonnage continues to rise by about 4% annually (Erbe et al., 2019). Fin whales (*Balaenoptera physalus*) are among the most struck cetacean species in the world (Laist et al., 2001; Redfern et al., 2020; Vanderlaan & Taggart, 2007), and their recovery since the end of commercial whaling in concert with steady increases in global shipping activities will likely lead to intensification of vessel impacts to whales.

Vessel traffic can impact whales in many ways, but two major impacts are ship strike, and acoustic interference. Vessel strikes represent an immediate and often lethal threat to whales and can have population consequences for large slow-reproducing marine mammals (J. V. Redfern et al., 2012; Schoeman et al., 2020). Whales are also vulnerable to acute and chronic noise threats. Acute threats such as military artillery testing that damage physical hearing infrastructure of whales and cause mass strandings and behavioural response (Dolman & Jasny, 2015; Richardson & Würsig, 1997; Thomas et al., 2016; Tyack, 2008). Chronic noise sources include global shipping fleets, which are responsible for an increase in the intensity of ambient ocean noise by approximately 11 decibels (McDonald et al., 2006). Noise pollution can reduce the communication range of whales (called call masking), cause them to alter their behaviour, and can reduce their foraging efficiency (Croll et al., 2001; Tyack, 2008). Chronic acoustic threats from shipping fleets are a particular concern for baleen whales because vessels emit noise in the same low frequency bands that baleen whales use to communicate (Weilgart, 2007).

Vessel traffic is not homogenous, however, and their behaviour (and associated threats) can vary among vessel types. Off the coast of Western North America, AIS (Automatic Identification System; Madon et al., 2022) data have been used to characterize different types of vessel traffic. Greig et al. (2020) identified different spatial patterns among vessel types and found commercial vessels (i.e., cargo ships, tankers, and tugs with a barge) stick to predefined routes while vessel types like private pleasure craft and fishing vessels were less organized along specific paths. The authors also showed that certain vessel types such as passenger ships on average traveled faster than other types like tankers, cargo ships, and tug vessels. This is likely why Laist et al. (2001) observed a high frequency of lethal strikes from tankers/cargo vessels. While a similar frequency of collisions occurred with whale watching ships, they rarely resulted in mortality. Threat differences between vessel types have since been attributed more explicitly to features of vessel size and movement. Specifically, higher travel speeds and larger vessels (longer and with deeper drafts) are less maneuverable, and associated with higher risk of lethal ship strike (Silber et al., 2010a; Vanderlaan & Taggart, 2007b). Generally, larger and faster ships produce the loudest underwater noise that travels the farthest, but other vessel factors like tonnage, horsepower, and hull design can also affect noise levels (McKenna et al., 2013). These vessel factors can also vary in time, and seasonal oscillations are common in vessel traffic (Cominelli et al., 2020). For instance, cruise ships have a slim window of economic activity during the northern hemisphere summer (Webb & Gende, 2015). Diurnal patterns in vessel traffic interactions with cetaceans are less easily investigated (Buscaino et al., 2016). Typically, investigations of cetacean vulnerability to vessel impacts do not consider vessel variation, and instead assume that patterns of spatial use (often derived from visual whale observations during the day) are consistent between day and night. Cetacean vocalizations have been associated, however, with different behaviours that vary over diurnal activity patterns.

Such temporal oscillations are vital in marine systems which are largely affected by the diel vertical migration of planktonic organisms (De Meester et al., 2009). Fin whales in the

Pacific also exhibit diurnal behaviour patterns that call types have been related to. Fin whales follow the diel vertical migration (DVM) of their primary prey krill; whereby whales perform deeper daytime dives to feed on krill when it is most densely clustered (therefore more easily captured) at depth (De Meester et al., 2009; Keen, Falcone, et al., 2019). In places where fin whales exhibit deeper daytime dives, and feed during daylight, the relative proportion of feeding (40Hz) calls was higher during daytime than nighttime, confirming this acoustic behavioural alignment (Širović et al., 2013). Fin whales producing 40Hz calls are associated with foraging behaviour as 40Hz calling has been directly associated with krill (prey) presence (Romagosa et al., 2021). Conversely, 20Hz calling is associated with social behaviours, especially when produced in repetitive sequences, otherwise known as song (Croll et al., 2002; Širović et al., 2013; Stimpert et al., 2015). Until recently, nocturnal lives of many animals were not considered, largely due to the limited ability to observe animals at night. Especially for marine cetaceans, substantial monitoring at night has always been difficult to achieve.

Understanding such variability in behaviours over different diurnal periods can be developed via newly accessible technologies such as Passive Acoustic Monitoring Arrays (PAM) with localization capacity. Passive acoustic monitoring of cetaceans is not itself new, but continued development of standardized detection, classification, and localization algorithms within the field of ecology enable automated extraction of relevant cetacean calls from large recordings that are otherwise very time-intensive to manually review. Such arrays can further discern the location of acoustically active cetaceans based on cross-referencing the same signal (call) between multiple sensors (hydrophones) (Gervaise et al., 2021; Hendricks, et al. , 2021; Mellinger et al., 2007). This technology facilitates collection of location-based behavioural data, continually in time and over a region of continuous space; which provides an opportunity for the study of cetaceans that are inherently difficult to observe, especially during darkness. Including animal behaviour in vulnerability assessment can supplement management options in complex regions where spatial separation strategies are limited. Coastal geographies for instance are spatially complex systems; therefore these regions require actionable, management-informing analyses that consider both anthropogenic and ecological patterns.

We pair the use of AIS data for vessels with spatial acoustic localization data of fin whales spanning all hours of the day; allowing for the unique opportunity to investigate both daytime and nighttime vulnerability of cetaceans among vessel types. This method allows for a comprehensive investigation of behavioural vulnerability in space and time, which can inform management of vessel-whale interactions. Our objective is to identify if certain fin whale behaviours, as defined by acoustic-temporal categories, are more vulnerable (in space and time) to different types of vessel traffic. First, we classify ship traffic based on AIS broadcast vessel type and size (length). We then use activity pattern analysis (Azevedo et al., 2018), to compare the occurrence of localized whale calls and vessel traffic over the 24-hour day to identify when ships and whales interact the most. Then we use Kernel Utilization Distributions (KUD) to illustrate activity cores of vessel (AIS data) and whale (acoustic localization data) co-occurrence. We then calculate and visualize overlap for all combinations to identify which whale vessel behaviours overlap the most in space and time, where largest overlaps imply greatest vulnerability.

Our analysis will contribute a unique perspective on interactions between ship and whale behaviour to understand vulnerability in complex coastal systems. Further, in an applied sense, it will contribute information on a baseline vulnerability of fin whales in Gitga’at Territory, coastal

British Columbia, which faces significant large vessel traffic increases in the near future as an additional 700 LNG vessel transits per year will bisect the study area starting 2023.

2. Materials and Methods

2.1. Study Site

Our research was conducted in Squally Channel on the north coast of British Columbia, Canada within the territory of the Giga'at First Nation (Figure 1). This area is known to have a year-round presence of fin whales with high interannual site fidelity (Keen et al., 2021). Whale observation data were collected from a hydrophone network installed that monitors an area of ~103 km^2. Within this area, vocalizing fin whale calls can be detected and classified as either 20Hz or 40Hz, while the stratification of the hydrophones provides localized geographic coordinates of whale call locations. For full details on the specifications of this hydrophone system see Hendricks et.al. (2019, 2021).

The study site is visited by multiple vessel types. In the spring to fall season, ecotourism boats, which operate regionally, and cruise ships that transit between Alaska and southern British Columbia are known to frequent this site as part of their route along the inside passage. Compared to harbours with over 200,000 vessel transits per km^2 per year such as the Salish Sea or Southern California Bight, north Squally Channel is a comparatively quiet area for vessel traffic with < 200 AIS vessel transits per km^2 per year (Marine Traffic, 2022). However, vessel activity for the region is set to increase dramatically in the next decade with the planned completion of several LNG projects in nearby Kitimat; vessels are planned to transit through our study site to offshore markets (Figure 1). These projects (LNG Canada, Cedar LNG) could bring upwards of 700 additional large vessel transits along this route by the end of the decade (Meisner, 2015b).

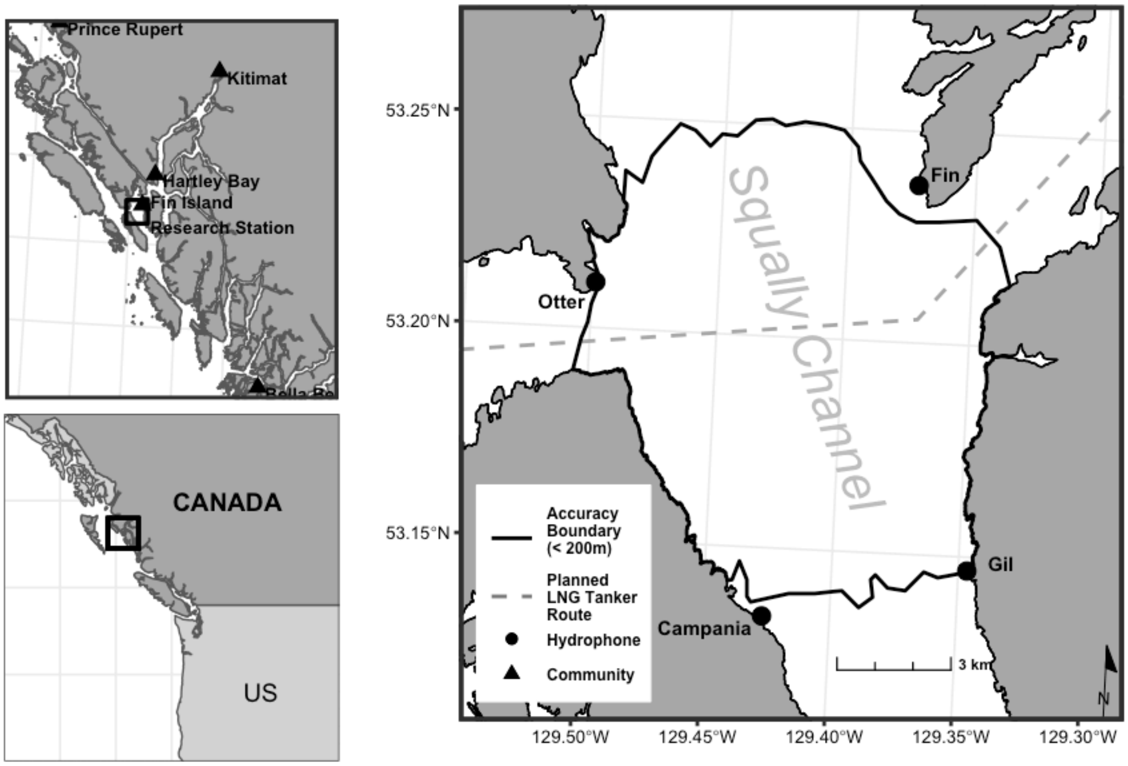

Figure 1. Study area map showing the study site location on the west coast of Canada, in relation to relevant communities, and the fine scale map of the study area boundary within Squally Channel and the location of hydrophone network locations and planned tanker route.

