A Review of Species Distribution Models and a Novel Approach to Including Soundscape Information for Species at Risk

A Review by Erin LaBrecque and Lynne Hodge

Abstract

Species distribution models (SDMs) are a suite of analytical tools that relate species distribution data with information on the environmental and/or spatial characteristics of those locations. SDMs typically incorporate static (e.g., depth and distance to shore) and dynamic (e.g., temperature, salinity, and distance to ephemeral oceanographic features) environmental variables that describe the physical environment. When parameterized by data from well-designed surveys, relevant predictors, and an appropriately identified model, SDMs can characterize the natural distributions of species and subsequently provide ecological insight and predict a species distribution across a seascape. Despite the importance of the acoustic environment for marine organisms, acoustic attributes have not been incorporated into SDMs. Given recent developments in the field of marine acoustics, we can now provide richer insights into species distributions related to the acoustic environment. Our ability to use acoustic detections of marine mammals in SDMs is challenged by the uncertainties inherent in passive acoustic data, such as animals being present but silent and masking during periods of increased ambient noise in addition to variability in detection distances of animal calls due to the dynamic nature of soundscapes. Adding to the complexity, sound can influence an animal's behavior and movement patterns in various ways, such as altering communication space, alerting predators to the presence of prey, and causing avoidance of the sound source. SDMs could be improved by the incorporation of soundscape data and acoustic species detection data.

Introduction

Understanding species distributions is an ecological underpinning for conservation and management. Species distribution models (SDMs), sometimes referred to as "habitat suitability models", are a suite of analytical tools that relate species distribution data (occurrence or abundance) to the environmental and spatial characteristics of the environment, or to physiological responses to the environment. When parameterized by data from well-designed surveys, relevant predictors, and an appropriately identified model, SDMs can characterize the natural distributions of species and subsequently provide ecological insight and predict a species distribution across a seascape. The most prevalent type of marine-focused SDMs typically incorporate static (e.g., depth and distance to shore) and dynamic (e.g., temperature, salinity, and distance to ephemeral oceanographic features) environmental information that reflect the ecological requirements of the species. Over the last two decades, the use of SDMs has dramatically increased, driven by a combination of the need to forecast responses to climate change and other anthropogenic disturbances (Guisan and Thuiller 2005), a greater access to data (Hochachka et al. 2012), and the availability of new estimation methods to predict distributions such as occupancy estimation (MacKenzie et al. 2002, 2003). Given recent developments in the field of marine acoustics, we can now provide richer insights into species distributions related to the acoustic environment.

In this review, we first give a brief introduction to the North Atlantic right whale and its conservation issues. Then we define and provide an overview of soundscapes, followed by a review of different sound and noise measurements. Next, we review the different types of species distribution models (SDMs) that could incorporate soundscape parameters and presence-only passive acoustic monitoring data, discussing the feasibility and limitations of using soundscape metrics in such models. Our goal is to suggest models and metrics that can use existing passive acoustic monitoring data to understand the relationship between soundscapes and the presence of vocalizing North Atlantic right whales and begin

incorporating all aspects of the species' environment. Finally, we present new modeling techniques that utilize passive acoustic detections to determine acoustic density and species density. The acoustic environment is an important feature of habitat and should be included in modeling efforts.

North Atlantic Right Whales

The North Atlantic right whale (*Eubalaena glacialis*) is one of three species of right whales (Committee on Taxonomy 2019) and one of the most endangered large whale species on the planet. Along with the North Pacific right whale (*Eubalaena japonica*) and Southern right whale (*Eubalaena australis*), all three right whale species were severely depleted by historical and commercial whaling. Over the last few decades, several of the breeding populations of Southern right whales (*Eubalaena australis*) have steadily increased in number and are now an IUCN Red List Least Concern species (Zerbini and Cooke 2017), although the Chili-Peru subpopulation is listed as "Critically Endangered" (Cooke 2017). The North Pacific right whale has two populations, a western population with uncertain numbers, and the eastern population with around 30 individuals (Wade et al. 2011). The North Atlantic right whale also has two populations. The western population is thought to be extinct or extirpated. Approximately 450 individuals (range 444-471) remained in the eastern population in 2015 (Pace III et al. 2017), and the most recently reviewed Stock Assessment Report estimates the population at 428 individuals (95% credible intervals 406-447) (Hayes et al. 2020).

North Atlantic right whales (hereafter, right whales) are an IUCN Red List Critically Endangered species (Cooke 2020). They are a migratory transboundary species that are protected in the US under the Endangered Species Act (since 1970) and the Marine Mammal Protection Act (since 1973), and in Canada under the Species at Risk and Fisheries Act (since 2003). Understanding the true size and distribution of the right whale population before 1750 is difficult given the inherent limitations of historical records, but research into whaling records suggests a minimum of 5,500 right whales, possibly

twice that number, were killed in the western North Atlantic between 1634 and 1950 (Kraus and Rolland 2007). After an international agreement to ban the hunting of right whales in 1935 was signed, the population in the western Atlantic slowly started to recover, but now the North Atlantic right whale faces new anthropogenic threats in the form of climate change (Record et al. 2019), ship strikes (Knowlton and Kraus 2001, Mullen et al. 2013), and entanglement in fixed and ghost fishing gear (Knowlton et al. 2012, Moore 2019). From 2017 through 2019, 30 right whale mortalities were detected while only 12 calves were born over the same time period (Pettis et al. 2020). Due to the small population size and high mortality rate of right whales, accurately describing their distribution and understanding the processes that drive their distribution, including the acoustic environment, has important conservation and management implications.

Overview of soundscapes

The term 'soundscape' refers to the acoustic environment, or the composition/collection of sounds in a particular location and time (Pieretti et al. 2011, Pijanowski et al. 2011). Soundscapes are made up of anthropogenic (ship noise, sonar, seismic exploration, etc.), geophysical (wind, rain, waves, ice, earthquakes, etc.), and biological (animal-made) sounds, also referred to as anthrophony, geophony, and biophony, respectively. Soundscapes vary from one place to another depending on the local and regional environments, the assemblage of sources, and the factors affecting sound propagation, including temperature, depth, and bathymetry. Thus, each habitat or local environment has a unique acoustic signature. Soundscapes are dynamic, varying over temporal and spatial scales and across frequencies (Miksis-Olds et al. 2018). The intensity and timing of sounds by each contributor can also vary, providing unique daily and seasonal soundscape patterns at different locations depending upon the makeup of sound producers. In the ocean, sound travels great distances and thus distant sounds, such as from far off shipping, can contribute significantly to the soundscape (Miksis-Olds et al. 2018). For

low frequencies (<500 Hz), ambient noise can include sounds originating from distances as far away as ocean basins, while for medium frequencies (500 Hz – 25 kHz), attenuation prevents sounds from propagating as far, and thus ambient noise in these frequencies is made up of more local or regional sounds (Hildebrand 2009). Common low-frequency (<1 kHz) underwater acoustic contributions come from ships, airguns, wind, and whales (Hildebrand 2009, Wiggins et al. 2016), as well as from fish and snapping shrimp (for shallower waters). Sound is the primary sensory modality for marine organisms as the other senses are limited. Many of these organisms use sound for sensing and orienting in their environment, communicating, and foraging, and thus they can be particularly sensitive to changes in ambient noise levels.

Some animals, such as some fish (Simpson et al. 2004, 2008, Montgomery et al. 2006), birds (Ward and Schlossberg 2004), amphibians (Goutte et al. 2013), and invertebrates (Montgomery et al. 2006, Stanley et al. 2012, Lillis et al. 2013, 2016), orient and find appropriate habitats to settle in by using cues from soundscapes. Coral reef soundscapes have been found to play a critical role in the recruitment of settlement-stage larval fish, corals, and invertebrates such as crustaceans (Simpson et al. 2004, Tolimieri et al. 2004, Montgomery et al. 2006, Radford et al. 2007, Vermeij et al. 2010, Lillis et al. 2016). Soundscapes can also affect the behavior of an animal, including its acoustic behavior, which can in turn alter the soundscape (Miksis-Olds et al. 2018). Because sounds are important habitat features for many marine organisms, acoustics should be included in habitat modeling efforts. The only known effort to incorporate soundscape information into habitat models was Goutte et al. (2013), who looked at characterizing frog habitat using traditional habitat variables (temperature, depth, etc.) and ambient sound pressure level (SPL). These authors found that ambient SPL improved occupancy predictions of calling site selection in acoustically active frog species (Goutte et al. 2013).

