FREE-RANGING MARINE MAMMALS: THE NEXT ACOUSTIC SHIPS OF OPPORTUNITY?

by

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Abstract

Understanding the nature of species interactions in the ocean is challenging because direct observation is usually impossible. The deployment of dual transmitting and receiving acoustic transceivers and satellite-linked GPS tags on mobile marine predators provides a unique opportunity to resolve species associations in space and time. However, an approach for how best to analyze and draw biological inferences from these data is lacking. I evaluated the detection efficiency of acoustic transceivers deployed on grey seals (*Halichoerus grypus*) in 2010 off Sable Island in response to changing field conditions using generalized linear models (GLM) applied to post-processed detection data and summarized raw transceiver data. Distance between seals, wind stress, and depth were the most important predictors of detection efficiency. Access to the raw acoustic transceiver data greatly improved our ability to identify legitimate periods of silence when the receiver recorded no part of an acoustic transmission. I demonstrated how the non-parametric Lagrangian method, T-LoCoH, may be applied to GPS location data to characterize patterns in the individual and collective movement of instrumented grey seals and account for uneven sampling effort. Consistent patterns in collective area-use emerged that may relate to seasonal energy requirements and prey distribution. At the individual-level, T-LoCoH can be used to identify behavioural patterns and to calculate the transmission reception per unit sampling effort (TPUE) using time and space-use metrics. This thesis represents a first step towards analyzing acoustic data collected by mobile marine animals. My findings highlight the importance of understanding the factors influencing tag performance and the biological processes driving animal movement in order to draw accurate biological inferences. In addition, these findings demonstrate effective approaches that may be used to quantify and account for changes in detection efficiency and uneven sampling effort.

List of Abbreviations Used

Argos	Advanced Research and Global Observation Satellite
ARS	Area Restricted Search
BB	Banquereau Bank
°C	Degrees Celsius
CB	Canso Bank
CTD	Conductivity Temperature Depth
DFO	Department of Fisheries and Oceans Canada
FB	French Bank
GLM	Generalized Linear Model
GPS	Global Positioning System
h	Hour
HMM	Hidden Markov Model
k	Number of nearest neighbours
kHz	Kilohertz
km	Kilometer
LoCoH	Lagrangian Convex Hull
m	Meter
MB	Middle Bank
MCP	Minimum Convex Polygon
N	Newton
OTN	Ocean Tracking Network
OFT	Optimal Foraging Theory
R^2	Coefficient of Determination
s	Time-scaled Distance parameter
s	Second
SB	Sable Bank
SE	Standard Error
T-LoCoH	Time Lagrangian Convex Hull
TDR	Time Depth Recorder
TPUE	Transmission reception Per Unit sampling Effort
TSD	Time-Scaled Distance
VHF	Very High Frequency
VMT	Vemco Mobile Transceiver

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Chapter 1

Introduction

Interactions among conspecifics and between species shape both social and ecosystem structures, and can affect population growth rates, distribution, diversity, and gene flow [1, 2]. However, direct observation of interactions in the ocean is challenging because most interactions take place below the surface where they are difficult to observe. As a result, scientists have used 'associations' between animals to infer interactions, where the "circumstances under which an association occurs are those in which interactions usually take place" [3]. Circumstances include the location, time, nature, and frequency of associations in addition to the identities of the players involved. Our ability to measure and interpret the circumstances under which an association takes place hovers on the edge of technological feasibility and scientific knowledge. Resolution of the location, timing, and frequency of associations varies depending on the observation techniques employed; for example, a diet sample may tell us that the seal ate a herring but not where this interaction occurred. The scale at which we are able to resolve an animal's behaviour also varies; the nature of an association may be determined at the level of behavioural events (e.g., breaches, prey feeding events) or behavioural states (e.g., travelling, foraging) [4, 5]. Likewise, a player's identity is defined by its species, sex, age, trophic level, and life history, yet in some cases we are only able to identify it by species. The level at which we are able to resolve the circumstances of an association has important implications for drawing ecological inferences.

The development of two-way acoustic transceivers provides a unique opportunity to resolve the circumstances under which animal associations occur. The dual transmitter and receiver capabilities of the acoustic transceivers effectively turn marine organisms instrumented with the devices into geo-referenced mobile receiving stations with the ability to detect other tagged conspecifics and non-surfacing tagged organisms for which there is otherwise no location information. By deploying transceivers on the marine animals of interest themselves, associations can be recorded at a scale relevant to the instrumented animal's behaviour over potentially large geographic ranges and inaccessible habitats. Transceivers record the time at which an association (received transmission) occurs as well as the identity of the transmitting tag, allowing one to record the frequency of associations between two known individuals. The deployment of these tags in conjunction with Global Positioning System (GPS) satellite telemetry enables us to determine the location at which associations occur and may be used to estimate the animal's behavioural state.

I begin my thesis introduction with an overview of the methods used to resolve association circumstances in the ocean, followed by an introduction to my case study where I explore the use of two-way coded acoustic tags as a potential tool to study the spatial and temporal patterns of associations between grey seals and other marine organisms.

Studies of the location, timing, and frequency of predator-prey, competitive, and social associations in marine species have largely been inferred from experiments [6], diet sampling [7], multi-species time series analyses [8,9], or direct observation [10]. Diet sampling provides direct evidence that an interaction occurred. However, diet samples are also subject to biases: some interactions may be underrepresented depending on the type of prey consumed [11] and the method of consumption [12]; samples typically only represent the last few meals (but see Quantitative Fatty Acid Analysis, [13]); samples are often difficult to tie to specific locations. Direct observation of associations and species distributions of large marine animals are limited to observations from land or at the sea-surface interface (e.g., colonies, rookeries, at-sea sightings data). Passive and active acoustics overcome this shortcoming by expanding observation ranges to include the underwater realm. Passive acoustic detectors make it possible to detect, localize, and track sound producing fish and marine mammals and have been employed to elucidate seasonal distribution and occurrence of numerous species such as humpback whales and haddock (see [14] for a review). Active acoustics give voice to individuals and species that are not active sound makers or whose sound projection range is limited, and can be employed to understand species distributions [15]. Advances in tracking and telemetry technology have allowed scientists to collect increasingly accurate and fine-scale animal location data both at (GPS satellite telemetry) and below (e.g., geolocation tags, hydroacoustic arrays) the ocean's surface. However, in order to resolve the nature of an association we need to know the behaviour of the players involved.

Researchers have devised novel methods of assigning behaviour to what cannot be directly observed. Behaviour may be defined in terms of states and events [5]. Whitehead and Van Parijs [5] define a behavioural state as a prolonged condition such as foraging and feeding, and behavioural events as instantaneous actions such as breaches or prey feeding events. Advancements in location telemetry (Argos, GPS, Fast-loc GPS, geolocation) and improvements in animal movement models have revolutionized our understanding of the movement patterns and behaviour of numerous marine organisms (e.g., [16–21]). Time-depth recorders (TDR) and accelerometers extend our understanding of the mechanics of animal movement below the surface [22–24]. Passive acoustics have been used to broadly identify mating behaviour based on call/sound characteristics in species such as bearded seals [25], humpback whales [26–28], and haddock [29–31]. Acceleration data loggers have been employed to study fine-scale interactions (events) between predators and prey and as a way to identifying mating events (e.g., nurse sharks, [32]). Echo-location buzzes produced by sperm whales have also been used to define short-term measurements of feeding [33]. More invasive techniques including underwater cameras [34], jaw movement sensors [35] and esophagus and stomach temperature probes [36, 37] have also been used to provide proxies for prey encounters. These technologies have aided our understanding of how animals use ocean environments both behaviourally (e.g., feeding, reproduction, travelling states) and across temporal scales. The level at which researchers are able to determine the identity of the players in an association, especially those involving conspecifics, determines the complexity of the ecological inferences they can draw (e.g., relationships, social structure, [3]).

Identifying the players in an association can be challenging. In some cases it is possible to directly identify the players using existing visual markings or passive tags (e.g., spaghetti tags, fish; fin tags, seals); however, these are often limited to what may be observed at the surface (e.g., photo identification, [38]; pelage recognition, [39]; branding, [40]) or over short temporal ranges (e.g., crittercams, [34]). Genetic analyses may also be used to identify individuals [5]. Passive acoustics have been shown to be effective in identifying individuals in some species based on call characteristics (e.g., bearded seals, [25]). Active acoustic tags (transmitting acoustic pings), and barcode tags (fish) may also be used to identify individuals [15]. In studies where instruments are deployed on animals, we are able to identify the subject animal deployed with the device; however, in the absence of behavioural patterns that differ depending on the individual or species they interact with, we are often unable to identify the other player(s). To overcome this problem in predator-prey interaction studies, researchers have employed tracking and hydroacoustic methods concurrently to identify the size and type of prey in an aggregation.

It is clear from the literature that the most successful means of studying species interactions in space and time are those that involve a multi-faceted approach to resolving the circumstances under which associations takes place.

Since 2009 the Ocean Tracking Network (OTN) has been instrumenting grey seals (*Halichoerus grypus*) with novel two-way transmitting and receiving coded acoustic tags (Vemco Mobile Transceiver, Vemco Ltd.) to study the spatial and temporal patterns of associations between grey seals and other acoustic transmitter-only tagged species including salmon (*Salmo salar*) and cod (*Gadus morhua*) which are of conservation concern [41,42].

Grey seals are large, size-dimorphic, marine carnivores with colonies in Atlantic Canada, on Sable Island and the southern Gulf of St. Lawrence, with smaller colonies in adjacent areas of Atlantic Canada and the northeastern US. Grey seals are wide-ranging foragers that exhibit marked seasonal changes in distribution, diet, and foraging effort [7, 43–47]. As bioprobes, individual animals equipped with sampling instruments (e.g., ocean temperature, coded acoustic transceivers), changes in environmental conditions and seasonal patterns in movement are likely to influence the quality of the data recorded and where and when data are collected.

The overarching question of my thesis is: How can novel acoustic transceivers paired with GPS satellite telemetry deployed on grey seals be effectively used to explore how, when, and where associations occur?

1.1 Chapter 2

Making biological inferences regarding the prevalence and distribution of species associations at the most basic level relies on knowing whether or not a tagged organism is present. In the second chapter of my thesis, I evaluate the probability of detecting a tagged organism given it is near a given receiver in relation to environmental characteristics and seal behaviour using post-processed and summarized acoustic tag data.

1.2 Chapter 3

Understanding how a bioprobe uses space is integral to how we account for uneven sampling effort, interpret the data collected, and for what data collection purposes the bioprobe is used. The third chapter of my thesis demonstrates how to quantify and characterize individual and collective area-use to account for uneven sampling effort (time spent and where) and to understand the biological importance of the data collected.

Chapter 2

Probability of Detecting Marine Predator-Prey and Species Interactions Using Novel Hybrid Acoustic Transmitter-Receiver Tags

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2.1 Introduction

Electronic tracking and telemetry data have greatly improved our knowledge about the ecology of many marine species at the individual and population levels [48]. However, few studies have used these methods to investigate the nature of associations between individual animals. Interactions among conspecifics and between species shape both social and ecosystem structures, and can affect population growth rates, distribution, diversity, and gene flow [1,2]. Studies of predator-prey, competitive and social associations in marine species have largely been inferred from experiments [6], diet sampling [7], multi-species time series analyses [8, 9], or direct observation [10]. These studies are often limited to accessible habitats (e.g., the intertidal, haul-out sites) and may not provide insight at the individual level (e.g., time series analysis). Acoustic telemetry can overcome some of these shortcomings by providing information about associations at the level of individuals from inaccessible marine environments, see Barnet et al. [49] and Barnet and Semmens [50] who simultaneously tracked predator and prey.

The deployment of dual transmitting and receiving acoustic Vemco Mobile Transceivers (VMT, www.vemco.com) and satellite-linked GPS tags or geolocation tags [51] on large marine vertebrates provides an opportunity to understand species associations in space and time. The VMT is a hybrid acoustic tag, housing a 69 kHz coded transmitter and a 69 kHz monitoring receiver. While arrays of stationary acoustic receivers are often necessarily confined to continental shelf areas (e.g., [52]), the deployment of VMTs on marine animals provides the ability to extend detection ranges of conspecific and other marine species to biologically interesting regions that may be missed by fixed arrays. The dual transmitter and receiver capabilities of the VMT create a mobile receiving station by which non-surfacing acoustic-tagged organisms, such as fish, can be detected. With these data we have the capacity to better understand the role of predators in ecosystems and to improve our understanding of their associations with commercial fish stocks and fish species of conservation concern.

To interpret associations between two organisms we must accurately describe the circumstance (locations, duration, and frequency) under which an association takes place. At the most basic level, interpreting an association relies on knowing whether or not a tagged organism is present. Quantifying the probability of detecting a tag if it is near a given receiver, particularly under changing field conditions, is vital for making accurate biological inferences when using these VMTs. In general, the probability of detecting a transmitter depends on the distance the transmitter is from the receiver, the properties of the medium and transmission (e.g., sound frequency), and the presence of physical obstructions and noise [53]. Sound intensity attenuates with the square of the range according to geometric spreading of the sound in water [53]. Therefore the distance a transmission travels in the ocean depends strongly on the sound frequency of the signal and characteristics of the propagation medium (i.e., sea water composition). Detection probability can also be affected if parts of the transmission are masked by background noise or distorted (e.g., changes in transmission frequency).

Changes in detection efficiency may occur in response to changes in oceanographic and environmental conditions: wind stress [54, 55]; water column stratification [56, 57]; water density [15, 56]; bottom topography [58]. Detection efficiencies have been quantified using a range of approaches including boat based, diver based, fixed sentinel tags, fixed tag with receiver at set distances, post-analysis, single tag at different distance [59]. While these studies provide valuable data on detection ranges, they cannot fully describe conditions experienced offshore, and therefore cannot be expected to assess the performance of the VMT when deployed on a free-ranging marine animal. Our case study is distinct from standard acoustic studies, where only the tag is in motion; in our case both the tag and receiver are in motion. The importance of understanding how a tagged marine animal's behaviour affects tag performance is therefore increased. Differences between VMTs may arise because some individuals spend a greater proportion of their time in noisier locations or near complex geomorphology, which may lead to more obstructed transmissions [60] than in other locations. Understanding these behavioural patterns and how they differ seasonally, by age, sex, and physiological state is of the utmost importance.

Pinnipeds are well suited for testing the performance of VMTs. Their frequent return to the surface provides highly accurate GPS locations. Grey seals (*Halichoerus grypus*) fitted with VMTs are known to interact frequently with each other [61], and exhibit high site fidelity, making them easy to recapture to retrieve archived data. Evaluating VMTs when deployed on grey seals provides an opportunity to assess the efficiency of VMTs under realistic behavioural and environmental conditions. Here, we define detection efficiency as how well VMTs are able to detect another VMT transmitter (i.e., with what probability) within a defined range.

