

**THE VOCAL BREEDING BEHAVIOUR OF
HARBOUR SEALS (Phoca vitulina) IN GEORGIA STRAIT,
CANADA: TEMPORAL PATTERNS AND VOCAL REPERTOIRE**

By

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Accepted in Partial Completion
of the Requirements for the Degree
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MASTER'S THESIS

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Katrina Nikolich

November 6, 2015

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In Partial Fulfillment

Of the Requirements for the Degree

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ABSTRACT

During the breeding season, male harbour seals (*Phoca vitulina*) produce underwater calls used in intra-sexual competition and advertisement. One call type, called a roar, has been documented in every population of this species that has been studied. Because calls vary in structure and temporal patterns among populations, it can be inferred that regional vocal dialects may exist, and that the influence of local environmental and biological conditions may affect the timing of calls. Breeding calls have only been studied in relatively few locations worldwide; however, the effect of ambient noise on the underwater vocal behaviour of harbour seals has not been studied. I investigated the temporal patterns, structure and complexity of harbour seal breeding calls at Hornby Island, British Columbia. Underwater recordings were made near the south end of Hornby Island in the summer breeding season of 2014 using a single omnidirectional hydrophone while concurrent visual observations were conducted at a nearby site on shore.

I investigated the relationships between roars per hour, tide level, ambient noise and time of day. Logistic regression showed that roars were over eight times more likely to be heard during night-time hours than during the day. When roars were heard, roar number was most influenced by time of day and the progression of the breeding season, with more roars heard later into the breeding season. Roar density was inversely related with ambient noise; however, ambient noise and time of day were highly auto-correlated, and therefore the effects of these two variables could not be assessed independently. Whereas harbour seal call timing in other areas has been attributed to tidally-driven haul-out patterns, the tide level at Hornby Island did not statistically correlate with roar density. I hypothesize that ambient noise may be a cause of the strong diel pattern of call density at Hornby Island, and suggest further study to determine the mechanistic link between ambient noise cycles and calling behaviour.

Four breeding call types were identified, one of which was the 'roar' call described in every population that has been studied. The structure of the roars at Hornby Island was comparable to those of other populations, but displayed wide variation in several parameters. Each of the three non-roar call types

were distinguished from roars qualitatively by aural-visual classification, and quantitatively by trained linear discriminants analysis (LDA). Agreement between these two classification systems was 88%, suggesting that the four call types were distinct. The three non-roar call types contained five call subtypes which were also identified through aural-visual and LDA classification. Agreement was slightly lower at 74%, but more variable, suggesting that some call subtypes were more distinct than others. One non-roar call type, the sweep, was distinct from any call previously described for harbour seals worldwide. I suggest that more than one of these call types are used by each individual, supporting the results of a previous study in California which identified several call types produced by harbour seals. If this is the case, then the vocal breeding repertoire of harbour seals at Hornby Island is more complex than that of most previously studied populations. Further study of this population with the ability to localize calls and identify individuals is required to support or refute the hypothesis that individual harbour seals at Hornby Island produce several call types.

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TABLE OF CONTENTS

ABSTRACT	iv
ACKNOWLEDGEMENTS	vi
LIST OF FIGURES	ix
LIST OF TABLES	x
GENERAL INTRODUCTION	1
Sexual Communication in Marine Mammals	2
Breeding Systems in Pinnipeds	3
Breeding Behaviour in the Harbour Seal	5
Acoustic Masking and Communication Space	8
Research Needs	9
Research Approach	11
TEMPORAL TRENDS IN BREEDING CALL OCCURRENCE AND DENSITY FOR HARBOUR SEALS IN GEORGIA STRAIT, BC	13
Introduction	13
Methods	16
Acoustic Recordings	18
Visual Observations	18
Data Processing and Analysis	21
Results	23
Factors Affecting Roar Presence/Absence	25
Factors Affecting Roar Density	25
Visual Observations	29
Ambient Noise Predictors	31
Haul-Out Behaviour	31

Discussion.....	34
QUANTIFYING THE DIVERSITY OF UNDERWATER VOCALIZATIONS OF BREEDING HARBOUR SEALS AT HORNBY ISLAND, BC, CANADA.....	41
Introduction.....	41
Methods.....	44
Data Collection.....	44
Data Processing and Analysis.....	45
Results.....	50
Aural-Visual Classification.....	50
Linear Discriminants Analysis Classification.....	56
Visual Observations.....	58
Discussion.....	60
GENERAL CONCLUSIONS AND FUTURE DIRECTIONS.....	65
Major Findings and Contributions.....	65
Future Directions.....	67
BIBLIOGRAPHY.....	69

LIST OF FIGURES

- Figure 1.** Map showing the Salish Sea and indicating the region of study (top right), the field of view visible from the observation site (bottom right), and a close-up view of the study site at Heron Rocks, including the location of the hydrophone, observation point and haul-out area. Created in ArcGIS using the North American 1983 datum and GCS NA1983 coordinate system. Units are in decimal degrees. Map created by Erin Harker.....17
- Figure 2.** Power spectral density calculated per minute and averaged over one hour when seal calls were heard in low (top) and high (bottom) ambient noise conditions. Likelihood at the 5%, 25%, 50%, 75% and 95% levels are shown, as well as the expected levels according to the Wenz curve (Wenz 1962).28
- Figure 3.** Average number of harbour seal roars \pm SE per h that were detected by spectrographic analysis, compared to time of day (N=20 days).30
- Figure 4.** Average number of seals \pm SE hauled out (open points) and in the water (closed points) each hour, compared to the number of hours since high tide (HT) or low tide (LT). Data points representing extreme tides with low sample sizes have been removed.33
- Figure 5.** Spectrograms of the four subtypes of harbour seal roars characterized at Hornby Island, BC. Spectrograms generated by Raven Pro 1.5 (Cornell Lab of Ornithology) with smoothed 2,456 point fast Fourier transform, Hann window and 50% overlap; a) Long Pulse; b) Short Pulse; c) Double Pulse; d) High Frequency. Axes are scaled the same in each spectrogram.52
- Figure 6.** Spectrograms of the three non-roar call types (containing five subtypes) of harbour seal breeding call characterized at Hornby Island, BC. Spectrograms generated by Raven Pro 1.5 (Cornell Lab of Ornithology) with smoothed 2,456 point fast Fourier transform, Hann window and 50% overlap; a) Short Growl; b) Long Growl; c) Step; d) Abrupt Call; e) Sweep. Axes are scaled the same in each spectrogram.55

LIST OF TABLES

Table 1a. Description of vessel types recorded at Heron Rocks during the summer of 2014.20

Table 1b. Description of vessel activities recorded at Heron Rocks during the summer of 2014.20

Table 2. Information on the 20 days in the 2014 breeding season that were randomly selected for acoustic analysis. An X under ‘Visual’ denotes that this day was one in which visual observations were conducted. ‘Hours of Roars’ indicates the number of hours in each day when roars were detected spectrographically, and ‘# of Roars’ gives the total number of roars that were detected on that day. *Killer whales were heard from 20:00 to 21:30 on the evening of July 30th, and only one roar was detected over the following day.24

Table 3. Model selection for predictors of roar occurrence (RoarPres) in a given hour. I used a generalized linear model with a binomial distribution (logistic regression). The best-fit model is represented by the lowest AIC value. The model was fit with the time of day (day or night; shown as TOD), the date (expressed in days after the first day of breeding season), and the tide (number of hours after high or low tide). Extreme tides were excluded for a final N=387 h.26

Table 4. Coefficients and significance values for the factors included in the best-fit model predicting roar occurrence. Odds ratios are exponentiated coefficient estimates. Values <0.005 are denoted with a ‘*’.27

Table 5. Model selection for predictors of ambient noise level to the fourth power (Ambient⁴) during daylight observation hours at Heron Rocks. I used a general linear model with a normal distribution. The best-fit model is represented by the lowest AIC value. The model was fit with the average number of vessels (#Vessels), the average precipitation (Precip), the average sea state (SS), and the relative tide (time after low or high tide; Tide). N=81 h.32

Table 6. Descriptions and shorthand codes of key features from the Noise Resistant Data Set (NRFS) in Osprey used to classify harbour seal mating calls.49

Table 7. Counts and summary statistics for the four subgroups of the roar call type, characterized for harbour seals at Hornby Island, BC. N=383 calls. For measurements taken using the NRFS in Osprey, means are presented with standard deviation in parentheses. Key features are denoted with an asterisk (*). See Table 1 for full names of measurements and descriptions.51

Table 8. Counts and summary statistics for the three non-roar call types (five subtypes) characterized for harbour seals at Hornby Island, BC. N=117 calls. For measurements taken using the NRFS in Osprey, means are presented with standard deviation in parentheses. Key features are denoted with an asterisk (*). See Table 1 for full names of measurements and descriptions.54

Table 9. Example association analysis table from the ten LDA models used to classify seal call types. High agreement between aural-visual (AV) and LDA classification is indicated in bold. Models were trained with a random subset of 100 calls, which was then used to predict classification of the remaining 400 calls. Classifications for call types are: Growl=G, Roar=R, Sweep=S, Short Call=SC.57

Table 10. Example association analysis table from the 10 LDA models used to classify seal non-roar call subtypes. N=117 calls. High agreement between aural-visual (AV) and LDA classification is indicated in bold. Models were trained with a random subset of 50 calls, which was then used to predict classification of the remaining 67 calls. Classifications for call subtypes are: Long Growl=LG, Abrupt=A, Sweep=S, Short Growl=SG, Step=ST.59

GENERAL INTRODUCTION

Communication is critical to animals reproducing sexually because it allows them to breed with a suitable mate. Effective communication is required to find, identify, attract or breed with another individual. Depending on the breeding system, different strategies will be used by individuals to achieve the maximum number of successful offspring (Emlen and Oring 1977; Cassini 1999). In the majority of systems, female choice plays a role in sexual selection. In theory, females choose mates based on physical cues that directly and honestly relate to the male's body condition, which may relate to their genetically-based fitness (Kodrik-Brown and Brown 1984; Bradbury and Vehrencamp 1998). These cues must be communicated effectively from male to female (and *vice versa*), and from male to male in the case of competition for mates.

A combination of visual, vocal and chemical modes of communication have evolved in animals (Kodrik-Brown and Brown 1984; Bradbury and Vehrencamp 1998). Accomplishment of mating depends not only on body condition, but also on an individual's ability to produce, perceive, comprehend and respond to signals effectively (Richardson et al. 1995; Bradbury and Vehrencamp 1998). By studying these signals, and the ways in which individuals ensure that they are noticed, we can learn more about the information these signals convey and which cues females use to identify fit mates. A more complete knowledge of the information that females look for in potential mates allows us to understand the drivers of sexual selection in a species (Bradbury and Vehrencamp 1998; Stirling and Thomas 2003). Such knowledge is usually accomplished by observing breeding behaviour and 'ground-truthing' this behaviour by examining the fitness and paternity of males (Bradbury and Vehrencamp 1998).

Studying breeding behaviour in marine mammals is difficult because individuals spend the majority of their lives underwater and range widely. In addition, many species of marine mammals are currently at risk; therefore invasive observation techniques are often undesirable. The development of remote visual and acoustic sensing technology has allowed us a better look at the sexual behaviour of many species

of marine mammals; however there remain many species for which our knowledge of sexual communication is incomplete.

Sexual Communication in Marine Mammals

Marine mammals face a few key challenges when attempting to locate and advertise to potential mates (Richardson et al. 1995). In addition to being widely dispersed, many species are solitary or travel in small kin groups for much of the year (Stern 2000), further reducing the chances of encountering potential mates by chance. Another challenge to communication is the fact that light attenuates much faster in water than in air; most wavelengths of visible light do not penetrate further than the first hundred meters of the water column under ideal conditions, and significantly less so in biologically productive or coastal waters (Urick 1983). This attenuation limits the effectiveness of visual signals over the distances by which most marine mammals are dispersed (Richardson et al. 1995).

Instead, many marine mammal species rely on acoustic cues to locate, attract, and select mates. Sound waves propagate farther and faster underwater than in air, and under certain conditions can travel thousands of kilometers in the ocean (Urick 1983; Richardson et al. 1995). Sound is used extensively by marine mammals to facilitate important life functions such as foraging, social cohesion, communication, orientation, predator avoidance, and to convey information about the fitness of a potential mate (review by Richardson et al. 1995). This prevalence of acoustic signals in breeding behaviour is advantageous for ecologists who wish to study the process of mate choice in marine mammals. Instead of relying on brief and occasional visual data, we are able to obtain much more information by recording acoustic breeding behaviour.

Marine mammals employ several tactics to face the challenge of communicating with potential mates across large spatial ranges. Baleen whales (Suborder Mysticeti) are often widely dispersed across a population's range, and can migrate tens of thousands of miles annually; they must rely on long-range

communication to identify and locate potential mates (Stern 2000). Balaenopterids such as the fin whale (*Balaenoptera physalus*) and blue whale (*B. musculus*) create loud, very low-frequency vocalizations in order to maximize propagation and minimize attenuation over distance (McDonald et al. 1995; Croll et al. 2002). Males of many mysticete species produce songs (a stereotyped series of shorter calls) that serve as advertisement displays (McDonald et al. 2001; Darling et al. 2006).

Some species, including many otariids (eared seals) and some baleen whales such as the humpback (*Megaptera novaeangliae*) and right (*Eubalaena* spp.) whales, aggregate during the breeding season at breeding sites that remain relatively constant across generations (Darling and McSweeney 1985; Boness 1991; Kenney 2002). Once within the relatively small area of the breeding grounds, short-range communication can be achieved both acoustically and visually. Humpback whales produce complex songs, the contents of which differ by population and by year (Payne and McVay 1971; Winn et al. 1981; Cerchio et al. 2001). Surface-active behaviour (e.g. breaching, fluking) is also common on breeding grounds, and may serve as visual signals as well as non-vocal acoustic signals (Silber 1986; Dunlop et al. 2010).

For marine mammals that have smaller ranges or live in conserved or semi-conserved groups, the chance of encountering conspecifics increases and vocal communication may be used to determine level of kin relationship, thus avoiding inbreeding. This is thought to be the case in resident killer whales (*Orcinus orca*) in the northeast Pacific, where variability in vocal dialect is directly related to genetic relatedness among groups (Barrett-Lennard and Ellis 2001; Yurk et al. 2002; Deecke et al. 2010).

Breeding Systems in Pinnipeds

The pinnipeds (Order Pinnipedia) are a taxon of marine mammals that spend a portion of time on land. Most pinnipeds, including all otariids and two genera of phocids (true seals), breed on land (Stirling

1983; Cassini 1999). Limited haul-out space for parturition and pup care causes spatial and temporal aggregations of receptive females in these taxa, leading to intense competition among males and often extreme polygyny wherein very few dominant males are responsible for all fertilization within a colony in a given year (Boness 1991; Cassini 1999; Fabiani et al. 2004). Polygynous matings are facilitated by males defending a harem of females (female defense polygyny) or by defending territory that contains resources required by females (resource defense polygyny; Emlen and Oring 1977). In fur seals and other otariids, males will establish territorial hierarchies on haul-out sites, thus monopolizing a resource that is required by females to rest and care for pups (Emlen and Oring 1977; Boness 1991). In this system, female choice is facilitated by dominance displays and by the quality of territory held by the male (Emlen and Oring 1977; Boness 1991; Cassini 1999).

