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

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EMC and SJ conceived of the idea; SJ carried out the optical modeling; EMC wrote the manuscript with input from SJ; both authors edited the manuscript and gave final approval for submission.

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

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7  
8                   **Abstract**

9                   Visual perception is, in part, a function of the ambient illumination spectrum. In aquatic  
10                   environments, illumination depends upon the water's optical properties and depth, both of which  
11                   can change due to anthropogenic impacts: turbidity is increasing in many aquatic habitats, and  
12                   many species have shifted deeper in response to warming surface waters (known as bathymetric  
13                   shifts). Although increasing turbidity and bathymetric shifts can result in similarly large changes to a  
14                   species' optical environment, no studies have yet examined the impact of the latter on visually-  
15                   mediated interactions. Here, we examine a potential link between climate change and visual  
16                   perception, with a focus on colour. We discuss: (1) what is known about bathymetric shifts; (2) how  
17                   the impacts of bathymetric shifts on visual interactions may be distributed across species; (3) which  
18                   interactions might be affected; and (4) the ways that animals have to respond to these changes. As  
19                   warming continues and temperature fluctuations grow more extreme, many species may move into  
20                   even deeper waters. There is thus a need for studies that examine how such shifts can affect an  
21                   organism's visual world, interfere with behaviour, and impact fitness, population dynamics, and  
22                   community structure.

23                   **Keywords:** Visual ecology, anthropogenic impacts, depth shift, colour, signalling

24  
25                   **Introduction**

26                   Human activities are affecting animals in numerous ways, such as range shifts [1] and  
27                   habitat loss (e.g. [2]). Recently, increased attention has been paid to understanding how  
28                   anthropogenic changes can impact animal sensory systems (e.g. [3]). Vision is particularly important  
29                   for information acquisition in many species, allowing animals to locate food, assess mates, signal to  
30                   territorial intruders, and find mutualistic partners. What an animal sees depends upon the source of  
31                   the light (our focus here being solar illumination), the spectral reflectance (the percentage of light a

32 surface reflects at each wavelength) of what is viewed, the optical properties of the medium that  
33 light passes through (e.g., air, water), the animal's visual system, and the ambient illumination.  
34 Changes to any of these factors can affect visual perception.

35         The ambient illumination an aquatic organism experiences depends upon both the optical  
36 properties of the water it inhabits and on the depth at which it lives, both of which can shift as a  
37 result of anthropogenic impacts. First, increased dissolved and particulate compounds, due to  
38 agricultural and septic run-off, soil erosion, and other sources can increase turbidity [4]. This makes  
39 waters darker, murkier, and more brown or green in colour (e.g. [5,6]). Second, many aquatic  
40 species are moving deeper in the water column (in what is known as a bathymetric shift) in  
41 response to warming surface waters. In addition to illumination decreasing with depth, the  
42 spectrum of underwater light narrows because different wavelengths of light attenuate at different  
43 rates. In essence, the range of visible colours grows more limited with increasing depth, changing  
44 the appearance of visual stimuli (Figure 1). As a result, bathymetric shifts can affect a species' visual  
45 environment in similar ways as increased turbidity. Although studies have correlated variation in  
46 colour vision across taxa with species' depth ranges (e.g. [7,8]), no studies have yet focused on how  
47 visually-mediated interactions may be impacted as a given species experiences a bathymetric shift.  
48 The need for such studies is immediate, however, as species are already shifting their depth  
49 distributions in response to anthropogenic change [9–13].

50         Here, we focus on how climate-induced changes to depth ranges could impact an animal's  
51 visual world, interfering with visually-mediated processes and altering the dynamics of interactions  
52 within and between species. We discuss: (1) what is currently known about climate-change-induced  
53 bathymetric shifts (hereafter, bathymetric shifts); (2) the conditions under which bathymetric shifts  
54 could impact visual perception; (3) how bathymetric shifts may alter signalling interactions; and (4)  
55 how animals may respond to these changes. We emphasize effects on colour perception, since  
56 colour is a source of information across many taxa and behavioural contexts [14], and because  
57 bathymetric shifts can have large impacts on illumination spectra and thus colour perception. We  
58 also focus on fish, a diverse group of highly visual animals in which the impacts of bathymetric shifts  
59 on visually-mediated communication could be significant, and in which behaviour and visual  
60 capabilities are well-studied. Lastly, we restrict our discussion to the epipelagic zone, the depth  
61 range at which photosynthesis can occur, because this is where the largest changes in both  
62 temperature and the spectral environment occur with increases in depth.

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

75

#### 76 **Light in Aquatic Environments: A Primer**

77 First, we provide a brief primer on light in aquatic environments; for detailed accounts, see  
78 [15–17].

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

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

92 Despite this variability, there are a few general rules for how light attenuates with depth in  
93 different water types. In oceanic and most tropical coastal waters, scattering is low, and light is

94 primarily absorbed by the water itself, with a small to moderate contribution to absorption from  
95 chlorophyll in phytoplankton and light scattering by the bodies of the phytoplankters themselves,  
96 which are almost exclusively found in the upper 200 meters. The dominant wavelength – especially  
97 below 200 meters – is typically ~480 nm (cyan to human eyes), and light at this wavelength  
98 decreases ten-fold roughly every 70-100 meters. In temperate and polar coastal waters, scattering  
99 and absorption are high, with absorption at long wavelengths dominated by water and absorption  
100 at short wavelengths dominated by moderate to strong contributions from chlorophyll. This results  
101 in green water with a dominant wavelength of ~550 nm. As one approaches land, scattering  
102 typically increases due to increases in suspended sediment and absorption by coloured dissolved  
103 organic matter (CDOM). This latter material absorbs all but long-wavelength light strongly, so water  
104 colour changes from green to brown. Fresh waters are highly variable. Some are clear and blue, but  
105 most are strongly scattering and absorbing systems with large contributions from both chlorophyll  
106 and CDOM. Certain freshwater systems (e.g. blackwater swamps), are atypical in having strong  
107 absorption with low scattering.

108

#### 109 **What is currently known about bathymetric shifts in aquatic organisms?**

110 There are multiple examples of aquatic organisms, from dinoflagellates to fish, shifting  
111 deeper due to increases in near-surface water temperatures [9–13,18]. Although the rate at which  
112 species are shifting varies considerably, [11] found that some fish species had shifted deeper at a  
113 mean rate of more than 1 meter/year between 1968 and 2007. Although the majority of  
114 documented bathymetric shifts come from northern temperate regions, there is emerging evidence  
115 of depth shifts in tropical reef species as well (e.g. [19]).

