A sense of scale: Foraging cetaceans' use of scale-dependent multimodal sensory systems

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Abstract

Research on cetacean foraging ecology is central to our understanding of their spatial and behavioral ecology. Yet, functional mechanisms by which cetaceans detect prey across different scales remain unclear. Here, I postulate that cetaceans utilize a scale-dependent, multimodal sensory system to assess and increase prey encounters. I review the literature on cetacean sensory systems related to foraging ecology, and hypothesize the effective scales of each sensory modality to inform foraging opportunities. Next, I build two "scale-of-senses" schematics for the general groups of dolphins and baleen whales. These schematics illustrate the hypothetical interchange of sensory modalities used to locate and discriminate prey at spatial scales ranging from 0 m to 1,000 km: (1) vision, (2) audition (sound production and sound reception), (3) chemoreception, (4) magnetoreception, and somatosensory perception of (5) prey, or (6) oceanographic stimuli. The schematics illustrate how a cetacean may integrate sensory modalities to form an adaptive foraging landscape as a function of distance to prey. The scale-of-senses schematic is flexible, allowing for case-specific application and enhancement with improved cetacean sensory data. The framework serves to improve our understanding of functional cetacean foraging ecology, and to develop new hypotheses, methods, and results regarding how cetaceans forage at multiple scales.

Key words: acoustics, baleen whale, cetacean, distance, dolphin, foraging, olfaction, scale, sensory system, vision.

Finding food in a big ocean is no small task. Ocean resources are notoriously patchy (Hyrenbach *et al.* 2000), mandating that marine predators have adept abilities to find and capture their prey within this dynamic environment (Fauchald and Tveraa 2006). Cetaceans (whales and dolphins) present one such group of marine predators that frequently range broadly and must search efficiently to encounter discrete foraging opportunities. Yet, this search for food is technically challenging, as the ability to gain effective prey localization and quality information is dependent on the dynamic use of sensory pathways as a function of distance to the target. For animals in search

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of food, the spatial scale of the pursuit at any given moment determines the importance of any given input of sensory information. To forage effectively, cetaceans must employ a multimodal, scale-dependent, sensory system that provides information on prey availability, much like other higher-order mammals (Davenport and Rogers 1970, Bryant *et al.* 1972).

The scale of search effort is particularly relevant to animals that move large distances, including cetaceans that use foraging strategies informed by sensory cues dependent on target proximity. Finding the Gulf Stream likely takes a different set of skills than finding a school of fish within the Gulf Stream. This hierarchical, scale-dependent search behavior is the basis of area restricted search theory (Kareiva and Odell 1987), Levy walks (Sims *et al.* 2008), and first passage time analyses (Fauchald and Tveraa 2003) that are frequently applied to analyses of movement data from marine predators.

Foraging ecology is a central theme in cetacean studies that advances our understanding of their ecology and biology, and enhances conservation management (Corkeron *et al.* 1990, Baumgartner and Mate 2003, Constantine *et al.* 2015, Pirotta *et al.* 2015). Distribution, habitat use, and behavior studies are frequently used to describe how, when, and where cetaceans find and capture prey (Heithaus and Dill 2002, Hastie *et al.* 2004, Torres *et al.* 2008). Yet, little consideration has been given to the sensory modalities at work that actually facilitate prey encounters, discrimination, and capture. Controlled studies of cetacean sensory abilities are inherently difficult due to animal size, needs, and marine habitat, forcing many foraging ecology studies to assume what role sensory modalities play rather than explicitly describing how sensory systems enable prey discrimination and capture. However, we know cetaceans regularly locate prey, evaluate prey type and quality (Witteveen *et al.* 2008, Au *et al.* 2009), adjust their foraging strategy accordingly (*e.g.*, Hoelzel *et al.* 1989, Heithaus and Dill 2002, Torres and Read 2009), and capture prey. Therefore, the focus of this review is to apply what is known or hypothesized about cetacean sensory abilities to discuss the scales at which their multimodal senses operate to facilitate foraging. With a better understanding of the spatial scales at which certain sensory modalities operate to aid prey localization and discrimination, we can improve the suitability of our questions, methods, and results regarding our understanding of cetacean foraging ecology.

In this review, I hypothesize that a cetacean forms an adaptive foraging landscape that accounts for distance to, and qualities of, prey patches derived through information gained from its sensory modalities. Kenney *et al.* (2001) presented a conceptual model of the scale-dependent mechanisms used by western North Atlantic right whales (*Eubalaena glacialis*) throughout an annual cycle. Here I expand upon this initial effort and present hypothetical schematics of the scale-of-senses for two general groups of cetaceans: baleen whales (mysticetes) and dolphins (Delphinidae). The dolphin group refers to the subfamilies Delphininae, Globicephalinae, Lissodelphininae, Orcininae, and Stenoninae; the whole odontocete group (all toothed whales and dolphins) are not used for this exercise due to the scarcity of information for many odontocete species, and the large diversity of this group. First, I define the applied spatial scales in these scale-of-senses schematics (Table 1). Next, I briefly summarize the sensory systems of baleen whales and dolphins, and their functional role in foraging ecology. These summaries are not meant to be exhaustive overviews of the literature but rather to provide background information on how each sensory modality informs foraging

Table 1. Definition of spatial scales applied in the scale-of-senses schematics for foraging cetaceans (see Fig. 1, 2).

Scale	Spatial range
Micro	0 to 100 m
Fine	100 m to 5 km
Meso	5 to 100 km
Large	100 to 500 km
Macro	500 to >1,000 km

efforts and the scales of utility. Then, I present the scale-of-senses schematics, through which I posit and compare the scales at which the sensory systems are effective in aiding foraging by baleen whales and dolphins. Finally, I discuss the implications and applications of these hypothesized scaled multimodal sensory schematics.

