

Review

# Implication of Altered Acoustic Active Space for Cetacean Species That Result from Soundscape Changes and Noise Additions

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**Abstract:** Organisms use multi-modal, scale-dependent, sensory information to decipher their surroundings. This can include, for example, recognizing the presence of con- or heterospecifics, including a predatory threat, the presence and abundance of prey, or navigational cues to travel between breeding or feeding areas. Here we advocate for the use of the concept of active space to understand the extent to which an individual might be sending and receiving habitat information, describing this as the active component of their niche space. We present the use of active space as a means to understand ecological interactions, giving focus to those species whose active space is acoustically defined, in particular, cetacean species. We show how the application of estimates of active space, and changes in extent, can help better understand the potential disturbance effects of changes in the soundscape, and be a useful metric to estimate possible adverse effects even when stress responses, or behavioral or calling modifications are not obvious.

**Keywords:** acoustics; active space; niche; disturbance; masking; mitigation measures



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## 1. Introduction

The application of the concept of active space to the ecological understanding of animals is presented in this review. Active space describes the area over which sensory information is received or exchanged by an individual. This may be an active or passive process. The information may guide navigation, prey detection, social interactions, including territory definition or defense and hierarchy, and mate selection. In particular, the ideas and parameters of active space given here are in reference to highly acoustic species, focused on cetaceans. Examples of the active space function for cetaceans, and how it might be incorporated into conservation and management are given, outlining its role in the ecological study of these species.

The idea of a circumferent acoustic space has been used in bird behavior and community ecology, (e.g., [1,2] and references therein) and has been applied to the concept of the niche (*sensu* [3]). The idea of an acoustic hypervolume describes the reality by which cetaceans interact with their surroundings and fulfill their life history requirements, by engaging in information exchange through their principal sense. While whale research is uncovering more details about ecology, habitat use, behavior, and the spatial behavior of individuals and populations, it does not have a framework that allows practitioners to interpret the results that rely on the whale's sensory perception of its surroundings.

Perhaps more importantly, the management of whales is a relatively crude pursuit that relies on marking spatiotemporal presence-absence, simple population estimates, and a reactive patchwork of actions to, most frequently, avoid extirpation and extinction. For management to succeed in marine environments, which are becoming much more difficult ecosystems to track and predict, it would benefit from a hierarchical set of boundaries that is firmly based on the individual and then integrated into the population, and the species level. Using a framework that incorporates the concept of active space gives a species-centric approach to understanding the potential disturbance, and efficacy of mitigation

measures. Even when calculated in a rudimentary way, the application of active space or range, centered around an individual, demonstrates their place in an ecosystem, and how things might be impacted by a source of disturbance (see [4]).

Whales, dolphins, and porpoises are highly mobile apex predators that exist in a dense, visually-opaque, three-dimensional medium. Humanity has interacted with them extensively and, for the most part, senselessly reduced populations and degraded habitats. An animal's senses are the major link between an individual and its environment. The acoustic sense is the most important for cetaceans and should be the locus of management. They will not survive without the ability to gain access to prey, find suitable mates, or avoid danger, all of which rely on sound perception and interpretation. Whales' acoustic sense defines the active space and the active con- and heterospecific and individual-habitat exchanges key to individual and population success and survival.

