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Source: Zoological Science, 30(2) : 69-75

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.30.69

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ZOOLOGICAL SCIENCE **30**: 69–75 (2013)

[REVIEW]

Somatosensation, Echolocation, and Underwater Sniffing: Adaptations Allow Mammals Without Traditional Olfactory Capabilities to Forage for Food Underwater

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Animals rely mainly on olfaction to locate and track food sources. However, mammals that have evolved to live partially or fully underwater are unable to use traditional olfaction in the foraging process. These animals have subsequently developed alternative underwater foraging techniques. Cetaceans (e.g. dolphins) live exclusively underwater, and most utilize a highly developed sonar system for navigation and tracking of prey. Pinnipeds (e.g. seals) live on land, but forage underwater. These animals' highly sensitive whiskers allow them to locate food sources. Sirenians (e.g. manatees), the only herbivorous aquatic mammals, also use highly developed whiskers during the grazing process. The semiaquatic mammals *Condylura cristata* (star-nosed mole) and *Sortex palustris* (water shrew) have developed the ability to sniff and detect semiochemicals underwater, a discovery that contradicts prior views on the evolutionary relationship between olfaction and aquatic adaptation. The current review details the anatomy of the olfactory systems of these mammals that live and/or forage underwater, and the adaptations they use to follow prey and forage underwater.

Key words: olfaction, vibrissae, bubble technique, Cetacea, Pinnipedia, Sirenia

INTRODUCTION

Most animals use olfaction and gustation cooperatively to locate and consume nutritious food. But mammals that forage for food underwater represent a unique group of organisms that are unable to use olfaction in the typical sense while foraging. Consequently, these mammals have adapted alternative methods to find sustenance in their habitats. The current review focuses on mammals from the orders Pinnipedia, Cetacea, and Sirenia, all of which have evolved from terrestrial mammals. Cetaceans, including whales and porpoises, and sirenians, including manatees and dugongs, are fully aquatic mammals. Pinnipeds, including seals and sea lions, breed on land but forage underwater. In this review, we will discuss what traces (if any) of functioning olfactory systems exist within these orders, and the primary non-olfactory strategies that mammals of these orders employ in the foraging process. We will also discuss research on a group of evolutionary disparate mammals (the water shrew, star-nosed mole, and river otter) that have developed a technique for underwater detection of semiochemicals, challenging prior notions on evolutionary reduction of olfactory features in aquatic mammals.

OLFACTORY SYSTEMS, OR LACK THEREOF

The vast majority of vertebrates have two distinct olfactory systems: the main olfactory system and the vomeronasal system (VNS). The main olfactory system includes the main olfactory epithelium and the main olfactory bulb, and typically serves to detect the quality of volatile odor molecules. The vomeronasal olfactory system includes the vomeronasal organ (VNO) and the accessory olfactory bulb, and primarily serves to detect fluid-phase odorants, many of which function as pheromones (Meisami and Bhatnagar, 1998). Most mammals efficiently locate food through the functioning of these two systems.

Unlike most mammals and fish, fully aquatic mammals have significantly reduced or absent olfactory systems. This inhibits such mammals' ability to forage for food underwater through odor detection. Members of the order Cetacea either have rudimentary olfactory systems, or lack an olfactory system altogether (Tyack, 2000). Kishida et al. (2007) demonstrated that members of Cetacea, including the dwarf sperm whale (*Kogia sima*), Dall's porpoise (*Phocoenoides dalli*), and the Minke whale (*Balaenoptera acutorostrata*) all have a significantly higher number of non-functional olfactory receptor pseudogenes than their close terrestrial relatives. This suggests a diminished role of olfaction, as the number of pseudogenes is inversely proportional to olfactory functionality.

Adult Odontocetes (e.g. sperm whales, beaked whales, dolphins) lack olfactory nerves or olfactory bulbs (Breathnach,

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doi:10.2108/zsj.30.69

1960). However, Buhl and Oelschläger (1986) found that the cetacean harbor porpoise (*Phocoena phocoena*), of the suborder Odontoceti, has an olfactory bulb during early embryonic development. They found that the anlage of the olfactory bulb grew smaller during later development, and that the placodal component disconnected from the telencephalon, effectively eliminating olfaction capabilities.