BRIEF DESCRIPTIONS OF CETACEAN SENSORY SYSTEMS AS RELATED TO FORAGING BEHAVIOR

Six sensory modalities potentially used by foraging cetaceans are reviewed here and considered in the scale-of-senses schematics: (1) vision, (2) audition (sound production and sound reception), (3) chemoreception, (4) magnetoreception, and somatosensory perception of (5) prey derived, or (6) oceanographic stimuli. The transmission properties of these signals in the marine environment, and subsequent detection range, vary. Tyack and Miller (2002, table 6.1) summarize the physical attributes of acoustic, light, chemical, and electrical cues underwater and suggest that the effective range of hearing is 10–100 km, vision is 1–100 m, and olfaction is 10–100 m. Here I review the literature for each sensory modality as related to prey localization and capture, and propose the effective scales of utility for foraging dolphins and baleen whales (Table 2).

VISION

Cetacean oculomotor muscles and nerves are well developed and comparable to other terrestrial mammals, and include a pupil adaptation that rapidly adjusts to changes in light levels (Mass and Supin 1997, 2007). However, due to the high density of water, light attenuates very quickly in the ocean, limiting the effective range of visual detection. Hence, vision is assumed to inform baleen whale and dolphin foraging at micro and lower end fine scales.

Dolphins—Despite being highly recognized for their echolocation capabilities, dolphins have roughly equivalent visual and acoustic acuity (Herman *et al.* 1975, Herman 1990, Pack and Herman 1995; except for the river dolphins that have poor visual acuity). With vision capabilities comparable to dogs and cats, dolphins can see farther in air (approximately 8.2 min of arc at 1 m)—potentially useful to detect surface cues regarding feeding opportunities, such as seabird activity—than in water (approximately 12.5 min of arc at 2.5 m) where nearby prey capture is critical (Herman *et al.* 1975, Herman 2010). Overall, dolphins have good visual resolution, acuity, brightness and contrast sensitivity, motion detection, rudimentary color sensitivity, and distance perception that serves important biological functions, including prey

Table 2. Maximum functional range as described in the literature review of sensory modalities employed by dolphins and baleen whales while foraging, and the assumed effective scales of each modality as applied to scale–of–senses schematics (see Fig. 1, 2).

Sensory modality	Dolphin		Baleen whale	
	Maximum distance	Assumed scale	Maximum distance	Assumed scale
Vision	12.5 min of arc at 2.5 m (in water)[a]	Micro, Fine	7–11 min of arc[b]	Micro, Fine
Audition: Sound production (echolocation)	<173 m[c]	Micro, Fine	No data	(Not included in schematic)
Audition: sound reception of prey signals (passive listening)	<630 m[d]	Micro, Fine	No data	Micro, Fine, Meso
Audition: acoustic signals from conspecifics and other sources	<25 km[e]	Micro, Fine, low end Meso	Jaw sounds: estimated 1.6 km;[f] Vocalizations: typically 9–45 km,[g] up to 1,000s of km[h]	Micro to Large, most significantly at Meso
Chemoreception	Olfaction: <2.5 m[i]	Micro, Fine (but minimal support for this modality)	No data	Fine, Meso, Large, Macro
Magnetoreception	No data	Meso, Large, Macro	No data	Meso, Large, Macro
Somatosensory perception: Prey-derived stimuli	No data	Micro	No data	Micro
Somatosensory perception: Oceanographic stimuli	No data	Fine to Macro	No data	Fine to Macro

[a]Herman et al. 1975.
[b]Murayama et al. 1992, Mass and Supin 1997.
[c]Au et al. 2009.
[d]Gannon 2003.
[e]Janik 2000.
[f]Watkins 1981, Brodie 1993.
[g]Stafford et al. 2007, Clark et al. 2010.
[h]Croll et al. 2002, Oleson et al. 2007.
[i]Kremers et al. 2016b.

detection (Herman 1990, Kremers *et al.* 2016*a*) and likely prey discrimination. In air, dolphins likely use their accurate vision to assist with air born prey capture (*e.g.*, Torres and Read 2009), while in water the visual sensitivity to depth perception and motion increases prey detection, discrimination, and capture at close range, where the utility of the forward-focused biosonar field deteriorates (Watkins and Wartzok 1985, Mobley and Helweg 1990).

Baleen whales—The visual acuity of minke (*Balaenoptera acutorostrata*) and gray (*Eschrichtius robustus*) whales is approximately 7 and 11 min of arc, respectively (Murayama *et al.* 1992, Mass and Supin 1997). These estimates are based on anatomical studies, not behavioral, and indicate that baleen whale visual acuity is lower than that of the cat, but similar to those of the rabbit and elephant (Murayama *et al.* 1992).

AUDITION

Due to the effective transmission of sound and limited penetration of light in water, the functional role of the auditory system in all cetaceans is highly evolved and used to aid foraging, predator detection, communication, and navigation (Tyack and Clark 2000, Johnson *et al.* 2009). Furthermore, the structure of the auditory system in both mysticetes and odontocetes allows for more complex signal processing mechanisms than in most land mammals (Ketten 1997). While cetaceans produce and receive acoustic signals across a broad range of frequencies and spatial scales for multiple purposes, the following synopsis is limited to acoustic signals related to prey localization and discrimination across various scales. Full reviews of dolphin and baleen whale acoustic sensory systems are available from (Au *et al.* 2000, Tyack and Clark 2000, Kremers *et al.* 2016*a*).

In general, dolphins are mid to high frequency specialists (10–80 kHz) with a shorter acoustic sensory range (<25 km; Janik 2000) due to attenuation properties than baleen whales that are low frequency specialists and are able to sense acoustic signals across larger distances, extending up to hundreds of kilometers (Wartzok and Ketten 1999, Tyack and Clark 2000). Audiograms have been generated for many species of dolphins held in captivity and generally indicate a peak in hearing sensitivity between 40 and 80 kHz, with species-specific variation in the lower frequencies (Wartzok and Ketten 1999). Relative to odontocetes, considerably less research has been conducted on the acoustic abilities of baleen whales because of the challenges associated with holding such large animals in captivity. Yet, anatomical studies show that baleen whales have the only mammalian ears fully adapted to underwater hearing and employ the broadest acoustic range of any mammal group, spanning from the infra- to ultrasonic range (Ketten 1997). The majority of most baleen whale vocalizations is below 1 kHz, and playback experiments on several baleen whale species have demonstrated good directional hearing capabilities based on orientation, localization, and predator response (Parks *et al.* 2007).

