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The sensory impacts of climate change: bathymetric shifts and visually mediated interactions in aquatic species

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Visual perception is, in part, a function of the ambient illumination spectrum. In aquatic environments, illumination depends upon the water's optical properties and depth, both of which can change due to anthropogenic impacts: turbidity is increasing in many aquatic habitats, and many species have shifted deeper in response to warming surface waters (known as bathymetric shifts). Although increasing turbidity and bathymetric shifts can result in similarly large changes to a species' optical environment, no studies have yet examined the impact of the latter on visually mediated interactions. Here, we examine a potential link between climate change and visual perception, with a focus on colour. We discuss (i) what is known about bathymetric shifts; (ii) how the impacts of bathymetric shifts on visual interactions may be distributed across species; (iii) which interactions might be affected; and (iv) the ways that animals have to respond to these changes. As warming continues and temperature fluctuations grow more extreme, many species may move into even deeper waters. There is thus a need for studies that examine how such shifts can affect an organism's visual world, interfere with behaviour, and impact fitness, population dynamics, and community structure.

1. Introduction

Human activities are affecting animals in numerous ways, such as range shifts [1] and habitat loss (e.g. [2]). Recently, increased attention has been paid to understanding how anthropogenic changes can impact animal sensory systems (e.g. [3]). Vision is particularly important for information acquisition in many species, allowing animals to locate food, assess mates, signal to territorial intruders, and find mutualistic partners. What an animal sees depends upon the source of the light (our focus here being solar illumination), the spectral reflectance (the percentage of light a surface reflects at each wavelength) of what is viewed, the optical properties of the medium that light passes through (e.g. air, water), the animal's visual system, and the ambient illumination. Changes to any of these factors can affect visual perception.

The ambient illumination an aquatic organism experiences depends upon both the optical properties of the water it inhabits and on the depth at which it lives, both of which can shift as a result of anthropogenic impacts. First, increased dissolved and particulate compounds, due to agricultural and septic run-off, soil erosion, and other sources can increase turbidity [4]. This makes waters darker, murkier, and more brown or green in colour (e.g. [5,6]). Second, many aquatic species are moving deeper in the water column (in what is known as a bathymetric shift) in response to warming surface waters. In addition to illumination decreasing with depth, the spectrum of underwater light narrows because different wavelengths of light attenuate at different rates. In essence, the range of visible colours grows more limited with increasing depth, changing the appearance of visual stimuli (figure 1). As a result, bathymetric shifts can affect a species' visual environment in similar ways as
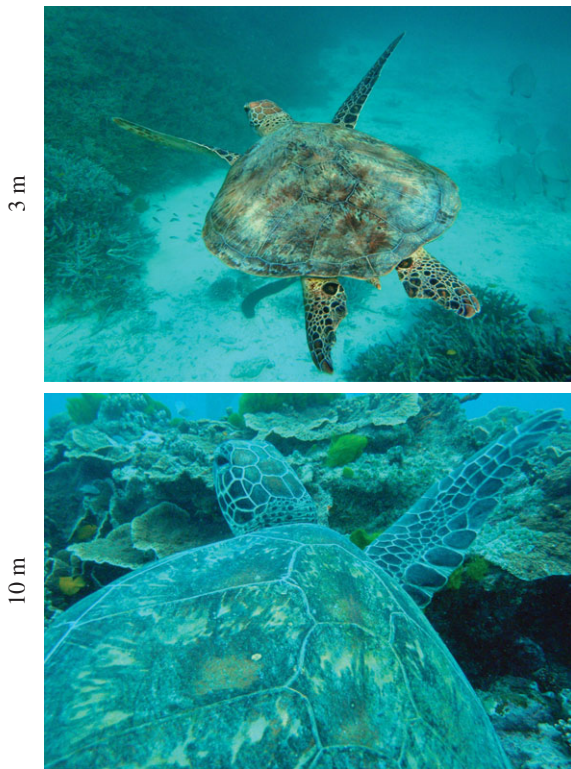
Figure 1. Photographs taken with no flash, but at different depths, illustrate how colours available in the marine environment change with depth. The green turtle shown at 10 m depth lacks the orange and yellow highlights seen on the turtle at 3 m depth—even though the former is photographed from a shorter distance—because orange and yellow wavelengths are no longer present in sufficient quantities in the illumination to be seen after reflecting off of the carapace. Photographs taken by S.J. at Heron Island, Australia. (Online version in colour.)

increased turbidity. Although studies have correlated variation in colour vision across taxa with species' depth ranges (e.g. [7,8]), no studies have yet focused on how visually mediated interactions may be impacted as a given species experiences a bathymetric shift. The need for such studies is immediate, however, as species are already shifting their depth distributions in response to anthropogenic change [9–13].

Here, we focus on how climate-induced changes to depth ranges could impact an animal's visual world, interfering with visually mediated processes and altering the dynamics of interactions within and between species. We discuss (i) what is currently known about climate-change-induced bathymetric shifts (hereafter, bathymetric shifts); (ii) the conditions under which bathymetric shifts could impact visual perception; (iii) how bathymetric shifts may alter signalling interactions; and (iv) how animals may respond to these changes. We emphasize effects on colour perception, since colour is a source of information across many taxa and behavioural contexts [14], and because bathymetric shifts can have large impacts on illumination spectra and thus colour perception. We also focus on fish, a diverse group of highly visual animals in which the impacts of bathymetric shifts on visually mediated communication could be significant, and in which behaviour and visual capabilities are well studied. Lastly, we restrict our discussion to the epipelagic zone, the depth range at which photosynthesis can occur, because this is where the largest changes in both temperature and the spectral environment occur with increases in depth.

While many studies have examined the effects of turbidity on the behaviour of aquatic species (see references throughout), the behavioural impacts that may result from bathymetric shifts are not well studied. However, the effects on the illumination spectrum of shifting to deeper water are analogous to those of increasing turbidity: both increase the absorption and scattering of underwater light—the former by increasing the light's path through the water, the latter by increasing the attenuation for a given path length—and both decrease brightness, shift the dominant wavelength, and restrict spectral breadth. Thus, here we draw on the literature regarding turbidity effects to understand how bathymetric shifts may affect behaviour. It should be noted, however, that the effects of turbidity and depth increases are not precisely the same, because bathymetric shifts have the potential to be global in scope and persistent over time, while turbidity is typically affected by local, sometimes short-term, events. Despite this, turbidity studies provide a useful guide to the potential impacts of bathymetric shifts.

2. Light in aquatic environments: a primer

First, we provide a brief primer on light in aquatic environments; for detailed accounts, see [15–17].

Even pure water is a strong absorber of visible and near-UV light (350–700 nm) at many wavelengths, especially at wavelengths greater than 590 nm. As depth increases, illumination decreases in both intensity (brightness) and spectral breadth (the range of wavelengths over which the illumination at a given depth is at least half the peak value at that depth; figure 2). This decrease at each wavelength is typically exponential. Therefore, if only 10% of surface light at a given wavelength remains at 10 m depth, only approximately 1% remains at 20 m.

Although water in the centres of the major oceans approaches the clarity of pure water, underwater illumination in many locations is strongly affected by both dissolved and suspended materials. These both absorb and scatter light, which together attenuate illumination. Due to the exponential attenuation of light, these added substances can have massive effects, with some coastal waters at 10 m depth having the same light levels as the open ocean at 1000 m. For this same reason, illumination in coastal and freshwater systems is highly variable compared to oceanic systems.

