# Listening to whales: Tying acoustics to ecology

by

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B.Sc., University of Bath, 2009
M.Sc., University of Victoria, 2012

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# Supervisory Committee

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# Abstract

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The acoustic sense is vital to all life processes for whales. It defines their ‘active space’, and the extent and nature of interactions with their surroundings. Yet, we are still learning the basics of most species’ acoustic behaviours and vocal repertoires.

The ecology of gray whales (*Eschrichtius robustus*) is well known, however vocal behaviours are not well described outside of breeding lagoons. Bottom-stationed acoustic monitoring devices were deployed in Clayoquot Sound, west coast Vancouver Island to explore acoustics use outside of these areas. During migration the use of low frequency moan calls are prevalent, perhaps for group cohesion, with lead whales guiding followers. During the summer more inter-group calls (knocks, upsweeps) are employed. Here I explored the use of ‘motherese’ calls between cow-calf pairs, and how this may mirror the weaning process. Photoperiod, increased ambient noise, threat perception, and vessel and aircraft presence elicited acoustic responses. Calling was also altered by social, behavioural, and physiological state. These results begin to show gray whales to be acoustically sensitive, with highly nuanced vocalising behaviours.

Acoustic methods afford monitoring at times and in places that would otherwise be impossible, and lends themselves to the study of rare or cryptic species. Ocean gliders with passive acoustic capacity were used to explore deep-coastal and shelf-break waters for large whale species. Humpback whales (*Megaptera novaeangliae*) were common on the shelf, whereas calls from fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sperm (*Physeter macrocephalus*), and possibly sei whales (*Balaenoptera borealis*) were heard in more offshore locations. Concurrent habitat data steams help establish area use and importance to these species. The surveys focus on submarine canyons that are thought to aggregate prey. Calls denote whale presence, whereas call type may suggest behaviour and habitat use. Calls described for feeding and breeding were heard for fin and blue whales, with distinct temporal distribution.

Acoustic techniques complement other ecological methods and can fill existing knowledge gaps in whale life histories. It can also help quantify the effect of human activities on whale populations and ocean soundscapes. These findings will inform management actions. I provide examples of management links to acoustic-ecological research.

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***All worthwhile endeavours are 90% effort and 10% love and only the love should show***

Chuck Jones (1912-2002)

## I. Theoretical Preamble: Whale Geography: Acoustics, Biogeography and Whales

### Preface

Organism-based biogeographical studies typically note presence and abundance over time on various scales. However, to be comprehensive, factors of environment and habitat, energetics, morphology and population dynamics should be examined also. Here I consider the idea of the 'geography' of whale species, and the spatial scales on which they operate, paying particular attention to the acoustical components of their landscape, or 'soundscape', to link acoustics to ecology.

I focus on the acoustic sensory modality for whales as it is their primary means of sending and receiving information about their surroundings and between conspecifics. Cetaceans have increased investment in auditory senses compared to vision, suggesting their reliance on sonic information (Ketten 1997). I consider the 'active space' of individuals; the acoustic range of an animal in which it can either send a signal to a receiver and it be enacted on as intended, or can send and receive its own signal to investigate its surroundings, to be a crucial variable. Using this definition, I use active space as a refining feature of whale ecology, as well as a key factor in habitat use for these species. Also, I discuss implications of forces changing active space, in particular human-derived noise. Foreshortening of active space by these sources has been likened to the effect of a persistent pollutant causing habitat degradation, and changes in species distribution (Slabbekoorn 2004). The largest change in ocean soundscape is derived from the introduction of propeller driven vessels. The growing reliance on ocean transportation has radically altered the acoustic landscape, with vessel noise permeating waters far removed from human activity (Jasny 2005, NRC 2005). Elevated ambient noise is predicted to continue, heightened by increased ocean temperature and acidity. Resulting alterations of behaviour, acoustics use, and overall geography of a whale may manifest itself as changes in individual, population, and species success.

The quantification of active space is multi-faceted, likely influenced by physiology and state of caller, the context the call is made, and the composition of call employed. By considering calling under different circumstances, the function of the call may be implied. Vocalisations may be inherent to behaviours, or their use varied due to circumstance. Classifying and measuring the metrics of calls under different circumstances will not in itself 'crack the code' of whales' communiqués, but may illuminate more of their ecology.

The work for this thesis references the idea of organism-centered study and the active space of an individual to describe the area over which it is able to sense its surroundings. The thesis is broadly separated in to three sections. The first uses the gray whale (*Eschrichtius robustus*) as a case study, and example of a species previously considered 'quiet' in most of its range, and now found to actually employ acoustics during migration and summer foraging, as well as in breeding lagoons, where the original acoustics research was conducted. This changes how we understand an individual may interpret the environment it is in, and in particular the influence acoustic disturbance might have to its life history. The second section describes surveillance of more deep-coastal and offshore waters for large whale species, using acoustics to monitor for presence. The occurrence of calls is used to infer habitat use over time. Finally, I discuss some of the management implications of incorporating acoustics into the ecological study of a species and assessments of human disturbance on marine environments.

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## Whale geography: Acoustics, biogeography and whales

### *Organism-centered study and active space*

In his seminal work Geographical Ecology, Robert MacArthur stated that the study of biogeography should consider the 'structure of the environment, the morphology of species, the economics of species behaviour, and the dynamics of population changes' (1972: 1). To address this proposition, we draw on evolutionary biology, ecology and population biology, and species' interactions with the environment over varied temporal and spatial scales.

However, the biogeographical study of a species is frequently limited to an examination of presence, location and geomatic components, and coarse time scales. The components of biogeography that MacArthur suggests are largely considered to sit outside the discipline of geography. To address the neglected processes that he delineated, we need to integrate taxa-specific adaptations and life history, specifically when those alter our fundamental perception of how an organism uses space. To move beyond simply mapping the area that an individual or species inhabits, biogeography now needs to apply knowledge of factors guiding movement and distributions, species interactions, both predation and competition, variation in physical properties of the environment, dispersal ability, and species requirements throughout life history stages.

I am advocating a species-specific emphasis to underpin biogeographical study, and I build my argument around the example of whales. Whale biogeography illustrates how the integration of information, with a focus on facets of biology unique to marine taxa and guided by the consideration of space and time scales common in geographical study, leads to a greater appreciation of an organism's ecology. I use MacArthur's postulate as the guiding principle to outline the biogeography of the cetaceans: the whales, dolphins and porpoises. I will address environment, morphology and physiology, energetics and population dynamics as outlined by MacArthur, and suggest that a more active and dynamic appreciation of these factors on spatial and temporal scales constructs the biogeography of these species. In doing so, I focus on the acoustic sense as a means of sending and receiving information, the predominant mode of cetaceans' interface with their surroundings. What has been missing, and still perhaps underappreciated as the key to most interactions between cetaceans and their environment, is the acoustic realm. Whereas vision is the primary sense for terrestrial animals, for marine mammals it is only useful at fine scales (Torres 2017). The structure of the auditory system allows for far more complex signal processing and so greater resolution and extent in sensing the surrounding seascape.

Cetaceans are morphologically adapted to underwater sound processing; for example, toothed whales have a bio-sonic echolocation process for fine scale navigation and prey identification, and baleen whale vocalisations occupy the lowest sound frequencies to facilitate long-range signalling (Payne & Webb 1971). Whales' adaptations of the middle and inner ear began with their isolation outside of the skull, to discriminate fine details and localize sound sources. Physiological examination by Ketten (1997) showed increased investment in audition in cetaceans by comparing the number of auditory and optic nerves. The ratio of fibre counts were two to three times in favour of acoustical senses in whales than in terrestrial animals, suggesting the strong reliance on sonic information (Ketten 1997). We can infer from this that acoustics is the primary means of information reception, environment imaging, and conspecific interaction for these animals.

Traditionally, the marine environment would be described by metrics such as water depth, topographic rugosity, substrate, pH, temperature, salinity, and current speed, or perhaps even through discussions of oceanic regimes and productivity patterns. These factors vary on a spectrum of scales. Here, I use principles from landscape ecology to describe process and pattern to guide the definition of 'soundscape ecology' and its application to the marine mammal environment, and then later how this plays a role in whale geography. Applying the concept of soundscape to interactions, trophodynamic linkages in ecosystems and the patchiness of resources will refine our grasp of habitat use by cetaceans.

In water, sound energy propagates more than four times faster, and at some depths also further, than in air. The transmission path is defined by characteristics of both the signal and the receiving environment. Water composition alters sound conduction, with gradients in temperature and salinity in both vertical and horizontal dimensions creating different sound propagating conditions (Urick 1983). Transmission properties define the soundscape and the broad scale over which acoustic information interacts with whales. Propagation coefficients alter with changing ocean conditions over space, for example as an animal migrates, or over time. The physical characteristics of the area the sound will propagate in, for instance substrate composition, topography or water mixing regimes, influences the sound transmission parameters, together forming the underwater soundscape of an area. Currently, there is a suite of changes in conditions that are altering ocean sonic environments. The effects of rising ocean temperatures may form new thermoclines (Sehgal et al. 2010), alter absorption and, thus, allow sounds to propagate further (Firestone & Jarvis 2007). Also, as seawater pH decreases due to carbon dioxide uptake, the sound absorption coefficient and attenuation of low frequency noise in particular is reduced, therefore increasing their propagation (Ilyina et al. 2009, Sehgal et al. 2010, Etter 2012).

Just as physical habitats are defined by their abiotic and biotic components, soundscapes are a composite of three distinct sonic energy sources: geophonies, the abiotic natural agents; anthrophonies, the human-derived acoustic additions; and biophonies, organism-derived noise (Farina 2014). Here, I give examples of each of these components and summarize the issues surrounding the structure and interaction of the abiotic and the living forms in the acoustic world.

Additions to noise from abiotic inputs (geophonies) come directly from sea-state, driven by wind speed, water turbulence, tide, currents and hydrostatic pressure, surface waves, or precipitation. They account for great variation in ambient noise conditions over time and space (Richardson et al. 1995, Wysocki et al. 2007, Coers et al. 2008, Lugli 2010, Ladich 2013).

Anthropogenic sources of underwater noise (anthrophonies) are derived from transportation, resource use, and military activity, including shipping, construction, and seismic or scientific exploration. Although the noise emissions may be considered as discrete spatial and/ or temporal events, for example air gun operation, a drill rig or a vessel traffic route, the distribution and extent of propagation of these human-added sounds is now becoming increasingly evident. The introduction of propeller driven vessels, especially into commercial shipping, has precipitated the largest single change in ocean ambient noise levels. The reliance of oceanic transport routes for global trade, representing approximately 95% of tonnage transported, has radically altered the marine acoustic landscape (Jasny 2005, NRC 2005: 142). Oceanic background noise is now several decibels higher than pre-industrial levels, even in the open ocean with no nearby anthropogenic noise source (Richardson et al. 1995). Decibels are units of a power or intensity level of sound intensity and are set on a logarithic scale, whereby, for example, a change in 3 dB would intensify the sound by a factor of 2, and a 10 dB change would intensify the sound by a factor of 10. In addition, coastal and offshore waters receive contributions from construction, pile driving, underwater explosions, seismic exploration and sonar use particularly tied to oil and gas exploration and extraction platforms (Johnson & Tyack 2003, Thomsen et al. 2011, Simmonds et al. 2014, Williams et al. 2014).

Biological noise arises from a variety of sources. Contributions from marine organisms to the ocean's sonic landscape are referred to as biophonies. The vocalisations of fish and marine mammals can elevate ambient noise in coastal environments significantly in specific frequency bands, and at times dominate the ambient noise with their vocal expressions (Widener 1967, Myrberg 1978, Dahlheim 1987, Cato 1992, Cato & McCauley 2001, Tyack & Janik 2013). The organism-based sound production is shaped by the amount and diversity of marine life in an area, related to habitat use and life history events such as migration. Together, these three components of the soundscape form a matrix within which cetaceans live. It follows, then, that we should focus on the basic biological nature of cetaceans as sound organisms, and the effects of a changing soundscapes.

The furthest reaches of auditory detection and discrimination of passive acoustic cues from biological and physical features of the soundscape by cetaceans is termed their 'reverberation space' (Clark et al. 2009). The spatial acoustic range of an animal in which it can send a signal to a receiver, and it be enacted on as intended, or can send and receive its own signal as an echo to discern its surroundings, is its 'active space'. This area is in part defined by distance and ambient signals, and in part by features of the signalling individual, including size. It is the application of the concept of active space to the description of a realized niche that will allow biogeographic study to become species oriented.

In general, animals with greater mass produce lower frequency (in hertz, Hz) signals, which propagate over larger distances (Rossing 2007, Stoeger et al. 2012, Farina 2014). If uninhibited by other variables, the acoustic range, and therefore active space, will be greatest for the larger whale species. The blue whale (*Balaenoptera musculus*) employs vocalisations in frequencies ranging from 16–25 Hz (Richardson et al. 1995), while also capable of producing long infrasonic calls below 10 Hz, that last over 10 seconds, to communicate over long ranges (Stafford et al. 1998). Fin whales (*Balaenoptera physalus*) too, with their characteristic 20 Hz pulsed calls, emit vocalisations which may be audible over hundreds of kilometres, and theoretically across ocean basins if projected at high amplitude with little absorption or impedance from ambient noise sources (Northrop et al. 1968, Payne & Webb 1971, Spiesberger & Fristrup 1990, Stafford et al. 1998, 2007, Mellinger & Clark 1997, Watkins et al. 2000, Tyack

& Janik 2013). In contrast, toothed whales have a smaller active space, but potentially greater efficiency and acuity as a result of a finer spatial resolution of auditory information (Madsen et al. 2007, Tyack & Janik 2013). The sperm whale (*Physeter macrocephalus*), the largest toothed whale, dedicates more than a third of its mass to sound production, and has the most powerful echolocation system ranging into mid-frequencies (100 Hz to 32 kHz; Morrissey et al. 2006), transmitting at a maximum source level of 232 dB re 1μPa that allows its signals to range up to 10 km (Tyack 1997, Møhl et al. 2000, Madsen et al. 2005, Zimmer et al. 2005, Rossing 2007, Tyack & Janik 2013). These measured or modelled propagation distances of vocalisations are the basis of the active space of a species, and give an indication of their potential spatial domain and, therefore, the niche they inhabit. Indeed, the distance over which these signals can travel in ideal conditions sets the furthest extent of active space.

The calls and songs projected by whales, although key to their functioning, are not without energetic cost. Estimates suggest that the direct cost of calling constitutes up to 5% of total metabolic energy production (Jensen et al. 2012, Tervo et al. 2012, Noren et al. 2017). Indirect costs are also incurred from exposure to predators, advertising of callers' presence to prey or reduced time budgeted for other activities, such as foraging. Together, however, it is unlikely that these costs act to limit vocal behaviours (Jensen et al. 2012) as vocalisations can also indicate the presence of an individual, a warning of danger, territory extent or physical or emotional state of the signaller, including sexual prowess. Changes in ambient noise conditions, particularly as a result of anthropogenic additions, could precipitate changes in calling behaviours and increase energy costs of vocalising.

Here, I do not present a detailed review of the effect of underwater sound on marine mammals (see Richardson et al. 1995, Nowacek et al. 2007, Shannon et al. 2016), instead I present examples of how anthropogenic additions to the ambient condition can result in altered spatial use and/or altered active space of cetaceans. Modified habitat use, diving behaviour or altered vocalisation rate and composition are potential compensation mechanisms of whales to increases in ambient noise. The acoustic aspects of compensation may include revision in call patterns, frequency shifts, modified energy levels of vocalisations, longer or more repetitive signals, or reduced calling until the noise levels fall (Dahlheim 1987, Miller et al. 2000, Buckstaff 2004, Morisaka et al. 2005, Nowacek et al. 2007, Parks et al. 2007, Weilgart 2007, Tyack 2008, Holt et al. 2009, Castellote et al. 2012, Rolland et al. 2012, Janik 2014, Veirs et al.

2016). Signalling costs may be higher when suboptimal frequencies are used, or redundancy in calling is increased, intensifying a whale's energy expenditure, perhaps to some threshold (Bradbury & Vehrencamp 1998, Weilgart 2007). The adaptations in call structure and timing may also make communications less effective, as changes in the interval and bandwidth of signals have the potential to limit the range of the vocalisation (Castellote et al. 2012).

Short-term behavioural responses of cetaceans to human-produced sound can include longer dive times, shorter surface intervals, increased swimming speed and evasive movements away from the source, particularly to shield young (Norris 1994, Gordon & Moscrop 1996, Frankel & Clark 1998,). Altered habitat use to avoid sound sources has also been observed whereby individuals redistribute themselves, altering both their ecological and sonic energy fields (e.g. Malme et al. 1983, 1984, Richardson et al. 1985, 1990, Tyack & Clark 1998, McCauley et al. 2000). For more chronic exposure or sustained ambient noise increases, whales have shown displacement over extended periods from breeding, rearing and feeding areas, as well as alteration in migration routes (e.g. Malme et al. 1983, 1984, Richardson et al. 1985, 1990, Tyack & Clark 1998, McCauley et al. 2000).

Avoiding areas significant for life history events, and abandoning behaviours such as feeding or mating in response to a sound source (e.g. Malme et al. 1988, Richardson et al. 1995, McCauley et al. 1998, 2000), may mean the animals incur great cost, depending on the extent and duration of the change (McCauley et al. 2000, Firestone & Jarvis 2007). In addition, the potential acoustic masking effect (Richardson et al. 1995, Weilgart 2007, Clark et al. 2009, Erbe et al. 2012, Hatch et al. 2012, Rolland et al. 2012) caused by increased ambient noise levels may have wider consequences in predator detection, foraging success or fitness. Preliminary modelling of whale energetics suggests that even small behavioural alterations can be costly, with repeated modifications over time potentially holding consequences for success at the population level, especially since many cetacean species are capital breeders and seasonal foragers (Jasny 2005). A detailed economic analysis of the cost of a changing soundscape is lacking for many species and should be integrated when, and if, it becomes available as the economics of energy expenditure and return is the currency of the natural world.

The biological significance of a behavioural response is dependent on the severity and context of exposure (Sivle et al. 2015). The reaction to a particular sound will be governed by the individual's age, sex, health, prior experience, sensitivity to the noise, anticipation of noise, behavioural state, distance from the sound source, and timing and duration of exposure (Wartzok & Ketten 1999, Firestone & Jarvis 2007, Weilgart 2007). It is key to recall that the effect of a particular noise will not be the same for all species or, indeed, for all individuals.

How individual responses consequently shape population dynamics is yet to be described for many species. Conclusive cause and effect relationships to changes in whale populations' success as a result of a modified soundscape have yet to be determined, with perhaps the full repercussions yet unseen. Whereas a behavioural or vocal response can give a tangible measure and some means to quantify the spatial or temporal extent of the effect, these are likely a naïve appreciation of the overall influence of a change in soundscape. Still, there is a need to interpret the small scale/individual actions to wider scale consequences.

The modification of marine soundscapes has been likened to the effects of a persistent pollutant leading to habitat degradation and changes in species distribution (Slabbekoorn 2004). Increases in ambient noise are predicted to continue, with anthropogenic influence heightened by increased ocean temperature and acidity. In this way, the geophonic and anthrophonic components of the soundscape drive changes in biophonies. Oceanographic and anthropogenic changes can be dramatic over relatively short time frames. They can, for example, change the spatial distribution of resources, and therefore the presence of top predators such as whales. In turn, displacement of these highly mobile predators can reshape ecosystem structure. Few studies have yet to explore the effects of noise over larger spatial or temporal scales, with the challenge being to isolate this effect from other sources of disturbance or habitat change (Costa 2012, Erbe et al. 2016, Shannon et al. 2016).

Cetacean populations are in a recent post-whaling scenario, which compounds the effects of a changing sonic environment. Numerous whale populations are recovering into ecosystems that have been altered by a number of processes, including ecosystems that have been damaged by over-fishing. This, coupled with their long lives and complex adaptations, increases uncertainty of the trajectory of cetacean species in the altered soundscape. Indeed, the speed of change forces modification of calling behaviour primarily relying on vocal plasticity and learning, rather than resulting from evolutionary adaptations (Wallschager 1980, Nowicki 1989, Prestwich et al. 1989, Ryan 1986, 1988, Sanborn 1997, Jasny 2005, Gillooly & Ophir 2010, Noren et al. 2013, Janik 2014). When considered in a wider context, teamed with our recent appreciation of the role of top predators in ocean ecology, the need to uncover whale biogeography becomes a pressing issue, and will be needed for effective conservation measures.

The assessment of habitat loss, degradation and abandonment, pollution accumulation, and ocean climate change as a consequence of human activities can be moved forward by biogeographic methods. In turn, the perspective of whale-based geographical studies is useful for the development of effective mitigation of the effects of a polluted soundscape on cetaceans. The application of acoustic research methods in whale biogeography may be the only means to study small and fragmented populations, such as the north Pacific right whale (*Eubalaena japonica*), for which sightings are rare and data on ecology and habitat use is sparse.

In line with MacArthur's (1972) description of the biogeographical approach to ecological study, I have presented the structural environment by focusing on the marine soundscape from the whale outwards. The use of acoustic signals is a property of the fundamental biology of cetaceans, shaped by natural selection in a sound dominated environment. They rely on acoustics for habitat and conspecific interaction, now depending increasingly on adaptive behaviours employed to counter disturbance. The concept of active space, or active niche space, shapes our interpretation of a whale-centred biogeography.

When trying to understand spatial behaviour of a cetacean species, we should recognize that they will position themselves according to preferences in static (e.g. topographic) and dynamic (e.g. oceanographic) variables on different temporal scales (Fernandez et al. 2017). Acoustics is a vital spatial component of whale biogeography, but is little studied, especially in reference to cetaceans' spatial use. Logistically, it is difficult to study or comprehend, yet it may be the most significant aspect of whale human interaction, and the most in need of unravelling if we are to protect cetaceans.

### *Thesis overview*

The work I present in this thesis considers the use of acoustics of large whale species in differing geographic, social, and behavioural context, always in reference to MacArthur's (1972) rendering of the approach that biogeographical studies should take. The overarching theme is to examine the additions that passive acoustic monitoring (PAM) techniques can make to the ecological study of whale species.

In the first 'Coastal' section I use the gray whale (*Eschrichtius robustus*) as a case study. Previously described as the 'quiet whale' (Rasmussen & Head 1965), I use recordings during periods of migration and foraging to add to the knowledge of its vocal repertoire and acoustics through its full range. The recordings describe a highly sonorous whale during north- and southward travel (Chapter 1.2). I then discuss how this may function as a means to maintain the 'herd' (Payne & Webb 1971) during migration (Chapter 1.3).

Recordings from foraging areas are made in Clayoquot Sound, on the west coast of Vancouver Island. This is a persistent feeding locale, as well as a nursing/weaning site for cow-calf pairs. The prey resources and habitat use is described in Chapter 1.4. The acoustic behaviours during summer foraging are then discussed in Chapter 1.5, with special reference to the use of 'motherese' vocalisations between mothers and their young.

Altered vocalisation in the presence of a perceived threat is also examined. First, in the case of increased ambient noise levels, I compare the acoustic response to natural and anthropogenic noise additions particularly whale watching traffic (Chapter 1.6), and then in the acoustic presence of killer whales (*Orcinus orca*, Chapter 1.7).

In the second, 'Offshore' section, static and mobile PAM systems are used to examine for the presence of large whale species in the offshore waters of Clayoquot Sound. The first chapter (Chapter 2.2) describes findings from PAM-capable ocean glider missions in the Canadian Pacific. The two chapters following show further analysis of the large whale species call presence from two offshore mobile and three deep-coastal water and one deep shelf-break stationary PAM system deployments. Chapter 2.3 describes the presence of large baleen and sperm whale calls over time, and the call types heard, with Chapter 2.4 presenting a more detailed analysis of the temporal separation of call types heard for fin whales in the study area.

The final section aims to show the management implications of the integration of acoustics in to ecological study. Chapter 3.2 shows how the use of acoustics data can be used in concert with visual data. Here I consider the visual sightings of a citizen science network, contributing data to compare to recordings from a stationary hydrophone in a coastal location off Flores Island, Clayoquot Sound. The last chapter puts forth suggestions for better whale watching management and regulatory actions, based on a growing body of scientific works on the disturbance effects of vessel present and noise on cetaceans (Chapter 3.3).

The use of acoustics by animals more generally us discussed in 4.1, where I muse on whether we will ever know the meaning of calling behaviours from their form and function. The lessons learned from this thesis work are given in Chapter 4.2, where the implications of increasing human-derived acoustic disturbance, in already altered ecosystems, on acoustically active species is discussed. The use of acoustics as another tool for ecologists to understand how individuals interact with their surroundings, each other, and other species is proposed. The strength of these relationships is discussed for whales in the light of the findings. Further the applications of PAM methods are suggested, as is the use of active space as a concept to refine the scale of ecological studies. I suggest that acoustics, as the primary modality, moderates species-species and species-habitat interactions and indeed all life processes for whales. Much more effort should be given to understanding vocalisation behaviours and soundscape interpretation, as well as the level of disturbance anthropogenic activities are introducing into the marine environment.

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## II. Acoustic methods overview

The data for this thesis was collected from recordings made by both bottom-stationed and mobile passive acoustic monitoring (PAM) platforms. More details are presented in the chapters that follow, but here I present a general overview on the deployments of PAM systems, data inspection and preparation for analysis.

### Acoustic data acquisition, inspection and analysis

*Coastal Recordings*

Deployments

The recordings for the coastal section (Chapters 1.2-1.7) were made by an Autonomous Multichannel Acoustic Recorder (AMAR G3A, JASCO Applied Sciences, Halifax NS.) with a calibrated hydrophone (sensitivity -165 dB re 1 V/µPa, effective 5 Hz-150 kHz, gain of 6 dB; GeoSpectrum M8E-132, Dartmouth, NS.) All deployments were set to record constantly up to 8 kHz. Duty cycling to recording into higher frequencies was used in some of the deployments.

Five deployments were made, three of which were positioned to record data during gray whale (*Eschrichtius robustus*) migration at a 51 m deep, coastal location. The AMAR was deployed approximately 5 nm/9.26 km southwest of Siwash Point, Flores Island, on the west coast of Vancouver Island (49.21028, -126.24667, Figure II.1). The same location was used for both northward and southward migrations. The PAM system was deployed between February 21 and April 25, 2015 (N1) and March 7 to May 5, 2016 (N2) for the northward migration recordings, and September 27, 2016 to January 25, 2017 (S) for southward migration (Table II.1, also see Appendix).

The range and probability of detection of gray whale calls for each deployment was estimated using ambient noise levels for each minute of the recording, the source of class 3 moan calls (156.9 ± 11.4 dB re 1µPa @ 1m as reported by Guazzo et al. 2017), and cylindrical spreading models for estimated transmission loss, including the assumption of no attenuation losses. This would approximate the maximum probable distance a call could be heard from (Figures II.1 and II.2, Appendix of Chapter 1.2 and 1.5).

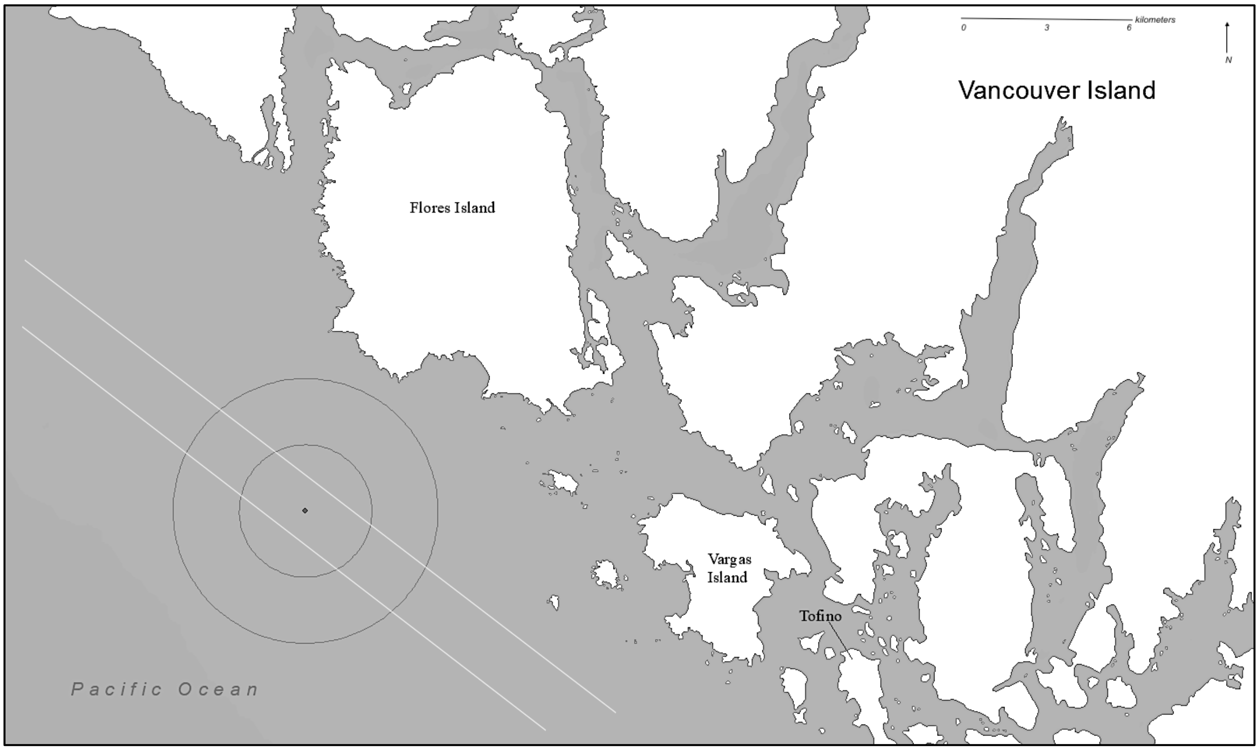

**Figure II.1:** Location of AMAR deployment for N1, N2, and S, with migratory corridor and likely range detection radii of gray whale class 3 moan calls. AMAR location is in the centre of the detection circles with the smaller circle representing the range of detection 80% of the time (3 km) and the larger 10 % of the time (6 km). The lines parallel to the coast line are 8 km, to indicate the migratory path of Phase A whales, and 5 km, for the cow-calves in Phase B.

Two deployments were made during the summer with the AMAR placed in the main feeding bay for gray whales in Clayoquot Sound on the south coast of Flores Island (49.25629, -126.15928, Figure II.2). Deployments were between May 6 and September 14, 2015 (F1) and May 30 and September 5, 2016 (F2).

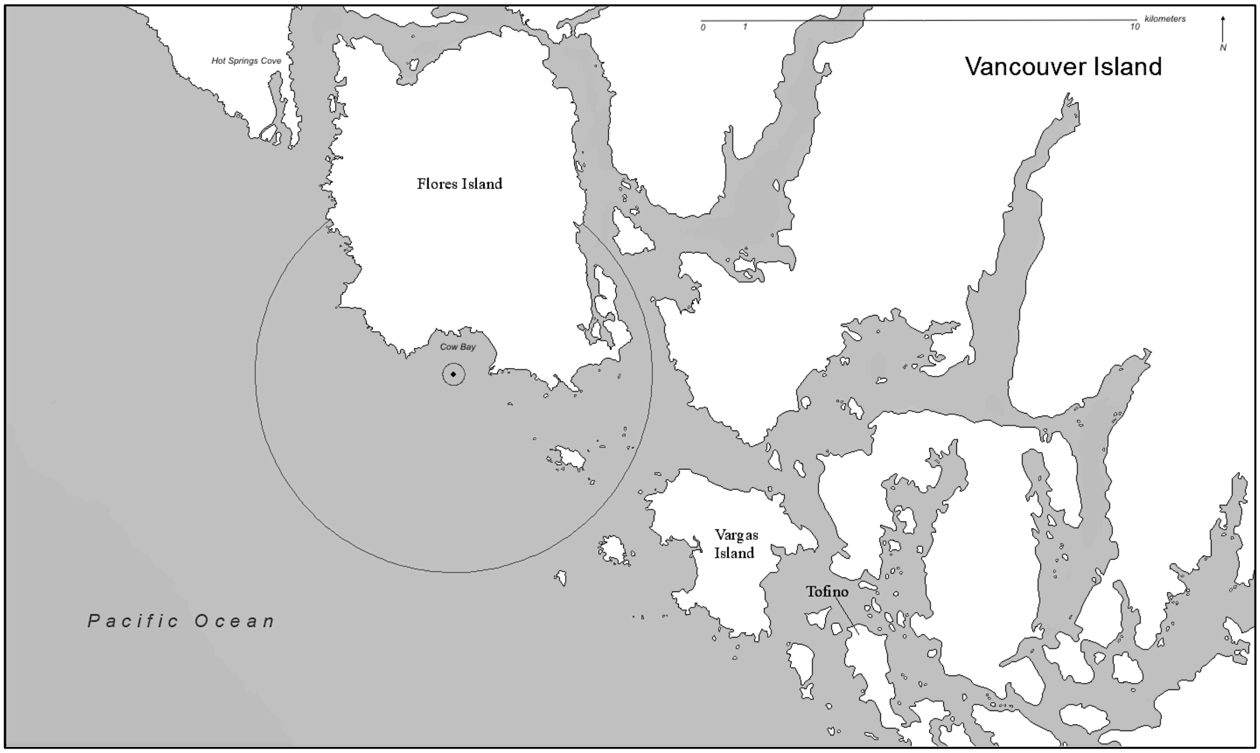

**Figure II.2**: AMAR deployment location (49.25629, -126.15928) for summer foraging recordings (F1 and F2). The circles display the likely detection radius for 90% of the time (500 m) and 10% of the time (9 km).

**Table II.1**: Summary of deployment timing, and proportion of recordings/amount of time inspected. Recording time is expressed YYYY-MM-DD, 24-time, GMT.

| Deployment | |
|---|---|
| N1 | Recording time: 2015-02-21, 21:02:47 — 2015-04-25, 19:38:27<br>AV inspection: 56.6%, 855 hr 11 min |
| N2 | Recording time: 2016-03-07, 18:01:16 — 2016-05-05, 18:37:14<br>AV inspection: 23%, 327 hr 57 min |
| S | Recording time: 2016-09-27, 17:17:17 — 2017-01-25, 05:17:17<br>AV inspection: 20.7%, 604 hr 30 min |
| F1 | Recording time: 2015-05-06, 18:47:00 — 2015-09-14, 13:47:00<br>AV inspection: 45%, 1221 hr 6 min |
| F2 | Recording time: 2016-05-30, 22:09:17 — 2016-09-05, 22:18:37<br>AV inspection: 28.5%, 670 hr 15 min |

### Call identification and classification

Manual identification of calls was made through aural and visual (AV) examination of sound files and respective spectrograms using Raven Pro Interactive Sound Analysis Software (Cornell Lab of Ornithology). Spectrograms were generated using a 256-point Hann window 1 s FFT with 50% overlap. For all deployments a minimum of every fifth day (20%), from the first full day of recording, was inspected for comparisons over time. For the first deployment (N1), a minimum of 340 s of every 900 s segment was analysed, in addition to the regularly spaced 20%, with an additional randomly selected 560 s segments (see Appendix). This deployment in particular was used to refine an automated detector for gray whale calls. Although the automated detection process is not presented or discussed in detail, precision and recall of the systems of gray whale calls were tested by comparing the AV inspected data to the detection results as part of a verification process for each deployment. For the coastal data analysis (with results also part of Chapter 3.1), PAM data were also subject to a detector to highlight the presence of killer whale (*Orcinus orca*) calls (Mahoney et al. 2014, Mouy et al. 2015). The inspection of these periods are part of the part of the period's analyses that extend past the minimum 20% (see Appendix).

Call identification and classification was made by reference to the literature. For gray whale calls Dahlheim (1987) was a primary source, with subsequent other studies (Crane & Lashkari 1996, Ollervides 2001, Wisdom et al. 2001, Stafford et al. 2007, Charles 2011, López-Urbán et al. 2016, Youngson & Darling 2016) used as reference where appropriate. Descriptions of both quantitative (call parameters) and qualitative (aural perception) qualities of calls noted in previous studies, as well as spectrogram comparison, were used to categorise calls identified in the AV inspection to type.

Gray whale calls are focused in the low frequencies (<2 kHz). I focused the AV analysis on these frequencies to identify calls. To aid with call recognition and classification, calls were amplified by a factor of 25. The playback speed was also manipulated during the AV process. Playing back at up to 3 times their produced rate allowed for clearer call cadence identification. The increase in speed also increased the pitch of the call features.

For each of the calls, a series of measurements were made. Call parameters were extracted through the selection call formants in spectrogram displays (Figure II.3). Call features were extracted from selections defined by the start and end time and harmonic extents (lowest and highest frequencies, see Figure II.3). Calls were  described by their duration (s), lower and upper frequency (Hz) extents, the frequency range (Hz) of the call harmonics, and peak frequency (Hz), where the acoustic energy of the call is greatest. These became metadata for each call identified. Comments on call qualities were also noted, to allow for later refinement of call categories. Any calls where background noise, particularly vessel noise, masked the accurate measurement of these metrics were excluded from further analysis, as were those calls labeled ‘other’. Care was taken, for example, that measurements were a true reflection of the call and not vessel noise (horizontal lines in Figure II.3) or wind or wave noise. These call details were tabulated to form a ‘call library’ of gray whale calls. Additional comments as to the presence of vessels and killer whale calling were also made per call in a binary coding (presence-absence, Table II.2). Each call was also correlated to ambient noise levels, and wave, wind, sea state, and tidal measures (Table II.2).

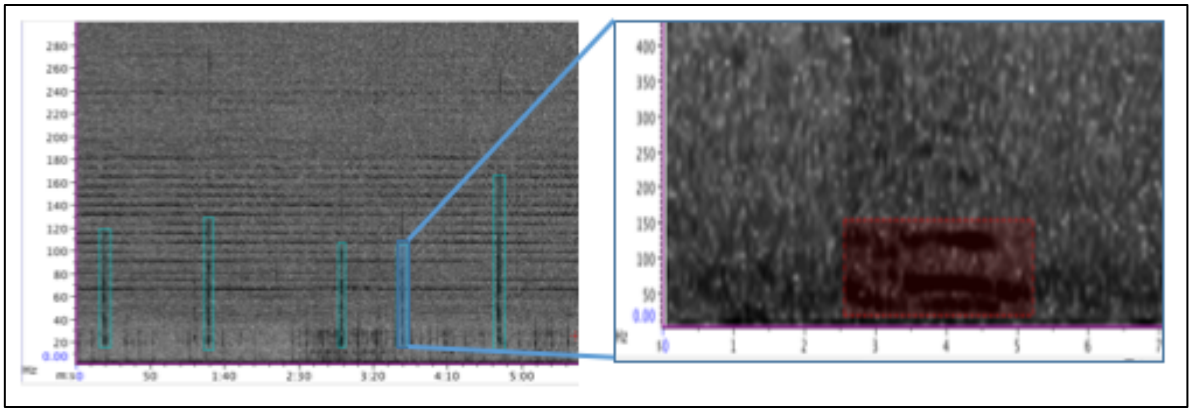

**Figure II.3:** Example of call selection, from which call parameters were derived. On the left five moan calls are highlighted in turquoise. The image on the right is one of these calls, where spectrogram extent (in time and frequency axes) has been adjusted to show call structure in more detail.

I compiled call data in a second data table to calculate rate by call type. For each full hour of data the acoustic presence of gray whales was noted. The number of each call type (classes 1-11) was totalled hourly. The presence of vessel or float plane noise and killer whales, from the presence of their calls, were noted in a binary code. The passage rate of vessels and float planes was quantified by totalling the number of Lloyd mirror curves per hour, which represent direct passage over the AMAR recorder (Figure II.4, Table II.2). Hourly ambient noise, wind speed and wave height (sea state), and tide height values were matched to each hour of call data (Table II.2).

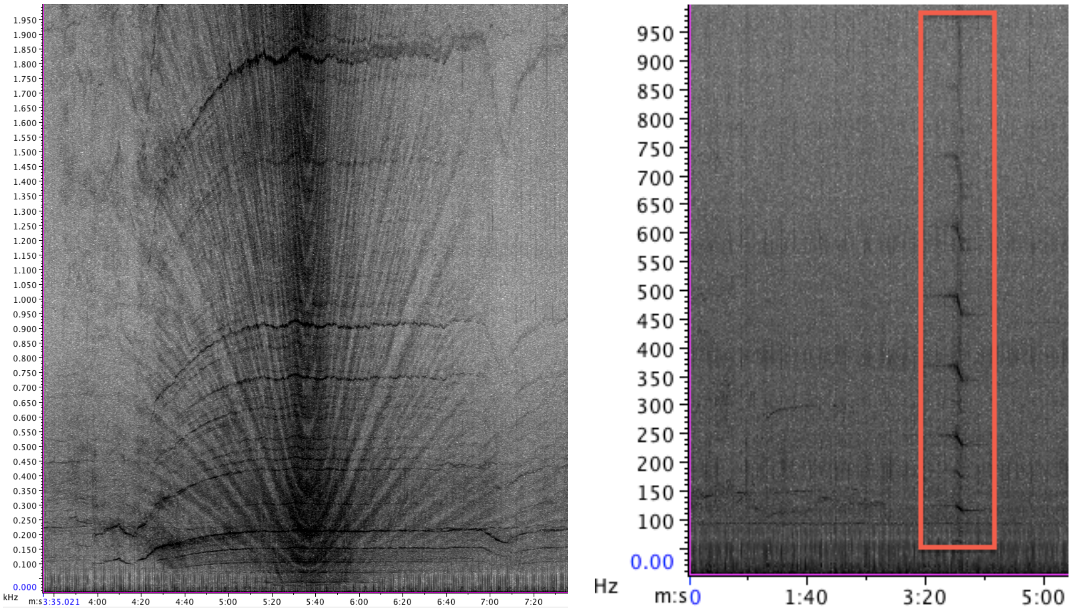

**Figure II.4:** Example of a Lloyd mirror curve from direct overhead vessel passage (left) and the more Z shaped sound signature of a float plane passage overhead (right, highlighted by red box).

Normalcy in the distributions of calls over time and call parameter values was tested using the Kologorov-Smirnov goodness-of-fit test. Modality was found in calls over time. Call parameters were found to be highly skewed, focussed in the low frequency/short call durations, with a long right-hand tail, and highly leptokurtic. Non-parametric tests were used on gray whale calling data as a result.

**Table II.2**: Summary of how comparisons between call parameters and calling rate were made to variables of ambient noise levels, sea state, and vessel and aircraft presence.

| Rate | Derived parameter and scale |
|---|---|
| For each call: | |
| Call parameters | Frequency extents, range and peak, and call duration<br>Call classified to class type using Dahlheim 1987, Ollervides 2001, Charles 2011 |
| Ambient noise | Minute-wise, summing 1/3 octave bands between 0-2000 Hz |
| Environmental factors | Reading of continuous and gusting wind speed (m/s) and wave height (m) take from the La Perouse weather station on hourly schedule and applied to all calls in that hour |
| Tide | Application of hourly tide level readings, and categorisation of high-slack or low-slack, 2 hours before and after the slack tide, or ebb or flood periods |
| Sea state | Beaufort Scale, derived from hourly wind speed and wave height readings, applied to each call |
| Vessel presence | Presence/absence at the time of call |
| Diurnal-patterning | Calls categorised as day or night, or day-night-dusk-dawn using nautical twilight times |
| | |
| Hourly: | |
| Call parameters | Number of calls, per call class |
| Ambient noise | Minute-wise, summing 1/3 octave bands between 0-2000 Hz, averaged over an hour |
| Environmental factors | Hourly reportings of continuous and gusting wind speed (m/s) and wave height (m) taken from the La Perouse weather station |
| Tide | Application of hourly tide level readings, and categorisation of high-slack or low-slack, 2 hours before and after the slack tide, or ebb or flood periods |
| Sea state | Beaufort Scale, derived from hourly wind speed and wave height readings |
| Vessel presence | Presence/absence during the hour<br>Vessel passage rate, derived from the number of Lloyd mirror curves |
| Aircraft presence | Presence/absence during the hour<br>Vessel passage rate, derived from the number of Lloyd mirror curves |
| Diurnal-patterning | Calls categorised as day or night, or day-night-dusk-dawn using nautical twilight times |

### *Offshore Recordings*

Acoustic data for the offshore section was collected from two bottom-stationed hydrophones, the deep-coastal (N2 and S) deployments of the AMAR system and a deep-shelf break recorder positioned at the base of Clayoquot Canyon. Ocean gliders with PAM capabilities linked the two fixed recorders (Figure II.5).

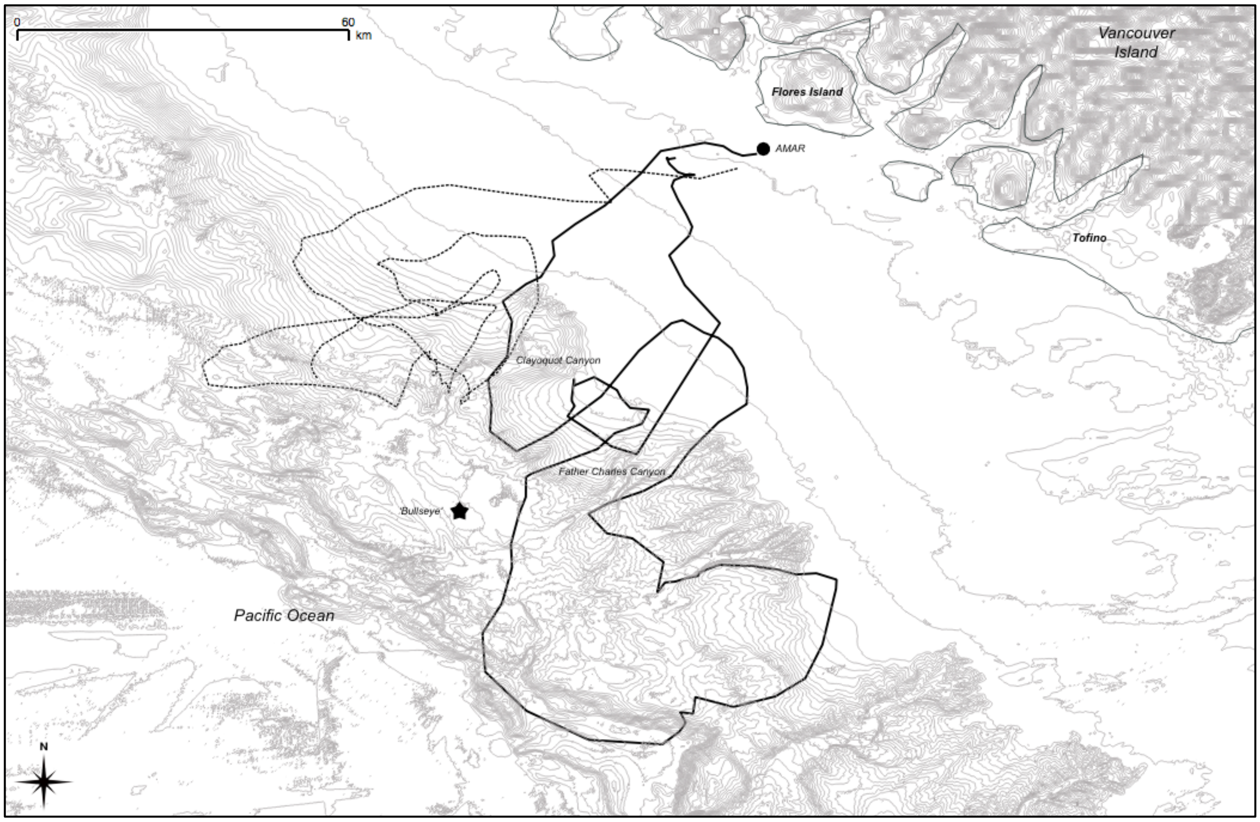

**Figure II.5:** Deployment site of AMAR (circle, 49.21028, -126.24667) and icListen 'Bullseye' (star, 48.6706, -126.8485) passive acoustic recorders, and routes of glider surveys. The solid line is the 2016 glider deployment and dashed line is the 2017 glider deployment.

Deployments

Two ocean glider (Webb Teledyne Slocum) deployments were made between March 17-April 16, 2016 and January 30-February 18, 2017 (see Appendix). Launched from the AMAR deployment site, the gliders were tasked in surveying deep-coastal and shelf-break zones. Passive acoustic recordings were made using a digital acoustic monitoring system (DMON, Woods Hole Oceanographic Institute) that records constantly up to 1 kHz throughout the deployments. Acoustic recordings were downloaded fully on glider retrieval, with the large data packets split into 5 minute files for ease of further analysis.

The DMON data are complemented by AMAR recordings (as described above) and an Ocean Sonics icListen AF Hydrophone 2504 (sensitivity -170 dB re 1 V/ µPa, effective 10 Hz-200 kHz, gain of 6 dB), named 'Bullseye', deployed by Ocean Networks Canada, approximately 45 nm from shore (48.6706, -126.8485, Figure II.5). This is a cabled device at 1256 m depth, recording constantly up to 16 kHz. Recordings between March 20-April 10, 2016 were used here, to match the on-shelf recordings of the first glider deployment. Acoustic data was retrieved from the Ocean Network Canada data archive (http://www.oceannetworks.ca) and downloaded in five-minute clips.

Call identification and classification

Recordings made by the DMON and the iClisten device 'Bullseye' were inspected in their entirety. The AMAR recordings were inspected as outlined above. I also sampled beyond the regularly spaced 20% (every fifth day), when an automated detector (Mouy et al. 2009) indicated call presence (see Appendix). Call presence was noted for all species. Particular emphasis was given to large baleen whale species. As above, the recordings were subject to an AV inspection process, using Raven Pro Interactive software to generate spectrograms (256-point Hann window 1 s FFT with 50% overlap). Parameters were derived for all gray, fin, blue, and sei whale calls heard (as above) to form a call library per species, whereas calls of humpback and sperm whales, and delphinid species were noted as present only. This approach was taken due to the limited recording capacity in frequency range of the DMON system.

Calls were assigned to day-night, or day, night, and twilight using the nautical twilight times for both glider and iClisten. The presence of vessels was also noted for each five minute clip. For the glider data each call and clip were identified as either on the continental shelf, or on the slope, as well in a submarine canyon, or along the shelf-break. For discussions of call rate the 5-minute clips were aggregated into hourly totals.

*Key terms and concepts*

- Ambient noise - the residual, background noise when all individual identifiable sound sources and equipment self-noise has been eliminated
- Decibels – a tenth of a Bell, used to compare sound intensities or sound energy densities. Not an absolute measure of acoustic sound pressure
- Dialect – social signal variation in vocal behaviours of different but potentially interbreeding groups (e.g. ecotypes or geographic subpopulations)
- dB re 1µPa – is the intensity of the plane wave of pressure equal to one micro Pascal.
- FFT size – the number of points or length of time step in each fast fourier transformation
- Frequency – the number of cycles per second, derived from the wavelength of the sounds Given in Hertz, Hz

- Low – 10-500 Hz; Mid – 500-25,000 Hz ; High frequency - > 25,000 Hz

- Fundamental frequency – the lowest frequency of a waveform.
- Frequency modulation – a change in pitch of the fundamental frequency through the call.
- Lloyd mirror curve – a distinctive sound signal created by surface interference in the sound field
- Lombard effect (Cocktail party effect) – compensation in signal production to elevated ambient noise conditions
- 'Motherese' – vocalisations reserved for communications between a mother and her young. These are distinct from those used by other group members
- Octave frequency bands – ranges in frequency, whereby the highest value of the band is double that of the lowest
- Peak frequency – the frequency (Hz) where most of the energy of a call is focused
- Precision (P) – used in reference to the use of automated detectors on PAM data

$$P = \frac{N_{TP}}{(N_{TP}+N_{FP})}$$

$N_{TP}$ – number of true positives; $N_{FP}$ – number of false positives; $N_{FN}$ – number of false negatives

- Prosody – the intonation, tone, syntax, stress, or emphasis in a vocal expression
- Recall (R) – used in reference to the use of automated detectors on PAM data

$$R = \frac{N_{TP}}{(N_{TP}+N_{FN})}$$

$N_{TP}$ – number of true positives; $N_{FP}$ – number of false positives; $N_{FN}$ – number of false negatives

- 'Song' – a highly patterned and repetitive sequence that comprises of syllables and phrases, and contrasts to other social calls which are typically projected in more simple, discrete units
- Sound Fixing and Ranging (SOFAR)/ Deep water sound channel (DSC) – a horizontal layer of water in the ocean at which depth the speed of sound is at its minimum, and formed as a consequence of the characteristic velocity profile of the deep sea
- Spectrogram – a visual representation of the spectrum of frequencies of a sound or signal as they vary with time
- Speed of sound in air - 340 m/s
- Speed of sound in water – 1500 m/s or 3,000 kts

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# Appendix

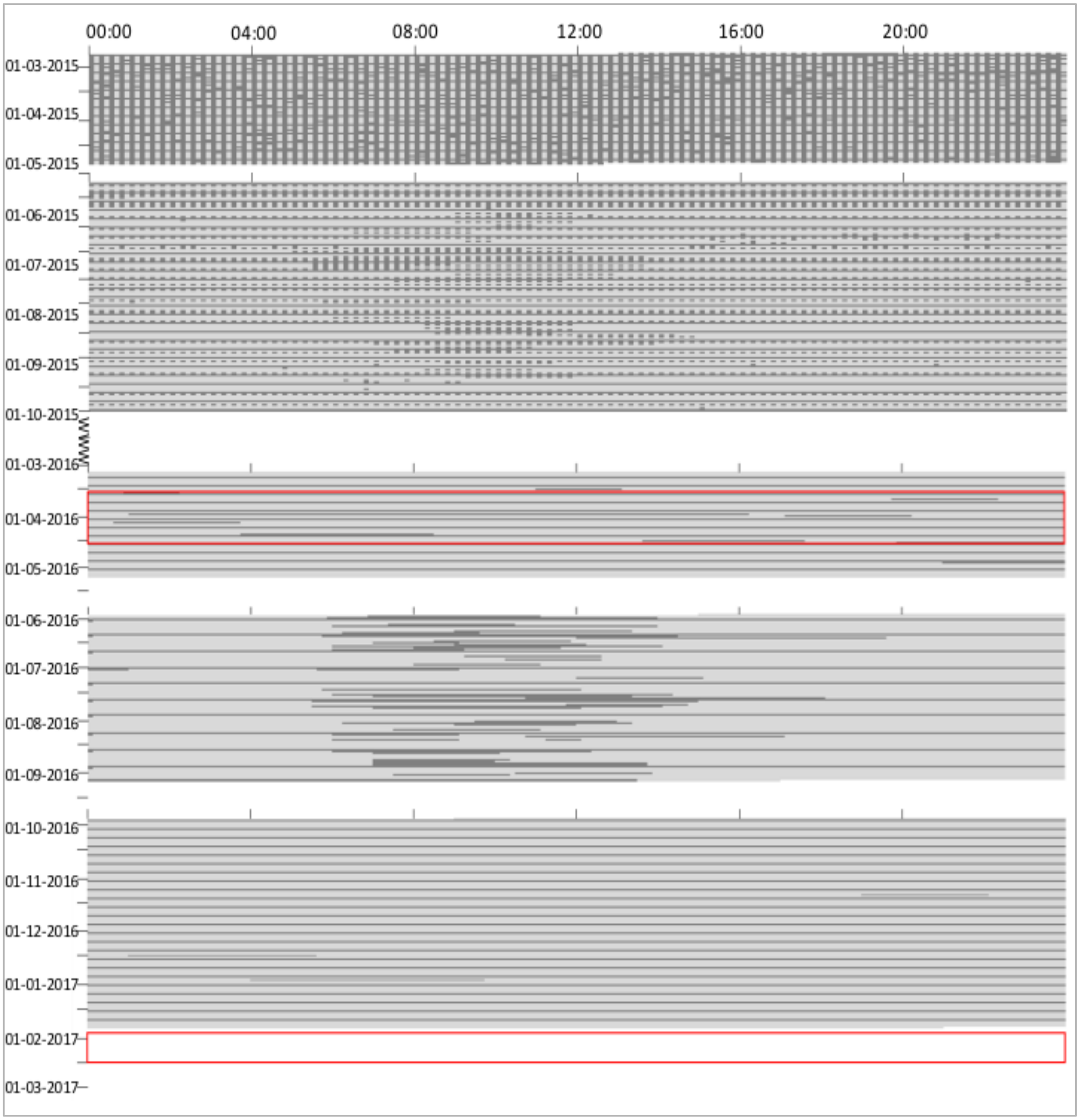

**Figure A.II.1:** Deployment of PAM systems between February 21, 2015 and March 1, 2017. AMAR recording periods is shown in light grey and the manually inspected data is shown in darker grey. The red boxes indicate ocean glider deployments, with the DMON data from these examined in its entirety. Data retrieved from the iClisten device 'Bullseye' matches the 2016 glider deployment and was also inspected for that whole period. Time of day is shown in twenty-four hour time across the top, with markers for each deployment showing 4 hour increments. The dates are given DD-MM-YYYY.

## 1. Part One: Coastal

*I must go down to the seas again, for the call of the running tide*
*Is a wild call and a clear call that may not be denied;*
*And all I ask is a windy day with the white clouds flying,*
*And the flung spray and the blown spume, and the sea-gulls crying.*

John Masefield (1878-1967)

## 1.1. Coastal Section: Introduction to the gray whale (*Eschrichtius robustus*) case study

Much is known about the life history of the eastern Pacific gray whale (*Eschrichtius robustus)*. An underexplored facet of its behavioral ecology is, however, its acoustic behaviour. Initial descriptions of gray whale vocalisations came from whalers, who reported them to 'sing' (Aldrich 1889), and use 'low pitched roars' (Tomlin 1957) in feeding grounds. From breeding grounds, intense sounds like that of hammering on the wooden hull of the ship were described by Rasmussen and Head (1965). Early recordings in dedicated acoustic studies did not find vocalisations to be prolific, leading the gray whale to be labelled 'the quiet whale' (Rassumussen & Head 1965, Appendix Chapter 1.8).

Since then, many studies have been conducted in the Mexican breeding lagoons to refine the call repertoire and its use. The call categorisation developed by Dahlheim (1987) is widely applied, whereby four 'core' call types, and two further acoustic projections of underwater exhalations were described. Knock-like calls formed by a sequences of pulses (class 1) were most frequently recorded from breeding areas, with other pulsed rumbles (class 4) noted. These calls were thought to be employed for within-group social contact, and over relatively short distance (Dahlheim 1987, Crane & Lashkari 1996, Charles 2011). Frequency modulated tones, for longer distance group cohesion, were also categorised as class 2 down- or up-sweeps and class 3 moans (Dahlheim et al. 1984, Dahlheim 1987, Crane & Lashkari 1996). More recent work has suggested the use of a type of 'motherese' vocalisation between cow-calf pairs, and suggest a period of learning, repertoire acquisition, and practise by young whales (Ollervides 2001, Charles 2011, López-Urbán et al. 2016). Application of these call types has been limited solely to breeding lagoons so far, with vocal refinement, and progression from 'motherese' to adult call types not yet clearly described.

Work outside of breeding areas is limited. Acoustic records of gray whales during migration and foraging are scant (Cummings et al. 1968, Moore & Ljungbald 1984, Dahlheim 1987, Crane & Lashkari 1996). The work that follows aims to address this. The deployment of a stationary hydrophone system in the migration route and in a productive feeding bay for long-term continuous recordings is intended to better describe the vocal behaviours of gray whales in their full range, and establish if call use is stereotyped to a locational, behavioural, or social setting. Findings from migration are described in Chapters 1.2 and 1.3, representing vocalisations during travel. Chapter 1.2 describes call type use and call structure compared to that described by Dahlheim (1987), whereas Chapter 1.3 looks more to calling rate, and how calls may be employed by gray whales to aid large-scale population movements. Also, I discuss how calling behaviours may be informative as to the timing, peaks, and modality of migration, using the PAM recordings as a remote census tool. Recordings for foraging are taken from the main feeding bay in Clayoquot Sound, a locale south of the principal Arctic feeding areas, and predominantly used by a population sub-group known as the Pacific Coastal Feeding Group (PCFG, Calambokidis et al. 2010, IWC 2010). A site description and details of the long-term use by foraging whales traced over a twenty year period is given in Chapter 1.4. Following this is an examination in Chapter 1.5 of calling behaviours during summer foraging. Here, I give extra attention to the presence and use of ‘motherese’-type calls by cow-calf pairs using the area as a nursing/weaning area. Drawing on data from a long-term study of gray whale use of Clayoquot Sound, I have an ecological foundation on which to place the findings from the acoustic recordings into context.

Call rate, type, and structure, may be nuanced to fit the whales surroundings. Modification of call use may be seen in response to varying ambient noise levels, for example, as discussed in Chapter 1.6. The strength and type of response, if any, may be directed by whether the driver is abiotic (e.g. wind, wave noise), biotic (presence of another species), or anthropogenically-derived. Clayoquot Sound is a busy whale-watching area, affording comparison between periods of vessel presence to those without. The examination of the acoustic response to human-introduced noise may help determine the level of disturbance these tourist activities have on a critical life stage for gray whales (Chapter 1.6). Altered calling behaviours may resemble those employed as a threat response (Lima & Dill 1990, Frid & Dill 2002), and so I also try to determine the vocal response to the acoustic presence of a predator (Chapter 1.7). This may help derive the threshold of response by gray whales in a period of perceived threat by comparing behaviours from overall soundscape change.

To find gray whales to be an acoustically active species may instigate a re-evaluation of what is known about this species, and the mechanisms underlying much of the behavioural ecology that has been described. It will also bring to bear an examination of the level of disturbance human has on this species, with its exposure to anthropogenic noise sources extensive when considering its full range.

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## 1.2. The not so quiet whale: Gray whale (*Eschrictius robustus*) call types recorded during migration off the west coast of Vancouver Island.

### Preface

Cetacean species adapt their acoustics use to the situation they are in, altering both the rate and type of call based on the behavioural, social, or geographical context in which they are made. Vocalisations for gray whales (*Eschrichtius robustus*) have been described from research in the breeding lagoons and, until recently, acoustic behaviour was thought to be almost non-existent in foraging areas and on migration routes. Indeed, scarcity of vocal behaviours is implied, with calls punctuating long periods of silence, earning the gray whale the moniker 'the quiet whale' (Rassmussen & Head 1965, Dahlheim 1987, Crane & Lashkari 1996). Vocalising behaviours of other baleen whale species has shown a breeding/feeding dichotomy in calling (e.g. Clark 1983, Parsons et al. 2008). For gray whales previous works have suggested this division to be more represented by signalling/silence, until very recently (Guazzo et al. 2017, Rannankari et al. 2018).

Here, I use passive acoustic recordings made during whale migration, from a location approximately half the distance, on the west coast of Vancouver Island, to investigate their acoustic behaviours during travel. Whales are in a negative energy state during northward migration, following a winter of fasting, and so it would follow that gray whales are silent migrators to conserve energy during this time. Southward migrations follow a summer of foraging and replenishing energy reserves. Any differences between recordings, then, might suggest a difference in physiological state.

Gray whales represents the largest biomass of whales in Canadian waters during their migration period, yet their acoustic behavior has not been considered. Here, I describe the rate of calling, and type of calls employed to sharpen our understanding of gray whales' acoustics use during this time. This could lead to a reassessment of their ecology and sensitivity to human activity in the coastal areas they frequent.

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# Gray whale (*Eschrictius robustus*) call types recorded during migration off the west coast of Vancouver Island.

## Introduction

For many whale species, calls have been correlated with either a behavioural, social or geographic context, with changes in call repertoire and call rate over a species range. Whereas vocalising behaviours of gray whales (*Eschrichtius robustus*) have been well documented in their calving/breeding lagoons (Dahlheim et al. 1984, Dahlheim 1987, Ollervides 2001, Charles, 2011, López-Urbán et al. 2016), studies have only recently added to the body of knowledge from the rest of their range (see for example Moore & Ljungbald, 1984, Stafford et al. 2007, Youngson & Darling 2016, Guazzo et al. 2017, Rannankari et al. 2018). The use of bottom-mounted passive acoustic monitoring (PAM) systems allows long duration recordings with sensitivity into the lowest frequencies, capturing their full vocal range. These acoustic survey techniques are insensitive to sea state, weather, or light conditions, and data collection that was previously difficult or impossible, particularly during migration periods, is now feasible. These data document a highly acoustic whale, with extensive calling the norm, rather than scarce, as noted in previous vessel-based studies (Rassmussen & Head 1965, Cummings et al. 1968, Fish et al. 1974, Crane & Lashkari 1996, Wisdom et al. 2001).

Research from breeding lagoons describes six primary call types in the frequency range of 20 Hz to 2 kHz: class 1, a series of metallic pulses or knocks, sometimes called bongo or conga calls; class 2, a longer duration, single, up- or down-sweeping metallic pulse; class 3, a low frequency modulated moan-like pulse, in some works described as a 'growl'; class 4, higher frequency modulated pulses forming grunt or rumble like calls; class 5, higher frequency 'bubble blasts', and class 6, extended sub-surface exhalations (Dahlheim et al. 1984, Dahlheim 1987). Additional call types have been described, including a potential 'motherese' used specifically by cow-calf pairs (Ollervides 2001, Charles 2011, López-Urbán et al. 2016), 'clicks' or 'pulses' sometimes suggesting echolocation potential (Asa-Doria Perkins 1967, Fish et al. 1974), 'rasping', 'grunts', 'chirps', 'pop', 'croak' or 'bongs', and vocalisations where more than one call type is super-positioned, for example 'knock-moans' or 'knock-grunts' (Eberhardt & Evans 1962, Painter 1963, Wenz 1964, Gales 1966, Hubbs 1966, Poulter 1968, Fish et al. 1974, Dahlheim 1987, Wisdom et al. 2001).

On the northward migration, previous studies have found class 3 moans most frequent, in contrast to the class 1 knocking calls that dominate in breeding areas. Moans comprise up to 87% of the total calls recorded during migration (Cummings et al. 1968, Dahlheim 1987, Crane & Lashkari 1996, Guazzo et al. 2017), and are presumed to aid long distance herd cohesion, with broader spectrum modulated calls like class 1 and 4 used for sub- or within-group communication. At a time of negative energy balance, such as northward migration, I assume acoustic behaviours would be limited as a conservation measure, but recent recordings taken in California show that not to be the case (Guazzo et al. 2017). Limited data is available for southward migratory behaviours, where calling behaviours may reflect an altered physiological state compared to northward travel.

Here I aim to add to the body of knowledge of gray whale acoustic behaviour with long duration recordings taken during two northward and one southward migration by deploying a PAM device in the migration corridor. I look to variation in call type and rate for temporal patterning, particularly diurnal, and within- and between seasons, to refine hypotheses about potential call function.

## Methods

An Autonomous Multichannel Acoustic Recorder (AMAR, JASCO G3A) fitted with a GeoSpectrum M8E-132 calibrated omnidirectional hydrophone (sensitivity -165 dB re 1 V/ µPa, effective 5 Hz-150 kHz, gain of 6 dB) was deployed at a location along the gray whale migration route approximately 5 nm/9.26 km southwest of Siwash Point, Flores Island, on the west coast of Vancouver Island (49.21028, -126.24667) in 51 m of water. The AMAR recorded continuously in the low frequency ranges 0-8000 Hz throughout each of the deployments. The location was chosen using previous knowledge of the migration route in this area (Duffus, Pers. Comms., 1984-2017), as well as periodic vessel-based observations prior to, and during the deployment. The migration corridor is estimated to be within 8 km of the shore for breeding and non-breeding adults and juveniles, and within 5 km for cow-calf pairs, with some observations as close as 200-400 m from shore (Poole 1984, Perryman et al. 2002, DeAngelis et al. 2011). The southward migration is similar, but with some observations of whales traveling up to 40 km offshore (Green et al. 1995, Shelden et al. 2000, Figure 1.2.1).

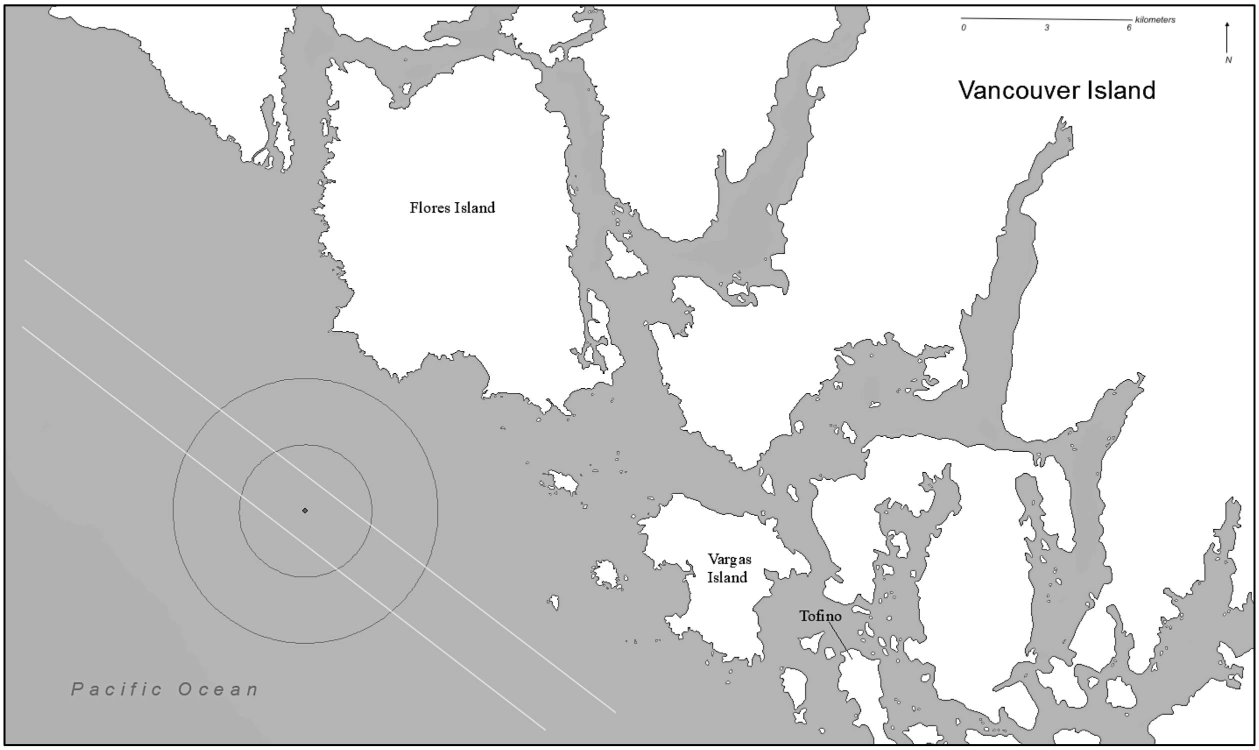

**Figure 1.2.1:** Location of AMAR deployment, with migratory corridor and likely range detection radii of gray whale class 3 moan calls. AMAR location is in the centre of the detection circles with the smaller circle representing the range of detection 80% of the time (3 km) and the larger 10 % of the time (6 km). The lines parallel to the coast line are 8 km, to indicate the migratory path of Phase A whales, and 5 km, for the cow-calves in Phase B.

The PAM system was deployed between February 21 and April 25, 2015 (N1) and March 7 to May 5, 2016 (N2) for the northward migration, and September 27, 2016 to January 25, 2017 (S1) for southward migration. Recordings were made constantly, covering the peak migration sightings off the west coast of Vancouver Island (Duffus, Pers. Comms., 1984-2017) and compared to data from California shore-counting and PAM survey stations (ACS Sighting data, Guazzo et al. 2017).

Manual identification of calls was made through visual and aural examination of sound files and respective spectrograms using Raven Pro Interactive Sound Analysis Software. For the 2015 northward migration (N1) the data was split into 900 s segments, and the first 340 s of every segment was manually examined. A random selection of 200 of the 900 s segments was fully analysed. For all deployments a minimum of every fifth day (20%) of the recording period was manually inspected, accounting for a total of 56.6% for N1, 23% for N2 and 20.7% for S1. Spectrograms were generated using a 256-point Hann-window FFT with 50% overlap.

Comparisons were made to the core call types, described by Dahlheim (1987) and subsequent others (Crane & Lashkari 1996, Ollervides 2001, Wisdom et al. 2001, Stafford et al. 2007, Charles 2011, López-Urbán et al. 2016, Youngson & Darling 2016) where appropriate. Calls were categorized as class 1-4, as described by Dahlheim (1987), possible 'motherese', or 'other' if they matched the descriptions from other studies or were still believed to be gray whale sounds due to frequency (Hz) and received volume of sound relative to ambient noise conditions. I modified the classification of class 1 calls to indicate frequency modulation (1a) or not (1b), and class 2 to distinguish between upsweeps (2a) and downsweeps (2b). Sub-surface exhalation sounds for class 5 and 6 (Dahlheim 1987) were noted, but used here only to indicate whale presence, and were not subject to further analysis. In addition, the full recordings were subject to an automated detection system (Mahoney et al. 2014, Mouy et al. 2015), to compare with the manual analysis. For gray whale call detection, the automated system uses a decision-tree like process, comparing recordings of high acoustic energy to definitions of calls, described by the sound's frequency (slowest and highest harmonic extents, range, and change in call/modulation) and duration. An estimated number of calls for the deployment was calculated based on the number of calls identified in the percentage of each deployment that was manually inspected, and extrapolated to the full deployment ((Number of calls identified/Amount of time verified) x Total recording time). This extrapolation presumed in this case that calling was at a consistent rate with no diurnal or seasonal patterning to vocal behaviours, and did not discern the number of callers at any time. Also a correction of call number, using a comparison of the results of the automated detector and manual verification was calculated to establish a level of detection accuracy (precision and recall calculations, as decribed in Chapter II).

For each of the calls, a series of measurements were made. Calls were described by their duration (s), lower and upper frequency (Hz) extents, the frequency range (Hz) of the call harmonics, and peak frequency (Hz), where the acoustic energy of the call is greatest. Comments on call qualities were also noted, to allow for later refinement of call categories. Any calls where background noise, particularly vessel noise, masked the accurate measurement of these metrics were excluded from further analysis, as were those calls labeled 'other'.

The appropriateness of the separate call categories, and subsequent subdivisions, was analysed for each call class and sub-class comparing call metrics of frequency extents, range, peak, and duration of all calls recorded during the migration periods.

An estimate of the range and probability of call detection was made using ambient noise levels taken at each minute of the recording, source levels for moan calls as reported by Guazzo et al. (2017; 156.9 ± 11.4 dB re 1µPa @ 1m), and an approximation of transmission loss using the spherical spreading law (Urick 1983). Given the low frequency nature of gray whale calls found in this and other works, attenuation was not included in the transmission loss estimation (see Figure A.1.2.1 in the Appendix for details). Moan calls are typically lower in frequency (Hz) and greater in amplitude (dB) than knock calls (Cummings et al. 1968) and so would approximate the furthest distance calls are likely received from during these recordings.