Factors affecting acoustic detections

Vocal rates and occurrence have been found to vary with factors such as behavioral state (Jones and Sayigh 2002, Cook et al. 2004, Nowacek 2005, dos Santos et al. 2005, Quick and Janik 2008, Hernandez et al. 2010), group size (Matthews et al. 2001, Jones and Sayigh 2002, Quick and Janik 2008, Hernandez et al. 2010), group composition (i.e., groups with calves as well as sex and age differences, Darling and Bérubé 2001, Croll et al. 2002, Oleson et al. 2007, Hawkins and Gartside 2010), time of year (Jacobs et al. 1993), and time of day (Goold 2000, Gordon et al. 2000, Matthews et al. 2001, Carlström 2005, Stafford et al. 2005, Wiggins et al. 2005, Mellinger et al. 2007, Baumgartner and Fratantoni 2008, Mussoline et al. 2012). In order to interpret temporal and spatial patterns of acoustic detections from autonomous passive acoustic recorders, not only is the classification of sounds to the species level needed but also an understanding of how vocal rates are correlated with each of these factors. Therefore, behavioral studies showing vocal rates during various behavioral states (vocal activity budgets) as well as daily behavioral activity budgets are needed for the interpretation of acoustic data that do not have concurrent visual data.

In addition to these factors that affect vocal rates and occurrence, it is also important to consider factors that might affect acoustic detections on the recording instrument itself. These factors include propagation conditions, source level of the calls, ambient noise levels, and receiver (in this case, instrument) sensitivity (Richardson et al. 1995). Thus, besides the recording equipment sensitivity, variations in detection distances are due to both the dynamic oceanographic conditions and ambient noise fluctuations.

Propagation efficiency is affected by depth, seafloor bottom type, bottom slope, the frequency range of the call, temperature (and thus season), salinity, and pressure. Deep water and shallow water propagation models differ, with spherical spreading as the main theoretical mode of sound transmission

for deep water and cylindrical spreading for shallow water (Richardson et al. 1995). The depths of the vocalizing animals and the receiver are important to consider as well, as they affect sound transmission and detection. Calls produced in the deep sound channel (sound fixing and ranging, or SOFAR, channel), for example, will propagate great distances because nearly-horizontal rays of sound become trapped within that channel. Thus, propagation losses due to reflections off of the surface and bottom can be minimized (Richardson et al. 1995). Sounds produced at the surface may become trapped in a surface duct that can cause recording instruments deployed at the bottom to be in shadow zones (and therefore those calls would not be detected). The Lloyd mirror effect, which involves the formation of interference patterns, also can come into play when calls are produced very close to the surface (Richardson et al. 1995).

Although the geoacoustic properties of the sediment are usually considered to be stable, different seafloor bottom types (sediment properties) affect sound propagation differently. The slope of the seafloor bottom, especially in shallow water, also affects sound propagation (Richardson et al. 1995). If sound encounters a downward sloping bottom, it can spread out into the increased volume. The deeper water also allows for fewer surface and bottom reflections, though. Thus, the net effect of such slopes is generally lower transmission loss. For sound encountering an upward sloping bottom, the reverse is true and thus the net effect is generally greater attenuation.

Lastly, propagation is affected by temperature, salinity, and pressure. Decreasing the water's temperature, salinity, or pressure results in a decrease in the speed of sound. Consequently, sound rays will refract towards these areas of lower sound speed (Richardson et al. 1995). These column properties (temperature, salinity, and pressure) that affect transmission loss can change quickly – even on a daily time scale – and so are considered dynamic.

Ambient noise also affects the ability of sounds to be detected. Examples of ambient noise, which is background noise that includes all noise other than the signals of interest, are noise from waves, wind, rain, animals, shipping, industrial activities, and sonar. With increasing ambient noise, signal-to-noise ratios (SNRs) decrease, which decreases the detection distance of signals and may even result in signals being masked (thereby being undetectable). Gordon et al. (2000) found that acoustic detection rates decreased with increasing sea state, wind speed, and background noise levels. Matthews et al. (2001) mention that high sea states and wind can create near-surface air bubbles which can increase the attenuation of calls produced at the surface. Thus, it is important to take all of these factors into consideration when trying to interpret and understand data from passive acoustic recorders. Finally, it is also important to realize that different ambient noise levels might also affect vocal production of different species, with some animals adapting their calls (by either intensity and/or frequency shifts/compensation) in louder environments, some choosing to be silent but remain present, and yet others choosing to leave. When incorporating acoustic detection data into models, false negatives can occur when animals are present but not vocal, for whatever reason, or when their vocalizations are masked due to high levels of anthropogenic noise.

For North Atlantic right whales, maximum detection distances can vary greatly depending on the factors mentioned above and thus are not only site specific but also temporally specific, with daily and seasonal differences in ambient noise and overall soundscape levels. Xu (2018) found that estimates for detection ranges for North Atlantic right whales at one location in St. Anns Bank at approximately 375 m depth varied from approximately 3-5 km in November to between 12.5-19 km in August, with directional/aspect differences due to bathymetry. Call type is another factor that can affect detection distances as different types of calls have different source levels. In addition, as mentioned above, it is important to note that some animals, such as birds (Cynx et al. 1998, Brumm 2004), monkeys (Sinnott et al. 1975, Halfwerk et al. 2016), bats (Hage et al. 2013, Luo et al. 2016), túngara frogs (Halfwerk et al.

2016), and whales (humpback whales: Dunlop et al. 2014; North Atlantic right whales: Parks et al. 2011), have been found to increase the amplitude of their calls with increased ambient noise levels, thereby demonstrating the Lombard effect. The estimates for St. Anns Bank were generated using an average source level for up-calls of 150 dB rms re 1μPa at 1m (based on Parks and Tyack 2005b), ambient noise measured from acoustic recordings, the location's bathymetry, and an ocean circulation model that estimated sound propagation. Detection distance in models is influenced by what is input for source level. Detection ranges for right whale up-calls have previously been reported to vary from 8-16 km (Laurinolli et al. 2003, Clark et al. 2009), but these authors may have used different source levels. For example, Mussoline et al. (2012) used an average source level of 165 ± 3.5 dB rms re μPa based on a study in the Stellwagen Bank National Marine Sanctuary. When including acoustic detections into models for habitat distributions, providing realistic, albeit estimated, detection distances are important. These detection distances should be estimated on not only a monthly or seasonal scale (as water column properties change considerably throughout the year), but also on a daily scale, as daytime and nighttime column properties also can be quite different (Xu 2018).

Types of sound and noise measurements

Typical soundscape measurements include metrics such as (broadband) SPLs, power spectral density (PSD), percentile PSD levels, octave analysis, and sound level exceedance percentiles. SPL, typically measured on a logarithmic scale due to the large range of pressures that mammals can perceive, is a ratio of the pressure of a sound to a reference pressure and uses a single number to describe the sound level over a specified range of frequencies (Merchant et al. 2015). The reference pressure for underwater sounds is 1 μPa. Measurements of underwater acoustic pressure are considered to be in RMS unless indicated (Hildebrand 2009). The RMS level, also called the arithmetic mean, is the most common averaging method used for ambient noise and calculates the mean before converting to

decibels. The PSD describes the energy found in linearly-spaced frequency bands, often 1-Hz bands, showing how the power is distributed over a range of frequencies. The Welch method (Welch 1967) is often used to make computing PSDs more efficient (Merchant et al. 2015). In octave band analysis, which is typically performed with 1/3-octave band levels (TOLs), frequency is typically plotted on a logarithmic scale such that the octaves, which widen exponentially as frequency increases, are evenly spaced and the power in these octave bands is measured (Merchant et al. 2015). Because TOLs are considered the most relevant for how mammals hear, they may be beneficial for characterizing habitat (Merchant et al. 2015) and are sometimes used in studies examining how noise affects marine mammals (Todd et al. 2015). Sound level exceedance percentiles, expressed as L_N, describe the sound level exceeded for N% of a specified measurement time (Miksis-Olds et al. 2018). Percentile levels are often used when calculating the noise in the environment. Plotting various percentile levels across the frequency spectrum can show a habitat's range of sound levels and indicate approximately how the sound levels are distributed, perhaps also indicating the amount of acoustic masking that might be occurring in the habitat for different species (Merchant et al. 2015). Dekeling et al. (2014) recommended that when examining soundscape measurements, daily statistics should be calculated in 1-minute windows and that the arithmetic mean and percentile PSD levels should be calculated in all 1/3 octave bands less than 1 kHz for each 24 h period.