We conducted two analyses of detection efficiency of VMTs deployed on grey seals using post-processed detection data (complete transmissions) and summarized raw VMT data (complete and incomplete transmissions), to explore the effect of environmental factors: wind stress, distance between VMTs, and temperature and depth gradients. The raw VMT data consists of a record of all acoustic pings (the smallest sound unit) recorded by the VMT receiver, and differs from the post-processed detection data in that it contains records of incomplete transmissions in addition to complete transmissions (confirmed detections) as well as pings from environmental and anthropogenic sources. Vemco provided us with summarized raw data for four VMTs consisting of acoustic pings classified by the time intervals between them and summed for each 10-minute period.

We evaluated the detection efficiency of VMTs using calculated distances (based on GPS locations) between seals to generate a series of instances when detections are likely to have occurred. Access to the summarized raw VMT data allowed us to focus on the physical and environmental factors that limit a receiver's ability to resolve a transmitter's identity.

2.2 Methods

2.2.1 Ethics Statement

This research was conducted in accordance with guidelines for the use of animals in research [62] and the Canadian Council on Animal Care. The research protocol for deployment of tags on grey seals was approved by the University Committee on Laboratory Animals, Dalhousie University's animal ethics committee (animal care protocol: 08-088) and the Department of Fisheries and Oceans (DFO), Canada (animal care permit: 10-65).

2.2.2 Study Site

The study was conducted between 8 September 2010 and 17 January 2011 on Sable Island, Nova Scotia, Canada (43°55'N, 60°00'W) and the Eastern Scotian Shelf in the northwest Atlantic Ocean (Figure 2.1). Sable Island is an important breeding site for grey seals [37] and the Eastern Scotian Shelf is an important foraging area [45, 61].

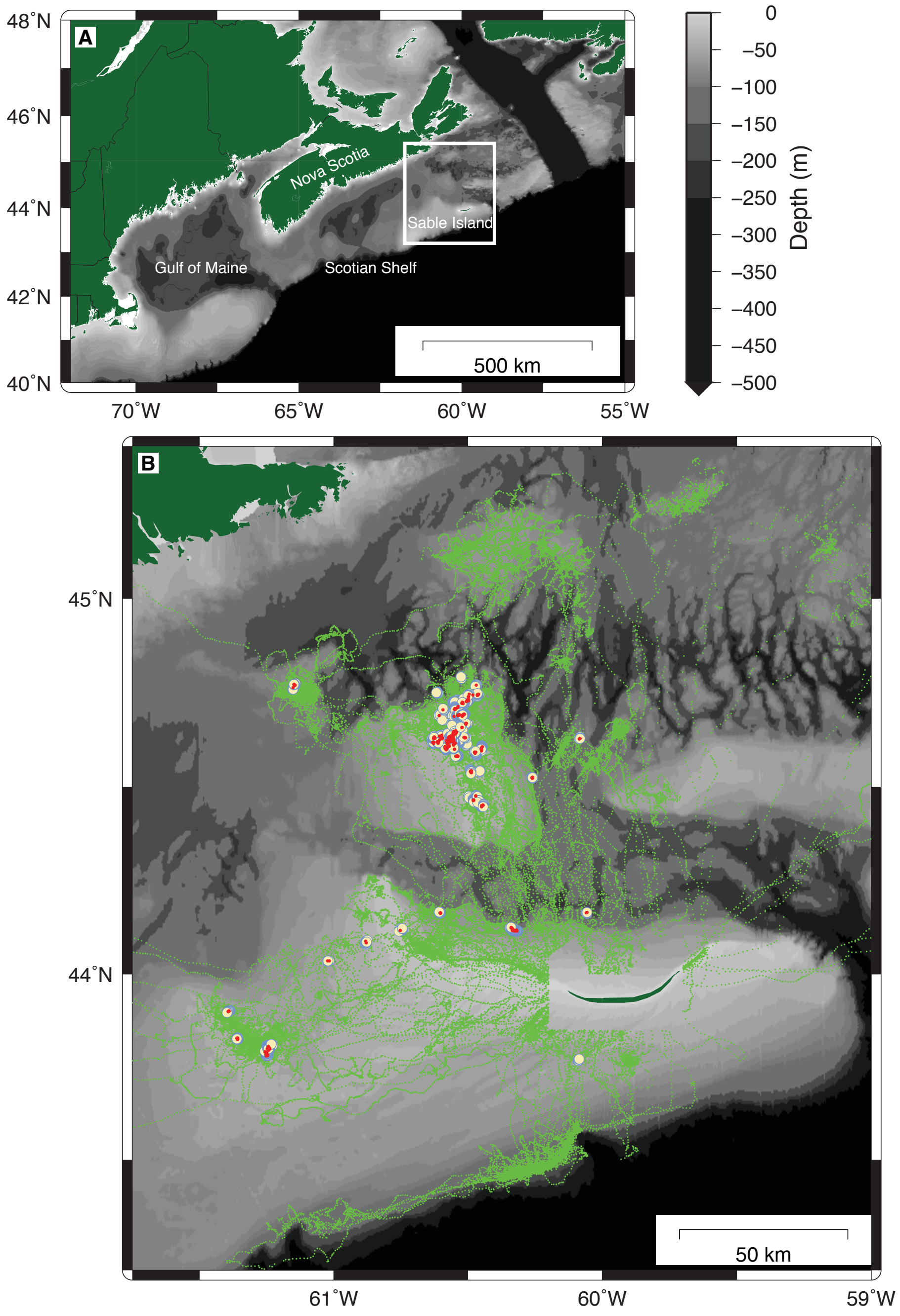

Figure 2.1. Nova Scotia and the Scotian Shelf (A) with the study area showing GPS tracks (green) and VMT expected (white) and observed (red) detections (B). The main shallow banks in the region are outlined with their 100 m isobaths (grey). Detection data around Sable Island was removed prior to analysis in the polygon outlined.

2.2.3 Study Animals

Seventeen adult grey seals, *Halichoerus grypus* (Fabricius, 1791), selected from a pool of known-age adults were captured between 8 and 18 September 2010 on Sable Island and fitted with a VHF transmitter (164-165 MHz, www.atstrack.com), GPS satellite-linked tag (MK10-AF, www.wildlifecomputers.com) and a VMT according to the methods described in Lidgard et al. [61]. Briefly, the VHF and GPS tags were attached just below the neck to maximize the time the GPS tag spent above water where it could record the satellites in range. The VMT was attached to the lower back of the seal to increase the time the VMT spent in the water transmitting and receiving detections and to reduce electrical interference with the satellite tag. The GPS tag was programmed to collect light intensity, depth (m), and temperature (°C) every ten seconds and to record a GPS location every 15 minutes. GPS attempts were suspended when the unit was dry more than 20 minutes or when a location had been attained.

Peak sensitivities for hearing in phocids are between about 10 and 50 kHz with a high frequency limit of 100 kHz [63]. It is likely that seals could hear the 69 kHz VMT transmissions, given the power output of the transmitters (146-149 dB re 1μPa SPL @1m) [64]. However, we did not observe any differences in behaviour: seals in this study exhibited similar foraging and breeding patterns to seals previously tagged with satellite transmitters without an acoustic tag [45], [65], [66]. Ambient background noise, reflection and refraction of the signal, and habituation to the signal over time, make it unlikely that seals could localize other VMT tagged seals. Individuals were recaptured on Sable Island during the subsequent breeding season (December 2010 to January 2011) and their tags retrieved (median deployment period = 112 d, range = 92-121 d).

2.2.4 Post-processed detection data vs. summarized raw VMT data

VMTs are coded transmitters, meaning they transmit a sequence of pings that form an acoustic code unique to each individual VMT. VMTs are programmed to transmit an acoustic code on an irregular schedule, every 60 to 180 seconds. During each code transmission the VMT turns off its receiver for approximately 3.5s to avoid receiving echos from its own transmission that could interfere with code validation, and records the date and time of the transmission. Each code transmission comprises a sequence of eight acoustic pings (acoustic code). Each acoustic code begins with a synchronisation interval (sync)—the time between the first two acoustic pings—that identifies the transmission format. The series of acoustic pings that follows each sync, specifically the interval between each of the eight acoustic pings, creates the unique identification code (Figure 2.2). A checksum is applied by the manufacturers to the entire acoustic code to identify the legitimacy of the transmission. Hereafter, we use the terms transmission and acoustic code synonymously.

Post-processed detection data, available to all VMT users, comprises the complete received 69 kHz transmission—which may originate from a VMT or other 69kHz transmitter—and a daily summary of the total number of acoustic pings, syncs, and rejected false detections. Received complete transmissions (detections), in VMT memory, comprise a date-time stamp and the identities of the transmitting and receiving acoustic tags. False detections are identified by VEMCO using proprietary software, and are removed from the dataset upon VMT retrieval. False detections may result from the collision of codes from other active transmitters that either generate a code that does not exist or an existing code that is known to be present elsewhere (e.g., tags deployed on freshwater species or on non-migratory species in other ocean basins).

The summarized raw VMT data is different from the post-processed detection data in that it includes all acoustic pings received by the transmitter, including those from incomplete transmissions. Acoustic pings may originate from a variety of sources such as other VMTs, acoustic transmitters and abiotic and biotic noise. Acoustic pings originating from VMTs and other VEMCO transmitters may be distinguished from background noise by the signature intervals between each ping in their acoustic codes (Table 2.1). VMTs are programmed such that consecutive acoustic pings in an acoustic code occur between 0.30 s and 0.70 s. Acoustic pings may also occur at intervals within 0.70 s and 1.50 s in cases where one or more acoustic pings in a code are missing (Figure 2.2). We therefore defined the range at which probable VMT pings occur as 0.30 s to 1.50 s. Acoustic pings occurring at intervals between 0.26 0 ss and 0.30 s are thought to indicate possible echos, multipath transmissions, or transmission collisions. Acoustic pings occurring at intervals greater than 1.50 s are likely the result of environmental noise or are cases where VMTs are near their acoustic range limit.

Table 2.1. Criteria used to determine ping origins

Interval Length	Description
0.26-0.29s	Possible echos or multipath transmissions
0.30-0.70 s	Interval range between consecutive pings
0.71-1.50 s	Interval range between 1 or more skipped pings
>1.50 s	Spurious pings or 3 or more skipped pings

*Ping origins deduced from intervals between consecutive pings.

2.2.5 Track Data and Expected vs. Observed detections

We determined GPS locations by analyzing archival GPS data from each tag using software from the manufacturer. To be considered accurate, locations had to be acquired from > 5 satellites with a residual error < 30m [67, 68].

To link encounters between instrumented seals to locations interpolated at 3-min intervals from the seal tracks, clocks in the VMT and GPS tags were synchronized upon deployment and time corrected upon retrieval based on the respective clock drift calculated from GPS and VMT tags over the deployment time [61]. Distances between seals (m) were calculated from the 3-min interpolated locations.

Each seal's travel rate (m/s) was calculated using the original archival GPS location

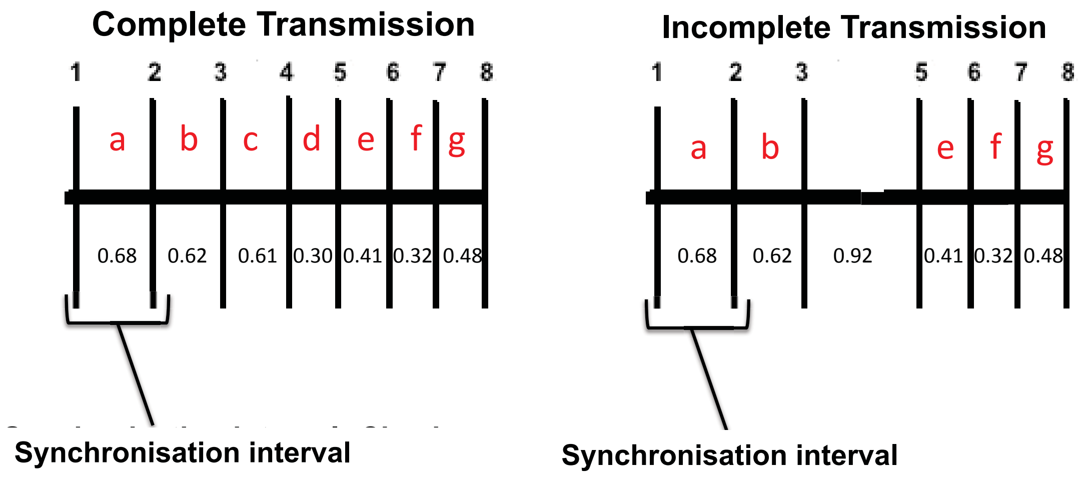

Figure 2.2. The difference between a complete and incomplete transmission. VMT transmissions comprise a series of 8 acoustic pings. Each 'acoustic ping string' contains a synchronization interval (between the first two pings), used to identify acoustic-tag transmission format, followed by a series of pings unique to each individual tag. Intervals between 0.30-0.70 s correspond to consecutive pings. An interval between 0.70-1.50 s may indicate that one ping (of duration 0.01 s) is missing, e.g., time interval of 0.92 s in the incomplete transmission diagram. All 8 acoustic pings must be received for a detection to be recorded.

data. We matched these estimates to the respective transmitting and receiving VMTs using a date-time stamp. We assumed expected detections to occur every 180 s based on tag specifications (every 60-180 s), when two VMTs encountered each other. We operationally defined an expected encounter as occurring when the VMTs were within 100-700 m of one another. We used 100 m as the lower limit of this range to avoid a decreased probability of detection, which may sometimes occur at close encounter ranges. We used 700 m as the upper limit of our range based on the manufacturer's specifications and inspection of our detection data (Figure 2.3).

Despite being within range of VMTs that recorded data, two VMTs (66487, 66548) failed to record any detections, and one VMT (66494) was only recorded once by another VMT. Closer inspection of the seal tracks associated with these VMTs indicated they were spatially peripheral to the majority of the VMT-tagged seals, but still within range of certain known working VMTs. We excluded these non-functioning VMTs (66487, 66548, 66494). Other confounding elements could have affected the summarized raw VMT and post-processed detection data around the VMT deployment point, Sable Island. VMTs do not record signals out of water; therefore, it is important to exclude any periods the seal is out of water from the analysis. Close to the island, it was difficult to determine if a VMT-tagged seal was out of water if these durations were shorter than the wet-dry sensors on the GPS tag could detect. Furthermore, due to the shallow bathymetry and thus high noise disturbance around the island, we expected the capability of the VMT to record transmissions to be compromised. Thus, detection data around Sable Island were removed prior to analyses (see polygon outlined in Figure 2.1B).

2.2.6 Conversion Efficiency

Vemco provided summarized raw VMT data for four of the VMTs (66556, 66504, 66555, 66541). From these data we calculated the VMT conversion efficiency. Conversion efficiency was defined as the ratio of acoustic pings translated into detections (complete VMT transmissions) to those received (complete and incomplete VMT transmissions, Figure 2.2).

2.2.7 Statistical Model and Environmental Variables

We used a generalized linear model (GLM) with a negative binomial distribution to model VMT detection and conversion efficiency, where the response variable was the number of observed detections from new encounters in a 12 h period. New encounters were identified as detections (expected or observed) occurring when there was at least a 30 min interval between consecutive detections for a defined pair of seals. The number of expected detections in each 12 h period was included in the model as an offset term to account for the time VMT-tagged seals spent near each other.