Studies of the baleen whale and toothed whale found evidence for embryonic development of an accessory olfactory system and terminalis system, and absence of a vomeronasal organ (Buhl and Oelschläger, 1986; Oelschläger, 1989). However, the baleen whale, unlike the toothed whale, shows intact olfactory features in later stages (Cave, 1988; Oelschläger, 1989). Thewissen et al. (2010) examined the anatomy of the olfactory systems of four bowhead whales (*Balaena mysticetus*). They found olfactory bulbs in their specimens, and reported that the olfactory bulbs in one whale weighed 3.7 g and comprised approximately 0.13% of the total weight of the brain, a comparable percentage to old and new world monkeys. Histologically, they found glomerular layers in the olfactory bulbs. This report suggests that these whales may have a functional olfactory system.

Interestingly, Hagelin et al. (2012) suggest that baleen whales may orient towards airborne chemical signals when they surface, and that this could allow them to home in on zooplankton, one of their primary food sources. Zooplankton, which are typically found near the surface of the water, feed on phytoplankton, and the chemical dimethyl sulfide (DMS) is released during this grazing (Dacey and Wakeman, 1986). Kowalewsky et al. (2006) demonstrated that harbor seals can detect ambient levels of DMS, which is associated with favorable feeding locations. Additionally, Nevitt, Veit, and Kareiva (1995) demonstrated that seabirds, such as Wilson's storm Petrel (*Oceanites oceanicus*), use DMS as an attractant airborne chemical cue to locate zooplankton, an underwater food source (also see Nevitt (2008) for a review on this topic). Hagelin et al. (2012) reported that baleen whales orient towards the direction of the wind above statistical chance levels. The hypothesis that they may be orienting towards an upwind odor plume is attractive, but additional experiments are required.

Pinnipeds have both a main olfactory system and a vomeronasal system, which allows detection of volatile and fluid-phase odorants. Pinnipeds cannot inspire air underwater, rendering underwater detection of odorants at the olfactory epithelium impossible, but they do possess olfactory capabilities on land (Reidman, 1990). Sea lions have been known to retreat into the ocean if they smell a human upwind. Additionally, a recent study found that the female Australian sea lion (*Neophoca cinerea*) can identify the scents of its pups through naso-nasal contact, a behavior frequently observed in mother-pup interactions (Pitcher, Harcourt, Schaal, and Charrier, 2011).

Mackay-Sim et al. (1985) examined formalin-fixed tissue from the West Indian manatee (*Trichechus manatus*) and found that the nasal cavity lacked ducts necessary for the vomeronasal system. However, they observed main olfactory structures like olfactory cilia, olfactory epithelium, a perforated cribriform plate where nerve fibers from the olfactory nerve would presumably enter the central nervous system, and rudimentary olfactory bulbs, although they reported that some of these structures were poorly fixed and decomposed.

Together, these results support the theory that mammals more adapted to aquatic life exhibit a greater reduction of olfactory features. Although cetaceans, pinnipeds, and sirenians do not possess traditional underwater olfactory capabilities, animals in these orders have adapted alternative strategies for underwater foraging.

UNDERWATER FORAGING STRATEGIES

Somatosensation

Pinnipeds (walrus, sea lions, seals) are a group of carnivorous mammals that breed on land but feed in the water. These mammals have highly developed mystacial vibrissae, or whiskers (see Fig. 1), that they use in conjunction with acute color vision to navigate their environment and track prey (Griebel and Schmid, 1996; Dehnhardt et al., 2001). The whiskers can detect and analyze changes in underwater vortices to Dehnhardt et al. (2001) demonstrated that the harbor seal (*Phoca vitulina*) can use its whiskers to detect wakes caused by swimming fish, allowing them to track the fish and ultimately feed on them. The experiments placed a small submarine into a tank and propelled it through the water. It was then removed, and a seal was quickly introduced into the tank. The seal was able to follow the trajectory of the submarine utilizing vortices left in its wake. Furthermore, the seal was able to complete this task while blindfolded, but not while its whiskers were covered. Researchers concluded that seals use their highly evolved whiskers to compensate for the lack of underwater olfactory capabilities. As demonstrated in another study of similar design, the California sea lion (*Zalophus californianus*) also uses its mystacial vibrissae for hydrodynamic trail following (Gläser et al., 2011). Unlike in harbor seals, the sea lions' performance degraded with increased delay between removing the submarine and placing the animal in the tank.

