The Tactile Senses of Marine Mammals

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The successful return of mammals to aquatic environments has presented numerous sensory challenges to overcome. Aquatic habitats reduce the utility of vision and the type of chemoreception important in terrestrial perception. In several orders, the sense of touch assumed greater importance, especially when enhanced by the development of vibrissal (sensory hair) systems. Species of two extant orders, Sirenia and Cetacea, have lost all of their hairs except for vibrissae. In the former, these hairs cover the entire bodies of the two families, Trichechidae and Dugongidae. Hairs in adult cetaceans are more constrained (e.g., they appear in some river dolphins and baleen whales) and are restricted primarily to rostral regions. Pinnipeds and sea otters retained their pelage, but in addition have elaborated their mystacial and other facial vibrissae. High numbers of vibrissal receptors, associated dense innervation, prominence of neural tracts, and hypertrophy of brain areas associated with touch suggest an importance of tactile senses for aquatic mammals. Experimental testing has demonstrated the exquisite tactile sensitivity of many marine mammal species. Sensory hairs contribute to that tactile sensitivity in both haptic and mechanosensory contexts. Several, if not most, pinniped species, seals and sea lions, can track prey based on mechanoreception alone. It remains unclear to what degree non-vibrissal skin receptors contribute to tactile sensation in most marine mammals. In this review we will discuss the neurobiological and behavioral evidence for the tactile senses of marine mammals.

Keywords: touch, mechanoreception, vibrissae, sensory hairs, follicle-sinus complex, marine mammals

Behavior is dynamic; there is ongoing integrated feedback between sensation and motor events. Furthermore, behaviors that we observe on the order of seconds involve a multitude of neural events that occur in the range of milliseconds. For example, limb movement results in feedback from muscle afferents (e.g., stretch receptors) that can alter excitability thresholds for incoming mechanosensory inputs, thus affecting the influence of the next descending motor signals to the spinal cord, and the course of a motor sequence. Similarly, strong sensory inputs can redirect a current motor sequence, which can then affect near-term excitability thresholds for mechanosensory signals. Thus, the mechanosensory and motor systems are highly interdependent with regard to behavioral function.

Although touch perception includes a variety of senses (e.g., kinesthesia, proprioception, interoception), the majority of research on tactile senses of marine mammals addresses mechanical interactions of the skin, including sensory hairs, and the environment. Within this domain, two types of touch are generally recognized, active and passive touch (Gibson, 1962). Active touch occurs when an organism touches something, and passive touch occurs when something touches the organism. Active touch is purposive or goal-directed (Prescott, Diamond, & Wing, 2011). In passive touch, stimuli impinge on the organism. In marine animals, an important origin of these stimuli is water movement. In both types of touching, reception may occur directly on the skin or indirectly through movement of vibrissae (sensory hairs).

Experimentally, it is much easier to control the sensory environment than to control motor output. Therefore, non-invasive experimental studies of the neural bases of behavior have often focused on the contribution of sensory systems. However, the richness and complexity of natural situations is not well captured by investigations of sensory capabilities that rely on controlled stimuli and repeatable conditions. Nevertheless, such studies have produced a wealth of information that is valuable within the limits of its

applicability. In this review, we will consider both observational and controlled studies, each of which has its strengths and limitations, emphasizing mechanosensation in the context of naturally occurring behavioral ecology. This addresses our short-term goal of pointing toward experiments that will further our understanding of the behavioral capacities of particular species, and the longer-term goal of understanding how sensory and motor neural events interact to create behavior.

In the transition from ancestral terrestrial habitats to aquatic environments, marine mammals developed extensive sensory innovations shaped by natural selection, many of which are focused on detecting prey or food. Among mammals, marine mammals illustrate the power of natural selection for producing often novel sensory innovations for detecting prey in the aquatic environment. The ancestors of sirenians and cetaceans underwent a major evolutionary radiation during the Eocene (~50 million years ago). The ancestors of pinnipeds radiated later, during the late Oligocene (~26-23 million years ago). The extant product of this evolution includes cetaceans (whales and dolphins), sirenians (sea cows), and pinnipeds (seals, sea lions, and walruses). Marine mammals are often defined as those mammals that depend upon the marine habitat for survival (Rice, 1998). Broad lists of marine mammals often include marine otters (*Lontra felina*), polar bears (*Ursus maritimus*), Arctic foxes (*Vulpes lagopus*), and fishing bats (*Noctilio leporinus*), because these species feed upon marine prey. However, in the context of mammalian sensory systems, the distinction of marine versus freshwater becomes irrelevant. Although pinnipeds and sea otters are known for their sensitive sense of touch using vibrissae, many mammals apprehend prey within freshwater aquatic environments and use well-developed sensory systems to do so. Surprisingly, these semi-aquatic mammals include some species of tenrecs, shrews, rodents, moles, possums, and platypuses. Food and prey of this diverse assemblage of aquatic mammals range from algae, zooplankton, benthic invertebrates, and fishes to other aquatic tetrapods (Marshall & Goldbogen, 2015). Concomitantly, a diverse range of sensory systems have evolved to detect these diverse food sources. In addition to foraging, tactile senses are relevant to various social behaviors, orientation, and navigation. Manatees frequently contact each other with flippers, rostrums, and torsos (Hartman, 1979; Marsh, O'Shea, & Reynolds, 2011). Dolphins also engage in a variety of social touching behaviors (Dudzinski, Gregg, Paulos, & Kuczaj, 2010; Dudzinski, Gregg, Ribic, & Kuczaj, 2009; Tavolga & Essapian, 1957), which Reynolds, Wells, and Eide (2000) have suggested are analogous to primate grooming. Although understanding the role of tactile mechanisms in foraging and social behavior is important, much of the research on cetacean mechanoception followed a different path driven by an attempt to determine if dolphins can minimize turbulence and induce laminar flow during swimming (Wartzok & Ketten, 1999).

Currently, for marine mammals, there is much more data on vibrissal-based mechanoreception than on other types of mechanoreception; thus, our review is necessarily skewed accordingly. Until more data on other forms of mechanoreception become available, vibrissal systems are the main thread that unites and differentiates the tactile sensory systems of different marine mammal families. Vibrissal systems may be particularly advantageous in sensing changes in the three-dimensional aquatic environment surrounding marine mammals, often caused by water currents and movement of other organisms, analogous to the function of the lateral line system in many non-mammalian aquatic vertebrates.

Sirenians

Sirenians are herbivorous marine mammals that possess innovations for grasping, excavating, and processing aquatic plants using modified vibrissae. Sirenians transitioned to fully aquatic environments ~50 million years ago, around the same time as cetaceans, but they did so independently (Domning, 2001; Velez-Juarbe, Domning, & Pyenson, 2012). Sirenians are comprised of four families, two extinct and two extant

(Reep & Bonde, 2006). The earliest were the Prorastomidae and Protosirenidae. Modern sirenians are comprised of the Trichechidae and the Dugongidae. Extant trichechids comprise three manatee species: West Indian manatees (*Trichechus manatus*), West African manatees (*T. senegalensis*), and Amazonian manatees (*T. inunguis*). Modern dugongids comprise two species, dugongs (*Dugong dugon*) and the recently extinct Steller's sea cow (*Hydrodamalis gigas*).

Over the course of sirenian evolution there have been ongoing adaptations of sirenians to efficiently gather the plants they eat. Extinct dugongids in the Caribbean exhibited a range of tusk lengths that varied depending on the type of sea grasses they fed upon (e.g., shallow or deep rooted). Later, about 3 million years ago, geological changes (e.g., uplift and creation of the Andes mountain chain in South America) led to increased silica content in aquatic plants, making them more abrasive. This produced the selection pressure for manatees to evolve unique mechanisms of tooth replacement to combat tooth wear and likely allowed manatees to persist in the Caribbean and outcompete dugongs, which lacked a tooth replacement system (Domning, 1982). Dugongs now inhabit mainly the western Pacific and Indian Oceans.

Manatees are usually solitary. The primary social interaction is cow-calf bonding, which includes an extended (~2 yr) period of suckling and learning where to go for food and warm water in more northern climes such as Florida (Reep & Bonde, 2006). Manatees have a low metabolic rate, related to their herbivory on comparatively low-quality food sources and the thermal demands of a fully aquatic existence. They spend many hours per day feeding and resting. It has been hypothesized that sirenian feeding mechanics are optimized for efficiency (Marshall, Clark, & Reep, 1998) due to the large amounts of vegetation (5-10% of body weight/day) that are consumed over many hours per day.

Sirenian sensory hairs. Mammalian sensory hairs are specialized to detect movement, either through direct contact with objects in the environment or due to passive deflection by the air or fluid medium in which they are immersed. Sensory hairs are also called vibrissae, tactile hairs, sinus hairs, or whiskers. Vibrissae are perhaps best studied in rodents, in which mystacial vibrissae (the largest field located on the cheeks) vibrate during rhythmic movements known as "whisking" behavior. Typically, vibrissae of terrestrial mammals function in direct contact with an object (but exceptions exist). The term "sinus hairs" references the circumferential blood sinus present in most sensory hairs. A single vibrissa is comprised of the externally visible hair shaft which is rooted in a subcutaneous follicle-sinus complex (F-SC). A F-SC is comprised of an outer dense connective tissue capsule, circumferential blood sinus, and dense innervation (Rice, Mance, & Munger, 1986). In manatees, as in other mammals, several types of innervated mechanoreceptors are distributed along the membranous wall surrounding the shaft of the sensory hair (Sarko, Rice, Reep, & Mazurkiewicz, 2007). Sufficient movement of the hair shaft causes it to contact the membranous wall of the F-SC, where it excites mechanoreceptors that transduce the energy of mechanical deformations into electrical signals that propagate along peripheral axons, which enter the central nervous system.