Conversion efficiency was evaluated by modeling the number of acoustic pings from complete VMT transmissions (observed detections x 8 pings), including the total number of pings from VMTs received (pings occurring at intervals between 0.3-1.5s) in 10 min intervals as an offset.

2.2.8 Environmental Variables

Environmental variables were selected according to their relevance to sound propagation on the Scotian Shelf and their availability (Table 2.2). To avoid temporal and spatial scale mismatches, most variables were limited to those that we could collect from the MK 10-AF tags which sampled every 10 seconds and at the seal's exact location. Temperature (°C) and depth gradients (m) between the transmitting and receiving seals were included in the model to test for the effect of water stratification and density changes. The directional (positive or negative) difference in depth and temperature was included because the direction of signal travel with respect to the temperature or depth gradient affects sound transmission differently. Horizontal distance (m) was included in the model to represent detection range.

Table 2.2. Environmental variables explored in VMT efficiency analyses

Variable	Description
negtempdif	Directional temperature difference (±°C)
mindepth	Depth of the shallowest seal (m)
distance	Horizontal distance between seals (km)
negdepdif	Directional depth difference (±m)
travel rate	Travel rate of the receiving seal (m/s)

*Description of environmental variables tested in VMT efficiency analyses.

0 m

Wind stress (N/m^2) was included in the model to test the effect of increased noise and changes in the air-sea interface through the introduction of air bubbles. Wind stress (N/m^2) was calculated from hourly estimates of wind speed on Sable Island (DFO) in

MATLAB (MathWorks, Inc.), using the function stresslp.m (air and sea package) following Large and Pond [69]. We hypothesized that the effect of noise and/or air bubbles generated by wind stress would be greatest at the surface; we therefore tested for a possible interaction between wind stress (N/m^2) and the depth of the shallowest seal (m) in the model. Seal identity was included as a factor to account for variation in VMT performance and differences in seal behaviour and movement patterns. Travel rate (m/s) was included to describe the seal's horizontal movement rates.

2.2.9 Model Selection

Terms in the model were added and subtracted using forward and backward selection [70]. Variable selection was based on hypothesis testing (p-values) and by comparing the pseudo adjusted R^2 calculated from the residual and null deviance of the model. Residual diagnostics were examined to determine goodness of fit. To explore how sensitive the results were to the subsample distance range, we explored the data subset by distance ranging from 100-250 m, 100-400 m, and 100-700 m. This was done to control for varying amounts of time spent by seals at different distances from one another.

2.3 Results

All 17 deployed VMT and GPS tags were recovered from seals upon their return to Sable Island during the breeding season. GPS locations were acquired with a median of 9 satellites (<15 m residual error). A total of 1,168 detections were recorded, occurring at distances between 4 m and 1880 m (median=320 m, mode=250 m). Fewer detections occurred at both close range and beyond 500 m. 60% of all detections occurred when the VMTs were within 500 m of one another (Figure 2.3A). We observed a decrease in the proportion of observed vs. expected detections with increased distance (Figure 2.3B). Only about half of the expected detections were recorded even when two VMT-tagged seals were estimated to be within 50-200 m. At a separation of 400 m, only about 15%

of expected detections were recorded. The summarized raw VMT data provided a clearer picture of whether any part of a transmission was received with distance (Figure 2.4): the ratio of pings from complete transmission to pings from complete and incomplete transmissions fluctuated around 70%, with a minimum of around 40% at 600 m and a maximum of about 85% at 50 m (Figure 2.4).

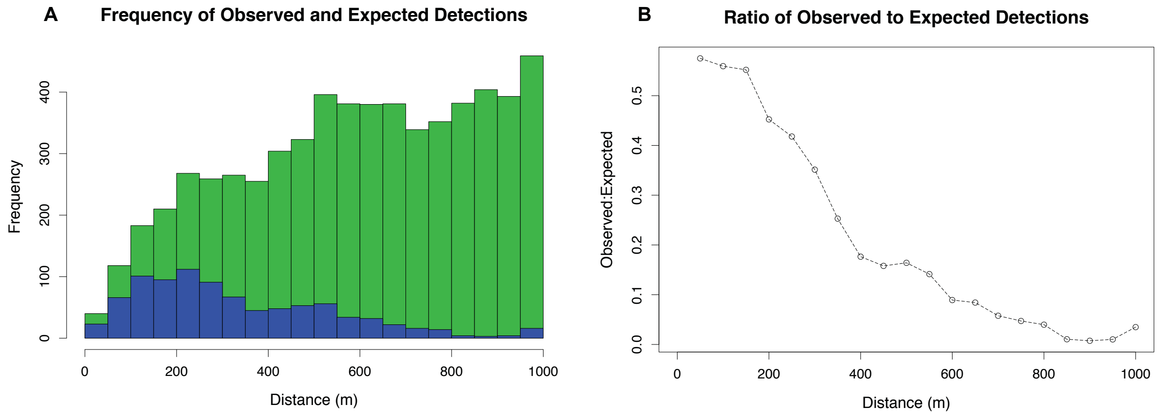

Figure 2.3. A. Density of observed (blue) and expected detections (green) with distance. B. Plot of the ratio of observed to expected detections.

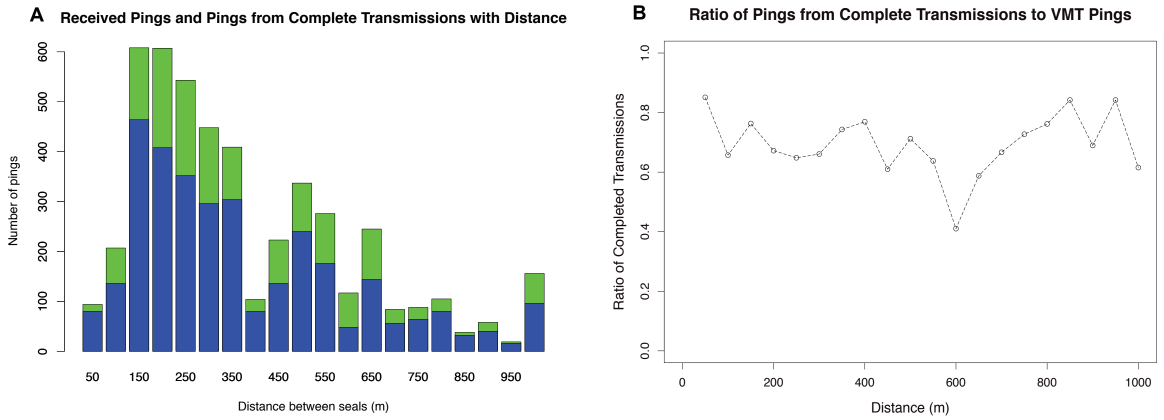

Figure 2.4. A. Density of VMT acoustic pings received (green) and acoustic pings from VMT complete transmissions (blue) with distance. B. Plot of the ratio of pings from complete transmission to VMT pings received.

2.3.1 Model 1: Expected and Observed Detections

The best model explained 35.7% of the variability in detection efficiency. The probability of detection decreased with increasing distance between seals (-2.77, SE: 0.64), wind stress (-7.40, SE: 1.87), and depth of the shallowest seal (-0.03, SE: 0.01), (Figure 2.5).

2.3.2 Model 2: Conversion Efficiency

Wind stress (-1.59, SE: 0.35) and distance (-0.54, SE: 0.14) were both important predictors of conversion efficiency. Conversion efficiency decreased with increasing wind stress and increasing distance (Figure 2.6). Wind stress had the most significant effect on detection efficiency.

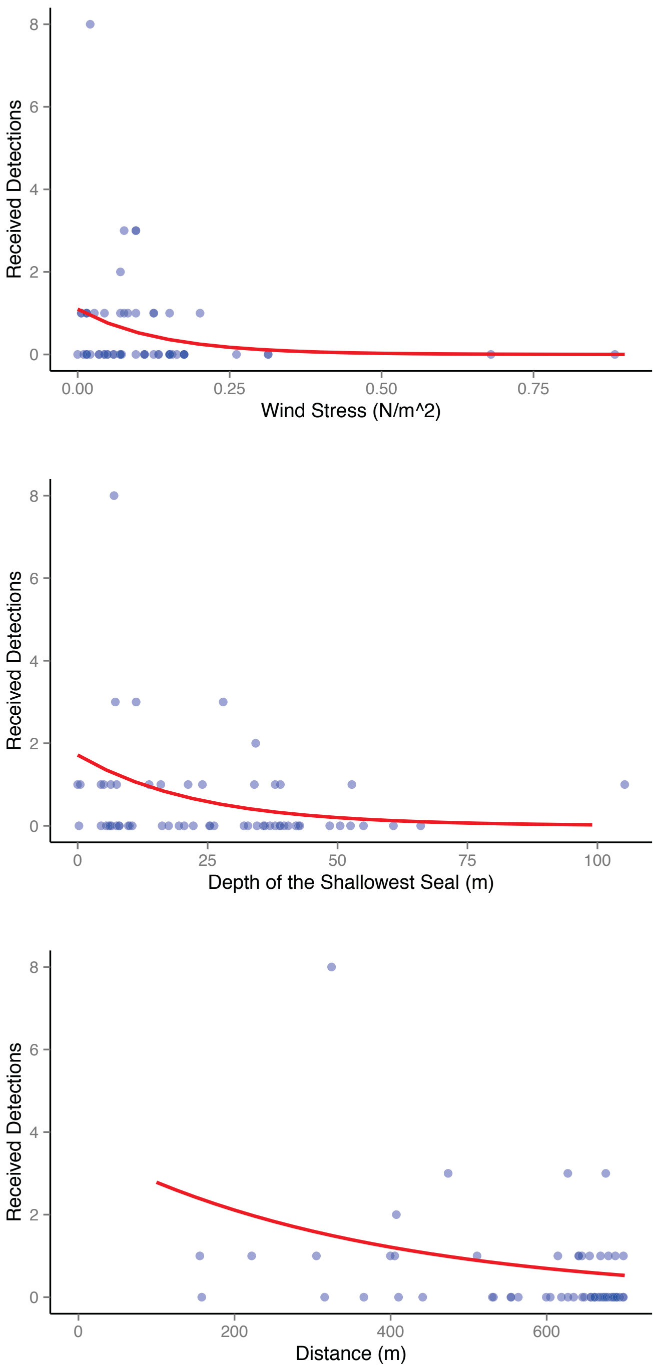

Figure 2.5. The predicted effect on detection efficiency of the significant variables (red line): wind stress, minimum depth, and distance. Fitted values (observed detections offset by expected detections) are shown as points. Points: dark blue indicates high intensity, light blue indicates low intensity.

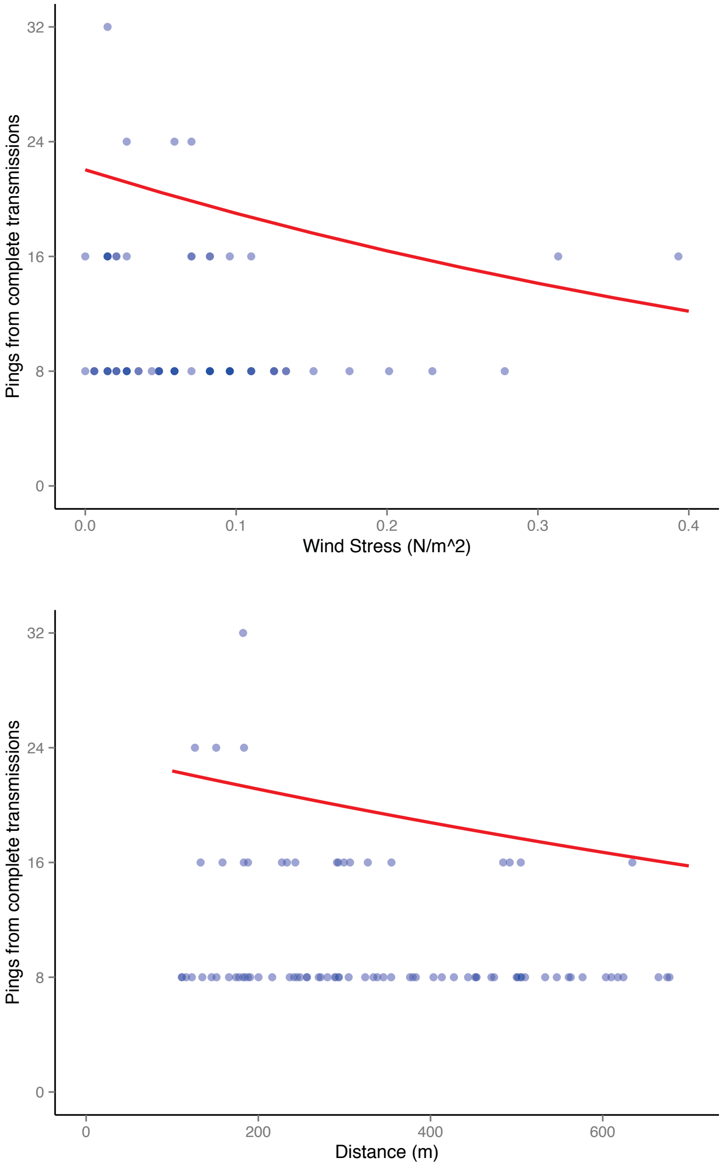

Figure 2.6. The predicted effect on conversion efficiency of the significant variables (red line): wind stress and distance. Fitted values (VMT acoustic pings from complete transmissions offset by total VMT acoustic pings received) as points. Points: dark blue indicates high intensity, light blue indicates low intensity.

2.3.3 Sensitivity of Detection Efficiency to Distance Range

The results from each data subset were generally consistent with those of the main analyses. When encounters were defined at the 100-400 m range, results were consistent with the main analysis (100-700 m), but when encounters were defined at the 100-250 m range depth of the shallowest seal did not have a significant effect on detection efficiency. The signs and coefficients of model terms were conserved across distance ranges. The pseudo R^2 values were 19.5%, 28.1%, and 35.72% for the interval ranges: 100-250 m, 100-400 m, and 100-700 m respectively. These changes in explanatory power are likely the result of the increased influence of distance on decreases in detection efficiency.

2.4 Discussion

While it is relatively easy to ascertain if a tagged animal is present (true positive), it is more difficult to determine with certainty that it is absent (true negative) as it could be present but not detected (false negative). Quantifying the proportion of VMT transmissions that are not received and determining to what extent this is due to physical and environmental factors and the behaviour of the tagged animals, is vital to form accurate ecological conclusions from VMT data. Without an appreciation of these issues, these effects may lead to erroneous inferences.