External factors that may affect calling behaviours were also explored, including photoperiod, tidal cycle, ambient noise and presence of vessel noise. Also, changes in call rate and call type was explored as the season progresses. For photoperiod, a day-night comparison was used, where day was defined as the time between nautical twilight start and stop times, where the sun crosses above 12 degrees below the horizon. Night is the opposing time, when the sun has crossed 12 degrees below the horizon. To include periods of twilight this definition was adjusted so that dawn is the time between the nautical twilight start and sunrise, day is sunrise to sunset times, dusk is between sunset and nautical twilight end, and night remains between nautical twilight times of dusk and dawn. Tidal effects were examined by correlating to tide levels, as well as grouping calls as either low or high slack tide, which was defined as 2 hours before and after the turning of the tide, and ebb and flood periods between slacks. Ambient noise levels were calculated per minute for 1/3 octave frequency bands. The overall ambient noise levels in the range of gray whale acoustics use was estimated by summing the 1/3 octave bands centered around 1-2000 Hz, to capture the full frequency range of calls. Ambient condition was correlated to each call identified, or converted to an hourly average to examine calling rate in changing background noise conditions. Finally, the calling rate and use of each call type was considered as the survey period progressed by correlating call number with the number of days elapsed since January 1 of that year.

## Results

A total of 13,749 calls were analysed from the northward migration from 2015 and 2016, and 3,691 were analysed for the southward migration. The appropriateness in combining the two northward deployments was tested, comparing calling rates, call distibutions and call parameters, and deployments were not found to be significantly different. All core call types were present for all deployments (see Figures A.1.2.2-5 in Appendix for example spectrograms of each call type), but in all cases, class 3 moan calls were dominant, with 83.69% for northward and 98.05% for southward travel. The number of calls identified by the auto-detector, corrected by the manually verified data is also given as a comparator for each deployment (Table 1.2.3). The number of calls, call duration, frequency extents, and peak were compared for northward and southward movement for this study as well as to previous studies. Calling rate is greater and calls typically lower during northward migration compared to southward travel, and similarly greater acoustics use and calls focused into the lower frequencies was seen when comparing calls from this study to previous works (Table 1.2.1, 1.2.2). The number of calls expected for the full deployment was extrapolated using the rate of calls per hour of the manually inspected data, under the assumption that the rate of calling was consistent in all time periods throughout the deployment ('calls/rate' in Table 1.2.3). Using a comparison of the auto-detector results and manually inspected data, estimates of a corrected call number were possible ('calls corrected' in Table 1.2.3). I compared the proportion of false positive and false negatives between the detector to the verified data (0.52-4.88% and 14.95-26.55% respectively), and analysed whether the number of calls correctly identified were accurate, or an over- or underestimate (50.96-60.55% and 4.16-41.12% respectively).

The distinction of call classes was tested by comparing the means for each call metric by class (T-test with Bonferroni correction (testing at p=0.0025 significance level), Table 1.2.4-1.2.8). Overall, significant differences in composition of call types were found for calls employed during migration. A pair-wise comparison of migration calls (both north and southward) found significant differences between call classes consistently, with class 4 the most like other call types (T-test with Bonferroni correction, Tables 1.2.4-1.2.8). In particular the appropriateness of sub-division was explored with calls 1a and 1b, 2a and 2b, and 3 and 3a, all being significantly different in all call metrics. Subdivision on class 1 calls was based on presence of frequency modulation of call, for class 2 it was whether the call swept up or down in frequency, and for class 3 the category of 'low moan'(class 3a) was used for moan calls focused in the lower frequencies and did not show call harmonics above the fundamental frequency (Tables 1.2.4-1.2.8, Figures in Appendix).

Calls identified as possible 'motherese', first described in breeding lagoons by Ollervides (2001) and Charles (2011), were noted for both northward and southward migrations, but comprised only 0.28% and 0.13% of calls respectively. Therefore, they were not included in the more detailed call analysis. Class 5 and 6 exhalations were noted, with increased prevalence in the latter part of northward migrations, with the opposite true for southward recordings.

There were proportionately more calls at night than during the day, and at night compared to both day and twilight periods (dusk and dawn, Table 1.2.9). Call rate differences between day and night periods, or day-night and twilight periods were tested (Table 1.2.10, Figure 1.2.2, 1.2.3). For northward migration, there was a significant difference when all call types are pooled (Mann-Whitney U, $p<0.001$), and between day-night calling behaviours in class 1 knock calls (Mann-Whitney U, class 1a: $p=0.009$; class 1b: $p=0.041$) and class 3 moans (Mann-Whitney U, $p=0.001$). For southward migration the trend was similar with overall calling (Mann-Whitney U, $p=0.008$) significantly changed between day and night periods, driven by increased use of moan calls (Mann-Whitney U, $p=0.011$). Light conditions had a significant influence on calling for both north- and southward travel when considering periods of twilight, particularly for class 3 moan calls (Kruskal-Wallis, NM: $p=0.008$; SM: $p=0.010$, Table 1.2.10). When considered by call type and travel direction, the mean number of calls per hour differed significantly for class 1a (Welch's $t(314.178)=-1.987$, $p=0.048$) and class 3 (Welch's $t(569.770)=-2.918$, $p=0.004$) on northward migrations when comparing day-night photoperiods. The use of class 1a modulated knocks also differed significantly between dawn and dusk (Welch's $t(36.391)=2.091$, $p=0.044$). Class 1 calls were not significantly different between day and night periods in their rate of use (mean number of calls/hour) on the southward migration, with all other call classes showing significant differences in response to photoperiod (T-tests, Table 1.2.11).

A similar analysis of call rate correlated to tide cycle was performed, grouping calls to those at either low or high slack tide, which was 2 hours before and after the turning of the tide, and ebb and flood periods between slacks. This showed no significant results for any call class in any deployment. Therefore tides are deemed ineffective to calling in this setting. Correlating call rate and metrics with ambient noise produced a negative correlation between frequency extent, frequency range, peak frequency and duration with increased ambient noise (Table 1.2.12). However, the rate of employment of each call type was not significantly altered in the presence of vessels. Call parameters for classes 2a, 3a and 4 were correlated to changes in ambient noise levels significantly to the p=0.05 level if not p<0.001 for northward migration (Spearman's rho, Table 5), with no significant correlation consistently seen for any call type on the southward migration (Spearman's rho, Table 1.2.12). Most of the correlations are weak, only a few are moderately strong. Rises in ambient noise levels are coupled with lower frequency calls, but the relationship again is not strong (Table 1.2.12).

In general, all call types showed a negative correlation with the seasonal progression of time, with the four core call types significant at the p=0.001 level (Spearman's rho, Table 1.2.13). For northward migration classes all core call types show significant negative correlation with time, except upsweeps (class 2a: $r_s$ =0.182, p<0.000) and low moans (class 3a: $r_s$ =0.068, p=0.661). For whales migrating south, only moan call use is significantly correlated with time, and negatively (class 3, south: $r_s$ = -0.210, p<0.000, Table 1.2.13).

The estimated detection probability of moan calls, the most prevalent call, by the recorder is shown graphically (see Figure A.1.2.1, Appendix) and spatially in relation to the hydrophone deployment site (Figure 1.2.1). Moans with the highest source levels are estimated to be detectable up to 3 km from the recorder 80% of the time and up to 6 km, 10 % of the time, encompassing the migration corridor and coastal and offshore waters that may be part of it. Recordings are unlikely to come from coastal feeding regions.

**Table 1.2.1:** Number of calls (N) and mean, standard deviation (St. Dev.) and coefficient of variation (CV) for each call metric by call type. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Frequency measures are in hertz (Hz), and length in seconds (s). Total northward calls is 13,749 and southward is 3,691.

| Call class | | Northward migration | | | | Southward migration | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | N | Mean | St. dev. | CV | N | Mean | St. dev | CV |
| 1a | Low freq. | 994 | 174.33 | 140.21 | 80.43 | 34 | 19.75 | 12.18 | 61.67 |
| | High freq. | 994 | 760.34 | 428.89 | 56.41 | 34 | 214.03 | 136.28 | 63.67 |
| | Peak freq. | 994 | 258.34 | 82.00 | 31.74 | 34 | 65.44 | 51.80 | 79.16 |
| | Length | 994 | 1.58 | 1.08 | 68.35 | 34 | 2.40 | 2.57 | 107.08 |
| | Freq. range | 994 | 588.41 | 130.20 | 22.13 | 34 | 194.28 | 150.70 | 177.57 |
| 1b | Low freq. | 21 | 42.43 | 91.60 | 215.88 | 8 | 99.04 | 93.41 | 94.32 |
| | High freq. | 21 | 219.68 | 251.98 | 114.70 | 8 | 406.25 | 171.34 | 42.18 |
| | Peak Freq. | 21 | 63.64 | 99.24 | 155.94 | 8 | 197.89 | 128.61 | 64.99 |
| | Length | 21 | 2.32 | 0.85 | 36.65 | 8 | 3.03 | 1.35 | 44.55 |
| | Freq. range | 21 | 177.25 | 184.01 | 103.81 | 8 | 307.21 | 112.35 | 36.57 |
| 2a | Low freq. | 998 | 43.58 | 26.60 | 61.04 | 26 | 33.43 | 20.19 | 60.39 |
| | High freq. | 998 | 179.93 | 68.23 | 37.94 | 26 | 159.10 | 26.45 | 16.62 |
| | Peak freq. | 998 | 79.34 | 39.69 | 50.03 | 26 | 68.55 | 30.72 | 44.81 |
| | Length | 998 | 1.65 | 0.59 | 35.76 | 26 | 2.78 | 1.21 | 0.44 |
| | Freq. range | 998 | 136.26 | 57.58 | 42.26 | 26 | 125.67 | 23.51 | 18.71 |
| 2b | Low freq. | 65 | 30.81 | 17.27 | 56.05 | 4 | 27.03 | 27.36 | 101.22 |
| | High freq. | 65 | 123.02 | 45.39 | 36.90 | 4 | 116.55 | 56.44 | 48.43 |
| | Peak freq. | 65 | 59.88 | 25.69 | 42.90 | 4 | 53.00 | 31.09 | 58.66 |
| | Length | 65 | 2.21 | 0.67 | 30.32 | 4 | 5.09 | 1.50 | 29.47 |
| | Freq. range | 65 | 92.22 | 49.54 | 53.72 | 4 | 89.53 | 51.06 | 57.03 |
| 3 | Low freq. | 11506 | 19.58 | 15.66 | 79.98 | 3619 | 16.09 | 7.49 | 46.55 |
| | High freq. | 11506 | 124.62 | 33.44 | 26.83 | 3619 | 114.27 | 31.38 | 27.46 |
| | Peak freq. | 11506 | 48.03 | 24.55 | 51.11 | 3619 | 48.73 | 25.34 | 52.00 |
| | Length | 11506 | 2.14 | 0.80 | 37.38 | 3619 | 2.52 | 1.14 | 45.24 |
| | Freq. range | 11506 | 105.05 | 33.53 | 31.92 | 3619 | 98.17 | 3.52 | 3.59 |
| 3a | Low freq. | 172 | 32.36 | 13.27 | 41.01 | 0 | | | |
| | High freq. | 172 | 58.61 | 20.50 | 34.98 | 0 | | | |
| | Peak freq. | 172 | 44.90 | 15.64 | 34.83 | 0 | | | |
| | Length | 172 | 2.27 | 0.94 | 41.41 | 0 | | | |
| | Freq. range | 172 | 23.15 | 13.34 | 57.62 | 0 | | | |
| 4 | Low freq. | 19 | 36.32 | 25.78 | 70.98 | 0 | | | |
| | High freq. | 19 | 151.44 | 67.65 | 44.67 | 0 | | | |
| | Peak freq. | 19 | 66.09 | 30.82 | 46.63 | 0 | | | |
| | Length | 19 | 2.37 | 0.84 | 35.44 | 0 | | | |
| | Freq. range | 19 | 115.12 | 55.54 | 48.25 | 0 | | | |

**Table 1.2.2:** Call proportion and descriptors for core call types for this and previous PAM of gray whale calls during migrating periods. Peak frequency and call duration values are mean values. For calls identified for this study class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'.

| Call Class | Direction | Proportion of calls (%) | Freq. range (Hz) | Peak Freq. (Hz) | Call length(s) | Reference |
|---|---|---|---|---|---|---|
| 1 | S | 4.76 | <350 | - | - | Cummings et al. 1968 |
| | N | 37 | 45-4520 | 665.5 | 0.9 | Crane and Lashkari 1996 |
| | N/S | 1.79 | - | 149 | - | Guazzo et al. 2017 |
| 1a | N | 7.23 | 11.7-733.60 | 258.34 | 1.58 | This study |
| | S | 0.92 | 2.7-633.20 | 65.44 | 2.40 | This study |
| 1b | N | 0.15 | 4.6-825.70 | 63.64 | 2.32 | This study |
| | S | 0.22 | 20.20-639.60 | 197.89 | 3.03 | This study |
| 2a | N | 7.26 | 3.7-684.60 | 79.34 | 1.65 | This study |
| | S | 0.70 | 6.90-205.30 | 68.55 | 2.78 | This study |
| 2b | N | 0.17 | 63.20-355.60 | 143.05 | 0.89 | This study |
| 3 | S | 87.00 | 20-200 | - | - | Cummings et al. 1968 |
| | N | 46.51 | 12.5-550 | 74 | - | Crane and Lashkari 1996 |
| | N/S | 22.24 | - | 38.1 | 1.79 | Guazzo et al. 2017 |
| | N | 83.69 | 1.80-738.10 | 48.03 | 2.14 | This study |
| | S | 98.05 | 1.80-417.90 | 48.73 | 2.52 | This study |
| 3a | N | 1.25 | 1.90-222.30 | 44.90 | 2.27 | This study |
| | S | 0 | - | - | - | This study |
| 4 | N | 4.26 | 147-1000 - | - | | Crane and Lashkari 1996 |
| | N | 0.14 | 4.60-324.60 | 66.09 | 2.37 | This study |
| | S | 0 | - | - | - | This study |

**Table 1.2.3**: Call numbers from manual verification and auto-detector. 'Calls identified' are the total number of calls identified during manual inspection (including 'motherese' and those excluded from call metrics analysis due to interference of background noise); 'Calls detected' are those indicated by the detector system; 'Calls/rate' is the number of calls expected if the rate of calling established from the proportion of manually inspected data is extrapolated to the full deployment, and 'Calls corrected' is the 'Calls detected' corrected using the proportion of false positives and negatives, and over or underestimates from correctly identified call presence when comparing the results from the detector and manual verification . 'Calls/day' is expressed using the calls corrected number and deployment length.

| Deployment | Length (days) | Percent verified (%) | Calls identified | Calls detected | Calls/ rate | Calls corrected | Calls/ day |
|---|---|---|---|---|---|---|---|
| N1 | 64 | 56.6 | 7,841 | 7,763 | 14,622 | 10,597 | 166 |
| N2 | 60 | 23 | 3,779 | 5,064 | 6,521 | 5,788 | 96 |
| S1 | 121 | 20.7 | 4,701 | 8,063 | 22,688 | 10,529 | 87 |

**Table 1.2.4**: T-test comparison of mean low frequency (Hz) measures of calls by type for calls identified in recording of both north and southward migration. The application of a Bonferroni correction means significance is tested at the p=0.0025 level. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Total northward calls is 13,749 and southward is 3,691. T and p values displayed.

| Low frequency (Hz) | 1a | 1b | 2a | 2b | 3 | 3a |
|---|---|---|---|---|---|---|
| 1a, t: | | | | | | |
| p: | | | | | | |
| 1b, t: | 6.176 | | | | | |
| p: | <0.001 | | | | | |
| 2a, t: | 28.130 | 0.844 | | | | |
| p: | <0.001 | 0.406 | | | | |
| 2b, t: | 28.417 | -5.490 | -1.561 | | | |
| p: | <0.001 | <0.001 | 0.129 | | | |
| 3, t: | 34.292 | 2.251 | 27.238 | 5.538 | | |
| p: | <0.001 | 0.032 | <0.001 | <0.001 | | |
| 3a, t: | 34.173 | 2.238 | 25.819 | 5.386 | -0.726 | |
| p: | <0.001 | 0.033 | <0.001 | <0.001 | 0.468 | |
| 4, t: | 18.051 | 1.179 | 1.055 | -0.911 | -2.970 | -2.928 |
| p: | <0.001 | 0.247 | 0.292 | 0.372 | 0.008 | 0.009 |

**Table 1.2.5**: T-test comparison of mean high frequency (Hz) measures of calls by type for calls identified in recording of both north and southward migration. The application of a Bonferroni correction means significance is tested at the p=0.0025 level. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Total northward calls is 13,749 and southward is 3,691. T and p values displayed.

| High frequency (Hz) | 1a | 1b | 2a | 2b | 3 | 3a |
|---|---|---|---|---|---|---|
| 1a, t: | | | | | | |
| p: | | | | | | |
| 1b, t: | 9.936 | | | | | |
| p: | <0.001 | | | | | |
| 2a, t: | 41.132 | 2.019 | | | | |
| p: | <0.001 | 0.053 | | | | |
| 2b, t: | 42.450 | -9.627 | -3.244 | | | |
| p: | <0.001 | <0.001 | 0.003 | | | |
| 3, t: | 45.846 | 3.279 | 26.874 | 0.126 | | |
| p: | <0.001 | 0.003 | <0.001 | 0.900 | | |
| 3a, t: | 52.288 | 5.204 | 66.666 | 15.954 | 151.837 | |
| p: | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | |
| 4, t: | 28.702 | 2.493 | 1.781 | -1.749 | -1.887 | -7.521 |
| p: | <0.001 | 0.018 | 0.075 | 0.094 | 0.075 | <0.001 |

**Table 1.2.6**: T-test comparison of mean peak frequency (Hz) measures of calls by type for calls identified in recording of both north and southward migration. The application of a Bonferroni correction means significance is tested at the p=0.0025 level. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Total northward calls is 13,749 and southward is 3,691. T and p values displayed.

| Peak frequency (Hz) | 1a | 1b | 2a | 2b | 3 | 3a |
|---|---|---|---|---|---|---|
| 1a, t: | | | | | | |
| p: | | | | | | |
| 1b, t: | 6.489 | | | | | |
| p: | <0.001 | | | | | |
| 2a, t: | 30.904 | 0.954 | | | | |
| p: | <0.001 | 0.348 | | | | |
| 2b, t: | 30.644 | -5.844 | -1.801 | | | |
| p: | <0.001 | <0.001 | 0.082 | | | |
| 3, t: | 37.306 | 2.315 | 24.645 | 3.778 | | |
| p: | <0.001 | 0.028 | <0.001 | <0.001 | | |
| 3a, t: | 41.422 | 3.325 | 41.506 | 10.913 | 52.258 | |
| p: | <0.001 | 0.002 | <0.001 | <0.001 | <0.001 | |
| 4, t: | 20.811 | 1.457 | 1.418 | -0.947 | -3.149 | -5.762 |
| p: | <0.001 | 0.155 | 0.157 | 0.346 | 0.002 | <0.001 |

**Table 1.2.7**: T-test comparison of mean call length (s) by type for calls identified in recording of both north and southward migration. The application of a Bonferroni correction means significance is tested at the p=0.0025 level. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Total northward calls is 13,749 and southward is 3,691. T and p values displayed.

| Call length (s) | 1a | 1b | 2a | 2b | 3 | 3a |
|---|---|---|---|---|---|---|
| 1a, t: | | | | | | |
| p: | | | | | | |
| 1b, t: | -4.929 | | | | | |
| p: | <0.001 | | | | | |
| 2a, t: | -2.373 | 4.566 | | | | |
| p: | 0.018 | <0.001 | | | | |
| 2b, t: | -6.297 | 5.734 | -0.820 | | | |
| p: | <0.001 | <0.001 | 0.416 | | | |
| 3, t: | -26.037 | 1.979 | -25.846 | 1.352 | | |
| p: | <0.001 | 0.048 | <0.001 | 0.176 | | |
| 3a, t: | -25.346 | -1.505 | -24.491 | -3.780 | -14.184 | |
| p: | <0.001 | 0.142 | <0.001 | <0.001 | <0.001 | |
| 4, t: | -3.897 | 0.679 | -4.641 | 0.034 | -0.675 | 2.466 |
| p: | 0.001 | 0.501 | <0.001 | 0.973 | 0.500 | 0.023 |

**Table 1.2.8**: T-test comparison of mean frequency range (Hz) of call harmonics by type for calls identified in recording of both north and southward migration. The application of a Bonferroni correction means significance is tested at the p=0.0025 level. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'. Total northward calls is 13,749 and southward is 3,691. T and p values displayed.

| Frequency range (s) | | 1a | 1b | 2a | 2b | 3 | 3a |
|---|---|---|---|---|---|---|---|
| 1a, | t: | | | | | | |
| | p: | | | | | | |
| 1b, | t: | 10.333 | | | | | |
| | p: | <0.001 | | | | | |
| 2a, | t: | 33.789 | 2.361 | | | | |
| | p: | <0.001 | 0.025 | | | | |
| 2b, | t: | 34.084 | -7.098 | -3.652 | | | |
| | p: | <0.001 | <0.001 | 0.001 | | | |
| 3, | t: | 36.632 | 3.364 | 18.111 | -1.911 | | |
| | p: | <0.001 | 0.002 | <0.001 | 0.060 | | |
| 3a, | t: | 43.441 | 6.055 | 66.785 | 12.872 | 225.473 | |
| | p: | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 | |
| 4, | t: | 25.403 | 2.799 | 1.583 | -1.758 | -0.920 | -7.804 |
| | p: | <0.001 | 0.008 | 0.114 | 0.082 | 0.370 | <0.001 |

**Table 1.2.9**: Total number of calls per hour for each light condition, also expressed as a proportion. NM= northward migration, SM= southward migration.

| Calls/hr | NM | % | SM | % |
|---|---|---|---|---|
| Day | 250 | 32.60 | 192 | 31.20 |
| Dawn | 125 | 16.30 | 96 | 15.60 |
| Dusk | 125 | 16.30 | 96 | 15.60 |
| Night | 267 | 34.80 | 231 | 37.60 |
| | | | | |
| Day | 371 | 48.40 | 288 | 46.80 |
| Night | 396 | 51.60 | 327 | 53.20 |

**Table 1.2.10**: Distribution of calls by light condition, comparing Day-Night calling using a Mann-Whitney U test, and periods of Day-Night-Dusk periods (both sunrise and sunset) using a Kruskal-Wallis test. Here class 2 only represents upsweeps. NM=northward migration, SM=southward migration.

| Call class | NM Day/Night | SM Day/Night | NM Day-Night-Twilight | SM Day-Night-Twilight |
|---|---|---|---|---|
| All | <0.001 | 0.008 | <0.001 | 0.009 |
| 1a | 0.009 | 0.230 | 0.072 | 0.782 |
| 1b | 0.041 | 0.783 | 0.073 | 0.912 |
| 2 | 0.904 | 0.062 | 0.786 | 0.340 |
| 3 | 0.001 | 0.011 | 0.008 | 0.010 |
| 3a | 0.760 | 1.000 | 0.926 | 1.000 |
| 4 | 0.770 | 1.000 | 0.947 | 1.000 |

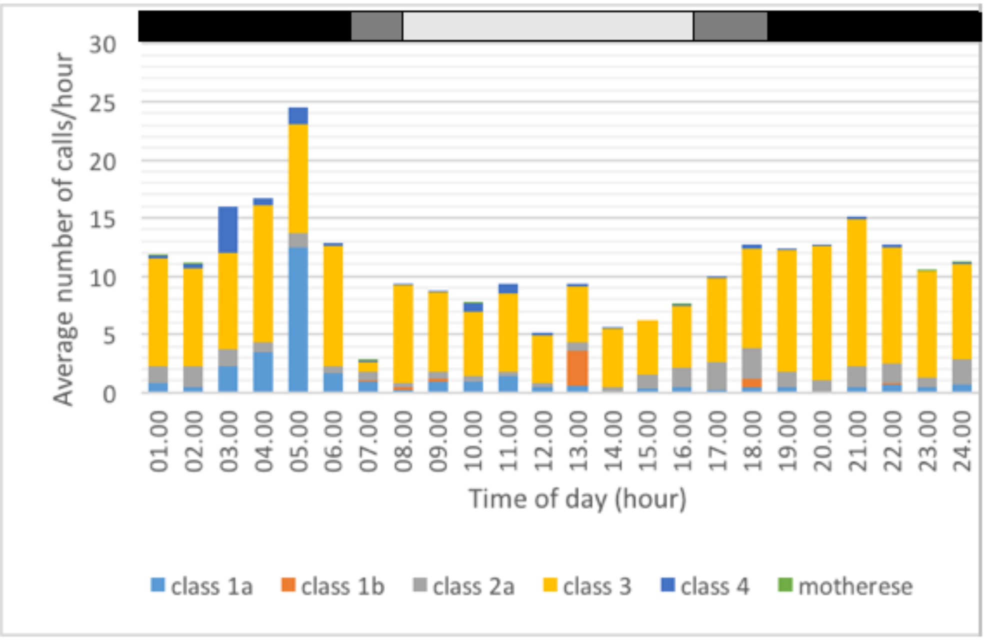

**Figure 1.2.2:** Mean number of calls per hour for each call type (for core call types, classes 1-4, and motherese call types pooled) through the day for northward migration. The shaded bar across the top of the chart represents night (black) twilight (dusk and dawn, dark grey) and day (light grey) according to nautical twilight time.

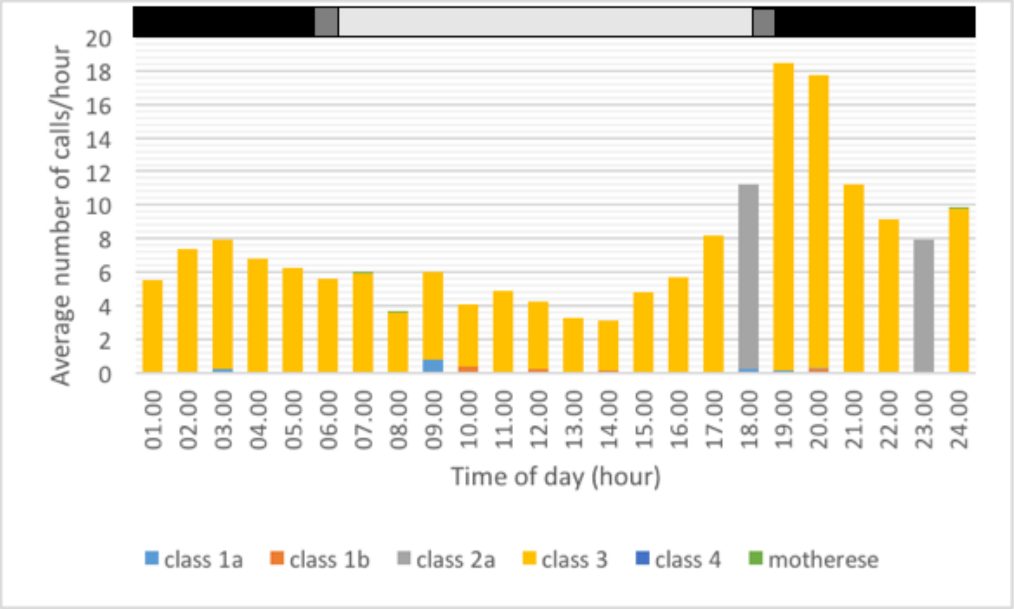

**Figure 1.2.3:** Mean number of calls per hour for each call type (for core call types, classes 1-4, and motherese call types pooled) through the day for southward migration. The shaded bar across the top of the chart represents night (black) twilight (dusk and dawn, dark grey) and day (light grey) according to nautical twilight time.

**Table 1.2.11**: Mean number of calls per hour across different light conditions. T-test t value and p values are given for the Day-Night comparison by call type. Here class 2 only represents upsweep calls. NM= northward migration, SM= southward migration

| Period | call class | Day | Dawn | Dusk | Night | Day | Night | t value | p value |
|---|---|---|---|---|---|---|---|---|---|
| NM | All | 8.19 | 10.70 | 12.88 | 13.274 | 8.79 | 13.72 | -3.508 | <0.001 |
| | 1a | 0.53 | 1.59 | 0.12 | 2.34 | 0.58 | 2.34 | -1.987 | 0.048 |
| | 1b | 0.11 | 0.00 | 0.00 | 0.01 | 0.09 | 0.01 | 1.627 | 0.104 |
| | 2 | 1.04 | 0.62 | 1.27 | 1.37 | 1.03 | 1.37 | -1.065 | 0.287 |
| | 3 | 6.39 | 8.73 | 10.93 | 10.01 | 6.97 | 10.01 | -2.918 | 0.004 |
| | 3a | 0.10 | 0.00 | 0.02 | 0.05 | 0.08 | 0.05 | 0.651 | 0.516 |
| | 4 | 0.24 | 0.14 | 0.02 | 0.42 | 0.21 | 0.42 | -1.084 | 0.279 |
| SM | All | 4.17 | 5.32 | 7.23 | 9.80 | 4.61 | 9.93 | -4.500 | <0.001 |
| | 1a | 0.01 | 0.00 | 0.00 | 0.05 | 0.01 | 0.05 | -1.359 | 0.175 |
| | 1b | 0.04 | 0.00 | 0.03 | 0.03 | 0.04 | 0.03 | 0.225 | 0.822 |
| | 2 | 0.01 | 0.04 | 0.00 | 0.07 | 0.01 | 0.07 | -2.012 | 0.045 |
| | 3 | 4.05 | 5.29 | 7.20 | 9.64 | 4.51 | 9.368 | -4.458 | <0.001 |

**Table 1.2.12**: Correlation, using Spearman's rho, between ambient noise condition and call metric for all call types during northward and southward migration. Parameters shown are call low frequency extent (Low freq.), high frequency (High freq.), peak frequency (Peak freq.), length, and frequency range (Freq. rang). Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b) and class 3 has a sub-group, 3a, of calls described as 'low moans'.

| | | Northward | | Southward | |
|---|---|---|---|---|---|
| | | Correlation | Significance | Correlation | Significance |
| 1a | Low freq. | -0.317 | <0.001 | -0.042 | 0.813 |
| | High freq. | -0.194 | <0.001 | -0.057 | 0.748 |
| | Peak freq. | -0.247 | <0.001 | -0.102 | 0.568 |
| | Length | -0.005 | 0.883 | 0.021 | 0.904 |
| | Freq. range | -0.0143 | <0.001 | -0.042 | 0.816 |
| 1b | Low freq. | -0.084 | 0.716 | -0.216 | 0.608 |
| | High freq. | -0.033 | 0.886 | -0.407 | 0.317 |
| | Peak freq. | -0.514 | 0.017 | 0.036 | 0.933 |
| | Length | 0.216 | 0.347 | 0.061 | 0.885 |
| | Freq. range | -0.068 | 0.767 | -0.683 | 0.062 |
| 2a | Low freq. | -0.242 | <0.001 | 0.352 | 0.078 |
| | High freq. | -0.343 | <0.001 | -0.116 | 0.572 |
| | Peak freq. | -0.199 | <0.001 | -0.295 | 0.143 |
| | Length | -0.178 | <0.001 | -0.400 | 0.043 |
| | Freq. range | -0.281 | <0.001 | -0.425 | 0.030 |
| 2b | Low freq. | 0.277 | 0.025 | 0.000 | 1.000 |
| | High freq. | -0.670 | <0.001 | -0.800 | 0.200 |
| | Peak freq. | 0.143 | 0.256 | 0.000 | 1.000 |
| | Length | -0.144 | 0.253 | -0.400 | 0.600 |
| | Freq. range | -0.593 | <0.001 | -0.800 | 0.200 |
| 3 | Low freq. | -0.247 | <0.001 | -0.217 | <0.001 |
| | High freq. | -0.024 | 0.002 | 0.046 | 0.006 |
| | Peak freq. | -0.112 | <0.001 | -0.239 | <0.001 |
| | Length | -0.247 | <0.001 | 0.027 | 0.108 |
| | Freq. range | 0.082 | <0.001 | 0.096 | <0.001 |
| 3a | Low freq. | -0.328 | <0.001 | -0.191 | <0.001 |
| | High freq. | 0.349 | <0.001 | 0.045 | 0.0224 |
| | Peak freq. | 0.348 | <0.001 | -0.139 | <0.001 |
| | Length | -0.111 | 0.147 | -0.054 | 0.149 |
| | Freq. range | 0.232 | <0.001 | 0.138 | <0.001 |
| 4 | Low freq. | -0.256 | 0.291 | | |
| | High freq. | -0.163 | 0.577 | | |
| | Peak freq. | -0.347 | 0.146 | | |
| | Length | -0.030 | 0.903 | | |
| | Freq. range | 0.186 | 0.446 | | |

**Table 1.2.13**: Correlation coefficients and significance of Spearman's rho correlation between calling rate (calls/hr) and year day (number of days elapsed since January 1), by call type and swimming direction.

| | Northward | | Southward | |
|---|---|---|---|---|
| Class | Correlation coefficient ($r_s$) | Significance level (p) | Correlation coefficient ($r_s$) | Significance level (p) |
| 1a | -0.195 | <0.001 | -0.045 | 0.265 |
| 1b | -0.010 | 0.774 | -0.043 | 0.292 |
| 2 | 0.182 | <0.001 | -0.210 | 0.611 |
| 3 | -0.214 | <0.001 | -0.210 | <0.001 |
| 3a | 0.068 | 0.661 | | |
| 4 | -0.248 | <0.001 | | |

## Discussion

These recordings are from a relatively uniform and stereotyped behaviour state dominated by linear, constant swimming. Migration is a continuous, protracted trail of whales, whose movements are consistent in direction and average speed (Perryman et al. 2002, Mate & Urbán-Ramirez 2003, Guazzo et al. 2017). The timing and location of the deployments largely excludes vocal behaviours associated with foraging and weaning (Burnham 2015). Although courtship and mating behaviours have been noted on the southbound migration (Gilmore 1960) and observed during northward migrations in Clayoquot Sound (Burnham, Pers. Obs., 2015) these are minor components of the whales' behaviour.

Gray whales call frequently during migration, which is in agreement with a recent study by Guazzo et al. (2017) on northward migrating whales in Californian waters, and demonstrates greater vocal activity than that suggested by earlier work (Rassmussen & Head 1965, Dahlheim 1987, Crane & Lashkari 1996). The average rate of calling concurs with recent reports for migration (Guazzo et al. 2017), and bottom mounted hydrophone recordings made in the breeding lagoons (5982 calls from three weeks, López-Urbán et al. 2016) and compares consistently to the corrected auto-detection data (Table 1.2.3).

The metrics of call duration and harmonics gives a rough approximation of the shape of the call and acoustic energy projected (see Appendix for example spectrograms). The calls identified in this study are in accordance with other PAM studies of gray whale migration. They are, however, typically longer and, in some cases, lower in frequency than those previously reported (Table 1.2.1, 1.2.2), suggesting a modification based on geographical location or perhaps water propagation properties. Comparison of call types over time showed a general decrease in frequencies employed this study and previous (Rassmussen & Head 1965, Dahlheim 1987, Crane & Lashkari 1996), and even between 2015 and 2016 for the northward migration, with moan calls consistently employing the lowest frequencies in frequency extents and peak frequency. This may represent a more general response to changes in soundscape, with blue (*Balaenoptera musculus,* McDonald et al. 2006) and fin whales (*Balaenoptera physalus*, Bradbury & Vehrencamp 1998) also noted to modify call structure over time to overcome anthropogenic additions to the ambient condition. The employment of 'low moans' by gray whales may also be part of the adaptation.

I employ a finer sub-division of classes than previous works, and present the description of a 'low moan' call type, referred to herein as class 3a. This study considers the use of all core call classes outlined by Dahlheim (1987), not seen in other previous studies, with manual inspection of the data allowing for a more nuanced consideration of vocal behaviours including these types of call subdivision, also seen in classes 1 and 2 (see Figures in Appendix). The 'low moan' calls show similarity to the fundamental frequency of a moan call, but do not contain call harmonics in higher frequencies. However, a crude comparison of the received amplitude of calls supports the subdivision of moan and low-moan, rather than the call being a result of information and harmonics loss in transmission and propagation. The low moans may represent, for example, variation in the size or state of the individual animal calling compared to moan calls, or an altered application of moan calls, discussed in more detail as part of another analysis (see Chapter 1.8).

Class 3 moan calls dominate migration vocalising. In each deployment, both north and southward, moan calls exceeded 80% of all calls manually verified. The rate of calling for northward migration was almost double that of southward, from manually verified data (NM=11.62 calls/hr, SM=6.11 calls/hr), and in the corrected auto-detector calling rate per day (Table 1.2.3). This rate of use of moans during migration is similar to other studies and contrasts to calling patterns noted for breeding areas, where their use is seen as almost negligible (Dahlheim 1987, Crane & Lashkari 1996). Also, moans show much less variation than the other call types (Table 1.2.1). A low-centred peak frequency and highly controlled call duration and frequency range, as well as the prominence of this call during migration, suggests this call type is linked to travelling behaviours. Moan calls may be a means to maintain herd cohesion as the whales migrate over larger spaces (see discussion in Chaper 1.3), whereas other call classes such as class 1 knocks, with their higher peak frequency and variability, are for within-group communication or possibly courtship behaviours (Crane & Lashkari 1996, Youngson & Darling 2016). Deployments for both north and southward migration were timed to capture the peak of the migrations past the recording site, substantiated by shore counts and data from the timing of whales entering and leaving the breeding lagoons (LSIESP 2014, 2015, ACS Sighting data, Guazzo et al. 2017, Chapter 1.3). The difference between call rates for north versus south movement (Table 1.2.1, 1.2.3) suggests that vocalisations may be a more necessary component of northward migration. The number of whales, and so potential callers, passing the recorder during migration periods presumed to be similar for north- and southward travel. Call number per day, particularly the number of moan calls per day, was found to be a good representation of the relative number of individuals passing the recorder, using shore counts as comparison to the acoustic data. Therefore, the progression and peaks of migration can be discerned from the number of calls detected but not the number of whales (see Chapter 1.3). Calling rate may be expected to be greater for southward migrations, as whales have restored their energy reserves and may also employ social calling for mate attraction, but this was not found. The function of calls, especially moans, may be nuanced to identify topographical/bathymetric features for navigation and a means to orientate less experienced whales to the migration route, as well as productive feeding areas or safe weaning sites as part of an overall cultural transmission of information (Calambokidis et al. 2010, Lang et al. 2011, Scordino et al. 2011, Chapter 1.3). My recording site is directly offshore from a heavily used summer foraging site and cow-calf requiem. Potential modifications to calling behaviours from whales traversing waters in or adjacent to feeding and weaning sites, for example to search for or advice conspecifics of prey resources, is outside the scope of this study and requires additional test sites.

Variation in calling, both in the rate and the composition of calls, may be trait specific to individual whales. The inherent rate of calling by an individual in the context of its social or behavioural setting is not known for gray whales, however, we can look at general patterns throughout a population using this migration data. There is variability in calling rate, call type, and within call classes, in the frequency extents, peak frequency and duration, throughout all deployments. Delivery of a call may be varied to amalgamate information on the caller identity and their physiological or emotional state, social or behavioural context of the call, as well as the message for the intended receiver. Changes in call features in relation to size of individuals signalling is not considered here. Also distance from hydrophone of the signaling whale, and how that affects the received call formant, is unknown. Calls, by type, are treated in this analysis equally whether they were received from Phase A or B on northward migration, or during the day or night which may have altered propagation distances (Figure 1, Poole 1984, Perryman et al. 1999, Perryman et al. 2002, DeAngelis et al. 2011). The call classes described here are an average of thousands of calls made by numerous individuals, possibly fulfilling multiple functions.

A preliminary analysis to tie the variation to an environmental context found calling to be greater at night than during the day, as suggested by Guazzo et al. (2017) and Rannankari et al. (2018). This suggests that visual cues may supplement acoustics during the day, particularly for fine scale navigation or orientation (Torres 2017). Diurnal changes in behaviour have been suggested for southward travel (Perryman et al. 1999), but not for northward migration (Perryman et al. 2002, Mate & Urbán-Ramirez 2003). Perryman et al. (1999) suggested that whales were socializing more during the day from observations made on southward migrating whales, which resulted in a slower swimming speed, however this was not mirrored by any acoustic alterations.

As well as photoperiod, a change in both calling rate and composition was heard in relation to ambient noise conditions and the presence of vessels. The acoustic reaction by whales to changes in the soundscape and presence of human-derived noise sources has not been studied in detail for baleen whale species. Gray whales are subjected to constant additions to natural background sound levels through much of their migration, following or cutting across shipping lanes and commercial fishing areas. Their potential adaptations and thresholds for call modifications in the presence of noise are yet to be fully examined, and are outside the scope of this work (see Chapter 1.6).

Studies of gray whales acoustics, including this one, have relied on categories described by Dahlheim (1987). All core call types were found, somewhat correlated to the seasonal passage of time (Table 1.2.7). Those call types proposed for within-group communication such as class 1 knocks and class 2 upsweeps have a significant positive correlation with time through the northward migration, with a higher occurrence in the latter part of the recordings. The reverse trend was seen for southward migrations, with moan calls decreasing significantly with time. This may be indicative of a switch from concentrated traveling behaviours to more social or prey searching/foraging behaviours in late April and May, with the opposite true for the southward migration, with some individuals still test-foraging prey patches as they return to the calving/breeding lagoons. A small proportion of calls were classified as potential 'motherese' calls (Ollervides 2001, Charles 2011) through the manual verification process, but not further considered for analysis. They were present in the latter part of the northward migration (late March-April), within the second phase of the migration. For the recordings of southward migration they are present only in September and October. Similarly, increased class 5 and 6 sub-surface exhalations during these periods suggest a shift shoreward during the second phase of the migration, particularly towards the end of April onwards for northward movements and a more offshore migration route taken after the early part of deployment recordings for southward migrations.

This study adds to the body of knowledge of gray whale acoustics use by contributing long-duration multi-year data from both north- and southward migrations. It hints at the need for more studies like this one, and more detailed analysis of the extensive vocal component of gray whales' ecology. Analysis of calling behaviour should extend past notation of presence, with results of PAM recordings complementing and enhancing studies on whales using and migrating in highly ensonified waters. Repeated and long term behavioural baseline studies such as this one may be able to give us an important cue to changes, if we can link them to altered ecosystem dynamics that migratory whales integrate over their extensive ranges and perceptual fields.

A version of the work described in this chapter has been published as:

Burnham, R.E, Duffus, D.A., Mouy, X. 2018. Gray whale (*Eschrichtius robustus*) call types recorded during migration off the west coast of Vancouver Island. *Front. Mar. Sci.* 5:329.

# Appendix

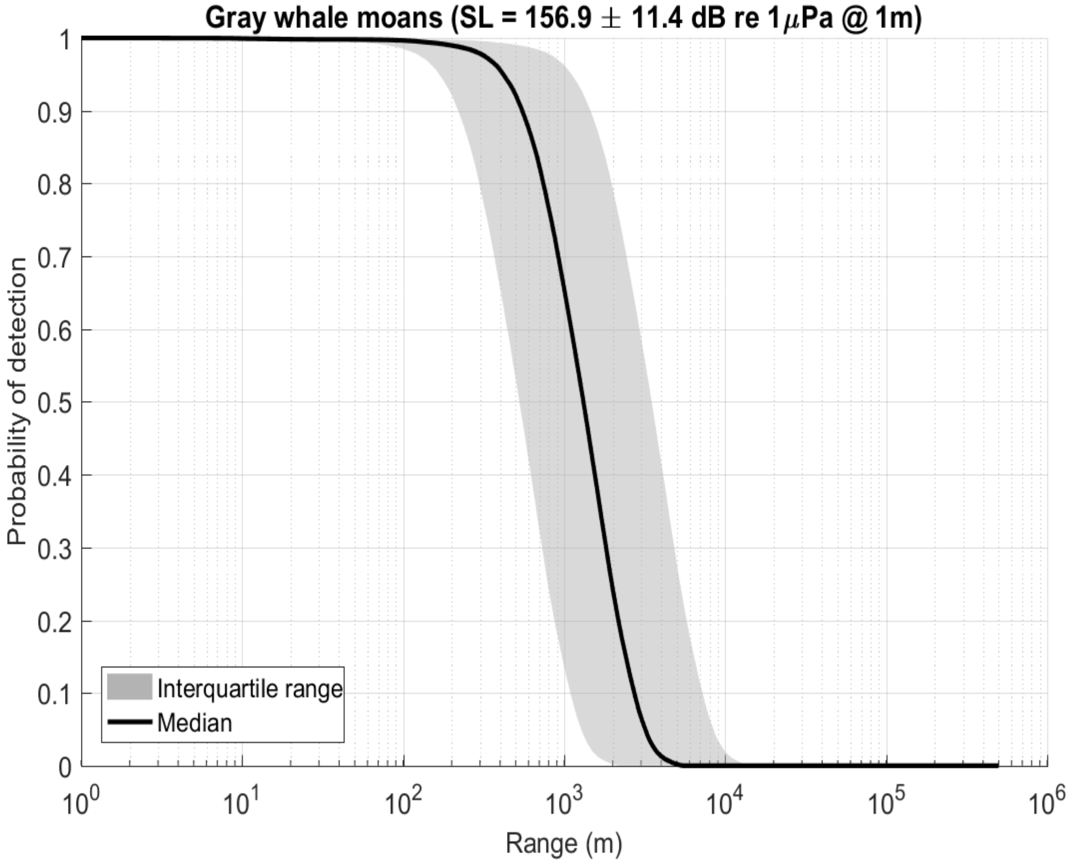

**Figure A.1.2**: Estimation of detection range of gray whale moans by the AMAR system throughout deployments. The range of detection of gray whale calls was estimated using ambient noise levels (NL) for each minute of recording, source levels (SL) of gray whale moans reported by Guazzo et al. (2017, 156.9 ± 11.4 dB re 1μPa @ 1m), and an estimate of the transmission loss (TL). The received sound level (RL) of a gray whale moan at the recorder is defined as RL = SL–TL(r), where r is the distance in meters between the whale and the recorder. The transmission loss was approximated to follow a spherical spreading law and was therefore estimated as TL(r) = 20 log10(r) (Urick 1983). Given the low frequency of the gray whale calls, attenuation was not included in the transmission loss estimation. The gray whale was considered to be an omnidirectional source. The detection range of a moan was estimated to be the distance from the recorder for which the received level of the gray whale moan equaled the noise level at the recorder (NL = RL). Noise levels used for estimating detection range were calculated for every minute of recording by summing the 1/3 octave bands centered between 20 and 100 Hz). The detection range was calculated for each minute of recording. The probability of detecting a gray whale moan at a given range was the number of 1 min recordings with a detection range equal to or greater than the given range divided by the number of 1 min recordings. A Monte Carlo method accounted for the measured variability in source levels. Detection ranges were re-calculated 300 times by randomly choosing 300 normally distributed source level values, with the means and standard deviations defined by Guazzo et al. 2017. Consequently, a distribution of probability is associated with each range.

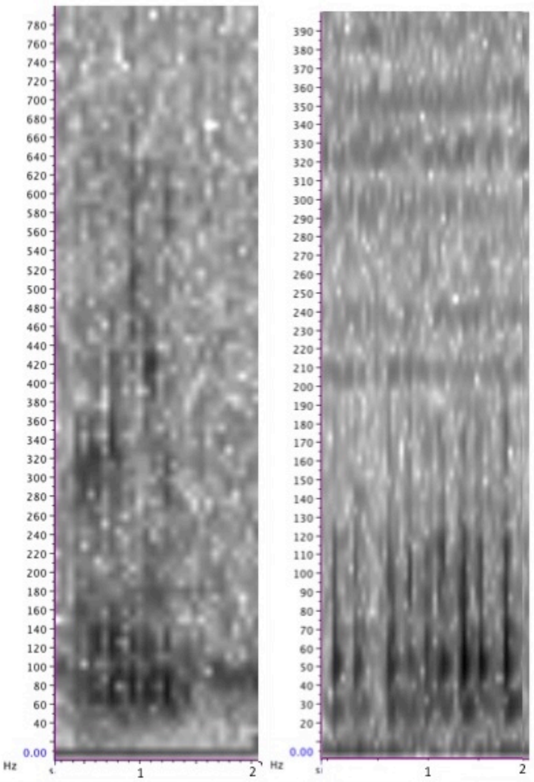

**Figure A.1.2.2:** Spectrogram of class 1 calls. Left: 1a, frequency modulated calls; Right: 1b, unmodulated. Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap. Note the frequency (Hz) scales are altered for clarity of each call type.

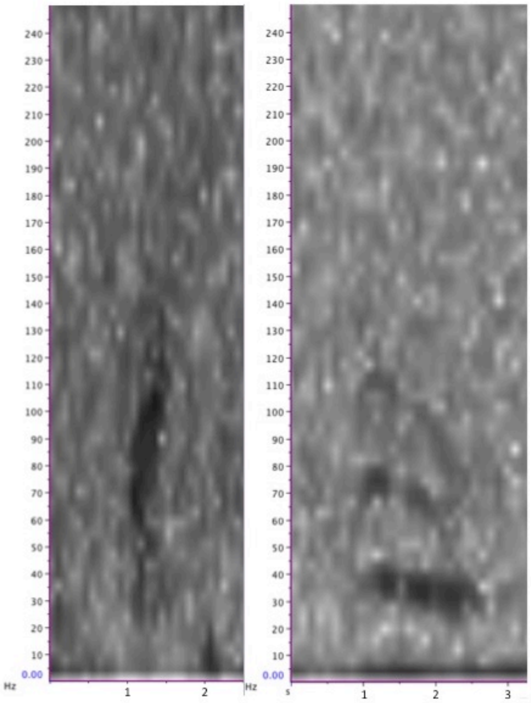

**Figure A.1.2.3**: Spectrogram of class 2 calls. Left: Upsweep, 2a; Right: Downsweep, 2b. Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

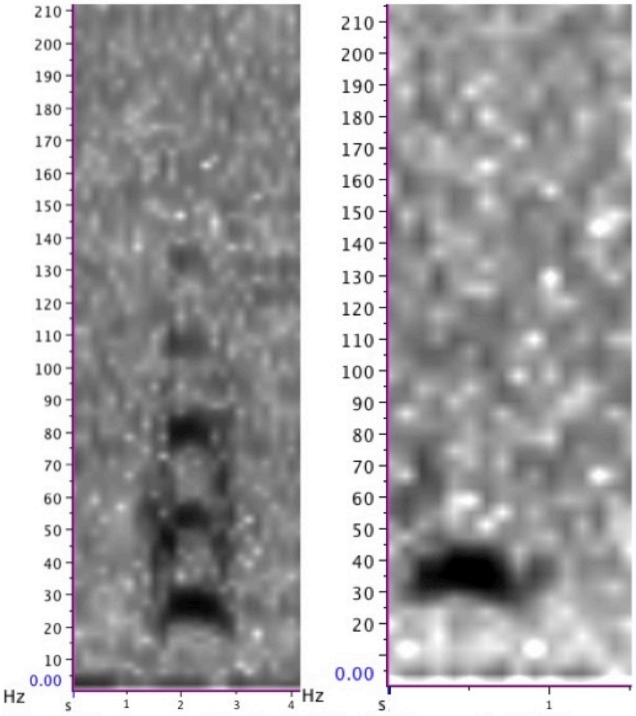

**Figure A.1.2.4:** Spectrogram of class 3 calls. Left: Class 3 moan call as described by Dahlheim (1987); Right: Low moan call, 3a. Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

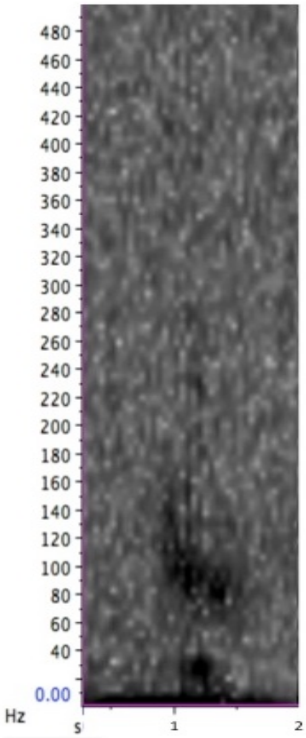

**Figure A.1.2.5:** Spectrogram of a class 4 call, as described first by Dahlheim (1987). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

## 1.3. Following the leader? Acoustic cue use in migration by gray whales

### Preface

The use of acoustics during periods of travel, and to aid navigation and group cohesion, has been noted for many species. Passively received soundscape information gives cues to location, with whales possibly interpreting signals from environmental features and conspecifics for orientation. In addition, some species actively employ acoustic signals to orientate and navigate. Here I discuss the acoustics use by gray whales during their lengthy, en-masse migration and how this may complement other, lesser employed, sensory systems. Navigation using returns of an individuals' own signals (echo-location) has only seen limited application to baleen whales (Norris 1966, 1969, Payne & Webb 1971, Thompson et al. 1979, Ellison et al. 1987, Clark & Ellison 2004, Oleson et al. 2007). For mysticetes, vocalisations are often assigned a social context, with contact calling for group cohesion likely to play a role during migration (Payne & Webb 1971, Würsig & Clark 1990, Edds-Walton 1997).

Because we cannot know the full spectrum of call functions, we are forced to piece together our interpretation of what a call is used for. Studies of the use of various call types in different habitats, and different life history situations will provide clues that we can put forward as hypotheses to unravel what may turn out to be a far more complex and important aspect of whales' lives. Chapter 1.2 showed gray whales to be much more sonorous during migration than previous research had described, suggesting an inherent use of acoustics in travel behaviours. Furthering the call descriptions from Chapter 1.2, in this Chapter, I discuss how calling and soundscape interpretation might play into both environmental imaging and group cohesion of whales during migration. I also explore the idea of whale calls acting as an acoustic census, comparing visual shore counts and call rates to test for possible associations between these two data streams in tracing the progression of migration.

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## Following the leader? Acoustic cue use in migration by gray whales (*Eschrichtius robustus*)

### Introduction

Migration is a non-trivial movement undertaken in response to endogenous rhythms or environmental signals typically between breeding and feeding, or breeding and refuge areas that are distant to each other (Baker 1978, Taylor 1986, Dingle 1996). This life history phenomenon is seen most frequently in species that rely on shifting or patchy habitats and prey resources (Dingle 1996), where migration likely enhances resource acquisition, reproductive success or survival of young. Destinations lie outside of the sensory range of the starting point, and so successful travel between locales is achieved by the use of orientating mechanisms, perceptual cues, or memory processes (Mueller & Fagan 2008).

Broadly there are three methods of navigation used in long-range movement: landmark navigation or 'piloting', following a sequence of reference points on a number of spatial scales, in in some cases with reinforcement markers to the target (Brown & Gass 1993); vector navigation, following a directional bearing for a given time or distance, which also may use cues to confirm orientation, and 'homing', or the use of a cognitive spatial map. These are formed by information garnered from landmark and vector navigation, incorporated with information from sensory streams, including physical, visual, olfactory and auditory inputs, to confirm direction and course, originating from the environment or from conspecifics. It allows for migration to an end-point despite displacement or obscured cues. First, I will discuss the navigational means of migrating species, especially those travelling as a group, flock, or herd, and then will focus on how this may apply to cetaceans, specifically baleen whales, with gray whales as a case study.

#### *The Senses*

The geomagnetic sense is the most widely applied physical navigational cue to animal navigation, where information of the location and angle of intersection of magnetic field lines, and the intensity of the signal, forms a bi-coordinate map (Wilschko & Wilschko 1996, 2005, Lohmann et al. 2007). Birds, particularly homing pigeons, bats, and small mammals, such as moles, rats and hamsters, are thought to use these cues (Lohmann et al. 1999, 2007, Bingham & Chen 2005,Wiltschko & Wiltschko 2005), additionally informed by barometric pressure (e.g. bees, Aidley 1981), or winds (e.g. birds and locus, Baker 1978). Birds also 'pilot' by landmarks, orientating to features such as shorelines, mountain ranges and other leading lines (Boinski & Garber 2000). Similar orientation techniques are also noted to primates (e.g. Mackinnon 1974). Several taxa orientate by the sun or skylight polarization, sun and moon position, and star patterns and other celestial cues, often tied to internal circadian rhythms (Aidley 1981, Wiltschko & Wiltschko 2003, Akesson & Hedenstrom 2007, Dacke et al. 2013). For some, these visual cues may be reinforced by other sensory cues also. Landscape features along the migration, as well as destination sites may have unique chemical signatures that could extend up to hundreds of kilometers, perhaps reflecting mountain ridges, river outlets, and coastlines (Benevenuti et al. 1994, Wallraff 2004, Nevitt & Bonadonna 2005). Scent can describe natal sites (e.g. birds Sinsch 1990, dung beetles Wallraff 2004), marks trails, and be used as a means to guide conspecifics, or demarcate a home range, which has been documented for wildebeest (Dingle 1996, Yahner 2012), and insects such as ants, termites, dungflies, bees, and wasps (Wilson 1965, Baker 1978, Kennedy 1983, Boinski & Garber 2000). Similarly, sites can have unique 'soundscapes'. Birds, for example use infrasonic sound resulting from wind off mountain ranges and ocean waves for broad scale spatial information (Aidley 1981, Hagstrum 2000). They may also use sonic-cues that result from the flapping of their wings when flying in formation as guidance (Stoker 2013). Passive listening to conspecifics is also seen in anuran species, with them following the breeding chorus of others to a particular site (Baker 1978). Conversely, active acoustics use such as echolocation in bats creates internal images of surroundings for navigation, orientation, and assessment of habitat suitability (Knörnschild et al. 2012).

### *Social elements*

Group migration allows for cultural transmission of information from more experienced individuals leading others, often incorporating behaviours to maintain contact and cohesion between individuals and/or coordinate movements. Primates, for example, travel with the rule 'keep at least one individual in sight'. Baboons, for example, maintain visual contact between conspecifics, supplemented with 'bark' calls if vision is obscured (Ingmanson 1996). Information transmission could be through communicative actions such as the honey bee 'waggle dance' (von Frisch 1967, Riley et al. 2005), or 'voting behaviours' in buffalo herds in pre-migration milling periods (Prins 1996). For more protracted herd migrations, trail markers may be created to mark travel trajectory, for example the seemingly deliberate breaking and disturbance of leaves and branches by bonobos (Ingmanson 1996), or the penal gland secretions of wildebeest that communicate direction and suitability of habitat (Baker 1978). Acoustic cues between conspecifics may be important to initiate travel, convey directional information, or aid group cohesion, and are often produced by mature, dominant group members (Laws et al. 1975). Calls like 'rallying' cries, as described for primates, wolves, hyenas, coyotes, and lions (Gautier & Gautier-Hion 1977), or 'let's go' rumbles heard from elephants (Poole et al. 1988) are noted early in migration, whereas calls that suggest the message 'travel in that direction' or 'continue traveling' described in howler monkeys are important to the troop throughout travel (Carpenter 1934). Additionally, information on route, ranging, and areas to be avoided is exchanged acoustically, as observed in mountain sheep (Geist 1971). Young frequently accompany their mothers on all or part of a migration circuit (Baker 1978), for the route to be learnt and committed to memory, as seen in terrestrial ungulate species (e.g. Bailey et al. 1996). Route communication and group cohesive techniques may be genetically determined or learnt through practise during this time (e.g. Gouzoules & Gouzoules 1989), and use then reinforced by social influence and learning (Whiten & Ham 1992, Janik & Slatter 1997).

### Migration in the marine setting

Organisms that swim often have the longest migrations, with marine species demonstrating large scale migrations similar to those described for bird species or terrestrial ungulates (Shaffer et al. 2006, Egevang et al. 2010). The means by which many aquatic species achieve these long-distance movements is not fully described, but likely involves the use of cognitive spatial maps informed by multi- faceted and scale inputs. Many of the senses described above have been applied to marine taxa. The use of geomagnetic cues are again considered common, supplemented by information derived by water currents and tidal rhythms (Aidley 1981, Dingle 1996). Visual and celestial cues may reinforce this (e.g. turtles, Avens & Lohmann 2003, Muheim et al. 2006, Lohmann et al. 2008 a,b), as might olfactory or acoustic signatures, for example in returning to natal sites by fishes (Sand & Kalrsen 1986, Farina 2014). Group contact may be maintained over a range of scales, varying from long range propagation of contact-calling of apparently 'lone whales' (see Payne & Webb 1971), to the 'queuing' behaviours of the spiny lobster, where physical contact is maintained by connection of antennae and feet throughout (Dingle 1996).

### *Baleen whales*

Migration in baleen whales is often between remote breeding and feeding sites, with the longest migrations seen in those species where food availability is highly seasonal and patchy. However it is 'more than just a long swim' (Brown & Corkeron 1995), and results from a balancing act between the want to reduce the risk of predation, especially in regards to calf vulnerability and survival (Connor & Corkeron 1999), to maximize reproductive success, and minimize energy expenditure traveling to and exploiting feeding sites (Boinski & Garber 2000).

Great precision in navigation between sites is likely achieved by the accumulation of information from topographical or landscape features (Kirschvink et al. 1986, Dalla Rosa et al. 2012, Garrigue et al. 2015), geomagnetic cues (Allen 2013), inputs from visual, olfaction, and chemosensory modalities (Bastian 1967), as well as acoustics (Pike 1962, Allen 2013). Navigation may be multi-faceted, integrating information from a number of scales (Torres 2017), with the route taken often more direct than that suggested by a singular means (in humpback whales, *Megaptera novaeangliae*, Allen 2013; fin whales, *Balaenoptera physalus*, Walker et al. 1992). Spatial maps may also be informed by water density, temperature, stratification, turbulence, currents or frontal location, and wave movement (Norris 1967, Tynan 1998, Baumgartner & Mate 2003, Lohmann et al. 2008a, Bost et al. 2009). Vision may confirm direction on a fine scale, rudimentary olfaction may detect chemicals indicative of high prey productivity, and gustation evaluate salinity levels of a locale, all perhaps used as navigational tools (e.g. Tynan et al. 2005, Torres et al. 2008). Acoustic signatures can be distinct to locales, with shore and surf noise from breaking waves providing information over greater distances (Wilson Jr. et al. 1985, Mate & Urbán-Ramirez 2003, Wladichuck et al. 2010, Allen 2013). In some cases projections from other marine species are loud enough to perhaps act as cues for migratory whales (e.g. snapping shrimp, family Alpheidae, see Allen 2013, McWilliam & Hawkins 2013). Echolocation has seen limited application to baleen whale species, yet echoes from an individual's own vocalisations could orientate them to bathymetric or topographical features, seen for instance in blue whales (*Balaenoptera musculus*) during migration, and bowhead whales (*Balaena mysticetus*) in under-ice travel (Norris 1966, 1969, Payne & Webb 1971, Thompson et al. 1979, Ellison et al. 1987, Clark & Ellison 2004, Oleson et al. 2007a,b). Also, long patterned calls with sweeps in frequency and high repetition rate are seen in humpback, blue, fin and right whales (*Eubalaena australis*) and may be used to maintain contact with conspecifics during travel (Payne & Webb 1971, Clark 1982, Wiley & Richards 1978, McDonald et al. 1995, Oleson et al. 2007b, Allen 2013, Širović et al. 2013). In addition to aiding group cohesion the calls may also serve as an orientating mechanism, either projecting information actively to intended receivers or as signals passively received by 'eavesdropping whales' (Allen 2013). Here, I examine in more detail the use of vocal behaviours during migration of gray whales (*Eschrichtius robustus*) as a means of both social contact and way-finding.

*Gray whale case study*

The eastern Pacific gray whales migrates between breeding lagoons in Baja California Sur and higher latitude feeding areas in the Bering and Chukchi Seas. Recent studies have shown them to vocalize frequently during this travel period, with some indication of periodicity in calling during the northward migration (see Guazzo et al. 2017, Rannankari et al. 2018, Burnham et al. 2018). Recordings from a passive acoustic monitoring (PAM) device in deep-coastal waters of Clayoquot Sound, west coast Vancouver Island (49.21028, -126.24667), deployed in the gray whale migration corridor for both north- (21 February to 25 April, 2015; 7 March to 5 May, 2016) and southward migration (27 September, 2015 to 25 January, 2016) were examined for calling behaviours, to better understand the role of vocalisations during travel, and how they may inform our understanding of large whale migration. Data from the PAM device (JASCO Applied Sciences AMAR G3, GeoSpectrum M8E-132 calibrated omnidirectional hydrophone with sensitivity - 165 dB re 1 V/µPa, effective bandwidth 5 Hz–150 kHz, gain of 6 dB) were manually analysed through aural and visual inspection by generating spectrogram (256-point Hann window FFT with 50% overlap), for calls for at least every fifth day of the recording (20%), and comparing to previous works, in particular Dahlheim (1987), who described calling categories from recordings taken primarily in breeding lagoons (also see Crane & Lashkari 1996, Ollervides 2001, Wisdom et al. 2001, Stafford et al. 2007, Charles 2011, López-Urbán et al. 2016, Youngson & Darling 2016). Call classification was to one of four 'core' call types (class 1 knocks, class 2 sweeping-pulses, class 3 moans, or class 4 rumbles). Sub-surface exhalations, class 5 and 6 in Dahlheim's (1987) work, were noted to indicate whale presence but not analyzed as a vocal projection. Calls types that resembled those described as possible 'motherese'

(Ollervides 2001, Charles 2011, López-Urbán et al. 2016), employed between mothers and calves, were also considered.

The timing and location of the recordings mean the vocal behaviours present reflect those typical of migration and travel, with feeding behaviours unlikely, and particularly scarce in whales returning to breeding areas (Best et al. 1995, Stockin & Burgess 2005, Stamation et al. 2007, Barendse et al. 2010). Courtship behaviours may be present, and have been noted for both north (Pers. Obs 2016) and southward migration (Gilmore 1960) in gray whales, but would only represent a small proportion of the vocalizations captured in the recordings.

The most prevalent call heard was class 3 moans for both north- (83.69%, both deployments pooled) and southward (98.05%) migrations (See Chapter 1.2.2, Figure 1.3.1, 1.3.2). This is in agreement with previous recordings of gray whales at this time (Crane & Lashkari 1996, Guazzo et al. 2017, Rannankari et al. 2018). Examples of all other 'core' call types were heard for each deployment, except for class 4 rumbles on southward travel. 'Motherese' calls were also heard, but in small numbers (0.28% calls northward, 0.11% calls southward).

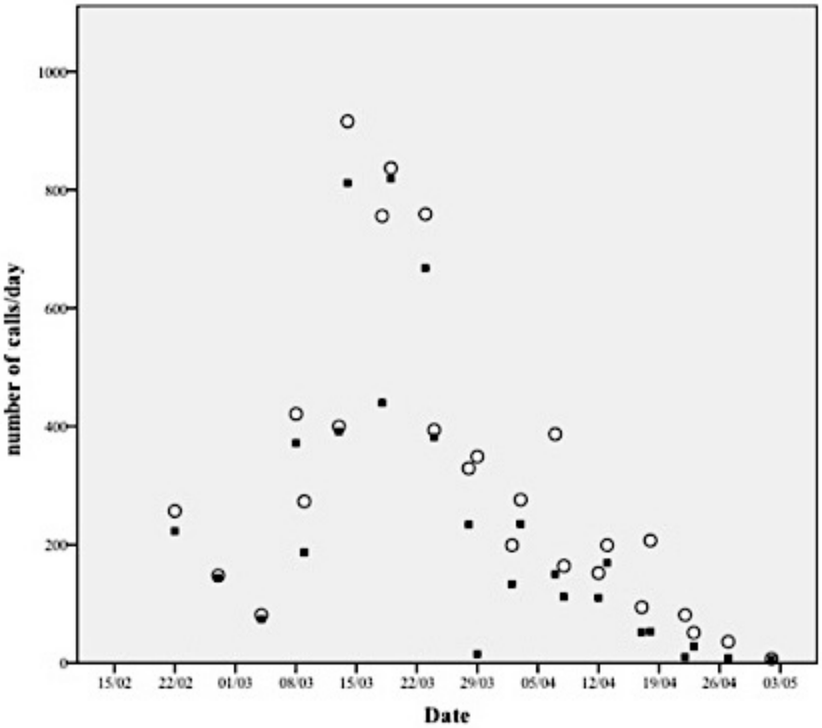

**Figure 1.3.2**: The number of calls heard per day through the AMAR deployment period for northward migration. Data from 2015 and 2016 are pooled. The open circles represent the number of total calls and black squares are the number of moans. Date is in the format DD/MM.

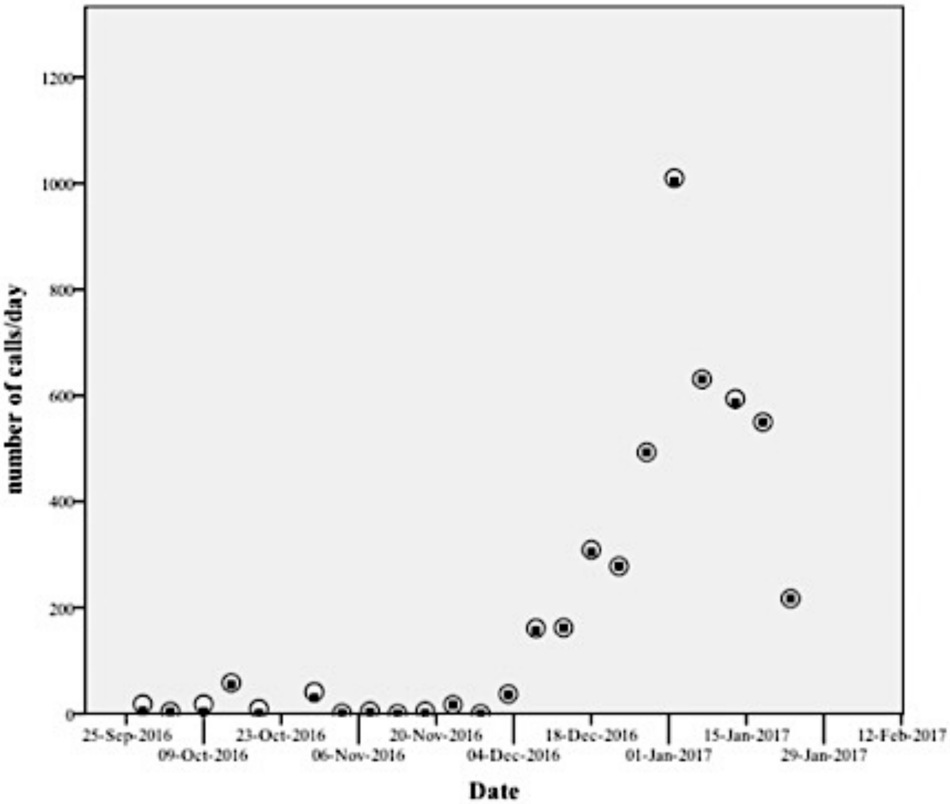

**Figure 1.3.3**: The number of calls heard per day through the AMAR deployment period for southward migration. The open circles represent the number of total calls and black squares are the number of moans.

Call number per day was compared to shore-based visual count data, to first examine whether this would approximate abundance of whales passing the recording site. Each call is treated individually without knowledge of the whether multiple calls are being projected from a single whale. For the shore-based surveys, on a clear day it is possible, from the cliff-side observation station at Point Vincente, that observations may extend approximately 24 km, with weather conditions and visibility noted at least hourly during the surveys. Care is also taken not to double count individuals.

The rate of vocalising showed some agreement with visual records when comparing dates of peak whale passage (ACS/LA gray whale census data taken from Pt. Vincent California, Table 1.3.1) and days with the highest rate of calling, when taking into account approximate travel time between monitoring locations. This is suggested to be approximately between 8-22 days to cover the estimated 2000 km between stations for northward travel and 7-16 days for southward (Mate & Urbán-Ramierez 2003, DeAngelis et al. 2010, Table 1.3.2, Figure 1.3.3).

Moan-calls in particular seemed to best track the movements past the recorder, with singular events of increased call number especially of class 1 knock calls suggestive of more within-group socialising and perhaps even courtship/mating behaviours. This suggests that in this case, calls are not just indicative of whale presence but could reflect whale abundance within the PAM detection range. Overall, a significant negative trend was found for call number over time as migration progresses for both directions ($r_s$ northward =-0.187, p<0.001; $r_s$southward=-0.229, p<0.001).

**Table 1.3.1**: Comparison of visual and acoustic data. Sighting data is from shore counting data from the ACS/LA gray whale census undertaken annually, and acoustic data is from the PAM system for this study. Peak whale number seen are those recorded during day light hours from Point Vincent, California. Peak call count is all calls amalgamated regardless of type, recorded for Siwash Point deployment site. Dates are expressed-DD.MM.YYYY

| Year | Direction | Survey dates | Type | Location | Peak date | Peak |
|---|---|---|---|---|---|---|
| 2014-2015 | N | 01.12.2014-27.05.2015 | visual | Point Vincent | 10.03.2015 | 79 |
| | | 21.02.2015-25.04.2015 | acoustic | Siwash Point | 14.03.2015 | 916 |
| 2015-2016 | N | 01.12.2015-31.05.2016 | visual | Point Vincent | 08.03.2016 | 96 |
| | | 07.03.2016-05.05.2016 | acoustic | Siwash Point | 23.03.2016 | 759 |
| 2016-2017 | S | 01.12.2016-25.05.2017 | visual | Point Vincent | 14.01.2017 | 46 |
| | | 27.09.2016-25.01.2017 | acoustic | Siwash Point | 02.01.2017 | 1010 |

**Table 1.3.2:** Estimated travel time between the shore-based observation stations in Point Vincent, CA, and Siwash Point, BC. Estimated speeds of travel are taken from Mate and Urbán-Ramierez (2003) for the overall estimate and DeAngelis et al. (2011) for the phased migration estimates.

| Direction | Phase | Location | Estimated speed (kts) | Estimated travel time (days) |
|---|---|---|---|---|
| Northward | A | CA | 1.8-2.8 | 9.6-15.0 |
| | | OR/WA | 2.6-3.8 | 4.7-6.9 |
| | B | CA | 1.3-2.3 | 10.0-13.9 |
| | | OR/WA | 2.3-3.3 | 5.5-7.8 |
| | | Overall average | 10.36 | 8.0 |
| Southward | | OR/WA | 2.9-4.3 | 4.2-6.2 |
| | | CA | 2.8-3.8 | 6.3-9.7 |

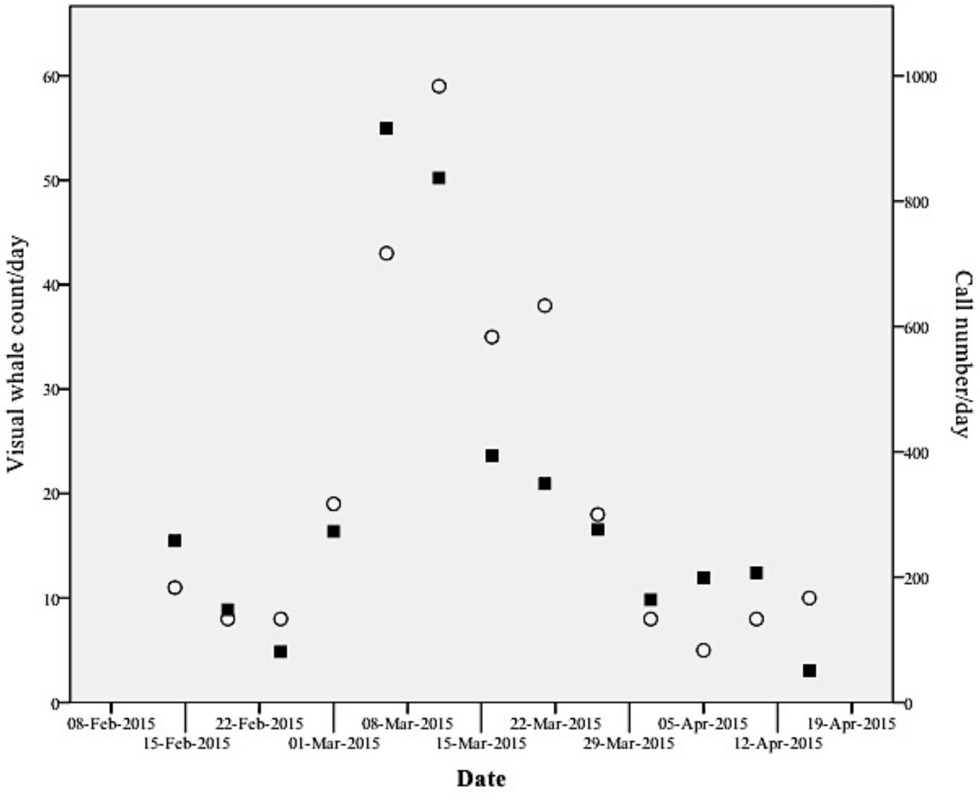

**Figure 1.3.4:** Comparison of visual and acoustic data for northward migration. Sighting data from 2015 and 2016 was averaged, and acoustic data from both northward deployments were pooled. Per day visual counts are represented by open circles and call counts by black square. Acoustic data was lagged -8 days, in accordance with the average swimming speed reported by Mate and Urbán-Ramirez (2003), to represent travel time between surveying locations.