116 Bathymetric shifts have the potential to be widespread. Most of Earth's aquatic ecosystems  
117 are warming (Figure 3), and global mean sea surface temperatures (SSTs) are predicted to increase  
118 by up to 4.8°C (relative to the 1896-2005 average temperature) by 2100 [20,21]. The rate of change  
119 and projected increases in SST vary widely across habitats and latitudes. In general, marine areas in  
120 northern temperate and polar latitudes are warming especially rapidly [22]. However, species-rich  
121 reef and tropical coastal ecosystems are also warming quickly, with SST trends across 207 coral reef  
122 sites showing average increases of 0.32°C/decade [23], and coastal waters warming at a rate of  
123 0.25°C/decade [24].

124 Climate change is also manifesting in aquatic habitats as increases in temperature  
125 variability. Many coastal and reef ecosystems are projected to experience increased numbers of SST  
126 anomalies, large short-term changes in temperature that have the potential to severely impact  
127 animals. In almost 40% of the world's coastal regions, extremely hot days are becoming more  
128 common [24], and on reefs, the frequency and intensity of bleaching events is increasing [23].

129 There is currently little evidence that fish thermal tolerances can adapt fast enough—in the  
130 short term or over evolutionary time—to cope with warming. [25] found that cardinalfish exhibited  
131 the same preferred temperature even after six weeks of exposure to increased temperatures. Thus,  
132 in the short term, preferred temperature ranges did not change, and fish instead behaviourally  
133 thermoregulated by moving to find cooler temperatures. Artificial selection experiments over six  
134 generations in zebra fish showed that evolution towards increased thermal tolerance was slow,  
135 with the rate of adaptation likely outpaced by the rate of warming, and indicated there may be a  
136 hard limit on upper thermal tolerance [26]. Even species with broad thermal tolerances have been  
137 observed shifting deeper in response to warming waters [10].

138

### 139 **Under which conditions could bathymetric shifts impact visual perception?**

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

145 For species that do experience bathymetric shifts, the effect on colour perception will  
146 depend strongly on the type of water in which the animal lives. Different wavelengths of light  
147 attenuate differently with depth depending on water type (Figures 2, 5). Thus, the impact of a  
148 depth shift on colour signalling is different in different habitats. In clear oceanic water, for example,  
149 long wavelengths (reds and oranges) attenuate first. In those habitats, species that display red or  
150 orange colouration, such as carotenoid-based ornaments, may be particularly affected. In  
151 freshwater systems by contrast, short wavelengths are usually absorbed most strongly, so blue and  
152 green colours are affected most. Ultraviolet (UV) light also attenuates relatively quickly in all but the  
153 clearest waters. Additionally, the magnitude of the change an animal experiences in its spectral  
154 environment depends on the depth at which it originally resided. The largest change in spectral

155 breadth occurs near the surface (Figure 2). Specifically, in shallow water, long (red and orange) and  
156 very short (ultraviolet) wavelengths are much more strongly absorbed relative to blue light. Thus,  
157 even though photons of a given wavelength may still be detectable by a photoreceptor if viewed in  
158 isolation, when viewed within a spectrum dominated by light at other wavelengths, they drop  
159 relatively quickly to a level at which they're no longer useful for colour vision (Figure 5).

160 The visual impact of a bathymetric shift also depends upon how quickly temperature and  
161 light change with depth. In waters that are clear and still, for example, the temperature gradient is  
162 often steep. As a result, animals will not have to shift much deeper to find appropriate  
163 temperatures, and minor changes in depth will have minimal impacts on colour signalling. By  
164 contrast, animals inhabiting murky waters that cool slowly with depth (for example, due to mixing)  
165 would have to shift much deeper, and the effects of depth shifts on the optical environment could  
166 strongly impact signalling.

167 Bathymetric shifts can also result from increased turbidity itself, since fish may move to  
168 avoid sub-optimal conditions in the turbid layer. For example, fish may shift their depth ranges to  
169 avoid hypoxic areas that result from the decomposition of algae (e.g. [28,29]). The effects of  
170 increased turbidity can also interact with those of warming surface waters. In habitats where  
171 agricultural runoff has changed the water colour and darkened the water (e.g. "brownification" of  
172 lakes and coastal waters, as in [5,30]). Browner surface waters adsorb more solar radiation than  
173 clear waters and exhibit reduced heat energy transfer to deeper waters [31]. Thus, species in some  
174 habitats will be doubly-impacted by the combination of increased turbidity and warming surface  
175 waters.

176

### 177 **What types of interactions might bathymetric shifts affect?**

#### 178 *Mate Choice and Reproductive Isolation*

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

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



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

198         Turbidity-induced changes in the light environment can also disrupt reproductive isolation.  
199 In Lake Victoria, assemblages of Haplochromine cichlids reproductively isolate by using colour  
200 signals to identify individuals as con- or hetero-specifics. However, in areas that have become turbid  
201 due to human-induced eutrophication, species diversity has decreased, and hybridization between  
202 species has increased, compared to clear environments [38]. Laboratory studies have linked the  
203 observed breakdown in reproductive isolation to changes in the illumination spectrum. Females of  
204 two congeneric cichlid species preferred conspecific over heterospecific males in the lab under  
205 broad-spectrum illumination, but mated indiscriminately under monochromatic lighting that  
206 masked colour differences between species [38]. Similar impacts would likely occur as a result of a  
207 bathymetric shift, given that it also reduces the range of colours in the ambient illumination.  
208 Although cichlids provide an illustrative example, they are not the only system in which colour  
209 signals facilitate species recognition. Overall, habitat shifts can have profound impacts on the  
210 evolution of sympatric species. Although in some cases this can lead to increased speciation, and  
211 thus increased biodiversity, the loss of information in mating signals that can result from a habitat  
212 shift can also pose a risk to biodiversity.

213

#### 214 *Predator-Prey Dynamics*

215         Because vision is often important for locating prey and hiding from predators, predator-prey  
216 dynamics can be impacted by increased turbidity. Some of these changes are attributable to

217 changes in the conspicuousness of colour patches or the quality of visual information, so we expect  
218 analogous changes to occur as a result of bathymetric shifts.

