

Review

Vision and photoentrainment in fishes: the effects of natural and anthropogenic perturbation

Shaun P. COLLIN and Nathan S. HART

School of Animal Biology and the Oceans Institute, The University of Western Australia, Crawley, W. A., Australia

Correspondence: Shaun P. Collin, School of Animal Biology and the Oceans Institute, The University of Western Australia, Crawley 6009, W. A., Australia

Email: shaun.collin@uwa.edu.au

Running Title: Photoreception of fishes in turbid conditions

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Abstract

Vision and photoentrainment in fishes are vital for feeding, avoiding predation, spatial orientation, navigation, social communication and the synchronization of many homeostatic functions such as activity patterns and sleep. The camera-like (image-forming) eyes of fishes are optimized to provide a clear view of their preferred ecological niche, while non-visual photoreceptors provide irradiance detection that mediates circadian photoentrainment, an endogenous time-keeping mechanism (biological clock) to respond to predictable changes in environmental conditions. Fish and fisheries are under pressure from both natural and anthropogenic perturbation, which in many cases, alters the intensity and spectral composition of the light environment on which they depend for their survival. This review examines the effects of a changing light environment and turbidity on the health of fishes within a developmental and ecological context. Understanding the sensory environment of fishes is vital to predicting their responses and, ultimately, their resilience to environmental change and the potential for maintaining sustainable levels of biodiversity.

Keywords: circadian rhythms, ecology, environment, photoreception, turbidity

INTRODUCTION

Within every aquatic ecosystem, the ability to detect environmental signals such as light, sound, odors, temperature, changes in water movement, small electric disturbances, and even changes in the earth's magnetic field strength all contributes to each species' capacity to regulate their activity patterns, find sustenance, avoid predation, interact socially and reproduce (Partridge & Pitcher 1980; Helfman 1986; Blaxter 1988; Derby & Sorenson 2008; Collin 2012). However, it has been revealed recently that fishes have varying capacities to acclimate to changes in temperature and ocean acidification, placing intense pressure on whole ecosystems (Scott & Sloman 2004; Hobday *et al.* 2006b; Belkin 2009; Nilsson *et al.* 2012; Munday *et al.* 2012). It is therefore important to understand the degree to which species are able to respond to environmental change. Although the nervous system has evolved to solve computational tasks that are relevant to the survival and fitness of an animal in a given environment, we are not yet in a position to understand how sensory perception will be altered in the face of environmental changes, especially rapid change, and whether at least some species may possess some inherent resilience to perturbation within specific ranges.

The evolution of different sensory systems has shaped speciation events and influenced animal biodiversity by improving the perception of environmental signals and the evolution of novel communication systems within specific environments. Therefore, in order to reliably assess the resilience and vulnerability of species to environmental perturbation, it is crucial to understand the perceptual, cognitive, and behavioral abilities of animals in a sensory context, while being cognizant of any evolutionary or physiological constraints. For example, for an understanding of the sensory environment (e.g., the visual lightscape) of fishes, it will be necessary to identify the constraints of information processing in the context of each species' microhabitat in the natural world. Predicting behavioral responses to an

environmental signal also relies on in-depth knowledge of the signal, its propagation, and the ability to detect (visual and non-visual organs) and process (relevant neural pathways within the central nervous system) biologically-relevant information.

