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Mestrado em Biologia Marinha

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Abstract

Increased vessel traffic and human activity have raised underwater noise levels in marine environments, significantly impacting species that rely on sound, such as the endangered Southern Resident killer whale population (*Orcinus orca*). Southern Residents rely on sound for foraging, navigation, group cohesion, and cultural transmission, but increasing noise levels can interfere with these behaviours by masking communication signals and prompting changes in call use. This study modelled acoustic data from two Southern Gulf Islands in British Columbia, Canada to examine how Southern Residents, and specifically J pod, modify their vocal behaviour under varying noise conditions. I investigated which discrete pulsed call types were being used by J pod and modelled the rates at which these calls were used in response to increases in sound pressure levels. Call proportions aligned with historical usage except for a marked dominance of the S04 call type on Saturna Island, a finding that contradicts previous studies identifying S01 as the most common J pod call type. Model estimates showed S04 usage decreased by 10.7% per every 1 dB increase in ambient noise. Overall, model estimates show that J pod members significantly reduce total discrete pulsed calling rate by 2.4% for every 1 dB increase in ambient noise and by 21% for every 10 dB increase in ambient noise. The S02i, S04, S05, S06, S07, S12, S42, S44 call types were all used significantly more in quieter conditions. Call types S01, S02ii and S41 showed no significant change in usage. This study provides further evidence that increases in ambient noise significantly affects Southern Resident killer whale vocal behaviour, leading to reduced call rates and possible shifts in call type use. The findings of this study highlight the importance of preserving quiet marine environments and improving our understanding of Southern Resident acoustic behaviour to inform effective conservation and management strategies.

Keywords

Anthropogenic noise; Call rates; *Orcinus orca;* Endangered; Behaviour

Resumo

O aumento do tráfego marítimo e da actividade humana tem contribuído para o aumento dos níveis de ruído subaquático nos ambientes marinhos, impactando significativamente espécies que dependem do som, como é o caso da população de orcas residentes do sul (O*rcinus orca*), também conhecidas como Southern Resident killer whales (SRKW). Esta população encontra-se classificada como “em perigo” ao abrigo da Lei Canadiana das Espécies em Risco (Species At Risk Act – SARA) e da Lei das Espécies Ameaçadas dos Estados Unidos (Endangered Species Act – ESA), sendo a baixa disponibilidade e acessibilidade de presas, os contaminantes, e as perturbações físicas e acústicas identificados como ameaças à sua recuperação. As Southern Resident do sul habitam tipicamente as águas costeiras do sul da Colúmbia Britânica, no Canadá, e do Estado de Washington, nos Estados Unidos. O seu habitat principal coincide com rotas internacionais de navegação comercial no Mar de Salish, incluindo o Haro Strait e o Boundary Pass. Embora o transporte marítimo comercial constitua a fonte de ruído mais prevalente e constante no ambiente marinho, o contributo de embarcações mais pequenas, bem como de actividades comerciais e recreativas de menor escala, não é negligenciável. O ruído provocado por estas embarcações pode mascarar faixas de frequência entre 1 kHz e 40 kHz, o que abrange em grande medida as bandas utilizadas pelas orcas para comunicação (0–15 kHz) e ecolocalização (20–70 kHz). Estudos anteriores que modelaram os efeitos do ruído antropogénico nas orcas sugerem que embarcações ruidosas podem provocar respostas comportamentais a distâncias inferiores a 200 metros e que a exposição prolongada pode causar um deslocamento temporário no limiar auditivo, podendo mesmo resultar em perda auditiva permanente. As orcas residentes dependem fortemente da acústica para caçar, manter a coesão do grupo e transmitir conhecimento cultural. O aumento dos níveis de ruído interfere nestes comportamentos, mascarando sinais de comunicação e levando a alterações na escolha e utilização dos chamamentos. Sabe-se que as orcas ajustam as suas vocalizações na presença de ruído, aumentando a amplitude dos seus sons — um fenómeno conhecido como efeito Lombard, também observado em humanos, aves, rãs e outras espécies de cetáceos, como as baleias-jubarte e as belugas. Outros efeitos observados incluem alterações no tom ou frequência dos sons, maior duração ou taxa de emissão dos chamamentos e, em alguns casos, a completa evasão de zonas ruidosas anteriormente incluídas no seu habitat de rotina.

As orcas residentes têm uma estrutura social matrilinear, descendendo de um único grupo ancestral. A tradição vocal e o repertório de chamamentos são transmitidos directamente da mãe para os descendentes. Os indivíduos permanecem ao longo da vida no seu grupo natal liderado pela matriarca, o que proporciona um ambiente propício à aprendizagem vocal. Com o tempo, a estrutura e o uso dos chamamentos pode evoluir independentemente, através de deriva cultural — ou seja, alterações na cópia vocal transmitidas entre gerações. As orcas residentes produzem três tipos principais de vocalizações: cliques de ecolocalização, assobios e chamamentos pulsados. Estes últimos subdividem-se em chamamentos aberrantes, variáveis e discretos. Os chamamentos pulsados discretos possuem propriedades estruturais e acústicas únicas, altamente estereotipadas, que permitem distinguir não só diferentes ecótipos, mas também clãs, grupos familiares (pods) e unidades matrilineares. A investigação existente sugere que o ruído antropogénico interfere com a emissão e recepção destes chamamentos social e ecologicamente importantes, podendo provocar disrupções na comunicação, coordenação de grupo e coesão social.

Este estudo modelou dados acústicos recolhidos em duas ilhas do Sul do Arquipélago do Golfo, na Colúmbia Britânica: a Ilha de Pender e a Ilha de Saturna, com o objectivo de examinar de que forma as orcas residentes do sul — nomeadamente o grupo J (J pod) — modificam o seu comportamento vocal perante diferentes níveis de ruído. Investigou-se quais os chamamentos pulsados discretos usados por este grupo e modelaram-se as taxas de emissão em resposta ao aumento dos níveis de pressão sonora ambiente. Um dos principais desafios encontrados na recolha de dados foi a presença de interferência eléctrica a 60 Hz provocada pela instalação do hidrofone na Ilha de Pender. Para garantir medições acústicas fiáveis, foi desenvolvido e aplicado um filtro notch, que permitiu identificar, remover e substituir as bandas de ruído autoinduzido em todos os registos afectados. Após esta correcção, cada ocorrência acústica foi analisada manualmente para identificar e classificar os chamamentos pulsados discretos ao longo de toda a duração do encontro. Para a análise estatística, foi construído um modelo linear generalizado misto com efeitos fixos para localização, tipo de chamamento, níveis de pressão sonora e as suas interacções, bem como um efeito aleatório para cada encontro acústico.

Os resultados mostraram que as proporções dos chamamentos estavam de acordo com os padrões históricos, com excepção de uma dominância acentuada do chamamento S04 na Ilha de Saturna — em contradição directa com estudos anteriores que identificavam o chamamento S01 como o mais dominante no grupo J. As estimativas do modelo indicaram que as orcas do grupo J reduzem significativamente a sua taxa total de emissão de chamamentos pulsados discretos em 2,4% por cada aumento de 1 dB no ruído ambiente, e em 21% por cada aumento de 10 dB.

Verificou-se que os chamamentos S02i, S04, S05, S06, S07, S12, S42, S44 foram usados significativamente mais em condições de menor ruído. A hipótese de que os chamamentos com componentes bifónicas ou de alta frequência seriam usados com maior frequência em ambientes ruidosos não foi necessariamente refutada, mas a análise inicial das taxas de emissão não revelou um padrão claro. A utilização preferencial do chamamento S04 em condições mais silenciosas levanta questões sobre a influência de factores locais na escolha e frequência dos chamamentos e merece investigação adicional.

Este estudo fornece evidências adicionais de que o aumento do ruído ambiente influencia significativamente o comportamento acústico das orcas residentes do sul, particularmente através da redução das taxas de chamamentos e de possíveis alterações na dominância dos tipos de chamamento. A diminuição geral da emissão vocal em contextos de ruído elevado pode indicar ajustes temporais ou uma supressão comportamental como resposta à perturbação — ambos com possíveis consequências ecológicas e energéticas. Acima de tudo, os resultados reforçam a importância de manter e proteger ambientes marinhos silenciosos, a fim de preservar a integridade do espaço acústico das orcas residentes. À medida que o ruído de origem humana continua a aumentar, uma compreensão aprofundada do comportamento acústico desta população será essencial para informar estratégias eficazes de conservação e gestão do seu habitat crítico.

Palavras-chave

Orcinus orca, Ruído subaquático, Chamamentos pulsados discretos, Perturbação acústica, Comportamento vocal, Conservação marinha

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List of abbreviations, acronyms and symbols

ANL – Ambient noise level
AIC – Akaike's Information Criterion
CPM – Calls per minute
COSEWIC - Committee on the Status of Endangered Wildlife in Canada
dB – Decibel
ESA – Endangered Species Act
GLMM – Generalized linear mixed model
HFBP – High-frequency burst pulse
HFC – High frequency component
ISZ – Interim Sanctuary Zone
LFC – Low frequency component
NRKW – Northern resident killer whale
PC – Pulsed call
SARA – Species at Risk Act
SNR – Signal-to-noise ratio
SPL – Sound pressure level
SRKW – Southern Resident killer whale

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Chapter 1 - General Introduction

This chapter explores the ecology, social organization, and the current threats to Southern Resident killer whale recovery to provide a better understanding of how anthropogenic noise pollution is contributing to and compounding the endangerment of their population.

1.0 Introduction

Noise pollution and its impact on marine life have become an important topic of study (Chapman & Price, 2011; Crystal et al., 2011; Erbe et al., 2019; Hildebrand, 2009; Tyack & Janik, 2013). Anthropogenic impacts are often visually obvious, as seen with oil spills, plastic pollution, overfishing, and coastal development. Even activities with good intention such as whale watching, can visibly alter natural behaviour through physical proximity (Noren et al., 2009; Williams et al., 2010; Williams, Trites, et al., 2002). In contrast, the influence of noise pollution in marine environments may not always be so obvious. For sound centered species such as killer whales (*Orcinus orca*), acoustic disturbance can significantly impact survivability. Killer whales rely on sound for hunting (L. Barrett-Lennard, 1996; Ford, 1989; Ford & Ellis, 2006), navigation (Miller, 2002), and social interaction (Deecke et al., 2010; Miller, 2002), all of which are critical for their survival. In 2008, Canada formally recognized underwater noise as a threat to its populations of killer whales (Fisheries and Oceans Canada, 2018; Heise, 2008). Since then, studies have begun to further to assess what types of acoustic disturbance impact killer whales and what can be done to mitigate or eliminate these influences (Cominelli et al., 2018; Holt et al., 2009, 2017; Tennessen et al., 2024; Veirs et al., 2016; Williams et al., 2014).

For the purposes of building familiarity to the reader, this chapter will focus on a broad overview of Southern Resident killer whale (SRKW) ecology, their social organization, and the currently identified threats to their survival. The chapter will conclude with a brief examination of anthropogenic noise, its implications for Southern Resident survival, and its relevance to the research of this thesis.

1.1 Southern Resident Killer Whale Ecology

1.1.1 Geographic Range and Life History

Southern Resident killer whales (*Orcinus orca*), are a part of a diverse and wide-ranging species with distinct populations in every ocean on Earth (Barrett-Lennard & Ellis, 2001; Bigg et al., 1990; Forney & Wade, 2007; Heimlich-Boran, 1988; Olesiuk et al., 1990). Killer whale populations with highly specialized diets and hunting traditions, that also differ in social structure, acoustic behaviour, and morphological traits, have been identified in various regions of the world and in many cases belong to distinct ecotypes (reviewed in de Bruyn et al., 2013, and Ford, 2019).

The Pacific northwest of North America is home to several ecotypes of killer whales that live in sympatry with one another without any form of genetic overlap (Bigg, 1982; Bigg et al., 1990; Olesiuk et al., 1990). The three main ecotypes found in the west coast of Canada and the United States are: offshore killer whales, Bigg's (Transient) "mammal-eating" killer whales, and two resident populations of "fish-eating" killer whales (Bigg, 1982). Resident killer whales are split into two distinct populations, also referred to as 'communities', the Northern Resident killer whales (NRKW), and the Southern Resident killer whales (SRKW) (Bigg, 1982; Olesiuk et al., 1990). The northern population ranges from Alaska to northern Washington state, while the southern population ranges from northern Haida Gwaii to southern California (Bigg et al., 1990; Olesiuk et al., 1990). Although both populations co-occupy similar geographical ranges and share food preferences, they are genetically distinct and have unique vocal characteristics that distinguish them (Barrett-Lennard & Ellis, 2001; Ford, 1989, 1991).

1.1.2 Identification & Population Status

Visually, individual killer whales can be distinguished through unique markings, nicks, and scratches on their dorsal fins and saddle patches. Individual identification was first applied to the species by Dr. Michael Bigg, who used it to distinguish populations, estimate their numbers and track maternal relationships (Bigg, 1982). Throughout the Pacific Northwest, Killer whale photo-identification studies have been used to understand much of what we know about the species, including their biology, life-histories, social systems and behaviours, and movement patterns. (Bigg, 1982; Olesiuk et al., 1990; Matkin et al., 2013;). In addition to visual identification, Ford (1984) observed that the various clans, populations and ecotypes of killer whales could be acoustically distinguished through distinct call repertoires of each family. The ability to recognize groups of whales through passive acoustic monitoring has allowed for a broader understanding of social structure and geographic usage (Ford, 1991; Samarra et al., 2015), acoustic behaviour in the presence and absence of physical and acoustic interference (Foote et al., 2004; Foote & Nystuen, 2008; Holt et al., 2009, 2011; Vagle et al., 2021) and has even supported the identification and reintegration of lost whales to their families (Jourdain et al., 2021). Passive acoustic monitoring has become a vital tool for killer whale research and conservation. The ability to recognize not only species, but for killer whales, their ecotypes, clans, and pods has enabled the detection of killer whale presence, identification, and understanding of both spatial and temporal patterns in critical habitats, without the necessity of a researcher being physically present (Riera et al., 2019; Emmons et al., 2021; Thornton et al., 2022; Pilkington et al., 2023).

1.1.3 Social and Acoustic Dynamics

Female resident killer whales have a life expectancy of approximately 50 years but may reach a maximum of 80-90 years (Olesiuk et al., 1990). On average, females start having calves of their own by age 15 and typically produce just over five viable offspring in their lifetime (Olesiuk et al., 1990). Males have a shorter life expectancy of around 29 years, but can reach a maximum of 50-60 years (Olesiuk et al., 1990). Males reach sexual maturity around the same time as females and are perceived to be fully grown at around 21 years (Olesiuk et al., 1990). Both Northern Resident and Southern Resident offspring, remain with their mothers for the entirety of their lives, forming small, stable matrilineal units, composed of related individuals descended from a single living female (Deecke, 1994; Olesiuk et al., 1990).

Some closely related matrilines often associate and travel together, forming pods that are genetically and acoustically related (Deecke, 1994; Ford, 1991; Miller & Bain, 2000). Killer whales produce three different types of vocalizations: echolocation clicks, whistles, and pulsed calls (Ford, 1984, 1989, 1991). Pulsed calls have unique structural and acoustic properties that can be used to differentiate between ecotypes, communities, clans, pods, and even matrilineal units (Ford, 1991; Miller & Bain, 2000). Resident killer whales produce three different types of vocalizations: echolocation clicks, whistles, and pulsed calls (Ford, 1991). Pulsed calls can be further classified into aberrant, variable, and discrete call types. Discrete pulsed calls have unique structural and acoustic properties that are highly stereotyped and enable the differentiation not only between ecotypes, but also between respective clans, pods, and matrilineal units (Ford, 1989; Miller & Bain, 2000).

Pods of resident killer whales are thought to be related by matrilineal descent from a single ancestral pod, with vocal traditions and call repertoires passed directly from mother to offspring (Deecke et al., 2000, 2010; Ford, 1991; Moore et al., 1988). Since individuals within resident communities spend nearly the entirety of their lives within one family (Barrett-Lennard & Ellis, 2001), it is likely that stable matrilineal units are an important environment for the learning and transmission of vocal traits (Deecke et al., 2000, 2010). Ford (1991) suggested the splitting and formation of new matrilines and pods may be accompanied by divergence in vocal repertoire. New pods initially retain their ancestral call repertoire, but may accumulate variations over successive generations suggesting that pods that share more call types have a more recent common ancestor (Deecke, 1994; Deecke et Ford et al., 2000; Ford, 1991). Over time, call structure and pattern of usage may evolve independently through cultural drift, resulting from vocal copying and the transmission of these changes across generations (Ford, 1991). However, Ford also states that some vocal variation can arise from unique vocal trends, rather than copying errors.

The highest level of association among resident killer whales are clans, which are groups of pods that share distinct vocal characteristics and are believed to have a single common ancestor (Bigg, 1982; Deecke et al., 2010; Ford, 1991). The formation of distinct clans, where no call types are shared, likely occurred under different circumstances than that of pods (Deecke, 1994b; Ford, 1989, 1991). Two possible explanations have been proposed: (1) the gradual loss of ancestral calls over time following an ancient divergence, or (2) the independent development of acoustic separation and vocal traditions in geographic isolation, arising from a series of unrelated founding events (Ford, 1991).

The Southern Resident killer whale population comprises a single clan, known as J clan, which includes three pods: J, K, and L and do not associate with Northern Residents. In comparison, the Northern Resident population consists of three acoustic clans — A, G, and R — each with its own distinct set of pods. Population specific pods often associate with one another and tend to form larger social groups (Ford, 1984, 1991). However, although it is not unusual to find all members of a pod together, matrilineal kin-based units appear to be the most important social unit as groupings within, and between pods, will fluctuate (Olesiuk et al., 1990, Ford 1991). One explanation for such fluctuations is that large groupings may at times be too inefficient or energetically costly in terms of resource procurement (Olesiuk et al., 1990). However, in Southern Residents, genetic relatedness within social groups may play a significant role to the maintenance of large groups, where the direct fitness costs are balanced by the benefits gained through behaviours such as cooperative care, altruism, and group foraging (Barrett-Lennard & Ellis, 2001; Ford, 1991; Olesiuk et al., 1990).

Resident killer whales exhibit strong inbreeding avoidance mechanisms and typically do not mate within their natal pods (Barrett-Lennard & Ellis, 2001). Instead, they mate with individuals from other pods within the same population. In the Northern Resident population, most matings occur between members of different clans, helping to maintain genetic diversity and avoid inbreeding despite the lack of dispersal from natal groups (Barrett-Lennard & Ellis, 2001). However, the Southern Resident population, consisting of a single acoustic clan, has no inter-clan mating opportunities. Both genetic isolation and small effective population size has led to elevated inbreeding within SRKWs, significantly impacting survival rates and reducing population growth potential (Barrett-Lennard & Ellis, 2001; Ford et al., 2018).

1.2 Population Status & Threats to Recovery

Killer whales have become an iconic species in the Pacific Northwest of North America, although they were not always viewed so kindly. Historically, killer whales were never the target of commercial whaling, however, they were viewed as a nuisance species that interfered with commercial fishing and as a hazard to small vessels (Bigg, 1982; Olesiuk et al., 1990). In the 1940s, the Royal Canadian Air Force used killer whales for bombing target practice, and in 1960 the Canadian government mounted a machine gun near Campbell River, BC with the intent to reduce the population (Olesiuk et al., 1990).

Resident killer whale populations were significantly impacted during the live-capture trade which removed individuals from both populations for display in marine parks and aquariums. From 1962 to 1977, a total of 68 killer whales were captured for this purpose (Olesiuk et al., 1990), including 47 individuals from the Southern Resident population alone, reducing an already small population to just 66 individuals (Bigg, 1982; Fisheries and Oceans Canada, 2018). After live captures ended, censuses were conducted annually and showed that the SRKW population recovered to 99 individuals in 1995 before falling to 72 in 2001 (Fisheries and Oceans Canada, 2018).

The optics around killer whales changed drastically as science began to unravel killer whale life history, diets, and social habits. Although controversial, captivity and the aquarium trade brought killer whales into the daily lives of people in an intimate way that would otherwise have been impossible. Major feature films such as “Free Willy”, the story of a captive whale being freed to return to the wild and his family, captured the hearts of generations and had a major influence on the change in perception of killer whales (Wearing et al., 2011). Around the same time, whale watching companies began to occupy locations up and down the coastlines of Washington and British Columbia, providing not only the experience to see whales in the wild, but also expanding the push for conservation and understanding of the species (Olesiuk et al., 1990). These companies benefited greatly from the cultural shift of fear to admiration, and as more vessels began to follow pods of whales, promising close encounters and life changing experiences, science began to question the impacts of proximity and noise.

In 2003, Southern Resident killer whales were listed as "endangered" under the Canadian Species at Risk Act (SARA), and in 2005 under the U.S. Endangered Species Act (ESA) (Fisheries and Oceans Canada, 2017, 2018; National Marine Fisheries Service, 2005). In the same period, the Northern Resident population increased from 125 individuals to an estimated 341 individuals, despite having similar life histories and diets as the Southern Residents (Fisheries and Oceans Canada, 2018; DFO, 2023. Northern Residents were designated as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2001, a designation that remains today.

In 2018, the Government of Canada determined that the Southern Resident killer whale population was facing imminent threats to its survival (Government of Canada, 2018), and management measures began to be implemented to promote their recovery. The immediate threats to SRKW survival were identified as: prey availability and accessibility, contaminants, and physical and acoustic disturbance (Lacy et al. 2017; Fisheries and Oceans Canada, 2017, 2018; Heise, 2008).