The recordings confirmed the biphasic nature of the northward migration (Mate & Urbán-Ramirez 2003, De Angelis et al. 2010), with the newly pregnant, anestrous females, adult males, and juveniles (Phase A) leading the cow-calf pairs (Phase B; Herzing & Mate 1984, Poole 1984). The movement to feeding grounds is led by those who have the most to gain by investing time in energy procurement. Phase B leave breeding areas last to allow for maximum calf growth before migration. The appearance of 'motherese'-type calls and higher incidence of ventilation sounds towards the end of the northward recordings in late April and May, indicates a movement towards shore of cow-calf pairs, and lends more evidence to the cow-calf separation from the general population when migrating north. Shore counts past Point Vincent indicate a higher incidence of cow-calf pairs from mid-April (ACS/LA gray whale census data) with the recording period for northward migration in this study ending around or just before the peak number of cow-calf pairs would likely pass the AMAR deployment site, depending on swimming speed

(Mate & Urban-Ramierez 2003, DeAngelis et al. 2010). This may go some way to explain the low incidence of ‘motherese’ calls in this data. In addition, a decreased calling rate as the migration progresses, shown by negative correlation of calling with time, suggests that mothers and calves may maintain attachment by more tactile means, complemented by acoustics, as seen in other baleen whale species (e.g. Szabo & Duffus 2008, Videsen 2017).

It is not known whether the southward journey is similarly segregated, but it is thought that pregnant females and those with calves borne en-route arrive first to the breeding lagoons (Rice & Wolman 1971). They are followed by females in oestrous, males, and juveniles (Herzing & Mate 1984). The recordings for southward migration show two peaks in calling, with ‘motherese’-type calls were present only in September and October. The timing and rate of employment of these call classes, much reduced from northward migration recordings, likely denotes the latter stages of weaning, and separation of cows from their calves from the late summer onwards (Pers. Obs. 2009-2017). The possibility of a phased migration towards the breeding grounds is suggested by an increase in calling rate in mid-October prior to the main peak in early January, however this is not yet corroborated with visual observations.

Patterns in call rate, the number of calls per hour, are driven by changes in the use of class 3 moan calls during migration. Diurnal patterning is seen, as with previous studies (Guazzo et al. 2017, Rannankari et al. 2018), with acoustics employed more at night when cues from other modalities are more limited. The use of moan calls was significantly, but weakly, correlated with ambient noise levels for northward travel but not southward ($r_s$north=0.082, p=0.023; $r_s$south=-0.075, p=0.064). A similar trend was seen when comparing calling rate per hour to sea state conditions, which contribute to back ground noise, including wave height and gusting windspeed ($r_s$waveheigh=0.221, p<0.001; $r_s$gusting windspeed=0.342, p<0.001). Increased calling was seen on the northward migration in the presence of vessels. Modifications in vocalising behaviours may be a compensation mechanism by gray whales, to ensure conspecific signalling remains effective in the presence of anthropogenic noise. Greater repetition and increased number of pulses in class 1 knock-call sequences have been noted in playback experiments of vessel and drilling noise in breeding lagoons (Dahlheim 1987, Dahlheim & Castellote 2016). A similar response may be present here, but with adaptive use of class 3 moan calls with their low frequency and long propagative features, as the dominant call type during migration.

The differences seen between calling on the north- and southward movements may be indicative of the necessity or intrinsic nature of calling during travel towards feeding grounds. Indeed, the rate of calls per hour on the northward migration was, on average, more than one and a half times that on the southward movement.

## Conclusions

These results suggest that gray whale calling during migration is a consistent behaviour, perhaps inherent to travel. The dominant use of low frequency class 3 moan calls implies that acoustics are being used on a wide spatial scale, likely as an adhesive mechanism between conspecifics. The changes in calling rate and composition in increased ambient or sea state indicates plasticity in gray whale vocalizations, likely applied to overcome the masking effect of increased background noise. This appears particularly true for northward migration, where the need of individuals to reach feeding grounds is greater, and where younger or less experienced individuals may use the calls of more mature leading whales as guidance.

This expenditure of energy in calling, especially on the northward migration for gray whales, when they are in a negative energy state following overwinter fasting, and for some calving and weaning, suggests the necessity for calling. As well, vocalizing to the herd suggests a level of altruism. The receiver of the 'donated' information may not always be known. This is particularly true in case of whales 'eavesdropping'(Allen 2013), which low frequency, far-propagating moan calls are likely more subject to than the frequency modulated calls of class 1 knocks and class 2 upsweeps.

The calling patterns seen during migration contrast with those described in breeding lagoons, where class 1 knock calls are most prevalent (Dahlheim et al. 1984, Dahlheim 1987), and feeding regions (Moore & Ljundbald 1984, Chapter 1.5). Call use and function can only be inferred given the call shape (frequency peak and range, frequency contour, and duration), and its known behavioural, social, temporal, or geographical context. The structure of class 3 calls modulated knock-like or sweeping calls used for within-group conspecific contact, with 'social/sexual' behavioural applications (Youngson & Darling 2016). Indeed, contact-calling has been noted in many species during travel, for example walrus (e.g. Charrier et al. 2011), bats (e.g. Doerrie et al. 2001, Schmidt 2013), and elephants (e.g. Rees 1963, Poole et al. 1988, Poole 2011, Poole & Granli 2011). This type of vocalization during migration is closely tied to social interaction and coordination of the group to maintain cohesion, perhaps summon group members, or even reunite individuals to the group and mobilizing them towards the migratory destination. In addition, calling may form or retain alliances or hierachies, and perhaps regulate inter-individual spacing (e.g. primates, Boinski & Garber 2000, humpback whales, Norris et al. 1999, Cholewiak et al. 2018). Calls may be multi-functional: aiding navigation, maintaining group cohesion, or affording guidance to less experienced whales. Lower frequency calls have longer wavelengths and afford baleen whales an extensive sensory range. It has been suggested that baleen whales use infrasonic calls to orientate to topographical features, such as seamounts or other physical features, using echolocation techniques to garner useful navigational information (George et al. 1989, Tyack & Clark 2000, Stimpert et al. 2007, Kobayashi et al. 2008, Dalla Rosa et al. 2012). This navigation by landmarks (e.g. Clark et al. 2009, Allen 2013, Garrigue et al. 2015) is analogous to techniques used by shorter-range navigators or non-migrators searching for food, but on a greater scale (Bingham & Cheng 2005).

The calling behaviours seen here are not unique to gray whales: bowhead whales in the Beaufort Sea showed clusters of calls in time and space matching visual surveys. The complex frequency-modulated calls employed during migration maintain group cohesion, with increased rate of calling at night (Blackwell et al. 2007); migrating humpbacks are known to sing (Kibblewhite et al. 1967, Payne & McVay 1971, Levenson & Leaply 1978, Cato 1984, 1991, Clapham & Mattila 1990, Norris et al. 1999, Noad et al. 2000, Noad & Cato 2001, Cato et al. 2001) with some components in the frequency ranges of 20-100 Hz which would be detectable to conspecifics at long distance and likely making it a source of environmental information (Wartzok & Ketten 1999, Clark & Ellison 2004). Blue and fin whales produce long, intense patterned sequences of calls focused in the lowest frequencies suggesting the signals are optimized for long-distance communication (Payne & Webb 1971, Clark & Ellison 2004).

There is increasing evidence to suggest that multi-sensory information is used in navigation (e.g. Lohmann & Lohmann 1996, Avens & Lohmann 2003, Cochran et al. 2004, Muheim et al. 2006, Lohmann et al. 2008a), with cues used both sequentially and in parallel by whales to localize the target area (Bingham & Cheng 2005). Acoustic cues are likely complemented with other sensory information, perhaps chemosensory or geomagnetic, and the scale over which information is received goes from large to fine as they approach a target locale, for example a feeding site (Torres 2017). We are just beginning to comprehend the range and extent of sensory mechanisms involved in orientation, way-finding and long range movements in animals. Acoustics, both active and passive, afford baleen whales a long range information stream. Other sensory information garnered through, vision, skin and vibrissae, chemoreception, magnetoreception, somatosensory perception/gustation, and prey derived or oceanographic stimuli on the micro (<100m) to macro (>1,000km) scale enhances locational awareness (Torres 2017). This allows spatial information to be discerned at high resolution, and perhaps calibrated and corrected through more fine scale inputs, affording the accuracy and site fidelity often seen in migrators (e.g. Hoelzel 1998, Calambokidis et al. 2010, Horton et al. 2011, Allen 2013, Baker et al. 2013, Fossette et al. 2014).

Comprehending the mechanisms of orientation and group cohesiveness granted by acoustics use in baleen whales is extremely challenging, with the extents over which cetacean are able to send and receive information, their active space (Tyack & Clark 2000, Clark et al. 2009, Burnham 2017), not yet accurately defined for many species.

Group maintenance by acoustic means may function in a similar way to primates (see Ingmasnon 1996), using vocalizations as a method of keeping other individuals 'in sight' and confirm direction of travel, as suggested for humpback whale singing during migration by Norris et al. (1999). Cultural or maternal transmission of information, or memory maps of migration, may be reinforced by calling, either by following lead individuals through 'eavesdropping' (e.g. see Allen 2013), or individuals relaying directional information. The recurring use of calls at times when an energetics approach suggests it should be reduced, particularly for northward migration, suggests that acoustics has a tangible function when whales are traveling. Calling behaviours are also likely a means to inform cognitive spatial maps, with the average call rate per hour much increased during migration, for both directions, than compared to feeding or breeding grounds (Dahlheim 1987). The dominant use of moan calls rather than knocks, which are most prevalent in breeding lagoons and feeding areas (Moore & Ljundbald 1984, Dahlheim 1987), suggests too that they are sending and receiving acoustic information over much greater spatial scales during migration. Calls may act as 'trail markers', similar to following the tracks of lead individuals (as seen in lemmings, Barker 1978), as well as carrying information regarding the route or habitat suitability (e.g. pheromone secretion by wildebeest, Barker 1978). In this way the class 3 moan calls could act as a 'pathway' of calls laid down by conspecifics. Indeed these far-ranging calls could form a 'highway of sound', illuminating the migration route with vocalizations, carrying information on the route and destination. This habit of sharing with individuals, that may not even be a member of a cooperative group, close kin or represent a potential mate, evolved with the underlying idea of reciprocity, either immediate or in the future (Baker 1978). This suggests that the calls heard in the recordings for this study might actually form a network of reciprocated acoustic information not just one-way signaling. Moving as a group, can aid in predator detection and avoidance, warding off potential threats to individuals or the group; allow for social learning or cultural transmission, through shared knowledge of route and destination (Boinski & Garber 2000, Scott et al. 2014), and increased accuracy of navigation (e.g. Hamilton 1967, Baker 1978, Mueller et al. 2013, Pettit et al. 2013). Movement by the group may be rather protracted, like that of gray whales, in which case acoustics can connect the herd through 'large vocally mediated communication networks', similar to that shown by Langbauer and colleagues (1991) in elephants, who employed low frequency 'rumbles' and infra-sonic vibrations extending over long ranges.

Passive acoustic methods can afford constant monitoring, regardless of weather or light/visibility restrictions. The manual verification, and discernment between call types allows for singular or short lived events to be discerned from more wide ranging patterns. In the case of gray whales, the moan call gives the best appreciation of the migration pattern overall, whereas class 1 and 2 modulated calls are social interactions over shorter spatial and temporal ranges. Migration timing seems intrinsically linked to reproductive strategy and success. Some calling may be tidied to social cohesion, perhaps even courtship. Other vocals may be rousing calls to initiate or continue travel, as seen as 'rally calls' in big cats (Gautier & Gautier-Hion 1977) and in elephants as 'let's go' calls (Poole et al. 1988). An increased knowledge of cetacean acoustics, particularly in baleen whales, whose signals can propagate over great distances, gives us an enhanced understanding to the designation of a 'lone whale' (Payne & Webb 1971), and the processes behind migratory, feeding and breeding behaviours and the scale on which they operate.

Acoustic methods are also useful to complement more traditional research methods such as shore, vessel or aerial surveys, with 'acoustic censuses' adding to observational work (see Guazzo et al. 2017 for acoustic tracking of whales through a hydrophone array). Changes in vocalizing behaviours are possibly a reflection of altered 'acoustic community' or soundscapes, not least anthropogenically-driven increases in ambient noise and, on a wider scale, the warming and decreased pH of the oceans affecting the propagation of calls (Ilyina et al. 2009, Sehgal et al. 2010). The concept of sentinel species to reflect soundscapes and habitat health has already applied to frog and bird species (e.g. Laiolo & Tella 2005, Laiolo et al. 2008, Ponce et al. 2012, Farina 2014), with gray whales possibly acting as a candidate in the marine setting. Further long term deployments of PAM systems, similar to this study, along the gray whale migration route may show adaptive use of acoustics, for example, in deeper water compared to coastal regions (see Crane & Lashkari 1996); as oceanographic conditions change, for example water temperature or salinity, in turn altering sound propagation, or behavioural distinctions in calling behaviours, for example those more tied to prey-finding or securing a mate, than purely travel. Borrowing insights from other taxa, as well as integrating knowledge of population dynamics, evolutionary ecology, physiology and behaviour may help us better understand the more complex life history components of cetacean species and the processes that drive them.

## 1.4. The continued use of Clayoquot Sound by gray whales to forage, based on a long-term ecological study

### Preface

Marine mammal ecosystem data with a long time series are rare. Here, I review twenty years of ecological study of gray whale use of Clayoquot Sound, establishing it as an important foraging and nursing/weaning area. Prior analysis of some of this data has shown top-down modification of habitat quality and system functioning by an apex predator (Burnham & Duffus, in press), whereby predation in a summer shapes the use of the site in subsequent years. Whales using this site are members of a wider population sub-group, the Pacific Coastal Feeding Group (PCFG, Calambokidis et al. 2010, IWC 2010), that utilize feeding sites south of the main Arctic regions during the summer.

It is only recently that predator-prey motifs have been established for the use of this feeding locale. It is the return of a 'core' group of whales, members to the PCFG, and the prey resource that determines the continued use of this site. The use of cow-calf pairs may present a special case, with site features thought to confer predation protection. This chapter introduces the use of Clayoquot Sound as a foraging site for gray whales as the basis on which to examine the acoustics use of whales using the area during the summer for feeding and calf rearing in later chapters.

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## The continued use of Clayoquot Sound by gray whales (*Eschrichtius robustus*) to forage, a summary of a long-term ecological study

The eastern Pacific gray whale (*Eschrichtius robustus*) completes one of the longest mammalian migrations from breeding lagoons in Baja California Sur, Mexico, to the Bering and Chukchi Seas for summer foraging (Pike 1962). This migration, and period of fasting overwinter, reduces body weight between 11-29% (Rice & Wolman 1971). The negative energy state is exacerbated in cows that also have the demands of pregnancy, birth and lactation. The 'feast-famine' cycle, and travel between geographically separated breeding and feeding areas, makes it essential that gray whales utilize areas of high prey abundance during summer foraging to restore internal energy reserves to allow the cycle to be repeated the subsequent year (Rice & Wolman 1971, Murison & Gaskin 1989, Highsmith & Coyle 1992).

Population recovery following intensive whaling, estimated to be 19,126 individuals (Laake et al. 2012), has placed increasing pressure on foraging areas, leading to the suggestion that numbers are reaching the carrying capacity of primary prey stocks in Arctic foraging locales (Highsmith & Coyle 1992, Le Boeuf et al. 2000, Moore et al. 2001, Coyle et al. 2007). As an opportunistic forager, gray whales have been increasingly observed foraging in areas on the southern extents of their principal feeding site, as well as those extending the length of their migration, particularly between Alaska and northern California (Kim & Oliver 1989, Moore et al. 2001, 2007, Perryman & Lynn 2002). In addition, they have been documented exploiting alternative prey sources, in particular epi-benthic and pelagic species such as mysid shrimp swarms (Family Mysidae; Dunham & Duffus 2001, 2002, Scordino et al. 2011), in place of their typical benthic prey source of ampeliscid amphipods (Ampelisca spp.; Bogoslovskaya et al. 1981, Nerini 1984).

Most of the gray whale stock migrate to feed in primary Arctic regions, however a group of whales, numbering several hundred, spend the summer foraging in coastal waters of the Pacific northwest, known as the Pacific Coastal Feeding Group (PCFG, Calambokidis et al. 2010, IWC 2010). The use of alternative foraging sites could be in response to prey availability and distribution, particularly in comparison to principle sites, environmental conditions, with oceanic regimes and changes in ice cover influencing the length of the foraging season (Stafford et al. 2007), or competition, and the energy requirements associated with age and reproductive state, with PCFG whales noted to differ from the wider population (Duffus 1996).

Here I review the spatial and temporal patterns of use by gray whales of Clayoquot Sound (between 49.24333, -126.10278 and 49.31417, -126.24167, which defines the transect route, Figure 1.4.1), on the west coast of Vancouver Island. This area has been a feeding locale for more than 40 years (Hatler & Darling 1974, Darling 1984, Calambokidis et al. 2010), with prey community composition and ecological processes mirroring those seen in more northern latitudes (Burnham & Duffus 2016). Its use as a nursing and weaning site by cow-calf pairs has also been noted. The physical characteristics of the site offers protection for calves from predation. Here I discuss patterns in spatial and temporal use of this foraging site, derived from a long-term ecological study spanning twenty-years. This site represents an opportunity for gray whales to replenish energy reserves while saving on the cost and time to travel to Arctic feeding sites.

Clayoquot Sound is a spatially discrete site, that is separated from adjacent foraging locales by approximately 25 km of deep, unproductive waters that are devoid of prey. In addition to the use by cow-calf pairs, individuals feeding in Clayoquot Sound are typically pre-breeding juveniles, and some post- or non-breeding adults that are distinct from the breeding nucleus (Duffus 1996). Of the whales sighted in the area (~low hundreds), many are members of the PCFG, exploiting prey reserves in the study site, and adjacent areas, in preference to foraging in principal Arctic regions. Some others may be opportunistic, and are perhaps ‘stragglers’ of the northward migration (Calambokidis et al. 2010).

Gray whale feeding was first noted in Clayoquot Sound in the sandy embayment of Ahous Bay on the west coast of Vargas Island (Hatler & Darling 1974, Figure 1.4.1). Here infaunal amphipods (Percardia, Amphipoda) once formed dense tube mats from the shallows to approximately 22 m water depth, with reefs and islands defining and surrounding the bay allowing whales to feed in relative protection from oceanic swell (Burnham & Duffus 2016, Figure 1.4.1). However, persistent predation by gray whales drove amphipod reserves into major decline by about 1997, effectively ending the use of Ahous Bay (Duffus 1996, Dunham & Duffus 2001, 2002, Burnham & Duffus 2016). The demise of amphipod populations led to a prey switch to epi-benthic mysid swarms as the principal prey item, pushing whales to forage in rocky reefs and kelp beds.

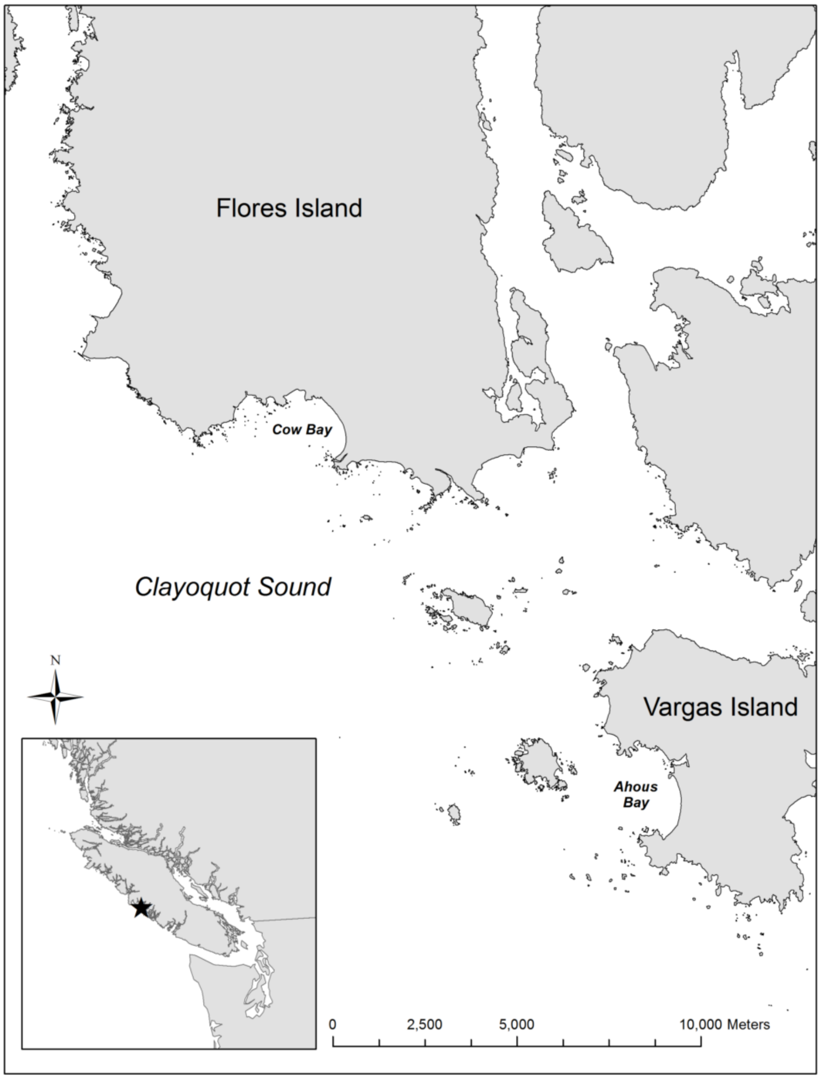

**Figure 1.4.1**: Map of the study site, Clayoquot Sound. Indicated are Ahous Bay, main gray whale foraging region for benthic amphipods, and Cow Bay, main feeding locale for epi-benthic mysid species.

Gray whale foraging habitat extends along the south, south-west coast of Flores Island encompassing exposed coastline, rocky headlands and bays. Currents and water flow are known to influence the formation and distribution of prey swarms in this area (Kopach 2004). Mysid species in Clayoquot Sound inhabit shallow water, with swarms, on average, in water 10 m deep and not more than 30 m deep, and within 1 km from shore. Species are bottom referent, and form dense swarms associated with rock reefs or headlands or other bottom structures (Clutter 1969, Kathman et al. 1986, Kim & Oliver 1989, Jumars 2007, Nelson et al. 2008, Laskin et al. 2010, Feyrer & Duffus 2011, 2014, Burnham 2015, Burnham et al. 2017). However, this area also provides habitat for crab larvae (Pachycheles and Petrolisthes spp.), and other occasional secondary prey species, as well as amphipod habitat in deeper waters with sandy substrate.

The main feeding area for gray whales in Clayoquot Sound is Cow Bay on the south coast of Flores Island, 5 km northeast of Ahous Bay (Figure 1.4.1, 1.4.2). Bathymetry within the bay is varied, with rock reefs and kelp beds defining its margins and gentle sloping sandy stretches of coastline in the southeast corner. Relatively calm waters and benthic complexity in this region aggregates and retains prey, with a convergence mid-bay at approximately the 10 m isobath (Kopach 2004, Laskin et al. 2010).

Key foraging sites in Clayoquot Sound have been identified through line transect boat-based surveys over 20 years (1997-2016). The survey route follows the 10 m isobath covering approximately 20 km$^2$ of the nearshore of the south-west coast of Flores Island (Figure 1.4.2). It was initially developed through intense observations, sampling, and surveying between 1994 and 1997 (Figure 1.4.2). The vessel speed remained constant at 13 km/h while surveying to avoid double counting, with a minimum of four observers constantly scanning 360° for whales. Surveys were aborted if visibility was reduced below 500 m in any direction or if sea state exceeded Beaufort 3 (Dunham & Duffus 2001, 2002, Burnham & Duffus, in press for more details). Surveys were conducted bi-weekly between May 24 and September 8 each year. A minimum of thirty surveys were conducted over each summer season. Only foraging whales were recorded on transect surveys, with the route designed to maximize the possibility of locating them by passing through known habitat of potential prey species. Foraging was determined by observations of behaviour, particularly those characteristic of area-restricted foraging behaviours, as well as dive location, length and distance travelled (Malcolm & Duffus 2000, Dunham & Duffus 2001, Stelle et al. 2008, Feyrer & Duffus 2014).

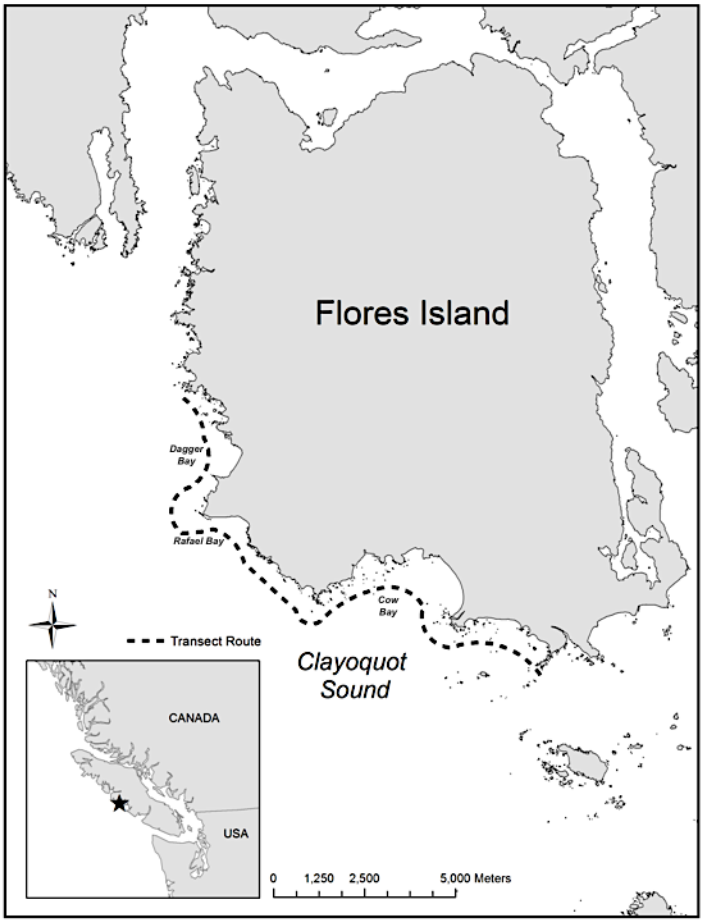

**Figure 1.4.2:** The study area, Clayoquot Sound. The survey route, indicated by the dotted line, follows the 10 m isobath, typically through rocky reef systems which are key mysid habitat.

Prey resources in the study site are the immediate determinants of the number and distribution of whales summering in Clayoquot Sound. Over the course of the 20 year ecological study in this area, the systematic repetition of the line transect survey, as well as analysis of fecal matter, underwater video, SCUBA surveys, benthic samples, plankton net tows, and active and passive acoustic surveys, has consistently confirmed the relationship between whales, foraging, and prey (Duffus 1996, Dunham & Duffus 2001, 2002, Nelson et al. 2008, Feyrer & Duffus 2011, 2014, Burnham & Duffus 2016, Burnham & Duffus, in press).

The number of individual whales documented foraging in Clayoquot Sound since 1998 may be as many as 300, with 237 unique individuals confirmed through the use of photographic identification techniques (Calambokidis et al. 2010). Whales were matched using unique identifying features on the right and left flanks of the whales body as well as distinctive profiles of dorsal humps and knuckles (Lien & Katona 1990, Calambokidis et al. 2010). Identification photographs of all foraging whales were taken for 1998-2000 and 2008-2013, no photographs were taken in 2001, and only opportunistically during only some of the site surveys from 2002-2007 and 2014-2016. Photographic identification techniques allowed both the annual number of whales and their annual residency time to be calculated. A little under half (48.52%) of the whales were sighted in only one foraging season ('visitor' whales), with 122 whales seen to return for two or more summers. The most frequent that a whale was seen to return was twelve of the twenty years (n=2). Of those whales seen foraging over multiple years, annual return counts ranged from 2 to 12 years with an overall average of 4.5 years, forming a 'core' group of foragers in Clayoquot Sound. This indicates that whales show multi-year site fidelity to Clayoquot Sound. However, this is not a closed population, with an increased number of new recruits or single time 'visitor' whales noted in years of high prey abundance. Site use by these whales may be through foraging habitat selection and cost-benefit analysis of swimming further, especially if they are individuals trailing the main body of the population on the northward migration as suggested by Calambokidis et al. (2010). The earliest whales testing foraging sites are seen in April, however this is before mysid prey swarms have become established and stable, with individual prey likely still to be small in size (Burnham 2015). The last to leave to migrate south can be mid-October to November, although some whales overwinter in Clayoquot Sound (Pers. Obs.).

In reaching a foraging area, whales should be edacious and firmly focused on prey capture. Indeed, foraging gray whales dedicate most of their efforts and time to foraging throughout the summer (Pers. Obs). Foraging effort, the proportion of time given to foraging behaviours, was found to be primarily driven by prey density on both regional/site and local/patch level (100m). Feyrer and Duffus (2014) found a significant positive relationship with individual whale foraging effort and prey density. Also, foraging behaviour did not occur if mysid patch density was below 2,300 mysids/m$^3$, suggesting a threshold response. Location of prey by gray whales occurs by distal and proximal cues (Torres 2017), with their fine scale foraging behaviours showing complex appreciation and response to prey availability in a patchy environment (Feyrer & Duffus 2014). The 'win stay/lose switch' rule (Shields et al. 1988) may in part explain fidelity to patches by certain whales (Pers. Obs.), with only the decay in successful prey capture past this threshold instigating a move to another prey patch.

Whales do not move through the site randomly through a summer season to exploit prey patches. Typically foraging efforts moved from south to north over the summer, with Cow Bay predominantly utilized from mid/late-May until the end of June. Areas to the north and extending to Rafael Bay (Figure 1.4.2) serve as ancillary prey areas from late July to Mid-August. In the latter part of the summer, from mid-August onwards, Cow Bay again becomes the dominant foraging location. Areas along the south coast of Flores, and perhaps deeper water regions of Cow and Ahous Bays, as the last remaining benthic prey reserves, may also experience test feeding by whales before they leave to migrate south (Unpublished Whale Lab data, Pers. Obs.). This pattern reflects the re-establishment of mysid swarms as broods from spring and mid-summer mature (Burnham 2015).

Foraging whale numbers peaked each season between mid-July to mid-August (Burnham & Duffus, in press). This period of higher whale numbers is coincident with mysid prey reaching its body length maximum, with swarms stabilized after spring and early summer broods (Burnham 2015, Burnham and Duffus, in press). Following this peak, the number of whales declined following significant removal of the prey base (Burnham & Duffus, in press). Only in years of very high prey abundance (2010, 2011), were whales seen to successfully forage into the late season in high numbers. In contrast, years where prey resources were particularly scarce (e.g. 2009), short-duration peaks in whale foraging were seen, often followed by complete site abandonment (Burnham & Duffus, in press).

Combining transect survey results with photographic identification data confirmed the number of whales per survey (foraging intensity); the residency time of each whale over a season, and the rate of return for each individual, or how many years previous they had been seen. These metrics all speak to site fidelity, a strategy often employed by wide-ranging animals as a means to maximise net energy gain by showing high rates of return to areas where resource availability is high and predictable (Arthur et al. 2015). Analysis of the whales catalogued on the site showed the mean residency time of whales foraging in Clayoquot Sound to be 23 days per year. The range was from a single day to nearly the full summer (113 days). A significant positive correlation was found between a whale's residency time and its return rate, whereby those whales that had been sighted in multiple years where most likely to forage in Clayoquot Sound for extended periods of the summer ($r_s$ =0.419, p<0.001, n=116). Also, a whale's residency time each summer was dependent on prey reserves, showing positive correlation with both annual foraging intensity and the total number of individual whales exploiting the site annually ($r_s$=0.933, p<0.001, n=9; $r_s$ =0.850, p=0.004, n=9). However, the peak in the number of whales foraging in the area each summer was coincident to a peak in 'visitor', single visit whales sighted, showing the opportunistic nature of their site use.

It was found in an average year, 42 different whales would be sighted in Clayoquot Sound; of these 8 would be 'visitors' and 34 would be returning whales, of which 7 were members of the 'core' group, with a high level of site fidelity. The annual foraging effort, or mean number of whales per transect survey is 7.1 foraging whales/survey over the full twenty year period (Figure 1.4.3). Whereas 'visitor' whales are sighted predominantly in high forage years, the whales forming a foraging 'core' were less influenced by prey density. The availability and predictability of prey reserves, and repopulation after predation, and perhaps familiarity with the area allows site use to persist for these re-sighted whales despite annual variations in energy availability (Arthur et al. 2015).

Predator-prey dependency is seen strongly in inter-annual foraging patterns, where years with high foraging intensity, and therefore number of foraging whales, are followed by at least one summer of lower numbers (Figure 1.4.3). Intense foraging in a summer season necessitates at least one year of reduced predation, allowing a reprieve for mysids in which to repopulate (Figure 1.4.3, Burnham & Duffus, in press). The exception is 2010-2011, which were both high prey years, but followed several years of limited foraging pressure. Over the twenty-year period, several inter-annual patterns were noted, including boom-bust cycles, extended periods of reduced foraging, and an overall declining trend. This overall trend is seen in repeating cycles: 1998-2001, 2002-2009, 2010-onwards, with declines followed by recovery, however ultimately leading to a depressed prey base and very few whales foraging in Clayoquot Sound in 2017-2018 (Figure 1.4.3, Pers. Obs. 2017-2018). Unlike the amphipod prey, however, once given a repose, the mysid species flock in Clayoquot Sound demonstrates significant population recovery, shown here by using the number of foraging whales as a proxy for prey reserves (Figure 1.4.3, Burnham & Duffus 2016, in press). Shorter life cycles, and the ability to capitalise on periods of lower predation, including overwinter, has so far allowed mysid prey to recover from annual gray whale predation (Burnham 2015, Burnham & Duffus, in press). The spatially discrete nature of the study site defines the extent to which prey re-populates from other areas. The re-establishment of prey in Clayoquot Sound must therefore be from small remaining populations within the site (Pers. Obs., Unpublished Whale Lab data).

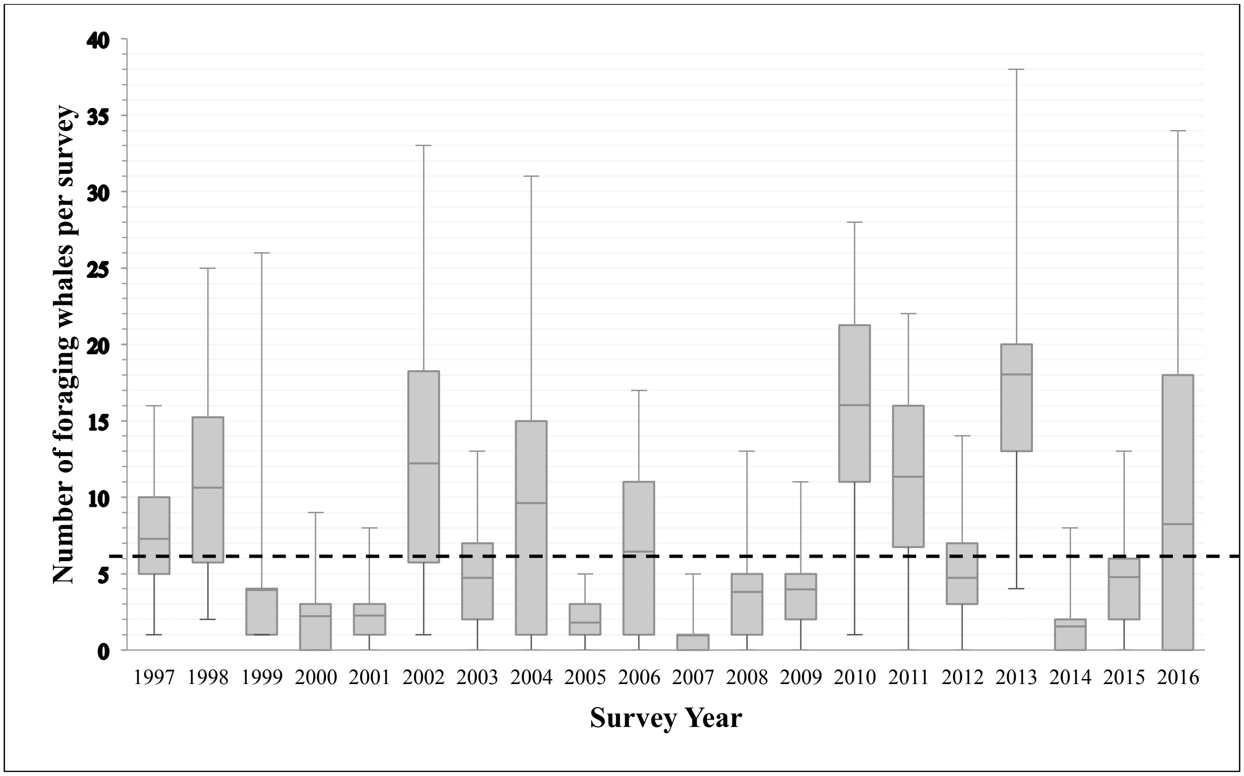

**Figure 1.4.3:** Boxplot to indicate foraging intensity in the study site, calculated by the number of foraging whales sighted per transect survey. The dashed line is the overall average for all years, and allows for comparison between years.

The use of the site does not appear to differ by the gender of the whale; of the 237 individuals identified in Clayoquot Sound, 101 have had their gender identified using genetic analysis and/or the presence of a calf. Of these 101, 62 are females and 39 are males. There was no significant difference found between gender and the average number of years a whale was re-sighted either in Clayoquot Sound (Student’s t-test, t(99)=0.325, p=0.746), or in the wider PCFG range (Students’s t-test, t(95)=1.153, p=0.252). There was also no difference between the genders in average residency time of a whale during a season to the study site (Student’s t-test, t(90)=-1.715, p=0.090). Although not significant, the average return rates to Clayoquot Sound were less for females, but residency time was greater by an average of 7 days (M: $\overline{x}$=17.05 days; F: $\overline{x}$=24.03 days). Similarly, of the calves that are brought to wean in Clayoquot Sound (n=27), 9 have had their gender identified, with no significant difference between return rate or residency time between male and females, despite female average values being consistently higher than male counterparts (Student's t-test, return: t(7)=-0.339, p=0.744; F: $\bar{x}$=4.33 years (n=3); M: $\bar{x}$=3.67 years (n=6); residency: t(7)=-1.381, p=0.210; F: $\bar{x}$=35.25 days; M: $\bar{x}$= 17.21 days).

The use of Clayoquot Sound by cow-calf pairs presents a special situation. The number of mother-young pairs using the site as a nursing and weaning area per summer is relatively consistent, and seems somewhat independent of the number of births to the overall population, estimated from counts in breeding lagoons and of northward migrants (Unpublished Whale Lab data, LSIESP data, ACS gray whale census data), and prey availability in Clayoquot Sound. Productive sites, such as Cow Bay, present foraging opportunities for mothers to replenish energy reserves, and calm shallow areas to nurse that also afford calves protection from predators.

Twenty seven cow-calf pairs have used Clayoquot Sound since 1998, with an annual average of 2.44 calves/yr. Mothers that bring calves to wean in Clayoquot Sound are either females that only use the area only when accompanied with a calf, or those that forage in the area with and without a calf (Unpublished Whale Lab data). The residency time of the females that only ever use the site when weaning is typically less than those that forage in the study site with and without a calf present ($\bar{x}$=13 days and $\bar{x}$=35 days respectively). Generally cow-calf pairs spend more time in the area than single whales, with this occupancy time not as closely associated with prey levels. The females of the latter group showed significantly increased residency times when accompanied by a calf ($r_s$ =0.435, p=0.048, n=21). The number of cow-calf pairs typically declined as the season progressed, presumably as weaning occurred. There were no mother-calf pairs noted in transects in September for any year, though solo calves have been observed in the late summer (Pers. Obs, Unpublished Whale Lab data).

Cow-calf pairs and other foraging whales use different parts of Cow Bay. The greatest number of pairs were recorded in waters less than 5 m deep, or shallower. Almost eighty percent (77.4%) of all sightings were shoreward of the of the 10 m isobath. The use of these areas, away from other foraging whales, may replicate site use in the breeding lagoons, where cow-calf pairs occupy the upper lagoons, with mature whales in the deeper waters closer to the lagoon mouth. The use of these areas is a prioritisation of the needs of the calf by the mother, as protection comes at the cost of being away from the largest prey patches in the area. This has been observed in other baleen whales. Humpback whale (*Megaptera novaeangliae*) cow-calf pairs exhibit ‘following’ behaviours during the first migration towards feeding areas, and cows modify ventilation and diving patterns to fit with the physiologically-limited dive depth and length of her calf. The use of shallow waters by gray whale cows could mediate this modification during foraging behaviours, by better suiting the calf’s lesser lung capacity, and the mother not having to leave the calf alone at the surface for extended periods of time. Being close to the shoreline also allows for increased vigilance for predators, as the shore affords protection from one direction (Szabo & Duffus 2008). The sonic characteristics of surf breaking may help ‘acoustically’ hide the mother and her young from killer whales. Also, the acoustic properties of kelp beds and soft bottom, as well as heavily turbid waters may offer further protection (Urick 1983, Ford & Reeves 2008, Wladichuck et al. 2010).

The use of tertiary feeding areas, like Clayoquot Sound, as weaning areas, and the subsequent return of calves in the following years suggest internal recruitment to the PCFG via maternal learning. Identification of migratory routes, foraging areas, and prey species may be transferred via vertical transmission through social learning (Rendell & Whitehead 2001). Genetic analysis has shown breeding to occur between whales irrespective of foraging site preferences, yet there are significant differences found in mitochondrial DNA (mtDNA), between whales utilising the primary Arctic feeding areas and the PCFG range (Calambokidis et al. 2010, Lang et al. 2011, Scordino et al. 2011). Return rates of calves in post-weaning years fit with these results. The return rate of the calf is significantly correlated with the return rate of the mother ($r_s$=0.839, p=0.001, n=18). Almost all calves sighted as weanlings in their first year in Clayoquot Sound returned for at least one year.

It is likely that Clayoquot Sound is one area in a complex of feeding sites of the PCFG whales (Calambokidis et al. 2010). Calambokidis and colleagues (2010), through compilation of photographic records, identified 872 individual whales foraging in the PCFG range. Of these whales more than half (51.9%) had been sighted more than once, with a slightly higher rate of returns for calves (54%, Calambokidis et al. 2010). Site use and residency time patterns throughout the PCFG range were seen to replicate those in Clayoquot Sound, with whales with the longest residency times also most likely to have the highest return rates (Calambokidis et al. 2004, 2010). Movement between areas within the full range (Calambokidis et al. 2010), was demonstrated, presumably reflecting prey reserves, yet individual whales did demonstrate fidelity to particular regions (Calamokidis et al. 2010). Of the 237 whales noted in Clayoquot

Sound, 205 whales were part of the wider population of PCFG whales with at least one sighting in one of the other 14 areas extending from southern California to Alaska. Whales from the Clayoquot Sound catalogue were most frequently seen foraging in areas in southern Vancouver Island to northern Puget Sound when not observed in the study area. The movement between areas may demonstrate gray whale sensitivity to influences on a range of scales, perhaps being able to appreciate relative prey availability on regional and local scales (Feyrer & Duffus 2014).

In Clayoquot Sound the 'core' whales of the area, returned with less regard to prey abundance, suggesting a number of factors may be at play (Arthur et al. 2015). However, the strongest influence on the average number of whales at this site in any year is the foraging pressure of previous years, suggesting a top-down forcing on the inter-annual predator-prey patterns (Burnham & Duffus, in press). The force of baleen whales as apex predators is yet to be fully understood, largely hindered by the size and range of their habitats, and a paucity of fundamental information about ecological interactions within it (DeMaster et al. 2006, Paine 2006). Studies such as this one, over long-time scales and in a spatially discrete area, can provide important insight into the role of predators in marine ecosystems. However, a more complete understanding of whale use of Clayoquot Sound may be garnered by considering push and pull factors from adjacent regions in the wider PCFG range. Gray whales have so far shaped their own prey's abundance in Clayoquot Sound, mediated by the reproductive behaviour of their primary prey. Considering the foraging behaviours of PCFG whales in other locales, as well as those outside of the PCFG, may aid a better population-wide understanding of the link between gray whales and their prey.

While 20 years of study has produced a useful appreciation of the ecological relationships between predator and prey, until now the mechanism by which site use was mediated was unknown. Whales seemed to have perfect knowledge of this small foraging area, as well as foraging sites along hundreds of kilometers of coastline. On finer scales, cows with calves moved to specific types of sites to take advantage of the proximity of good prey and good cover from killer whales. Prey density cues and distribution of patches are obvious forces in the behavioural ecology and decision-making of the individual animals, but a higher level of organization between animals and sub-groups of core residents and single time visitors is also implicated. That higher level now appears to be driven by acoustic behaviour, whether it be directed communication, passive listening, or some combination of the two, that forms a network that connects gray whales.

## 1.5. Gray whale acoustic behaviour in foraging and weaning areas

### Preface

The acoustic repertoire of gray whales is well described for breeding areas, and increasingly for migration routes, as discussed in Chapter 1.2 and 1.3. It is, however, poorly known for foraging areas (Stafford et al. 2007). It is possible that vocal behaviours are restricted in this situation, to focus energy on prey acquisition as seen in other baleen whales (e.g. Clark 1983, Mellinger et al. 2007, Baumgartner & Fratantoni 2008, Parsons et al. 2008, Parks et al. 2011, Vu et al. 2012). Here I use recordings from the main foraging bay in Clayoquot Sound (Chapter 1.4), to examine the whales' vocal repertoire and behaviours during this time.

Acoustic recordings often cannot move past noting the presence of whales. Here I added visual observations to give social, demographic, and behavioural context to the acoustic data. I am looking for a route to refine the interpretation of vocal behaviours during this time. Several dynamic processes are occurring during the summer that I can use to underpin my thinking. For example, satiation may be approached, as the whales replenish energy reserves following overwinter fasting. A movement from foraging to more social behaviours as the summer months progress has been noted anecdotally, specifically before the southward migration begins and the site is abandoned (Pers. Obs.), which may be reflected in the acoustic data. Also, there is a progression of the weaning process, which may be expressed in the use of 'motherese' calling between cow and calf, until now only suggested from the natal lagoons, which may be abandoned as the calf gains independence (Ollervides 2001, Charles 2011).

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# Gray whale (*Eschrichtius robustus*) acoustics use in a foraging and weaning area

## Introduction

Clayoquot Sound, on the west coast of Vancouver Island, is a foraging and weaning site for gray whales (*Eschrichtius robustus*). The physical characteristics of the area, including topographical complexity and depth, create the foundation for whale prey habitat (Laskin et al. 2010). Gently sloping sandy stretches adjacent to rocky outcrops and kelp beds create nursing/weaning areas for calves, in close proximity to high quality, but variable foraging areas. Productive foraging sites present opportunities for mothers to forage and replenish energy reserves, following the demands of migration, pregnancy, birth, and lactation, as well as protection of the calf. Maternal learning and cultural transmission of site use is suggested by the recruitment patterns of whales to this area. Individuals return repeatedly to take advantage of both ephemeral and more persistent prey types (Dunham & Duffus 2001, 2002, Feyrer & Duffus 2011, 2014, Burnham 2015).

Vocal behaviours of gray whales have been well described in calving/breeding areas (Dahlheim et al. 1984, Dahlheim 1987, Ollervides 2001, Charles 2011, Ponce et al. 2012, López-Urbán et al. 2016), however only limited recordings have been made in foraging areas that examine calling during feeding and weaning (Moore & Ljungbald 1984). I consider several lines of inquiry based on these general themes. Vocalising rate may be reduced as whales focus on prey capture, as noted in other species (e.g. Clark 1983, Mellinger et al. 2007, Baumgartner & Fratantoni 2008, Parsons et al. 2008, Parks et al. 2011, Vu et al. 2012). Perhaps acoustic use changes as whales progress from an energy deficient, to a satiated state as summer foraging progresses. Calling behaviours may also alter if energy expenditure for foraging increases, for example by rough seas or tidal cycle (e.g Nuutila et al. 2017), or if the ability to maintain contact with conspecifics decreases, such as in increased ambient noise, either by abiotic action or vessel presence. Calling could also increase as darkness limits the utility of visual cues (Guazzo et al. 2017, Rannankari et al. 2018).

My examination of the recordings made over two summers first aims to describe calling during foraging, and how this may change as the season progresses looking for indicators of a shift from foraging-dominated activity to more social behaviours. Calling patterns in relation to photo- and tidal period and soundscape conditions are also considered. The effect of whale watching activities in the area are touched on, but considered in more detail elsewhere (Chapters 1.6, 3.3). Given the use of the study site for nursing/weaning, the recordings are also examined for the presence of ‘motherese’-type calls (Ollervides 2001, Charles 2011, López-Urbán et al. 2016). Indeed, cues of weaning and cow-calf separation may be suggested in the acoustic data, with the possibility that these call types will be abandoned as the calf matures. Surface observations made concomitant to the acoustic recordings allow us to describe calling with some behavioural context.

## Methods

An Autonomous Multichannel Acoustic Recorder (AMAR, JASCO G3A), fitted with a GeoSpectrum M8E-132 calibrated omnidirectional hydrophone (sensitivity -165 dB re 1 V/µPa, effective bandwidth 5 Hz-150 kHz, gain of 6 dB) was deployed in Cow Bay (49.25629, -126.15928), the main feeding area for gray whales in Clayoquot Sound (Figure 1.5.1). Continual recording onto solid state flash memory was made from May 6 to September 14, 2015 and May 30 to September 5, 2016. Visual and aural inspection of the acoustic data was through spectrograms generated using a 256-point Hann window FFT with 50% overlap using Raven Pro Interactive Sound Analysis Software. Manual inspection of the recordings for gray whale calls was made for every fifth day (20%) from the first full day of the AMAR deployment to allow for comparisons over time. In addition, periods where visual observations were made were also manually analysed (see Appendix of Chapter II).

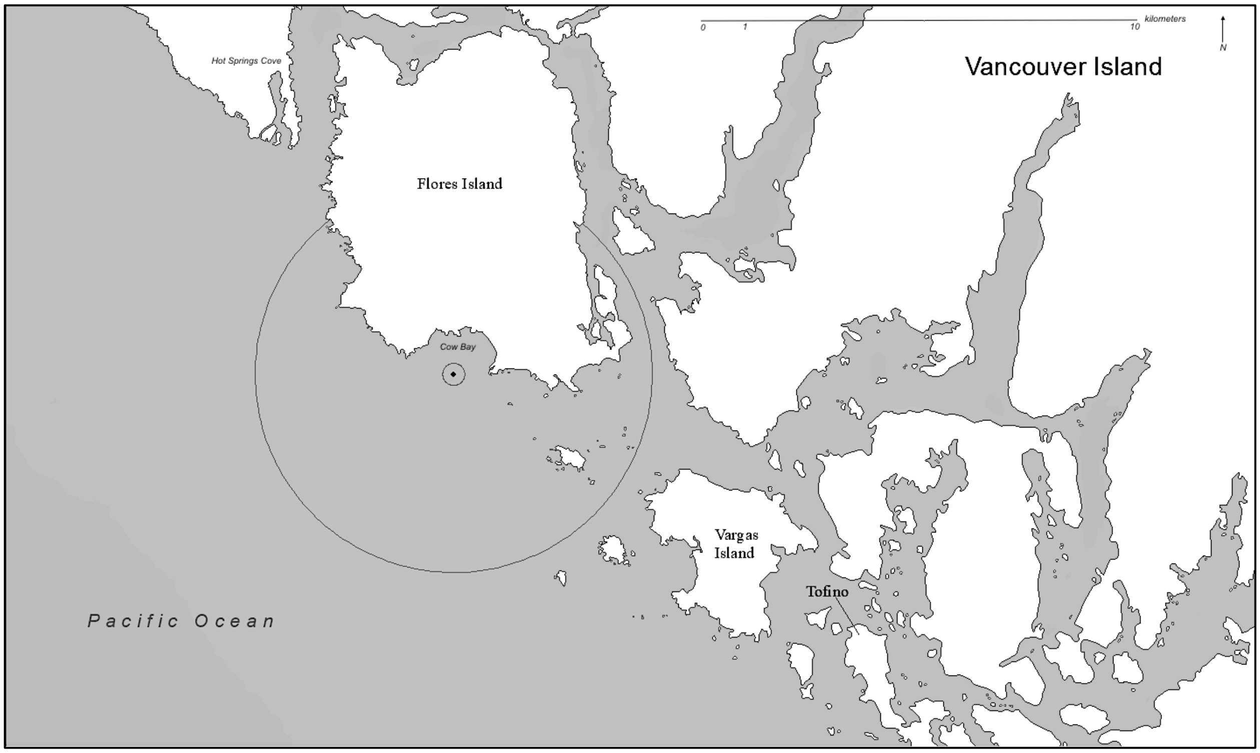

**Figure 1.5.1**: AMAR deployment location (49.25629, -126.15928) for summer foraging recordings. Circles around AMAR show likely range detection radii of gray whale class 3 moan calls. AMAR location is in the centre of the detection circles with the smaller circle representing the range of detection 90% of the time (500 m) and the larger 10 % of the time (9 km).

Gray whale calls were classified by spectrogram comparison to previous gray whale acoustic studies (Dahlheim 1987, Crane & Lashkari 1996, Ollervides 2001, Wisdom et al. 2001, Stafford et al. 2007, Charles 2011, Dahlheim & Castellote 2016, López-Urbán et al. 2016). Core call types are class 1 knocks, a series of pulses, that here are subdivided to distinguish modulated (a) and non-modulated (b) calls; class 2 sweepings pulses, an upsweep (here labelled 2a), or downsweep (2b); class 3, low frequency modulated moan-like calls, sometimes described with 'growl' like qualities, and class 4, higher frequency modulated rumble calls (Dahlheim 1987). An additional five call types, outlined as possible 'motherese' were also analysed, including class 7, complex tonal growl sounds; class 8, short single knock-like vocals described as 'uggs'; class 9, roar-like, complex tones; class 10, grunt-like rumbles, with broader bandwidth than class 4, more like a creaking sound, and class 11, a large bandwidth 'rattle', possibly from the baleen (Ollervides 2001, Charles 2011). Sub-surface exhalations of class 5 and 6, 'bubble blasts' and extended outbreaths respectively (Dahlheim 1987), were used as indicators for whale presence, but not subject to further acoustic analysis. Vocal projections that were seemingly twinned, for example ‘knock-moan’ or ‘knock-grunt’ (Fish et al. 1984, Dahlheim 1987), or those believed to be part of the gray whale repertoire due to call structure, frequency range (Hz), or amplitude (dB re 1µPa) relative to background noise were recorded and labeled ‘other’, but were not subject to further examination.

For each call, the lowest and highest frequencies (Hz), and frequency range, peak frequency, call timing, and duration (s) were derived. Each was further annotated with call class and descriptive comments. Vessel noise was noted, with Lloyd mirror curves (Urick 1983) used to determine the passage of vessels directly through the bay.

Patterns in call type use and call rate in response to photoperiod, tide, and sea state, were examined. A day-night comparison was made, where day and night were defined by nautical twilight dawn and dusk times. As well, twilight periods were considered, where night is unchanged, but dawn is defined as the time between nautical twilight start and sunrise, day between sunrise and sunset and dusk between sunset and nautical twilight end. Tidal effects were considered by correlating tide level to calls, as well as between calls assigned to categories of ebb, flood, or slack tide (high or low), defined as two-hours before and after the tide turns. Measures of wave height, wind speed, and gusting wind speed were used as proxies to sea state, and correlated per call and per-hour for calling rate. Changes in calling over the summer were examined by correlating vocal behaviours to the number of days elapsed since January 1 of that year.

The detection of gray whale calls was presumed to be largely confined to Cow Bay (Figure 1). The range and probability of detection of whales was estimated using ambient noise levels (NL) for each minute of the recording, source levels (SL) of gray whale moans from Guazzo et al. (2017, 156.9 ± 11.4 dB re 1µPa @ 1m), where the received level (RL) at the recorder is RL=SL-TL(r). In this case transmission loss (TL) estimation follows the assumption of cylindrical spreading appropriate for shallow water (Urick 1983), with attenuation not included due to the low frequency of the calls (see Appendix Figure A.1.5.1 for probability curve).

Observations were made to complement the recordings. These were made from an anchored research vessel, with engines off, from mid-Cow Bay that allowed unobstructed views of the entire bay, as well as of areas from which whales or vessels entered from or exited to. Observers were positioned to maintain 360-degree coverage around the boat, and recorded whale number and location; group composition, especially the presence of cow-calf pairs; behaviours and movements of the whales; the presence of other species, especially killer whales, and the presence and movements of vessels or aircraft, or whale watching platforms, and their distance and behaviours in reference to the whales. More opportunistic observations were made during line transect surveys as part of an ecological study in Clayoquot Sound (outlined in Chapter 1.4), which allowed for the comparison of calling behaviours and the number of whales inside Cow Bay and in the wider study area.

## Results

All core call types, as described by Dahlheim (1987), and all 'motherese' call types except class 11 baleen rattles, as outlined by Ollervides (2001) and Charles (2011), were recorded in 2015 and 2016 (Table 1.5.1a, b, see Appendix for example spectrograms). Call number differed by year (2015: 2,795; 2016: 2,956), possibly reflecting the numbers of whales present, with all call information pooled for further analysis.

Calling rate differed significantly by photoperiod. There were proportionately more calls during the day than night or twilight (Table 1.5.2, 1.5.3, Figure 1.5.2), particularly for class 2 and 3 call types (class 2: $t(1715.613)=6.173$, $p<0.001$; class 3: $t(1597.351)=6.397$, $p<0.001$). The mean number of calls per hour of 'motherese' calls 9 and 10 were also found to differ significantly between day and night (class 9: $t(1403.000)=2.725$, $p=0.007$; class 10: $t(1700.740)=3.053$, $p=0.002$) when accounting for twilight periods. Although spatial use of the bay was seen to differ with the tide, with cow-calf pairs frequenting shallow, sandy nursing sites most at flood or high slack tides, tidal cycle had no effect on calling. Calling was generally negatively correlated with sea state, with the most significant responses seen for modulated calls such as class 1a and 2, however all correlations were weak (Table 1.5.4). Wave height and wind speed variables are abiotic sources of low- and mid- frequency noise in ambient noise conditions (Wenz 1962, Tyack 2008, Tyack and Janik 2013, Farina 2014), so changes in calling may represent a conservative strategy. Calling rate is negatively correlated with time, when calling per hour is compared to the number of days elapsed in the year (Table 1.5.4). This may be a function of calling behaviours or a reflection of lowered whale counts, both in Cow Bay and the study area, as the number of foraging whales were reduced after mid-July.

**Table 1.5.1a:** Number of calls (N) and mean, standard deviation and coefficient of variation, mode, minimum and maximum values for each call metric by call type. 'Core' call types presented. Class 1 is divided to distinguish modulated (1a) from non-modulated calls (1b), class 2 is divided to indicate upsweeps (2a) and downsweeps (2b). Total calls is 5,751 for Table 1a and 1b.

| Class | Metric | N | Mean | St. Dev. | CV | Mode | Min. | Max. |
|---|---|---|---|---|---|---|---|---|
| 1a | Low freq. | 1388 | 43.31 | 52.57 | 121.38 | 122.80 | 1.80 | 507.00 |
| | High freq. | 1388 | 229.62 | 248.15 | 108.07 | 120.00 | 57.30 | 1486.60 |
| | Peak freq. | 1388 | 81.90 | 82.01 | 100.13 | 50.80 | 6.80 | 715.60 |
| | Length | 1388 | 2.37 | 0.79 | 33.33 | 1.78 | 0.44 | 4.88 |
| | Freq. range | 1388 | 186.41 | 214.33 | 114.98 | 91.60 | 21.10 | 1274.20 |
| 1b | Low freq. | 421 | 122.53 | 108.33 | 88.41 | 10.10 | 4.60 | 464.80 |
| | High freq. | 421 | 332.97 | 233.86 | 70.23 | 261.00 | 73.30 | 1432.80 |
| | Peak freq. | 421 | 180.11 | 144.75 | 80.37 | 25.40 | 6.30 | 671.40 |
| | Length | 421 | 2.36 | 0.87 | 36.86 | 1.33 | 0.44 | 5.88 |
| | Freq. range | 421 | 210.44 | 165.51 | 78.65 | 113.70 | 48.90 | 1146.40 |
| 2a | Low freq. | 1110 | 46.73 | 33.09 | 70.81 | 24.70 | 4.60 | 464.80 |
| | High freq. | 1110 | 180.96 | 55.72 | 30.79 | 142.00 | 75.10 | 447.80 |
| | Peak freq. | 1110 | 94.62 | 54.57 | 57.67 | 73.20 | 5.90 | 378.40 |
| | Length | 1110 | 2.25 | 0.81 | 36.00 | 1.83 | 0.44 | 4.89 |
| | Freq. range | 1110 | 134.31 | 40.77 | 30.36 | 128.30 | 33.00 | 341.80 |
| 2b | Low freq. | 20 | 47.91 | 32.77 | 68.40 | N/A | 13.70 | 142.00 |
| | High freq. | 20 | 190.19 | 66.70 | 35.07 | 189.70 | 88.00 | 339.10 |
| | Peak freq. | 20 | 73.34 | 47.74 | 65.09 | 25.40 | 25.40 | 179.70 |
| | Length | 20 | 3.39 | 1.55 | 45.72 | 2.22 | 1.78 | 7.10 |
| | Freq. range | 20 | 142.28 | 58.97 | 41.45 | 165.90 | 58.00 | 288.70 |
| 3 | Low freq. | 1622 | 19.83 | 18.51 | 93.34 | 9.40 | 2.30 | 176.50 |
| | High freq. | 1622 | 140.10 | 50.26 | 35.87 | 103.30 | 58.20 | 623.50 |
| | Peak freq. | 1622 | 43.60 | 43.86 | 100.60 | 16.60 | 4.40 | 246.10 |
| | Length | 1622 | 2.86 | 0.94 | 32.87 | 2.35 | 0.44 | 5.88 |
| | Freq. range | 1622 | 120.27 | 41.81 | 34.76 | 84.50 | 27.40 | 580.30 |
| 4 | Low freq. | 13 | 66.56 | 32.27 | 48.48 | 8.20 | 8.20 | 103.30 |
| | High freq. | 13 | 284.93 | 69.23 | 24.30 | 139.30 | 139.30 | 415.50 |
| | Peak freq. | 13 | 142.28 | 69.85 | 49.09 | 129.90 | 23.40 | 256.80 |
| | Length | 13 | 3.30 | 1.53 | 46.36 | 1.22 | 1.22 | 5.88 |
| | Freq. range | 13 | 218.38 | 58.91 | 26.98 | 103.60 | 103.60 | 319.30 |

**Table 1.5.1b:** Number of calls (N) and mean, standard deviation and coefficient of variation, mode, minimum and maximum values for each call metric by call type. 'Motherese' call types presented. Total calls is 5,751 for Table 1a and 1b.

| Class | Metric | N | Mean | St. Dev. | CV | Mode | Min. | Max. |
|---|---|---|---|---|---|---|---|---|
| 7 | Low freq. | 77 | 48.40 | 35.11 | 72.54 | 37.60 | 5.60 | 156.70 |
| | High freq. | 77 | 174.93 | 78.59 | 44.93 | 162.20 | 62.30 | 392.70 |
| | Peak freq. | 77 | 86.11 | 57.97 | 67.32 | 48.80 | 8.80 | 250.50 |
| | Length | 77 | 3.41 | 1.49 | 43.70 | 2.22 | 1.07 | 7.99 |
| | Freq. range | 77 | 126.53 | 66.56 | 52.60 | 50.40 | 48.50 | 360.10 |
| 8 | Low freq. | 496 | 50.28 | 38.33 | 76.23 | 15.60 | 4.60 | 321.60 |
| | High freq. | 496 | 164.77 | 60.29 | 36.59 | 110.00 | 77.00 | 532.40 |
| | Peak freq. | 496 | 88.87 | 53.73 | 60.46 | 107.70 | 5.90 | 343.50 |
| | Length | 496 | 2.08 | 0.83 | 39.90 | 1.83 | 0.61 | 4.70 |
| | Freq. range | 496 | 114.49 | 39.46 | 34.47 | 85.20 | 28.70 | 310.30 |
| 9 | Low freq. | 214 | 23.51 | 9.95 | 42.32 | 22.90 | 10.10 | 97.10 |
| | High freq. | 214 | 197.64 | 57.28 | 28.98 | 202.50 | 68.70 | 426.10 |
| | Peak freq. | 214 | 89.95 | 22.84 | 25.39 | 95.70 | 25.40 | 144.50 |
| | Length | 214 | 3.29 | 1.34 | 40.73 | 1.78 | 1.33 | 4.00 |
| | Freq. range | 214 | 174.13 | 59.11 | 33.95 | 176.80 | 16.20 | 368.40 |
| 10 | Low freq. | 390 | 81.93 | 38.95 | 47.54 | 43.10 | 11.90 | 226.30 |
| | High freq. | 390 | 264.23 | 53.85 | 20.38 | 255.70 | 93.50 | 492.10 |
| | Peak freq. | 390 | 159.28 | 59.11 | 37.11 | 183.60 | 15.10 | 320.30 |
| | Length | 390 | 2.59 | 0.99 | 38.22 | 1.83 | 0.61 | 7.33 |
| | Freq. range | 390 | 182.29 | 50.98 | 27.97 | 133.80 | 72.40 | 474.70 |

**Table 1.5.2:** Total number of calls per hour for each light condition, also expressed as a proportion. In the first instance day and night are defined by nautical twilight times. For twilight inclusion, dawn is nautical dawn to sunrise, day sunrise to sunset, dusk is sunset to nautical dusk and night is nautical dusk to dawn.

| Frequency/hr | Call number | % |
|---|---|---|
| Day | 1408 | 67.92 |
| Dawn | 102 | 4.92 |
| Dusk | 109 | 5.26 |
| Night | 454 | 21.90 |
| Day | 1619 | 78.10 |
| Night | 454 | 21.90 |

**Table 1.5.3**: Calling rate, defined as mean number of calls per hour, for each photoperiod. Differences in calling between periods of day-night-dusk (both sunrise and sunset) was tested using a Kruskal-Wallis test (K-W, p), Day-night using a Mann-Whitney test (M-W,p.) and t-tests to compare means between day and night (t-value and p-value shown). Day is sunrise to sunset, dawn is nautical dawn to sunrise, dusk is sunset to nautical dusk, night is nautical dusk to dawn. For day-night comparison day is nautical dawn to dusk, with night nautical dusk until dawn. 'M.' is an abbreviation for 'motherese' calls.

| Class | $\bar{x}$,day | $\bar{x}$,dawn | $\bar{x}$,dusk | $\bar{x}$,night | K-W,p | $\bar{x}$,day | $\bar{x}$,night | M-W, p | t-value | p-value |
|---|---|---|---|---|---|---|---|---|---|---|
| All | 2.02 | 0.54 | 0.83 | 1.10 | <0.001 | 1.84 | 1.10 | <0.001 | 2.977 | 0.003 |
| 'M.' | 0.21 | 0.05 | 0.12 | 0.04 | 0.079 | 0.19 | 0.04 | 0.009 | 3.278 | 0.001 |
| | | | | | | | | | | |
| 1a | 0.15 | 0.00 | 0.00 | 0.10 | <0.001 | 0.13 | 0.10 | 0.789 | 0.643 | 0.532 |
| 1b | 0.72 | 0.07 | 0.21 | 0.49 | <0.001 | 0.65 | 0.49 | 0.015 | 0.787 | 0.432 |
| 2 | 0.38 | 0.14 | 0.11 | 0.10 | <0.001 | 0.35 | 0.10 | <0.001 | 5.848 | <0.001 |
| 3 | 0.54 | 0.15 | 0.37 | 0.18 | <0.001 | 0.50 | 0.18 | <0.001 | 6.053 | <0.001 |
| 4 | 0.00 | 0.00 | 0.00 | 0.00 | 0.992 | 0.00 | 0.00 | 0.631 | -0.706 | 0.481 |
| 7 | 0.03 | 0.03 | 0.00 | 0.02 | 0.789 | 0.02 | 0.02 | 0.541 | 0.566 | 0.572 |
| 8 | 0.10 | 0.00 | 0.05 | 0.02 | 0.239 | 0.09 | 0.02 | 0.050 | 1.503 | 0.133 |
| 9 | 0.04 | 0.00 | 0.00 | 0.00 | 0.175 | 0.04 | 0.00 | 0.034 | 2.724 | 0.007 |
| 10 | 0.04 | 0.02 | 0.07 | 0.01 | 0.191 | 0.04 | 0.01 | 0.012 | 3.191 | 0.001 |

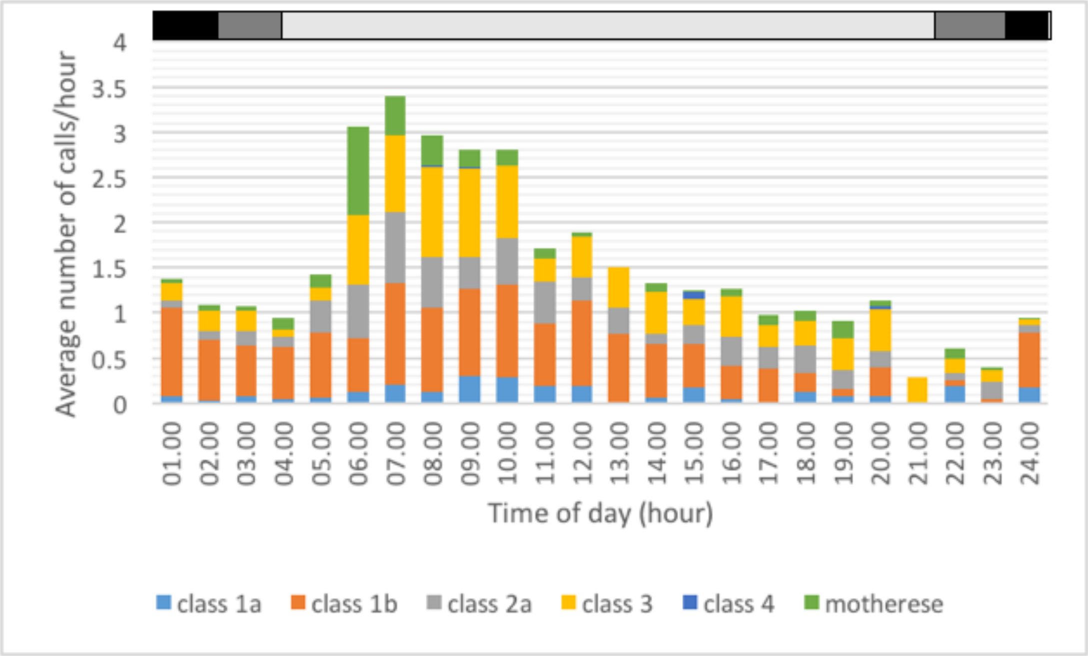

**Figure 1.5.2:** Mean number of calls per hour for each call type (for core call types, classes 1-4, and motherese call types pooled) through the day for recordings made during the summer feeding period. The shaded bar across the top of the chart represents night (black) twilight (dusk and dawn, dark grey) and day (light grey) according to nautical twilight time.

**Table 1.5.4:** Spearman's correlations, with correlation coefficient (coef.) and significance value (sign.) of calling rate (number of calls per hour) and ambient (dB), tidal level (m), waveheight (m), continuous and gusting wind conditions (m/s) and year day, the number of days elapsed since January 1 of that year.

| | Coefficient | Significance | Coefficient | Significance |
|---|---|---|---|---|
| Ambient average | | | Year day | |
| All | 0.079 | <0.001 | -0.407 | <0.001 |
| 'motherese' | -0.113 | <0.001 | -0.083 | <0.001 |
| 1a | 0.130 | <0.001 | -0.231 | <0.001 |
| 1b | 0.128 | <0.001 | -0.391 | <0.001 |
| 2 | 0.068 | 0.002 | -0.285 | <0.001 |
| 3 | 0.037 | 0.088 | -0.275 | <0.001 |
| 4 | 0.021 | 0.330 | 0.008 | 0.729 |
| 7 | -0.116 | <0.001 | -0.060 | 0.006 |
| 8 | -0.021 | 0.342 | -0.049 | 0.027 |
| 9 | -0.020 | 0.346 | -0.113 | <0.001 |
| 10 | -0.063 | 0.004 | 0.200 | 0.355 |
| Tidal level | | | Waveheight | |
| All | -0.083 | <0.001 | -0.086 | <0.001 |
| 'motherese' | -0.069 | 0.002 | -0.048 | 0.031 |
| 1a | -0.059 | 0.007 | 0.014 | 0.510 |
| 1b | -0.063 | 0.004 | -0.028 | 0.207 |
| 2 | -0.074 | 0.001 | -0.052 | 0.019 |
| 3 | -0.056 | 0.011 | -0.010 | 0.658 |
| 4 | -0.052 | 0.017 | 0.014 | 0.521 |
| 7 | -0.006 | 0.796 | -0.060 | 0.006 |
| 8 | -0.063 | 0.004 | 0.004 | 0.868 |
| 9 | -0.084 | <0.001 | -0.014 | 0.524 |
| 10 | -0.005 | 0.826 | -0.007 | 0.764 |
| Continous windspeed | | | Gusting windspeed | |
| All | -0.034 | 0.162 | -0.107 | <0.001 |
| 'motherese' | -0.003 | 0.908 | -0.023 | 0.334 |
| 1a | -0.016 | 0.518 | -0.060 | 0.011 |
| 1b | 0.049 | 0.047 | -0.049 | 0.039 |
| 2 | 0.013 | 0.602 | -0.066 | 0.005 |
| 3 | -0.012 | 0.616 | -0.041 | 0.081 |
| 4 | -0.022 | 0.380 | -0.019 | 0.411 |
| 7 | 0.001 | 0.955 | 0.003 | 0.908 |
| 8 | 0.031 | 0.203 | 0.017 | 0.460 |
| 9 | 0.036 | 0.138 | 0.003 | 0.891 |
| 10 | -0.046 | 0.059 | -0.054 | 0.020 |

Visual observations were made over 243 hours, 11.7% of the total acoustic data analyzed. Of those, 109 hours were from transect surveys in Cow Bay and 134 hours from designated observation periods. Also, 96 hours were without whales and 142 were without cow-calf pairs. These observations allowed us to analyse how the number and demographics of whales in the bay, and wider study area (Figure 1.5.3, 1.5.4), occurs with altered vocal behaviours. The use of all call types, except class 4, showed an increased call rate when whales were physically present in the bay, with the presence of single whales ($r_s = 0.460$, $p<0.001$) and cow-calf pairs correlating with calling ($r_s = 0.352$, $p<0.001$), albeit with only weak to moderately strong coefficients. The use of 'motherese' call types was unchanged when compared to the number and type of whales in the bay (Table 1.5.5). Class 1b calls were significantly correlated with numbers of whales recorded in Clayoquot Sound (total whales: $r_s$ =0.433, p=0.001; cow-calf pairs: $r_s$ =0.300, p=0.001), with class 2 upsweeps and single foraging whales ($r_s$=0.264, p=0.010) and class 3 moans and cow-calf pairs ($r_s$=0.302, p=0.003) were correlates, but only weakly to moderately so.