The neural basis of behavior in fishes is broadly seated in understanding how the nervous system is organized and how evolution has shaped it in different species. External stimuli (such as light) play a large part in determining behavior, but for most species this (sensory or afferent) input is separated into a series of parallel pathways that begin at the peripheral sense organs, for example, the eye and non-visual (non-imaging forming) aggregations of photoreceptive tissue, and end at the neuromuscular junctions, which are ultimately responsible for a specific (efferent or motor) output. Therefore, the neural bases of visual behavior can be divided into a series of stages, each having a profound effect on the resultant behavioral output. These stages can be divided into: (1) the light signal; (2) the propagation of this signal through the aquatic environment where part of the signal may be lost or modified; (3) the sampling or reception of light by a specialized sensory organ (retina and/or photoreceptive cells within the pineal, dermis, iris, and other body regions (Van Gelder 2003; Peirson *et al.* 2009), which may be arranged to provide spatial information; (4) the transduction of light energy into a form that can be recognized by the central nervous system (CNS); (5) mechanisms for the rapid dissemination (divergence), summation (convergence), protection (no loss of signal), or further processing (excitatory, inhibitory or reflex) of the signal; (6) the representation of this sensory (afferent) input within the CNS, where it will be integrated with the outputs of both afferent and efferent neurons to ultimately regulate the output of information to the descending pathways; and finally, (8) the behavioral output generated by reflex pathways to individual muscle groups (Collin 2012).

The perception of light for image formation (vision) and setting of circadian rhythms varies enormously across fishes, depending on each species' reliance on light in their natural

life history. For species where light plays an important role, either during development or when individuals are mature, any perturbation of the environment can markedly change behavior. Natural (high tidal flows and run-off) and anthropogenic (dredging) perturbations that result in increased levels of turbidity, which radically change the aquatic light environment, would all affect light-guided behaviors. For species relying on vision, this form of “sensory pollution” affects the physical environment by changing the intensity and the spectral composition of the ambient light environment and, therefore, how objects are visualized within the visual field against the background of suspended particles. This ultimately changes the visual abilities of each species, the distance at which fish react to potential prey, the conspicuousness of prey, and ultimately whether vision can be used reliably against each species’ sensory repertoire. Sustained changes in the intensity and spectral composition of down-welling light may also affect each species’ ability for circadian synchronization of the time of day and many other homeostatic functions, such as activity patterns, orientation and taxis, levels of arousal, and body pigmentation. If the spectral input regulating the chronobiological clock is disrupted, this may also influence some species’ ability to survive under such conditions.

This review will highlight the complex nexus of the ambient light environment and photoreception in cartilaginous and bony fishes, the ability of the visual and non-visual systems to overcome natural and anthropogenic perturbations and neurobiological options for species faced with a compromised light environment, and how/if other sensory modalities may provide a viable alternative.

Light in the sea

As light propagates through water it is absorbed and scattered. this has a marked effect on the quality of light at different depths in the sea, and, therefore, visual and non-

visual photoreception. The intensity of light, as well as its spectral composition and degree of polarization, is significantly altered as it travels through the ocean. (Warrant *et al.* 2003). At the surface, the light spectrum available for vision spans from about 300 nm to 750 nm. In a clear ocean, light becomes progressively bluer with depth, with the orange-red part of the spectrum (beyond 550 nm) being almost completely absorbed within the first 100 m (Tyler & Smith 1970). Ultraviolet light is also absorbed, but not quite as rapidly, with biologically relevant intensities remaining to at least 200 m (Frank & Widder 1996; Losey *et al.* 1999). Below 200 m, the down-welling daylight is almost monochromatic (475 nm). The intensity of light, even in the clearest oceans and lakes, reduces by approximately 1.5 orders of magnitude for every 100 m of depth. The spectral composition and intensity of light also differs with water type and the amount of dissolved organic matter within the water column (Jerlov 1968, 1976; Smith & Baker 1981).

The spatial distribution of light in the water column is greatly influenced by turbidity. Close to the surface (during the day and in water sufficiently deep that the substrate reflectance can be ignored), the radiance distribution is dominated by the position of the sun, and the downwelling sunlight is much brighter than the upwelling light created by scattering. However, as depth increases, scattering by water molecules and other suspended particles diffuses the downwelling light and renders the radiance distribution more uniform about a given point in the water. Below the so-called ‘asymptotic depth’, which is about 400 m in the clearest ocean water, the radiance distribution is vertically symmetric (Jerlov 1976). The effect of increasing water turbidity is to drastically reduce the asymptotic depth, as well as the overall intensity of light at all depths.