Elephant seals (*Mirounga* spp.) and gray seals (*Halichoerus grypus*) are phocids that breed on land, and share many reproductive characteristics with otariids including extreme sexual dimorphism, gregariousness of females during the breeding season, and dominance polygyny (Cassini 1991). In elephant seals, females are defended directly by dominant males, who can mate with a large number of females within a harem (LeBoeuf 1974; Emlen and Oring 1977; Fabiani et al. 2004). Gray seal males defend their tenure within an aggregation of females, and mating strategies depend upon the kind of substrate (e.g. ice, rock, or sand) on which the females are hauled out. In a study in eastern Canada, the success of ice-breeding gray seals depended not on male size, but on the amount of time the male spent with females on land and his ability to defend his tenure against other males (Tinker et al. 1995).

Most phocid species breed underwater, and as a result show very different mating systems from land-breeding pinnipeds (Sullivan 1981; Cassini 1999; Van Parijs et al. 2003a). While females in aquatic-breeding species give birth on land, they tend to take longer foraging trips late in lactation and during the oestrus period than females of land-breeding species. Consequently, receptive females are much less gregarious in aquatic-breeding pinnipeds, which makes it virtually impossible to monopolize females (Emlen and Oring 1977; Van Parijs et al. 2003a). Males thus engage in less direct competition

and exhibit less sexual dimorphism. They instead display their fitness through physical and vocal displays (Emlen and Oring 1977; Bradbury and Vehrencamp 1998). Many species of aquatically-mating phocids have been associated with a male-only call performed during the breeding season, which is hypothesized to attract females as well as display dominance to other males (Stirling and Thomas 2003; Schusterman and Van Parijs 2003). The diversity and complexity of vocalizations in a population of any species may be related to its habitat, geographical location, mating system, degree of female gregariousness during oestrus, and a number of other life-history and evolutionary factors (Stirling and Thomas 2003). Therefore the vocal repertoire of any population cannot be assumed based on those of other populations, and should be investigated to identify the factors that increase its diversity and complexity.

Breeding Behaviour in the Harbour Seal

The harbour seal (*Phoca vitulina*) is an aquatic-mating phocid. This species has one of the most extensive global ranges of any pinniped, inhabiting coastal waters throughout the northern hemisphere (Bigg 1969a; Burns 2009). Though harbour seals may travel long distances to forage throughout the year, it is believed that most individuals are philopatric (Stanley et al. 1996), and can be found in their home ranges in breeding season. This philopatry has led to genetic isolation and the rise of four subspecies (Stanley et al. 1996) as well as genetically distinct parapatric populations within subspecies (Burg et al. 1999).

Female harbour seals haul out to give birth to a single precocial pup during the early summer, and will spend the majority of her time around the haul-out while the pup is nursing (Bowen et al. 1999; D'Agnesse 2015). Females begin taking longer foraging trips post-lactation, resulting in a staggered distribution of oestrus females in space and time (Bigg 1969a; Cassini 1999; Boness 2006). These constraints preclude female defense or resource defense mating systems; however harbour seals are

considered promiscuous breeders, implying some degree of male dominance polygyny (Stirling and Thomas 2003).

Harbour seals show very little sexual dimorphism (Burns 2009; Howard 2009), and males do not display any Fisherian ornamentation (Bradbury and Vehrencamp 1998). Sullivan (1981) observed that male harbour seals in northern California occupy discrete territories around a central haul-out area during mating season. These males will produce visual displays on the surface including tail-lobbing, flipper-slapping and rolling. This displaying within a common arena suggests a lek-like system of male dominance, in which females choose the most dominant male with which to mate (Sullivan 1981). About 20 years ago it was discovered that male harbour seals produce underwater calls during the breeding season, often concurrent with these visual displays (Hanggi and Schusterman 1994; Van Parijs et al. 1997). This calling suggests a multiple signal competition system, in which some aspects of the visual and/or vocal behaviours display dominance to other males and potentially to females as well. It is unclear whether these visual and vocal signals are redundant (convey the same information about fitness), additive (both signals are needed to accurately assess fitness), or dishonest (one signal conveys honest information regarding fitness, and the other is the product of Fisherian selection and is misleading; Bradbury and Vehrencamp, 1998).

The hypothesis that male vocal signals are a breeding display is supported by the fact that only males are known to produce underwater vocalizations as adults (Ralls et al. 1985), and they are produced most frequently during or just before the breeding season (Coltman et al. 1997; Van Parijs et al. 1997; Hayes et al. 2004a). One call in particular, the 'roar', is cosmopolitan to every harbour seal population that has been studied, and is believed to be an indicator of fitness (Hanggi and Schusterman 1994). This hypothesis is supported by evidence showing that roars appear to be highly stereotyped within an individual (Hanggi and Schusterman 1994; Van Parijs et al. 2000a), but show variation in key vocal parameters among individuals (Hanggi and Schusterman 1994; Van Parijs et al. 2000a; Hayes et al. 2004b). In playback experiments in California, these individual differences were perceived by other

males, who responded aggressively to the roar of a subdominant male within their territory (Hayes et al. 2004b). This response suggests that the roar is used to establish dominance and maintain spatial dispersion in displaying males (Hayes et al. 2004b). The dominance of the individual was positively correlated with roar duration and negatively correlated with roar center frequency (Hayes et al. 2004b). This same pair of vocal parameters (duration and low frequency) varied between individual males in Scotland (Van Parijs et al. 2000a), suggesting that these parameters may in fact be an honest signal of fitness.

While it is well established that the roar is used in male-male dominance interactions, it is still unclear whether it is also used by females as an indirect, honest measure of male fitness. This additional function of roars would explain why males tend to roar more often at times when females are receptive and best able to hear them (Coltman et al. 1997; Van Parijs et al. 1997; 1999; Hayes et al. 2004a). For instance, two populations in Scotland had different temporal patterns of vocalizations, based upon differences in environmental constraints and timing of female mating receptivity between the two sites (Van Parijs et al. 1999). However, in Monterey Bay, harbour seals exhibited very different timing of roars, with some males roaring most before the breeding season in a central location, and others roaring most during the oestrus period while spread out along a travel corridor which females use to forage post-pupping (Hayes et al. 2004a). This individual variation in mating tactics was seen previously in Scottish populations, and in both cases the same individuals tended to employ the same tactics over a period of 2-4 years (Van Parijs et al. 2000b; Hayes et al. 2004a). This variation in display strategies suggests that individuals within and among populations use alternative mating tactics; therefore, studying the patterns of roaring and spatial distribution of males can provide clues about these tactics and, in turn, the purpose and reliability of male vocal signals.

Along with mating tactics, the vocal structure of the roar itself shows marked differences between populations and across geographical distance. The vocalizations of two populations in Scotland showed more variation between sites than among individuals within a site (Van Parijs et al. 2000a), and roars

from six colonies throughout the Baltic Sea were almost 90% distinguishable to site based on call frequency contours (Bjørgesæter et al. 2004). Van Parijs et al. (2003b) compared roar parameters of ten sites across the harbour seal's global range and found that roars varied at the subpopulation, population and subspecies level. Differences in vocal parameters did not always reflect geographic or genetic differences among sites, and there was no certain parameter that correlated exclusively with increased vocal differences. There also existed differences in vocal parameters between two sites within a genetic population, from which one may infer that the structure of a harbour seal roar is not completely determined by genetics, but may be a learned behaviour resulting in regional dialects (Van Parijs et al. 2003b). Unlike resident killer whales (Barrett-Lennard and Ellis 2001; Deecke et al. 2010), these dialects may not reflect genetically-related differences, and unlike humpback and blue whales (Winn et al. 1981; McDonald et al. 2006), call characteristics may not indicate discrete populations.

Acoustic Masking and Communication Space

Producing an honest and clear breeding signal is not enough to reproduce. In order to affect breeding success, the signal must also be received and comprehended (Richardson et al. 1995; Bradbury and Vehrencamp 1998). In the case of underwater vocal signals, the audibility of a signal depends upon its source level (energy at the source), the auditory sensitivity of the receiving individual, and the propagation conditions between the two animals (Urlick 1983; Richardson et al. 1995). Propagation conditions depend on the properties of the medium (density, temperature, reflective surfaces), and the interference of other signals (noise). Information in a signal can be lost due to absorption or reflection, or it can be masked by other signals (Richardson et al. 1995; Clark et al. 2009). These other signals may include natural ambient noise produced by wind, waves, seismic events and other animals, or it can come from anthropogenic sources (Richardson et al. 1995; Clark et al. 2009; Merchant et al. 2014). Acoustic masking is a term used to describe a loss of perceptibility of a signal due to interference by signals not of interest to the receiver (Clark et al. 2009). To mask a biological signal, the noise must be

loud enough to obscure at least part of the call, and be in a similar enough frequency bandwidth to make the noise indistinguishable from the call (Richardson et al. 1995; Clark et al. 2009). Masking reduces the communication space: the effective distance over which two animals can communicate (Clark et al. 2009; Hatch et al. 2012). Masking causes behavioural changes in marine mammals, such as increasing the source level (the ‘Lombard effect’; Holt et al. 2011) calling rate, or duration of calls (Foote et al. 2004), switching to non-vocal communication (Dunlop et al. 2010), or displacement from important habitats (Rako et al. 2013). It has been proposed that the additional energy costs associated with these behavioural responses could incur losses of fitness in individuals (Jensen et al. 2009; Tyack 2009; Holt et al. 2011; Rako et al. 2013).

While the behavioural effects of masking have been studied in a number of cetaceans, they have not yet been investigated in the harbour seal. Harbour seals have a wide audible range in air and underwater (Kastak and Schusterman 1998; Reichmuth et al. 2013), and exhibit behavioural changes in response to underwater acoustic harassment devices (Yurk and Trites 2000). The broadband noise produced by boat motors and shipping vessels overlaps the frequency bandwidth in which much of the energy of seal roars is concentrated (25Hz-1500Hz; Hanggi and Schusterman 1994); therefore, the acoustic masking of breeding calls is a distinct possibility in this species. If this is the case, anthropogenic influence may play a role in male breeding strategies: in order to ensure that their breeding calls are heard, males may change their calling behaviour in areas or at times of high noise. This phenomenon has been observed in the breeding calls of many birds and amphibians in response to natural and anthropogenic noise (Brumm and Slabbekoorn 2005; Slabbekoorn and Ripmeester 2007). This effect has not, to my knowledge, been investigated in pinnipeds.

Research Needs

While it is strongly suspected that harbour seal vocalizations serve as an attraction signal to females as well as displaying dominance to other males, the process of female mate choice in harbour seals is still

poorly understood (Hayes et al. 2004a; 2004b; Boness et al. 2006). In order to understand the process of mate choice in this species, we must first understand the diversity of male strategies, and how they relate to regional patterns that affect success, such as female availability and communication space. If we can determine the amount of effort that males put into sounding attractive and being heard, we can begin to assess whether it is important that females perceive these calls, and to what degree they convey fitness.

It is likely that acoustic masking of breeding vocalizations will cause changes in vocal behaviour in areas of high anthropogenic presence. However, acoustic masking and reduction of communication space has never been investigated in harbour seals. If behavioural changes in response to masking occur, then human activities would have become one of the drivers of breeding strategies in populations of harbour seals exposed to noise on a consistent basis.

Previous studies on vocal variation and displaying strategies of harbour seals have focused on one or two closely-related populations (Van Parijs et al. 1999; 2000a; Hayes et al. 2004b; Bjørgesæter et al. 2004), or on a small subset of populations (Van Parijs et al. 2003b). Despite decades of study in a few populations, there are large areas of the harbour seal's range in which their breeding behaviour has not been described. This discrepancy precludes a complete comparison of breeding strategies and vocalizations across all populations. Basic descriptions of the breeding behaviour of understudied populations is essential to drawing wide-scale conclusions about the evolutionary function of signals produced during the breeding season.

The Pacific subspecies of harbour seals inhabits much of the west coast of North America (*Phoca vitulina richardii*; Stanley et al. 1996); however the breeding behaviour and vocal characteristics of this subspecies has been described in detail in only one location: Monterey Bay, California (Hanggi and Schusterman 1994; Hayes et al. 2004a; 2004b). The inland waters of Washington State and British Columbia, collectively called the Salish Sea, support a very high population density of harbour seals whose vocal breeding behaviour has never been described. This population is maintained at carrying

capacity (Jeffries et al. 2003; Olesiuk et al. 2010), despite heavy anthropogenic influence due to industry, urbanization and ecotourism (Lusseau et al. 2009; Erbe et al. 2012). This resiliency makes Salish Sea harbour seals a good model population to compare to others in the harbour seal's global range, and an ideal system in which to study how anthropogenic noise may impact breeding behaviour in this species. Studying the vocal breeding behaviour of this population could reveal the strategies that males use in order to breed successfully despite large amounts of anthropogenic interference.

Research Approach

I used passive acoustic monitoring and concurrent visual observations to describe the vocal breeding behaviour of harbour seals at a haul-out in Georgia Strait, British Columbia, Canada. My objectives in Chapter 2 were to characterize the temporal patterns of roar density in this population, and compare them to environmental and anthropogenic cycles to determine the extent to which these cycles influence the displaying strategies of male harbour seals at this site. This study will be the first to examine ambient noise as one of these possible influences. My findings may be compared with similar information in other populations to determine whether males are competing for the attention of females, thus supporting the hypothesis that roars are an inter-sexual advertisement call. If anthropogenic noise is related to male roaring behaviour, then this study will provide a basis to investigate the mechanism underlying this relationship, and to determine whether similar relationships exist in other populations of harbour seal.

In Chapter 3, I set out to characterize the vocal parameters of roars in this region. I describe an unprecedented diversity of roars produced in this one small site, suggesting either drastic individual variation, the existence of discrete call types within this population, or perhaps a combination of these two factors. This information will fill a gap in our knowledge of roar variation between and among populations, allowing more comprehensive comparison with other sites.

By describing the vocal diversity and potential for anthropogenic interference in the breeding behaviour of harbour seals in Georgia Strait, it is my hope that this work will bring about further study of the breeding behaviour of this population of harbour seals. This information will allow us to understand their ability to breed successfully, despite high amounts of anthropogenic interference, and to apply this knowledge to other, more at-risk populations.

TEMPORAL TRENDS IN BREEDING CALL OCCURRENCE AND DENSITY FOR HARBOUR SEALS IN GEORGIA STRAIT, BC

Introduction

The impacts of noise pollution upon marine mammals have been an important foci of conservation research for the past few decades. Among animal species that communicate vocally, a diversity of behavioral mechanisms have evolved or developed in response to increased naturally and anthropogenically-generated ambient noise levels (Brumm and Slabbekoorn 2005; Tyack 2009). In cetaceans, for example, sound is an important mode of communication which, when impaired, can impact the ability to perform basic life functions and lead to stranding and other mortality events (Jensen et al. 2009; Tyack 2009; Holt et al. 2015). Anthropogenic contributions to ambient noise in the world's oceans have increased markedly in the past few decades, and these contributions are expected to rise with increased urbanization, resource exploration and renewable energy projects (Nowacek et al. 2007). Many studies have focused upon the impact of noise on the vocal behaviour of cetaceans (Nowacek et al. 2007; Tyack 2009). In contrast, few studies have investigated the effects of underwater noise on the vocal behaviour of pinnipeds. One species of phocid, the harbour seal (*Phoca vitulina*), occupies a range encompassing most coastal regions of the northern hemisphere (Burns 2009). Harbour seals vocalize underwater during the breeding season, and these vocalizations appear crucial to mating success (Hanggi and Schusterman 1994). While several studies have been conducted on the underwater hearing sensitivity of this species to loud sounds (e.g. Kastelein et al. 2013), to my knowledge no study has yet investigated the effects of increased anthropogenic noise on their vocal behaviour.