Qualitative differences between the whiskers of sea lions and seals may explain variations in the animals' performance. Miersch et al. (2011) isolated single whiskers of both animals and tested the whiskers' response to underwater wakes. For both types of whiskers the researchers cal-

Fig. 1. A close-up picture of a sea lion (*Zalophus wollebaeki*) reveals a dense matrix of vibrissae. These tactile end-organs function to detect particles and vortices in the underwater environment. Photo by RM Hallock.

culated a signal-to-noise ratio (SNR), or ratio of the power between ‘wanted’ signals and background noise. Results showed that while both whisker types responded accurately to vortices in the water tank, as supported by the aforementioned studies of these species, harbor seal whiskers significantly reduced background noise compared to California sea lion whiskers (Miersch et al., 2011). Walruses are the other members of the pinnipeds, but the role of their whiskers is largely unexplored. Future experiments should examine whether walruses use their whiskers to respond to underwater vortices and ultimately locate food sources.

Little research has focused on the foraging techniques of sirenians, but mammals of this order have a highly developed somatosensation system that may aid in the foraging process. As with pinnipeds, sirenians have sensitive vibrissae that help these animals navigate the environment, with the aid of color vision (Griebel and Schmidt, 1996; Newman and Robinson, 2006). The West Indian manatee has over 5300 vibrissae covering its entire body; about 2000 of these vibrissae are located in the facial region (Reep et al., 1998). Manatees use their facial hairs for different functions (Bachteler and Dehnhardt, 1999) and both facial and postfacial vibrissae help the manatee detect hydrodynamic stimuli and navigate its environment (Reep et al., 2011). However, only facial vibrissae are used for tactile exploration. When a manatee investigates a potential food source or novel object, it extends oral vibrissae to increase tactile acuity and analyze the object’s qualities. The manatee’s vibrissae are extremely sensitive compared to the nasal appendage of the star-nosed mole or the trunk of an elephant (Bauer et al., 2005). Sarko et al. (2007) investigated the brain anatomy of the manatee, and found that nuclei devoted to somatosensation (particularly stemming from facial vibrissae) were disproportionately large compared to nuclei of other sensory inputs. These findings further support the notion that the manatee’s primary adaptation is their advanced vibrissae. Interestingly, perioral vibrissae (thick pairs of vibrissae around the mouth) are also used to grasp plants during feeding.

Unlike pinnipeds and cetaceans, sirenians are herbivorous and thus tracking is less of the focus than the proper identification of stationary food sources. Future research should test the exact roles of vision and somatosensation in the foraging process. This may be tested using a mask that disrupts the vibrissae from receiving information, or alternatively a blindfold that masks the animal’s vision. Manatees can be observed grazing along the bottom of the water, so it is also possible that contact between postfacial vibrissae and food sources are the animal’s primary food detection mechanism. Yet experimental masking of postfacial vibrissae is unnecessary, as the role of facial vibrissae and color vision can be tested with greater ease.

Echolocation

Dolphins do not have a sense of smell to aid in the food foraging process (Cahill, 2000), and although dolphins do have an acute visual sense, their primary foraging adaptation is of course a highly specialized echolocation system. Echolocation is the production of sound waves and the subsequent obtainment of information from the waves’ reverberations. The returning sounds are variations of the initial sounds produced, and through comparison of these returning signals, dolphins effectively perceive the topology of their surroundings (Jones, 2005).

Dolphins’ vocalizations are produced by air movements in the nasal passage and not the larynx. Recently it has been proposed that the structural “monkey lips”/dorsal bursae (MLDB) complexes on either side of the head are crucial for sound production (Cranford and Amudin, 2004). The MLDB includes phonic lips, which vibrate in response to an increase in air pressure, generating signals upwards of 130 kHz (Cranford and Amundin, 2004). The signals then pass through the melon on the forehead, a structure consisting of special fats that serve to focus outgoing sound waves and project the waves forward (see Fig. 2); interestingly, the melon may filter out frequencies higher than 160 kHz (Madsen et al., 2010; Jones, 2005). Recent research demonstrates that in short-distance prey tracking, the harbor porpoise only produces clicks with the right pair of phonic lips, despite possessing a pair on the left side as well (Madsen et al., 2010). Using just the right pair, dolphins are still able to vary sound output and direction of echolocative clicks (Madsen et al., 2010). Future research should describe the function (if present) of the left pair of phonic lips.

