Editorial: biodiversity of sensory systems in aquatic vertebrates

Editorial on the Research Topic

[Biodiversity of Sensory Systems in Aquatic Vertebrates](#)

Introduction

Many sensory systems are more commonly known than others, but all are critical for survival. These include those senses typically described by Aristotle around 300–400 Before the Common Era (BCE), such as sight (vision), hearing (audition), touch (somatosensation), smell (olfaction), and taste (gustation). However, many years of scientific endeavor have shown that these five senses represent only a part of the sensory abilities that are now known throughout the aquatic animal kingdom. The extended repertoire of senses includes the ability for vestibular control (equilibrioception), the sensation of temperature (thermoreception), postural awareness (proprioception), the monitoring of pain (nociception), the use of sonar (echolocation), and the detection of weak electric (electroreception) and magnetic (magnetoreception) fields.

The papers presented in this Research Topic were greatly welcomed and consist of a collection of exciting and well-received articles that incorporated new knowledge on almost all of the known senses in a range of aquatic vertebrates, such as the sarcopterygian lungfishes, both freshwater and marine teleosts, elasmobranchs, marine reptiles, and cetaceans (marine mammals). The papers target many of the known senses in aquatic vertebrates, but are biased toward vision, which reflects the number of active research programs that concentrate on this sensory modality.

Research Topic Contributions and Their Wider Biological Contexts

Kremers et al. extend the breadth of knowledge on the vocal and echolocating abilities in dolphins by examining other aspects of audition, such as context relatedness, and the social function of vocalizations and socio-sexual recognition. However, they also present an excellent review of anatomical, physiological, and behavioral data on vision, electroreception, magnetoreception, somatosensation and chemoreception (olfaction and taste), and emphasize the degree by which dolphins, and other cetaceans, utilize a diverse array of senses (Kremers et al.). These same authors (Kremers et al.) also present novel experimental approaches to determine the little-known chemoreceptive abilities of dolphins by examining their spontaneous behavioral responses to chemical stimuli (Kremers et al.). Collectively, these studies reveal that dolphins may discriminate both odors and flavors, as well as many other critical stimuli. However, it should be emphasized that further research is required, especially with respect to the perception of chemical and auditory cues via water and air, as well as the influence of natural environmental changes and/or human-induced climate-related effects as discussed below (Kelley et al.).

Fasick and Robinson reveal that the eyes of cetaceans (marine mammals) are a great example of an evolving visual system that has become adapted to the visual demands of foraging at different depths within the water column. While most terrestrial mammals have dichromatic color vision that is based on the presence of two classes of cone photoreceptors [containing short-wavelength-sensitive (SWS) and long-wavelength-sensitive (LWS)

photopigments] (Davies et al., 2012), all cetaceans studied thus far lack cone-based color vision: having lost the SWS photopigment and would be considered LWS or L-cone monochromats (Newman and Robinson, 2005). Among the dolphins, porpoises, and beaked whales, the absorbance spectra of rod visual photopigments are shown to be spectrally-tuned to the available radiance spectra at foraging depths, with an inverse relationship between the wavelength of maximum sensitivity of the rod photopigment and depth (Fasick and Robinson, 2000). The average common diving depth of most marine mammals is around 300 m (Ponganis, 2011), reaching an average maximum depth of 1, 300 m (Ponganis, 2011). However, some species of whale (e. g., the sperm whale, *Physeter macrocephalus*) commonly dive to 1, 200 m, but may reach as far as 3, 000 m from the surface (Watkins et al., 1993). Others, such as the two elephant seals *Mirounga angustirostris* and *M. leonina* can dive to depths of over 1, 500 m (Leboeuf et al., 1988 ; Delong and Stewart, 1991 ; Hindell et al., 1991). Due to the filtering of particular wavelengths of light (as well as a reduction in light intensity) with increasing depth (Loew and McFarland, 1990), namely shorter and longer wavelengths, the predominant wavelengths of down-welling sunlight that penetrate to deeper regions of the water column are around 480 nm. As such, rod photopigments in cetaceans (as well as most deep-sea fishes) have adapted to this attenuated light environment and have become spectrally-tuned to shorter wavelengths (Fasick and Robinson, 2000). This also holds true for the spectral tuning of the conserved LWS cone visual photopigments (Newman and Robinson, 2005). It appears that the melanopsins (encoded by one or more *OPN4* genes) in monochromatic