No measured audiograms currently exist for any species of mysticete (Tubelli *et al.* 2012). Yet, models indicate that the functional hearing of baleen whales commonly extends to 20 Hz, with several species (blue, *Balaenoptera musculus*; fin, *B. physalus*; and bowhead whales, *Balaena mysticetus*) predicted to hear at infrasonic frequencies as low as 10–15 Hz, and the upper functional range predicted to extend to 20–30 kHz (Ketten 2004, Yamato *et al.* 2008, Tubelli *et al.* 2012). The low frequency calls produced by baleen whales facilitate large propagation distances, dependent on transmission loss due to environmental conditions and source level. Baleen whale vocalizations often propagate 9–45 km away from the source depending on

conditions and species (Stafford *et al.* 2007, Clark *et al.* 2010), and extreme detection ranges of blue and fin whale calls in oceanic environments have been made at hundreds to thousands of kilometers (Stafford *et al.* 1998, Tyack and Clark 2000).

Sound Production

Dolphins—The echolocation capabilities of dolphins, using specialized anatomical adaptations (Hemilä *et al.* 2010), are well recognized and have been studied extensively (Wartzok and Ketten 1999). The maximum target detection range of a 30-cm-long Atlantic cod (*Gadus morhua*) by a bottlenose dolphin (*Tursiops truncatus*) and harbor porpoise (*Phocoena phocoena*) using echolocation was 173 m and 27 m, respectively (Au *et al.* 2007). Extrapolation based on the interclick intervals of baiji (*Lipotes vexillifer*), finless porpoises (*Neophocaena phocaenoides*), and bottlenose dolphins determined that the echolocation of free-ranging dolphins is adapted to various distances, sometimes up to 140 m (Akamatsu *et al.* 1998). Additionally, Au and Snyder (1980) demonstrated that bottlenose dolphins are able to detect a small object (~8 cm) at distances over 100 m. In addition to prey localization, distinction of prey type and quality is critical to foraging success, and bottlenose dolphins may be capable of such prey discrimination through echolocation, as studies have shown that dolphins are able to discern objects by using the echo spectrum shape, changes in target strength, peak and center frequency (DeLong *et al.* 2006), and receive acoustic cues that can distinguish among multiple species of fish (Au *et al.* 2009). Sound production through echolocation is assumed to inform dolphin foraging at micro and fine scales.

Baleen whales—While echolocation capabilities in baleen whales have not been demonstrated, it has been hypothesized that mysticetes use echoes from low frequency sounds to detect topography, conspecifics, the deep scattering layer, and prey (Tyack and Clark 2000), including the description of "megapclicks" in foraging humpback whales (*Megaptera novaeangliae*; Stimpert *et al.* 2007). Many fish species that are prey of baleen whales, such as anchovies (*Engraulidae* spp.), have gas-filled swim bladders with low resonant frequencies, which are well suited for long-range detection by baleen whales that are tuned to low-frequency signals (Tyack and Clark 2000). Baleen whales often produce sounds while foraging (D'Vincent *et al.* 1985, Oleson *et al.* 2007), but it remains unknown whether the functional role of these sounds is for communication, prey detection through a type of low-frequency sonar, or other purpose. In the baleen whale scale-of-senses schematic presented (Fig. 2), sound production through echolocation is not assumed to inform baleen whales at any scale.

Sound Reception

Dolphins—In addition to echolocation as a means of acquiring information about prey, there is evidence of passive listening by dolphins for prey, which also facilitates prey discrimination (Barros 1993, Barros and Wells 1998, Gannon *et al.* 2005). Dolphins prey on many species of soniferous fish so that an effective foraging strategy may be to search for prey by listening for their calls. For example, aggregations of Atlantic croaker (*Micropogonias undulates*), an important prey species for bottlenose dolphins in the coastal regions of the northwest Atlantic Ocean, may be audible for up to 630 m (Gannon 2003), much farther than an echolocation range. Gannon *et al.* (2005) hypothesized that the optimal search mode for dolphins may be a combination

of echolocation and passive listening. Acoustic signals from prey through passive listening is assumed to inform dolphin foraging at micro and fine scales.

Baleen whales—There is no evidence of passive listening by baleen whales for prey aggregations. However, given the well-developed auditory system of baleen whales and its fundamental sensory role in the aquatic environment, it is logical that whales process acoustic information on prey density, type, and location gained through passive listening. Certain types of baleen whale prey, such as anchovy, herring, and krill, produce low-frequency sounds while schooling (Moulton 1960, Wiese and Ebina 1995, Tyack and Clark 2000, Wilson *et al.* 2004) that may act as prey location and quality cues for listening whales. It has also been suggested that baleen whales use passive listening for navigation by listening for relative levels of surface and benthic noise (Norris 1967). Although no experimental evidence currently exists to support the speculation that baleen whales use passive listening to encounter prey patches, for the scale-of-senses schematics (Fig. 2), I hypothesize that baleen whales perceive and respond to biological sounds derived by their prey at micro, fine, and meso scales, based on presented theories and documented acoustic signals from prey.