We present one of the first studies to investigate the detection efficiency of acoustic VMT receivers deployed on marine animals and to analyze detection efficiency using summarized raw VMT data. Wind stress, depth of the shallowest seal, and distance between seals were significantly correlated with VMT performance. The summarized raw VMT data allowed us to determine the extent to which within-range VMTs are successfully detected and provided a clearer picture of whether any part of a VMT transmission is received. The ratio of VMT pings from complete transmissions to VMT pings received fluctuated around 70% with a minimum of around 40% at 600 m and a maximum of about 85% at 50 m. This shows a vast improvement when compared with at best 50% of expected detections received between 50-200 m, dropping to 15% at 400 m when using only the post-processed detection data. Examining conversion efficiency (the ratio of complete transmissions to all transmissions received) provides additional insight into

VMT detection efficiency by focusing on factors that limit a transceiver's ability to resolve a transmitter's identity.

To date, GPS tags provide the best location estimates for *in situ* studies of this nature. GPS locations were obtained with a small residual error (<15 m) [67], resulting in little uncertainty in the GPS locations and subsequently, little uncertainty in the actual detection distances observed. Therefore, although it is possible for the seals to be 60 m closer or further away than that reported, the chance of this occurring is low.

2.4.1 Environmental Factors Affecting VMT performance

Distance between seals was a significant predictor of detection and conversion efficiency. In both cases, the probability of detection or conversion decreased with distance as expected. Detection range has long been identified as an important factor affecting the detection of acoustic tags [20]. Detection probability is hypothesized to decline proportionally to the decline in sound intensity, which is a combination of geometric and exponential decline due to sound spreading and attenuation resulting from water viscosity [53]. However, the exact shape of this relationship is unknown and modeling approaches vary. We were unable to resolve the shape of this relationship from our data due to the observational nature of the data. However, results from our sensitivity analysis illustrate that the detection range, assumed *a priori*, did not affect the relationships observed.

We also observed a decrease in detection efficiency and conversion efficiency with increasing wind stress. Wind stress can introduce noise as well as air bubbles into the marine environment. Noise makes it difficult to distinguish the acoustic signal above the background noise and may result in failure to detect one or more of the pings. Air bubbles absorb sound transmission because the acoustic signal has to pass between water and air. The absence of a significant interaction between wind stress and the depth of the shallowest seal suggests that the effect of wind stress on detection efficiency is not confined to surface waters. The observed decrease in detection efficiency with increasing depth may be indicative of sound attenuation occurring as a result of bathymetric effects [58].

Despite well established effects on sound transmission, we observed no effect of the propagation medium (temperature/depth gradients) on detection efficiency [53]. Sound propagation may be absorbed and deflected when traveling through density gradients (i.e., pycnocline). The coastal currents that transport source waters to the Scotian shelf exhibit strong seasonal cycles as well as significant interannual variability [71]. The Nova Scotia current reaches a peak velocity in winter, transporting low salinity and low temperature water originating in the Gulf of St. Lawrence [72] into the inshore waters. These forces generally result in a low salinity and low temperature signature inshore that is more pronounced during winter months [71]. Temperature and depth gradients are therefore more likely to affect detection efficiency from January-March, than during our deployment period (September-December) .

As animal-borne acoustic telemetry evolves beyond stationary receivers, it is unclear how factors such as the orientation of the VMT with respect to the animal or the size of the animal affect VMT performance. VMTs were placed on the lower back of the seal to maximize the time the VMT spent in the water receiving and transmitting signals. However, the seal's body might attenuate acoustic signals being transmitted to or received from a certain direction, regardless of VMT positioning. Although this effect has not been formally investigated, it would be extremely difficult to quantify *in situ*. A triaxial accelerometer could be deployed to measure the seal's speed and VMT orientation, however, these devices also have limitations. Controlled experiments will be needed to investigate the influence of such factors on VMT performance. Other factors known to affect detection efficiency that were not included in our model are biotic and/or anthropogenic noise, (e.g., [73, 74]). These, in addition to characteristics of the seals behaviour (e.g., the animal's orientation during diving), may account for some of the unexplained variation in the model.

2.4.2 VMT engineering

To interpret associations we must accurately define their location, duration, frequency, and confidently identify legitimate periods of silence (i.e., the absence of transmissions). For a detection to occur, the VMT receiver must be able to distinguish the acoustic signal from background noise. The background noise strength is dependent on weather and the fluid environment and other sources, including anthropogenic noise [53]. Distinguishing legitimate transmissions from background noise is an important component of measuring VMT performance. Simpfendorfer et al. [60] used syncs to estimate the volume of received incomplete and complete transmissions for a given period relative to the number of recorded transmissions; however, syncs are not precise. When tag transmissions collide, syncs can be created that are not from a tag transmission; consecutive pings from different tags may create a pseudo sync interval. The use of summarized raw VMT data addresses this shortcoming by using aspects of the transmission that are less susceptible to false positives. With access to the summarized raw VMT data, users can examine the interval between consecutive pings to determine their origin and thus authenticity (i.e., whether the pings arose from echoes, multi-path collisions, environmental noise or are legitimate pings from a VMT).

Observational data in the ocean are often limited due to the technological, environmental, and physical challenges that accompany data collection. These constraints make it important to maximize what can be gleaned from such data. Currently, access to the summarized raw data is not routinely available. Wider access to data of this sort will provide users with an additional indicator of their tag's performance, and inform their analyses through the ability to identify false negatives. In cases where the identity of the tagged individual is not pertinent, it may be sufficient to simply know that a seal was detected when part of a VMT transmission reached the VMT, even if we cannot account for the factors affecting the reception of the full VMT transmission.

Without understanding the factors affecting detection efficiency, biological inferences regarding the prevalence and nature of species associations via VMT/acoustic data will very likely be biased. For example, seasonal changes in environmental factors, that could reduce received transmissions, may be falsely attributed to seasonal changes in encounter rate. It is therefore vital that we account for changes in detection efficiency, as without this information, it is impossible to interpret what any given detection event represents.

Chapter 3

Quantifying Spatial Behaviour of Female Grey Seals and Associated Detections of Acoustically Tagged Prey Species

3.1 Introduction

The miniaturization of environmental sensors and acoustic tags has allowed these instruments to be deployed on an increasing number of animals [61, 75–77]. Animal-borne instruments such as temperature-salinity (CTD) tags, underwater cameras, and acoustic transceivers present a unique opportunity to study local oceanographic conditions, predator-prey interactions, and interspecies associations. Paired with GPS satellite location telemetry, animal-borne instruments allow for the collection of spatially-linked, fine-scale information at a scale relevant to the animal's behaviour [37, 75].

Diving animals can sample the water column multiple times each day [78, 79] and often at a higher spatio-temporal resolution than other ocean observing systems [80]. Bioprobes, individual animals equipped with sampling instruments (e.g., ocean temperature, coded acoustic transceivers), are also not constrained by the same financial and logistic constraints as human sampling platforms and fixed acoustic-receiver arrays; they therefore have the potential to advance our understanding of the physical environment and species interactions in habitats that are inaccessible and/or inhospitable to humans [81]. Bioprobes have already made important contributions to global data collection including approximately 70% of all oceanographic profiles south of 60°S [82]. However, this method of sampling the physical or biological environment differs markedly from traditional vessel-based surveys. I define sampling as the collection of any type of data about the physical or biological environment (e.g., temperature, acoustic noise). The data a bioprobe collects are intrinsically linked to the bioprobe's behaviour. Sampling locations are non-random in space and time and where a particular instrumented animal may go is difficult to predetermine, although general patterns in their movement may be known (e.g., certain marine mammals tend to forage at given points during their seasonal cycle). Understanding how a bioprobe uses space is therefore integral to how one accounts for uneven sampling effort when interpreting the physical and biological data they collect.

An animal's use of space is a fundamental aspect of their ecology [83]. How and where they spend their time has important implications for resource acquisition, mate searching, energy budgets, and species interactions, including avoidance of predation [84]. Space-use patterns can change over time in response to environmental variability (e.g., changes in temperature, prey distribution, predator density) and an individual's age, sex, and life stage. When animals are used as bioprobes, these biological processes/responses have important implications for the biological inferences drawn from these data. How one interprets data collected by bioprobes depends on the research aim and whether the bioprobe is i) the subject of the study or ii) a sampling platform (e.g., Ship of Opportunity) (Figure 3.1). In both cases, the underlying movement patterns and the biological processes that drive them are the same; however, the inferences differ. In the first case, one is collecting data to understand the bioprobe and uses the bioprobe's behaviour to understand the biological importance of the data, whereas in the second case, the bioprobe is a platform from which to collect data. As the subject of the study, a bioprobe's behavioural state and/or frequent visits to an area may indicate the ecological importance of the area to the animal and provide relevant biological context for the data collected. As a sampling platform, a bioprobe's movement patterns determine where, when, and how many samples are collected. These patterns have important consequences for sampling. The distribution of sampling determines the area over which one can extend their findings, the biological and physical conditions sampled (e.g., bathymetry, substrate type, etc.), and the performance of sampling devices such as acoustic tags. The intensity and overlap of sampling influences the accuracy of one's measurements and one's ability to characterize and compare areas over time. When sampling is conducted simultaneously by multiple platforms carrying identical sensors, the overall coverage and intensity of sampling is a result of the total sum of their movements. In these cases, sampling effort can be viewed in terms of collective time spent in an area.

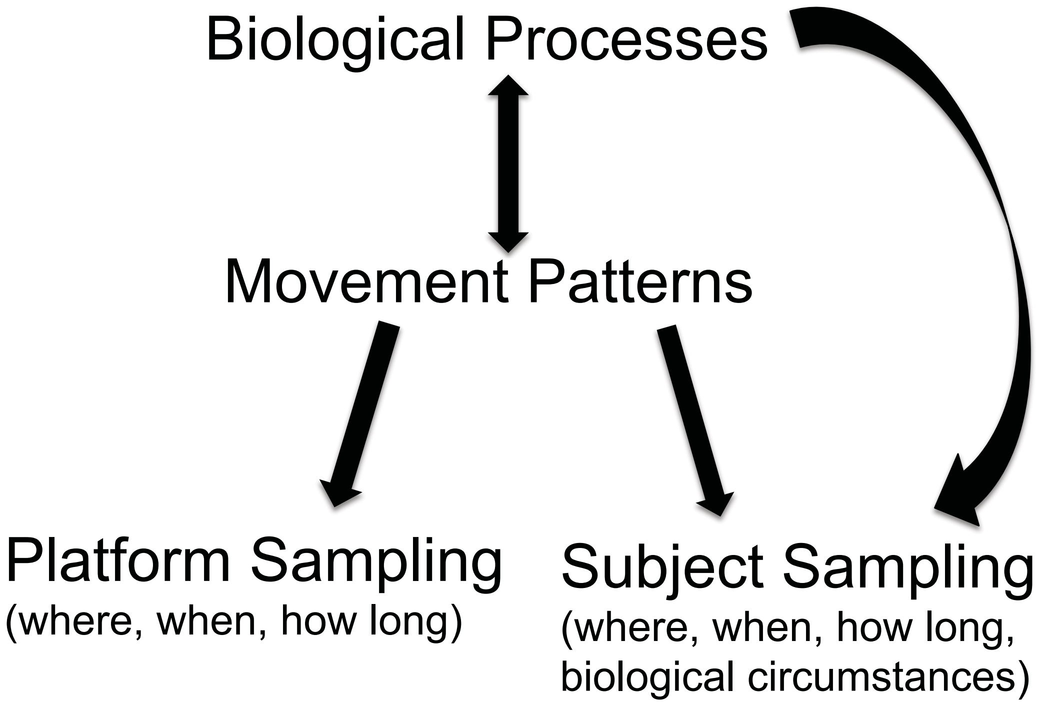

Figure 3.1. Bioprobe sampling schema showing the difference in data interpretation when the bioprobe is used as a platform vs. as the subject.

It is impossible to separate where and when sampling occurs from a bioprobe's behaviour. However, one can use their knowledge of the biological processes influencing movement behaviour to better predict and understand sampling patterns, quantify movement patterns to account for uneven sampling effort, and relate these patterns (e.g., behavioural states) to understand the biological context of the data collected.

Ecologists have developed a suite of methods for identifying the area(s) used by an animal (e.g., home range) and those used most intensely (utilization distribution) based on location data (see [85] for a review of these methods). Many of these methods are based on the assumption that the time an animal spends in an area reflects the importance of that area to the animal, and has been used to infer what behaviour the animal is exhibiting (i.e., their behavioural state). Here I use a specific type of method, Lagrangian Convex Hull (LoCoH), which estimates an animal's utilization distribution based on local nearest-neighbour minimum convex polygons (MCP) constructed from the relative frequency distribution of animal locations, using density as a third dimension to portray the intensity of area-use [86]. An advantage of LoCoH methods is that they tightly 'hug' the data making them suitable to study space use over areas that incorporate distinct habitat, geographical, or physical boundaries [87]. LoCoH methods have been shown to outperform traditional kernel-smoothing techniques in excluding areas known not be used [87]. LoCoH methods are also well suited to the study of the collective area-use of multiple organisms that exhibit possibly diverse individual space-use patterns. Recent developments have expanded these methods to include time in the construction and aggregation of MCPs (e.g., T-LoCoH: [88]). T-LoCoH offers an advantage over traditional approaches because it further improves the user's ability to partition area use and study patterns over time [88]. These same concepts can be extended to characterize sampling effort by viewing area use and intensely-used areas in terms of both area sampled and intensely-sampled areas. I therefore use the terms 'use' and 'intensely-used' to encompass both the extent and intensity of where the animal has been, and consequently sampled, when regarded as a sampling platform.

Since 2009, the Ocean Tracking Network (OTN) has been instrumenting grey seals (*Halichoerus grypus*) with novel two-way (transmitting and receiving) coded acoustic transceivers (Vemco Mobile Transceiver, Vemco Ltd.) to study the spatial and temporal patterns of associations between grey seals and acoustically tagged species such as cod (*Gadus morhua*) and salmon (*Salmo salar*). Coincident with this work, OTN partners have been acoustically tagging cod and salmon as part of ongoing studies of the movement of these species [89, 90]. These tagged fish represent species that grey seal bio-probes may detect. The dual capabilities of the transceivers effectively turn instrumented grey seals into geo-referenced mobile acoustic receiving stations with the ability to detect other instrumented grey seals and non-surfacing acoustic-tagged fish for which there is no independent location information. Recently, I was given access to the summarized raw acoustic data from the tag manufacturers, allowing me to increase my acoustic information to include incomplete acoustic transmissions known to originate from 69 kHz transmitters [91]. While it is difficult to determine from which species or individual incomplete acoustic transmissions originated from, these data are invaluable for identifying legitimate silent periods, that is when there is not an acoustic tagged organism in the vicinity of the transceiver.