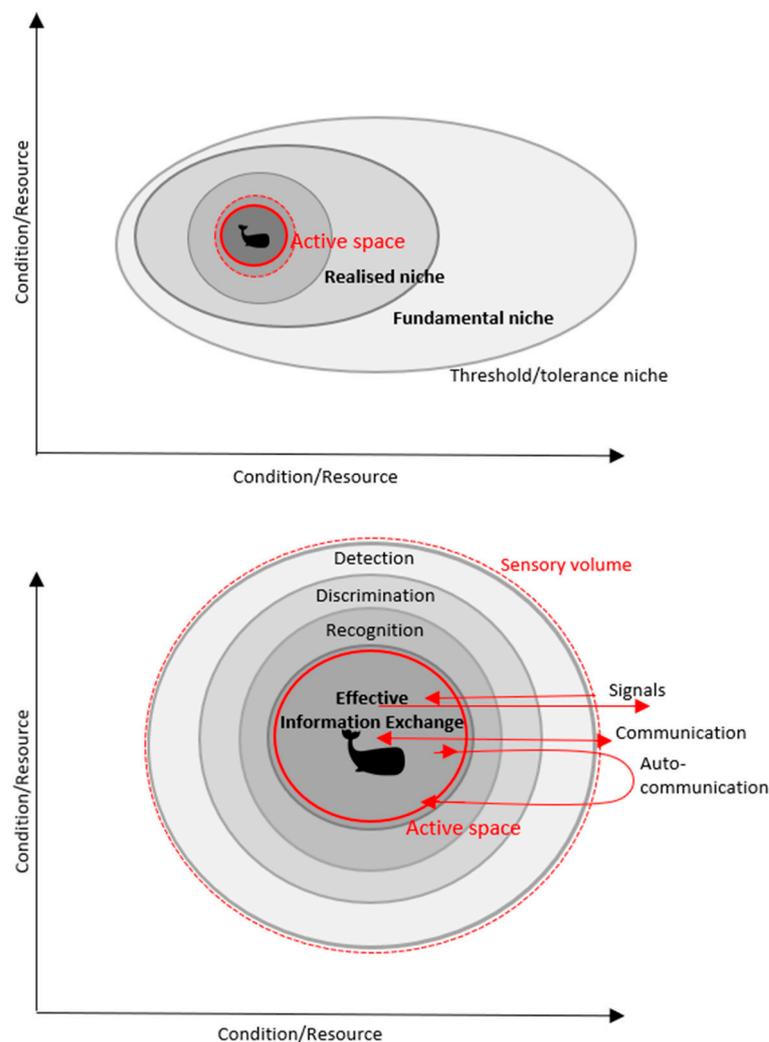
## 2. Background

A species' interaction with its environment can be portrayed by the concept of niche. Using Hutchinson's concept [3], niche space, habitat use, and observations of species-species and species-environment interactions are centered around the individual (Figure 1). It is not defined by anchors to a geographical location, rather it is continuously redefined as the individual travels, with the 'operational' [5] or 'realized' niche [3] defining the area over which active, reactive, or interactive exchanges are made (Figure 1). The word 'niche' comes from the French to 'make a nest', and describes the adaptations of an organism to its habitat in the fullest sense, whereby an organism's niche both describes the habitat it inhabits and its role or function within that system. As the idea of niche is refined (from threshold to realized, Figure 1), it increasingly represents the interrelationships of an organism or species with other species and the environmental conditions. The broadest scale of niche space describes an organism's threshold niche, defined by the biotic and abiotic conditions that it can withstand. Within this, the fundamental niche represents the conditions that are favorable for a species' survival and optimal for reproduction. Biotic interactions are modified by predation or competition to form the realized niche, which can also be referred to as the post-competitive niche space (Figure 1). The area over which information from its surroundings is received by an organism can first be described as its sensory volume. However, when this surpasses pure signal detection this then describes an organism's active space: the area over which they actively and passively send and receive sensory stimuli that provides cues on the surrounding environment, directs behavior, and influences affective state and arousal (Figure 1). It is a dynamic attribute of niche, and a product of selection, learning, and signal processing, that is central to an animal's survival.

The area or extent of the active space can be calculated theoretically, establishing the distance over which a signal from the environment or between conspecifics could be received and interpreted accurately by an organism (Figure 1). This extent is first defined by the strength and type of signal, and constrained by the environment and conditions it is projected into. Active space can also be modified by factors concerning the receiver of the signal. For example, an individual's sensory acumen can be defined by morphological specializations for species or a level of familiarization for that kind of signal.

This theoretical definition of active space focuses on the principle means an individual is capable of sending and receiving information. However, it is multi-modal sensory information that fills the volume of the active space. The maximum range is quantified by the dominant sensory mechanism that operates within the active space envelope, but this can be augmented by other sensory streams. For terrestrial animals, the active space may be delineated by visual acuity and ambient light levels, or be based on chemical signaling of pheromone plumes (e.g., [6–9]), whereas for marine organisms the acoustic sense dominates, influenced by background soundscape sound levels. The extent of the active space adapts to changes in sensory inputs over time and space, shaped also by life history, experience, and the reception and processing of environmental cues. It is the interplay and confluence of physical and biological inputs. The physics is captured as wave

energy, whether it be reflected light through air, acoustical energy in water, or chemical signals emanating from hormonal secretions or digestive by-products. These are the basis of signals, either actively sought, or passively received, by animals to interpret. The biological aspect is somewhat captured by the definitions of the functional niche but is smaller than an animal’s territory. It is more closely aligned to the fight or flight distance [10], or the area over which they can actively monitor resources, navigational cues, and the presence of con- and hetero-specifics, including predators. It goes beyond what Hofman et al. [11] described as the sensorimotor loop of ‘active sensing’, which is the process of an animal producing and emitting sound energy, which is modulated by its surroundings and then returned as information to be decoded. Active space encompasses echolocation, electro-sensory, and electro-location mechanisms (see Figure 1), and defines the area over which animals process all incoming sensory information to direct their responses.



**Figure 1.** A theoretical schematic depicting active space within the realized niche (**top**), and how active space differs from sensory volume (**bottom**). The conditions or resources on the axes could be environmental conditions, resource/prey abundance, or a condition of the morphology, genotype, or phenotype of the organism at the center of the concentric circles.