Despite this variability, there are a few general rules for how light attenuates with depth in different water types. In oceanic and most tropical coastal waters, scattering is low, and light is primarily absorbed by the water itself, with a small to moderate contribution to absorption from chlorophyll in phytoplankton and light scattering by the bodies of the phytoplankters themselves, which are almost exclusively found in the upper 200 m. The dominant wavelength—especially below 200 m—is typically approximately 480 nm (cyan to human eyes), and light at this wavelength decreases 10-fold roughly every 70–100 m. In temperate and polar coastal waters, scattering and absorption are high, with absorption at long wavelengths dominated by water and absorption at short wavelengths dominated by moderate to strong contributions from chlorophyll. This results in green water with a dominant wavelength of approximately 550 nm. As one approaches land, scattering typically increases due to increases in suspended sediment and
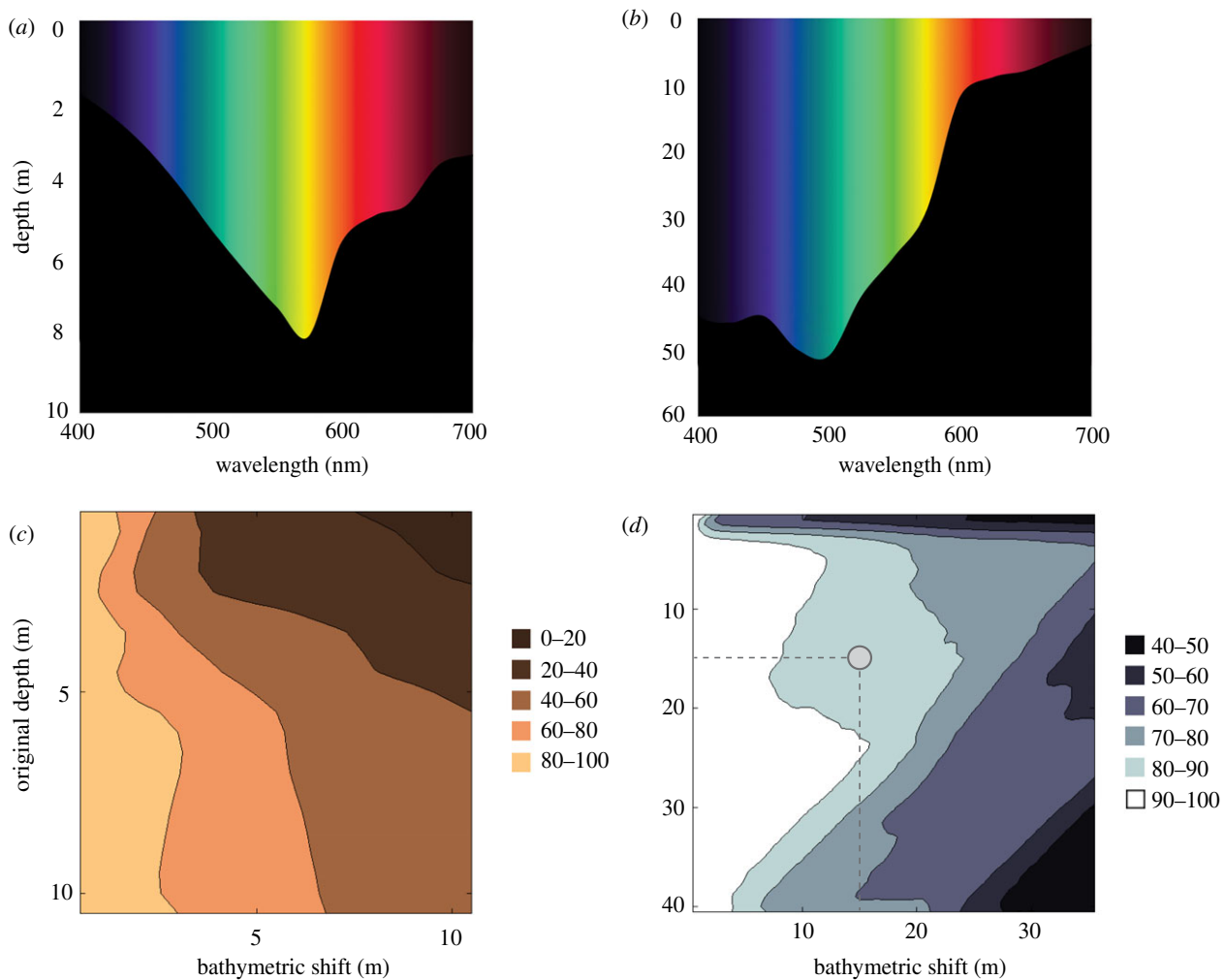
Figure 2. The effect of a bathymetric shift depends on the size of the shift, the original depth, and the water type. First, the range of wavelengths available decreases with depth, as illustrated here in (a) near shore coastal and (b) clear coral reef water. The dark regions show where light of a given wavelength is less than 5% of its surface value. The y-axis scales differ between (a) and (b) to better show the depth profile of near shore coastal water. Second, the spectral breadth of illumination at any depth decreases after a bathymetric shift. (c,d) The per cent of spectral breadth remaining after a bathymetric shift—as a function of original depth—in the water types shown in (a,b), respectively. For example, if an animal normally lives at 15 m depth in coral reef water and is forced to move 15 m deeper (dashed lines), then the spectral breadth of the ambient illumination is now only 80–90% of what it was (illustrated by the grey circle). Spectral breadth is strongly affected by bathymetric shifts in near-surface waters, because many short and long wavelengths are absorbed in the first few metres. At deeper depths, the effects of bathymetric shifts are more complex, but far stronger in near shore coastal water. (a,c) Made using inherent optical properties of Jerlov type 7C near shore temperate water [16]. (b,d) Made via a radiative transfer model (Hydrolight 5.3) using the inherent optical properties for oligotrophic water with a chlorophyll concentration of 0.5 mg m^{-3}, typical of coral reefs. (Online version in colour.)

absorption by coloured dissolved organic matter (CDOM). This latter material absorbs all but long-wavelength light strongly, so water colour changes from green to brown. Fresh waters are highly variable. Some are clear and blue, but most are strongly scattering and absorbing systems with large contributions from both chlorophyll and CDOM. Certain freshwater systems (e.g. blackwater swamps) are atypical in having strong absorption with low scattering.

3. What is currently known about bathymetric shifts in aquatic organisms?

There are multiple examples of aquatic organisms, from dino-flagellates to fish, shifting deeper due to increases in near-surface water temperatures [9–13,18]. Although the rate at which species are shifting varies considerably, Nye et al. [11] found that some fish species had shifted deeper at a mean rate of more than 1 m yr^{-1} between 1968 and 2007.

Although the majority of documented bathymetric shifts come from northern temperate regions, there is emerging evidence of depth shifts in tropical reef species as well (e.g. [19]).

Bathymetric shifts have the potential to be widespread. Most of Earth's aquatic ecosystems are warming (figure 3), and global mean sea surface temperatures (SSTs) are predicted to increase by up to 4.8°C (relative to the 1896–2005 average temperature) by 2100 [21,22]. The rate of change and projected increases in SST vary widely across habitats and latitudes. In general, marine areas in northern temperate and polar lati-tudes are warming especially rapidly [23]. However, species-rich reef and tropical coastal ecosystems are also warming quickly, with SST trends across 207 coral reef sites showing average increases of 0.32°C/decade [24], and coastal waters warming at a rate of 0.25°C/decade [25].