219 For example, turbidity can affect prey choice in predators who locate prey using colour  
220 patches. The European perch (*Perca fluviatilis*) preferentially preys upon more colourful courting  
221 stickleback males, who are overall more conspicuous, but in eutrophic habitats, predation rate on  
222 conspicuous males was reduced [39]. Turbidity (and likewise bathymetric shifts) could also be  
223 advantageous for prey organisms, since under lower-light conditions, prey may be better-concealed  
224 and thus harder for predators to detect. Turbidity can also reduce the ability of prey to recognize  
225 predators. For example, [40] trained fathead minnows (*Pimephales promelas*) to recognize  
226 predatory brown trout, and subsequently examined minnow responses to predatory brown and  
227 rainbow trout in clear or turbid conditions. In clear water, minnows exhibited antipredator  
228 responses towards brown trout, but also generalized their recognition to novel rainbow trout. In  
229 turbid water, however, responses towards brown trout were lessened, and minnows exhibited no  
230 antipredator responses to rainbow trout. Thus, turbidity can alter the quality and quantity of visual  
231 information used in recognizing prey or predators.

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

237

### 238 *Community Scale Processes*

239 In aquatic environments, the light environment can impact the distribution and movement  
240 of animals (e.g. [43]) and social interactions like shoaling and group formation (e.g. [44,45]).  
241 Additionally, [46] have suggested that depth shifts may be accompanied by decreases in  
242 abundance, because species moving deeper are often forced into less optimal habitats. Of  
243 relevance to visually-mediated interactions, processes that lower local species abundance can cause  
244 communication between individuals to become scarce or infrequent. Thus, information-mediated  
245 Allee effects [47], in which decreases in population size or density are associated with decreases in  
246 individual fitness, can ultimately lead to, or exacerbate, population declines [48]. As species shift in  
247 depth, they may also be shifting into niches that are not usually free, which could affect competitive

248 regimes, displace species, and disrupt the local community. For example, various models (e.g.  
249 [49,50]) show that changes in depth or water optical properties can dramatically affect the outcome  
250 of competition for food resources, and the structure of marine communities and food chains.

251

### 252 **How might species respond to bathymetric shift-induced changes to visual perception?**

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

257

#### 258 *Altering signal colouration or visual physiology*

259 Several species of fish alter their signal colouration (colour patch size, saturation, or  
260 brightness) in response to changes in the light environment. Such changes can be plastic and even  
261 reversible (e.g. [51]). For example, western rainbowfish (*Melanotaenia australis*) exposed for 15  
262 days to red-shifted environments, like those rich in dissolved organic matter, increased the area and  
263 brightness of colour patches that serve as signals during shoaling [44]. Male red shiner *Cyprinella*  
264 *lutrensis* display carotenoid-based colouration during the breeding season, and males from turbid  
265 habitats have brighter nuptial colouration than those from less turbid waters [52]. There is also  
266 some evidence that colouration has adapted over evolutionary timescales, to maintain signal  
267 function under variable light conditions at the population level, as in, for example guppies  
268 (reviewed in [53]) and Burtoni cichlids [54]. However, even over evolutionary timescales, fish don't  
269 always alter their signal colouration when faced with changes in light environment. For example,  
270 [55] examined sticklebacks that have inhabited "tea-stained" lakes in Scotland, which heavily  
271 absorb UV wavelengths, for more than 10,000 generations. They found that despite the low  
272 transmission of UV wavelengths in this habitat, males in tea-stained lakes still reflect UV light when  
273 reproductively active, and female sticklebacks still preferred males with UV reflectance.

274 One way in which colour signals would be unaffected by a bathymetric shift is if they are  
275 based on a fluorescent pigment. Fluorescence involves absorption of energy from shorter-  
276 wavelength light, a (typically small) fraction of which is subsequently emitted as light at a longer  
277 wavelength. A few animals are known use fluorescence in signalling (reviewed in [56]), and a variety  
278 of natural compounds, from carotenoids to pterins to guanine, fluoresce. However, a specific set of

279 conditions must be met in order for fluorescence to be functionally significant in a natural signalling  
280 context. At minimum, the wavelength that excites the fluorescent compound must be present in  
281 the environment at sufficient intensity and must differ sufficiently from the wavelength that is  
282 subsequently emitted that the two will be viewed as different colours [56]. Furthermore the  
283 viewer's colour vision system must be tuned to the emission spectrum (see [56]) and, as with any  
284 signal, some visually-guided behaviour must be related to the fluorescent structure. Thus, we urge  
285 caution in assuming that fluorescent structures are signals. However, fluorophores—for example  
286 that absorb blue wavelengths and emit green in oceanic waters, or absorb green and emit red in  
287 coastal waters—could provide a mechanism by which colour signals remain useable with increasing  
288 depth.

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

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

305

### 306 *Switching within the visual modality to non-colour stimuli*

307 Another way to potentially compensate for the effects of bathymetric shifts is to switch  
308 within the visual modality from assessing colour to assessing other stimuli that are less affected by  
309 the optical environment. In theory, signal receivers could rely more on patterns (such as the

310 arrangements of spots and stripes) for signal assessment in conditions where colour perception is  
311 altered.

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

321 Beyond signal receivers altering which signal criteria they rely on most, signal senders could  
322 amplify non-colour aspects of a signal. For example, in the laboratory, stickleback females visited  
323 males in clear conditions more often and for longer than males in turbid conditions [65]. Thus, the  
324 authors concluded that for males in turbid conditions to receive the same amount of interest from  
325 females as males in clear conditions, they would need to court significantly more, potentially  
326 introducing selection for higher courtship activity among males in turbid environments. Support for  
327 this was found in an experiment where male sticklebacks from mildly and very turbid habitats were  
328 allowed to court females under standardized lab conditions. Males from the most turbid habitats  
329 courted more intensely [66], consistent with the idea that signallers can compensate for the  
330 reduced visibility of colour signals by increasing signal intensity along other axes.

331 Overall, patterns are known to be important features in processes such as species  
332 recognition (e.g. in Chaetodontid butterfly fishes, [67]). Studies have shown that a variety of  
333 organisms rely on achromatic (brightness) cues for detecting and discriminating small targets, while  
334 for large objects, chromatic (colour) cues are more salient (as in domestic chicks [68] and triggerfish  
335 [69]). However, whether signal receivers increase their reliance on patterns, or other achromatic  
336 cues, with changes in ambient light has not been explored. Importantly, as an organism shifts  
337 deeper, it adapts to the ambient brightness, so the apparent contrast between colour patches does  
338 not change, although the ability to *detect* contrast declines [70]. Additionally, with decreases in  
339 light, many organisms employ spatial summation, in essence grouping a number of photoreceptors

340 together to collect more light, but at the expense of resolution [70]. Thus, at very low-light depths,  
341 even achromatic patterns won't be useful as signalling traits.