In one of the first studies to suggest that dolphins use echolocation, Kellogg (1958) demonstrated that these animals are able to distinguish between different sizes and types of fish. Though initially making some errors, over time the dolphins were able to accurately choose target fish, even in darkness and in turbid water. The dolphin emitted sounds under the water that increased in frequency and intensity when a target fish was introduced. The author concluded that dolphins are able to distinguish various sizes of stimuli, and navigate the surrounding environment by using echolocation.

Norris et al. (1961) also studied bottlenose dolphins to investigate echolocation and the ability to discriminate stimuli. Though the dolphins were blindfolded with latex cups, the animals were still able to locate targets suspended randomly below the water surface. In a subsequent test, a

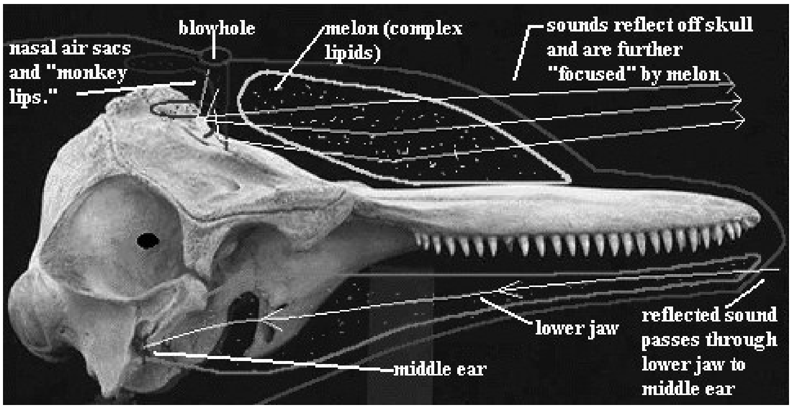

Fig. 2. Right lateral view of Tursiops skull showing current model of echolocation. Figure kind courtesy A.T. White.

maze was created in the dolphin's tank using poles, and fish were dropped into the water near the poles. The blindfolded dolphin was able to get to the fish while avoiding the poles in all but one case. The combined results from these experiments helped demonstrate that echolocation, rather than vision, is primarily responsible for the bottlenose dolphin's ability to avoid obstacles and locate food sources. Research has subsequently demonstrated that the amplitude of the emitted sound waves depends on the range to the target, the ambient noise level in the environment, and the difficulty of the task (Au, 1993; Li et al., 2011).

Herman et al. (1998) used object pairings to determine if the dolphins use vision or echolocation to match novel stimuli. The results indicated that bottlenose dolphins are able to generate a direct shape percept from echolocation, which allows for the accurate matching of various objects. They suggested that echolocation yields a representation of an object that directly corresponds to a vision-derived percept. Additionally, these experiments demonstrate that bottlenose dolphins do not seem to rely on specific details or features of the objects in question, but rather perceive the objects holistically (Herman et al., 1998). Similar findings by Kellogg (1958) and Norris et al. (1961) provide evidence that echolocation in bottlenose dolphins seems to replace sight and smell in the water and allow these mammals to encode their surroundings.

While bottlenose dolphins are used as model organisms for echolocation research, the ability to use echolocation for feeding and navigation is seen in other mammals of the order Cetacea, including various species of toothed whales (Barrett-Lennard et al., 1996; Simonis et al., 2012; Johnson et al., 2004). As in dolphins, toothed whales have two pairs of phonic lips capable of producing vocalizations (Cranford et al., 1996). Lammers and Castellote (2009) suggested that toothed whales actuate both pairs of phonic lips to produce one strong, directional echolocative click. However, Madsen et al. (2010) demonstrated that the harbor porpoise only utilizes its right pair of phonic lips for echolocation, establishing this species as an exception. Unlike toothed whales, baleen whales do not use echolocation. Advanced adaptations past the baleen filter system are presumably unnecessary for foraging. Though echolocation is an effective tool for navigation and locating prey, it is unable to detect pheromones or other semiochemicals in the marine environment.

Although it has been shown that cetaceans rely on echolocation rather than a sense of smell to navigate their habitat and forage for food, the relationship between the acquisition of echolocation and the loss of olfactory capabilities is not well documented. Two hypotheses have been proposed to explain the loss of smell in cetaceans that utilize echolocation verses those that rely on filter-feeding (including the mysticetes): the echolocation priority hypothesis, which suggests that the acquisition of echolocation caused the reduction in importance of olfaction, and the filter-feeder hypothesis, which proposes that the filter-feeders maintain an olfactory system so that they can locate prey based on the particular odor given off by clouds of plankton (Kishida and Thewissen, 2012). These latter authors' analyses of the selective evolutionary pressures on the olfactory marker protein (OMP) genes in various species of cetaceans supported the disparate foraging methods (echolocation versus filter-feeding), providing evidence for the filter-feeder hypothesis over the echolocation priority hypothesis.