Climate change is also manifesting in aquatic habitats as increases in temperature variability. Many coastal and reef ecosystems are projected to experience increased numbers of SST anomalies, large short-term changes in temperature
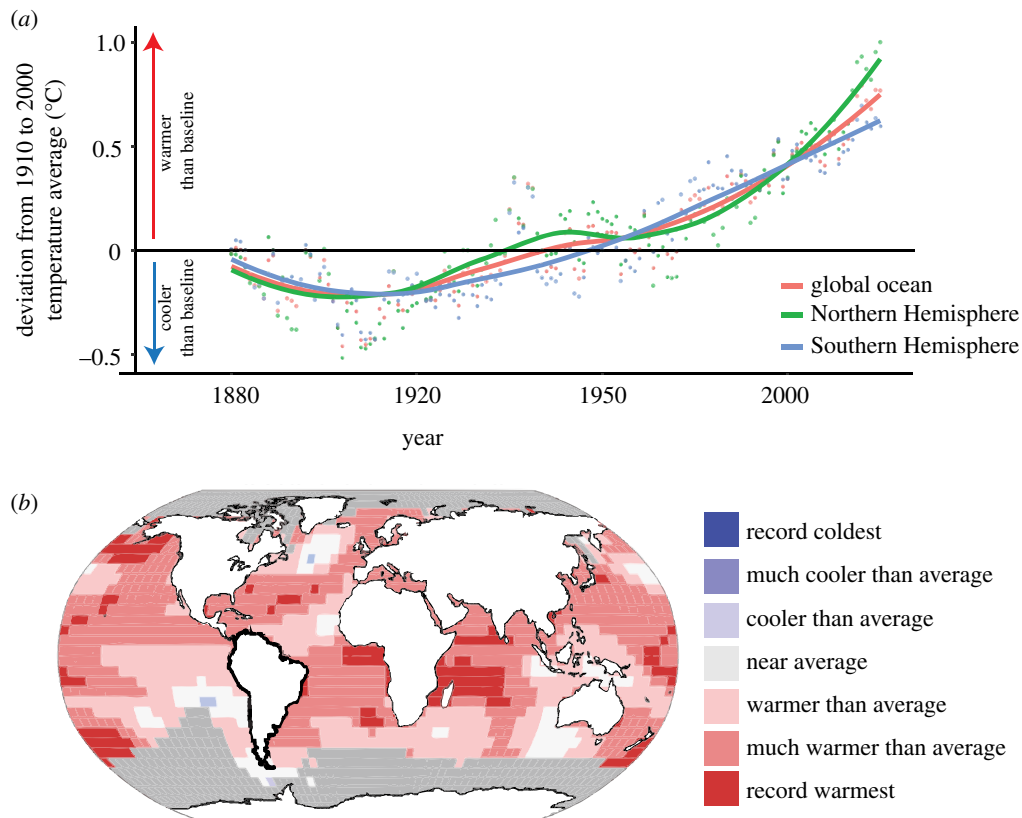
Figure 3. The world's oceans have warmed over the last hundred years. (a) Annual SSTs of the global ocean and Northern and Southern Hemispheres have increased since 1880. This graph uses the 1910–2000 average as a baseline for depicting change. (b) 2019 ocean temperature departure from average, with respect to a 1981–2010 base period. Data from the United States National Oceanographic and Atmospheric Administration Centers for Environmental Information [20]. (Online version in colour.)

that have the potential to severely impact animals. In almost 40% of the world's coastal regions, extremely hot days are becoming more common [25], and on reefs, the frequency and intensity of bleaching events is increasing [24].

There is currently little evidence that fish thermal tolerances can adapt fast enough—in the short term or over evolutionary time—to cope with warming. Nay *et al*. [26] found that cardinalfish exhibited the same preferred temperature even after six weeks of exposure to increased temperatures. Thus, in the short term, preferred temperature ranges did not change, and fish instead behaviourally thermoregulated by moving to find cooler temperatures. Artificial selection experiments over six generations in zebra fish showed that evolution towards increased thermal tolerance was slow, with the rate of adaptation likely outpaced by the rate of warming, and indicated there may be a hard limit on upper thermal tolerance [27]. Even species with broad thermal tolerances have been observed shifting deeper in response to warming waters [10].

4. Under which conditions could bathymetric shifts impact visual perception?

The impacts of bathymetric shifts on visual perception are unlikely to be equally distributed across species. First, bathymetric shifts will likely be more widespread in species that cannot shift poleward to cooler waters. This includes species in east–west oriented habitats and species constrained by geography from shifting in latitude (as in [13]; figure 4). Species that are reliant on fragmented or patchy habitats,

such as coral reefs, may also be constrained from shifting poleward.

For species that do experience bathymetric shifts, the effect on colour perception will depend strongly on the type of water in which the animal lives. Different wavelengths of light attenuate differently with depth depending on water type (figures 2 and 5). Thus, the impact of a depth shift on colour signalling is different in different habitats. In clear oceanic water, for example, long wavelengths (reds and oranges) attenuate first. In those habitats, species that display red or orange colouration, such as carotenoid-based ornaments, may be particularly affected. In freshwater systems by contrast, short wavelengths are usually absorbed most strongly, so blue and green colours are affected most. UV light also attenuates relatively quickly in all but the clearest waters. Additionally, the magnitude of the change an animal experiences in its spectral environment depends on the depth at which it originally resided. The largest change in spectral breadth occurs near the surface (figure 2). Specifically, in shallow water, long (red and orange) and very short (UV) wavelengths are much more strongly absorbed relative to blue light. Thus, even though photons of a given wavelength may still be detectable by a photoreceptor if viewed in isolation, when viewed within a spectrum dominated by light at other wavelengths, they drop relatively quickly to a level at which they are no longer useful for colour vision (figure 5).