Species most impacted by altered soundscapes are those whose active space is defined by their acoustic capability. For these species, other sensory streams are limited and contribute primarily to meso- to macro-scale information [12]. In this case, the sensory volume describes the furthest extent over which auditory detection and discrimination can occur. This includes both active and passive acoustic inputs, and either signaling or contact

calling between conspecifics. Therefore, active space defines the distance between the signaler and the receiver so that the message may be received, interpreted, understood, and enacted in the intended way. It equally could be the distance that auto-communications, such as echolocation in bats or odontocete whales or electro-location in fishes is projected, and the echo of that signal returns and be interpreted. It also captures the area from which passive reception of acoustic cues and ‘soundmarks’ [13] occurs. This could be abiotic, environmental sounds, or acoustic projections from other species, including ‘eavesdropping’ on conspecific calls which may aid in orientation, prey location, navigation, or habitat use choices [14,15].

Active space is a ‘time-space-organism’ conception of the environment, whereby the extent responds to both temporal and spatial variables, and it is centered around an individual. If defined by the acoustic sense, it could be described as the ‘dynamic spatio-spectral-temporal acoustic habitat’ [16] or as the operational ambisonic niche of an individual [4]. The active space extent reflects the variability in the transmission of signals given properties of the air or water the sounds are emitted in and traits of the signal itself. While active space refers to a three-dimensional area, it can be simplified to a two-dimensional distance for ease of expression. This two-dimensional representation is a snapshot or a time-averaged area [7] and designates the zone or extent that an acoustic signal promotes a behavioral response. In its simplest form, it can be calculated as the distance or area over which a signal could be detected by a receiver at a signal-to-noise ratio (SNR) greater than zero. That is the received level of the signal exceeds background ambient sound levels, or an SNR that reflects the auditory sensitivity of the species if that is known.

Erbe et al. [17] described concentric zones of signal exchange (similar to Figure 1), which aid our understanding of the concept of active space in the reception of biologically important signals. The range of comfortable communication (‘effective information exchange’ in Figure 1) encompasses the area where vocalizations from a signaler can be heard by a conspecific, but also the clear reception of range finding signals if echolocating. This is the innermost range and is centered around the individual. Next, the zone of recognition depicts the area where an individual receives cues from other species, defining a ‘predator space’, or the extent over which cues to prey and predator presence can be monitored. Cues from biological and physical features, termed ‘reverberation space’, define the distance over which an organism is receiving soundscape information [17]. This forms the final, and most extensive zone of acoustic information transfer (‘detection’ in Figure 1).

Acoustic signals and their emission, transmission, and reception are defined by frequency, amplitude, length, and modulation. The higher the frequency of the signal, the shorter the signal wavelength and so the more spatially restricted the signal propagation. Therefore, without obstruction or interference, high-energy, low-frequency tones propagate furthest. Thus, species that are sensitive to and utilize the low frequencies have a greater active space than those using higher frequency signals [16,18]. A signal’s propagation is modified by the transmission properties of the medium and the soundscape that it is projected into (e.g., [19–21]). Soundscapes are composites of biological, non-biological, and anthropogenic noise, which together form a complex acoustic environment that modifies sound pathways (e.g., [22,23]).

Animals that primarily use the acoustic senses devote considerable time and energy to communication and sonic information processing. The projection of acoustic signals can be energetically costly and is not done without intention [24–28]. Although taxon-specific, it can require a high aerobic capacity (as in frogs, e.g., [29]), and may be correlated with the calling individual’s metabolic rate [24,28,30–33]. Calculations of active space from signal transmission calculations, adapted to compare the propagation and distance of detection under differing levels of ambient noise, have been made (e.g., see [19,21,34]). However, the work to fully describe the active space, even in this rudimentary way, is still in the formative stages. If refined, this could help with the understanding of the extent to which

changes in an organism's surroundings and soundscape could be impactful, and aid with our understanding of the function and use of these acoustic signals.

Calling may be to signal or communicate, with the latter meaning an acoustic response is expected (see Figure 1). They are both distinguished from acoustic cues, which lack intention or evolutionary specialization, such as the noise made as a by-product of presence. They are also distinguished from indices, which express a property of the signaler, that is interesting to the receiver, known also as 'unfakeable', 'honest', or 'assessment' signals [35–37]. The use of the acoustic mode by terrestrial animals and birds is particularly heightened when the perceptual ability of their closest conspecifics by visual or olfactory cues, are obscured.