2.2. Data

Acoustic whale localizations (n = 5,701) were collected between 2019 – 2021 for the months of June through October. We only used points for which location accuracy was within 200 m (Figure 1) assessed with acoustic transmission experiments (Hendricks et al., 2019). Call proportions differed among years and in 2019 the greatest proportion of localized calls were 20Hz while in 2021 the largest proportion were 40Hz and 2020 represented an intermediate year (Table 1).

Vessel locations were collected from automatic information service (AIS) data acquired from the Canadian Coast guard (CCG) (Canadian Coast Guard, 2021). AIS data were available for six years between 2014 and 2021 (Table 1). Most traffic in our site occurred during the day (n = 713 unique vessels; Table 1). During this time a yearly average of 133 unique vessels across ~14 distinct vessel types transmitting AIS transited our study site. While there was a decrease in detections during 2020, counts this year were still higher than those in preceding years (2014, 2015 and 2018) which may be related to improved AIS technology, and a change in AIS regulations in 2019 mandating a wider range of vessels to carry AIS (Transport Canada, 2019). Canadian maritime law mandates that several vessel categories must carry and transmit AIS data; these include all vessels > 20m in length except for pleasure craft, vessels carrying over 50 passengers, vessels transporting IMO (International Maritime Organization) regulated materials like bulk pollutants, stationary dredging and floating plants that pose a collision hazard, and towboats > 8m in length (Government of Canada, 2022). In addition, for vessels embarking on voyages beyond sheltered waters, requirements are extended to all passenger vessels and any vessel > 8m and carrying a passenger. While not mandatory on small pleasure craft, such vessels may also voluntarily participate in AIS transmission for safety benefits. To ensure analysis of moving vessels traveling at realistic speeds, we filtered AIS observations to entries with speed over ground (SOG) values between 0.5 and 40 knots. We also trimmed vessel data to the same month range (June - October) for which whale data were available. Due to data access agreements, MMSI (Maritime Mobile Service Identity) numbers were dubbed with an ID code, which was unique to each year, thus the same vessel transiting the study site in multiple years will have three different codes (one for each year) and is therefore counted as a distinct vessel.

The most numerous vessel types in our region were pleasure craft, tug/towing, and fishing vessels respectively (Figure 2). Highest travel speeds and largest vessel lengths were found for the cruise and tanker/cargo categories respectively. The ship type with largest 2020 decline occurred for pleasure-craft class, which recovered substantially in 2021 (Figure S7).

Decline also occurred for cruise ships, which did not recover substantially in 2021. Fishing vessels numbers remained essentially stable through the pandemic.

Table 1. Vessel and whale data inventories and category proportions within the 200m accuracy boundary of the study site.

	Year	Days in Season	Start Date	End Date	Total Points	Hydrophone	# 20Hz	# 40Hz	Day	Night	20 DAY	20 NIGHT	40 DAY	40 NIGHT
Whales	**2019**	112	Jul 1	Oct 21	4416	3	3968 88.3%	522 11.7%	3342 75.7%	1074 24.3%	3028 68.6%	872 19.7%	314 7.1%	202 4.6%
	2020	48	Sept 9	Oct 27	742	4	478 61.1%	301 38.9%	359 48.4%	383 51.6%	237 31.9%	216 29.1%	122 16.4%	167 22.5%
	2021	126	Jun 10	Oct 29	412	4	20 4.4%	412 95.6%	270 65.5%	142 34.5%	6 1.5%	12 2.9%	264 64.1%	130 31.6%

					Points	Unique Vessels	Unique Vessel Types
Vessels	**2014**	126	Jun	Oct	3145	111	15
	2015	126	Jun	Oct	3453	125	12
	2018	126	Jun	Oct	4499	175	13
	2019	126	Jun	Oct	5822	169	13
	2020	126	Jun	Oct	4607	80	15
	2021	126	Jun	Oct	8177	143	13
TOTAL					29,602	803 (133 Yearly Avg.)	20 (13.5 Yearly Avg.)

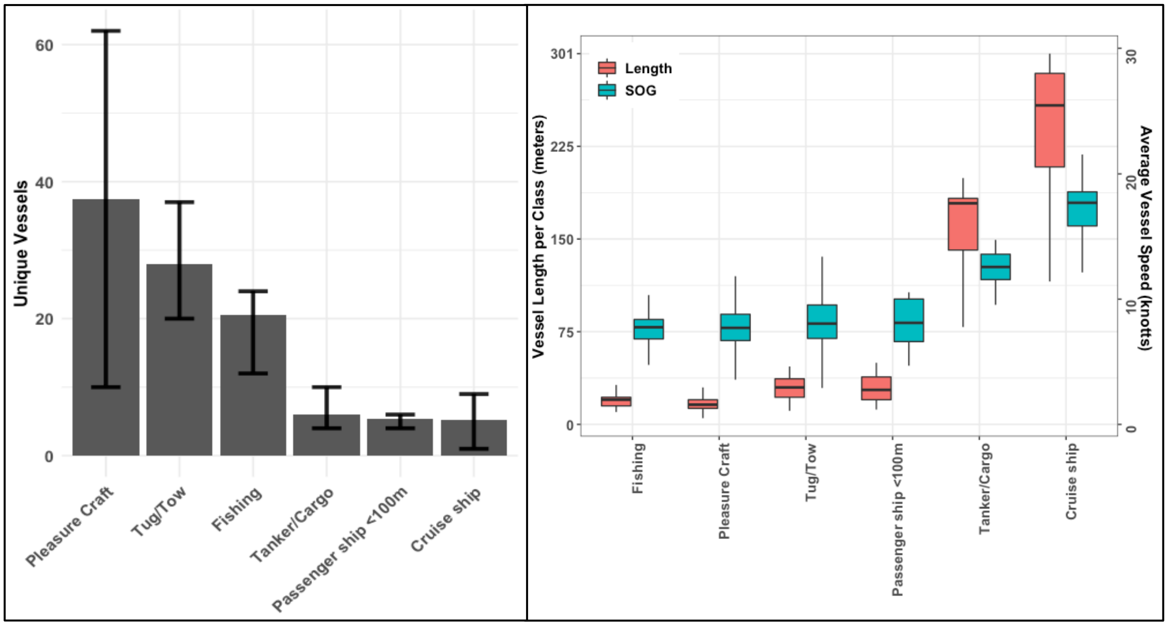

Figure 2. Annual unique AIS vessel count per category (left) with error bars showing the spread of interannual variation in counts and the spread of vessel lengths (meters) and average travel speed (knots) per vessel category investigated (right).

2.3. Analysis

We performed temporal and spatial comparisons between whale and vessel categories to estimate when and where acoustically active fin whales experience the greatest vulnerability to AIS transmitting vessel traffic (Figure 3). We also distinguish whether distinct behaviours are more vulnerable to different kinds of traffic.

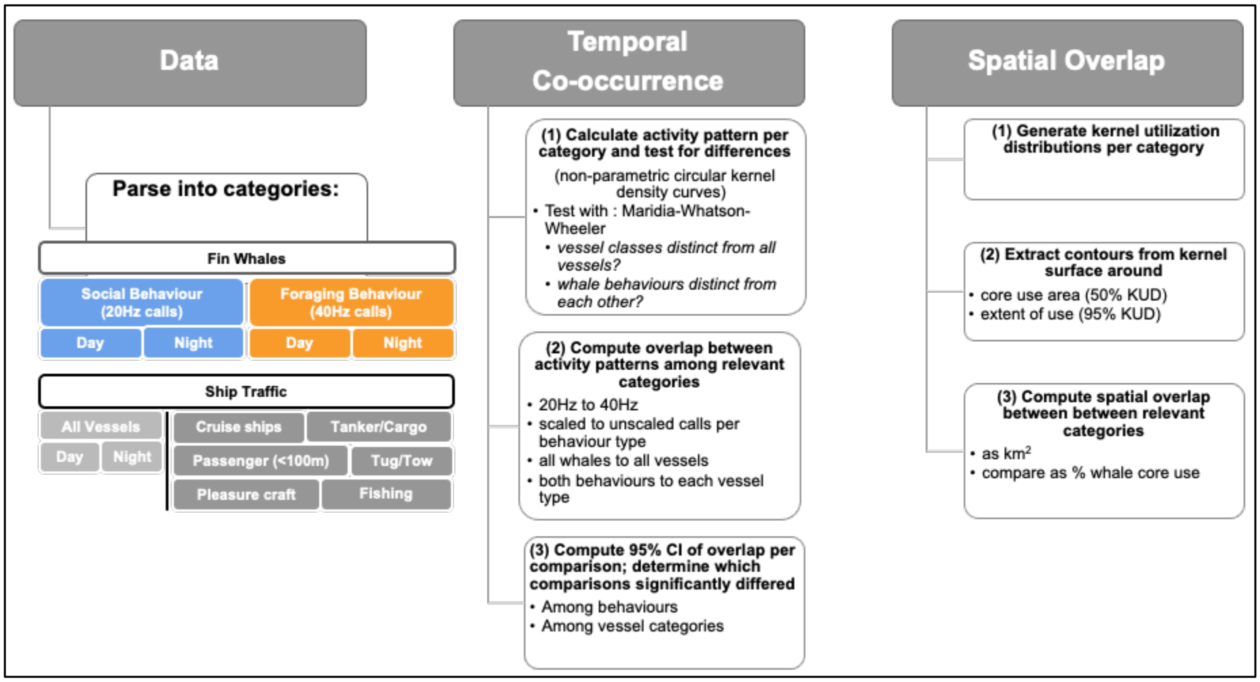

Figure 3. Flowchart of methods.

2.3.1. Category Selection

Behavioural categories were chosen according to call type and whether they occurred during the day (solar angle > -12) or the night (solar angle < -12), which reflect distinct whale behaviours identified in the literature. Similar to whale categories, we parsed vessel traffic by time of day (solar angle > -12 = day; solar angle < -12 = night), and by vessel type according to a combination of listed AIS data vessel "type", and "length". We categorized vessel data into a total of nine categories: cruise ships, passenger ships (<100m in length), pleasure craft, fishing vessels, tankers/cargo ships, and tug/towing vessels (Table S2).