Sirenians possess only sensory hairs, and these are distributed over the entire body, though about 30 times denser on the face and head region (Reep, Marshall, & Stoll, 2002; Reep, Marshall, Stoll, Homer, & Samuelson, 2001). Three categories of sensory hairs may be distinguished: perioral bristles that are thick and have large follicles that are densely innervated; bristle-like hairs of the oral disk that are intermediate in thickness, follicle size, and innervation; and, postfacial body hairs that are thin, have small follicles, and receive less innervation. In sirenians, mechanoreceptors have not been identified in the skin itself. It is possible that the presence of sensory hairs distributed over the entire body largely supersedes the need for skin mechanoreceptors.

In the head region, the perioral bristles are located in six fields; some of these bristles are markedly stiff and engage in true grasping to gather and ingest plants during foraging (Marshall, Clark, & Reep, 1998; Marshall, Huth, Edmonds, Halin, & Reep, 1998; Reep, Marshall, Stoll, & Whitaker, 1998). We have named this unique behavior *oripulation* to denote grasping or handling by the sensory hairs and associated facial musculature, in contrast to *manipulation*, which connotes use of the manus, or hand. The oral disk, the expanded upper lip and mystacial region of the sirenian face, contains a dense array of bristle-like hairs that are used during tactile investigation of novel objects and food items (Bachteler & Dehnhardt, 1999; Hartman, 1979; Marshall, Huth, et al., 1998). There are about 2,000 sensory hairs on the head and face region. Each follicle is supplied with 50-225 axons, for a total of ~110,000 axons. The postfacial body exhibits about 3,300 vibrissae, each with a relatively independent field of movement (Reep et al., 2002). Each postcranial follicle is supplied by 20-50 axons, for a total of ~100,000 axons. A similar body-wide distribution of vibrissae is present in dugongs as well as manatees (Bryden, Marsh, & McDonald, 1978; Dosch, 1915; Kamiya & Yamasaki, 1981).

Information from the sensory hairs enters the central nervous system, and a large amount of the manatee brainstem, thalamus, and cortex appears devoted to processing somatosensory information, including that related to hydrodynamic stimuli (Marshall & Reep, 1995; Reep, Johnson, Switzer, & Welker, 1989; Sarko, Johnson, Switzer, Welker, & Reep, 2007; Sarko & Reep, 2007). There is prominent representation of somatosensation in the brainstem and thalamus that appears to represent the fluke, flipper, tactile hairs of the postcranial body, perioral face, and the oral disk topographically (Sarko, Johnson et al., 2007). The presumptive (i.e., defined anatomically but not physiologically) somatosensory cortex is more extensive than the presumptive auditory or visual cortex and represents ~25% of the total cortical area (Sarko & Reep 2007). Cortical representations of the facial hairs are hypothesized to be present in Rindenkerne of area CL1; postcranial hairs are hypothesized to be localized in the small Rindenkerne in area CL2 (Reep et al., 1989; Reep et al., 2002). Rindenkerne are neuronal aggregations found in layer VI of five cortical areas (Marshall & Reep, 1995); they may be similar to the somatosensory barrels of layer IV that process information from single mystacial vibrissae in other taxa, such as rodents.

Murphy (Bauer et al., 2016; C. T. Murphy, personal communication, February 16, 2018) pointed out that manatees do not appear to have developed some of the vibrissal adaptations found in pinnipeds (e.g., elliptical shape in cross-section and beading along the longitudinal access) that reduce sensory interference from turbulence caused by vortex shedding (Hanke et al., 2010). The cylindrical cross-section of manatee hairs might suggest a problem with vortex shedding; however, their hairs are much more compliant than those of pinnipeds, and the animals move at slower speeds. Water may simply flow around or over the hairs without shedding a vortex street (i.e., the flexibility of the hairs and operating speeds resolve the problem of turbulence). This difference between manatees and pinnipeds also suggests that pinniped whiskers and manatee hairs may interact differently with the fluid medium and may receive signals differently. This hypothesis should be explored.

Vibrissal-based feeding behavior. The use of vibrissae to acquire plant material by sirenians is unique among mammals in that both motor and sensory modalities are used extensively. Sirenian mystacial vibrissae differ from other mammalian sensory hairs; they are short, thick, and often referred to as bristles. The perioral bristles of sirenians are organized in a series of discrete fields located on the broad and expanded upper lip margins; a complementary set of bristle fields are located on the lower lip (Marshall et al., 2003; Marshall, Huth, et al., 1998; Reep et al., 2001; Reep et al., 1998). The perioral bristles are enclosed in a series of orofacial

muscles that are hypertrophied (Domning, 1978; Marshall, Clark, & Reep, 1998). Collectively, this assemblage forms a muscular hydrostat (Kier & Smith, 1985). Muscular hydrostats are muscular organs (such as elephant trunks and tongues or squid tentacles) that are capable of highly complex and varied movements (Marshall, Clark, & Reep, 1998; Marshall et al., 2003). This muscular-vibrissal complex is an efficient plant-gathering apparatus. The coordinated actions of bristles are used to crop or clip the blades of aquatic vegetation, and the apparatus can be quite forceful. In fact, the bristles of dugongs can literally excavate the below-ground root system (including rhizomes) from the sea floor. As dugongs feed along the seafloor, this leaves a signature "feeding trail" behind (Anderson & Birtles, 1978). However, manatees and dugongs exhibit different patterns of these movements related to the generalist feeding habits of the former and the exclusively bottom grazing of the latter.

Marshall (Marshall, Huth, et al., 1998) used underwater videography to investigate the movement patterns made by captive Florida manatees during grasping and ingestion of plants that had been placed in holes on a transparent plexiglass surface. Rhythmic movements of the oral region produced a grasping cycle ~600 ms in duration that was repeated for as long as it took to consume the vegetation presented. Each cycle consisted of five component movements: snout contraction, eversion of the stout upper lip bristles with simultaneous jaw opening, grasping of vegetation through lateral to medial movements of the right and left upper lip bristle fields, closure of the lower jaw, and sweeping of vegetation further into the oral cavity by the everted lower lip bristles. In a later study, Marshall et al. (2003) compared feeding mechanics among all extant sirenians; all three living manatee species exhibited the pattern of movement described above, but dugongs used a semicircular medial to lateral to medial sweeping pattern, perhaps related to their benthic foraging on rhizomes. Grasping by the bristles is unique to sirenians. In all other mammals studied, the vibrissae of the facial region are used during tactile investigation but do not perform a grasping function. Marshall also noted that in addition to the bilaterally symmetric movement cycle described above, the right and left bristle fields could be used independently in cases where it was advantageous to do so to obtain food that challenged the performance of the grasping apparatus (i.e., food was presented so that it was difficult to attain). Such behavior clearly shows the integration of tactile sensation with motor response. Likewise, independent reverse movements of the upper lip bristles were also observed during the dislodging of ingested food, which may have been distasteful, from the oral cavity. These observations, incidental to the main focus of defining the mechanics of feeding behavior, are important because they identify unexpected capabilities that expand our appreciation of the range of behavior. This illustrates a strength of controlled studies – the ability to create a novel environment that increases the range of observed behaviors.

These investigations of foraging behavior not only demonstrate the functional characteristics of the exquisite active touch of manatees, but also illustrate the behavioral inseparability of motor and many tactile sensory domains. Motor activity, the movement of facial anatomy, and vibrissae are integral to the act of tactile sensing during feeding; sensory and motor functions occur simultaneously, as food is grasped and ingested.

Manatee tactile behavior and psychophysics. Reports of richly innervated sensory hairs covering facial areas and the body suggest that manatees might have good tactile sensitivity (Dosch, 1915; Reep et al., 1998; Reynolds, 1979). In lieu of comparative cortical and electrophysiological data, F-SC innervation in whiskers serves as an indicator of sensitivity (Marshall, Rozas, Kot, & Gill, 2014). Similarly, neural proxies have been used in inferring facial sensation from crocodyliform trigeminal nerve morphology (George & Holiday, 2013). Wild manatees were observed to use the facial vibrissae during investigations of novel objects; Marshall, Huth, Edmonds, Halin, and Reep (1998) noted that most often the oral disk was used during initial exploration. This involves the eversion of the bristle-like hairs in a "flare" response, whereby facial muscles

act to expand and flatten the oral disk, causing protrusion of the bristle-like hairs just prior to contact. The perioral bristles were often used during subsequent investigation (e.g., interactions with anchor lines), much like the use of macrovibrissae by rodents (Brecht, Preilowski, & Merzenich, 1997). Psychophysical studies on captive manatees confirmed this hypothesis in both active and passive contexts. Active haptic touch was tested through discrimination of textured targets consisting of different width grooves (Bachteler & Dehnhardt, 1999) or different width ridges and grooves (Bauer et al., 2012). West Indian manatees investigated targets with the facial area, including bristle-like hairs on the oral disc, as well as with bristles in the perioral areas. Bachteler and Dehnhardt (1999) reported that an Antillean manatee (*Trichechus manatus manatus*) could discriminate 2.28 mm grooves from a 2 mm standard at a 75% threshold level. Bauer et al. (2012) also used a 2 mm standard in a study of two captive male Florida manatees (*Trichechus manatus latirostris*). They found slightly lower thresholds for the Florida manatees, a related subspecies, with limens of 2.05 and 2.15 mm. Threshold differences between the two subspecies are difficult to support with so few test subjects and might be attributed to variation in methods or individuals. Noteworthy are the low Weber fractions (just-noticeable differences) for both of k = 0.025—0.14, comparable at the higher end of the range to Asian elephants, *Elephus maximus*, using their trunk tips (k = 0.14) (Dehnhardt, Friese, & Sachser, 1997), and comparable to human index finger sensitivity at the lower end (k = 0.04) (Morley & Goodwin, 1983).