The visual impact of a bathymetric shift also depends upon how quickly temperature and light change with depth. In waters that are clear and still, for example, the temperature gradient is often steep. As a result, animals
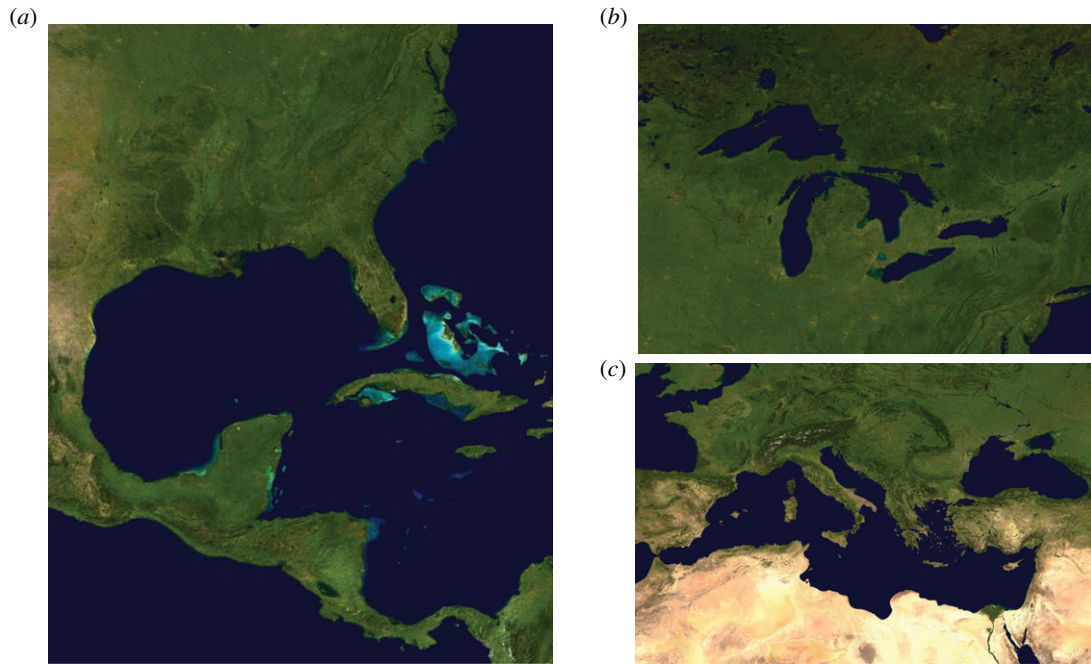
Figure 4. Species inhabiting certain geographical areas will be constrained from shifting poleward, such as those in (*a*) the northern Gulf of Mexico, or in east–west oriented habitats like (*b*) some of North America's Great Lakes or (*c*) the Mediterranean and Black Seas. Note that in (*a*), while species in the northern Gulf of Mexico cannot shift northward, those along the Atlantic coast of the USA could (as in [13]). Images from NASA/Goddard Space Flight Center. (Online version in colour.)

will not have to shift much deeper to find appropriate temperatures, and minor changes in depth will have minimal impacts on colour signalling. By contrast, animals inhabiting murky waters that cool slowly with depth (for example, due to mixing) would have to shift much deeper, and the effects of depth shifts on the optical environment could strongly impact signalling.

Bathymetric shifts can also result from increased turbidity itself, since fish may move to avoid suboptimal conditions in the turbid layer. For example, fish may shift their depth ranges to avoid hypoxic areas that result from the decomposition of algae (e.g. [30,31]). The effects of increased turbidity can also interact with those of warming surface waters. In habitats where agricultural run-off has changed the water colour and darkened the water (e.g. 'brownification' of lakes and coastal waters, as in [5,32]). Browner surface waters adsorb more solar radiation than clear waters and exhibit reduced heat energy transfer to deeper waters [33]. Thus, species in some habitats will be doubly impacted by the combination of increased turbidity and warming surface waters.

5. What types of interactions might bathymetric shifts affect?

(a) Mate choice and reproductive isolation

Changes in illumination due to increased turbidity can impact mate choice, and many of the documented effects of turbidity on mate choice and reproductive isolation are attributable to changes in the appearance or effectiveness of colour signals in turbid environments. Thus, the potential effects of bathymetric shifts are likely to be largely analogous.

In the three-spined stickleback *Gasterosteus aculeatus*, males perform courtship dances to attract females, who also assess the male's red carotenoid-based colour patches, a signal of mate quality. Stickleback males in poor condition

exhibit decreased courting effort relative to males in good condition; however, the magnitude of the difference in courting effort between poor- and good-condition males is greater in clear than in turbid conditions [34]. In essence, male colouration is less correlated with male quality in turbid waters than in clear waters, indicating that the ability of a female to gather accurate information on male quality from colouration is affected by the light environment. Supporting this finding, Candolin *et al.* [35] found that female sticklebacks in turbid conditions are more likely to mate with males that sire low-viability offspring, showing that changes to the light environment can hamper the ability of females to choose high-quality mates. In the sand goby *Pomatoschistus minutus*, females prefer to mate with larger males; in turbid conditions, however, mating success is more evenly distributed among males of all sizes [36]. Thus, increased turbidity can alter the dynamics of mate choice, relaxing selection on sexually selected traits. Because signals of mate quality are often costly to produce [37], these signals have the potential to be lost entirely if reduced visibility persists over evolutionary timescales.

Turbidity-induced changes in the light environment can also disrupt reproductive isolation. In Lake Victoria, assemblages of Haplochromine cichlids reproductively isolate by using colour signals to identify individuals as con- or hetero-specifics. However, in areas that have become turbid due to human-induced eutrophication, species diversity has decreased, and hybridization between species has increased, compared to clear environments [38]. Laboratory studies have linked the observed breakdown in reproductive isolation to changes in the illumination spectrum. Females of two congeneric cichlid species preferred conspecific over heterospecific males in the laboratory under broad-spectrum illumination, but mated indiscriminately under monochromatic lighting that masked colour differences between species [38]. Similar impacts would likely occur as a result of a bathymetric shift, given that it also reduces the range
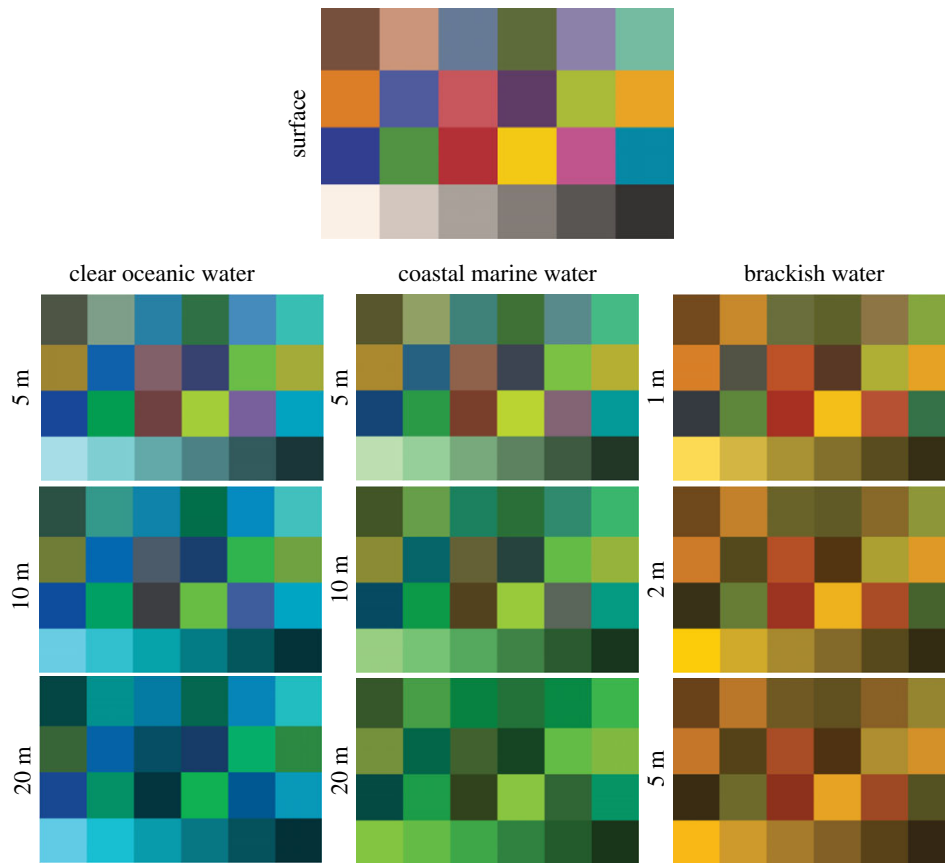
Figure 5. The effect of increased depth on the appearance of colours. Here, a GretagMacbeth ColorChecker Chart is viewed in (left) clear oceanic, (middle) coastal marine, and (right) brackish water at varying depths. The depth changes in brackish water are presented on a different scale, given how quickly brackish water attenuates light. Note that in the bottom row, most colours are distinguishable only by their brightness. Colours have been modified using an optical model that incorporates information about the downwelling illumination spectrum at given depths for a given water type and turbidity (Hydrolight 5.3 Software, Sequoia Scientific, WA, USA). The water parameters used are for oceanic water in the equatorial central Pacific [28], coastal marine water about 80 km east of Portsmouth, New Hampshire, USA [29], and brackish water from Waquoit Bay, Cape Cod, USA (S Johnsen 2000, unpublished data). (Online version in colour.)