In harbour seals, the breeding season typically occurs in summer and early fall, after females have weaned their pups (Bigg 1969b; Temte et al. 1991). Males contract their wide foraging ranges during late lactation into smaller aquatic territories near areas that are frequented by females (Van Parijs et al. 1997; Hayes et al. 2004a). Males defend these reduced territorial ranges with visual and auditory dominance displays (Sullivan 1981; Hayes et al. 2004b) and show strong site fidelity between years

(Hayes et al. 2004a; Van Parijs et al. 2000b). The proximity of harbour seal males displaying near female haul-out areas resembles leks. Displays include surface-active behaviours (flipper-slapping, rolling and lob-tailing; Sullivan 1981) and short dives during which underwater vocal displays are produced (Hanggi and Schusterman 1994; Coltman et al. 1997). These vocal displays consist primarily of stereotyped calls referred to as 'roars' (Hanggi and Schusterman 1994). Roars show individual variation, and are hypothesized to be used in male-male competition for territory (Hanggi and Schusterman 1994; Van Parijs et al. 2000a; Hayes et al. 2004b). Roars may also be used to advertise fitness to females, although this hypothesis has not been carefully investigated (Boness et al. 2006).

Individual males show variation not only in the vocal qualities of their roars but also in their overall displaying tactics. Differences in calling behaviour among and within populations may be due to small-scale differences with respect to environmental conditions such as tide and bathymetry, and/or differences in spatiotemporal proximity of females (Coltman et al. 1997; Van Parijs et al. 1997, 1999; Hayes et al. 2004a; Boness et al. 2006). For instance, in Scotland some males occupy displaying territories close to a haul-out site while others occupy territories along a feeding corridor or near a foraging area (Van Parijs et al. 1997). Variability in the temporal patterns of displays has been recorded between two parapatric haul-outs in Monterey Bay, California (Hayes et al. 2004a): at one location, calls peak about a month before the onset of mating receptivity (oestrus) of females, whereas in two other locales, males displayed the most during the peak of the mating season. Males in Monterey Bay also showed a bimodal diel pattern of call density (number of calls per hour), calling most just before sunrise and after sunset, when females were most likely to be in the water (Hayes et al. 2004a). Temporal patterns also differ between two haul-outs in Scotland: males roared most at peak oestrus in both sites, despite peak oestrus occurring several days apart between the two locales (Van Parijs et al. 1999). Call density in one location was significantly related to tide, with more vocalizations being produced at high tide when, presumably, there are more female seals in the water. In the other location in Scotland, calls are related to both tide and time of day, with more calls being produced at night (Van

Parijs et al. 1999). In Nova Scotia, males perform more shallow display dives, typically associated with vocal activity, during the evening and night, when females are moving between haul-out and foraging sites (Coltman et al. 1997). A reasonable inference about the relationship of call density to temporal patterns of haul-out by harbour seal females is that males choose to vocalize when it is more likely that females will hear them (Coltman et al. 1997; Hayes et al. 2004a).

A source of variation that has not been examined in relation to harbour seal vocal behaviour is the impact of anthropogenic underwater noise. Acoustic masking occurs when ambient noise in an important bandwidth increases to a level over which signals of interest (e.g. calls) cannot be perceived by a listener (Richardson et al. 1995; Clark et al. 2009). Interference by acoustic masking reduces communication space in cetaceans and pinnipeds, and is associated with changes in behaviour (reviews by Clark et al. 2009; Tyack 2009). Most of the energy of harbour seal roars occupies the bandwidth from 50Hz to 5kHz (Van Parijs et al. 2003b), which is also occupied by noise from vessel motors, submarine tectonic activity and, in shallow water, surface wind noise (Richardson et al. 1995). If males call most when females are likely to hear them, then it is reasonable to assume that acoustic masking may play a role in the choice of breeding strategy in vocalizing male harbour seals. However, such an effect has not been studied in this species.

Harbour seals are among the most widely-encountered pinnipeds in the world. Yet, their vocal breeding behaviour has been studied in detail in only a few populations in Scotland (Van Parijs et al. 1997, 1999, 2000a,b; Bjørgesæter et al. 2004), California (Hanggi and Schusterman 1994; Hayes et al. 2004a, b), Norway and Sweden (Bjørgesæter et al. 2004), and eastern Canada (Coltman et al. 1997; Boness et al. 2006). The inland waters of Washington State and British Columbia, known as the Salish Sea, support a very high density of harbour seals, comprising several genetically and geographically discrete populations (Burg et al. 1999; Huber et al. 2012). No study has been conducted on the breeding behaviour of these populations, including patterns of vocal behaviour. Despite heavy anthropogenic presence in the form of urban development, ecotourism, recreational and shipping vessel traffic in the

Salish Sea (Lusseau et al. 2009; Erbe et al. 2012, 2014), these populations are maintained at carrying capacity (Jeffries et al. 2003; DFO 2010). The populations appear to be reproducing effectively, hence one may infer that males employ behavioural strategies that allow their calls to be heard despite the noise. In other marine mammals, these strategies often result in changes to an individual's energy budget (Clark et al. 2009; Holt et al. 2011, 2015). Understanding these strategies can help to determine the threat that acoustic masking poses to the health of harbour seal populations. The inland waters of British Columbia are an ideal system to examine these strategies in a healthy population that is consistently exposed to high noise levels.

To investigate for the first time in harbour seals the influence of human activities on their underwater vocal behaviour, I employed passive acoustic and visual observations to describe the diel and seasonal patterns of harbour seal vocal displays in Georgia Strait, British Columbia, and relate them to natural (tide, daylight, and progression of breeding season) and anthropogenic (broadband noise) variables. Acoustic recordings were used to measure ambient noise and to determine roar density (roars/hour). Visual observations were used to collect data on weather conditions, the number and behaviour of vessels in the area, and the number of seals hauled out and in the water.

Methods

Acoustic and visual observations were made from June through September 2014 at Heron Rocks, a known harbour seal haul-out site near the southern end of Hornby Island, British Columbia, Canada. Hornby Island is one of the Northern Gulf Islands, located in Georgia Strait near the east coast of Vancouver Island (Figure 1). This site was selected due to its high abundance of harbour seals (Olesiuk 2010) and its proximity to Hornby Island, making it easily observable from shore. The water around Heron Rocks is ideal for moored hydrophone deployment due to its low current flow (6 km/h maximum) and soft mud/gravel substrate (Canadian Hydrographic Service, Chart #3527). This site is also acoustically sheltered from a nearby shipping lane to the east of Hornby Island (Figure 1).

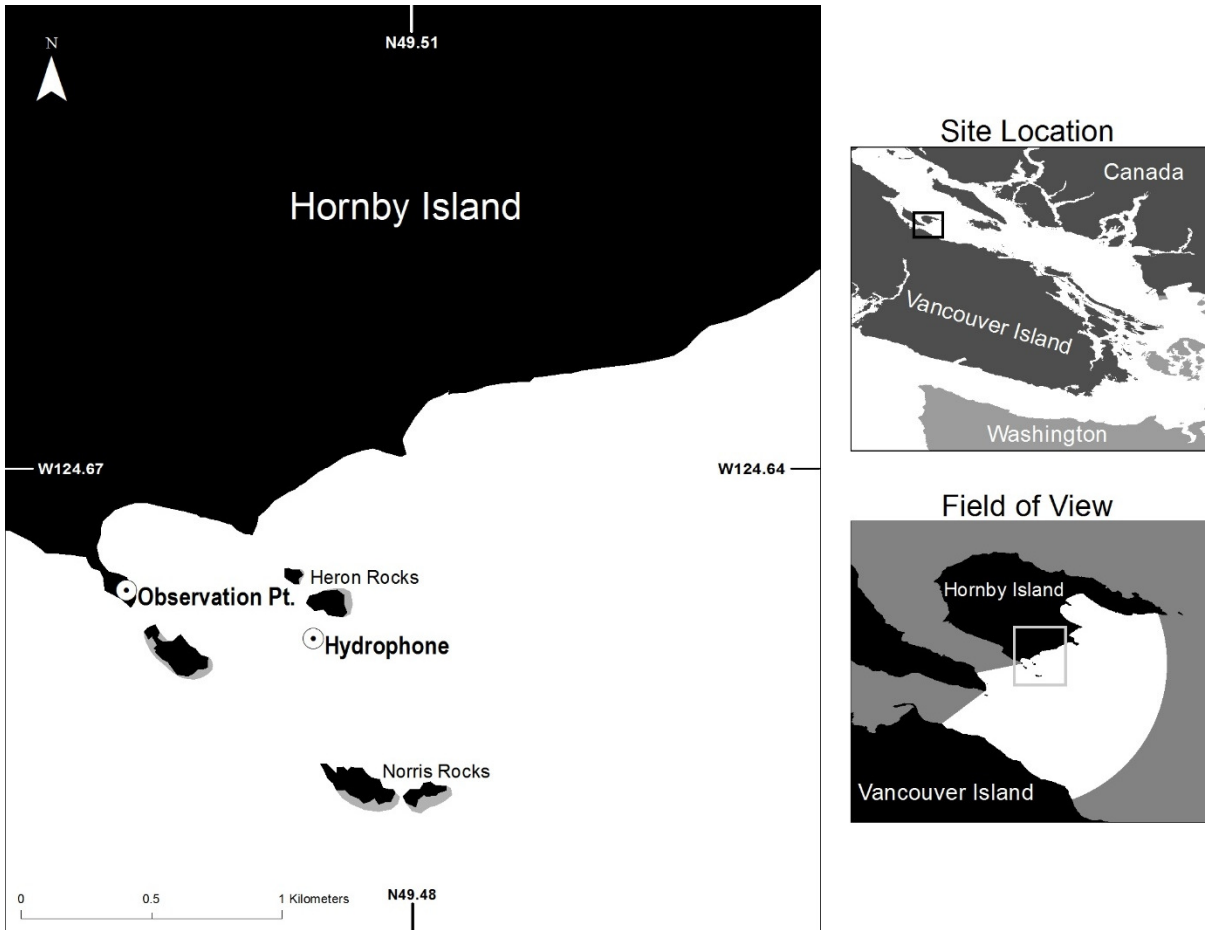


Figure 1. Map showing the Salish Sea and indicating the region of study (top right), the field of view visible from the observation site (bottom right), and a close-up view of the study site at Heron Rocks (left), including the location of the hydrophone, observation point and haul-out area. Created in ArcGIS using the North American 1983 datum and GCS NA1983 coordinate system. Units are in decimal degrees. Map created by Erin Harker (Western Washington University); used with permission.

Acoustic Recordings

Acoustic data were collected with an Autonomous Multichannel Acoustic Recorder (AMAR) system (JASCO Applied Sciences), fitted with a calibrated omnidirectional standard acoustic hydrophone (M8E from GeoSpectrum Technologies Inc.; nominal sensitivity -165 dB re: 1 V/ μ Pa; flat frequency response 10-24,000 Hz). The AMAR system was anchored to a steel plate with the hydrophone element suspended by elastic cables approximately 50 cm from the seafloor. The AMAR was deployed at approximately 6.4 m deep at mean sea level in a central area of the Heron Rocks haul-out site (49°29.307'N, 124°39.313'W; Figure 1) on June 15, 2014, and was retrieved on September 10, 2014. The AMAR recorded continuously in the bandwidth of 10 Hz - 24,000 Hz during its deployment time (24-bit sampling resolution; 48,000 Hz sampling rate), which falls well within the vocalizing frequency range of harbour seal calls (Hanggi and Schusterman 1994; Van Parijs et al. 2003b).

Upon retrieval, calibration settings were checked and found that the sensitivity was within an acceptable range of error (\pm 0.3 dB). Data were automatically saved to a secure digital memory card. Upon retrieval of the hydrophone, data were downloaded to a hard drive at JASCO Applied Sciences in Victoria, BC.

Visual Observations

Visual observations of the haul-out site were taken from the shoreline of Hornby Island, approximately 300 m from the nearest haul-out site at Heron Rocks (Figure 1). The observation site (49°29.380'N, 124°39.845'W) has an elevation of 5.7 m above mean sea level; this height afforded an unobstructed view of the area which allowed all vessels to be reliably counted. Seals in the lee of the islands may not have been visible at all times. As these blind spots were consistent throughout all observations, and the relative number of seals was more important than the exact number, seal counts were not adjusted.

Three observation sessions were carried out: June 16-28, July 21-August 2, and August 25-September 6, 2014.

Visual surveys were conducted during daylight hours for up to 12 h each day. Surveys were truncated or paused if the tide rose over 3.9 m above mean sea level, or if weather conditions (i.e. fog, high sea state, heavy rain) prohibited adequate visibility of the entire study area. The maximum sighting distance to the horizon from the observation site was 10 km. The maximum tidal difference during summer months at Hornby Island is approximately 4 m, causing a notable change in the amount of haul-out space at Heron Rocks throughout the tidal cycle. Visual surveys were conducted using reticle binoculars (Steiner Commander III, 7x50 magnification) and a digital theodolite (Leica TC605L [± 5 in. (127mm) accuracy]); data were recorded in real-time on a notebook computer.

Each visual survey lasted 20 min as follows: first, the number of seals seen on land and in the water were recorded; then, the number of vessels within the study region was recorded. Following the vessel count, the position of each vessel was fixed at a single point in time for each survey by scan-sampling from one side of the visual area to the other over 15 min (Martin and Bateson 2007). Vessel positions at a certain time were fixed by taking a range with reticle binoculars and a simultaneous bearing with the theodolite. The type and activity of each vessel was also recorded (Table 1). Weather conditions were recorded at the top of each hour, and updated as large changes occurred. The presence of other marine mammal species was noted when it occurred.

Table 1a. Description of vessel types recorded at Heron Rocks during the summer of 2014.

Vessel Type	Description
Motor Yacht	Larger boat, likely inboard motor
Sailboat	Boat with sail, with or without motor
Outboard	Solid hull, outboard motor
RHIB	Rigid hull inflatable vessel, outboard motor
Tug (& Tow)	Tugboat, alone or carrying cargo/barge/log boom
Cargo/Ferry	Large vessel carrying cargo containers/passenger ferry over ~30 meters

Table 1b. Description of vessel activities recorded at Heron Rocks during the summer of 2014.

Vessel Behaviour	Description
Running	Moving faster than the current
Sailing	Actively sailing; motor, if present, not active
Idling	Motor running, but no movement relative to current
Drifting	Motor does not appear to be running, no movement relative to current
Unknown	Too far to tell, cannot see trajectory

Data Processing and Analysis

Acoustic data were analyzed spectrographically using Raven Pro 1.5 acoustic analysis software (Cornell Lab of Ornithology) with 2450-point Fast Fourier Transform, Hann window and 50% overlap. For analysis, 20 days (480 hours) in which seal roars were detected were randomly selected (Table 2) and reviewed in their entirety. This form of subsampling was designed to catch diurnal patterns and track the progression of the breeding season, but did not represent the full spread of conditions that were recorded. Therefore these data may not be reliable for absolute density estimates or presence/absence patterns at this site (Thomisch et al. 2015). The recordings were manually reviewed and the number of roars per h was counted for each hour beginning at the top of the hour. The first day when seal calls was heard was deemed the first day of breeding season, as harbour seals typically call only during breeding season (Hanggi and Schusterman 1994).

Ambient noise (sound pressure level [SPL] in dB re: 1 μ Pa) was averaged over 60 s intervals in 1/3 - octave bands using SpectroPlotter acoustic analysis software (JASCO Applied Sciences Ltd.). The hourly average was computed for the bandwidth with center frequencies from 1.5-20 kHz; the lower limit was selected to avoid the bandwidth of the majority of harbour seal roars, so that the presence of roars would not skew the approximation of ambient noise in that bandwidth. The upper limit of the chosen bandwidth corresponds to the Nyquist limit of our recordings, which is well within the auditory range of a harbour seal (Richardson et al. 1995; Reichmuth et al. 2013).