Acoustic Signals Transmitted by Conspecifics and Other Sources

Acoustic signals received from conspecifics can also inform individuals regarding foraging opportunities. Dolphins are known to forage cooperatively in groups over small distances (*e.g.*, Würsig 1986, Pitman and Durban 2012), while baleen whales may forage cooperatively using acoustic signals over small (*e.g.*, humpback whales: D'Vincent *et al.* 1985, Parks *et al.* 2014) and large distances (Croll *et al.* 2002, Oleson *et al.* 2007). Delphinid use of whistles for communication is well studied (Sayigh *et al.* 1999, Au *et al.* 2000, Janik and Sayigh 2013). The transmission range of bottlenose dolphin whistles has been estimate to be between 1.5 and 25 km depending on frequency and environmental conditions effecting transmission loss (Janik 2000). Baleen whales also may use the acoustic signals of other whales to locate prey patches, especially if whales acoustically advertise foraging opportunities, as hypothesized by Croll *et al.* (2002). There is evidence that fin whales produce distinct nonvocal sounds from jaw movements or water and surface noise while feeding that other whales respond to from over a mile away (Watkins 1981, Watkins and Wartzok 1985, Brodie 1993). Furthermore, the diet of many cetaceans overlap with other marine mammal, seabird, and fish species, and therefore individuals may eavesdrop on acoustic signals produced by other species to inform foraging opportunities (Evans 1982, Clua and Grosvalet 2001, Davoren *et al.* 2010, Thiebot and Weimerskirch 2013). Likewise, cetaceans may use acoustic signals from anthropogenic noise sources as foraging opportunity cues, such as ship propeller cavitation (Thode *et al.* 2007) and acoustic pingers (Cox *et al.* 2004). Acoustic signals from conspecifics and other sources is hypothesized to inform dolphins at micro, fine, and low end meso scales in the scale-of-senses schematic (Fig. 1), and to inform baleen whale foraging at scales between micro and large, but most significantly at the meso scale (Fig. 2).

CHEMORECEPTION

Few studies on cetacean chemoreception, including gustation and olfaction, have been conducted and the results from such studies are often contradictory (see Kremers *et al.* 2016*b* for review). Furthermore, chemoreceptive structures common in terrestrial mammals may be modified, displaced, reduced, or absent in modern cetaceans
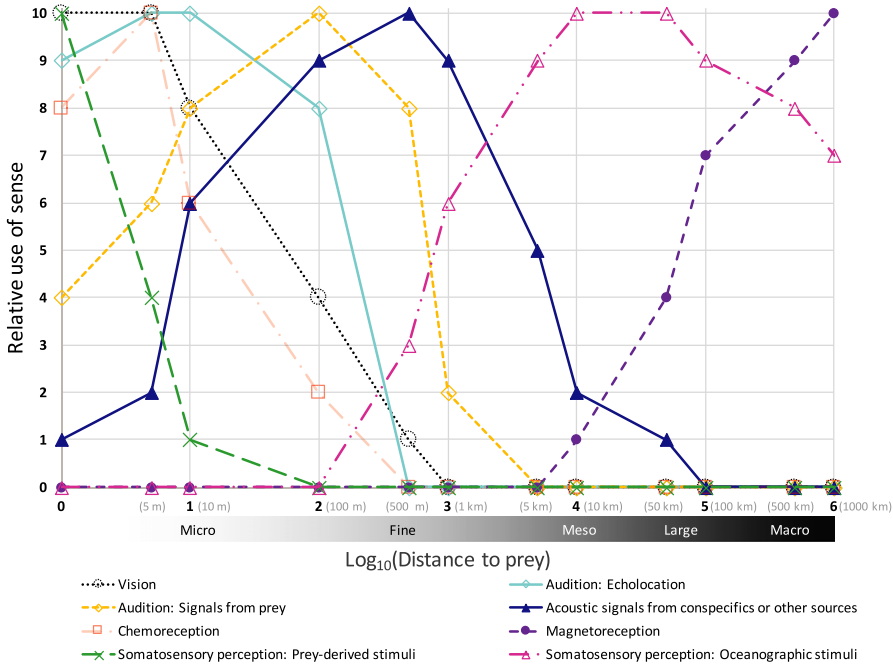
Figure 1. Scale-of-senses schematic of the hypothetical interchange of sensory modalities used by dolphins to locate prey at variable scales. The line for chemoreception is faded to denote a lack of support for the sensory system in dolphins. *X*-axis on log scale, with equivalent metric distance given in gray type, and associated scale below. *Y*-axis ranks the relative use of each sensory modality between 0 (no contribution) and 10 (highest contribution) relative to its own information capacity, not relative to other senses.

due to evolutionary adaptation to life in an aquatic environment (Kremers *et al.* 2016*a*). Genetic evidence indicates that all cetaceans lack functional receptors for sweet, bitter, and umami flavors (Kishida *et al.* 2015). However, the salt taste receptor genes are intact and there is behavioral evidence that dolphins can detect salt, bitter, sour, and sweet flavors (Nachtigall and Hall 1984, Friedl *et al.* 1990, Kishida *et al.* 2015). Again, although genetic and some anatomical studies indicate that odontocetes have also lost olfactory capability (Pihlström *et al.* 2008, Kishida *et al.* 2015), other evidence indicates well-developed olfactory tubercle in odontocetes (Oelschläger and Oelschläger 2009) and chemoreception in the nasal cavity of harbor porpoise (Behrmann 1989). A recent study demonstrated that bottlenose dolphins are capable of perceiving the odor of a dead fish in air at a distance of 2.5 m, and discriminate between fish and nonfish flavors (Kremers *et al.* 2016*b*). Small fungiform papillae that may be associated with taste buds were recently documented on the dorsal surface of a gray whale calf tongue (Kienle *et al.* 2015), demonstrating evidence of gustation in baleen whales. These indications of chemoreception ability suggest that individual cetaceans may use olfaction and gustation cues to localize and discriminate prey (Kremers *et al.* 2016*b*), or potentially sense salinity levels to evaluate local oceanographic conditions (see Oceanographic stimuli). In the dolphin scale-of-senses schematic (Fig. 1), chemoreception is hypothesized to inform foraging behavior at
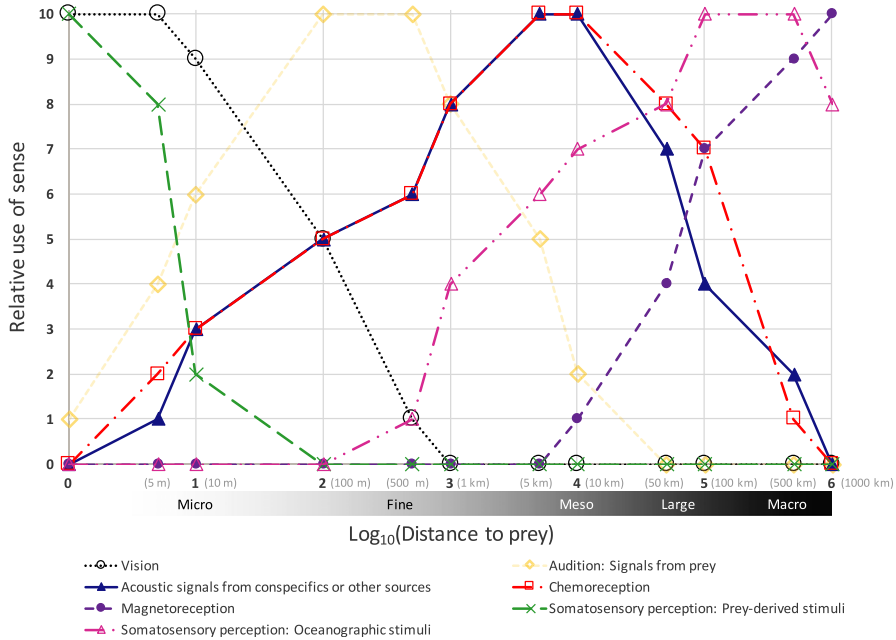
Figure 2. Scale-of-senses schematic of the hypothetical interchange of sensory modalities used by baleen whales to locate prey at variable scales. The line for audition of signals from prey is faded to denote a lack of evidence for this sensory system in baleen whales. *X*-axis on log scale, with equivalent metric distance given in gray type, and associated scale below. *Y*-axis ranks the relative use of each sensory modality between 0 (no contribution) and 10 (highest contribution) relative to its own information capacity, not relative to other senses.