342

### 343 *Switching to signals in other modalities*

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

352 In other species, relying on a non-visual modality did not make up for the reduced efficacy  
353 of visual signals. For example, in sex-role-reversed broad-nosed pipefish (*Syngnathus typhle*), the  
354 presence or absence of female olfactory cues did not affect male mate choice in turbid versus clear  
355 conditions [73]. In three-spined sticklebacks, females relied more on olfactory mate choice cues in  
356 turbid water, but preferred different males in turbid versus clear conditions, indicating that  
357 switching to a non-visual modality actually altered mate preferences [74]. Finally, [75] found that  
358 colour was necessary and sufficient for assortative mating in a pair of cichlid species. The ability of  
359 females to choose conspecific over heterospecific mates broke down in the absence of colour  
360 information, despite potentially informative species-specific chemical cues being present. Thus,  
361 switching to a different sensory modality may help overcome reduced visual information in some  
362 behavioural tasks, and in some species, but not others.

363

### 364 **Conclusions**

365 Bathymetric shifts are occurring in response to climate change, sometimes at rates higher  
366 than one meter/year, and temperature anomaly events are increasingly frequent. We know that  
367 the visual world changes with increasing depth, and that these changes in near-surface waters are  
368 particularly pronounced for colour perception. Precisely which colours are most affected, and the  
369 magnitude of effects on colour perception, depends on the depth at which a species lives prior to a  
370 bathymetric shift, as well as the water type in which a species lives. Bathymetric shifts will be

371 potentially global in scope, and large numbers of species could be affected, particularly shallow-  
372 dwelling, colourful species such as those on coral reefs.

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

385

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389

### 390 **Literature cited**

- 391 1. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009 The velocity of  
392 climate change. *Nature* **462**, 1052–1055. (doi:10.1038/nature08649)
- 393 2. Mac Nally R, Bennett AF, Thomson JR, Radford JQ, Unmack G, Horrocks G, Vesk PA. 2009  
394 Collapse of an avifauna: Climate change appears to exacerbate habitat loss and  
395 degradation. *Divers. Distrib.* **15**, 720–730. (doi:10.1111/j.1472-4642.2009.00578.x)
- 396 3. Dominoni DM *et al.* 2020 Why conservation biology can benefit from sensory ecology.  
397 *Nat. Ecol. Evol.* , 1–10. (doi:10.1038/s41559-020-1135-4)
- 398 4. Smith VH, Joye SB, Howarth RW. 2006 Eutrophication of freshwater and marine  
399 ecosystems. *Limnol. Oceanogr.* **51**, 351–355. (doi:10.4319/lo.2006.51.1\_part\_2.0351)
- 400 5. Roulet N, Moore TR. 2006 Browning the Waters. *Nature* **444**, 3–4.

- 401 6. Sandén P, Håkansson B. 1996 Long-term trends in Secchi depth in the Baltic Sea. *Limnol.*  
402 *Oceanogr.* **41**, 346–351. (doi:10.4319/lo.1996.41.2.0346)
- 403 7. Cronin TW, Marshall NJ, Caldwell RL. 2000 Spectral tuning and the visual ecology of  
404 mantis shrimps. *Philos. Trans. R. Soc. B Biol. Sci.* **355**, 1263–1267.  
405 (doi:10.1098/rstb.2000.0680)
- 406 8. Schweikert LE, Fitak RR, Caves EM, Sutton TT, Johnsen S. 2018 Spectral sensitivity in ray-  
407 finned fishes: diversity, ecology and shared descent. *J. Exp. Biol.* **221**, jeb189761.  
408 (doi:10.1242/jeb.189761)
- 409 9. Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005 Climate change and distribution shifts in  
410 marine fishes. *Science* **308**, 1912–1915. (doi:10.1126/science.1111322)
- 411 10. Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR. 2008 Climate  
412 change and deepening of the North Sea fish assemblage: A biotic indicator of warming  
413 seas. *J. Appl. Ecol.* **45**, 1029–1039. (doi:10.1111/j.1365-2664.2008.01488.x)
- 414 11. Nye JA, Link JS, Hare JA, Overholtz WJ. 2009 Changing spatial distribution of fish stocks in  
415 relation to climate and population size on the Northeast United States continental shelf.  
416 *Mar. Ecol. Prog. Ser.* **393**, 111–129. (doi:10.3354/meps08220)
- 417 12. Tunin-Ley A, Ibañez F, Labat JP, Zingone A, Lemée R. 2009 Phytoplankton biodiversity and  
418 NW Mediterranean Sea warming: Changes in the dinoflagellate genus *Ceratium* in the  
419 20th century. *Mar. Ecol. Prog. Ser.* **375**, 85–99. (doi:10.3354/meps07730)
- 420 13. Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA. 2013 Marine taxa track local  
421 climate velocities. *Science* **341**, 1239–1242.
- 422 14. Osorio D, Vorobyev M. 2008 A review of the evolution of animal colour vision and visual  
423 communication signals. *Vision Res.* **48**, 2042–2051.
- 424 15. Johnsen S. 2012 *The Optics of Life*. Princeton, NJ: Princeton University Press.
- 425 16. Jerlov NG. 1976 *Marine optics*. Elsevier.
- 426 17. Johnsen S. 2014 Hide and seek in the open sea: Pelagic camouflage and visual  
427 countermeasures. *Ann. Rev. Mar. Sci.* **6**, 369–392. (doi:10.1146/annurev-marine-010213-  
428 135018)
- 429 18. Engelhard GH, Righton DA, Pinnegar JK. 2014 Climate change and fishing: A century of