Response characteristics suggest that the manatee detection thresholds for active touch are a conservative estimate (i.e., real discrimination thresholds are probably lower). Both Florida manatees investigated by Bauer et al. (2012) always investigated the left target first in a two-alternative forced-choice procedure and made a choice to select that target or shift to the alternative target. Rarely (<1.5%) did they return to the original target after touching the second. The Antillean manatee's performance was also characterized by a side bias on the first choice, in its case, to the right, and infrequent investigation after the second target. That is, both subspecies turned a more sensitive forced-choice procedure into a less sensitive go/no-go procedure (Gescheider, 1997), one that relied on memory for the grating widths across trials rather than simultaneous comparison. The persistence of memory for this tactile task over longer periods is further illustrated by 100% correct performance after durations up to 22 months without rehearsal for the Florida manatees (Bauer et al., 2012).

In naturally occurring behavior, sensory hairs can be stimulated by active movement, which brings them into contact with objects during foraging and exploration. The hairs can also be passively stimulated by water movement. As described below, the sensitivity of this type of mechanoreception was tested with the same two Florida manatees in a series of experiments at Mote Marine Laboratory.

In all of the experiments of passive touch, stimuli were generated by an oscillating underwater sphere, with computer control of frequency and amplitude, which generated vibratory hydrodynamic stimuli. The first experiments tested sensitivity of the facial area, the same area tested in the active touch studies. Both animals detected oscillation-generated water movements between 5 – 150 Hz at about 14 cm from the source (Gaspard et al., 2013), well below their hearing frequency limit of about 250 Hz (Gaspard et al., 2012; Gerstein, Gerstein, Forsythe, & Blue, 1999). Detection thresholds declined from about a micron of particle displacement at 10 Hz to as low as a nanometer at 150 Hz. We do not actually know if manatees are detecting particle displacement, velocity, or acceleration, but because they are simple mathematical transformations of each other, we report only the displacement values.

The role of the vibrissae, as distinct from direct skin reception, was assessed by restricting the vibrissae with masks of variable sized mesh, which allowed a differential number of hairs to protrude. As the numbers of hairs were reduced, the detection thresholds rose (Gaspard et al., 2013), indicating a loss of sensitivity as

the number of mobile vibrissae was reduced. Subsequently, three locations (forward, middle, and rear third) about 20 cm from the stimulus source on the right side and one on the left side (forward) of the postcranial body of the same subjects were tested at the same frequencies as used in the facial experiment (Gaspard et al., 2017). Because the four locations yielded similar thresholds, they were combined and referred to as postcranial sites. Detection thresholds were about one standard deviation higher for postcranial hairs than for facial hairs. To evaluate the contribution of vibrissae to hydrodynamic sensitivity, a 50 cm square was shaved on the side of each manatee and the tests were repeated. Shaving reduced sensitivity by three to four times at 75 Hz, the one frequency at which detection was tested (Gaspard et al., 2017).

The role of vibrissae versus direct skin reception remained ambiguous in these hydrodynamic flow experiments. Although active and passive touch thresholds were elevated when vibrissae were restricted or trimmed, detection still occurred. Reception might be attributed to residual hair movement at the experimental sites or direct activation of the F-SCs. Alternatively, detectable threshold levels might have occurred through movement of full, unrestricted hairs surrounding the restricted site. Although the spatial attenuation of the hydrodynamic stimulus is rapid, following an inverse cube function, it was still likely that hairs outside the mask in the facial study and at the periphery of the 50 cm square in the postcranial shaving experiment were stimulated at above threshold levels. Also, the rough skin of manatees made it impossible to shave the hair completely, leaving remaining stubble perhaps capable of mediating particle flow detection, albeit with reduced sensitivity (Gaspard et al., 2017).

Experiments to test how the passive tactile sense might be used in natural conditions have been implemented to only a limited extent. The hypothesis that the vibrissae provide complex orientation information through the passive touch system suggests that manatees should be able to navigate in opaque conditions by sensing changes in water flow as sea and river bed topography changes or as objects enter their tactile fields. A first step in assessing this functional use of passive touch was a test of stimulus localization (Gaspard et al., 2017). Two manatees discriminated left and right sources of water movement generated by oscillating spheres at frequencies from 25 – 125 Hz at levels greater than 83% for one manatee and more than 92% for the other.

A mammalian lateral line? The sensory hairs of manatees are utilized passively to detect low frequency hydrodynamic stimuli in the range of 5-150 Hz, supporting the hypothesis that they act as a sensory array analogous to the lateral line system of the fish, which operates in a similar range of frequencies. Based on its multiplicity of mechanoreceptors, substantial neural investment, and elaborations of the somatosensory processing regions of the central nervous system (Sarko, Johnson et al., 2007; Sarko & Reep, 2007; Sarko, Rice, et al., 2007), we have hypothesized that the body-wide array of sirenian sensory hairs, together with its central nervous system representations, computes the intensity and direction of water displacements and low-frequency vibrations impinging on the body surface (Reep et al., 2011). This information would be useful for detecting and localizing approaching conspecifics, other animals, water currents, and tidal flows. We are not the first to make such a suggestion. Hartman (1979) hypothesized that the body hairs were used to sense water movements. He suggested that this could facilitate detection of approaching conspecifics and could also be the means by which a group of animals resting on the substrate with their eyes closed rises in unison to breathe. Reynolds (1979) also made a similar conjecture and used the term "lateral line" as an analogy to describe the presumed function of the postcranial hairs. Based on their study of manatee auditory capabilities, Gerstein and colleagues proposed that manatee postcranial sensory hairs might detect low frequency acoustic energy in the form of near-field particle displacements (Gerstein et al., 1999). They found improved detection at low

frequencies when the manatee oriented its postcranial body towards the stimulus. Detection occurred within the range of frequencies (100-200 Hz) that correspond to lateral-line detection in fish.

The sensory hairs on the body of a manatee appear to constitute a three-dimensional array capable of aiding navigation. Manatees are large-bodied aquatic mammals and are often found in turbid water. It is not known what cues they use for orientation as they navigate through their environment and migrate between summer and winter locations. Tracking of manatee movements suggests that individuals are aware of the spatial configuration of their environment and utilize preferred paths to navigate (Slone, Reid, Kenworthy, diCarlo, & Butler, 2012). One example of a complex environment navigated by manatees is the Ten Thousand Islands area of southwest Florida that features numerous small islands. The sirenian array of sensory hairs may be used to detect and localize fixed objects in the underwater environment, including limestone formations and boundaries such as river banks and sand bars. Objects in aquatic media produce a boundary layer and they generate turbulence when introduced in flow fields. Manatees and dugongs may be able to detect these perturbations and utilize them as orientation and/or navigational cues. As mentioned below, hydrodynamic reception in other taxa allows for information about object size and distance to be detected. If the distributed system of postcranial sensory hairs in the Florida manatee is used in a similar way, the large body size of manatees might facilitate this capability by providing a larger detector array.

Pinnipeds

Pinniped vibrissal mechanoreceptive systems. Pinnipeds (seals, sea lions, fur seals, and walruses) made the transition back to aquatic environments ~26-23 MA during the late Oligocene, much later than cetaceans and sirenians. As a consequence, they are amphibious. The sensory ecology of pinnipeds took another evolutionary path compared to cetaceans and sirenians. Although they have substantial tactile sensation capabilities, the pinniped evolutionary path has emphasized enlargement, refinement, and innovation of homologous vibrissal fields (e.g., mystacial and other facial fields) that date back to the origins of mammals, rather than departing from a more traditional body plan regarding vibrissae. In fact, pinnipeds possess the largest mystacial vibrissae of any mammal today (Ling, 1966, 1977); however, even among pinnipeds, vibrissal number, geometric arrangement, morphology, and innervation vary. The largest vibrissal group is the mystacial field, but others exist such as superorbital (above the eyes), rhinal (along the rostrum or nose) vibrissae, and, among terrestrial species, additional fields include mandibular or mental (also found in sirenians), genal (along the cheek), and even carpal (wrist) vibrissae. In general, otariids tend to have fewer mystacial vibrissae that are located more laterally on a long rostrum relative to phocids. This is in stark contrast to the broad, expanded, and mostly anteriorly placed mystacial vibrissae of walruses (*Odobenus rosmarus*; Fay, 1982). The geometric arrangement of walrus whiskers is an adaptation for benthic feeding (Fay, 1982). Many phocids display a spectrum in snout morphologies from broad and short to narrow and long, in which mystacial vibrissae are located anteriorly, or laterally, respectively. For example, bearded seals (*Erignathus barbatus*) are ecologically similar to walruses and possess a broad, short muzzle with anteriorly oriented vibrissae (Marshall, 2016; Marshall, Amin, Kovacs, & Lydersen, 2006; Marshall, Kovacs, & Lydersen, 2008). This benthic foraging phenotype is also associated with an increase in the number of vibrissae in both walruses and bearded seals (Fay, 1982; Marshall, 2016; Marshall et al., 2006; Marshall et al., 2008).