Scattering of light also greatly affects the visibility of objects in the sea as perceived by any animal. Light reflected from the surface of an object travelling toward the viewer’s eye will be scattered out of the optical path. Similarly, light coming from above, below, and

the side will be scattered into the optical path between the object and the viewer, producing a veiling haze of light. Such scattering greatly reduces the apparent contrast of objects and limits the furthest distance at which they can be reliably detected (Lythgoe 1979, 1988; Jagger & Muntz 1993). In the brightest and clearest ocean water, the veiling space light zeros the contrast of a dark object at a range of about 40 m (Lythgoe 1979). In turbid water, this distance is dramatically reduced. There are also temporal differences in the quality of the ambient, underwater light environment, which can be attributed to changes in meteorological conditions on a daily or yearly (seasonal) basis and the phases of the moon (tidal).

The eyes and visual abilities of fishes

Image formation in fishes is mediated by the dioptric apparatus (cornea, lens, intraocular lens muscle) that focuses light on the neural retina at the back of the eye to form an image. However, the neural process of vision begins with the absorption of light by the retinal photoreceptors. It follows, therefore, that the ability of an organism to detect a light stimulus depends upon the spectral absorption properties of the visual pigments located within the photoreceptors and the photokinetics of the receptor class (rods that operate in dim light and cones that operate in bright light). Most vertebrates possess a number of different cone photoreceptor classes, each expressing a different visual pigment. The peak absorption of the visual pigment (λ_{\max}) can be “tuned” to the spectral composition of the ambient light environment, optimizing light capture to satisfy visual demands (for reviews, see Bowmaker & Hunt 1999, 2006). Teleost fishes, with their wide range of natural habitats, have become the model for examining the relationship between ambient light and the spectral sensitivity of visual pigments; it has been shown that species from bodies of water with differing spectral irradiance tend to possess visual pigments that are related to the most abundant wavelengths (Bowmaker *et al.* 1994; Bowmaker & Hunt 2006; Douglas *et al.* 2003; Loew & Lythgoe

1978; Lythgoe *et al.* 1994; Partridge *et al.* 1989, 1992). Furthermore, the ontogenetic migration of fishes from one body of water to another or to greater depths is accompanied by changes in the spectral sensitivity of the retina in many species (for reviews, see Beaudet & Hawryshyn 1999; Collin & Shand 2003). For example, those that migrate to deeper water during ontogeny exhibit a narrowing in the spectral range of their visual pigments as the spectral range of the light environment also narrows (Bowmaker & Kunz 1987; Shand *et al.* 1988, 2008; Shand 1993; Hope *et al.* 1998).

The spacing of the photoreceptors governs the spatial resolving power within the visual field and the detection limit of each species is dependent on the abundance, size and photokinetics of the two major receptor systems: rods active in low light (scotopic) conditions and cones active in bright light (photopic) conditions. Two or more cone types with different spectral sensitivities provide the basis for color vision in bright light conditions. Recent research on the evolution of visual pigments has revealed that the representatives of the earliest vertebrates (Agnatha or jawless fishes dating back 540 million years) possess the potential to discriminate complex colors by the neural comparison of up to five (pentachromatic) photoreceptive channels (Collin *et al.* 2003, 2009), while the cartilaginous jawed fishes (the Chondrichthyes) possess a diversified visual capacity with elephant sharks (Holocephali) and rays (Batoidea) possessing trichromatic color vision (Davies *et al.* 2009; Hart *et al.* 2004, 2006; Theiss *et al.* 2007) and sharks possessing a single cone type and, therefore, being color blind (Hart *et al.* 2011; Theiss *et al.* 2012). The speciose bony fishes, which occupy a large number of ecological niches, show marked variations in photoreceptor machinery ranging from pure rod retinæ (Locket 1971; Partridge *et al.* 1988), to mono-, di-, tri- and tetra-chromatic retinæ for discrimination of objects underwater based on either color or contrast (Losey *et al.* 2003; Marshall *et al.* 2003; Sabbah *et al.* 2013).