Optimal foraging theory (OFT) predicts that an animal in a favourable habitat ought to remain in that habitat for an extended period of time [92]. This theory provides a useful framework within which to view the animal's movement. Grey seals are large, size-dimorphic, marine carnivores with breeding colonies in the Eastern Scotian Shelf on Sable Island, the southern Gulf of St. Lawrence, and with smaller colonies in adjacent areas of Atlantic Canada and the northeastern U.S [93]. Grey seals are wide-ranging foragers that exhibit marked seasonal changes in distribution, diet, and foraging effort [7, 43–47]. Both male and female grey seals have large energy demands, with a large portion of their time dedicated to foraging. Female grey seals are capital breeders, relying on body energy stores to fuel reproduction; males also rely on large energy stores for courtship and mating [66, 94]. I therefore expect their movement to reflect the patchy distribution of their prey whose distributions or availability may change over time [47]. Using OFT I assume that when a grey seal remains in a small area for an extended period of time that the seal is exhibiting area restricted search (ARS). ARS is a term used to describe the tendency of predators to focus their foraging attention to a restricted area in the vicinity of recent captures before continuing exploration [95]. Previous studies have characterized presumed foraging in grey seals using state-space models that predict the probability of being in area-restricted search based on turning angles and persistence of movement [47]. The location and size of presumed foraging areas have also been estimated using hidden Markov-models (HMM) that estimate the probability of exhibiting fast vs. slow movement behaviour, with fast behaviour indicating travel and slow behaviour indicating area-restricted search [19]. These studies rely on Argos satellite or GPS locations from the seal to identify behaviours. T-LoCoh presents a geometric approach to studying individual movement from GPS locations, where a high density of neighbouring GPS locations in time and space indicates area-restricted search patterns [88]. Although these statistical approaches are very different, they can be used to reveal similar aspects of the animal's biology and behaviour.

I demonstrate how the home-range package T-LoCoH [88] can be used to characterize and quantify spatial and temporal patterns in the individual and collective movements of grey seals equipped with GPS tags and with two-way acoustic transceivers on the Scotian Shelf (Nova Scotia, Canada). I illustrate how this method may be applied in new ways to address research questions from both the perspective of grey seals as the *subjects* of study and grey seals as *platforms*. Specifically, as subjects of the study: How does the frequency of associations between the grey seal and acoustically tagged fish species relate to the grey seal's behavioural state? And as platforms: What are the spatial and temporal trends in collective area-use? What are their implications for sampling? In addition to demonstrating this method, I discuss the biological processes driving patterns in individual and collective movement and make recommendations for future sampling.

3.2 Methods

3.2.1 Study Site

The study was conducted between 11 June 2011 and 31 December 2011 on Sable Island, Nova Scotia; the Eastern Scotian Shelf; and the southern Gulf of St. Lawrence (Figure 3.2). Sable Island is the largest breeding colony for grey seals in Eastern Canada [96] and the Eastern Scotian Shelf an important foraging area [45, 61, 97].

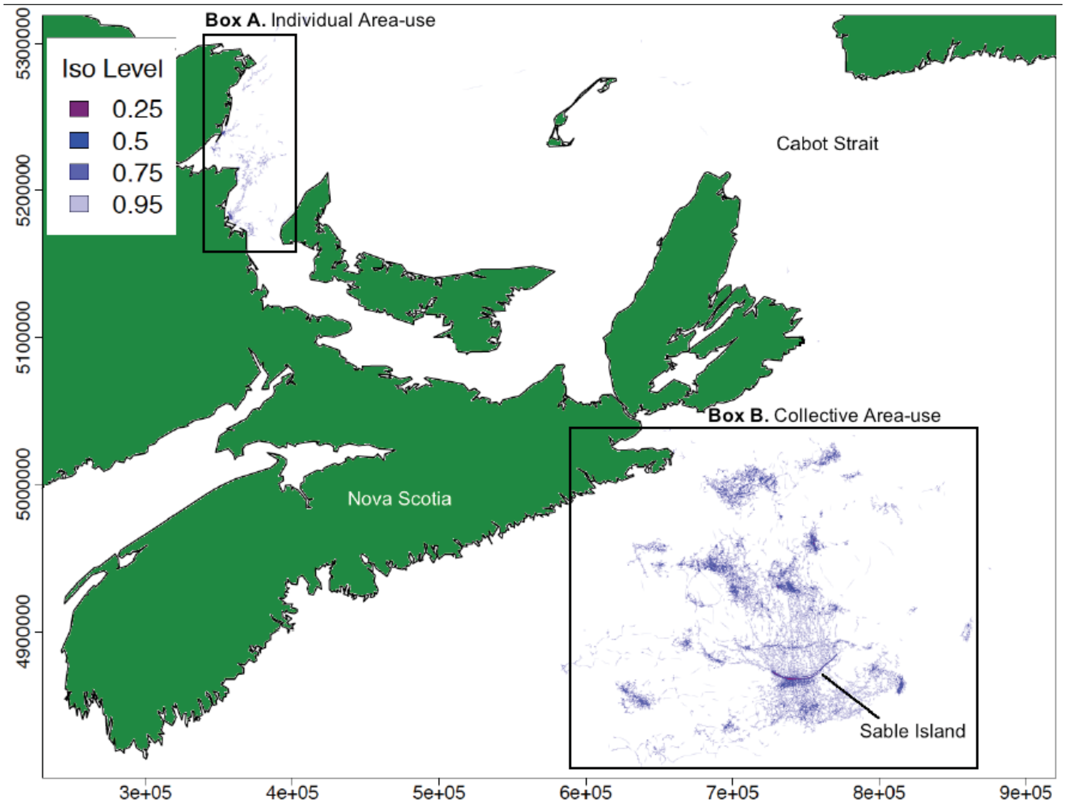

Figure 3.2. Bioprobe collective area use. Grey seal bioprobes collectively used an area of 11,308.28 km^2 (light blue, 95% density quantile) and intensely used an area of 31.07 km^2 (purple, 25% density quantile). One seal travelled to the southern Gulf of St. Lawrence and was used to study individual area-use (Box A). The majority of seals stayed on the Scotian Shelf surrounding Sable Island and were used to study collective area-use (Box B).

3.2.2 Bioprobe and Fish Tagging

Twenty female adult grey seals were captured between 11 and 15 June 2011 on Sable Island and each fitted with a VHF transmitter (164-165 MHz, www.atstrack.com), GPS satellite-linked tag (MK10-AF, www.wildlifecomputers.com) and an acoustic transceiver (VMT) according to the methods described in Lidgard et al. [61]. Briefly, the VHF and GPS tags were attached behind the cranium to maximize the time the GPS tag spent above water where it could detect the satellites in range. The transceiver was attached to the lower back of the seal to increase the time the transceiver spent in the water transmitting and receiving detections and to reduce electrical interference with the satellite tag. Although the tags transmitted GPS location via satellite link, we used the larger number of stored GPS positions in this study. The tag was programmed to record a GPS location every 15 minutes. GPS attempts were suspended when the unit was dry $>$ 20 minutes or when a location had been previously attained. Sixteen seals were recaptured on Sable Island during the subsequent breeding season (December 2011 to January 2012) and their tags were retrieved (median deployment period = 188 d, range = 173-198 d). A total of 623 Atlantic cod were tagged with Vemco V13 acoustic transmitters in the southern Gulf of St. Lawrence (249 between May 2009 and May 2011) and the Eastern Scotian Shelf (374 between November 2010 and November 2012) using methods outlined in Lidgard et al. [98]. During the same period, OTN in collaboration with the Atlantic Salmon Federation tagged 298 Atlantic salmon with V9 or V13 Vemco acoustic transmitters as outlined in Halfyard et al. [90]. All transmitters were programmed to transmit an acoustic signal every 60-180 s.

3.2.3 Tag Data Processing

As noted above, I determined GPS locations by analyzing archival GPS data from each tag using software from the manufacturer. To be considered accurate, locations had to be acquired from $>$ 5 satellites with a residual error $<$ 30 m [67, 68]. Received complete transmissions (detections) from tagged fish recorded by the transceiver are comprised of a date-time stamp and the identities of the transmitting and receiving acoustic tags. The summarized raw data includes all acoustic pings received by the transmitter, including those from incomplete transmissions. I distinguished acoustic pings originating from 69 kHz Vemco transmitters from background noise by the signature intervals between each ping in their acoustic codes (Table 2.1). False detections were identified by VEMCO using proprietary software, and removed from the dataset upon transceiver retrieval. To link detections of acoustic tagged fish and partial acoustic transmissions to locations interpolated at 15 min intervals from the seal tracks, clocks in the VMT and GPS tags were synchronized upon deployment and time corrected upon retrieval based on the respective clock drift calculated from GPS and VMT tags over the deployment time [61].

3.2.4 Individual and Collective Area-use

I selected one month from the track made by seal 106716 to illustrate individual area-use (Figure 3.2. Box A). Seal 106716 was an ideal bioprobe to use to relate individual space-use patterns to acoustic transmissions because it was the only instrumented seal that travelled to the southern Gulf of St. Lawrence and thus, spent little time near other acoustic-tagged seals. Seals that remained on the Scotian Shelf were used to study collective area-use over this area (Figure 3.2. Box B).

3.2.5 Estimation of Area Use and Intensity

I estimated patterns in area-use and intensity using the R-Forge package, T-LoCoH [88]. T-LoCoH is a non-parametric Lagrangian method for constructing utilization distributions from GPS locations. T-LoCoH expands the base LoCoH algorithm [86] to incorporate the date-time stamp of each location in the selection of nearest neighbours using a time-scaled distance metric (TSD) [88]. The TSD transforms the time interval between any two locations into a third axis of Euclidean space through adaptive scaling of the maximum distance the individual could have travelled during the time interval [88]. Nearest neighbours are therefore determined based on proximity in space and proximity in time. I used the k-method of sampling to construct polygons around each location and its k nearest neighbours (Figure 3.3) [88]. This allowed me to standardize the approximate temporal sampling interval of each polygon by including a fixed number of GPS locations. As GPS locations are obtained about every 15 minutes, each polygon was equivalent to approximately the value of k chosen multiplied by 15 minutes.

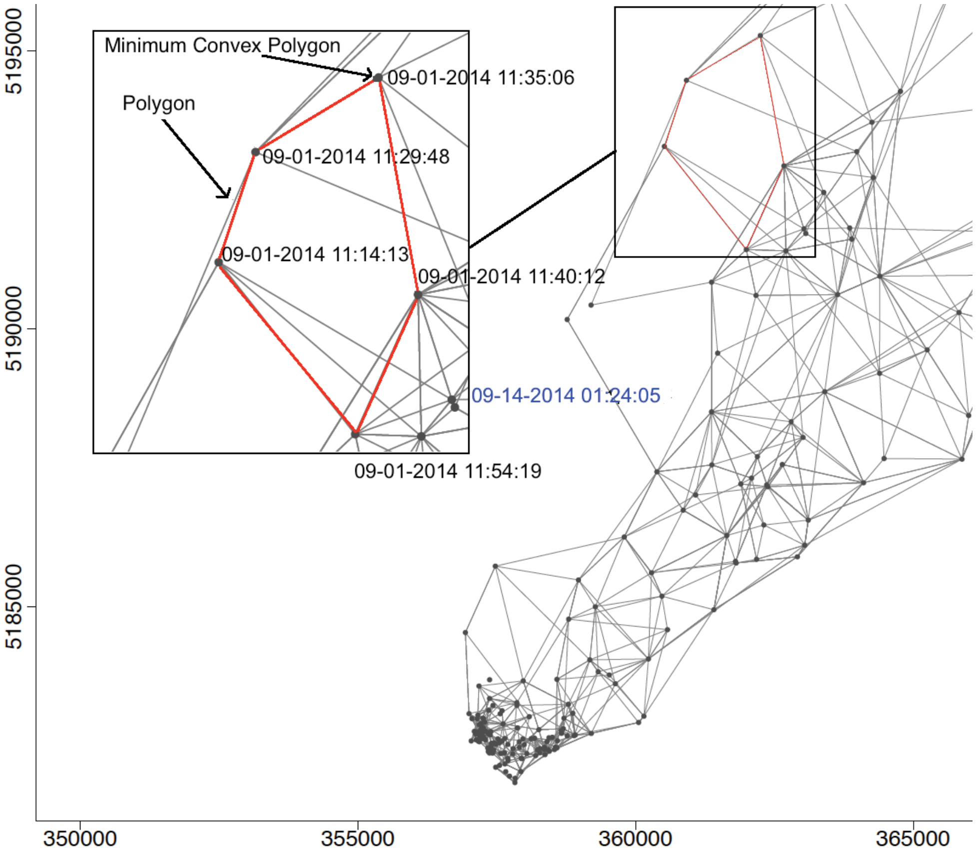

Figure 3.3. Polygon Construction. Polygons (red) are constructed to include each GPS location (points) and its nearest neighbours using a time-scaled distance metric *s* that takes into account the time and distance between GPS locations. As a result GPS locations close in space but far away in time (e.g., blue time-stamp) are not included in the same polygon.

The T-LoCoH algorithm aggregates local minimum convex polygons (MCPs) constructed around each GPS location to form polygons to include the starting location and its nearest-neighbours (Figure 3.3) [88]. Polygons are then sorted based on ascending area. After sorting, polygons are cumulatively merged by taking their union and used to construct density quantiles containing a percentage (25,50,75,95) of locations. I used density quantiles as a proxy for intensity of use. I used the 25% density quantile to represent the most intensely used areas (containing 25% of locations). I used the 95% density quantile to represents overall area-use in line with traditional home-range methods [86].

3.2.6 Individual Bioprobes

I used the graphical tools specified in Lyons et al. [88] to select the time-scaled distance metric s=0.03 that resulted in 60% of polygons being time selected, that is, surface GPS locations were included or excluded based on time (Appendix B, Figure 1). I selected a nearest-neighbour value of k=10, which allowed me to capture the seal's movement patterns over a 2.5 h period. I inspected the estimated area by quantile and compared the perimeter:area estimates (edge:area) to ensure that the value of k chosen did not result in a sudden jump in area (Appendix B, Figure 2).

3.2.7 Multiple Bioprobes

I selected a nearest-neighbour value of k=5 to closely fit the GPS locations and standardize polygon temporal range to approximately 75 minutes. I did not incorporate time into my selection of nearest neighbours as the wide geographic spread of locations at any one time produced spurious results when using the time-scaled distance metric. I was conservative in my choice of k because collective area-use estimates are more susceptible to the inclusion of unused areas than individual area-use estimates for two reasons: (1) time cannot be easily included in my estimate of nearest neighbours, and (2) GPS locations near one another are not necessarily part of the same animal's track, making it difficult to know the path trajectory and therefore what areas are used vs. not used. I examined surrounding values of k and inspected the estimated area by quantile and edge:area curves [88] to ensure that the value of k chosen did not result in a sudden jump in area (Appendix B, Figure 3).

3.2.8 Spatial and Temporal Trends in Collective Area-use

I stratified the data by month to test for temporal trends in collective area use. In addition to spatial trends in seal distribution and the distribution of intensely-used areas, I compared three metrics of area-use at the 95% and 25% density quantiles: time-at-sea, area covered (km^2), and the degree to which surface GPS locations were aggregated as an indicator of spread. I used the number of GPS locations as a proxy for time-at-sea. I used area-use relative to time-at-sea as a metric to compare the degree seals' surface locations were aggregated or dispersed at the 25% (intense-use) and 95% (overall-use) density quantiles relative to other months. The degree to which surface locations are aggregated/dispersed is a combination of the overlap/proximity of seal tracks, that is how close individual seals are to one another, and how close an individual's consecutive surface locations are from one another. If all of these components are constant (i.e., seals keep a certain distance from one another and the distance between where an individual surfaces are evenly spread) then the area of each density quantile should be proportional to the number of points they contain (e.g., 95%, 25%) (Null Bar, Figure 3.4). Under constant conditions no areas are more intensely used than others.