1.2.1 Diet & Prey Availability

Early studies of prey preferences analyzed scale and tissue samples from successful foraging events, revealing that salmon comprised approximately 96-97% of resident killer whale diet, with flatfish (including sole and halibut), sablefish, and rockfish making up the remainder (Ford & Ellis, 2006; Hanson et al., 2010, 2021). Chinook salmon (*Oncorhynchus tshawytscha*) were the predominant salmon species in their diet, followed by chum salmon *(Oncorhynchus keta*) and, less-commonly, coho salmon (*Onchorhynchus kisutch*) (Ford & Ellis, 2006; Hanson et al., 2021), but pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*Oncorhynchus nerka*) do not appear to be a significant contributor to resident killer whale diet despite their high abundance in areas of resident foraging (Chasco et al., 2017; Hanson et al., 2021). Preference for Chinook salmon may be due to their larger size, relatively high lipid content and year-round presence in coastal waters (Hanson et al., 2010, 2021).

Southern Resident movement patterns closely reflect those of migrating Chinook populations (Hanson et al., 2010). From June to August SRKWs feed almost exclusively on Chinook in the inland waters from Juan de Fuca to Puget Sound. This percentage of Chinook drops in their diet to about 50%, with most of the remainder comprising chum and then coho (Hanson et al., 2021). In winter they range from central California to northern BC's outer coastal waters (Hanson et al., 2010) where their diet includes a mix of Chinook, coho, and chum salmon and other species such as steelhead salmon and several non-salmonids, before returning to a predominantly Chinook salmon diet in spring (Hanson et al., 2021).

The reliance on chinook impacts Southern Resident killer whale survival and fecundity as most stocks of chinook along the west coast of Canada and the United States are also in decline (Atlas et al., 2023; COSEWIC, 2018, 2020; Ohlberger et al., 2018). In 2020, COSEWIC listed 19 designatable stocks of concern for chinook salmon as either "endangered" or "threatened", 8 of these stocks were from the Fraser River alone (COSEWIC, 2018, 2020), a watershed of primary importance to Southern Resident (Chasco et al., 2017; Hanson et al., 2010, 2021; Ohlberger et al., 2018). Chinook salmon stocks that dominate mid-winter/early spring SRKW diet include the Sacramento River, Columbia River, and Puget Sound, all of which are listed as threatened or endangered under the ESA (National Marine Fisheries Service, 2005). Habitat degradation is the primary reason for the prominent decline of Chinook salmon (Crozier et al., 2021; Ohlberger et al., 2018; Stewart et al., 2023). Human driven activity including climate change, urban and industrial expansion (cities, ports and pipelines), and dam construction on spawning streams reduce viable habitat, disrupting salmonid life cycles (Atlas et al., 2023; Crozier et al., 2021; Lewis et al., 2015; Ohlberger et al., 2018). Further compounding variables include commercial and recreational fishing, where over-harvesting and size-selective fisheries may have led to further reductions and drive evolutionary shifts toward smaller and younger Chinook cohorts (Atlas et al., 2023; Lewis et al., 2015).

The decline in both Chinook and SRKW populations is happening in parallel and points to nutritional stress being a significant threat to SRKW recovery (Couture et al., 2022; Fearnbach et al., 2011). Photogrammetric surveys carried out over the summer months, when SRKW are primarily feeding on Fraser River and Puget Sound salmon stocks, demonstrated a decline in body condition with a concurrent decline in respective significant chinook habitat (Fearnbach et al., 2011). Further studies found other indicators of nutritional stress in SRKW feces (Yehle, 2022;

Wasser et al., 2017). By analyzing thyroid and glucocorticoid hormone metabolites researchers were able to assess pregnancy occurrences and failures and link these outcomes to periods of low chinook availability (Wasser et al., 2017). SRKW had pregnancy failure rates of approximately 69%, with nutritional stress likely to be the main contributor, especially in late stages of reproduction when costs of failure are high (Wasser et al., 2017). Prey availability and reaching nutritional thresholds remain a significant concern for the Southern Resident population.

1.2.2 Contaminants

Numerous persistent and harmful industrial and agricultural chemicals produced during the twentieth century have been found to accumulate in the fatty tissues of animals at higher trophic levels within aquatic food chains (Krahn et al., 2007, 2009; Ross et al., 2000). As large, apex predators, killer whales experience the full impacts of bioaccumulation and are among the most contaminated marine mammals in the world (Ross et al., 2000). Potential causes of Southern Resident killer whale population decline include high levels of environmental pollutants such as persistent organic pollutants (POPs) and chlorinated (PCBs, DDTs) and brominated environmental contaminants (Krahn et al., 2007; Ross et al., 2000). Exposure to organochlorine contaminants in marine mammals can lead to deleterious biological effects such as immune dysfunction and reduced reproductive and endocrine capabilities (Krahn et al., 2007, 2009; Ross et al., 2000). High levels of POPs have historically been found in all North Pacific killer whale populations (Ross et al., 2000), and more recently, studies have shown that most SRKW blubber samples contained PCB levels that far exceeded thresholds for negative health effects in other marine mammals (Hickie et al., 2007; Ross et al., 2000). Environmental contamination is often most pronounced in large males because of gross prey intake, however juvenile whales exhibit higher concentrations of POPs compared to adults, likely due to maternal transfer during development, potentially increasing their risk for surviving early stages of life (Krahn et al., 2009; Ross et al., 2000).

Interestingly, the ratios of pollutants such as DDTs/PCBs differ between K/L pods and J pod, likely because of their tendencies to forage in different locations such as California or Puget Sound/Georgia Basin respectively (Hickie et al., 2007; Ross et al., 2000). J pod exhibited significantly lower DDT/PCB rations than K or L pods suggesting that prey found in Puget Sound, where J pod spends significant time in the fall and winter, contained lower levels of DDTs than prey that reside in California (Hickie et al., 2007; Krahn et al., 2007, 2009; Ross et al., 2000).

Although PCB concentrations have declined rapidly since regulations in the 1970s, for long-lived species such as killer whales, it will take a long time for their metabolism to break down and reduce their concentration (Hickie et al., 2007; Krahn et al., 2007, 2009; Ross et al., 2000). Studies suggest that SRKW may not fall below a safe threshold concentration of PCBs until at least 2063, posing a continued vulnerability to infectious disease, reduced reproductive performance, and irregular growth and development (Hickie et al., 2007; Ross et al., 2000). Compounding the effects of contamination with reduced prey availability and physical and acoustic disturbance may have severe consequences for the recovery of Southern Resident killer whales.

1.2.3 Physical and Acoustic Disturbance

Noise pollution is a major threat to killer whales and often occurs alongside physical disturbance. Its impacts have been widely studied and has been linked to changes in rates of respiration (Williams et al., 2014), elicitation of surface behaviours (Noren et al., 2009; Williams et al., 2002) and changes to typical activity budgets such as foraging, travelling and socializing (Tennessen et al., 2024; Williams et al., 2002). Significant noise exposure can cause alterations to movement and directionality and in some cases has led to long-term avoidance of specific locations altogether (Williams et al., 2014; Morton & Symonds, 2002;). One of the most impactful effects that noise pollution has on marine mammals is auditory masking. Masking occurs when an acoustic signal becomes difficult to recognize, or detect, because of the presence of another sound (Erbe, 2016). Although masking naturally occurs in marine systems, where wind-driven sea states largely determine ambient noise levels, growing vessel traffic in busy urban areas and commercial shipping lanes now dominate the marine environment (Erbe, 2016; Tyack and Janik, 2013).

Noise pollution and physical proximity go hand-in-hand. Some of the earliest studies on vessel activity in proximity to SRKWs found that close approaches by vessels elicited surface active behaviours (SABs) such as tail slaps, breaches, and spy hops (Erbe, 2002; Noren et al., 2009; Williams et al., 2002). Although these behaviours may entertain the casual observer, they are energetically costly given the concern over food-limitations and nutritional deficiencies

(Williams et al., 2002, 2006; Williams & Ashe, 2006). Williams et al. (2006) estimated that behavioural changes and reduced time spent foraging in response to vessel presence may cause substantial reductions (18%) in energy acquisition by northern residents. Similarly, Southern Residents spend more time travelling and less time foraging when approached at distances of 100m to 400m (Williams et al., 2010). The effect of these disruptions decreased with increasing distance, but significant behavioural changes were still observed at 400m.

At the time these studies were conducted, vessels were permitted to approach Southern Resident killer whales as close as 100m. Today, regulations prohibit approaches closer than 400m and 1000m for Canada and the United States respectively (Fisheries and Oceans Canada, 2018; National Marine Fisheries Service, 2005). In contrast, the minimum approach distance for all other killer whale populations remains at 200m in both Canada and the United States. While whale watching receives much of the attention regarding physical proximity, similar concerns apply to other vessel types such as recreational and commercial fishers, tourists and pleasure craft operators, and large commercial tankers and cargo ships (Bain et al., 2006; Lusseau et al., 2009; Vagle et al., 2021).

Acoustic disturbance compounds these effects and is arguably the more significant factor. Prior to current government regulations, SRKWs could find themselves surrounded by boats for 8-10 hours per day, 7 days a week during peak whale-watching season (Erbe, 2002). Between 1995 and 1999, an average of 21 boats could be observed following a group of whales, with a maximum of 60-70 at one time (Erbe, 2002). Individual boat noise alone may not be enough to cause permanent hearing loss, but large aggregations of vessels or continuous exposure to transiting vessels over long periods may reach critical levels associated with both temporary and permanent hearing loss (Erbe, 2002). Erbe (2002) used sound propagation and acoustic impact assessment models to determine the ranges over which boat noise was audible to killer whales and assessed its potential to interfere with killer whale communication and behavioural responses. Erbe's study observed that fast boats could be audible to killer whales over 16km and could mask killer whale calls at distances of 14km. Her study showed that exposure to fast moving vessels for 30-50 minutes within 450m could be enough to cause a temporary threshold shift in hearing of 5 dB. Temporary threshold shifts may occur at distances as close as 20 m, while slower vessels produce similar effects at ranges of up to 1 km.

Erbe’s study suggested that decreasing speed and increasing distance requirements for whale watchers could benefit killer whale quality of life, and many of these recommendations were later implemented. Although whale watching is what is the focus of Erbe’s study, these disturbances apply to all vessels in the vicinity of whales. Recreational fishermen, pleasure boat operators, and tourist boats all make up local marine traffic and share physical space with Southern Resident killer whales (Cominelli et al., 2018; Holt et al., 2011; Joy et al., 2019; Williams et al., 2014). Whale watchers are typically aware of, and adhere, to the guidelines put into place by government and regulatory organizations, however the general public may not be as well informed (Burnham et al., 2021).

Over the past 50 years, acoustic disturbance from human activity has caused a progressive increase in background noise levels in marine ecosystems (Chapman & Price, 2011; Cominelli et al., 2018; Erbe et al., 2019; McDonald et al., 2008). Sources of marine noise caused by human activity include seismic activity, navy sonar exercises, pile driving and commercial and recreational vessels (Hildebrand, 2009; McDonald et al., 2008; Vagle et al., 2021). Of these sources, commercial shipping is the most widespread and consistent in most marine environments (Cominelli et al., 2018; Hildebrand, 2009). Southern Resident core habitat overlaps with international commercial shipping lanes that are the gateways to ports in large urban areas such as Vancouver, BC and Seattle, WA (Crystal et al., 2011; Thornton et al., 2022; Veirs et al., 2016).

Earlier research suggested that large commercial vessels produced noise predominantly at frequencies below 1 kHz, lower than the typical range of most pulsed call types used by killer whales (Cominelli et al., 2018; Veirs et al., 2016). However, more recent studies demonstrated that ship noise within critical Southern Resident killer whale habitat, such as Haro Strait and Juan de Fuca Strait, could elevate background noise levels not only in the low-frequency domain, but also in the 10 kHz to 40 kHz band at distances of up to 3km (Veirs et al., 2016). These frequencies directly overlap with those used for echolocation and communication, increasing the risk of acoustic masking even when several kilometers away from the source (Clark et al., 2009; Erbe et al., 2016; Veirs et al., 2016).

Research has suggested that anthropogenic noise negatively affects Southern Resident foraging behaviour, by reducing foraging time and displacing residents from ideal foraging locations (Bain et al., 2006; Lusseau et al., 2009). Tennessen et al. (2023) used bio-logging tags attached to individuals during bouts of foraging to examine the effects of noise on SRKW foraging behaviour. Their study observed that for every 1 dB increase in noise, the odds of searching behaviour increased by 4%, while the odds of pursuit and capture dropped by 58% (females) and 12.5% (both sexes), respectively (Tennessen et al., 2024). Deep dives, which are often associated with prey capture, were more likely to result in failure when exposed to high noise levels than deep dives exposed to low or medium noise levels (Tennessen et al., 2024). Tennessen's results support evidence that vessel noise interferes with foraging through auditory masking and highlights the need to reduce ocean noise to acoustically sensitive marine mammals.

Continued research has led to mandatory and voluntary slowdowns implemented within SRKW summer core habitat to help reduce broadband noise exposure (Clarke et al., 2024; Joy et al., 2019). In 2017, a voluntary vessel slowdown was implemented in Haro Strait during months when SRKW presence was high. The slowdown was successful in reducing broadband noise and demonstrated that reducing vessel speeds is a viable strategy to improve habitat quality of important summer foraging hotspots (Burnham et al., 2021; Joy et al., 2019). Potential SRKW foraging time could increase by 22-40% depending on vessel engagement and minimum speeds (Joy et al., 2019). Further slowdowns have since been implemented throughout Haro Strait, Swiftsure Bank and Boundary Pass. Most recently, vessel restriction zones, formerly Interim Sanctuary Zones (ISZs) have been placed in high traffic areas that are deemed key foraging areas for SRKWs. Additionally, the government has recommended voluntary mitigation measures, including stopping fishing or hauling up gear, reducing transit speeds to less than 7 knots, turning off echo sounders and fish finders, and placing engines in neutral idle to allow disturbing nearby whales (Fisheries and Oceans Canada, 2024).

In response to both natural and anthropogenic sources of noise, killer whales have demonstrated the ability to actively modify their vocalizations. Vocal modification is described by Holt et al. (2009, 2011), who observed SRKWs increasing the amplitude of their calls in response to rising noise levels, likely to communicate over the noise in free acoustic space (Burnham et al., 2021; Holt et al., 2009; Poupard et al., 2021). This phenomenon of "speaking up" is a process known as the Lombard Effect which was first seen in humans (Brumm & Zollinger, 2011), but can also be observed in fishes (Luczkovich et al., 2017), frogs (Halfwerk et al., 2016) and other cetacean species such as humpback (*Megaptera novaeanglia*), minke (*Balaenoptera acutorostrata)*, and beluga (*Delphinapterus leucas*) whales (Guazzo et al., 2020; Helble et al., 2020; Scheifele et al., 2005). Increases in vocal output to compensate for excessive environmental noise could have negative energetic costs and affect normal activity budgets (Holt et al., 2009).

Additional evidence of vocal modification includes shifts in frequency, call duration, and changes in bandwidth. Antarctic killer whale populations have been shown to shift their vocal frequency to avoid competition with other co-existing soniferous species such as leopard seals (*Hydrurga leptonyx*) (Mossbridge & Thomas, 1999), and there is evidence of SKRWs doing the same in response to vessel noise (Murphy, 2023). Murphy (2023) explored these concepts further, finding that some SRKW call types are lengthened under noisy conditions, supporting prior research of increases in call duration (Foote et al., 2004; Wieland et al., 2010), and that other call types may also increase in bandwidth used. Furthermore, structural features of some call types may reflect adaptive responses shaped by evolutionary pressures to facilitate communication in noisy environments. Miller et al. (2006) investigated biphonic pulsed call types which contain both a low (LFC) and high frequency component (HFC). They demonstrated that the HFC are directional, often correlating with the orientation of the signaler, suggesting a role in group orientation and direction of movement. Since HFCs occur in higher energy bands, they may be less affected by noise. The issues of acoustic disturbance and the compensatory vocal behaviors that result from it are examined in greater depth in the introduction and discussion of Chapter 2.

1.3 Conclusions and Relevance to Study

With the current conservation concerns for at-risk SRKWs, there has understandably been a distinct acknowledgement of the impacts of anthropogenic noise on killer whale foraging ability (Joy et al., 2019; Lusseau et al., 2009; Tennessen et al., 2024). The specific effects of noise on killer whale vocal behaviour are less known, despite growing evidence of its influence. Research increasingly demonstrates that anthropogenic noise interferes with the transmission and reception of socially and ecologically important vocalizations in resident killer whales, disrupting communication, group coordination, and social cohesion (Foote et al., 2004; Foote & Nystuen, 2008b; Holt et al., 2009, 2011; Miller, 2006).

Southern Resident call types have been categorically identified since the 1990s, but how these call types vary in varying noise conditions has not been well investigated. This study aims to build on prior research by focussing on one pod of Southern Residents and their specific call types to improve sample resolution and remove potential biases introduced by more dominant call types from other pods. Specifically, I will investigate whether Southern Residents preferentially select specific call types for communication during bouts of increased ambient noise, and whether these call types exhibit structural features that enhance their transmission in noisy environments. Evaluating changes in call usage provide a direct and easily measurable way to assess the effects of anthropogenic noise on SRKW acoustic behaviour. For a species that is so heavily reliant on the acoustic world, any changes or increased efforts for communication or foraging may have significant impacts on survivability and recovery.

2.0 References

Atlas, W. I., Sloat, M. R., Satterthwaite, W. H., Buehrens, T. W., Parken, C. K., Moore, J. W., ... & Potapova, A. (2023). Trends in Chinook salmon spawner abundance and total run size highlight linkages between life history, geography and decline. *Fish and Fisheries*, *24*(4), 595-617.

Bain, D. E., Smith, J. C., Williams, R., & Lusseau, D. (2006). Effects of vessels on behavior of Southern Resident killer whales (Orcinus spp.). *NMFS Contract Report No. AB133F03SE0959 and AB133F04CN0040*.

Barrett-Lennard, L. G., Ford, J. K., & Heise, K. A. (1996). The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal behaviour*, *51*(3), 553-565.

Barrett-Lennard, L. G., & Ellis, G. (2001). Population structure and genetic variability in northeastern Pacific killer whales: towards an assessment of population viability.

Bigg, M. (1982). An assessment of killer whale (Orcinus orca) stocks off Vancouver Island, British Columbia. *Report of the International Whaling Commission*, *32*(65), 655-666.

Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., & Balcomb, K. C. (1990). Social organization and genealogy of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission*, *12*, 383-405.

Brumm, H., & Zollinger, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, *148*(11-13), 1173-1198.

Burnham, R. E., Vagle, S., O'Neill, C., & Trounce, K. (2021). The efficacy of management measures to reduce vessel noise in critical habitat of Southern Resident killer whales in the Salish Sea. *Frontiers in Marine Science*, *8*, 664691.

Chapman, N. R., & Price, A. (2011). Low frequency deep ocean ambient noise trend in the Northeast Pacific Ocean. *The Journal of the Acoustical Society of America*, *129*(5), EL161-EL165.

Chasco, B., Kaplan, I. C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M. J., ... & Ward, E. J. (2017). Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(8), 1173-1194.

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A., & Ponirakis, D. (2009). Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Marine Ecology Progress Series*, *395*, 201-222.

Clarke, C. M. K., Stredulinsky, E., Toews, S., Rani, V., Bouvier-Brown, M., Smyth, D., ... & Thornton, S. J. (2024). Assessing the efficacy of ecological reserves: killer whale beach rubbing behaviour and vessel disturbance. *Endangered Species Research*, *53*, 555-567.

Cominelli, S., Devillers, R., Yurk, H., MacGillivray, A., McWhinnie, L., & Canessa, R. (2018). Noise exposure from commercial shipping for the Southern Resident killer whale population. *Marine pollution bulletin*, *136*, 177-200.

COSEWIC. (2018). COSEWIC assessment and status report on the Chinook Salmon Oncorhynchus tshawytscha, Designatable Units in Southern British Columbia (Part One – Designatable Units with no or low levels of artificial releases in the last 12 Years), in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxxi + 283 pp. (http://www.registrelep-sararegistry.gc.ca/default.asp?lang=en&n=24F7211B-1).

COSEWIC. (2020). COSEWIC assessment and status report on the Chinook Salmon Oncorhynchus tshawytscha, Designatable Units in Southern British Columbia (Part Two - Designatable Units with high levels of artifical releases in the Last 12 Years), in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxxv + 203 pp. (https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry.html).

COSEWIC. (2023). COSEWIC assessment and status report on the Killer Whale Orcinus orca, Northeast Pacific Southern Resident population, Northeast Pacific Northern Resident population, Northeast Pacific Transient Killer Whale population, Northeast Pacific Offshore population, and Northwest Atlantic / Eastern Arctic population in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxxi + 114 pp. (https://www.canada.ca/en/environment-climate-change/services/species-riskpublic-registry.html).

Couture, F., Oldford, G., Christensen, V., Barrett-Lennard, L., & Walters, C. (2022). Requirements and availability of prey for northeastern pacific Southern Resident killer whales. *PLoS One*, *17*(6), e0270523.

Crozier, L. G., Burke, B. J., Chasco, B. E., Widener, D. L., & Zabel, R. W. (2021). *Climate change threatens Chinook salmon throughout their life cycle. Commun. Biol. 4, 222*.