- 430 shifting distribution in North Sea cod. *Glob. Chang. Biol.* **20**, 2473–2483.  
431 (doi:10.1111/gcb.12513)
- 432 19. Lenanton RCJ, Dowling CE, Smith KA, Fairclough D V., Jackson G. 2017 Potential influence  
433 of a marine heatwave on range extensions of tropical fishes in the eastern Indian  
434 Ocean—Invaluable contributions from amateur observers. *Reg. Stud. Mar. Sci.* **13**, 19–31.  
435 (doi:10.1016/j.rsma.2017.03.005)
- 436 20. Hartmann DL *et al.* 2013 Observations: atmosphere and surface. In *Climate change 2013*  
437 *the physical science basis: Working group I contribution to the fifth assessment report of*  
438 *the intergovernmental panel on climate change*, pp. 159–254. Cambridge University  
439 Press.
- 440 21. Collins M *et al.* 2013 Long-term climate change: projections, commitments and  
441 irreversibility. In *Climate Change 2013-The Physical Science Basis: Contribution of*  
442 *Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*  
443 *Climate Change*, pp. 1029–1136. Cambridge University Press.
- 444 22. Sherman K, Belkin IM, Friedland KD, O’Reilly J, Hyde K. 2009 Accelerated warming and  
445 emergent trends in fisheries biomass yields of the world’s large marine ecosystems.  
446 *Ambio* **38**, 215–224. (doi:10.1579/0044-7447-38.4.215)
- 447 23. Goreau TJ, Hayes RL. 2005 Global coral reef bleaching and sea surface temperature  
448 trends from satellite-derived hotspot analysis. *World Resour. Rev.* **17**, 254–293.
- 449 24. Lima FP, Wetthey DS. 2012 Three decades of high-resolution coastal sea surface  
450 temperatures reveal more than warming. *Nat. Commun.* **3**. (doi:10.1038/ncomms1713)
- 451 25. Nay TJ, Johansen JL, Habary A, Steffensen JF, Rummer JL. 2015 Behavioural  
452 thermoregulation in a temperature-sensitive coral reef fish, the five-lined cardinalfish  
453 (*Cheilodipterus quinquelineatus*). *Coral Reefs* **34**, 1261–1265. (doi:10.1007/s00338-015-  
454 1353-4)
- 455 26. Morgan R, Finnøen MH, Jensen H, Pélabon C, Jutfelt F. 2020 Low potential for  
456 evolutionary rescue from climate change in a tropical fish. *Proc. Natl. Acad. Sci.*  
457 (doi:10.1073/pnas.2011419117)
- 458 27. 2020 NOAA National Centers for Environmental Information, Climate at a Glance: Global

- 459 Time Series. See <https://www.ncdc.noaa.gov/cag/> (accessed on 14 January 2021).
- 460 28. Bell GW, Eggleston DB. 2005 Species-specific avoidance responses by blue crabs and fish  
461 to chronic and episodic hypoxia. *Mar. Biol.* **146**, 761–770. (doi:10.1007/s00227-004-  
462 1483-7)
- 463 29. Karlson K, Rosenberg R, Bonsdorff E. 2002 Temporal and Spatial Large-Scale Effects of  
464 Eutrophication and Oxygen Deficiency on Benthic Fauna in Scandinavian and Baltic  
465 Waters ,À a Review. *Oceanogr. Mar. Biol. An Annu. Rev.* **40**, 427–489.  
466 (doi:10.1201/9780203180594.ch8)
- 467 30. Williamson CE, Overholt EP, Pilla RM, Leach TH, Brentrup JA, Knoll LB, Mette EM, Moeller  
468 RE. 2015 Ecological consequences of long-term browning in lakes. *Sci. Rep.* **5**, 1–10.  
469 (doi:10.1038/srep18666)
- 470 31. Read JS, Rose KC. 2013 Physical responses of small temperate lakes to variation in  
471 dissolved organic carbon concentrations. *Limnol. Oceanogr.* **58**, 921–931.  
472 (doi:10.4319/lo.2013.58.3.0921)
- 473 32. Johnsen S. 2002 Cryptic and conspicuous coloration in the pelagic environment. *Proc. R.*  
474 *Soc. B Biol. Sci.* **269**, 243–256. (doi:10.1098/rspb.2001.1855)
- 475 33. Johnsen S, Sosik HM. 2003 Cryptic coloration and mirrored sides as camouflage strategies  
476 in near-surface pelagic habitats: Implications for foraging and predator avoidance.  
477 *Limnol. Oceanogr.* **48**, 1277–1288.
- 478 34. Wong BBM, Candolin U, Lindström K, Lindstro K. 2007 Signals of Male Quality in Three-  
479 Spined Sticklebacks. *Am. Nat.* **170**, 184–189.
- 480 35. Candolin U, Tukiainen I, Bertell E. 2016 Environmental change disrupts communication  
481 and sexual selection in a stickleback population. *Ecology* **97**, 969–979.
- 482 36. Järvenpää M, Lindström K. 2004 Water turbidity by algal blooms causes mating system  
483 breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proc. R. Soc.*  
484 *B Biol. Sci.* **271**, 2361–2365. (doi:10.1098/rspb.2004.2870)
- 485 37. Searcy WA, Nowicki S. 2005 *The Evolution of Animal Communication*. Princeton, NJ:  
486 Princeton University Press.
- 487 38. Seehausen O, Alphen JJM Van, Witte F. 1997 Cichlid fish diversity threatened by

- 488 eutrophication that curbs sexual selection. *Science* **277**, 1808–1811.
- 489 39. Johnson S, Candolin U. 2017 Predation cost of a sexual signal in the threespine  
490 stickleback. *Behav. Ecol.* **28**, 1160–1165. (doi:10.1093/beheco/ax080)
- 491 40. Ferrari MCO, Lysak KR, Chivers DP. 2010 Turbidity as an ecological constraint on learned  
492 predator recognition and generalization in a prey fish. *Anim. Behav.* **79**, 515–519.  
493 (doi:10.1016/j.anbehav.2009.12.006)
- 494 41. Ajemian MJ, Sohel S, Mattila J. 2015 Effects of turbidity and habitat complexity on  
495 antipredator behavior of three-spined sticklebacks (*Gasterosteus aculeatus*):  
496 Antipredator behavior in sticklebacks. *Environ. Biol. Fishes* **98**, 45–55.  
497 (doi:10.1007/s10641-014-0235-x)
- 498 42. Leahy SM, McCormick MI, Mitchell MD, Ferrari MCO. 2011 To fear or to feed: The effects  
499 of turbidity on perception of risk by a marine fish. *Biol. Lett.* **7**, 811–813.  
500 (doi:10.1098/rsbl.2011.0645)
- 501 43. Nakayama S, Doering-Arjes P, Linzmaier S, Brieger J, Klefoth T, Pieterek T, Arlinghaus R.  
502 2018 Fine-scale movement ecology of a freshwater top predator, Eurasian perch (*Perca*  
503 *fluviatilis*), in response to the abiotic environment over the course of a year. *Ecol.*  
504 *Freshw. Fish* **27**, 798–812. (doi:10.1111/eff.12393)
- 505 44. Kelley JL, Phillips B, Cummins GH, Shand J. 2012 Changes in the visual environment affect  
506 colour signal brightness and shoaling behaviour in a freshwater fish. *Anim. Behav.* **83**,  
507 783–791. (doi:10.1016/j.anbehav.2011.12.028)
- 508 45. Modarressie R, Rick IP, Bakker TCM. 2006 UV matters in shoaling decisions. *Proc. R. Soc.*  
509 *B Biol. Sci.* **273**, 849–854.
- 510 46. Rutterford LA, Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön PJ, Sims DW,  
511 Tinker J, Genner MJ. 2015 Future fish distributions constrained by depth in warming seas.  
512 *Nat. Clim. Chang.* **5**, 569–573. (doi:10.1038/nclimate2607)
- 513 47. Schmidt KA, Johansson J, Betts MG. 2015 Information-mediated Allee effects in breeding  
514 habitat selection. *Am. Nat.* **186**, E162–E171.
- 515 48. Gil MA, Baskett ML, Schreiber SJ. 2019 Social information drives ecological outcomes  
516 among competing species. *Ecology* **100**, e02835.