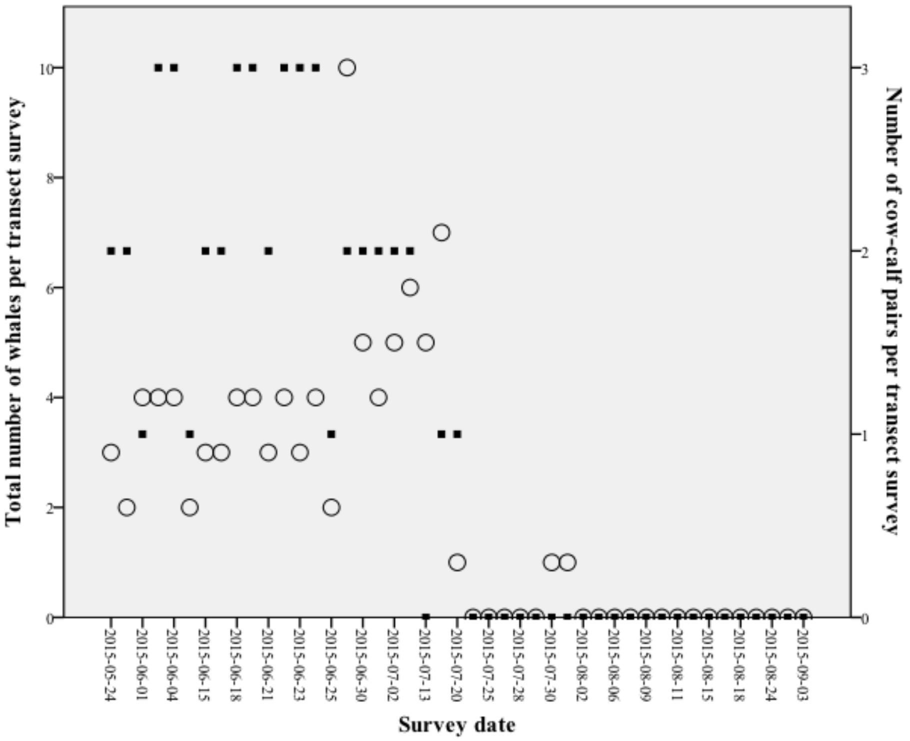

**Figure 1.5.3:** Transect and observational data from within Cow Bay for 2015, showing the number whales (total, open circles) and cow-calf pairs (part of total, black squares)

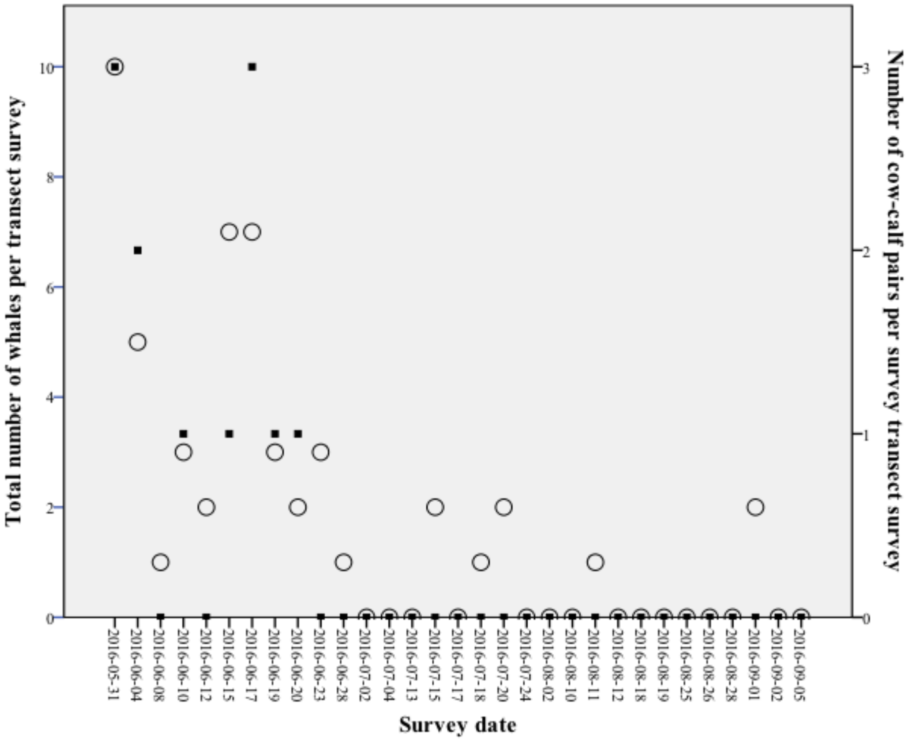

**Figure 1.5.4:** Transect and observational data from within Cow Bay for 2016, showing the number whales (total, open circles) and cow-calf pairs (part of total, black squares)

**Table 1.5.5**: Comparing rate of calling with the known presence and absence of whales and cow-calf pairs only using Mann-Whitney U testing, with significance values shown (M-W, p.) Spearman's correlation between the rate of calling to the number of whales seen, the number of single adults only and the number of cow-calf pairs only is also shown with the correlation coefficient (coef.) and significance value (sign.). 'M.' is an abbreviation for 'motherese' call types.

| Class | whale | cow-calf | number of whales | | single adults | | cow-calf pairs | |
|---|---|---|---|---|---|---|---|---|
| | M-W, p | M-W, p | coef. | sign. | coef. | sign. | coef. | sign. |
| All | <0.001 | <0.001 | 0.485 | <0.001 | 0.460 | <0.001 | 0.352 | <0.001 |
| 'M.' | 0.028 | 0.161 | 0.172 | 0.007 | 0.234 | <0.001 | 0.031 | 0.635 |
| | | | | | | | | |
| 1a | <0.001 | 0.035 | 0.219 | 0.001 | 0.210 | 0.001 | 0.119 | 0.064 |
| 1b | <0.001 | 0.004 | 0.300 | <0.001 | 0.322 | <0.001 | 0.178 | 0.005 |
| 2 | <0.001 | 0.106 | 0.235 | <0.001 | 0.289 | <0.001 | 0.108 | 0.092 |
| 3 | <0.001 | <0.001 | 0.402 | <0.001 | 0.271 | <0.001 | 0.415 | <0.001 |
| 4 | 0.419 | 0.236 | 0.096 | 0.137 | 0.096 | 0.136 | 0.079 | 0.220 |
| 7 | 0.055 | 0.013 | 0.198 | 0.002 | 0.268 | <0.001 | 0.093 | 0.150 |
| 8 | 0.200 | 0.717 | 0.047 | 0.467 | 0.089 | 0.166 | -0.021 | 0.745 |
| 9 | 0.045 | 0.035 | 0.311 | 0.311 | -0.040 | 0.532 | 0.059 | 0.359 |
| 10 | 0.201 | 0.727 | 0.138 | 0.138 | 0.158 | 0.014 | 0.014 | 0.832 |

## Discussion

Few studies have recorded gray whale acoustic behaviour during foraging or nursing/weaning, or considered the use of 'motherese' outside of breeding lagoons. Vocal patterns and call type use differ from those described for breeding areas (Dahlheim 1987, Ollervides 2001, Charles 2011, Ponce et al. 2012, López-Urbán et al. 2016) and during migration (Rassmussen & Head 1965, Cummings et al. 1968, Crane & Lashkari 1996, Guazzo et al. 2017, Burnham et al. 2018). Work in Arctic feeding grounds reports class 1, low-frequency knock-like pulses as the most common. Recordings from this study agree, both modulated (class 1a) and unmodulated (class 1b) calls, when pooled total 31.45% of calls, however their dominance is less than that reported from northern feeding areas. Prevalence of knock-like calls were highest in recordings from June, when whale number in the bay was also at its highest.

The use of the frequency-modulated call types of class 1 and 2 suggest that gray whales retain contact in the same feeding bay or between adjacent prey patches when foraging. These vocal projections are believed to be used for inter-group communications, and have been described to have a 'social/sexual' role (Youngson & Darling 2016). The use of class 3 moan calls, which propagate over greater distances, suggests that the whales may also be sending and receiving acoustic information over a wider spatial scale than from just within the foraging bay. Acoustics may form part of the whales' proximal and distal mechanisms to locate and exploit prey aggregations (Torres 2017) over large stretches of coastline that forms their range.

It was presumed that all or most of the calling behaviours recorded would be from whales in the bay, confirmed by the detection probability radius (See Appendix for details). Calls were propagating from within 500m of the AMAR for 90% of the recordings and extended to the range of the entire bay (~ 2 km) for 45% of the recording time. At the quietest times, likely overnight with calm seas, recordings could extend to a maximum of 9 km (10% of recordings). Finding vocalisations when whales are absent from the bay means that calls were propagating from outside or on the outskirts of the bay, with low frequency moan calls having the highest call rate during these times.

Calls described as possible 'motherese' (Ollervides 2001, Charles 2011) accounted for 20.53% of the calls in the recordings, with class 8 'uggs' the most common. Although calls from this study matched the descriptions and spectrograms reported from breeding lagoons, frequency ranges and peak frequencies were more restricted and lower in pitch, and call length was several times greater in vocalisations from Cow Bay compared to Bahia Magdalena. This may suggest that call parameters change as the calf grows, and has greater physical ability to make lower frequency, longer duration calls. A decline in the use of these call types perhaps represents the progression of the weaning process. Together this suggests that calls described as 'motherese' may, in fact, be precursors for the core call types during periods of vocal learning and repertoire refinement by calves, as has been noted for odontocete species (Janik & Slater 1997, Falk 2004, see Chapter 1.8 for discussion).

Greater calling rates during the day contrasts to patterns reported for migration (Guazzo et al. 2017, Rannankari et al. 2018, Chapters 1.2, 1.3) and recordings in the breeding lagoons. For migration calling rates (call/hr) are at their greatest at night, and in the breeding lagoons Ponce et al. (2012), describe a calling peak in the early morning around dawn, particularly for class 1 and 4 calls, with a secondary peak in the twilight. Diurnal vertical migration patterns have been shown for many mysid species (Mauchline 1980), the main prey species for gray whales at this foraging site (Dunham & Duffus 2001, 2002, Feyrer & Duffus 2011, 2014, Burnham 2015), which would dissipate swarms and possibly hamper feeding success at night. However, these behaviours have not been recorded for any species in Clayoquot Sound (Burnham 2015). Feeding behaviours is, therefore, not thought to differ between day and night, however changes in acoustics use may allude to a more subtle modifications in foraging schedules. Heightened calling during the day may be due to increased vessel presence at this time, rather than calling connected directly to foraging behaviours. This patterning in calling may reflect the roughly 12 hour diel cycle in ambient noise in Cow Bay resulting from whale watching activities (see Chapter 1.6, 3.3). Ponce et al. (2012) suggested that a counter-calling to vessel noise underscored daily patterns in the breeding lagoons. On a seasonal scale, the calling rate may have been expected to increase as the whales approach satiation and are more social, but in fact there is a decrease in vocal behaviours. This may, however, be a reflection of the whale number in the study area, with foraging whales in Cow Bay much reduced in the latter part of the summer.

Calling rates were significantly different when whales were located in the bay during our observations (Table 1.5.5). Ponce et al. (2012) suggest that the call count increased in a non-linear manner, particularly when the number of whales increases quickly, and rather than be used as a remote means of counting whales, could instead be used to infer the number of connections present in the network, or how many conspecifics are communicating with each other. A similar relationship may be true for feeding areas, with this network active both within and between feeding patches in the study area. This concurs with the long term work on the study site where the number and identity of the foraging whales is dynamic, and linked to prey resource levels. It suggests that information is being passed by vocal means, as in over 20 years of work in the bay there have been no examples of direct competition for food or foraging sites observed (Whale Lab unpublished data, Chapter 1.4).

Class 1b knocks have the highest mean rate of employment during the hours that visual observations were made and whales were present, and again in periods when cow-calves were present. This pattern was also seen in transect data, for single foraging whales and cow-calf pair numbers in the wider study area. 'Motherese' calling rate was significantly reduced when no cow-calf pairs were seen in Cow Bay, except for class 8 and 10. These calls may have a function in reuniting calves with their mothers during periods of separation, or in times of threat or stress, or perhaps come from whales in less visible areas in or among the rock outcrops in Cow Bay.

The use of passive acoustic methods uncovers subtleties in behaviour that would not be possible to observe, or may be altered in the presence of a research vessel. Although not presented as part of the acoustic analysis, sub-surface exhalations and sounds of surfacing events were frequent, particularly at night, and notably overnight during the latter part of the summer when whales were not present in the bay during the day. Movements at night, and to areas that have less prey, indicates a possible shift in priorities. For both summer 2015 and 2016 whales were present in Clayoquot Sound into the late summer but frequented areas that offered benthic forage away from Cow Bay. The recordings suggest that while they were test-foraging in alternative locations, at night at least some whales returned to Cow Bay, with this site perhaps offering a haven to rest as well as forage.

The use of Cow Bay likely balances lower energy gains, with its smaller resource base, and the potential stress from frequent vessel presence than in high latitude areas, with protection from predators, and calm areas to nurse/wean. Residency time and return rates of whales between years (Chapter 1.4) signifies the importance of this foraging area, and the willingness for whales to withstand disturbance from whale watching activities to feed. This study adds to the knowledge of gray whale vocal repertoire and acoustics use throughout its range. Few previous studies have focussed on calling in foraging sites, or gray whale acoustics in the nursing and weaning process.

# Appendix

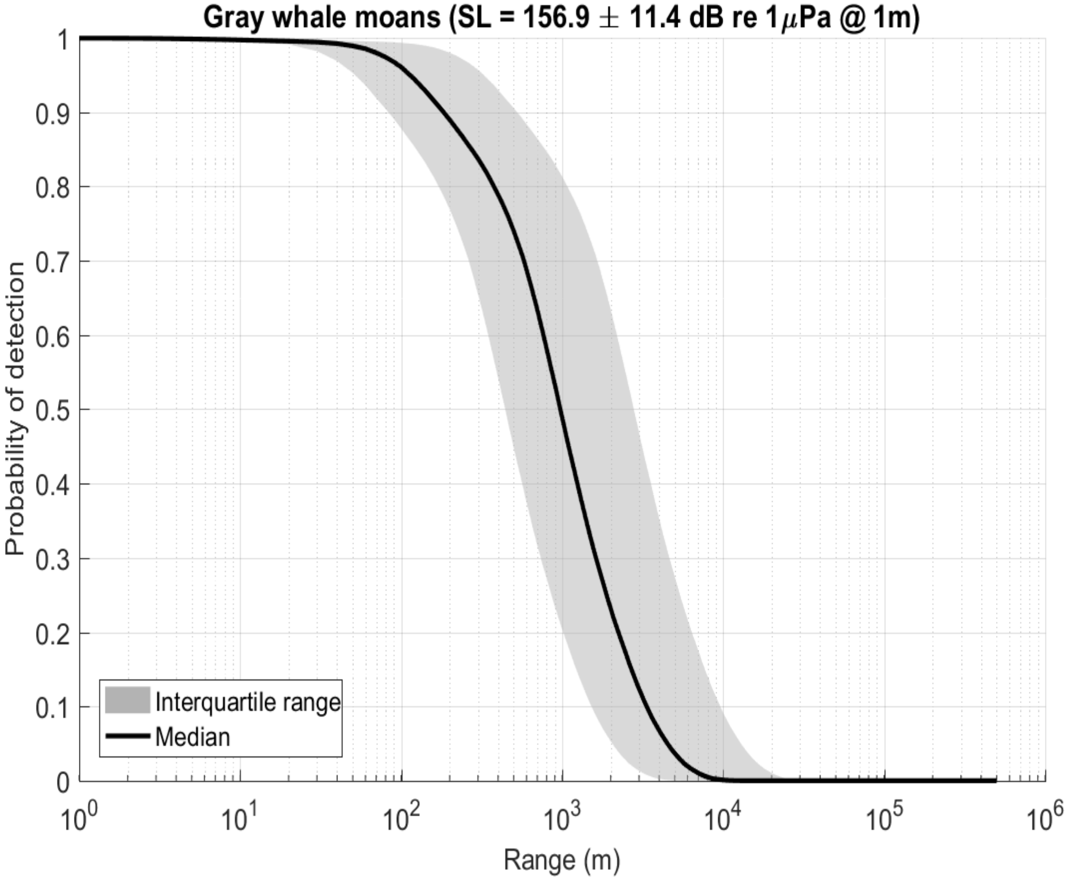

**Figure A.1.5.1**: Estimation of detection range of gray whale moans by the AMAR system throughout deployments. The range of detection of gray whale calls was estimated using ambient noise levels (NL) for each minute of recording, source levels (SL) of gray whale moans reported by Guazzo et al. (2017, 156.9 ± 11.4 dB re 1μPa @ 1m), and an estimate of the transmission loss (TL). The received sound level (RL) of a gray whale moan at the recorder is defined as RL = SL–TL(r), where r is the distance in meters between the whale and the recorder. The transmission loss was approximated to follow a spherical spreading law and was therefore estimated as TL(r) = 20 log10(r) (Urick 1983). Given the low frequency of the gray whale calls, attenuation was not included in the transmission loss estimation. The gray whale was considered to be an omnidirectional source. The detection range of a moan was estimated to be the distance from the recorder for which the received level of the gray whale moan equalled the noise level at the recorder (NL = RL). Noise levels used for estimating detection range were calculated for every minute of recording by summing the 1/3 octave bands centred between 20 and 100 Hz. The detection range was calculated for each minute of recording. The probability of detecting a gray whale moan at a given range was the number of 1 min recordings with a detection range equal to or greater than the given range divided by the number of 1 min recordings. A Monte Carlo method accounted for the measured variability in source levels. Detection ranges were re-calculated 300 times by randomly choosing 300 normally distributed source level values, with the means and standard deviations defined by Guazzo et al. 2017. Consequently, a distribution of probability is associated with each range.

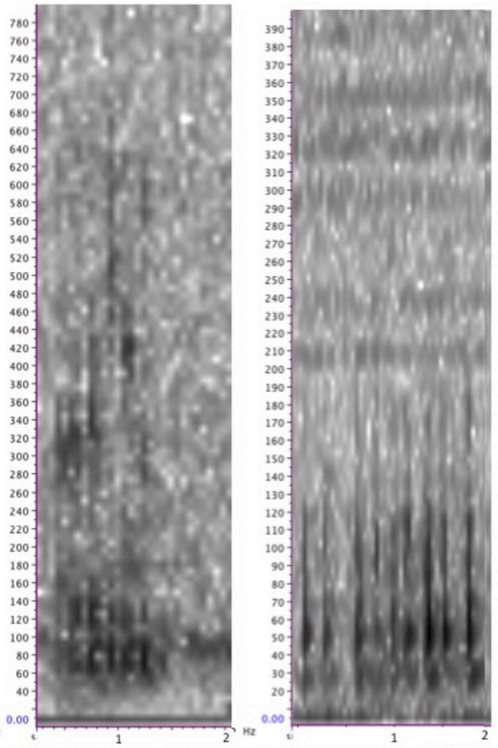

**Figure A.1.5.2**: Spectrogram of class 1 calls. Left: 1a, frequency modulated calls; Right: 1b, unmodulated. Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap. Note the frequency (Hz) scales are altered for clarity of each call type.

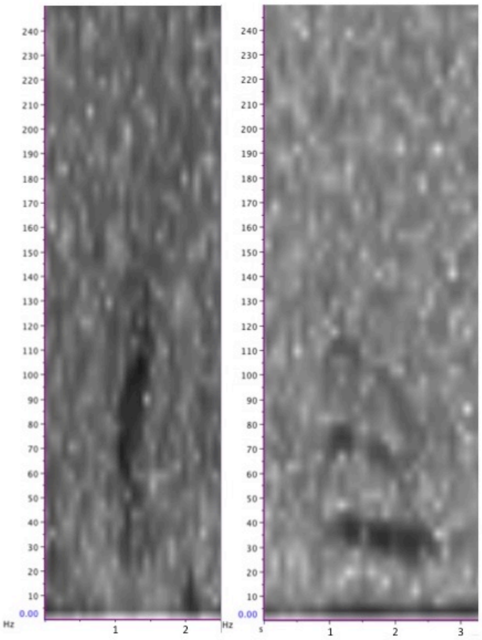

**Figure A.1.5.3**: Spectrogram of class 2 calls. Left: Upsweep, 2a; Right: Downsweep, 2b. Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

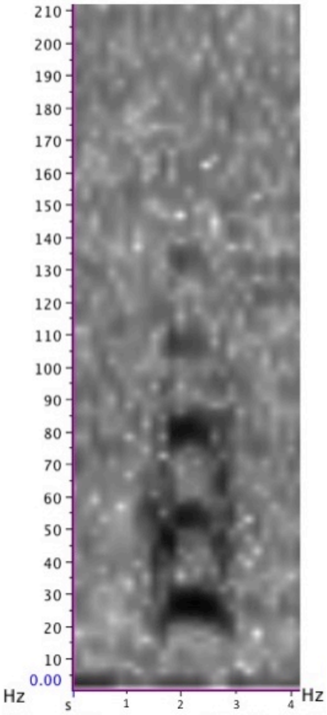

**Figure A.1.5.4**: Spectrogram of class 3 calls. Left: Class 3 moan call as described by Dahlheim (1987); Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

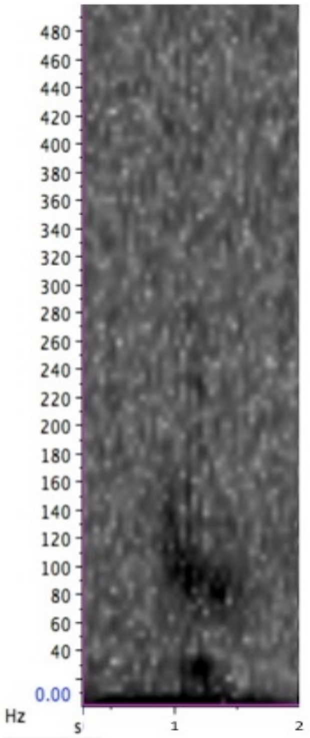

**Figure A.1.5.5**: Spectrogram of a class 4 call, as described first by Dahlheim (1987). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

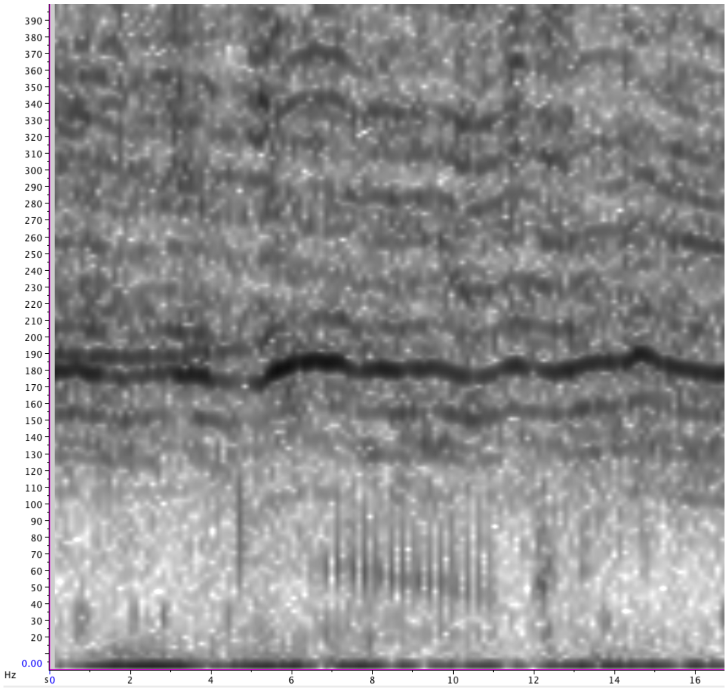

**Figure A.1.5.6:** Spectrogram of a class 7 call, part of the ‘motherese’ repertoires as described first by Ollervides (2001). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap. Dark horizontal lines are vessel noise.

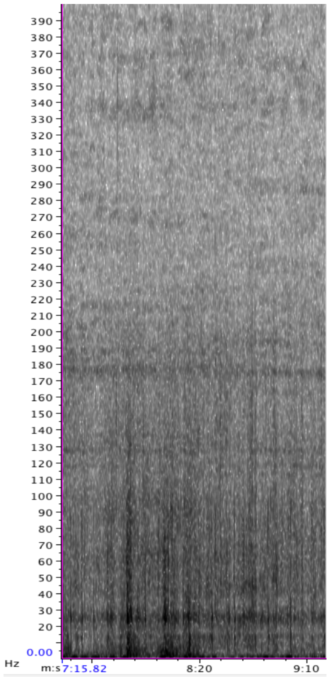

**Figure A.1.5.7:** Spectrogram of a class 8 call, part of the ‘motherese’ repertoires as described first by Ollervides (2001). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap. Dark horizontal lines are vessel noise.

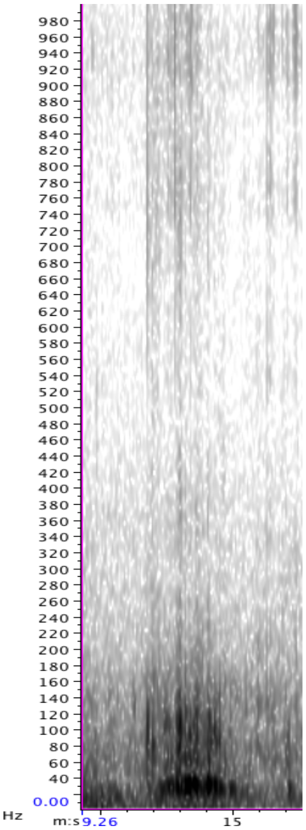

**Figure A.1.5.8**: Spectrogram of a class 9 call, part of the 'motherese' repertoires as described first by Ollervides (2001). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap. Dark horizontal lines are vessel noise.

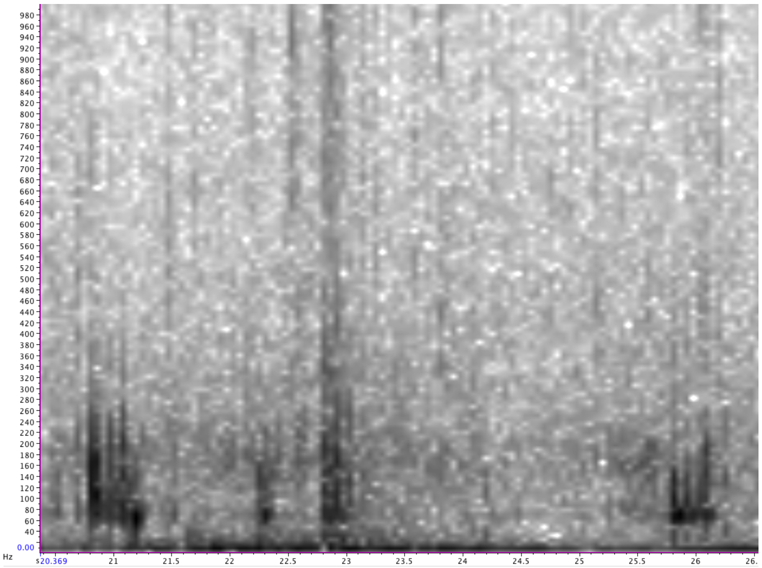

**Figure A.1.5.9**: Spectrogram of a class 10 call, part of the 'motherese' repertoires as described first by Ollervides (2001). Spectrogram was generated using a 256-point Hann-window FFT with 50% overlap.

## 1.6. The acoustic behaviours of gray whales in increased ambient noise conditions during migration and summer foraging

### Preface

Findings from previous chapters, suggest that gray whale acoustics use has been underestimated. This facet of their behavioural ecology has not been well explored, suggesting that their sensitivity to human activity and changing ocean soundscapes should also be re-evaluated.

Gray whales encounter various soundscapes as they move through their life cycle. During migration, much of the route follows or directly crosses shipping lanes, putting them into contact with considerable human derived noise. While foraging in Clayoquot Sound, gray whales are subject to vessel noise, predominantly from whale watching vessels.

Much research based on surface observations of disturbance effects from increased noise levels and vessel presence has been done (Malme et al. 1983, 1984, 1986, 1988, 1989, Bryant et al. 1984, Dahlheim et al. 1984, Dahlheim 1987, Jones et al. 1994, Richardson et al. 1995, Ollervides 1997, 2001, Würsig et al. 1999, Moore & Clarke 2002, IWC 2005, 2007). Here I look for a response in gray whale acoustics use, which may be more subtle or nuanced than that seen in swimming/diving behaviours. I compare various soundscape settings to give context to the response heard. Increased ambient noise levels resulting from natural sea state measures, and human pressures focussed on recreational/whale watching vessel presence are the backdrop for measuring changes in vocalisation behaviour. Recordings from north- and southward migration as well as from summer foraging are compared, perhaps allowing for findings to be set within the broad physiological, behavioural, and social context in which behaviours occur.

There are several processes at work here, some of which will be difficult to gauge. For example, the role of habituation cannot be examined, or the effect of the whale's individual experience on their responses. Inferences of effect may be made, but vocalisation is likely highly refined, with our level of understanding limited and simply on a cursory level, which we may have difficulty moving beyond.

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## The acoustic behaviours of gray whales in increased ambient noise conditions during migration and summer foraging

### Introduction

Acoustic alteration of the marine environment is a result of noise additions that can produce far ranging and complex effects on wildlife. Underwater soundscapes are composites of abiotic, biological, and man-made sound, each well characterised (Urick 1983, Richardson et al. 1995, Farina 2014). However, how these then effect organisms is poorly understood, thus mitigation or management may be ineffective. Whales are acoustic animals that rely heavily on sound to communicate and sense their environment, as well as a group that has been subjected to highly destructive human interaction. Here I use the study of gray whale (*Eschrichitus robustus*) acoustic behaviour to shed some light on the complexity of responses by one species to noisy soundscapes.

The eastern Pacific gray whale population has recovered since the cessation of whaling. The current estimate equals or exceeds pre-whaling numbers (Laake et al. 2012). Its proclivity for coastal habitats makes it relatively easy to study, and its life history is well described. In much of its range it is subject to ambient noise additions, especially from anthropogenic sources. This includes vessel noise, construction, and seismic and scientific exploration, with much of the acoustic contribution of these in the low frequencies (< 1000 Hz; Urick 1983, Clark 1990, Moscrop & Simmonds 1994, Richardson et al. 1995, Ross 2005, McDonald et al. 2006). Field observations of gray whale behavioural reactions to acoustic stimuli contributed to the development of the 120 dB re 1μPa exposure limit now widely applied to other marine mammals and ocean settings. Acoustic reactions to noise have been explored in playback experiments conducted in the Mexican breeding lagoons, whereby increased use and call structure modification of the dominant call type, a knock-like projection, was noted as ambient noise levels increased (Dahlheim 1987, Dahlheim & Castellote 2016). Using the same parameters as Dahlheim and Castellote (2016), here I examine changes in acoustic behaviours during migration and foraging periods, using passive acoustic recordings taken in Clayoquot Sound, on the west coast of Vancouver Island.

Gray whales have a core call repertoire of 6 acoustic projections, limited to the lower frequencies (<2 kHz; Dahlheim et al. 1984, Moore & Ljungblad 1984, Crane & Lashkari 1996, Ollervides 2001, Wisdom et al. 2001, Stafford et al. 2007, Charles 2011, Burnham et al. 2018). Calls described as 'metallic knocks' (class 1) dominate in breeding and feeding areas (Dahlheim et al. 1984, Dahlheim 1987, Moore & Ljungblad 1984), and low-frequency moan calls (class 3) dominant during migration (Crane & Lashkari 1996, Guazzo et al. 2017, Burnham et al. 2018; Rannankari et al. 2018). Other call types are described as sweeping tones (class 2), rumbles (class 4), and acoustic by-products of sub-surface exhalations (classes 5 and 6) (Dahlheim 1987). The use of 'motherese' call types between cow and calf pairs has also been described, giving an additional 5 call types. These include, growl-like tonals (class 7); short, single pulses described as 'uggs' (class 8); complex, roar-like tones (class 9); grunt-rumble, forming a creak-like sound (class 10); and, a large bandwidth 'rattle', possibly from the baleen (class 11) (Ollervides 2001, Charles 2011). The presence of 'motherese' calls has so far only been described for breeding lagoons, but they will be examined for here in the summer recordings as Clayoquot Sound is used as a nursing and weaning site. Vocal behaviours, including calling rate, call type use, and call structure, in different ambient conditions will be examined first, followed by a comparison between responses to wind and wave noise, quantified together as sea state, and anthropogenic noise, in particular vessel and aircraft noise. The reactions of gray whales will then serve as a basis for a wider discussion of the implication of altered soundscape conditions on marine mammal species.

## Methods

An Autonomous Multichannel Acoustic Recorder (AMAR, JASCO G3A), fitted with a GeoSpectrum M8E-132 calibrated omnidirectional hydrophone (sensitivity -165 dB V/µPa, effective bandwidth 5 Hz-150 kHz, gain of 6 dB), was deployed to record constantly in frequencies 0-8000 Hz.

Recordings during the gray whale migration were made from a site approximately 5 nm southwest of Siwash Point (49.21028, -126.24667, Figure 1.6.1), off Flores Island in water 51 m deep. Northward migration recordings were made between February 21-April 25, 2015 and March 7-May 5, 2016 and southward migration recordings were made from September 27, 2016-January 25, 2017. Summer foraging recordings were made in Cow Bay, the main feeding area for gray whales on the south coast of Flores Island (49.25629, -126.15928, Fig. 1.6.1). The

AMAR was deployed in 20 m water depth between May 6-September 14, 2015 and May 30-September 5, 2016. This is also a primary site for seasonal whale watching.

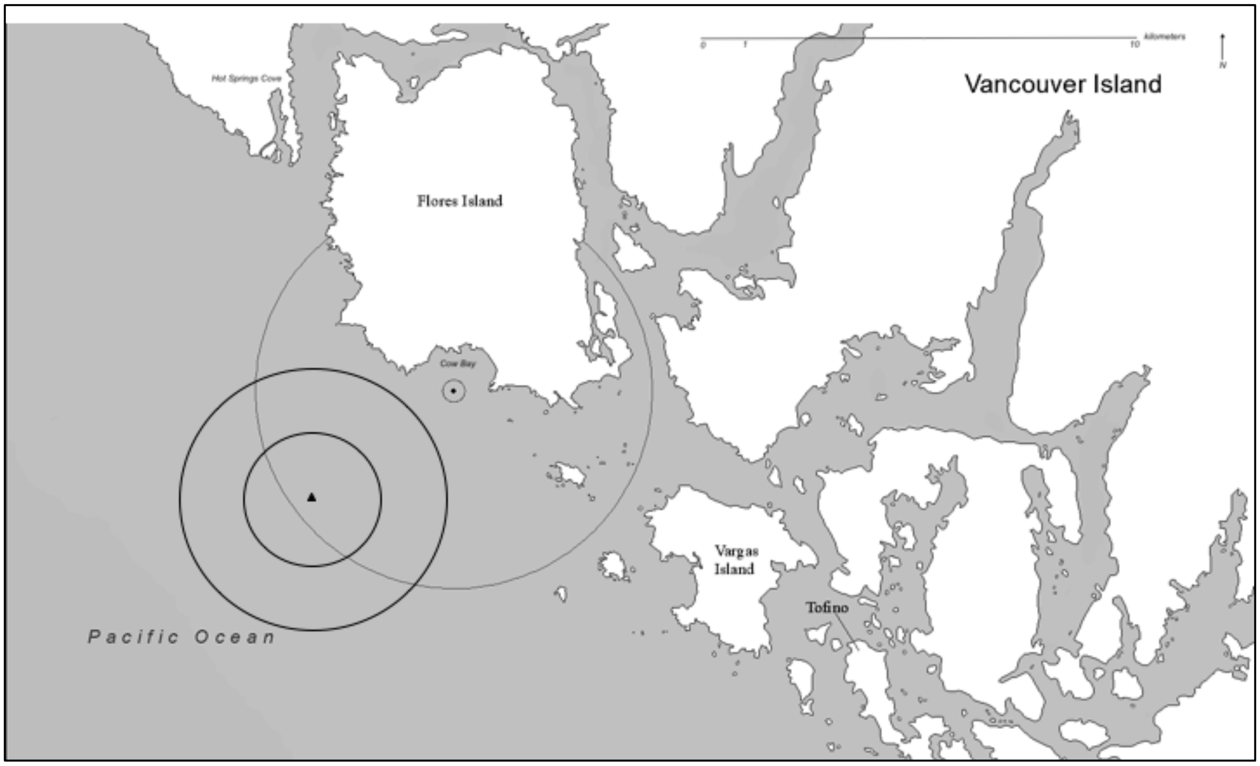

**Figure 1.6.1**: Offshore AMAR deployment location (triangle, 49.21028, -126.24667) for migration recordings, with surrounding bold-line circles to represent the likely detection range 80% of the time (3 km) and 10% of the time (6 km); inshore AMAR deployment location (circle, 49.25629, -126.15928) and surrounding circles that representing the likely detection radius for 90% of the time (500 m) and 10% of the time (9 km) for summer foraging recordings.

Visual and aural inspection of the recordings were made using spectrograms generated using a 256-point Hann window FFT with 50% overlap. Manual inspection was conducted for every fifth day of each deployment, and at all times when the research vessel was in the detection range. For northward migration 1183.13 hours/39.12% of the recordings were inspected, pooling data from 2015 and 2016, 604.5 hours/20.7% of the southward migration was inspected, and a total of 5065.31 hours/37.34% of foraging recordings were inspected, again pooling 2015 and 2016 (see Appendix of Chapter II).

Calls were identified and classified using previous gray whale acoustic studies (Dahlheim et al. 1984, Dahlheim 1987, Crane & Lashkari 1996, Ollervides 2001, Charles 2011, Dahlheim &

Castellote 2016, López-Urbán et al. 2016). Class one calls were distinguished as either modulated (1a) or unmodulated (1b) knock calls. Calls that did not easily conform to one of the call categories described, or were super-positioned to another call type (e.g. knock-moan), but had been previously noted as gray whale vocalisations (Eberhardt & Evans 1962, Painter 1963, Wenz 1964, Gales 1966, Hubbs 1966, Poulter 1968, Fish et al. 1974) were classified as 'other', but were not part of further analysis. For each call, descriptive parameters were derived using Raven Pro Interactive Sound Analysis Software. These metrics included the lowest and highest frequency (Hz) of the call, which also gives frequency range, the peak frequency, and call duration (s), with each categorised to a call type. This follows the parameters used by Dahlheim and Castellote (2016) in the breeding lagoons. Analysis focuses on the dominant call types of each period. 'Motherese' calls are specifically examined to better understand the response of cow-calf pairs in increased ambient noise and anthropogenic disturbances.

Ambient noise levels were measured for each minute of the recordings. The 1/3 octave bands centered between 1-2000 Hz, the gray whale vocalization range, were summed per minute to quantify the background noise level. This was matched to each call, along with the identifiable acoustic signature vessels and aircraft (presence-absence), and sea state. Sea state was derived from hourly reports of wind speeds and wave heights from La Perouse weather buoy (48.83N, 126.0W) using the Beaufort Scales, with that variable (0-12) applied to each call within that hour. Calling rate was quantified by the number of calls by class, per hour. Minute-wise ambient noise levels were averaged to give hourly readings to be matched to these calling rates, and hourly sea state readings were again applied. Vessel and float plane presence was noted present or absent, with an hourly passage rate directly over the AMAR also determined from the cumulative number of Lloyd mirror curve signals (Urick 1983, Richardson et al. 1995) in spectrograms per hour, most pertinent to summer recordings. Using observation data from when vessels were able to be identified, and were the only vessel present, acoustic signatures were taken from the point of closest passage and compared using hull size, shape and material, engine configuration (inboard/outboard), size and number, and speed of passage as categorising variables.

The range and probability of detection of gray whale calls were calculated for migration and foraging periods using ambient noise levels quantified for each minute of the recording, the source level of class 3 moans calls (156.9 ± 11.4 dB re 1µPa @ 1m as reported by Guazzo et al.

2017), and cylindrical spreading models for estimated transmission loss, including the assumption of no attenuation losses. This approximates the maximum probable distance a call could be heard from during the recordings.

## Results

All core call types were present for northward migration and foraging periods, with class 4 rumbles missing from southward migration recordings. 'Motherese' call types are also present for all recordings, but were negligible during migration (Table 1.6.1). Class 3 moan calls dominate both north- (83.69%) and southward (98.05%) migration calling. Class 1 (1a and 1b pooled) calls dominate in foraging sites (31.45%), with class 3 moans and class 2 sweeping tones almost equally present. For foraging periods 'motherese' calls exceed 20% of the calls (Table 1.6.1).

Measures of ambient noise, sea state condition, and vessel presence were significantly different between north- and southward migration and foraging recordings (Kruskal-Wallis, $p<0.001$).

**Table 1.6.1**: For northward migration (NM), southward migration (SM) and foraging (F) the proportion of each call type; correlation to ambient noise (dB re 1µPa) via Pearson's R; mean value comparison to 120 dB re 1µPa threshold, and vessel presence is presented for each core call type, and 'motherese' (M) pooled. O is for 'other', representing calls that do not fit into the described classes

| Call class | | Proportion | Ambient | 120dB | | Vessel | | sea state | |
|---|---|---|---|---|---|---|---|---|---|
| | | (%) | Coef. | Sign. | t | p | t | p | p |
| NM | All | | 0.117 | 0.001 | -0.869 | 0.230 | -4.517 | <0.001 | <0.001 |
| | 1a | 7.23 | 0.083 | 0.022 | 1.099 | 0.272 | 0.139 | 0.890 | 0.001 |
| | 1b | 0.15 | 0.022 | 0.552 | -0.588 | 0.557 | 0.073 | 0.942 | 0.846 |
| | 2 | 7.43 | -0.023 | 0.531 | -2.956 | 0.004 | 0.239 | 0.811 | 0.001 |
| | 3 | 83.69 | 0.056 | 0.121 | -0.296 | 0.767 | -5.337 | <0.001 | <0.001 |
| | 4 | 0.14 | 0.117 | 0.001 | 2.299 | 0.025 | 3.693 | <0.001 | <0.001 |
| | M | 0.28 | 0.000 | 0.994 | -0.704 | 0.482 | -0.246 | 0.806 | 0.502 |
| | O | 1.08 | - | - | - | - | - | - | - |
| SM | All | | -0.067 | 0.097 | -1.203 | 0.230 | 0.172 | 0.864 | <0.001 |
| | 1a | 0.92 | -0.027 | 0.499 | -2.159 | 0.031 | 0.627 | 0.531 | 0.890 |
| | 1b | 0.22 | -0.050 | 0.214 | -0.423 | 0.672 | 0.659 | 0.510 | 0.154 |
| | 2 | 0.70 | -0.052 | 0.197 | -2.699 | 0.004 | 0.021 | 0.984 | 0.344 |
| | 3 | 98.05 | -0.055 | 0.172 | -1.120 | 0.264 | 0.128 | 0.898 | <0.001 |
| | 4 | 0 | - | - | - | - | - | - | - |
| | M | 0.11 | -0.040 | 0.321 | 0.605 | 0.546 | 0.959 | 0.338 | 0.903 |
| | O | 1.11 | - | - | - | - | - | - | - |
| F | All | | 0.079 | <0.001 | 1.167 | 0.243 | 5.069 | <0.001 | <0.001 |
| | 1a | 24.13 | 0.130 | <0.001 | 0.292 | 0.004 | 0.247 | 0.805 | 0.689 |
| | 1b | 7.32 | 0.128 | <0.001 | 1.089 | 0.276 | 1.804 | 0.071 | <0.001 |
| | 2 | 19.65 | 0.068 | 0.002 | 1.089 | 0.276 | 5.331 | <0.001 | 0.002 |
| | 3 | 28.20 | 0.037 | 0.088 | 0.541 | 0.588 | 6.642 | <0.001 | 0.084 |
| | 4 | 0.23 | - | - | 1.265 | 0.207 | -0.439 | 0.660 | 0.608 |
| | M | 20.46 | -0.113 | <0.001 | -1.024 | 0.306 | 3.067 | 0.002 | 0.252 |
| | 7 | 1.34 | -0.116 | <0.001 | -4.802 | <0.001 | 3.856 | <0.001 | 0.134 |
| | 8 | 8.62 | -0.021 | 0.342 | -0.515 | 0.607 | 1.904 | 0.057 | 0.643 |
| | 9 | 3.72 | -0.020 | 0.364 | -0.737 | 0.461 | -0.144 | 0.885 | 0.157 |
| | 10 | 6.78 | -0.063 | 0.004 | -0.444 | 0.615 | 4.289 | <0.001 | 0.351 |
| | O | 1.01 | - | - | - | - | - | - | - |

*Migration*

Vessels were present in 92% of the recordings examined during northward, and 77% of southward migration, primarily from fishing vessels. For both north- and southward migration, patterns of ambient noise were also influenced by increased sea state and storm events, though correlations are weak (northward, r=0.096, p=0.008, southward, r=0.436, p<0.001). The greatest proportion of recordings exceeding the 120 dB re 1µPa disturbance threshold occurred with the greatest wave heights and wind speed. Northward migration recordings (2015 and 2016) show elevated ambient noise (>120 dB re 1µPa) in 7.3% of the recordings sampled, and only 5.5% of recordings made in Beaufort sea state 3 or less. Southward migration recordings showed a greater proportion of elevated ambient noise (19.5%) and less calm seas (5.0% Beaufort sea state 3 or less), with sea states extending to violent storm force conditions, sea state 11.

In total 13,749 calls were identified in northward migration recordings (2015 and 2016 pooled), and 3,691 calls for southward migration (see Chapter 1.2). The likely detection range of gray whale moan calls during migration recordings was up to 3 km, 80% of the time, and extended to 6 km at the quietest times (10% of recordings) (Figure 1.6.1).

Calling was significantly increased with elevated ambient noise levels during northward migration ($r=0.117$, $p=0.001$, Table 1.6.1), for both modulated knocks, class 1a, and rumbles, class 4 (Table 1.6.1). When using the 120 dB re 1μPa threshold, call classes 1a, 2, and 4 were significantly altered (Mann-Whitney U, class 1a: $p=0.013$; class 2: $p=0.05$; class 4: $p<0.001$), where mean calling rate of sweeping tones, class 2, decreased significantly (Table 1.6.1). Only unmodulated knock call rate, class 1b, was not altered with changes in sea state (Table 1.6.1). Reduced vocalising in the presence of vessels resulted from a significant decrease in the use of class 3 moan calls (Table 1.6.1). This call also showed a significant, yet weak negative correlation with call rate and number of vessel passages per hour ($r_s= -0.081$, $p=0.025$).

Acoustic responses to elevated background noise were less evident for calling during the southward migration. Correlation to ambient conditions were weak. The use of modulated call types 1a, and 2 were significantly reduced when noise levels exceeded 120 dB re 1μPa. Wind and wave additions precipitated a change in moan calls, with increased use of the dominant call type for this period, and no significant change with increased vessel noise (Table 1.6.1).

Moan calls parameters were significantly altered in elevated ambient condition for both migration directions (Table 2), and more so than any other call type. The peak frequency, where the acoustic energy is focused, was significantly decreased in calls heard when 120 dB re 1μPa in background noise was exceeded (Table 1.6.2). The frequency range of moan calls was altered in the presence of vessels, due to altered frequency extents (Table 1.6.2). Significant negative correlations were seen for moan calls in lowest frequency extent and peak frequency for both north- and southward migration when examining the response to elevated gusting wind speed (NM, low: $r_s= -0.105$, $p<0.001$, peak: $r_s= -0.060$, $p<0.001$; SM, low: $r_s=-0.146$, $p<0.001$, peak: $r_s= -0.088$, $p<0.001$) and wave height measures (NM, low: $r_s= -0.138$, $p<0.001$, peak: $r_s= -0.085$, $p<0.001$; SM, low: $r_s=-0.146$, $p<0.001$, peak: $r_s= -0.021$, $p<0.001$).

*Foraging*

Recordings made during gray whale foraging showed ambient levels to exceed 120 re 1μPa for 14.3% of the recordings sampled. The abiotic addition to background noise was less than during migration, whereby a quarter of the time examined had a sea state of Beaufort 3 or less. Patterns in ambient noise levels follow the whale watching tour schedules, where mean vessel passage rates during the day ($\bar{x}$=0.73 vessels/hr) greatly exceed that heard at night ($\bar{x}$=0.02 vessel/hr). At least one direct passage over the AMAR was heard in 22.9% of the sample. The shape of the Lloyd mirror curve, indicating direct overhead passage, differs based on hull size, shape and material, engine configuration (inboard/outboard), size and number, and speed of passage (see Chapter 3.3, Appendix for example spectograms of vessel passage). The hull material (Kruskal-Wallis, p=0.031) and engine number (Mann-Whitney U, p=0.032) made a significant difference to the amplitude of the acoustic signature in a direct passage over the recorder. Aircraft, usually float planes, signals were also present in the summer recordings, 8.3% of hours had at least one passage, with their acoustic additions in the lower frequencies (<1000 Hz). They only operate during daylight hours, with an average passage rate of 0.19 planes/hr.

A total of 5,751 calls were identified in the foraging recordings manually inspected (see Chapter 1.5). Class 1 calls (modulated and unmodulated) were the most frequent (31.55%) with class 2 sweeping tones (19.36%) and class 3 moans (28.20%) and 'motherese' call types making up the rest (Table 1.6.1). The likely detection range for the summer recordings was 500 m for 90% of the recording time, meaning the majority of calls heard were likely from whales within Cow Bay. The furthest extent in quiet conditions was 9 km (10% of recording time, Figure 1.6.1).

Knocks, class 1a and 1b, and sweeping tones, class 2, were significantly correlated to ambient noise, although with weak coefficients (Table 1.6.1). Of these, modulated knocks showed a significant increase in average hourly use in ambient conditions exceeding 120 dB re 1μPa, and the use of classes 1b and 2 were significantly altered dependent on sea state (Table 1.6.1). Whereas core call use increased coincident to increases in ambient noise, the use of 'motherese' calls decreased, significantly for classes 7 and 10 (Table 1.6.1). Float plane presence reduced class 10 (Mann-Whitney U, p<0.001).

Consistently, calls in elevated ambient conditions showed alteration in parameters, predominantly to lower the call structure and shorten the frequency range and length (Table

1.6.2). ‘Motherese’ call types showed much less alteration coincident to soundscape condition. Most alteration in call structure for these call types was heard in the presence of vessels (Table 1.6.2)

**Table 1.6.2:** Call parameters for dominant call types during northward (NM), southward migration (SM) and foraging (F) periods correlated with ambient noise levels (dB re 1µPa) via a Pearson's R test, and comparing mean values in elevated noise, using 120 dB re 1µPa threshold, and vessel presence.

| | | Ambient | | 120 dB threshold | | Vessel p/a | |
|---|---|---|---|---|---|---|---|
| | | Coef. | Sign. | t | p | t | p |
| NM class 3 | Low freq. | -0.246 | <0.001 | -23.097 | <0.001 | -4.583 | <0.001 |
| | High freq. | 0.046 | 0.011 | 1.839 | 0.066 | 11.902 | <0.001 |
| | Peak freq. | -0.112 | <0.001 | -10.556 | <0.001 | 1.825 | 0.068 |
| | Length | -0.247 | <0.001 | -29.383 | <0.001 | -4.750 | <0.001 |
| | Freq. range | 0.082 | <0.001 | 8.278 | <0.001 | 13.911 | <0.001 |
| SM class 3 | Low freq. | -0.217 | <0.001 | -13.668 | <0.001 | 11.984 | <0.001 |
| | High freq. | 0.046 | 0.006 | 3.555 | <0.001 | 4.774 | <0.001 |
| | Peak freq. | -0.239 | <0.001 | -14.285 | <0.001 | 12.799 | <0.001 |
| | Length | 0.027 | 0.108 | 3.179 | 0.001 | -1.250 | 0.211 |
| | Freq. range | 0.096 | <0.001 | 6.764 | <0.001 | 2.190 | 0.029 |
| F class 1a | Low freq. | 0.050 | 0.062 | 3.931 | <0.001 | 4.471 | <0.001 |
| | High freq. | 0.174 | <0.001 | 8.166 | <0.001 | 3.975 | <0.001 |
| | Peak freq. | 0.072 | 0.007 | 3.248 | 0.001 | 3.896 | <0.001 |
| | Length | -0.094 | <0.001 | -5.949 | <0.001 | -1.536 | 0.125 |
| | Freq. range | -0.042 | 0.816 | 8.516 | <0.001 | 3.536 | <0.001 |
| F class 1b | Low freq. | -0.299 | <0.001 | -3.071 | 0.002 | -4.619 | <0.001 |
| | High freq. | -0.337 | <0.001 | -4.728 | <0.001 | -5.758 | <0.001 |
| | Peak freq. | -0.324 | <0.001 | -3.667 | <0.001 | -3.931 | <0.001 |
| | Length | -0.187 | <0.001 | -5.726 | <0.001 | 1.298 | 0.195 |
| | Freq. range | -0.207 | <0.001 | -5.043 | <0.001 | -5.035 | <0.001 |
| F class 2 | Low freq. | -0.146 | <0.001 | -8.918 | <0.001 | 6.243 | <0.001 |
| | High freq. | -0.074 | 0.014 | -5.345 | <0.001 | 7.685 | <0.001 |
| | Peak freq. | -0.068 | 0.023 | -6.137 | <0.001 | 6.392 | <0.001 |
| | Length | -0.154 | <0.001 | -3.287 | 0.001 | 0.812 | 0.417 |
| | Freq. range | -0.035 | 0.240 | -3.989 | <0.001 | 5.588 | <0.001 |
| F class 3 | Low freq. | -0.015 | 0.538 | -2.904 | 0.004 | -0.292 | 0.770 |
| | High freq. | -0.033 | 0.188 | 0.411 | 0.682 | -3.002 | 0.003 |
| | Peak freq. | 0.004 | 0.868 | -3.501 | 0.001 | 1.985 | 0.047 |
| | Length | -0.166 | <0.001 | -6.785 | <0.001 | -0.218 | 0.827 |
| | Freq. range | -0.220 | 0.372 | 1.569 | 0.117 | -3.483 | 0.001 |
| F class 7 | Low freq. | -0.038 | 0.741 | -0.944 | 0.348 | 3.535 | 0.001 |
| | High freq. | -0.025 | 0.828 | -1.727 | 0.092 | 5.326 | <0.001 |
| | Peak freq. | -0.064 | 0.580 | -2.137 | 0.048 | 4.158 | <0.001 |
| | Length | -0.129 | 0.265 | -0.530 | 0.598 | -1.348 | 0.185 |
| | Freq. range | -0.082 | 0.480 | 0.047 | 0.963 | 3.601 | 0.001 |
| F class 8 | Low freq. | -0.251 | <0.001 | -5.749 | <0.001 | 6.789 | <0.001 |
| | High freq. | 0.010 | 0.647 | -4.227 | <0.001 | 6.334 | <0.001 |
| | Peak freq. | -0.166 | <0.001 | -3.648 | 0.001 | 4.763 | <0.001 |
| | Length | 0.110 | 0.014 | -0.608 | 0.544 | -2.907 | 0.004 |
| | Freq. range | 0.174 | <0.001 | 0.529 | 0.597 | 2.997 | 0.003 |
| F class 9 | Low freq. | -0.008 | 0.902 | -0.334 | 0.738 | -1.634 | 0.116 |
| | High freq. | -0.129 | 0.059 | -0.701 | 0.484 | 7.366 | <0.001 |
| | Peak freq. | 0.181 | 0.008 | -4.708 | <0.001 | 0.875 | 0.392 |
| | Length | -0.237 | <0.001 | -1.112 | 0.235 | -2.192 | 0.029 |

Table 1.6.2 continued

| | Ambient | 120 dB threshold | | Vessel p/a | | | |
|---|---|---|---|---|---|---|---|
| | | Coef. | Sign. | t | p | t | p |
| | Freq. range | -0.117 | 0.087 | -1.084 | 0.284 | 7.497 | <0.001 |
| F class 10 | Low freq. | 0.063 | <0.001 | -1.205 | 0.229 | -0.297 | 0.766 |
| | High freq. | -0.101 | <0.001 | -2.101 | 0.036 | 3.306 | 0.001 |
| | Peak freq. | 0.003 | <0.001 | -1.537 | 0.125 | 2.246 | 0.025 |
| | Length | 0.153 | 0.003 | -0.064 | 0.949 | -2.190 | 0.029 |
| | Freq. range | -0.165 | 0.001 | -1.291 | 0.198 | 4.422 | <0.001 |

## Discussion

Significant changes in call rate and in call structure were heard in elevated ambient noise, surpassing a 120 dB re 1µPa threshold, when sea state is heightened, and in the presence of human generated noise, such as vessels and aircraft, for both migration and foraging. The findings here generally agree with the playback experiments of Dahlheim and Castellote (2016), where the number of class 1 knock calls, and the number of pulses comprising the call, were increased in response to increased ambient noise levels, and at the presentation of outboard motor noise. However, changes in parameters such as call frequencies and length were not seen (Dahlheim 1987, Dahlheim & Castellote 2016), as they were in this study.

During the northward migration, whales are in a state of negative energy balance from the exertions of migrating and overwinter fasting while in breeding grounds. Calling behaviours were modified in altered wind and wave conditions, and with the presence of vessels, with an overall positive correlation between calling and ambient noise condition. The use of the dominant call type, class 3 moans, was however not significantly altered relative to background noise, speaking to the consistency of calling behaviours at this time (Burnham et al. 2018, Chapter 1.2, 1.3). Acoustic contact with conspecifics both remote and possibly more within-group or in shorter range may be maintained by employing both low frequency moan and modulated calls respectively (Crane & Lashkari 1996). Indeed, class 1a is the only call class not to show a reduced use at time when ambient noise exceeded 120 dB re 1µPa, perhaps being more distinguishable over background noise (Wiley & Richards 1978). In the presence of anthropogenic noise sources calling rate is reduced significantly for much of the gray whale vocal repertoire (Table 1.6.1). Less significant changes were seen in calling rate for southern migration (Table 1.6.1), although modification in call structures were evident (Table 1.6.2). Differences in vocal behaviours between north and southward migrations may represent a change in physiological state of individuals, an altered perception of vulnerability, especially if vessel noise is considered a threat, or an altered behavioural context.

Summer foraging is an important time in gray whale life history, where energy reserves are replenished. In Cow Bay, it is also a period of weaning. Calling rate rose as ambient noise levels increased, with significantly more modulated knocks heard when background noise exceeded 120 dB re 1µPa. At times of heightened ambient noise, calls were mostly likely from whales within Cow Bay (Figure 1.6.1), and modulated calls may be used for short-range contact (Table 1.6.1, 1.6.2). In these recordings differences were seen in the response to naturally-derived and human-added noise. In broad terms, acoustic additions from wind and vessel noise are similar in their composition (broadband, <500 Hz; Wenz 1962), however anthropogenic noise often differs in intensity and frequency range (McGregor et al. 2013). The ability of whales to adapt to these human generated additions is much less than those from an altered sea state (Dunlop 2016). An extention of this work may be to examine calling adaptation considering the ambient noise in its compositional 1/3 octave bands, which may better discern the effects of abiotic from anthropogenic noise.

'Motherese' call use decreased with increased ambient noise and increased sea state. However, acoustic responses were strongest in the presence of vessels. Calling in this case may be a startle reaction, or a call to reunite calf with cow for protection. Lesser modification may represent a physiological threshold of calves, especially in producing lower or longer calls.

The changes seen in gray whale calling in this study give us a first look at vocalising behaviours in differing soundscape conditions. From the summer recordings both vessel and float plane noise overlapped with the principal frequencies of gray whale vocalizations, and may result in acoustic masking of calls (Clark et al. 2009). Thus these changes in the soundscape may have implications, for example in finding prey patches, or for conspecifics to reunite, especially cow-calf pairs when still nursing. It may also impair the ability to detect and interpret acoustic signals, for example those important to way-finding or assessing danger (Richardson & Würsig 1997), or curtailing the whales 'active space' (Clark et al. 2009, Castellote et al. 2012, Burnham 2017).

The continued acoustic use in the presence of potentially masking stimuli, and the modification in call parameters, shows the importance of acoustic behaviours to gray whales, both to navigate during migration, particularly northward, and gather information on prey during summer foraging. More work is needed to establish baselines of undisturbed patterns of calling during migration (Guazzo et al. 2017, Burnham et al. 2018, Rannankari et al. 2018) and foraging, to estimate how calling is modified by social and physiological context, and soundscape, to understand the implications of altered vocal behaviours. For example, the comparisons of calling rate presented here do not take into account the number of individuals present, and how that may influence vocal behaviours (Ponce et al. 2012). Also, distance of the individual calling to the AMAR, and how call propagation may be altered in various ambient conditions, is unknown. It may be that calling behaviours are changed to incorporate call context and modifications cumulatively or hierarchically, and use both the rate of use and alteration of call parameters to project a highly nuanced message to conspecifics, or tailor vocal behaviours to allow the acoustic sense to be used successfully. Also, the degree to which whales can tolerate acoustic additions is still unknown, and may be dependent on factors integral to the sound, including frequency, onset, spectral characteristics, and received intensity (Weilgart 2007, Erbe 2008), or factors internal to the whale receiving the sound, such as age, health, and past experience as well as anticipation of noise and distance from the source (Wartzok & Ketten 1999, Firestone & Jarvis 2007, Weilgart 2007). Clearly, vocal behaviours of whales may be more complex and nuanced than we have previously entertained; if so, the net effect of noise pollution is more influential.

Strategies of altered call composition and calling rate, either calling more frequently or reducing vocalisation to complete cessation has been noted for other species (Miller et al. 2000, Buckstaff 2004, Morisaka et al. 2005, Nowacek et al. 2007, Weilgart 2007, Tyack 2008, Holt et al. 2009, Castellote et al. 2012, Rolland et al. 2012, Janik 2014, Veirs et al. 2016). There may be, however, a physiological or energetic limit to call alteration, or indeed a threshold before the call meaning becomes too distorted (Richardson et al. 1995, Noweck et al. 2007, Southall et al. 2007, Weilgart 2007). The energetic demand in call modifications, perhaps using suboptimal frequencies or a higher rate of redundancy in calling (Bradbury & Vehrencamp 1998) can be heightened when it is twinned with displacement from optimal feeding or breeding sites, or altered migration routes are taken to avoid acoustic stimuli, as has been seen for gray whales (Malme et al. 1983, 1984, 1986, 1988, 1989, Bryant et al. 1984, Würsig et al. 1999, Moore & Clarke 2000, IWC 2005, 2007).

The acoustic sense is the principal means by which whales send and receive information. The threat posed by increasing anthropogenic contributions to ambient noise is growing, as too is the potential for abiotic additions, with more intense storm and precipitation events (see Osterberg et al. 2017), as well as altered underwater sound propagation (Sehgal et al. 2010), particularly the decline in absorption of low frequency sounds (Ilyina et al. 2009). To understand the full impact of chronic and acute noise pollution on whales we need to be clear on the level at which acoustic additions to the environment influence the success of important functions, such as foraging, mate selection, or predator-prey interactions. The threshold used here to describe an elevated ambient noise condition (120 dB re 1 μPa) was developed from field studies of gray whales and finding consistent behavioural responses when stimuli were presented at this amplitude (Malme et al. 1983, 1984, 1988). More recently this criterion has been adapted to reflect response limits to continuous (120 dB re 1 μPa) or impulsive sound sources (160 dB re 1 μPa; NOAA 2013) and is widely applied to other marine mammal species. An acoustic response may occur sooner, and be more sensitive to acoustic additions than those seen from surface observations of overt behaviour. Also, if response by an individual is in some way based on a signal to noise ratio, as background soundscapes become increasingly nosier, these thresholds will need re-evaluation, and tailoring to be appropriate for individual species or life history settings.

While it is well known that whales sensory modes are primarily acoustic, they are only interpreted in simple, narrow terms in conservation and management programs. The fine tuning of sound production and hearing by natural selection has taken place over lengthy periods in much different oceans than whales experience today. To be precautionary and conservative the consideration of the effect of noise pollution should begin from a broader perspective that whales use acoustics in constant, complex, and critical ways.

# Appendix

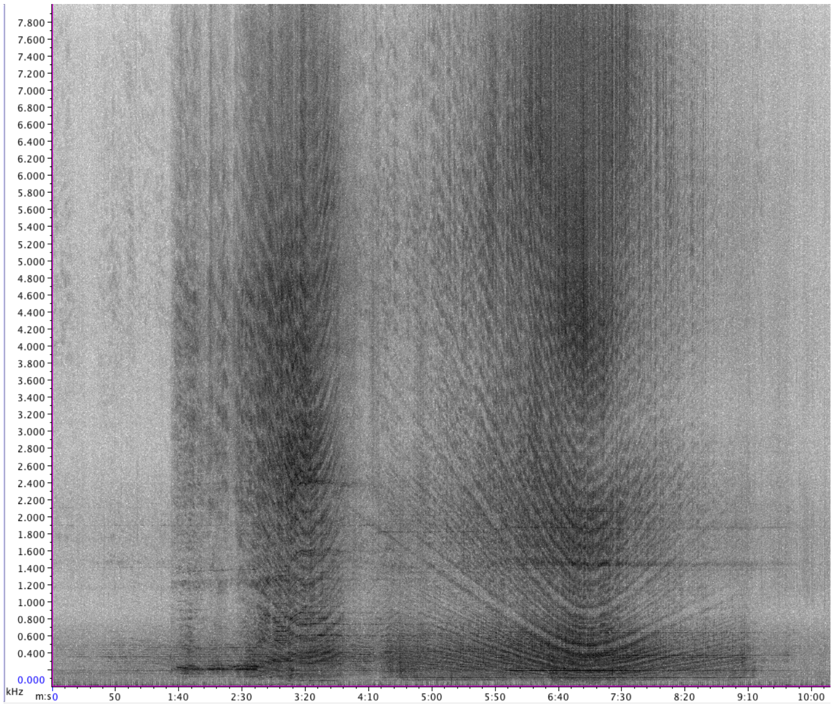

**Figure A.1.6.1**: Example Lloyd mirror curve of covered, aluminum, 33 ft vessel with Inboard engine.

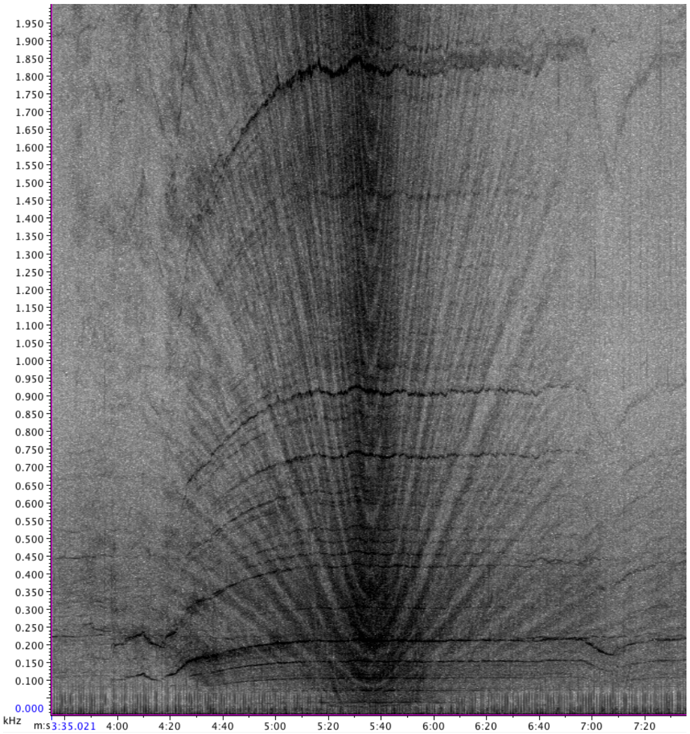

**Figure A.1.6.2**: Example Lloyd mirror curve of a rigid hull Inflatable, 31 ft twin vessel with twin outboard, engines (200 HP).

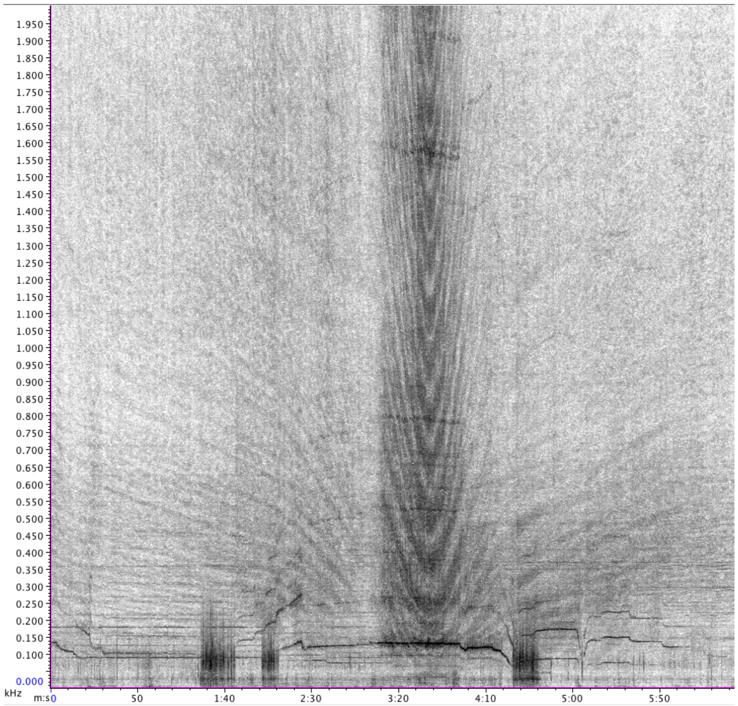

**Figure A.1.6.3**: Example Lloyd mirrorcurve of a covered, aluminum, twin inboard, split hull vessel.

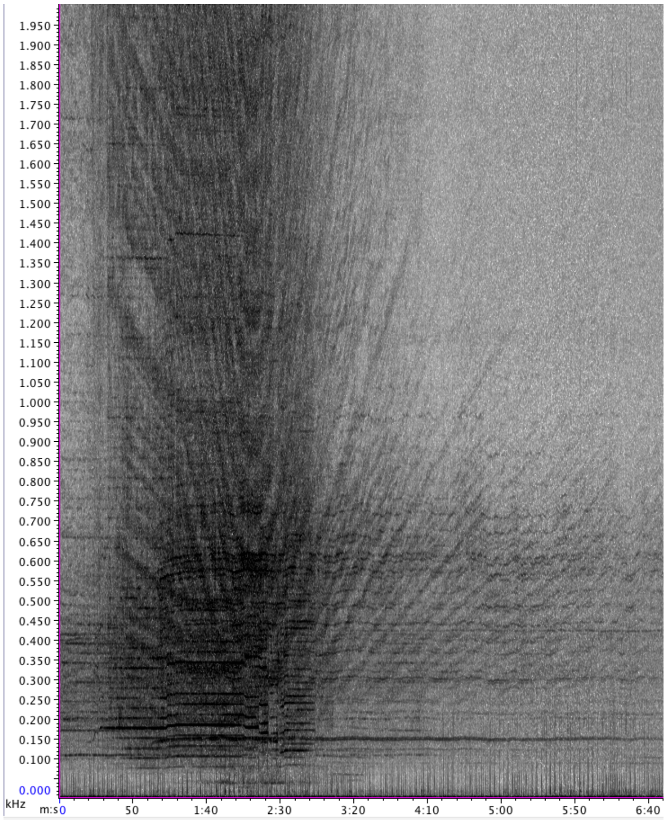

**Figure A.1.6.4:** Example Lloyd mirror curve of open,  fibreglass, 24 ft vessel with twin outboard engines.

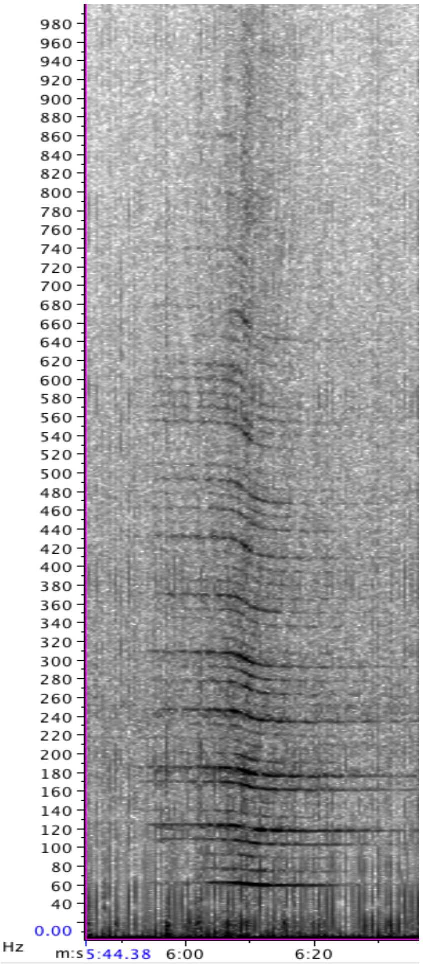

**Figure A.1.6.5**: Example of a float plane (Cessna 185) passage overhead of AMAR.

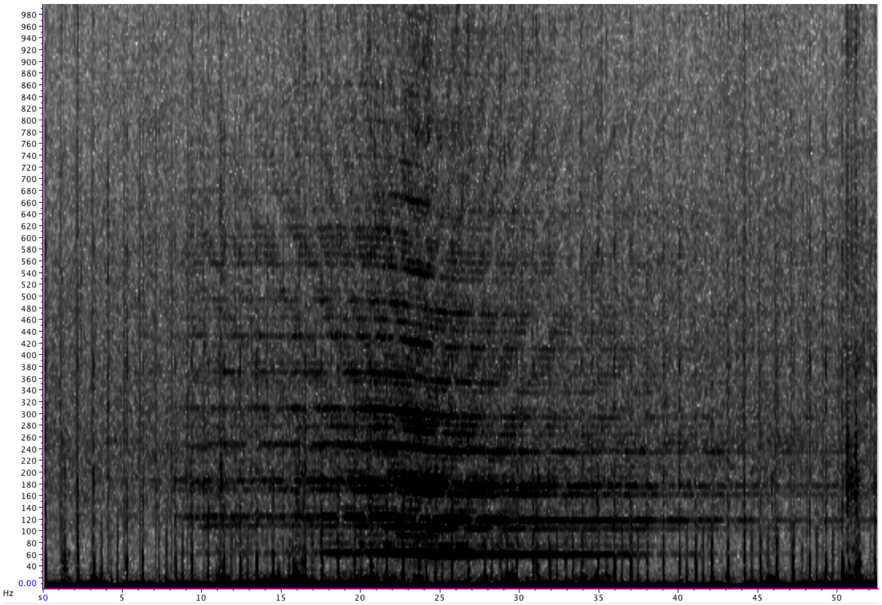

**Figure A.1.6.6:** Example Lloyd mirror curve of a float plane (Cessna 185) on an overhead passage of AMAR.

## 1.7. Acoustic predator-prey reactions: gray whales and killer whales

### Preface

In Chapter 1.6, I discussed the acoustic behaviour of gray whales in the face of increased ambient noise, and the addition of anthropogenic noise to the soundscape. Here I examine the behaviour when they are facing a potential predation threat by analysing periods when both gray whales and killer whales are acoustically present. Although attacks on gray whales from killer whales are rarely seen in Clayoquot Sound, avoidance behaviours have been noted. The study area is an ideal site to do this comparison as it is a known habitat for cow-calf pairs, with probable physical and acoustic anti-predation mechanisms.