micro and fine scales, yet I acknowledge the minimal evidence to support this sensory modality.

Mysticetes appear to have maintained a functional olfactory system, indicating that they can smell in air (Berta *et al.* 2014, and literature cited therein). In particular, there is mounting evidence that baleen whales use olfaction of air molecules to detect prey patches by sensing the odor dimethyl sulfide (DMS; Thewissen *et al.* 2011, Kishida and Thewissen 2012), which is a volatile compound released by certain species of phytoplankton when they are consumed by zooplankton (Dacey and Wakeham 1986), a common prey item of baleen whales. DMS is detectable within a few meters of the ocean surface, overlapping with the breath intake zone of baleen whale blowholes. Genetic studies also support the hypothesis that baleen whales sense DMS through their olfactory system in order to locate their prey (Kishida *et al.* 2007, Thewissen *et al.* 2011, Kishida and Thewissen 2012) and a preliminary study indicates that foraging baleen whales orient upwind toward odor plumes.[2]

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[2]Hagelin, J., J. Straley, L. Nielson and A. Szabo. 2012. Baleen whales and tubenose seabirds—a colossal chemosensory convergence. 34th Association for Chemoreception Sciences, Huntington Beach, CA. April.

The DMS scent tends to be associated with oceanographic features, including upwelling zones, seamounts and fronts (Nevitt and Bonadonna 2005). Multiple large-scale global studies have found spatial correlations between DMS and productive marine environments (*e.g.*, Simó and Dachs 2002, Belviso *et al.* 2004). Furthermore, DMS features are not ephemeral, but can persist for several days or weeks, with seasonal predictability (Nevitt and Bonadonna 2005). There is strong evidence that the procellariiform group of seabirds (tubenose albatrosses and petrels) use DMS signals at large and fine scales to navigate and detect prey (Nevitt and Bonadonna 2005). The use of DMS olfaction by baleen whales to obtain spatial and temporal cues on the location and density of prey fields has been demonstrated in other far-ranging marine predators including procellariiform seabirds (Nevitt 1999, 2008), loggerhead sea turtles (*Caretta caretta*; Endres and Lohmann 2012), harbor seals (*Phoca vitulina*; Kowalewsky *et al.* 2006), and African penguins (*Spheniscus demersus*; Wright *et al.* 2011). Like these species, baleen whales must locate patchy prey over the vast ocean. However, not all phytoplankton release DMS upon senescence, and not all baleen whales eat zooplankton in surface waters that would enable the release of DMS. Yet, a baleen whale targeting zooplankton with associated DMS off-gassing may build an odor landscape through olfaction that describes the distribution and quality of foraging opportunities.

Olfaction of DMS scents by procellariiforms operates across a continuum of scales, including large scales to aid navigation toward productive zones and fine scales to help locate prey items (Nevitt 2000, Nevitt and Bonadonna 2005, Nevitt 2008). Proximity to the source of DMS production likely regulates the strength of the signal perceived by the individual. DMS may be dispersed over large distances by air currents, providing a relatively faint signal used for general orientation, while olfaction of stronger DMS levels may indicate more immediate foraging opportunities. Therefore, chemosenses of DMS through olfaction is assumed to inform baleen whale foraging primarily at fine, meso, and large scales.

Magnetoreception (Biomagnetism)

Magnetoreception, sometimes called biomagnetism, is the ability to sense and interpret the earth's magnetic field. It has been posited that cetaceans use magnetoreception to sense the spatial and temporal variation of magnetic fields to navigate across large distances. However, anatomical studies remain equivocal regarding the amount of magnetic material in cetacean brains (reviewed in Bauer *et al.* 1985, Wartzok and Ketten 1999, Kremers *et al.* 2016*a*). Yet, fin whale migration routes have been correlated with geomagnetic fields (Walker *et al.* 1992). Additionally, experimental evidence indicates that dolphins can discriminate magnetic properties of objects (Kremers *et al.* 2014), and two studies demonstrated correlations between live stranding locations of cetaceans and anomalies in coastal geomagnetic fields (Klinowska 1985, Kirschvink *et al.* 1986). Therefore, biomagnetism is hypothesized to inform both baleen whales and dolphins at meso, large, and macro scales in the presented scale-of-senses schematics (Fig. 1, 2).

Somatosensory Perception

Somatosensory perception includes the sense of touch (*via* pressure), pain, temperature, and body position (Kremers *et al.* 2016*a*). Cetacean skin is well-innervated and very sensitive to touch (Ridgway and Carder 1990), and most cetaceans possess vibrissae at birth, which are quickly lost in odontocetes, but common in adult mysticetes

(Ling 1977, Drake *et al.* 2015). In the scale-of-senses schematics, somatosensory perception is differentiated between detection of prey signals through vibrissae and skin, and reception of ocean property signals (*e.g.*, temperature).