Crystal, D., Moseley, K., Paterson, C., Ryvola, R., & Wang, S. (2011). Commercial shipping noise impacts on the critical habitat of the Southern Resident killer whale (Orcinus orca).

Deeke, V. B. (1998). *Stability and change of killer whale (Orcinus orca) dialects* (Doctoral dissertation, University of British Columbia).

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (Orcinus orca). Naturwissenschaften, 97(5), 513–518.

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (Orcinus orca). *Naturwissenschaften*, *97*, 513-518.

DFO. 2023. Population status update for the Northern Resident Killer Whale (Orcinus orca) in 2022. DFO Can. Sci. Advis. Sec. Sci. Resp. 2023/031.

Emmons, C. K., Hanson, M. B., & Lammers, M. O. (2021). Passive acoustic monitoring reveals spatiotemporal segregation of two fish-eating killer whale Orcinus orca populations in proposed critical habitat. *Endangered Species Research*, *44*, 253-261.

Erbe, C. (2002). Underwater noise of whale‐watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model. *Marine mammal science*, *18*(2), 394-418.

Erbe, C., Marley, S. A., Schoeman, R. P., Smith, J. N., Trigg, L. E., & Embling, C. B. (2019). The effects of ship noise on marine mammals—a review. *Frontiers in Marine Science*, *6*, 606.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine pollution bulletin*, *103*(1-2), 15-38.

Fearnbach, H., Durban, J. W., Ellifrit, D. K., & Balcomb III, K. C. (2011). Size and long-term growth trends of endangered fish-eating killer whales. *Endangered Species Research*, *13*(3), 173-180.

Fisheries and Oceans Canada. 2017. Action Plan for the Northern and Southern Resident Killer Whale (*Orcinus orca*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa. v + 33 pp.

Fisheries and Oceans Canada. 2018. Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada [Proposed]. Species at Risk Act Recovery Strategy Series, Fisheries & Oceans Canada, Ottawa, x + 84 pp.

Fisheries and Oceans Canada. 2024. Watching marine wildlife. [Online, DFO webpage]

Foote, A. D., & Nystuen, J. A. (2008). Variation in call pitch among killer whale ecotypes. *The Journal of the Acoustical Society of America*, *123*(3), 1747-1752.

Foote, A. D., Osborne, R. W., & Hoelzel, A. R. (2004). Whale-call response to masking boat noise. *Nature*, *428*(6986), 910-910.

Ford, J. K. B. (1984). *Call traditions and dialects of killer whales (Orcinus orca) in British Columbia* (Doctoral dissertation, University of British Columbia).

Ford, J. K. (1989). Acoustic behaviour of resident killer whales (Orcinus orca) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*(3), 727-745.

Ford, J. K. (1991). Vocal traditions among resident killer whales (Orcinus orca) in coastal waters of British Columbia. *Canadian journal of zoology*, *69*(6), 1454-1483.

Ford, J. K., & Ellis, G. M. (2006). Selective foraging by fish-eating killer whales Orcinus orca in British Columbia. *Marine Ecology Progress Series*, *316*, 185-199.

Ford, M. J., Parsons, K. M., Ward, E. J., Hempelmann, J. A., Emmons, C. K., Bradley Hanson, M., ... & Park, L. K. (2018). Inbreeding in an endangered killer whale population. *Animal conservation*, *21*(5), 423-432.

Forney, K. A., Wade, P. R., & Estes, J. A. (2006). Worldwide distribution and abundance of killer whales. *Whales, whaling and ocean ecosystems*, *145*, 162.

Guazzo, R. A., Helble, T. A., Alongi, G. C., Durbach, I. N., Martin, C. R., Martin, S. W., & Henderson, E. E. (2020). The Lombard effect in singing humpback whales: Source levels increase as ambient ocean noise levels increase. *The Journal of the Acoustical Society of America*, *148*(2), 542-555.

Halfwerk, W., Lea, A. M., Guerra, M. A., Page, R. A., & Ryan, M. J. (2016). Vocal responses to noise reveal the presence of the Lombard effect in a frog. *Behavioral Ecology*, *27*(2), 669-676.

Hanson, M. B., Baird, R. W., Ford, J. K., Hempelmann-Halos, J., Van Doornik, D. M., Candy, J. R., ... & Ford, M. J. (2010). Species and stock identification of prey consumed by endangered Southern Resident killer whales in their summer range. *Endangered Species Research*, *11*(1), 69-82.

Hanson, M. B., Emmons, C. K., Ford, M. J., Everett, M., Parsons, K., Park, L. K., ... & Barre, L. (2021). Endangered predators and endangered prey: Seasonal diet of Southern Resident killer whales. *PloS one*, *16*(3), e0247031.

Heimlich-Boran, J. R. (1988). Behavioral ecology of killer whales (Orcinus orca) in the Pacific Northwest. *Canadian Journal of zoology*, *66*(3), 565-578.

Heise, K. A. (2008). *Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada*. Fisheries and Oceans Canada.

Helble, T. A., Guazzo, R. A., Martin, C. R., Durnbach, I. N., Alongi, G. C., Martin, S. W., ... & Henderson, E. E. (2020). Lombard effect: Minke whale boing call source levels vary with natural variations in ocean noise. *The Journal of the Acoustical Society of America*, *147*(2), 698-712.

Hickie, B. E., Ross, P. S., Macdonald, R. W., & Ford, J. K. (2007). Killer whales (Orcinus orca) face protracted health risks associated with lifetime exposure to PCBs. *Environmental Science & Technology*, *41*(18), 6613-6619.

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5-20.

Holt, M. M., Hanson, M. B., Giles, D. A., Emmons, C. K., & Hogan, J. T. (2017). Noise levels received by endangered killer whales Orcinus orca before and after implementation of vessel regulations. *Endangered Species Research*, *34*, 15-26.

Holt, M. M., Noren, D. P., & Emmons, C. K. (2011). Effects of noise levels and call types on the source levels of killer whale calls. *The Journal of the Acoustical Society of America*, *130*(5), 3100-3106.

Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., & Veirs, S. (2009). Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise. *The Journal of the Acoustical Society of America*, *125*(1), EL27-EL32.

Jourdain, E., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K., Karoliussen, R., Towers, J. R., & Vongraven, D. (2021). Natural entrapments of killer whales (Orcinus orca): A review of cases and assessment of intervention techniques. *Frontiers in Conservation Science*, *2*, 707616.

Joy, R., Tollit, D., Wood, J., MacGillivray, A., Li, Z., Trounce, K., & Robinson, O. (2019). Potential benefits of vessel slowdowns on endangered Southern Resident killer whales. *Frontiers in Marine Science*, *6*, 344.

Krahn, M. M., Hanson, M. B., Schorr, G. S., Emmons, C. K., Burrows, D. G., Bolton, J. L., ... & Ylitalo, G. M. (2009). Effects of age, sex and reproductive status on persistent organic pollutant concentrations in "Southern Resident" killer whales. *Marine Pollution Bulletin*, *58*(10), 1522-1529.

Krahn, M. M., Hanson, M. B., Baird, R. W., Boyer, R. H., Burrows, D. G., Emmons, C. K., ... & Collier, T. K. (2007). Persistent organic pollutants and stable isotopes in biopsy samples (2004/2006) from Southern Resident killer whales. *Marine pollution bulletin*, *54*(12), 1903-1911.

Lewis, B., Grant, W. S., Brenner, R. E., & Hamazaki, T. (2015). Changes in size and age of Chinook salmon Oncorhynchus tshawytscha returning to Alaska. *PLoS One*, *10*(6), e0130184.

Luczkovich, J. J., Krahforst, C. S., Kelly, K. E., & Sprague, M. W. (2016, July). The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments. In *Proceedings of Meetings on Acoustics* (Vol. 27, No. 1). AIP Publishing.

Lusseau, D., Bain, D. E., Williams, R., & Smith, J. C. (2009). Vessel traffic disrupts the foraging behavior of Southern Resident killer whales Orcinus orca. *Endangered Species Research*, *6*(3), 211-221.

Matkin, C. O., Ward Testa, J., Ellis, G. M., & Saulitis, E. L. (2014). Life history and population dynamics of southern Alaska resident killer whales (Orcinus orca). Marine Mammal Science, 30(2), 460-479.

McDonald, M. A., Hildebrand, J. A., Wiggins, S. M., & Ross, D. (2008). A 50Year comparison of ambient ocean noise near San Clemente Island: A bathymetrically complex coastal region off Southern California. *The journal of the Acoustical Society of America*, *124*(4), 1985-1992.

Miller, P. J. (2002). Mixed-directionality of killer whale stereotyped calls: a direction of movement cue? *Behavioral Ecology and Sociobiology*, *52*, 262-270.

Miller, P. J. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A*, *192*, 449-459.

Miller, P. J., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, Orcinus orca. *Animal Behaviour*, *60*(5), 617-628.

Moore, S. E., Francine, J. K., Bowles, A. E., & Ford, J. K. (1988). Analysis of calls of killer whales, Orcinus orca, from Iceland and Norway. *Rit Fiskideildar*, *11*, 225-250.

Mossbridge, J. A., & Thomas, J. A. (1999). An "acoustic niche" for antarctic killer whale and leopard seal sounds 1. *Marine Mammal Science*, *15*(4), 1351-1357.

National Marine Fisheries Service. (2005). Endangered and Threatened Wildlife and Plants; Endangered Status for Southern Resident Killer Whales. Federal Register 70, 222, 69903–69912.

Noren, D. P., Johnson, A. H., Rehder, D., & Larson, A. (2009). Close approaches by vessels elicit surface active behaviors by Southern Resident killer whales. *Endangered Species Research*, *8*(3), 179-192.

Pilkington, J. F., Stredulinsky, E. H., Gavrilchuk, K., Thornton, S. J., Ford, J. K., & Doniol-Valcroze, T. (2023). Patterns of winter occurrence of three sympatric killer whale populations off eastern Vancouver Island, Canada, based on passive acoustic monitoring. *Frontiers in Marine Science*, *10*, 1204908.

DFO. (2019). Population Status Update for the Northern Resident Killer Whale (Orcinus orca) in 2018. DFO Can. Sci. Advis. Sec. Sci. Resp.

Ohlberger, J., Ward, E. J., Schindler, D. E., & Lewis, B. (2018). Demographic changes in Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries*, *19*(3), 533-546.

Olesiuk, P. F., Bigg, M. A., & Ellis, G. M. (1990). Life history and population dynamics of resident killer whales (Orcinus orca) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission, Special*, *12*, 209-243.

Poupard, M., Symonds, H., Spong, P., & Glotin, H. (2021). Intra-group orca call rate modulation estimation using compact four hydrophones array. *Frontiers in Marine Science*, *8*, 681036.

Riera, A., Pilkington, J. F., Ford, J. K., Stredulinsky, E. H., & Chapman, N. R. (2019). Passive acoustic monitoring off Vancouver Island reveals extensive use by at-risk Resident killer whale (Orcinus orca) populations. *Endangered Species Research*, *39*, 221-234.

Ross, P. S., Ellis, G. M., Ikonomou, M. G., Barrett-Lennard, L. G., & Addison, R. F. (2000). High PCB concentrations in free-ranging Pacific killer whales, Orcinus orca: effects of age, sex and dietary preference. *Marine Pollution Bulletin*, *40*(6), 504-515.

Scheifele, P. M., Andrew, S., Cooper, R. A., Darre, M., Musiek, F. E., & Max, L. (2005). Indication of a Lombard vocal response in the St. Lawrence River beluga. *The Journal of the Acoustical Society of America*, *117*(3), 1486-1492.

Stewart, J. D., Cogan, J., Durban, J. W., Fearnbach, H., Ellifrit, D. K., Malleson, M., ... & Balcomb, K. C. (2023). Traditional summer habitat use by Southern Resident killer whales in the Salish Sea is linked to Fraser River Chinook salmon returns. *Marine Mammal Science*, *39*(3), 858-875.

Tennessen, J. B., Holt, M. M., Wright, B. M., Hanson, M. B., Emmons, C. K., Giles, D. A., ... & Deecke, V. B. (2024). Males miss and females forgo: Auditory masking from vessel noise impairs foraging efficiency and success in killer whales. *Global Change Biology*, *30*(9), e17490.

Thornton, S. J., Toews, S., Stredulinsky, E. H., Gavrilchuk, K., Burnham, R., Noren, D. P., ... & Vagle, S. (2022). *Southern Resident killer whale (Orcinus orca) summer distribution and habitat use in the southern Salish Sea and the Swiftsure Bank area (2009 to 2020)*. Canadian Science Advisory Secretariat (CSAS).

Tyack, P. L., & Janik, V. M. (2013). Effects of noise on acoustic signal production in marine mammals. In *Animal communication and noise* (pp. 251-271). Berlin, Heidelberg: Springer Berlin Heidelberg.

Vagle, S., Burnham, R., Thupaki, P., Konrad, C., Toews, S., & Thornton, S. J. (2021). *Vessel presence and acoustic environment within Southern Resident killer whale (Orcinus orca) critical habitat in the Salish Sea and Swiftsure Bank area*. Canadian Science Advisory Secretariat (CSAS).

Veirs, S., Veirs, V., & Wood, J. D. (2016). *Ship noise extends to frequencies used for echolocation by endangered killer whales. PeerJ 4, e1657*.

Wasser, S. K., Lundin, J. I., Ayres, K., Seely, E., Giles, D., Balcomb, K., ... & Booth, R. (2017). Population growth is limited by nutritional impacts on pregnancy success in endangered Southern Resident killer whales (Orcinus orca). *PLoS One*, *12*(6), e0179824.

Wearing, S., Buchmann, A., & Jobberns, C. (2011). Free Willy: the whale-watching legacy. *Worldwide Hospitality and Tourism Themes*, *3*(2), 127-140.

Wieland, M., Jones, A., & Renn, S. P. (2010). Changing durations of Southern Resident killer whale (Orcinus orca) discrete calls between two periods spanning 28 years. *Marine Mammal Science*, *26*(1), 195.

Williams, R., & Ashe, E. (2006). Northern resident killer whale responses to vessels varied with number of boats. *NMFS Contract AB133F04SE0736.(Available from R. Williams, Pearse Island, Box 193, Alert Bay, BC V0N1A0, or E. Ashe, 2103 N. 54th St., Seattle, WA 98103.)*.

Williams, R., Ashe, E., & Lusseau, D. (2010). Killer whale activity budgets under no-boat, kayak-only and power-boat conditions. *Contract via Herrera Consulting, Seattle, Washington*.

Williams, R., Erbe, C., Ashe, E., Beerman, A., & Smith, J. (2014). Severity of killer whale behavioral responses to ship noise: A dose–response study. *Marine pollution bulletin*, *79*(1-2), 254-260.

Williams, R., Lusseau, D., & Hammond, P. S. (2006). Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). *Biological conservation*, *133*(3), 301-311.

Williams, R., Trites, A. W., & Bain, D. E. (2002). Behavioural responses of killer whales (Orcinus orca) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, *256*(2), 255-270.

Yehle, K. E. (2022). *Fecal hormone metabolites as indicators of stress in the southern and northern resident killer whale (Orcinus orca) populations in coastal waters of British Columbia, Canada* (Doctoral dissertation, University of British Columbia).

Chapter 2 – Manuscript

Call type modification in Southern Resident killer whales (*Orcinus orca*) in response to variable ambient noise levels

Keywords
Southern Resident killer whale, anthropogenic noise, call types, modification, masking

Abstract

Increased vessel traffic and human activity have raised underwater noise levels in marine environments, significantly impacting species that rely on sound, such as the endangered Southern Resident killer whale population (*Orcinus orca*). Southern Residents rely on sound for foraging, navigation, group cohesion, and cultural transmission, but increasing noise levels can interfere with these behaviours by masking communication signals and prompting changes in call use. This study modelled acoustic data from two Southern Gulf Islands in British Columbia, Canada to examine how Southern Residents, and specifically J pod, modify their vocal behaviour under varying noise conditions. I investigated which discrete pulsed call types were being used by J pod and modelled the rates at which these calls were used in response to increases in sound pressure levels. Call proportions aligned with historical usage except for a marked dominance of the S04 call type on Saturna Island, a finding that contradicts previous studies identifying S01 as the most common J pod call type. Model estimates showed S04 usage decreased by 10.7% per every 1 dB increase in ambient noise. Overall, model estimates show that J pod members significantly reduce total discrete pulsed calling rate by 2.4% for every 1 dB increase in ambient noise and by 21% for every 10 dB increase in ambient noise. The S02i, S04, S05, S06, S07, S12, S42, S44 call types were all used significantly more in quieter conditions. Call types S01, S02ii and S41 showed no significant change in usage. This study provides further evidence that increases in ambient noise significantly affects Southern Resident killer whale vocal behaviour, leading to reduced call rates and possible shifts in call type use. These findings highlight the importance of preserving quiet marine environments and improving our understanding of Southern Resident acoustic behaviour to inform effective conservation and management strategies.

1.0 Introduction

In recent years, increases in vessel traffic and other anthropogenic activities have caused a progressive increase in background noise levels in marine ecosystems (Chapman & Price, 2011; Cominelli et al., 2018; Erbe et al., 2019; McDonald et al., 2008). Sources of marine noise caused by human activity include seismic surveys, navy sonar exercises, pile driving and commercial and recreational vessel traffic (Hildebrand, 2009; McDonald et al., 2008; Vagle et al., 2021). Commercial shipping is the most prevalent and consistent source of noise in most marine environments (Cominelli et al., 2018; Hildebrand, 2009), but the contribution from small vessels, and small scale commercial and recreational activity may also be considerable (Erbe, 2002; Joy et al., 2019; Vagle et al., 2021).

The effects of noise on marine mammals are wide and varied (Erbe, 2009; Tyack and Janik, 2013). Anthropogenic noise has been linked to changes in marine mammal behaviour such as rates of respiration and activities such as foraging, travelling and socializing (Tennessen et al., 2024; Williams et al., 2021; Lusseau, 2004; Blair et al., 2016; Pirotta et al., 2012). In some cases, significant noise exposure has altered movement patterns, with certain species being displaced or avoiding specific habitats altogether (Jones et al., 1994; Lusseau, 2005; Morton & Symonds, 2002;)

One of the most impactful effects that noise pollution has on marine mammals is auditory masking. Masking occurs when an acoustic signal becomes difficult to recognize, or detect, because of the presence of another sound (Erbe, 2016). Although masking naturally occurs in marine systems, where wind-driven sea states largely determine ambient noise levels, growing vessel traffic in busy urban areas and commercial shipping lanes now dominate the marine environment (Erbe, 2016; Tyack and Janik, 2013). In response to masking, cetaceans have been observed to actively modify the amplitude of their vocalizations, a phenomenon known as the Lombard Effect. This effect has been described in mysticetes - including humpback (*Megaptera novaeangliae* - Guazzo et al., 2020), minke (*Balaenoptera acutorostrata* - Helble et al., 2020) and right whales (*Eubalaena glacialis* - Parks et al. 2011), and odonotocetes such as beluga whales (*Delphinatperus leucas* - Scheifele et al., 2005) and killer whales (*Orcinus orca* - Holt et al., 2009). The Lombard effect has also been well documented in humans (Brumm & Zollinger, 2011), fish (Luczkovich et al., 2017) and frogs (Halfwerk et al., 2016) to name a few.

Vocal modification involves more than simply increasing volume. Other documented strategies include both short- and long-term shifts in vocal frequency (Lesage et al., 1999; Parks et al., 2007), as well as increases in call duration and bandwidth (Foote et al., 2004; Murphy, 2023; Wieland et al., 2010). Changes in calling rate have also been observed in both natural and anthropogenic contexts. For example, bottlenose dolphins (*Tursiops truncatus*) reduce whistle rates when group size becomes large enough for self-masking to occur (Quick & Janik, 2008), while harp seals (*Pagophilus groenlandicus*) and Blainville's beaked whales (*Mesoplodon densirostris*) have been shown to decrease call rates in response to vessel or sonar noise (Terhune et al., 1979; Tyack et al., 2011). For killer whales, the effects of noise on innate behaviours have become a prominent area of study, and research into its specific effects on acoustic behaviour is growing (Foote et al., 2004; Foote & Nystuen, 2008; Holt et al., 2009, 2011; Miller, 2006).

Southern Resident killer whales (SRKW) are an endangered population of killer whales whose critical habitat overlaps with international commercial shipping lanes in the Salish Sea. These waters serve as key gateways to major urban ports in both southern British Columbia and northern Washington State (Cominelli et al., 2018; Crystal et al., 2011; Veirs et al., 2016). SRKWs are listed as "endangered" under Canada's Species At Risk Act (SARA) and under the United States' Endangered Species Act (ESA), with low prey availability and accessibility, contaminants, and physical and acoustic disturbance all listed as threats to their recovery (Fisheries and Oceans Canada, 2018; Heise, 2008; National Marine Fisheries Service, 2005). Chronic underwater noise poses a significant threat to these fish-eating killer whales by disrupting critical behaviours (Williams et al., 2002, 2009), including coordinated hunting strategies and foraging efficiency (Lusseau et al., 2009; Tennessen et al., 2024), as well as communication within and between family groups (Foote et al., 2008; Holt et al., 2011; Miller, 2002).