3.2.9 Relating Acoustic Data to Individual Area-use

Seal 106716 was used to illustrate individual movement patterns and demonstrate how to determine the true rate of partial acoustic transmissions by accounting for uneven sampling effort. Seal 106716 spent the majority of its time in the southern Gulf of St. Lawrence far from other acoustic-tagged seals thus simplifying the interpretation of the data. Incomplete acoustic transmissions originating from 69 kHz Vemco transmitters closely resemble one another, as such, it is difficult to distinguish an incomplete transmission originating from transceivers deployed on grey seals and those originating from receivers attached to other marine organisms such as cod and salmon. The absence of

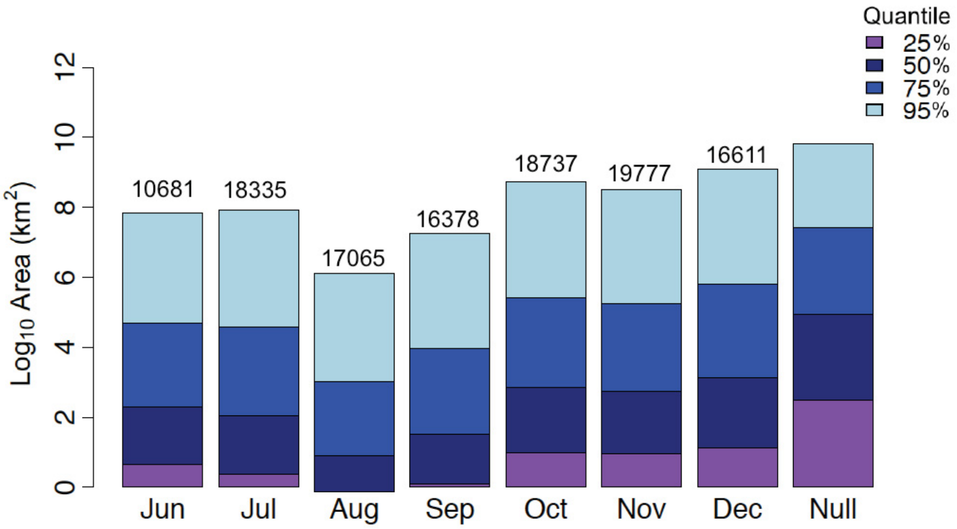

Figure 3.4. Monthly area-use estimates (km^2 on log10 scale) for each density quantile (25, 50, 75, 95). Each density quantile contains a percentage of GPS surface locations (25, 50, 75, 95) and is colour coded based on intensity of use (purple=highest, light blue=lowest). The number of GPS surface locations attained in each month is shown above each bar. The null bar shows the case where no area was more intensely covered than others.

other instrumented seals therefore allows for the study of patterns in encounter rates between seals and fish species and the spatial and temporal distribution of these species for which there is otherwise no independent location information. I focused on the month of September for three main reasons: firstly, during this month a high number of 69 kHz acoustic transmissions were received yielding a large sample size (n=40); secondly, the seal was isolated from other instrumented seals for the entire month; thirdly, the seal exhibited a range of space-use patterns I was interested in comparing to the rate of acoustic transmissions received. I chose to focus on 69 kHz transmissions, rather than detections, because only one detection of an Atlantic salmon was recorded in this month.

I used the Intersect tool in ArcMap [99] to relate the number of 69 kHz transmissions to the time and space-use metrics characterizing the polygon in which they were received and to the probability the seal was in ARS. The locations of ARS for the seal in the study were previously estimated [98]. The polygon data contained information on the polygon reference number, the density quantile the polygon belonged to, the area of the density quantile (km^2), the timespan (minutes) the polygon was occupied for, the polygon area (km^2), and the probability of being in ARS. We summarized these results for the 25%, 50%, and 75% density quantiles, which had sample sizes of 4 transmissions received or more.

3.3 Results

In 2011, grey seals collectively used an area of 11,308 km^2 (95%), and intensely-used an area of 31 km^2 (25%) during the 7-month post-moult and pre-breeding periods (June-December) (Figure 3.2).

3.3.1 Individual Area-use

In September, 40 transmissions were received, of which more than half (52.5%) were received at the most intensely-used part of the seal's movement (25% density quantile). Increasingly fewer transmissions were received at the 50%, 75%, and 95% density quantiles with 8, 4, and 2 transmissions received, respectively (Table 3.1). The probability of the seals being in area-restricted search when transmissions were received was highest for the 25% density quantile (0.74, SE: 0.05) and 50% density quantile (0.62, SE: 0.15) (Table 3.1, Figure 3.5). The probability of being in area-restricted search was markedly lower at the 75% density quantile (0.03, SE: 0.02).

Transmissions were received from a broad geographic distribution but few detections occurred outside the 75% density quantile (n=7) (Table 3.1, Figure 3.5). A large cluster of transmissions were received over the course of the month at location (x= 355000, y=5180000, Figure 3.5). The highest transmission reception per unit sampling effort (TPUE) occurred in the 25% density quantile (35.37, SE: 8.94) roughly seven times higher than at the 50% density quantile (5.26, SE: 1.83).

Table 3.1. Polygon Time and Space-use Metrics for Transmissions Received Summarized by Density Quantile. Average polygon time and space-use metrics for polygons where transmissions were received are summarized by density quantile. Density quantiles are used to represent intensity of space-use (25%= high intensity, 75%= low intensity). Polygon area and occupancy time are used to calculate the overall sampling effort (km^2/h) and estimate the transmission reception per unit sampling effort (TPUE).

Quantile	Trans.	Mean Area (km^2)	Mean Time (h)	Probability	TPUE (km^2/h)
0.25	21	0.21 ± 0.10	1.30 ± 0.16	0.74 ± 0.05	35.27 ± 8.94
0.5	8	2.51 ± 1.18	2.58 ± 0.78	0.62 ± 0.15	5.26 ± 1.83
0.75	4	6.59 ±2.87	4.17 ± 1.87	0.03 ± 0.02	2.26 ± 1.26

*N.B. A total of 7 transmissions were heard outside of the 75% density quantile.

3.3.2 Collective Area-use

The geographic spread in area-use and areas intensely-used by seals was similar from June through September. In these months, seals spent a large amount of time inshore near Sable Island, which is evident in the high density of locations that outline the island (Figure 3.6). Seals tended to make trips immediately south of Sable Island to the edges of Sable Bank (SB) and as far north as Canso Bank (CB), with some foraging east of Canso Bank in June, July, and September (Figure 3.6). In the autumn and winter months, seals spent increasingly more time at-sea and less time near Sable Island. Seals began increasingly using French (FB) and Middle Banks (MB) from September-November, with use decreasing slightly in December (Figure 3.6). From October to December, seals used areas on the lower part of Banquereau Bank (BB) and immediately above the bank. In October and November area-use occurred in large patches over Middle Bank, and over Canso Bank in October. In December, seals intensely used small areas to the north and west of Sable Island along Sable Bank, with fewer and more directed paths between Sable Island and outlying areas (Figure 3.6). These patterns suggest that seals made longer trips and returned less frequently to Sable Island later in the year.

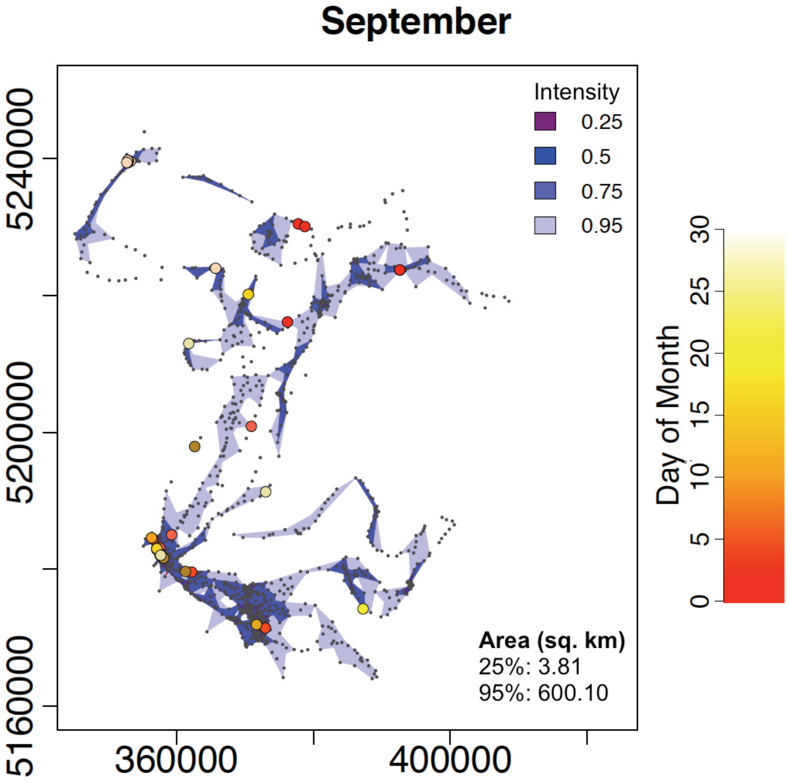

Figure 3.5. Monthly bioprobe individual sampling effort. Intensity of area-use is represented by density quantiles. Each density quantile contains a percentage of GPS surface locations (25, 50, 75, 95) and is colour coded based on intensity of use (purple=highest, light blue=lowest). Small grey points represent GPS surface locations. Larger, coloured points represent 69 kHz transmissions colour coded by day of the month. Area estimates (km^2) for the 25% and 95% density quantiles are shown in the lower right hand corner.

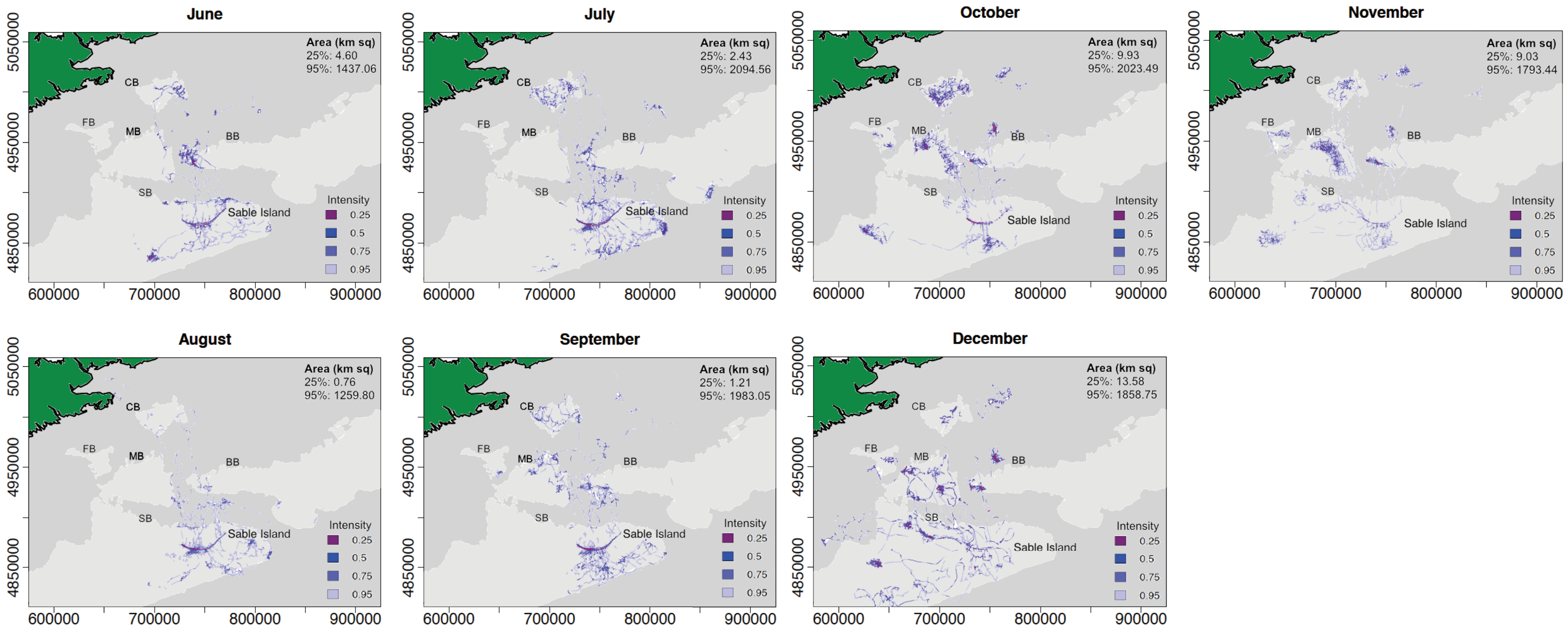

Figure 3.6. Monthly bioprobe collective area use. Collective area-use on the Scotian Shelf by 15 female adult grey seals during the 7-month post-moult pre-breeding period (mid June to December). Banks on the Scotian Shelf are outlined at the 100 m isobaths, and include French (FB), Canso (CB), Middle (MB), Banquereau (BB) and Sable Banks (SB). Intensity of area-use is represented by density quantiles containing a percentage of GPS surface locations (25, 50, 75, 95). The 25% density quantile (purple) corresponds to the highest density of GPS surface locations and represents the area (km^2) most intensely-used by seals. The 95% density quantile (light blue) corresponds to the overall collective area-used (km^2). Area estimates (km^2) for the 25% and 95% density quantiles are shown in the upper right hand corner.

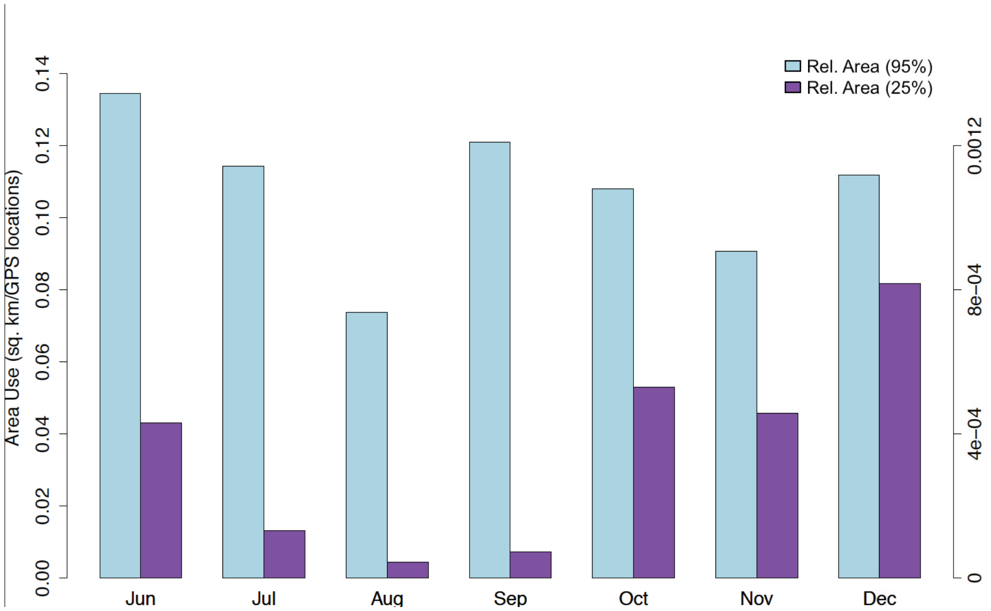

Figure 3.7. Monthly area use relative to activity. Area use (km^2) relative to activity (GPS locations) at the 95% (light blue) and 25% density quantile (purple). The 95% density quantile represents the overall area covered; the 25% density quantile represents the most intensely-used area.