Recently, ecoacoustic metrics, such as the acoustic complexity index (ACI), the acoustic diversity index (ADI), the bioacoustic index (BI), acoustic entropy (H), and the normalized difference soundscape index (NDSI), have been used as proxies for indicating ecosystem biodiversity, species richness, species composition, and biological acoustic activity (Sueur et al. 2008, Towsey et al. 2014, Pieretti et al. 2017), although several have been shown to be sensitive to anthropogenic noise (Depraetere et al. 2012, McWilliam and Hawkins 2013, Parks et al. 2014, Gasc et al. 2015, Desjonquères et al. 2015, Fairbrass et al. 2017). These acoustic indices, which are statistical analyses of the sound levels or acoustic energy of

the soundscape that can be used to estimate the diversity of sounds, were originally developed for

terrestrial habitats, mainly to look at bird composition and the number of vocal species in an area

(Pieretti et al. 2011), and have been used to compare different habitats (characterizing variability and

differences) with mixed results (Towsey et al. 2014, Lellouch et al. 2014). Even more recently, the

application of these acoustic indices (especially ACI) for freshwater (Desjonquères et al. 2015, Bolgan et

al. 2017, Linke et al. 2020) and marine environments (McWilliam and Hawkins 2013, Parks et al. 2014,

Staaterman et al. 2014, Kaplan et al. 2015, Butler et al. 2016, Harris et al. 2016, Buscaino et al. 2016,

Bertucci et al. 2016, Pieretti et al. 2017, Buxton et al. 2018, McKenna et al. 2018) has been explored with

mixed success (see Table 1). Because they were originally developed for terrestrial environments, this

adaptation to aquatic environments needs further research to determine their robustness and how well

they correspond to various ecological metrics, especially in noisy aquatic environments (and especially

when noise occurs in the same frequency bands as various species' vocalizations). In addition to

including more standard soundscape measurements in modeling efforts described in more detail below,

including ecoacoustic indices, which granted do not focus on single species but instead communities,

could potentially help identify areas of ecological importance and thus should be considered, especially

since they can be calculated quickly (such as with the R package 'seewave' (SUEUR et al. 2008)) and thus

inexpensively. Incorporating information that includes what marine animals' perceive in their

environment (e.g., levels of ambient noise, anthropogenic sources, such as shipping or seismic activity,

and intensity of those sounds, conspecific and nonconspecific vocalizations, etc.) might help with

predicting what habitats are preferred (i.e., using sound to predict animal distribution) if in fact the focal

species uses sound to choose habitats, as some species have been found to do (see "Overview of

soundscapes"). As Risch and Parks (2017) suggested, these metrics can also help determine and

document changes in a habitat's acoustic signature, the biological component of which might change as

a result of changes in biodiversity possibly caused by increased anthropogenic noise levels, for example.

Table 1. Studies that applied ecoacoustic metrics in aquatic environments, with information about study area, ecoacoustic metric(s) used, and findings.

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
McWilliam and Hawkins (2013)	Protected inlet in Ireland	ACI, ADI	Found ACI (and ADI, but not as strongly) to be directly correlated to the number of snapping shrimp snaps; authors cautioned that high snap levels could mask other biological sounds and ecoacoustic metrics might not provide such detailed information; found ACI and ADI to be sensitive to both anthrophony and geophony
Parks et al. (2014)	South Atlantic, Indian, and North Pacific ocean basins	Acoustic biodiversity index (acoustic entropy index (H))	Found H to be sensitive to anthrophony; after modifying H by subtracting out seismic exploration signals from background noise (thereby creating a noise compensated entropy index, H_N), they found this new index to be more representative of biological patterns
Staaterman et al. (2014)	Coral reefs in the Florida Keys (USA)	ACI	Found ACI values strongly agreed with the "visual patterns of the soundscapes"; stated that more work

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
			needs to be done for ecological metrics to be linked to acoustic measures
Desjonquères et al. (2015)	3 temperate ponds in Paris, France	ACI, temporal entropy (Ht), spectral entropy (Hf), acoustic richness (AR), median envelope energy (M), number of major peaks (NP) of mean frequency spectrum	Found ACI, M, and NP to be positively correlated with abundance and richness but also SNR; found Ht and Hf to be negatively correlated with abundance, richness, and SNR; found AR to be negatively correlated with SNR and not correlated with abundance or richness - HOWEVER, if background noise was used as a control variable, then AR was found to be positively correlated with both abundance and richness and thus "a good candidate for revealing acoustic diversities within ponds"; found all metrics were sensitive to background noise
Kaplan et al. (2015)	3 tropical reefs in U.S. Virgin Islands	ACI, acoustic entropy index (H)	Neither ACI nor acoustic entropy index provided results that agreed with other analyses; snapping shrimp

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
			affected acoustic entropy values
Bertucci et al. (2016)	Coral reefs of Moorea Island, South Pacific	ACI	Found a positive correlation between ACI and fish species diversity
Busciano et al. (2016)	Mediterranean Sea – shallow-water marine protected area	ACI	Found ACI corresponded to fish vocalization counts and to the SPLs for the octave bands in which fish sounds occur; found ACI to be correlated with snapping shrimp sounds in the octave bands occupied by such sounds; did not find ACI to be correlated with anthrophony or geophony
Butler et al. (2016)	3 near-shore tropical habitats in the Florida Keys (USA)	ACI	Found ACI to be correlated with snapping shrimp snaps, which do not add to the soundscape 'complexity' (in terms of variability in the frequency and amplitude of sounds as they are broadband sounds encompassing many frequencies); authors stated that in places, such as reefs, where fish calls are prominent, the ACI could be a good indicator of 'complexity' since fish calls have

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
			smaller frequency ranges
Harris et al. (2016)	Temperate reefs of NE New Zealand	ACI, acoustic richness (AR), acoustic entropy index (H)	Found ACI and H to be robust indices with strong potentials for analyses of temperate reefs; ACI was a good indicator of evenness; H was positively correlated with number of species; AR failed to meet authors' requirements for being a successful ecoacoustic metric
Bolgan et al. (2017)	Windermere Lake, UK	ACI	Found ACI was influenced/positively correlated by fish spawning activities (mainly noise from gravel displacement but also fish air passage sounds) and insect sounds; also found lower ACI values when anthropogenic noise increased (peaks in SPL) which was expected due to the more constant intensity values of the anthrophony
Pieretti et al. (2017)	Mediterranean Sea – rocky bottom	ACI	For frequencies > 620 Hz, found ACI was positively correlated to diurnal patterns of snapping shrimp snaps; for frequencies < 620 Hz, ACI was associated

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
			with fish choruses at night but failed to find the peak in fish vocal activity (off by 2 hrs), instead peaking with an increase in the intensity of snapping shrimp activity during that time
Buxton et al. (2018)	8 marine sites in Everglades National Park (USA) (and 43 terrestrial sites)	ACI, temporal entropy (Ht), spectral entropy (Hf), total entropy (H), normalized difference soundscape index (NDSI), ADI, acoustic evenness, acoustic richness (AR), roughness, and other various acoustic metrics	Found that acoustic indices did not perform as well in marine (versus terrestrial) environments in terms of predicting bioacoustic activity; authors noted that the frequencies of biological sounds and anthropogenic noise often overlap in marine environments unlike in terrestrial environments; these authors included combinations of indices in modeling efforts and found that combinations of indices, versus a single index, were more effective for making predictions of bioacoustic activity (looking at diversity of animal sounds)
McKenna et al. (2018)	Gulf of Maine	ACI	Found that incorporating ACI was helpful in predicting

Study	Study area	Ecoacoustic metric(s) used	Findings in relation to ecoacoustic metrics
			habitats at the community level; models performed better when using broad acoustic indices ("community" metrics) versus species-specific ones
Linke et al. (2020)	River in northern Australia	ACI, acoustic entropy index (H), median of the amplitude envelope (M)	Found ACI focused on specific frequency bands ($ACI_{500-1000\ Hz}$) to be correlated to the dawn fish chorus; found $ACI_{500-1000\ Hz}$ and H to be correlated with stream flow noise; found ACI and M to be sensitive to geophony (stream flow noise) and associated also with insect choruses – with authors suggesting these sounds overrode other acoustic events; none of the measured indices "picked up the high acoustic richness between 6 and 10 a.m."