Prey-derived Stimuli

Dolphins—The skin of bottlenose dolphins is furrowed by small ridges that may function in tactile sensing (Ridgway and Carder 1990). Furthermore, the sensitivity of dolphin skin to tactile stimuli is greatest around the blowhole, eyes, snout, lower jaw, and melon, where sensitivity is equivalent to the most sensitive areas of human skin (Ridgway 1986; genital region not examined). This cephalization of increased tactile sensitivity corresponds to the most proximate body regions with prey encounters; therefore somatosensory perception of prey is assumed to inform dolphin foraging at micro scales. Additionally, electroreception, which is the ability to sense electric fields, has recently been documented in hairless vibrissal crypts on the rostrum of the Guiana dolphin (*Sotalia guianensis*), and Czech-Damal *et al.* (2011) hypothesize that this species, as well as potentially other dolphins that forage benthically or in turbid areas, use electroreception to detect prey. For the purpose of the scale-of-senses schematics, electroreception is grouped with somatosensory perception because it is poorly understood in cetaceans and, if electroreception informs dolphin foraging behavior, it is likely to do so at micro scales.

Baleen whales—Although odontocetes possess only a few hairs or none (except Indian river dolphins, *Platanista* spp.), mysticetes have extensive vibrissae primarily around the upper and lower jaws, which are thought to aid tactile detection of food (Ling 1977). These vibrissae are highly enervated, so that the frequency and magnitude of deflection caused by encounters with zooplankton denote information on prey biomass density to the whale (Ling 1977, Kenney *et al.* 2001). Functional links have been hypothesized between the foraging strategies and targeted prey items of baleen whale species with the density and location of vibrissae on the species of whale (Yablokov and Klezeval 1969). Additionally, a newly discovered sensory organ embedded between the two mandibles of the lower, unfused jaw of rorqual whales (Balaenopteridae: blue, fin, sei [*B. borealis*], Bryde's [*B. brydei*], minke, humpback whales) is believed to provide mechanosensory information for coordinating rapid and complex lunge-feeding events (Pyenson *et al.* 2012). Hence, it is assumed that baleen whales use vibrissae and/or the lower jaw sensory organ for tactile sensations of prey fields at micro scales.

Oceanographic Stimuli

A multitude of studies have correlated cetacean distributions with oceanographic patterns at many scales (Hamazaki 2002, Cotté *et al.* 2011, Torres *et al.* 2013), including associations with water temperature or frontal location (Tynan 1998, Bost *et al.* 2009). However, no information on how cetaceans functionally sense these oceanographic patterns is available, including temperature (Ridgway 1999). Baumgartner and Mate (2003) hypothesized that northern right whales use a variety of cues to detect the bottom mixed layer, above which their prey aggregates, including shear at the top of the layer, turbulence within the layer, or temperature and salinity properties. Norris (1967) suggested that cetaceans use water mass characteristics, including temperature and stratification, to navigate. Although unconfirmed, it has also been hypothesized that the vibrissae and follicles of whales function as pressure

receptors that are capable of detecting currents (Ling 1977). Additionally, cetaceans have retained the ability to taste salty flavors (see Chemoreception), which I hypothesize assists cetacean navigation through their ability to sense ocean salinity gradients, as many studies have documented correlations between cetacean distribution and salinity levels (Tynan *et al.* 2005, Torres *et al.* 2008) and proximity to river mouths (Derville *et al.* 2016).

Given the impressive navigational feats of cetaceans to travel vast distances and arrive at precise locations that are often associated with oceanographic features, I build on Norris' hypothesis by suggesting that whales and dolphins gain information about their location and desired direction of travel through skin, vibrissae, or gustation sensory mechanisms that enable individuals to gauge water temperature and salinity. Sensitivity to oceanographic conditions, through somatosensory perception or gustation, is assumed to inform both baleen whale and dolphin foraging at fine to macro scales.

THE SCALE-OF-SENSES SCHEMATICS

The scale-of-senses schematics illustrate the hypothetical interchange of information derived from six sensory modalities (vision, audition, chemoreception, magnetoreception, and somatosensory perception of prey or oceanographic stimuli) used by dolphins (Delphinidae; Fig. 1) and baleen whales (Fig. 2) to locate and evaluate prey at various scales. As described above, there are many knowledge gaps concerning the effective range and sensitivity of sensory modalities to prey signals. Therefore, these schematics are intended to assist with hypothesis generation and identification of knowledge gaps concerning how cetaceans localize, discriminate, and capture prey, which is an important, yet minimally discussed, aspect of foraging ecology research. At each scale, each sensory modality is subjectively rated by the user (myself in this case) based on taxa, ecosystem, and sensory knowledge between 0 (no contribution to prey localization or evaluation) and 10 (highest contribution to prey localization or evaluation) relative to its own information capacity, not relative to other senses. Hence, a 10 indicates the scale at which that sense provides maximum information to the individual, regardless of what other modalities might also be contributing. These subjective ratings between 0 and 10 allow for relative comparison within each modality, so a sensory modality rating of 6 is twice as informative to an individual as a rating of 3 for that modality. Therefore, these conceptual models are flexible, allowing users to proceed despite knowledge gaps, while also fostering hypothesis testing, identification of these gaps, and revision when new information becomes available. The discussions below regarding the scale-of-senses schematics for dolphins (Fig. 1) and baleen whales (Fig. 2) are based on my review (above sections) and evaluation of scale-specific use of senses to inform foraging opportunities, including hypothesized relationships when data gaps exist.