- 517 49. Eiane K, Aksnes DL, Giske J. 1997 The significance of optical properties in competition  
518 among visual and tactile planktivores: A theoretical study. *Ecol. Modell.* **98**, 123–136.  
519 (doi:10.1016/S0304-3800(96)01909-6)
- 520 50. Haraldsson M, Tönnesson K, Tiselius P, Thingstad TF, Aksnes DL. 2012 Relationship  
521 between fish and jellyfish as a function of eutrophication and water clarity. *Mar. Ecol.*  
522 *Prog. Ser.* **471**, 73–85. (doi:10.3354/meps10036)
- 523 51. Hornsby MAW, Sabbah S, Robertson RM, Hawryshyn CW. 2013 Modulation of  
524 environmental light alters reception and production of visual signals in Nile tilapia. *J. Exp.*  
525 *Biol.* **216**, 3110–3122. (doi:10.1242/jeb.081331)
- 526 52. Dugas MB, Franssen NR. 2011 Nuptial coloration of red shiners (*Cyprinella lutrensis*) is  
527 more intense in turbid habitats. *Naturwissenschaften* **98**, 247–251. (doi:10.1007/s00114-  
528 011-0765-4)
- 529 53. Sandkam B, Dalton B, Breden F, Carleton K. 2018 Reviewing guppy color vision:  
530 Integrating the molecular and physiological variation in visual tuning of a classic system  
531 for sensory drive. *Curr. Zool.* **64**, 535–545. (doi:10.1093/cz/zoy047)
- 532 54. Theis A, Roth O, Cortesi F, Ronco F, Salzburger W, Egger B. 2017 Variation of anal fin egg-  
533 spots along an environmental gradient in a haplochromine cichlid fish. *Evolution* **71**, 766–  
534 777. (doi:10.1111/evo.13166)
- 535 55. Hiermes MH, Reher SR, Rik IPR, Bakker TCMB. 2021 Influence of lighting environment on  
536 social preferences in sticklebacks from two different photic habitats . I . mate  
537 preferences of wild-caught females. *Curr. Zool.* , 1–21.
- 538 56. Marshall J, Johnsen S. 2017 Fluorescence as a means of colour signal enhancement.  
539 *Philos. Trans. R. Soc. B Biol. Sci.* **372**, 20160335. (doi:10.1098/rstb.2016.0335)
- 540 57. Sakai Y, Ohtsuki H, Kasagi S, Kawamura S, Kawata M. 2016 Effects of light environment  
541 during growth on the expression of cone opsin genes and behavioral spectral sensitivities  
542 in guppies (*Poecilia reticulata*). *BMC Evol. Biol.* **16**, 1–10. (doi:10.1186/s12862-016-0679-  
543 z)
- 544 58. Fuller RC, Claricoates KM. 2011 Rapid light-induced shifts in opsin expression: Finding  
545 new opsins, discerning mechanisms of change, and implications for visual sensitivity.

- 546 *Mol. Ecol.* **20**, 3321–3335. (doi:10.1111/j.1365-294X.2011.05180.x)
- 547 59. Fuller RC, Noa LA, Strellner RS. 2010 Teasing apart the many effects of lighting  
548 environment on opsin expression and foraging preference in bluefin killifish. *Am. Nat.*  
549 **176**, 1–13. (doi:10.1086/652994)
- 550 60. Nandamuri SP, Yourick MR, Carleton KL. 2017 Adult plasticity in African cichlids: rapid  
551 changes in opsin expression in response to environmental light differences. *Mol. Ecol.* **26**,  
552 6036–6052.
- 553 61. Luehrmann M, Stieb SM, Carleton KL, Pietzker A, Cheney KL, Marshall NJ. 2018 Short-  
554 term colour vision plasticity on the reef: Changes in opsin expression under varying light  
555 conditions differ between ecologically distinct fish species. *J. Exp. Biol.* **221**.  
556 (doi:10.1242/jeb.175281)
- 557 62. Chang CH, Yan HY. 2019 Plasticity of opsin gene expression in the adult red shiner  
558 (*Cyprinella lutrensis*) in response to turbid habitats. *PLoS One* **14**, 1–16.  
559 (doi:10.1371/journal.pone.0215376)
- 560 63. Stieb SM, Carleton KL, Cortesi F, Marshall NJ, Salzburger W. 2016 Depth-dependent  
561 plasticity in opsin gene expression varies between damselfish (Pomacentridae) species.  
562 *Mol. Ecol.* **25**, 3645–3661.
- 563 64. Seehausen O, Van Alphen JJM. 1998 The effect of male coloration on female mate choice  
564 in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behav. Ecol.*  
565 *Sociobiol.* **42**, 1–8. (doi:10.1007/s002650050405)
- 566 65. Engström-Öst J, Candolin U. 2007 Human-induced water turbidity alters selection on  
567 sexual displays in sticklebacks. *Behav. Ecol.* **18**, 393–398. (doi:10.1093/beheco/arl097)
- 568 66. Tuomainen U, Sylvén E, Candolin U. 2011 Adaptive phenotypic differentiation of courtship  
569 in response to recent anthropogenic disturbance. *Evol. Ecol. Res.* **13**, 697–710.
- 570 67. McMillan WO, Weigt LA, Palumbi SR. 1999 Color pattern evolution, assortative mating,  
571 and genetic differentiation in brightly colored butterflyfishes (Chaetodontidae). *Evolution*  
572 **53**, 247–260. (doi:10.1111/j.1558-5646.1999.tb05350.x)
- 573 68. Jones CD, Osorio D. 2004 Discrimination of oriented visual textures by poultry chicks.  
574 *Vision Res.* **44**, 83–89. (doi:10.1016/j.visres.2003.08.014)