The value and function of the exchange of acoustic information relies on the geographical, behavioral, social, or physiological context in which it is made. Bats, for example, adjust their echolocation signals to localize, identify and capture prey. The dynamic control of the direction, timing, and frequency of the biosonar projection forms a cognitive map of the environment for navigation [38]. Bat sonar calls can also communicate the age, lactation stage, fitness, and aggressive state of the signaling individual [38–42], by calls distinct from those used in wayfinding or prey pursuit [43,44]. These calls have been used to signal conspecifics in excess of 50 m from the caller. Complexity and length are variables that distinguish birdsong from alarm or contact calls [45]. Mobbing calls to attract conspecifics contrast with these alarm calls by typically being repetitive, having a sharp onset, and covering a broad frequency range, whereas the high-pitched alert signals are more difficult to localize, which may be an anti-predator mechanism [46].

Calling between conspecifics aids in reunion, via pairing or contact calls. This supports the re-aggregation of animals that are fission-fusion species, or seemingly lone individuals. Calls shared by a group or herd are typically stable over time and have a supportive function during movements or re-aggregations after separation, and direct mate selection and kin care efforts (e.g., [47–51]). Features inherent in the call project the species, group membership, and even the identity of the caller [52–54], indicating whether it is a friend, a known conspecific, or a 'foe' in immediate proximity. Acoustic niche partitioning and separation in the call structure such as frequency and modulation is used to distinguish sympatric species in the same area calling at the same time (e.g., frog species [55]).

Calls also establish a form of 'social buffering' in bonding, as seen in mammals (e.g., [56,57]) and nesting birds (e.g., [58,59]). Therefore, maintaining acoustic contact can reduce the stress that might result from separation, especially noted for mother-young pairs, or ameliorate any aversive experiences when conspecifics are remote [60]. Mating choice can also be mediated by acoustic exchanges. Typically, calls promote male signalers' attractiveness to potential female mates. Must and estrous rumbles of elephants, for example, are specific reproduction-related long-distance projections that advertise the physiological state of the caller for up to 4 km [61–65]. Equally, calls may be made to advertise size, prowess, or social rank, and maintain territory and spacing, in particular by males (e.g., [29,66–70]).

### 3. Active Space and Marine Mammals

Many taxa, across terrestrial and aquatic habitats, have specialized auditory systems that receive and process acoustic information that focuses on their ecological function. Much of the research effort involves birds and marine mammals [71] to clarify auditory capacities, the behavioral context of acoustic use, levels of sound exposure, and noise sources in their surrounding environments. There is an increasing body of evidence that shows the sensitivity of fishes and aquatic invertebrates to changes in their acoustic habitat, however, here, we use whales and dolphins as our focal species to discuss the impact of changes in underwater soundscapes on animals, using the active space concept. By doing so, we work toward a more animal-centric approach, and an appreciation of the interaction of an individual with the ecosystem by defining the extent of this organism-habitat interchange based on its functional use of acoustics (see Figure 1).

Cetaceans are morphologically adapted to underwater sound processing, as the acoustic sense is their primary method to send and receive information. In the marine environment, the acoustic transmission of information is far superior to visual means, with all cetaceans believed to be capable of sound production and reception that is critical to navigation and orientation, signaling, foraging, and communication [72–74]. Marine mammals have an increased number of auditory nerves, with two to three times the number of fibers than their terrestrial counterparts [75].

The baleen whales more closely resemble their terrestrial ancestors in terms of their acoustic morphology. Calls are produced by the manipulation of airflow through the larynx [76]. In contrast, toothed whales have an asymmetrical cranium that houses a complex system of nasal passages and fatty tissues (the melon) for sound generation and projection of high-frequency whistles or short, pulsed biosonar calls [77]. This enables odontocete echolocation where the returning echo of their own signals is interpreted to create a mental map of the underwater landscape and preyscape (see Figure 1). In a medium where visual cues are limited, whales use sound for the creation, mediation, and maintenance of social relationships, navigation, prey location, and successful competition. Call function may be interpreted from the season, group association and proximity, or behavioral, emotional, or physiological state concomitant to the vocalization. However, it is the estimation of the active space which allows us to better understand how an animal associates with its habitat and makes sense of its surroundings from the whale's perspective [4,23,78].