Rather than the development of echolocation *causing* the sense of smell loss, it may be that the evolutionary pressures led to a decrease in importance of olfaction in those cetaceans that found echolocation more adaptive to their aquatic habitat. Furthermore, Kishida and Thewissen (2012) suggested that the cetacean sense of smell decreased gradually, and that it is possible that the olfactory marker protein may still have some functionality. Thus, the acquisition of echolocation may not have caused the loss of smell in cetaceans, but instead the evolutionary pressures of the habitat may have led to both. The relationship between the development of echolocation and the loss of a sense of smell in fully aquatic mammals is an important evolutionary question that warrants further research.

Underwater sniffing

Intriguingly, the semiaquatic mammals *Condylura cristata* (star-nosed mole) and *Sortex palustris* (water shrew) have adapted a process that allows underwater detection of semiochemicals. These animals exhale air bubbles onto underwater objects or scent trails and then inhale them through their nose, allowing diffusion of the newly-airborne odorant molecules into the olfactory epithelium (Catania, 2006). This underwater sniffing behavior is known as the bubble technique. A sniff is defined as a sequence of nasal inhalations that increases the velocity and alters the duration of airflow in the nose to obtain olfactory information (Kepecs et al., 2006; Scott, 2006). Experimentation on rodents indicates that only a single sniff is necessary for animals to discriminate between odors and to accurately sample the olfactory environment (Kepecs et al., 2006). Indeed the kinematics of underwater sniffs parallel the kinematics of terrestrial rodent sniffs, in terms of the volume of air (corrected for body weight) exhaled and inhaled, rate of airflow, and frequency (Catania, 2006, 2009). Such similarities support the notion that the underwater sniffing behavior is in fact an olfactory process.

The star-nosed mole is recognized for its ornate soma-

Fig. 3. The star-nosed mole's unique somatosensory organ, composed of 11 pairs of fleshy appendages for tactile perception. The image on the left features the star-nosed mole (*Condylura cristata*) in the midst of an underwater sniff, with bubbles being re-inhaled by the nose. The image on the right zooms in on the nose and the air bubble. Photo courtesy of Kenneth Catania.

tosensory organ (see Fig. 3), but video recordings have also suggested that the animal uses the bubble technique to forage for food underwater (Catania, 2005). In order to determine if the pattern of exhalations and re-inhalations observed underwater were a means of odor sampling, Catania et al. used a forced choice paradigm in which moles were trained to follow a trail of earthworm scent laid on one of two underwater paths (Catania, 2009). To ensure that only olfactory cues were used to choose/follow the path, trails were laid in a channel and covered with a steel grid that allowed the air bubbles to pass through freely, but prevented contact with the mole's nose. Moles chose the correct trail with 85% accuracy. When a finer mesh grid prevented bubbles from contacting the scent trail, performance dropped to chance levels. Such results indicate that the star-nosed mole uses the bubble technique to locate and track prey underwater.

Catania et al. (2008) also recorded water shrews exhibiting the bubble technique. Two shrews were trained to follow an underwater fish scent trail and were able to follow the path in 80% and 85% of the trials, but performed at chance when a grid blocked their bubbles. Interestingly, when a terrestrial shrew (*Blarina brevicauda*) was trained to retrieve food from a shallow well, they were able to retrieve the reward but did not use underwater sniffing (Catania, 2009). This evidence suggests that the bubble technique is an olfactory strategy that has been exclusively adopted by semiaquatic species. Given that the water shrew and star-nosed mole do not share a common semiaquatic ancestor, and seem to have evolved this mechanism of olfaction independently (Catania, 2009).

A recent BBC program, "Halcyon River Diaries," showed footage of river otters exhaling and then re-inhaling bubbles that they expelled directly on the river substrate (James, 2010) (see Fig. 4). Future research should use controlled feeding experiments to test whether these otters use the bubble technique to sniff underwater. The independent acquisition of the technique in different species suggests that it is an efficient and effective means of underwater olfaction. This technique has been found in a range of animals and further investigation may discover additional semi-aquatic mammals that have adapted the bubble technique for underwater foraging.