Previous playback experiments in breeding lagoons (Dahlheim 1987, Dahlheim & Castellote 2016) have shown cessation in calling in the presence of Bigg's killer whale calls. Crane and Lashkari (1996) also suggest silence as a strategy, employed in areas on the migration where killer whales are a greater threat.

Here I compare instances where killer whales and gray whales are both present, indicated by calls, for north- and southward migration and summer foraging periods. I focus on changes of vocal use by cow-calf pairs, with young whales the most vulnerable to predation. I am also interested here to test the ability of gray whales to distinguish true threat, by comparing the vocal reaction to the presence of the Bigg's ecotype, the mammal eating whales, from the resident, fish eating, killer whale ecotype. While data is sparse at this time, this fits into the seascape of fear concept developed by Dill and colleagues (Lima & Dill 1990, Frid & Dill 2002), and will continue to build as more PAM deployments are completed.

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# Acoustic predator-prey reaction: gray whales (*Eschrichtius robustus*) acoustic response to killer whales (*Orcinus orca*)

Killer whale (*Orcinus orca*) predation can have a significant effect on gray whale (*Eschrichtius robustus*) demographics, and may be responsible for a large proportion of their natural mortality (Rice & Wolman 1971, Ljungblad & Moore 1983). Matkin and Durban (2011) state that in Unimak Pass, mammal-eating Bigg's (formerly transient) killer whales remove between 5-50% of the calf production per year. Both fight and flight behaviours by gray whales have been noted in the presence killer whales (Cummings & Thompson 1971, Dahlheim 1987, Ternullo & Black 2002, Ford & Reeves 2008), however the acoustic response is less well described. Playback experiments have shown that gray whales employ near, to complete, silence as a tactic in the presence of killer whale calls (Cummings & Thompson 1971, Dahlheim 1987, Dahlheim & Castellote 2016). During presentation of recordings of natural and anthropogenic sounds to whales in San Ignacio breeding lagoons, the projection of Bigg's killer whale sounds resulted in the cessation in calling, an effect only replicated by the presence of an unfamiliar test tone (Dahlheim & Castellote 2016). Furthermore, experiments conducted by Cummings and Thompson (1971) using the projection of killer whale 'screams' to whales transiting Point Loma, San Diego, during two consecutive southward migrations found just 2 gray whale phonations in recordings during play back periods (n=36), whereas 47 had been noted in control periods where random noise (n=10) or pure tones (n=10) were projected. In Monterey Bay, recordings of migrating whales found they vocalized less, and were often silent when transiting over deep (>100m depth) water where the masking effects of ambient noise are less (Crane & Lashkari 1996). Reduced phonation in these cases, it is speculated, affords lower detectability from killer whales. Silence was also noted during observations of killer whales pursing feeding gray whales in the northern Bering Sea (Ljungblad & Moore 1983).

Here we report the response in gray whale calling during migration and foraging in naturally occurring killer whale acoustic presence. We compare calling rate and structure when killer whale vocalisations are heard to periods when they are absent. Also the responses to the acoustic presence of Bigg's (mammal-eating) and resident (fish-eating) killer whales is compared. Following previous research, the expectation is for acoustic silence by gray whales, particularly in the presence of Bigg's killer whales.

Recordings were made by an Autonomous Multichannel Acoustic Recorder (AMAR JASCO G3) with GeoSpectrum M8E-132 calibrated omnidirectional hydrophone (sensitivity -165 dB V/µPa, effective bandwidth 5 Hz-150 kHz, gain of 6 dB) in Clayoquot Sound, on the west coast of Vancouver Island. Migration recordings come from deployments timed for two northward (N1: February 21 to April 25, 2015, 1510.6 hrs; N2: March 7 to May 5, 2016, 1422.7 hrs) and one southward (September 27, 2016 to January 25, 2017, 2920.3 hrs) migration, with the AMAR positioned in the migration corridor (49.21028, -126.24667), approximately 5 nm from Siwash Point on the coast of Flores Island and in 51 m water depth. Summer foraging recordings were made in two consecutive summers (F1: May 6 to September 14, 2015, 3138.9 hrs; F2: May 30 to September 5, 2016, 2351.8 hrs), in Cow Bay on the south coast of Flores Island (49.25629, -126.15928). This is a productive feeding bay in Clayoquot Sound, also used for nursing and weaning by gray whale cow-calf pairs.

The recordings were examined for acoustic co-occurrence of killer whales, both resident and Bigg's ecotypes, and gray whales, with the detection range for killer whale vocalizations presumed to encompass, or be exceeded by that of gray whales (Burnham et al. 2016, 2018, see Appendix). Data was manually inspected by aural and visual analysis of spectrograms (256-point Hann window FFT with 50% overlap). In addition, the recordings were subjected to automated detection software that logged killer whale clicks and whistles (Mahoney et al. 2014, Mouy et al. 2015). A minimum of every fifth day (20%) of recordings were manually inspected. Additional recordings were scrutinised if killer whales presence were found, to encompass the full encounter, sometimes several hours in length, and where killer whale calls were identified by the auto-detector. The total amount inspected for northward migration was 1183.13 hours, or 39.12%, pooling data from 2015 and 2016; southward migration was 604.5 hours or 20.7%, and foraging periods were 5065.31 hours, or 37.34%, again pooling 2015 and 2016.

Gray whale calls were identified and classified according to descriptions by Dahlheim (1987). Core call types include class 1 knocks, here distinguished by the presence of frequency modulation (1a) or not (1b); class 2 sweeping tones, class 3 moans and class 4 rumbles. Class 5 and 6 represent acoustic bi-products of sub-surface exhalations (Dahlheim 1987), and as such are not considered further in this analysis. Also, calls described as possible 'motherese' were included, including class 7 complex tonal growls; class 8 grunt-like 'uggs'; class 9 roar-like tones; class 10 grunt-like rumbles, and class 11 rattle sounds (Ollervides 2001, Charles 2011).

Call rate was determined by the number of calls per call type, per hour. For each call, parameters of low and high frequency (Hz) extent of harmonics, frequency range, peak frequency, where most of the energy is focused, and length (s) were derived using Raven Pro Interactive Sound Analysis Software. This allows for examination of changes in call structure, by type, in the presence of killer whales.

Killer whale presence was determined using the automated detector output and confirmed manually as outlined in Burnham et al. (2016) and Chapter 3.2. Echolocation clicks were not used as a reliable indicator of killer whale presence, with encounters defined by the presence of whistles or other pulsed or tonal calls. Designation of calls to ecotype were done using reference to calling known to distinguish resident and Bigg's killer whales (Ford, 1984, 1987, 1991).

A total of 3455 hours of data were analysed, of which 111 showed killer whale acoustic presence. During those periods of killer whale acoustic presence, the average gray whale call rate increased for class 1 knocks and class 4 rumbles, and decreased for class 2 sweeping tones, predominantly upsweeps, class 3 moans and all 'motherese' call types. The use of modulated knock calls increased significantly in the presence of killer whales (Mann-Whitney U, p=0.033) as did overall average call number per hour (Mann-Whitney U, p=0.039). Knock calls (both classes 1a and 1b) were the most affected in playback experiments in breeding lagoons, with increased use and greater repetition in call structure when an acoustic stimulus was presented (Dahlheim 1987, Dahlheim & Castellote 2016). No significant differences in calling rate were seen when comparing calling in the acoustic presence of Bigg's or resident killer whale ecotypes, with calling rate typically higher in the presence of the mammal-eaters. This trend does not agree with results of playback (Cummings & Thompson 1971, Dahlheim 1987, Dahlheim & Castellote 2016) or natural observations (Ljungblad & Moore 1983).

The more useful comparison may be made between responses in different behavioural settings. Killer whales were heard most during the northward migration. These encounters also afforded a comparison between the Bigg's and resident ecotype (Table 1.7.1). Significant decreases were heard in the call rate of upsweeps (Student's t-test, $t(482.396)=-4.876$, $p<0.001$), and moans (Student's t-test, $t(163.666)=-8.206$, $p<0.001$, Mann-Whitney U, $p<0.001$) when killer whales were present during northward migration. Moans are dominant during this time, exceeding 83% of calls, with knock and upsweep calls making up the rest of the vocal repertoire approximately equally (Burnham et al. 2018, Chapter 1.2, 1.3). Therefore, the decreased use of moan calls resulted in a significant change in the overall calling in the presence of killer whales (Mann-Whitney U, $p<0.001$). There was no significant difference in acoustic reaction when comparing the mammal- and fish-eating killer whale ecotypes during this time, both instilling decreased calling from gray whales. This agrees with findings from previous studies (Cummings & Thompson 1971, Crane & Lashkari 1996).

Generally the opposite acoustic reaction was seen for southward migration, with a significant increase in calling rate (Mann-Whitney U, $p=0.009$), and the use of class 3 moan calls (Mann-Whitney U, $p=0.023$), in the acoustic presence of killer whales. The changes in use of moan calls dominated the overall trend, being the main call (>98%, Burnham et al. 2018) during this period. However, all other call types except for non-modulated knock calls (class 1b) also increased in rate. The comparison between ecotypes is not possible for southward migration, with the killer whale vocalisations not positively identified to an ecotype (Table 1.7.1).

**Table 1.7.1:** Acoustic presence of killer whales (in hours of recording) for each deployment period, with the number of encounters identified to ecotype shown.

| Behaviour | KW presence | Bigg's | Resident | Unknown |
|---|---|---|---|---|
| Migration (north) | 59 | 15 | 13 | 31 |
| Migration (south) | 24 | - | - | 24 |
| Foraging | 28 | - | 4 | 24 |

The call structure of moan calls and upsweep class 2 calls were altered significantly in at least one parameter when produced in the acoustic presence of killer whales. For both call types, on both north- and southward migration, the lowest frequency harmonic of the call was altered, in conjunction with either the frequency range or focal formant of the call (Table 1.7.2). There is little employment of class 1b on migration in the presence of killer whales, with no calls in classes 1a or 4 during southward migration when killer whales were heard.

The difference in call strategies between north- and southward migration may represent the different physiological state the whales are in, and vulnerability to predation. During the northward migration, gray whales are in a negative energy state, and so a strategy of reduced calling may be an anti-predation tactic while also avoiding energy use. During southward migration, the use of moan calls increases significantly. The frequency extents and range of the harmonics are significantly altered (Table 1.7.2). This may reflect the use of alarm or warning calls, as seen in other animals (Gill & Bierema 2013, Zuberbühler 2009, Suzuki 2013), or represent information transfer of the type or proximity of threat, a phenomenon also well described for other species (Leavesley & Magrath 2005, Templeton et al. 2005, Zuberbühler 2009, Gill & Bierema 2013, Suzuki 2013, Cunningham & Magrath 2017).

**Table 1.7.2:** Changes of gray whale call parameters, by call type, in the presence of killer whale calls for north and southward migration using a t-test. T and p values shown. There was only one 1b call on northward migration in the presence of killer whales, no class 1a or 1b, 4 or calls heard in presence of killer whales on southward migration.

| Call class | | Northward migration | | Southward migration | |
|---|---|---|---|---|---|
| | | T | P | T | P |
| 1a | Low freq. | -1.150 | 0.250 | | |
| | High freq. | -0.861 | 0.392 | | |
| | Peak freq. | -1.189 | 0.238 | | |
| | Length | -2.798 | 0.006 | | |
| | Freq. range | -0.390 | 0.697 | | |
| 1b | Low freq. | | | | |
| | High freq. | | | | |
| | Peak Freq. | | | | |
| | Length | | | | |
| | Freq. range | | | | |
| 2 | Low freq. | -2.490 | 0.013 | 5.307 | <0.001 |
| | High freq. | -1.718 | 0.091 | 5.424 | <0.001 |
| | Peak freq. | -2.096 | 0.036 | 1.554 | 0.133 |
| | Length | -0.964 | 0.335 | -0.271 | 0.794 |
| | Freq. range | -0.325 | 0.745 | 0.061 | 0.952 |
| 3 | Low freq. | 2.256 | 0.025 | -3.571 | <0.001 |
| | High freq. | 3.157 | 0.002 | 12.383 | <0.001 |
| | Peak freq. | 4.181 | <0.001 | -2.577 | 0.007 |
| | Length | 2.132 | 0.033 | 0.561 | 0.104 |
| | Freq. range | 1.446 | 0.148 | 15.330 | <0.001 |
| 4 | Low freq. | -1.386 | 0.184 | | |
| | High freq. | -2.561 | 0.020 | | |
| | Peak freq. | -0.901 | 0.401 | | |
| | Length | 1.571 | 0.180 | | |
| | Freq. range | -1.316 | 0.206 | | |

During foraging, calling behaviours differ from migration periods and have a higher use of within- and between-group vocalization types, class 1 and 2 (Moore & Ljungbald 1984, Chapter 1.5). The presence of killer whales, however, does not instill a notable difference in rate, or call type. While core call types are increased, and 'motherese' call types are decreased, none are statistically significant. The structure of modulated knock calls show significant changes in the presence of killer whales, with altered frequency ranges for class 2, 3, 8 and 9 calls, often in conjunction with an adjusted lowest frequency extent (Table 1.7.3). There were no call class 4 or 7 calls heard when killer whales were acoustically present.

**Table 1.7.3:** Changes of gray whale call parameters, by call type, in the presence of killer whale calls during summer foraging using a t-test. T and p values shown. No calls for class 4 or 7 were heard in the presence of killer whales.

| Call class - core | | | | Call class- 'motherese' | | |
|---|---|---|---|---|---|---|
| | | T | P | | T | P |
| 1a | Low freq. | -4.754 | <0.001 | 8 | -6.000 | <0.001 |
| | High freq. | -3.206 | 0.002 | | 0.171 | 0.867 |
| | Peak freq. | -6.479 | <0.001 | | -1.547 | 0.123 |
| | Length | 3.623 | <0.001 | | -0.353 | 0.724 |
| | Freq. range | -2.735 | 0.007 | | 7.237 | <0.001 |
| 1b | Low freq. | 1.770 | 0.077 | 9 | -3.997 | <0.001 |
| | High freq. | 0.689 | 0.491 | | 4.312 | <0.001 |
| | Peak Freq. | 1.153 | 0.250 | | 0.138 | 0.890 |
| | Length | 1.710 | 0.088 | | -0.886 | 0.377 |
| | Freq. range | -0.704 | 0.501 | | 6.211 | <0.001 |
| 2 | Low freq. | 0.875 | 0.446 | 10 | 0.538 | 0.602 |
| | High freq. | -0.939 | 0.348 | | -0.883 | 0.378 |
| | Peak freq. | 1.052 | 0.293 | | 0.632 | 0.528 |
| | Length | 0.026 | 0.979 | | 0.117 | 0.907 |
| | Freq. range | -21.777 | <0.001 | | -1.185 | 0.237 |
| 3 | Low freq. | 2.239 | 0.025 | | | |
| | High freq. | 3.667 | <0.001 | | | |
| | Peak freq. | -0.654 | 0.521 | | | |
| | Length | -3.485 | 0.003 | | | |
| | Freq. range | 3.412 | 0.001 | | | |

Increased calling during foraging periods does not agree with previous studies, however this is the first time a dedicated comparison between vocal behaviours in the acoustic presence of killer whales has been made, as well as the first to consider the use of 'motherese' calls during these times. The decreased use of 'motherese', and shift of calls to lower frequencies and shorter lengths, suggests mothers and young become quiet. The areas that cow-calf pairs frequent in

Cow Bay may add to their acoustic hiding tactic, often staying close to breaking surf or hidden in kelp beds (Pers. Obs., Ford & Reeves 2008, Wladichuck et al. 2010).

Resident, fish-eating killer whales are strongly tied to the seasonal movements of their salmonid prey (Nicol & Shackelton 1996), with their overwinter presence greater than expected (also see Burnham et al. 2016). This ecotype frequently uses echolocation, and often communicate with and between hunting groups (Ford 1987, 1991, Ford & Ellis 1999). Conversely, mammal-eating, Bigg's killer whales hunt with little to no calling. Vocalizing is largely limited to surface-active and post-feeding behaviours (Ford 1984, Morton 1990, Guinet 1992, Barret-Lennard et al. 1996, Deecke 2003, Deecke et al. 2005). The differences in prey preference and acoustics use between ecotypes may instill a different acoustic reaction in gray whales, but this was not the case where the comparison was possible during northward migration. The reaction may be precautionary, to reduce calling despite the killer whale not being a predatory threat. Taking a precautionary approach has been suggested by Crane and Lashkari (1996), who propose the use of silence in areas where the presence of killer whales is expected to be high.

The continued use of calling in all cases demonstrates the importance of shared acoustic information to gray whales in each period of their life history. It may be that responses in this study balance the cost and benefit of calling (Lima & Dill 1990), and sharing information with conspecifics, especially if modification of call parameters are required (Bradbury & Vehrencamp 2011). It may be that the calls used, and the modifications employed in the acoustic presence of killer whales, placing the acoustic energy of calls made below the frequency ranges that killer whales' hearing is most sensitive (Hall & Johnson 1972, Symanski et al. 1999, Miller 2006, Branstetter et al. 2017). If this is true, the use of lower frequency calls and sweeping tones, focused between 20-200 Hz, should be favoured over the knock-like calls of class 1, that have a wider and typically higher frequency range (Dahlheim et al. 1984, Dahlheim 1987, Burnham et al. 2018). In this study, killer whale vocalisation harmonics were present in spectrograms down to approximately 150 Hz, suggesting a significant overlap in the hearing and vocalising range of gray whales and killer whales (see Appendix).

Modifications in calling rate and call structure shows plasticity in gray whale acoustic behaviours. Alterations in call parameters may be a method for gray whales to encode information through graded variation, already seen in increased calling rate and note repetition in the playback study of Dahlheim and Castellote (2016). The difference in responses between the observations of this study and the experimental playback studies may be the context in which the recordings are made. Also, the sensitivity to a stimulus could vary due to an individual's age, reproductive status, and prior experience. Vulnerability of individuals to predation may be higher in breeding lagoons or migrating with calves, or in areas of high presence of killer whales (e.g. Monterey Canyon, Crane & Lashkari 1996, Unimak Pass, Alaska, Matkin & Durban 2011). In these cases silence is the safest strategy.

The ability of killer whales to shape the behaviours of their prey has been well documented (Schevill 1964, Cummings & Thompson 1971, Fish & Vania 1971, Morgan 1979, Dahlheim 1987, Finley1990, Crane 1992, Crane & Lashkari 1996, Corkeron & Connor 1999, Lésage et al. 1999, Karlsen et al. 2002, Van Parijs et al. 2003, Nowacek et al. 2004, Castellote & Fossa 2006, Ford & Reeves 2008, Baird 2011, Matkin & Durban 2011) with this study adding to these examples. However, much work still remains to be done to understand the perception of predation risk over the life history stages of gray whales, and how acoustics plays into the anti-predator strategy and response.

# Appendix

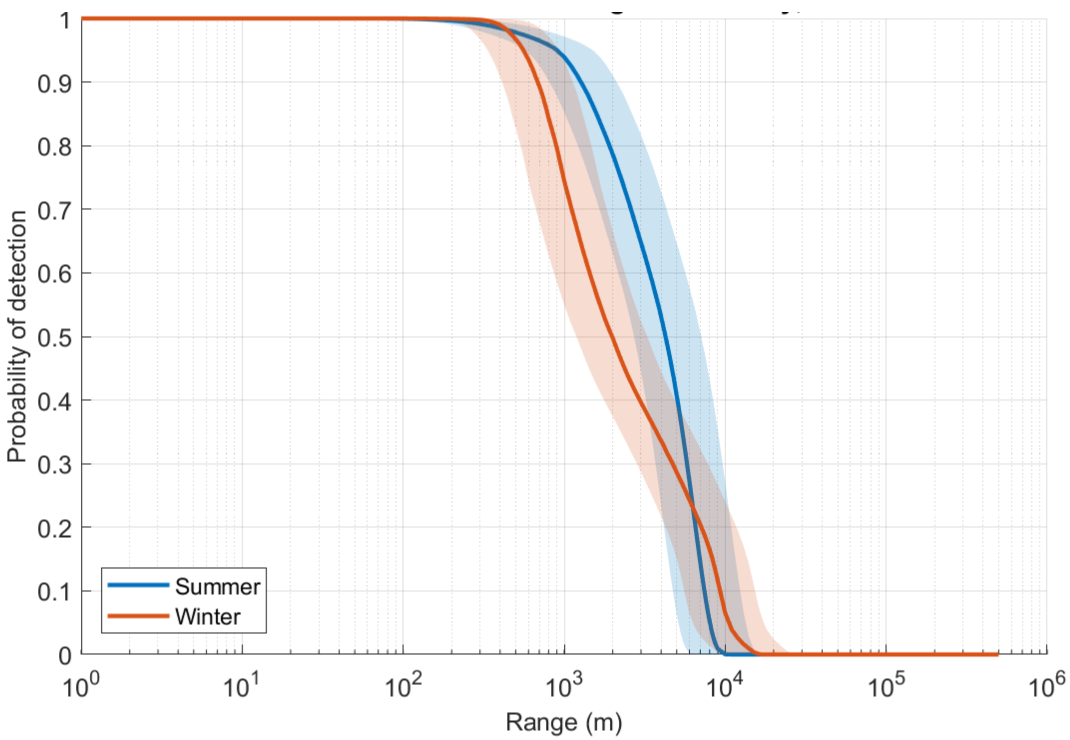

**Figure A.1.7.1**: Estimation of detection range of gray whale moans by the AMAR system throughout deployments. The range of detection of gray whale calls was estimated using ambient noise levels (NL) for each minute of recording, source levels (SL) of killer whale vocalisations reported by Holt et al. (2009) as 133–174 dB re 1 µPa at 1 m with a mean of 155.1 ± 6.5 dB re 1µPa @ 1m), and an estimate of the transmission loss (TL). The received sound level (RL) of a gray whale moan at the recorder is defined as RL = SL–TL(r), where r is the distance in meters between the whale and the recorder. The transmission loss was approximated to follow a spherical spreading law and was therefore estimated as TL(r) = 20 log10(r) (Urick 1983). The detection range was estimated to be the distance from the recorder for which the received level of the gray whale moan equalled the noise level at the recorder (NL = RL). Noise levels used for estimating detection range were calculated for every minute of recording by summing the 1/3 octave bands centred between 1,000 and 8,000 Hz. The detection range was calculated for each minute of recording. The probability of detecting killer whale calls at a given range was the number of 1 min recordings with a detection range equal to or greater than the given range divided by the number of 1 min recordings. A Monte Carlo method accounted for the measured variability in source levels. Detection ranges were re-calculated 300 times by randomly choosing 300 normally distributed source level values, with the means and standard deviations defined by Holt et al. 2009. Consequently, a distribution of probability is associated with each range. Estimations for both migration (winter) and foraging (summer) deployments are shown.

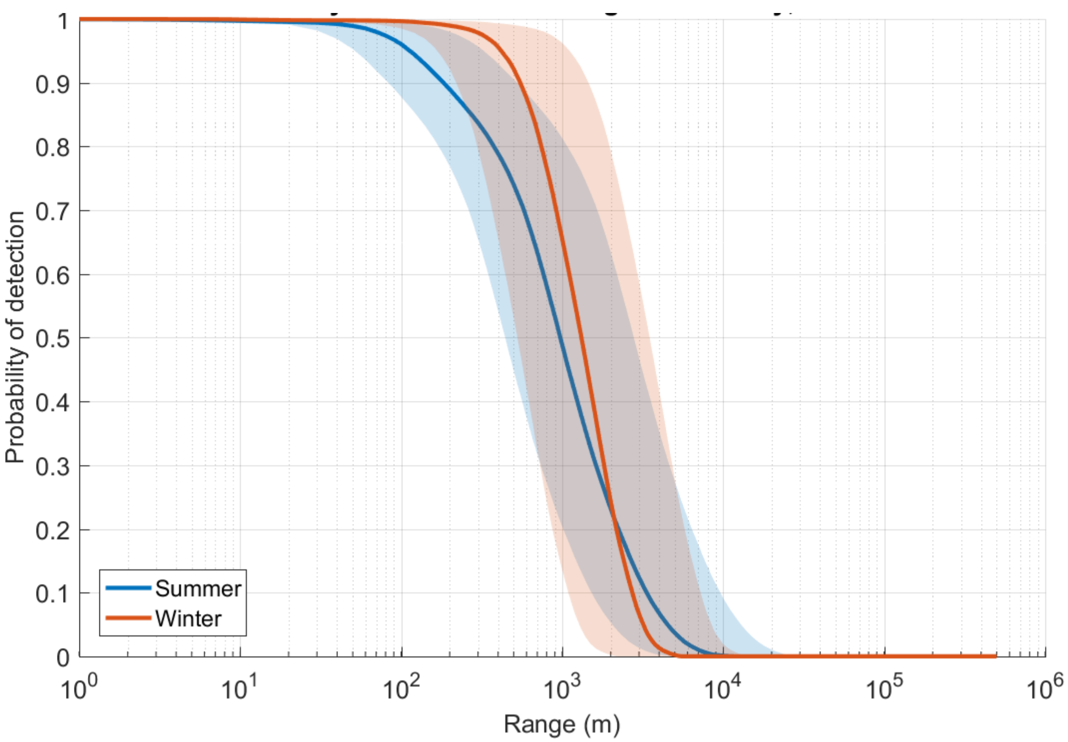

**Figure A.1.7.2**: Estimation of detection range of gray whale moans by the AMAR system throughout deployments. The range of detection of gray whale calls was estimated using ambient noise levels (NL) for each minute of recording, source levels (SL) of gray whale moans reported by Guazzo et al. (2017, 156.9 ± 11.4 dB re 1µPa @ 1m), and an estimate of the transmission loss (TL). The received sound level (RL) of a gray whale moan at the recorder is defined as RL = SL–TL(r), where r is the distance in meters between the whale and the recorder. The transmission loss was approximated to follow a spherical spreading law and was therefore estimated as TL(r) = 20 log10(r) (Urick 1983). Given the low frequency of the gray whale calls, attenuation was not included in the transmission loss estimation. The gray whale was considered to be an omnidirectional source. The detection range of a moan was estimated to be the distance from the recorder for which the received level of the gray whale moan equalled the noise level at the recorder (NL = RL). Noise levels used for estimating detection range were calculated for every minute of recording by summing the 1/3 octave bands centred between 20 and 100 Hz. The detection range was calculated for each minute of recording. The probability of detecting a gray whale moan at a given range was the number of 1 min recordings with a detection range equal to or greater than the given range divided by the number of 1 min recordings. A Monte Carlo method accounted for the measured variability in source levels. Detection ranges were re-calculated 300 times by randomly choosing 300 normally distributed source level values, with the means and standard deviations defined by Guazzo et al. 2017. Consequently, a distribution of probability is associated with each range. Estimations for both migration (winter) and foraging (summer) deployments are shown.

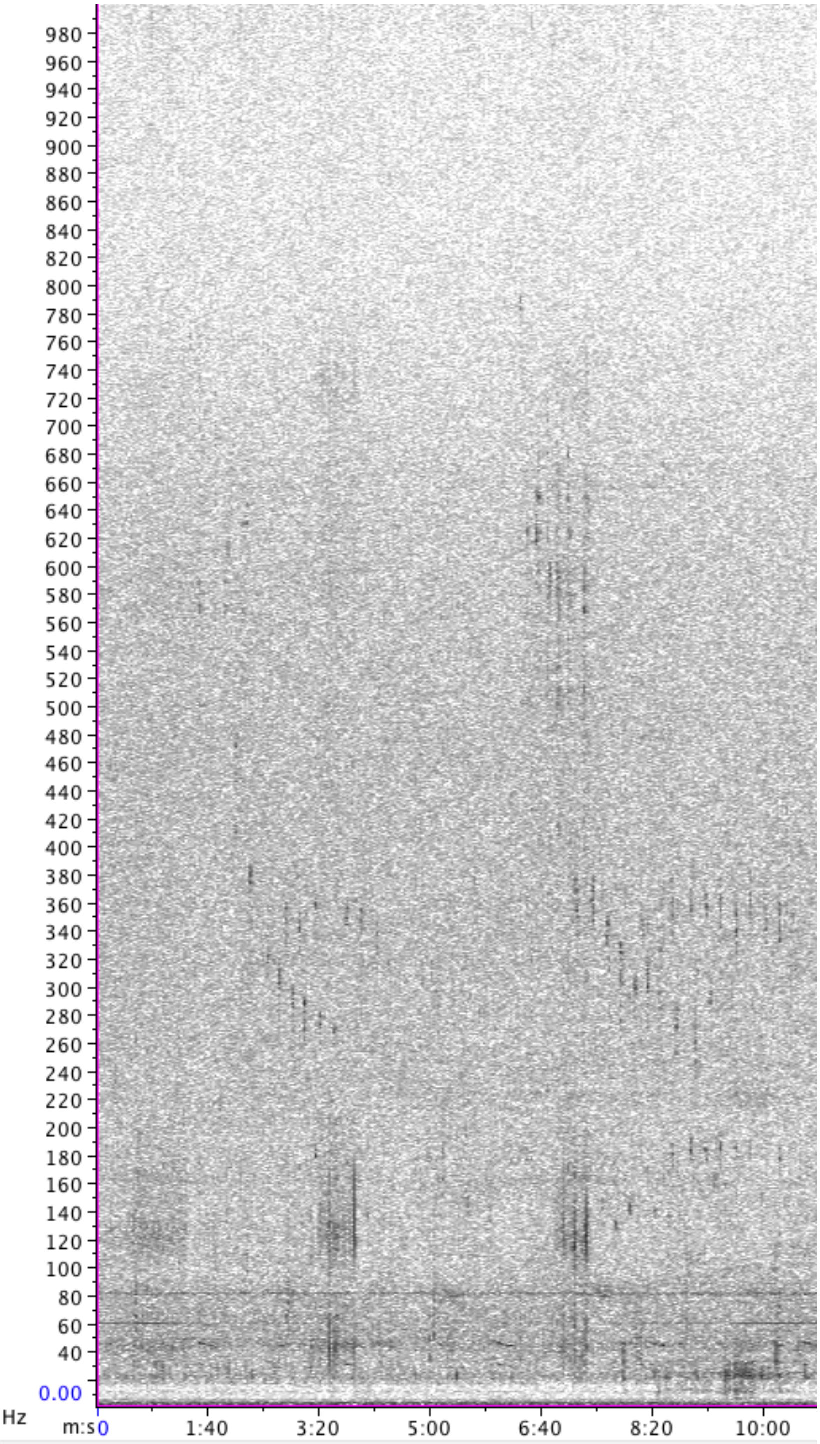

**Figure A.1.7.3:** Example spectrogram showing killer whale calls extending into the low frequencies, and into the vocalisation range of gray whales.

## 1.8. Case study conclusions: The acoustic repertoire of gray whales

*The 'not so quiet' whale*

Once described as 'the quiet whale' (Rasmussen & Head 1965), the vocal behaviours for gray whales (E*schrichtius robustus*) have been well described from works in breeding lagoons. It is only more recently that recordings have been used to discern their acoustics use in foraging areas (Stafford et al. 2007) and on migration (Guazzo et al. 2017, Rannankari et al. 2018, Appendix Figure A.1.8.1). Prior recordings at these times found vocal behaviours to be more limited than in breeding areas, with calls described as infrequently punctuating long periods of silence (Rasmussen & Head 1965, Dahlheim 1987, Crane & Lashkari 1996). The work described in the previous chapters of this section (see Chapters 1.2, 1.3, 1.5) from passive acoustic recordings made in Clayoquot Sound, off the west coast of Vancouver Island, begins to redress the balance of time spent examining gray whale acoustic use outside of breeding/calving regions, and adds to knowledge of gray whale vocal behaviours over its entire range.

The initial works dedicated to gray whale acoustics were performed in breeding lagoons (Dahlheim et al. 1984, Dahlheim 1987). This resulted in the description of six core call types, which are still applied in current research. All calls sit in the frequency range below 2000 Hz, and the energy focused (the peak frequency of the call) below 300 Hz. Dahlheim (1987) suggested that the structure of calls took advantage of an 'acoustic window' in the soundscape, below other large amplitude contributions to the ambient condition.

Additions to the 'core' call repertoire have been described for interactions between cows and their young, also resulting from work in breeding lagoons. Ollervides (2001) suggested an additional five call types. These call types, and two further vocalisations described by López-Urbán and colleagues (2016) are used by both adult whales and cow-calf pairs. These call types have not been widely applied outside of the studies that initially described them, with the work in Chapter 1.5 the first to examine for 'motherese' presence outside of the lagoons.

*Feeding and weaning*

Recordings have been made concomitant to gray whale foraging in the Beaufort, Chukchi and Bering Seas (Moore & Ljungbald 1984). Prior to this work, descriptions of gray whales vocalisations were only anecdotal, where Aldrich (1889) described a type of 'singing', and

Tomlin (1957) noted a low frequency roar-like call (Appendix Figure A.1.8.1). In Chapter 1.5 I describe the vocal behaviours during foraging periods on a tertiary feeding ground, primarily frequented by whales that are part of the Pacific Coastal Feeding Group (PCFG, Calambokidis et al. 2010, IWC 2010). Patterns in call use and timing were much like those described in breeding lagoons, with 'bursts' or 'bouts' of calling (Stafford et al. 2007). The feeding-breeding dichotomy, as suggested for other baleen whale species (e.g. Clark 1983, Parsons et al. 2008) was not, however, substantiated in this work, with the calls heard perhaps to maintain contact with conspecifics, or even attract others to the food sources, or coordinate feeding effort (Janik 2000).

*Migration*

Gray whale calling patterns diverge most from that of breeding or feeding behaviours during migration. Here the low frequency class 3 moan dominates (83.69% of calls during northward and 81.67% during southward migration). I suggest in Chapters 1.2 and 1.3 that calling during migration, especially the use of moan calls, may be a means to navigate. This may be through reverberation and interpretation of an individual's own low frequency calls, or conspecific calls that provide information, as described for blue (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*, Evans & Raga 2001, Clark & Ellison 2004). They may leave an acoustic trail, created by leading whales for conspecifics to follow. The use of similar frequency modulated calls have been seen from other baleen whales, including humpback (*Megaptera novaeangliae*, Watkins 1981) blue, fin (Clark & Ellison 2004), and bowhead whales (*Balaena mysticetus*, Blackwell et al. 2007). The structure and use of these calls are optimised for long range maintenance of contact with others, described by Payne and Webb (1971) as retention of the 'range herd'. The use of acoustics by baleen whales, either active or passive, as an orientation cue has not received much attention (Allen 2013), despite the recognition that low frequency signals can travel up to hundreds of kilometers (Norris 1967, Payne & McVay 1971).

The addition of a sub-group of moan calls, labelled in Chapter 1.2 as 'low moans', class 3a, was suggested, and were prevalent in both north- and southward migration recordings. They were found to be distinct in call structure from other calls including class 3 moans. These calls, focused on average at 44.90 Hz (Table 1, Chapter 1.2), likely complement the use of moans, and may be the most far reaching means of sending and receiving information during migration.

Call rates were matched to shore based visual surveys of the gray whale migration (ACS gray whale census data) in Chapter 1.3, establishing that calling, in particular the use of moan calls, could be used as a proxy to whale number. The expected peaks of whale passage tied closely to peaks of calls. Until this and some other recent studies (Guazzo et al. 2017, Rannankari et al. 2018), vocal behaviours were not thought to be common during migration, perhaps as a conservative measure after a period of overwinter fasting.

*Vocal repertoire and referential calling*

The information coded into a call, or its 'referent' is anything becoming knowable or predictable via interpretation of the signal (Smith 1981). Vocalisations can carry complex information including location, behavioural state, or social context of signaller; the caller identity and their and group membership, as well as the physiological or internal state of the individual (Markl 1985, Maynard Smith & Harper 2003, Wiley et al. 2013). Communication signals can also refer to events external to the signaller, and in this case are 'functionally referential' (Rendall et al. 2009). Descriptive vocalisations likely incorporate both behavioural and identity referents of the whale in the signal (Smith 1981). Referential signals should display specificity to a stimulus or situation (Macedonia & Evans 1993), however the strength of this association may depend on the function of the call (e.g. food-associated versus alarm signals, Scarantino & Clay 2015).

Baleen whale acoustics use is typically assigned a role in social interactions and group dynamics. As well as group cohesion, this may also include conflict resolution, intra-sexual competition, hierarchy, or territory establishment (e.g. Cummings et al. 1972, Tyack 1981, Helweg et al. 1992, Clapham 1996, Darling & Bérube 2001, Darling et al. 2006, Oleson et al. 2007a,b, Smith et al. 2008). Calling may form or retain alliances or hierarchies, and perhaps regulate inter-individual spaces as seen in humpback whales (Norris et al. 1999, Chloewiak et al. 2018).

The use of calls labelled as 'motherese' between gray whale a mother and young is analogous to 'baby babble' or 'toddler jargon' in human children, or 'sub-song' in birds (Marler 1965, 1970). Charles (2011) reported that gray whale groups in breeding lagoons with calves present were never silent. This suggests that calling is a means for the pair to retain contact, with perhaps mother giving constant cues to her young. Calling between mother and calf in other baleen whale species has been found to be more similar than between other conspecifics, indicating perhaps a modification of vocal use by the cow during nursing and weaning which may aid in the learning process for the calf (e.g. right whale (*Eubalaena glacialis*), Baumgartner et al. 2008). However, studies have yet to determine the developmental mechanisms used by baleen whale calves in learning and refining their ensemble of calls (Fish et al. 1974, Ljungbald et al. 1980, Würsig et al. 1985, Wisdom et al. 2001).

The resemblance between call classes 7-10 (Ollervides 2001, Charles 2011) and the 'core' call types of classes 1-4 (Dahlheim 1987) suggest that 'motherese' may be a precursor for the adult repertoire. This type of development of call catalogue, where a juvenile version matures into an adult call, has been noted in oscine birds (Petrinovich & Baptista 1987) and bats (Esser & Schmidt 1989). Even if the call repertoire of gray whales were innate, the use of particular sounds at a particular time, in a certain context, with intonation, or as an appropriate response, may be reinforced by experience (Wisdom et al. 2001). The study of a captive gray whale calf shows the use of class 1a, 3, and 4 calls developed with no exposure to adult calling. However, modification of repertoire as the calf grew suggests a role for social context and/or reinforcement in calling (Wisdom et al. 2001).

I hypothesize that 'motherese' call types (Ollervides 2001, Charles 2011) are antecedents to the 'core' vocalisations of the gray whale repertoire (Dahlheim 1987). This hypothesis, that draws on spectrogram comparison as well as the use of calls in different settings, will be difficult to test. The increasingly limited use of 'motherese' calls may simply be a product of the weaning process and not repertoire evolution. It is likely that cow-calf pairs, if not mothers at least, use the 'core' call types in addition to those described for 'motherese'.

The complex growl sounds of class 7 are similar to class 4 rumbles (Charles 2011). Although not frequently recorded in this study, they are heard approximately twice as much in foraging grounds as on migration. The tonal class 8 'ugg' is representative of class 3 moan calls. It was the most frequently heard call type in recordings from Cow Bay when mother-young pairs were not visually present, with increased employment at night, leading to the suggestion that this call may be used during periods of separation of cow-calf pairs, and aid in their reuniting (see Chapter 1.5). The number of class 3 calls heard during summer deployments correlated with the number of cow-calf pairs visually present, as well as being present in the repertoire of the captive calf very early in life (Wisdom et al. 2001). However, its continued use may need to be reinforced, perhaps by return signals from conspecifics, as Wisdom and colleagues (2001) showed the call type have limited use as the calf matured.

Class 9 are complex pulsive sounds, that resemble the upsweeps of class 2. Upsweeps form contact-calling sequences in other baleen whale species (e.g. southern right whales, Clark 1980). Class 2 calls have been recorded for both migration and foraging (see Chapters 1.2, 1.3, 1.5). This, however, contrasts with other recordings made during foraging in higher latitudes that did not record any type 2 calls (Moore & Ljungbald 1984). Its increased relative use heard in summer recordings suggest a role in foraging. However, both class 2 and 9 calls show modification in the presence of vessel noise. This potential reaction to disturbance, as well as apparent sensitivity to social context suggests that it communicates change of state or threat presence to conspecifics.

Lastly, class 10 calls are a series of grunts, forming a rumble or creak sound, and maybe the predecessor of the class 1 knock calls. Call type 1a were present within 1.5 months for the captive calf, whereas class 1b developed several months later (Wisdom et al. 2001), and although both are suggested for social calling and group contact, the application of each sub-type may be nuanced. The increased rate of use of class 1b in the presence of both vessels and killer whales, both likely perceived as threats at some level by gray whales. Following this line of thought, they may be alarm calls indicating perceived or impending threat or other important situation changes (Caro 2005, Cunningham & Magrath 2017).

The development of the repertoire, if it is refinement and not abandonment of 'motherese' call types, may be an example of cultural learning. Maternal transmission of migration routes and foraging areas is known for gray whales (Calambokidis et al. 2010, Chapter 1.4). As well, cetaceans are believed to be capable of vocal learning through mimicry, an ability only otherwise present in parrots, hummingbirds, songbirds, bats, elephants and humans (Janik & Slater 1998, 2000, Jarvis 2006). A period of 'babbling' is noted before the adult vocalisations are stabilized (Lenneberg 1976, Marler & Peters 1982, McCowan & Reiss 1997, Lipkind et al. 2013). Also, periods of practice of manipulating airflow and phonic structures have been described, with skills increasing as the whale matures (Cazau et al. 2013). The ability to recycle air, as well as to match calls is mastered over time with repetition and imitation (Guinee et al. 1983, Edds et al. 1993, Janik & Slater 1997, Tyack & Sayigh 1997, Jarvis 2006).

Divining call function is the 'holy grail' of whale acoustics. To date, no other study of gray whale acoustics use has attempted to tie phonation to behaviour. The function of calls may vary from one setting to another, or remain steadfast across behaviour and life history states. Analysis of gray whale calling behaviours in various behavioural, social, and soundscape conditions from this work, and others (see Dahlheim et al. 1984, Dahlheim 1987, Ollervides 2001, Ponce et al. 2012, Dahlheim & Castellote 2016) show the plasticity in vocalising behaviours of this species. Dahlheim (1987) suggests that calls are focused within an 'acoustic window' and may have developed in reference to background noise, with multiple acoustic strategies employed to ensure that signaling remains effective (Dahlheim & Castellote 2016).

### *A highly sonorous whale*

Acoustic techniques in whale research provides knowledge of whale presence, and habitat use over space and time. As yet, our knowledge of gray whale acoustics is not detailed enough to make broader contributions without having recordings tied to visual observations and/or other data streams. Yet, to now consider gray whales as highly acoustic, rather than relatively silent, has wider implications on the way we use acoustic data for this species.

Forays into the idea of call function, tied with estimates of how far calls propagate can offer novel and exciting insights into the use of acoustics and how that plays into an animal's life history. It also opens a route to understanding the impacts that anthropogenic-introduced noise have on gray whales. Chapter 1.6 indicates that, through modification in calling behaviour and structure, elevated ambient noise conditions can be somewhat circumvented. However, this and other studies (Dahlheim & Castellote 2016), show that there may be a threshold to call plasticity, either defined by physiology, or how far the call can be changed without altering the meaning.

The results from Chapters 1.2, 1.5, and 1.6 highlight the acoustic sensitivity of gray whales to human-induced noise, and the vulnerability of cow-calf pairs. For gray whales acoustic disturbance is a particular concern. They are subject to chronic exposure of anthropogenic noise throughout their range and ambient noise levels in shallow water can be as much as seven times greater than deep (Elles 1982, Nichols 1987). Clearly, the management implications of a sonorous species is different from a non-acoustic animal. Our relative ignorance of the fundamental nature of one of the most commonly encountered coastal whales raises suspicions as to how much uncertainty and misinterpretation guides our approach to co-existing with cetaceans.

# Appendix

1770 - Propellor suggested for submarine use
1776 - First steam powered boat
1789 - First whaling activities in the Pacific (Henderson 1972)
1798 - Four bladed propellor experiments on a ship (Robert Fulton)
1819 - First Atlantic Ocean crossing of a propellor driven vessle
1840 - Sailboats phased out to be replaced by steam power
1845-1846 - First gray whale take in Magdalena Bay
1855-1856 - Scammon whaling in Magdalena Bay
1857-1858 - Scammon whaling in Ojo De Liebre (Scammon's Lagoon)
1864-1865-Shore-based whaling for gray whales initiated (cow-calfs the focus)
1874 - gray whale whaling abandoned
1889 - Gray whale (devilfish) described as 'singing' on nothern feeding grounds -Aldrich
1903 - First diesel engines
1910 - Piston engine powered jet unit tested
1914 - first catches from factory ships
1919 - Fixed pitch propellors introduced
1937 - International Agreement for Regulation on Whaling
1940 - Japanese Whaling begins
1946 - Gray whales afforded protection but IWC, enforced in 1949
1957 - 'Low pitched roars' decribed from the Bering and Chukchi Seas - Tomlin
Scientific whaling 1959-1970 - US remove 316
1960-1970: 'Croaker like grunts',"low frequency rumbles' described from Laguna Ojo de Liebre - (Evans 1962)
Low grunting (Painter 1963); Clicks during migration (Wenz & Asa-Dorian 1964); knocking (Rassmussen & Head 1965)
Pulses, moans, whistels' lagoons/San Diego (Asa-Dorian & Perkins 1967); 'Grunts, rumbles, cries, rasps, pulses, clicks' in Laguna Ojo de Liebre (Poulter 1968)
1974 - Growl, moan, pulses, clicks recorded in captivity - Fish et al. 1974; 'Noisy pulsation' - Ray & Schevill
1978 - Reclassified and protected, population estimated ~17, 000 (Rugh & Braham 1979)
1978 - Knocks, pulses, snorts, slamming, bubble blasts, squeaking and moans recorded in Laguna San Ignacio lagoon
First call classification system from work in lagoons - Dahlheim et al. 1984, Dahlheim 1987
Recordings of knocks in the Bering - Moore & Ljungbald 1984
Moans found to be most prevalent during migration by Crane & Lashkari 1996
Motherese' call types described from work in lagoons - Ollervides 2001, Charles 2011, Urban-Lopez et al. 2016
1007 - Knock calls of gray whales heard year-round in the Bering - Stafford et al. 2007
2012 - Population estimate 19,126 individuals (Laake et al. 2012)
Periodicity in calling on migration, phasic progression seen in acoustics - Guazzo et al. 2017, Rannakari et al. 2018

**Figure A.1.8.1:** Timeline to show the progression of awareness in acoustics use of gray whales. The history of whaling of gray whales and select marine vessel use landmarks are given for context.

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## 2. Part Two: Offshore

*THE SEA! the sea! the open sea!*
*The blue, the fresh, the ever free!*
*Without a mark, without a bound,*
*It runneth the earth's wide regions round;*

Barry Cornwall (1787- 1874)

## 2.1. Introduction: Offshore Clayoquot Sound and the use of ocean gliders

Whale numbers and distribution were significantly altered by whaling throughout the north Pacific. There is now great uncertainty regarding population size and habitat use by large whale species in Canadian Pacific waters. Although some species, like the gray whale (*Eschrichtius robustus*), that was the focus of the Coastal Section, have recovered, perhaps even to pre-whaling numbers (Laake et al. 2012), we have limited data for other species. Much of what we know about their life histories and habitat use comes from historic data, including whaling records, as well as few rare encounters. Species that were once the most prolific have scant sighting records since the cessation of whaling in the late 1960s.

The much needed surveys to re-establish baseline knowledge of population size and habitat use of large whales are expensive and often weather limited. The proclivity of these species, such as fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), and sperm (*Physeter macrocephalus*) whales to inhabit the shelf break or deeper offshore waters, and/or low population numbers, as for Pacific right (*Baleaena japonicus*) and sei whales (*Balaenoptera borealis*), further hinders this work. This is where the use of acoustics, particularly autonomous ocean gliders with passive acoustic monitoring (PAM) capabilities may come to the fore. The use of gliders opens the possibility of surveying for species presence at times and in locations that would otherwise be difficult to impossible, and in an unobtrusive way to the species of interest.

Chapter 2.2 describes the deployment of PAM-capable gliders on the coast of British Columbia, in the waters offshore of Clayoquot Sound. The mandate for the first deployment was to cover as much water as possible, with special reference to areas of bathymetric relief which were examined for increased prey density, as suggested by Freeland & Denman (1982), Allen & Hinkey (2010), and Moors-Murphy (2014). The second deployment returned to these bathymetric features, namely oceanic canyons, to further explore the draw these locales may have on whale species. The hope was to further establish if these areas are biological ’hotspots’ for whales, and if so, why.

The observation of whale calls is a proxy for presence; when a call is heard at least one individual of that species must be present. In Chapter 2.3, I tie the recordings made during the glider missions to those made by a stationary hydrophone deployed in the coastal waters of

Clayoquot Sound (see previous section for details), to describe the minimum presence of large whales species. As our knowledge of call repertoires with regards to geographic, behavioural, or social context increases, we can tentatively draw parallels between the calls and the setting of the signaller. Chapter 2.4 describes the different call types heard in both mobile and stationary PAM recordings for fin whales, and discusses what can be inferred from a distinct temporal pattern.

Considered together, the data presented in this Offshore Section begins to re-form a baseline of presence and habitat use of large whale species of the west coast of Vancouver Island, which can be fed into better protection and management systems to further aid population recovery of these species. Acoustic surveys like those presented here may revolutionize species distribution and habitat mapping, with monitoring over fine spatial and long temporal scales possible.

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## 2.2. Using passive and active acoustics to identify whale habitat on the west coast of Vancouver Island

### Preface

Chapters in Section 1 have a nearshore focus, primarily on a coastal species, the gray whale. Here I describe the exploration of waters offshore from Clayoquot Sound outward to the continental shelf break. Autonomous underwater vehicles (AUV) with passive acoustic data collection capacity allows surveys for whales beyond the capabilities of traditional methods. Acoustic survey work can continue at night, in poor weather, and under conditions that vessel based visual methods cannot, also often detecting cetacean presence more frequently than surface observations (McDonald & Moore 2002, Širović et al. 2004, Barlow & Taylor 2005, Mellinger et al. 2007a, Rankin et al. 2007). The offshore waters of British Columbia were once habitat for large toothed and baleen whale species, including sperm (*Physeter macrocephalus*), blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus)*, Pacific right (*Baleaena japonicus*) and sei whales (*Balaenoptera borealis*). Following removals by whaling, populations of these species are small, and habitat use patterns largely unknown. Acoustics represents a relatively cost effective way to monitor for whales over time and space, using their vocalisations as a cue to presence. In addition, data streams measuring habitat quality and the preyscape can outline areas that are important to large whale species. I focus on submarine canyons and regions of bathymetric relief, as these are thought to enhance upwelling or downwelling along the shelf break (Freeland & Denman 1982, Allen & Hinkey 2010).

Here I outline findings from two AUV ocean glider deployments in the offshore waters of Clayoquot Sound. These are the first steps taken to establish important or ‘critical’ habitat areas by tying passive acoustic recordings of large whale species to data from an echosounder, that estimates potential prey abundance, as well as instruments to measure oceanographic properties of the waters. The limitations of the application of acoustics to these kinds of surveys is discussed, as well as stressing the advances that acoustics affords in terms of stretching the limits of time and space over which surveillance is possible.

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## Using passive and active acoustics to identify whale habitat on the west coast of Vancouver Island

### Introduction

Populations and distributions of whale species in the marine waters of western Canada have been much altered by unmanaged whaling. Coastal species such as the eastern Pacific gray (*Eschrichtius robu*stus) and the humpback whale (*Megaptera novaeangliae*) have partly recovered to their pre-whaling numbers, whereas the sei (*Balaenoptera borealis*) and the Pacific right whale (*Baleaena japonicus*) have had only a handful of possible sightings since the end of whaling. Our current knowledge on presence, distribution, and habitat use of these, and other large whale species inhabiting the pelagic, continental shelf, and shelf-break regions is sparse. Moreover, small population size makes tracing seasonal movements or outlining important habitat difficult (Gregr et al. 2006).

Locating areas of high prey abundance is a first step in outlining important habitat for whales. The west coast of Vancouver Island is a productive region due to the confluence of the northernmost extent of the California current, and the southern reaches of the northward flowing Alaska current (Thomson 1981). Oceanographic conditions allow nearshore primary productivity to be translated into high concentrations of offshore zooplankton (Mackas & Galbraith 1992, Gregr & Trites 2001, Mackas et al. 2001). In the offshore waters, topographical features of the continental slope and shelf break show increased biological productivity (Hickley 1995, Smith et al. 2010). In particular, submarine canyons are sites of enhanced upwelling (Freeland & Denman 1982, Hickey 1997, Vindeirinho 1998, Allen & Hinkley 2010), and play an important role in nutrient exchange across the shelf break (Kunze et al. 2002, Allen & Hinkley 2010). Submarine canyons in other regions have been associated with large numbers of cetaceans, although the mechanisms affecting the strength of attraction are unknown (Moors-Murphy 2014).

Here, ocean gliders were deployed in the offshore waters of Vancouver Island to identify whale species and associated habitat variables. The gliders use passive acoustic monitoring (PAM), to identify species by their calling behaviour. The occurence of calls alone denotes presence, but the repertoire employed may suggest other aspects of habitat use. Habitat variables including water conductivity, temperature and density, as well as backscatter measures from a high frequency echosounder, were collected concurrent with the PAM recordings. Submarine canyon regions in particular are explored to establish their potential to aggregate prey and whales.

## Methods

A Teledyne Webb Slocum electric glider was equipped to measure water temperature, conductivity, and density via a pumped Seabird Glider Payload Conductivity, Temperature and Depth (GPCTD) sensor. Acoustic backscatter was recorded to identify potential whale prey using a 300 kHz Imagenex active acoustic echosounder. Whale calls were collected by a digital acoustic monitoring (DMON) instrument (Woods Hole Ocean Institute), capable of omnidirectional recording in frequencies up to 1000 Hz. The DMON records continually in the range of baleen whales and sperm whale (*Physeter macrocephalus*) vocalizations.

Two deployments were made to the offshore waters of Clayoquot Sound (Figure 2.2.1), on the west coast Vancouver Island, between March 17-April 16, 2016, and January 30-February 18, 2017. The first deployment covered on- and off-shelf regions, crossing the shelf break and areas of interest. It was released approximately 5 nm off Siwash Point, Flores Island, (49°12’37” N, -126°14’48” W), first travelling west to the shelf break to traverse areas of topographical relief and canyons while moving southward towards La Perouse Bank (Figure 2.2.1, 2.2.2). The second deployment was a more detailed survey of Clayoquot Canyon following our examination of the recordings from the initial deployment (Figure 2.2.1, 2.2.3). The glider profiled to a maximum depth of 200 m.

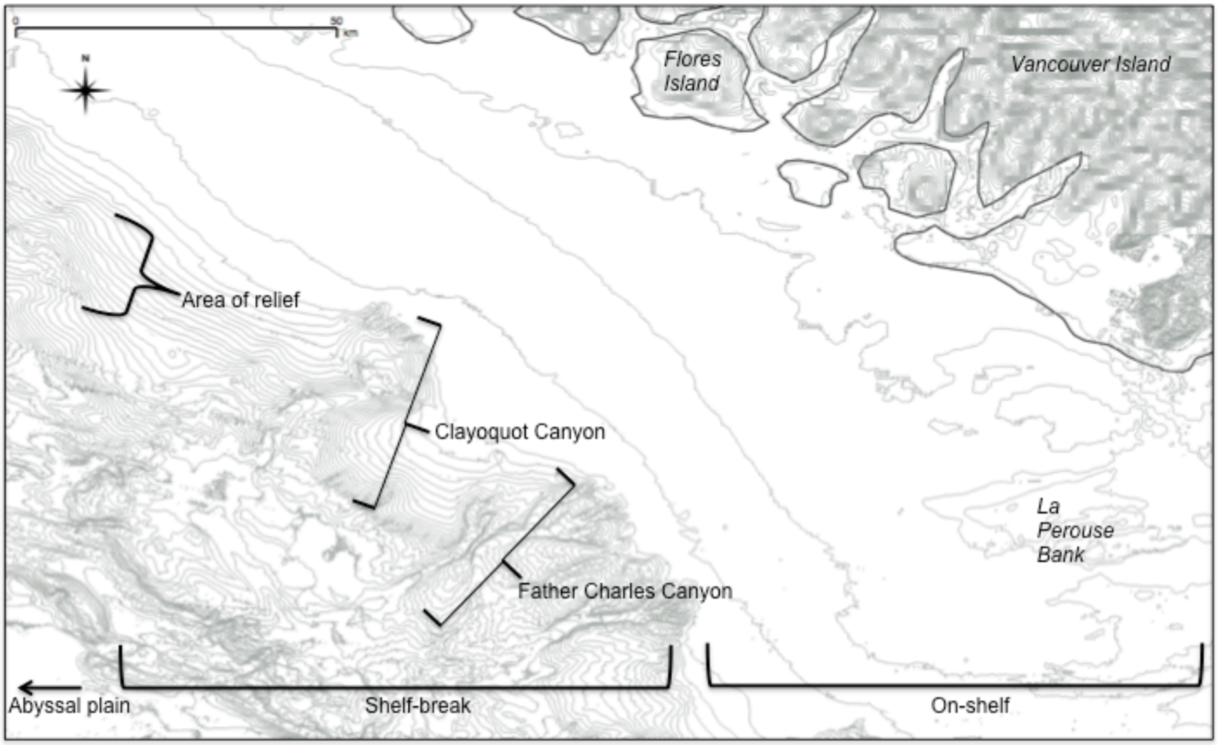

**Figure 2.2.1:** Area of study. Deployment is 5nm from Siwash Point, Flores Island. The three regions of interest, on-shelf, shelf-break, and abyssal plain, indicated. Canyons and areas of relief of particular note are marked.

The PAM recordings were split into 5 minute clips for manual inspection of the data in its entirety. Spectrograms were generated using Raven Pro Interactive Analysis software using a 256-point Hann-window FFT with 50% overlap to visualise the recordings. Whale calls were identified and classified by making reference and spectrogram comparison to previous research. This gave a call number per species for every 5 minute clip of the recordings, which were matched to mean latitude and longitude of the glider, water depth, temperature, salinity (derived from conductivity and temperature measures), and acoustic backscatter as volume scattering strengths.

The echosounder collected observations of acoustic backscatter on descent. Given its high operating frequency, it is most sensitive to scatterers greater than 1.6 mm in size (Davis et al. 2016), and in the near range, of approximately 1-20 m from the glider. Volume scattering strengths (Sv) recorded for each dive were averaged over the full water column, and in depth bands of 0-50 m, 50-100 m, 100-150 m and 150-200 m. These values (in dB re m^-1), which had an average temporal separation of about 30 minutes (dependent on local water depth), were matched to the better resolved 5 minute acoustic clips to explore the whale calls relationship with backscatter.

To examine temporal patterns, each clip was classified as day or night, using nautical twilight dawn and dusk times, to allow for diurnal comparison. They were also labelled with the number of days elapsed since January 1 of the year of deployment. To provide coarse scale spatial analysis it was noted whether the glider was on or off the continental shelf, or on the shelf break (Figure 2.2.1), and in or outside of a canyon. Comparison between on-shelf, shelf break and off-shelf recordings were made, as were data recorded inside canyons to that outside along the shelf break. The species and the number and type of calls present, and oceanographic and prey measures were compared for each region.

Vessel noise was also noted for each 5 minute clip. Periods at the surface were dominated by water noise, with the glider's pump motor and electronic noise, obscuring whale calls. This, however, accounted for no more than ten minutes per surfacing.

### Results

The 2016 deployment covered 452.8 km of shelf and shelf-break habitat, with a total of 737.55 hours of recording (8560 five-minute clips). Three-quarters of the recording time was spent in the self-break region, with the remainder on the continental shelf. The 2017 deployment covered 327.1 km with recordings from 547.03 hours (5411 five-minute clips). The second deployment was aimed more specifically at canyons, but similar time proportions were spent on the shelf and along the shelf break as the first deployment. The gliders approximately followed the planned routes, but were affected by currents, especially in the head of canyons (Figure 2.2.2, 2.2.3).

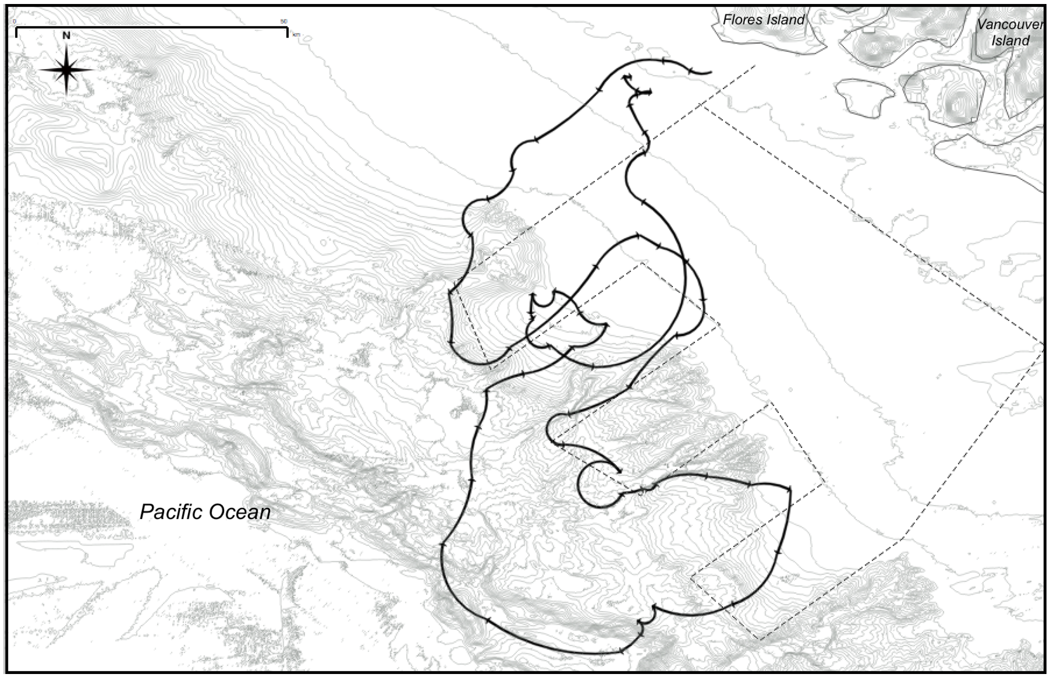

**Figure 2.2.2:** Planned (dashed line) and completed route (solid line) of the ocean glider for the 2016 deployment. The direction of travel is indicated by the chevrons.

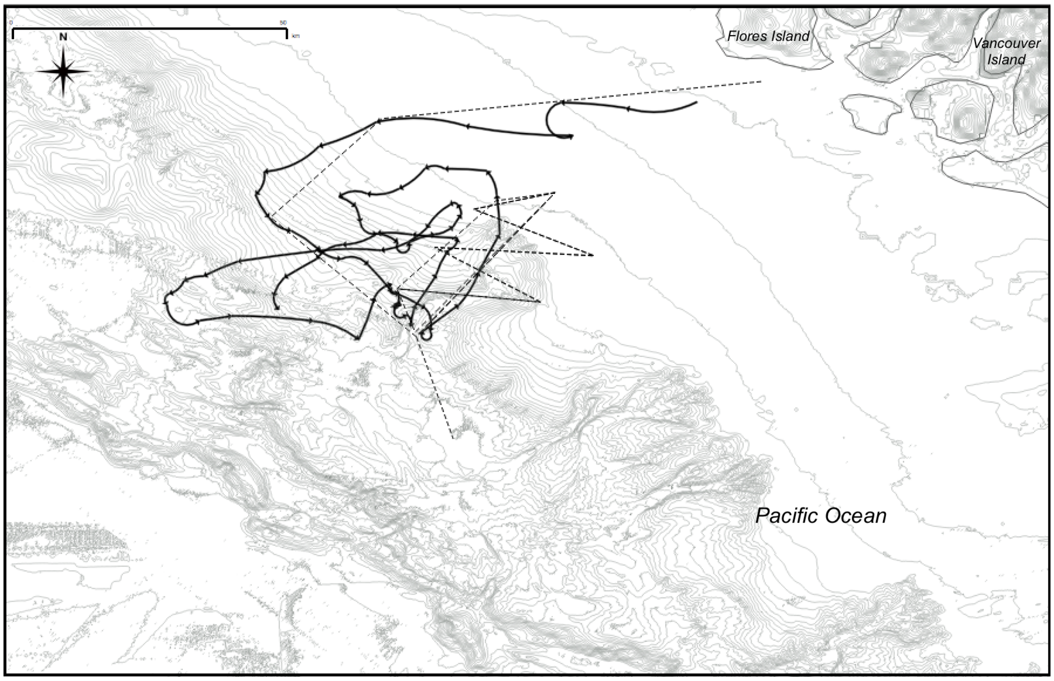

**Figure 2.2.3:** Planned (dashed line) and completed route (solid line) of the ocean glider for the 2017 deployment. The direction of travel is indicated by the chevrons.

*Whale calls*

Of the 8560 five-minute clips for 2016, 999 had at least one whale call. A total of 1,394 calls were recorded and measured for further analysis. Due to their ubiquity and varied repertoire, humpback calls were simply marked as present when heard. Similarly, sperm whale calls are only marked as present, with the number and type of clicks not analysed here. With my instrumentation, I cannot discern whether it is one whale calling repeatedly or multiple whales, and so all calls were treated independently. For initial spatial analysis of whale calls, the position of the glider when receiving the call is used. This, however, is done cognizant that the vocalising whale could to be distant from the glider. Low frequency calls can propagate over great distances, up to thousands of kilometers under certain conditions (Payne & Webb 1971). For example, using recordings from a stationary hydrophone deployed in deep coastal waters just north of the glider survey area, Koot (2015) estimated fin whale 20-Hz calls to have a detection range of 112 km at average ambient noise conditions, and up to 1,498 km in conditions of low background noise. Links between calls and habitat use are done with this in mind.

The 2017 deployment had a much higher call count than in 2016. More than half of recordings included calls (51.53% of the 5410 clips), nearly 5 times greater than in 2016 (11.67%). Humpback whales were heard most frequently in 2016, whereas fin whales dominated in 2017 (Table 2.2.1). The proportion of clips with calls by survey area (on-shelf, shelf break, and in canyon), is shown in Table 2.2.2, and the spatial separation of calling behaviours per species is shown in Table 2.2.3.

When considering both deployments and all calls, acoustic activity differed diurnally (Mann Whitney U, $p<0.001$) and was generally greater at night. The number of calls also differed when comparing on-shelf and shelf break areas. Calls increased significantly when the glider was surveying past the continental shelf break (Welch's $t(10073.052)=-11.411$, $p<0.001$), but were reduced when the glider was inside a canyon, such as Clayoquot Canyon (Welch's $t(1644.715)=5.302$, $p<0.001$). I examine each species in turn.

**Table 2.2.1:** The presence of whale calls by species expressed as a proportion of the full deployment time and from the clips that have shown the presence of at least one whale call.

| Species | Deployment year | Proportion of deployment (%) | Proportion of whale presence (%) |
|---|---|---|---|
| All whales | 2016 | 11.67 | |
| | 2017 | 51.53 | |
| Gray whales | 2016 | 0.50 | 4.30 |
| | 2017 | 0.01 | 0.07 |
| Humpback whale | 2016 | 6.19 | 5.31 |
| | 2017 | 21.16 | 41.07 |
| Fin whale | 2016 | 5.51 | 47.25 |
| | 2017 | 40.55 | 78.69 |
| Blue whale | 2016 | 0.06 | 0.50 |
| | 2017 | 0.26 | 0.50 |
| Sperm whale | 2016 | 0.00 | 0.00 |
| | 2017 | 0.20 | 0.39 |

**Table 2.2.2:** Call counts received by the glider and proportions of time the whale calls by species are present from the survey time spent on the shelf and along the shelf-break

| Species | Deploy. | Count | | Proportion | |
|---|---|---|---|---|---|
| | | On-shelf | shelf-break | On-shelf | shelf-break |
| Gray whale | 2016 | 43 | 0 | 2.02 | 0.00 |
| | 2017 | 2 | 1 | 0.13 | 0.03 |
| Humpback whale | 2016 | 323 | 213 | 15.17 | 3.31 |
| | 2017 | 456 | 694 | 28.81 | 18.13 |
| Fin whale | 2016 | 109 | 366 | 51.20 | 5.69 |
| | 2017 | 462 | 1726 | 29.19 | 45.09 |
| Blue whale | 2016 | 1 | 4 | 0.05 | 0.06 |
| | 2017 | 11 | 3 | 0.69 | 0.08 |
| Sperm whale | 2016 | 0 | 0 | 0.00 | 0.00 |
| | 2017 | 0 | 11 | 0.00 | 0.29 |

**Table 2.2.3**: Call counts received by the glider and proportions of time the whale calls by species are present from the survey time spent in a canyon and adjacent shelf-break area.

| Species | Deploy. | Count | | Proportion | |
|---|---|---|---|---|---|
| | | In canyon | shelf-break | In canyon | shelf-break |
| Gray whale | 2016 | 0 | 0 | 0.00 | 0.00 |
| | 2017 | 0 | 0 | 0.00 | 0.00 |
| Humpback whale | 2016 | 36 | 177 | 2.66 | 3.48 |
| | 2017 | 171 | 523 | 21.24 | 17.30 |
| Fin whale | 2016 | 146 | 220 | 10.80 | 4.33 |
| | 2017 | 320 | 1406 | 39.75 | 46.51 |
| Blue whale | 2016 | 0 | 4 | 0.00 | 0.08 |
| | 2017 | 0 | 3 | 0.00 | 0.10 |
| Sperm whale | 2016 | 0 | 0 | 0.00 | 0.00 |
| | 2017 | 0 | 11 | 0.00 | 0.36 |

**Table 2.2.4**: Call counts received by the glider and proportions of time the whale calls by species are present from the survey time spent on the shelf, along the shelf break, and in canyon regions.

| Species | | Count | | | Proportion | | |
|---|---|---|---|---|---|---|---|
| | Deploy. | On-shelf | shelf-break | canyon | On-shelf | shelf-break | canyon |
| Gray whale | 2016 | 43 | 0 | 0 | 100.00 | 0.00 | 0.00 |
| | 2017 | 2 | 0 | 0 | 100.00 | 0.00 | 0.00 |
| Humpback whale | 2016 | 323 | 177 | 36 | 60.26 | 33.02 | 6.72 |
| | 2017 | 456 | 523 | 171 | 39.65 | 45.58 | 14.87 |
| Fin whale | 2016 | 109 | 220 | 146 | 22.95 | 46.35 | 30.74 |
| | 2017 | 462 | 1406 | 320 | 21.12 | 64.26 | 14.63 |
| Blue whale | 2016 | 1 | 4 | 0 | 20.00 | 80.00 | 0.00 |
| | 2017 | 11 | 3 | 0 | 78.57 | 21.43 | 0.00 |
| Sperm whale | 2016 | 0 | 0 | 0 | 0.00 | 0.00 | 0.00 |
| | 2017 | 0 | 11 | 0 | 0.00 | 100.00 | 0.00 |

*Gray whales*

Gray whale calls were recorded near the coast soon after deployment. A triumvirate breeding group was observed and recorded soon after deployment in 2016. In 2017 calls were also coastally focused, recorded inside the 50 m isobath (Figure 2.24a,b, Table 2.2.2, 2.2.3) within approximately 6 km from shore. There was no significant difference between the backscatter measures taken in the vicinity of the gray whale calls (Student's t(13885)=-0.805, p=0.421), as expected. The whales are migrating north at the time, and if they do forage it is in shallow coastal waters not surveyed by the gliders. The calls heard were class 3 moans which have the frequency characteristics to carry long distances (Dahlheim et al. 1984, Dahlheim 1987).

There was more calling at night when data was pooled from both years, which is consistent with other studies of gray whales during northward migration (Guazzo et al. 2017, Rannankari et al. 2018, Chapter 1.2). However, results between diurnal periods are not statistically different here, likely due to the limited number of calls heard.

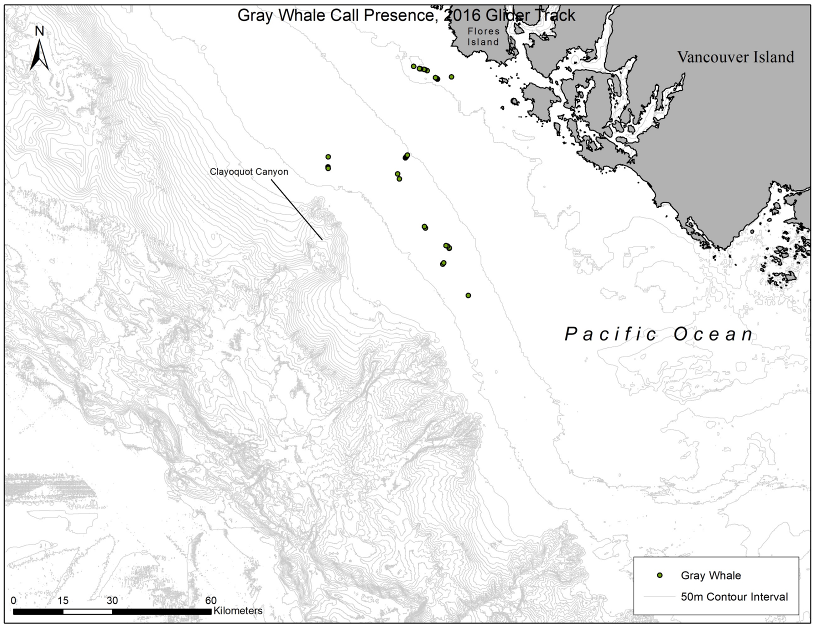

**Figure 2.2.4a**: Location of gray whale calls received from the 2016 deployment of the ocean glider

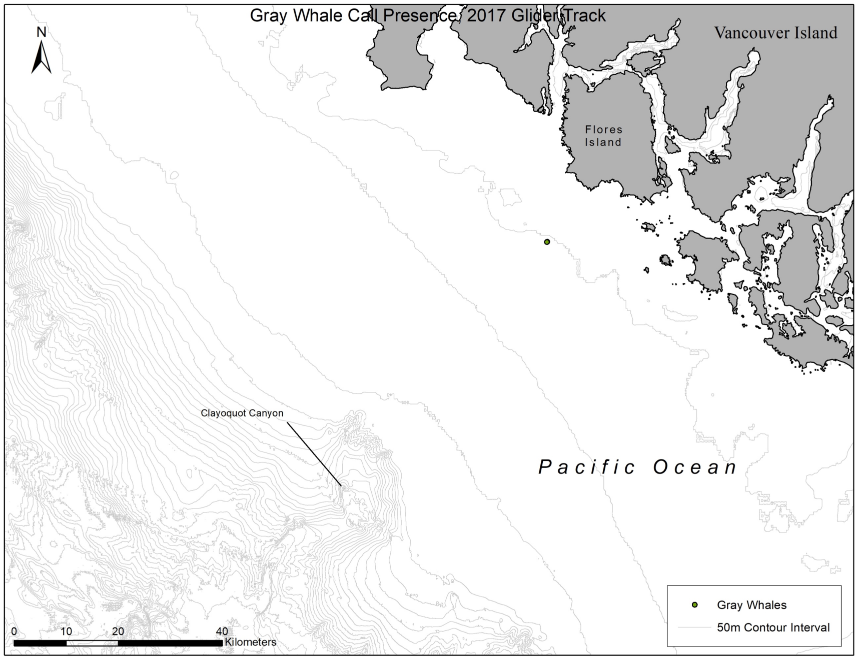

**Figure 2.2.4b**: Location of gray whale calls received from the 2017 deployment of the ocean glider

*Humpback whales*

Humpback whales were heard in all areas surveyed (Table 2.2.2, 2.2.3). In 2016 they were recorded most frequently in the deeper waters of the continental shelf (Table 2.2.3). In 2017 more calls were heard closer inshore (Figure 2.2.5a,b, Table 2.2.3).