Species distribution models

There are three types of model approaches to estimate a species distribution: a mechanistic approach, a process-oriented approach, and a correlative approach. A mechanistic SDM is a coupled, environmental-life history model that incorporates information on a species' known physiological tolerances to environmental conditions (Kearney and Porter 2009, Melle et al. 2014). These models are less prevalent because physiological responses of a species to environmental factors are often unknown. In a recent literature review of marine SDMs, Melo-Merino et al. (2020) found only 13 articles that developed mechanistic SDMs out of the 328 articles selected for their review. None of the 13 articles focused on marine mammals. Process-oriented SDMs consider demographic processes that influence a species range, such as life and death rates and dispersal. This model type is considered a "hybrid" model (Peterson et al. 2015) when it is combined with correlative approaches. For example, Young et al. (2020) combined habitat, oceanographic, and biological data within a dispersal model (Treml et al. 2015) to understand the patterns of Australia's blacklip abalone population connectivity. Correlative SDMs are the most widely used form of the species distribution model and assumes that the current species distribution is a good indicator of its ecological requirements. Correlative SDMs relate presence-only or presence-absence data with environmental predictors and fit a relationship between the environmental predictors and presence-only or presence-absence data (Redfern et al. 2006). When SDMs are used to predict a species distribution in geographic space, they are referred to as "predictive habitat distribution models" or "spatially explicit habitat suitability models" (Franklin 2010). Predictive SDMs have recently been developed for near real-time monitoring of highly migratory species (Hazen et al. 2017, Abrahms et al. 2019, Blondin et al. 2020) and used to evaluate and mitigate ship-strike risk (Redfern et al. 2019, 2020). Most correlative SDMs are developed with presence-absence data, but due to the presence-only nature of passive acoustic monitoring, we restrict the scope of our correlative SDM model suggestions to those that focus on presence-only data and then provide suggestions on variable selections.

Envelope models

One of the first approaches developed to quantitatively describe environmental conditions associated with species distributions was the envelope model. Envelope models are based on simple rules and assumptions, and use presence-only data without the need to create background data or pseudo-absence data (Guisan et al. 2017). These models use the observed range of environmental conditions as the definition of habitat with rules defined by the minimum and maximum values or quantiles (e.g., 5th and 95th quantiles) of environmental variables. Environmental conditions above or below the quantiles (or minimum and maximum values) are considered locations outside of the envelope and therefore not suitable habitat (see Figure 1). This approach assumes that all environmental variables considered are relevant and that locations must be within the envelope of all variables.
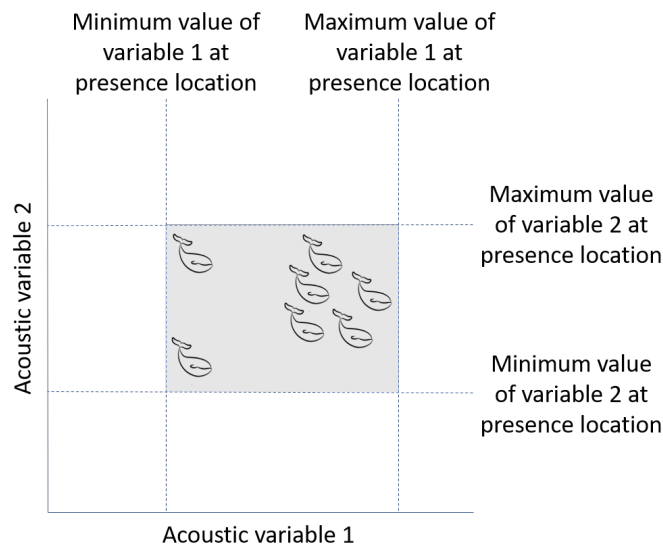

Figure 1: Acoustic envelope model using the minimum and maximum values of two acoustic environmental metrics to define the acoustic habitat for the species.

Envelope models are simple and can provide an initial description of the physical and acoustic environment, but these models are spatially and temporally coarse. We found one peer-reviewed article that developed a rule-based envelope model for marine mammals (Kaschner et al. 2006). Kaschner et al. (2006) used bottom depth, mean annual sea surface temperature, mean annual distance to ice edge, and distance to land to define niche categories (habitat usage) for 115 species of marine mammals world-wide. When projected into geographic space, the niche categories broadly predict habitat ranges.

Envelope models are also intolerant of outliers and can easily inflate predicted habitat areas (Guisan et al. 2013), so while they are good for exploratory analyses, we do not suggest using an envelope model for spatial or temporal predictions.

Maximum Entropy Models

A more robust model that can be developed using acoustic detections and soundscape metrics is a maximum entropy model. Unlike most correlative SDMs that rely on presence and absence information, a maximum entropy model, or MaxEnt (Phillips et al. 2006, Phillips and Dudík 2008), was designed to utilize presence-only information. Initially developed to take advantage of the plethora of specimen records in museum databases (Elith et al. 2011), MaxEnt models are now widely applied in terrestrial systems (Merow et al. 2013) and are gaining a foothold in marine studies in general and marine mammal studies in particular (Smith et al. 2012, Bombosch et al. 2014, Tobeña et al. 2016, Derville et al. 2018, Passadore et al. 2018, Kent et al. 2020). MaxEnt models have shown good predictive ability with small sample sizes (Hernandez et al. 2006, Wisz et al. 2008) and can account for potential sampling biases inherent in sighting data (Phillips et al. 2006). With the high cost of ship-based and aerial systematic surveys that are needed to obtain presence-absence data for regression habitat modeling techniques, it is not surprising that marine mammal ecologists are increasingly exploring ways to utilize less expensive data collected with presence-only methods. Although MaxEnt was initially presented as a

machine learning technique, Elith et al. (2011) present MaxEnt in statistical terms that are likely more familiar to ecologists.

Unlike an envelope model, MaxEnt models require environmental information at background locations. In general, a MaxEnt method models a species distribution by estimating the density of environmental covariates conditional on species presence (Franklin 2010). The maximum entropy theory states that a "probability distribution with maximum entropy (i.e., a distribution that is the most spread-out or closest to a uniform distribution) is the best approximation for an unknown distribution because it agrees with everything that is known but avoids assuming anything that is not known" (Elith et al. 2011). In maximum entropy, multivariate distribution of suitable habitat conditions (environmental and acoustic information) is constrained by the expected values of the environmental and acoustic data estimated from the set of species presence observations (Figure 2). In the case of a species distribution model, the unconstrained distribution comes from the background points as the environmental factors in the study area. The constraint is the distribution of the expected values from the observations/detections of species presence (Franklin 2010, Elith et al. 2011). Constraints are expressed in terms of simple functions (known as features in the machine learning literature) that are an expanded set of transformations of the original covariates, and the output of a MaxEnt model is a logistic format that estimates the probability of presence (Phillips and Dudík 2008).
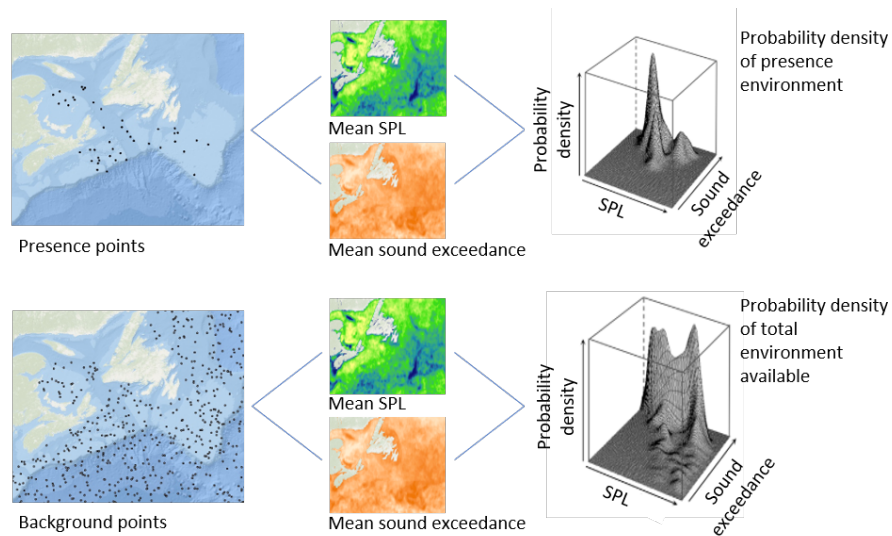
Figure 2: Schematic of a MaxEnt model. Figure adapted from Elith et al (2011).

One important caveat of a MaxEnt model is that it assumes that all habitat variables, both acoustic and environmental, represent all the environmental conditions and are available from the entire study area. Acoustic variables might have to be interpolated between recorders, or more recorders would need to be deployed to fill in the gaps.