As in sirenians, pinniped follicle-sinus complexes are comprised of a hair shaft and the underlying follicle. Vibrissal hair-shaft morphologies and material properties vary among pinnipeds. Vibrissal hair shafts of pinnipeds are typically classified as smooth or beaded (also, bumpy or corrugated). All phocids possess a beaded or bumpy profile along the tapered shaft length with the exception of bearded seals and monk seals

(Ling, 1977), and possibly Ross seals (*Ommatophoca rossii*; Ling, 1972). All other pinnipeds possess smooth or nonbeaded hair-shaft morphologies. The beaded profile is a repeating sequence of crests and troughs resulting in a three-dimensional sinusoidal profile (Dehnhardt & Kamiski, 1995; Ginter, DeWitt, Fish, & Marshall, 2012; Ginter, Fish, & Marshall, 2010; Hanke et al., 2010; Hanke et al., 2013). Specifically, "The sinusoidal wavelength is on the order of millimeters and the greater and smaller diameters of the cross-section are out of phase by approximately 180 degrees" (Summarell, Ingole, Fish, & Marshall, 2015, p. 2 of 15). However, quadratic discriminant function analyses based on fused traditional morphological and geometric morphological data of vibrissal hair-shaft profiles demonstrated that several functional groups exist among phocids with beaded profiles (Ginter et al., 2012). It is probable that these morphological groups have functional significance and therefore have ecological consequences (Ginter et al., 2012). Also of interest was that at least two functional groups were demonstrated among otariids, which only possess smooth hair shafts, and that they were separated in morphospace from a bearded seal group, which also possess smooth hair shafts (Ginter et al., 2012). Furthermore, cross-sectional profiles of hair shafts vary from elliptical to circular (Murphy, Eberhardt, Calhoun, Mann, & Mann, 2013). These properties directly impact the flexural stiffness of vibrissal hair shafts (Summarell, Ingole, Fish, & Marshall, 2015), resulting in a diversity of potential vibrational frequencies of the hair shaft. Understanding the biomaterial properties of vibrissal hair shafts is critical because the shaft acts as a biomechanical filter (Dykes, 1975; Sane & McHenry, 2009) that modulates the environmental vibrotactile cue that is eventually received by sensory mechanoreceptors within the F-SC. Experiments by Hanke et al. (2010) in which flow and force measurements were integrated with numerical simulations suggest that the beaded profile of harbor seal vibrissal hair shafts, and through inference, other phocids, reduced vibrations by changing the pattern of vortical shedding off the shaft. This results in lower hydrodynamic forces relative to a simply elliptical or circular hair shaft. The functional consequence is that beaded vibrissal hair shafts may suppress self-generated noise during swimming.

Recent comparative data regarding F-SC microstructure and innervation among pinnipeds are beginning to show functional patterns. Available data for phocid F-SCs demonstrate a tripartite organization of blood sinuses (this differs from sirenians and cetaceans); the upper cavernous sinus is apical followed by the ring sinus and the lower cavernous sinus basally. The upper cavernous sinus consistently comprises 40-60% of the total follicular length (Hyvärinen, 1989; Ling, 1966; Marshall et al., 2006; Mattson & Marshall, 2016; McGovern, Marshall, & Davis, 2015; Sprowls, 2017) and is not innervated by a superficial vibrissal nerve as reported in terrestrial taxa (Dörfl, 1985; Rice et al., 1986). The elongated, aneural upper cavernous sinus in phocids is thought to provide thermal protection to underlying mechanoreceptors (Dehnhardt, Mauck, & Hyvärinen, 2003; Mauck, Eysel, & Dehnhardt, 2000). Comparative axon counts of large, ventrolateral macrovibrissae among pinnipeds demonstrate a range of mean number of axons/F-SC from 1,350 to 1,600. However, maximum values in the largest whiskers range from 1,500-2,150 and are related to size of F-SCs (Hyvärinen, 1989; Marshall et al., 2006; Marshal, Rozas, Kot, & Gill, 2014; Sprowls, 2017). Therefore, the innervation investment per F-SC, while 5-10 times greater than terrestrial mammals, is relatively consistent among phocids (Dehnhardt, Hyvärinen, Palviainen, & Klauer, 1999; Hyvärinen & Katajisto, 1984; Hyvärinen, Palviainen, Strandberg, & Holopainen, 2009), and possibly extends to all pinnipeds (Sprowls, 2017).

Micro- and macrovibrissae functional morphology and innervation. The mystacial vibrissal field is divided into macro- and microvibrissae in rodents (e.g., Brecht et al., 1997). Similar morphological and function divisions have also been described in pinnipeds (Dehnhardt, 1994; Dehnhardt, Sinder, & Sachser, 1997; Grant, Wieskotten, Wengst, Prescott, & Dehnhardt, 2013; Kastelein & Van Gaalen, 1988; Mattson & Marshall, 2016; Sprowls, 2017). For pinnipeds performing object recognition tasks (active touch), the behavioral trend is for large, lateral macrovibrissae to be used to determine size, orientation, and general shape

of an object, whereas shorter, more numerous medial microvibrissae are used for fine-scale tactile resolution. This latter behavior is accomplished with multiple contact points using the most ventromedial vibrissae (Grant et al., 2013). This functional region acts as a "tactile fovea" (*sensu* Catania & Remple, 2004). This behavior is similar to manatees using the large perioral bristles to explore novel objects then follow up using bristle-like hairs of the oral disk for finer tactile discrimination (Marshall, Huth, et al., 1998, 2000).

Recent studies have investigated microstructural and innervation differences across the mystacial vibrissal field, which include both macro- and microvibrissae. Using harp seals (*Phoca groenlandica*) as a model system, Mattson and Marshall (2016) reported that the cross-sectional shape of vibrissal hair shafts changes from elliptical laterally to more circular medially. Additionally, the difference in dermal capsule thickness is greatest laterally and diminishes medially. Furthermore, the distribution of axon bundles around the hair shaft within the lower cavernous sinus is asymmetrical laterally and symmetrical medially. The asymmetry of axon bundles is hypothesized to be related to the variation in dermal capsule thickness. Areas of thick dermal capsule in lateral macrovibrissae are likely regions of muscle attachment for protraction of whiskers; the lateral mystacial vibrissae in phocids display the greatest range of movement (from retracted to protracted). Although using axon bundle distribution as a proxy for mechanoreceptor distribution should be done with caution, the data suggest a functional segregation in vibrissal movement and possibly mechanoreception in the most lateral macrovibrissae that may be related to hydrodynamic trail following (see next section below). The number of axons innervating each F-SC decreases from lateral macrovibrissae to medial microvibrissae (1600 to 500 axons/F-SC, respectively). Although this may be a function of size and surface area, Mattson and Marshall (2016) did not detect a significant difference in axon density (number axons/surface area) across the mystacial field. A similar study in California sea lions (*Zalophus californianus*) (Sprowls, 2017) showed a different trend; California sea lions possess smooth elliptical vibrissal hair shafts, and this shape is maintained from large lateral macrovibrissae to the smaller medial microvibrissae. As in harp seals, axon bundles were asymmetrically distributed around hair shafts, but this asymmetry was maintained from macro- to microvibrissae. Innervation (axons/F-SC) also decreased laterally to medially; however, axon densities (axons/surface area) increased and were highest in the ventromedial microvibrissae. This suggests greater sensitivity for these F-SCs and supports psychophysical testing that demonstrates highly sensitive tactile discrimination capability for California sea lions (Dehnhardt, 1994; Dehnhardt & Dücker, 1996).

Tactile discrimination capability of pinnipeds. Early electrophysiological experiments (Dykes, 1975) recorded direct vibrissal stimulation from the maxillary branch of the trigeminal nerve in harbor and gray seals (*Halichoerus grypus*). Approximately 85% of afferent fibers in the infraorbital nerve supplied vibrissae. Approximately 2/3 of all afferent fibers were rapidly adapting and 1/3 were slowly adapting fibers. Dykes (1975) concluded that few rapidly adapting fibers were active at frequencies < 500 Hz and that they required a large stimulus amplitude. Therefore, it was assumed that these seals' vibrissal systems functioned through active touch and that information gained included surface texture as well as shape and size of objects in their environment.

Although using innervation investment and electrophysiological studies are good proxies for sensitivity, psychophysical performance testing is still the standard despite its labor-intensive drawbacks. Harbor seals and California sea lions are the two most studied pinniped species to date regarding mystacial vibrissal function and performance (e.g., Dehnhardt, 1994; Dehnhardt, Mauck, & Bleckmann, 1998). The behaviors for which we have data are active touch behaviors (haptics) and passive touch, including hydrodynamic trail following. Psychophysical testing has been used to quantify the performance of tactile discriminatory capabilities of harbor seals and California sea lions. Two-alternative forced-choice active touch experiments on harbor seals demonstrated that seals could distinguish size differences among a series of

standard disks (Dehnhardt & Kaminski, 1995). Harbor seals were able to achieve Weber fractions of 0.29 (male) and 0.26 (female) for the smallest disks and Weber fractions of 0.13 and 0.08 for larger standardized disks. This performance is as efficient as monkeys using their hands for active touch experiments (Dehnhardt & Kaminski, 1995). When discriminating the smallest of disks, harbor seals would make lateral head movements while keeping the ventromedial-most microvibrissae still, indicating that kinesthesis in addition to mechanosensation is important at this scale. Kinesthesis was not as important for larger disks.