Marine mammals use multi-modal, scale-dependent, sensory information to decipher their surroundings. The auditory system of cetaceans allows for more complex signal processing than land mammals [75]. Audio perception and hearing sensitivity studies have focused on odontocetes. Audiograms have been generated through experimentation for delphinids. Less work has been possible for baleen whale species, although their hearing ranges span the infra- to ultrasonic range [65,79]. Sensitivity to the low frequencies facilitates information exchange over large distances. Baleen whale vocalizations have been recorded to travel 9–45 km from the source [80,81], yet the maximum detection range can extend from several hundred to thousands of kilometers from the caller [82,83]. This compares to the higher frequencies used by toothed whales, that use their acoustic sense on micro- (<100 m) to fine scales (<5 km [12]). Passive listening and reception of sonic cues may, however, occur over wider spaces. Whales may use magnetoreception and somatosensory cue perception of ocean conditions on the broadest scales, but these cues may not have the resolution needed for immediate navigation or foraging decisions [12]. Yet simply considering sound perception when considering an individual's active space fails to consider the dynamic nature of the response of whales and dolphins to their surroundings, and the variability they experience in their surroundings and in the information perceived. The transmission of sound and the detection range of conspecific calls is dependent on the frequency and amplitude of the signal and the environmental conditions that impact transmission loss. The soundscape is composed of natural biological and non-biological components, as well as additions from human actions. In marine settings, sea states, wind, wind-driven waves, water turbulence, tides, currents, and precipitation form the abiotic components. The biological additions come from the vocalizations and sonic by-products of conspecifics and other organisms.

The anthropogenic noise additions result from transportation and resource use of the oceans. The introduction of propeller-driven vessels, and now the increase in the number and capacity of commercial vessels, has precipitated large changes in the ambient sound levels and has shaped soundscapes even in remote regions [84,85]. The propagation of sound energy of each of these sources changes dynamically alongside ocean conditions over time and space. Properties such as water depth, topography, substrate, pH, temperature, and salinity create sound speed profiles that define propagation coefficients and influence the sonic environment ('conditions' on the axes in Figure 1). Ambient noise may also vary daily and seasonally, as the dominant sound sources change over time and space. Modified

soundscapes arise from changes in the presence of one or more of the geophonic, biophonic, or anthrophonic variables. The increase in ocean temperature, for example, could alter a thermocline [86] and, thus, sound absorption, as could a decrease in pH from acidifying oceans, by attenuating and absorbing low-frequency sound in particular [86–88].

The use of the active space concept allows us to consider the impacts of changes in the soundscape in a way that is meaningful to individuals and populations and how the presence of noise alters auditory detection, rather than just a simple description of the variation of sound levels. It focuses on the study of impact on the individual, and the species, and is a dynamic means to consider the changes in pattern and process across seascapes and time periods as they are experienced by an individual animal. Active space encompasses the relationship of the individual to changes in its surroundings or in the ecosystem structure, or in the mechanisms it is a part of. It may also help predict how the animal might respond to change. By extension, this bears on the population, especially so if it is small or sparsely distributed. An understanding of active space and signal masking could be incorporated as a metric of impact to estimate the effectiveness of management measures designed to reduce disturbance. A masking metric, calculated by expressing the active space or range that an individual can maintain communication or use echolocation under different noise scenarios as a proportion of the extent of the same signals under ideal soundscape conditions, has been suggested as such a tool (see [4,21,89]). Other metrics, such as the level of noise exposure that results in either temporary or permanent changes in hearing sensitivity or physiological stress of an organism can be a means to assess impact also but only speak to the potential changes in signal reception and processing that occur at the receiver. The use of a metric that incorporates the concept of active space takes this and the changes in the conditions surrounding the individual into account.

The active space defines a meaningful scale on which we consider these relationships and responses, giving rise to a dynamic individual-based view of ecological networks and ecosystem function. Using active space to define the extent of an individual's conspecific network also orients us to the spatial extent of the 'range herd' [18]. Despite individual cetaceans appearing to be solitary, we need to adjust our sense of spatial extent through active space to allow us to recalibrate the nature of the animal's group. This helps redefine the idea of herds or groups for cetaceans, where individuals maintain contact with conspecifics over large areas, but are still afforded space, for example, to find prey without competition [18]. It may be that whales are in constant contact [18], and are able to re-aggregate via vocally mediated communication networks. It also credits the complexity of the acoustic sensory mode for cetaceans whereby, for example, conspecific vocalizations are distinguished from other sounds in the environment, and the use of both enables an individual to locate prey patches or a mate.

The study of cetacean bioacoustics is pivotal for understanding the ways in which whales and dolphins interact with each other and their environment. Within this, estimates of active space suggest the function of the calls and their behavioral outcomes. Generally, the larger the animal, the lower the frequency of the vocalizations [90]. Baleen whales produce powerful, low-frequency sounds used for environmental imaging, signaling, or communication. Blue whales (*Balaenoptera musculus*), the largest whale species, are able to employ infrasonic calls below 10 Hz lasting in excess of 10 s to communicate over long ranges [82]. Similarly, 20 Hz pulsed fin whale (*Balaenoptera physalus*) calls may be audible over hundreds of kilometers, and theoretically across ocean basins if projected at high amplitude with little absorption or external impedance from ambient noise sources [18,80,82,91–95]. This contrasts with toothed whales, which use higher frequencies for tonal calls and 'clicks' to determine closer-range targets, usually limited to hundreds of meters [95–97]. The sperm whale (*Physeter macrocephalus*), the largest toothed whale, dedicates more than a third of its mass to sound production, and has the most intense echolocation system ranging into mid-frequencies (100 Hz to 32 kHz, [98]), transmitting at a maximum source level of 232 dB re 1  $\mu$ Pa that allows its signals to project

up to 10 km [72,95,99–101]. Generally, however, toothed whales have a smaller active space, but potentially greater efficiency and acuity in information acquisition [95,102].