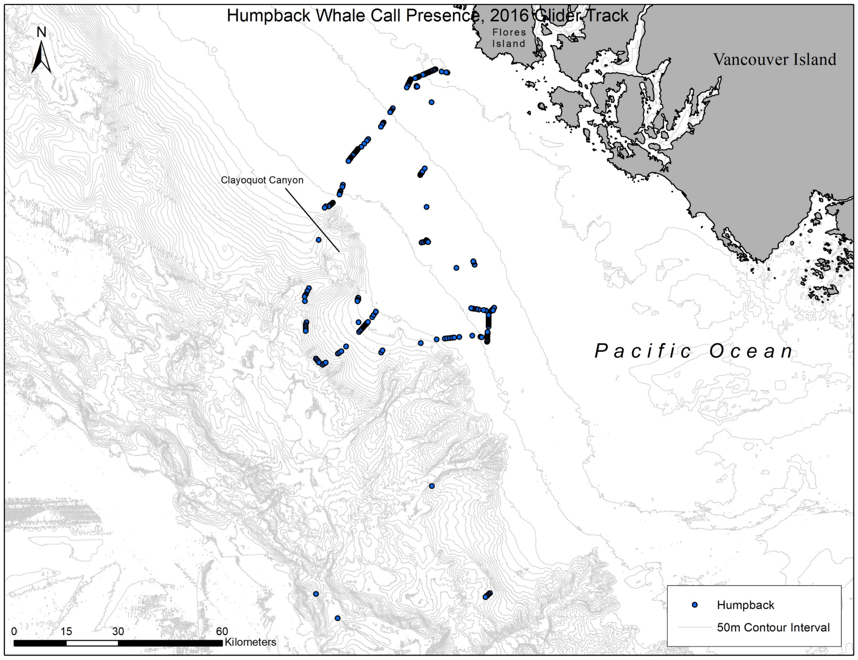

**Figure 2.2.5a**: Location of humpback whale calls received from the 2016 deployment of the ocean glider.

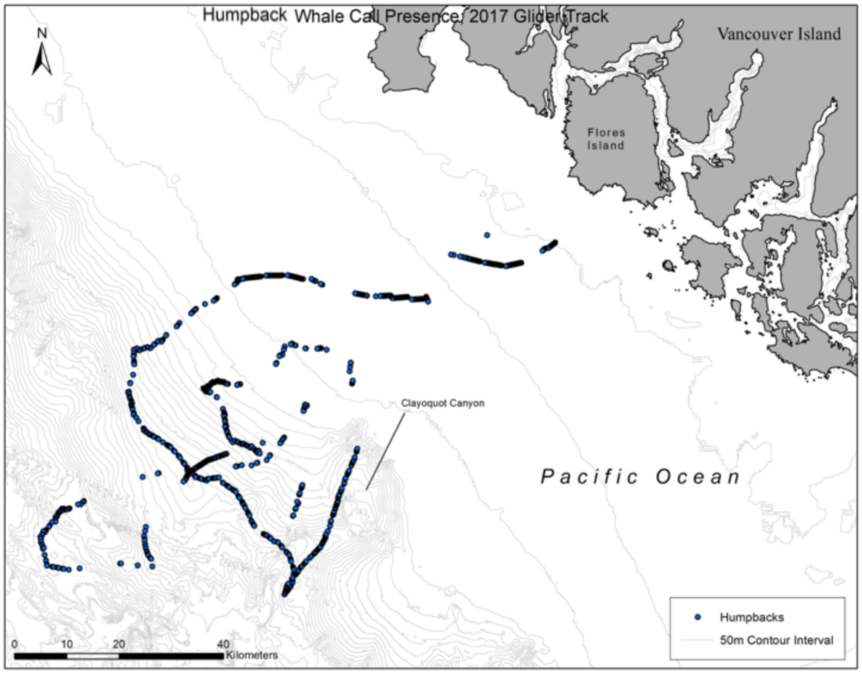

**Figure 2.2.5b**: Location of humpback whale calls received from the 2017 deployment of the ocean glider.

*Fin whales*

Fin whale calls were recorded most frequently in waters deeper than 200 m, along the continental shelf break, and in areas of bathymetric complexity (Table 2.2.2, 2.2.3). The greatest number of calls were recorded traversing Clayoquot Canyon and in areas to the north and west (Figure 2.2.6a,b, 2.2.7, Kruskal-Wallis, $p<0.001$).

The water column mean volume scattering strength associated with the calls showed, on average, stronger reflectance in the 2016 deployment than in 2017 (2016: $\bar{x}=-52.08\pm4.22$ dB re m^-1; 2017, $\bar{x}=-62.60\pm2.11$ dB re m^-1). This is, however, recorded where the glider is, and not necessarily where the vocalising whale might be. The rate of calls received (number of calls/clip) did not differ significantly with volume scattering strength in 2017, and only for the readings below 150 m deep (Kruskal-Wallis, $p=0.007$) in 2016. Call number was not correlated with volume scattering strength in either deployment (2016: $r_s=-0.287$, $p=0.640$; 2017: $r_s = -0.047$, $p=0.341$). The latitude, longitude, water depth, water temperature and salinity, as well as volume scattering strength below 50 m, all significantly change with the call rate (Kruskal-Wallis, $p<0.001$). Call rate was negatively correlated with year-day, although only weakly decreasing through March into April for 2016, and increasing as February progressed in 2017 ($r_s= -0.109$, $p=0.026$). This may indicate a changing behavioural or contextual state for whales between the two deployments.

The number of calls were significantly greater at night (Welch's $t(2525.534)=-6.684$, $p<0.001$). Calls also differed in number and type between deployments. Almost all were 40 Hz calls (99.90%), as described by Širović and colleagues (2013), on the 2016 deployments. In 2017, however, 99.39% were the stereotyped 20-Hz call, with some (11.92%) resembling short doublet song (Širović et al. 2017). This is discussed in greater detail in Chapter 2.3 and 2.4.

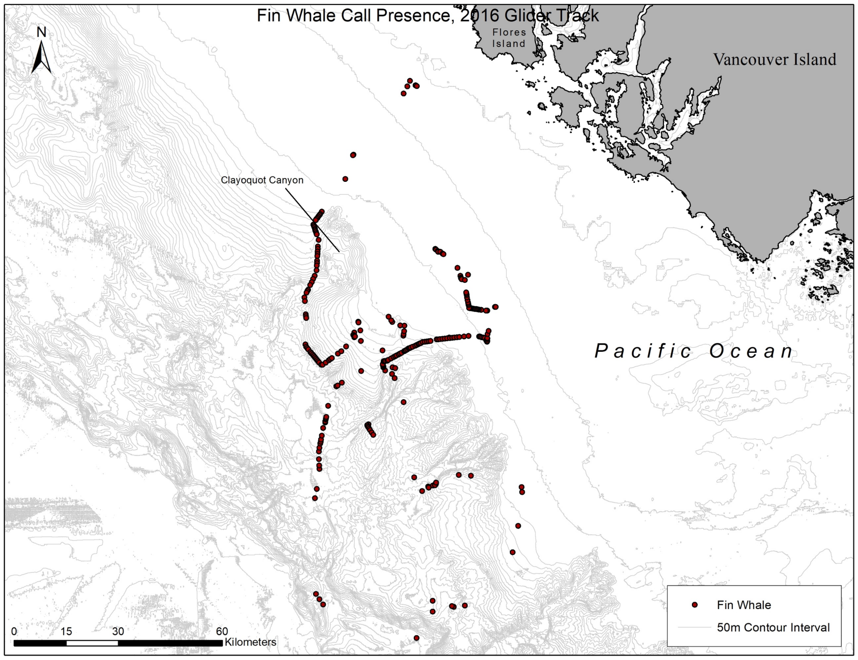

**Figure 2.2.6a**: Location of fin whale calls received from the 2016 deployment of the ocean glider.

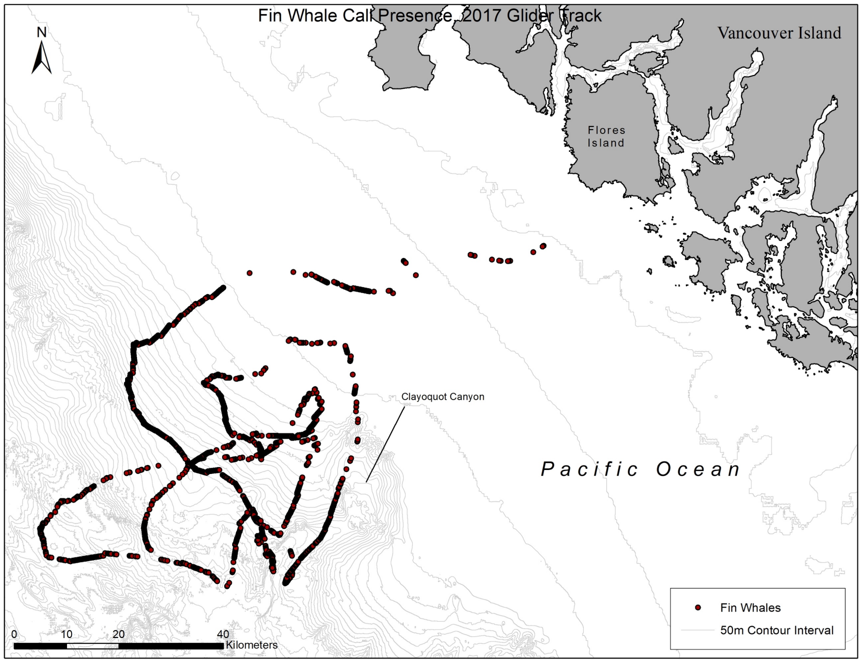

**Figure 2.2.6b**: Location of fin whale calls received from the 2017 deployment of the ocean glider.

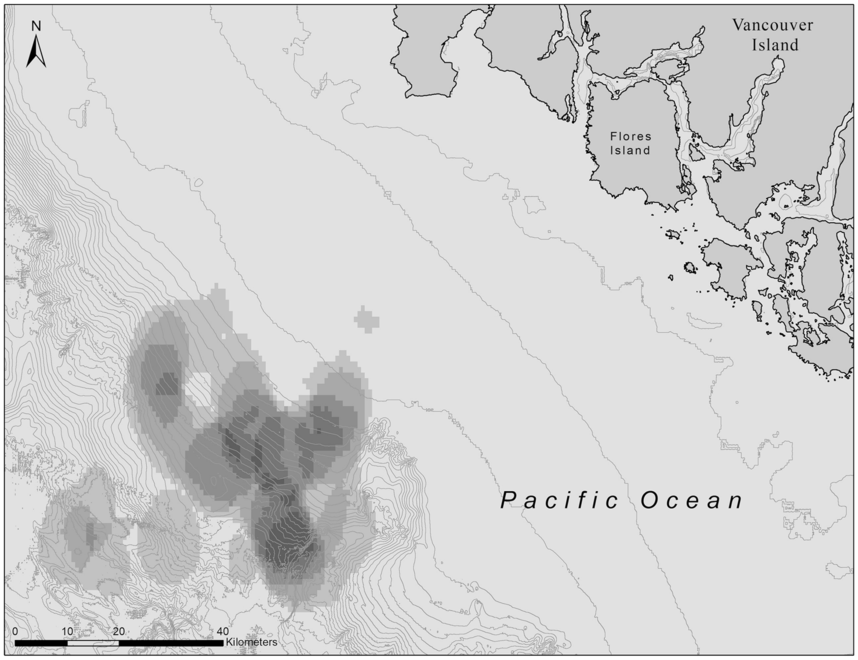

**Figure 2.2.7**: Heat map of fin whale calls, aggregating call data from both the 2016 and 2017 deployments.

*Blue whales*

Blue whale calls (n=19) were recorded from beyond the shelf break (Figure 2.2.8a,b, Table 2.2.2, 2.2.3). For clips with blue whale calls, the average call rate was x̄=2.11 calls/clip, and were predominantly D type downsweeps, (Thompson et al. 1996, Oleson et al. 2007a, b). These occur with both feeding and socialising behaviours (Oleson et al. 2007a). B type calls were also noted.

Although more calls were recorded at night, the difference was not significant (day: x̄=1.93±1.11; night: x̄=2.75±1.5; Student's t(17)=-1.230, p=0.236), nor was call number significantly correlated with year day ($r_s$ =0.225, p=0.439).

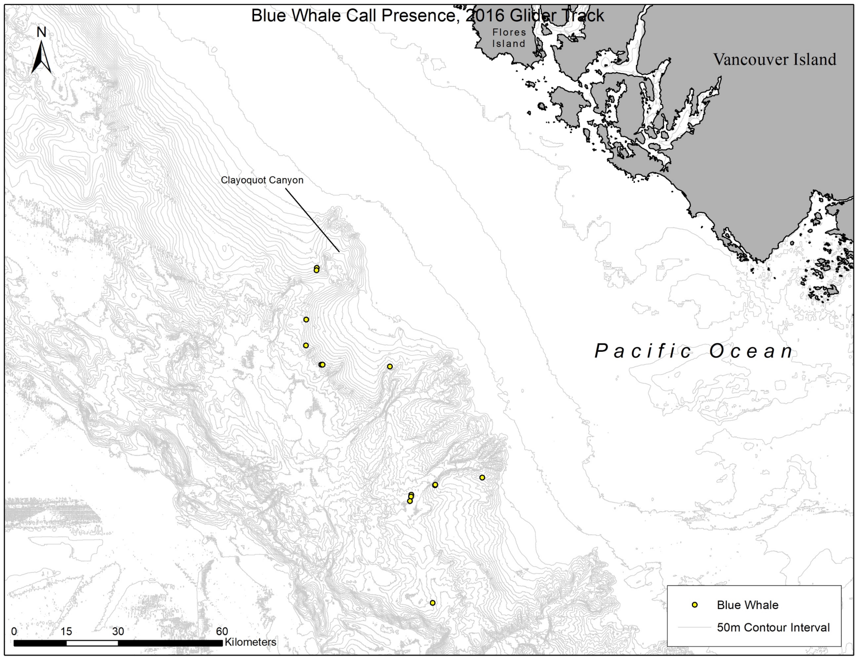

**Figure 2.2.8a**: Location of blue whale calls received from the 2016 deployment of the ocean glider.

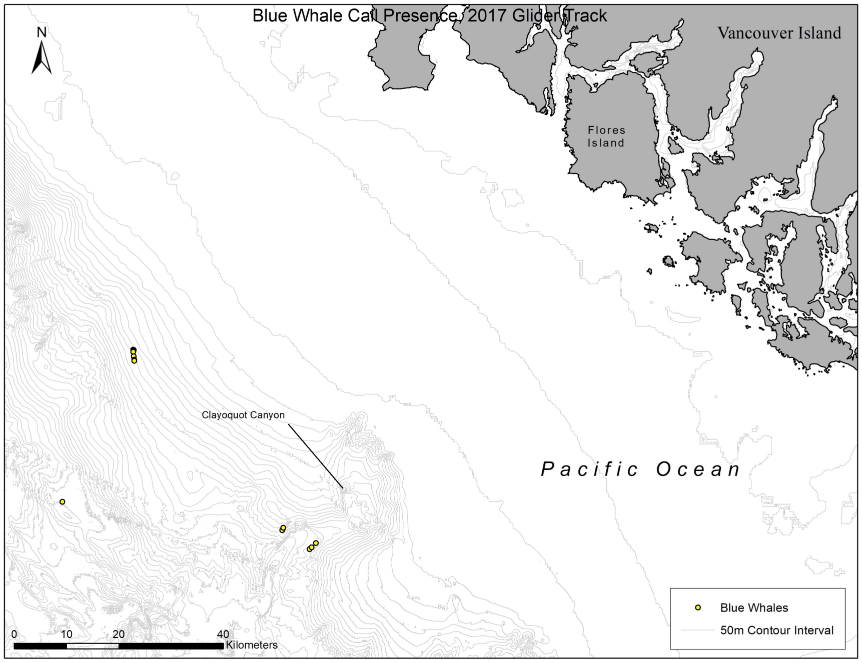

**Figure 2.2.8b**: Location of blue whale calls received from the 2017 deployment of the ocean glider.

*Sperm whales*

The 2017 deployment recorded sperm whale calls, all within a 2 hour period overnight on February 6-February 7, 2017. These calls were recorded in waters along the continental shelf break (Figure 2.2.9). At the location where calls were received, the water column average volume scattering strength was -58.23±2.07 dB re m^-1, with the strongest signals in the 100-150 m depth range. The frequencies of the calls employed suggest the signalling sperm whale is likely within 2 km of the glider (Watkins 1980).

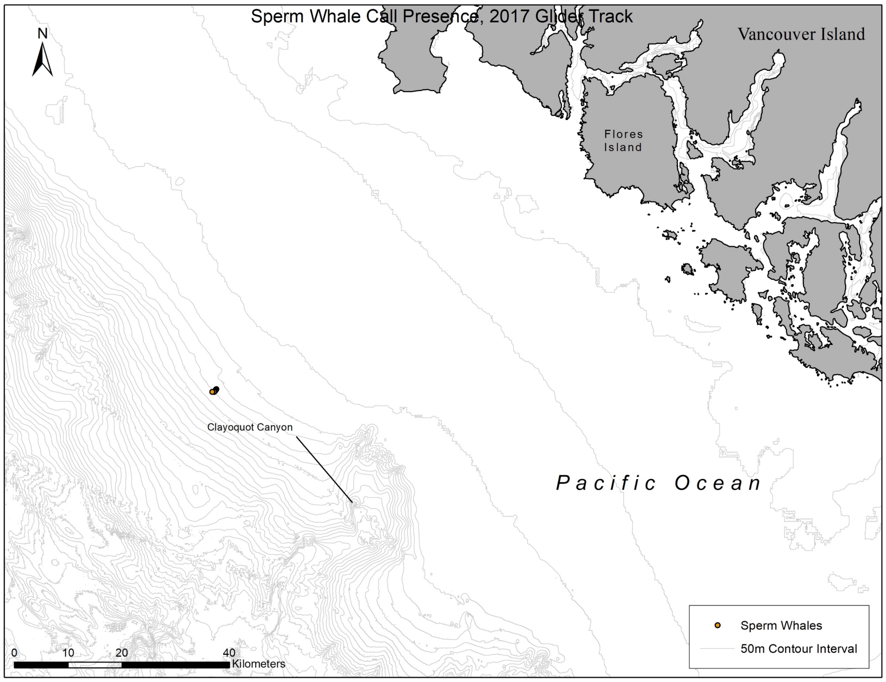

**Figure 2.2.9**: Location of sperm whale calls received from the 2017 deployment of the ocean glider.

*Sei, north Pacific right, and minke whales*

Calls resembling sei whale calls were heard in the 2016 deployment in small number, but they are difficult to definitively identify. The presence of these calls is discussed in more detail in Chapter 2.3. No minke or right whale calls were positively identified for either of the deployments.

*Backscatter, Structure and Soundscape*

My interpretation of whale habitat is based on three elements, measures of volume scattering strength indicating potential prey, water structure which influences prey productivity and distribution, and the ambient sound level. Although dive rate was slower than the 5-minute intervals used for whale call detection, the average volume scattering strengths were mapped to correspond to this schedule. Values were averaged over the full water column for each dive (to 200 m), as well as separated into 50 m depth increments to explore diurnal vertical migration

(DVM) of zooplankton. Many of the dives were in water exceeding the glider's depth limit (68.74% of pooled data). Water column-mean volume scattering strengths ranged from -82 dB to -32 dB re m^-1. The deployment in 2016, was during the spring transition from downwelling to upwelling (Chandler et al. 2017), and water column-mean volume scattering strengths values were stronger, suggesting there was greater prey presence and/or density during the transition phase than during the downwelling in 2017 (x̄=-62.71±0.01dB re m^-1 in 2016, x̄=-55.31±7.40 dB re m^-1 in 2017).

Average volume scattering strengths considering both deployments increased significantly in the 0-50m (Student's t(13862)=-16.895, p=<0.001) and 50-100 m (Welch's t(12179.983)=-3.863, p<0.001) depth bands, and decreased in the 100-150 m (Student's t(12132)=6.715, p<0.001) and 150-200 m bands at night (Welch's t(8782.696)=8.970, p<0.001) suggesting diurnal vertical migration of potential prey.

The study area is classified into three zones (Figure 2.2.1): continental shelf waters, surveying from the deployment site approximately 5nm from the coast to the shelf break, 50-180 m in depth; the shelf break which is steeply sloped and bathymetrically complex, from 180 m to 3,000 m deep, and the abyssal plain beyond the shelf break. Both glider deployments surveyed the first two zones for comparison. Average volume scattering strength values were significantly weaker past the shelf break in the upper 150m (0-50 m: Welch's t(6715.505)=11.088, p<0.001; 50-100 m: t(5237.873)=36.162, p<0.001; 100-150 m: t(4214.895)=26.164, p<0.001) with a pycnocline described around this depth (Howatt et al. 2018). Comparison between deployments begins to show the difference due to upwelling, with average volume scattering strengths in the upper 150 m of the water column increasing along the shelf break and in more coastal waters for 2016 (0-50 m: Student's t(8538)=10.083, p<0.001; 50-100 m: t(8397)=42.409, p<0.001; 100-150 m: Welch's t(2487.393)=38.770, p<0.001), whereas this trend is seen the full depth of glider dives in 2017 (Figure 2.2.12; 0-50 m: Welch's t(3665.737)=7.353, p<0.001; 50-100 m: t(2008.173)=22.256, p<0.001; 100-150 m: t(1643.288)=41.681, p<0.001; 150-200 m: t(665.315)=20.749, p<0.001). The results from the 2017 deployment show a stronger deference in in-shore and shelf-break volume scattering strengths, though this difference is observed in data from both years (Figure 2.2.10, 2.2.11)

Higher average volume scattering strengths are generally found in canyons and areas of complexity. The strongest signals were from Clayoquot Canyon, followed by Father Charles

Canyon to the south, and then an area of relief to the north of Clayoquot Canyon (for locations see Figure 2.2.1). This trend is present in both deployments, although average volume scattering strengths are greater in 2016 (Figure 2.2.10a,b). When considering depth bands through the water column, in 2016 the upper 50 m shows stronger returns in the canyons compared to the shelf break (2016: Welch's t(1845.987)=6.201, p<0.001), with then significantly decreased average volume scattering strengths within the canyon from 50 to 200 m (50-100 m: Welch's t(2020.998)=-4.652, p<0.001; 100-150 m: t(1910.438)=-7.433, p<0.001; 150-200 m: t(2327.392)=-7.460, p<0.001). This switch occurs in the 100-150 m band for 2017, with the surface 50 m not significantly different in- or outside of a canyon (0-50 m: Welch's t(1016.250)=1.317, p=0.188; 50-100 m: t(1806.038)=-9.884, p<0.001; 100-150 m: t(1135.827)=-4.875, p<0.001; 150-200 m: Student's t(3564)=3.347, p=0.001).This may again be indicative of the pycnocline (Howatt et al. 2018), zooplankton being entrained by oceeanic discontinuities such as halo- or thermoclines (Steele & Henderson 1992, Jónasdóttir et al. 2005) or possibly in diapause.

When considering longitude, measures from the 2016 deployment did not show a noticeable difference when crossing the shelf break, whereas the average volume scattering strengths from waters past the shelf break were lower than those from in-shore waters for 2017 (Figure 2.2.11a,b).

Salinity and temperature were significantly different between the continental shelf and the shelf break. Both salinity and temperature in the upper 20 m of the water column were significantly higher in the shelf break waters compared to shelf waters for 2016 (Welch's t(1873.388)=-13.376, p<0.001 and t(1581.544)=-23.410, p<0.001 respectively), whereas waters were cooler but still more saline in 2017 (Welch's t(2199.397)=2.666, p=0.008 and t(1596.277)=-26.598, p<0.001 respectively).

Just under 90% of both of the deployments recorded some form of vessel noise (2016: 89.72%, 2017: 88.83%). Indeed, Lloyds mirror curves (Urick 1983) were seen in spectrograms indicating vessels in very close proximity, if not overhead of the glider while surveying.

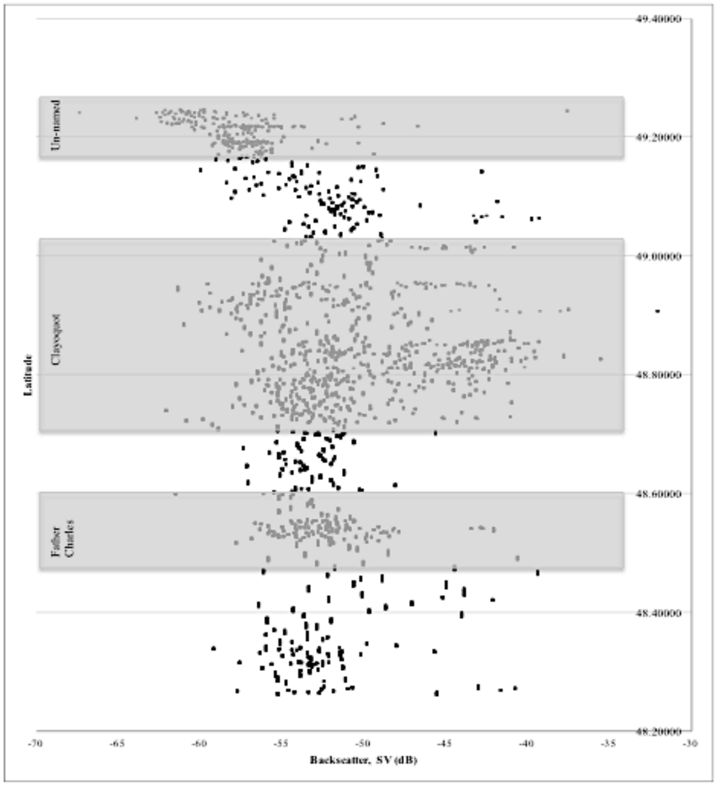

**Figure 2.2.10a:** Backscatter (water column average volume scattering strengths, Sv, dB re m^-1) values plotted against latitude for the 2016 deployment. Canyons and a bathymetric relief region (unnamed) are indicated.

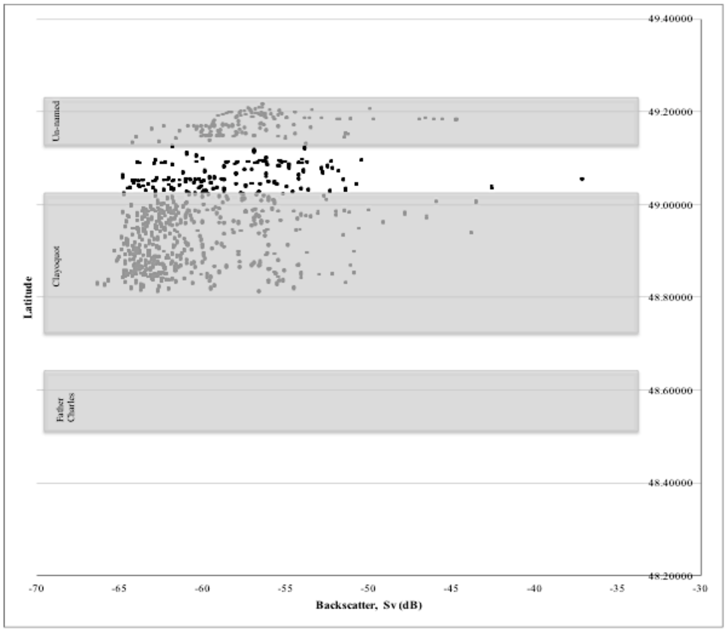

**Figure 2.2.10b:** Backscatter (water column average volume scattering strengths, Sv, dB re m^-1) values plotted against latitude for the 2017 deployment. Canyons and a bathymetric relief region (unnamed) are indicated.

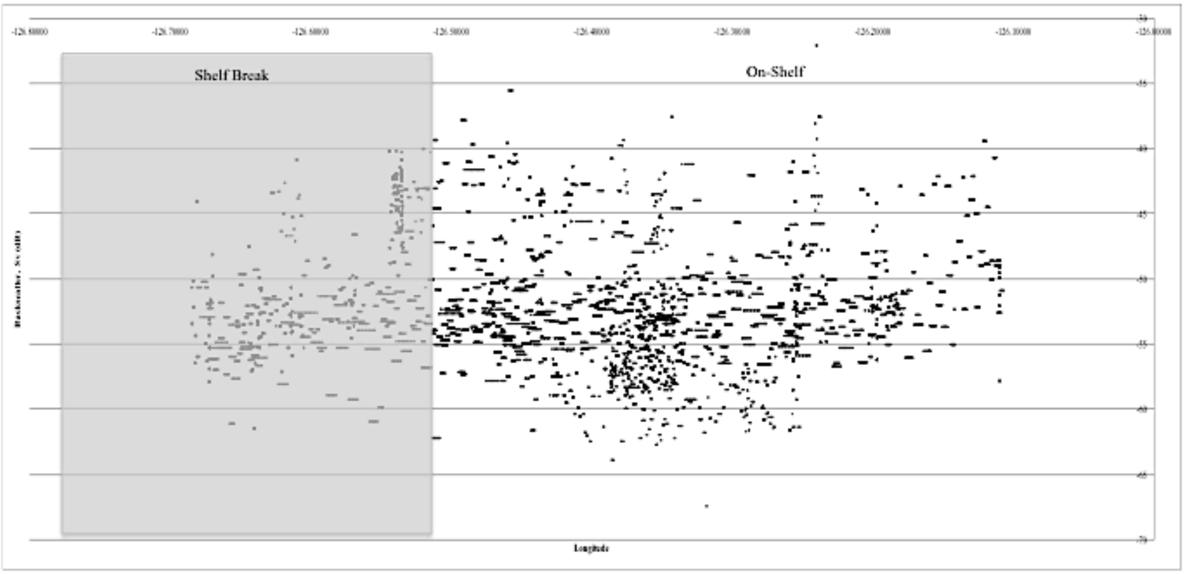

**Figure 2.2.11a:** Water column average backscatter (water column average volume scattering strengths, Sv, dB re m^-1) values plotted against longitude for 2016 deployment. Shelf break is marked.

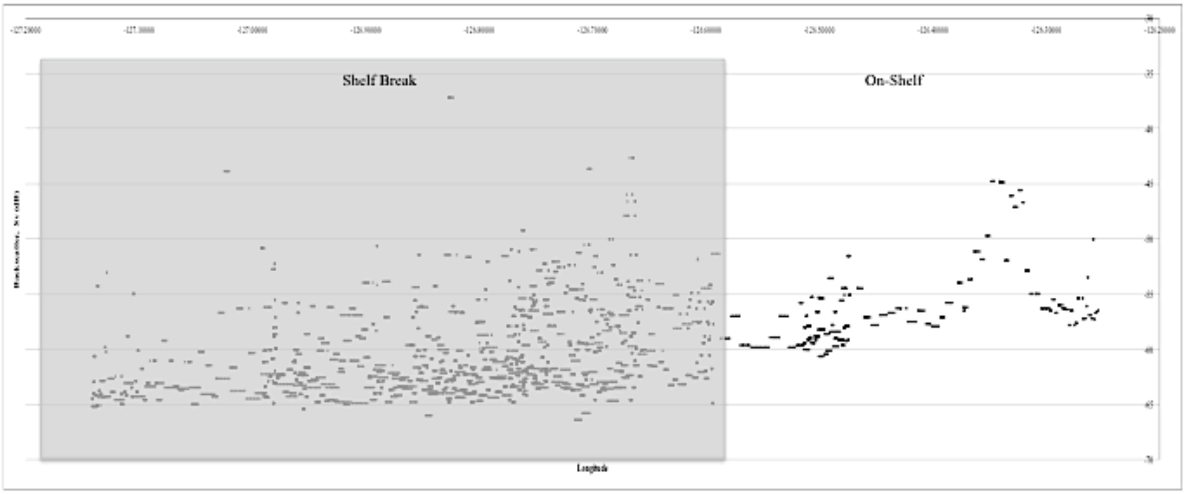

**Figure 2.2.11b:** Water column average backscatter (volume scattering strengths, Sv, dB re m^-1) values plotted against longitude for 2017 deployment. Shelf break is marked.

## Discussion

Information on whale distribution and abundance is integral to any plan aimed at population recovery. However, this information is lacking for whales inhabiting Canada's Pacific coast. This study reports the first use of PAM capable AUV in the waters off the west coast of

Vancouver Island, and can be a first step to re-establish the baselines of species presence and habitat use.

### *Whale calls*

Acoustic communication underlies group cohesion, social interaction, navigation, and foraging in cetaceans. In this study, vocalisations are a proxy for presence, and also suggest the behavioural state of the animal, as indicated by previous studies that employed visual observations or tag data concurrent with recordings.

The low number of gray whales calls in the recordings is due to the area and habitat surveyed. Gray whales are coastally focused, with their northward migration corridor usually within 8 km of shore (Poole 1984, Perryman et al. 2002, DeAngelis et al. 2011). Differences in presence and call numbers between the two deployments likely reflects the progression of the migration. Mid-March is the typical migration peak past the study site (Rannankari et al. 2018, Chapter 1.2, 1.3). The diurnal pattern in calling found here agrees with other PAM records of northward migrating gray whales (Guazzo et al. 2017, Rannankari et al. 2018).

Humpback whales were recorded in all areas. They have a diverse acoustic repertoire ranging from the lowest frequencies to approximately 6 kHz, lasting typically less than one second (Stimpert et al. 2011). The calls identified in this study are ‘social sounds’, produced during all life history events. At the time of the glider deployments, humpback whales are migrating off Vancouver Island in groups. Social sounds play a role in the composition and cohesion of these groups (Dunlop et al. 2008). The water column average volume scattering strengths taken coincident to calls suggest that humpback whales are moving through areas that support shoals of mesopelagic fish (Axenrot et al. 2009, Manik 2015), a common prey item,with a shift to both onshore and shelf break areas for 2016, matching areas of stronger scattering strengths.

Fin whales were recorded frequently during both deployments, but differed in call type (Chapter 2.4). The most common fin whale signal is its stereoptyped 20-Hz call, a downsweeping note that descends from about 25 to 18 Hz in about one second (Watkins et al. 1987, Edds 1988, Thompson et al. 1992, Hatch & Clark 2004). These calls were most frequent in 2017. Also, some of these 20-Hz calls heard in the 2017 deployment formed sequences of paired pulses with a ‘backbeat’ and stable inter-pulse interval (see Chapters 2.3, 2.4 for more details).

This type of vocal projection has been described as ‘song’ (see Širović et al. 2017), and is produced during the breeding season. It can last several hours and is believed to be produced only by males (Watkins et al. 1987, 2000, Croll et al. 2002, Hatch & Clark 2004, Delarue et al. 2009). Additional acoustic monitoring in waters of northern British Columbia reported fin whale calling at its peak from November to January, coinciding with the breeding season (Mizroch et al. 2009). These waters could function as breeding, and possible calving areas for fin whales (Chandler et al. 2015). The fin whale 40-Hz call dominates the 2016 recordings. It is less well characterised (Watkins 1981), but has been associated with groups, and has an apparent foraging function (Watkins 1981, Širović et al. 2013). While these calls are produced repeatedly they do not form a pattern (Watkins 1981).

Calls were typically recorded on the shelf break, however fin whales were also recorded while the glider surveyed on the continental shelf during 2017. Recordings from a static, bottom-stationed PAM system in 51 m water depth, 5nm from shore, for this same period has similar calls, though these may be propagated from the shelf break (See Chapter 2.3).

Diel variation in call rate has been noted for fin whales, tying this pattern to foraging driven by the prey’s DVM (Širović et al. 2013). The change of call rate as time progressed in the 2016 deployment may also be related to foraging, demonstrating the feeding-breeding dichotomy in acoustic behaviours seen in several baleen whale species (e.g. Clark 1983, Mellinger et al. 2007b, Baumgartner & Fratantoni 2008, Parsons et al. 2008, Parks et al. 2011, Vu et al. 2012).

Blue whale calls were recorded in the deepest waters, furthest from shore, and tied to the continental shelf break. Very little is known about the numbers or distribution of this species in the northeast Pacific. Catch records from Canadian whaling stations indicate their presence in waters ‘well offshore’ of Vancouver Island (Pike & MacAskie 1969, Rice 1974). Blue whale vocalisations extend into infrasonic frequencies, and can propagate sufficiently to retain contact with distant conspecifics (Payne & Webb 1971, Clark 1990). The calls heard here were predominantly D calls, linked to foraging (Oleson et al. 2007a,b). Previous studies also suggest a social role for D calls, with alternating call patterns between closely associated whales and greater production in groups (Thode et al. 2000, Berchok et al. 2006, Oleson et al. 2007b). Type B calls were also recorded, as well as by a stationary hydrophone positioned at the glider deployment site (see Chapter 2.3). The received amplitude of the calls suggests blue whales may be on the continental shelf or at the shelf break. There was no diurnal pattern, consistent with previous blue whale studies (Wiggins et al. 2005).

Sperm whale clicks were heard in the 2017 deployment most likely attributable to an individual foraging on the shelf break region. Only presence is noted in this study, with sightings (Palm, Pers. Comms.) and strandings of sperm whales a further confirmation of their presence.

A small number of possible sei whale calls were heard during the 2016 deployment, but are not discussed here (see Chapter 2.3). No calls were recorded for the north Pacific right whales. Both of these species, once abundant in the study area (Pike & MacAskie 1969), have only a handful of possible sightings since the end of whaling on the coast. The acoustic records show a similar trend, with identification of vocalisations usually tentative. Their existence in the eastern north Pacific is assumed, but their population number and range is unknown (Gregr et al. 2006).

These acoustic data fits into expected habitat use patterns. Gray whale movements are largely contained within the migration corridor. Humpback whales are common on the continental shelf, particularly in the spring (2016) deployment (Table 2.2.2, 2.2.3) when they are likely foraging. Increased calls at the shelf–break in winter (2017) suggest a shift offshore by humpback whales, either migrating or foraging. Fin and blue whale calls were prevalent in areas of greater bathymetric complexity along the shelf break and in canyons. This corroborates the observations of winter distributions of these whales in the northeast Atlantic, where these species are recorded in higher density on the outer margins of the continental shelf (Baines & Reichelt 2014). Modelling physical factors in conjunction with whaling data suggests that the shelf break zone was an ‘important area’ for blue, fin, sei and sperm whales (Gregr & Trites 2001).

This PAM data for the large whales in offshore waters is valuable. Acoustic surveys are a powerful means of locating and tracking whales, which can then be translated to presence and relative abundance on various scales (Clark & Ellison 1989, Thompson et al. 1992, Clark et al. 1996, Clark & Fristrup 1997, Clark & Charif 1998, Moore et al. 1998, Stafford et al. 1998, 1999). However, with this kind of data it is only possible to say that a whale is definitely present when there are calls recorded. The lack of calling does not necessarily translate to whale absence, just an absence in vocalising. Also, for many of the species discussed, the calling rate for each behavioral state is not well known. Therefore, it is difficult to establish if there is more than one signaling animal present. Repetition of glider studies in similar and different time periods may show a seasonal change in calling behaviours, lending support to the geographic, social or behavioural function of calls.

A whale call in itself has important caveats when inferring a behavioral or ecological context. Although calls are mapped as point data, previous studies show baleen whale vocalisations propagate over large distances. As our hydrophone is omnidirectional, each call should be represented by a buffered point. For each individual call, the source level, the received level, ambient noise, the depth of both the glider and water, as well as the water properties are required to formulate a sound propagation model, and so estimate the size of the buffer. This would then only give the likelihood of the call emanating from within a certain range. The estimation would rely on several assumptions, including that the source level is within certain levels and that the likelihood of detecting the call is the same in all directions. Indeed the detection range of blue and fin whale calls in certain conditions may extend into the thousands of square kilometers (Cummings & Thompson 1971, Payne & Webb 1971, Clark 1995, Stafford et al. 1998, 1999, Tyack & Clark 2000, Širović et al. 2007, Stafford et al. 2007, Simard et al. 2008, Clark et al. 2010, Delarue et al. 2013, Koot 2015).

### *Preyscape*

Measures of productivity and zooplankton biomass are typically higher in waters on the continental shelf, than offshore (Mackas & Sefton 1982, Harris et al. 2009). This is seen in the data of these deployments, where the volume scattering strength averaged over different portions of the watercolumn is stronger on the continental shelf than those from the shelf break (Figure 2.2.11).

The transition from a downwelling to upwelling state occurred during the 2016 glider deployment. This transition was earlier than average, although the strength of the upwelling was normal (Chandler et al. 2017, Gower & King 2017). Although the oceanographic conditions resemble a more spring-summer system, dominated by northerly winds and currents running equator-ward along the shelf break, the increased productivity that this brings is not captured in the preyscape measurements derived from measures taken by the echosounder. Productivity reaches a peak in March-April for coastal and offshore regions, followed by a lag time for the primary production to be assimilated by potential whale prey (Mackas & Sefton 1982, Harris et al. 2009). The effects of productivity and environmental variables on zooplankton are, however, typically studied on seasonal and longer time scales, with some of these seasonal differences seen between deployments when comparing spring (2016) and winter (2017) conditions (e.g. Roesler & Chelton 1987, Brinton & Townsend 2003, Rebstock 2003, Urmy & Horne 2016). No clear patterns were distinguished, although stronger average volume scattering strength measures were observed for 2016 compared to 2017, and at the shelf break for both deployments (Table 2.2.2, Figures 2.2.10, 2.2.11).

Canyons are biologically active regions that are thought to aggregate zooplankton (Hickey 1995, Mackas et al. 1997, Allen et al. 2001, Smith et al. 2010). This is suggested here with both glider deployments showing stronger volume scattering strengths in canyons rather than outside along the shelf break (Table 2.2.3). Also, these measures were stronger closer to the head of the canyon (Howatt et al. 2018). The possible link between calling and prey is seen here, where calling, primarily by fin whales, was less from inside canyons than the surrounding waters, possibly indicative of feeding.

The prey species composition in the study region differs by season, with the most abundant zooplankton species being *Oithona* spp., *Pseudocalanus* spp., *Metridia pacifica*, and increasingly towards offshore waters, primarily *Neocalanus* spp. (Goldblatt et al. 1999). These organisms aggregate at specific depths and locations. The data suggests that the oxygen concentrations (oxyclines) and pycnocline depths in the water column define the depths to which zooplankton migrate vertically (Howatt et al. 2018). This is also seen in the trends in average volume scattering strengths through the water column, which is generally stronger below 150 m. These measures may also be species in diapause over the winter, with torpid animals aggregating below the stable thermocline to prevent premature returns to the surface (Jónasdóttir et al. 2005).

Understanding how oceanic processes are tied to physical features would be advantageous for conservation and management. Comparisons between canyons in this area may be possible in the future to refine the idea of what makes these areas attractive to cetaceans. Bathymetric features are fixed over time and so can be more easily protected (Hyrenbach et al. 2000)

### *Oceanographic and habitat features*

Though not considered in depth in this study, the differing temperature and salinity profiles help describe ocean fronts. The GPCTD measured warmer, more saline waters along the continental shelf than along the shelf break. Thermo- and haloclines structure biomass and species distribution, albeit usually on a wider scale than those measured during glider deployments (Lefevre 1986, Sournia 1994). These larger scale ocean convergences (Polovina et al. 2001) are persistent in time and space and predictably occur with continental shelf breaks (Munk et al. 2003). Sea surface temperature, primary productivity, salinity and fronts do, however, show variation, and can change rapidly. This creates problems in protecting a region that has fluid features that may be short lived (Hyrnebach et al. 2000). Annotating the acoustics data with habitat and prey measures, cognizant of the disparity in scales at which this information is collected and the limitations of the data, creates a more detailed understanding of ecosystem function in offshore waters, and further research will provide baselines with which to assess change.

The presence of cetaceans does relate to oceanographic features and water mass characteristics, with environmental variables influential at fine to macro scales (Hamazaki 2002, Cotté et al. 2011, Torres et al. 2013, Torres 2017). Variation in water masses may present proximal and distal cues to animals seeking foraging areas, which I suggest Clayoquot Canyon and surrounding shelf break zones are for the large whales (Torres 2017). Indeed, Powell and Ohman (2015) suggest that physical gradients alone could be used by mobile predators such as whales to locate prey concentrations. Using CTD measures to locate the conditions that symbolize processes that are important to these whales is a preliminary method to outline habitat units. However, making the link between whale presence and the habitat/prey conditions must be done on the appropriate scales and must consider the high potential for empty habitat given whale populations size and distribution. The measures of backscatter, as a proxy for prey, and oceanographic conditions, that could drive prey presence, are measured on fine temporal and spatial scales. This may be one stream of the multi-sensory data that large whales integrate when assessing habitat quality.

## Conclusions

The use of ocean gliders as surveying tools affords a connection between the coastal and open oceans, as the deployments in this study show. In addition to the PAM capabilities, to locate whale presence in deep-coastal and offshore waters, monitoring oceanic conditions such as productivity blooms, ocean fronts, and shelf break features allows us to analyse whale habitat and ask broader ecological and conservation questions. Notations of vessel noise in the PAM recordings is a preliminary means of establish the use of this area by vessel traffic, and in so doing describe the potential acoustic disturbance to whales using this area. The oceanographic measures allow us to track changes in potential whale habitat, here comparing spring/upwelling (2016) and winter/downwelling (2017) regimes. This may translate into changes in prey abundance and, thus, whales. The use of the area may also differ, for example switching from foraging in the spring to mating behaviours overwinter (further discussed in Chapters 2.3, 2.4) The results from this study highlight the presence of rare and endangered species in the offshore waters of Vancouver Island, and their use of these areas for important life history events. This work is a first step in describing offshore habitat use by whales, which may lead to delineating habitat units important to large whale species. The focus on canyons provides a tangible habitat unit that could be protected to support whale population recovery.

## 2.3. The presence of large whale species in Clayoquot Sound and its offshore waters

### Preface

In its very simplest form, passive acoustic monitoring (PAM) documents the presence of cetacean species in an area over time. This sets a minimum indicator of presence, with only animals vocalising within the detection radius of the recorder captured. That said, PAM methods allow for monitoring at times and locations that were previously not possible, and done regardless of weather or visibility conditions (Moore et al. 2006). Here, I combine results from both stationary and mobile PAM recorders for a first look with this combinations of instruments at the presence of large baleen and toothed whale species in the deeper-coastal and offshore waters of Clayoquot Sound over time. Although presence has been noted anecdotally (Palm, Pers. Comms.), little dedicated time or effort has been given to survey for whale presence in offshore waters. The use of acoustics, as outlined here, also supports research for rare and endangered species, and the re-establishment of baselines of presence and habitat use for these large whale species as populations try to recover from large scale removals by whaling. Here, calls are a proxy for presence, with call type, and time and position of call detection informative as to the use of the offshore waters of Pacific Canada.

### References

Moore, S.E., Stafford, K.M., Mellinger, D.K., Hildebrand, J.A. 2006. Listening for large whales in offshore waters of Alaska. *BioScience*. 56:49–55.

## The presence of large whale species in Clayoquot Sound and its offshore waters

### Introduction

Whales were decimated by whaling in the north-east Pacific. Though some species, like the eastern Pacific gray (*Eschrichtius robustus*) and the humpback whale (*Megaptera novaeangliae*), have made population recoveries, for many others the severe reduction in numbers has had a lasting impact, and populations remain well below their pre-whaling numbers (Clapham et al. 1999, Baker & Clapham 2004, Thomas et al. 2016). Here I discuss the presence of large whale species in Clayoquot Sound, on the west coast of Vancouver Island, in reference to their historic use of this area, using passive acoustic monitoring (PAM) as survey tools. In particular, fin (*Balaenoptera physalus)*, blue (*Balaenoptera musculus*), and sperm whales (*Physeter macrocephalus*), and recordings tentatively identified as sei whales (*Balaenoptera borealis*) are discussed, with the current population size and habitat use for these species unknown. This is further hindered by them predominantly inhabiting deep-coastal, continental shelf-break, or offshore waters. The current status of these species is poorly known, with acoustic data collectors perhaps the best tools for filling gaps in our knowledge of these whale populations.

Fin whales were once the most prevalent baleen whale species on the British Columbia coast, but whaling reduced them to a possible minimum of 2,316 individuals in the northeast Pacific (Pike & MacAskie 1969, Oshumi & Wada 1974, Gregr et al. 2006). Similar removals were seen for other large baleen whale species, with sei whales targeted as a substitute for fin and blue whales when catch number diminished. Now only a remnant north Pacific population is assumed, with very few confirmed sightings. The immediate requirements are to re-establish knowledge on their presence and patterns of distribution, as well as the importance of specific areas to feeding, weaning, breeding or migration. Recordings taken from stationary and mobile PAM systems in deep-coastal, continental shelf, shelf-break and deep shelf-break regions of Clayoquot Sound and adjacent waters will first be examined for whale vocalisations, as a simple cue to presence. Call type and timing may provide further clues to the use of the area, or behavioural state of the signaller. This will acoustically map the presence of species from coastal to offshore waters in the Canadian Pacific, and add to the little existing knowledge we have for larger species use of waters of or past the shelf-break zone. Although here I report on surveys with a few instruments over a limited area, I hope to demonstrate the potential for PAM techniques in future surveillance programs mapping the large whale ecosystems of Canada's Pacific coast and what they can add to traditional survey techniques.

## Methods

Recordings were taken from two stationary recording systems. An Autonomous Multichannel Acoustic Recorder (AMAR JASCO G3A) with a calibrated hydrophone (sensitivity -165 dB re 1 V/µPa, effective 5 Hz-150 kHz, gain of 6 dB; GeoSpectrum M8E-132) was deployed on the ocean floor in 51 m of water approximately 5 nm offshore (49.21028, -126.24667, Figure 2.3.1). The AMAR recorded constantly up to 8 kHz between March 6-May 5, 2016 and between September 27, 2016 - January 25, 2017. The second, an Ocean Sonics icListen AF Hydrophone 2504 (sensitivity -170 dB re 1 V/ µPa, effective 10 Hz-200 kHz, gain of 6 dB), named 'Bullseye', was stationed by Ocean Networks Canada in a deep shelf-break location, approximately 45 nm from shore (48.6706, -126.8485, Figure 2.3.1). This is a cabled device, with recordings between March 20-April 10, 2016 used here. These recordings are constant, up to 16 kHz. A third recorder, a mobile platform, moved between these two static recorders. Ocean glider borne recorders were deployed from the AMAR deployment location to survey deep-coastal and shelf-break zones between March 17-April 16, 2016 and January 30-February 18, 2017 (Figure 2.3.1, Chapter 2.2). The ocean glider was equipped with a low frequency (>1000Hz) recording system (Digital Acoustic Monitor, DMON, Woods Hole Oceanographic Institute) that recorded constantly throughout the deployments.

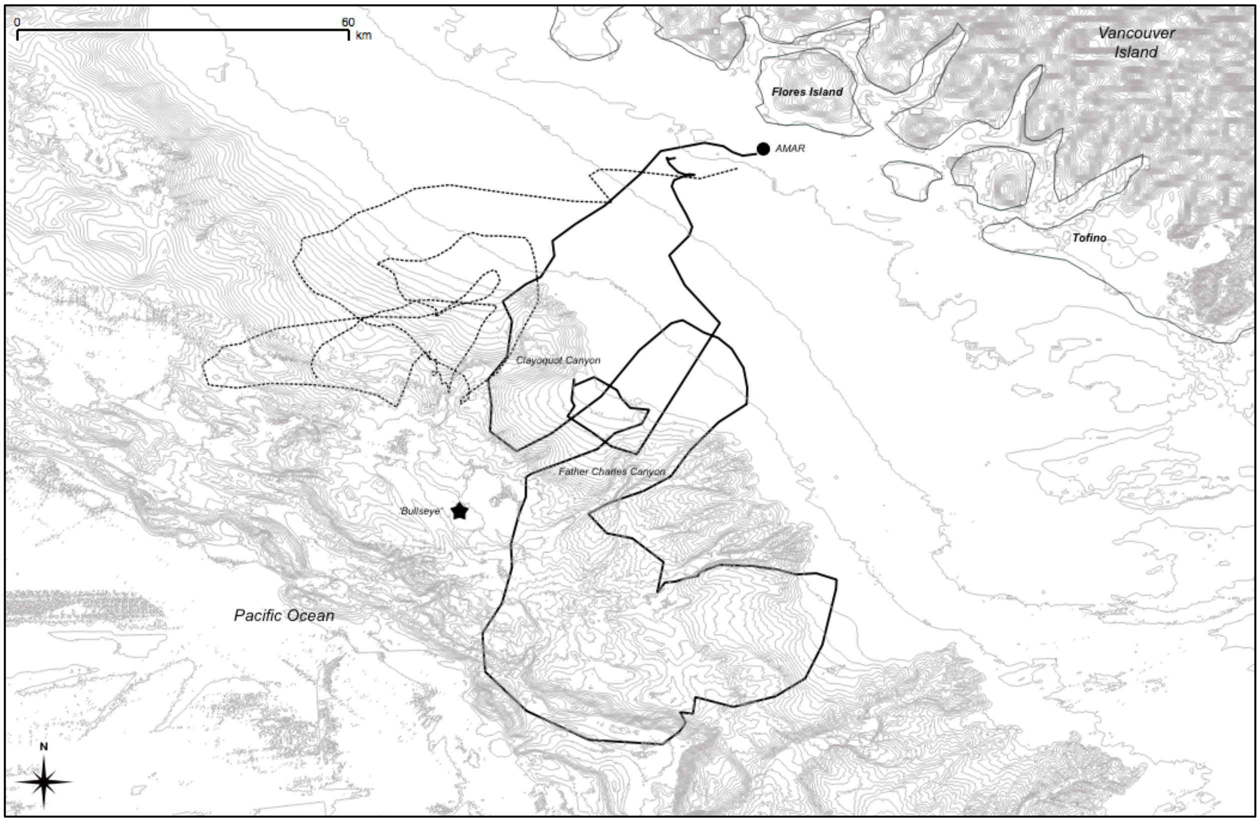

**Figure 2.3.1:** Deployment site of AMAR (circle, 49.21028, -126.24667) and icListen 'Bullseye' (star, 48.6706, -126.8485) passive acoustic recorders, and routes of glider surveys. The solid line is the 2016 glider deployment and dashed line is the 2017 glider deployment.

Recordings were visually and aurally inspected manually through the generation of spectrograms (256-point Hann window 1 s FFT with 50% overlap) in Raven Pro Interactive software. The mobile and deep shelf-break data were analysed in their entirety. The AMAR deployments were inspected for every fifth day of the deployment period (20%), and at times when an automated detector indicated the presence of a species of interest, specifically the presence of blue, fin, or sperm whales (Mouy et al. 2009). Call presence was noted for all species, with call number given for gray, fin, blue and sei whales, with the full characterisation of these calls possible from all recorders. Whale calls were identified and classified by making reference to previous acoustic studies. For fin whales descriptive and spectrogram comparisons were made for the 20-Hz (Watkins et al. 1987, Edds 1988, Thompson et al. 1992, Hatch & Clark 2004) and 40-Hz calls (Širović et al. 2013); for blue whales, calls from the Pacific are A, B, A-B, C and D type (Cummings & Thompson 1994, Širović et al. 2004, 2007, Stafford et al. 1998 1999, 2005, Mellinger & Clark 2003, Rankin et al. 2005), sei whale downsweeps (McDonald et al. 2005, Rankin and Barlow 2007, Baumgartner et al. 2008, Baumgartner & Mussoline 2011), and sperm whale clicks (Gero et al. 2016).

## Results

Calls for gray, killer (*Orcinus orca*), humpback, fin, blue, sperm and possibly sei whales were found on the recordings from the PAM sensors (see Appendix for example spectograms). The proportion of each species presence differed between receivers when recording the same period (March 17-April 16, 2016): gray and killer whale calls were almost only found on the deep-coastal AMAR, humpback whale calls were found predominantly from recordings made on the continental shelf and inshore waters, and fin, blue, and sperm whales were found in the deepest waters, and dominated the recordings made at the deep shelf-break location (Table 2.3.1).

**Table 2.3.1:** Proportion of calls (%) heard per species by each recorder during the period March 17-April, 2016. Deep-coastal is the AMAR system; on-off, mobile is the ocean glider; deep shelf-break is the icListen system, 'Bullseye'. Species are: gray (*Eschrichtius robustus*), killer (*Orcinus orca,* both resident and Bigg's ecotype), humpback (*Megaptera novaeangliae*), fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sperm (*Physeter macrocephalus*) and sei whales (*Balaenoptera borealis*), and dolphin species (delphind sp.)

| Species: | gray | killer | humpback | fin | blue | sperm | sei | delphind sp. |
|---|---|---|---|---|---|---|---|---|
| Deep-coastal, static | 62.85 | 9.91 | 14.55 | 0.93 | 0.00 | 0.00 | 0.62 | 0.00 |
| On-off shelf, mobile | 2.42 | 0.00 | 14.92 | 20.70 | 0.27 | 0.00 | 0.40 | 0.00 |
| Deep shelf-break, static | 0.00 | 0.00 | 6.82 | 35.04 | 3.22 | 22.16 | 0.95 | 2.84 |

The prevalence and type of calls differed over time (Figure 2.3.2). Both 20-Hz and 40-Hz fin whale calls were present, with the latter dominant in the 2016, spring deployment and 20-Hz calls dominant in the 2017 deployment. Consistent inter-pulse intervals between calls suggested fin whale song (Watkins et al. 1987, McDonald & Fox 1999, Clark & Gagnon 2002, Clark et al. 2002, Croll et al. 2002, Delarue et al. 2013, Oleson et al. 2014, (see Appendix for example spectograms) in a proportion (~12%) of the 2017 winter deployment calls (see Chapter 2.4). A similar temporal separation in call type use was heard for blue whales, with D calls, thought to be tied to foraging (Oleson et al. 2007a), more prevalent in the 2016 deployment (Figure 2.3.2). Delphinid species, most likely Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), were heard only in recordings from the icListen 'Bullseye' in the deep shelf-break location (Figure 2.3.2).

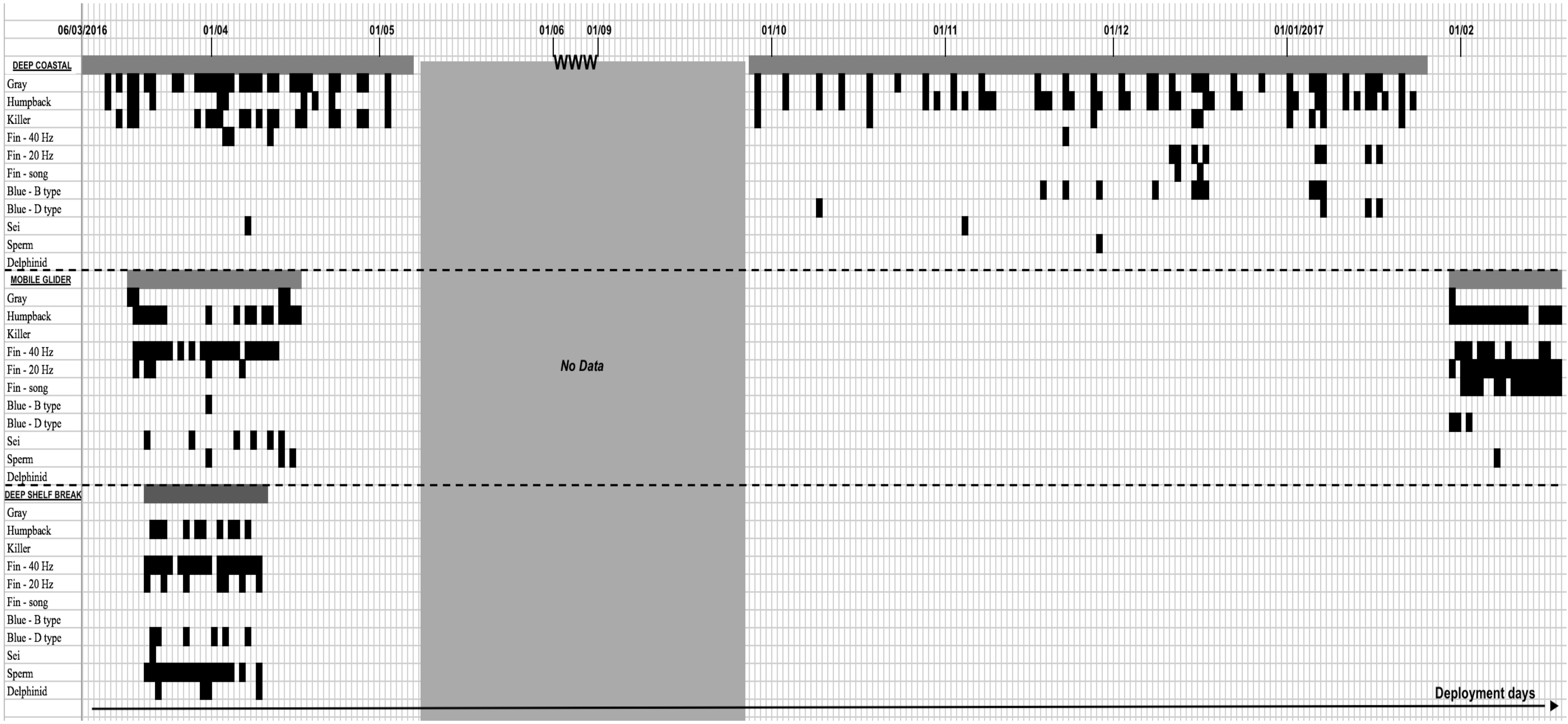

**Figure 2.3.2:** Call presence over time, marking presence by species and type. Deployment periods of each recording system (Deep-coastal AMAR system, mobile ocean glider, and deep shelf-break icListen system, 'Bullseye') are marked in grey and call presence marked in black. Presence is marked by day throughout the deployment. Species are: gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), killer (*Orca orcinus,* both resident and Bigg's ecotype), fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sperm (*Physeter macrocephalus*) and sei whales (*Balaenoptera borealis*), and dolphin species (delphind sp.). The presence of different call types have been displayed for fin (40-Hz, 20-Hz and song patterns) and blue whales (B and D type).

## Discussion

Recordings in the deep-coastal locations were dominated by migrating gray whales, with killer and humpback whale calls also present. The deep shelf-break recorder demonstrated none of these species, but indicated the presence of fin, blue and sperm whales. The mobile ocean glider represents a transition between these two zones in both its survey route and the calls noted (Figure 2.3.1, Table 2.3.1). The dominant calls heard in coastal recordings were those tied to travelling behaviours of gray whales (Burnham et al. 2018). Humpback whale calls were approximately equal on the deep-coast and glider recording, with social calls (Stimpert et al. 2011) heard. The presence of fin, blue, sperm and sei whales in the recordings are of greater interest as their seasonal movements, migrations routes, and general life histories are less well described (Lockyer 1984, Mizroch et al. 2009, Simon et al. 2010).

Fin whales utilise a short-duration, frequency modulated, stereotypic 20-Hz call, that has been noted in all ocean basins (Watkins 1981, Watkins et al. 1987, Edds 1988, Thompson et al. 1992, Clark & Fristrup 1997, Clark & Charif 1998, Watkins et al. 2000, Hatch & Clark 2004, Širović et al. 2004, Castellote et al. 2012, Delarue et al. 2013, Oleson et al. 2014). This call type dominated calls heard between December and February, and is believed to form the basis of conspecific communications, with also a likely role in navigation or prey localisation (Patterson & Hamilton 1964, McDonald et al. 1995, Clark & Ellison 2004). Song sequences, found in recordings made from fall to spring, suggest the presence of breeding and calving in the offshore waters of Clayoquot Sound. The use of 40-Hz calls is less well defined. Its use is less well understood, but has been attributed to social calls within groups, and during foraging (Watkins 1981, Edds 1988, Širović et al. 2013). It was found in spring recordings, and in lesser numbers than the 20 Hz call. The temporal separation of the use of these call types suggests a change in the prevailing behavioural state and/or habitat use (see Chapter 2.4 for more discussion).

Similar call patterns as those described for the fin whale were found also for blue whales, although far fewer blue whale calls were recorded (Table 2.3.1, Figure 2.3.2). Calls were most present on the deep shelf-break recorder, and were recorded from the furthest offshore areas that the gliders surveyed. Tonal call type B, tied to travelling and song are more frequently heard in the winter recordings (Oleson et al. 2007a,b), whereas downsweeping D type calls usually correlated with foraging (Oleson et al. 2007a,b, Calambokidis et al. 2008, Akamatsu et al. 2013) were present in recordings from January to late March. Blue whales feed in mid-to high-latitudes throughout the summer and fall in areas of upwelling and prey aggregation (Miller 2012), moving to lower latitudes when prey becomes unavailable in the winter (Clapham et al. 1999). They have previously been noted off the coast of Vancouver Island from the late summer and through the winter (Burtenshaw et al. 2004), which agrees with the recordings from this study. As with fin whales, blue whale migrations are not well defined, and so it is possible that they are present in the offshore waters of Clayoquot Sound year-round (Baines & Reichelt 2014).

Historically common in the north Pacific, but heavily targeted to substitute for fin and blue whale catch, the size and range of the remnant sei whale population in the north Pacific is unknown (Gregr et al. 2006). Much of what we do know is derived from whaling records, or comparisons to other regions. They are thought to typically inhabit deeper waters and shelf-break areas, and zones of upwelling, mixing or dynamic features in the water properties, such as eddies, that would presumably aid prey capture (Nasu 1966, Gregr & Trites 2001, COSEWIC 2003, Gregr et al. 2006, Nichol & Ford 2011). Little is confirmed for their vocal repertoire for the Pacific, and so recordings taken in close proximity to sei whales from other regions (Thompson et al. 1979, Knowlton et al. 1991, Stafford et al. 1999, McDonald et al. 2005, Rankin & Barlow 2007, Baumgartner et al. 2008) have guided the identification of calls, call type and vocal behaviours in this study, albeit tentative. The calls heard here add to those noted by previous studies (Ford et al. 2010), creating an acoustic record of presence. Calls resembling feeding calls described by Rankin and Barlow (2007) and Baumgartner et al. (2008) were heard on both mobile and stationary recorders, all after the date of transition from a downwelling to an upwelling dominated oceanic system in the spring (Chandler et al. 2017, Gower & King 2017). This suggests that the productive waters of Vancouver Island (Mackas & Galbraith 1992) are still used by foraging sei whales.

The continental shelf and shelf-break region is also used by foraging sperm whales. The vocalisations on our recordings are foraging clicks, employed presumably during feeding dives. The lower frequency components of the call (<4 kHz) is most audible within 2 km of the signalling whale (Watkins 1980). The presence of sperm whale clicks on the AMAR recordings (Figure 2.3.2), and this shorter propagation distance suggests that they do hunt in waters on the continental shelf. However, the majority of sperm whale calls were recorded on the deep shelf-break recorder, suggesting that feeding is predominantly in this zone and in offshore waters.

These recordings add to anecdotal sightings from offshore surveys (R. Palm, Pers. Comms.) and stranding records that confirm the presence of sperm whales in this area.

Dephinid species were heard on the deep shelf-break recorder only, with this the only system capable of recording into the high frequencies of their vocalisations. It is most likely that these calls are from Pacific white-sided dolphins given the call structure but, but may also be from northern right whale (*Lisodelphis borealis*) or possibly Risso's dolphins (*Grampus griseus*) or perhaps offshore killer whales (Soldevilla et al. 2008, Henderson et al. 2011).

The use of acoustics is an effective means by which to mark species occurrence in time and space. The results shown here represent the minimum presence of whale species in Clayoquot Sound and its offshore waters. Although a good proxy for presence, we remain cognizant of several caveats of acoustic data. The first is that the absence of calling does not mean an absence in whales. Although some studies have used vocalising data to estimate number or demographics of calling individuals in an area (McCordic et al. 2016), the discussions here do not make any inference about the number of whales present when calls are heard, using vocalisations just as a marker of at least one individual of that species within an area. The relative presence of calls may be representative of the number of whales present, or be more a reflection of the social, geographical, or behavioural context of the calling. For example a breeding-feeding dichotomy has been identified in baleen whales where calling is much reduced to focus on prey capture, compared to mating activities (Clark 1983, Mellinger et al. 2007b, Baumgartner & Fratantoni 2008, Parsons et al. 2008, Parks et al. 2011, Vu et al. 2012).

The second factor to keep in mind is that the received location of the call, either by static or mobile recorders, is not necessarily the position of the calling whale. Indeed, the low frequency calls employed particularly by the large baleen whales can propagate over large distances (Payne and Webb 1971). This contrasts with the ondontocete species, whose calls propagate much less due to the higher frequencies employed. Using an array of recorders with each receiver positioned in a different zone (coastal, continental shelf, shelf-break), as in this study, allows the comparison of the relative presence of species calls in these areas. The results (Table 2.3.1) hint at niche partitioning between species in their use of habitat, with the largest whale species most prevalent in the deeper offshore waters, and more coastally-focussed species such as gray whale and resident and Bigg's killer whales found only on the inshore AMAR recorder or when the glider was surveying closest to shore.

The call type and timing give clues as to the use of the area. Increased knowledge of call repertoire could lead to the ability to locate and track signalling individuals. If a PAM array is employed we could identify stocks or population sub-groups from dialects or patterns in calling, for example fin whale song (Širović et al. 2017). As well we can determine seasonal distributions and patterns of relative abundance (Clark & Ellison 1989, Thompson et al. 1992, Clark et al. 1996, Clark & Fristrup 1997, Clark & Charif 1998, Moore et al. 1998, Stafford et al. 1998, 1999). Acoustics can also be used as an indicator for habitat change, whereby prey abundance or climate change may stimulate altered distribution or vocalization patterns (e.g. MacLeod et al. 2007, Wright 2009, Pace et al. 2015).

This work is explorative and aimed at adding to survey efforts for large whale species, particularly for those that are rare and endangered. If we can develop firmer inferences for a behavioural or social context to calling, we can begin to identify areas of importance to these species, which should be afforded protection as a means to support population recovery. Species are trying to recover into a much changed ocean, with altered oceanic regimes, increased vessel traffic, and heightened acoustic pollution. This makes the current uncertainty on species population size and habitat use more problematic when trying to put in place suitable management actions to aid recovery.

# Appendix

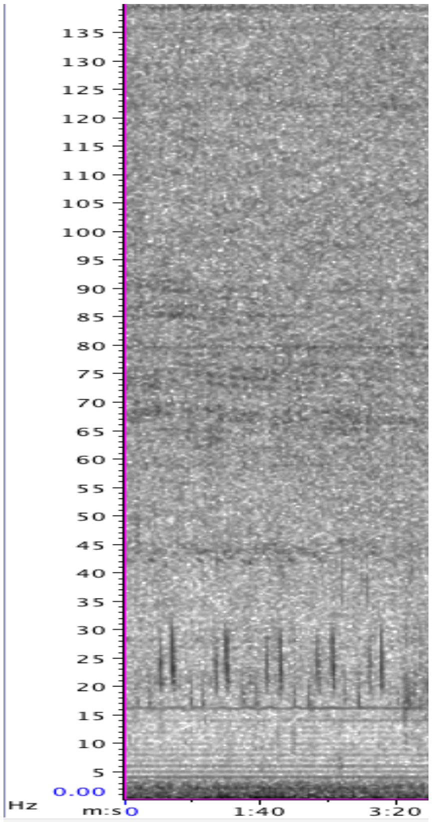

**Figure A.2.3.1**: Example of paired fin whale calls.

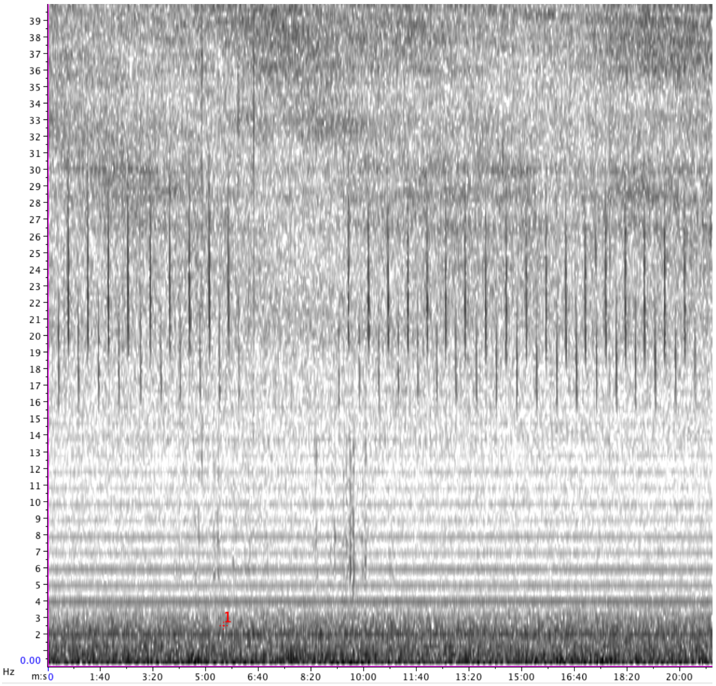

**Figure A.2.3.2:** Example of fin whale doublet song.

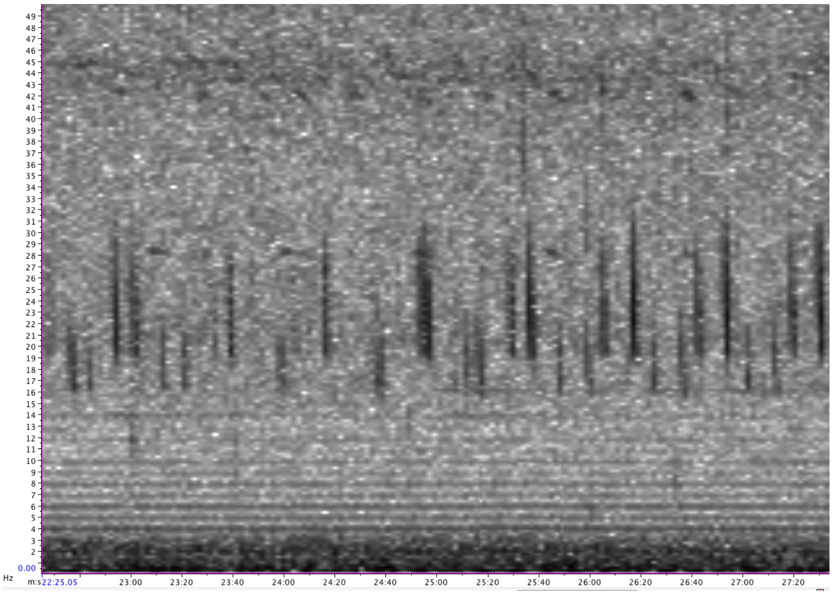

**Figure A.2.3.3:** Example of fin whale doublet song, with backbeat and 20-Hz pulse alternating. Blue whale B call also present.