In an effort to measure harbor seal whisker sensitivity, subjects were tested using a waterborne oscillating sphere (Dehnhardt, Mauck, & Bleckmann, 1998). Harbor seals detected hydrodynamic stimuli (distance was controlled and ranged from 5 to 50 cm) throughout the tested frequency range of 10 to 100 Hz, in line with data reported by Dykes (1975) but in a narrower range of frequencies. Particle displacement thresholds were under 5 μm (because data were reported graphically it was difficult to determine peak sensitivity levels). Dehnhardt and colleagues (1998) suggested that harbor seals were responding to the acceleration component of the stimulus at frequencies of 10 – 50 Hz and particle displacement at higher frequencies. Using newer technology, Murphy, Reichmuth, Eberhardt, Calhoun, and Mann (2017) revisited this question and tested harbor seal sensitivity using a vibrating plate coupled with a sinusoidal stimuli delivery system within a psychophysical paradigm. The subject responded to a range of frequencies with peak sensitivity at 0.09 mm/s (0.179 μm particle displacement) at 80 Hz and decreasing sensitivity below 20 Hz and above 250 Hz, describing a U-shaped function. This is 100 times more sensitive than reported for in-air measures. These values agree well with excised whiskers exposed to water flow in a water tunnel; in these experiments, whiskers produced low frequency signals that were < 300 Hz (Murphy et al., 2013). This level of sensitivity is needed for hydrodynamic trail following.

In addition to high tactile discriminatory capability during active touch experiments, harbor seals are also able to detect hydrodynamic trails using their mystacial whiskers only. This is the ability to detect turbulent trails laid down by fleeing fish. Behavioral experiments, in which harbor seals were only able to use hydrodynamic stimuli, demonstrated that they could follow a turbulent trail laid down by a small remotely operated vehicle (Dehnhardt, Mauck, Hanke, & Bleckmann, 2001), as well as a biogenic trail laid down by another swimming harbor seal (Schulte-Pelkum, Wieskotten, Hanke, Dehnhardt, & Mauck, 2007). Seals were able to follow the trails perfectly and could also detect the direction of prior movement when encountering a trail perpendicular to the seal's own line of movement.

Dehnhardt (Dehnhardt, 1990; Dehnhardt & Dücker, 1996) demonstrated that California sea lions are able to distinguish between objects of different shapes and circular disks of different sizes using only their mystacial vibrissae. Sea lions were able to discriminate a difference in size of objects within 5% and an absolute difference within 0.33 cm in disk size. The relative size difference in terms of Weber fraction was 0.26, similar to harbor seals. As with harbor seals, sea lions are able to discriminate holding their microvibrissae still and making small, precise, lateral head movements. Head movements were similar regardless of disk size; therefore, vibrissae must have been detecting differences in deflection. Again, this indicates that kinesthesis is involved in their discrimination capability as well as mechanosensitivity of the F-SCs, although this might be more important in California sea lions compared to harbor seals.

California sea lions are also capable of hydrodynamic trail following. As in harbor seals, sea lions were able to detect turbulent trails within the water using mystacial vibrissae alone (Gläser, Wieskotten, Otter, Dehnhardt, & Hanke, 2011). Although subjects were able to follow linear trails with high accuracy, their performance, although very effective, was not as high as that found for harbor seals (Dehnhardt, Mauck, Hanke, & Bleckmann, 2001; Schulte-Pelkum et al., 2007). One possible functional hypothesis that explains the

difference in trail following performance is the beaded versus smooth vibrissal hair shafts of harbor seals and the smooth hair shafts of California sea lions, respectively.

The capability of discriminating between objects of varying shape and size, as well as following hydrodynamic trails is a function of the underlying vibrissal hair shaft biomechanics, the microstructure and innervation of the F-SC, but also segregation of tactile information from the peripheral nervous system through the central nervous system primary somatosensory cortex. Although data regarding harbor seals are lacking for central nervous system innovations, much more is now known for California sea lion central sensory systems. It is known that tactile information from vibrissae is communicated via the maxillary branch of the trigeminal nerve in pinnipeds. In California sea lions, afferent inputs into the brainstem are segregated into barreloid-like structures (e.g., Sp5c, Sp5v, Pr5). Compartmentalization is continued into the thalamus via an enlarged VPM (ventral posterior) nucleus that represents the head, including vibrissae (Sawyer, Turner, & Kaas, 2016). Although no barrel-like structures are found within S1 (primary somatosensory cortex), there is anatomical evidence of segregation of tactile information via gyri and sulci of S1 (Sawyer, Turner, & Kaas, 2016). Support for segregation of mystacial vibrissae information processing within S1 is available for northern fur seals (*Callorhinus ursinus*) (Ladygina, Popov, & Supin, 1985). Electrophysiological recordings of S1 show a somatotopic map of all body regions, as well as vibrissae. Recordings demonstrate F-SC afferents to S1, despite the lack of a barrel system, are somatotopically organized as distinct regions of somatosensory cortex that receive input from specific column and rows of F-SCs (Ladygina, Popov, & Supin, 1985).

Few data are available for the tactile discrimination capability of walruses. Psychophysical testing of a single walrus, however, demonstrated that they use mystacial vibrissae to detect size differences down to a surface area of 0.4 cm^2 in test objects (Kastelein & Van Gaalen, 1988). As in other pinnipeds, the subject used "longer vibrissae," presumably macrovibrissae, to locate the test object and smaller, most ventromedial vibrissae above the upper lip to discriminate between the smallest objects. As with harbor seals and sea lions, walruses moved their heads suggesting that kinesthesis was as important as mechanoreception. Additional sensory cues may be important to walruses, such as mechanoreception of the lips and perhaps the tongue. It was reported that this individual walrus would often touch the test object with the lips and the tongue (Kastelein & Mosterd, 1989). The diet of walruses is primarily bivalves (Fay, 1982), and they have an unusual method of excavation that includes hydraulic jetting of water (Kastelein & Mosterd, 1989). Because this method of foraging creates substantial bioturbation, vision is not likely a viable sensory mode. It remains to be determined if the tactile sensory abilities of walruses are greater than other pinnipeds. However, their broad short rostrum, expanded lip region, and increased number of vibrissae (~400; Fay, 1982) suggest enhanced discriminatory capabilities. Such a capability may be used for detecting bivalves in the sediment but also perhaps their size, shape, texture, and even species. It is estimated that walruses can excavate and remove the body of a clam from its shell rapidly, up to 6 clams/min (Oliver, 1983).

Although innervation investment, axons/F-SC, is a proxy that is commonly used in lieu of behavioral performance data (George & Holliday, 2013), the relationship between number of axons entering F-SCs and the number of mechanoreceptors that they terminate upon is not well known. To date, the only estimate of mechanoreceptor abundance for pinnipeds is that of Hyvärinen (1995). The number of Merkel-Neurite complexes within a ringed seal F-SC ranged from 10,000 to 20,000. The number of lanceolate endings ranges from 1,000 to 4,000 (Hyvärinen, 1995). As in numbers of axons/F-SC, these mechanoreceptor estimates are much higher than terrestrial mammals. Merkel-Neurite complexes and lanceolate mechanoreceptors of terrestrial mammals range from 500 to 2,000 and 20 to 100, respectively, per F-SC (Hyvärinen, 1995). Although such data suggest that pinnipeds rely heavily on tactile senses and possess more sensitive

discrimination abilities than terrestrial taxa, it also demonstrates the strong selection pressure of the aquatic environment for mechanoreception.

Cetaceans

Cetacean fossils first appear in the record of mammalian radiations of the Eocene epoch, about 50 MA. The earliest whales, archaeocetes, which appeared at this time, included the ancestors of the two extant radiations of cetaceans: mysticetes (baleen whales) and odontocetes (toothed whales). Baleen whales are large, ranging from about 6 m and 3,000 kg for pygmy right whales, *Caperea marginata* (Kemper, 2009) to 32 m and 170,000 kg for blue whales, *Balaenoptera musculus* (Sears & Perrin, 2009). They are primarily pelagic animals, although some species come into shallow waters for breeding or foraging on small invertebrates (e.g., zooplankton, crustaceans, amphipods) and small fish. Odontocetes range in size from under 1.4 m (Rojas-Bracho & Jaramillo-Legoretta, 2009) and 54 kg for the vaquita, *Phocoena sinus,* to enormous male sperm whales (*Physeter macrocephalus*) up to 16 m and weighing over 40,000 kg (Rice, 1989). Toothed whales are ecologically diverse with some species living exclusively in freshwater or in seawater, while others are euryhaline. Species live in rivers, coastal habitats, and open ocean. Prey ranges in size from small crustaceans and fish to giant squid, eaten by sperm whales (reviews in Perrin, Würsig, & Thewissen, 2009). Even within species there can be substantially different diets. For example, resident killer whales (*Orcinus orca*) in the northeast Pacific eat mainly fish, while other sympatric orcas called transients eat other mammals such as pinnipeds and porpoises (Ford et al., 1998). The great differences in morphology and ecology among the cetaceans suggest caution in generalizing from the few species described in detail.

Tactile behavior and sensitivity. Cetacean behavior suggests sensitive tactual receptivity for a variety of functions including navigation, foraging, and social interactions. Various researchers have suggested that dolphins facilitate swimming efficiency by tactually monitoring water flow and adjusting their integument to reduce turbulence (reviewed by Wartzok & Ketten, 1999). Another navigational use of touch is illustrated by Indus River dolphins (*Plantanista indi*), an essentially blind species lacking a focusing lens; they swim on their sides, using one of their flippers to maintain contact with the substrate, presumably to establish their orientation (Pilleri, 1974).