cetacean species are, incidentally, also spectrally-tuned to 480 nm, and are ideally placed to detect the remaining down-welling sunlight (and the bioluminescence that is emitted by over 80% of organisms) that occur at these greater depths. The spectral tuning of melanopsin to 470–480 nm is also common for terrestrial vertebrates (Davies et al., 2010 , 2014), where its main functional role is to detect blue-enriched light at dusk and dawn for the photoentrainment of circadian rhythms, such as the sleep-wake cycle (LeGates et al., 2014). This may also be true for monochromatic cetacean species, where melanopsin may be detecting either (or both) down-welling sunlight and/or bioluminescence for photoentrainment (or the maintenance) of daily biological oscillations of the circadian clock. In addition, some cetacean species may possess a mechanism that inhibits relatively rapid deactivation of light-activated melanopsin photopigments. This process would result in prolonged pupil constriction that results in a useful cellular process for the prevention of rod photopigment photobleaching under photopic conditions (Fasick and Robinson); however, further studies are required to determine if this potentially advantageous adaptation is commonplace in all cetacean species, and perhaps even in a broader range of aquatic organisms that also express melanopsin.

The adaptive capacity for vision underwater in biodiverse extant representatives of the lobe-finned fishes (the ancient sarcopterygian lungfishes, *Protopterus dolloi* , and *Lepidosiren paradoxa*) is revealed in the study by Appudurai et al. . Specifically, they showed that the complement of retinal photoreceptor types (one rod and a single cone-type in adult *L. paradox* , compared to one rod and two cone photoreceptor types in juvenile

P. dolloi) indicates that there are major differences in the capacity to discriminate color in these two " living fossils" and that the visual needs of both species may differ (Appudurai et al.). This is in contrast to the Australian lungfish, *Neoceratodus forsteri* , that possesses three different cone classes in addition to a large rod, thereby optimizing both color sensitivity and wavelength discrimination (photopic vision), and sensitivity to low intensities of light (scotopic vision) (Bailes et al., 2006 , 2007).

The relationship between photoreceptor sensitivity, the underwater spectral environment, and the perception of specific visual stimuli is taken one step further by Pauers et al. . In this paper, the authors investigate the co-evolution of spectral sensitivity and body color patterns in Lake Malawi cichlids as a mechanism for enhancing visual communication. They reveal that distinct spectrally-tuned SWS photopigments serve different functions in fishes, and that the communication of " public" signals [i. e., those widely visible to conspecifics and allospecifics alike, such as the advertisement of services by " cleaner" fishes to " client" species for the removal of ectoparasites Grutter, 1999] is found in species with eyes possessing ultraviolet (UV) sensitivity and that the communication of " private" signals [i. e., those restricted to certain species, such as conspecific nuptial coloration for sexual selection (Endler, 1992), but not predators] is found in species with eyes that lack UV-sensitivity. Species with (vertical) barred patterns have SWS peak sensitivity values at wavelengths that are shorter than either of the other patterns (solid and horizontal stripes). Their results indicate that visual sensitivity and color patterns co-evolved in a correlated fashion, and that the ancestral cichlid was likely to be a UV-sensitive (UVS)

fish with a barred color pattern that first changed its design from barred to striped, followed by a loss of UV-sensitivity (Pauers et al.). Their work reveals that both the arrangement and contrast of color pattern elements may be just as important as color in mate recognition. However, future work is required to elucidate the cellular mechanisms involved in body coloration more broadly in aquatic vertebrates, where sensing external photo-stimuli (e. g., from local lighting environments or coloration/patterns of predators, prey, or potential mates) may be determined either directly via the skin (for example, see Kelley and Davies, 2016) or indirectly via the eye and other photoreceptive organs such as the pineal gland and/or deep brain structures (e. g., the hypothalamus). These ongoing and future studies will be critical in linking the detection of diverse, rapidly changing photic conditions, and physiological/behavioral activities such as camouflage, mate recognition, and the establishment of complex predator/prey relationships.