Noise level for each 30-min sound file was rated quantitatively by a single observer on a scale of 0 (lowest noise) to 4 (highest noise), based on the relative strength of background noise seen on the spectrogram for that file. If ambient noise fluctuated within a file from one rating to another, the average over the length of the file was taken. To ensure that roar density was not biased due to varying levels of ambient noise, power spectral density (power per unit frequency, in dB re: 1 μ Pa²/Hz) was calculated each minute and averaged for a one-hour period, then plotted against frequency. Plots of an hour when seal calls were heard in the presence of noise rating 4 were compared to plots of an hour when seal

calls were heard in noise rating 0. Peaks in energy that were seen in the low-noise graph are assumed to indicate seal calls. If these same peaks are visible in the high-noise graph, it can be said that seal calls would be detectable even in high noise conditions.

Logistic regression was used to model the best predictors of roar occurrence at Hornby Island; specifically, a GLM (general linear model) defined by a binary response variable (presence or absence of seal calls). This type of logistic model was useful for determining which variables contributed most to call occurrence, as well as producing the likelihood of seal calls occurring for any value of these variables (Hosmer and Lemeshow 2000). Density plots were used to confirm normality and homoscedasticity of all predictor variables. Predictors were selected by modelling every possible combination of predictors and choosing the model with the lowest Akaike Information Criterion (AIC) score (Bolker et al. 2009). The selected model was then used to produce odds ratios for each predictor variable, denoting the likelihood of roars occurring in an hour with a certain value of that variable.

When roars were heard (beginning with a single roar, thus roar count in an hour was >0), the numbers of roars per hour (roar density) was compared to ambient noise level using Kendall's rank correlation; this correlation was selected for its robustness in departures from normality and homoscedasticity in the data (Abdi 2007). Roar density was compared between day and night by using a Wilcoxon paired test, chosen also for its robustness to departures from parametric assumptions and uneven sample sizes.

Visual observations were compiled and measured variables were averaged over each hour of observations. I selected for analysis days of visual observations that corresponded to any of the 20 days that were acoustically analyzed ($n=9$ visual observation days, 86 h total). A one-way analysis of variance (ANOVA) was used to compare daytime haul-out patterns across tide levels to determine whether tide had a significant effect on the number of seals hauled out or in the water during daytime observations. The relationships between haul-out patterns and other environmental variables including cloud cover, precipitation and time of day were also tested using non-parametric methods (Kruskal-

Wallis test for cloud cover and precipitation, and Spearman's rank correlation for time of day), because the predictor variables did not meet parametric assumptions of normality and homoscedasticity.

For the same dataset, a generalized linear model with a normal distribution was used to determine which factors contributed most strongly to ambient noise level during daylight hours (Bolker et al. 2009). The dependent variable was transformed to fit a normal distribution. The factors included in the full model were the average number of vessels, the average number of motor vessels running, the relative tide level (number of hours past high or low tide, as a proxy for relative current speed), average precipitation, average wind speed and average sea state. Predictor variables were tested for autocorrelation using a Pearson's correlation matrix, after testing to ensure that all parametric assumptions were met for each variable. In cases where autocorrelation was found, the strongest predictor variable was included in the model and the correlated variable was excluded. The best-fit model was determined to be the model with the lowest AIC value (Bolker et al. 2009).

Results

Over the 88 days of hydrophone deployment, approximately 2,112 h of acoustic data were collected. Over three two-week observation sessions, approximately 962 twenty-min visual surveys were completed, equalling approximately 320 h of visual observations during daylight hours. Harbour seal roars were heard during 185 h of recordings between July 25th and September 10th, which I used to represent the breeding season. Of these 48 days of breeding season that were recorded, 20 were randomly selected for analysis (Table 2). The number of hours that roars were heard and the number of roars heard per day increased as the breeding season progressed, and neither variable had decreased by the time the hydrophone was retrieved.

Table 2. Information on the 20 days in the 2014 breeding season that were randomly selected for acoustic analysis. An X under ‘Visual’ denotes that this day was one in which visual observations were conducted. ‘Hours of Roars’ indicates the number of hours in each day when roars were detected spectrographically, and ‘# of Roars’ gives the total number of roars that were detected on that day. *Killer whales were heard from 20:00 to 21:30 on the evening of July 30th, and only one roar was detected over the following day.

Date	Visual	Hours with Roars	# of Roars
07/26		4	56
07/28	X	5	118
07/31	X	1*	1*
08/01	X	5	17
08/05		2	40
08/14		4	169
08/15		9	111
08/16		10	272
08/20		5	94
08/21		9	93
08/23		8	412
08/24		10	345
08/25	X	11	354
08/27	X	9	194
08/28	X	13	446
08/29	X	10	318
09/02	X	21	1161
09/03	X	17	895
09/08		14	966
09/09		18	1453

Factors Affecting Roar Presence/Absence

The full logistic regression model of occurrence of roars was fit with time of day (day/night, based on sunset and sunrise times), relative tide level (number of hours after high or low tide), and the date (expressed in number of days past July 25th). The best-fit model included time of day and date but not tide level (Table 3). Odds ratios indicated that it was 8.7 times more likely that roars would be present during night time hours than during the day (Table 4) and that with each additional day past July 25th, the probability that roars would be present in each hour increased by 8.35%.

Factors Affecting Roar Density

In examining the spectral power density plots, a peak in energy was seen at approximately 50 Hz in each graph (Figure 2), as well as between 100-700 Hz, which is where the majority of power in seal roars was concentrated. These peaks are likely associated with seal roars, as they are the highest-energy portion of the low-noise hour graph. The high-noise plot showed an increased level of noise in the frequency band from 1,000-10,000 Hz (1-10 kHz); however, the lower-frequency peaks of energy were still visible. While examining the spectrograms, it was noted that even at times when noise was high, concentrated energy below 1,000 Hz could be used as an indication that seals were calling. Therefore graphical analysis and spectrographic examination both show that the low-frequency components of seal calls could be detected by an observer even in high-noise conditions. Narrow peaks at 150 Hz in both plots likely correspond to an artifact of recording such as hydrophone self-noise (Figure 2).

Table 3. Model selection for predictors of roar occurrence (RoarPres) in a given hour. I used a generalized linear model with a binomial distribution (logistic regression). The best-fit model is represented by the lowest AIC value. The model was fit with the time of day (day or night; shown as TOD), the date (expressed in days after the first day of breeding season), and the tide (number of hours after high or low tide). Extreme tides were excluded for a final N=387 h.

Model	df	AIC	ΔAIC
RoarPres ~ TOD + Date	384	388.1	-
RoarPres ~ TOD + Date + Tide	375	395.1	7.0
RoarPres ~ TOD	385	453.1	58.0
RoarPres ~ TOD + Tide	376	461.8	8.7
RoarPres ~ Date	385	465.3	3.5
RoarPres ~ Date + Tide	376	476.4	11.1
RoarPres ~ Tide	377	536.6	60.2

Table 4. Coefficients and significance values for the factors included in the best-fit model predicting roar occurrence. Odds ratios are exponentiated coefficient estimates. Values <0.005 are denoted with a '*’.

Factor	Estimate	Std. Error	z Value	p-value	Odds Ratio
(Intercept)	-3.64094	0.40249	-9.046	<2e-16 *	0.02623
Time of Day	2.16696	0.26593	8.149	3.68e-16 *	8.73169
Date	0.08019	0.01111	7.219	5.22e-13 *	1.08349

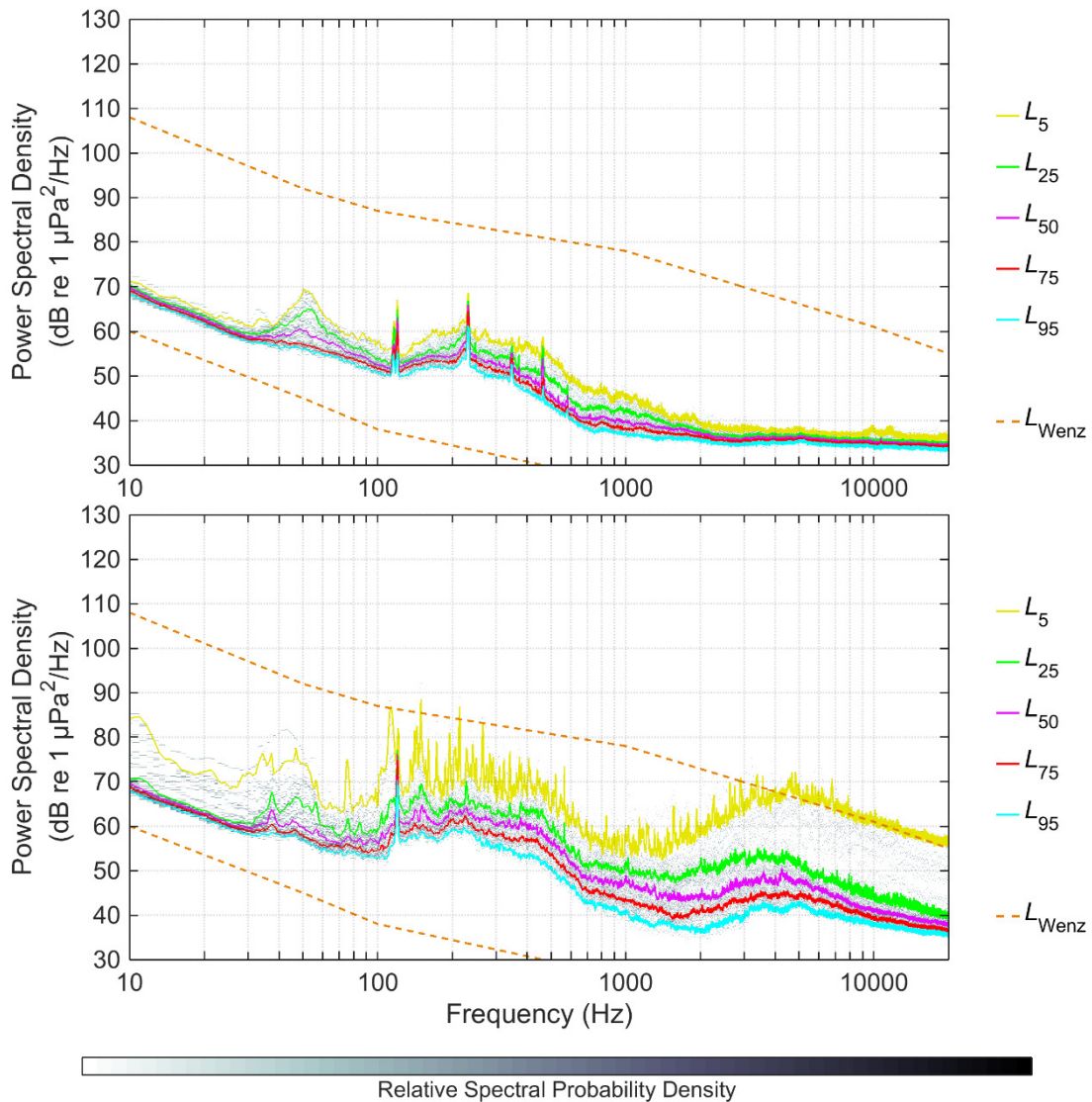


Figure 2. Power spectral density calculated per minute and averaged over one hour when seal calls were heard in low (top) and high (bottom) ambient noise conditions. Likelihood at the 5%, 25%, 50%, 75% and 95% levels are shown, as well as the expected levels according to the Wenz curve (Wenz 1962). Peaks seen at ~50 Hz and 100-700 Hz in the low-noise graph are assumed to indicate seal calling. These peaks are visible in the high-noise graph as well, despite high energy in higher bandwidths.

During hour periods when seal roars occurred, time of day had a very strong statistical relationship to the number of roars detected per h. Roar density was significantly higher during the night than during the day (Wilcoxon $W=12983$, $p<0.001$; Figure 3). Ambient noise was also significantly correlated to roar density (Kendall's $\tau = -0.286$, $p<0.001$); however, these two factors were auto-correlated: ambient noise was significantly higher during the day than at night (Wilcoxon $W=52901$, $p<0.001$).

Visual Observations

Over the 3 two-week visual observation sessions, 961 visual surveys were completed (approximately 320 h of data). The time period where roars were heard (a proxy for the breeding season) included the second and third visual observation sessions. Of the 20 randomly selected days that were acoustically analyzed from this time period, 9 days had associated daytime visual observations during daytime (Table 2), totalling 86 h when acoustic analysis and visual observation overlapped.

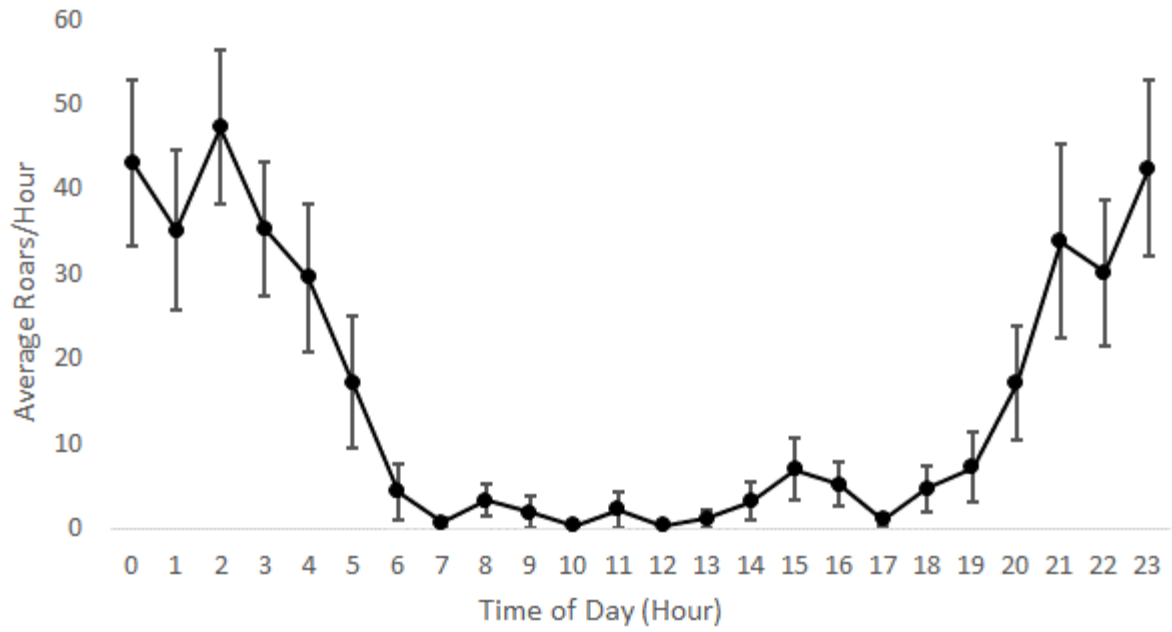


Figure 3. Average number of harbour seal roars \pm SE per h that were detected by spectrographic analysis, compared to time of day (N=20 days).

Ambient Noise Predictors

For general linear models, the total broadband ambient noise levels for each hour were transformed to fit a normal distribution by multiplying it to the fourth power (Ambient Noise⁴). Average wind speed and average sea state were found to be highly correlated (Spearman's $\rho=0.46$, $p<0.001$); only sea state was included in the model. Average number of vessels and average number of vessels under power were also highly correlated (Pearson's $r=0.65$, $p<0.001$). I chose to include the average number of vessels in the model, because it correlated more strongly with ambient noise level. Relative tide level was included in the model after eliminating data points that represented extreme tides, to maintain a balanced sample size across tide levels. These variable selections reduced the total sample size to 81 hours. The full, fitted model contained the average number of vessels, average sea state, average precipitation, and relative tide level. The best-fit model only included the average number of vessels (Table 5), though the change in AIC value was small between all models containing the average number of vessels. When number of vessels was excluded from the model, the fit of the model was greatly reduced (Table 5).