In the social domain, dolphins and other odontocetes contact each other with flippers, flukes, and trunk when they are engaged in social and sexual behavior (Dudzinski et al., 2009, 2010; Tavolga & Essapian, 1957). Self-rubbing, variously attributed to pleasure, play, (Hill & Ramirez, 2014; Kritzler, 1952; Kuczaj, Makecha, Trone, Paulos, & Ramos, 2006), and hygiene (e.g., parasite control, removal of old epidural cells) (O'Corry-Crowe, 2009), suggest tactile sensitivity. Furthermore, Johnson and Norris (1986) speculated that dolphin echolocation may serve a tacto-acoustic communication function. Supporting this speculation are observations that humans can feel dolphins' echolocation signals (e.g., Norris, 1974).

The path for investigating mechanosensory functions in cetaceans has followed a different trajectory from the other marine mammals we have discussed. Traditional behavioral psychophysical experimentation has not been pursued in studies of cetacean touch. Instead, much of the early motivation for studying cetacean tactile senses was related to the speed at which some species swim, putatively much faster than would be expected given their size, body contours, and musculature (Gray, 1936; Wartzok & Ketten, 1999). Gray proposed that reduction in turbulence around the body of a dolphin as it moved through water would reduce the drag sufficiently to explain observed swimming speeds. The search for integument mechanisms for reducing turbulence and increasing laminar flow to increase swimming efficiency generated considerable

subsequent research. More recently, Fish, Howle, and Murray, (2009) determined that no conclusive lines of research support laminar flow over the entire body; rather, drag is minimized by the shape of the body and appendages. Although a major speed/morphology disjunction, Gray's paradox, has not held up to careful scrutiny (i.e., speeds are within expected ranges), skin damping by cetaceans to reduce turbulence remains a viable hypothesis, one that suggests tactile sensitivity.

To understand the skin's role in damping turbulence, it is necessary to understand the skin's sensitivity to pressure and the motor response that alters skin topography. Ridgway and Carder (1990, 1993) following-up on studies by Lende and Welker (1972) and Kolchin and Bel'kovich (1973) studied tactile sensitivity in a bottlenose dolphin using evoked potential techniques to measure somatic responses to tactile stimuli. Using electroencephalograms, they measured responses to a moving coil, piezo-ceramic bimorph, finger taps, and water drops to generate somatic evoked potentials (SEPs). They found greatest sensitivity around the head, including the jaws and around the eyes and blowhole. The most sensitive areas were at the gape of the jaws and around the eyes. Unexpectedly, the heavily innervated area around the jaw crypts was not found to be among the most sensitive. Earlier, Kolchin and Bel'kovich (1973), measuring galvanic skin response (GSR), found similar levels of sensitivity in a common dolphin (*Delphinus delphis*) but in somewhat different areas with most sensitivity under the eye and around the blowhole, with less sensitivity on the snout, and still lower around the dorsal fin. The pressure thresholds reported by Kolchin and Bel'kovich (1973) (10 mg/mm^2 for the head and 40 mg/mm^2 for the trunk) were comparable to those of human hands and lips and sufficient to detect water turbulence.

The sensitivity of dolphin skin needs to be accompanied by a mechanism for damping turbulence if drag is to be reduced. Ridgway and Carder (1993) suggested that motor adjustments of dolphin microvibrations, small tremor-like vibrations constantly present on the bodies of warm-blooded animals, might provide such a mechanism. In their study, a bottlenose dolphin responded to a vibrating stimulus by approximately matching the frequency of that stimulus and increasing the amplitude of the vibratory response. The motor response might provide the means for reducing drag by matching water vibrations impinging on the skin.

The integument of bottlenose dolphins contains post-caudal dermal ridges and rich innervation that might be specialized for pressure transduction (Palmer & Weddell, 1964; Ridgway & Carder, 1990, 1993). Ridgway and Carder (1993) characterized this complex skin structure as "…instrumental in enabling the dolphin to become aware of its body image in relation to the water around it. In other words that the skin had both tactile and proprioceptive functions." (pp. 83-84). As a caveat in interpreting these perpendicular ridges common in odontocetes (Shoemaker & Ridgway, 1991) as contributing to the enhancement of laminar flow, Ridgway and Carder (1993) note that the ridges correspond to "roughness," which should increase turbulence. Clearly, understanding the role of these ridges and microvibrations in active damping of turbulence around swimming dolphins requires more research.

Foraging. Cetaceans, lacking prehensile limbs, capture prey with their mouths suggesting rostral sensory involvement, of which the sense of touch appears to be prominent. Although vision may be used for tracking prey in clear water, turbid and lightless conditions are likely to minimize its importance. Slow rates of chemical diffusion and currents in water relative to air suggest a minor role for taste in orientation toward prey. Olfaction is precluded by the lack of olfactory bulbs in odontocetes. Odontocetes likely use echolocation, the use of reflected sound, to locate prey, as bats do (Pollack & Casseday, 1989), but although the physical characteristics and psychophysics of dolphin echolocation are well studied, its use in feeding behavior is not.

Furthermore, the likely interplay of echolocation and touch at close range has not been investigated to our knowledge. Both baleen and odontocete whales may be able to sense the presence of prey in waters surrounding them through mechanoreception. In addition, several species of cetacean forage in bottom sediments, including gray whales (*Eschrichtius robustus*) (Jones & Swartz, 2009; Nerini, 1984) and bottlenose and river dolphins, presumably sensing prey by touch. Although bottlenose dolphins use echolocation for detecting prey in mud (Nachtigall, Au, Roitblat, & Pawloski, 2000; Roitblat, Au, Nachtigall, Shizumura, & Moons, 1995), they may use touch senses to complement auditory mechanisms.

Basic behavioral psychophysical experiments are needed to establish functional thresholds for sensitivity of the rostral area of odontocetes. In addition, much work remains to be done to establish the tactile reception characteristics of the flippers, flukes, and trunk.

Structure of cetacean hair. In general, in taxa with reduced hair, the distribution of hair that is present is focused in areas of the body that appear to be most important with regard to sensation (Sarko et al., 2011). All cetaceans have vibrissae en utero, but, in most species, hair shafts fall out and the follicles become nonfunctional shortly after birth. Among adult cetaceans, hair is more commonly observed in mysticetes than odontocetes and is present in the head region, where sensitivity is greatest (Ridgway & Carder, 1990, 1993). Vibrissae are present in all the baleen whales studied, including bowhead whales (*Balaena mysticetus),* minke whales *(Balaenoptera acutorostrata),* sei whales *(Balaenoptera* borealis), blue whales (*Balaenoptera musculus),* fin whales *(Balaenoptera physalus),* humpback whales *(Megaptera novaeangliae) (*Japha, 1912; Nakai & Shida, 1948; Yablokov & Klevesal, 1969*),* and north Atlantic right whales *(Eubalaena glacialis)* (C.D. Marshall, personal observation, 1996*).* In bowhead whales (*Balaena mysticetus*), vibrissal hair shafts are present in patches on the upper and lower lips and around the blowhole. The follicles exhibit a dense connective tissue capsule that surrounds an elongated blood sinus that is divided into numerous internal spaces by connective tissue trabeculae. A large nerve bundle enters the base of the follicle. Within the tissue lining the blood sinuses are smaller nerve bundles and corpuscles that appear to be mechanoreceptors (Drake Crish, George, Stimmelmayr, & Thewissen 2015). Similar distribution, microstructure, and innervation have been observed in North Atlantic right whales (C.D. Marshall, personal observation, 1996) and fin whales (Yablokov & Klevezal, 1969). In right whale calves, single hair shafts over the rostrum are associated with raised proturbances on the head that will ultimately become callosities (C.D. Marshall, personal observation, 1996), indicating that callosities may be mechanosensory in function. More recently, this hypothesis has been supported by Mercado (2014; see below). A similar distribution and architecture of stiff hairs is seen in gray whales. Lamellated corpuscles having the appearance of mechanoreceptors are numerous in the lining of the follicle sinus (Berta et al., 2015). Among most species of odontocetes, only rudimentary hairs are seen postnatally, which then disappear (Ling, 1977). However, some odontocetes, primarily river dolphins, have a few hairs distributed on the face postnatally in species-typical patterns; *Pontoporia blainvillei*, one of the river dolphin species, retain rostral hairs as calves (Brownell, 1989). There also is some evidence that kogiids have persistent follicles as juveniles that disappear by adulthood (C.D. Marshall, personal observation, 2004).

Mercado (2014) summarized evidence that humpback whale tubercles are sensory structures. There are ~50 tubercles on the head of a humpback whale, concentrated along the upper and lower jaws, chin, and around the blowhole (similar to the distribution of putative sensory hairs in mysticetes). Each tubercle contains a centrally located hair and its follicle, which exhibits a blood sinus and innervation by ~400 nerve fibers. Some of the nerve endings may be mechanoreceptive, because they form nets with enlarged or spiky endings. It may be that deformations of the tubercle initiate mechanosensation. Such deformations could be produced

by pressure changes, water currents, turbulence, or acoustic stimuli. Mercado (2014) speculated that the tubercles may function analogously to the lateral line system of fishes and amphibians.