The detection range of a call is defined by its type and its parameters (frequency, modulation, amplitude, length, inter-pulse, or call interval); the active space requires some knowledge of the hearing threshold and critical signal-to-noise ratio (SNR) of the call. Here we consider the extent of the active space of a call to be the distance over which the information encoded in these parameters is transferred effectively. This differs from a detection range estimation (or ‘sensory volume’ in Figure 1) centered around an individual whale that might be referred to as its communication [16] or echolocation space [19]. The calculations to define these spaces are concerned with the extent of the propagation of the signal and attenuation only, and not the process of information exchange. We would estimate these communication and echolocation extents using  $\text{SNR} > 0$ , and not determine whether the received level of the signal allowed for accurate decoding. The calculation of active space extent starts with these detection range calculations. However, in this review, we use active space as a means of acoustic information exchange, rather than pure detection of the signal (the ‘sensory volume’; Figure 1) through either a directed signal or eavesdropping [103–106]. This definition requires the ability to decrypt the information that the call contains as well as background communication noise from conspecifics [106,107].

If the signal strength of calls diminished purely through transmission loss, as outlined by Urick [108], then the ability to discern the content of the signal from source to receiver will diminish with increased distance only [17]. In this case, active space is defined by the distance between the signaler and receiver with no other interfering variables. However, other factors, including but not limited to, attenuation, ambient sound levels, directionality of signal, orientation of signaler and receiver, and attentiveness and processing ability of receiver also regulate the extent of an organism’s active space [22].

Functionally, call use, structure, and timing play a role in social behavior, foraging, and reproduction [109–111]. Quantifying the attenuation of calls at a particular time and specific location adds to what is known about the use of the acoustic sensor to support critical life functions. For example, estimates of active space for coda echolocation signals of sperm whales by Jacobs [34] altered the perceived use of calls. The estimated maximum radial distance suggested that codas should not be considered long-distance signals as they were traditionally described [112], but rather as a more spatially restricted signal to mediate within-group relationships [34]. Coda calls have been described to display membership of a cultural group, but knowledge of the signals’ structure suggests that their use is better suited to communicating to closer conspecifics. This work hints at the complexity and use of communication in structuring social systems.

Call type and structure reflect the behavioral context and motivation of the signaler, and so transmission extent must be tied to the intended influence of the call on the receivers, and be optimized for that function. Mate advertisement by bowhead whales, for example, is through calls of a higher frequency than might be expected for its body size and comparison to other baleen whales [90]. However, the distance over which these reproductive calls are utilized is limited to well-established annual breeding areas, so propagation over a large distance is not needed. Moreover, the use of the higher frequencies allows for greater variation in the calls’ frequency modulation, and so likely includes a greater transfer of information on relevant traits of the caller [90]. Changes in the extent of active space can result from modification of the call or an altered soundscape in which the call is projected. Indeed, call modification and compensatory mechanisms such as changes in frequency, amplitude, and calling rate have been noted as a response to elevated background sound levels [113–118].

The foreshortening of the cetacean active space equates to a spatially restricted exchange of sonic information. This may limit the extent of the cognitive maps they form to aid in wayfinding, due to reduced acoustic cues for navigation and orientation [118], a smaller search range for prey, and a reduced ability to use acoustic signals for prey capture, as well as changes in social group dynamics. The contact and coordination between

individuals may be reduced [118], or indeed, the distance between individuals is reduced to be able to maintain contact. Changes in soundscape degrade auditory cues critical for predator or threat detection [119]. Novel or unpredictable sounds have elicited responses similar to antipredator startle or flight behaviors (e.g., see [120–122]).

#### 4. Anthropogenic Noise Effects on a Cetacean

Anthropogenic noise additions to underwater soundscapes have been likened to the effect of a persistent pollutant causing habitat degradation and changes in species distribution [123]. The most pervasive instigator of change in the marine environment is the addition of vessel noise. However, a variety of sound sources contribute to the underwater ambient sound field, for example, seismic air guns, sonar, and telemetry devices [122]. The low-frequency components of these sounds can contribute to ambient levels over millions of square kilometers in some cases [123]. For example, seismic surveys can raise the background noise levels by 20 dB over 300,000 square kilometers continuously for several days [124]. Seismic air gun arrays are increasingly being used for oil and gas explorations in deep water, although currently, work focuses on the continental shelf. Coastal waters may experience acoustic inputs from sonar, attributed to naval, fisheries, or research use, as well as acoustic deterrents or harassment devices.