Many species of fishes possess ocular specializations to optimize vision within a preferred ecological niche, including: (1) corneal, lenticular, and retinal spectral filters to tune the incoming light to enhance absorption of the complement of photoreceptor visual pigments (Douglas & Marshall 1999); (2) corneal iridescence to either tune the incident light and/or camouflage the pupil (Lythgoe & Shand 1989; Collin & Collin 2001); (3) pupillary mobility and the ability to change the shape of the pupillary aperture to control the amount of light entering the eye and reduce the effects of lenticular spherical aberration (Douglas *et al.* 2002); (4) structural mechanisms to increase sensitivity (increases in eye, lens, and photoreceptor size, the presence of a tapetum lucidum); (5) increases in the summation of information between the input cells (photoreceptors) and output cells (ganglion cells) (Collin 1997); and (6) localized increases in neuronal sampling to increase spatial resolving power (Collin & Pettigrew 1988a,b; Lisney & Collin 2008). Localized increases in retinal neuron density (both photoreceptors and ganglion cells) differentially sample specific regions of the visual field in fishes and define the visual axis and the limits of visual acuity (Litherland & Collin 2008; Temple *et al.* 2010). These types of retinal specializations are closely allied with the ability of fishes to scan their environment with their eyes (Collin & Shand 2003). Species with specializations of the temporal retina (area centralis, fovea), that part of the eye receiving information from the frontal part of the visual field, often have pronounced eye movements; species with an elongated or horizontal increase in retinal sampling across the retinal meridian (horizontal streak), viewing a panoramic scene across a large part of the visual field, are able to perceive the environment without saccadic eye movements.

Light detection and photoentrainment

In fishes, mere light detection and the ability to align activity patterns to changes in lighting conditions are mediated by aggregations of photoreceptive cells located either within

the eye (non-rod, non-cone photosensitive retinal neurons) and/or within specialized cells in the iris, CNS, and skin (Drivenes *et al.* 2003; Bellingham *et al.* 2006; Cheng *et al.* 2009; Davies *et al.* 2012). Non-visual pigments provide irradiance detection that mediates circadian photoentrainment, an endogenous time-keeping mechanism or biological clock to respond to predictable changes in environmental conditions, for example, seasons, tides, light cycles and temperature. The receptors that sense these regular, environmental perturbations are diverse in their structure, function, location, and role, but the light sensitive cells in the brain (pineal and parapineal), skin, cornea and iris of the eye all have specific actions and interactive influences on circadian behaviors. Recent research has revealed that one of the most ancient, non-visual pigment genes, melanopsin, dates back over 400 million years. The elephant shark, *Callorhynchus milii* Bory de Saint-Vincent (1823), represents one of the earliest stages in the evolution of jawed vertebrates and possesses three melanopsin genes (*opn4m1*, *opn4m2* and *opn4x*), all expressed in multiple tissue types, including the eye and brain but also the fins, gills, liver, and testes (Davies *et al.* 2012). The significance of this differential pattern of expression is unclear, but may be related to the movement of the elephant shark from the deep ocean to shallow water in order to spawn, where it is exposed to a bright-light environment. Different melanopsin genes may be involved in the spatial and temporal regulation of photoentrainment at particular stages of the lifecycle. Unlike the relatively rapid phototransduction kinetics exhibited by typical visual photoreceptors (Lamb & Pugh 2004), melanopsin-based photoreceptive kinetics appear to integrate photons over longer periods of time (Sekaran *et al.* 2005). Melanopsin-based pigments are generally sensitive to shorter wavelengths that peak between 475 nm and 500 nm (Koyonagi *et al.* 2005; Davies *et al.* 2011; Davies *et al.* 2012). There is still a marked paucity of studies investigating the importance of non-visual photoreception in Chondrichthyes.