Haul-Out Behaviour

Seal haul-out behaviour appeared to be driven by tidal cycles during daylight hours. After eliminating data points with extreme tides, a one-way ANOVA showed that the number of seals hauled out was significantly lower around high tide than around low tide ($F_{10,70}=2.406$, $p=0.016$; Figure 4). A different one-way ANOVA determined that the number of seals in the water was significantly lower at low tide than at high tide ($F_{10,70}=2.904$, $p=0.004$; Figure 4). The overall number of seals observed on and around the haul-out remained constant across tide levels (ANOVA, $p>0.20$), which suggests that the total number of seals did not influence the proportion of seals seen in the water or hauled out.

Table 5. Model selection for predictors of ambient noise level to the fourth power (Ambient⁴) during daylight observation hours at Heron Rocks. I used a general linear model with a normal distribution. The best-fit model is represented by the lowest AIC value. The model was fit with the average number of vessels (#Vessels), the average precipitation (Precip), the average sea state (SS), and the relative tide (time after low or high tide; Tide). N=81 h.

Model	df	AIC	ΔAIC
Ambient ⁴ ~ #Vessels	76	2842	-
Ambient ⁴ ~ #Vessels + Precip	75	2843	1
Ambient ⁴ ~ #Vessels + Precip + SS	74	2844	1
Ambient ⁴ ~ #Vessels + Precip + SS + Tide	74	2845	1
Ambient ⁴ ~ #Vessels + SS + Tide	65	2846	1
Ambient ⁴ ~ SS	76	2865	19
Ambient ⁴ ~ Precip + SS + Tide	65	2867	2
Ambient ⁴ ~ SS + Tide	66	2874	7

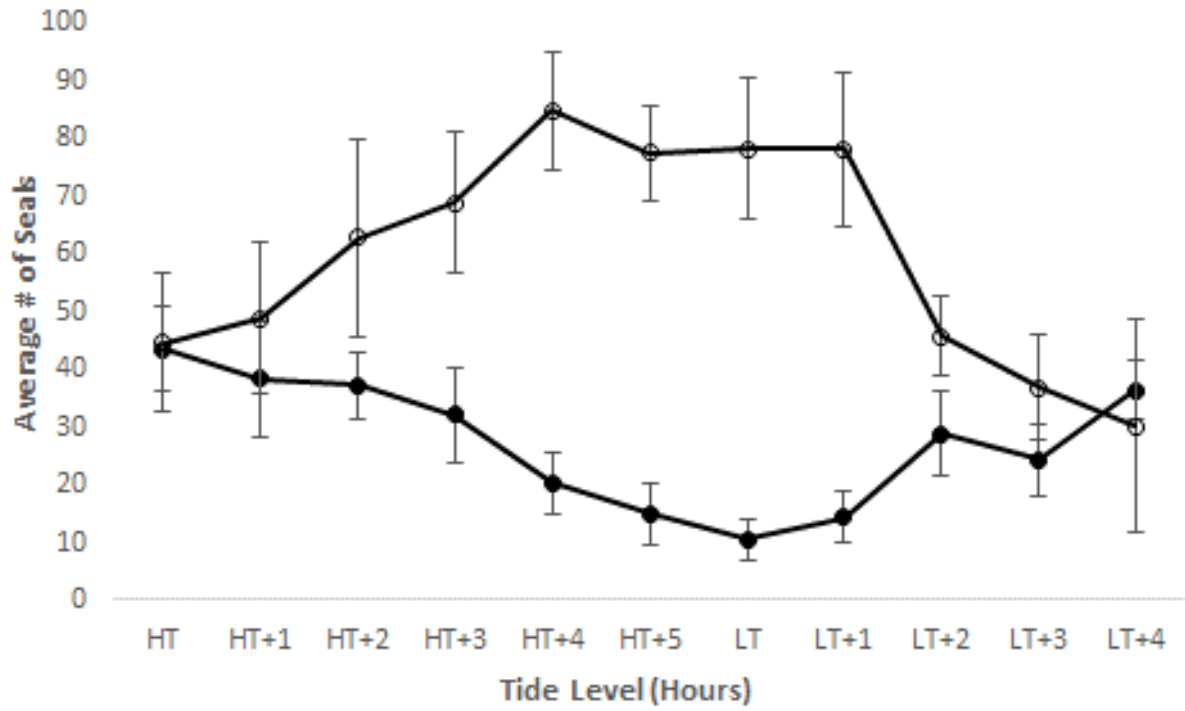


Figure 4. Average number of seals \pm SE hauled out (open points) and in the water (closed points) each hour, compared to the number of hours since high tide (HT) or low tide (LT). Data points representing extreme tides with low sample sizes have been removed.

The number of seals hauled out was not related to cloud cover (CC), but the number of seals in the water was significantly greater when there was no cloud cover (CC=1) than when there were any clouds at all (CC=2-5; Kruskal-Wallis $X^2=9.02$, $p=0.03$). This result may be the product of sampling bias, considering that the number of surveys in the sample set that had CC=1-2 was much greater than those with CC=3-5. Similarly, time of day had no effect on the number of seals hauled out during the day (Spearman's rank correlation, $\rho=0.186$, $p=0.09$). A weak negative correlation was found between the number of seals in the water (small sampling period, 86 h) and time of day (Spearman's rank correlation, $\rho=-0.258$, $p=0.02$), with the fewest seals in the water seen in the early afternoon and the most seen in mid-morning. No relationship was found between precipitation and number of seals either hauled out or in the water (Kruskal-Wallis, $p>0.05$). The effect of tide was the strongest effect seen on any environmental variable tested on haul-out patterns.

Discussion

In Georgia Strait, calls at night were more than eight times more likely than calls during the day. . Also, when roars were heard, the number of roars per hour (roar density) was much higher at night than during the day (Figure 2). The density of roars was lower at times of high ambient noise; however, ambient noise level was significantly higher during the day, confounding whether roar density was more dependent on time of day or noise level. Visual observations showed that during the day, haul-out behaviour was related to tide. During the night, however, roar presence and density were not related to tide.

Seals at Hornby Island showed a very clear diel pattern of roaring behaviour, a pattern previously observed in other populations (Coltman et al. 1997; Van Parijs et al. 1999). In Moray Firth, Scotland, a similar pattern of nocturnal roaring was observed, but it was also significantly related to tide (Van Parijs et al. 1999). Seals at Sable Island, Nova Scotia, make more shallow dives at night (Coltman et al. 1997). Vocalizations were not measured directly, but short, shallow dives have been associated with

roaring behaviour in Scotland (Van Parijs et al. 1997). The Sable Island study did not relate the nocturnal trend in dive behaviour to tide; instead the authors posited that this trend was related to the foraging behaviour of females. A similar hypothesis was proposed for a population in Monterey Bay, where vocalizations peaked at dawn and dusk, when females were likely transiting between foraging grounds and haul-out sites (Hayes et al. 2004a). Relating male-calling behaviour to female movements supports the hypothesis that males roar to advertise fitness to females, and not only to other males.

It is reasonable to infer that if males use roars to attract females, then males would call more when more females are within hearing range. These nocturnal activity patterns of males have been associated with times when female availabilities were higher, such as when females were foraging or at high tide when haul out space was unavailable (Coltman et al. 1997; Van Parijs et al. 1999; Hayes et al. 2004a). But, in contrast, during daylight, roar density was not related to tidal period at Hornby Island, even though haul-out behaviour was strongly related to tide (Figure 3). Haul-out behaviour may not be the only explanation for this nocturnal predominance of roaring; thus, other factors such as ambient noise patterns may cause the relative paucity of roars during the day. For example, acoustic masking may pose opportunity costs (wasted time) as noise increases, because the distance at which calls can be heard and the information that can be perceived from that call decreases (Clark et al. 2009; Jensen et al. 2009). Moreover, both energetic costs and opportunity costs may be reduced if male harbour seals call more often at times when their roars would convey the most information to conspecifics: namely when females are in the water and the acoustic environment is favourable.

Females in other harbour seal populations are more available during foraging at high tide (Van Parijs et al. 1999), whereas in this study high tide did not correlate with roar density in this study. Presumed foraging behaviour was observed during daylight hours, but because seal behaviour was not observed at night in this study, the nocturnal foraging behaviour of females cannot be confirmed. Harbour seals are adapted for nocturnal activity as well as diurnal (Burns 2009). It is therefore likely that females at

Hornby Island forage equally during the day and night, with males choosing to call more during night-time foraging trips to avoid acoustic masking by vessel noise.

In analyzing the relationship between broadband noise level and call density, it was important to verify that any acoustic masking that may have occurred did not bias the call density results. I ascertained from power spectral density analysis that acoustic masking occurred because I found peaks in power around 50 Hz and between 100 and 1,000 Hz that were higher in power than ambient noise when noise was both low and relatively high. These peaks were also noted upon spectrographic examination, and confirmed by graphical analysis. Masking of the higher frequency components of seal calls was also noted visually, and confirmed by graphical analysis: power levels were much higher in the frequency band from 1-10 kHz when ambient noise was high, which includes the highest frequencies of seal roars (Van Parijs et al. 2003b). Thus I infer from these results that, although seal calls can still be detected during high ambient noise, some masking takes place when ambient noise (in this area mostly produced by anthropogenic sources) is high.

Clark et al. (2009) describe two kinds of masking: energetic masking (when the masking noise contains energy in a similar bandwidth of the call, rendering the call inaudible) and informational masking (the call is still audible, but parts of it are unable to be disentangled from masking noise with similar characteristics). I suggest here that harbour seal roars may not be energetically masked by anthropogenic ambient noise, but that some informational masking is taking place. If the higher-frequency characteristics of seal roars (e.g. pulse length, high frequency; Van Parijs et al. 2000a) are important for conveying information on body condition or other fitness aspects, then informational masking of this type could be detrimental to seal communication despite the low frequency component of roars still being audible to conspecifics. This would suggest that seals would benefit from roaring preferentially at times of low noise. If males are temporally avoiding noise in order to have a better chance of being heard without expending more energy, this may be a strategy which allows this

population to maintain high reproductive output despite high levels of anthropogenic disturbance in the form of vessel noise.

Predator avoidance may also provide a link between roar density and ambient noise levels. When killer whale vocalizations were heard the night of July 30th, no roars were heard until the following evening. Since transient killer whales are thought to hunt by listening for prey vocalizations (Barrett-Lennard et al. 1996), perhaps seals in this region prefer not to vocalize at times when ambient noise levels are high, because calling makes them vulnerable to auditory predators while the noise would prevent them from receiving auditory warning of predator approach in the form of distant whale vocalizations.

Ambient noise level in this study depended on the number of total boats in the area, and the best model contained sea state and precipitation as well. Similar results were found in a study of shipping noise in Moray Firth, UK (Merchant et al. 2014). Vessel movements accounted for a significant portion of recorded noise levels at most frequency bands. In the absence of shipping noise, ambient noise level was correlated to wind speed (highly related to sea state) at middle frequencies, and current speed and tide level at low and high frequencies, respectively (Merchant et al. 2014). At Hornby Island, tide level (used as a proxy for current speed) was not correlated to ambient noise. The lack of significant correlation may be attributable to the generally slow current around Hornby Island (maximum 10 km/h; Canadian Tide and Current Tables). Additionally, cumulative broadband noise measurements were analyzed in this study, because harbour seal hearing and vocalizations are broadband and I wished to measure the effect of noise level overall on seal vocalizations. Merchant et al. (2014) analyzed each 1/3-octave band separately, because they wished to break down the sources of noise by frequency band. The discrepancy in the relationship between tide and noise level in their study and this one may then be attributable to the concentration of current noise in a particular frequency band, which I was unable to resolve with broadband ambient noise measurements.

Precipitation had a stronger correlation with noise than expected, which may be explained by the lack of variability in the precipitation level throughout this study. In the 86 h of visual observations that

were analyzed, only four had a precipitation score higher than 0. These four values may have artificially inflated the importance of this variable. The increased effect of rain on noise at this site could also be explained by the shallow positioning of the hydrophone, which would allow it to record more surface noise than a deeper instrument. Harbour seals vocalize during short dives that can reach 10 m depth (Coltman et al. 1997); thus a deeper deployment would still be expected to record roars without as much surface noise.

Surprisingly, ambient noise was correlated more strongly with the number of boats in general than with the number of boats running their engines in any given hour (Table 5). This may be due to the survey methods – the observation point lacked the height of eye necessary to measure exact distance with the theodolite. Previous studies measuring boat impacts have used theodolite tracking to measure minimum approach distance, speed and other metrics for each vessel (e.g. Johnson and Acevedo-Gutiérrez 2007); however this study's goal was to locate and count all vessels that may have contributed to ambient noise (Merchant et al. 2014; Fournet 2014). Future studies in this area would benefit from a haul-out sight that could be viewed from a higher vantage, and in addition to counting total vessels, use of the theodolite to track vessels that approach within a certain radius of the haul-out site may provide more accurate comparison between boat behaviour and ambient noise level.

Other marine mammal species increase the duration, frequency (pitch) or source level of their calls in the presence of noise (Brumm and Slabbekoorn 2005). These vocal changes have metabolic and overall fitness implications (Jensen et al. 2009; Holt et al. 2015). Few roars were heard at times of high ambient noise levels in this study, and no notable changes in roar duration or roar frequency were observed during periods of high ambient noise. Source level (power of calls at the point of origin) could not be assessed in this study because I did not have the number of hydrophones necessary to localize the roar location, but it is notable that many roars detected at high noise levels had relatively high received levels. This perceived change in received level may be due to noise bias and bears further investigation. Certain species of cetacean increase repetition of calls in high noise (Brumm and Slabbekoorn 2005),

but the opposite temporal pattern was seen with harbour seals in Georgia Strait. This temporal avoidance of high noise may serve the same function as the avoidance of noisy areas (spatial displacement) by odontocetes (spatial displacement; Morton and Symonds 2002; Rako et al. 2013) and spatial avoidance of acoustic harassment devices by harbour seals (Yurk and Trites 2000). Spatial avoidance can be a concern if a population is displaced from favourable foraging areas or resting grounds (Morton and Symonds 2002; Tyne et al. 2015). The effects of temporal noise avoidance in harbour seals are potentially less concerning, provided that 1) males are able to forage during times when they are not vocalizing, and 2) vocalizing at night is efficacious.

Another important factor that influenced the occurrence of calls in a given hour was the number of days after the first day of the presumed breeding season (designated July 25th, as this was the first day in which roars were detected). Calling by males began later and extended longer in the year than expected based on the breeding times of nearby populations (Huber et al. 2001; DFO 2010; D'Agnese 2015). Because I documented a linear increase in number of calls per day, with no subsequent decline (Table 2), I infer that only the first half of breeding season was recorded. The established paradigm of seal breeding times in Pacific harbour seals (*Phoca vitulina richardii*) is a latitudinal cline from California to Washington State, with later breeding times as latitude increases (Bigg 1969b). Temte et al. (1991), however, showed that harbour seals in the Salish Sea breed ~65 days later than one would expect, given their latitude. This delay could be due to latency in biological productivity of inland waters compared to coastal waters, but is not affected by photoperiod (Temte et al. 1991). In addition, seals on the outer coast of Vancouver Island were heard roaring much later than expected in 1999; roars were observed in November of that year (Van Parijs et al. 2003b).