Acoustic Distance

Our last suggestion involves calculating acoustic detection distances to compile summary statistics on the detections and acoustic metrics. We call this sampling the acoustic distance. Xu (2018) calculated the estimated detection range of North Atlantic right whales in different months from an acoustic recorder on St. Anns Bank. These calculations were based on right whale up-call detection distances and varied greatly depending on the month (Figure 3). The detection distance estimates for St. Anns Bank were generated using an average source level for up-calls based on Parks and Tyack (2005), ambient noise measured from acoustic recordings, bathymetry, and an ocean circulation model that estimated sound propagation. Although there is interest in what these data present in terms of call rates and

potential masking, these data also provide a way to explore the environment within which an animal is calling and can be detected. For example, if we know the expected source level of an animal vocalizing a specific type of call, and we know the range estimate for that animal in a given time period, we can determine the distance an animal is from the hydrophone. We cannot determine an exact location with one hydrophone, but we create concentric distance bins from the hydrophone's location and determine how many calls occur within each distance bin. Summarizing the calls within each bin provides information on far away or how close the animals are when calling in relation to the hydrophone. The environmental and acoustic metrics within each distance bin can also be summarized and might provide finer scale information about an animal's environment compared to an area estimate that encompasses the entire detection area. Additionally, when including acoustic detections into models for habitat distributions, providing realistic, even if only estimated, detection distances are important. As previously mentioned, these detection distances should be estimated on not only a monthly or seasonal scale (as water column properties change considerably throughout the year), but also on a daily scale, as daytime and nighttime column properties also can be quite different.
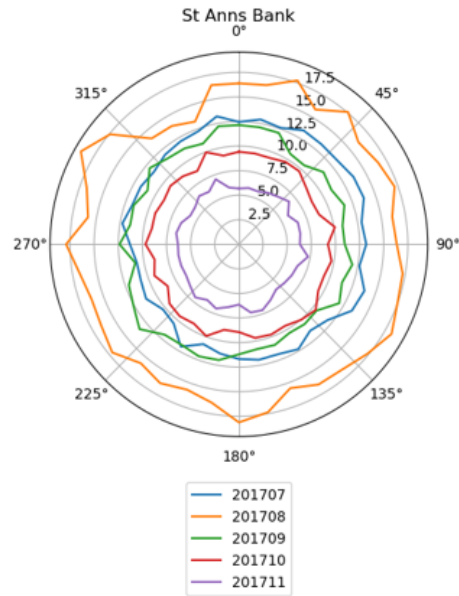
Figure 3: Acoustic detection range estimates of North Atlantic right whales off St. Anns Bank from July 2017 to November 2017. Analysis by Jinshan Xu.

Integrating sound and noise measurements into SDMs

The acoustic parameters we suggest processing and including in these models are: octave band SPLs,

TOLs for the frequencies of the focal species' main call type (for North Atlantic right whales: 63-200 Hz

encompasses the main frequencies of up-calls), sound level exceedance percentiles[1], and the acoustic

detections. We suggest including octave bands up to 1 kHz in order to potentially provide more

information about habitat suitability. As mentioned previously, some animals use sound from the

environment to choose habitats (i.e., some animals might be more attracted to areas with lower levels

of anthropogenic noise and some animals might be more attracted to areas with higher levels of call

diversity). We also recommend processing these parameters in 1-hr (for acoustic detections) and 3-hr

(for soundscape measurements) bins. Acoustic detections are often reported in hourly bins (often times

as presence/absence data, especially when using automated detectors), and soundscapes change

---

[1] Sound level exceedance percentiles can be used to determine how much of the time there might be masking.

throughout the day, often times with diel patterns that can change over longer time periods (seasonally). A 3-hr bin would capture many of these changes in the soundscape as well as allow for better estimations of detection distances, as different noise levels can affect detection probabilities and ranges.

When looking more broadly at a community level (versus species level), ecoacoustic metrics, as mentioned previously, have been used as proxies for indicating ecosystem biodiversity, species richness, species composition, and biological acoustic activity (Sueur et al. 2008, Towsey et al. 2014, Pieretti et al. 2017). As their incorporation into models for aquatic environments is relatively new and limited with mixed results, we suggest first focusing on including only one or two ecoacoustic metrics into species distribution models: the ACI and/or the acoustic entropy index. We suggest incorporating the ACI, which quantifies soundscape complexity by computing the variability of amplitude in acoustic recordings, because it is one of the most popularly used ecoacoustic metrics (see Table 1 for aquatic examples), and although there have been mixed results using it, this metric has often times been correlated with diversity and richness. The ACI has been found to be efficient in filtering out anthropogenic noise in the terrestrial environment as it is based on the assumption that such noise has more constant values than biotic sounds (Blondel and Hatta 2017). While this assumption may still be mostly true in the marine environment, anthropogenic noise in this environment often overlaps with marine animal sounds (i.e., fish and baleen whale vocalizations) and thus this ecoacoustic metric does not always work as well. Still, the ACI has often been used as a proxy for marine sounds of biological origin and thus should be explored further, especially since McKenna et al. (2018) had some success determining community richness and diversity when incorporating this metric into a random forest model[2]. The acoustic entropy

---

[2] McKenna et al. (2018) ran a random forest model using habitat features (sea surface temperature, seafloor composition, sea floor complexity, sea surface cholorphyll), meta features (depth, time of year), vessel features (fishing vessels, commercial vessel traffic), and acoustic features (27 different features). The 27 acoustic features included SPL metrics, time-domain impulsiveness metrics, spectrogram complexity metrics (involving the ACI and

index is made up of temporal (H_t) and spectral entropy (H_f) and has been found to increase with the number of singing species, at least in terrestrial environments. We recommend including this ecoacoustic index because Parks et al. (2014) examined its usefulness in the marine environment and found it had potential in representing biological patterns after it was modified with a simple background removal technique, which helped remove noise from seismic activity that was masking biological sounds.

Recommendations

The acoustic environment is an important habitat feature for marine mammals and other marine organisms that use sound; therefore, it should be included in habitat modeling efforts. With the advances in marine acoustic technologies resulting in the ability to collect large amounts of acoustic data at a relatively affordable costs, and the fact that marine mammal acousticians have described and catalogued many sounds produced by marine mammals, the data are now available to explore not just acoustic detections, but also the acoustic environment. Prior to including the suggested acoustic parameters metrics into SDMs, we recommend first performing a Principal Component Analysis (PCA) to determine which acoustic parameters might be more important (see Goutte et al. 2013).

We also need to collect acoustic soundscape data on the full spatial range of a species to provide ecological inferences within the entire range of the species distribution. With the acoustic collaborations along the East Coast of the US and Canada, most of the known right whale habitat range has been acoustically sampled, albeit on a coarse spatial scale. Now is the time for acousticians and distribution

---

day and night), and raw detections from an automated detector. They used singular value decomposition to condense 768 sound level metrics (based on hour of day, frequency range (including the full frequency spectrum as well as octave bands between 16-1000 Hz), sound level exceedance percentiles (L_{90}, L_{50}, and L_{10}) and the equivalent continuous sound pressure level (L_{eq})) down to 12 SPL features. They found that acoustical features did have predictive power, with the models working best with broad community ecological metrics (i.e., ACI), which are useful for predicting habitats at the community level (looking at community richness and diversity) but not at the species level.

modelers to come together and work to combine these fields. For example, Davis (2020) worked with modelers to present a way to combine visual and passive acoustic monitoring data in the form of occupancy models to address North Atlantic right whale distribution questions. We believe that this type of collaboration to combine different data sources is the forefront in marine mammal species distribution modeling and conservation of protected species.

Even though we suggested presence-only models to limit our recommendations to the current availably of data sources, new techniques are being developed using passive acoustic monitoring to estimate marine mammal species density. Barlow et al. (2021) and Thode et al. (2020) provide new statistical techniques to address detection functions using passive acoustic monitoring data, including using PAM data in spatial capture-recapture methods. These methods rely on a single vocalization being recorded on multiple hydrophones. Additionally, we only made suggestions based on data from stationary hydrophones. There is potential to discern soundscape information from towed hydrophones and relate the acoustic environment to sighting data from visual and acoustic line-transect surveys which would provide a more statistically robust analysis of species abundance.

We also did not address model validation. Although this is a critical component to any modeling endeavor, we did not think it prudent to venture into model validation for this exercise without having datasets to test.

This is an exciting time to start probing the depths of coupling soundscape information and species sightings and acoustic detections to better understand North Atlantic right whale ecology and by extension, provide better conservation efforts for this critically endangered species.

References

Abrahms, B., E. L. Hazen, E. O. Aikens, M. S. Savoca, J. A. Goldbogen, S. J. Bograd, M. G. Jacox, L. M. Irvine, D. M. Palacios, and B. R. Mate. 2019. Memory and resource tracking drive blue whale migrations. Proceedings of the National Academy of Sciences:201819031.

Barlow, J., S. Fregosi, L. Thomas, D. Harris, and E. T. Griffiths. 2021. Acoustic detection range and population density of Cuvier's beaked whales estimated from near-surface hydrophones. The Journal of the Acoustical Society of America 149:111–125.