Several of the mature river dolphins have prominent stiff hairs or hair crypts along the rostrum (Simpson & Gardner, 1972). Based on photographic evidence provided by Simpson and Gardner (1972, p. 368) from an Amazon River dolphin, *Inia geoffrensis,* the associated follicles appear to have cavernous sinuses and a surrounding dense capsule, suggesting that they are sensory hairs. Layne and Caldwell (1964) described the hairs of *Inia* as flat, non-tappering, bent at the top, and with pits at their base and concluded that they are specialized for tactile sensitivity. In contrast, Hanke and Dehnhardt (2016) reported that these hairs more closely resemble guard hairs, course outer hairs found in the fur of terrestrial mammals. In addition, Dehnhardt (personal communication, February 13, 2018) reported that *Inia* did not exhibit the thermal responses to infrared scanning indicative of a follicle blood sinus as were found in tucuxi (*Sotalia fluviatilis*) (Mauk et al., 2000). The sensitivity of these hairs remains to be established by behavioral tests. Another caution is provided by the fact that although the hairless follicle pits found in other species, such as bottlenose and common dolphins, are heavily innervated (Palmer & Weddell, 1964), functions other than touch may have evolved as hairs were lost during evolution. For example, the facial crypts in tucuxi serve as electrical detectors (Czech-Damal et al., 2012); this is demonstrated both behaviorally and histologically. In *Sotalia,* the F-SCs appear to function analogously as ampullae rather than mechanoreceptors. This is the first account of electroreception in a eutherian mammal. Although the evolution of electroreceptors from mechanoreceptors in mammals is independent phenomenon, the modification of mechanoreceptors to functional electroreceptors is not unknown. Electroreceptive ampullae of Lorenzini in chondrichthyans and electroreceptive ampullae from other fishes are derived embryonically from the lateral line system placodes (Baker, Modrell, & Gillis, 2013).

Unlike studies of pinniped vibrissae, relatively little work has been done on the functional implications of the morphology of cetacean hairs. Murphy (Bauer et al., 2016; C. T. Murphy, personal communication, February 16, 2018) has taken an initial step in studying the vibrissal form of the North Atlantic right whale. These vibrissae are similar in form (circular in cross section) and circumference to manatees, representing a small sensor on a large body platform. Murphy speculated that the vibrissae are scaled to relevant hydrodynamic stimuli such as eddies (i.e., the hair size may relate to the size of the stimuli they are detecting).

Specialization and Convergence of Tactile Sensation Using Vibrissae: Terrestrial to Semiaquatic to Aquatic Vibrissal Innervation

Among mammals, there is evidence for increased aquatic specialization and convergence associated with a progressive increase in F-SC innervation. A comparative method for studying specialization and convergence serves scientists well when trying to understand the function of vibrissae in aquatic habitats (marine or freshwater) as well as the evolution of vibrissae and tactile sensation. Freshwater semi-aquatic carnivory has evolved repeatedly among rodents, shrews, tenrecs, and moles (Benstead, Barnes & Pringle, 2001; Catania, Hare, & Campbell, 2008; Olsen, 2008; Peterhans & Patterson, 1995; Rowe, Achmadi, & Esselstyn, J, 2014; Sorenson, 1962; Stone, 1985; Veron, Patterson, & Reeves, 2008; Voss, 1988). Common aquatic attributes in many of these groups are webbed feet, elongated metatarsals, dense body hair, small pinnae, and particularly stiff mystacial vibrissae (Veron et al., 2008; Voss, 1988). In general, semiaquatic and fully aquatic mammals (e.g., Australian water rat (*Hydromys chrysogaster)* and river otters (e.g., *Lutra sp.*)) have higher vibrissal innervation than terrestrial mammals (Dehnhardt, Hyvärinen, Palviainen, & Klauer, 1999; Hyvärinen

et al., 2009). The innervation investment of F-SCs in terrestrial mammals (e.g., rodents, rabbits, cats, and monkeys) is ~200 axons/F-SC or less (Halata, 1975; Halata & Munger, 1980; Rice, Fundin, Arviddson, Aldskogius, & Johansson, 1997; Rice et al., 1986). However, semi-aquatic mammals possess substantially more innervation per F-SC than terrestrial mammals. Beavers (*Castor sp*) possess 120 axons/F-SC (Hyvärinen & Katajisto, 1984), and Australian water rats (*Hydromys chrysogaster*) have 500 axons/F-SC (Dehnhardt, Hyvärinen, Palviainen, & Klauer, 1999). This trend is exemplified in a comparison of European polecats (*Mustela putorius*, a terrestrial mustelid), European river otters (*Lutra lutra*), and ringed seals (*Phoca hispida*) that demonstrate fully aquatic and semi-aquatic species have 10-fold and 4-fold increases in axons/F-SC, respectively, compared to terrestrial species (Hyvärinen et al., 2009).

A recent example of convergent evolution of tactile sensation using vibrissae is found in sea otters. The innervation investment of sea otters (*Enydra lutris*; Marshall et al., 2014) supports this trend of increased innervation from semi-aquatic to aquatic and, in conjunction with Hyvärinen et al. (2009), provides a direct comparison within Mustelidae. Additionally, sea otters are the most recent group of marine mammals. They arose in the North Pacific during the Pleistocene (Leffler, 1964; Mitchell, 1966; Repenning, 1976) and have only become fully aquatic in the last 1–3 million years (Berta & Sumich, 1999). Due to this relatively recent arrival back to the sea, it was hypothesized that sea otters might have vibrissae that were more similar to terrestrial mammals. Although sea otters may leave the ocean to bask, rest, and give birth on land (Kenyon, 1975), they are significantly more aquatic than river otters (*Lontra sp.* and *Lutra sp.*). The microstructure of sea otter F-SCs are remarkably similar to that of pinnipeds. They possess a tripartite F-SC, the deep vibrissal nerve enters the base (not laterally as in terrestrial species), and the UCS comprises ~40% of the total follicular length and lacks innervation. While this percentage is at the low end compared to pinnipeds, it is similar to that found in southern elephant seals (Ling, 1966). The mean innervation per F-SC is 1339 ± 408.3 axons similar to that of bearded seals (Marshall et al., 2006). Based on sulcal patterns of sea otters (Radinsky, 1968), the somatosensory cortex has been hypothesized to possess two specializations related to their tactile discrimination capabilities. These specializations are increased tactile performance of the manus (paws) and vibrissae. The research of Marshall et al. (2014) supported the hypothesis that the disproportionate expansion of the coronal gyrus in somatosensory cortex of sea otters was also related to the high innervation investment of the mystacial vibrissal array, and that quantifying innervation investment was a good proxy for tactile sensitivity (George & Holliday, 2013). Recently, the hypothesis of sea otter vibrissae and paw sensitivity was confirmed by the behavioral research of Strobel, Sills, Tinker, and Reichmuth (2018). Despite the recency of sea otter return to the marine environment, their F-SC microstructure, innervation, and, presumably, function have converged with pinnipeds.

Discussion

This review summarizes data on tactile sensation in marine mammals and points toward experimental approaches that would further our appreciation of the various ways tactile sensation is used during naturally occurring behaviors. Explorations into the role of mechanosensation in marine mammals, largely done in the last 20 years, have been very fruitful. However, across marine mammal taxa, there is a lack of data that would allow for in-depth comparisons. Much more anatomical data exist than psychophysical data. Knowledge of anatomical variations across taxa, together with comparative behavioral observations, can generate testable hypotheses such as those outlined in the section above on pinnipeds. For the relatively well-studied vibrissal systems, there are more experimental data for sirenians and pinnipeds than for cetaceans. Thus, for a well-defined natural behavior like feeding, there are data on the role of mechanosensation in sirenians and a few pinnipeds and suggestive evidence in some cetaceans, but we are not at the point where a comprehensive theory

can be constructed for marine mammals generally. At present, the data suggest that sensitive vibrissal systems can be advantageous for feeding in the aquatic environment and are used in a variety of ways by different taxa.

In recent decades, a wealth of new knowledge has resulted from applying the comparative approach in a behavioral neurobiological context and has led to the appreciation of convergent solutions to similar behavioral ecological problems. For example, since the 1970s, studies of rodent vibrissae led to a virtual cottage industry linking the peripheral anatomy of hair follicles and their associated mechanoreceptors with the central nervous system pathways that process this information and its role in behavior. This system represents a rich model system for continued research into the neural mechanisms of mechanosensation, specifically factors that might influence sensation and behavior. The rodent research drove our interest in manatee vibrissae, leading to an appreciation of the role of vibrissae in feeding behavior and active touch, as well as in hydrodynamic reception. Similarly, the ubiquity of hydrodynamic reception throughout the animal kingdom (Bleckmann, 1994) informed the fascinating studies of trail following in harbor seals. Likewise, comparisons of behavioral performance reveal much regarding the selection pressures involved in increased tactile sensitivity.

Marine Mammal Sensory Hairs

It is evident that sirenians, pinnipeds, cetaceans, and other aquatic mammals utilize sensory hairs in a variety of ways. This is reflected in variations in hair distribution and F-SC structure, not only between species, but within the body of individual animals. As presented above, mechanoreceptor diversity and innervation density are potent anatomical indicators of the range of complexity that exists at the level of single F-SCs. However, development of a comprehensive theory that applies across taxa will depend upon advances in quantification of peripheral mechanoreceptor types, axon numbers and branching patterns, and resultant peripheral innervation density. The central nervous system regions that process this information are known but remain largely unexplored anatomically and physiologically among marine mammals. We need comparative volumetric data on the sizes of these regions, their neuronal types, and densities. How much variation exists in the patterns of neural activity that result in coordination of sensory input with ongoing motor behavior is also virtually unknown. Lessons from other model systems suggest that although there is great benefit in detailed explorations of single systems, there is much to be gained by studies across taxa because, in many cases, single taxa represent particular experiments done by nature – at the least, variations on a theme and sometimes novel compositions.