- 575 69. Newport C, Green NF, McClure EC, Osorio DC, Vorobyev M, Marshall NJ, Cheney KL. 2017  
576 Fish use colour to learn compound visual signals. *Anim. Behav.* **125**, 93–100.  
577 (doi:10.1016/j.anbehav.2017.01.003)
- 578 70. Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014 *Visual Ecology*. Princeton, NJ:  
579 Princeton University Press.
- 580 71. Hartman EJ, Abrahams M V. 2000 Sensory compensation and the detection of predators:  
581 The interaction between chemical and visual information. *Proc. R. Soc. B Biol. Sci.* **267**,  
582 571–575. (doi:10.1098/rspb.2000.1039)
- 583 72. Suriyampola PS, Cacéres J, Martins EP. 2018 Effects of short-term turbidity on sensory  
584 preference and behaviour of adult fish. *Anim. Behav.* **146**, 105–111.  
585 (doi:10.1016/j.anbehav.2018.10.014)
- 586 73. Sundin J, Berglund A, Rosenqvist G. 2010 Turbidity hampers mate choice in a pipefish.  
587 *Ethology* **116**, 713–721. (doi:10.1111/j.1439-0310.2010.01787.x)
- 588 74. Heuschele J, Mannerla M, Gienapp P, Candolin U. 2009 Environment-dependent use of  
589 mate choice cues in sticklebacks. *Behav. Ecol.* **20**, 1223–1227.  
590 (doi:10.1093/beheco/arp123)
- 591 75. Selz OM, Pierotti MER, Maan ME, Schmid C, Seehausen O. 2014 Female preference for  
592 male color is necessary and sufficient for assortative mating in 2 cichlid sister species.  
593 *Behav. Ecol.* **25**, 612–626. (doi:10.1093/beheco/aru024)
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605 **Figure Captions**

606 **Figure 1.** Photographs taken with no flash, but at different depths, illustrate how colours available  
607 in the marine environment change with depth. The green turtle shown at ten meters depth lacks  
608 the orange and yellow highlights seen on the turtle at three meters depth – even though the former  
609 is photographed from a shorter distance – because orange and yellow wavelengths are no longer  
610 present in sufficient quantities in the illumination to be seen after reflecting off of the carapace.  
611 Photographs taken by SJ at Heron Island, Australia.

612  
613 **Figure 2.** The effect of a bathymetric shift depends on the size of the shift, the original depth, and  
614 the water type. First, the range of wavelengths available decreases with depth, as illustrated here in  
615 (A) near-shore coastal and (B) clear coral reef water. The dark regions show where light of a given  
616 wavelength is less than 5% of its surface value. The y-axis scales differ between (A) and (B) to better  
617 show the depth profile of near-shore coastal water. Second, the spectral breadth of illumination at  
618 any depth decreases after a bathymetric shift. (C,D) show the percent of spectral breadth remaining  
619 after a bathymetric shift – as a function of original depth – in the water types shown in (A) and (B),  
620 respectively. For example, if animal normally lives at 15 m depth in coral reef water and is forced to  
621 move 15 meters deeper (dashed lines), then the spectral breadth of the ambient illumination is now  
622 only 80-90% of what it was (illustrated by the grey circle). Spectral breadth is strongly affected by  
623 bathymetric shifts in near-surface waters, because many short and long wavelengths are absorbed  
624 in the first few meters. At deeper depths the effects of bathymetric shifts are more complex, but far  
625 stronger in near-shore coastal water. Panels (A, C) made using inherent optical properties of Jerlov  
626 type 7C near-shore temperate water [16]. Panels (B, D) made via a radiative transfer model  
627 (Hydrolight 5.3) using the inherent optical properties for oligotrophic water with a chlorophyll  
628 concentration of 0.5 mg/m<sup>3</sup>, typical of coral reefs.

629  
630 **Figure 3.** The world's oceans have warmed over the last hundred years. (A) Annual sea surface  
631 temperatures of the global ocean and northern and southern hemispheres have increased since  
632 1880. This graph uses the 1910 to 2000 average as a baseline for depicting change. (B) 2019 ocean  
633 temperature departure from average, with respect to a 1981-2010 base period. Data from the  
634 United States National Oceanographic and Atmospheric Administration Centers for Environmental  
635 Information [27].

636

637 **Figure 4.** Species inhabiting certain geographic areas will be constrained from shifting poleward,  
638 such as those in (A) the northern Gulf of Mexico, or in east-west oriented habitats like (B) some of  
639 North America's Great Lakes or (C) the Mediterranean and Black Seas. Note that in (A), while  
640 species in the northern Gulf of Mexico cannot shift northward, those along the Atlantic coast of the  
641 United States could (as in [13]). Images from NASA/Goddard Space Flight Center.

642

643 **Figure 5.** The effect of increased depth on the appearance of colours. Here, a GretagMacbeth  
644 ColorChecker Chart is viewed in (left) clear oceanic, (middle) coastal marine, and (right) brackish  
645 water at varying depths. The depth changes in brackish water are presented on a different scale,  
646 given how quickly brackish water attenuates light. Note that in the bottom row, most colours are  
647 distinguishable only by their brightness. Colours have been modified using an optical model that  
648 incorporates information about the downwelling illumination spectrum at given depths for a given  
649 water type and turbidity (Hydrolight 5.3 Software, Sequoia Scientific, WA, USA). The water  
650 parameters used are for oceanic water in the equatorial central Pacific [32], coastal marine water  
651 about 80km east of Portsmouth, New Hampshire, USA [33], and brackish water from Waquoit Bay,  
652 Cape Cod, USA (SJ unpubl data).

653



3 meters



10 meters



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 ten meters depth lacks the orange and yellow highlights seen on the turtle at three meters 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 SJ at Heron Island, Australia.