In the paper by Anthes et al. , it was shown how numerous species of marine fishes display intricate patterns of fluorescence by transforming ambient blue-green light into red light. Based on a series of *a priori* hypotheses regarding adaptive functions, they compare the prevalence of red fluorescence among groups of species based on ecological or biological characteristics, while controlling for shared ancestry. Putative functions of fluorescence include background matching for camouflage in " sit-and-wait" predators, prey localization in species with bright irides, and sexual communication in species showing sexual dimorphic patterns of fluorescence (Anthes et al.). As more ecological data regarding the phylogeny and behavioral ecology of fishes become available, the function of fluorescence

and the environmental conditions under which it operates will be better understood.

[Ladich and Schulz-Mirbach](#) explore one of the main riddles of fish bioacoustic systems: what selective forces and/or constraints led to the evolution of diversity in the inner ear, including accessory hearing structures, and how is morphological variability linked to hearing abilities? They consider that eco-acoustical constraints are more likely to explain the level of diversity in fish hearing sensitivities rather than to facilitate intraspecific acoustic communication. They also propose that low ambient noise levels may have facilitated the evolution of accessory hearing structures, thereby enabling fish to detect low-level abiotic noise and sounds from con- and hetero-specifics, including both predators and prey ([Ladich and Schulz-Mirbach](#)). As more acoustic environments are characterized and assessed with respect to the demands placed on hearing abilities in different species, these relationships will be able to be tested more widely. This should be aided by the ongoing technological advances in bioimaging of the inner ear using magnetic resonance imaging (MRI) and micro-computed tomography (µCT).

Predictions of the roles of vision and olfaction during development in deep-sea grenadier fishes, which occupy some of the deepest regions of the ocean (e. g., 2, 000–6, 000 m) is the subject of the paper by [Lisney et al.](#) . They reveal that at least two species of grenadiers undergo ontogenetic shifts in the relative size of the optic tectum and the olfactory bulbs. Concomitant changes in axonal input (as determined by ultrastructural assessment of nerve axon numbers) are also shown to be associated with the hypertrophy

of these sensory brain lobes, suggesting a shift from a reliance on vision to olfaction during ontogeny, in association with a move to a more scavenging lifestyle and a change in diet. This study shows that sensory demands on teleosts in the deep-sea are high and change during development to optimize survival (Lisney et al.). This emphasizes that not one sensory modality operates in isolation, but that the interplay of multiple senses may be important to all aquatic vertebrates that undergo continual growth of both their peripheral and central nervous systems (such as cartilaginous and bony fishes), especially those that live in extreme environments or naturally move from one environment to another during development. It is predicted that many further investigations will demonstrate the vital importance of integrating different modes of sensory information for species behavior and ultimate survival, especially in the rapidly emerging fields that link systems biology with functional genomics.

Finally, Kelley et al. examine how anthropogenic threats to the aquatic environment impact the senses or determine the reactive responses of particular species to environmental change. The authors review in detail how different sensory modalities can act to influence genetic and non-genetic (developmental) responses to environmental change, which, in turn, may cause knock-on effects in a range of other biological systems. They propose that sensory systems lie at the forefront of how various species respond to environmental perturbation and that urgent efforts should be made to recognize the important role they play in determining fitness, which is critical for understanding the effects of external processes such as habitat degradation and climate change (Kelley et al.). As many aquatic

environments continue to be degraded by human activities, it is critical that the effects of acidification, elevated levels of carbon dioxide, increases in temperature, chemical and noise pollution, and changes in the transmission and detection of sensory signals are monitored ([Kunc et al., 2016](#) ; [Sharma and Chatterjee, 2017](#) ; [Amoatey and Baawain, 2019](#) ; [Chapuis et al., 2019](#) ; Kelley et al.).