2.3.2. Temporal Overlap

The objectives of the temporal overlap analysis were to (1) identify whether vessel types display activity patterns distinct from vessel traffic generally, (2) determine if whales co-occurred more with certain vessel types than others, and (3) determine if co-occurrence differed between whale behaviours. We use each call as the independent sample because we are investigating acoustic activity patterns and interested in calling activity itself. We compared diurnal temporal activity patterns of different whale calls and vessel traffic categories with a non-parametric circular kernel density function (Ridout and Linkie 2009). First, we adjusted observation times to each day's sunrise and sunset times to account for the changing sun position (Azevedo et al., 2018). Each activity pattern per category was estimated separately. Differences among activity patterns were tested with the nonparametric Mardia–Watson–Wheeler (MWW) test, which compares the shape of activity pattern density curves (Batchelet, 1981, Lund et al., 2022).

We then calculated the *coefficient of overlapping* (Δ) for all important comparisons between vessel and whale categories. This coefficient quantifies the overlapping area shared under the density curves of the activity patterns, and ranges from 0 (no overlap) to 1 (complete overlap) (Linkie & Ridout, 2011; Meredith & Ridout, 2021). The estimator for large sample sizes (Δ^4) was used when both categories had $n > 50$, which occurred for all samples. Bootstrap runs of 10,000 resamples were then used to generate the 95% confidence interval of overlap per comparison, and differences were deemed significant when confidence intervals did not overlap (Meredith & Ridout, 2021). All analyses were performed in R (version 4.1.0; R Core Team, 2021) with the packages "overlap" (Meredith & Ridout, 2016) and "circular" (Lund et al., 2022).

Finally, we compared the density distributions across solar angles (a metric of darkness) of different categories and to available environmental ranges during the same time period. Kolmogorov-smirnov tests (D statistic) were used to test for differences among categories and available solar angles. Differences from available solar angles would reveal preferential selection, and differences in solar angle preferences among whale behaviours would suggest different calls are used in different portions of the diurnal cycle.

2.3.3. Spatial Overlap

We performed a spatial overlap analysis among core use areas (CUA's) for vessel and whale categories. CUA's represent the spatial area within which a certain proportion of an animals' activity occurs. First, kernel utilization distributions (KUD's) were generated for each whale and vessel behaviour across the same resolution grid with the "adehabitatHR" package (Calenge, 2006) in the R statistical environment (version 4.1.0; R Core Team 2021). The smoothing parameter was selected with the reference bandwidth ("h-ref") method and then consistently applied across categories for comparability. Next we extracted activity space contours per category around the core use, and use extent, respectively defined by the 50%, and 95% contours (Udyawer et al., 2013). We then computed the area of overlap between core use contours of whale and vessel categories and converted overlap areas to the proportion of whale CUA to identify classes and call types with higher overlap. We consider greater overlap as higher spatial vulnerability. While we apply these techniques to different call types instead of individuals' telemetry relocations (as the function was originally designed for), our goal was to investigate patterns of different acoustic whale behaviours, not individuals.

3. Results

3.1. Analysis

3.1.1. Temporal Overlap

Foraging and social related call types exhibited divergent diurnal activity patterns. While 20Hz calling peaked during mid-afternoon and was lowest just before sunrise, 40Hz callers had a peak of activity just before sunrise, and just after sunset, while 40Hz activity was lowest during the afternoon (Figure 4). MWW tests determined that activity patterns were distinct among call types ($W = 9.28$, $P < 0.009$; Table S3). We also determined that 40Hz calls occurred towards significantly more negative solar angles than 20Hz calls ($D = 0.31$, $P <0.001$; Table S4; Figure S9), and environmentally available solar angles ($D = 0.19$, $P <0.001$) within the same seasonal window. However, 20Hz calling activity did not vary significantly from environmental ranges ($D = 0.13$, $P > 0.9$).

Vessel traffic types also displayed different activity patterns. Cruise ships and passenger ships were largely diurnal with most of their activity between sunrise and sunset (Figure 4). Fishing and pleasure craft vessels also displayed mid-day activity peaks but were still occasionally active at night. Tanker/cargo and tug/towing vessels had highest levels of nighttime activity and tug vessels showed little preference for any time of day. MWW tests showed activity patterns of vessel types differed significantly ($P < 0.001$) from the activity pattern of all vessel traffic for all categories although differences were smallest for passenger ships (<100m), fishing vessels and tanker/cargo vessels respectively (Table S3).

Temporal co-occurrence (Δ) between whales and vessel traffic also differed among call types and vessel categories, and ranged from 0.27 to 0.79 (Figure 5). Fin whales producing 20Hz calls co-occurred more with overall vessel traffic than 40Hz callers. Comparison of confidence intervals demonstrated that co-occurrence with vessel types was significantly different between whale behaviours for all vessel types except tug/towing and passenger vessels; both behaviours showed similar vulnerability to these vessels (Figure 5). Co-occurrence of whale behaviours with unique vessel classes was significantly different from co-occurrence with all ships for all vessel types except passenger and fishing vessels, which were among the less numerous vessel types (Figure 2). We found diurnal co-occurrence peaked in September (Figure S10). Patterns also varied somewhat across months and years, although 40Hz calls consistently had lower solar angles compared to both 20Hz and available angles in all months other than July (Figure S11).

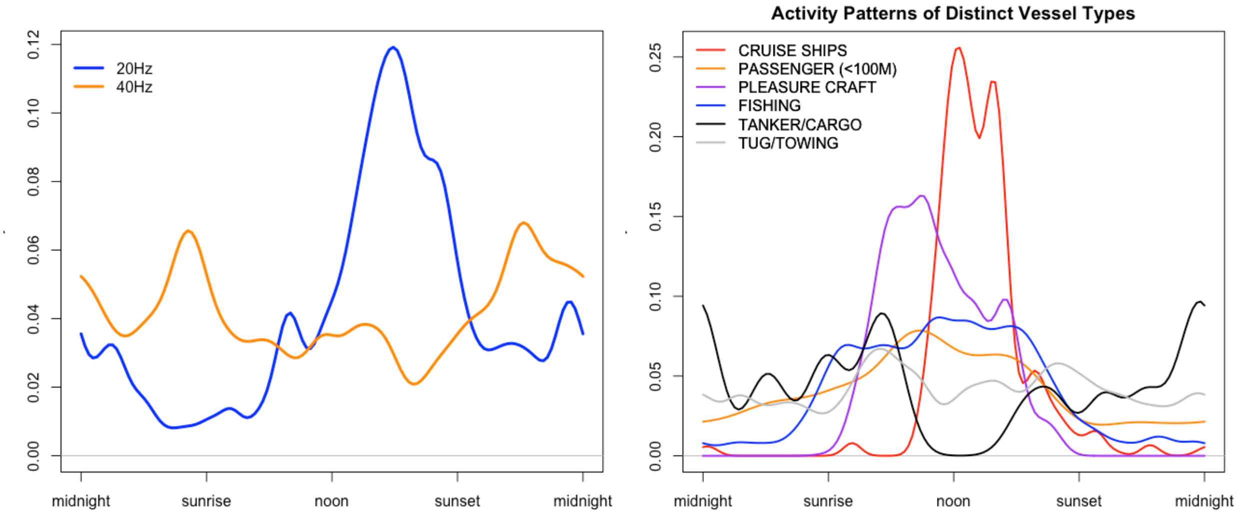

Figure 4. Activity patterns (non-parametric circular kernel density curves) of 20Hz and 40Hz call behaviours (left) and of distinct vessel traffic types (right).

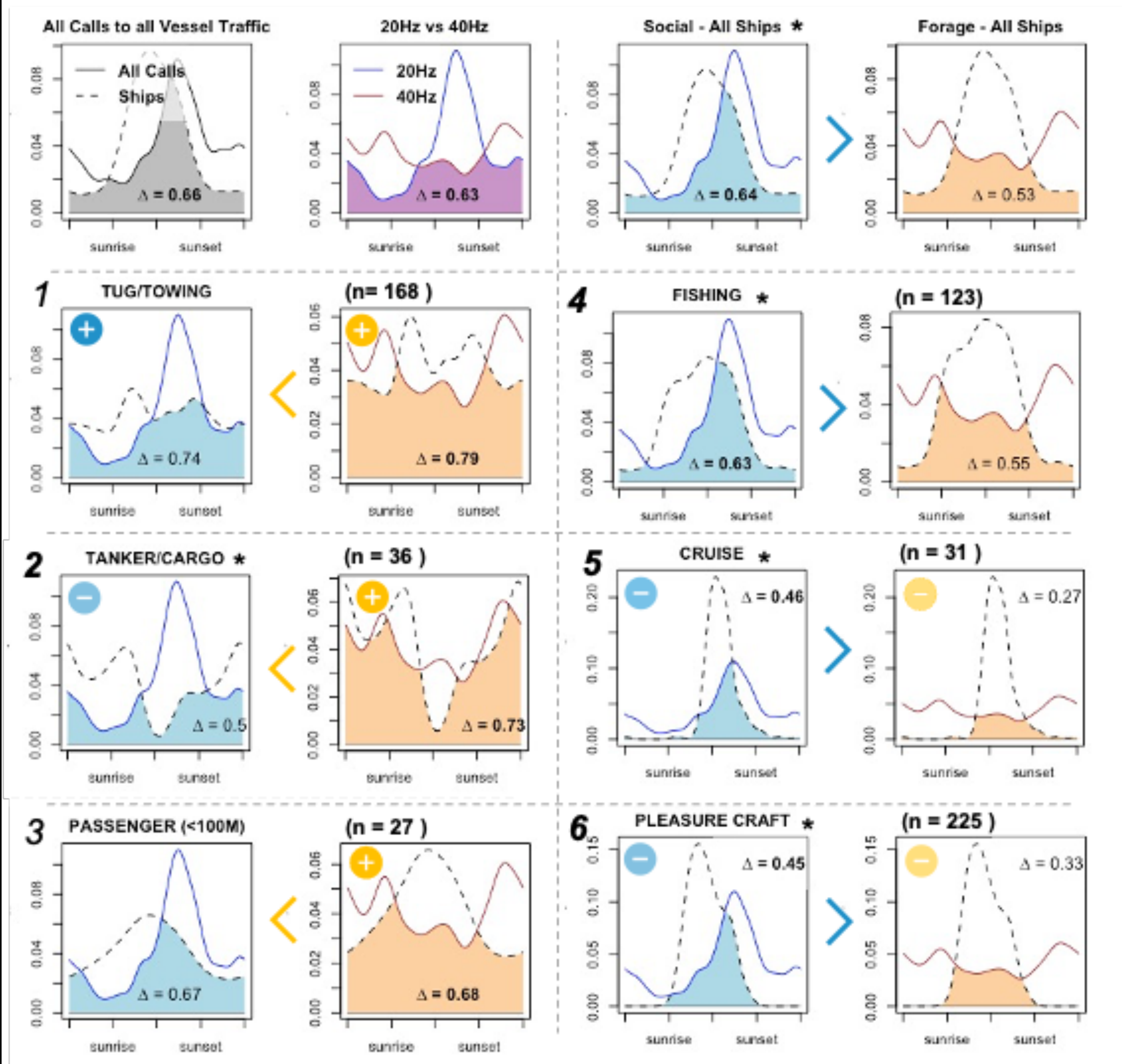

Figure 5. Plots of temporal overlap among call and vessel types; the estimated coefficient of overlap (Δ) per comparison is listed in bold for the call type with greater co-occurrence per ship type; asterisk (*) accompanies the name of vessel classes for which differences between whale behaviours were significant; the count of unique vessels for which activity patterns are calculated is listed (n); numbers show rank from highest overlap to least overlap; and circular icons show whether Δ with that vessel type was significantly higher (+) or lower (-) than Δ with all vessel traffic for that behavior.