Hydrodynamic Reception in Other Taxa

Hydrodynamic reception appears to be of great ecological value, as evidenced by its widespread distribution throughout animal taxa. Various invertebrates and vertebrates use highly sensitive mechanosensory structures to detect unsteady hydrodynamic flow patterns and perturbations caused by potential prey or predators or to monitor their own movements (Budelmann, 1989; Bleckmann, 1994; Leitch & Catania, 2012). Often, these mechanical biosensing structures are small, hair-like, and abundant. Some freshwater insects use these structures to sense benthic flow patterns in streams (Hart & Finelli, 1999; Statzner, 2008). Other small marine crustaceans, like copepods, use hair-like structures called setae to detect very small hydrodynamic signals at depth and near the sea surface (Fields & Yen, 1997; Jiang & Paffenhöfer, 2008; Kiorboe, 2008; Weatherby & Lenz, 2000; Yen, Lenx, Gassie, & Hartline, 1992). Even single-celled protozoans also use hair-like cilia (which are microscopic) to sense flow patterns (Cheer & Koehl, 1987). The smallest

filiform hairs found on insects and crustaceans are some of the most discriminatory sensory organs in the animal kingdom, operating on a microscopic level to detect water particle displacement (Casas & Dangles, 2010). This small scale involves very low Reynolds numbers (Re), indicative of laminar flow and low turbulence, and non-negligible effects from any associated boundary layer, although larger invertebrates like crayfish with relatively long sensory hairs may reach above the boundary layer (Casas & Dangles, 2010). At such small scales, the emergent properties from groups of small hairs may act collectively as the functional sensory unit (Casas & Dangles, 2010). These examples illustrate the myriad of ways in which sensory appendages have been appropriated to facilitate hydrodynamic reception in various taxa and suggest that mammalian sensory hairs are but one form by which animals have enabled hydrodynamic energy to become ecologically useful.

A comparative approach to understanding mechanoreception can provide new insights into marine mammal tactile mechanoreception. For example, much of our knowledge regarding how vibrissae perform in water is based on single vibrissal hair shafts. Groups of vibrissae may react differently when exposed to flow and comparative data may provide indications as to how marine mammal vibrissae may react similarly or differently.

Biomechanical reception of hydrodynamic stimuli has attributes that are intermediate between touch and hearing (Bleckmann, 1994), suggesting that marine mammal sensory hairs may serve a function complementary to audition at low frequencies. In non-mammals, hydrodynamic sensors on the body surface convey useful information about the spatial distribution of a stimulus (Bleckmann, 1994; Teyke, 1989). As an example, many fish use the lateral line for discrimination and avoidance of objects in the aquatic environment (Hassan, 1986). Blind cavefishes utilize self-produced hydrodynamic stimuli to detect objects while moving (Campenhausen, Riess & Weissert, 1981; Hassan, 1989; Weissert & Campenhausen, 1981). Stationary underwater objects create distortions in the flow fields generated by moving animals, and information about object size and distance is obtained by analyzing the velocity distribution of the flow field over the body (Bleckmann, 1994; Hassan, 1989; Windsor, 2014). These capacities may be enhanced in marine mammals due to their large body size.

Behavioral Studies of Touch

Basic behavioral and psychophysical studies of touch have been reported for sirenians (manatees), pinnipeds (harbor seals and sea lions), and an aquatic mustelid (sea otters). These studies have included tests of both active and passive touch in manatees and pinnipeds and just active touch in the sea otter. Bottlenose dolphin touch sensitivity has been studied using evoked potential techniques, but touch in other cetaceans has emphasized morphological studies of the integument, primarily vibrissae or observational studies of behavior. Although the evidence varies among marine mammal families, all species studied show highly sensitive mechanoreception.

As comparative data become available, it will be important to identify metrics that can be used to assess performance across taxa and within sensory modalities. For example, recent data from sea otter paws show that the tactile sensitivity of their paws is greater than with their vibrissae (Strobel et al., 2018). The discrimination threshold with paws was $\Delta I = 0.27$ mm, Weber fraction, $k = 0.13$ versus $\Delta I = 0.47$ mm, Weber fraction $k = 0.23$ for vibrissae, where ΔI is the minimum discriminable difference between the standard and alternative targets. Sensitivity was the same in air and underwater. Similarly to manatees (Bachteler & Dehnhardt, 1999; Bauer et al., 2012) and harbor seals (Dehnhardt & Kaminski, 1995), the subject always went

to the same side target first and either selected that plate or switched and selected the other. Rarely did the subject inspect the same plate more than once; it made between zero and one sequential comparisons. As was the case for sirenians and pinnipeds, this investigation pattern essentially turned a two-alternative forced-choice procedure into a less sensitive go/no-go procedure. In other words, the threshold estimate was conservative.

Comparison of species using vibrissae to make a discrimination indicates that the active touch difference threshold for sea otters (k = 0.23) was less sensitive than for an Antillean manatee (k = 0.14) (Bachteler & Denhardt, 1999) or harbor seals (k = .09) (Denhardt, Mauck, & Hyvärinen, 1998). The difference threshold for a Florida manatee using vibrissae was lower, still (k = 0.05) (Bauer et al., 2012), but somewhat different stimuli were used. Bauer and colleagues used stimuli in which both ridges and grooves varied in width, whereas the other studies used stimuli that varied only in the width of the grooves; ridge width was held constant. In contrast, the threshold for paws fell between the Antillean manatee and harbor seal. Perhaps some of the fine tactile exploratory functions served by the vibrissae in marine mammals without paws are met by the paws in sea otters. Alternatively, individual differences might account of threshold differences, a plausible scenario in studies that tested only one to two animals.

The majority of behavioral studies of touch have emphasized those laboratory procedures we characterized as static measures. More can be learned from this psychophysical research but although these studies are important for understanding receptor and organism processing capabilities, they may not be especially informative about how an animal might use their sensory capacity in natural settings. Gibson (1979) emphasized the necessity of studying perception in ecologically valid formats (i.e., ones that demonstrated what an organism could do under natural circumstances) to fully understand evolved capacities. This type of testing requires subjects to be in motion; it requires detection and discrimination of stimuli within the rich contexts of real life. This level of understanding can be approached in carefully constructed laboratory experiments, such as were seen in the tracking experiments in which pinnipeds followed the trails of miniaturized submarines and conspecifics (Dehnhardt et al., 2001; Schulte-Pelkum et al., 2007).

Reep et al. (2002) hypothesized that manatees might be able to use their exquisite ability to sense minute levels of water movement to orient in dim light conditions. Laboratory experiments in which blindfolded, free-swimming subjects were required to report the presence of objects or discriminate among objects based on physical parameters (e.g., size, form, texture) could illuminate the capacity of manatees to navigate under natural circumstances, something that they clearly do in turbid water conditions or during night-time travel. Similarly, study of the microstructure of manatee food consumption in captive animal conditions elucidated the prehensile and lateralized nature of the manatee sensory/motor utilization of vibrissae (Marshall, Huth, Edmonds, Halin, & Reep, 1998).

It is difficult to study animal senses in the wild; it is hard to identify the specific senses and attention parameters an organism uses without the benefit of laboratory control. Nevertheless, motor activity can be objectively observed and sensory response inferred from that activity. Dehnhardt's and Reichmuth's research groups (Dehnhardt et al., 2001; Murphy et al., 2017; Schulte-Pelkum et al., 2007) inferred tactile sensing from the tracking behavior (motor activity) of blindfolded pinnipeds. Marshall's work (Marshall, Clark, & Reep, 1998; Marshall, Huth, et al., 1998; Reep et al., 1998) inferred touch in describing the fine motor activity involved in manatee eating. Analogous procedures can be used in the wild, although observations might be difficult.

An ideal sense for study in the wild is echolocation. Echolocation provides objective measures not only of active hearing, but also of attention, a difficult factor to measure even in the laboratory. An example

of how echolocation provides attentional information is provided by prey capture studies of bats. Attention to the prey is reflected in changes of echolocation characteristics as a bat approaches and consumes an insect (e.g., Pollak & Casseday, 1989). Active touch provides similar advantages for study. The behavioral action provides a measure of attention and the response topography demonstrates sensory/motor interaction. Study of passive touch, such as demonstrated in pinniped tracking experiments, is a little more ambiguous in the wild because vision and olfaction are not controlled. Olfaction would be controlled if dolphins were studied, as they have no olfaction. In addition, experiments with ocean-trained pinnipeds and dolphins (Ridgway, 1987; Wood, 1973) would allow introduction of some controls, such as blindfolds to control vision and recordings to verify absence of echolocation.

The study of touch within the context of behavioral ecology has lagged behind neurobiological and psychophysical approaches for marine mammals. The notable exceptions of tracking behavior by pinnipeds (Dehnhardt et al., 2001; Murphy et al., 2017; Schulte-Pelkum et al., 2007) and foraging behaviors by manatees (Marshall, Clark, & Reep, 1998; Marshall, Huth, et al., 1998; Reep et al., 1998) provide models for future research on natural behavior and follow Gibson's (1979) proposal for an ecological approach to understanding the senses. The behavioral activity required in these ecological approaches also more clearly links the sensory/motor processes inherent in the umwelts (von Uexküll, 1957) of marine mammals.

Acknowledgements

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