Concluding Remarks

The evolution of complex, integrated sensory systems has allowed organisms to sense and respond to continuously changing local and global environmental stimuli. Together, the interplay of these vital biological systems promotes survival via optimized sexual selection strategies, the establishment of hierarchical predator/prey relationships, and the detection and evasion of toxic conditions. This Research Topic consists of a plethora of in-depth original and review articles that provides an overview of different sensory modalities that function in many aquatic vertebrates. Due to the large network of researchers in the field of photobiology, it is not surprising, perhaps, that many papers presented herein focus on vision (or light detection in general), which is regarded as one of the most important and specialized sensory systems to evolve. Nonetheless, other significant senses are discussed in detail, such as chemoreception and audition. In particular, this special assembly of publications highlights the significant increase in recent years of human-induced noise and light pollution, as well as contaminating chemical outflows (e. g., microplastics) into various local and global aquatic systems. Thus, the degree of impairment and species survival will ultimately be dependent upon each physiological level of tolerance and

the propensity for compensatory plasticity (or sensory switching) under natural and anthropogenic environmental changes. Such studies are moving toward the forefront of active research in many interdisciplinary scientific fields and will be vital in determining conservation efforts and influencing environmental policy in the foreseeable future. Finally, as hosts of this stimulating Research Topic, sincere gratitude is offered to all authors for their important contributions to this special issue.

Author Contributions

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

Funding

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Acknowledgments

acknowledge the multitude of expert reviewers that offered their in-depth comments.

References

Amoatey, P., and Baawain, M. S. (2019). Effects of pollution on freshwater aquatic organisms. *Water Environ. Res.* 91, 1272–1287. doi: 10. 1002/wer. 1221

PubMed Abstract | CrossRef Full Text | Google Scholar

Bailes, H. J., Davies, W. L., Trezise, A. E., and Collin, S. P. (2007). Visual pigments in a living fossil, the Australian lungfish *Neoceratodus forsteri* . *BMC Evol. Biol.* 7: 200. doi: 10. 1186/1471-2148-7-200

CrossRef Full Text | Google Scholar

Bailes, H. J., Robinson, S. R., Trezise, A. E., and Collin, S. P. (2006). Morphology, characterization, and distribution of retinal photoreceptors in the Australian lungfish *Neoceratodus forsteri* (Krefft, 1870). *J. Comp. Neurol.* 494, 381–397. doi: 10. 1002/cne. 20809

PubMed Abstract | CrossRef Full Text | Google Scholar

Chapuis, L., Collin, S. P., Yopak, K. E., McCauley, R. D., Kempster, R. M., Ryan, L. A., et al. (2019). The effect of underwater sounds on shark behaviour. *Sci. Rep.* 9: 6924. doi: 10. 1038/s41598-019-43078-w

PubMed Abstract | CrossRef Full Text | Google Scholar

Davies, W. I., Collin, S. P., and Hunt, D. M. (2012). Molecular ecology and adaptation of visual photopigments in craniates. *Mol. Ecol.* 12, 3121–3158. doi: 10. 1111/j. 1365-294X. 2012. 05617. x

PubMed Abstract | CrossRef Full Text | Google Scholar

Davies, W. I. L., Foster, R. G., and Hankins, M. W. (2014). " The evolution and function of melanopsin in craniates", in *Evolution of Visual and Non-visual Pigments* , eds D. M. Hunt, M. W. Hankins, S. P. Collin, and N. J. Marshall (New York, NY: Springer), 23–63.