3.1.2. Spatial Overlap

Fin whale spatial core use areas (CUA) varied by behaviour. Although all call categories shared a predominantly center channel distribution, daytime 20Hz calls had the most eastern and north-south distribution, while 40Hz callers' CUA was oriented more east-west (Figure 6 A-D). From day to night distribution of 20Hz callers shifted to the south-west while 40Hz caller distributions shifted to the north-east.

Spatial distributions also varied among vessel types. Smaller vessel types (i.e., pleasure craft, fishing) were concentrated closer to shore than larger vessel types like tanker/cargo and cruise ships (Figure 6). Commercial vessel classes (cruise, tanker/cargo, and tug/towing) had smaller core use areas and narrower extent boundaries than more recreational categories like pleasure craft and passenger ships (<100m) that had a more even distribution across the study area (Figure 6). Among vessel types, one common CUA patch oriented north-south developed in the eastern portion of the study site, and another at the western entrance to Squally Channel.

The spatial use areas among fin whale and vessel categories showed distinct overlaps. Overall, vessel traffic overlapped with 40Hz calls more with 20Hz calls, and overlap was greater during nighttime than daytime for both call types (Figure 6A-D). Fin whale 40Hz callers at night had greatest exposure to vessel traffic; 34.5% of the whales' core use area overlapping with the nighttime vessel traffic CUA's (Figure 6). Of the vessel types investigated, recreational passenger ships (<100m in length) overlapped most with all whale calls with 52.8% and 10.5% of 40Hz and 20Hz CUA's overlapping respectively (Figure 6E). For 40Hz callers, pleasure craft, fishing, and tug/towing vessels were also important exposure sources with overlap proportions of 26%, 23% and 15% respectively (Figure 6F,G,H). Tanker/cargo were an important exposure class to 20Hz callers with 6.2% CUA overlap (Figure 6I). Among vessel types, cruise and tanker/cargo ships were the only vessel types with which 20Hz calls had higher overlap than 40Hz calls (Figure 3I, J). While we report on the comparison of CUA's (50% UD's), visual inspection shows that whale core use overlaps almost completely with use extent boundaries (95% UD) of most vessel types. These 95% use extents nearly overlap entirely among most vessel classes and whale behaviours, which is an important consideration given the low frequency-high impact nature of ship strikes. Fin whales are large bodied mammals meaning they are slow to re-produce so any mortalities are catastrophic; thus the precautionary principal should be applied in the consideration of such high-impact events like ship strike.

Seasonal and interannual variation in fin whale KUD's found that 40Hz calls at night had the most consistent overlap at the western entrance of Squally Channel (Figure S12). Monthly patterns again reveal a persistent concentration in the middle and at the western entrance of Squally Channel, especially in August and September (Figure S13).

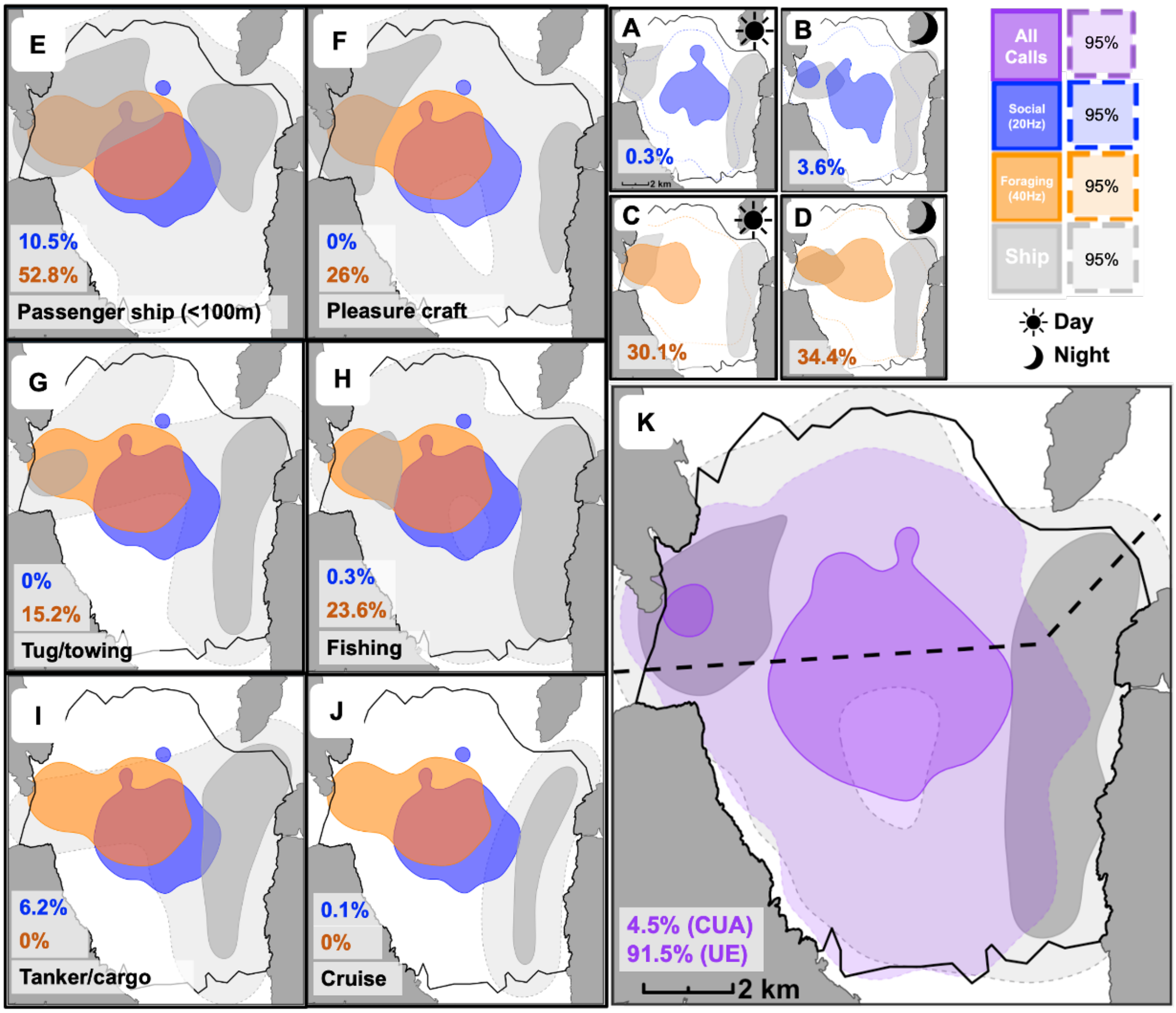

Figure 6. Spatial overlap between vessel traffic and fin whale Social (20Hz; blue) and Foraging (40Hz; red) behaviours are displayed with core use areas (CUA; 50% KUD) defined by solid lines and use extent (UE; 95% KUD) defined by dashed lines. Polygon colours call frequency; sun and moon symbols represent day and night variations of the respective temporal-behavioural comparison; labels give the area of overlap as a proportion of whale core use areas (%) where text colour follows the legend. Panels A-D show independent temporal-behaviour comparisons to diurnal vessel traffic with the extent of use by whales shown by a dashed boundary. Panels E-J show overlap between pooled 20Hz and 40Hz CUA's with different vessel types; dashed boundary shows use extent by vessel category. Panel K shows interaction among all whale calls and all vessel traffic; with dashed black line showing planned LNG traffic route.

4. Discussion

We investigated how vulnerability of acoustically active fin whales to vessel traffic might vary among whale behaviours and different types of vessel traffic. We first investigated whether space-time patterns varied among behaviour and vessel type categories, then compared temporal co-occurrence and spatial overlap among categories using activity pattern techniques and overlap analyses of core use areas. We emphasized the role of behaviours in this analysis due to its importance in understanding whale conservation. Understanding variability across vessel types may also facilitate improved risk mitigation strategies.

Our approach, which observed whales during day and night, yielded new insights. While previous studies using binned comparisons found no significant difference in calling activity between day and night (Hendricks et al., 2021), we investigated calling activity over the continuous 24-hour day for two different call types and found meaningful variation among call types. Fin whale 20Hz calling was more diurnal with a peak towards late afternoon and evening relative to 40Hz calling, which had greater occurrence during lower solar angles and nighttime hours (Figure 5; Figure S9). Importantly, we compared diurnal whale and vessel patterns to available sun angles during the duration of data collection and found 40Hz calls occurred more often during significantly lower sun angles than available and lower sun angles compared to 20Hz calls, although 20Hz calls did not vary distinctly from the available pattern of sun angles. We also contextualized diurnal patterns within these broader temporal scales and found that, although there was variation among months and years, the trend of higher sun angles for 20Hz calls compared to 40Hz calls persisted in all months except July, which may be due to less available data in this month (Figure S11).

Our analysis of two call types over continuous time revealed distinct activity patterns and observation of more crepuscular peaks in foraging associated 40Hz calls can be explained in the context of optimal foraging and diurnal oceanic cycles. Fin whales of the Pacific are thought to feed primarily during the day because they perform deeper daytime dives associated with the diel vertical migration of krill (DVM) (Friedlaender et al., 2015; De Meester et al., 2009). Higher proportions of daytime 40Hz calls have also observed in places where fin whales express these diurnal dive patterns, such as the Bearing Sea and off the coast of Southern California (Širović et al., 2013). This pattern of deeper daytime dives was also observed in Squally Channel, confirming that daytime foraging likely occurs here (Nichol & Heaslip, 2018). Given this evidence of diurnal foraging in our study site, and the association of 40Hz calls with foraging, we might have expected to observe greater occurrence of 40Hz calls during daytime in our site, but instead found a more crepuscular pattern, and preference towards darker hours. Other baleen species exhibit crepuscular and night-time foraging activity however and our observation of nighttime foraging calls by fin whales is not unexpected within the context of balaenopterid foraging. Blue whales for instance have been observed to feed during crepuscular periods to optimize the trade-off between prey capture efficiency (density of krill schools), with prey accessibility (depth) and the need to make energy intensive deep dives requiring long recovery windows (Doniol-Valcroze et al., 2011). Humpback whales have even been found to feed almost exclusively at night when krill becomes available near the surface at night (Ware et al., 2011). Notably, feeding at night on shallower prey inherently occurs in shallower waters butting feeding whales at night at particular risk of strike. Similar to our findings, acoustic analyses in the Gulf of California of both call types found a higher proportion of 40Hz calls at night despite observation of daytime foraging dives there (Širović et al., 2013). Furthermore, coastal environments like fjords can produce greater variability in environmental drivers potentially leading to more diverse patterns of prey availability in such environments (Cloern & Jassby, 2010). More dynamic nutrient cycling here may facilitate more predictable nighttime foraging and associated 40Hz call production. Such behavioural patterns may serve to expose whales to different vessel threats throughout the diurnal cycle, in particular a higher threat of strike during the night.