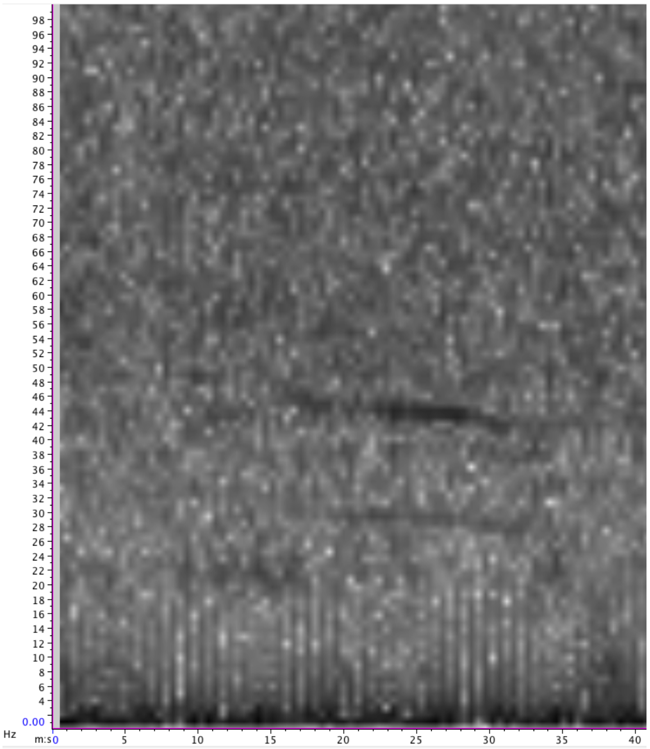

**Figure A.2.3.4:** Example of blue whale B call.

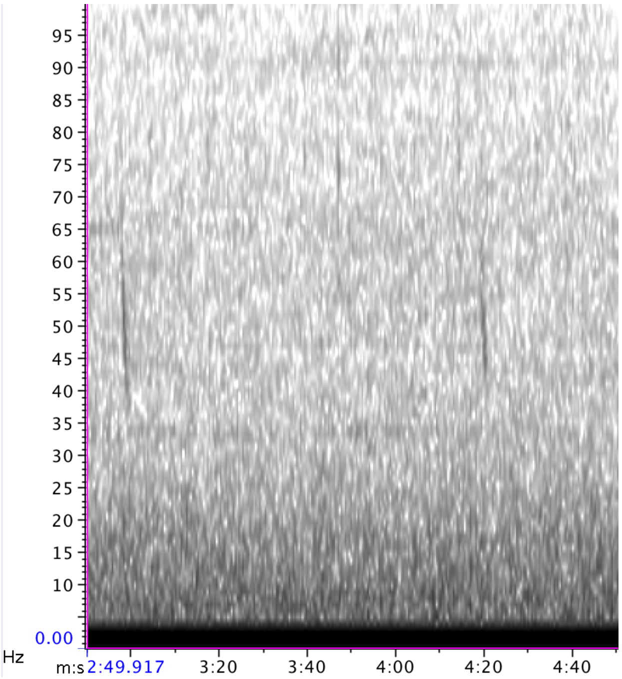

**Figure A.2.3.5:** Example of blue whale D call.

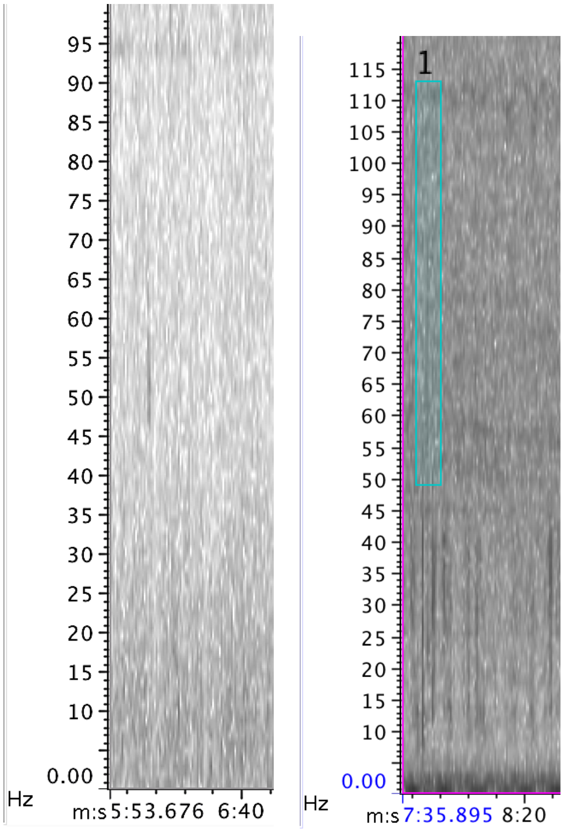

**Figure A.2.3.6:** Example of possible sei whale call. Call on the left recorded April 13, 2015 and call on right recorded April 8, 2016. In this case call is highlighted in turquoise as it is faint compared to ambient noise.

## 2.4. Variation in fin whale calling in Clayoquot Sound and its offshore waters

### Preface

This chapter presents a discussion of the fin whale (*Balaenoptera physalus*) call types heard during passive acoustic monitoring (PAM) recordings made in deep-coastal waters and offshore regions of Clayoquot Sound. Fin whales were one of several baleen whales to see large population reductions as a result of whaling, with its presence, abundance, habitat use, and seasonal patterns in Pacific Canada ill-described (Mizroch et al. 2009). In the first instance, calls act as a marker for presence. The call type employed is a hint towards the population group membership of the caller (Širović et al. et al. 2017), or behaviour, or context of calling (Oleson et al. 2007a,b, Širović et al. 2013, 2017).

Previous Chapters (Chapters 1.2, 1.3, 1.5) have outlined the gray whale calling repertoire, with descriptions of call type and patterns of use dependent on context. Although not all baleen whales vocalising behaviours are well defined (Gedamke et al. 2001), it is believed that they too adapt their acoustics use to varying situations. Here the changes in calling behaviours over time may represent altered behavioural state or use of habitat, with this the first discussion of that kind for fin whales in waters off the west coast of Vancouver Island. This short analysis provides an example of what may be accomplished with PAM techniques.

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## Variation in fin whale calling in Clayoquot Sound and its offshore waters

Baleen whales use refined acoustic systems for many life processes. At its simplest, passive acoustic monitoring (PAM) can mark species presence over time and space, using call presence as an indicator of whale presence. The type of call, its timing, and location can be indicative of habitat use, as different vocalizations are employed for communication, wayfinding and prey location (Norris 1969, Payne & Webb 1971, Oleson et al. 2007b, Torres 2017). More nuanced vocal patterns display group membership (Baumgartner et al. 2008), coordinate conspecifics (Thompson et al. 1986, Edds-Walton 1997, Cerchio & Dahlheim 2001, Parks et al. 2014), or are part of sexual displays (Clapham 1996, Oleson et al. 2007a).

Fin whales (*Balaenoptera physalus*) were one of the most common species on the British Columbia coast (Pike & MacAskie 1969), but were severely depleted by whaling. Surveys have resulted in few sightings, and the current population and habitat use in the Canadian Pacific is uncertain (COSEWIC 2005). Acoustic monitoring can supplement vessel-based surveys to form a clearer picture of habitat use patterns.

Fin whales employ various short duration, frequency-modulated calls in the low to infrasonic frequencies (Watkins 1981, Watkins et al. 1987, Thompson et al. 1992, Širović et al. 2007). The 20-Hz and 40-Hz pulse call types are the most commonly described,. The 20-Hz pulse is the best characterized, and has been attributed to fin whales in all ocean basins (Oleson et al. 2014). It is a downsweep from approximately 25 Hz to 18 Hz of about a one second duration (Watkins 1981, Watkins et al. 1987, Edds 1988, Thompson et al. 1992). It may have a role in conspecific communications, or navigational cues. The 20-Hz pulses have also been noted to form repetitive sequences, whereby the down-swept pulses form patterned doublet or triplet call groupings, with stable inter-note (INI) and inter-pulse (IPI) intervals (Watkins et al. 1987, Clark et al. 2002, Croll et al. 2002, Delarue et al. 2013, Oleson et al. 2014, Koot 2015). In the northeastern Pacific, four distinct song types have been identified, with the short-doublet song form the most common (Koot 2015, Širović et al. 2017). Alternating 'classic' 20-Hz (Koot 2015) and 'backbeat' notes form the repeating unit, the backbeat note may act as a marker to song presence (Clark & Gagnon 2002).

The 40-Hz call is also used regularly by fin whales, and has been attributed to calling during social interaction and foraging (Watkins 1981). It is a downsweeping note, similar to the 20-Hz note, but is less well described, and does not form repetitive sequences.

Here, I use PAM techniques to explore the fin whale presence in deep-coastal and offshore waters of Clayoquot Sound, off the west coast of Vancouver Island. The presence of calls in the first instance will mark the presence of fin whales in the area of interest. Call repertoire identifies the principal behaviours undertaken at that time and place. The use of both a moored and mobile PAM system allows acoustic surveillance over extended times and space. This will add to efforts to ascertain distribution, habitat use, and abundance information of fin whales in the northeastern Pacific.

Recordings were made from a deep-coastal site by an Autonomous Multichannel Acoustic Recorder (AMAR, JASCO G3A). This system was fitted with a calibrated, omnidirectional hydrophone (GeoSpectrum M8E-132, sensitivity of -165 dB re 1 V/ µPa, effective 5 Hz-150 kHz, gain of 6 dB) and deployed from March 7–May 5, 2016 and September 27, 2016–January 25, 2017 approximately 5 nm offshore from Siwash Point, Flores Island (49.21028, -126.24667, Figure 1) in 51 m of water. The AMAR recorded constantly up to 8000 Hz.

A Webb Teledyne Slocum glider with a Woods Hole Oceanographic Institute (WHOI) Digital Acoustic Monitor (DMON) instrument was tasked to survey the on-shelf, shelf break, and deep-shelf break habitat. It was deployed between March 17–April 16, 2016, and January 30–February 18, 2017. It route focussed on areas of topographic complexity, such as Clayoquot Canyon (Figure 2.3.1), as a type of habitat that attracts whales (Moors-Murphy 2014). The DMON recorded constantly up to 1000 Hz for both deployments.

Fin whale calls were identified by reference to existing studies, using aural and visual inspection of the data. Spectrograms were generated using a 256-point Hann window with 1 s FFT 50% overlap by Raven Pro Interactive Analysis Software. The AMAR deployments were manually inspected for every fifth day of the deployment periods (20%), and when the presence of fin whale calls were indicated by an automated detector (Mouy et al. 2009). This totaled 328 hours, 23% for the first deployments and 604.5 hours, 21% for the second. The glider data were inspected in their entirety. For all calls, descriptive parameters were recorded, including the lowest and highest frequency extent, to also give frequency range; peak frequency, where most of the call energy is focused, and call duration, measured from start and stop times, that were also used in the calculation of the INI and IPI of song-like calls. Each call was identified as either 40-Hz or 20-Hz, with the 20-Hz calls also inspected for song characteristics. Calls were marked as either being made during daylight or night, using nautical sunrise and sunset times to define these periods. Changes in IPI and INI for song notes over time was tested by correlating duration of intervals (s) with the number of days elapsed since January 2016. For the calls identified on the glider recordings, the location of the glider when receiving the call was estimated by interpolation between the position of surfacing events, and the speed and direction of travel.

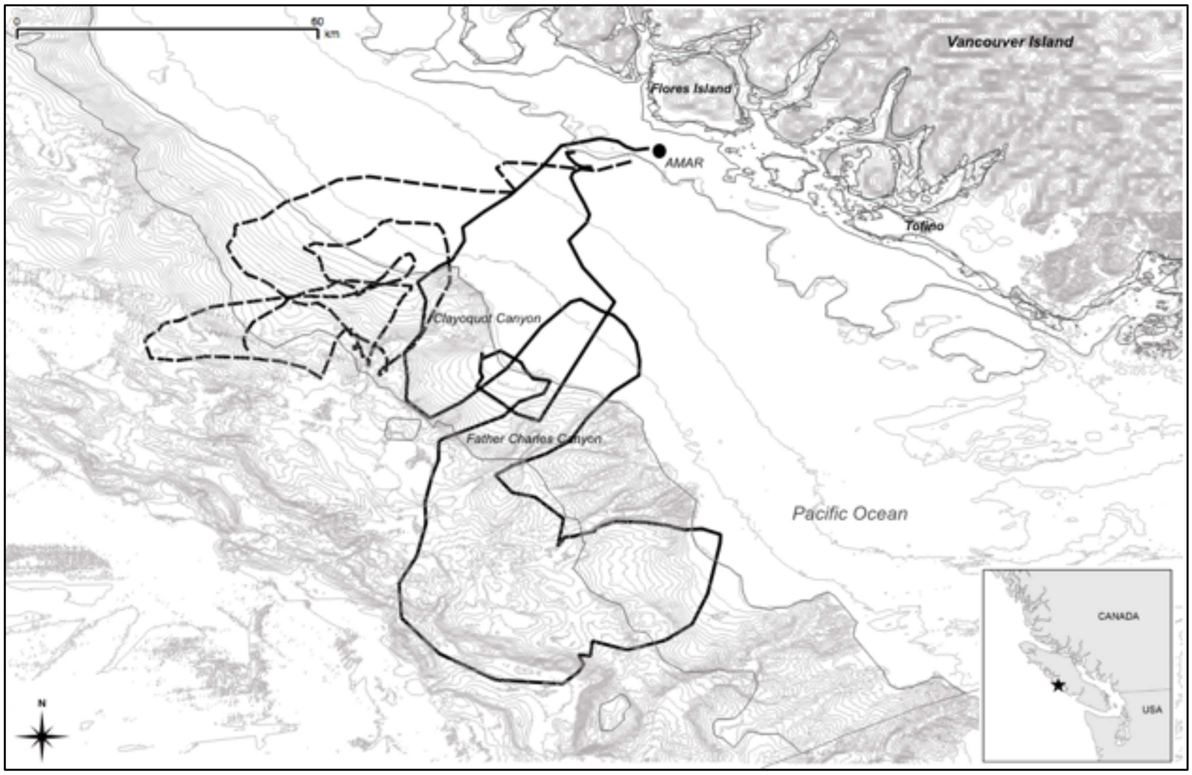

**Figure 2.4.1.** Location of Autonomous Multichannel Acoustic Recorder (AMAR, black circle at 49.21028, -126.24667), and survey routes of the Webb-Teledyne gliders, with the 2016, spring route in solid black and 2017, winter a dashed black line. Contours show the benthic topography and relief surveyed by the gliders during both deployments.

Fin whale calls were heard on both AMAR deployments, but in fewer numbers than those received by the DMON (Table 2.4.1). Calls recorded by the glider were received predominantly when in deeper waters and along the shelf-break (Figure 2.4.2), although care must be taken in the interpretation between where the call is received and the location of signalling whale. The number of calls received, and their received amplitude, suggest those recorded on the AMAR could have propagated from the survey areas of the glider (Figure 2.3.1, 2.3.2). Fin whale calls were not heard in recordings made by the AMAR system from mid-April to May, or from late September through until the end of November (Table 2.3.1). The greatest number of calls were recorded in late-January to mid-February, and the least number of calls in March (Table 2.3.1).

**Table 2.4.1:** Weekly representation of calls heard from both the AMAR and DMON data. N=total call number with contribution from each recorder show, and the relative proportion for each call type for the duration of the PAM deployments.

| Date | n | PAM receiver | | Call type, proportion (%) | | |
|---|---|---|---|---|---|---|
| | | AMAR | DMON | 40-Hz | 20 Hz | Doublet song |
| 2016-03-06 | -- | | | | | |
| 2016-03-13 | 4 | 4 | | 75.00 | 25.00 | -- |
| 2016-03-20 | 461 | -- | 461 | 100.00 | | |
| 2016-03-27 | 83 | 8 | 75 | 90.36 | 9.64 | -- |
| 2016-04-03 | 180 | 4 | 176 | 99.44 | 0.56 | -- |
| 2016-04-10 | 304 | 1 | 303 | 100.00 | -- | -- |
| 2016-04-10 | -- | | | | | |
| 2016-04-17 | -- | | | | | |
| 2016-04-24 | -- | | | | | |
| 2016-05-01 | -- | | | | | |
| -- | | | | | | |
| 2016-09-27 | -- | | | | | |
| 2016-10-04 | -- | | | | | |
| 2016-10-11 | -- | | | | | |
| 2016-10-18 | -- | | | | | |
| 2016-10-25 | -- | | | | | |
| 2016-11-01 | -- | | | | | |
| 2016-11-08 | -- | | | | | |
| 2016-11-15 | -- | | | | | |
| 2016-11-22 | -- | | | | | |
| 2016-11-29 | -- | | | | | |
| 2016-12-06 | 91 | 91 | -- | -- | 100.00 | 100.00 |
| 2016-12-13 | 1071 | 1071 | -- | -- | 100.00 | 23.16 |
| 2016-12-20 | -- | | | | | |
| 2016-12-27 | -- | | | | | |
| 2017-01-03 | 669 | 669 | -- | -- | 100.00 | 35.72 |
| 2017-01-10 | 723 | 723 | -- | 0.69 | 99.31 | 33.33 |
| 2017-01-17 | 5 | 5 | -- | 20.00 | 80.00 | -- |
| 2017-01-24 | 22 | -- | 22 | -- | 100.00 | -- |
| 2017-01-31 | 8883 | 8883 | -- | 0.74 | 99.26 | 3.02 |
| 2017-02-07 | 7374 | 7274 | -- | 0.38 | 99.62 | 20.88 |
| 2017-02-14 | 3489 | 3489 | -- | 0.89 | 99.11 | 16.60 |
| 2017-02-21 | -- | | | | | |

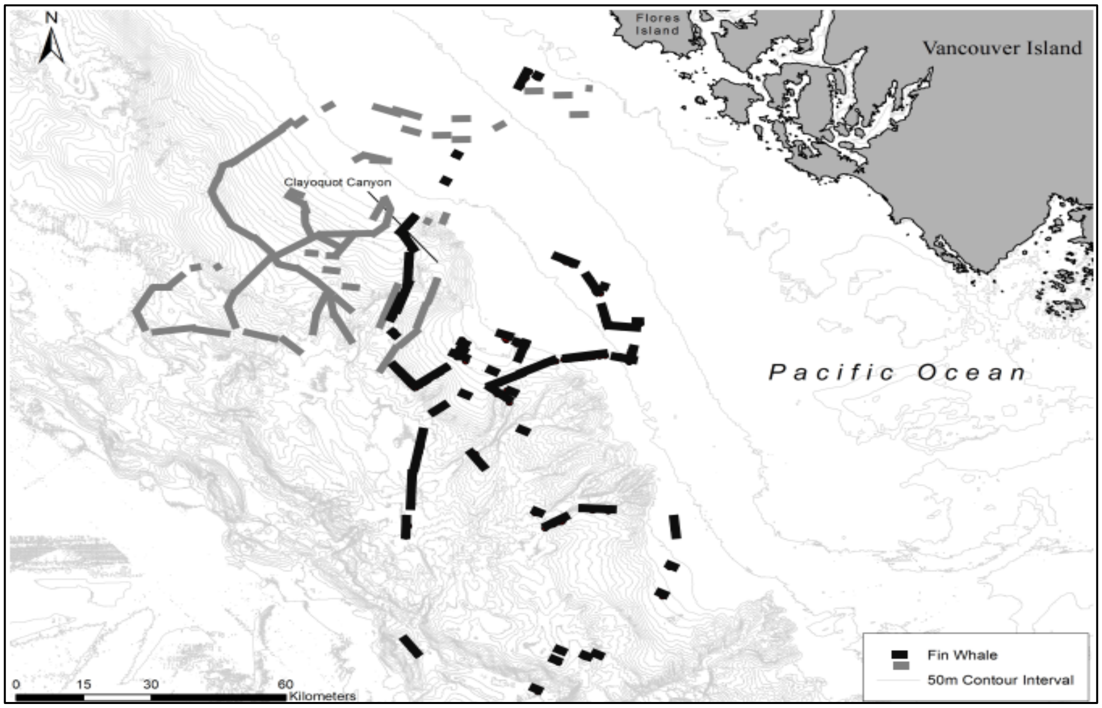

**Figure 2.4.2.** Survey routes of glider missions highlighted to show where fin whale calls were heard. Black lines indicate calls heard from the 2016, spring deployment and grey from 2017, winter.

The first AMAR and glider deployment were dominated by 40-Hz calls (Table 2.4.1). This call type was present during late January and February (2017), through until mid-April (2016, Table 2.4.1). In represented 99.03% of calls heard in March and April. Similarities in glider and AMAR data allowed for pooling of data when deployments overlapped in time (Table 2.4.1). A greater percentage of 40-Hz calls (68.3%) were heard during the day, with call structure not showing any diurnal variation.

The 20-Hz pulse was most frequently heard from December to February from both moored and mobile PAM recorders (Table 2.4.1). Again, calls were most frequent when surveying shelf-break zones (Figure 2.4.2). Between December 2016 to February 2017, 20-Hz calls comprise 99.43% of the sample, of which 14.35% had song sequences. Song was identified from the presence of repeated two-note units, a 20-Hz pulse and a backbeat, with regular INI and IPI intervals (Figure 2.4.3), and matched the description of doublet song by Širović et al. (2017). The sequences were also similar to those reported by Koot (2015) who made recordings north of the study area, whereby INI and IPI lengths (Figure 2.4.3) and patterning between months are similar to this study (Table 2.4.2). Song sequences were prevalent from December to mid-February, peaking in early January (Table 2.4.1). INI and IPI were longer in December-January

(AMAR) than in February (DMON). The inter-pulse intervals (IPI) were also significantly positively correlated with the passing of time from December to February (IPI(20Hz-backbeat), $r_s = 0.307$, $p < 0.001$; IPI(backbeat-20-Hz), $r_s = 0.603$, $p < 0.001$), though inter-note intervals declined over time (INI, $r_{s,} = -0.481$, $p < 0.001$). Possible triplet song was noted, but may be a result of irregular single notes overlapping with doublet-song, and so was not subject to further analysis.

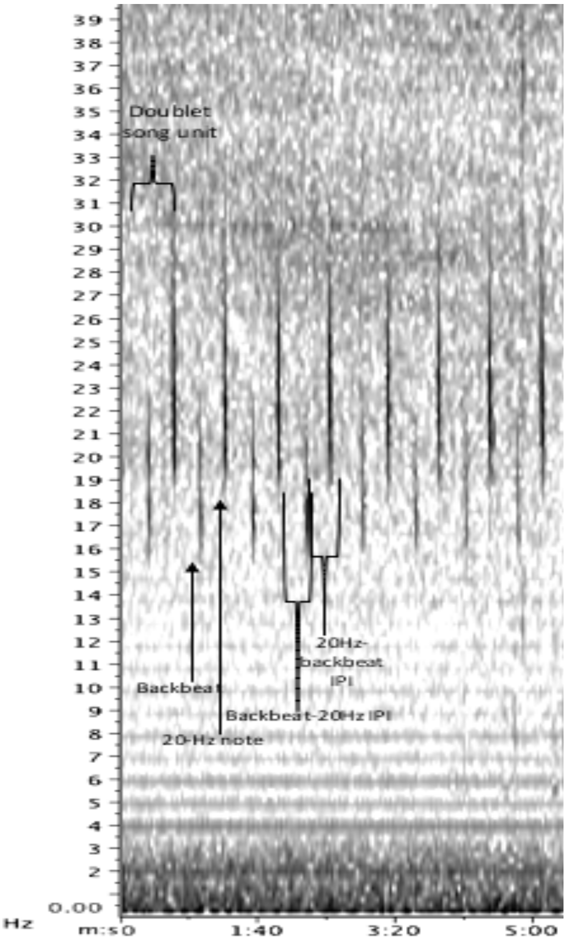

**Figure 2.4.3.** Example of fin whale doublet song from this study's recordings. Backbeat and single notes are indicated, with the inter-pulse (IPI) measures also shown. Inter-note intervals (INI) are derived from the difference between IPI(20-Hz to backbeat) minus IPI(backbeat to 20-Hz pulse).

**Table 2.4.2:** Inter-note and inter-pulse intervals for doublet song over time, with mean lengths (s), standard deviation (st.dev) and coefficient of variance (cv) shown monthly, and compared to findings from recordings from waters to the north of the study area by Koot 2015.

| | Inter-note interval | | | Inter-pulse (20-Hz-backbeat) | | | Inter-pulse (backbeat-20-Hz) | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Month | mean | st.dev | cv | mean | st.dev | cv | mean | st.dev | cv | |
| Dec | 3.02 | 1.90 | 0.63 | 17.29 | 1.76 | 0.10 | 13.91 | 1.48 | 0.11 | AMAR |
| Jan | 2.88 | 1.90 | 0.66 | 16.72 | 2.04 | 0.12 | 13.86 | 1.99 | 0.14 | AMAR |
| Feb | 3.53 | 2.53 | 0.72 | 17.72 | 1.87 | 0.11 | 16.86 | 1.98 | 0.12 | DMON |
| Dec | 4.20 | 0.72 | 0.45 | 17.40 | 1.09 | 0.10 | 13.20 | 0.73 | 0.06 | Koot 2015 |
| Jan | 3.80 | 0.77 | 0.56 | 16.90 | 0.97 | 0.08 | 13.00 | 1.03 | 0.05 | Koot 2015 |
| Feb | 4.30 | 0.97 | 0.56 | 17.30 | 1.55 | 0.14 | 13.10 | 1.20 | 0.08 | Koot 2015 |

The 20-Hz pulses occurred together in recordings in irregular and song-like sequences. However, the 20-Hz and backbeat notes comprising song differed in structure from other 20-Hz notes heard at the same time. The 20-Hz note in the song sequence was significantly lower in its frequency extents (low, t(873.023)= -8.875, p <0.001; high, t (815.774) = -9.685, p<0.001; range, t(777.867) = -5.628, p < 0.001); peak, t (824.378) = -8.640, P < 0.001), and duration t(18297) = -8.018, p<0.001) than non-sequenced 20-Hz notes. The backbeat note to the 20-Hz note in the song sequence also differed (low, t(1424)= -43.279; high, t(1423.419)= -42.541; range, t(1367.827)= -24.224; peak, t(1424)= -40.213; duration, t(1424)= -3.535, all p<0.001). The use of 20-Hz calls increased at night (57.9%) compared to daylight hours (42.1%). Changes in call metrics were seen on a diurnal basis for single and paired calls and also in structure for song phrases. From the glider recordings the 20-Hz calls significantly increased in frequency range (t(18204.773) = -12.727, p<0.001) and decreased in length (t(18611.537) = 2.934, p<0.003) at night. This, however, was not found in the AMAR recordings.

At their simplest, these recordings show fin whales using the deep-coastal and offshore waters of Clayoquot Sound. In the past, their presence has been largely unnoticed in visual surveys (R. Palm, Strawberry Isle Marine Research Society, Pers. Comms. 1993-2009), but more recent PAM studies have noted them in waters adjacent to Clayoquot Sound. This adds to an acoustic record for fin whales on the west coast of Vancouver Island, with other recordings taken from Union Seamount, 420 km west of Nootka Sound, in 2006, La Perouse Bank, 50 km southwest of Barkley Sound, in 2007 (Ford et al. 2010), and Brooks Peninsula in 2011 (Koot 2015). These studies identified primarily 20-Hz calls. This is the first to note distinct temporal patterns in calling and separation of the dominant call type use.

The prevalence of 40-Hz calls suggests foraging behaviour during the transition from an ocean downwelling system to an upwelling system (Chandler 2017, Gower & King 2017). The increased primary productivity at this time translates into aggregations of zooplankton, which are advected and entrained around topographical features, such as submarine canyons along the shelf-break (Freeland & Denman 1982, Vindeirinho 1998). The decreased use of calling at night may be indicative of feeding, when prey migrate vertically and become more available. Higher numbers of calls recorded when surveying these regions suggests increased whale presence, although call number is not a reliable indicator of whale numbers.

The 20-Hz call is most commonly described for fin whales, and may play a role in a number of behaviours. For other baleen whales, similar low-frequency to infrasonic calls are linked to conspecific contact and navigational cues (Allen 2013, Burnham et al. 2018, Chapter 1.3). However, movement and migration patterns are not well described for fin whales (Mizroch et al. 2009).

Song sequences are produced by male whales, and so have been linked to breeding behaviors. Koot's (2015) comparison of song and non-song calling found that the 20-Hz note in the doublet sequences was focussed in the lower frequencies, and that the spectral properties of the backbeat were distinct from other calls. This was also found here. The repeated patterns last for up to several hours, as they did in the recordings for this study (Watkins et al. 1987, Clark & Gagnon 2002, Clark et al. 2002, Croll et al. 2002, Delarue et al. 2013, Oleson et al. 2014). A doublet song form, similar to that described by Koot (2015) and Širović et al. (2017) was the prominent pattern heard. The short-doublet form, as found here, is the dominant song type described to the north Pacific (Širović et al. 2017). The broad use of this doublet pattern suggest a widely distributed and connected population (Oleson et al. 2014, Širović et al. 2017), yet subtleties in INI and IPIs within a song phrase may allow for identification of an individual, its group membership, or geographic region (Watkins et al. 1987, Edds 1988, Clark et al. 2002, Delarue et al. 2009).

Seasonal patterns in calling, including the lengthening of INIs and IPIs over time, could indicate changes in physiology, reproductive state, or dominant behavior (Morano et al. 2012). The use of song patterns on feeding grounds can promote female-male pairing in the following season, and suggests a longer-term mate assessment period; however, song sequences were not noted here at the times when foraging calls were dominant.

The use of the 40-Hz and 20-Hz calls, and song-sequences suggests that waters off the west coast of Vancouver Island form part of the feeding range and breeding areas for fin whales. These behaviours dominate at different times of the year. Similar breeding calls have been recorded in Hecate Strait and Queen Charlotte Strait in northern British Columbia, peaking in November to January (Chandler et al. 2015). This is similar to the call patterns seen in this study, which coincides with the breeding season for fin whales in this area (Mizroch et al. 2009). Song may be used to attract a mate or as a display of fitness, as well as perhaps function in mate guarding, territory defence, male-male interactions, or social competition.

I present the temporal separation between calling behaviours, but care must be taken when drawing conclusions on spatial use and whale abundance from the vocalisations. The prevalence of calls along the shelf-break and in zones of topographical complexity support the idea of fin whales foraging in the area, as prey aggregations are stronger (Mackas et al. 1997, Allen et al. 2001), as well as possibly using the vocal returns from these same bathymetric features to form navigational cues for large-scale movement (Allen 2013, Garrigue et al. 2015). However, the low-frequency calls described here can propagate over great distances with low attenuation. Koot (2015) estimated a detection range of nearly 1,500 km for a 20-Hz pulse in low ambient noise on recordings made from a moored recorder in waters north of this study area. This is in line with other estimates for calls of a similar nature (Cummings & Thompson 1971, Payne & Webb 1971, Clark 1995, Stafford et al. 1998, Širović et al. 2007, Delarue et al. 2013), leading to considerable uncertainty in locating a calling whale. The differences in call number between the spring and winter recordings (Table 2.4.1) may be indicative of an increase in whale numbers during breeding periods, or perhaps reflect a breeding-feeding dichotomy commonly described for baleen whales, where energy is dedicated to foraging leading to reduced calling (Mellinger et al. 2007b, Baumgartner & Fratantoni 2008, Parks et al. 2011).

The acoustic record of fin whales will grow with repeat deployments of ocean gliders and moored PAM units similar to those described here. Not show here is the presence of other rare and endangered species also recorded during these deployments, the blue (*Balaenoptera musculus*) and possibly sei whale (*Balaenoptera borealis*) (Chapter 2.3). Placing PAM units in an array will more clearly define whales' use of space over time, and perhaps even track their movement through the area. Further recordings will also establish the temporal patterns in calling more definitively, and will move the use of PAM data past simply noting presence, to suggest the importance of specific habitat units. This work adds to the body of research being completed to determine current abundance estimates and habitat use for whales species in the northeastern Pacific, especially those most effected by whaling. The integration of PAM methods with other traditional techniques, as well as historical data, adds another facet to the ecological study of these whale populations.

## 2.5. Conclusions: Listening for whales

Whales were decimated by whaling in the north-east Pacific. Many populations that once dominated ocean ecosystems are yet to recover to pre-whaling, or in some cases, viable population numbers. The chapters in this section (Chapters 2.2-2.4) show how acoustic monitoring is an effective and efficient way of re-establishing whale presence and habitat use, especially in offshore regions. Passive acoustic methods are increasingly being used to augment or replace traditional survey methods, because they are not hampered by limitations such as light, weather, and remoteness. Visual surveys for fin whales in the northern hemisphere, for example, have been limited often to a single season and a restricted number of surveys, with most areas having been only surveyed once (Edwards 2015). The use of passive acoustic monitoring, such as those described in this section, and indeed in the previous section (Chapters 1.2-1.7), can be employed to survey through conditions that would make visual observations impossible, and often detect cetacean presence more readily compared to visual methods (McDonald & Moore 2002, Širović et al. 2004, Barlow & Taylor 2005, Mellinger et al. 2007b, Rankin et al. 2007).

In this section I have started to build a picture of the spatial and temporal presence of whale species in the deep-coastal and offshore waters of Clayoquot Sound. At its very basic I ask what species are present and when (Chapters 2.2, 2.3), and then link that to what is known about the habitat and how whales may be using it (Chapters 2.2, 2.4). Reduced population sizes makes tracing seasonal movements or outlining areas of importance for life history events, such as feeding, weaning, or breeding, even more difficult (Gregr et al. 2006). The use of gliders with the capacity to make passive acoustic recordings allows for surveillance of potentially large areas for extended periods, providing us with critical data for population recovery.

The acoustic surveys work on the premise that cetaceans use sound as their primary means for environmental imaging, navigation, prey location, and communication. Here I use these calls as a cue to presence. This in itself can be valuable, especially for more cryptic species and/or in areas more difficult to survey (see Chapters 2.2, 2.3). Habitat use may be informed by a number of other factors including timing and location of calls, prey availability in the area, and the conditions that encourage growth and aggregation of prey patches. These variables are explored in Chapter 2.2 where whale calls are compared to preyscape surfaces formed by extrapolating echosounder data collected concurrently to the passive acoustic monitoring (PAM) for whale calls. In this case I am comparing patterns in large habitat regions: on the continental shelf, and along the shelf break to off-shelf regions. Also, measures taken inside submarine canyons were compared to adjacent shelf-break areas. Generally more calls were heard from the deeper waters surveyed, and areas past the shelf break. Submarine canyons are thought to aggregate prey and enhance productivity along the shelf break (Freeland & Denman 1982, Allen & Hinkley 2010, Smith et al. 2010), which is why I focused on these with glider deployments. The strongest average volume scattering strengths recorded from the glider deployments were indeed from canyon regions. The presence of whales may then be expected to be increased, as seen in other locations (Moors-Murphy 2014), however call numbers were proportionately less, which may be because of a number of factors including; calls being a true reflection of the number of whales present, call number representing conspecific contact lines and not number of individuals; call propagation and call reception differing within canyons compared to open water, and perhaps differing whale behaviours in and around canyons, for example engaged in foraging rather than calling. It must be remembered, however, that the calling animal can be sometimes very removed from the location that the calls are received, and so perhaps it would be better to distinguish regions of the shelf break that are steep and topographically complex than those that are not, rather than individual canyons. Also, their effect in prey aggregation may work as a singular region, as well as stimulating increased productivity by the actions in a single canyon become compounded by several canyons in close proximity to one another.

The comparison of mobile and stationary recorders (Chapter 2.3) goes some way in outlining habitat use as well as giving greater spatial coverage. The calls described in this section (Chapters 2.2-2.4) are allochthonous, with the PAM systems having large detection ranges, especially for low frequency calls of large whales, which can travel up to thousands of kilometers (Cummings & Thompson 1971, Payne & Webb 1971, Clark 1995, Stafford et al. 1998, 1999, Tyack & Clark 2000, Širović et al. 2007, Stafford et al. 2007, Simard et al. 2008, Clark et al. 2010, Delarue et al. 2013, Koot 2015). Passive acoustic surveillance, especially if using bottom-fixed and spatially dynamic recorders in concert, allows for tentative delineation of areas important to each species over time. It can also allow for the most spatially effective surveying program for some of the rarest species, including north Pacific right (*Baleaena japonicus*) and sei whales (*Balaenoptera borealis*), of which I describe calls for the latter in Chapter 2.3, but only cautiously due to a lack of comparison materials. If it were possible to triangulate the calls, conclusions on spatial niche partitioning by species may become stronger. For this work calls are described from a single omnidirectional receiver (Chapters 2.2-2.4), but still some coarse spatial patterns can be seen. The gray whale (*Eschrichtius robustus*) calls from the glider where typical to those described for migration (Chapters 1.2, 1.3, Guazzo et al. 2017, Rannankari et al. 2018) and were only heard in coastal waters. Humpback whale (*Megaptera novaeangliae*) calls were most prevalent in recordings made on the continental shelf, but were the most ubiquitous in time and space as well as demonstrating the most varied repertoire. Fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), sei, and sperm whale (*Physeter macrocephalus*) calls were heard in deeper waters, mostly along the shelf break (Chapter 2.2). Further deployments, and those with multiple PAM receivers, may better describe these differences in habitat use of each species.

Calls carry more information than purely a presence marker. They may indicate the underlying behaviour behind the call, for example travelling, feeding or mating. Just as was found for gray whales in Section 1 (Chapters 1.2-1.7) calling behaviours, and the call type employed, can vary in response to behavioural, geographical, social, or emotional context of the whale signalling. It can also allude to group membership of the individual (Thompson et al. 1996, Rivers 1997, McDonald et al. 2006, Oleson et al. 2007 a,b, Širović et al. 2013, Koot 2015, Gero et al. 2016). Each call heard was compared to those described in the literature with reference to behaviours observed during signalling. The sperm whale clicks heard are likely being employed during a foraging bout, for example. Temporal separation in the employment of call types was heard for both blue and fin whales (Chapter 2.3), suggesting both feeding and breeding behaviours in the area of interest. Chapter 2.4 focuses on the fin whale calls recorded and how call type use changes over time. This, and other studies suggest that offshore regions of the Canadian Pacific are used by fin whales for breeding and calving.

We currently only have fragmentary knowledge of both whale populations and the quality of the habitat they are recovering into. Populations reduced by whaling initially are further threatened by coastal development, release of waste produces, and acoustic disturbance from oceanic transportation routes. The work documented in Chapters 2.2-2.4 shows how PAM techniques help to piece the evidence of whale presence, habitat use, and importance of habitat for life history events together. Here, reliance on the recordings are absolute, showing that acoustic data adds to knowledge in its own right, as well as highly complementing more traditional methods. The recordings, and oceanographic and habitat mapping data streams can also establish the potential levels of stress imposed on whales by increased ocean noise from anthropogenic activities, and reductions in prey and habitat availability as a result of changing ocean conditions. There are still many geographical and temporal data gaps in our knowledge of cetacean species' use of coastal and offshore waters in the Canadian Pacific, and its importance.

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## 3. Part 3: Management implications

*The sea is the land's edge also, the granite*
*Into which it reaches, the beaches where it tosses*
*Its hints of earlier and other creation:*
*The starfish, the horseshoe crab, the whale's backbone;*
*The pools where it offers to our curiosity*
*The more delicate algae and the sea anemone.*

T.S. Elliot (1888-1965)

## 3.1. Introduction: Bringing acoustics and ecology to inform management action

Our understanding of whale presence, habitat use and behavioural ecology can be hampered by the high cost of field research and the conditions needed for accurate and repeatable data collection. Long time-series data for whale species, like that referenced in the Coastal Section, are rare. The use of passive acoustic monitoring (PAM) techniques, used in concert with more traditional methods, can be used to begin to fill knowledge gaps. In this Section I discuss how data streams enhanced with PAM findings can better inform management actions aimed at protecting species and habitat regions critical to their life history processes.

Chapter 3.2 is a test case of how acoustic and visual monitoring studies can complement each other to form a complete picture of a species' ecology. Here I use overwinter killer whale presence in Clayoquot Sound as an example. Calls at their most basic, mark presence in the study site, with aspects of calling indicative of the eco-type and possible behaviour at the time of calling interpretable. Although in this instance, data is derived from only one winter deployment, it represents a time when other data streams are more limited, with fewer vessels on the water making observations. Further deployments of PAM systems will only add to our ability to describe species ecology, which should in turn better inform management action.

This is also the message presented in Chapter 3.3, where I draw on the material presented in the Coastal Section, as well as the 20-year ecological study of gray whales in Clayoquot Sound (see Chapter 1.4) to illustrate where scientific study can and should inform protective actions. In this instance I suggest a more adaptive management approach for whale watching activities, implying that the full impact and energetic draw on cetacean species by tourist-based activities has not yet been fully realised. Until this is the case, I suggest a cautionary approach, listing areas where greater consideration should be given when making recommendations of best practise. In short, I propose that the ecological setting and vulnerability of an individual or population to disturbance at the time and/or in the place of whale watching should be considered before it becomes part of the activity's resources. I end by recommending that these disturbance events should be considered in terms of their contribution to a much wider ranging anthropogenic-derived intrusion into the species lives.

Acoustics-based study has much to add to our comprehension of whale ecology, but we are still in the infancy of our understanding. Further integration of PAM systems into ecological study will only aid our interpretation of behaviours and habitat use, likely adding interesting nuances.

## 3.2. Combined use of visual and acoustic techniques for winter killer whale observations in Clayoquot Sound

### Preface

Systematic observations of cetaceans during the winter are difficult, yet knowledge of their presence and behaviour during this period is important for conservation and management. Typically, observations come from vessel surveys, with citizen science networks adding significantly to sighting data. However, this work is hampered by high costs of field research, weather, and data collection limited to daylight hours. In contrast, acoustic recorders can be deployed to collect information over long periods, and in almost any conditions. Used in combination, these data collection techniques will fill knowledge gaps. Here I use data from a well-established citizen science group, whose reporting network extends from Amphitrite Point, Ucluelet, to Sharp Point/Hot Springs Cove on the west coast of Vancouver Island, and an Autonomous Multichannel Acoustic Recorder (AMAR) positioned off the southern coast of Flores Island to measure killer whale presence during winter months in Clayoquot Sound as an example of how the two data-streams can be used in complement to provide a wider view of a species ecology. The combination of several data streams, affording year-round, or increased spatial and/or temporal coverage, will be a valuable in to informing management actions.

# Combined use of visual and acoustic techniques for winter killer whale observations in Clayoquot Sound

## Introduction

Data on species distribution over long time periods or great spatial extents is difficult to collect in the marine environment. Observations of free-ranging cetaceans are hampered by high costs of field research, weather, and limited data collection periods, for example to daylight hours. Field research is more difficult, if not impossible, during the winter in many locations.

Typically, observations come from dedicated vessel-based surveys, with citizen science networks increasingly used to add significant to sightings data. These networks potentially have a wide spatial extent, but are dependent on the chance encounters of whales, and normal activities of vessels in any given area. Night or inclement weather observations are uncommon. Data, if garnered by an experienced observer may, however, provide more information than simple presence, such as group size, individual identity, or behavioural context.

Remote data collection devices, such as passive acoustic monitors (PAM) are being used to collect marine data over long periods, in areas and at times it might otherwise be problematic to survey. Once deployed, they can record data continuously without regard to sea-state or visibility, but are spatially restricted to a defined detection radius from its location. In the case of acoustically sensitive species, PAM may also offer a less intrusive alternative to vessel-based surveying.

Here I assess the input of the more traditional against the more technological data collection method to knowledge of whale presence, habitat use, and behaviour. Opportunistic visual observations from a well-established citizen science network are compared to underwater acoustic recordings to analyse the winter presence of killer whales (*Orcinus orca*) in Clayoquot Sound on the west coast of Vancouver Island, Canada. Together they form a novel examination of whales' use of the area.

Killer whales are common year-round inhabitants of coastal waters in the northeastern Pacific (Ford 2014). In the near shore waters of British Columbia three sympatric and genetically distinct ecotypes have been described: resident, Bigg's (transient), and offshore (Ford et al. 2000). They differ in morphology, social structure, diet and foraging behaviour, and acoustic behaviour (Bigg et al. 1987, Ford 1987, Baird & Stacey 1988, Ford & Ellis 1999, Ford et al. 2014). The resident killer whale ecotype is distinguished into a northern and southern cohort, with a number of pods or clans arranged into each. Each pod shares an acoustic dialect, with pods with similar calls collectively referred to as clans. Residents often utilize echolocation and communicate within and between hunting groups, with the seasonal presence of their salmonid prey strongly influencing the distribution of resident groups throughout their range (Nichol & Shackleton 1996, Baird et al. 2005). A pod can have a repertoire of 7–17 discrete calls, whose use varies depending on the group dialect (Ford 1987, Ford 1991, Ford & Ellis 1999). In contrast, Bigg's killer whales are mammal hunters, with much of their time devoted to foraging, markedly more than resident groups (Heimlich-Boran 1988, Ford & Ellis 1999). They tend to travel in smaller groups of 2–6 individuals, with a very dynamic social order (Ford & Ellis 1999). Bigg's killer whales are believed to vocalise significantly less than residents, with calling predominantly limited to surface-active and post-feeding behaviours (Morton 1990, Guinet 1992, Barrett-Lennard et al. 1996, Deecke 2003, Deecke et al. 2005). Deecke et al. (2005) suggests that they remain silent as a strategy, so as to not incur extra cost to foraging from being heard by their prey on approach. Stealth and surprise are important elements of foraging success; therefore both vocalising and echolocating are limited (Barrett-Lennard et al. 1996, Ford & Ellis 1999, Deecke et al. 2002). When vocalising they use a smaller repertoire of calls (4–6), demonstrating some regional distinction in use, but with a less discrete dialect identity than residents (Ford & Ellis 1999). The offshore killer whale ecotype is estimated to have diverged from the resident killer whale lineage approximately 200,000 years ago, and feed on fish, specializing on shark prey (Herman et al. 2005, Ford et al. 2011, 2014). Offshore groups have been noted in inside waters around Vancouver Island infrequently (Ford et al. 2014), and are predominantly sighted in waters off the coast between California and south-east Alaska (Herman et al. 2005). This group will not be considered further in this study.

Despite efforts to map abundance, distribution, and life histories of these groups spanning more than 40 years (Bigg et al. 1976, 1990, Ford et al. 1998), questions still remain. For example, although the distribution and use of inshore waters around Vancouver Island by killer whales has been studied intensely, little is known about movement patterns outside of these areas and during winter months (Ford et al. 1998, Ford 2006, Riera et al. 2013). Similarly, their use of space and behaviour through the night remains poorly known. Previous studies have used passive acoustic monitoring for killer whale presence in the northern Pacific (e.g. Newman & Springer 2008, Oleson et al. 2009, Širović et al. 2011, Hanson et al. 2013, Riera et al. 2013); in this study, I amalgamate visual and acoustic data sets to try to describe killer whale use of Clayoquot Sound during the winter. The data from a long-term citizen science network of observers provides the visual data. I compare this to a 64-day deployment of a bottom mounted acoustic recorder, as an assessment of passive acoustic monitoring for presence that may otherwise be impossible. Although the quantity and scale of data collected by each method differs, together these databases fill gaps in our knowledge of coastal killer whale habitat use, which is vital to species management plans.

## Methods

### *Visual data set*

Strawberry Isle Marine Research Society (SIMRS) and their reporting network recorded visual sightings of killer whales in Clayoquot Sound. The range of reporting for SIMRS between February and May 2015 extended from Amphitrite Point, Ucluelet, to Sharp Point/Hot Springs Cove, Vancouver Island. The daily sighting records are summarized into hourly reports, with observations of presence and behaviour of killer whales reported from an extensive network. They trace movements of whale groups through the network area for as long as possible, with observational data provided by private and recreational boaters, commercial vessels such as the whale-watching fleet and fishermen, as well as SIMRS scientists. Opportunistic photographs taken during a sighting are used to determine group size and identity, residency time and return rate.

### *Acoustic data set*

An Autonomous Multichannel Acoustic Recorder (AMAR G3, JASCO Applied Sciences) was deployed on the ocean floor on February 21, 2015 and recorded continuously for 64 days. It was positioned approximately 5 nm southwest of Siwash Point, Flores Island, at a depth of 51 m. Recorded ambient noise levels were used to estimate the killer whale detection range, calculated for every minute of the recording by summing the 1/3-octave-band levels, assuming a spherical spreading of sound from the source. The source level of killer whale vocalisations used were those reported by Holt et al. (2009) as 133–174 dB re 1 μPa at 1 m with a mean of 155.3 dB re 1 μPa at 1 m (±7.4 SD). Thus, the maximum detection range, given the lowest ambient noise levels and greatest killer whale call source levels, was 30 km, representing approximately 1% of the recording time. The median value (50%) was calculated at 1.8 km, with the upper quartile of killer whale detections extending to 3 km assuming high source levels of vocalisations (Figure 1). Detection range is influenced by the frequency specific propagation of calls, using the parameters defined by Holt et al. (2009) and known transmission parameters for the area (Mahoney et al. 2014, Mouy et al. 2015) as well as ambient noise quantifications. The AMAR was fitted with an M8E calibrated omnidirectional hydrophone (GeoSpectrum Technologies Inc.) and set for a gain of 6 dB. The recorder sampled for 340 s (5 min and 40 s) at 16 ksps/0–8 kHz, alternating with 560 s (9 min 20 s) at 64 ksps/0–32 kHz, recording with equal sensitivity for all frequencies. The recordings were first passed through detection software that noted presence of killer whale clicks or whistles (Mahoney et al. 2014, Mouy et al. 2015). Presence was then confirmed manually, selecting those clips shown to have killer whale vocals present by the detector, and those temporally adjacent (directly before and after), to define the length of the acoustic ‘encounter’. Each file, and respective spectrogram, was visually and aurally inspected to verify an acoustic encounter, when at least one killer whale call or whistle was heard in the clip. Echolocating clicks were not used as a reliable indicator of killer whale presence. A further percentage of the recordings, approximately 5%, were randomly selected for manual verification to determine confidence in the detection software and eliminate false negatives or positives from the data to be processed further.

Whistles, characteristic pulsed and tonal calls denoted killer whales presence. An ‘encounter’ was defined by a string of positive killer whale acoustic detections book-ended by recordings that did not have audible calling. Although vocalisation is not a continuous activity, acoustics are typically more consistently used by odontocetes. It is presumed that killer whales remain present between temporally adjacent sound files (those either directly before or after those confirmed to contain killer whale calls, and within a 15 min period), despite calls not consistently heard. The vocalisations were further analysed to determine the ecotype of the killer whale group, either resident, transient or unknown. This was determined by identification of stable, stereotypical discrete calls, which distinguishes the caller to ecotype, clan and in some cases pod, as categorized by Ford (1987, 1991). In this case it is the type of vocalisation, and its repetition rate that helps determine call characteristics and caller identity (Ford 1987).

**Results**

Both data collection systems work at different scales and resolution, with only two occurrences of killer whales detected concurrently by both acoustic and visual means. The SIMRS network collected 14 visual encounters of killer whales throughout its larger spatial range (Hot Springs Cove to Ucluelet, Figure 2.3.1) for the period of February 21 to April 25, 2015. Network sightings within the maximum AMAR acoustic detection radius were noted on several different occasions (Figure 3.2.1), however matching notations for visual and acoustic presence were only made on February 25 and March 17, 2015. All other on-water observations are beyond the limit of the recorder (Table 3.2.1). Analysis of acoustic data with its smaller range, but higher acuity, recorded 17 acoustic encounters, ranging from 9 min to 11 h 30 min. Thus the PAM recorded 15 encounters that were not located by the SIMRS network. The time of day of these encounters were determined as either day (06.00–18.00), or night, (18.00–06.00) with several spanning both day and night. In this case it is counted as a single encounter and listed under the period the encounter begins determined by the time whale calls were first detected.

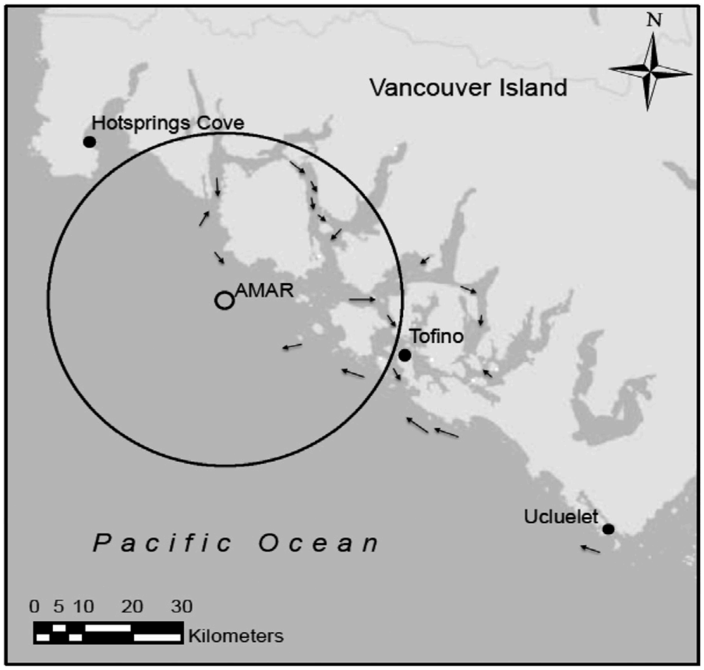

**Figure 3.2.1**:Location of AMARs deployment and likely range of acoustic detections. AMARs location is the centre of the detection circles, with the smaller circle representing the range of detection 50% of the recording time (1.8 km) and the larger circle the maximum extent (30 km). The extent of the SIMRS network extends from Hotsprings Cove to Ucluelet with arrows used to denote individual sighting events from the location they are first observed and the swimming direction.

Although sounds made by vocalising whales could suggest group number or animal density, in this study they were used solely as an indicator of presence, and in further analysis to detect recognizable dialects of killer whale groups and identify ecotype, classifying calls in accordance with work by Ford (1987). Both resident and transient groups have been noted to the area, with the PAM recordings confirming both during the winter (Table 3.2.1).

**Table 3.2.1:** Presence of killer whales during AMARs deployment period. An 'x' in PAM denotes acoustic presence, and in visual represents that a sighting was also recorded in the detection area. An 'x' in Reported denotes a visual sighting recorded in the full range of SIMRS. Date and time of day represents when the observation was made, with this representing when whale vocalisations were first heard for acoustic encounters. For killer whale ecotype (KW type) NR = Northern Resident, SR = Southern Resident, T = Transient/Bigg's whales.

| Date | Time of Day | PAM | Duration | KW type | Visual | Reported |
|---|---|---|---|---|---|---|
| 2015-02-21 | Day | | | | | x |
| | Night | x | 9 m | NR | | |
| 2015-02-23 | Day | x | 11 h 30 m | NR | | |
| 2015-02-25 | Day | x | 4 h 24 m NR | | x | x |
| | Night | x | 6 h 53 m | | | |
| 2015-02-28 | Day | | | | | x |
| 2015-03-01 | Day | | | | | x |
| | Night | x | 4 h 6 m | NR | | |
| 2015-03-02 | Day | x | 7 h 9 m | NR | | |
| 2015-03-03 | Night | x | 1 h | T | | |
| 2015-03-05 | Day | x | 6 h 9 m | NR | | |
| | Night | x | 1 h 51 m | T | | |
| 2015-03-06 | Day | x | 9 m | Unknown | | |
| 2015-03-07 | | | | | | x |
| 2015-03-08 | Day | x | 5 h 15 m | Unknown | | |
| 2015-03-11 | Day | | | | | x |
| 2015-03-12 | Day | | | | | x |
| 2015-03-16 | Day | x | 1 h 15 m | Unknown | | |
| | Night | x | 5 h | T | | |
| 2015-03-17 | Day | x | 15 m | T | x | x |
| 2015-03-18 | Day | | | | | x |
| 2015-03-20 | Day | | | | | x |
| 2015-03-21 | Day | | | | | x |
| 2015-03-28 | Day | | | | | x |
| 2015-03-31 | Day | x | 3 h 39 m | NR | | |
| 2015-04-07 | Day | | | | | x |
| 2015-04-08 | Night | x | 6 h 9 m | NR | | |
| 2015-04-09 | Day | | | | | x |
| 2015-04-11 | Night | x | 15 m | Unknown | | |

## Discussion

Clayoquot Sound is a significant habitat for several species of cetaceans. Killer whales and gray whales (*Eschrichtius robustus*) as well as harbor porpoise (*Phocoena phocoen*a) are common and significant parts of the coastal ecosystem (Burnham 2015, Burnham & Duffus, in press). The area is designated as a UNESCO Biosphere reserve, and holds several other marine area protective designations, as well as supports a thriving whale watching industry, both of which speak to the utility of detailed whale knowledge. However, we are only now grasping the importance of killer whales at the apex of the food webs in diversity and stability of local marine ecosystems (Estes et al. 1998).

In this study, passive acoustics collects killer whale data at times when it is otherwise difficult to gather information. Passive acoustic monitoring complements and extends the data from visual surveys, with long-term acoustic studies used to fill knowledge gaps in presence, seasonal movements, distribution and behaviour for these whales. This study follows those conducted by Riera et al. (2013) and Hanson et al. (2013) examining year-round presence of killer whales in coastal waters and over the continental shelf respectively.

First, the consistent presence of killer whales during the winter was greater than previously thought. In the area of detection there was 17 encounters noted acoustically, of which two were also reported visually. On a number of occasions observations were made by the sightings network outside the spatial range of the PAM recorder. Considered together, these data sets demonstrate a high overwinter whale presence. Also, with 9 acoustic encounters during the day and 8 noted at night, in this data set there is no discernible diurnal patterning to the calling as you might expect from previous studies (e.g. Baird 2001, Newman & Springer 2008). Second, the number of vocalisations recorded was also greater than expected, with acoustic analysis in most cases able to identify the ecotype of the individuals vocalising. Both resident and Biggs' (transient) killer whale groups were noted, although the majority of vocalisations recorded were from the northern resident dialect. This ecotype is considered the least likely visitor from the local populations around Vancouver Island to be present, due to presumed scarcity of prey resources (Ford et al. 2000, Palm, Pers. Comms.). Vocal detection rate may be a function of life history, with Bigg's whales less acoustically active to avoid 'eavesdropping' by mammal prey (Deecke et al. 2005), or could simply represent greater site use by resident whale groups. The acoustic data opens up the possibility that Clayoquot Sound may be an important overwinter foraging area for the resident ecotype, which focuses on salmon. However, call type and frequency has not been conclusively tied to behavioural context. During summer months, resident whale habitat use is more predictable following salmon runs, which often form in narrow straits in the inside waters of Vancouver Island (Heimlich-Boran 1986, Heimlich-Boran 1988, Ford 1989, Guinet 1990, Nichol & Shackleton 1996, Ford et al. 1998, Osborne 1999, Hanson et al. 2013, Holt et al. 2013). However, during the winter months distribution is tied to dispersed salmon populations, making the whales much more sporadic in space and time. This first look at winter presence using acoustics in addition to visual detections allows documentation of patterns of occurrence of killer whales in Clayoquot Sound, and has implications for both northern resident and transient eco-type foraging ecology.

Whale residency time is an important metric to inform management planning. Autonomous acoustic recorders, like the AMAR, can be deployed to collect data continuously and unobtrusively for long time periods, over known areas, and in all weather and light conditions. For the most accurate recording of marine mammal presence, however, we cannot yet rely solely on acoustic data. Little is currently known about vocalisation rate of individual whales, or how this may be linked to circadian rhythms, activity state or the behavioural context (Ford 1987, Deecke et al. 2005). Acoustic presence is an underestimate of both use of the area, and residency time. In addition, although recognition of acoustic signals can identify groups to ecotype, if not clan or pod level, this does not extend to the individual level, as photo-identification does, and so falters for data such as a whale's range, residency time, or return rate. An expanded array of recorders and/or more dedicated visual observations concurrent to acoustic recording could aid in annotating the calls heard with ecotype identity, whale number, and behaviour.

The detection of killer whales by the AMAR provides the minimum rate of presence, and over-winter site use. Whales may not be detected because they are not actively vocalising, they are beyond the detection range of the hydrophone, or faint calls are not detected over ambient noise levels, so the absence of detection does not necessarily mean absence from the study site. The average swimming speed of a killer whale is between 3 and 10 km/h depending on behaviour (Ford 1989, Barrett-Lennard et al. 1996) suggesting transition time through the area of detection could as little as 2 hours if behaviour was purely travelling. As many of the acoustic encounters exceed this, it could be interpreted that the whales are foraging, resting or socializing.

Therefore, acoustic monitoring is complementary to more traditional research methods such as vessel or aerial survey, observation or tracking experiments. Passive acoustic data could, as visual observations do, inform habitat-based density models to allow the prediction of cetacean presence over space and time (Küsel et al. 2011, Harris et al. 2013). Acoustics can also inform us on conspecific or interspecific interactions, which may be unseen from the surface, particularly as the acoustic range of cetaceans far exceeds that of visual detection. This forms another interesting facet of acoustic data, with several sound clips of the recordings for this study indicating killer whale and either gray whale, humpback whale, or sea lion vocalisations co-occurring, possibly representing predator–prey contact between Bigg's whales and mammal prey (see Chapter 1.7). Killer whales are an influential apex predator. They may shape interactions through direct predation, as well as instigating avoidance behaviours in prey, reacting to fear of predation (Baird 2011). As pack-hunters, they may be important in regulating prey populations, both fish and marine mammal species in this area.

Although beyond the scope of this chapter, the final useful observation is the potential for acoustic interaction between whales and vessels. Passive acoustic arrays are a tool to advise managers as to the vulnerability of cetacean species, such as killer whales, to the effects of increased underwater noise, particularly from anthropogenic sources. Thresholds of acoustic pollution, or mitigation measures to lessen the disturbance or potential acoustic masking effect can be derived from recordings such as those used in this study.

Although PAM methods are becoming feasible for measuring temporal and spatial distribution of marine mammals, they still have limitations. Also, with many systems, such as the AMAR used here, the data is not accessible until retrieval of the recorder. Conversely, experienced citizen networks, that coordinate, compile and accurately log data provide information over wide spatial areas and in near real time. Citizen science groups can, therefore, accumulate large data sets that, if they include photographs or notes on behaviour, can be analysed for relative change.

Complementary acoustic monitoring and visual observations fills knowledge gaps of presence and area use by cetaceans. This two pronged approach allows surveys to adapt to a range of species, from those commonly seen but rarely acoustically recorded, to those more vocal but elusive. Data from citizen science networks can support any other methods that may be applied, and have been used to great advantage in many places with many species throughout the world (Dickinson et al. 2012). Not only do these groups provide information, they also provide a route where local communities can actively participate in research and conservation of species in their local waters. This investment pays off when new management action is proposed, and in events such as strandings and entanglements. Researchers working in coastal communities have relied on local boaters and in particular whale watching fleets for support and value the addition of time tested local knowledge of waters and wildlife. In this example, the visual surface data from the citizen science network gives behavioural context to the acoustic data, which itself expands the accuracy of local habitat use estimates.

A version of the work described in this chapter has been published as:

Burnham, R.E., R.S. Palm, D.A. Duffus, X. Mouy, A. Riera. 2016. The combined use of visual and acoustic data collection techniques for winter killer whale (*Orcinus orca*) observation. *Global Ecology and Conservation,* 8:24-30.

## 3.3. Towards an enhanced management scheme for recreational whale watching

### Preface

Changes in call rate and structure (Bradbury & Vehrencamp 1998, Costa 2012, Dahlheim & Castellote 2016, Veirs et al. 2016), and changes in diving and swimming patterns (Corkeron 1995, Ollervides 2001, Williams et al. 2002, Lusseau, 2003, Christiansen et al. 2010, Stamation et al. 2010, Matsuda et al. 2011, Visser et al. 2011) have been noted for several cetacean species in the presence of vessels. Chapter 1.6 outlines the potential acoustic disturbance vessel noise can have on gray whales' acoustics use. In particular the additions from whale watching to whales foraging in Clayoquot Sound were examined. Here I expand on that discussion, with suggestions for management actions that could be applied to local whale watching, and to species and locations further afield. Drawing on the findings from a long-term ecological study of Clayoquot Sound as case study material, I suggest that further thought should be given to whale watching practises. I suggest four areas where further discussion is needed, as new data has become available, which, in turn, should be applied to management. These include recognition of the ecological setting of the whales used as resources for the tourist activity; the acoustic disturbance of these activities, drawing on data presented in part in Chapter 1.6; the impact on more vulnerable species and/or individuals, which may hamper population success (Weilgart 2007), and cumulative effects of anthropogenic activities over the range and life history of whale species. This chapter presents another example of how acoustic information supplements and strengthens ecological and social data to provide managers with improved options to protect whales.

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# Towards an enhanced management scheme for recreational whale watching

## Introduction

Whale watching is a major global tourist activity, with more than a thousand cetacean populations interacting routinely with tour boats (Hoyt 2001, O'Connor et al. 2009). Estimates suggest that 13 million tourists participate annually in whale watching in 119 countries (Garrod & Fennell 2004, O'Connor et al. 2009, Cisneros-Montemayor et al. 2010, Parsons 2012). These numbers are, however, potentially an underestimate, with substantial informal cetacean viewing undertaken on a non-commercial basis.

The potential impact of tourist vessels on whales and dolphins is widely acknowledged (e.g. Baker & Herman 1989, Christiansen & Lusseau 2014, Corkeron 2004, Lusseau & Bejder 2007, Parsons 2012, Lusseau 2014, Higham et al. 2016). Most research that has demonstrated behavioural alterations is based on proximity and density of whale watching vessels (Orams 2000, Higham et al. 2014), but the length of the interaction and how vessels manoeuvre around whales (e.g. speed, approach, predictability) is also important (Gordon et al. 1992, Bejder et al. 1999, Nowacek et al. 2001, Williams et al. 2002). Regulations or guidelines that reduce the disturbance are often 'semi-formal' or voluntary in nature (Garrod & Fennell 2004). They have been developed in absence of strong regulatory frameworks (Higham et al. 2009, Malcolm & Penner 2011) that consider broader biological and ecological consequences (Corkeron 2006), instead resting on the axiom that whale watching is a benign, non-consumptive activity (Duffus & Dearden 1990). Indeed, these regulations rely on the untested foundation that the activity promotes nature conservation, and thus renders no harm (Neves 2010). Most measures are not sensitive to species' behavioural, geographic or temporal context, demographics, life-history stage, or the importance of habitats to individuals or populations. This is extraordinary, given the emotional and economic importance of conserving cetacean resources (Higham et al. 2014).

The almost ubiquitous use of approach guidelines for whale watching, for example, simply limits the distance that vessels can approach a whale. This highlights the over simplification of regulation currently in place. While a safety aspect exists, these directives have little scientific foundation or biological significance, and are used largely because they provide the foundation for an enforceable regulatory procedure. Given that industry success leans on predictable rates of encounter with cetaceans, it follows that whale watching management should make explicit reference to the underlying ecology and life histories of species that brings them to waters within economical viewing domains. Whale watching only succeeds due to the strong ecological or life history attachment to that area by the focal species. Whale and dolphin species often approach coastal waters, and therefore whale watching sites, as part of their life history cycle (Arguelles et al. 2016). These areas may be important for feeding, weaning, reproduction, socializing or resting. The occurrence of these critical life history elements, however, may also make the focal populations more susceptible to stress effects as a result of disturbance. It follows then that we can improve the strength of managing whale-based tourism by modification of conduct to suit the whales more than the operators or managers.

The response to interactions between cetaceans and whale watching vessels has been studied for many species. Effects, if any, are described in the short-term and are focused on changes in activity budgets, respiratory patterns, vital rates, movement and diving patterns, and avoidance behaviours (e.g. Blane & Jaakson 1995, Corkeron 1995, Au & Green 2000, Nowacek et al. 2001, Williams et al. 2002, Hastie et al. 2003, Lusseau 2006, Richter et al. 2006, Stamation et al. 2010, Steckenreuter et al. 2012, Lundquist et al. 2013, Christiansen & Lusseau 2014, Constantine 2014, Lusseau 2014). Disturbance may lead to modified speed and directionality in swimming, cessation of feeding or socialising behaviour, in some cases, increased time spent 'milling' at the surface (e.g. Dahlheim et al. 1984, Dahlheim & Castellote 2016). These changes in behaviour and habitat use can lead to altered distributions of whales over time, affect foraging and reproductive success, increase energetic expenditure and ultimately reduce survival (e.g. Constantine & Baker 1997, Berrow & Holmes 1999, Heckel et al. 2001, Williams et al. 2002, Lusseau et al. 2006). The biological impact of disturbances, alone or cumulatively in time and space, can be assessed from changes in behaviour, which themselves reflect a change in the energy budgeting of an individual or population. For animals that are capital breeders, as many cetaceans are, the consequences of those changes will influence reproductive success.

If cetacean-based tourism is to be sustainable and non-consumptive (Tremblay 2001), then it is necessary to understand the extent and consequences of whale-human interactions, especially if the response of the whale is to divert time and energy from fitness enhancing activities (Frid & Dill 2002, Christiansen & Lusseau 2014). Here, I propose four areas that, if addressed, will strengthen recreational whale watching management. First, regulation should illuminate the significance of habitat units for each species, ideally with baselines and long-term records of ecological variability. The significance of a specific habitat may vary within a population due to age, life stage, behavioural state, or situation. Thus, detailed ecological data is needed to sort natural variability from disturbance-induced change. Second, I suggest a change in the breadth of disturbance-response studies to consider more stressors than simply physical boat presence. I emphasize the need to better understand the impact of anthropogenic acoustic additions to whale habitats. Acoustic disturbance and reduced efficacy of acoustic signalling, including conspecific communications, is particularly important for cetaceans. A third area of reconsideration should be addressed to those individuals and/or populations most at risk. In particular, I target whale watching that focuses on endangered species or populations, and those at a critical life stage, notably cow-calf pairs. This has been recognized in some situations, and more finely nuanced management is applied to some species and areas, but still may not be sufficient. Lastly, I discuss the problem of cumulative effects of stressors. Management actions currently tend to isolate singular events for mitigation, without discussion of dose-response from multiple stressors over time and space.

I will discuss each one of these management components in turn, in each case offering an example based on our long-term research site on the west coast of Vancouver Island, Canada, where eastern Pacific gray whales (*Eschrichtius robustus*) form the core of a whale watching industry during northward migration and summer foraging. I believe the research outcomes act as a guide that is readily transportable to other species and other sites, while acknowledging that site and species specific modifications will be required.

### *Behavioural-ecological value of venue*

Whale aggregation at any site is ecologically or behaviourally mediated (Constantine 2014). Locations used for foraging, migration, mating, calving, or a combination thereof, thrusts whales onto the human recreational stage. Human use may range from single periods, sporadic interactions, to repeated use on both short and long-term cycles. Migratory pathways and breeding/calving areas appear to be the most stable over decades to centuries, while foraging sites vary within, and between years, tied to pulses of ocean productivity and predation pressure (e.g. Burnham & Duffus 2016). Habitat use by whales may continue despite disturbance, representing a trade-off between aversion and fulfilling an energetic need. For example, whales may continue to forage in areas they perceive as high-risk if prey availability is high. Whale watching takes advantage of these ecologically-driven aggregations and will usually focus on the most predictable scenario of presence available.

For this case study, I focus on whale watching in Clayoquot Sound (between 49.24333, -126.10278 and 49.31417, -126.24167, Figure 3.3.1, Chapter 1.4), where foraging gray whales are the focal species for tourism. These whales are part of the Pacific Coastal Feeding Group (PCFG, Calambokidis et al. 2010, IWC 2010), which utilise a network of feeding sites along the migration range, in preference to the primary foraging areas in the Bering and Chukchi Seas. Foraging drives most gray whale behaviour in this area, and so prey productivity is the ecological foundation for commercial whale watching (Dunham & Duffus 2001, 2002, Duffus et al. 2013, Feyrer & Duffus 2014, Burnham & Duffus 2016). Whale foraging census surveys have been conducted during 20 consecutive seasons (Figure 3.3.2, 3.3.3). High foraging intensity in a single season is followed by one to three years of reduced foraging efforts (Feyrer 2010, Burnham & Duffus, in press). Both the highest number of whales in a single survey (n=38) and the highest mean number of whales per survey for a season (n=18.0), were recorded in 2013. This follows several high-prey years (2010-2012), precipitated by an extended period of low foraging efforts in the preceding years (2007-2009, Figure 3.3.3). However, prey stocks in 2016 and 2017 were very low, with the study site largely unused for foraging. This boom-bust cycle, which reflects the capacity of the prey to recover (Family Mysidae; Feyrer 2010, Burnham 2015), creates a variable whale watching environment. Indeed, an earlier whale watching foci, Ahous Bay, only 5 kms to the south (Figure 3.3.1) saw so much foraging pressure that its benthic ecosystem, dominated by ampeliscid amphiods (Percardia Amphipoda), collapsed (Duffus 1996, Burnham & Duffus 2016).

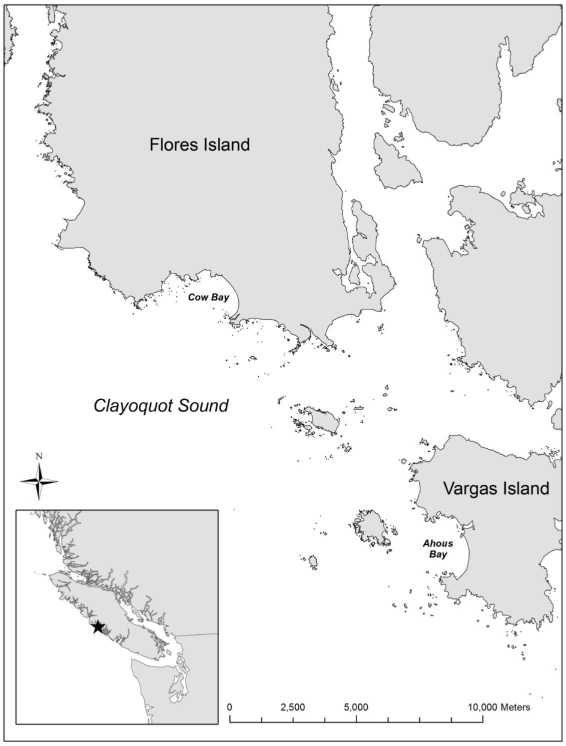

**Figure 3.3.1**: Map of the study site, Clayoquot Sound. Indicated are Ahous Bay, main gray whale foraging region for benthic amphipods, and Cow Bay, main feeding locale for epi-benthic mysid species.