Commercial vessels generate the most energy at frequencies below 1 kHz (Cominelli et al., 2018), overlapping only partially with the frequency range of most killer whale pulsed call types (Ford, 1984, 1991). However, recent studies have demonstrated that ship noise can also elevate noise levels up to 40 kHz at distances of up to 3km, overlapping substantially with the frequency bands used by killer whales for communication (0-15 kHz) and echolocation (20-70 kHz) (Veirs et al., 2016). Additional sources of anthropogenic noise in the Salish Sea include daily traffic from ferries, recreational fishers, pleasure craft operators, and smaller commercial venues such as ecotours and whale watching boats (Joy et al., 2019; Veirs et al., 2016). Early studies found that vessel proximity could trigger behavioural changes in killer whales, including increased surface-active behaviours (Noren et al., 2009) as well as reduced foraging efficiency and increased time transiting (Lusseau et al., 2009; Williams et al., 2002, 2006). These findings suggest that noise could be a primary contributor to the responses observed. Erbe (2002) modelled the effects of anthropogenic noise on killer whales showing that loud vessels could mask killer whale calls from 14km away and prolonged exposure could cause a temporary threshold shift in hearing and perhaps even permanent hearing loss. More recently, Tennessen et al. (2023) used data loggers attached to killer whales and found that increased noise was associated with longer search times for prey, and less time spent pursuing and capturing that prey.

While the effects of anthropogenic noise on SRKW foraging ability are well recognized (Williams et al., 2006; Lusseau et al., 2009; Tennessen et al., 2024), its impacts on their acoustic behaviour, which are equally vital to survival, deserve closer attention. Resident killer whales are thought to be related by matrilineal descent from a single ancestral pod, with vocal traditions and call repertoire passed directly from mother to offspring (Deecke et al., 2010; Ford, 1991). Individuals within resident communities remain with their natal matriarchal group throughout their lives (Barrett-Lennard & Ellis, 2001), and these stable matrilineal units provide an important environment for learned vocal traits (Deecke, 1994; Deecke et al., 2000, 2010). Over time, call structure and pattern of usage may evolve independently through cultural drift, which is the result of errors in vocal copying and the transmission of changes across generations (Deecke et al., 2000; Ford, 1991). Resident killer whales produce three different types of vocalizations: echolocation clicks, whistles, and pulsed calls (Ford, 1991). Pulsed calls can be further classified into aberrant, variable, and discrete call types. Discrete pulsed calls have unique structural and acoustic properties that are highly stereotyped and enable the differentiation not only between ecotypes, but also between respective clans, pods, and matrilineal units (Ford, 1989; Miller & Bain, 2000). Variable calls are sounds that cannot be clearly defined into structural categories and include squeaks, trills, or squawks, and aberrant calls are variations of discrete calls that are highly distorted or excited to be distinctly characterized. Classification of killer whale pulsed call types has advanced scientific understanding of killer whale social structure and geographic distribution (Ford, 1991; Samarra et al., 2015) and has been relied on in the identification and reintegration of lost whales to their families (Jourdain et al., 2021).

The vocal frequencies of killer whales likely evolved in response to their prey's auditory range and to the natural ambient noise of their respective environments (Foote & Nystuen, 2008). Killer whales have been observed to be able to shift these frequencies in response to the vocalizations of other species (Mossbridge & Thomas, 1999) and to increases in ambient noise (Murphy, 2023). Additional evidence of active vocal modification is described by Holt et al. (2009, 2011), who observed SRKWs increasing the amplitude of their calls in response to rising noise levels. Murphy (2023) explored these concepts further, finding evidence that some call types had longer durations under noisy conditions, supporting prior research (Foote et al., 2004; Wieland et al., 2010). In addition, some call types increased in both bandwidth and peak frequency during loud conditions (Murphy 2023).

The structural features of some call types may reflect adaptive responses shaped by evolutionary pressures to facilitate communication in noisy environments. Miller et al. (2002) investigated biphonic pulsed call types which contain both a low (LFC) and high frequency component (HFC) and demonstrated that the HFC are directional and vary with the orientation of the signaler. Miller suggests that these directional HFC may act as a cue for group orientation and direction of movement, and their presence in higher energy bands may mean they are less susceptible to masking by noise. These studies suggest that anthropogenic noise interferes with the transmission and reception of socially and ecologically important vocalizations in resident killer whales, leading to disruptions in communication, group coordination, and social cohesion.

This study examined how SRKW vocal behaviour changes in response to varying noise conditions, using hydrophone recordings collected from passive acoustic monitoring stations on Pender and Saturna Island in the Southern Gulf Islands. Specifically, the objectives were to: (1) identify Southern Resident call types as groups moved through the listening range of recorders, (2) model the relative frequency of different call types under quiet to increasingly loud conditions and (3) assess how total call rates respond to increasing noise levels. This study specifically focussed on J pod due to a higher rate of acoustic encounters compared to K or L pod. I hypothesized that call rates would decrease as ambient noise levels increased, potentially because the energetic cost of calling more frequently may not be outweighed by gains in signal effectiveness. Additionally, I predicted that calls with distinct structural features, such as high-frequency components, would be used often in loud environments, as these features may enhance signal transmission or detectability. This study contributes to a growing understanding of how noise impacts vocal behavior in a sound-dependent species and serves as a reminder that limited human understanding of complex vocal communication in endangered killer whales does not diminish the cultural and communicative significance of these vocalizations.

2.0 Materials & Methods

2.1 Study Location

All recordings were collected from pre-installed hydrophone monitoring stations on Pender Island and Saturna Island (Figure 1). The Pender Island hydrophone is located on the western side of Wallace Point and listens towards Haro Strait and Swanson Channel, the shadow of Wallace Point likely hides much of the acoustic signal that would come from Boundary Pass. Recordings from Saturna Island came from two different installations, Monarch Head and East Point. Both hydrophones have an unimpeded listening view of Boundary Pass. The use of two listening stations on Saturna Island was used to align with Pender Island functional dates and any outages of the East Point hydrophone. Specifically, the Monarch Head recordings were only used between July and October of 2023 when the East Point hydrophone was non-operational. Monarch Head and East Point have a very similar listening area and were not used simultaneously at any point to avoid duplicating encounter data.

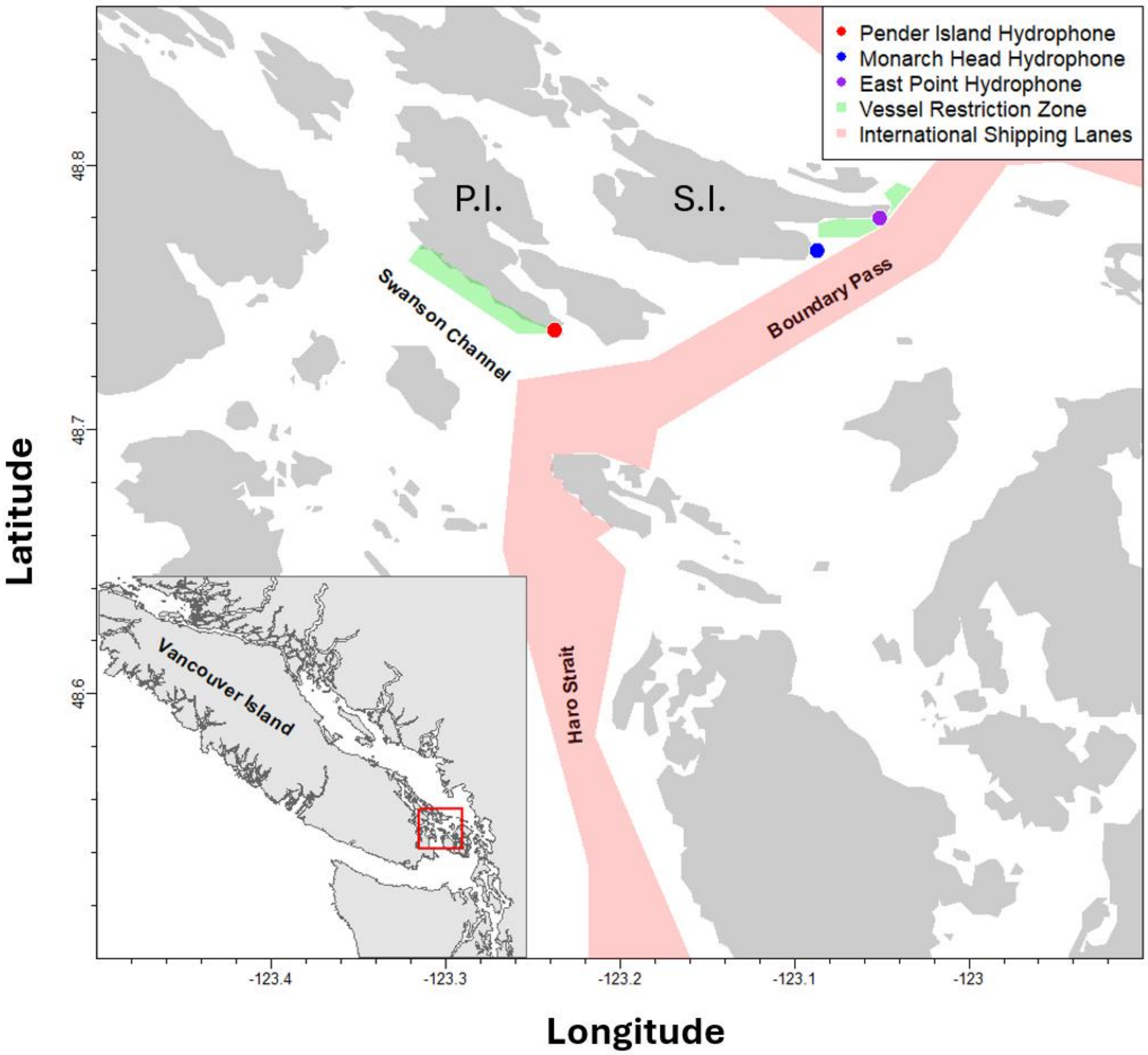

Figure 1. Locations of the three hydrophones used for this study on Pender Island (P.I.) and Saturna Island (S.I) and their relative proximity Boundary Pass and Haro Strait. Commercial international shipping lanes are marked in red, and Vessel Restriction Zones are marked in green.

2.2 Ambient Noise Recordings

All hydrophones recorded continuously and all recordings from the months of June 2023 to December 2024 were analyzed for killer whale vocal activity. An HTI -99-HF (High Tech, Inc.) with a flat frequency response from 2-125 kHz (±3 dB), and an end-to-end sensitivity of -204 dB re 1 V/µPa, 16-bit resolution and a sampling rate of 250 kHz was deployed on Pender Island in the Spring of 2023. Saturna Island used icListen HF (Ocean Sonics) hydrophones for both

Monarch Head and East point. All icListen's had a frequency response of 10-200 kHz, 24-bit resolution and a sampling rate of 128 kHz. Monarch Head had an end-to-end sensitivity of -177.1 dB re 1 V/µPa, and East Point had two different sensitivity values of -176.6 dB re 1 V/µPa and -177.2 dB re 1 V/µPa due to hydrophones being swapped for routine maintenance and a faulty initial installation. Ambient noise levels represent the noise received at each hydrophone listening station. When operational, all hydrophones recorded continuously and all recordings from June 2023 to December 2024 were analyzed for killer whale vocal activity.

2.3 Acoustic Encounters

All recordings were processed using PAMGuard's Whistle & Moan Detector (PAMGuard V2.02.16) with custom settings to maximize killer whale detections. Automatic detections were manually verified to confirm killer whale presence and ecotype (e.g. Southern Resident or Bigg's). For confirmed SRKW encounters, pulsed calls were extracted and sorted by date for each study site and all pods were identified within each encounter. An acoustic encounter was defined as the time of the first identifiable discrete pulsed call type until the last identifiable discrete pulsed call type. A time threshold was considered to define acoustic encounters, however, without concurrent visual information there was no way to verify if whales had left the acoustic range of the recorders or if they were just being silent. Any encounters that did not include J pod were excluded from the study.

Acoustic files were visually analyzed using Raven Pro 1.6 (Cornell Lab of Ornithology) with standardized pre-set spectrogram settings for both Pender Island and Saturna Island. All SRKW pulsed calls were annotated to the level of call type by manually drawing a selection box around each call within the encounter. Other vocalizations such as whistles, buzzes or echolocation clicks were not annotated due to time constraints. Any pulsed call that was audible but not identifiable, either due to low signal to noise ratios, excessive overlapping of calls, or because of the aberrant nature of a call, was labelled as "PC" for "pulsed call" and excluded from the dataset. To maximize inclusion of calls, calls that were difficult to identify were reviewed by an expert in SRKW communication prior to being removed, ensuring removals were limited to as few calls as possible. The number of each discrete call type was then summed into 60-second time windows to assess call rates with paired ambient noise levels for the entirety of each encounter.

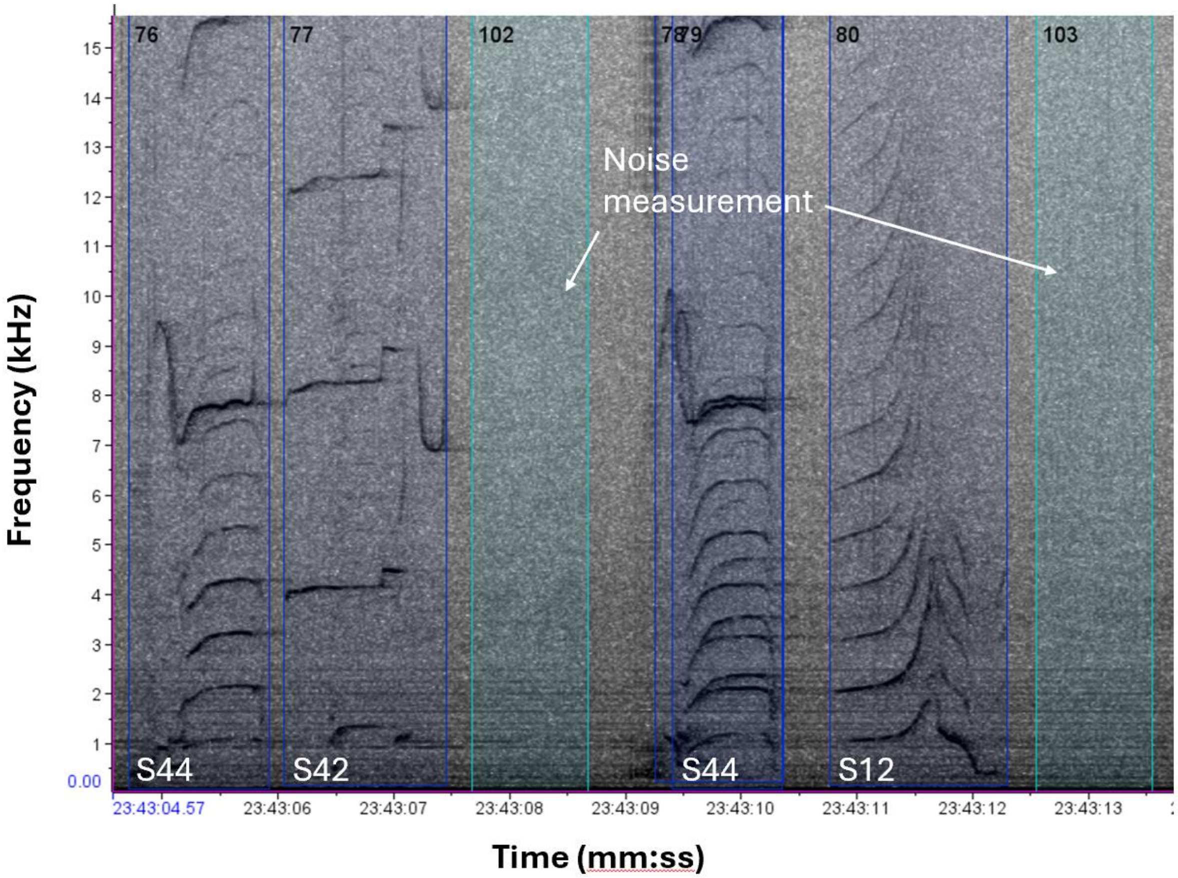

Figure 2. An example of annotated J pod discrete call types (dark blue) and annotated 1-second long selection boxes (light blue) for sound pressure level (SPL) noise measurements that are void of killer whale vocal activity. This is a magnitude spectrogram showing sound frequency (y-axis) and SPL amplitude (darker greyscale indicating higher SPL) over time (x-axis).

2.4 Ambient Noise Analysis

Ambient noise levels (ANL) were measured from 1-second long selection boxes that were manually drawn approximately once every 10 seconds in instances without killer whale vocal activity for the entire duration of an acoustic encounter (Figure 2). In this study, ANLs were measured as broadband sound pressure level (SPL) (dB re 1 μPa), ranging from 0-15 kHz: the frequency range where vessel noise and SRKW communication has the most overlap (Ford, 1991; Veirs et al., 2016). Code provided by Dr. Ben Hendricks (Sound Space Analytics) was used to calculate SPL for each study location using respective calibration information for each hydrophone. Each 1-second selection was averaged to create an ambient noise level for each 60-second window of an encounter. In cases when killer whale vocal activity was too continuous to allow a measurement every 10 seconds, SPL for that 60-second window was averaged with what gaps in activity were available. Calls that occurred within each 60-second time window were then associated within their respective SPL measurements, which served as the ANL for that sampling period.

2.5 60 Hz Self-Noise Removal

The Pender Island hydrophone was installed with the intent to be able to live-stream both video and audio to the public. When the livestream became operational, sometime after July 5th, 2023, a 60 Hz band of electrical energy interference deriving from the streaming equipment became both audible and visible on the spectrogram within the subsequent recordings (Figure 3.).

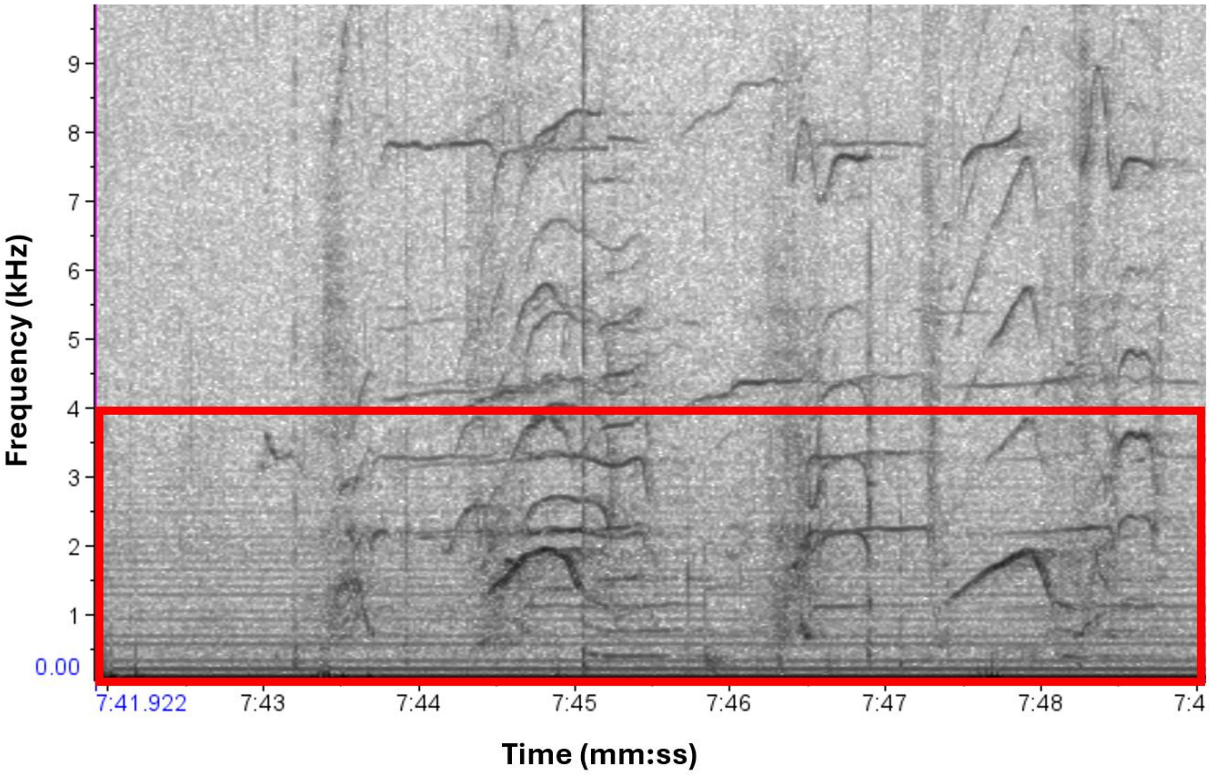

Figure 3. Example spectrogram from Pender Island containing both 60 Hz self-noise and J pod Southern Resident killer whales from a one-minute sample. Affected frequencies lay within the 0-4 kHz bands.

The 60 Hz band produced additional bands of energy bands at odd-integer multiples of the fundamental frequency, i.e. at 180 Hz, 300 Hz, 420 Hz, and so on, although system self-noise was not limited to these frequencies alone. Most self-noise occurred within the 0 Hz – 4 kHz range (Figure 4). System self noise meant that ANL were artificially inflated, particularly within the 0-1 kHz bands. Since SPL was calculated across the 0-15 kHz range, this self-noise introduced errors of up to 7 dB, with the greatest impact occurring below 1 kHz, SPL measurements at frequencies above 1 kHz were less affected.