In contrast to the cartilaginous fishes, irradiance detection systems have been studied more widely in bony fishes, at least with respect to the diversity of non-visual pigments present (see recent review by Porter *et al.* 2012). However, few of these studies have revealed the localization and/or function of these photosensitive pigments in the context of a species' preferred light environment. The melanopsin gene has been investigated in the retina of the zebrafish (*Danio rerio* Hamilton, 1822) and found to be present in five different cell-specific forms (Davies *et al.* 2011). The finding that all neurons within the retina (cone photoreceptor, bipolar, amacrine, horizontal, and ganglion cells) are potentially intrinsically photosensitive, each expressing a different form of melanopsin with a peak spectral absorption (λ_{\max}) between 451 and 470 nm, suggests that the eyes of this species (and possibly others) may be “fine tuned” to the dynamic changes in underwater light levels to which this species is exposed, and that retinal visual processing may be under more complex circadian control than previously thought (Davies *et al.* 2011). However, the mediation of gross changes in environmental light (irradiance) for setting of circadian rhythms, levels of arousal, orientation and taxis, body pigmentation, temperature regulation, and pupil size may occur over a much narrower region of the visual spectrum.

Although the pineal organ cannot distinguish between discrete, rapidly changing light stimuli, and, therefore, functions primarily as a non-visual luminance detector (Bowmaker & Wagner 2004), it may possess some directional light perception, which has been classified as ‘semi-visual’ photoreception in some species of bony fishes and in the parietal eye of reptiles (Hartwig & Oksche 1982; Vigh *et al.* 2002). The pineal complex in cartilaginous fishes (Vigh *et al.* 2002) and the pineal/parapineal complex in bony fishes (Ekström & Meissl 1997) respond to changes in ambient illumination often via a pineal window or a reduction in either the pigmentation or thickness of the overlying region of the cranium (Wagner & Mattheus 2002). Light controls melatonin production, which oscillates daily and seasonally (Falcón

1999; Kulczykowska & Vázquez 2010) and is also directly involved in the adaptation of skin melanophores in response to the changing intensity of the ambient light (Vanecek 1998). The pineal photoreceptors of only a few species of chondrichthyans have been examined and, despite showing ultrastructural similarities to retinal cone photoreceptors, the receptors appear to be rod-like, containing a rod opsin and a peak spectral sensitivity (λ_{\max}) of 500 nm (Rüdeberg 1969; Hamasaki & Streck 1971). The pineal and deep brain (suprachiasmatic and cerebrospinal fluid-contacting cells; Vigh & Vigh-Teichmann 1998; Kojima *et al.* 2000) possess a range of light absorbing, non-visual pigments that respond to light in the range of 495-530 nm: exo-rhodopsin, extra-retinal rod-like opsin, vertebrate ancient opsin, pinopsin and parapinopsin (Ekström & Meissl 2003; Soni & Foster 1997; Kojima & Fukuda 1999; Philp *et al.* 2000; Moutsaki *et al.* 2000).

Both image and non-image forming light detection systems in fishes are able to operate over eight log units of light intensity, with some deep-sea fishes able to detect a single quantum of light (Warrant *et al.* 2003). Such a finely-tuned system of photoreception would surely be markedly affected by even small perturbations in light transmission.

DISCUSSION

Environmental and anthropogenic perturbations and their impacts on the visual abilities of fishes

Environmental perturbations affecting the transmission of light through the water column vary from terrestrial run-off, dredging, high tidal fluxes, seasonal algal blooms, rainfall, melting of ice formations, eutrophication, and meteorological forcing. All produce short and long term changes in turbidity and the level of suspended particles. While suspended sediments are often the main contributors to turbidity, other non-sediment sources that affect light transmission, such as natural tannins and algae, can also influence turbidity.