of colours in the ambient illumination. Although cichlids provide an illustrative example, they are not the only system in which colour signals facilitate species recognition. Overall, habitat shifts can have profound impacts on the evolution of sympatric species. Although in some cases, this can lead to increased speciation, and thus increased biodiversity, the loss of information in mating signals that can result from a habitat shift can also pose a risk to biodiversity.

(b) Predator–prey dynamics

Because vision is often important for locating prey and hiding from predators, predator–prey dynamics can be impacted by increased turbidity. Some of these changes are attributable to changes in the conspicuousness of colour patches or the quality of visual information, so we expect analogous changes to occur as a result of bathymetric shifts.

For example, turbidity can affect prey choice in predators who locate prey using colour patches. The European perch (*Perca fluviatilis*) preferentially preys upon more colourful courting stickleback males, who are overall more conspicuous, but in eutrophic habitats, predation rate on conspicuous males was reduced [39]. Turbidity (and likewise bathymetric shifts) could also be advantageous for prey organisms, since under lower-light conditions, prey may be better concealed and thus harder for predators to detect. Turbidity can also reduce the ability of prey to recognize predators. For example, Ferrari *et al.* [40] trained fathead minnows (*Pimephales promelas*) to recognize predatory brown trout, and subsequently

examined minnow responses to predatory brown and rainbow trout in clear or turbid conditions. In clear water, minnows exhibited antipredator responses towards brown trout, but also generalized their recognition to novel rainbow trout. In turbid water, however, responses towards brown trout were lessened, and minnows exhibited no antipredator responses to rainbow trout. Thus, turbidity can alter the quality and quantity of visual information used in recognizing prey or predators.

Many prey species alter the frequency of antipredator behaviours in turbid compared to clear conditions, by increasing use of sheltered habitats, reducing activity and foraging levels, or altering the timing of activities such as foraging (e.g. [41,42]). Some of these changes are at least partly attributable to the decreases in light level that occur with turbidity, so we would expect similar changes to occur with bathymetric shifts.

(c) Community-scale processes

In aquatic environments, the light environment can impact the distribution and movement of animals (e.g. [43]) and social interactions like shoaling and group formation (e.g. [44,45]). Additionally, Rutterford *et al.* [46] have suggested that depth shifts may be accompanied by decreases in abundance, because species moving deeper are often forced into less optimal habitats. Of relevance to visually mediated interactions, processes that lower local species abundance can cause communication between individuals to become scarce or infrequent. Thus, information-mediated Allee effects [47],

in which decreases in population size or density are associated with decreases in individual fitness, can ultimately lead to, or exacerbate, population declines [48]. As species shift in depth, they may also be shifting into niches that are not usually free, which could affect competitive regimes, displace species, and disrupt the local community. For example, various models (e.g. [49,50]) show that changes in depth or water optical properties can dramatically affect the outcome of competition for food resources, and the structure of marine communities and food chains.

6. How might species respond to bathymetric shift-induced changes to visual perception?

There are several ways in which species can respond plastically to variation in the spectrum of the ambient environment. Species could also adapt to deeper environments over evolutionary time, but whether species can adapt to overcome the reduced efficacy of colour signals before a signalling system breaks down is unknown.

(a) Altering signal colouration or visual physiology

Several species of fish alter their signal colouration (colour patch size, saturation, or brightness) in response to changes in the light environment. Such changes can be plastic and even reversible (e.g. [51]). For example, western rainbowfish (Melanotaenia australis) exposed for 15 days to red-shifted environments, like those rich in dissolved organic matter, increased the area and brightness of colour patches that serve as signals during shoaling [44]. Male red shiner Cyprinella lutrensis display carotenoid-based colouration during the breeding season, and males from turbid habitats have brighter nuptial colouration than those from less turbid waters [52]. There is also some evidence that colouration has adapted over evolutionary timescales, to maintain signal function under variable light conditions at the population level, as in, for example, guppies (reviewed in [53]) and Burtoni cichlids [54]. However, even over evolutionary timescales, fish do not always alter their signal colouration when faced with changes in light environment. For example, Hiermes et al. [55] examined sticklebacks that have inhabited 'tea-stained' lakes in Scotland, which heavily absorb UV wavelengths, for more than 10 000 generations. They found that despite the low transmission of UV wavelengths in this habitat, males in tea-stained lakes still reflect UV light when reproductively active, and female sticklebacks still preferred males with UV reflectance.

One way in which colour signals would be unaffected by a bathymetric shift is if they are based on a fluorescent pigment. Fluorescence involves absorption of energy from shorter-wavelength light, a (typically small) fraction of which is subsequently emitted as light at a longer wavelength. A few animals are known to use fluorescence in signalling (reviewed in [56]), and a variety of natural compounds, from carotenoids to pterins to guanine, fluoresce. However, a specific set of conditions must be met in order for fluorescence to be functionally significant in a natural signalling context. At minimum, the wavelength that excites the fluorescent compound must be present in the environment at sufficient intensity and must differ sufficiently from the wavelength that is subsequently emitted that the two will be viewed as different colours [56]. Furthermore, the viewer's colour vision system must be

tuned to the emission spectrum (see [56]) and, as with any signal, some visually guided behaviour must be related to the fluorescent structure. Thus, we urge caution in assuming that fluorescent structures are signals. However, fluorophores—for example, that absorb blue wavelengths and emit green in oceanic waters, or absorb green and emit red in coastal waters—could provide a mechanism by which colour signals remain useable with increasing depth.

Fish can also tune their colour vision in response to changes in the light environment. Juveniles can plastically change their visual systems during development in response to the light environment (e.g. [51,57]), and there is also evidence for visual adaptations in adult fish in response to rapidly changing environmental conditions. These changes are usually adjustments in the expression of genes that encode light-sensitive opsin proteins, and can occur within days or weeks (e.g. [58–61]) in response to environmental changes like increased turbidity [62]. Some evidence suggests, however, that plasticity in opsin gene expression is species specific (e.g. [63]), so not all species are equally able to tune their visual systems.

These changes are likely to result in, at best, limited return of signal function. First, signal colouration is constrained by physiology, and thus, the opportunity for plastically altering signal colouration—at least over short time frames—may be limited. Second, as a given wavelength disappears from the ambient illumination, less and less of it is left to reflect from a colour patch or be absorbed by a photoreceptor. Thus, increasing the brightness, saturation, or reflectance of a colour patch, or increasing the tuning of the visual system to a specific wavelength, even on an evolutionary timescale, will likely have little to no effect if that wavelength has been strongly absorbed in the water column.