To still make use of these data and accurately assess ambient SPL, a filter was created with the help of Dr. Farid Jedari-Eyvazi (Dalhousie University). This filter 1) identified spectral peaks of energy resulting from system noise, and 2) suppressed the tonal noise at each identified band and replaced them with the average SPL surrounding them (Figure 4). Background SPL measurements were then taken for the entirety of the file as previously described for all other recordings not plagued by system self-noise.

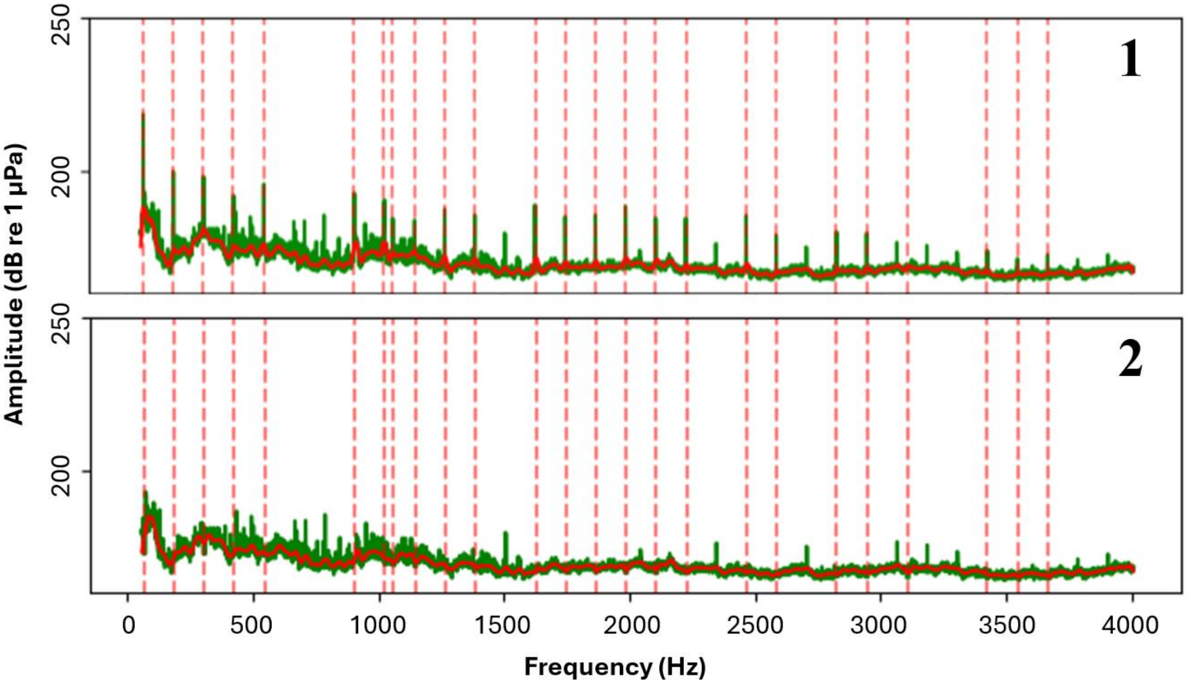

Figure 4. Average spectrum over time for 8 samples of Pender Island acoustic recordings subject to 60 Hz self-inflicted noise. Vertical dashed lines show system noise channels, the green curve indicates the average spectrum over time, and the red curve indicates the filtered signal using a 5000 Hz Butterworth low-pass filter. 1) Average spectrum pre-noise filter. 2) Average spectrum post-noise filter. Image provided by Dr. Farid Jedari-Eyvazi, Dalhousie University, Nova Scotia.

To ensure the filter was working as intended, mean and median broadband (0-15 kHz) SPL were measured across six encounters, three of which were recorded before the 60 Hz noise band from the livestream started, and three after. These broadband mean and median SPL measurements were then compared with and without the application of the noise-removal filter (Figure 5). The provided graphic (Figure 5) demonstrates that the filter had little effect on files without the hum and effectively reduced self-noise for files with the hum. The encounters used prior to the 60 Hz hum were quieter than the encounters post 60 Hz hum, therefore it should not be interpreted that files that were obtained after the 60 Hz hum occurred were inherently louder. All reported post band-filter SPL values should closely reflect accurate ambient noise levels at the location of the hydrophone. All files from East Point and Monarch Head did not have this issue so no filter was applied.

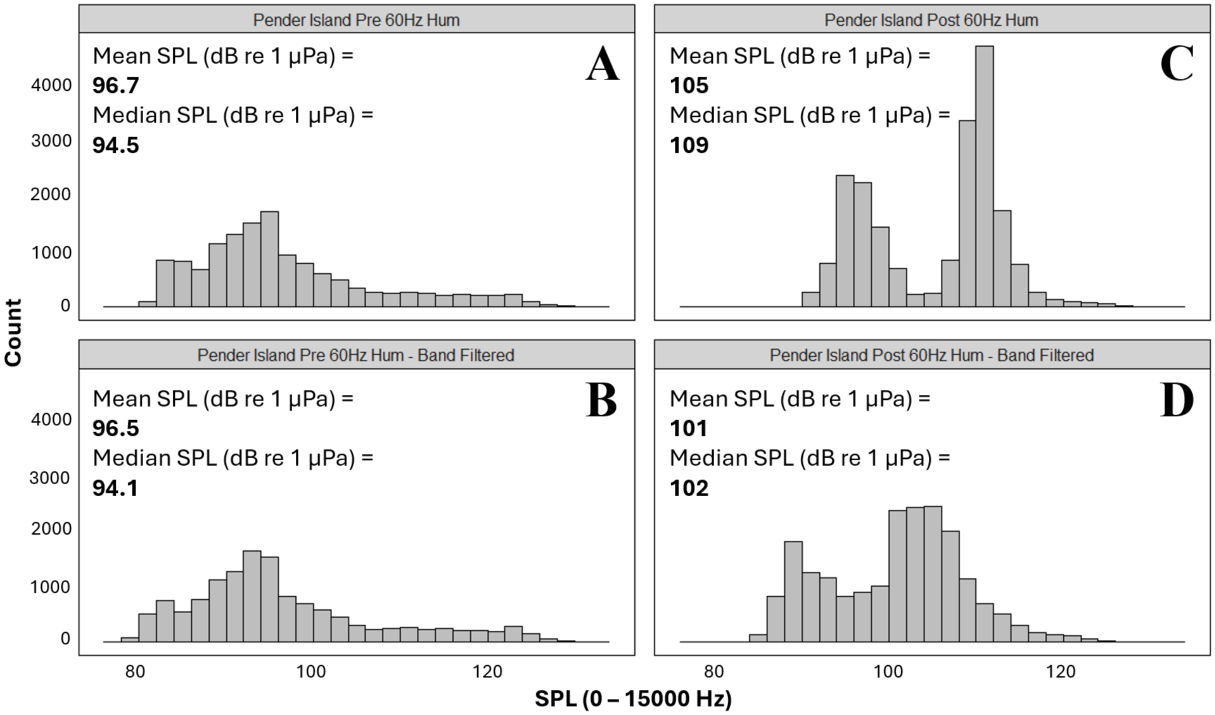

Figure 5. Broadband SPL measurements for the Pender Island hydrophone before (A) and after (C) livestream implementation as well as broadband SPL measurements after application of noise-removal filter (C, D). A notable shift can be seen in SPL measurements when comparing plot D with plot C. Count (y-axis) represents the number of seconds measured at each SPL. Count distributions each represent a total of three encounters.

2.6 Statistical Analysis

2.6.1 Total Call Rates

A generalized linear mixed model (GLMM) with a negative binomial error distribution was used to analyse the relationship between J-pod's total pulsed-call call rate (counts of call types combined per 1-minute file) and mean SPL. The model accounted for spatial variation through hydrophone location as a fixed effect, temporal autocorrelation using an AR(1) covariance structure based on the number of calls in consecutive time bins, and encounter variability through a random intercept for each encounter.

Long periods of silence were often a part of acoustic encounters resulting in many 60-second windows without calls present, producing excess zeros in the count data. To address this excess absence of call activity, we adapted the negative binomial GLMM with a zero-inflation (intercept-only) term. This approach addressed three biological reasons for J-pod not calling: 1) natural periods of no calling such as resting behaviours, 2) noise conditions were too loud therefore masking communication effort, or 3) individuals moving out of the range of the hydrophone for periods of the encounter. This was chosen to explicitly model the zero-generating process distinct from the negative binomial count process and avoid overfitting, and because of a lack of visual evidence to support the inclusion of specific predictors in the zero-inflation process.

2.6.2 Call rates per call type

To understand how noise affects specific call types differently, the Total Call Rates model looking at generic vocal effort was expanded by incorporating call type into the model as a fixed effect, with interaction terms between call type and SPL to test for differential noise sensitivity. Call rates per call type were modelled using a GLMM, and a zero-inflated negative binomial error distribution; spatial variation, AR(1) covariance structure, and random effect model choices mirrored the previous model for comparability.

2.6.3 Statistics

Candidate models were fitted using the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2024) via RStudio (version 2023.12.1+402; Posit team 2025). The optimal model was identified by selecting that with the lowest Akaike's Information Criterion (AIC) (see Table A1 in the Appendix). Model assumptions—including overdispersion, zero-inflation, and residual patterns—were assessed using the DHARMa package (Figure A3) (Hartig, 2016). All plots were generated using the ggplot2 (Wickham, 2016) and sjPlot (Ludecke et al., 2015) packages. Acoustic plots, measurements, and noise reduction procedures were performed in Python 3.12.7 using Spyder 5.5.1.

3.0 Results

3.1 Acoustic Summary

After applying the 60 Hz self-noise filter to all affected encounters from Pender Island, the mean broadband (0-15 kHz) SPL for all encounters was 98.8 dB re 1 µPa, approximately 7 dB re 1 µPa higher than the mean SPL at Saturna Island, which was 91.5 dB re 1 µPa (Table 1). The loudest encounter on Pender Island had a mean SPL of 117.2 dB re 1 µPa reaching a maximum of 124.45 dB re 1 µPa and the quietest encounter had a mean SPL of 89.7 dB re 1 µPa (Figure 6) reaching a minimum of 86.96 dB re 1 µPa. At Saturna Island, the loudest encounter had a mean SPL of 103.3 dB re 1 µPa reaching a maximum of 106.22 dB re 1 µPa and the quietest encounter had a mean SPL of 80.1 dB re 1 µPa (Figure 7) reaching a minimum of 78.58 dB re 1 µPa.

Soundscape power spectral density plots for each SRKW encounter were created to better display where the most energy occurred for all acoustic encounters of both Pender Island and Saturna Island acoustic encounters (Figure 6 and 7).

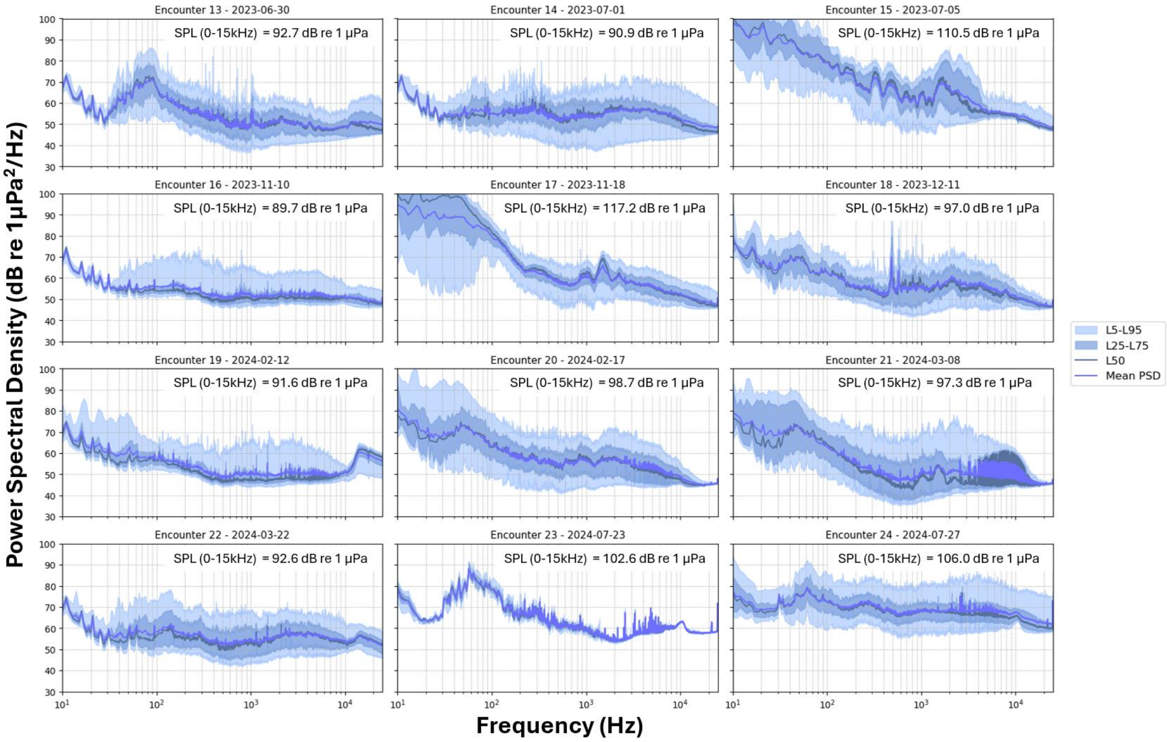

Figure 6. Power spectral densities (PSD) reported as dB re 1 µPa²/Hz for encounters 13-24 on Pender Island. Broadband mean SPL values for each encounter are displayed in the top right of each plot. PSD plot frequencies are binned logarithmically at 1/1000 hybrid-millidecade intervals. The median (L50), interquartile range (L25–L75), and 5th–95th percentile range (L5–L95) of PSD are shown as progressively lighter shades of blue, with the mean PSD overlaid as a solid line.

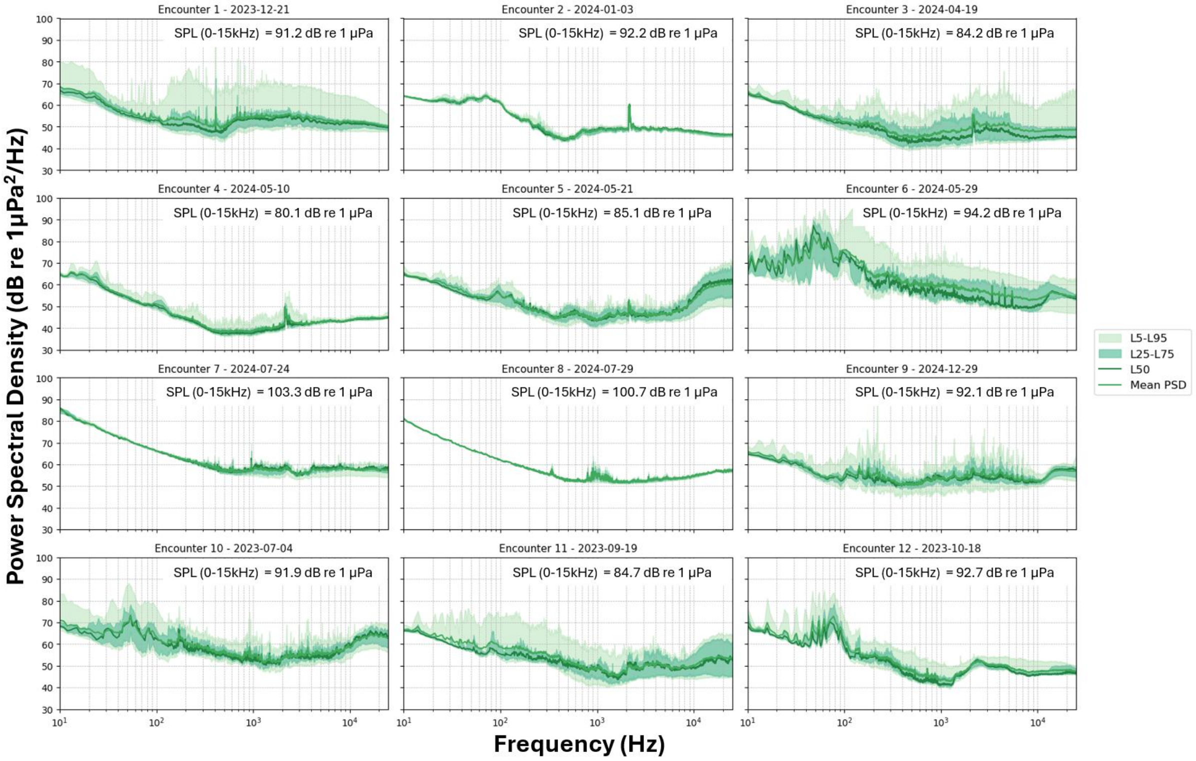

Figure 7. Power spectral densities (PSD) reported as dB re 1 µPa²/Hz for encounters 1-12 on Saturna Island. Broadband mean SPL values for each encounter are displayed in the top right of each plot. PSD plot frequencies are binned logarithmically at 1/1000 hybrid-millidecade intervals. The median (L50), interquartile range (L25–L75), and 5th–95th percentile range (L5–L95) of PSD are shown as progressively lighter shades of green, with the mean PSD overlaid as a solid line. Encounters 1-9 are taken from the East Point hydrophone and encounters 10-12 are taken from the Monarch Head hydrophone.

Table 1. Cumulative acoustic encounter summaries for Pender and Saturna Island including duration, call counts and sound pressure level measurements.

Location	Mean Duration (minutes)	Mean # of Calls	Max # of Calls	Min # of Calls	Mean SPL (dB re 1 µPa)	Max SPL (dB re 1 µPa)	Min SPL (dB re 1 µPa)
Pender	107	267	858	13	98.8	124.5	89.7
Saturna	67	236	767	23	91.5	103.3	78.6

3.2 Call Summary

Across the Saturna and Pender Island hydrophones, a total of 41 unique SRKW acoustic encounters were detected, 20 from Saturna Island and 21 from Pender Island. Of these, 35 encounters included J pod calls, and 5 encounters had acoustic evidence of J, K, and L pods, representing the full SRKW acoustic repertoire. Twenty-four of the 35 encounters that included J pod were selected for analysis.

A total of 6049 calls were annotated to call type, with 3214 recorded from Pender and 2835 from Saturna Island. The number of calls per encounter ranged from a maximum of 858 to a minimum of 13 (Table 1). The most common call type recorded was the S04 (n=1837) making up approximately 30% of the call share, while the S06 (n = 44) was the least common call making up less than 1% of all calls.

Call proportions appeared to be different between Pender and Saturna Island. At Pender Island, S01 was the most common call, comprising approximately 32% (n = 1024) of all calls recorded across 21 encounters. At Saturna Island, however, the S04 call was the most common, accounting for 45% (n = 1318) of calls of the 20 encounters. Saturna Island had 4 encounters that consisted of only S04 calls, (n = 23, 44, 41, 230 calls respectively) while only one such encounter was observed at Pender Island (n = 13 calls). Mean encounter duration was 107 minutes for Pender Island and 67 minutes for Saturna Island.

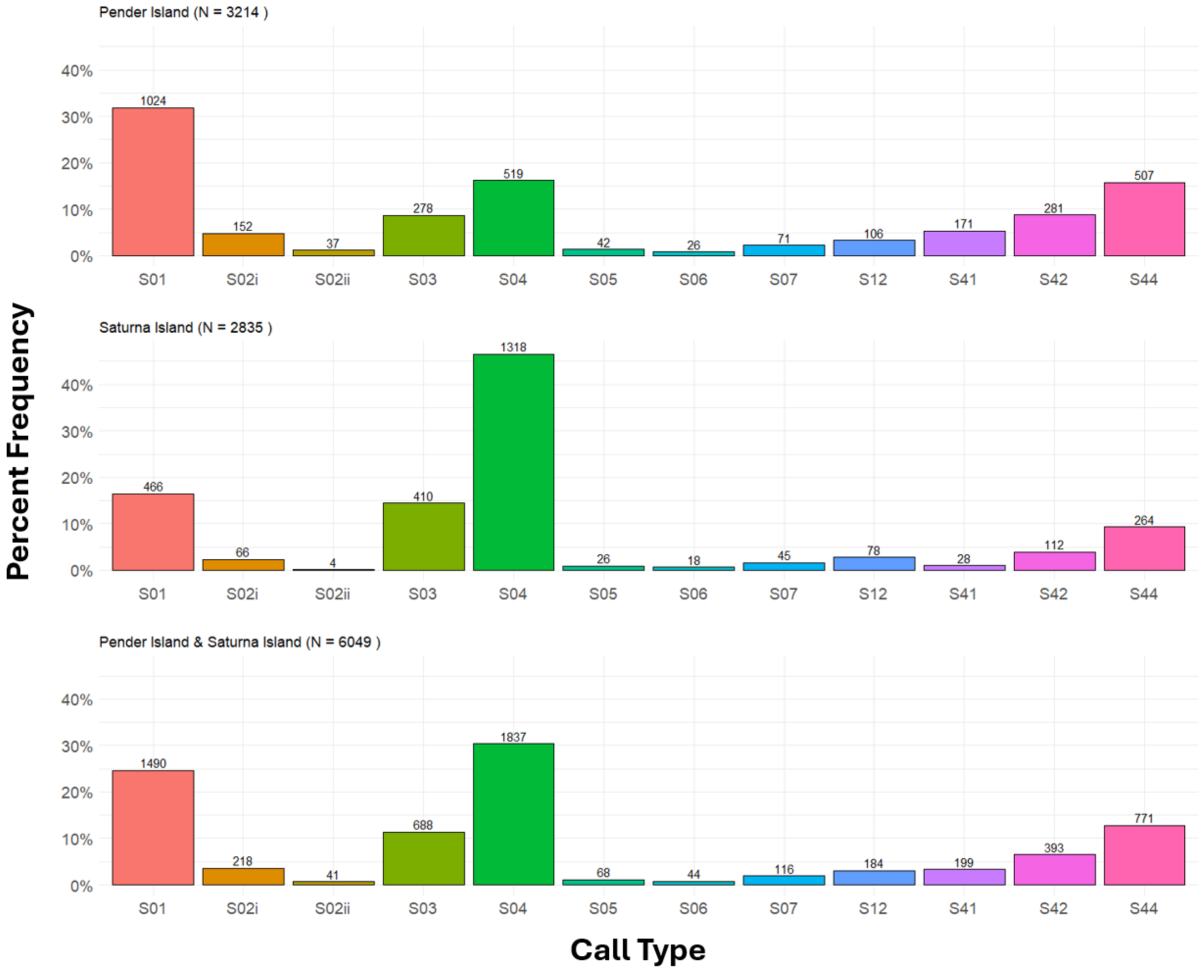

Figure 8. Percent frequency distributions of call types produced by J pod for Pender Island (top), Saturna Island (middle) and combined locations (bottom).