The introduction of motorized commercial shipping over the last century precipitated the largest change in ambient noise particularly in low frequencies. Both local and global scales are impacted by the expansion of the global marketplace [85]. The sound is generated primarily from propeller cavitation and propulsion noise from the engine, gears, and machinery, and is predominantly in the 20–200 Hz range from larger vessels, however, it can radiate up to 100,000 Hz [84,116,125–127]. Studies monitoring the trends in ambient noise have found that there has been an overall 10–12 dB increase in noise less than 80 Hz since the 1960s, which is coincident with the doubling of the global shipping fleet [123,125,127,128].

Vessel presence creates stress for whales [128–143]. Behavioral responses have been frequently observed (e.g., [134,137–142], with implications for group size and cohesion [143,144]). A number of studies that have assessed the effect of vessel noise on marine mammals (e.g., [129,144–148]), typically consider the direct and indirect impact of a single noise source in proximity to individual animals. Research efforts focused on determining disturbance effects from increased noise and vessel presence frequently use surface observations (e.g., [84,124,137,149–160]). Behavioral responses may be subtle or nuanced, and not be immediately noted as readily as changes in swimming/diving or vocalizing. Whales may also be negatively impacted by vessels without any obvious changes in behavior [161,162]. Physiological responses to stress have not been fully defined for cetaceans, although altered vital rates and levels of stress hormones suggest disturbance [129,163,164]. Considered together, the overt expressions of disturbances and more covert stress responses may change whale distributions and habitat use, reproductive success, and survival [123,124,161–167]. For species, groups, or individuals that are already vulnerable, this is a particular concern.

Active space calculations are a means to assess the potential acoustic disturbance from noise additions to the soundscape (e.g., see [4]). They may also support an estimate of acoustic stress on an individual when changes in behavior are not observable, for example when whales are willing to withstand disturbance to continue to exploit prey reserves. Habitat use by whales may continue despite disturbance, representing a trade-off between aversion and fulfilling an energetic need. Moreover, avoidance behaviors such as altered swimming patterns, and changes in calling have predominantly been classed as short-term, sub-injurious [123], and sub-lethal effects. That may or may not be true as we know little about the accumulation of stress and thresholds that may be breached and create significant consequences.

Estimating reductions in the extent of an animal's active space provides some of the fundamental information needed to understand the consequences of changes in their sonic environment on a biologically meaningful level. Establishing the effect of short-term, small-scale, high-intensity, acute exposures to increased noise on marine mammals, with

regards to injury and masking is the focus of much of the research, although long-term, larger-scale chronic low-intensity noise exposure may be more detrimental to individuals and populations [16,18,84]. Acoustic masking is a failure to recognize the occurrence of a stimulus or to not distinguish a signal of interest, as a result of interference from other noise. It also describes a reduction of active space. It occurs when elevated ambient noise, or the presence of a noise source in the sound field, obscures or fully erases the audibility of signals of interest. Masking as a result of noise from human activities is an increasing threat to marine life, particularly low-frequency specialists such as baleen whales.

Auditory masking is the most widespread impact on cetaceans as a result of noise additions [17,84]. Calculations to assess the potential for masking or proportional changes in active space have been undertaken for several whale species and presented as a metric of effect or disturbance. Acoustic masking can impact the extent to which audio detection and discrimination of acoustic cues are received from the soundscape, termed as their 'reverberation space' [16], or more specifically a loss of communication and echolocation space.

An assessment of the change in active space and the repercussions of soundscape changes on individuals and populations occur over a wide range of animal taxa (e.g., [84,118,123,124]). It considers more than the reduced capacity to communicate (e.g., [168–173]), but also a whale's ability to gather acoustic information pertinent to its success and survival, including orientation when traveling (e.g., [169,170]) or foraging (e.g., [147,171]). To estimate the effect, researchers have sought to show the change in the absolute extent of call reception, or as proportional reductions of this distance comparing the whales' calling ranges under noise conditions to those during ideal or historical conditions [21,118].