In recent years, seals in south Puget Sound were observed pupping (and thus females were entering oestrus) several weeks earlier than the Hornby Island population (D'Agnese 2015). Similarly, seals in Johnstone Strait, immediately north of Georgia Strait, were heard roaring in 2013 from the beginning of July to the end of August (J. Towers, Marine Research and Education Society, Alert Bay, BC,

unpublished data). Based on this information, the deployment at Hornby Island was expected to encompass the majority of the breeding season. Because hydrophone deployment in this study appears to have excluded the second half of breeding season, however, the positive linear trend in roar occurrence is not unexpected. Seal roar activity in other populations increases with time leading up to peak breeding season, and decreases toward the end of the season (Van Parijs et al. 1999; Hayes et al. 2004a). If the recordings had extended into early October, I assume that seal call occurrence would have peaked in mid-September followed by a steep decline. It is possible that the late breeding season observed in 2014 is a product of oceanic conditions, such as a strong El Niño season underway at the time (US National Atmospheric and Oceanic Society). Further study in this region will help to determine whether the Hornby Island population in fact breeds later than adjacent populations, or if this one-year study represents an anomaly.

The Georgia Strait population of harbour seals is not of conservation concern, despite high levels of anthropogenic influence (DFO 2010). By comparing vocal breeding behaviour to anthropogenic noise levels, I hoped to determine whether underwater noise affected seal vocalization patterns, and whether harbour seals employ strategies similar to those observed in other marine mammals in order to overcome noise disturbance. The primary inferences to draw from my results are that male harbour seals at Hornby Island preferred to call at night and at times of low noise. I believe that the most parsimonious explanation for this behavioural pattern is that it is energetically favourable for males to call at times when they are most likely to be heard. Because this study could not isolate noise as a variable separate from the strong diel pattern of vessel traffic, further study is recommended to understand how ambient noise affects seal roaring behaviour, independently of time of day.

QUANTIFYING THE DIVERSITY OF UNDERWATER VOCALIZATIONS OF BREEDING HARBOUR SEALS AT HORNBY ISLAND, BC, CANADA

Introduction

Among marine mammals, vocal communication is essential to critical behaviours such as foraging, navigation and mate selection (review by Richardson et al. 1995). The complexity of vocal communication varies across species. For example, killer whales (*Orcinus orca*) in the northeast Pacific utilize a wide vocal repertoire in addition to echolocation (Ford 1989), and humpback whales (*Megaptera novaeangliae*) produce a number of different calls on both breeding (Payne and McVay 1971) and foraging grounds (Stimpert et al. 2011; Fournet and Szabo 2013). Some species have only had a small number of underwater calls associated with them, such as many balaenopterids (Winn and Perkins 1976; McDonald et al. 1995) and several phocids (Hanggi and Schusterman 1994; Stirling and Thomas 2003). Understanding the context or ‘meaning’ of certain call types can provide researchers insight into the behaviour of marine mammals without the need for visual observation. However, to assess the behaviour of a population based on its vocalizations, all of the call types produced by this population must be clearly defined and classified.

It is assumed that most marine mammal vocalizations are learned (Janik 2014; Reichmuth and Casey 2014). This assumption is based on the observation that within a species, genetically or geographically isolated stocks develop unique dialects that may or may not have shared calls with one another (Cerchio et al. 2001; Yurk et al. 2002). Such unique dialects may allow conspecifics to distinguish desirable mates based on genetic similarity, as proposed for the resident killer whales of the northeast Pacific (Ford 1991; Deecke et al. 2010). Vocal dialects within species also allow researchers to distinguish between populations when using acoustic methods to study them. In addition, humpback whales singing on breeding grounds modify their songs each year from the beginning to the end of breeding season, with each whale adopting the same changes (Parsons et al. 2008). This also suggests vocal learning. Understanding the patterns of vocal changes and dialect formation can lead to a better

understanding of the patterns of dispersal and extent of social and genetic exchange between populations (Winn et al. 1981; Deecke et al. 2000; McDonald et al. 2006). To enable comparisons of dialects among populations, acoustic datasets should be representative of the species' entire range and differences should be compared in the context of genetic and geographic distance. For species that occupy a wide global range with limited individual ranges, there may exist a number of breeding stocks in a relatively small geographical area. It is then important to sample among these stocks extensively to achieve a representative sample. The harbour seal (*Phoca vitulina*) is one such wide-ranging species. Harbour seals are phocids that occupy coastal ranges throughout the northern hemisphere (Stanley et al. 1996). Until recently, it was believed that harbour seals did not vocalize underwater in non-captive environments, although studies on captive and wild harbour seals revealed that males and females vocalize in air as pups (Khan et al. 2006) and as adults (Ralls et al. 1985; Van Parijs and Kovacs 2002). Hanggi and Schusterman (1994) first described underwater vocalizations for adult harbour seals *in situ* in Moss Cove, central California, and hypothesized that these calls were related to breeding activity. During the summer breeding season harbour seals engage in lekking, a mating system wherein males aggregate in an area frequented by females and perform visual and/or vocal displays (Emlen and Oring 1977). The traits upon which females base their choices are still unclear in this species, and are thought to be a combination of surface-active displays and underwater vocalizations (Sullivan 1981; Hanggi and Schusterman 1994).

Hayes et al. (2004b) performed playback experiments in Elkhorn Slough, USA, and determined that one of these vocalization types, the 'roar', showed significant individual variation. Roars from subdominant males elicited agonistic responses from dominant males when played in their displaying territory (Hayes et al. 2004b). Hayes et al. (2004b) hypothesized that this call comprises part of the advertising display which males use to defend their dominance during lekking. Male harbour seal underwater vocalizations have since been described for populations in Norway and Sweden (Bjørgesæter et al. 2004), Scotland (Van Parijs et al. 1997; 1999; 2000a; 2000b; Bjørgesæter et al.

2004) and eastern Canada (Coltman et al. 1997; Boness et al. 2006). In each of these populations, the roar call has been associated with male breeding behaviour, and is often heard during short dives between bouts of surface active behaviour (Coltman et al. 1997; Van Parijs et al. 1997).

There is vocal variability in roars among harbor seal populations. For instance, males in Orkney and Moray Firth, Scotland, separated by over 100 miles, displayed more variation between sites than between individuals within a site (Van Parijs et al. 2000a). Harbour seals from six locations in the North Sea also varied in the contours of their roars (Bjørgesæter et al. 2004). Harbour seal roars from all the locations mentioned above were compared and were found to be ~90% distinguishable among populations (Van Parijs et al. 2003b). These clear differences among populations support the conclusion that roar vocalizations are learned behaviours, leading to the formation of population-specific dialects (Van Parijs et al. 2003b). Interestingly, there is no correlation between the amount of difference in vocal parameters across populations and increasing geographic or genetic differences, as is seen in vocal dialects of other marine mammal species (Winn et al. 1981; Ford 1991; Stanley et al. 1996; Van Parijs et al. 2003b).

Roars of an individual male are considered highly stereotyped (Van Parijs 2000a), and the roars of individuals within a site differ in both duration and frequency parameters such as maximum and center frequency (Van Parijs et al. 2000a; Hayes et al. 2004b). This variability in roar structure supports the hypothesis that roars indicate varying body sizes and conditions of the callers. The playback experiments in Elkhorn Slough used roars with different durations and center frequency to denote dominance, with more dominant roars being longer and lower in frequency (Hayes et al. 2004b). Van Parijs et al. (2000a) described two roar types at a single study site in Orkney, Scotland. At this site, however, individual harbour seals had highly stereotyped vocalizations. This suggests that each individual harbour seal used only one roar type. Similarly, Bjørgesæter et al. (2004) found two distinct call types within two sites in Norway. Bjørgesæter et al. (2004) could not confirm whether this finding reflected differences within or among individuals at each site. Intra-individual variation in vocalizations

was described by Hanggi and Schusterman (1994), who identified and described five unique call types in Monterey Bay, California, USA, that were used to varying degrees by each individual male. Vocal plasticity within individuals (i.e. distinct call types) has not been described for any population of harbour seals since Hanggi and Schusterman (1994) described this behaviour in Monterey Bay.

The coasts of Oregon, Washington and Alaska, USA, and British Columbia, Canada, comprise a significant portion of the range of the Pacific harbour seal subspecies *P. v. richardii* (Stanley et al. 1996). Despite the potential for vocal variation within this subspecies, harbour seal vocal breeding behaviour has not been described for any populations north of Monterey Bay (Hanggi and Schusterman 1994; Hayes et al. 2004a; 2004b). To obtain a more representative dataset from this subspecies, the vocalizations of other populations in its range should be described. The inland waters of Washington State and southern British Columbia, collectively called the Salish Sea, support a high density of harbour seals (Olesiuk 2010). This sea is therefore an advantageous location to begin characterizing the roars of the Pacific Northwest populations of harbour seals.

Vocalizations of harbour seals were recorded at a haul-out site in the northernmost waterway of the Salish Sea: Georgia Strait, British Columbia. From this single haul-out, a wide variability was detected in the acoustic parameters of roars, as well as distinctive calls which do not fit the typical definition of a roar. This study describes for the first time the within-site vocal variability exhibited in this population of harbour seals, and I suggest that this population has a more extensive repertoire of calls than any previously studied population of the species.

Methods

Data Collection

Acoustic and visual observations were conducted during the summer of 2014 at a haul-out site on Heron Rocks, which are located near the southwestern tip of Hornby Island, BC. Hornby Island lies about 10

km off the east coast of Vancouver Island, near the northern end of Georgia Strait. An Autonomous Multichannel Acoustic Recorder (AMAR; JASCO Applied Sciences) system, fitted with a single omnidirectional hydrophone (M8E from GeoSpectrum Technologies Inc.; nominal sensitivity -165 dB re: 1 V/ μ Pa; flat frequency response 10-24,000 Hz), was deployed on a weighted mooring at approximately 6.4 m depth (low tide) in a location central to the haul out (49°29.307'N, 124°39.313'W). The AMAR was deployed on June 15th and recorded continuously in the bandwidth of 10 Hz to 24 kHz (24-bit sampling resolution; 48,000 Hz sampling rate) until it was retrieved by a diver on September 10th.

Visual observations were conducted from a nearby vantage (49°29.380'N, 124°39.845'W) on the shoreline of Hornby Island, approximately 300 m from the haul-out at the nearest point, at an elevation of 5.7 m above mean water (9.0 m above chart datum). Harbour seal behaviour was recorded opportunistically on a continual basis during daylight hours for 41 days, including three sessions: June 16-28, July 21-August 2, and August 25-September 6, 2014. Observations were made for a maximum of 12 h each day, subject to weather and tidal constraints. Discrete behavioural events by seals in the water (splashing at the surface, above-water vocalizations and fights) were reported in near-real time, and a range and bearing was taken if possible using reticle binoculars (Steiner Commander III, 7x50 magnification) and a digital theodolite (Leica TC605L [\pm 5in. (127mm) accuracy]). Because the vast majority of seal vocalizations were produced at night, the measurements taken from visual observations were not used in further analysis.

Data Processing and Analysis

Twenty days were randomly selected from the breeding season for analysis, and only files containing seal calls were examined for call variability. Acoustic recordings were viewed spectrographically and calls were annotated using the Matlab-based program Osprey (Mellinger 1994) with a 2,048 point fast Fourier transform (FFT), Hann window and 50% overlap. Each call was measured using the Noise

Resistant Feature Set (NRFS) in Osprey (Mellinger and Bradbury, 2007), which includes parameters that produce the same results in varying levels of ambient noise. This feature set was designed for calls such as seal roars, which tend to fade at high frequencies and overlap with natural background noise, making it difficult to use traditional spectrographic measurements to define them (Mellinger and Bradbury 2007). Whereas many spectrographic measurements are taken from a manually-drawn annotation box, the NRFS reduces a manual annotation box into a 'feature box'. The feature box is defined as the frequency and time vectors within the annotation box where 90% of the energy in the annotation box is located, thus defining the call relative to ambient noise. Measurements are then taken from this feature box, making them robust to varying noise levels (Mellinger and Bradbury 2007). The NRFS took a total of 29 measurements for each call, including the mean signal-to-noise ratio (MSNR). For analysis, only seal roars that had a definitive start and end time, judged visually and audibly in Osprey, were measured. All roars with null values for any of the 29 NRFS measurements was excluded, and only roars with a MSNR > 30 dB were used for analysis. A threshold of 30 dB was judged visually and audibly to be that at which all calls were clearly defined and that all measurements would therefore be most accurate, regardless of noise level.

Of the calls that had all measurements and an acceptable MSNR, a subset of 500 was randomly selected. Because the recordings had no directionality, calls could not be attributed to an individual seal. I attempted to avoid individual bias by verifying that this sample contained representative numbers of calls from each day of breeding season, as well as a representative distribution of call durations and bandwidths. This subset of calls was analyzed both aurally and visually and placed into hierarchical classes. Roars were considered to be any call over 5 s in duration that had a low-frequency component and a broadband 'pulse' component, as defined by Van Parijs et al. (2000a). Differences in the duration of the pulse and the total roar, as well as differences in the bandwidth of the roar's two components, are a product of individual variation in other populations (Van Parijs et al. 2000a; Hayes et al. 2004b). Therefore, variability in roars was classified aurally and visually into subclasses, but were not

considered unique call types. Calls that were < 5 s or did not contain both low-frequency and broadband components were considered non-roar call types, and were similarly placed into hierarchical call type groups.

Quantitative verification of aural-visual classification was conducted using linear discriminants analysis (LDA; Klecka 1980) from the MASS library in R version 3.1.3 (R Foundation for Statistical Computing 2012). Discriminant function analyses such as LDA have been used to verify classification in previous studies of cetacean vocalizations (Dunlop et al. 2007; Fournet and Szabo 2013). Although previous studies of harbour seal in-air vocalizations have been analyzed using principal components analysis (PCA; Van Parijs and Kovacs 2002), LDA outperformed PCA in quantitatively analyzing underwater calls in this study because it can be trained on a subset of data. Before running LDA, redundant variables (defined as having a correlation value greater than |0.85| using a Spearman's correlation matrix) were identified and excluded from further analysis. When appropriate, variables were log-transformed to better conform to the assumptions of normality and homoscedasticity among call types. Graphical analysis was used to determine whether each remaining variable contributed to separation of the candidate call types. Those variables that showed differences among call types were considered 'key variables' (Table 6), and were used in the LDA. The subset of 500 randomly-selected calls that were classified by aural-visual analysis were also classified using LDA, and the predicted classifications for each call were then compared to determine agreement between classification systems.

To avoid overfitting the model, I trained the LDA model with a subset of the data, then used the resulting model to predict classifications of the remaining dataset. Firstly, LDA was used to verify the proposed call types. These models were trained by randomly selecting 100 calls to build the model, then predicting classifications for the remaining 400 calls based on this model. Roars were then excluded from the dataset and a subset of 50 of the remaining calls were used to train a model classifying non-roar call subtypes. The agreement between aural-visual and LDA classification systems

was then tested using chi-squared association analysis, with a null hypothesis of random classification (chi-squared values <0.05 were considered to be non-random classification and thus to indicate agreement), and by comparing error rates between the two classification systems. The LDA models were each trained 10 times with different random samples of calls; if the results were consistent across models, I interpreted as an indication that the classification was non-random.

Table 6. Descriptions and shorthand codes of key features from the Noise Resistant Data Set (NRFS) in Osprey used to classify harbour seal mating calls.