Increased turbidity can lead to an increase in sedimentation and/or reduced light penetration within the water column, which not only reduce the intensity but also alter the spectral composition of light available for vision in fishes living at different depths. Fish assemblages are initially governed by patterns of settlement of larval fishes (Wenger *et al.* 2011), for whom settlement is driven by a variety of sensory cues (including visual stimuli). If suitable habitat cues are not available to larvae, due to degradation of their habitat or elevated levels of suspended sediment, habitat choice can be impaired (Wenger *et al.* 2011). Fisheries resources may also be affected because of the potential for degrading and/or decreasing spawning and rearing habitats (Jones *et al.* 2004; Partridge & Michael 2010).

Increased turbidity generally reduces visibility and decreases the ability of visual specialists to obtain food (Blaxter 1968, 1969; Gardner 1981; Berg & Northcote 1985; Utne-Palm 2004) and limits visual range for localizing mates, predator surveillance, and social interactions. Reaction distance was found to decline as a decaying power function of light (0.17-261 lux), prey size (55, 75, and 139 mm), and turbidity (0.09, 3.18, and 7.40 nephelometric turbidity units) in adult lake trout (*Salvelinus namaycush* Walbaum, 1792), rainbow trout (*Oncorhynchus mykiss*, Walbaum 1792) and cutthroat trout (*Oncorhynchus clarki* Richardson, 1836) (Vogel & Beauchamp 1999). The reaction distance of the two-spotted goby (*Gobiusculus flavescens* Fabricius, 1779), to mobile and immobile copepod prey has also been studied in water conditions with different turbidity levels or spectral composition. Changes in both prey contrast and prey mobility caused reaction distance of *G. flavescens* to increase in turbid conditions, with the longest reaction distances (lowest contrast threshold) observed at shorter wavelengths (blue–green part of the spectrum) (Utne-Palm 1999).

Unless compensated for by physiological (e.g., longer integration times) or anatomical (e.g., increased outer segment length for enhanced light absorption) adaptations or

changes in behavior (e.g., changes in depth or time of activity), a reduction in the penetration of light in the water may also cause a loss or alteration of chronobiological synchronization of circadian or even circannual rhythms, which could have long term effects on a range of homeostatic functions such as activity patterns, body coloration, and sleep. The likely absorption of short wavelength light (~ 480 nm) would also reduce irradiance detection via melanopsin and deregulate the photoentrainment of circadian rhythms.

One may expect that visual specialists (those with high acuity vision) would be most at risk, with increased predation from non-visual specialists, where the relative importance of other senses such as the lateral line (Bleckmann 1986; Montgomery *et al.* 1995; Englemann *et al.* 2000; Wueringer *et al.* 2011), chemoreception (Finger 1988; Hara & Zielinski 1989; Hansen & Reutter 2004) and audition (Corwin 1981; Popper *et al.* 2003; Fay 2009) is higher than vision. In fact, in juvenile Atlantic cod (*Gadus morhua* Linnaeus, 1758) turbidity did not affect reactive distance to chemical cues, and had only a weak negative effect on reactive distance to visual cues (Skiftesvik *et al.* 2003; Meager *et al.* 2005). In the cartilaginous fishes, electroreception would also allow these apex predators to localize bony fishes in low visibility environments, thereby increasing the predatory risk on visual species (Kajiura & Holland 2002; Collin & Whitehead 2004; Kempster *et al.* 2013).

The effects of increased Total Suspended Sediments (TSS) on fishes may be direct, such as physical damage and/or abrasion, and indirect, for example feeding impairment (Kerr 1995; Buermann *et al.* 1997; Partridge & Michael 2010). Suspended sediments are usually silt and clay particles (typically in the range of 2 - 60 μm in diameter), and the level of exposure is dependent on the frequency, duration, particle size, particle type, and fish life stage. Research has found that duration of exposure plays a more dominant role than TSS concentration (Anderson *et al.* 1996). Long-term exposure to elevated TSS conditions may also cause endocrine stress responses (elevated plasma cortisol, glucose, and hematocrit