PubMed Abstract | Google Scholar

Davies, W. L., Hankins, M. W., and Foster, R. G. (2010). Vertebrate ancient opsin and melanopsin: divergent irradiance detectors. *Photochem. Photobiol. Sci.* 9, 1444–1457. doi: 10. 1039/c0pp00203h

PubMed Abstract | CrossRef Full Text | Google Scholar

Delong, R. L., and Stewart, B. S. (1991). Diving patterns of Northern elephant seal bulls. *Mar. Mammal Sci.* 7, 369–384. doi: 10. 1111/j. 1748-7692. 1991. tb00112. x

CrossRef Full Text | Google Scholar

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139, s125–s153. doi: 10. 1086/285308

CrossRef Full Text | Google Scholar

Fasick, J. I., and Robinson, P. R. (2000). Spectral-tuning mechanisms of marine mammal rhodopsins and correlations with foraging depth. *Vis. Neurosci.* 17, 781–788. doi: 10. 1017/s095252380017511. x

PubMed Abstract | CrossRef Full Text | Google Scholar

Grutter, A. S. (1999). Cleaner fish really do clean. *Nature* 398, 672–673. doi: 10. 1038/19443

CrossRef Full Text | Google Scholar

Hindell, M. A., Slip, D. J., and Burton, H. R. (1991). The diving behavior of adult male and female Southern elephant seals, *Mirounga leonina* (Pinnipedia, Phocidae). *Aust. J. Zool.* 39, 595–619. doi: 10. 1071/Zo9910595

CrossRef Full Text | Google Scholar

Kelley, J. L., and Davies, W. I. L. (2016). The biological mechanims and behavioral functions of opsin-based light detection by the skin. *Front. Ecol. Evol.* 4: 106. doi: 10. 3389/fevo. 2016. 00106

CrossRef Full Text | Google Scholar

Kunc, H. P., McLaughlin, K. E., and Schmidt, R. (2016). Aquatic noise pollution: implicatons for individuals, populations and ecosystems. *Proc. Biol. Sci.* 283: 20160839. doi: 10. 1098/rspb. 2016. 0839

PubMed Abstract | CrossRef Full Text | Google Scholar

Leboeuf, B. J., Costa, D. P., Huntley, A. C., and Feldkamp, S. D. (1988). Continuous, deep diving in female Northern elephant seals, *Mirounga angustirostris* . *Can. J. Zool.* 66, 446–458. doi: 10. 1139/z88-064

CrossRef Full Text | Google Scholar

LeGates, T. A., Fernandez, D. C., and Hattar, S. (2014). Light as a central modulator of circadian rhythms, sleep and affect. *Nat. Rev. Neurosci.* 15, 443–454. doi: 10. 1038/nrn3743

PubMed Abstract | CrossRef Full Text | Google Scholar

Loew, E. R., and McFarland, W. N. (1990). *The Underwater Visual Environment.* London: Chapman and Hall.

Google Scholar

Newman, L. A., and Robinson, P. R. (2005). Cone visual pigments of aquatic mammals. *Vis. Neurosci.* 22, 873–879. doi: 10. 1017/S0952523805226159

PubMed Abstract | CrossRef Full Text | Google Scholar

Ponganis, P. J. (2011). Diving mammals. *Comp. Physiol.* 1, 447–465. doi: 10. 1002/cphy. c091003

PubMed Abstract | CrossRef Full Text | Google Scholar

Sharma, S., and Chatterjee, S. (2017). Microplastic pollution, a threat to marine ecosystem and human health: a short review. *Environ. Sci. Pollut. Res. Int.* 24, 21530–21547. doi: 10. 1007/s11356-017-9910-8

PubMed Abstract | CrossRef Full Text | Google Scholar

Watkins, W. A., Daher, M. A., Fristrup, K. M., Howald, T. J., and Disciara, G. N. (1993). Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mammal Sci.* 9, 55–67. doi: 10. 1111/j. 1748-7692. 1993. tb00426. x

CrossRef Full Text | Google Scholar