Baumgartner, M. F., and D. M. Fratantoni. 2008. Diel periodicity in both sei whale vocalization rates and the vertical migration of their copepod prey observed from ocean gliders. Limnology and Oceanography 53:2197–2209.

Bertucci, F., E. Parmentier, G. Lecellier, A. D. Hawkins, and D. Lecchini. 2016. Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Scientific Reports 6:33326.

Blondel, P., and A. A. Z. Hatta. 2017. Acoustic Soundscapes and Biodiversity - Comparing Metrics, Seasons and Depths with Data from the NEPTUNE Ocean Observatory offshore British Columbia. Pages 763–768. Skiathos, Greece.

Blondin, H., B. Abrahms, L. B. Crowder, and E. L. Hazen. 2020. Combining high temporal resolution whale distribution and vessel tracking data improves estimates of ship strike risk. Biological Conservation 250:108757.

Bolgan, M., J. O'Brien, E. Chorazyczewska, I. J. Winfield, P. McCullough, and M. Gammell. 2017. The soundscape of Arctic Charr spawning grounds in lotic and lentic environments: can passive acoustic monitoring be used to detect spawning activities? Bioacoustics 27:57–85.

Bombosch, A., D. P. Zitterbart, I. Van Opzeeland, S. Frickenhaus, E. Burkhardt, M. S. Wisz, and O. Boebel. 2014. Predictive habitat modelling of humpback (Megaptera novaeangliae) and Antarctic minke

(Balaenoptera bonaerensis) whales in the Southern Ocean as a planning tool for seismic surveys. Deep Sea Research Part I: Oceanographic Research Papers 91:101–114.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. Journal of Animal Ecology 73:434–440.

Buscaino, G., M. Ceraulo, N. Pieretti, V. Corrias, A. Farina, F. Filiciotto, V. Maccarrone, R. Grammauta, F. Caruso, A. Giuseppe, and S. Mazzola. 2016. Temporal patterns in the soundscape of the shallow waters of a Mediterranean marine protected area. Scientific Reports 6:34230.

Butler, J., J. A. Stanley, and M. J. Butler. 2016. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. Journal of Experimental Marine Biology and Ecology 479:89–96.

Buxton, R. T., M. F. McKenna, M. Clapp, E. Meyer, E. Stabenau, L. M. Angeloni, K. Crooks, and G. Wittemyer. 2018. Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Conservation Biology 32:1174–1184.

Carlström, J. 2005. Diel Variation in Echolocation Behavior of Wild Harbor Porpoises. Marine Mammal Science 21:1–12.

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

Committee on Taxonomy. 2019. List of marine mammal species and subspecies. http://marinemammalscience.org.

Cook, M. L. H., L. S. Sayigh, J. E. Blum, and R. S. Wells. 2004. Signature-whistle production in undisturbed free-ranging bottlenose dolphins (Tursiops truncatus). Proceedings of the Royal Society B: Biological Sciences 271:1043–1049.

Cooke, J. 2017, December 21. IUCN Red List of Threatened Species: Southern Right Whale Chile-Peru

Subpopulation. https://www.iucnredlist.org/en.

Cooke, J. G. 2020. Eubalaena glacialis (errata version published in 2020). The IUCN Red List of

Threatened Species 2020: e.T41712A178589687. https://dx.doi.org/10.2305/IUCN.UK.2020-

2.RLTS.T41712A178589687.en.

Croll, D. A., C. W. Clark, A. Acevedo, B. Tershy, S. Flores, J. Gedamke, and J. Urban. 2002. Only male fin

whales sing loud songs. Nature 417:809–809.

Cynx, J., R. Lewis, B. Tavel, and H. Tse. 1998. Amplitude regulation of vocalizations in noise by a

songbird,Taeniopygia guttata. Animal Behaviour 56:107–113.

Darling, J. D., and M. Bérubé. 2001. Interactions of Singing Humpback Whales with Other Males. Marine

Mammal Science 17:570–584.

Davis, G. E. 2020, May. Using Passive Acoustic Data to Track Changes in Baleen Whale Distrubtion

Throughout the Western North Atlantic Ocean. Dissertation, University of Massachusetts

Boston.

Depraetere, M., S. Pavoine, F. Jiguet, A. Gasc, S. Duvail, and J. Sueur. 2012. Monitoring animal diversity

using acoustic indices: Implementation in a temperate woodland. Ecological Indicators 13:46–

54.

Derville, S., L. G. Torres, C. Iovan, and C. Garrigue. 2018. Finding the right fit: Comparative cetacean

distribution models using multiple data sources and statistical approaches. Diversity and

Distributions 0.

Desjonquères, C., F. Rybak, M. Depraetere, A. Gasc, I. Le Viol, S. Pavoine, and J. Sueur. 2015. First

description of underwater acoustic diversity in three temperate ponds. PeerJ 3:e1393.

Dunlop, R. A., D. H. Cato, and M. J. Noad. 2014. Evidence of a Lombard response in migrating humpback whales (*Megaptera novaeangliae*). The Journal of the Acoustical Society of America 136:430–437.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Fairbrass, A. J., P. Rennert, C. Williams, H. Titheridge, and K. E. Jones. 2017. Biases of acoustic indices measuring biodiversity in urban areas. Ecological Indicators 83:169–177.

Franklin, J. 2010. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge University Press, Cambridge.

Gasc, A., S. Pavoine, L. Lellouch, P. Grandcolas, and J. Sueur. 2015. Acoustic indices for biodiversity assessments: Analyses of bias based on simulated bird assemblages and recommendations for field surveys. Biological Conservation 191:306–312.

Goold, J. C. 2000. A Diel Pattern in Vocal Activity of Short-Beaked Common Dolphins, Delphinus Delphis. Marine Mammal Science 16:240–244.

Gordon, J. C. D., J. N. Matthews, S. Panigada, A. Gannier, and G. Notarbartolo di Sciara. 2000. Distribution and relative abundance of striped dolphins, and distribution of sperm whales in the Ligurian Sea cetacean sanctuary: results from a collaboration using acoustic monitoring techniques. Journal of Cetacean Research and Management 2:27–36.

Goutte, S., A. Dubois, and F. Legendre. 2013. The Importance of Ambient Sound Level to Characterise Anuran Habitat. PLoS ONE 8.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology letters 8:993–1009.

Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press, Cambridge.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, Tulloch Ayesha I. T., Brotons Lluis, McDonald-Madden Eve, Mantyka-Pringle Chrystal, Martin Tara G., Rhodes Jonathan R., Maggini Ramona, Setterfield Samantha A., Elith Jane, Schwartz Mark W., Wintle Brendan A., Broennimann Olivier, Austin Mike, Ferrier Simon, Kearney Michael R., Possingham Hugh P., P. R. Sutcliffe, Buckley Yvonne M., Arita Hector, and Arita Hector. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.

Hage, S. R., T. Jiang, S. W. Berquist, J. Feng, and W. Metzner. 2013. Ambient noise induces independent shifts in call frequency and amplitude within the Lombard effect in echolocating bats. Proceedings of the National Academy of Sciences of the United States of America 110:4063–4068.

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

Harris, S. A., N. T. Shears, and C. A. Radford. 2016. Ecoacoustic indices as proxies for biodiversity on temperate reefs. Methods in Ecology and Evolution 7:713–724.

Hawkins, E. R., and D. F. Gartside. 2010. Whistle emissions of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) differ with group composition and surface behaviors. The Journal of the Acoustical Society of America 127:2652–2663.

Hayes, S., E. Josephson, K. (ed.) Maze-Foley, and P. E. Rosel. 2020. US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments - 2019. Page 479. NOAA Technical Memorandum, National Marine Fisheries Service.

Hazen, E. L., D. M. Palacios, K. A. Forney, E. A. Howell, E. Becker, A. L. Hoover, L. Irvine, M. DeAngelis, S. J. Bograd, B. R. Mate, and H. Bailey. 2017. WhaleWatch: a dynamic management tool for predicting blue whale density in the California Current. Journal of Applied Ecology 54:1415–1428.

Hernandez, E. N., M. Solangi, and S. A. Kuczaj. 2010. Time and frequency parameters of bottlenose

dolphin whistles as predictors of surface behavior in the Mississippi Sound. The Journal of the

Acoustical Society of America 127:3232–3238.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species

characteristics on performance of different species distribution modeling methods. Ecography

29:773–785.

Hildebrand, J. 2009. Anthropogenic and natural sources of ambient noise in the ocean. Marine Ecology

Progress Series 395:5–20.