(b) Switching within the visual modality to non-colour stimuli

Another way to potentially compensate for the effects of bathymetric shifts is to switch within the visual modality from assessing colour to assessing other stimuli that are less affected by the optical environment. In theory, signal receivers could rely more on patterns (such as the arrangements of spots and stripes) for signal assessment in conditions where colour perception is altered.

One relevant study comes from mate choice trials in two species of African cichlids [64], one in which males are red and another in which males are blue. Under broad-spectrum lighting where colour is visible, females exhibit species-assortative mate choice. However, males from the blue species are also larger and display more frequently than red males. Under monochromatic light where colours were no longer discernible, females of both species responded more frequently to blue males than red males. Thus, despite potentially informative differences between males in display rate and body size, females exhibited non-assortative mate choice in the absence of colour signals. It may be that only over evolutionary timescales can females from the red species evolve to use body size, or other non-colour signals, as informative signals during mate choice.

Beyond signal receivers altering which signal criteria they rely on most, signal senders could amplify non-colour aspects of a signal. For example, in the laboratory, stickleback females visited males in clear conditions more often and for longer than

males in turbid conditions [65]. Thus, the authors concluded that for males in turbid conditions to receive the same amount of interest from females as males in clear conditions, they would need to court significantly more, potentially introducing selection for higher courtship activity among males in turbid environments. Support for this was found in an experiment where male sticklebacks from mildly and very turbid habitats were allowed to court females under standardized laboratory conditions. Males from the most turbid habitats courted more intensely [66], consistent with the idea that signallers can compensate for the reduced visibility of colour signals by increasing signal intensity along other axes.

Overall, patterns are known to be important features in processes such as species recognition (e.g. in Chaetodontid butterfly fishes, [67]). Studies have shown that a variety of organisms rely on achromatic (brightness) cues for detecting and discriminating small targets, while for large objects, chromatic (colour) cues are more salient (as in domestic chicks [68] and triggerfish [69]). However, whether signal receivers increase their reliance on patterns, or other achromatic cues, with changes in ambient light has not been explored. Importantly, as an organism shifts deeper, it adapts to the ambient brightness, so the apparent contrast between colour patches does not change, although the ability to *detect* contrast declines [70]. Additionally, with decreases in light, many organisms employ spatial summation, in essence grouping a number of photoreceptors together to collect more light, but at the expense of resolution [70]. Thus, at very low-light depths, even achromatic patterns will not be useful as signalling traits.

(c) Switching to signals in other modalities

Another way that animals can compensate for changes in visual perception is by relying more on signals in other modalities, such as olfactory signals. For example, fathead minnows were more likely to respond to chemical alarm cues from conspecifics, rather than visual cues, in turbid environments where visual information was absent [71]. Adult zebra fish housed in periodically turbid water decreased their response to visual stimuli while increasing responses to olfactory stimuli in foraging contexts, but behaviours such as shoal cohesion and activity level did not differ between clear and turbid treatments [72]. Thus, the magnitude or effects of shifts in modality may depend on the specific behaviour being considered.

In other species, relying on a non-visual modality did not make up for the reduced efficacy of visual signals. For example, in sex-role-reversed broad-nosed pipefish (*Syngnathus typhle*), the presence or absence of female olfactory cues did not affect male mate choice in turbid versus clear conditions [73]. In three-spined sticklebacks, females relied more on olfactory mate choice cues in turbid water, but preferred different males in turbid versus clear conditions, indicating that switching to a non-visual modality actually altered mate preferences [74]. Finally, Selz *et al*. [75] found that colour was necessary and sufficient for assortative

mating in a pair of cichlid species. The ability of females to choose conspecific over heterospecific mates broke down in the absence of colour information, despite potentially informative species-specific chemical cues being present. Thus, switching to a different sensory modality may help overcome reduced visual information in some behavioural tasks, and in some species, but not others.

7. Conclusion

Bathymetric shifts are occurring in response to climate change, sometimes at rates higher than 1 m yr^{-1}, and temperature anomaly events are increasingly frequent. We know that the visual world changes with increasing depth, and that these changes in near-surface waters are particularly pronounced for colour perception. Precisely which colours are most affected, and the magnitude of effects on colour perception, depends on the depth at which a species lives prior to a bathymetric shift, as well as the water type in which a species lives. Bathymetric shifts will be potentially global in scope, and large numbers of species could be affected, particularly shallow-dwelling, colourful species such as those on coral reefs.

Currently, however, there are large gaps in our understanding of the range, distribution, and magnitude of effects that bathymetric shifts are having, or may have, on visually mediated interactions. Although studies on the impacts of turbidity provide a sense of how ambient illumination changes can affect visually mediated interactions, studies directly examining depth changes are rare. There is a need for field studies that document the occurrence and magnitude of depth shifts in response to temperature variation, and experimental studies that examine what behavioural changes occur as a direct result of changes to the light environment like those that occur during bathymetric shifts. Lastly, theoretical studies could inform our understanding of whether species will be able to adapt to the challenges posed by changes to the visual environment before signalling systems break down. Understanding how bathymetric shifts may disrupt visual function and thus behaviour may help us to better direct conservation efforts, and perhaps mitigate some of the effects of anthropogenic change.

References

1. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009 The velocity of climate change. *Nature* 462, 1052–1055. (doi:10.1038/nature08649)

2. Mac Nally R, Bennett AF, Thomson JR, Radford JQ, Unmack G, Horrocks G, Vesk PA. 2009 Collapse of an avifauna: climate change appears to exacerbate habitat loss and degradation. *Divers. Distrib.* 15, 720–730. (doi:10.1111/j.1472-4642.2009.00578.x)

3. Dominoni DM *et al*. 2020 Why conservation biology can benefit from sensory ecology. *Nat. Ecol. Evol.* **4**, 502–511. (doi:10.1038/s41559-020-1135-4)

4. Smith VH, Joye SB, Howarth RW. 2006 Eutrophication of freshwater and marine ecosystems. *Limnol. Oceanogr.* **51**, 351–355. (doi:10.4319/lo.2006.51.1_part_2.0351)

5. Roulet N, Moore TR. 2006 Browning the waters. *Nature* **444**, 3–4. (doi:10.1038/444283a)

6. Sandén P, Håkansson B. 1996 Long-term trends in Secchi depth in the Baltic Sea. *Limnol. Oceanogr.* **41**, 346–351. (doi:10.4319/lo.1996.41.2.0346)

7. Cronin TW, Marshall NJ, Caldwell RL. 2000 Spectral tuning and the visual ecology of mantis shrimps. *Phil. Trans. R. Soc. Lond. B* **355**, 1263–1267. (doi:10.1098/rstb.2000.0680)

8. Schweikert LE, Fitak RR, Caves EM, Sutton TT, Johnsen S. 2018 Spectral sensitivity in ray-finned fishes: diversity, ecology and shared descent. *J. Exp. Biol.* **221**, jeb189761. (doi:10.1242/jeb.189761)

9. Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005 Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915. (doi:10.1126/science.1111322)

10. Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. 2008 Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J. Appl. Ecol.* **45**, 1029–1039. (doi:10.1111/j.1365-2664.2008.01488.x)

11. Nye JA, Link JS, Hare JA, Overholtz WJ. 2009 Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* **393**, 111–129. (doi:10.3354/meps08220)