Measurement	Notation	Description
Duration (s)	Duration	The length of the feature box
Temporal Interquartile Range (s)	Time Quartile	The amount of time where a cumulative 25%-75% of the energy in the call is represented
Temporal Concentration	Time Concent.	The number of time blocks (21.3 ms each) that contain a cumulative 50% of the energy in the call
Amplitude Modulation Rate	AM Rate	The dominant rate of amplitude modulation (in the call
Overall Entropy	Entropy	Average measure of how evenly the energy is spread among frequency blocks in every time block
Upsweep Mean (Hz)	Upsweep	Average change in median frequency between successive time blocks in the trimmed spectrogram

Results

Aural-Visual Classification

A total of 1,764 seal calls were determined to be of sufficient quality for classification. Of these calls, 500 were randomly selected for analysis. Roars formed the majority of the calls analyzed (383 out of 500 calls), and were sorted into four subtypes: long pulse, short pulse, double pulse and high frequency (Figure 5). Long pulse was defined as a roar where the broadband pulse occupied greater than one-quarter of the total duration of the roar; if the pulse was less than one-quarter of the total duration, it was considered a short pulse. Any roar with more than one pulse was called a double pulse. Any roar that had a component that extended to a higher frequency than 6 kHz was considered a high frequency roar, regardless of relative pulse length. The four roar subtypes exhibited a poor separation of means in some measured parameters (Table 7), making quantitative verification difficult.

Three additional non-roar call types were distinguishable both visually and audibly from the roar. I have termed these non-roar call types the growl, the short call and the sweep (Figure 6). The growl is named after the bubbly growl, following the naming scheme described by Hanggi and Schusterman (1994). A growl was characterized as any call that lacks a component above 1,000 Hz. Growls comprised only 27 of the 500 calls analyzed (Table 8). Growls were characterized by their narrow bandwidth and low frequency, but were variable in duration. Growls were further subdivided by aural-visual classification: growls ≤ 7 s in duration were classified as short growls (Figure 6a), and growls >7 s were termed long growls (Figure 6b).

Table 7. Counts and summary statistics for the four subgroups of the roar call type, characterized for harbour seals at Hornby Island, BC. N=383 calls. For measurements taken using the NRFS in Osprey, means are presented with standard deviation in parentheses. Key features are denoted with an asterisk (*). See Table 1 for full names of measurements and descriptions.

Subtype	Long Pulse	Short Pulse	Double Pulse	High Frequency
# Sampled	211	129	24	19
% of Sample Size	55.1	33.7	6.3	5.0
Duration (s)*	9.6 (2.1)	9.1 (2.4)	8.8 (3.4)	7.6 (2.0)
Low Freq. (Hz)	40.0 (11.8)	41.8 (12.0)	40.0 (13.8)	56.1 (30.1)
Bandwidth (Hz)	527 (273)	453 (168)	522 (307)	690 (361)
Time Quartile (s)*	6.8 (2.2)	6.2 (2.5)	4.8 (3.6)	5.5 (2.4)
Time Concent.*	7.3 (3.1)	6.4 (3.6)	6.8 (4.2)	6.5 (2.8)
Entropy*	70.0 (14.2)	64.4 (12.5)	64.7 (20.7)	80.8 (31.3)

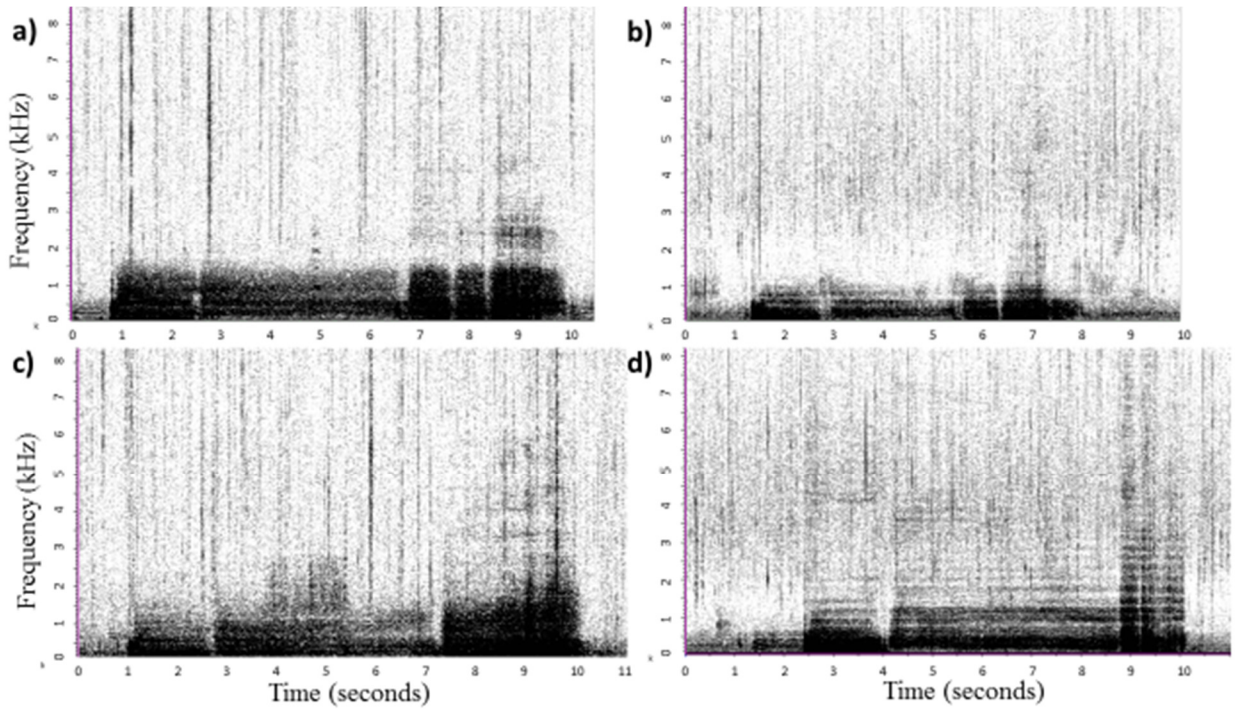


Figure 5. Spectrograms of the four subtypes of harbour seal roars characterized at Hornby Island, BC. Spectrograms generated by Raven Pro 1.5 (Cornell Lab of Ornithology) with smoothed 2,456 point fast Fourier transform, Hann window and 50% overlap; a) Long Pulse; b) Short Pulse; c) Double Pulse; d) High Frequency. Axes are scaled the same in each spectrogram.

The short call was defined as a call with a duration <5 s and an upper frequency $>1,000$ Hz. This call type was more common than the growl, with 78 examples in 500 calls (Table 8). Short calls were subdivided into two subtypes: the step and the abrupt call. Steps were calls that contained a low-frequency component as well as a pulse over 1,000 Hz; much like a roar but with a duration < 5 s (Figure 6c). Abrupt calls were $> 1,000$ Hz, contained no low-frequency component, and appeared to be the pulse section of a normal roar with the low-frequency component absent (Figure 6d).

The sweep call type was characterized as a call lasting 2-3 s and consisting of a broadband knock followed by a noisy upswing with an upper frequency that extends up to 6 kHz (Figure 6e). Sweep calls were the rarest call type, comprising only 12 of the 500 calls classified (Table 8). This call type was the most easily distinguishable, and was heard throughout the breeding season, almost always in association with a bout of calls that included roars.

Table 8. Counts and summary statistics for the three non-roar call types (five subtypes) characterized for harbour seals at Hornby Island, BC. N=117 calls. For measurements taken using the NRFS in Osprey, means are presented with standard deviation in parentheses. Key features are denoted with an asterisk (*). See Table 1 for full names of measurements and descriptions.

Call Type	Growl		Short Call		Sweep
Subtype	Short	Long	Step	Abrupt	Sweep
# Sampled	10	17	64	14	12
% of Sample Size	8.5	14.5	54.7	12.0	10.3
Duration (s)*	5.1 (1.2)	10.1 (2.5)	4.3 (0.9)	3.4 (0.7)	2.5 (0.2)
Low Freq. (Hz)	39.8 (9.9)	42.0 (11.0)	38.2 (9.6)	38.5 (8.5)	43.0 (15.3)
Bandwidth (Hz)	352 (72)	425 (196)	343 (99)	353 (90)	279 (87)
Time Quartile (s)*	2.1 (1.9)	5.9 (2.5)	1.5 (1.0)	0.7 (0.6)	0.4 (0.2)
Time Concent.*	1.8 (2.4)	4.9 (4.4)	1.2 (1.3)	0.6 (0.9)	0.2 (0.3)
AM Rate*	0.3 (0.3)	0.3 (0.6)	0.9 (0.6)	1.0 (0.7)	2.4 (1.6)
Entropy*	51.8 (7.0)	58.6 (11.8)	59.4 (12.0)	48.9 (11.4)	38.8 (5.9)
Upsweep (Hz)*	-6.0 (13.0)	-5.2 (11.5)	-14.5 (16.5)	-12.4 (16.0)	-18.8 (9.3)

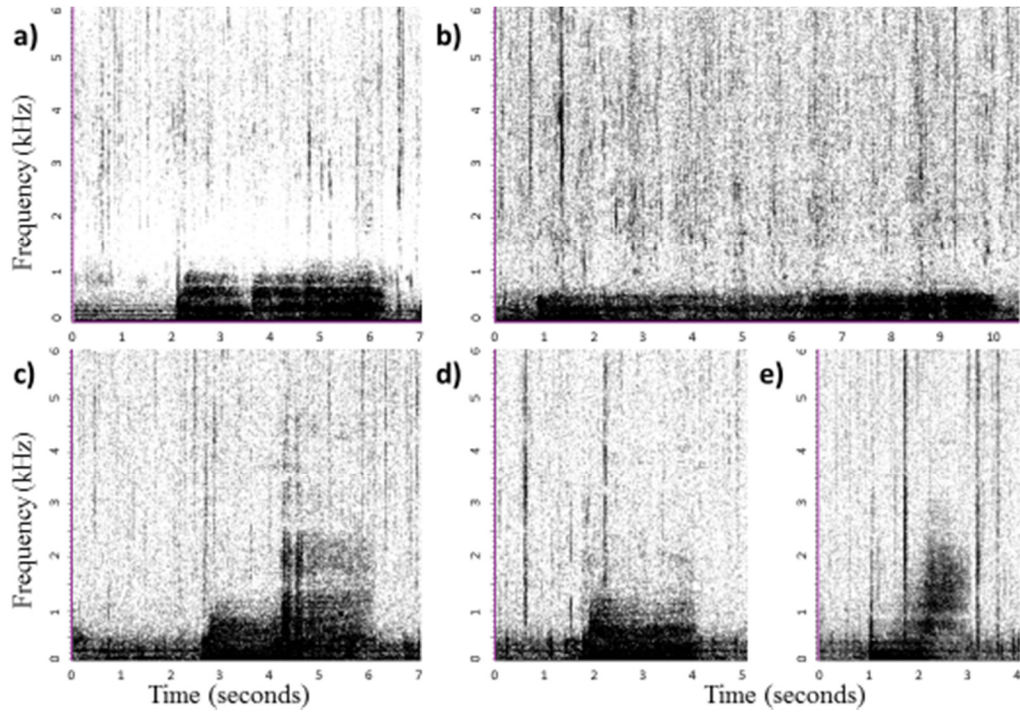


Figure 6. Spectrograms of the three non-roar call types (containing five subtypes) of harbour seal breeding call characterized at Hornby Island, BC. Spectrograms generated by Raven Pro 1.5 (Cornell Lab of Ornithology) with smoothed 2,456 point fast Fourier transform, Hann window and 50% overlap. Growl: a) Short Growl, b) Long Growl; Short Call: c) Step, d) Abrupt Call; Sweep: e) Sweep. Axes are scaled the same in each spectrogram.

Linear Discriminants Analysis Classification

To verify call type classification (roar, growl, short call or sweep) quantitatively, all calls that were classified using aural-visual analysis were assessed using LDA. Five of the six key variables (all but temporal interquartile range) were log-transformed to better conform to the assumptions of the model. Because some upsweep mean values were less than zero, these data were log transformed by their absolute value. After 10 independent trials using different training sets, LDA classification agreed with aural-visual classification for 83-90% of calls (mean \pm SD=87.9 \pm 2.0%). The percentage of variation explained in the first linear discriminant was 91.8 \pm 3.4%, indicating that the model was trained sufficiently to interpret the untrained data. The majority of roars were classified correctly; however some were often misclassified as short calls or growls. Growls were often misclassified as roars or short calls, and short calls were often classified correctly, although some were often misclassified as other call types. Sweeps were the most unique call type, and as a result were rarely misclassified; when they were misclassified, they were grouped as short calls (Table 9). High weightings were given to amplitude modulation rate, duration and temporal interquartile range in the first two linear discriminants. These variables most often showed good separation of means among different call types; however growls had a similar duration and amplitude modulation rate to roars.

Before a trained LDA model was used to classify non-roar calls into subtypes, four of the six key variable variables (namely Duration, Time Quart, Time Concent, and AM Rate) were log-transformed to meet the assumptions of the model. Average agreement with aural-visual classification after 10 independent trials was lower than for call types (73.6 \pm 4.5%), and much more variable. The percentage of variation explained by the first linear discriminant was 91.7 \pm 3.4%, which was slightly higher but more variable than the model for call types (Table 10). The high percentage of variation explained indicated that the model was sufficiently trained. The agreement of the model and percentage of trace were variable depending on the training set. Training sets that contained more abrupt calls and short

Table 9. Example association analysis table from the 10 LDA models used to classify seal call types. High agreement between aural-visual (AV) and LDA classification is indicated in bold. Models were trained with a random subset of 100 calls, which was then used to predict classification of the remaining 400 calls. Classifications for call types are: Growl=G, Roar=R, Sweep=S, Short Call=SC.

AV Class	LDA Classification			
	G	R	S	SC
G	4	13	0	6
R	8	283	0	12
S	0	0	10	0
SC	0	5	3	56

$X^2 = 579.7, p < 0.0001$
 Agreement between AV and LDA: 88.3%
 Variance explained by 1st LD: 94.3%

growls tended to have higher agreement, as these were the subtypes that were most often misclassified in the remainder sets. Long growl, sweep and step subtypes were often classified correctly. When steps were misclassified, they were most often misclassified as abrupt calls. Conversely, abrupt calls were almost always classified incorrectly as steps. Short growls were also often misclassified as steps. As with the LDA for call types, high weighting was attributed to duration, AM rate and temporal interquartile range in the first two linear discriminants. These three variables showed varying amounts of separation between means among subtypes. For instance growls were clearly separated by duration and temporal interquartile range, and sweeps were clearly separated by AM rate. This is the likely cause of the variation in agreement between training sets containing more or less of these subtypes, and suggests that some subtypes are not as distinguishable as others.

Visual Observations

A total of 961 20-minute surveys were completed. The pre-breeding session included 264 surveys, the early breeding season session included 371 surveys, and the peak-breeding session included 326 surveys. Visual observations all took place during the day; therefore no inferences could be made as to the number or behaviour of male harbour seals at night when the majority of calling took place. Daytime visual observations showed no major difference in the total number of seals throughout the breeding season (Kruskal-Wallis test, $p > 0.05$), and an increase in the amount of surface-active behaviour from the pre-breeding to breeding seasons, as would be expected if this behaviour was associated with breeding vocalizations (86 display events were recorded in the pre-breeding observation session, and 147 were observed in both breeding season observation sessions). However, few of these surface events corresponded to calling. Conversely, percussive sounds associated with surface behaviour were heard only rarely in association with recorded calls at night.