Hochachka, W. M., D. Fink, R. A. Hutchinson, D. Sheldon, W.-K. Wong, and S. Kelling. 2012. Data-

intensive science applied to broad-scale citizen science. Trends in Ecology & Evolution 27:130–

137.

Jacobs, M., D. P. Nowacek, D. J. Gerhart, G. Cannon, S. Nowicki, and R. B. Forward. 1993. Seasonal

Changes in Vocalizations during Behavior of the Atlantic Bottlenose Dolphin. Estuaries 16:241.

Jones, G. J., and L. S. Sayigh. 2002. Geographic Variation in Rates of Vocal Production of Free-Ranging

Bottlenose Dolphins. Marine Mammal Science 18:374–393.

Kaplan, M., T. Mooney, J. Partan, and A. Solow. 2015. Coral reef species assemblages are associated with

ambient soundscapes. Marine Ecology Progress Series 533:93–107.

Kaschner, K., R. Watson, A. W. Trites, and D. Pauly. 2006. Mapping world-wide distributions of marine

mammal species using a relative environmental suitability (RES) model. Marine Ecology Progress

Series 316.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial

data to predict species' ranges. Ecology Letters 12:334–350.

Kent, C. S., P. Bouchet, R. Wellard, I. Parnum, L. Fouda, and C. Erbe. 2020. Seasonal productivity drives aggregations of killer whales and other cetaceans over submarine canyons of the Bremer Sub-Basin, south-western Australia. Australian Mammalogy.

Knowlton, A. R., P. K. Hamilton, M. K. Marx, H. M. Pettis, and S. D. Kraus. 2012. Monitoring North Atlantic right whale Eubalaena glacialis entanglement rates: a 30 yr retrospective. Marine Ecology Progress Series 466:293–302.

Knowlton, A. R., and S. D. Kraus. 2001. Mortality and serious injury of northern right whales (Eubalaena glacialis) in the western North Atlantic Ocean. Journal of Cetacean Research and Management (special issue) 2:193–208.

Kraus, S. D., and R. Rolland, editors. 2007. The Urban Whale: North Atlantic Right Whales at the Crossroads. Harvard University Press.

Laurinolli, M. H., A. E. Hay, F. Desharnais, and C. T. Taggart. 2003. Localization of North Atlantic Right Whale Sounds in the Bay of Fundy Using a Sonobuoy Array. Marine Mammal Science 19:708–723.

Lellouch, L., S. Pavoine, F. Jiguet, H. Glotin, and J. Sueur. 2014. Monitoring temporal change of bird communities with dissimilarity acoustic indices. Methods in Ecology and Evolution 5:495–505.

Lillis, A., D. Bohnenstiehl, J. W. Peters, and D. Eggleston. 2016. Variation in habitat soundscape characteristics influences settlement of a reef-building coral. PeerJ 4:e2557.

Lillis, A., D. B. Eggleston, and D. R. Bohnenstiehl. 2013. Oyster Larvae Settle in Response to Habitat-Associated Underwater Sounds. PLoS ONE 8:e79337.

Linke, S., E. Decker, T. Gifford, and C. Desjonquères. 2020. Diurnal variation in freshwater ecoacoustics: Implications for site-level sampling design. Freshwater Biology 65:86–95.

Luo, J., H. R. Goerlitz, H. Brumm, and L. Wiegrebe. 2016. Linking the sender to the receiver: vocal adjustments by bats to maintain signal detection in noise. Scientific Reports 5.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site

occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology

84:2200–2207.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002.

Estimating site occupancy rates when detection probabilities are less than one. Ecology

83:2248–2255.

Matthews, J. N., S. Brown, D. Gillespie, M. Johnson, R. McLanaghan, A. Moscrop, D. Nowacek, R. Leaper,

T. Lewis, and P. Tyack. 2001. Vocalisation rates of the North Atlantic right whale (Eubalaena

glacialis):12.

McKenna, M., D. Mennitt, M. Thompson, J. Stanley, S. van Parijs, K. Fristrup, and L. Hatch. 2018.

Including acoustical features in marine ecological prediction: A case study in the Gulf of Maine.

Woods Hole, MA.

McWilliam, J. N., and A. D. Hawkins. 2013. A comparison of inshore marine soundscapes. Journal of

Experimental Marine Biology and Ecology 446:166–176.

Melle, W., J. Runge, E. Head, S. Plourde, C. Castellani, P. Licandro, J. Pierson, S. Jonasdottir, C. Johnson,

C. Broms, H. Debes, T. Falkenhaug, E. Gaard, A. Gislason, M. Heath, B. Niehoff, T. G. Nielsen, P.

Pepin, E. K. Stenevik, and G. Chust. 2014. The North Atlantic Ocean as habitat for Calanus

finmarchicus: Environmental factors and life history traits. Progress in Oceanography 129:244–

284.

Mellinger, D., K. Stafford, S. Moore, R. Dziak, and H. Matsumoto. 2007. An Overview of Fixed Passive

Acoustic Observation Methods for Cetaceans. Oceanography 20:36–45.

Melo-Merino, S. M., H. Reyes-Bonilla, and A. Lira-Noriega. 2020. Ecological niche models and species

distribution models in marine environments: A literature review and spatial analysis of evidence.

Ecological Modelling 415:108837.

Merchant, N. D., K. M. Fristrup, M. P. Johnson, P. L. Tyack, M. J. Witt, P. Blondel, and S. E. Parks. 2015. Measuring acoustic habitats. Methods in Ecology and Evolution 6:257–265.

Merow, C., M. J. Smith, and J. A. Silander. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36:1058–1069.

Miksis-Olds, J. L., B. Martin, and P. L. Tyack. 2018. Exploring the Ocean Through Soundscapes. Acoustics Today 14:9.

Montgomery, J. C., A. Jeffs, S. D. Simpson, M. Meekan, and C. Tindle. 2006. Sound as an Orientation Cue for the Pelagic Larvae of Reef Fishes and Decapod Crustaceans. Pages 143–196 Advances in Marine Biology. Elsevier.

Moore, M. J. 2019. How we can all stop killing whales: a proposal to avoid whale entanglement in fishing gear. ICES Journal of Marine Science 76:781–786.

Mullen, K. A., M. L. Peterson, and S. K. Todd. 2013. Has designating and protecting critical habitat had an impact on endangered North Atlantic right whale ship strike mortality? Marine Policy 42:293–304.

Mussoline, S., D. Risch, C. Clark, L. Hatch, M. Weinrich, D. Wiley, M. Thompson, P. Corkeron, and S. Van Parijs. 2012. Seasonal and diel variation in North Atlantic right whale up-calls: implications for management and conservation in the northwestern Atlantic Ocean. Endangered Species Research 17:17–26.

Nowacek, D. P. 2005. Acoustic Ecology of Foraging Bottlenose Dolphins (tursiops Truncatus), Habitat-Specific Use of Three Sound Types. Marine Mammal Science 21:587–602.

Oleson, E., J. Calambokidis, W. Burgess, M. McDonald, C. LeDuc, and J. Hildebrand. 2007. Behavioral context of call production by eastern North Pacific blue whales. Marine Ecology Progress Series 330:269–284.

Pace III, R., M., P. J. Corkeron, and S. D. Kraus. 2017. State–space mark–recapture estimates reveal a

      recent decline in abundance of North Atlantic right whales. Ecology and Evolution 7:8730–8741.

Parks, S. E., M. Johnson, D. Nowacek, and P. L. Tyack. 2011. Individual right whales call louder in

      increased environmental noise. Biology Letters 7:33–35.

Parks, S. E., J. L. Miksis-Olds, and S. L. Denes. 2014. Assessing marine ecosystem acoustic diversity across

      ocean basins. Ecological Informatics 21:81–88.

Parks, S. E., and P. L. Tyack. 2005a. Sound production by North Atlantic right whales (Eubalaena glacialis)

      in surface active groups. The Journal of the Acoustical Society of America 117:3297–3306.

Parks, S. E., and P. L. Tyack. 2005b. Sound production by North Atlantic right whales (*Eubalaena glacialis*

) in surface active groups. The Journal of the Acoustical Society of America 117:3297–3306.

Passadore, C., L. M. Möller, F. Diaz-Aguirre, and G. J. Parra. 2018. Modelling Dolphin Distribution to

      Inform Future Spatial Conservation Decisions in a Marine Protected Area. Scientific Reports

      8:15659.

Peterson, A. T., M. Papeş, and J. Soberón. 2015. Mechanistic and Correlative Models of Ecological

      Niches. European Journal of Ecology 1:28–38.

Pettis, H. M., R. Pace III M., and P. K. Hamilton. 2020. North Atlantic Right Whale Consortium 2019

      Annual Report Card. Annual Report.

Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic

      distributions. Ecological Modelling 190:231–259.

Phillips, S. J., and M. Dudík. 2008. Modeling of species distributions with Maxent: new extensions and a

      comprehensive evaluation. Ecography 31:161–175.

Pieretti, N., A. Farina, and D. Morri. 2011. A new methodology to infer the singing activity of an avian

      community: The Acoustic Complexity Index (ACI). Ecological Indicators 11:868–873.

Pieretti, N., M. Lo Martire, A. Farina, and R. Danovaro. 2017. Marine soundscape as an additional biodiversity monitoring tool: A case study from the Adriatic Sea (Mediterranean Sea). Ecological Indicators 83:13–20.

Pijanowski, B. C., A. Farina, S. H. Gage, S. L. Dumyahn, and B. L. Krause. 2011. What is soundscape ecology? An introduction and overview of an emerging new science. Landscape Ecology 26:1213–1232.

Quick, N. J., and V. M. Janik. 2008. Whistle rates of wild bottlenose dolphins (Tursiops truncatus): Influences of group size and behavior. Journal of Comparative Psychology 122:305–311.

Radford, C. A., A. G. Jeffs, and J. C. Montgomery. 2007. Directional swimming behavior by five species of crab postlarvae in response to reef sound. BULLETIN OF MARINE SCIENCE 80:10.

Record, N., J. A. Runge, D. Pendleton, W. Balch, K. Davies, A. Pershing, C. Johnson, K. Stamieszkin, R. Ji, Z. Feng, S. Kraus, R. Kenney, C. Hudak, C. Mayo, C. Chen, J. Salisbury, and C. Thompson. 2019. Rapid Climate-Driven Circulation Changes Threaten Conservation of Endangered North Atlantic Right Whales. Oceanography 32:163–169.

Redfern, J. V., E. A. Becker, and T. J. Moore. 2020. Effects of Variability in Ship Traffic and Whale Distributions on the Risk of Ships Striking Whales. Frontiers in Marine Science 6.

Redfern, J. V., M. C. Ferguson, E. A. Becker, K. D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M. F. Baumgartner, K. A. Forney, L. T. Ballance, and others. 2006. Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310:271–295.

Redfern, J. V., T. J. Moore, E. A. Becker, J. Calambokidis, S. P. Hastings, L. M. Irvine, B. R. Mate, and D. M. Palacios. 2019. Evaluating stakeholder-derived strategies to reduce the risk of ships striking whales. Diversity and Distributions 25:1575–1585.

Richardson, W. J., C. R. G. Jr, C. I. Malme, and D. H. Thomson. 1995. Marine Mammals and Noise. Gulf Professional Publishing.

Risch, D., and S. E. Parks. 2017. Biodiversity Assessment and Environmental Monitoring in Freshwater

      and Marine Biomes using Ecoacoustics. Pages 145–168 Ecoacoustics. John Wiley & Sons, Ltd.

dos Santos, M. E., S. Louro, M. Couchinho, and C. Brito. 2005. Whistles of Bottlenose Dolphins

      (<I>Tursiops truncatus</I>) in the Sado Estuary, Portugal: Characteristics, Production Rates, and

      Long-Term Contour Stability. Aquatic Mammals 31:453–462.

Simpson, S. D., M. G. Meekan, A. Jeffs, J. C. Montgomery, and R. D. McCauley. 2008. Settlement-stage

      coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef

      noise. Animal Behaviour 75:1861–1868.

Simpson, S., M. Meekan, R. McCauley, and A. Jeffs. 2004. Attraction of settlement-stage coral reef fishes

      to reef noise. Marine Ecology Progress Series 276:263–268.

Sinnott, J. M., W. C. Stebbins, and D. B. Moody. 1975. Regulation of voice amplitude by the monkey. The

      Journal of the Acoustical Society of America 58:412–414.

Smith, J. N., H. S. Grantham, N. Gales, M. C. Double, M. J. Noad, and D. Paton. 2012. Identification of

      humpback whale breeding and calving habitat in the Great Barrier Reef. Marine Ecology

      Progress Series 447:259–272.

Staaterman, E., C. Paris, H. DeFerrari, D. Mann, A. Rice, and E. D'Alessandro. 2014. Celestial patterns in

      marine soundscapes. Marine Ecology Progress Series 508:17–32.

Stafford, K. M., S. E. Moore, and C. G. Fox. 2005. Diel variation in blue whale calls recorded in the

      eastern tropical Pacific. Animal Behaviour 69:951–958.

Stanley, J. A., C. A. Radford, and A. G. Jeffs. 2012. Location, location, location: finding a suitable home

      among the noise. Proceedings: Biological Sciences 279:3622–3631.

SUEUR, J., T. AUBIN, and C. SIMONIS. 2008. SEEWAVE, A FREE MODULAR TOOL FOR SOUND ANALYSIS

      AND SYNTHESIS. Bioacoustics 18:213–226.

Sueur, J., S. Pavoine, O. Hamerlynck, and S. Duvail. 2008. Rapid Acoustic Survey for Biodiversity Appraisal. PLoS ONE 3:e4065.

Thode, A. M., S. B. Blackwell, A. S. Conrad, K. H. Kim, T. Marques, L. Thomas, C. S. Oedekoven, D. Harris, and K. Bröker. 2020. Roaring and repetition: How bowhead whales adjust their call density and source level (Lombard effect) in the presence of natural and seismic airgun survey noise. The Journal of the Acoustical Society of America 147:2061–2080.

Tobeña, M., R. Prieto, M. Machete, and M. A. Silva. 2016. Modeling the Potential Distribution and Richness of Cetaceans in the Azores from Fisheries Observer Program Data. Frontiers in Marine Science 3.

Todd, V., I. Todd, J. Gardiner, and E. Morrin. 2015. Marine Mammal Observer and Passive Acoustic Monitoring Handbook. Pelagic Publishing Ltd.

Tolimieri, N., O. Haine, A. Jeffs, R. McCauley, and J. Montgomery. 2004. Directional orientation of pomacentrid larvae to ambient reef sound. Coral Reefs 23.

Towsey, M., J. Wimmer, I. Williamson, and P. Roe. 2014. The use of acoustic indices to determine avian species richness in audio-recordings of the environment. Ecological Informatics 21:110–119.

Treml, E. A., J. R. Ford, K. P. Black, and S. E. Swearer. 2015. Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. Movement Ecology 3:1–16.

Vermeij, M. J. A., K. L. Marhaver, C. M. Huijbers, I. Nagelkerken, and S. D. Simpson. 2010. Coral Larvae Move toward Reef Sounds. PLoS ONE 5:e10660.

Wade, P. R., A. Kennedy, R. LeDuc, J. Barlow, J. Carretta, K. Shelden, W. Perryman, R. Pitman, K. Robertson, B. Rone, J. C. Salinas, A. Zerbini, R. L. Brownell, and P. J. Clapham. 2011. The world's smallest whale population? Biology Letters 7:83–85.

Ward, M. P., and S. Schlossberg. 2004. Conspecific Attraction and the Conservation of Territorial Songbirds. Conservation Biology 18:519–525.

Welch, P. 1967. The use of fast Fourier transform for the estimation of power spectra: A method based on time averaging over short, modified periodograms. IEEE Transactions on Audio and Electroacoustics 15:70–73.

Wiggins, S. M., J. M. Hall, B. J. Thayre, and J. A. Hildebrand. 2016. Gulf of Mexico low-frequency ocean soundscape impacted by airguns. The Journal of the Acoustical Society of America 140:176–183.

Wiggins, S. M., E. M. Oleson, M. A. McDonald, and J. A. Hildebrand. 2005. Blue Whale (*Balaenoptera musculus*) Diel Call Patterns Offshore of Southern California. Aquatic Mammals 31:161–168.

Wisz, M. S., R. J. Hijmans, J. Li, A. T. Peterson, C. H. Graham, and A. Guisan. 2008. Effects of sample size on the performance of species distribution models. Diversity and Distributions 14:763–773.

Xu, J. 2018. Integrated ocean-acoustic approach for North Atlantic right whale passive acoustic detection range modelling on Scotian Shelves. Poster.

Young, M. A., E. A. Treml, J. Beher, M. Fredle, H. Gorfine, A. D. Miller, S. E. Swearer, and D. Ierodiaconou. 2020. Using species distribution models to assess the long-term impacts of changing oceanographic conditions on abalone density in south east Australia. Ecography 43:1–13.

Zerbini, A., and J. Cooke. 2017, December 21. IUCN Red List of Threatened Species: Southern Right Whale. https://www.iucnredlist.org/en.