Although there was less vessel traffic overall at night in Squally Channel, we found higher spatial overlap occurred among vessels and whales at night, especially for 40Hz callers. Cetaceans are already difficult animals to observe, and during nighttime whales are nearly impossible for vessel operators to identify let alone avoid. Thus, different vessel categories sharing space at night have little capacity to detect and avoid whales and are more likely to have a collision. In Squally, tug/towing, fishing craft, and passenger vessels (<100m) remained operational after darkness, although tanker/cargo had the most nocturnal pattern (Figure 4). Fin whales are more vulnerable to ship strike at night because they usually make shallower dives during darkness (Keen, et al., 2019; Rockwood et al., 2017a), a pattern which has been confirmed in Squally Channel (Nichol & Heaslip, 2018). Consequently, finding greater shared use of space at night in Squally Channel raises concern that whales are indeed more vulnerable to strike at night in this region.

In our site, foraging calls (especially at night) exhibited the most consistent interannual spatial occurrence. Specifically, this occurred at the western entrance of Squally, which likely indicates dependable prey access here (Abrahms et al., 2019). This location also coincides with the core use of several vessel types; passenger, fishing, tug/towing for which 40Hz calls were highly spatially vulnerable (52.8%, 23.6%, and 15.2% respectively; Figure 6). Cetaceans inhabit inherently resource patchy environments, meaning that foraging behaviour is constrained spatially by spatial patterns of their food, and temporally by how accessible that food might be (Benoit-Bird et al., 2013). As a consequence, foraging whales may be unwilling to abandon a rewarding prey source when it is accessible, or may even be less aware of vessel traffic presence while engaged in foraging (Laist et al., 2001a; Lima & Dill, 1990). Our findings indicate that if foraging is occurring while engaged in 40Hz calling, as many sources suggest (Romagosa et al., 2021; Širović et al., 2013), feeding may occur during darkness in Squally Channel, thereby increasing vulnerability to strike at night. Especially considering the shallower depth of prey at night, sometimes < 20m, would directly encourage fin whale occupancy of the ship strike zone when they might be least aware of approaching threats, and least willing to depart from rewarding prey schools (Doniol-Valcroze et al., 2011; Keen, et al., 2019). Further, while 40Hz calling activity did not overlap with current tanker/cargo core use, the 40Hz CUA was almost entirely within the tanker/cargo vessel use extent boundary, and notably directly along the route of proposed vessel traffic increases for the region (Figure 6I; Figure 1). Tanker/cargo vessels had the largest temporal co-occurrence with whales between sunset and sunrise and was significantly higher for 40Hz calls (Figure 5). This vessel category represents the most similar vessel behaviour (spatial use, size, travel speed) to proposed LNG vessel traffic for the region (Figure 2), and such large, fast traveling vessels represent a significant threat of strike and acoustic interference.

Observed whale-vessel interactions across space and time can be considered in the context of proposed expansion to shipping. Specifically, liquid natural gas (LNG) carriers transporting product from the LNG Canada terminal in Kitimat BC are set to contribute an additional 700 transits of Squally Channel per year beginning in 2025 (Meisner, 2015b). LNG

Canada proposes to use carriers with up to 177,000m^3 capacity, meaning they will have lengths of ~ 200m, and drafts of ~8m (Bai & Jin, 2016; Meisner, 2015b). Such vessel dimensions represent high lethal strike threats for whales. Further, LNG vessels can emit sounds above cetacean behavioral response thresholds over average distances of 1.8 kilometers (Carr et al., 2006). In this fjord environment with narrow channels (i.e., western entrance to Squally Channel is < 2km wide), acoustic impacts of LNG vessel could threaten natural whale behaviours here. Foraging callers may be most temporally and spatially vulnerable to LNG vessel traffic increases if they maintain current schedules of tanker/cargo vessels along the proposed route, although acoustic disruption to social activity remains a concern.

In contrast, social behaviours might be less specifically constrained to specific locations than foraging behaviours, which might explain the low spatial overlap of 20Hz calling with vessels. However, 20Hz callers did overlap with tanker/cargo and cruise ships, which were the only two vessel types that 40Hz calls did not overlap at all with. Tanker/cargo and cruise ships are also the two largest, fastest traveling vessel types in the study site and present the largest potential threat of strike (Silber et al., 2010). Further, during bouts of repetitive 20Hz call production, fin whales have been documented to perform long shallow dives, often only to maximum depths 15 m (Stimpert et al., 2015). Whales at these depths are still vulnerable to strike from large vessels like tankers and cargo ships, as larger vessels have deeper drafts and the strike zone can extend several times below the depth of the vessel's draft (Rockwood et al., 2017b; Silber et al., 2010). Temporal co-occurrence with cruise ships was also significantly higher for 20Hz calling activity than 40Hz (Figure 5), meaning that in space and time, cruise ships represent a larger threat of strike for 20Hz callers, and social calling fin whales may be more vulnerable to current vessel strike threats, especially during daytime in Squally Channel.

Despite low spatial overlap, temporal co-occurrence among vessels and social behaviour was significantly higher than with foraging behaviour. Co-occurrence varied significantly among behaviours for four vessel types, and 20Hz calls were higher for fishing, cruise, and pleasure craft. Fishing and pleasure craft were among the most numerous vessels in our study, and although these classes are generally smaller and slower traveling, it is increasingly understood that small vessels still represent risk of lethal injury to whales (Raverty et al., 2020). Further, pleasure craft may represent the most similar vessel behaviour to small recreational vessels that are not required to carry AIS, which can be primary contributors to marine noise in more coastal soundscapes (Hermannsen et al., 2019). This is important as acoustic threats extend beyond the location of a vessel, and chronic noise pollution may present a larger problem for social calling activity despite lower direct spatial interaction.

Both foraging and social behaviours co-occurred most with tug/towing vessels that had an almost consistent activity pattern throughout the 24-hour day and may represent a large threat of chronic noise and acoustic masking. Tug/towing vessels were also the second most prevalent vessel category in the study. While tug/towing vessels do not produce sounds as loud as larger faster vessels (i.e., tugs may emit sounds ~9 decibels below cargo traffic; Jansen & De Jong, 2017), their slower transit speeds mean they could present higher risk of chronic noise pollution in our spatially constricted site given their potentially longer residence times when traveling at lower speeds (Figure 2). This becomes particularly relevant in constricted coastal environments where occupancy duration becomes important and even few vessel transits can increase noise levels above whale behavioural response thresholds (Cominellie, 2020). Although fin whales are likely capable of communication over the expanse of this study site with ease (Širović et al., 2007), chronic noise pollution can mask cetacean calls and may be more problematic to social behaviour given the inherent need for male song (which is a breeding display) to reach farther audiences (Erbe, 2002).

Such consideration of diverse threats offered by different types of vessels area also important because different vessel types be more responsive to different management measures. For instance, previous research found high compliance of cargo vessels with mandatory speed restrictions aimed at whale protection, while lower compliance was noted for passenger ships (Silber et al., 2014). Among vessel types, fishing vessels sowed lowest compliance with spatial whale protection (Guzman et al., 2020). Human operators of smaller vessels, and people on passenger vessels (Ryu et al., 2010), may also be more vulnerable to injury from a vessel-whale collision (Schoeman et al., 2020). Distinct vessel characteristics like maneuverability could affect the management measures that may be applied. For instance, smaller private vessel types may be better targeted with educational programs, while fines may be required to achieve compliance from larger commercial vessels.

We have employed analysis of acoustic whale behaviours and suggest that precautionary interpretation should be applied, given that whales may be present and not calling. While acoustic habitats have received comparatively little attention, and are important to consider, places with calling activity are not the only places of importance to whales and areas used even when whales are not-vocalizing are also important. The spaces we have identified represent important acoustic habitat for a highly sound-dependent species. Further, we have used AIS in the representation of anthropogenic activities, yet due to constraints of signal transmission, and user-defined ship-characteristics, this data source inherently underrepresents vessel traffic (Pallotta et al., 2013; Teixeira & Guedes Soares, 2018). AIS transmission is also still not mandated on smaller vessel categories, which can still dominate impacts on coastal marine soundscapes, especially in shallower waters (Hermannsen et al., 2019). Given the already high proportion of pleasure craft and small passenger ships in this area, smaller non-AIS transmitting vessels likely comprise a large proportion of local traffic; as such, future studies should incorporate their movements. While this site shows immense importance to fin whales (Keen et al., 2021), and the potential of this site serving a particular role for pacific fin whales requires meaningful consideration, we note that in the context of Pacific fin whale habitat, Squally Channel represents a small proportion of total habitat. Therefore, the capacity to make regional management recommendations based on direct observations within the network boundary is constrained. Nonetheless, findings from this system have implications for understanding how fin whale diurnal vulnerability varies across vessel traffic types and hold relevance beyond the boundaries of our study site.

5. Conclusion

This vulnerability assessment based on examining distinct vessel types and whale behaviours has contributed new insights on vessel-whale interactions, particularly in constricted geographies. We determined that differences exist among spatial and temporal activity patterns of vessel types and whale behaviours, which leads to variability in risk among them. We revealed that social calling fin whales may be more vulnerable to strike threats from cruise ships during the day. Foraging callers persisted at the mouth of a narrow channel entrance to Squally Channel shared by several vessel classes, and were especially vulnerable during darker periods, which could put them at greater risk of vessel strike during nighttime. Such information can assist identification of more effective management solutions in constricted coastal environments.

6. Supplementary Information

6.1. Tables

Table S2. Chosen Vessel Traffic categories and their descriptions.