levels), suggesting an increased physiological burden that could influence growth, fecundity, and longevity (Lloyd 1987; Servizi & Martens 1991; Au *et al.* 2004). Sediment particle size affects mortality and there is a decrease in lethal tolerance as particle size increases (Servizi & Martens 1991). Finer particles tend to clog gill rakers, erode gill filaments, cause ‘gill flaring’ and ‘coughing’ responses (Berg & Northcote 1985; Servizi & Martens 1992; Au *et al.* 2004) in addition to reducing growth rate (Sigler *et al.* 1984; Au *et al.* 2004). Tolerance also appears to be related to ambient water temperature (Servizi & Martens 1991). Other impacts (tolerance) with respect to specific perturbation (such as dredging) are determined by the regional size of the disturbance, the settlement rate of suspended particles and consequent changes in oxygen levels, water chemistry, noise, currents, and vibration.

Water that has become turbid as a result of eutrophication may constrain color vision, where the increased turbidity interferes with mate choice, relaxes vision-based sexual selection, and potentially blocks one mechanism of reproductive isolation. In this way, anthropogenic perturbation that increases turbidity can interfere with mate choice. For example, mate choice based on coloration in cichlids produces strong assortative mating and the sexual isolation of color morphs; increased turbidity can destroy both the mechanism of diversification and that which maintains diversity (Seehausen & Schluter 2004). Dull fish coloration, few color morphs, and low species diversity will ultimately result from turbid water conditions. As with other causes of turbidity, algae-induced eutrophication in marine and brackish water regions show that algae-induced water affects both direct (e.g., feeding and habitat choice) and indirect (e.g., weight) qualities of pike larvae (*Esox lucius*), thereby affecting larval survival and potentially even recruitment into the population (Engström-Ost & Mattila 2008).

Low levels of turbidity may also be beneficial and may protect fish from predation from visual specialists. Fish that remain in turbid water experience a reduction in predation

from piscivorous fish and birds (Gregory & Levings 1998). Gregory (1993) showed that turbid water acts as protective cover and allows fish to exist in otherwise ‘riskier habitats.’ An enhanced (altered) veiling light may also increase the contrast of some prey against the background, thereby enhancing feeding success. Moderate levels of turbidity actually enhance schooling behavior in ayu (*Plecoglossus altivelis* Temminck & Schlegel, 1846) and Japanese anchovy larvae (*Engraulis japonicus* Temminck & Schlegel, 1846), whereas this same level of turbidity has an inhibitive effect on schooling of juvenile yellowtail (*Seriola quinqueradiata* Temminck & Schlegel, 1845), reinforcing the need to understand the habitat characteristics of each species in order to predict any changes in behavior (Ohata *et al.* 2012). In fact, it is possible that those species of fishes with polarization vision may have improved object detection in turbid waters, as is accomplished by cuttlefishes (Hawryshyn 1992; Cartron *et al.* 2013).

However, avoidance is the primary behavioral response of fishes to local changes in turbidity. Avoiding areas with elevated TSS may lead to fishless areas in natural systems (Birtwell 1999). Salmonids have been observed to move laterally away from areas of disturbance (Servizi & Martens 1992) and/or downstream to avoid turbid areas (McLeay *et al.* 1987). Utne-Palm (2002) considers that the positive effect of turbidity is more pronounced for larval fishes, given that their visual field is short and there are more suspended particles to scatter light and interfere with detection. Interestingly, in a study of Atlantic herring (*Clupea harengus*) larvae attack rates on plankton in increasing levels of water turbidity (after the addition of diamaceous earth), intermediate levels of turbidity (35 Jackson Turbidity Units, JTU) had a positive effect on the attack rate of smaller larvae (20 mm), while high levels of turbidity (80 JTU) had a negative effect on attack rate of all tested larvae size groups (Utne-Palm 2004). Therefore, turbid environments may be more optimal for some species and size groups of fishes (planktivores and fish larvae) than for others (adult piscivore fish) (Utne-

Palm 2002) and may produce a structuring effect on a fish community (De Robertis *et al.* 2003).