12. Tunin-Ley A, Ibañez F, Labat JP, Zingone A, Lemée R. 2009 Phytoplankton biodiversity and NW Mediterranean Sea warming: changes in the dinoflagellate genus *Ceratium* in the 20th century. *Mar. Ecol. Prog. Ser.* **375**, 85–99. (doi:10.3354/meps07730)

13. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013 Marine taxa track local climate velocities. *Science* **341**, 1239–1242. (doi:10.1126/science.1239352)

14. Osorio D, Vorobyev M. 2008 A review of the evolution of animal colour vision and visual communication signals. *Vision Res.* **48**, 2042–2051. (doi:10.1016/j.visres.2008.06.018)

15. Johnsen S. 2012 *The optics of life*. Princeton, NJ: Princeton University Press.

16. Jerlov NG. 1976 *Marine optics*. Amsterdam, The Netherlands: Elsevier.

17. Johnsen S. 2014 Hide and seek in the open sea: pelagic camouflage and visual countermeasures. *Annu. Rev. Mar. Sci.* **6**, 369–392. (doi:10.1146/annurev-marine-010213-135018)

18. Engelhard GH, Righton DA, Pinnegar JK. 2014 Climate change and fishing: a century of shifting distribution in North Sea cod. *Glob. Chang. Biol.* **20**, 2473–2483. (doi:10.1111/gcb.12513)

19. Lenanton RCJ, Dowling CE, Smith KA, Fairclough DV, Jackson G. 2017 Potential influence of a marine heatwave on range extensions of tropical fishes in the eastern Indian Ocean—invaluable contributions from amateur observers. *Reg. Stud. Mar. Sci.* **13**, 19–31. (doi:10.1016/j.rsma.2017.03.005)

20. NOAA National Centers for Environmental Information. 2020 Climate at a glance: global time series. See https://www.ncdc.noaa.gov/cag/ (accessed 14 January 2021).

21. Hartmann DL *et al*. 2013 Observations: atmosphere and surface. In *Climate change 2013—the physical science basis: working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change*, pp. 159–254. Cambridge, UK: Cambridge University Press.

22. Collins M *et al*. 2013 Long-term climate change: projections, commitments and irreversibility. In *Climate change 2013—the physical science basis: contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*, pp. 1029–1136. Cambridge, UK: Cambridge University Press.

23. Sherman K, Belkin IM, Friedland KD, O'Reilly J, Hyde K. 2009 Accelerated warming and emergent trends in fisheries biomass yields of the world's large marine ecosystems. *Ambio* **38**, 215–224. (doi:10.1579/0044-7447-38.4.215)

24. Goreau TJ, Hayes RL. 2005 Global coral reef bleaching and sea surface temperature trends from satellite-derived hotspot analysis. *World Resour. Rev.* **17**, 254–293.

25. Lima FP, Wethey DS. 2012 Three decades of high-resolution coastal sea surface temperatures reveal more than warming. *Nat. Commun.* **3**, 1–6. (doi:10.1038/ncomms1713)

26. Nay TJ, Johansen JL, Habary A, Steffensen JF, Rummer JL. 2015 Behavioural thermoregulation in a temperature-sensitive coral reef fish, the five-lined cardinalfish (*Cheilodipterus quinquelineatus*). *Coral Reefs* **34**, 1261–1265. (doi:10.1007/s00338-015-1353-4)

27. Morgan R, Finnøen MH, Jensen H, Pélabon C, Jutfelt F. 2020 Low potential for evolutionary rescue from climate change in a tropical fish. *Proc. Natl Acad. Sci. USA* **117**, 33 365–33 372. (doi:10.1073/pnas.2011419117)

28. Johnsen S. 2002 Cryptic and conspicuous colouration in the pelagic environment. *Proc. R. Soc. Lond. B* **269**, 243–256. (doi:10.1098/rspb.2001.1855)

29. Johnsen S, Sosik HM. 2003 Cryptic colouration and mirrored sides as camouflage strategies in near-surface pelagic habitats: implications for foraging and predator avoidance. *Limnol. Oceanogr.* **48**, 1277–1288. (doi:10.4319/lo.2003.48.3.1277)

30. Bell GW, Eggleston DB. 2005 Species-specific avoidance responses by blue crabs and fish to chronic and episodic hypoxia. *Mar. Biol.* **146**, 761–770. (doi:10.1007/s00227-004-1483-7)

31. Karlson K, Rosenberg R, Bonsdorff E. 2002 Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic Waters—a review. *Oceanogr. Mar. Biol. Annu. Rev.* **40**, 427–489. (doi:10.1201/9780203180594.ch8)

32. Williamson CE, Overholt EP, Pilla RM, Leach TH, Brentrup JA, Knoll LB, Mette EM, Moeller RE. 2015 Ecological consequences of long-term browning in lakes. *Sci. Rep.* **5**, 1–10. (doi:10.1038/srep18666)

33. Read JS, Rose KC. 2013 Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. *Limnol. Oceanogr.* **58**, 921–931. (doi:10.4319/lo.2013.58.3.0921)

34. Wong BBM, Candolin U, Lindström K, Lindstro K. 2007 Signals of male quality in three-spined sticklebacks. *Am. Nat.* **170**, 184–189. (doi:10.1086/519398)

35. Candolin U, Tukiainen I, Bertell E. 2016 Environmental change disrupts communication and sexual selection in a stickleback population. *Ecology* **97**, 969–979. (doi:10.1890/15-1090)

36. Järvenpää M, Lindström K. 2004 Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proc. R. Soc. Lond B* **271**, 2361–2365. (doi:10.1098/rspb.2004.2870)

37. Searcy WA, Nowicki S. 2005 *The evolution of animal communication*. Princeton, NJ: Princeton University Press.

38. Seehausen O, Van Alphen JJM, Witte F. 1997 Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811. (doi:10.1126/science.277.5333.1808)

39. Johnson S, Candolin U. 2017 Predation cost of a sexual signal in the threespine stickleback. *Behav. Ecol.* **28**, 1160–1165. (doi:10.1093/beheco/arx080)

40. Ferrari MCO, Lysak KR, Chivers DP. 2010 Turbidity as an ecological constraint on learned predator recognition and generalization in a prey fish. *Anim. Behav.* **79**, 515–519. (doi:10.1016/j.anbehav.2009.12.006)

41. Ajemian MJ, Sohel S, Mattila J. 2015 Effects of turbidity and habitat complexity on antipredator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*): antipredator behavior in sticklebacks. *Environ. Biol. Fishes* **98**, 45–55. (doi:10.1007/s10641-014-0235-x)

42. Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO. 2011 To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biol. Lett.* **7**, 811–813. (doi:10.1098/rsbl.2011.0645)

43. Nakayama S, Doering-Arjes P, Linzmaier S, Briege J, Klefoth T, Pieterek T, Arlinghaus R. 2018 Fine-scale movement ecology of a freshwater top predator, Eurasian perch (*Perca fluviatilis*), in response to the abiotic environment over the course of a year. *Ecol. Freshw. Fish* **27**, 798–812. (doi:10.1111/eff.12393)

44. Kelley JL, Phillips B, Cummins GH, Shand J. 2012 Changes in the visual environment affect colour signal brightness and shoaling behaviour in a freshwater fish. *Anim. Behav.* **83**, 783–791. (doi:10.1016/j.anbehav.2011.12.028)

45. Modarressie R, Rick IP, Bakker TCM. 2006 UV matters in shoaling decisions. *Proc. R. Soc. B* **273**, 849–854. (doi:10.1098/rspb.2005.3397)