Dolphins—For oceanic dolphins traveling across ocean basins to encounter prey aggregations at macro scales >1,000 km, information on directionality is likely dominated by magnetoreception and somatosensory perception of oceanographic conditions such as water temperature and salinity. Due to attenuation of acoustic, visual, chemical, and prey-derived somatosensory signals through water, the other sensory modalities do not transmit pertinent information at these large scales. For nonoceanic dolphins with home-ranges less than 100 km, the relative use of biomagnetism may be reduced based on functionality, while somatosensory perception of oceanographic stimuli may be most effective at fine to meso scales, such as detection of salinity

gradients in coastal environments. Once the dolphin (oceanic or neritic) begins to search for prey at meso and fine scales of 10 km to 100 m, I postulate that information capacity of magnetoreception is eliminated, and that the acoustic pathways provide the greatest information of prey availability from echolocation, and acoustic signals from prey (passive listening) and conspecifics or other sources. As the dolphin hones in on prey for capture at fine scales of less than 100 m, sensory information from vision starts to provide important information along with acoustic cues. Only at the finest scales of under 10 m does somatosensory perception (and possibly electroreception) of prey provide useful information to a foraging dolphin. (Chemoreception may also inform dolphins of prey occurrence at these micro scales, but little is known of this ability; therefore the coloration of this line is faded in Fig. 1.)

Baleen whales—At the largest macro scales, as a baleen whale migrates toward a foraging ground over 1,000 km away, the individual's primary pathway for information on directionality is likely magnetoreception. Somatosensory perception of large-scale oceanographic patterns, such as temperature and salinity that may denote location of currents and frontal gradients, also primarily contributes at macro and large scales as the individual uses these features to navigate toward foraging grounds. As the whale nears a foraging ground at large scales of 100–10 km, the individual may still use somatosensory cues of oceanographic variation, but will likely begin use of acoustic signals from conspecifics or other marine animals about the location of foraging opportunities, and possibly to search for prey aggregations using chemosenses of DMS for information on persistent, large-scale patterns of DMS distribution (if this is a relevant prey signal to the whale). According to my depiction of baleen whale foraging in this scale-of-senses schematic, when the scale of prey search reduces toward meso scales of 10–1 km, both olfaction of DMS and acoustic signals from conspecifics and other sources are the dominant senses used to encounter prey patches, with some information provided by somatosensory perception of oceanographic conditions. These senses remain informative to the whale at fine scales, and if low-frequency acoustic signals from prey are available, the whale may perceive and respond to this information primarily between 5 km and 10 m. Yet, given the lack of data regarding this information pathway, the coloration of this line is faded in the schematic shown in Figure 2. At micro-scales <100 m, I posit that the whale becomes most reliant on information transmitted through visual and somatosensory cues of prey density and distribution to encounter and capture localized prey patches.

Discussion

Like humans (Bryant *et al.* 1972) and great apes and monkeys (Davenport and Rogers 1970), cetaceans likely integrate multimodal sensory systems to assess their environment. In order for cetaceans to forage efficiently, and potentially employ theoretical processes like optimal foraging (Emlen 1966, Krebs 1978) and marginal value (Charnov 1976), the individual must respond dynamically to sensory cues. Although such integration of sensory information has not been proven scientifically, it has previously been suggested that dolphins physiologically integrate visual and auditory sensory streams of information (Herman 1990, Mobley and Helweg 1990). With these scale-of-senses schematics, I hypothesize that the sensory modalities of cetaceans operate at many scales as an individual moves between phases of migration, large-scale search for prey aggregations, fine-scale search for prey patches, discrimination of prey quality, and ultimately prey capture.

Logistics of animal care and the marine environment limit our experimental ability and hence knowledge on the functional range of most sensory modalities used by foraging cetaceans. Many cetacean sensory modalities have not been thoroughly examined (Table 2), and the schematics presented here are intended to be hypotheses regarding the scales over which cetaceans perceive their environment. However, this framework can serve as a starting point to develop and test hypotheses regarding how cetaceans integrate various information sources at multiple scales to increase foraging success. Much is still unknown about the senses used by cetaceans to locate prey, especially at fine-scales (Tyack and Clark 2000), such as how a baleen whale localizes a discrete zooplankton aggregation. Examples of hypothesis generation based on a scale-of-senses schematic can be derived by my attempts at illustrating how dolphins (Fig. 1) and baleen whales (Fig. 2) use sensory information to find food:

- In the baleen whale schematic (Fig. 2), given the high degree of overlap between chemoreception (due to DMS olfaction) and acoustic signals from conspecifics and other sources, perhaps mysticetes have evolved to predominantly employ one mechanism or the other, dependent on prey type and behavior.
- The maximum contribution (subjective rating of 10) for each sensory modality appears to be staggered across scales in both schematics (except chemoreception and acoustic signals from conspecifics and other sources; see above hypothesis). Is this spreading of sensory information across spatial scales an evolutionary adaption to increase foraging efficiency?
- Baleen whales may rely heavily on somatosensory perception of oceanographic conditions at large to macro scales to encounter foraging areas (Fig. 2). Movement and habitat use analysis of baleen whale orientation of travel between tracking data and a broad suite of oceanographic variables (*e.g.*, temperature at depth, salinity, pH) when greater than 50 km from a foraging area may reveal important oceanographic cues and functional migration pathways.
- A conservation application of these schematics is to consider how, and at what distance, cetaceans perceive fishing gear. These answers are undoubtedly species, ecosystem and gear specific. Application of a scale-of-sense schematic to each case may help managers develop gear modifications or spatio-temporal mitigation strategies to reduce entanglements based on a species' scale-dependent sensory abilities. For instance, if vision and prey-derived somatosensory stimuli are the major sensory pathways at micro scales less than 10 m (Fig. 2), where entanglement with pot-line fishing gear is problematic, then perhaps efforts to differentiate the look and feel of fishing line material are worth further exploration.

The schematics also highlight the scales at which sensory knowledge gaps are relevant and therefore necessitate increased research efforts. Furthermore, the scale-of-senses schematics are completely adaptable to new data, and species, prey and ecosystem specific information. The simple Microsoft Excel spreadsheets used to develop these schematics are available as a template (Appendix S1) and can be easily modified by any user to examine the functional scales of sensory modalities to enable foraging opportunities. Case-specific modification of the scale-of-senses schematic can guide studies of habitat use, foraging behavior, and movement and spatial ecology by highlighting relevant senses, scales, and environmental covariates to be emphasized during study design and data analyses. Therefore, regardless of disagreement over my hypothesized effective scales of cetacean sensory modalities in Figures 1 and 2, the flexibility of this exercise allows any user to apply these schematics to inform and

guide their spatial and behavioral ecology studies. Furthermore, this scale-of-senses approach can be easily applied to other taxa.