Category	Filter	Points	Unique Vessels	Description
All Vessel Traffic	All AIS vessels	26,706	794	A pooled category of all available AIS traffic to show largest overall patterns.
Daytime Vessel Traffic	Only AIS points with solar angle > -12	22,002	713	Represent risk during daylight.
Nighttime Vessel Traffic	Only AIS points with solar angle < -12	4,704	231	Represent risk during darkness.
Pleasure craft	AIS Type = pleasure craft	5678	225	This AIS ship category primarily includes private Yachts. While small vessel AIS is rare, vessels in this class are most likely to represent small vessel traffic patterns.
Tug/towing	AIS Type = tug, towing, towing(200/25)	5514	168	Tug and towing vessels in this region are generally traveling slowly while transporting barges bearing heavy commercial loads, although this AIS type will also be transmitted by Pilot ships which may travel faster.
Fishing	AIS Type = fishing	6694	123	This AIS type is generally transmitted by commercial fishing vessels. This vessel class also maintains near equivalent density between day and night.
Passenger ships (<100m)	AIS Type = passenger Vessel & Length < 100m	1190	27	AIS type "passenger Vessel" will be transmitted by passenger carrying ships, ferries, or any accommodation ship. Likely represents ecotourism vessels in this site.
Cruise ships	AIS Type = passenger & length > 100m	1181	31	We can infer these vessels are cruise ships which are currently the largest, fastest vessel traffic category transiting the study area. This category represents a large potential risk of for strike to fin whales.
Tanker/cargo	AIS Type = tanker, tanker:DG,HS,MP(OS), tanker:DG,HS,MP(X) , cargo ship	367	36	Tanker routes are most representative of future vessel traffic proposed for the region that will transport LNG from Kitimat.

Table S3. Tabulated Meridia-Watson-Wheeler test results where statistic (W) shows how different the two activity patterns are (larger W is more different) and the associated P where asterisks denotes significance of the difference (* ; P < 0.001).

Comparison	**MWW Statistic (W)**
40Hz - 20Hz	537.3*
Cruise - ALL Vessels	791.4*
Passenger (<100) - ALL Vessels	49.5*
Fishing - ALL Vessels	52.7*
Pleasure Craft - ALL Vessels	746.0*
Tanker/Cargo - ALL Vessels	95.1*
Tug/tow - ALL Vessels	1030.7*
Vessel Present - Vessel Absent	322.5*

Table S4. Tabulated Kolmogorov-smirnov test results and associated P values comparing solar angles among behaviours, vessels, and available habitat.

Comparison Groups ***(mean solar angle)***				**Tolmogorov-smirnov tests (two-sided) D-Statistic**	**k test p value**
Available	*(+6.4)*	20Hz	*(+10.3)*	0.13	1
Available	*(+6.4)*	40Hz	*(-0.73)*	0.19	< 2.2e-16
Available	*(+6.4)*	Ships	*(+25.5)*	0.32	< 2.2e-16
20Hz	*(+10.3)*	40Hz	*(-0.73)*	0.31	< 2.2e-16

6.2. Figures

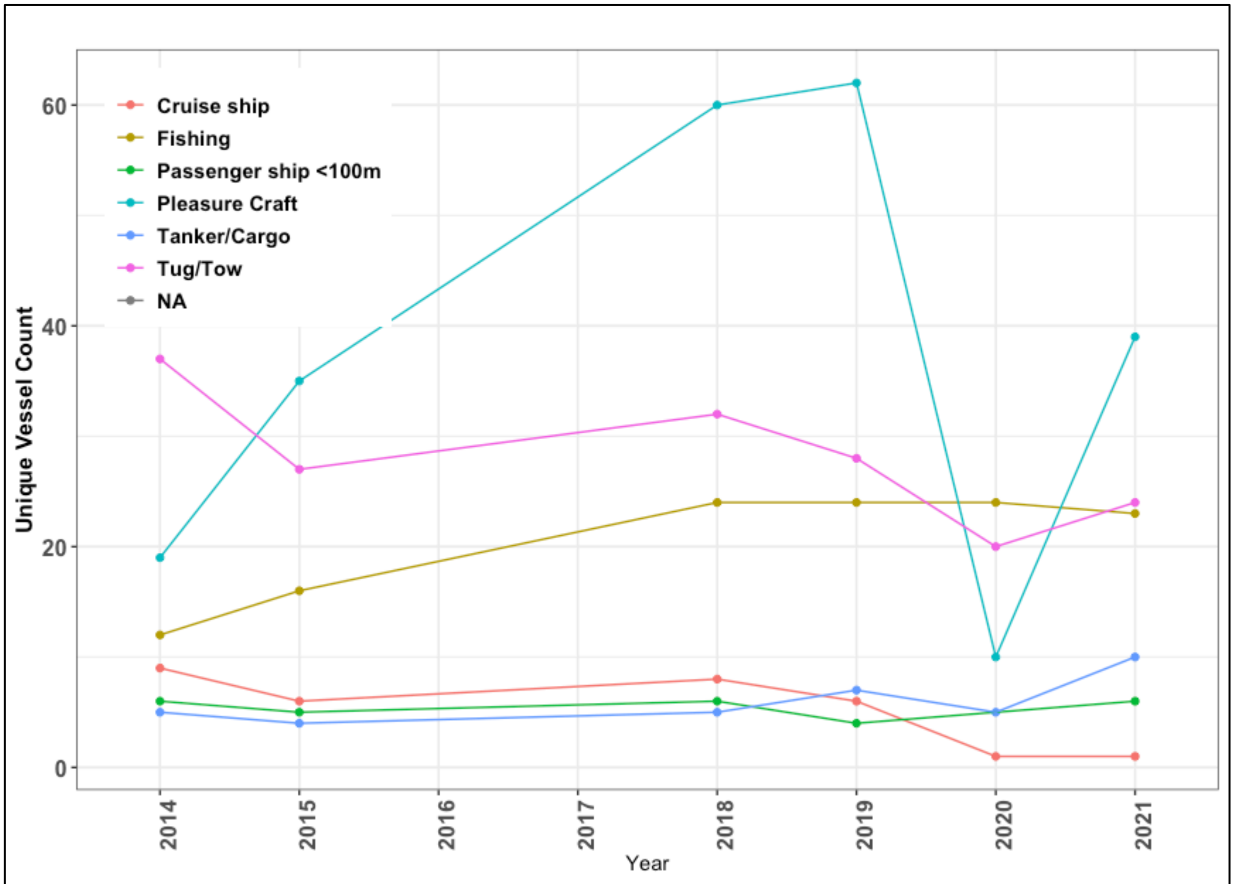

Figure S7. Interannual unique vessel counts per vessel type.

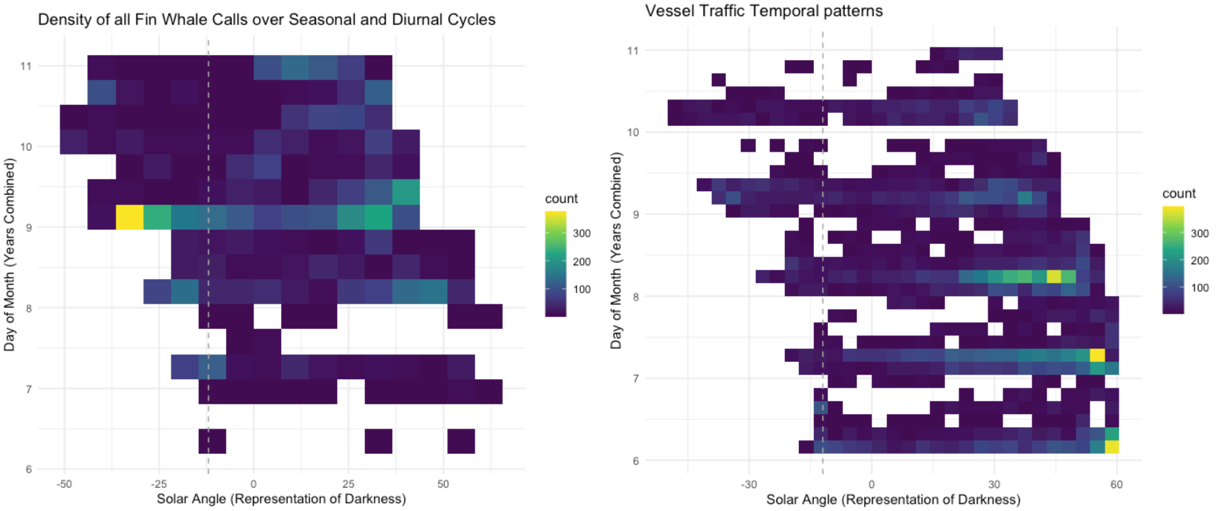

Figure S8. Two way histogram of temporal activity for whale calls (left) and vessel traffic (right) across solar angle (x-axis) throughout the study season (day of month on y-axis). All years of data are combined, virtical grey dashed line shows the solar angle threshold of -12 used to define day and night.