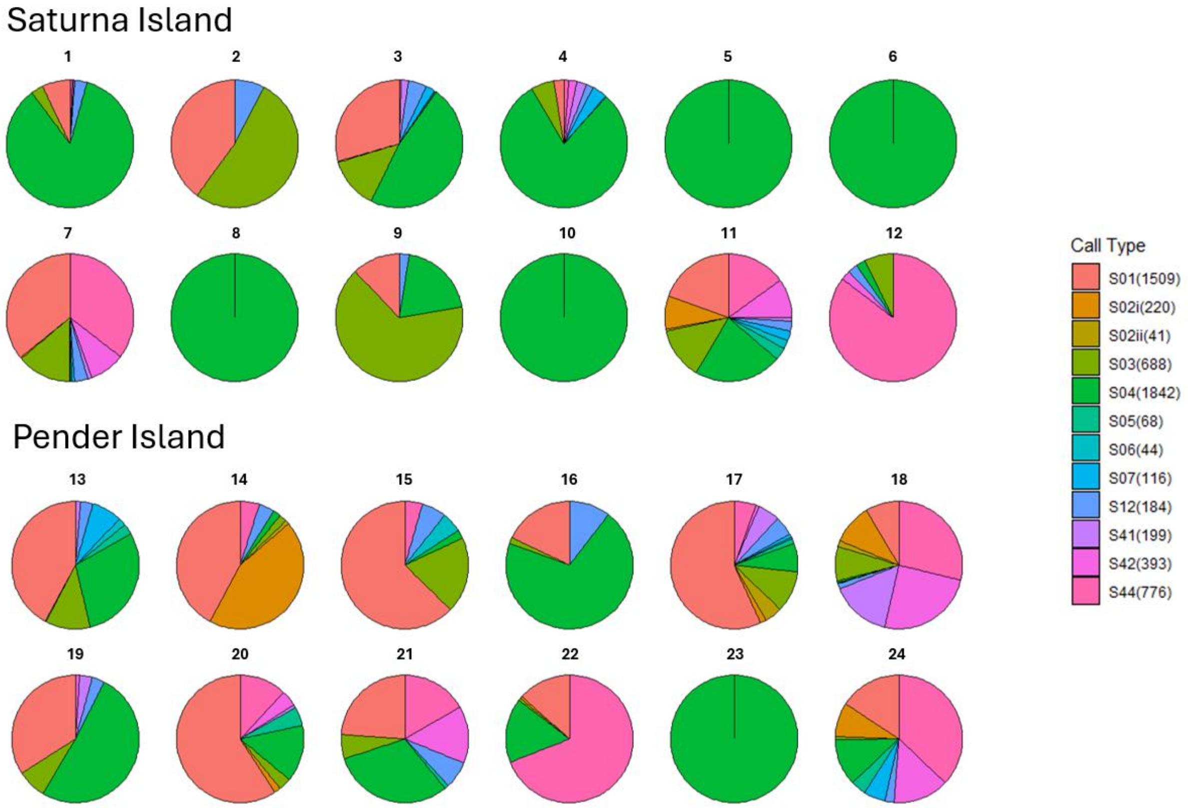

Figure 9. Call type proportions by Island. Pie charts 1-12 represent individual encounters from Saturna Island, and charts 13-24 correspond to encounters from Pender Island.

3.3 Total Call Rates

The average number of all SRKW calls summed across all call types was 3.24 calls per minute. Call rates ranged from 0 CPM (n = 1167) during periods of silence to 60 CPM (n=1) during periods of intense vocal activity (Figure 8). The model suggests that call rates significantly decreased with increasing background noise ($p < 0.01$) (Figure 11), and for every 1 and 10 dB re 1 μPa increase in mean SPL, total call rates declined by 2.4% and 21.0% respectively (Table 2). The highest predicted calls per minute (CPM) was in quiet conditions at just over 4 CPM, and lowest expected CPM was around 1.6 in the loudest conditions (Figure 11).

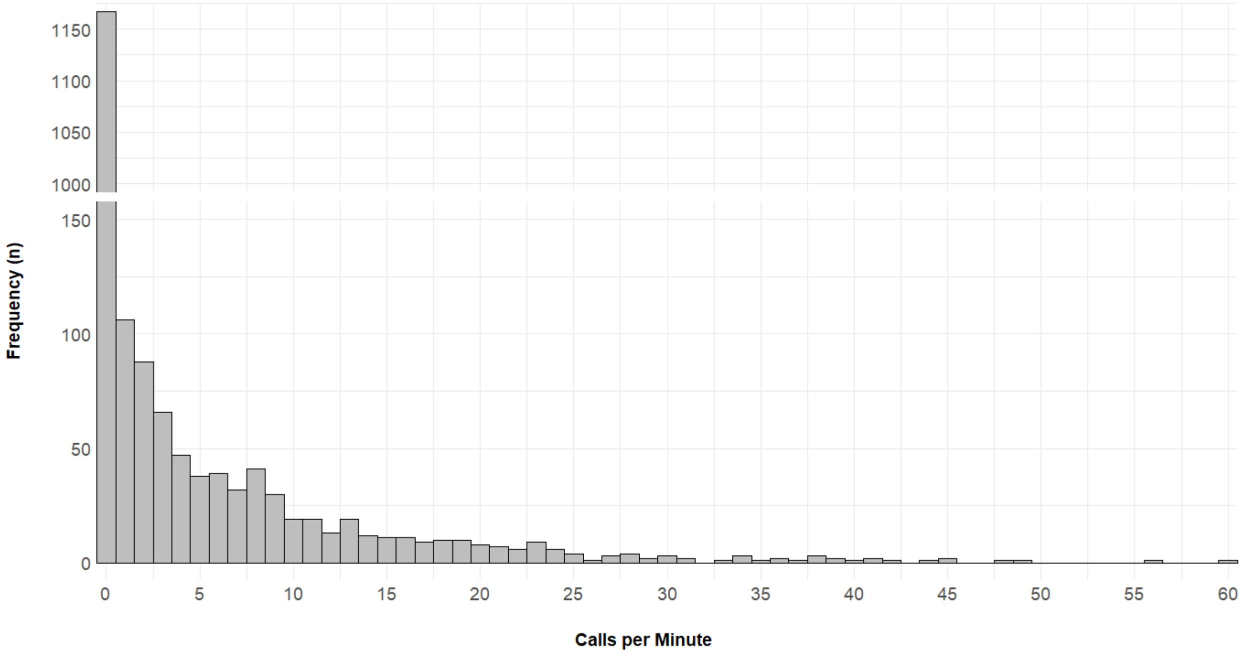

Figure 10. Frequency distribution of calls per minute (CPM) for J pod across all acoustic encounters for Pender Island and Saturna Island. Y-axis breaks at n = 150 and starts again at n = 1000 to avoid compression of all CPM when n =/= 0.

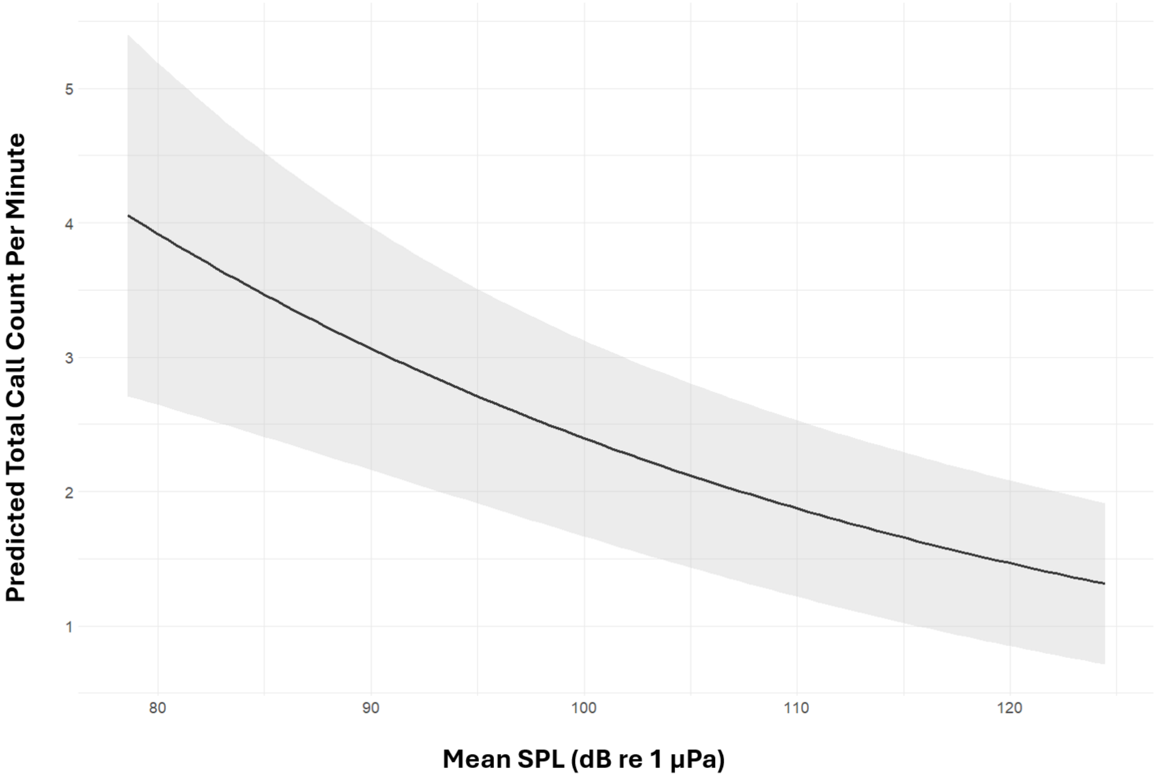

Figure 11. Predicted relationship between total discrete pulsed-call rate and mean sound pressure level (SPL) for J pod. Estimates derived from a generalized linear mixed model (GLMM) with a negative binomial distribution, including fixed effects for SPL, location, temporal autocorrelation, and random effects for encounter. The shaded area represents 95% confidence intervals.

3.4 Call Type Response to SPL

Model predictions suggest that for 8 of 12 call types investigated, the interaction between call type and mean SPL was statistically significant, indicating that increases in SPL were typically associated with reduced call rates (Figure 12). For S04s, the most used call during this study, a higher mean SPL was associated with significantly fewer calls (interaction $\beta = -0.1136$, $p < 0.001$), corresponding to a 10.7% decrease in call rate for every 1 dB re 1 µPa increase in mean SPL (Table 2). Similarly, call types S07, S42 ($p < 0.001$), S02i ($p < 0.01$), S05, S06, and S12 ($p < 0.05$) all showed significant negative associations with increasing SPL (Figure 10). No calls showed a significant positive association. All other call types did not show statistically significant differences between the quietest and loudest conditions, suggesting no clear SPL effect.

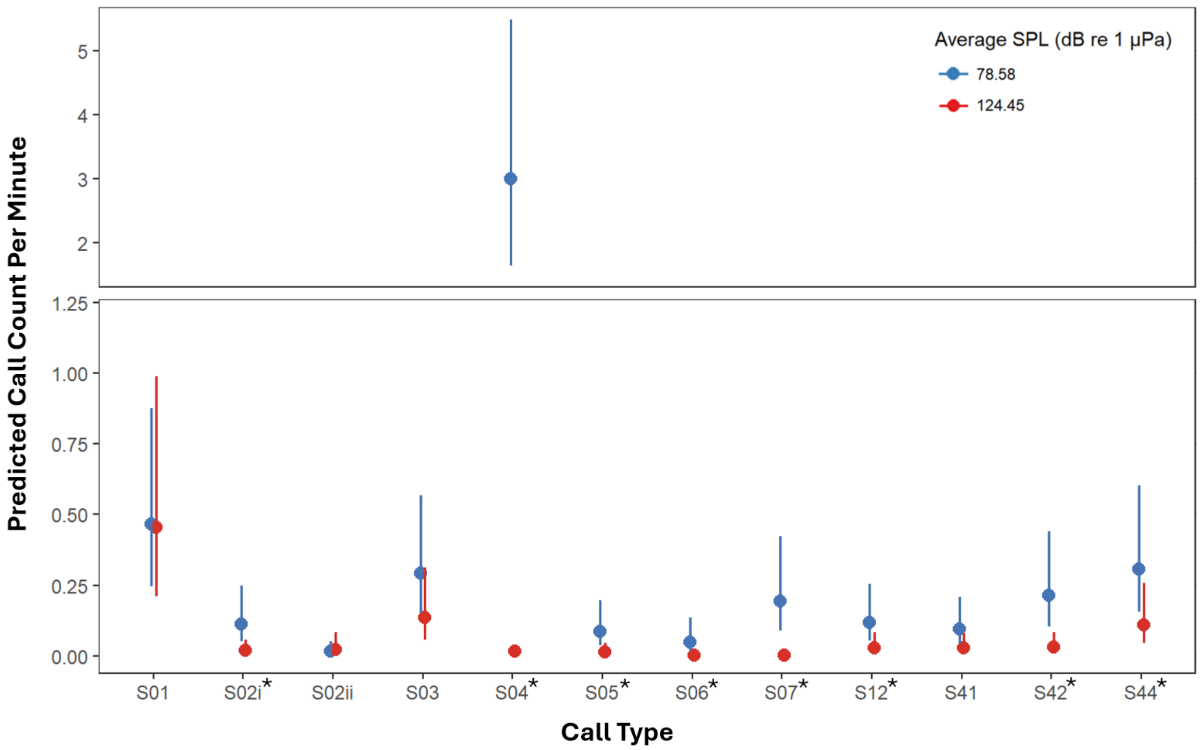

Figure 12. Predicted call rates for J pod call types at low (blue) and high mean (red) sound pressure levels (SPL). Predictions are from a generalized linear mixed model (GLMM) with a negative binomial distribution, modeling call count per minute as a function of call type, mean SPL, their interaction, and location (Pender vs. Saturna Island). The y-axis has been split and scaled to better visualize call counts below 1 CPM. Error bars represent 95% confidence intervals. Eight of 12 call types (with an asterix (*) next to their names) had significantly lower call counts under high SPL.

Table 2. Effect of sound pressure level (SPL) on total call rates and for significant call type interactions. Model 1 results are indicated in bold and model 2 results are indicated by each individual call type.

Call Type	Total SPL Effect (β)	Change per 1 dB SPL	Change per 5 dB SPL	Change per 10 dB SPL
All Calls	**- 0.0246**	**- 2.4%**	**- 11.5%**	**- 21.0%**
S02i	–0.0388	- 3.8%	- 17.7	- 32.7%
S04	-0.1136	- 10.7%	- 42.8%	- 67.8%
S05	-0.400	- 3.9%	- 18.0%	- 33.0%
S06	-0.0565	- 5.5%	- 24.7%	- 44.0%
S07	-0.0840	- 8.1%	- 33.7%	- 55.9%
S12	-0.0302	- 3.0%	- 14.0%	- 23.6%
S42	-0.0424	- 4.2%	- 19.3%	- 35.1%
S44	-0.0224	- 2.2%	- 10.6%	- 20.0%

4.0 Discussion

SRKW call usage followed similar proportions as those reported by Ford (1991), based on recordings from 1979-1983. Ford observed that calls S01, S04 and S07 were most commonly used during foraging, while S02(i,ii), S44, S42 and S01 were most common during travelling. The most common calls observed within this study were the S01, S03, S04, S42, and S44. Considering Ford's findings, these calls could imply that foraging and travelling were the most likely behaviours occurring during the recorded encounters. However, other studies have found limited evidence linking specific call types to distinct behaviours (Foote et al., 2008; Ford, 1984; Miller, 2002; Weiss et al., 2006; Weiß et al., 2007). Since behavioural information was not available, this study cannot add to the former body of work, but it is reasonable to assume that similar behavioural states were occurring as foraging and travelling typically dominate SRKW activity budgets (Heimlich-Boran, 1988; Noren & Hauser, 2016; Williams et al., 2010). Overall, these findings are consistent with historical trends in J pod call type proportions documented since studies began in the late 1980s.

Historically, the S01 has been the most common call produced by J pod, followed by the S04 (Foote et al., 2008; Ford, 1984, 1991). In this study, however, we observed the S04 dominating the call share because of a high influence of S04s recorded from Saturna Island, marking a stark contrast in previous documentation on SRKW call usage. In contrast, call proportions at Pender Island more closely reflected patterns reported in previous research. Six out of 12 acoustic encounters from Saturna had S04s making up more than ~80% of the calls observed, 4 of which were 100%. Murphy (2023) was the first to describe this reversal and described S04 call type usage more than doubling that of the S01 in the same study area. I observed S04 usage to be nearly triple that of the S01. Murphy's research included all call types from J, K and L pods, and suggested the dominance of the S04 could be attributed to a greater J pod presence during her study period (Murphy, 2023), however, this does not account for the deviation from historical trends within J pod alone.

The model indicated that S04 call usage decreased by 10.4% for every 1 dB increase in SPL, and under the loudest conditions S04 usage dropped to nearly zero. Saturna Island was, on average, 7 dB quieter than Pender Island. Although both locations are exposed to commercial shipping lanes in Boundary and Haro pass, as well as daily small vessel traffic, Pender Island is also exposed to hourly ferry traffic to the west which could explain the notable increase in noise levels (Cominelli et al., 2018; Joy et al., 2019; Vagle et al., 2021). The quieter conditions on Saturna Island could have an influence on the expression of certain behaviours. When S04's were detected at the Saturna hydrophones, they often occurred in large, dominant batches where they were the only call produced over long periods of time. Anecdotally, in acoustic encounters where S04s were not the only call present, this call dominance often occurred either before or after periods of increased acoustic activity or apparent excitable states.

In some of the earliest work done on resident call types, similar observations were documented for the N03 call type in A-clan northern residents. Low-arousal states, such as resting, or intermediate states between socializations and foraging were often associated with a dominance in N03 production (Ford, 1989, 1991). This association could suggest the importance of certain call types to indicate lower physical and acoustic activity levels, or perhaps as a transitionary call between behaviour states. Ford described the N03 not only as indicative of low-arousal states, but also as occurring during other socially important behaviours that often include excitable states such as beach-rubbing (Ford, 1989, 1991), a behaviour that has since been shown to be disrupted by increases in vessel traffic and ambient noise levels (Bouvier, 2020; Clarke et al., 2024; Williams et al., 2006). In a more recent study on NRKW call rates, researchers observed the N03 being emitted in dominant batches following elevated energy states after the passing of a cruise ship where surfing and increases in call rates were both observed (Poupard et al., 2021). This could suggest a shift in behavioural state from high-arousal to low-arousal and could lend evidence to the previously suggested usage of the N03 marking such transitions in behaviour.

The S04 shares spectrogram-based visual and acoustic similarities with the N03, and its situational dominance may suggest parallels in call usage and associated behavioral contexts. Interestingly, Ford (1991) found no evidence of calls being associated with resting activity in J-clan. Due to the lack of concurrent behavioural observations, this study cannot definitively associate S04s with resting behaviours or the bookending or transitioning of arousal states. Resting behaviour itself, however, is a well documented example of how marine mammals modify their activities in response to elevated noise and may provide a useful parallel for understanding how behavioural and acoustic adjustments are interconnected. (Constantine et al., 2004; Lusseau, 2004; Mikkelsen et al., 2019; Williams et al., 2010). In bottlenose dolphins in New Zealand, resting behaviour significantly declined with increasing vessel counts and the likelihood of dolphins engaging in this behaviour decreased the longer vessels remained nearby (Constantine et al., 2004; Lusseau, 2004). Similarly, in other marine mammals such as seals, resting behaviour was disrupted by anthropogenic noise on both land and sea (Mikkelsen et al., 2019). Mikkelsen et al. (2019) observed resting dives being aborted after vessels passing nearby and seals that were hauled out on land retreated into the water when exposed to ship noise.

Disruptions to resting behaviour extend to land based species as well. North American prairie dogs were found to decrease bouts of resting by half when exposed to road traffic noise (Shannon et al., 2014) and male great tits were observed sleeping longer than females in noisier environments possibly due to typical auditory cues being masked by excessive noise, or perhaps to make up for poor quality of sleep (Grunst et al., 2023). Although my research cannot assign a specific behavioural state to S04 production, the observed trends underscore the importance of quieter environments for acoustic behaviours that are poorly understood or undocumented.