Seal exhibited more variable patterns of space use during the summer months. Seals covered the smallest area (1437 km^2) and spent the least amount of time at-sea in June (10,681 GPS locations), although this may due to the fact that seals were tagged in mid-June (Figure 3.4). During this month, surface locations were highly dispersed at both the 25% and 95% density quantiles (Figure 3.7). Seals spent a large amount of time at-sea in July (18,335 GPS locations), covering the largest area of the entire study period (2094 km^2), which was 1.5 and 1.6 times larger than in the preceding and following months (Figure 3.4). While surface locations were highly dispersed at the 95% density quantile, surface locations were densely aggregated over a small area (2.4 km^2) at the 25% density quantile (Figure 3.7). In August, seals spent relatively less time at-sea (17,065 GPS locations) and more time inshore near Sable Island than in July, making only small trips from Sable Island (Figure 3.6). During this time seals covered the smallest overall area (1259 km^2) and intensely-used area (0.8 km^2), exhibiting the densest aggregation of surface locations (Figure 3.7).

The September-November period was marked by a steady increase in time at-sea, spatial extent, and dispersal. At the 25% quantile of use, spatial extent increased from September (1.2 km^2) to October and November (9.9 and 9.0 km^2, respectively), reflecting a change from high density to low density aggregation of surface locations (Figure 3.7). In December seals spent relatively less time at-sea (16,611 GPS locations) than in October and November. Surface locations were distributed over a large spatial extent at the 95% and 25% density quantiles (1858 km^2 and 13 km^2 respectively), exhibiting relatively high levels of dispersion (Figure 3.7).

3.4 Discussion

This work illustrates that T-LoCoH, previously used to estimate home range size, is a flexible tool that may be used to quantify the spatial coverage, degree of aggregation, and temporal patterns of the movement of a large marine predator. This method is particularly well suited to the study of collective area-use because it is able to exclude areas not used by the instrumented animal. At the individual-level, T-LoCoH provides a useful way to classify individual movement patterns and to identify presumed foraging locations. T-LoCoH also provides an approach for dealing with data types for which large-scale oceanographic models do not exist. I demonstrate how time and space-use metrics derived using this method may be used to determine the true rate of transmissions received independent of the time a bioprobe spends in the area.

3.4.1 Individual Area-use

Biological Processes

In September, the majority of acoustic transmissions were received when seals had a high probability of exhibiting ARS behaviour. Acoustic transmissions likely originated from Atlantic cod or Atlantic salmon because they are the only organisms I am aware that were tagged with 69 kHz tags in this region and because they were recorded in other months [98]. The highest transmission reception per unit effort occurred at the most intensely used part of their range (25% density quantile) which coincided with the highest probability of being in ARS. This indicates that the seal encountered more acoustic-tagged species when exhibiting this behaviour independent of the time it spent in the area. Transmission reception per unit effort decreased as the area-use quantiles got larger, which may reflect the fact that both foraging seals and acoustically-tagged fish co-occur in productive regions. Overlap could also indicate that seals may be preying on these species. However, while overlap is a prerequisite for consumption [100], additional information is needed to infer predation.

Without receipt of the full transmission, the species or individual to which the acoustic transmission belongs cannot be determined with full confidence, although I could narrow the identity down to two species, cod and salmon, in my study. Nevertheless, I have demonstrated how T-LoCoH may be employed as a useful technique to classify individual behaviour and may be widely applied to acoustic data of these kind to resolve the true rate of detections or transmissions received and can be used to determine the underlying distribution of non-surfacing acoustic tagged species such as salmon and cod.

Sampling Implications

In large-scale oceanographic models, uneven sampling is accounted for in the data assimilation process whereby measurements, such as those collected by bioprobes, are used to adjust the model output and reduce the model uncertainty locally. Regions poorly sampled will typically have a higher uncertainty relative to regions that are well sampled. Data collected by instrumented animals have greatly contributed to these types of large-scale predictive models [82]. Sea temperature measurements collected by elephant, crabeater, and Weddell seals in the Southern Ocean were used to improve large-scale model predictions by constraining estimates from oceanographic models [101]. While this is a useful approach for data sets for which large-scale oceanographic models exist, they are not appropriate for all data types collected by bioprobes. I present an approach that can be used to analyze other data types such as acoustic data. Time and space-use metrics derived using the geometric method, T-LoCoH, may be used to determine the true rate of transmissions received independent of the time a bioprobe spends in the area. These estimates can be used to study the distribution and local movement of acoustically-tagged fish, such as cod, and can be used to complement studies of their movement based on vessel-based trawl surveys.

3.4.2 Collective Area-use

These findings show that grey seal bioprobes use a small portion of the overall shelf area. Consistent patterns in the distribution and intensity of area-use within seasons were apparent. These patterns appear to reflect seasonal changes in grey seal energy requirements and perhaps prey distribution [7, 46].

Biological Drivers of Spatial and Temporal Trends

I found striking differences in area-use patterns between months. In the summer months of June and August and in the early fall (September) seals spent more time inshore near Sable Island than in other months (Figure 3.6). This translated to a high density of surface locations and a relatively small area covered at the most intensely-used part of the seals' range. This trend is consistent with previous studies that have found that grey seals, especially females, tend to remain inshore near haul out sites from May through August [46]. During this period, seals also made shorter foraging trips (distance and time) which suggest that adequate prey sources are readily available close to Sable Island [46]. The steady increase in time-at-sea, spatial extent, and aggregation of surface locations in the late autumn are characteristic of increased foraging efforts by grey seals as they near the January breeding period. As capital breeders, grey seals rely heavily on accumulated energy stores to successfully reproduce [43, 94]. In the months leading up to the breeding season (autumn, early winter) female grey seals traditionally experience the largest rate of mass gain [43]. Fatty acid analyses of female diets during this time reveal that sandlance (*Ammodytes dubius*) comprises a major proportion of their diet [7]. A female seal's need to acquire energy stores coincides with a time when many prey species migrate offshore to deeper water [102, 103]. During the autumn and early winter months grey seal movement occurs over a much larger distribution range reflecting changes in the distribution of their prey. The pursuit of this migration is particularly evident in December when foraging areas are markedly more distant and scattered with small concentrated areas at the end of these pursuits though which suggests that when prey are encountered offshore, seals spend little time searching for a more profitable patch. During the autumn months, seals also spent time in larger patches such as those over Middle and Canso Bank in October and November (Figure 3.6). Grey seals' preference for Middle and Canso Banks over other equally accessible areas during these months has been hypothesized to be due to an abundant, predictable supply of sandlance [7, 104, 105]. The use of Middle Bank was restricted to September to November, whereas Canso Bank was used in nearly all months, with the most intense use occurring in July and October (Figure 3.6). These patterns suggest that prey can be more or less predictably found on Canso Bank but are more profitable in certain months. I also observed a high fidelity to specific, small, isolated patches such as those on Banquereau Bank and directly east of Canso Bank in October-December. These patterns suggest that these are small profitable patches returned to by seals.

Sampling Implications of Spatial and Temporal Trends

Consistent seasonal trends emerge in collective area-use that suggest these patterns are more predictable than previously supposed [46]. In the summer and early autumn, sampling occurs over a relatively small portion of the Scotian Shelf, with small patches of heavily sampled areas north and immediately south of Sable Island and the majority of sampling concentrated inshore near Sable Island. In contrast, autumn is marked by increasingly little sampling inshore near Sable Island, with the majority of sampling occurring over a large distribution. During this time, sampling is concentrated in a few large patches providing solid coverage, and repeatable measurements at certain banks. In December, sampling is spread over a much larger expanse of the Scotian Shelf; intense sampling occurs in many small patches in deeper water at the outer limits of this range, with sampling paths connecting these areas to Sable Island.

Very few technologies are stand-alone and many research questions rely on multiple sensors, different sampling regimes, and an extensive network to study both fine and broad-scale processes [106]. Strategic use of other acoustic monitoring devices coincident with the deployment of acoustic transceivers on mobile marine animals could help to address broad-scale research questions such as the overlap between predators and prey. Consistent seasonal trends may be used to direct further sampling in areas where bioprobes do not typically go using ship-based surveys, gliders, and acoustic arrays.

3.5 Conclusions

My work illustrates that T-LoCoH, previously used to estimate home range size, is a flexible tool that may be used to identify and quantify spatial and temporal trends in individual and collective area-use/sampling by a large marine predator. This method is particularly well suited to the study of collective area-use because it is able to exclude areas not used by the instrumented animal. At the individual-level, T-LoCoH provides a useful way to classify individual movement patterns and to identify presumed foraging locations. Time and space-use metrics derived using T-LoCoH provide an alternative approach to account for biases arising from changes in sampling effort.

Chapter 4

Discussion

Effective, scalable, and sustainable technological innovations are central to advancing our ability to study the environment. The process of trialing a new technology has been described as a pipeline involving three components (1) proof of concept, (2) pilot, (3) mature [107]. Part of the trialing process involves assessing the current capabilities of a technology, what can be improved in terms of data quality, and how to effectively analyze the data gathered in the context of the research network and the questions it is applied to. A new technology may pass through many iterations of this process as the technology is added to, refined, and modified.

Early work has forecasted the potential to use acoustic transceivers to study the location and timing of intraspecific interactions such as schooling, spawning aggregations, and mate pair formation as well as interspecific interactions such as predator-prey interactions and mixed species aggregations [108]. However, despite the great potential for use of this technology, there has been little advancement beyond the proof of concept and pilot stages since a prototype of the tag was first trialed in 2009 by Holland et al. [108]. My thesis focuses on two of the challenges associated with using these data: (1) Changes in tag performance; (2) Analysis of non-traditional sampling data. I discuss my thesis findings and the future direction of acoustic transceivers in the broader context of trialing a new technology.

4.1 Current Capabilities

Acoustic transceivers paired with global positioning system (GPS) telemetry allow for the study of associations at a scale relevant to the instrumented animal's behaviour. The dual transmitter and receiver capabilities of the acoustic transceivers effectively turn marine organisms instrumented with the devices into geo-referenced mobile receiving stations with the ability to detect other tagged conspecifics and non-surfacing tagged organisms for which there is otherwise no location information. Acoustic transceivers record the time at which a transmission is received as well as the identity of the transmitting tag. Paired with fast acquisition GPS technology surface locations may be linked to where a detection event occurred. With this information one can begin to resolve the location, timing, and identity of the players in an association.

4.2 Application to Research Questions

Interactions among conspecifics and between species shape both social and ecosystem structures, and can affect population growth rates, distribution, diversity, and gene flow [1, 2]. Acoustic transceivers provide a means to study these interactions; however, one of the challenges in using acoustic transceivers is it is difficult to determine the nature and importance of interactions from detection events. Without the aid of additional technology (e.g., pop-up tags [109]; towed arrays [49, 50], or fixed acoustic arrays [21]) it is difficult to determine the behaviour of non-surfacing marine animals instrumented with the device. For surfacing marine animals, GPS telemetry opens the door to a number of methods that can be used to determine the animal's behavioural state (e.g., state-space modeling [16–20]). However, behavioural state (e.g., foraging or traveling) is still a coarse measure of behaviour and may not accurately represent the animal's behaviour at the time of detection. The number and timing of detections may be used to estimate the duration of an association; however, it is difficult to determine from this information alone the nature of an association. Lidgard et al. [98] hypothesized that continual bouts of acoustic detections of individual prey recorded by seals exhibiting area restricted search might indicate the pursuit and ingestion of prey. However, while this gives a measure of the time the seal and fish were within the vicinity of one another, this area is potentially vast (e.g., several hundred metres, [91]); as a result, it is difficult to determine the strength of the association (was the seal aware of the fish and vice versa?) and whether the seal was pursuing that tagged fish. To identify proximity, and perhaps awareness, requires a measure of the distance between two organisms.

Knowing the distance between two organisms can greatly improve our ability to study intraspecific and interspecific interactions and determine the strength of an association. Previous work has used distance between animals to study group cohesion and dynamics in birds, fishes, and mammals [110]. A similar measure could be applied to understand the nature of species interactions in the marine environment using acoustic data. In a predator-prey interaction, consecutive measures of distance between the two organisms might allow one to identify if and when the predator is closing in on the prey (i.e., the distance between predator and prey is decreasing). I discuss how distance may be calculated in section 4.4.1 Devising a Distance Measure.

4.3 Data Quality

Changes in transceiver performance in response to prevailing conditions can affect the quality of the data recorded. Understanding and accounting for how prevailing conditions affect tag performance can help prevent inaccurate biological inferences. In the second chapter of my thesis I focused on how data quality can be improved by quantifying the uncertainty of detecting a tagged organism in the vicinity of a transceiver under realistic field conditions. I found that our ability to determine whether an acoustic tagged organism is near a receiver decreases with increasing wind stress, depth of the shallowest seal, and the distance the tagged organism is away from the receiver. Access to the summarized raw data greatly improved the ability to determine whether a tagged organism is absent and not merely undetected. Determining the effect of prevailing conditions on detection probability will be aided by finer scale measurements of physical and environmental factors including depth, bathymetry, distance between organisms, wind stress, temperature, and salinity. By recording these measurements one can more accurately calculate the effect of prevailing conditions on sound propagation using established equations [111].

4.4 Future Directions

4.4.1 Devising a Distance Measure

In passive acoustic monitoring distance of a sound producing organism from a receiver has been measured using a variety of approaches. Distance has been estimated by measuring the received signal level if estimates of the source level and propagation loss as function of distance are known [112]. Distance of a source has also been determined by the time of arrival differences to 3 hydrophones which allows one to determine the location from where the source was made [112]. Model-based approaches have been used whereby the source is localized by finding the position that gives predicted arrival times that best match those measured [113]. This is achieved by creating a likelihood surface that gives the probability of an animal at any position in space using the information available. Information can include measured and modeled time of arrival, time difference of arrival, estimated uncertainties, and other *a priori* information [113]. In model-based approaches the maxima of the surface provide the estimated animal positions. Nosal has extended these methods to the tracking of multiple marine animals using source separation methods [114]. This extension would be particularly useful if expanding these data to include acoustic data from incomplete transmissions (see section 4.4.2 Analysis Techniques for a discussion of potential methods incorporating incomplete transmissions). Distance has also been measured using towed arrays by taking cross bearings which reduce the ambiguity surrounding the direction of the source [115].