Global climate change and its influences on the sensory ecology and biodiversity of fishes

Jawed (cartilaginous and bony) fishes in freshwater and marine (shallow water and deep-sea) environments encounter a diverse range of sensory environments (during development and as adults), which play a crucial role in their survival and longevity. It is now well documented that global warming is having a major effect on our aquatic ecosystems. Average global sea surface temperature (SST) has risen by 0.67° C in the last century (1901 to 2005) (Belkin 2009). By 2070, the SST around Australia is projected to warm a further 1 - 2°C, and water temperature at depth (up to 500 m) may rise 0.5 - 1° C (Hobday *et al.* 2006a, 2006b). These increases in temperature and pCO₂ levels (and the associated ocean acidification) have been shown to have a dramatic effect on a wide range of behaviors and sensory responses of reef fishes (altering the action of the GABA-A receptor in the brain), with consequences for the timing of settlement, habitat selection, predator avoidance, and individual fitness (Nilsson *et al.* 2012; Munday *et al.* 2012). At this stage, it is unknown whether these changes will have an effect on the visual system, but such changes may be responsible for shifts in the range and abundance of fishes (Perry *et al.* 2005; Cheung *et al.* 2009; Sorte *et al.* 2010). The ability to make shifts in their range will depend upon the new “sensoriscape” and each species’ adaptive capacity to receive, process, and react behaviorally to these altered environmental conditions.

Warming is occurring faster along the West Australian coast than the global average, with waters off the south-western corner having warmed by an average of 0.2° C per decade, compared to the global rate of 0.16° C per decade over the past 50 years (Pearce & Feng

2007). Moreover, future climate change is also expected to result in changes to regional oceanography, including possible weakening of the Leeuwin Current off Western Australia (Hobday & Lough 2011), which exerts substantial influence on productivity. With the continued reliance on our undersea natural resources, there is a high risk of localized disturbances (turbidity), which will undoubtedly influence the behavioral repertoire of resident fish populations. Further work is needed to assess the resilience of fish species to a changing light environment. Interestingly, some species of reef fishes from waters where UV radiation was attenuated quickly (as a result of the riverine outflow of suspended particles) had UV-absorbing epithelial mucous (sunscreen) that differed significantly from that of fishes from clearer waters. The two species showed different methods of acclimatizing to UV radiation: the labrid *Halichoeres bivittatus* Bloch (1791) from clearer waters shifted the spectral quality of its mucus toward the absorbance of shorter, more damaging wavelengths, while the parrotfish *Scarus iseri* Bloch (1789) from clearer waters increased the overall UV absorbance of its mucus with minimal spectral shifting (Zamzow 2007).

Although tagging and visual monitoring programs are providing important information about the movement patterns and abundance of individuals and groups, there is little information on what environmental stimuli are used to influence behavior and, thereby, why species aggregate to some geographical locations, migrate along well-defined paths, are able to navigate long distances, and are restricted to a specific home range (Carey & Sharold 1990; Klimley 1993; Holland *et al.* 1999; Klimley *et al.* 2002; Weng & Bloch 2004; Skov *et al.* 2010). Sensory systems are adapted over evolutionary timescales to a species' habitat characteristics and home range, and they may not be resilient or tolerate rapid/forced changes

in the physical parameters of that habitat. The survival of most aquatic organisms is therefore dependent on the complex sensoriscape to which they are adapted. A range of cues have been implicated in influencing behavior in fishes (Rowland 1999; Simpson *et al.* 2005, 2011; Leis 2006; Munday *et al.* 2009), especially in the face of ocean acidification, homing behavior, and larval fish settlement. However, a full understanding of the influence(s) of environmental stimuli, the sensitivity of the peripheral sense organs that detect these signals (against the masking effects of “sensory pollution”), the integration of different signals within the CNS, and how these ultimately determine a behavioral response are vital if we are to predict the effects of perturbation.

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