Table 10. Example association analysis table from the ten LDA models used to classify seal non-roar call subtypes. N=117 calls. High agreement between aural-visual (AV) and LDA classification is indicated in bold. Models were trained with a random subset of 50 calls, which were then used to predict classification of the remaining 67 calls. Classifications for call subtypes are: Long Growl=LG, Abrupt=A, Sweep=S, Short Growl=SG, Step=ST.

AV Class	LDA Classification				
	LG	A	S	SG	ST
LG	6	0	0	0	0
A	0	2	0	0	5
S	0	0	6	0	0
SG	3	0	0	0	6
ST	0	2	0	1	36

$X^2 = 123.3, p < 0.0001$
 Agreement between AV and LDA: 74.6%
 Variance explained by 1st LD: 90.5%

Discussion

Harbour seals at Hornby Island showed a wide vocal variation, including variation within the universal ‘roar’ call as well as three other proposed call types. Within-site vocal variation has been noted in other populations for roars (Van Parijs et al. 2000a; Bjørgesæter et al. 2004); however non-roar call types have not been proposed since Hanggi and Schusterman (1994) first described seal roars at Point Lobos, California. Although the Hornby Island population falls within the same subspecies as the California population (Stanley et al. 1996), the call types that I propose are not the same as those found for harbour seals in either Point Lobos (Hanggi and Schusterman 1994) or Elkhorn Slough (Hayes et al. 2004a; 2004b). This vocal variation supports previous studies that have shown significant differences in vocalizations among (Van Parijs et al. 2003b) and within subspecies of harbour seal (Van Parijs et al. 1999; 2000b; Bjørgesæter et al. 2004). However, this first description of Pacific harbour seal vocalizations north of California suggest that breeding vocalizations are more variable and complex than previously thought for this species.

Rather than discrete call types, harbour seal vocalizations appear to form a continuum, making objective classification difficult. Through the use of aural-visual analysis, four distinct call types were identified. Linear discriminants analysis (LDA) confirmed that three call types (the roar, sweep and short call) were able to be classified quantitatively, while the fourth (growl) was only distinguishable from other call types by the long growl subtype. The discriminant function model was likely driven mainly by the roar call type, as this call type had by far the largest sample size. The growl had similar values to the roar in the two highest-weighted variables in the first two linear discriminants (duration and AM Rate), which may have led to the poorer separation of these two call types. I infer from quantitative classification that the two subtypes of short call (the step and the abrupt call) were not distinguishable from the short growl subtype. This inability is likely due to the high weight given to duration in the linear discriminants. These three subtypes have similar durations but dissimilar call contours. Upsweep mean, a contour-related variable, was given low weight in linear discriminants.

Further analysis using call contour comparison methods (e.g. Bjørgesæter et al. 2004) might help to verify these subtypes.

The most common call type at Hornby Island was the roar, which was unsurprising given that roars have been heard in all harbour seal populations worldwide (Van Parijs et al. 2003b). Because this call shows individual variation in other populations, it is considered to be the primary means by which males display reproductive fitness (Van Parijs et al. 1997; Hayes et al. 2004b). Population-specific dialects exist in this species as the result of roars being a learned behaviour (Van Parijs et al. 2003b), and can be diagnostic of a particular population (Van Parijs et al. 2000a; 2003; Bjørgesæter et al. 2004). The roars heard at Hornby Island were on average several seconds longer than those heard in Moray Firth (average \pm SE = 4.8 ± 0.4 s) and shorter than those heard in Orkney, Scotland (average \pm SE = 14.6 ± 0.4 s; Van Parijs et al. 2000a). The bandwidth of roars at Hornby Island had a slightly smaller bandwidth than those heard at Moray Firth (average 1.06 kHz); however the high-frequency subtype was closer to the bandwidth of roars in Orkney (average 2.38 kHz; Van Parijs et al. 2000a). Hornby Island roars had a similar bandwidth to roars heard in the southern Norwegian Sea (~1.5 kHz), but were on average slightly shorter in duration (8-12 s; Bjørgesæter et al. 2004). Roars at Point Lobos, California, were described as being much shorter than those at Hornby Island (average 4.9 s), with a higher average bandwidth (average maximum frequency 810 Hz; Hanggi and Schusterman 1994). This description fits better with what I have called the abrupt call. Roars measured at two sites in Eastern Canada were similar in duration to those heard at Hornby Island (average \pm SD = 7.5 ± 3.2 s), with a slightly higher minimum frequency (average 0.4 kHz; Van Parijs and Kovacs 2002). With respect to roars heard in other populations of harbour seals, the roars heard at Hornby Island were similar in overall spectrographic parameters but displayed a wide variability not described in other populations. Aural-visual analysis identified four possible subtypes of roars. Within each of these subtypes, variability was high and quantitative analysis proved unsuccessful. This failure is likely because the subtypes are arranged along a continuum, rather than being distinct. This could be due to variation

within or among individual males. Van Parijs et al. (2000a) found that roars in Moray Firth were 73% identifiable to individual males, but cautioned against using roars alone as a method to identify individuals, as only a few individuals had roars distinguishable from those of other males. At Elkhorn Slough, the 'roar' was considered to be only the broadband section of the overall call, described by Van Parijs et al. (2000a) as the 'pulse'. These sections were longer in more dominant individuals, which could explain the difference between 'short pulse' and 'long pulse' roars seen at Hornby Island.

I was unable to confirm individual variability at Hornby Island as the majority of vocalizations were heard during night-time hours (see Chapter 2). Therefore no visual observations were available to confirm the number of males in the area when vocalizations took place. Additionally, it was impossible to localize any vocalizations due to the use of a single omnidirectional hydrophone. The observed variability in roars may then be the result of several individuals with distinct roars, or individuals whose vocalizations are more plastic than previously found for harbour seals. Further investigation using a hydrophone array equipped for localization purposes may help to determine the extent to which individual males at Hornby Island vary the contour of their roars.

The three non-roar call types that were identified in this study have not been explicitly described before for harbour seals. While harbour seals have a variety of calls above water (Van Parijs and Kovacs 2002), underwater calls have almost exclusively been called roars, despite variability within this call type. Hanggi and Schusterman (1994) describe a call much like the growl call type, which they termed a 'bubbly growl'. Their 'roar' call more closely resembles the short call from this study. Three other calls were described for harbour seals at Point Lobos, which were not seen at Hornby Island. The growl call type that I describe was relatively uncommon; this scarcity may reflect the overlap of the bandwidth of this call type with the bandwidth of low-frequency ambient noise, leading many growls to be excluded from analysis due to low MSNR. At Point Lobos, individual males made use of more than one call type in different combinations during the breeding season, to the extent that Hanggi and Schusterman (1994) suggested that harbour seals could be identified by the content and sequence of

their displays. Despite my inability to localize calls or attribute calls to individuals, it may be considered that males at Hornby Island also utilize more than one call type in their displays. This vocal plasticity within an individual would suggest that breeding vocalizations may not be as stereotyped for each individual as has been found in other populations.

As I was unable to localize any calls, I could not determine whether any non-roar calls were produced by more than one animal. One hypothesis is that vocalizations in harbour seals is a learned behaviour. Captive juvenile males in New England were recorded producing vocalizations much like our abrupt calls and short growls (Ralls et al. 1985), and playbacks have determined that more dominant (and presumably larger and older) males produce roars with longer pulses (Hayes et al. 2004b). Harbour seals have been shown to mimic other animals (Ralls et al. 1985), presumably as a form of vocal learning. Perhaps the shorter calls (the step and abrupt call subtypes as well as the short growl) are the calls of juveniles mimicking the adults. This may explain the ambiguity found among these calls in quantitative analysis.

Of the four call types identified in this study, the sweep call was the most distinctive and the most unlike any call that has been previously described for harbour seals. Sweeps are very short calls, and lack the components of roars (low-frequency lead-in followed by a broadband pulse). Instead, sweeps consist of a broadband concussive ‘knock’ followed by an upsweep with a rising fundamental frequency. The pulsed, non-tonal nature of the upsweep and its auditory and structural similarity to other seal calls lead me to believe that these calls are produced by harbour seals. Additionally, they were always heard during bouts of other calls (often roars). Sweeps were not documented as call types seen in captive harbour seals, either juvenile or sexually mature (Ralls et al. 1985). Further study at this site and nearby populations with the ability to localize calls will allow us to learn more about this novel call type.

Visual observations showed more surface activity during breeding season sessions (July 21-August 2 and August 25-September 6) than during the pre-breeding season observations (June 16-28). This may

have been due to an increase in observer effort (more surveys were conducted in breeding season sessions than in pre-breeding season sessions). It was also notable that surface displays during the day were only rarely associated with vocalizations, whereas vocalizations heard at night were only rarely associated with percussive sounds that would indicate surface activity. This may indicate that surface activity and breeding vocalizations are not as tightly-linked in this population that believed elsewhere (Hanggi and Shcusterman 1994; Van Parijs et al. 1997).

Despite an inability to attribute calls to individuals, the results of this study show a wide variability in breeding vocalizations within a single haul-out site in the Salish Sea. This is the first study to describe underwater calls of *P. vitulina richardii* north of California, and the first to investigate the presence of non-roar call types in this subspecies since 1994. I describe an ostensibly novel call type and show that the vocal repertoire of breeding harbour seals in this area is perhaps larger and more varied than previously thought for this species. Further investigation into the call repertoire of this population is needed to understand the extent to which the observed vocal variability is the product of individual variation, or vocal plasticity within individuals.

GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

The goals of this thesis were to describe the breeding calls of male harbour seals in Georgia Strait, British Columbia (BC), Canada, and to determine which environmental factors have the most influence on the presence and density of calls. Using passive acoustic monitoring, I was able to describe the vocal repertoire and characteristics of harbour seal calls near Hornby Island, BC. I also described the patterns of call timing by diel cycle and define the beginning of breeding season. By pairing acoustic recordings with visual observations, I related seal haul-out activity to tide and other environmental factors, in order to evaluate haul-out behaviour as an influence upon call density. The analyses performed in this thesis provide statistical models for the occurrence and density of harbour seal calls in Georgia Strait, based on environmental variables (Chapter 2), and a qualitative and quantitative analysis of call diversity in this population. These two related studies provide evidence to allow me to infer that harbour seal calling patterns at Hornby Island 1) may depend on a different set of factors from sets of factors that influence call patterns in other populations, and 2) may have a more diverse and complicated vocal repertoire than documented in other populations.

Major Findings and Contributions

In Chapter 2, I used counts of calls (including all call types) for 20 days of recordings to determine which environmental factors corresponded best with patterns of call occurrence (presence/absence of calls in an hour) and density (number of calls detected in an hour). Call presence was strongly influenced by time of day: calls were more than eight times more likely to be found in a given hour during the night than during daytime. Call presence was also influenced by day of the year, with the chance of hearing calls increasing as the breeding season progressed. I assume that if the recordings had not been terminated near the presumed peak of the breeding season, a decline in calls would have been seen toward the end of breeding season. For hours in which calls were heard, call density was significantly higher at night than during the day, and was negatively correlated with ambient noise

level. Because ambient noise level and time of day were highly correlated (noise was significantly higher during the day than at night), the effect of noise and time of day could not be assessed independently. Previously studied populations' call patterns corresponded with female foraging patterns and/or tide height; this study did not investigate diel patterns of foraging behaviour, and no correlation was found with temporal patterns of tides. I hypothesize that ambient noise level may play a role in the timing of male breeding calls by limiting their audibility during daytime hours.

My analysis in Chapter 3 classified harbour seal vocalizations into call types, and further into nested call subtypes. Aural-visual analysis by a human observer gave four call types including the roar, short call, growl and sweep. Roars were further divided into four subtypes, short calls into two subtypes, and growls into two subtypes. Sweeps were not divided into subtypes, as they were the rarest and least variable call type. Quantitative analysis using trained linear discriminants showed that the short call and sweep call types were distinguishable from roars and from each other, and that growls were less distinguishable from roars. When roars were excluded, classification of non-roar calls into subtypes was less successful using linear discriminants, with only three out of five subtypes classified correctly. Thus I infer that, like for many other mammal species, harbour seal vocalizations form a continuum and are not discrete. As localization was not possible with my recording set-up, I was unable to attribute variability within call types to individual animals. The existence of call types other than the roar has not been explored for this species for twenty years, and the seals at Hornby Island showed a high degree of vocal variation which may or may not be attributable to individual variation. The sweep call type was the most unique in its duration and spectral contour; surprisingly, it has not been described in other populations. I suggest that the vocal variability exhibited by harbour seals in Georgia Strait is higher than that seen in other populations, and that individual variation does not account for all of this variability. Therefore, I hypothesize that harbour seals in Georgia Strait make use of more than one call type per individual, and that individual males in this region exhibit vocal plasticity undetected in many other populations.

This thesis presents several novel results. This study is the first to describe the underwater vocalizations and call timing of Pacific harbour seals north of central California. This is also the first study to examine the influence of ambient noise on the timing and density of breeding calls in harbour seals, and while the results are unclear due to auto-correlation, the trend is compelling. The existence of call types other than roars in the breeding repertoire of harbour seals has not been described since Hanggi and Schusterman (1994) first described harbour seal breeding calls in Monterey Bay, California. Whereas the roar, growl and short call subtypes appear to form a vocal continuum and thus are more difficult to classify objectively, the sweep call type found in Georgia Strait is unique when compared to any call previously described for harbour seals. No function for different call types has been thoroughly examined, but it had been suggested that this species might use combinations of call types as part of a song-like display that may vary among individuals in its content and complexity (Hanggi and Schusterman 1994).

By describing the temporal range and complexity of harbour seal breeding calls in Georgia Strait, I have made a contribution toward understanding the evolutionary and functions and evolution of breeding vocalizations in this species. These new and novel results also open the door to many new lines of inquiry, including 1) the functions of different call types, 2) how those call types vary within and among individuals and 3) an investigation of the role of ambient noise on vocal behaviour in harbour seals.

Future Directions

The nature of this thesis was exploratory, and as such the results produced as many questions as they answered. While I am confident that the strong nocturnal trend of calling behaviour was not an artifact of noise bias, the driving cause(s) of this trend remains uncertain. Further study is required to draw a direct link between ambient noise level and call density, and to investigate the potential mechanisms between them. Observation of this site at night may give a better idea of haul-out patterns during the

times when most calls are heard. Furthermore, recordings taken in future years will help to determine whether this nocturnal trend holds true across breeding seasons. Recordings at haul-outs in the same region that have less of a diurnal pattern of ambient noise level would shed more light on whether seals in this region truly call only at night, or whether they simply prefer to call when noise is at its lowest. If noise level does have an effect on seal calling behaviour, then further study is recommended to determine the extent of the potential impact of noise on overall fitness and breeding success of individuals, especially in areas where harbour seals are seen to be shifting habitats or in decline. Even if populations are steady, as with Georgia Strait, this may not necessarily indicate that the fittest partners with respect to roaring, are always chosen by females. Further study should also investigate whether ambient noise masking may then have an impact upon the genetically-related fitness of a population.

The existence of a vocal continuum for the Hornby Island breeding site has been described in the absence of the ability to localize calls. Further study in this region on the prevalence and use patterns of the four call types found in this study would help us begin to understand the context and purpose of call types, and the reason that this particular population has such a wide vocal variation. Recordings at this site with the ability to ascribe calls to a particular display territory (and presumably a specific individual) would confirm that different call types are utilized by different individuals. By examining the ratio and pattern of call types used by each male, a better understanding of the purpose of these call types could be hypothesized.

In conclusion, this study has uncovered several new lines of research into the complexity, context and possible anthropogenic impacts upon harbour seal vocal breeding behaviour in Georgia Strait, with implications for other populations. Further research on the effect of anthropogenic noise on calls and on the function and context of novel call types found in this region are future directions for the research presented in this thesis.

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