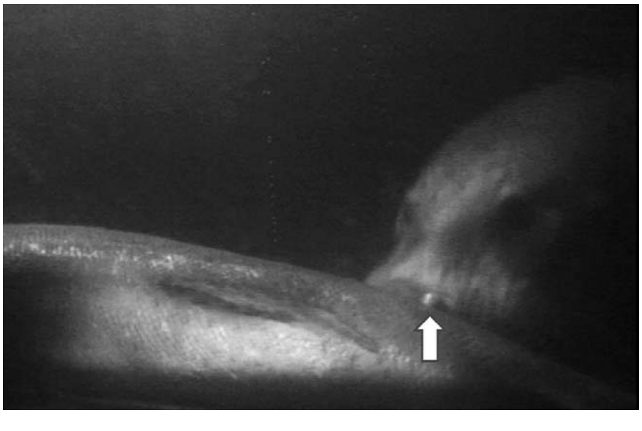

Fig. 4. This image shows a small bubble (white arrow) released from the nostril of a river otter (*Lutra lutra*) that comes into contact with the river substrate. The bubble was re-inhaled, and may represent usage of the bubble technique to sample particles from the underwater milieu. Photo used with kind permission from Charlie Hamilton James.

CONCLUSION

Recent studies provide convincing evidence that ecological adaptation plays a strong role in shaping mammalian olfactory subgenomes (Niimura, 2009). Functional olfactory receptor gene repertoires were reduced independently in the multiple origins of aquatic mammals (Niimura, 2009). Semiaquatic mammals, on the other hand, have variably maintained their olfactory receptor genes and olfactory structures (Kishida et al., 2007). For instance, while *Trichechus manatus* (West Indian manatee) displays evidence of a rudimentary olfactory system (Mackay-Sim et al., 1985), seals have a main olfactory bulb and an accessory olfactory bulb associated with a vomeronasal organ (Freitag et al., 1998). In the case of cetaceans, Kishida and Thewissen (2012) presented evidence suggesting that cetacean olfactory capabilities decreased gradually after adaptation to water, and some of these animals, like the baleen whales, still use olfaction to detect above-water odor plumes (e.g., Hagelin et al., 2012). In addition, Yu et al. (2010) suggested that complete adaptation to an aquatic environment seems to have caused the loss of vomeronasal functionality. Intriguingly, the partially aquatic platypus has a larger repertoire of vomeronasal receptors than many exclusively land-dwelling vertebrates, such as rats, mice, and dogs (Grus et al., 2007), contradicting the prior notion that semi-aquatic mammals necessarily exhibit a reduction in olfactory function as they become further equipped to an aquatic habitat. Future research should explore the importance of these receptors in this animal.

'Birth and death' evolution describes the large gene gains and losses through evolution based on an animal's environment, and further suggests that changes in olfactory receptor genes are quick and dynamic (Niimura, 2009). It is thus reasonable to posit that the bubble technique would be obsolete already if it were simply an intermediary step in the transition to a fully somatosensory underwater foraging adaptation, such as pinnipeds' system of vibrissae. Given that the bubble technique evolved independently in multiple species, it is unlikely to be the result of an evolutionarily degrading olfactory system. Considering the water shrew and star-nosed mole's reliance on underwater sniffing in the foraging process, the bubble technique is obviously an extremely advantageous trait. Although prey may be able to stop movement to avert capture, they may be unable to disguise their scent. The development of the underwater sniffing technique further evidences the lack of a correlation between increased aquatic adaptation and decreased olfactory functioning.

In sum, mammals that forage underwater have developed alternative foraging techniques that allow underwater tracking of food sources. Though previously it seemed that as mammals evolved to a more aquatic lifestyle, their olfactory capacities diminished. However, knowledge of these alternative techniques, such as semiaquatic mammals' use of the underwater sniffing technique, and evidence that baleen whales sniff the air above water to locate underwater food sources, provides evidence that olfaction and underwater adaptation coevolved. These recent discoveries highlight striking ways that some mammals have adapted to foraging underwater, and it is likely that these or other adaptations as used by other species still await discovery.

ACKNOWLEDGEMENTS

The authors thank Kris Banowetz, as well as the anonymous reviewers, for constructive comments that significantly improved the quality of the manuscript.

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(Received May 27, 2012 / Accepted September 10, 2012)