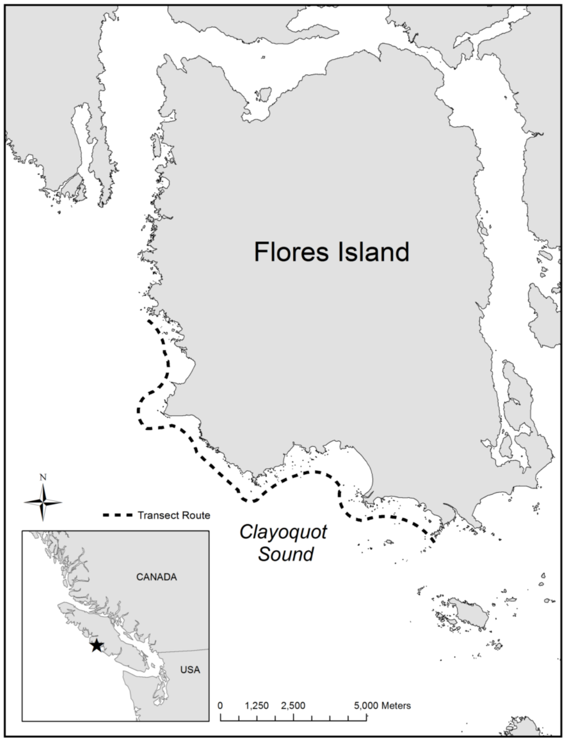

**Figure 3.3.2**: The study area, Clayoquot Sound. The survey route, indicated by the dotted line, follows the 10 m isobath, typically through rocky reef systems which are key mysid habitat.

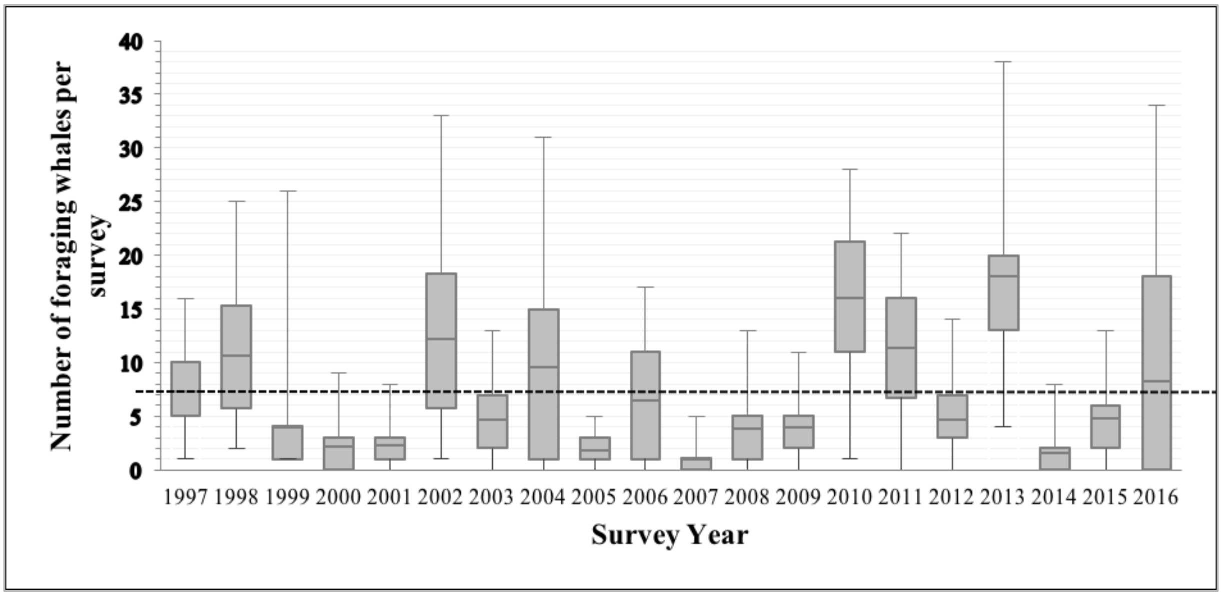

**Figure 3.3.3**: Boxplot to indicate foraging intensity in the study site, calculated by the number of foraging whales sighted per transect survey. The dashed line is the overall average for all years, and allows for comparison between years.

To focus on the issue of how whale watchers respond to differing ecological conditions, the fleet was observed over a two-year period in the summers of 2012 and 2013 (see Stevenson 2014 for detailed methods). During this study, 54 individual whales were subject to whale watching, all of which were identified in our photographic identification catalogue, and had used the study site to forage in at least one previous year. In spite of potential disturbance from whale watching, individual animals continue to return to Clayoquot Sound if prey is available, with more than half (51.48%) of whales documented to have used the site known to have foraged there for 2 or more summers.

The ecological message is the variation in significantly different foraging effort. In 2012 the mean number of foraging whales was 4.7 per survey, and in 2013 18.0 per survey. The overall 20-year mean value is 7.1 whales per survey, used as a means to differentiate ‘low’ foraging (2012) from ‘high’ foraging (2013) years (Figure 3.3.3). In 2012, the mean number of boats per whale watching encounter was 3.8 ±2.39 (n=97), while that same measure for 2013 was significantly lower (t(130.75)=7.1, p<0.001) at 1.94 ±1.19 (n=113). Similarly the whale watching encounter lengths differed, averaging 21 m 11 s in 2012 (n=94), and 17 m 35 s in 2013 (n=134).

Whale numbers were high in 2013, but it may have been difficult for vessel drivers to find whales in 2012. In 2013, whale watching vessels were able to be selective and search out a whale on their own, whereas this was limited in 2012. A typical day in 2013 would find between 15 and 20 whales in the core whale watching area, allowing for one or two boats with a single animal. This contrasts to 2012 where vessels had to share the typically 2 to 4 whales in the study area with 2 or 3, and occasionally many more, other vessels. Scenarios of multiple vessels per encounter, for longer viewing periods, can have both cumulative and multiplicative effects (Richardson et al. 1985, Blane & Jaakson 1996, Erbe 2002). This altered behaviour of the fleet is a direct product of ecological changes wrought by the predator induced depression and recovery process of the whales' prey, and shows that ecological dynamics alter whale watching practises. In a low prey year, each foraging whale could experience greater vessel presence in number and/or time of vessel encounters, creating a scenario of increased stress from whale watching when the individual is already subject to the ecological stress of reduced foraging opportunities.

Industry pressure on whales changes depending on the ecological dynamics that influence whale presence, which in turn has been influential in studies of vessel compliance to whale watching regulations (e.g. Wiley et al. 2008). Management of whale watching in Clayoquot Sound does not currently account for year-to-year variation in whale presence. Vessel number and duration of encounters are typically based on opportunity, and proximity to port (Duffus 1996). If the industry is to mediate activity based on the ecological scenario, relevant tools may include limiting the number of boats allowed in an encounter with individual whales, as well as limits on the encounter length, particularly during 'low whale' years. It is conceivable that the encounter time for each individual whale accumulates through the season, and it could reach a limit after which a negative, long-term impact is introduced. Also, for whales in Clayoquot Sound the timing of the most intense whale watching pressure on an individual may influence the level of impact. If a whale experiences disturbance in the early summer, while edacious to recoup energy stores, this may have greater influence on overall summer foraging gains, than if the same pressure is experienced later in the season.

Experimenting with management proposals, while simultaneously measuring behavioural responses from whales and visitor satisfaction, can reveal the influences of these limits on ecological and social variables. The challenge of site specific solutions reflecting ecological fluctuations will mean that management actions would need to be dynamic and flexible. Explanations of ecological considerations from the vessel operator, as an interpreter, to tourists may better manage the expectation of close approach and types of encounters with whales (e.g. Finkler 2001, Malcolm et al. 2017).

### *Acoustic disturbance by whale watching*

Many factors play into the response of whales to vessels (Williams et al. 2001). Interactions between whales and whale watching vessels are often measured as a response observed in surfacing behaviours elicited from a vessel. They are based on presence-absence of boats as the impact-control experiment. Here, I consider the invisible yet significant additions of human generated noise to ambient soundscapes of cetaceans from whale watching. I examine the effect of sonic additions to whales foraging in our study area in Cow Bay by examining the acoustic behaviour in the presence of vessels and aircraft. In terms of acoustic disturbance in a whale watching scenario, research has not frequently focussed on vessel-whale interactions, and if there is a discernable response in the whales' acoustic behaviour. Even less attention has been given to the noise emitted from aircraft that crosses the air-water barrier (Luksenburg & Parsons 2009).

A species is considered most sensitive to noise in the frequencies it employs for conspecific communications (Thompson et al. 1979, Watkins & Wartzok 1985, Clark 1990, Matthews et al. 1999, Wartzok & Ketten 1999, Hastie et al. 2003, Parks et al. 2009, Mooney et al. 2012, Cranford & Krysl 2015). Baleen whale hearing extends from 10 Hz to 30 kHz, with most sensitivity in the 20 Hz to 2 kHz range (Cummings & Thompson 1971, Ketten 2002). This also encompasses the frequency range of gray whales vocalisations. Their vocal repertoire consists of four 'core' call types, with additional call classes that describe a possible 'motherese' employed only by mothers and calves during the weaning period (Dahlheim et al. 1984, Dahlheim 1987, Ollervides 2001, Charles 2011). Noise from vessels, increasing the ambient levels, can mask calls and, if in sufficient amplitude or duration, create a physiological change in hearing sensitivities (Erbe 2002, 2012, Weilgart 2007). Conspecific vocalisations may be indistinguishable from vessel noise because both signal and noise are in the same frequencies, or the amplitude of the noise overpowers the calls. Both can impact an acoustically sensitive species' ability to perform auditory scene analysis, and shorten the range over which they are able to send and receive information, their active space (Clark et al. 2009, Merchant et al. 2015, Burnham 2017). This in turn affects their ability to detect predators, locate prey, and maintain contact with conspecifics. Whales can mitigate this affect by altering calls, in rate, type, or composition, but that may have energetic costs.

Here, I examine the acoustic signatures of the Clayoquot Sound whale watching fleet, and the changes in calling by foraging gray whales. A passive acoustic monitoring (PAM) system was deployed in Cow Bay (Figure 3.3.1), for summer 2015 and 2016. Visual observations were made concomitant to the recordings to annotate the acoustics (see Chapters 1.5, 1.6 for more detail on the deployments and methods). The presence, number and demographics (single whales, cow-calf pairs or both) of gray whales were noted, as was the presence and proximity of whale watching vessel(s) or aircraft, vessel or aircraft type. Spectrograms (256-point Hann window FFT with 50% overlap), were used to visualise recordings, and extract characteristics of gray whale calls and vessel disturbance. The acoustic parameters of each vessel type (distinguished by size, single or twin engine, and inboard or outboard motors) were defined for transiting vessels and for those in the bay and within 2 km of foraging whales, as well as whale watching float planes (see Chapter 1.6 review for more detailed methods).

All vessel signatures significantly altered the average ambient noise levels in the frequencies pertinent to gray whale calls (Welch's t(1920.253)=-3.957, p<0.001), however proximity of vessel and passage directly into Cow Bay (Welch's t(557.008)=-1.880, p=0.061) did not. The presence of whale watching vessels shaped the diurnal patterns of ambient noise, whereby a twelve-hour cycle of increased ambient noise levels occurred in daylight hours through the summer, with a slight depression in levels midway through the day, when vessels return to port to exchange customers (Figure 3.3.4). Ambient levels were also elevated over weekends and statutory holiday days for both 2015 and 2016, possibly resulting from an increased number of tours.

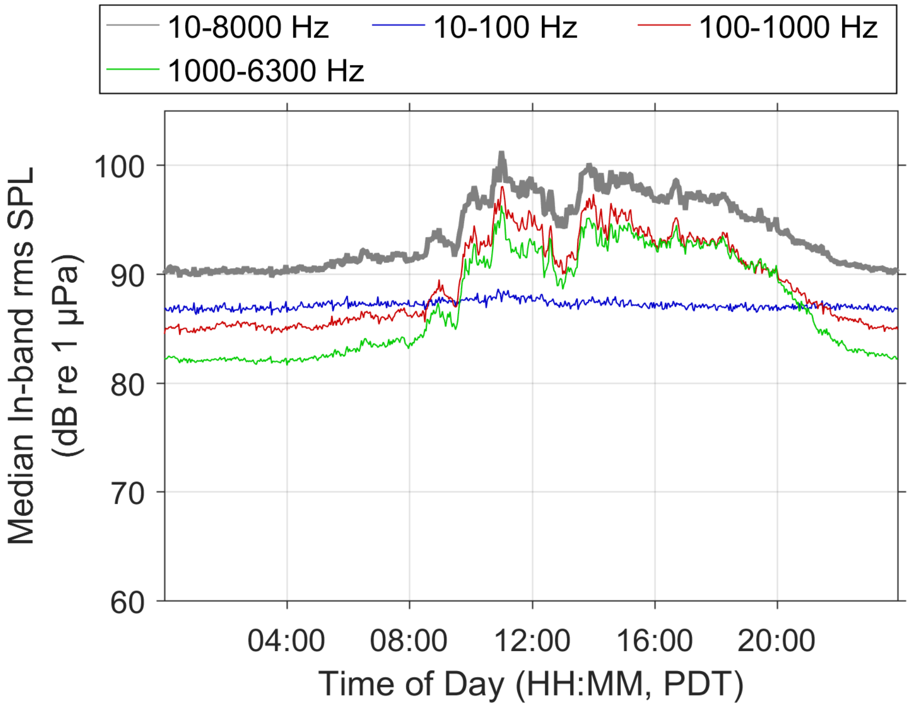

**Figure 3.3.4**: The average daily patterning of ambient noise levels received by the AMAR during deployments during summer foraging periods for gray whales. The changes seen in sound pressure level (SPL) received reflects vessel presence in the area

Typically, small whale watching vessels are considered to emit higher frequency noise due to their smaller, shallower propellers (Erbe et al. 2012). Here the acoustic signatures for all whale watching vessels and aircraft extended into the low frequencies, many below 200 Hz (Table 3.3.1). This means that noise from vessels and planes is almost certainly detectable by gray whales, and has the potential to impact their ability to communicate with conspecifics. This may be especially true for vessels actively watching whales where the distance between the whale and the vessel may be no more than 100 m, if the operator is adhering to ‘Be Whale Wise’ guidelines of approach (Strawberry Isle Research 1995, Schaffar et al. 2009, Matsuda et al. 2011, Tseng et al. 2011, Visser et al. 2011, DFO 2013).

**Table 3.3.1**: Metrics from acoustic signatures of vessel passages. 'Curve' represents those measures taken from Lloyd mirror curves representing a direct passage over the AMAR. Transit are those vessels passing, but not entering, Cow Bay.

| | Vessel Type | Size (ft) | Engine config. | Low freq. | Peak freq. | Center freq. | Approach time |
|---|---|---|---|---|---|---|---|
| Curve | Covered, aluminum | 35 | Twin, inboard | 84.58 ±65.10 | 207.35 ±87.71 | 357.25 ±143.40 | 234.47 ±123.42 |
| Curve | RHIB | 29 | Twin, outboard | 55.66 ±35.87 | 198.64 ±114.90 | 245.87 ±130.36 | 157.29 ±88.78 |
| Curve | Covered, aluminum | 30 | Twin outboard | 61.62 ±25.68 | 419.92 ±605.70 | 415.09 ±592.28 | 157.11 ±66.33 |
| Curve | Covered, aluminum | 30 | Inboard | 54.12 ±29.69 | 328.22 ±467.67 | 367.47 ±444.84 | 135.02 ±64.94 |
| Curve | Covered, aluminum, split hull | 42 | Twin, inboard | 30.20 ±19.00 | 113.93 ±26.83 | 272.17 ±123.46 | 94.67 43.58 |
| Curve | Open, Fibre glass | 24 | Twin, outboard | 55.50 ±41.51 | 191.90 ±101.53 | 198.70 ±116.54 | 129.09 ±91.69 |
| Curve | Recreation | 22 | Twin, outboard | 51.55 ±16.88 | 143.67 ±50.75 | 213.63 ±75.15 | 192.62 ±82.29 |
| Transit | Covered, aluminum | 35 | Twin, inboard | 87.20 ±24.04 | 318.60 ±193.04 | 412.60 ±44.83 | |
| Transit | RHIB | 29 | Twin, outboard | 52.10 ±48.08 | 82.25 ±75.59 | 101.55 ±51.12 | |
| Transit | Covered, aluminum | 30 | Twin, outboard | 58.90 - | 132.8 - | 374.00 - | |
| Transit | Covered, aluminum | 30 | Inboard | 69.24 - | 108.19 - | 146.5 - | |
| Transit | Open, Fibre glass | 24 | Twin, outboard | 72.5 - | 128.4 - | 190.9 - | |
| Overhead | Float plane | | Cessna 185 | 60.56 ±25.12 | 238.64 ±401.32 | 256.68 ±270.16 | 59.52 ±46.52 |

During the summer months, human-generated noise is a persistent feature of the underwater soundscape in Clayoquot Sound. How this is received and interpreted by the whales is unknown, however, I observed some alterations in vocalizations in the presence of human introduced underwater noise (Chapter 1.6). Shorter range modulated call use significantly increased as ambient noise levels increased ($r_s$ =0.130, p<0.001). Calling was significantly altered in the acoustic presence of vessels (Mann-Whitney U, p<0.001), driven, in this case, by changes in more long-range call type use (class 2 upsweeps and 3 moans, Mann-Whitney U, p<0.001). All these core call classes showed alteration in the presence of vessels in the immediate area, using Lloyd mirror curves as an indicator of vessel proximity (Mann-Whitney U, class 1a: p=0.049; 1b: p=0.012; class 2: p<0.001; class 3: p<0.001, call classes according to

Dahlheim 1987). The passage of aircraft also significantly increased calling, replicating the response to vessels (class 2: Welch's t(195.813)=-2.024, p=0.044; class 3: t(191.226)=-2.481, p=0.014). Calls were typically lowered in the extent of their harmonics and peak frequency, and were significantly shortened in a state of elevated ambient noise.

The rate of use of 'motherese' call types declined with elevated ambient noise ($r_s$ = -0.113, p<0.001). Also, a significant decrease in overall use of these call types (Welch's t(2647.389)=2.336, p=0.020) occurred when vessels were present, and in close proximity (Welch's t(638.298)=3.349, p=0.001). The calling rate in the presence of overhead aircraft was also significanty decreased (Welch's t(182.630)=2.154, p=0.033). Again, call parameters of frequency extent and peak frequency were shifted into the lower frequencies. Call length was typically longer in elevated noise conditions (see Chapter 1.6). Reduced calling and proclivity to complement low-amplitude vocals with tactile cues, may make reunion of separated cow calf pairs, typical during nursing and weaning, more difficult. Indeed, the 'motherese' calls types may be employed to strengthen and maintain bonds during the mother's foraging bouts, to re-instate close contact for nursing, or warn of predators. The overlap in the frequencies used in these call classes, and the acoustic signatures of the whale watching fleet show potential to obscure call projection.

The lengthening of calls or call phrasing, increased repetition in calls and call sub-units, and elevated amplitude of calls, as well as alteration of the fundamental frequency or frequency extent of the calls have been noted for mysticete species in the presence of noise (Bradbury & Vehrencamp 1998, Miller et al. 2000, Parks et al. 2007, 2009, Rolland et al. 2012). Indeed, increased calling and repetition within calls has been noted for gray whales when in the presence of vessel noise from outboard engines (Dahlheim & Castellote 2016). However, modified calling rate and composition, with the use of suboptimal frequencies, can increase signalling costs, and reduce the efficacy of the calls (Bradbury & Vehrencamp 1998, Castellote et al. 2012). Acoustic masking is considered an increasing threat to marine mammals, in particular low frequency specialists such as baleen whales. Importantly, masking may cause the separation of cow-calf pairs, whose specific 'motherese' signals are likely limited in their capacity for modification to overcome added noise.

Policy makers have not yet proposed explicit, quantitative limits on noise emissions applicable to whale watching. Most vessel operators are likely unaware of the extent of their acoustic additions into the whales' soundscape. In other noise generating scenarios, managers have relied on the '120 dB criterion' exposure, derived from noise played during in-field experiments at this level consistently eliciting avoidance behaviours (Malme et al. 1983, 1984, Richardson et al. 1985, 1990). I suggest that management take a more conservative approach and should simply aim to keep quiet areas quiet and quieten noisy areas. At the operator level, acoustic disturbance can be reduced by shutting engines down, where feasible, in proximity of whales, minimising vessel manoeuvring, as well as increasing approach distance. Vessels can be quietened by using propellers designed to limit cavitation, and increased engine maintenance which limits mechanical noise (Southall 2005). Regulatory action could outline time-area restrictions to vessel presence, or the designation of 'quiet zones'. These would need to be both species and area specific, with the minimum distance and/or noise exposure defined at the point which stress is first noted.

### *Whale watching of endangered species or during vulnerable life history stages*

The physical presence of whale watching vessels as well as the noise they introduce may elevate stress for whales (Blane & Jaakson 1995, Bejder et al. 1999, Au & Green 2000, Nowacek et al. 2001, Williams et al. 2002, Lusseau 2006, Nowacek et al. 2007, Williams et al. 2011, Pirotta et al. 2013). Visually identified responses have been frequently noted (Corkeron 1995, Ollervides 2001, Williams et al. 2002, Christiansen et al. 2010, Stamation et al. 2010, Matsuda et al. 2011, Visser et al. 2011), with implications for group size and cohesion (Bejder et al. 2006, Arcangeli & Crosti 2009). However, whales may also be negatively impacted by vessel presence without any obvious changes in behaviour (Beale & Monaghan 2004a,b). Physiological responses to stress have not been fully defined for cetaceans, although altered vital rates and expressions of stress hormones suggest disturbance (Christiansen & Lusseau 2014, Senigaglia et al. 2016). Considered together, the overt expressions of disturbances and more covert stress responses may change whale distributions and habitat use, reproductive success, and survival (Berrow & Holmes 1999, Constantine & Baker 1997, Heckel et al. 2001, Lusseau 2006). For species, groups, or individuals that are already deemed vulnerable this is a particular concern.

In important habitat areas during critical times the impact of disturbance from whale watching may be disproportionately greater than others (Lusseau & Bedjer 2007). Responses by individuals are likely to endanger the viability of small populations, with reduced levels of the ‘threshold of concern’, where disturbance may limit population growth (Lusseau 2006, Lusseau & Bejder 2007, Villegas-Amtmann et al. 2017). For species that experience negative energy states, such as baleen whales following migration and fasting during breeding periods, this may be of even greater concern.

There is an increasing demand from tourists to interact with animals that are rare or endangered (Rodger et al. 2007, Semeniuk et al. 2010). Re-defining whale watching to reduce impacts on endangered populations is challenging, with management at the very least establishing exclusion zones around ecologically important habitat. Indeed, Lien (2001:3) suggests that whale watching should not affect ‘life processes’, so as to retain viability in the focal population. However, understanding these processes and the thresholds to disturbance are difficult, as everything concerning a live whale is a life process.

In my case study, gray whale populations have recovered following the cessation of whaling (Laake et al. 2012), however the whales foraging in Clayoquot Sound are members of a genetically-distinct sub-group (Calambokidis et al. 2010, Lang et al. 2011, Scordino et al. 2011), the PCFG, that number in the mid-hundreds. A recent reassessment by COSEWIC (2017) now classifies this group as Endangered in Canadian waters. In gray whales, migration and overwinter fasting has been shown to reduce body weight as much as 29%. Animals in an energy-deficient physiological state likely experience exacerbated energetic draws when modifying behaviour. Therefore, costs of mitigation behaviours are likely at their greatest at the beginning of the foraging season when the need to replenish reserves is highest (Bradbury & Vehrencamp 1998, Costa 2012, Veirs et al. 2016).

Avoidance behaviours such as altered swimming pattern and speed, and shorter ventilation intervals have been noted for gray whales in the presence of vessels (Malme et al. 1983, 1984, 1986, Würsig et al. 1999, Ollervides 2001, Dahlheim et al. 1984, Dahlheim 1987). On a physiological level, to understand sub-injurious (Moore et al. 2006) and sub-lethal effects of anthropogenic disturbance, a behavioural threshold needs to be determined. In turn, the cost of surpassing this threshold should be estimated. It is significant if whale watching elicits behavioural changes that affect the energetic balance of an individual, for example the cessation of feeding when a whale was being observed by a tour boat or aircraft. Abandonment of a feeding location may come with several costs, including possibly the need to re-establish territory, increased predation, or lesser quality prey in the alternative habitat. Distinct behavioural change and site abandonment has not been described for the whales foraging in Clayoquot Sound, but this may be representative of a balance between stress costs and the need to replenish energy reserves. It is still unclear how the acoustic response may be tied to other behaviours. In light of this lack of knowledge I suggest that endangered populations, or population sub-groups, should be removed from the recreational resource base or at least subject to more adaptable, detailed management programs. We can readily assess why populations are endangered, but mechanisms of recovery are more complex, and likely not static (Clapham et al. 2008). We can, however, make the simple assessment that any addition of human induced stress will not support population growth.

The demands of pregnancy, birth and lactation presumably intensify the negative energy state in cows with calves. The stress resulting from maternal demands, and protection and maintenance of the calf, may further enhance this, increasing sensitivity to disturbance. Mothers with un-weaned young are easy targets for whale watchers as they typically move more slowly, have shorter dive intervals, and spend more time at the surface (Szabo & Duffus 2008).

Mothers and calves are generally more sensitive to whale-watching boat interactions. They are believed to interpret the presence of tourist vessels as a risk (van Parijs & Corkeron 2001, Stensland & Berggren 2007, Stamation et al. 2010, Christiansen & Lusseau 2014). It has also been suggested that calves are more prone to vessel strikes (Cartwright et al. 2012), with vessels maneuvering between a mother and its calf to afford better views for customers (Garrod & Fennell 2004). Cow-calf pairs use Clayoquot Sound as a nursing and weaning site, even in periods with depressed prey resources. They frequent shallow sandy sites, with some separation from other foraging whales (Chapter 1.4, Unpublished Whale Lab data). These provide calmer waters for nursing, while affording predator protection. The pairs are acoustically hidden in the surf noise (see Chapters 1.4, 1.5, 1.7), and protected from one angle of approach. However, evasive movements away from boats may expose them.

For cow-calf pairs the energetic budget is more finely balanced; compromised foraging opportunities for the mother may lead to less energy delivered to the calf, reducing its body size, increasing its susceptibility to predation or mortality. Particularly for mother-calf pairs, response to stressors seem to mirror anti-predator tactics, whereby the strength of response my represent the level of perceived risk (Frid & Dill 2002).

Understanding how and why an animal responds to stressors requires the integration of knowledge of behaviour, physiology, ecology and population dynamics. As with more vulnerable species, I suggest that individuals more sensitive to stressors, in this case by life history stage, should not be part of the recreational resource base. There should be greater restrictions on viewing cow-calf pairs or cetacean groups with calves.

### *Risk assessment and cumulative effects*

Quantifying exposure to a disturbance is the first step in evaluating the risk and impact of whale watching on an individual or population. Location and behaviour are important elements; a migrating gray whale that moves through a whale watching site may, for example, be less affected than an individual of a resident group inhabiting or spending prolonged periods in a site to feed (Christiansen & Lusseau 2014). The schedule of disturbance is also key, where being disturbed multiple times in a day, or over consecutive days, may have a greater effect than the same number of encounters with whale watching boats over the summer season (New et al. 2014). The migrating gray whale may be subjected to whale watching vessel approaches once or twice in total in these waters, while resident individuals may encounter tourist vessels on a daily basis.

For assessing risk and implications of disturbance it is important to distinguish between ‘aggregate exposure’, which is the combined exposure of one stressor (e.g. whale watching), and ‘cumulative risks’, which is the combined effect from exposure to multiple stressors over a single period of time (e.g. whale watching, larger commercial and cargo vessels, reduction of a prey source). The spatial and temporal scale of these considerations can vary from singular events or a focal area to the lifetime and full range of the animal.

In foraging areas, the energetic cost should simply be calculated by estimating energy expended and not acquired (Costa et al. 2016), but the currency of this relationship is difficult to measure. The graduation of responses to and recovery times from stressors are also not fully understood. In some cases the response to the disturbance, for example vessel noise, can be high, but the cumulative exposure low, and so overall little to no effect is determined (e.g. Christiansen & Lusseau 2015). The cost to individual fitness is mediated by the behavioural response and the rate at which this is generated, especially when energy is redirected from fitness-enhancing activities to stress response (Frid & Dill 2002, Christiansen & Lusseau 2014). Mitigation and management strategies must also understand the process of risk perception in cetacean species (Pirotta et al. 2015). For example whales are likely subject to acoustic additions to the soundscape on a much wider spatial scale than currently appreciated.

To sharpen the characterisation of cumulative effects, behavioural studies should focus on the relationship between the level of disturbance and the level of response, and the role of the behavioural and ecological context in the dose-response relationship. Although stressors are considered additive in terms of dose, different stressors may produce a synergistic response (NASEM 2017). To make matters more complex, the tolerance level of an individual should be determined, as well as the dose, or accumulative doses for several stressors simultaneously. There is a threshold that causes an animal to change reactionary strategies, for example, changing from a graduated linear response to vessel presence to that of complete habitat abandonment (Lusseau & Bejder 2007). That threshold of disturbance is the switch from short to long term responses (Constantine 2014, Lusseau & Bejder 2007), which is difficult to identify before it is reached (Corkeron 2004).

Human induced disturbances of whales interact and increase in complex ways. Few studies quantify the effect of a single stress on the population level (Wartzok et al. 2005, Tyack 2008), yet fewer still the synergistic effects of multiple sources (Jasny 2005, New et al. 2014). The Population Consequences of Disturbance model (PCoD) (NRC 2005, New et al. 2014, King et al. 2015) proposes a theoretical framework to determine meaningful population responses, with assumptions of reduced maternal condition and reproductive viability, increased offspring mortality, and eventually increased adult mortality resulting from disturbance. As capital breeders, changes to the reproductive success of baleen whale species is likely where the full implications of stressors will manifest (Stephens et al. 2009), resulting from reduced body condition of females subject to periods where energy expenditure is increased and/or energy acquisition is decreased. From this perspective, PCoD creates the structure to understand non-lethal disturbances, such as whale watching, as a consumptive ‘take’ activity, incorporating the consequences of behavioural compensation and altered body condition (Beale & Monaghan 2004a, Christiansen & Lusseau 2014, 2015).

There is little empirical evidence in the literature from which to build experimental models to this end, however King et al. (2015), developed an interim model of PCoD to apply to populations where empirical evidence is sparse, in their case based on harbour porpoise

(*Phocoena phoceona*). In their model, the authors suggest using explicit population or spatial management units within which to identify ‘a set of measurable behavioural or physiological responses that may affect individual fitness’ (King et al. 2015:1151). This mirrors some of the facets that I have outlined here applied to whale watching as the dominant stressor, then scaling disturbance to reflect duration, repetition and other cumulative effects.

The coastal nature of gray whale habitat use affords us relative ease in studying their life history and ecology. However, this habitat preference also increases their exposure to human disturbance. Here I have examined disturbance in a foraging locale, but gray whales are also the focal animal of whale watching activities in their breeding lagoons and along the southern half of their migration route. Also, along that route, for much of its extent, the whales follow or traverse heavily used shipping lanes. In this case I am examining a sub-population of foraging gray whales, the PCFG, classed as ‘Endangered,’ that do not simply migrate through, and are therefore often subject to repeated whale watching encounters over the summer months, more akin to a resident population than a transiting individual (Christiansen & Lusseau 2014).

The example of acoustic disturbance demonstrates the difficulty in typifying the effect from a singular stressor, and yet the whales deal with many stressors simultaneously. Food limitation and dwindling prey resources, and changing ocean regimes will heighten their sensitivity. Few management schemes are nuanced enough to incorporate acoustics, ecology and life history, while also considering the cumulative effect of vessel presence and the associated behavioural change. Also, part of the challenge is to apply this to the whales’ full range and determine the overlap of stressors. A piecemeal approach may be the first step in understanding the interaction of cumulative effects, but would likely be a misrepresentation as these impacts could be additive, synergistic, or antagonistic (Williams et al. 2016). Whales utilising Clayoquot Sound represent a test subject for this kind of to work, as the ecology of the animal is well known and a long-term time-series data is available. However, there are still significant knowledge gaps in the spatial and temporal scales of disturbance.

## Conclusions

Whale watching has grown into a major tourist activity, but for each tourism site, operations rely on a predictable and stable presence of whales. Managers and operators seem perplexed when whales desert sites that have been assumed to be permanent. Those assumptions arise because the ecological and life history ties to habitat use have not been recognised. As a result, regulations and guidelines for conduct around whales lacks the scientific foundation needed to accomplish the primary goal of management, to reduce disturbance of whales.

Here I suggest four areas of consideration for management to encourage sustainable whale watching. The key is being able to determine which aspect of, and at what level, the stressor becomes ‘biologically relevant’. I have focussed on ecological foundations and acoustic disturbance. Increased noise competes with successful signalling for navigation, prey location, and group cohesion. I suggest spatio-temporal restrictions (Tyne et al. 2014), such as ‘quiet zones’/‘noise requiems’, resting areas, and limited access by tourism operations to critical habitat units, as well as viewing restrictions on vulnerable species and life stages. Selecting the appropriate context and species-specific spatial and temporal management units will be critical to the success of the management.

It could be argued that whale watching activities in areas such as Clayoquot Sound have matured to a point they now surpass the ‘limits of acceptable change’ (Duffus & Dearden 1990), where carrying capacity of the number of operators exceeds a sustainable level in both the local human community and the ecological community. In some years the number of vessels surpasses that of the number of whales annually returning to forage. This will mean more seasons like 2012, with higher encounter rate and time per individual, and perhaps pressure on drivers to violate rules of approach and code of conduct to ensure customer satisfaction.

In the general case, however, the disturbance by whale watching vessels is considered small in comparison to that resulting from shipping or seismic surveys (New et al. 2015). I challenge that consideration based on the significance we give to the difference between a human-centred and a whale-centred approach to management. Industry growth of whale watching has been rapid. It was not long ago that businesses were small, with few vessels engaged in whale viewing. Equally, early research efforts were few and preliminary in nature. That is no longer the case. Whale watching is an important contributor to community economies in numerous places, and research has built a solid foundation in many locales. However, results from these works increasingly raise suspicion we have not met the needs of the whales, and are moving ever more away from the ‘no-take’ directive originally stated for whale watching. Whereas many cite whale watching as a medium for increased awareness of cetacean conservation issues (e.g. Mayes & Richins 2008, Weaver 2008, Zeppel & Muloin 2008, O'Connor et al. 2009, Cisneros-Montemayor et al. 2010, Orams, 2013, Filby et al. 2015, Malcolm et al 2017), I suggest that practises can and must advance significantly for this tourism-centered activity to fulfil its non-consumptive promise.

## 3.4. Conclusions: Talking to managers not yet listening to whales

This section draws on findings of the coastal research in Clayoquot Sound, both long-term ecological studies implementing visual survey techniques, and the more recent use of passive acoustic monitoring (PAM). Clayoquot Sound is important for cetacean species, as well as a key site for a thriving whale watching industry. The area is a foraging and weaning site for several whale species, in particular gray whales (*Eschrichtius robustus)* (Chapters 1.2-1.7) and occasionally humpback whales (*Megaptera novaeangliae),* as well as being frequented by both resident and Bigg's killer whale (*Orcinus orca*) ecotypes (Chapter 3.2). The tourist industry here, based out of Tofino, is reliant on the consistent use of these waters by whales, but themselves likely add to the stressors that may eventually lead to whales abandoning the site.

Chapter 3.2 shows the additions that passive acoustic monitoring can make when used in complement with visual methods to form a more comprehensive, year-round view of whale site use. Existing and ongoing monitoring of ocean ecosystems and ecological processes are sporadic in time and patchy in space (Okey 2018). The case presented in Chapter 3.2 is of killer whales overwintering in Clayoquot Sound, where acoustic recordings are compared to the sighting records of a citizen science network. It also tells of the difference in results when data is collected over differing spatial and temporal scales, whereby non-uniform effort may bias conclusions on the geographical or spatial distribution of whale use of an area. The use of several methods concurrently, here PAM, visual observation and photo-identification, allows any future management action to be based on the most thorough data possible.

Chapter 3.3 acts as a summary of findings from a long-term study of gray whale ecology in Clayoquot, in addition to that presented in Chapter 1.4, as well as highlighting results from this study that act as examples of how whale watching is currently mismanaged, and may be detrimental to the species that form the foundation of their business. Amongst the points highlighted is the potential sensitivity of gray whales to anthropogenic noise, here using whale watching vessels and aircraft (also see Chapter 1.5) as noise sources, and how being subject to consistent vessel noise may affect their ability to successfully forage at a time when replenishing blubber reserves is paramount. In the light of growth of cetacean-based tourism and the increase in the breadth and depth of research on whale species, I suggest a stronger ecological and life history grounding of the codes of conduct imposed on vessel operated, aimed at minimizing whale disturbance. This comes at a time when, first, a re-assessment of the gray whale population has designated the local population as endangered, with its numbers only into the several hundred (Calambokidis et al. 2010, COSEWIC 2017). Then, most recently, in the summer of 2018, the Department of Fisheries and Oceans amended regulations regarding vessel-marine mammal interactions, increasing vessel approach distances for some threatened whale species (DFO 2018). These are good first steps, however in Chapter 3.3 I suggest that approach distances, while offering an enforceable regulation, are not scientifically grounded, and so instead I offer four areas needing greater consideration to form better regulation for cetacean-based activities. First, the ecological setting of these interactions needs to be considered more. Greater recognition and quantification of stress sources is needed, both singularly, here using the example of acoustic disturbance, and as part of the many stresses a whale faces on various temporal and spatial scales. Finally, and perhaps most controversially, I suggest the exclusion of the most threatened species, or most sensitive individuals in a population, from the resource base of whale watching altogether.

In recognising the use and importance of acoustics by whale species (see Sections 1 and 2), it becomes apparent that we have been underestimating the area over which individuals are gaining and sharing information, as well as the negative impacts anthropogenic activities might have on important processes. While it is argued that whale watching has a role in education and the conservation of cetaceans, considering the impacts of vessel- or aerial-based viewings for approximately 12 hours a day, 7 days a week for several months as is the case for gray whales in my example, and in light of findings in previous chapters, it is questionable whether this tourist activity remains ‘no take’. The suggestions made in Chapter 3.3 are meant to act as stimulants for a reconsideration of regulation in vessel-whale interactions. Without action, the whales themselves will likely become the indicators of the switch from non-consumptive to detrimental, with the negative effect of stressors outweighing the ecological benefits of that area possibly precipitating site abandonment.

## 3.5. Management Implications Section References

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# 4. Part 4: Context and Conclusions

*By seeking and blundering we learn.*

Johann Wolfgang von Goethe (1749-1832)

## 4.1. Acoustic communication in animals: from function to meaning

The material presented in the gray whale case study, brings together evidence of vocal repertoire learning, the use of a 'motherese', and the possibility of call types being tied to a behaviour or referent to an internal state (Chaptet 1.8).

Vocal repertoires of whales and dolphins are acquired through vocal learning; likely an interaction between innate processes and learning through copying, mimicry, and practice. There is a period of 'babbling' described before the use of the adult repertoire is fully stabilised (Lenneberg 1967, Marler & Peters 1982, McCowan & Reiss 1997, Lipkind et al. 2013). This period maybe marked by the use of adaptive mother-calf calls ('motherese', in gray whales see Ollervides 2001, Charles 2011). Mastery of phonic structures and their production, including the ability to manipulate airflow to produce calls, increases as the whale matures (Cazau et al. 2013).

The repertoire and call structures differ between species, especially comparing baleen and toothed whale vocalisations. The identity of a cetacean to the species, group, clan, pod, and even individual level is possible from the structure and form of its vocalisations. Group-derived repertoires and dialects are most clearly described for killer whale matrilines (e.g. Ford & Fisher 1982, 1983, Ford 1991, Musser et al. 2004) and the click-codas in sperm whales (e.g Watkins & Schevill 1977b, Alder-Fenchel 1980, Watkins et al. 1985, Whitehead & Weilgart 1990, Richardson et al. 1995, Weilgart & Whitehead 1997, Gero et al. 2016). In baleen whales the geographically distinct calls have been noted and group membership conferred in song (e.g. humpback whales, Garland et al. 2013, and fin whales, Širović et al. 2013, 2017).

Vocalisations tied to behaviours, for example those with a role in traveling, feeding and mating, have been described (see Chapters 1.2-1.8, 2.4). Whereas echolocation is used to navigate and locate prey in odontocetes (*Phocoena phocoena,* Verfuss et al. 2009, Wiseniewska et al. 2015), narwhals (*Monodon monoceros*, Miller et al. 1995), sperm whales *(Physeter macrocephalus,* Madsen et al. 2002, Miller et al. 2004) and beaked whales *(Hyperoodontidae spp.,* Johnson et al. 2004, 2008, Madsen et al. 2005), described as a kind of auto-communication, baleen whales rely on counter-calling between conspecifics, and returns from low frequency signals forming echo-sensing processes to perform the same tasks (Patterson & Hamilton 1964, Norris 1969, 1966, Payne & Webb 1971, Thompson et al. 1979, Ellison et al. 1987, McDonald et al. 1995, Clark & Ellison 2004, Oleson et al. 2007a, b, Širović et al. 2013, Burnham et al. 2018, Chapter 1.2, 1.3). ‘Food calls’ may be represented by stereotypic foraging calls, to both synchronise prey capture (e.g. humpback whale ‘feeding cries’ Thompson et al. 1986, Gong et al. 2014, Parks et al. 2014, Rossing 2007), or prey sharing (killer whales Ellis et al. 2017, Matkin et al. 2017).

Breeding calls and ‘song’ have also been recorded for whale species, and were noted for fin whales in Chapter 2.4. The song of humpback whales is the most complex of the whale species. Evolutions and revolutions in song structure occur between male singers synchronously (Payne et al. 1983, Payne & Payne 1985). It does not appear to result from erroneous repetition or forgetfulness, or indeed an alteration in the message projected (Payne et al. 1983, Tyack & Clark 2000), but a result of cultural influences incorporated by vocal learning (Guinee et al. 1983, Payne et al. 1983, Janik & Slater 1997, Tyack & Sayigh 1997, Jarvis 2006).

The study of cetacean acoustics is still an emerging discipline. The much more established study of acoustics in terrestrial animals sheds new light on aspects of acoustic signaling in marine mammals.

Observations and playback studies provide a foundation for researchers to unravel the use and function of calling in terrestrial animals. As described for whales and dolphins, acoustic signals transfer information about an animals position and surroundings; project physical or emotional state; aid in navigation and prey detection; locate conspecifics or identify intrusion to the group; act in defence or outline territory; support social hierarchy and group cohesion, and aid searching and competing for a mate. Calling in most animals is thought to be an innate process, where differences in calls represents genetic divergence (e.g. suboscine passerines, Touchton et al. 2014). Call structuring may be limited by phylogeny or morphology, however repertoire structure and use may occur via cultural drift and reinforcement (Cure et al. 2012). Modification of calls can also occur through learning, shaped by experience (Janik & Slater 1998).

The vocal repertoire of parrots, hummingbirds, songbirds, bats, and elephants results from an interaction between genetics and conspecific learning. These species acquire their acoustic repertoire through imitation and mimicry through vocal leaning (Jarvis 2006). This shows calling to be more than pure instinct. Repertoire, rather than being innately derived, may be learned from the animal’s mother or from a tutor, with individuals often passing through phases of practise and refinement (Ramus et al. 2000, Toro et al. 2003, 2005, Tincoff et al. 2005, Naoi et al. 2012).

For social, or herd animals, contact-calling aids with group cohesion, especially during periods of travel. Contact calls to facilitate group aggregation and reunion have been noted in walrus (e.g. Charrier et al. 2011), bats (e.g. Doerrie et al. 2001, Schmidt 2013), and in elephants (e.g. Rees 1963, Poole et al. 1988, Poole 2011, Poole & Granli 2011). Vocalisations described as 'rallying calls' have been noted for primates, wolves, hyenas, coyotes, and lions (Gautier & Gautier-Hion 1977), and 'let's go' rumble from elephants (Poole et al. 1988). Trill calls in white-faced capuchin (*Cebus capucinus*), have been associated with initiation of movement, leading of the group, and reinforcing the troop's movement (Boinski & Campbell 1995). Baboons (*Papio spp.*) moving through thick forest have been noted to use 'bark' calls to maintain group contact if visual contact is obscurred (Ingmanson 1996).

Food-related calling, or vocalizations made in the feeding context, have been noted for a number of bird and mammal species (Hauser & Marler 1993, Evans & Evans 1999, Bugnyar et al. 2001, Di Bitetti 2003, Slocombe & Zuberbühler 2005, Kitzmann & Caine 2009). Primate calls are thought to be a physiological response triggered by finding a desirable food item (Clay & Zuberbühler 2011). The call also carries information on the foods quality or quantity (Elowson et al. 1991, Benz et al. 1992, Benz 1993, Boinski & Campbell 1996, Roush & Snowdon 2000, Gros-Louis 2004). Calls may also express the callers personal food preference, found in the 'rough grunt' call of chimpanzees (*Pan troglodytes*, Slocombe & Zuberbühler 2005). Part of the call structuring or components may encourage the approach of conspecifics to the caller. For example, spider monkeys (*Ateles spp.)* produce 'whinnies' to attract conspecifics to a food source, but can also use a similar call for social recruitment in situations unrelated to feeding (Chapman & Lefebvre 1990). The call's function maybe more closely tied to attracting conspecifics, rather than to food sharing specifically.

The use of song-like acoustic patterns have been described for aves, anurans, and primates (Slater & Mann 2004, Brumm & Zollinger 2013, Farina 2014) and, like the song projection in whales, are formed by pairing or patterning in call sequences, which comprise of repetitive 'syllables' or 'phrases' (McDonald et al. 2006, Smith et al. 2008, Hall 2009). Calls may be modified or reorganised over time to convey a different (Winn et al. 1981, Ackers & Slovodchidkoff 1999) or 'more attractive' message (Catchpole & Slater 1995). Many studies, from birds (Eriksson & Wallin 1986, Johnson and Searcy 1996, Nowicki & Searcy 2004), bats (Davidson & Wilkinson 2004), primates (Cowlishaw 1992), and whales (Payne & McVay 1971, Thompson et al. 1979) suggest that song complexity and production is influenced by female choice. Generally song displays are longer and more complex than other vocalisations, and form part of an 'honest communication' (Markl 1985, Maynard Smith & Harper 2003) of individual fitness. Social synchrony in song performance, such as chorusing in arthropods, anurans, aves, mammals, and sciaenids (Zelick et al. 1999, Gerhardt & Huber 2002, Brumm & Zollinger 2013, Farina 2014) or duetting between passerine bird partners (Todt & Naguib 2000, Hall 2009) maximises the effectiveness the vocal projections.

The presence of alarm calls are part of the reaction to predator presence (see Chapters 1.7, 1.8 for a discussion of alarm call use by gray whales). These calls are usually short, broadband calls with an abrupt onset (Rendall et al. 2009), to optimise the ability of the call to capture attention of neighbouring conspecifics. The calls can encode information on the type, level, and proximity of threat (Seyfarth et al. 1980, Zuberbühler et al. 1999, Zuberbühler 2003, Suzuki 2014, Suzuki et al. 2016) to guide listeners' responses, seen for example in vervet monkeys (*Chlorocebus pygerythrus*), green monkeys (*Chlorocebus sabaeus* Cartmill & Byrne 2010), red squirrels (Digweed & Rendall 2009) and chick-a-dees (Smith 1972, Gaddis 1985, Ficken et al. 1994). Calls are paired, or a suffix is added to change the specificity of the alarm call. For example, the Campbell's monkeys (*Cercopithecus campbelli*) call repertoire includes a non-predatory call, and calls that are used to raise an alert for specific ground-based or aerial predators. They also add a suffix to these specific call types, an '-oo', to represent a general alert, but still indicating whether the threat is terrestrial or aerial (Ouattara et al. 2009, Sclenker et al. 2014).

Non-predatory alarm calls employ similar components, but are used in response to more social disturbances, or agnostic interactions with con- or hetero-specific individuals (Fichtel & Kappeler 2002; Digweed et al. 2005; Fichtel & van Schaik 2006). Song projections can mediate male hierarchies and territorial spacing in baleen whales (Tyack 1981, Helweg et al. 1992, Darling & Bérube 2001, Darling et al. 2006), however aggressive responses to conspecifics have not yet been reported. These call types, produced particularly to protect territory, have been noted in bats for roosting sites (e.g. Knörnschild et al. 2012), in songbirds between neighbours and strangers (e.g. Beecher et al. 2000, Burt et al. 2001, Slater & Mann 2004, Vehrencamp et al.

2007), between alpha males in hippopotamus (e.g. Barklow 2004), and maintaining space between individual frogs (e.g Brenowitz et al. 1984, Wilczynski & Brenowitz 1988, Brenowitz 1989, Gerhardt et al. 1989). Calling may also be to protect a harem in pinnipeds (e.g. Bartholomew 1970, Van Parijs et al. 2004, Van Opzeelan et al. 2010), and as mediation for calling site fights in frogs (e.g. Wells 1988, Gerhardt & Huber 2002), or confirm rank, as seen in ring-tail lemurs *(Lemur catta*, e.g Koyama et al. 2005).

Vocalisations such as the food and alarm calls are 'functionally referential' and so should have discrete call structure and be specific to their application (Schlenker et al. 2016). They may help receivers to respond in an appropriate way, irrespective or even in the absence of other sensory or contextual cues (Marler et al. 1992, Macedonia & Evans 1993, Evan 1997). They have been described for many species, including primates (Zuberbühler 2003, 2009), birds (Evans & Marler 1994, Evans & Evans 1999, Bugnyar et al. 2001, Templeton et al. 2005), and mammals (Manser et al. 2001). Vocal signals between signaler and receiver have been seen to have many roles. Although presumed to be simply functional, they likely hold much more meaning. Discerning this meaning, however, would mean being able to understand both the message in the call, and how that message is perceived by the receiver. Analysis of variation and modification in call structure, rate, and use can guide our understanding on how vocal behaviours are employed.

As described for marine mammals, cues to the identity, age, and arousal state of the signaller may be encoded in vocalizations. Individuality in calling has been recognised for many mammals species (Fay 1988, Scherer 1989, Fitch 2006, 2010), including bats (e.g. Brown 1976, Gelfand & McCracken 1986, Esser & Schmidt 1989, Kastein et al. 2013), primates (e.g. Cheney & Seyfarth 1980, 1988, Snowdon & Cleveland 1980, Rendall et al. 1996, 2009, Sproul et al. 2006, Sliwa et al. 2011), rodents (e.g. Hare 1998, Blumstein & Daniel 2004), carnivores (e.g. Holekamp et al. 1999, McCulloch & Boness 2000, Insley 2001, Charrier et al. 2002, 2003, Frommolt et al. 2003, Müller & Manser 2008, Pitcher et al. 2010), proboscideans (e.g. McComb et al. 2000), perissodactyls (e.g. Lemasson et al. 2009, Proops et al. 2009, Lampe & Andre 2012), artiodactyls (e.g. Watts & Stookey 1999, Searby & Jouventin 2003, Terrazas et al. 2003), and pinnipeds (e.g. Serrano & Miller 2000). Acoustic projections can also confirm species, group or colony membership (Lakshminarayanan et al. 2003, Rickheit et al. 2003, Sidtis & Kreiman 2012). Birds are able to use call features and syntax to distinguish calls of conspecifics and intruder species (e.g. Krams & Krama 2002, Bloomfield et al. 2005, Magrath et al. 2007, Goodale & Kotagama 2008, Haff & Magrath 2013, Wheatcroft & Price 2013). The ability to identifying the caller as a herd or flock-mate can limit time or energy used for defensive actions, and recognition of the caller as a male or female would help in courting. Playback experiments in shearwaters have, for example, shown birds to respond with a territorial call to conspecifics, but show no response to heterospecific calls (Becker 1982, Catchpole & Slater 1995, Cure et al. 2012). Similar reactions have also been seen in songbirds (Peters et al. 1980, Baker & Baker 1990, Soha & Marler 2000, Cure et al. 2012).

Individualism in calling can facilitate mother-offspring reunion, and prevent mid-directed parental care. Contact calls between mother and young can show more similarity in acoustic structure than those directed to other group members (e,g, Siberian wapiti, *Cervus elaphus sibiricus*, Sibirakova et al. 2018). Typically the maturity of the individual is reflected in the frequency (Hz) of the call, with juvenile calls substantially higher pitched than adults, for example in ruminants (e.g. Torriani et al. 2006, Sibiryakova et al. 2015, 2017, Volodin et al. 2014, 2017). However, calls employed between a mother and her show vocal structures to be more aligned, with vocalizations between lambs and kids and their mothers in the first few days of life almost acoustically indistinguishable (Arnold et al. 1975, Lenhardt 1977, Shillito Walser et al. 1982).

Arousal, motivational, or emotional state may be referenced either by a specific call type or in modifications in the projection of calls. (e.g. Zahavi 1981, Manteuffel et al. 2004, Ehret 2005, Brudzynski 2007, Briefer 2012). Bark acoustics of dogs, for example, vary predictably according to the context they are made, with lower frequency barks used when a stranger is approaching, and low pitch growl sounds used in antagonistic situations or when feeling threatened (Yeon 2007, Handelman 2012). Higher frequency barks are employed when dogs are alone or in isolation (Yin & McCowan 2004, Pongrácz et al. 2005, Siniscalchi et al. 2018). Several studies have shown the link between the inner state of an animal and the vocalizations it produces, for example, in goats and cattle (Watts & Stookey 1999, Briefer et al. 2015), elephants (Stoeger et al. 2012), and primates (Masataka 2003). Ordering of the call components may, for example, represent the urgency of the response or priority of actions needed from the receivers, ranging perhaps from purely a warning from signaler to listeners (e.g. Richardson's ground squirrel *Spermophilus richardsonii,* Swan & Hare 2008) to mobbing behaviours (e.g. Carolina chickadees *Poecile carolinensis* Freeberg 2008).

Hormone levels, and receptiveness to mating, can be encoded into courtship signals. Musth and estrous rumbles of elephants are specific calls for long distance projections (up to 4 km) of physiological state, using long, strong, frequency modulated, repeated signals (Langbauer et al. 1991, Langbauer 2000, Payne et al. 2003, Garstang 2004, O'Connell-Rodwell 2007). The emphasis on these acoustic mating displays are to provide females with cues of the male callers' health or sexual prowess. Mate selection may be based on song type or the performance of the song by an individual, where for example humpback whales maintain a similar song between individuals in a region (Janik & Slater 1997, Noad et al. 2000, Rendell & Whitehead 2001). Though the mating function of the song may be discerned, the meaning of the individual elements and how they contribute to the overall sequence is mostly unknown. Bird (Cheng & Peng 1997) and frog (Wilczynski & Chu 2001) auditory systems have been directly linked to neuroendocrine processes which, in the case of receiving reproductive displays, can alter the motivation and perceptivity in females, and make her more receptive to mating (Wilczynski et al. 2005).

The calls so far describe animal signalling. The function of these calls is derived from the context in which they are made. Vocal exchanges between individuals can be coordinated in their timing over extended periods seen for example in marmosets (Takahashi et al. 2013), where individuals paused for approximately 5 seconds before responding to a signal, despite call rate changing to maintain the coupling (Takahashi et al. 2013). The initial signaler elicits a response from a receiver, with the context of the sender and receiver, and the interaction between the two, core to the communication.

It has been suggested that for calls to display meaning they must be produced intentionally, and aimed to alter the behaviour or at least mental state of the receiver (Grice 1957, 1969, Dennerr 1983). Cartmill and Byrne (2010) state that discerning intentionality is central to understanding whether animals have meaningful communication. Here the goal of eliciting a particular outcome in a recipient is the intention of the call. Scott-Phillips (2015) argued that for signals to be meaningful, the listener should also be able to recognise the callers intention.

In many cases meaning is seen to be equal to the function of calls, whereby the affect in the receiver is what was meant by the signaler (see Scott-Phillips 2010, 2015 for discussion). The term ‘meaning’ is applied more loosely in studies of animal communication, and with a simpler definition than when discussing human communication or language. It seems to be universally applied to the concept of calls carrying an intention from a signaller to a receiver. However, the specificity of calls to a function, and whether the modification of call structure is discrete or graduated to incorporate contextual cues is unknown. Meaning of calls observed in natural settings may be garnered by noting the contextual correlates (e.g. Smith 1972), however meaning may be encoded in the syntax of the call, whereby notes or calling units, and their patterning, may represent encoded information, and decoding may require memory or social knowledge (Seyfarth & Cheney 2017).

Whereas playback experiments can help unravel functional meaning through experimental manipulation of stimulus, this method is less useful for understanding the intention, or the nuances encoded in vocal behaviours. Functionally referent calls could, however, demonstrate intentionality, where food and alarm calls can change the orientation and actions of receivers. Yet the complexity of the message, and how it is interpreted, is still not fully appreciated. Spierings et al. (2014) tested the sensitivity of zebra finches to prosodic cues, examining pitch, duration, and amplitude patterns in calling. The greatest reactions were seen when each feature was altered on its own rather than in concert with others, and altered pitch the most salient (Spierings et al. 2014). These features may be important in telling the receiver the distance and setting of the signaler (Jusczyk et al. 1999, Nazzi et al. 2000, Thiessen & Saffran 2003, Seidl & Johnson 2006, Johnson & Seidl 2009), or represent nuances in calls that represent caller identity or arousal.

The difficulty in discerning meaning from animal calls can be seen if we take sexually selected signals or ‘song’ as an example. Although the function can be ascribed to courtship and mating, the qualities of the singer encoded in the song, and how the repetition and format of phrases present those physiological traits, are ambiguous except to the intended receiver. Indeed, Love (2017) suggests that in communication there is much information, but perhaps not content transmitted. Marler (1998, 11-12) described birdsong as ‘impoverished in referential content, but rich in idle emotional content’. Inferences of meaning may be oversimplified both when understanding the message, and the individuality encoded into it. Overall, we as researchers underestimate what the receiver fully infers from a signal. An emerging field of ‘primate linguistics’ (Schlenker et al. 2016b) borrows from contemporary linguistics studies to appreciate the structure and syntax of calling and the encoded semantics, which describe the rules by which the calls are interpreted. Schlenker and colleagues (2016a) suggest that trying to understand monkey utterances as a language promotes research where more precise predictions about the form, use, and structure of calls are made. Meaning of the information conveyed by a call or call sequence is derived from its semantic structure and the pragmatic inferences which come from the signaler's motives, and choice of vocal sequence (see Schlenker 2016, Seyfarth & Cheney 2014, 2016). Also, experimentation on monkeys is starting to provide insights into the neural encoding of information on numerical intuition (Neider & Miller 2004), social environment (Platt et al. 2016), and abstract rules in communication (Miller et al. 2002).

Language has four key components. It is comprised of communicative elements, for example calls, notes, words, or phonemes. These elements form units or sequences based on combinatorial rules, or compositional syntax. Finite set of units are combined, using these structural rules to form an infinite number of meanings (Suzuki et al. 2016). Last, language is defined by its use to refer to events in the present, the past and in the future.

The units in animal vocalising might be calls, notes or utterances. These are used in a known structural way. Calls then form referential communications as described above. Whether the combination of calls or call-units creates more complex meanings is unknown (Hauser et al. 2007, Hurford 2011), but there are examples of animals altering the sequence of elements, or using pre- or suffixes to alter meaning (Clarke et al. 2006, Clay & Zuberbühler 2011, Engesser et al. 2015, Suzuki et al. 2015). In experiments, several animal species recombine acoustically different elements, and these altered calling sequences affect listeners differently than the original message. The plasticity in humpback whale song demonstrates rapid evolution and even revolutions in song structure that reflects cultural transmission of acoustic information. Indeed, Marler (1965) suggested that the limited vocal repertoire of animals was overcome by the use of 'composite' signals.

Finally many argue that animals can only communicate their state or behaviour in the present. Also, there is the argument that animals are not capable of a complete theory of mind, which means they are not able to, as either the signaler or receiver, perceive others beliefs, knowledge or mental states when communicating (Grice 1957). However, as described above, the signal structure, and even the decision to call at all is based on context and experience of either one or both of the signaler and receiver, as well as the relationship between the two (Seyfarth & Cheney 2012).

### *Conclusions*

Hauser et al. (2002) stated that a wide variety of studies indicate birds and non-human mammals to have rich conceptual representations, but did not believe that their vocalisations expressed these complexities well. The apparently genetic determinacies of calling, and possible lack of flexibility in communications, due to morphological restraints (Seyfarth et al. 1980, Marler et al. 1992, Macedonia & Evans 1993, Evans 1997) are often cited in animal acoustic studies as the defining limitation between their calls and meaningful communication or language use. I would argue that, despite the perceived simplicity of their behaviours, we are really only scratching the surface on the complexities of animal communication, especially for those in the marine setting where the reliance on the acoustic sense is much more acute.

At its simplest, acoustics use for signaling and communicating is a process of encoding, transmission and decoding. However, for animal communication to be fully understood we must keep in mind that the key elements are the sender, the receiver, and the interaction between the two. Understanding the influence that the signal may have (Scott-Phillips 2010) and the potential asymmetry in this relationship (Rendall et al. 2009) is also important. The factors shaping signal design (Rendall et al. 2009) should also not be overlooked, where the understanding of meaning may come from the semantic or pragmatic components of the vocalisations. Although attributing calls to a specific behaviour or function seems to be the aim of many acoustic studies, perhaps instead we should be focussing on the individuality encoded and the nuanced way that call types are produced by conspecific individuals. How internal and external environments of the signaller are expressed in calls may become a key factor in changing soundscapes.

The change in receiver as a result of a signal implies a function, but more subtle components including context, caller and recipient identity, and the nature of their experience and past interactions may also be encoded. There is also asymmetry in the system of communication, with the vocal production of sounds in some animals fairly restricted whereas their use and comprehension, measured by their multiple responses, is much greater. As we have seen, small repertoires of calls can be modified or restructured to give rise to a rich ‘vocabulary’. If meaning in calling is conferred by intent expressed to the receiver (Scott-Phillips 2010), the study of animal communication must take into consideration the audience as much as the signal itself. However, this can only really be done on a crude level and will likely underestimate the full complexities and nuances of the signal components.

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## 4.2. Acoustics to ecology: Thesis conclusions

Ecology seeks to understand how individuals interact with their surroundings, conspecifics, and other species. For cetaceans, acoustics seems to be the underlying mechanism for these interactions. Although environmental information is likely multimodal, providing proximal and distal cues (e.g. Chapter 1.3, Torres 2017), usually a dominant sensory stream prevails. This will be apparent in either the relative strengths of signal propagation, or the mode that the signal is interpreted in, and acted upon by the receiver (Higham & Hebets 2013, Laidre & Johstone 2013). The acoustic sense dominates cetacean processes of communication, orientation, and prey location. Indeed, acoustics facilitates most vital life process, and underlies finding a mate, detecting prey, and avoiding predation. Whales and dolphins are morphologically adapted to underwater sound emission and processing, with more physiological investment in the acoustic sense than any other (Ketten 1997). The draw on energy for acoustic behaviours appears to be low, as species will still vocalise in negative-energy states (Jensen et al. 2012, Tervo et al. 2012, Noren et al. 2017). This indicates perhaps the reliance on this sense.

Acoustics may play an important role in the population structure and dynamics of whale species. Regional differences in vocalisations, that we refer to as 'dialects', have been described for several species (Ford 1987, 1991, Ford & Ellis 1999, Gero et al. 2016, Širović et al. 2017), as have geographically founded variations in many other species vocalisations. Whales of the same population or sub-group could be linked via an intricate network of vocalisations, receiving information from remote conspecifics about prey resources, habitat quality, or directional information (see Chapters 1.3, 1.5). Despite appearing solitary or disparate from the 'herd', often seen in baleen whale or odontocete 'fission-fusion' species (Soltis 2010), it may be that whales are in constant contact (Payne & Webb 1971). Calling may then act to re-aggregate individuals, for example, coordinating congregations to mate, or conversely, to establish territory or hierarchy (Cummings et al. 1972, Tyack 1981, Helweg et al. 1992, Clapham 1996, Darling & Bérube 2001, Darling et al. 2006, Oleson et al. 2007, Smith et al. 2008).

The underlying processes of previously unexplained or apparently stochastic behaviours are now becoming more clear; orientation and navigation during long migrations (Allen 2013), prey location (Torres 2017), and cooperative foraging (Baker 1978, D'Vincent et al. 1985, Cerchio & Dahlheim 2001) are just a few examples. The employment of active (echo-location, Norris 1966, 1969, Payne & Webb 1971, Thompson et al. 1979, Ellison et al. 1987, Clark & Ellison 2004, Oleson et al. 2007) and passive (hearing/eavesdropping, McGregor & Peake 2000) acoustics may be the directing force.

Considering the use of acoustics by whales can help us understand the pattern and process of behaviours as the individual progresses through life history events. Levin (1992) suggests this is one of the key problems of ecology, drawing on aspects of evolutionary ecology, ethology, and population biology (MacArthur 1972, Burnham 2017, Chapter I). Repetition of a specific call, in a particular context, forms a pattern of use. This can give us clues as to the potential function of the vocalisation, or the message it conveys. Deviations from the 'normal pattern' are important to recognise. As well, certain calls are inherent to a particular behaviour (e.g. Chapters 1.3, 1.8), or employed at a particular life stage (e.g. 'motherese', Chapters 1.5, 1.8).

In the Coastal Section, the use of the gray whale (*Eschrichtius robustus*) as a case study (Chapters 1.1-1.8) shows how acoustics can be used to describe the patterns of behaviour and interaction of species, and species groups, over time. It is also is a good example of how lacking our acoustics knowledge is, with other life history details of gray whales well studied thanks in part to their use of coastal waters.

Vocal behaviours were examined on an hourly, daily, seasonal, and annual scales, as well as a preliminary examination of patterns in ontological time ('motherese', see Chapters 1.5, 1.8). Through examination of call type use and structure, it is possible to see how different facets of a whale's situation, as well as perhaps its internal and physiological state, plays into the patterning of acoustics use. The employment of different call types in different parts of their range, as well as call structure and propagative value, can suggest call function. In time, calls can be used to elucidate not just the presence of whales to an area but also the area use, all without the researcher being present. For example, during migration (Chapters 1.2, 1.3) low frequency, modulated, moan-like calls are predominantly employed. I suggest this may be a means of acoustic navigation, and actively employing these far-reaching signals for social cohesion, and perhaps as a guide for less experienced conspecifics. The proportional use of these calls is much reduced during the summer months (Chapter 1.5), when calls with more within-group function (Dahlheim 1987, Crane & Lashkari 1996, Youngson & Darling 2016) are employed, perhaps to share information. It may be that crude classifications may be possible, for example moans are the ‘travel call’, knocks are the ‘breeding call’, and upsweeps are the ‘feeding call’ (see Chapter 1.8 for a more detailed discussion). The proposed use of a ‘motherese’ between cow-calf pairs by gray whales suggests that the acoustic repertoire of whale species is learned, or at the very least socially reinforced (Wisdom et al. 2001, Chapter 1.8). A more thorough examination may demonstrate the active acquisition and practise of vocal behaviours, similar to those seen in other cetaceans (Tyack & Sayigh 1997, Fripp et al. 2005, Miksis-Old et al. 2008). Call use may also indirectly show a change of state; in this case the use of the more mature repertoire may be an indication of a lessened reliance on the mother by the calf, and more independent sensory interpretation rather than simply ‘following’ (Szabo & Duffus 2008).

Acoustic responses to potential threats were examined in the recordings (Chapters 1.6, 3.3). These may represent an anti-predator strategy (Ford & Reeves 2008), stress/threat reaction (Frid & Dill 2002), or alert calls to conspecifics (Suzuki 2014). For gray whales there may be a graded threat response in calling behaviours. However, if a threshold is surpassed, silence is employed rather than modification (Dahlheim 1987, Dahlheim & Castellote 2016, Chapter 1.6). I would argue, however, that our knowledge for most species is still not sufficient to distinguish a deviation from the norm. Also, it is not yet possible for us to discern whether this changed pattern in vocal projection is biologically important or significant to the individual (Farina 2014).

A distinct feeding or breeding response in acoustic activity has been suggested for baleen whales (Clark 1983, Mellinger et al. 2007b, Baumgartner & Fratantoni 2008, Parsons et al. 2008, Parks et al. 2011, Vu et al. 2012). Calling behaviours, particularly in call rate and type, may be a key indicator of the habitat use. This divergence in call type was particularly prevalent in recordings analysed in the Offshore Section, where a temporal separation of calling behaviours was distinct for fin whales (*Balaenoptera physalus*), and, less so by blue whales (*Balaenoptera musculus*). For species where seasonal presence and movements are murky (Mizroch et al. 2009), acoustics can be used to establish the use and importance of habitat units.

The scale at which species-species and species-habitat interactions are considered can very much affect any conclusions about pattern and process (Levin 1992, Cao & Lam 1997, Pereira 2002). In the thesis preamble (Chapter I) the use of the concept of an individual’s ‘active space’ is advocated. This is a departure from the usual process by which scale is selected for research. The extent of a study is often biased by the observer, using, for example, visual limits or a logistically convenient areal unit to define the boundaries. This may mean work is not conducted on a scale pertinent to the species in focus (Stelle 1978, Levin 1992, Soberón & Arroyo-Peña 2017). In the marine setting, study areas might be defined by bathymetry, water depth or distance from shore, for example a coastal-offshore comparison like the set-up of this thesis, or shelf-shelf break-off shelf as in the Offshore Section (see Chapters 2.2-2.4). These definitions allows for comparison to broad patterns of ocean regimes including water circulation and productivity (Pickard & Emery 1990), but do not represent boundaries to organism movement, and certainly not to the propagation of sound (see the discussion of large baleen whale calls Chapter 2.3).

The application of an active, dynamic 'operational niche' definition, where the organism is central to the investigation (*sensu* Hutchinson 1979) is the underpinning of the work presented in this thesis, with 'active space' a king-pin in this concept. The original use of the term by Bossert and Wilson (1963), described the deliberate use of a sensory modality, pheromone release in ants in this case, that is modulated for short- to long-range communication (Bossert 1968). This is analogous to 'communication space' of an individual in a marine setting (Clark et al. 2009), defined as the area over which it can communicate with conspecifics. In its application here, 'active space' also encompasses an individual's 'sensory volume' (Lima & Zollner 1996) or region of 'active sense' (Hofmann et al. 2013); the area it is receiving information from, which is modified by ambient noise levels (Chapter 1.6).

For whales, acoustic active space is determined by the signal type, call structure and amplitude, its propagation path and rate of attenuation, and conditions of the environment it is projected into. The receptivity and physiological sensitivity of the receiver is also a determinant of how far a signal can travel and elicit the intended response (Bradbury & Vehrencamp 2011). Although active space really encapsulates an area (Bossert & Wilson 1963), it is often distilled into a two-dimensional distance over which signal-action responses operate, either internal to the individual (echolocation) or eliciting a response in a conspecific (communication; Hofman et al. 2013). Taking the organism-centered perspective, and using active space as a working scale will redefine the area over which biologically meaningful actions should be measured. It can also define the area over which selective pressures are acting on an individual. Active space extent can help modularise a complex species community into those relationships that are strongest and most pertinent at any given time to individuals. This moves away from the pure 'eat or be eaten' relationships outlined in interaction webs, and comes to appreciate the intricacies of species interactions, incorporating theories such as landscape of fear (Lima & Dill 1990, Frid & Dill 2002), altruism (Baker 1978), and symbiosis, for example in eavesdropping on others' signals (McGregor & Peake 2000, Deecke et al. 2005).

Baleen whales calls can propagate over areas exceeding that which ecological studies typically operate. This accentuates the need to integrate information from a range of scales including the population, community and ecosystem, rather than assuming closed or distinct habitat areas in an organisms range (Loreau & Holt 2004). This perspective may be much more applicable to blue and fin whales (Chapters 2.2-2.4), where they are employing infrasonic calls over long distances with, as yet, no discernable clear habitat units or migratory routes (Mizroch 2009).

The use of passive acoustic monitoring (PAM) techniques in the study of whales can add greatly to data collection, complementing results from traditional methods. As has been demonstrated in a number of the chapters of this thesis, the use of PAM allows for continuous data collection regardless of weather, visibility, distance from shore, season and time of day. This means that we can start to fill in knowledge gaps about life histories, for example over winter behaviours, when data collection would otherwise be difficult to impossible (e.g. see the Offshore Section and Chapter 3.2). Acoustic monitoring may come into its own for monitoring more transient use of a habitat by a species (for example killer whales, see Chapter 3.2), for rare or cryptic species, or for species where patterns of migration or residence are not well described (for example blue and fin whales, see Offshore section, Mizroch et al. 2009).

Although we will never discern the meaning of calls, unravelling their function may be possible by appreciating patterns of application and the processes driving them. The principle aim of PAM studies should be in establishing a baseline description of species' repertoire and calling behaviours in reference to its spatial, social or behavioural setting. Once general rules of application are known, then deviations encountered may indicate change in the individual, or the habitat it occupies.

The work in this thesis shows the additions that acoustic data can make to ecological studies, but there are still some limitations and caveats to PAM use. Care must be taken in interpreting acoustic behaviours, and when trying to interpret patterns and functions in vocalisations. Acoustic surveys can monitor distribution through time and suggest habitat preferences (Thomsen et al. 2001), but it is still difficult to establish abundance (Notarbartolo Di Sciara & Gordon 1997, Küsel et al. 2011, Ponce et al. 2012, Harris et al. 2013).

The amount of raw data is often cited as a hindrance in PAM studies. Increasingly automated detection systems are being used to identify whale calls in recordings. This may be done by using recognition of frequency-time parameters of a call (e.g. start-stop times and the extent of the lowest and highest frequency harmonics), or the shape of the dominant frequency of a call, known as a frequency-contour or pitch-track. Automated detectors were applied several times in the work for this thesis, in this case to highlight areas of the recordings most likely to contain calls from the species of interest, followed by manual analysis to verify calls and extensive sampling of the entire data base (see Chapters 1.2, 2.2, 3.2). Yet, many auto-detectors only recognise calls that exceed a certain amplitude relative to ambient noise, and so may miss quieter calls, or vocalisations from whales further away from the recorder. Calls demonstrating variance from the standard form may also be missed. Thus, total reliance on these systems should be avoided, with some level of manual analysis always needed.

The final section of the thesis shows how acoustic information, and the use of PAM in ecological studies can inform management action. It also, I think, shows how relevant the adage 'know your song well before you start singing' is. The integration of acoustics into ecological studies will help managers and policy makers make better decisions. With more deployments of PAM, the less likely we are to take actions that misrepresent or underestimate our impacts. For example, the gray whale was not considered acoustically active in most of its range (Rasmussen & Head 1965, Cummings et al. 1968, Dahlheim 1987, Crane & Lashkari 1996) and so would likely not have been considered at significant risk from anthropogenic noise additions. In fact, it is likely one of the species most subject to anthrophonic additions to the soundscape throughout its range, and it most certainly is a very acoustically active animal. Our lack of understanding of the use and importance of the acoustic sense to an individual and species likely means the consequences of disturbance are still misjudged. Acoustic 'pollution' may be the invisible killer, with anthropogenic additions to soundscapes implicated in a range of physiological and behavioural disturbances including habitat loss, injury, and reduced fecundity, leading ultimately to individual fatality and reduced population success. Despite a growing body of knowledge and the popularity of PAM system use, our appreciation of acoustics use by cetacean species is still poor, especially for baleen whales.

This work adds to the body of knowledge of whale acoustics use, particularly for the gray whale but also large whale species in Pacific Canada. At a time when ocean regimes are changing, habitat degradation is ongoing, prey availability has been reduced and, in some cases, populations are still recovering from intense removal, much work remains to assess the cumulative anthropogenic influences on ocean soundscapes, and whale habitat in general. Indeed a magic bullet would be needed to mitigate this fully. Works such as this one begin by re-establishing the basics; whale presence and behaviour, and the variables shaping these over time and space.

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