Both Pender and Saturna Island have “vessel restricted zones”, formerly “interim sanctuary zones (ISZ)”, to help reduce acoustic and physical disturbance from vessels within historically important SRKW foraging areas. Although well intentioned, these zones still have high levels of infringement and only voluntary slowdowns and voluntary lateral displacements away from shore have been implemented in the nearby commercial shipping lanes of Haro or Boundary Pass (Burnham et al., 2021; Joy et al., 2019; Vagle et al., 2021). Slowdown trials in SRKW critical habitat have shown that reduced vessel speeds could significantly reduce underwater noise despite longer passage times (Burnham et al., 2021; Joy et al., 2019; Vagle et al., 2021). Reductions of 1.2 dB were measured in median broadband noise (10-100,000 Hz) and model predictions suggested that SRKWs could experience up to 40% less disruptions during foraging if 100% of vessels slowed to a maximum of 11-knots, adhering to Haro Strait vessel slowdown recommended speed (Joy et al., 2019). Although an increase in foraging efficiency does not necessarily equate to more resting or socializing, it is reasonable to assume that activity budgets could be re-balanced if the quality of foraging time is improved, allowing for other behaviours to occur. The significant reduction in S04 production suggests that loud environments may be restricting certain behavioural states and that the preservation of quiet conditions may encourage relevant vocal activity. Ensuring consistent enforcement and implementation of these vessel restriction zones should be a high priority to improve the quality of SRKW critical habitat.

Model results suggest that at the highest observed noise levels, the S01 call re-emerged as the most dominant, despite an overall decrease in their cumulative rates. This result is highlighted by the significant decrease in the S04 call rates described previously. S01 call characteristics have been shown to be significantly affected by increasing noise. Holt et al., (2009, 2011) found that for every 1 dB increase in background noise, the S01 call source level increased by 1 dB. Although Holt et al. did not find adjustments to call duration, other studies have reported significant increases in the presence of vessel noise compared to absence of vessel noise (Foote et al., 2004; Wieland et al., 2010). Furthermore, there is evidence that both bandwidth and peak frequency of S01s increase significantly under high-noise conditions (Murphy, 2023). Given the S01s long-standing prominence in the J pod call repertoire, it is unsurprising that it may be the most obvious call for J pod to fallback to under noisy conditions. These findings underscore the need for further investigation into how noise affects the usage, structure, and function of this historically important call type.

I hypothesized that calls with HFCs would be used more frequently as ambient noise increased; however, for all calls containing HFCs that were tested, usage decreased. The calls with a biphonic HFC included S02(i,ii), S41, S42 and S44. S02i, S42 and S44 were used significantly less as SPL increased, and S02iii and S41 showed no significant change. Miller (2006) described calls with HFCs as “long-range” due to increased directionality, higher source levels, and greater active space relative to other “short-range” calls (Miller, 2002, 2006; Holt et al., 2011). In seawater, acoustic energy is more easily lost from sounds with higher frequencies than those of lower frequencies (Urick 1983). For Cetaceans, long range communication is often associated with low frequency vocalizations which can be detected over thousands of kilometers (Stafford et al., 1998; Watkins et al., 1987). However, “long-range” is a relative term—and its definition can be flexible based on the needs of species-specific communication.

In urban birds, for instance, Slabbekoorn and Peet (2003) observed that great tits (*Parus major*) shift to higher frequency calls in noisy environments, and in a further study, Slabbekoorn and den Boer-Visser (2006) suggest that the need for long-range, low-frequency signals is reduced when individuals live and interact in closer proximity. This principle also applies to killer whales. The use of these calls is thought to aid group coordination and be important when noise conditions limit acoustic proximity. (Miller & Bain, 2000). Although these calls may not propagate as far as other cetacean signals, they appear to be functionally sufficient at the range in which killer whales need to communicate effectively.

Miller (2006) found that for northern residents, available active space for long-range sounds was less affected by naturally occurring noise from increasing sea-state conditions, implying a natural partitioning of acoustic repertoire and usage. Similarly, Foote and Nystuen (2008) found that the offshore ecotype of killer whale in the Northeastern Pacific, an area associated with loud sea-states, produced calls with significantly higher minimum frequencies than that of either the resident or transient (Bigg’s) ecotypes. They suggest these differences could be the result of genotypic selection or ontogenetic time scales to deal with masking in noisy, wind-prone offshore environments. With the former research in mind, it is interesting that the findings of this study do not reveal a significant shift toward call types containing structural features that would be advantageous in mitigating the effects of noise. However, the consistent nature in call usage of the S02i and the S41, regardless of noise levels, could point towards the flexibility of such calls.

For example: a study on St. Lawrence estuary belugas found that high-frequency burst pulse (HFBP) calls remained constant before, during and after noise events whereas rates of contact calls and other call types were higher before noise events. The consistent nature of HFBP regardless of noise could suggest resilience to masking and an adaptive strategy to maintain communication in noisy environments (Vergara et al., 2025). By comparison, the S02i, S42 and S44 in the present study were used less as noise increased, however, the S02ii and S41 showed consistent use. Although a consistent result across all HFC call types would be preferred, there is a potential interpretation that the unaltered usage of S02ii and S41 may suggest they are less susceptible to louder conditions. With that said, HFBP in belugas spanned much higher frequencies (36.4±6.5 to 144 kHz) than the typical fundamental frequencies of SRKW discrete call types (0.1 – 6 kHz, harmonics up to 30 kHz - Ford, 1984, 1991; Veirs et al., 2016) which may provide belugas with greater resilience to noise. This makes a direct comparison difficult.

Acoustic masking provides a likely explanation for the significant reduction in the total call rates observed in this study. Masking is a primary means of disturbance from both natural and anthropogenic noise pollution by interfering with an animal's ability to send and receive acoustic signals (Dominoni et al., 2020; Erbe et al., 2016; Veirs et al., 2016). Veirs et al., (2016) showed that vessel noise in critical SRKW habitat regularly exceeds median background noise and overlaps with the typical frequency range of SRKW vocalizations. These frequencies are well within the range of their hearing sensitivity (18-42 kHz) (Branstetter et al., 2017; Szymanski et al., 1999). In locations such as the Southern Gulf Islands, acoustic masking may be more prominent as SRKWs travel paths can be within 2km of the center of commercial shipping lanes making sound absorption very minimal at such close quarters (Veirs et al., 2016).

Active vocal modification to overcome masking has been widely documented in marine mammals through louder vocalizations (Helble et al., 2020; Holt et al., 2009; Scheifele et al., 2005) and through shifts of vocal frequencies as seen in right whales (*Eubalaena glaciali*) (Parks et al., 2007), belugas (*Delphinapterus leucas*) (Lesage et al., 1999) and multiple dolphin species (*Delphinus delphis* - Ansmann et al., 2007; *Tursiops truncatus* - Fouda et al., 2018). While our study is not the first to document vocal modification in resident killer whales in response to noise, most research has investigated into changes in call parameters such amplitude, peak frequency and call duration, rather than call rates (Foote et al., 2004; Holt et al., 2009, 2011; Murphy, 2023). In my study, Southern Residents appeared to significantly reduce their total rate of vocal output under noisier ambient conditions. Thus, killer whales appear to not only alter the acoustic properties of their calls in response to masking conditions, but also adjust the overall amount of calling they choose to engage in.

Evidence of acoustic masking can also be observed in beluga whales, where contact calls and other variable call types were significantly reduced during exposure to vessel noise (Vergara et al., 2025). In contrast, a study on Northern Resident killer whales, found that call rates increased during and after a singular noisy event, possibly to ensure specific information was effectively communicated between and within co-travelling pods (Poupard et al., 2021). Evidence of a call rate modification in response to noise also extends to land species. Three acoustically active species of frogs *Microhyla butleri, Rana nigrovittata* and *Kaloula pulchra* all decreased their calling rates when exposed to airplanes flying nearby or playbacks of low-frequency motorcycle sounds (Sun & Narins, 2005). Another species of frog, *Rana taiphensis*, increased its calling rate under the same conditions. Sun et al., (2005) suggests that temporal and spectral separation are a possible means for ensuring acoustic communication. As mentioned previously, a spectral separation in response to noise has been well documented in killer whales, however, a temporal adjustment may also be at play, particularly in the observed decrease in call rates in conditions that are conducive to acoustic masking.

Since discrete pulsed call types in resident killer whales are likely involved in inter and intra-group behaviours such as initial contact and group orientation (Ford, 1991; Miller, 2002; Weiß et al., 2007), travelling and foraging (Ford, 1991; Miller & Bain, 2000; Weiss et al., 2006), and socialization and mate attraction (Yurk et al., 2002), a reduction in the ability to properly receive and interpret acoustic information across environmental space likely has costly impacts.
It’s possible that Southern Resident killer whales refrain from vocalizing when noise exceeds a certain threshold, potentially waiting for more favorable acoustic conditions. This strategy may help minimize the risk of acoustic masking and reduce the energetic costs associated with high rates of calling or louder vocalizations.

Although my results demonstrate significant modification to call rate behaviours, it is important to address some of the limitations of the study. Human influence and potential sources of error must always be considered when manipulating data. One of the most prominent limitations in this study may be artificially elevated SPL values caused by self-noise from the Pender Island hydrophone installation. While an effective method to mitigate the 60 Hz interference was implemented, it would have been preferable to identify and address the issue at the source prior to the study. Although the post-filter SPL values may lack absolute accuracy, the 60 Hz filter is a monotone transform, and the inclusion of a random intercept for each encounter in the GLMM should minimize any effect of this limitation on the interpretation of results. Although I am confident in the overall reliability of my measurements, it remains possible that some frequency bands affected by self-noise remained undetected.

When annotating the data, a degree of subjectivity is inherent in call type identification, particularly for calls that are similar, overlapping, or recorded under low SNR conditions. For example, the S01 and S03 call types can sound and appear quite similar, making them prone to misidentification—especially during long annotation sessions. Although all annotations were performed by a single, experienced technician to ensure consistency, the potential for human error remains and may have influenced model outputs.

From a study design perspective, the inclusion of concurrent visual observations and behavioural data for each acoustic encounter would have greatly enhanced the interpretation of call usage patterns. Uncertainty surrounding the whales' behaviours or their proximity to the hydrophones during recording likely introduced additional variability into the dataset and may have contributed to the observed zero-inflation in the models. Future research could benefit from incorporating additional contextual data, such as concurrent vessel counts and baseline ambient noise levels in the absence of vessel traffic, to more precisely isolate the influence of anthropogenic noise. Analyses of call type parameters—such as duration, peak frequency, and bandwidth—would also enhance our understanding of why certain calls may be more advantageous under varying acoustic conditions.

Finally, the observed dominance of the S04 call type warrants further investigation. Future studies should aim to clarify its situational relevance and assess whether similar patterns of S04 prevalence occur in potentially unidentified critical habitats. Given the strong vocal traditions exhibited by resident killer whales, a consistent deviation from historically dominant call types, such as the S01, may reflect emerging behavioural or ecological shifts, or perhaps represent a previously undocumented pattern in ecologically important locations.

This study provides further evidence that increases in ambient noise significantly influences the acoustic behaviour of Southern Resident killer whales, particularly through reductions in call rates and potential shifts in call type dominance. The overall decline in vocal output under elevated noise levels may point toward temporal adjustments or behavioral suppression in response to disturbance—both of which could carry ecological and energetic costs. Most importantly, this work underscores the value of maintaining and protecting quieter marine environments to preserve the integrity of acoustic space. As anthropogenic noise continues to rise, an understanding of Southern Resident acoustic behaviour will help to better inform conservation and management plans for their critical habitat.

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References

Ansmann, I. C., Goold, J. C., Evans, P. G. H., Simmonds, M., & Keith, S. G. (2007). Variation in the whistle characteristics of short-beaked common dolphins, *Delphinus delphis*, at two locations around the British Isles. *Journal of the Marine Biological Association of the United Kingdom*, *87*(1), 19–26.

Barrett-Lennard, L. G., & Ellis, G. (2001). *Population structure and genetic variability in northeastern Pacific killer whales: towards an assessment of population viability*.

Blair, H. B., Merchant, N. D., Friedlaender, A. S., Wiley, D. N., & Parks, S. E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. *Biology letters*, *12*(8), 20160005.

Bouvier, M. (2020). *Playgrounds by a highway: Understanding the effects of increased ambient noise levels on Northern Resident killer whales (Orcinus orca) during beach rubbing Project Submitted in Partial Fulfilment of the Requirements for the Degree of Master of Science in the Ecological Restoration Program Faculty of Environment (SFU) and School of Construction and the Environment (BCIT)*.

Branstetter, B. K., St Leger, J., Acton, D., Stewart, J., Houser, D., Finneran, J. J., & Jenkins, K. (2017). Killer whale (Orcinus orca) behavioral audiograms. *The Journal of the Acoustical Society of America*, *141*(4), 2387–2398.

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., ... & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling.

Brumm, H., & Zollinger, S. A. (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour*, *148*(11–13), 1173–1198.

Burnham, R. E., Vagle, S., O'Neill, C., & Trounce, K. (2021). The efficacy of management measures to reduce vessel noise in critical habitat of Southern Resident killer whales in the Salish Sea. *Frontiers in Marine Science*, *8*, 664691.

Chapman, N. R., & Price, A. (2011). Low frequency deep ocean ambient noise trend in the Northeast Pacific Ocean. *The Journal of the Acoustical Society of America*, *129*(5), EL161–EL165.

Clarke, C. M. K., Stredulinsky, E., Toews, S., Rani, V., Bouvier-Brown, M., Smyth, D., Joy, R., & Thornton, S. J. (2024). Assessing the efficacy of ecological reserves: killer whale beach rubbing behaviour and vessel disturbance. *Endangered Species Research*, *53*, 555–567.

Cominelli, S., Devillers, R., Yurk, H., MacGillivray, A., McWhinnie, L., & Canessa, R. (2018a). Noise exposure from commercial shipping for the Southern Resident killer whale population. *Marine Pollution Bulletin*, *136*, 177–200. https://doi.org/10.1016/j.marpolbul.2018.08.050

Cominelli, S., Devillers, R., Yurk, H., MacGillivray, A., McWhinnie, L., & Canessa, R. (2018b). Noise exposure from commercial shipping for the Southern Resident killer whale population. *Marine Pollution Bulletin*, *136*, 177–200.

Constantine, R., Brunton, D. H., & Dennis, T. (2004). Dolphin-watching tour boats change bottlenose dolphin (Tursiops truncatus) behaviour. *Biological Conservation*, *117*(3), 299–307.

Crystal, D., Moseley, K., Paterson, C., Ryvola, R., & Wang, S. (2011). *Commercial shipping noise impacts on the critical habitat of the Southern Resident killer whale (Orcinus orca)*.

Deecke, V. B. (1994). *Stability and change of killer whale (Orcinus orca) dialects*.

Deecke, V. B., Barrett-Lennard, L. G., Spong, P., & Ford, J. K. B. (2010). The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (Orcinus orca). *Naturwissenschaften*, *97*(5), 513–518. https://doi.org/10.1007/s00114-010-0657-z

Deecke, V. B., Ford, J. K. B., & Spong, P. (2000). Dialect change in resident killer whales: Implications for vocal learning and cultural transmission. *Animal Behaviour*, *60*(5), 629–638. https://doi.org/10.1006/anbe.2000.1454

Dominoni, D. M., Halfwerk, W., Baird, E., Buxton, R. T., Fernández-Juricic, E., Fristrup, K. M., McKenna, M. F., Mennitt, D. J., Perkin, E. K., & Seymoure, B. M. (2020). Why conservation biology can benefit from sensory ecology. *Nature Ecology & Evolution*, *4*(4), 502–511.

Erbe, C. (2002). Underwater noise of whale-watching boats and potential effects on killer whales (Orcinus orca), based on an acoustic impact model. In *MARINE MAMMAL SCIENCE* (Vol. 18, Issue 2).

Erbe, C., Marley, S. A., Schoeman, R. P., Smith, J. N., Trigg, L. E., & Embling, C. B. (2019). The Effects of Ship Noise on Marine Mammals—A Review. In *Frontiers in Marine Science* (Vol. 6). Frontiers Media S.A. https://doi.org/10.3389/fmars.2019.00606

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, *103*(1–2), 15–38.

Fisheries and Oceans Canada. (2018). *Amended Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada Killer Whale Species at Risk Act Recovery Strategy Series* (Species at Risk Act).

Foote, A. D., & Nystuen, J. A. (2008). Variation in call pitch among killer whale ecotypes. *The Journal of the Acoustical Society of America*, *123*(3), 1747–1752. https://doi.org/10.1121/1.2836752

Foote, A. D., Osborne, R. W., & Hoelzel, A. R. (2004). Whale-call response to masking boat noise. *Nature*, *428*(6986), 910.

Foote, A. D., Osborne, R. W., & Rus Hoelzel, A. (2008). Temporal and contextual patterns of killer whale (Orcinus orca) call type production. *Ethology*, *114*(6), 599–606.

Ford, J. K. B. (1984). *Call traditions and dialects of killer whales (Orcinus orca) in British Columbia*.

Ford, J. K. B. (1989). Acoustic behaviour of resident killer whales (Orcinus orca) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, *67*(3), 727–745.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (Orcinus orca) in coastal waters of British Columbia. *Canadian Journal of Zoology*, *69*(6), 1454–1483. https://doi.org/10.1139/z91-206

Fouda, L., Wingfield, J. E., Fandel, A. D., Garrod, A., Hodge, K. B., Rice, A. N., & Bailey, H. (2018). Dolphins simplify their vocal calls in response to increased ambient noise. *Biology Letters*, *14*(10), 20180484.

Gillespie, D., & Macaulay, J. (2025). PAMGuard (V2.02.16). Zenodo. https://doi.org/10.5281/zenodo.15056259

Grunst, A. S., Grunst, M. L., Raap, T., Pinxten, R., & Eens, M. (2023). Anthropogenic noise and light pollution additively affect sleep behaviour in free-living birds in sex-and season-dependent fashions. *Environmental Pollution*, *316*, 120426.

Government of Canada. (2018). Southern Resident killer whale: Imminent threat assessment. Assessment prepared under the Species at Risk Act. https://www.canada.ca

Halfwerk, W., Lea, A. M., Guerra, M. A., Page, R. A., & Ryan, M. J. (2016). Vocal responses to noise reveal the presence of the Lombard effect in a frog. *Behavioral Ecology*, *27*(2), 669–676.

Hartig, F. (2016). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. *CRAN: Contributed Packages*.

Heimlich-Boran, J. R. (1988). Behavioral ecology of killer whales (Orcinus orca) in the Pacific Northwest. *Canadian Journal of Zoology*, *66*(3), 565–578.

Heise, K. A. (2008). *Recovery Strategy for the Northern and Southern Resident Killer Whales (Orcinus orca) in Canada*. Fisheries and Oceans Canada.

Helble, T. A., Guazzo, R. A., Martin, C. R., Durbach, I. N., Alongi, G. C., Martin, S. W., Boyle, J. K., & Henderson, E. E. (2020). Lombard effect: Minke whale boing call source levels vary with natural variations in ocean noise. *The Journal of the Acoustical Society of America*, *147*(2), 698–712.

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5–20. https://doi.org/10.3354/meps08353

Holt, M. M., Noren, D. P., & Emmons, C. K. (2011). Effects of noise levels and call types on the source levels of killer whale calls. *The Journal of the Acoustical Society of America*, *130*(5), 3100–3106. https://doi.org/10.1121/1.3641446

Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K., & Veirs, S. (2009). Speaking up: Killer whales (Orcinus orca) increase their call amplitude in response to vessel noise . *The Journal of the Acoustical Society of America*, *125*(1), EL27–EL32. https://doi.org/10.1121/1.3040028

Jones, M. L., Swartz, S. L., & Dahlheim, M. E. (1994). Census of gray whale abundance in San Ignacio Lagoon: a follow-up study in response to low whale counts recorded during an acoustic playback study of noise effects on gray whales. *Rep. No. NTIS PB94195062 to the US Marine Mammal Commission, Washington, DC*.

Jourdain, E., Barrett-Lennard, L. G., Ellis, G. M., Ford, J. K. B., Karoliussen, R., Towers, J. R., & Vongraven, D. (2021). Natural Entrapments of Killer Whales (Orcinus orca): A Review of

Cases and Assessment of Intervention Techniques. *Frontiers in Conservation Science*, *2*. https://doi.org/10.3389/fcosc.2021.707616

Joy, R., Tollit, D., Wood, J., MacGillivray, A., Li, Z., Trounce, K., & Robinson, O. (2019). Potential benefits of vessel slowdowns on endangered Southern Resident killer whales. *Frontiers in Marine Science*, *6*(JUN). https://doi.org/10.3389/fmars.2019.00344

Lacy, R.C., Williams, R., Ashe, E., Balcomb III, K.C., Brent, L.J., Clark, C.W., Croft, D.P., Giles, D.A., MacDuffee, M. and Paquet, P.C., 2017. Evaluating anthropogenic threats to endangered killer whales to inform effective recovery plans. Scientific reports, 7(1), p.14119.

Lehtonen, L. (1983). The changing song patterns of the great tit *Parus major*. Ornis Fennica, 60(1), 16-21.

Lesage, V., Barrette, C., Kingsley, M. C. S., & Sjare, B. (1999). The effect of vessel noise on the vocal behavior of belugas in the St. Lawrence River estuary, Canada. *Marine Mammal Science*, *15*(1), 65–84.