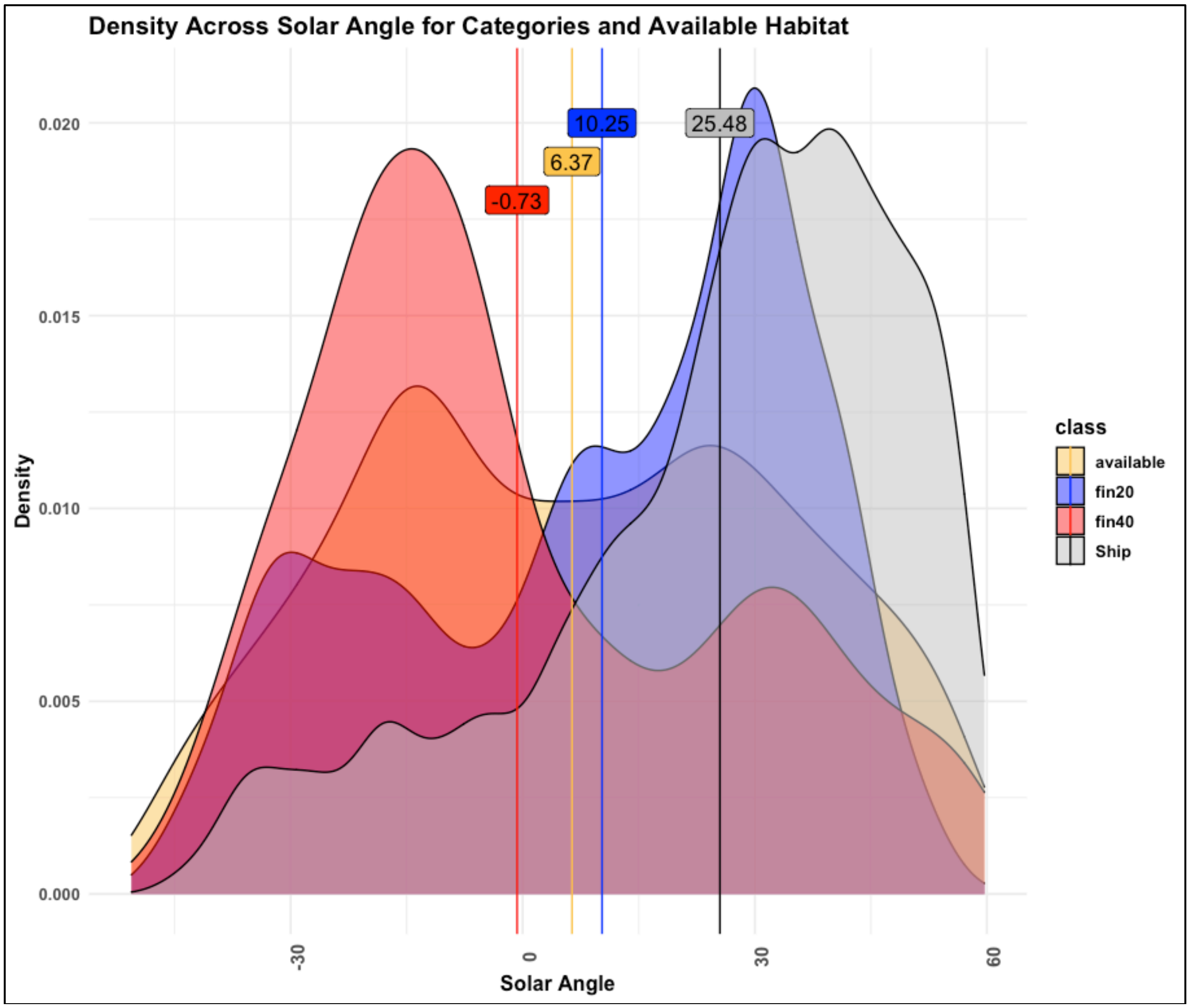

Figure S9. Density distributions of solar angles for different call types and vessel traffic compared against available habitat; vertical lines and attached values indicate median values per category.

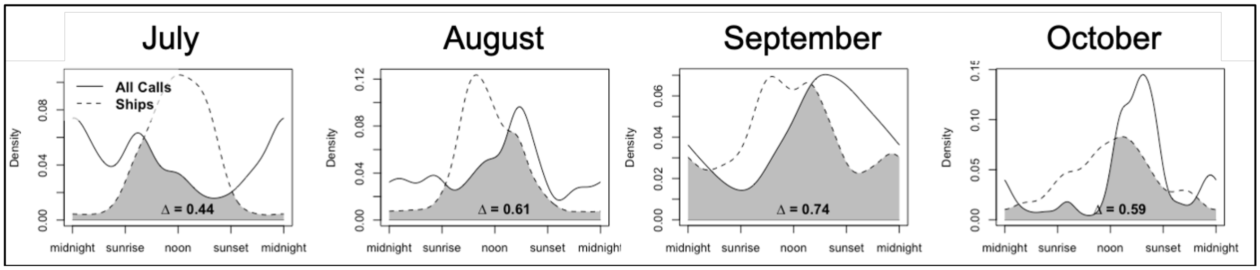

Figure S10. Diurnal activity patterns of vessels and whales among months (all years of data combined).

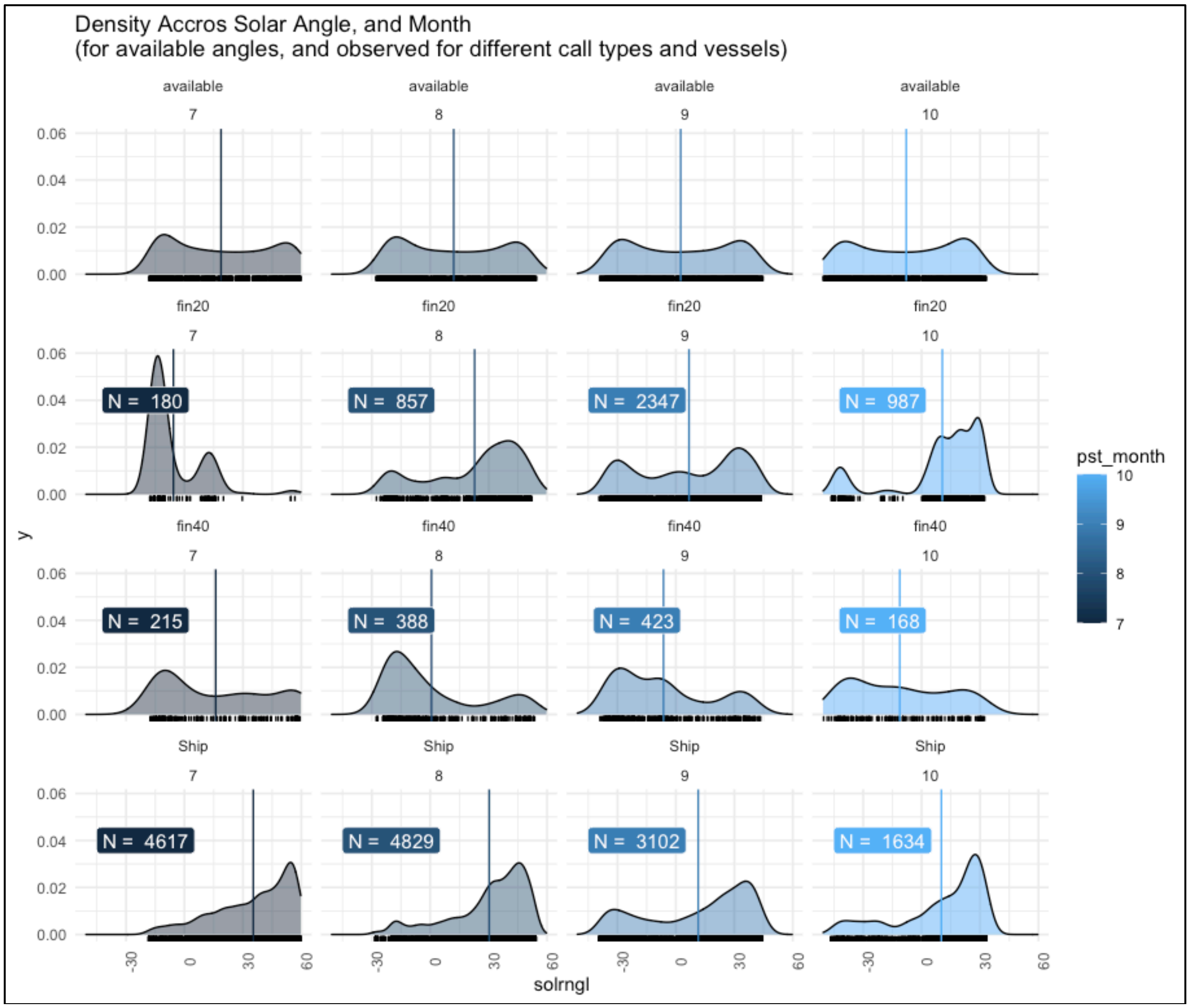

Figure S11. Seasonal variation in density across solar angle for available angles, different whale call types and vessel traffic; vertical lines show median solar angle; curves are compiled across years, n gives sample size per plot.

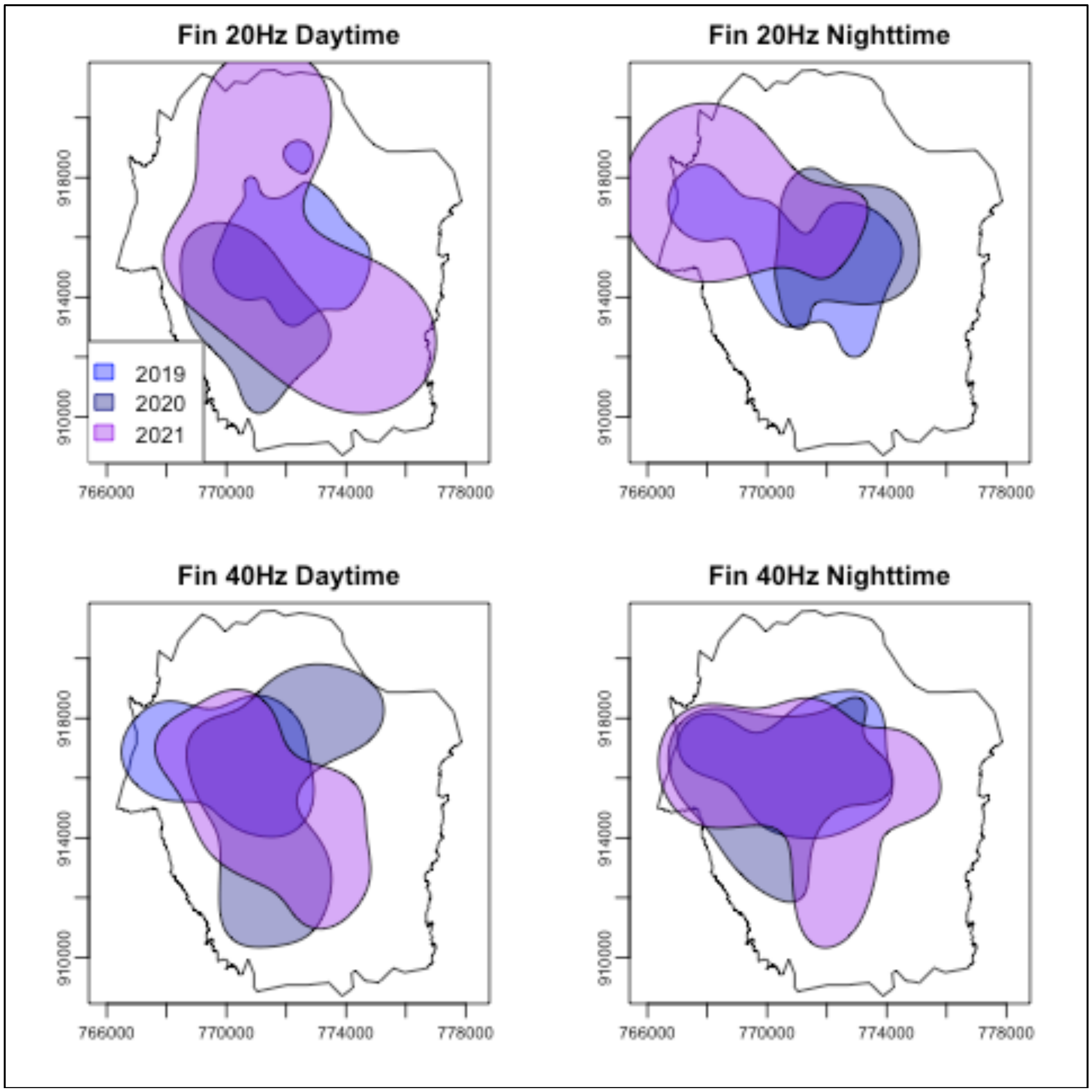

Figure S12. Interannual 50% KUD for each call category shows that nighttime 40Hz calls have a more consistent distribution between years while fin whale 20Hz calls during daytime appear to have the most variable distribution across years.