Payne and Webb [18] showed the potential for masking in one of the first descriptions of reduced call propagation distance. They demonstrated substantial reductions in call range, and, therefore, communication space, under moderate noise conditions. In doing so, were unknowingly the first to apply the concept of active space in a simplistic manner to understand the impact. It was the first study to highlight the importance of sound to whale species, and the need for regulation and management of noise emissions. Clark et al. [16] demonstrated the potential of masking for different species of the same sound source, dependent on the frequency range. This highlighted that when taking a species-centric approach, the consideration of impact needs to be driven by sounds pertinent to each species. This species-specific approach was also taken in the analysis by Hatch et al. [118], who showed that North Atlantic right whale (NARW, *Eubalaena glacialis*) communication space could be reduced by nearly 70% on average when compared to a pre-industrial ocean noise level. These estimates of effect are made more biologically relevant by focusing on the frequencies that are pertinent to the species that are affected, referencing their communication and/or echolocation frequencies, and understanding the behavioral and social consequences of the masking [21]. The zone of masking must then be applied to the estimates of active space to assess the consequences for behaviors that are mediated by acoustics. Signal frequency is species-specific. Vocalizations are also likely context-dependent. The ratio of source level to ambient amplitude, the critical ratio (CR), is decisive in determining if the signal will be discriminated from background noise by the intended receiver [22,90,172–174]. Properties of both the signal and the transmitting medium, including ambient noise levels, define the active space over which a signal will instill the intended response.

Taking this approach changes the consideration of altered soundscapes from short-term, acute noise, to chronic additions that degrade the perception of vital acoustic cues. Few studies have considered the repercussions of animals' soundscape changes on a landscape scale and/or over long time periods. This is needed, however, to be able to consider the cumulative and aggregate effects of exposure on individuals and populations as well as the wider ecological consequences, in particular habitat use.

## 5. Application of Active Space in Ecological Study

Pattern and scale are central themes in ecology. There is no single natural scale that describes the forces that drives life histories, competition pressure, or species interactions (e.g., [174]). Influences on the scale of the active space will have impacts on animal behavior, dispersal, and mechanisms that form a community and dictate success. The observable aspects of behavior are driven by the biological imperative to find food and mates and avoid predators. Individuals respond to cues related to these needs on different spatial and temporal scales, but predominantly within the constraints of their active space extent. As described before, active space is a means to describe the operational and active component of an animal's niche (Figure 1), akin to the spatially and temporally distinct individual-centered 'hypervolumes' described by Hutchinson [3]. Comprehension of active space will also lead us to realize our underestimation of how seemingly distant influences could have implications on whale behavior.

Active space is a key component of soundscape ecology, a more holistic means to understand sound. Most studies of active space and application of it as an ecological tool are still based on the theoretical (essentially volumes estimated from call detection radii with adapted SNR), or perhaps empirical manipulation and playback experimentation (see [34]). Clear responses by animals to sounds of a particular received level, the sensitivity, tolerance, and perhaps even habituation to the noise source are typically not well defined. However, as discussed, behavioral responses can be subtle and may be imperceptible or deemed not significant to a human examiner. Something like the masking metric of proportional reduction from a minimum ambient [21] or historic sound level (e.g., 'ancient ambient' [118]) is a useful means to compare the impact over time and space.

To understand the effect of changes to soundscapes on wildlife, the fundamental unit and scale of study should be defined by active space. It provides a means to understand broad-scale changes on the individual, population, and species levels that are organism centered, directed, timed, and spaced. It also transforms the presence of a whale from point data to a radius of energy in a soundscape map; representing the area where information can be both sent and received. It moves away from the idea that animal behaviors and responses are arbitrary or random, but shows the acoustic sense to be the mediator for all key behaviors and social interactions.

Moreover, it highlights the need for a widespread, coordinated international response in management. Our ability to interpret meaning and information encoded in calls is very limited, but active space at least allows us to consider the use of the acoustic modality in an ecologically relevant way. To understand the full impact of chronic noise pollution on marine mammals, we will need to know the level at which behaviors and predator-prey interactions are disturbed and when this becomes significant to a population (e.g., [123,148,174]). Until now, noise maps overlaid with maps of important habitats have supported management action [175], whereby high acoustic energy spaces and areas of high ecological importance could be identified as 'hot spots' for protection or mitigation [123]. Much is still to be learned about the call repertoires and function, and their structural features before acoustics can be used as an indicator or predictor of change. Exposure level quantification and thresholds have been suggested, although, so far the adaptation of their application has been based on a limited criterion, only taking into account whether the animal is mysticete, odontocete, or pinniped, and if the noise source is impulsive or continuous [176].

Several nations have committed to controlling underwater noise pollution to limit disturbance to marine life. These, however, are typically single sources, not an attempt to regulate cumulative noise or form ecologically relevant 'noise budgets' [177]. It is difficult to translate this and the concept of reduced active space through masking into tangible quantitative goals and operational targets which can be implemented to inform regulation or mitigation [178].

The biological impact of disturbances, alone or cumulatively in time and space, can only be assessed when we are able to determine when acoustic stressors and changes in

soundscapes become ecologically relevant; the application of the concept of active space in determining effect may be the first step in being able to do that.

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