Luczkovich, J. J., Krahforst, C. S., Kelly, K. E., & Sprague, M. W. (2017). *The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments*. 010035. https://doi.org/10.1121/2.0000340

Ludecke, D., Bartel, A., Schwemmer, C., Powell, C., Djalovski, A., & Titz, J. (2015). Data visualization for statistics in social science. *Comprehensive R Archive Network (CRAN)*.

Lusseau, D. (2004). The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecology and Society*, *9*(1).

Lusseau, D. (2005). Residency pattern of bottlenose dolphins Tursiops spp. in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series*, *295*, 265-272.

Lusseau, D., Bain, D. E., Williams, R., & Smith, J. C. (2009). Vessel traffic disrupts the foraging behavior of Southern Resident killer whales Orcinus orca. *Endangered Species Research*, *6*(3), 211–221. https://doi.org/10.3354/esr00154

McDonald, M. A., Hildebrand, J. A., Wiggins, S. M., & Ross, D. (2008). A 50Year comparison of ambient ocean noise near San Clemente Island: A bathymetrically complex coastal region off Southern California. *The Journal of the Acoustical Society of America*, *124*(4), 1985–1992.

Mikkelsen, L., Johnson, M., Wisniewska, D. M., van Neer, A., Siebert, U., Madsen, P. T., & Teilmann, J. (2019). Long-term sound and movement recording tags to study natural behavior and reaction to ship noise of seals. *Ecology and Evolution*, *9*(5), 2588–2601.

Miller, P. J. O. (2002). Mixed-directionality of killer whale stereotyped calls: A direction of movement cue? *Behavioral Ecology and Sociobiology*, *52*(3), 262–270. https://doi.org/10.1007/s00265-002-0508-9

Miller, P. J. O. (2006). Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, *192*(5), 449–459. https://doi.org/10.1007/s00359-005-0085-2

Miller, P. J. O., & Bain, D. E. (2000). Within-pod variation in the sound production of a pod of killer whales, Orcinus orca. *Animal Behaviour*, *60*(5), 617–628. https://doi.org/10.1006/anbe.2000.1503

Morton, A. B., & Symonds, H. K. (2002). Displacement of Orcinus orca (L.) by high amplitude sound in British Columbia, Canada. *ICES Journal of Marine Science*, *59*(1), 71–80.

Mossbridge, J. A., & Thomas, J. A. (1999). An “acoustic niche” for Antarctic killer whale and leopard seal sounds. In *Marine Mammal Science* (Vol. 15, Issue 4, pp. 1351–1357). Society for Marine Mammology. https://doi.org/10.1111/j.1748-7692.1999.tb00897.x

Murphy, O. B. (2023). *Analysing marine vessel noise impacts on endangered Southern Resident killer whale acoustic behaviour during transits of Boundary Pass in the Salish Sea*.

National Marine Fisheries Service. (2005). Endangered and Threatened Wildlife and Plants; Endangered Status for Southern Resident Killer Whales. *Federal Register 70*, *222*, 69903–69912.

Noren, D. P., & Hauser, D. D. W. (2016). Surface-based observations can be used to assess behavior and fine-scale habitat use by an endangered killer whale (Orcinus orca) population. *Aquatic Mammals*, *42*(2).

Noren, D. P., Johnson, A. H., Rehder, D., & Larson, A. (2009). Close approaches by vessels elicit surface active behaviors by Southern Resident killer whales. *Endangered Species Research*, *8*(3), 179–192. https://doi.org/10.3354/esr00205

Parks, S. E., Clark, C. W., & Tyack, P. L. (2007). Short-and long-term changes in right whale calling behavior: The potential effects of noise on acoustic communication. *The Journal of the Acoustical Society of America*, *122*(6), 3725–3731.

Pirotta, E., Milor, R., Quick, N., Moretti, D., Di Marzio, N., Tyack, P., ... & Hastie, G. (2012). Vessel noise affects beaked whale behavior: results of a dedicated acoustic response study.

Posit Team. (2025). RStudio: Integrated Development Environment for R. Posit Software, PBC. http://www.posit.co/.

Poupard, M., Symonds, H., Spong, P., & Glotin, H. (2021). Intra-group orca call rate modulation estimation using compact four hydrophones array. *Frontiers in Marine Science*, *8*, 681036.

Quick, N. J., & Janik, V. M. (2008). Whistle rates of wild bottlenose dolphins (Tursiops truncatus): influences of group size and behavior. *Journal of Comparative Psychology*, *122*(3), 305.

R Core Team. (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Samarra, F. I. P., Deecke, V. B., Simonis, A. E., & Miller, P. J. O. (2015). Geographic variation in the time-frequency characteristics of high-frequency whistles produced by killer whales (Orcinus orca). *Marine Mammal Science*, *31*(2), 688–706.

Scheifele, P. M., Andrew, S., Cooper, R. A., Darre, M., Musiek, F. E., & Max, L. (2005). Indication of a Lombard vocal response in the St. Lawrence River beluga. *The Journal of the Acoustical Society of America*, *117*(3), 1486–1492.

Shannon, G., Angeloni, L. M., Wittemyer, G., Fristrup, K. M., & Crooks, K. R. (2014). Road traffic noise modifies behaviour of a keystone species. *Animal Behaviour*, *94*, 135–141.

Slabbekoorn, H., & den Boer-Visser, A. (2006). Cities change the songs of birds. *Current biology*, *16*(23), 2326-2331.

Slabbekoorn, H., & Peet, M. (2003). Birds sing at a higher pitch in urban noise. *Nature*, *424*(6946), 267-267.

Stafford, K. M., Fox, C. G., & Clark, D. S. (1998). Long-range acoustic detection and localization of blue whale calls in the northeast Pacific Ocean. The Journal of the Acoustical Society of America, 104(6), 3616-3625.

Sun, J. W. C., & Narins, P. M. (2005). Anthropogenic sounds differentially affect amphibian call rate. *Biological Conservation*, *121*(3), 419–427.

Szymanski, M. D., Bain, D. E., Kiehl, K., Pennington, S., Wong, S., & Henry, K. R. (1999). Killer whale (Orcinus orca) hearing: Auditory brainstem response and behavioral audiograms. *The Journal of the Acoustical Society of America*, *106*(2), 1134–1141.

Tennessen, J. B., Holt, M. M., Wright, B. M., Hanson, M. B., Emmons, C. K., Giles, D. A., Hogan, J. T., Thornton, S. J., & Deecke, V. B. (2024). Males miss and females forgo: Auditory masking from vessel noise impairs foraging efficiency and success in killer whales. *Global Change Biology*, *30*(9). https://doi.org/10.1111/gcb.17490

Terhune, J. M., Stewart, R. E. A., & Ronald, K. (1979). Influence of vessel noises on underwater vocal activity of harp seals. *Canadian Journal of Zoology*, *57*(6), 1337–1338.

Tyack, P. L., & Janik, V. M. (2013). Effects of noise on acoustic signal production in marine mammals. In *Animal communication and noise* (pp. 251–271). Springer.

Tyack, P. L., Zimmer, W. M. X., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., Clark, C. W., D'Amico, A., DiMarzio, N., & Jarvis, S. (2011). Beaked whales respond to simulated and actual navy sonar. *PloS One*, *6*(3), e17009.

Vagle, S., Burnham, R., Thupaki, P., Konrad, C., Toews, S., & Thornton, S. J. (2021). *Vessel presence and acoustic environment within Southern Resident Killer Whale (Orcinus orca) critical habitat in the Salish Sea and Swiftsure Bank area*. Canadian Science Advisory Secretariat (CSAS).

Veirs, S., Veirs, V., & Wood, J. D. (2016). Ship noise extends to frequencies used for echolocation by endangered killer whales. *PeerJ*, *2016*(2). https://doi.org/10.7717/peerj.1657

Vergara, V., Mikus, M. A., Chion, C., Lagrois, D., Marcoux, M., & Michaud, R. (2025). Effects of vessel noise on beluga (Delphinapterus leucas) call type use: ultrasonic communication as an adaptation to noisy environments? *Biology Open*, *14*(3). https://doi.org/10.1242/bio.061783

Watkins, W. A., Tyack, P., Moore, K. E., & Bird, J. E. (1987). The 20-Hz signals of finback whales (*B alaenoptera physalus*). The Journal of the Acoustical Society of America, 82(6), 1901-1912.

Weiss, B. M., Ladich, F., Spong, P., & Symonds, H. (2006). Vocal behavior of resident killer whale matrilines with newborn calves: The role of family signatures. *The Journal of the Acoustical Society of America*, *119*(1), 627–635.

Weiß, B. M., Symonds, H., Spong, P., & Ladich, F. (2007). Intra-and intergroup vocal behavior in resident killer whales, Orcinus orca. *The Journal of the Acoustical Society of America*, *122*(6), 3710–3716.

Wickham, H. (2016). Programming with ggplot2. In *Ggplot2: elegant graphics for data analysis* (pp. 241–253). Springer.

Wieland, M., Jones, A., & Renn, S. P. (2010). Changing durations of Southern Resident killer whale (Orcinus orca) discrete calls between two periods spanning 28 years. *Marine Mammal Science*, *26*(1), 195.

Williams, R., Ashe, E., & Lusseau, D. (2010). Killer whale activity budgets under no-boat, kayak-only and power-boat conditions. *Contract via Herrera Consulting, Seattle, Washington*.

Williams, R., Bain, D. E., Ford, J. K. B., & Trites, A. W. (2002). Behavioural responses of male killer whales to a 'leapfrogging'vessel. *J. Cetacean Res. Manage.*, *4*(3), 305–310.

Williams, R., Bain, D. E., Smith, J. C., & Lusseau, D. (2009). Effects of vessels on behaviour patterns of individual Southern Resident killer whales Orcinus orca. *Endangered Species Research*, *6*(3), 199–209.

Williams, R., Erbe, C., Ashe, E., Beerman, A., & Smith, J. (2014). Severity of killer whale behavioral responses to ship noise: A dose–response study. *Marine pollution bulletin*, *79*(1-2), 254-260.

Williams, R., Lusseau, D., & Hammond, P. S. (2006). Estimating relative energetic costs of human disturbance to killer whales (Orcinus orca). *Biological Conservation*, *133*(3), 301–311. https://doi.org/10.1016/j.biocon.2006.06.010

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: vocal clans in resident killer whales in southern Alaska. *Animal Behaviour*, *63*(6), 1103–1119.

Appendix

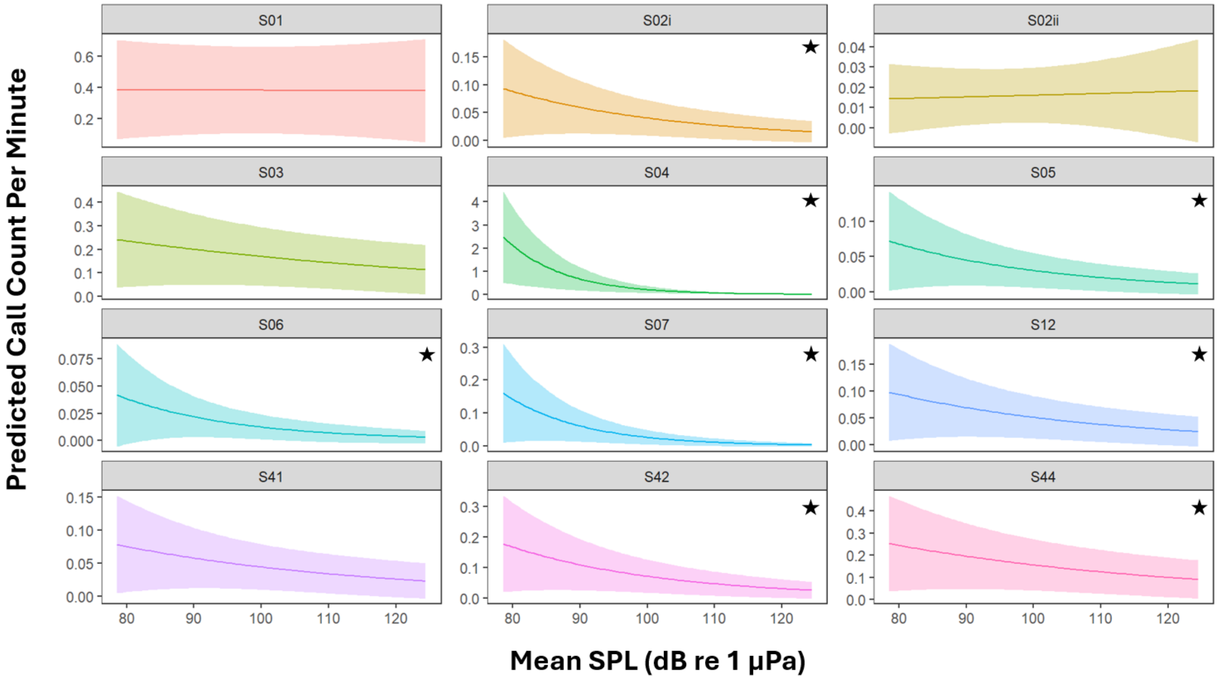

Figure A1. GLMM output and predicted call rates for call type across a gradient of mean ambient noise levels. Y-axis is not fixed to better show rates of change for each call type. Shaded regions represent 95% confidence intervals. Asterisks indicate statistically significant interactions between SPL and call type.

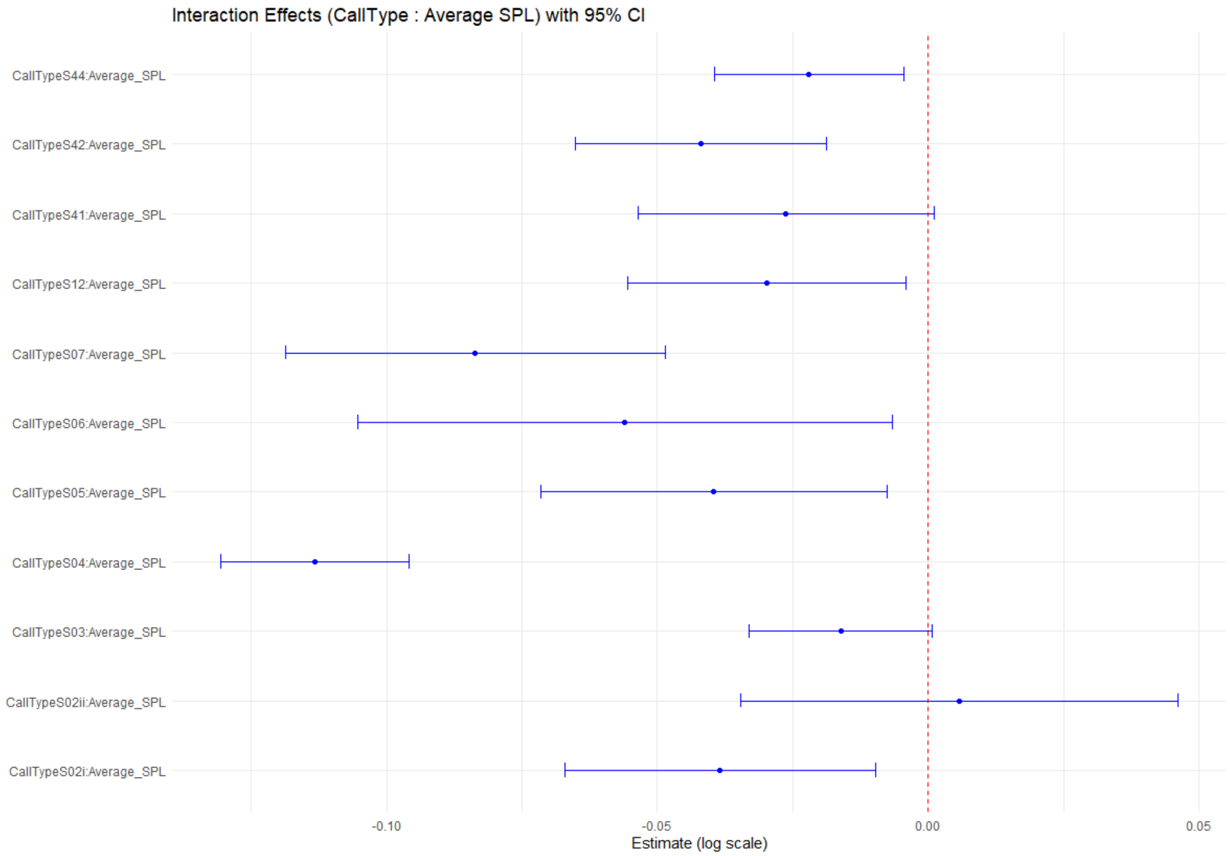

Figure A2. Estimated interaction effects (log scale) between call type and mean SPL on call rates for J pod, including 95% confidence intervals, as modeled by a zero-inflated negative binomial generalized linear mixed model (GLMM) with encounter-level random effects and first-order autoregressive structure.

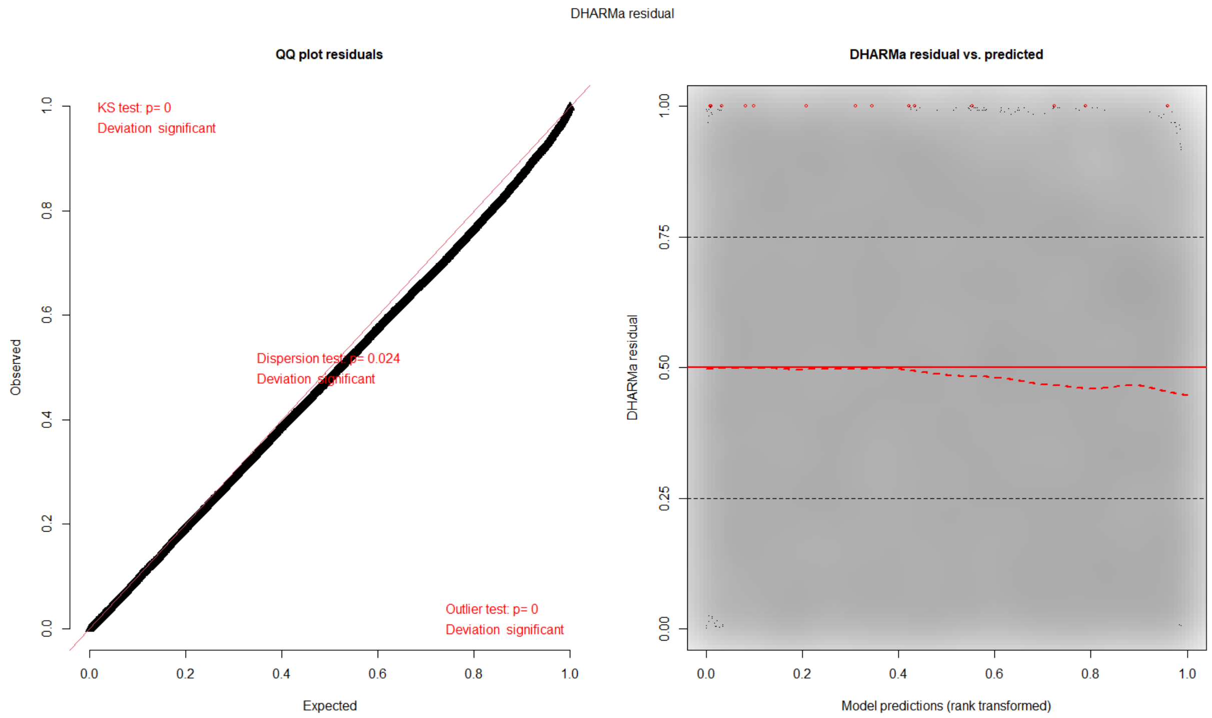

Figure A3. DHARMa residual diagnostics for the negative binomial mixed-effects model of TotalCalls. **Left**: Quantile-quantile (QQ) plot of DHARMa residuals, comparing observed and expected quantiles. The residuals closely follow the 1:1 line, indicating good overall model fit. Formal statistical tests detect significant deviations (KS test: p = 0; Outlier test: p = 0; Dispersion test: p = 0.024), likely as a result of the large sample size and minor deviations in the tails. **Right:** DHARMa residuals plotted against rank-transformed model predictions show no substantial structure or trend, supporting adequate model fit.

Table A1. Model comparison based on Akaike Information Criterion (AIC) for both models presented: Total Call Rates and Call Type Response to SPL. Models were initially tested for appropriate distributions and subsequent additions were made and retested for fit and AIC score. Acronyms for terms added to the model have been applied to for table legibility. Further information on model specifics can be found in the Materials & Methods section. Negative Binomial (NB), Hydrophone Location (HL), Encounter Variability (EV), Temporal Autocorrelation (AR1), and Zero Inflation (ZI). Final models selected are highlighted in bold.

Model	Model Name	df	AIC	ΔAIC
Total Call Rates	**NB + HL + EV + AR1 + ZI**	**7**	**6087.366**	**0.0**
	NB + HL + EV + AR1	6	6309.760	222.394
	NB + HL + EV	5	6352.102	264.736
	NB + HL	4	6779.412	692.046
Call Type Response to SPL	**NB + HL + EV + AR1 + ZI**	**30**	**13622.04**	**0.0**
	NB+ HL + EV + AR1	28	13644.68	22.64
	NB + HL + EV	27	14587.15	965.11
	NB + HL	26	15869.62	2247.59
	Negative Binomial	25	15885.50	2263.47
	Poisson	24	34233.26	20589.22
	Gaussian	25	79854.40	62803.44