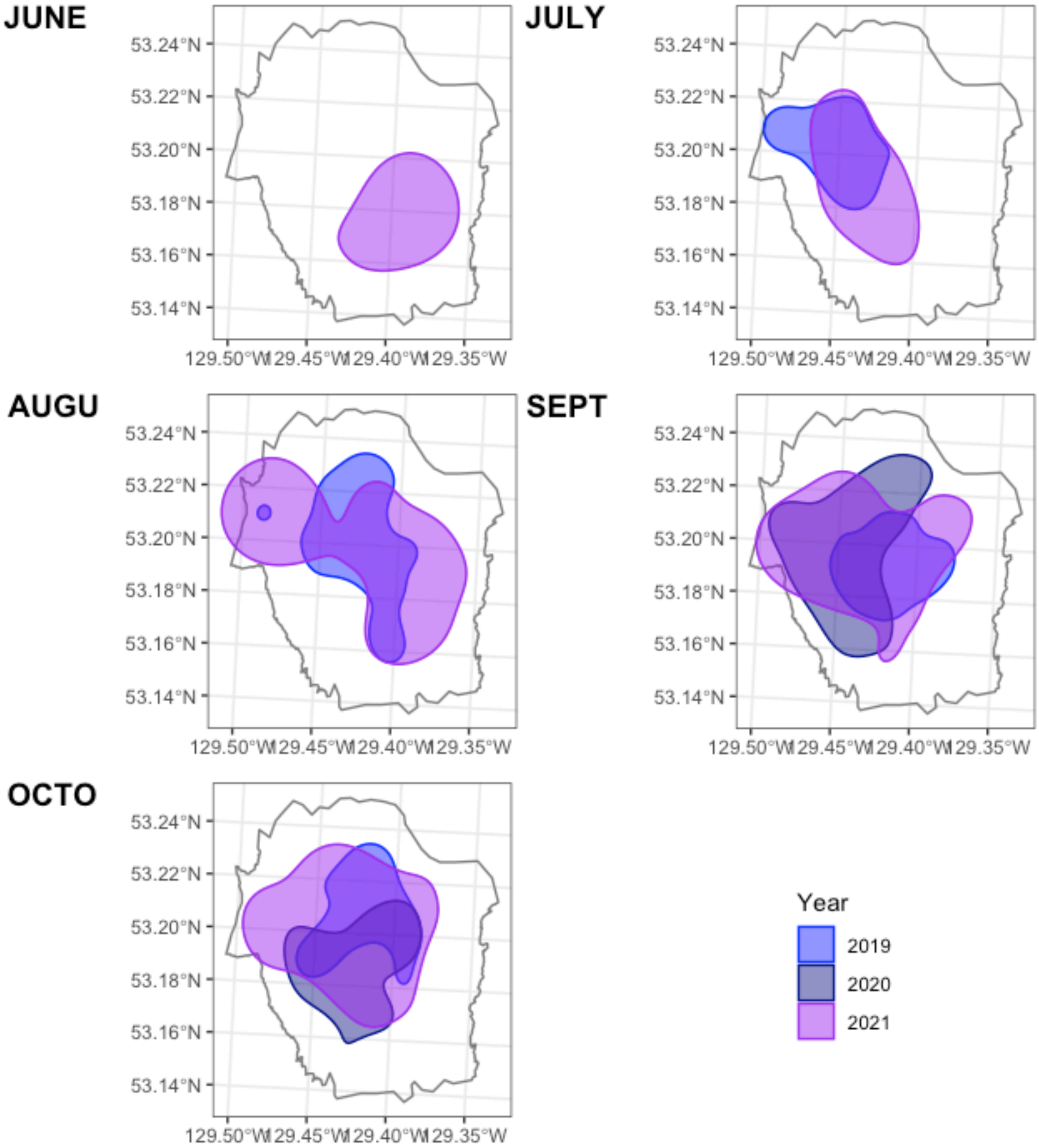

Figure S13. Interannual monthly fin whale distribution differences; 50% KUD core use areas plotted on top of each other so that denser areas represent most consistent seasonal use interannually.

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Chapter 4: Conclusion

1. Summary

The goal of this thesis was to employ acoustic localizations to better understand fin whale behaviours and vulnerability in a fjord system. The first part of this thesis investigated variation in the habitat requirements among acoustic behaviours with species distribution modeling, while the second evaluated how behaviours may be uniquely vulnerable to different vessel traffic types which also exhibit spatial temporal variability. In the first study, species distribution models were developed for each call behaviour to understand how environment relationships varied among fin whale acoustic behaviours. Habitat characteristics varied among call types and between day and night showing that the variables associated with fin whale locations can vary depending on their behaviour. Foraging related 40Hz calls aligned more with environment features expected to promote foraging conditions, while 20Hz calls were less associated with those features. Contrary to expectation, nighttime acoustic habitat also aligned more with foraging features and may suggest that coastal habitats provide ecological advantages allowing for more varied fin whale foraging schedules compared to more open ocean systems. Alternatively, fin whales may adapt acoustics to such nearshore environments given the drastically different soundscape between open ocean systems and nearshore environments. The species distribution model surfaces resulting from this study exhibited low predictive ability, likely owing to, amongst other things, the small and complex study site that is characterized by a highly variable bathymetry and narrow channels. While important findings were gleaned from this study, it was decided that an alternative modelling approach would be more appropriate for assessing the next component of this research.

The second study focused on evaluating variation in spatial and temporal vulnerability of whale behaviours to different types of vessel traffic. Temporal activity patterns of different vessel traffic types have rarely been described as we have accomplished here. We determined that there was significant variation in the temporal and spatial habits of different whale behaviours and vessel types, thus demonstrating a variation in whale vulnerability. Social calling activities were more temporally vulnerable owed to the larger coinciding activity peak during afternoon with primarily diurnal vessel categories (i.e. pleasure craft). Both acoustic whale behaviours temporally co-occurred most with tug/towing vessels, which may represent risk of chronic noise pollution and call masking. One potential mitigation measure may be a form of the convoy method for this vessel type if increasing temporal predictability could allow for a reduced duration of noise impacts. Conversely, foraging acoustic activity was more vulnerable in space, as it persisted at a geographic bottleneck (western entrance) that was utilized by several vessel classes. The results from this study also show that, for each vessel type, whale behaviours were either vulnerable in time and not space, or vulnerable in space and not time. This observation might suggest that whales exhibit behavioural adaptation to vessel traffic as animals can maximize fitness by avoiding threats in space and, or, time depending on the predictability of the threat and needs of the behaviour.

2. Management Implications

Overall, this research advances our understanding of fin whale acoustic habitat associations and shows how the vulnerability of acoustic behaviours can vary across different types of vessel traffic in an important ecological, cultural, and economic region. As this thesis has shown, different vessel types exhibit different size, speed, and spatial and temporal use patterns. Interacting activity patterns of animal and anthropogenic use in the marine realm requires greater attention now that tools are available for such investigation. Distinct types of vessel traffic ultimately represent different groups of people, a classification of which may be useful for devising more effective strategies that are vessel-specific. For instance, studies of vessel compliance to cetacean protection measures found varied compliance among vessel types, with more commercial ships having high compliance given existing regulatory mechanisms (Conn & Silber, 2013). Flexible strategies that account for human needs are also more likely to have higher compliance and ultimately higher ecological benefit (Parrott et al., 2016).

Several management strategies have been developed and applied to reduce vessel impacts to cetaceans, including spatial and temporal partitioning between vessels and whales as well as vessel speed control techniques. Each may be better suited to address different anthropogenic threats in different environments. Spatial restrictions on vessel activity have successfully reduced strike vulnerability (Crum et al., 2019; Guzman et al., 2013), but are less applicable in constrained coastal waters, especially for larger vessels with limited navigational flexibility. Adding spatial partitioning constraints, however, can also instigate longer and less direct transits that cause vessels to travel faster (thus increasing strike risk and noise pollution) or longer (increasing the duration and area of noise exposure) to maintain their schedules. This illustrates that mitigation measures directed at a singular threat (i.e. strike) may lead to unintended consequences for whales, and integrative approaches should be prioritized that consider mitigating acoustic and strike threats.

Unlike spatial restrictions, slowing vessel traffic serves to reduce both noise impacts and strike vulnerability. "Go Slow Zones" have been one of the most common methods employed because it costs relatively little for the industry, and compliance is high when appropriately regulated (Chion et al., 2017; Conn & Silber, 2013; McKenna et al., 2012). This strategy can reduce strike risk and also the intensity of vessel noise; however, it will increase the duration that vessel noise is present. This strategy may be one of few management options in certain geographies.

Vessel traffic impacts may also be mitigated through temporal separation of whales and vessels. This might look like seasonal restrictions on the space (i.e., "No-Go Zone" only active seasonally) or speed (i.e., "Go Slow Zone" only active seasonally) of vessel activity during times of critical whale use (Williams et al., 2019). A related technique is the 'convoy method', in which all vessel transits are organized to occur during a set period of time (Williams et al., 2019). This technique is directed more at mitigating acoustic impacts because it concentrates noise to certain time windows but does not restrict vessel speed or sound intensity during active vessel transit times. Thus, the convoy method prioritizes quiet time over reduced sound levels or strike risk. The convoy strategy may be beneficial if there are strong and predictable temporal patterns in marine mammal activity which traffic schedules can organize around.

To synthesize, these diverse management measures each have different capacity to mitigate different types of vessel impacts to whales. Spatial restrictions can be most effective in discrete spatial regions but are challenging to implement in complex coastal regions. Temporal restrictions can be tailored to address different threats of noise and strike. Speed restrictions target strike threat and noise pollution to a lesser extent. Due to political and logistical challenges, each of these measures are often implemented separately. However, unintended consequences can result from this decision to manage for only type of vessel threat as evidenced by the different costs and benefits of the abovementioned management strategies. Consequently, future management decision support tools should be developed that focus on the trade-offs between acoustic and strike-related threats. These tools should help to optimize solutions that minimize potential harm to whales and would be particularly valuable in environments that limit management strategies such as coastal fjords.

3. Conclusion

Cetaceans offer an important focal species on the development of humans' capacity to self-regulate environmental impacts. Whales are a charismatic megafauna with a large share of public interest in their wellbeing. From commercial whaling and use of whale oil to the global conservation efforts and observed recovery of certain whale populations, the human-cetacean relationship has been one of the most public and drastically transformative in the past century. Humans continue to drive environmental change at unprecedented rates, which in turn is affecting the environmental and social context under which animals make decisions to unparalleled degrees (Owen, 2017). This research has shown that how we approach the management of our activities must take into consideration the complex nature of interacting whale and human behaviours for best selection of mitigation measures.

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