46. Rutterford LA, Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön PJ, Sims DW, Tinker J, Genner MJ. 2015 Future fish distributions constrained by depth in warming seas. *Nat. Clim. Chang.* **5**, 569–573. (doi:10.1038/nclimate2607)

47. Schmidt KA, Johansson J, Betts MG. 2015 Information-mediated Allee effects in breeding habitat selection. *Am. Nat.* **186**, E162–E171. (doi:10.1086/683659)

48. Gil MA, Baskett ML, Schreiber SJ. 2019 Social information drives ecological outcomes among competing species. *Ecology* **100**, e02835. (doi:10.1002/ecy.2835)

49. Eiane K, Aksnes DL, Giske J. 1997 The significance of optical properties in competition among visual and tactile planktivores: a theoretical study. *Ecol. Modell.* **98**, 123–136. (doi:10.1016/S0304-3800 (96)01909-6)

50. Haraldsson M, Tönnesson K, Tiselius P, Thingstad TF, Aksnes DL. 2012 Relationship between fish and jellyfish as a function of eutrophication and water clarity. *Mar. Ecol. Prog. Ser.* **471**, 73–85. (doi:10.3354/meps10036)

51. Hornsby MAW, Sabbah S, Robertson RM, Hawryshyn CW. 2013 Modulation of environmental light alters reception and production of visual signals in Nile tilapia. *J. Exp. Biol.* **216**, 3110–3122. (doi:10.1242/jeb.081331)

52. Dugas MB, Franssen NR. 2011 Nuptial colouration of red shiners (*Cyprinella lutrensis*) is more intense in turbid habitats. *Naturwissenschaften* **98**, 247–251. (doi:10.1007/s00114-011-0765-4)

53. Sandkam B, Dalton B, Breden F, Carleton K. 2018 Reviewing guppy color vision: integrating the molecular and physiological variation in visual tuning of a classic system for sensory drive. *Curr. Zool.* **64**, 535–545. (doi:10.1093/cz/zoy047)

54. Theis A, Roth O, Cortesi F, Ronco F, Salzburger W, Egger B. 2017 Variation of anal fin egg-spots along an environmental gradient in a haplochromine cichlid fish. *Evolution* **71**, 766–777. (doi:10.1111/evo.13166)

55. Hiermes M, Reher S, Rick IP, Bakker TCM. 2021 Influence of lighting environment on social preferences in sticklebacks from two different photic habitats. I. Mate preferences of wild-caught females. *Curr. Zool.* zoab008. (doi:10.1093/cz/zoab008)

56. Marshall J, Johnsen S. 2017 Fluorescence as a means of colour signal enhancement. *Phil. Trans. R. Soc. B* **372**, 20160335. (doi:10.1098/rstb.2016.0335)

57. Sakai Y, Ohtsuki H, Kasagi S, Kawamura S, Kawata M. 2016 Effects of light environment during growth on the expression of cone opsin genes and behavioral spectral sensitivities in guppies (*Poecilia reticulata*). *BMC Evol. Biol.* **16**, 1–10. (doi:10.1186/s12862-016-0679-z)

58. Fuller RC, Claricoates KM. 2011 Rapid light-induced shifts in opsin expression: finding new opsins, discerning mechanisms of change, and implications for visual sensitivity. *Mol. Ecol.* **20**, 3321–3335. (doi:10.1111/j.1365-294X.2011.05180.x)

59. Fuller RC, Noa LA, Strellner RS. 2010 Teasing apart the many effects of lighting environment on opsin expression and foraging preference in bluefin killifish. *Am. Nat.* **176**, 1–13. (doi:10.1086/652994)

60. Nandamuri SP, Yourick MR, Carleton KL. 2017 Adult plasticity in African cichlids: rapid changes in opsin expression in response to environmental light differences. *Mol. Ecol.* **26**, 6036–6052. (doi:10.1111/mec.14357)

61. Luehrmann M, Stieb SM, Carleton KL, Pietzker A, Cheney KL, Marshall NJ. 2018 Short-term colour vision plasticity on the reef: changes in opsin expression under varying light conditions differ between ecologically distinct fish species. *J. Exp. Biol.* **221**, jeb175281. (doi:10.1242/jeb.175281)

62. Chang CH, Yan HY. 2019 Plasticity of opsin gene expression in the adult red shiner (*Cyprinella lutrensis*) in response to turbid habitats. *PLoS ONE* **14**, 1–16. (doi:10.1371/journal.pone.0215376)

63. Stieb SM, Carleton KL, Cortesi F, Marshall NJ, Salzburger W. 2016 Depth-dependent plasticity in opsin gene expression varies between damselfish (Pomacentridae) species. *Mol. Ecol.* **25**, 3645–3661. (doi:10.1111/mec.13712)

64. Seehausen O, Van Alphen JJM. 1998 The effect of male colouration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav. Ecol. Sociobiol.* **42**, 1–8. (doi:10.1007/s002650050405)

65. Engström-Öst J, Candolin U. 2007 Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behav. Ecol.* **18**, 393–398. (doi:10.1093/beheco/arl097)

66. Tuomainen U, Sylvin E, Candolin U. 2011 Adaptive phenotypic differentiation of courtship in response to recent anthropogenic disturbance. *Evol. Ecol. Res.* **13**, 697–710.

67. McMillan WO, Weigt LA, Palumbi SR. 1999 Color pattern evolution, assortative mating, and genetic differentiation in brightly colored butterflyfishes (Chaetodontidae). *Evolution* **53**, 247–260. (doi:10.1111/j.1558-5646.1999.tb05350.x)

68. Jones CD, Osorio D. 2004 Discrimination of oriented visual textures by poultry chicks. *Vision Res.* **44**, 83–89. (doi:10.1016/j.visres.2003.08.014)

69. Newport C, Green NF, McClure EC, Osorio DC, Vorobyev M, Marshall NJ, Cheney KL. 2017 Fish use colour to learn compound visual signals. *Anim. Behav.* **125**, 93–100. (doi:10.1016/j.anbehav.2017.01.003)

70. Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014 Visual ecology. Princeton, NJ: Princeton University Press.

71. Hartman EJ, Abrahams MV. 2000 Sensory compensation and the detection of predators: the interaction between chemical and visual information. *Proc. R. Soc. Lond. B* **267**, 571–575. (doi:10.1098/rspb.2000.1039)

72. Suriyampola PS, Cacéres J, Martins EP. 2018 Effects of short-term turbidity on sensory preference and behaviour of adult fish. *Anim. Behav.* **146**, 105–111. (doi:10.1016/j.anbehav.2018.10.014)

73. Sundin J, Berglund A, Rosenqvist G. 2010 Turbidity hampers mate choice in a pipefish. *Ethology* **116**, 713–721. (doi:10.1111/j.1439-0310.2010.01787.x)

74. Heuschele J, Mannerla M, Gienapp P, Candolin U. 2009 Environment-dependent use of mate choice cues in sticklebacks. *Behav. Ecol.* **20**, 1223–1227. (doi:10.1093/beheco/arp123)

75. Selz OM, Pierotti MER, Maan ME, Schmid C, Seehausen O. 2014 Female preference for male color is necessary and sufficient for assortative mating in 2 cichlid sister species. *Behav. Ecol.* **25**, 612–626. (doi:10.1093/beheco/aru024)