The use of mobile marine animals to detect acoustic transmissions is distinct from other active and passive acoustic monitoring programmes where the receiver(s) are in a fixed location and only the tagged animal or sound producing animal is in motion. Treating instrumented mobile marine mammals as towed or ship based detectors may be one approach to resolving the distance between the transmitting tag and the receiver. To do this would require determining the instrumented animal's path and the locations along the track where transmissions from the same tagged animal were received. In order to calculate accurate arrival times clocks on the transceivers would also need to be improved (pers. comm. Dale Webber, Vemco Ltd.).

4.4.2 Analysis Techniques

Non-traditional Sampling Design

Distribution data of acoustic-tagged organisms recorded by acoustic transceivers are akin to opportunistic ship survey data because both are non-random and are determined by others needs (in this case the instrumented animal's) [116]. Opportunistic surveys violate the assumption that all points in a study area have an equal probability of being sampled [117]. Williams et al. [118] overcome this assumption by using a generalized additive modeling approach to model Antarctic Baleen whale density along the ship's track as smooth or linear functions of spatial or environmental covariates. They then used the resulting relationship to predict density throughout the study area. This same technique could be applied to data collected by instrumented animals to model the density of associations, given that the distance to the tagged animal recorded can be determined and a detection function quantified.

In the absence of a distance measure, other approaches are needed to determine the spatial and temporal distribution of associations. In Chapter 3 I demonstrated how time and space-use metrics calculated from area-use polygons can be used to calculate the transmission reception per unit sampling effort (TPUE). Estimates of TPUE may be used to determine the rate of associations in an area independent of the time the bioprobe spends in that area. Further analyses could extend these findings to relate the rate of associations to the area and environmental conditions in which they occur using a generalized additive modeling approach similar to that used by Williams et al. [118].

Using Cue Rates to Analyze Incomplete Transmission Data

In Chapter 2 I demonstrated how access to the summarized raw data greatly improved our ability to determine the presence or absence of an organism in the vicinity of the transceiver. However, a limitation of expanding the analysis of associations to include the summarized raw data is the identity of the transmitting tag cannot be resolved from incomplete transmissions. In their current form, acoustic transceivers are coded such that 8 acoustic pings must be received in order to determine the identity of the tag. It may be possible to identify more tags if future versions of the tag require fewer acoustic pings to resolve the identity of the transceiver. Likewise, an algorithm similar to those used in passive acoustic call identification may be developed that uses the time intervals between received pings to determine a candidate set of tags that the transmission may have originated from [112]. Cue rate methods [119, 120] may be one approach that could be applied to incomplete transmission data.

In passive acoustic monitoring, researchers have used cue rates (e.g., the rate of individual calls) to estimate abundance by assuming or estimating a cue rate per individual [119, 120] and localizing the source of the call [114]. Active acoustic monitoring is in many ways more simple than passive acoustic methods because the cue rate is programmed into the tag and therefore quantifiable. Likewise, the source strength is fixed instead of depending on the behaviour of the animal. However, many of these methods are contingent on the ability to localize the source which require a distance measure.

4.5 Transceivers as Part of a Wider Research Network

Very few technologies are stand alone and many research questions rely on multiple sensors, different sampling regimes, and an extensive network to study both fine and broad-scale processes. The eXpendable Bathy Thermographs (XBTs) sampling programme is one example of a global network that uses different spatial and temporal resolutions of sampling to study ocean variability on a variety of scales [106]. A similar global acoustic sampling programme could be coordinated by networks like OTN. The majority of acoustic tags deployed by OTN operate on a common frequency (69 kHz) providing the means to communicate across a range of transmitters and receivers. Strategic use of other acoustic monitoring devices coincident with the deployment of acoustic transceivers on mobile marine animals could help to address both fine-scale and broad-scale research questions such as the overlap between predators and prey. In the case of grey seals and fish, in order to interpret the extent and importance of overlap between the species requires an independent measure of tagged fish distribution to that measured by grey seals [100]. Many fish do not surface, precluding the use of satellite telemetry; however, fixed acoustic arrays and gliders are two possible means to collect additional acoustic information on the spatial movements of tagged fish independent of tagged seals. In Chapter 3, I identified consistent patterns in where seals go and at what times of year [46]; this information can be used to complement future OTN deployments of instrumented grey seals by collecting data using ship based surveys, gliders, and acoustic arrays from areas where it is known that seals do not go.

In order to scale biological inferences gained from acoustic data up to the population level requires strategic planning about the number of animals tagged. In the case of predator-prey interactions where prey are caught and released is also important. If the research aim is to understand the spatial and temporal distribution of associations between predator and prey species over a fixed area, a more representative coverage will be achieved by stratifying locations where prey are tagged and released. If the aim is to study the nature of predator prey associations (e.g., predation attempts), increasing the number of detection events is imperative. A larger number of detection events may be achieved by tagging and releasing greater numbers of prey in areas known to be heavily-used by instrumented predators.

4.6 Conclusions

In conclusion, my thesis has highlighted the importance of evaluating acoustic tag performance under changing conditions (Chapter 2), accounting for uneven sampling effort (Chapter 3), and relating acoustic transmissions to seal behaviour (Chapter 3) in an effort to improve our ability to draw accurate biological inferences about the location, timing, and frequency of species associations. However, in order for this technology to mature additional measures are required. These include, but are not limited to, gathering additional physical and environmental data to automate quality control; working with acoustic tag engineers to devise a distance measure that may be used to determine the nature of interactions; expanding analyses to include data from incomplete transmissions; and lastly, complementing bioprobe deployments within the large research network to answer fine-scale and broad-scale questions.

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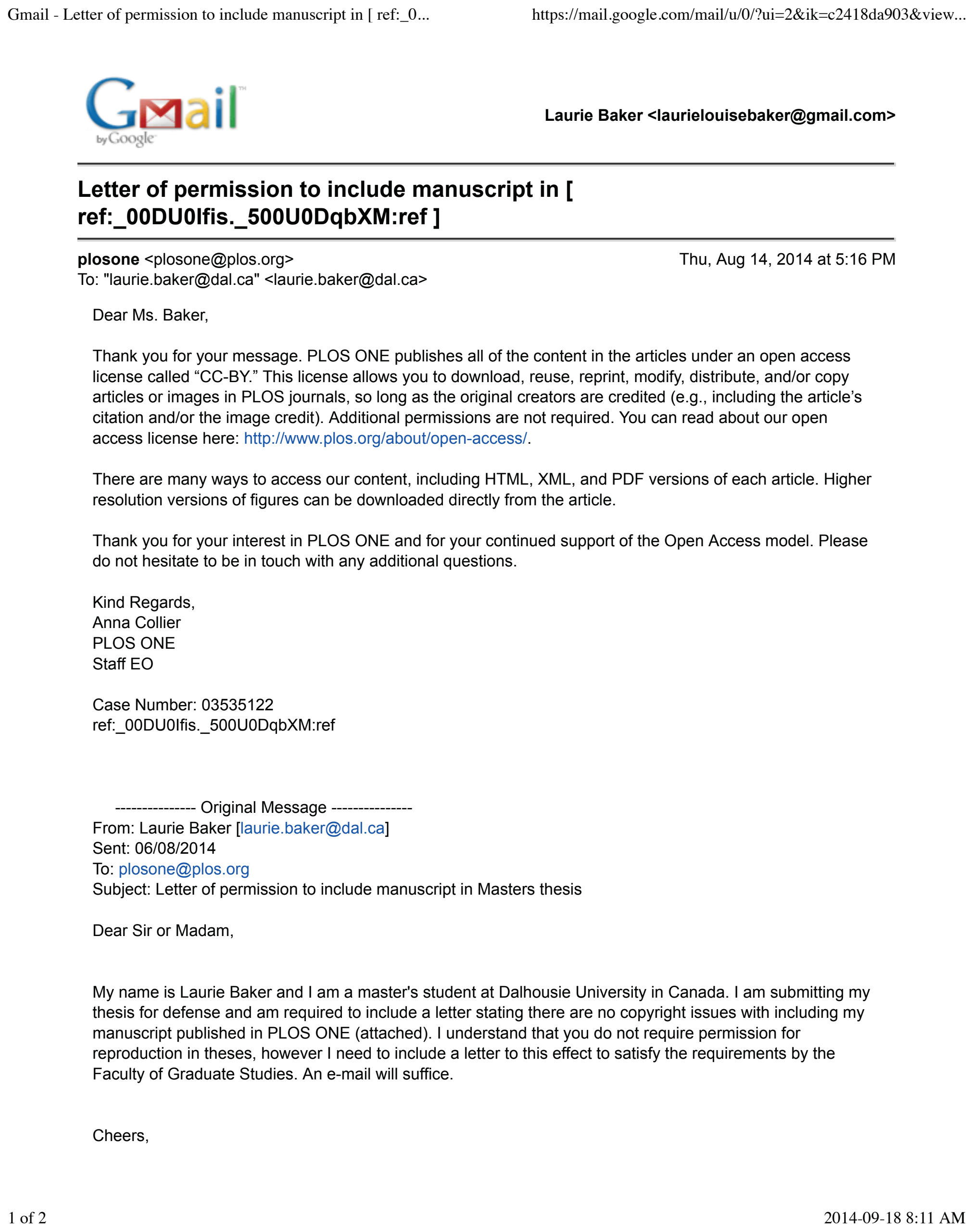

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Appendix B: Supporting Figures

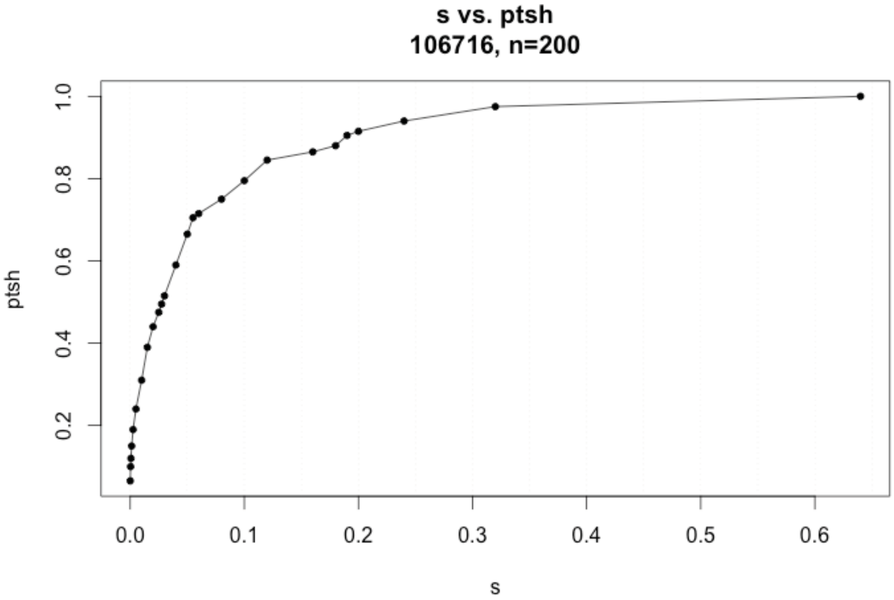

Figure 1. Time Scaled Distance Metric s vs. Percentage of Polygons Time Selected. When s is equal to 0.03 around 60% of GPS location polygons are time-selected

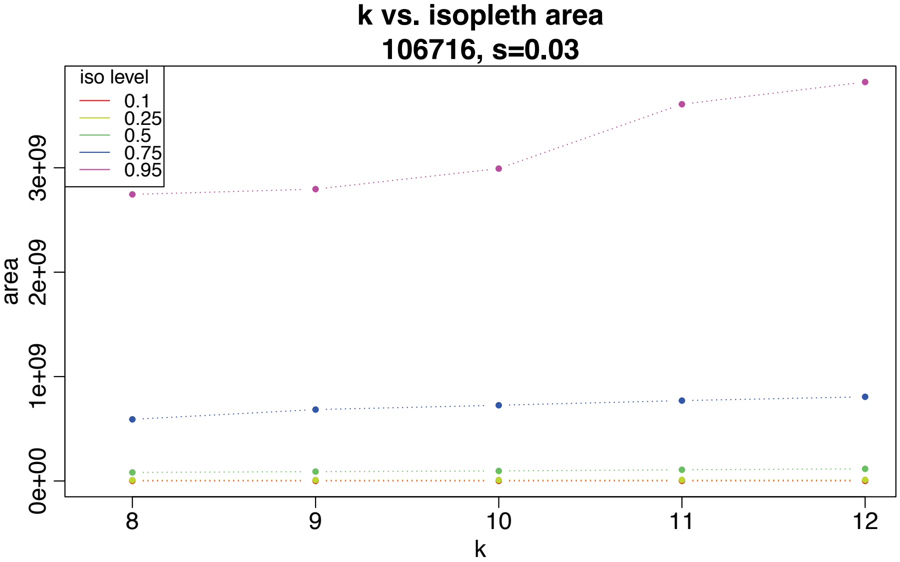

Figure 2. Individual area use estimated for each density quantile for a set value of s,0.03, and the k values surrounding k=10. A jump is observed in estimated area at k=11, with area values more or less similar from k=8 to k=10.

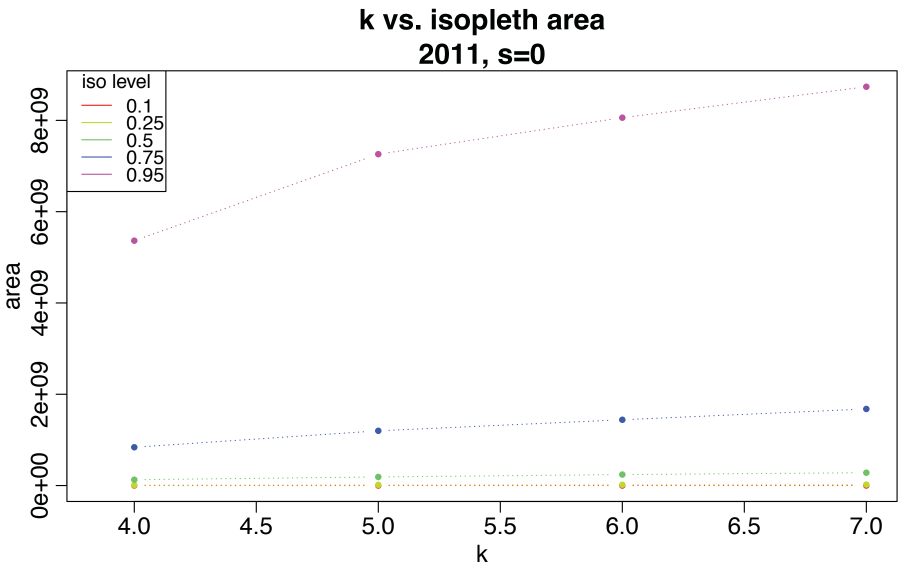

Figure 3. Collective area use estimated for each density quantile for the values of k surrounding k=5. The method did not converge for a k=3.