Although memory is not a traditional sensory modality, it could also be included in the schematics because memory provides individual cetaceans with information on desired directionality during large scale movements, or navigation at fine scales based on habitat features. There is strong evidence in multiple cetacean species of maternally directed fidelity to migratory destinations, including foraging grounds (Baker *et al.* 1990, Carroll *et al.* 2015). These traditional pathways may be culturally (Rendell and Whitehead 2001) and/or genetically facilitated (Carroll *et al.* 2015), but ultimately the individual can use this information as memory for directionality. Although matrilineal inheritance likely cannot account for sub-meso scale environmental variability that drives prey dynamics, this mechanism may also be used as meso, macro, and large scale guides to foraging grounds, especially in migratory baleen whales. There is strong empirical evidence of high memory capacity of dolphins (Herman 2010). Therefore, it is probable that dolphins memorize features within their home-range seascape that are associated with foraging opportunities, such as particular channels, mudbanks, or seagrass beds. Memory may enhance dolphin foraging ability at fine to micro scales.

Efforts to understand and accurately predict cetacean distribution patterns at all scales are prolific and frequently provide important information for conservation management (Gregr and Trites 2001, Vanderlaan *et al.* 2009, Torres *et al.* 2013). Habitat models attempt to accurately describe the multiple, nested scales of species-environment relationships (Scales *et al.* 2017), and the choice of analysis scales and environmental data layers dramatically influences model accuracy and reliability. The scale-of-senses schematic can aid these habitat use and modeling efforts by identifying the functional senses at work relative to the study's scale, thus highlighting appropriate environmental layers for assessment based on the dominant sensory modalities employed at the scale of interest, and recognizing scales at which we have gaps in knowledge about cetacean response to environmental cues. For instance, to the best of my knowledge, no species distribution model for a baleen whale has included the odor field of DMS as a predictor variable. This omission could be a large oversight in efforts to understand the habitat use patterns of certain baleen whales, especially at meso scales where olfaction may be an important sensory modality (Fig. 2). Due to potentially significant temporal and spatial lags between prey aggregations and areas of high productivity typically captured through satellite images of chlorophyll-*a* concentrations (Scales *et al.* 2017), a DMS layer that directly describes zooplankton grazing may be a more useful predictor of foraging baleen whale distribution patterns. Spatial models of two seabird species that included climatologies of sea surface DMS concentrations produced high predictive capacity of distribution patterns across a large-scale marine landscape (Humphries *et al.* 2012).

Cetacean movement data collected through tracking efforts can also be interpreted within these scale-of-senses schematics because animals change their movement patterns relative to information received from the different sensory modalities. With high-resolution GPS track data we are recording an animals' response to a different set of sensory information than recorded through lower resolution satellite transmitted data. These schematics can also facilitate hypothesis driven tracking studies on sensory cues employed by animals relative to foraging strategy, such as Nevitt *et al.* (2008). Furthermore, we can use novel methods and technologies to fill our knowledge gaps on the effective range of cetacean sensory modalities (Table 2). Meso and fine scale response of baleen whales to DMS could be examined through controlled

behavior studies using deployment of high-resolution multisensory tags (with GPS and accelerometer sensors) and systematic release of the DMS odour in variable concentrations and distances (*i.e.*, Nevitt *et al.* 1995). Additionally, high-resolution tags equipped with video and acoustic capability and ambient water sensors (*e.g.*, temperature, salinity) may be able to address questions related to animal response to acoustic signals from prey, conspecifics and other marine animals, as well as somatosensory perception of signals derived from prey and oceanographic stimuli (*e.g.*, Goldbogen *et al.* 2016, Mate *et al.* 2017).

Additionally, the scale-of-senses schematics can aid our ability to understand how anthropogenic impacts may influence or interfere with cetacean foraging behavior by diagnosing what scales may be disrupted. For instance, increased localized turbidity from seabed dredging may disrupt a baleen whale's sensory modalities at finer scales (vision, somatosensory perception of prey, audition), while shifting habitat availability caused by climate change will likely disrupt the effectiveness of large scale sensory modalities to encounter foraging grounds (somatosensory perception of oceanographic patterns, magnetoreception). Furthermore, as concerns regarding the impacts of ocean noise on cetaceans rise (Nowacek *et al.* 2007, Clark *et al.* 2009, Klinck *et al.* 2012, Holt *et al.* 2015), these schematics can allow us to generate predictions on how anthropogenic sound sources may affect foraging efficiency at various scales. For instance, if acoustic masking from vessel traffic within 50 km of a baleen whale foraging ground is a concern, Figure 2 illustrates that prey localization at distances between 50 km and 100 m may be significantly reduced because whales are highly dependent on acoustic signals (either from prey or conspecifics and other sources) at these scales. For dolphins, acoustic signals are the dominant sources of prey localization and discrimination information between 10 m and 1 km from a foraging opportunity (Fig. 1). Dolphins living in human-dominated coastal environments may be detrimentally effected by acoustic masking of important informational signals at these micro to fine scales (particularly if vessel noise is within the species' hearing range; Dyndo *et al.* 2015, Veirs *et al.* 2016). Again, these scale-of-senses schematics can be tailored to particular species and ecosystems to explore such impacts of anthropogenic activities more precisely.

Conclusions

To forage effectively, cetaceans must build hierarchical foraging landscapes by integrating multimodal sensory systems. The scale-of-senses schematic describes how a foraging cetacean transitions between sensory information as the scales to a prey target changes. Development and interpretation of these schematics can focus cetacean foraging ecology research questions, methods, and results. Furthermore, these scale-of-senses schematics provide a fresh perspective on the mechanistic drivers of cetacean-environment relationships over various scales, fostering a broadened understanding of cetacean foraging ecology. Although simplistic, the scale-of-senses approach to understanding cetacean foraging ecology provides a method to identify scale-specific processes of functional prey detection.

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SUPPORTING INFORMATION

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12426/suppinfo.

Appendix S1. Template for scale-of-senses schematics for baleen whales and dolphins.