53x69mm (300 x 300 DPI)

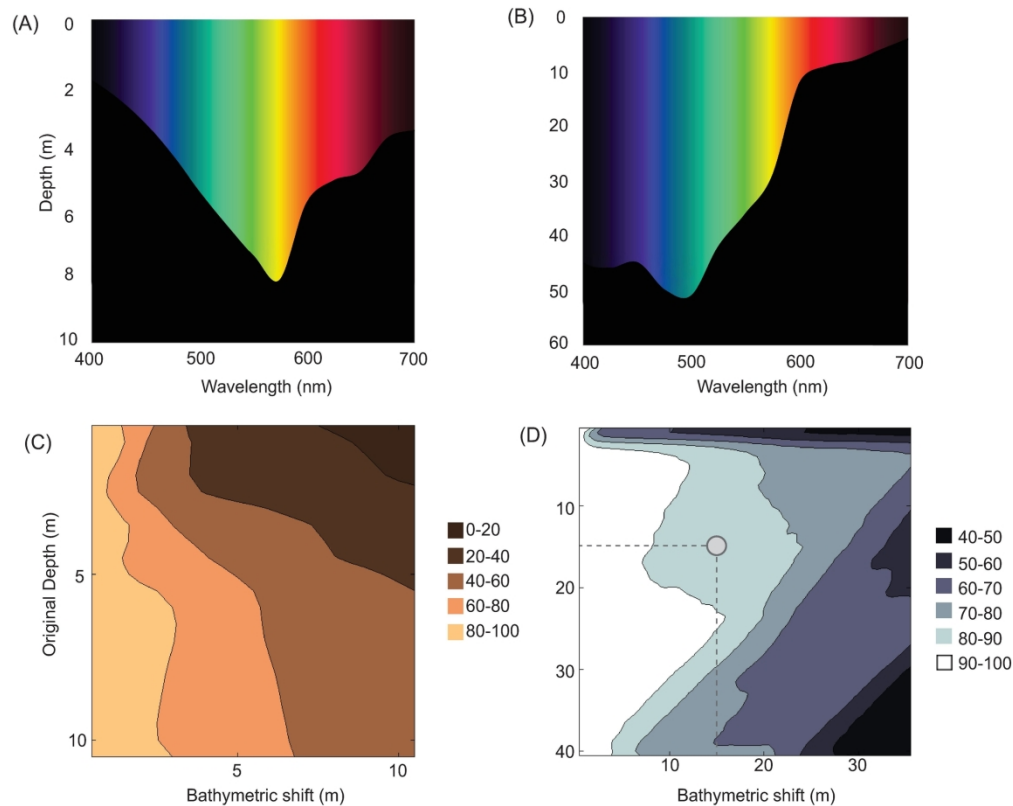


Figure 2. The effect of a bathymetric shift depends on the size of the shift, the original depth, and the water type. First, the range of wavelengths available decreases with depth, as illustrated here in (A) near-shore coastal and (B) clear coral reef water. The dark regions show where light of a given 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) show the percent of spectral breadth remaining after a bathymetric shift – as a function of original depth – in the water types shown in (A) and (B), respectively. For example, if animal normally lives at 15 m depth in coral reef water and is forced to move 15 meters 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 meters. At deeper depths the effects of bathymetric shifts are more complex, but far stronger in near-shore coastal water. Panels (A, C) made using inherent optical properties of Jerlov type 7C near-shore temperate water [16]. Panels (B, D) made via a radiative transfer model (Hydrolight 5.3) using the inherent optical properties for oligotrophic water with a chlorophyll concentration of  $0.5 \text{ mg/m}^3$ , typical of coral reefs.

206x166mm (300 x 300 DPI)

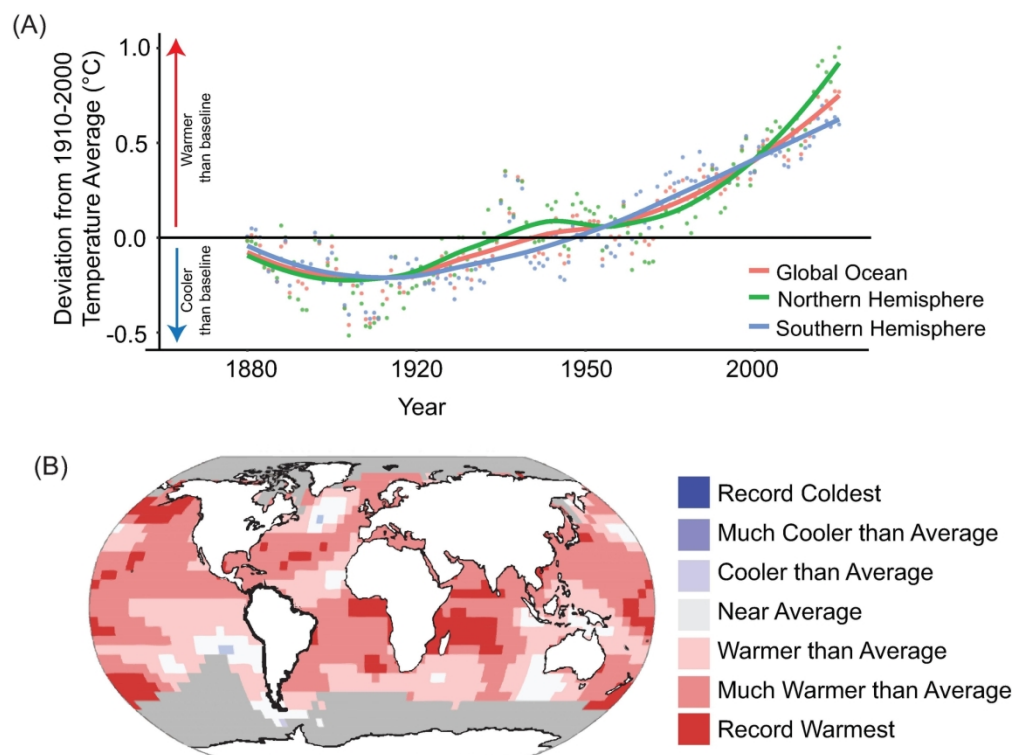


Figure 3. The world's oceans have warmed over the last hundred years. (A) Annual sea surface temperatures of the global ocean and northern and southern hemispheres have increased since 1880. This graph uses the 1910 to 2000 average as a baseline for depicting change. (B) 2019 ocean temperature departure from average, with respect to a 1981-2010 base period. Data from the United States National Oceanographic and Atmospheric Administration Centers for Environmental Information [27].

163x122mm (300 x 300 DPI)

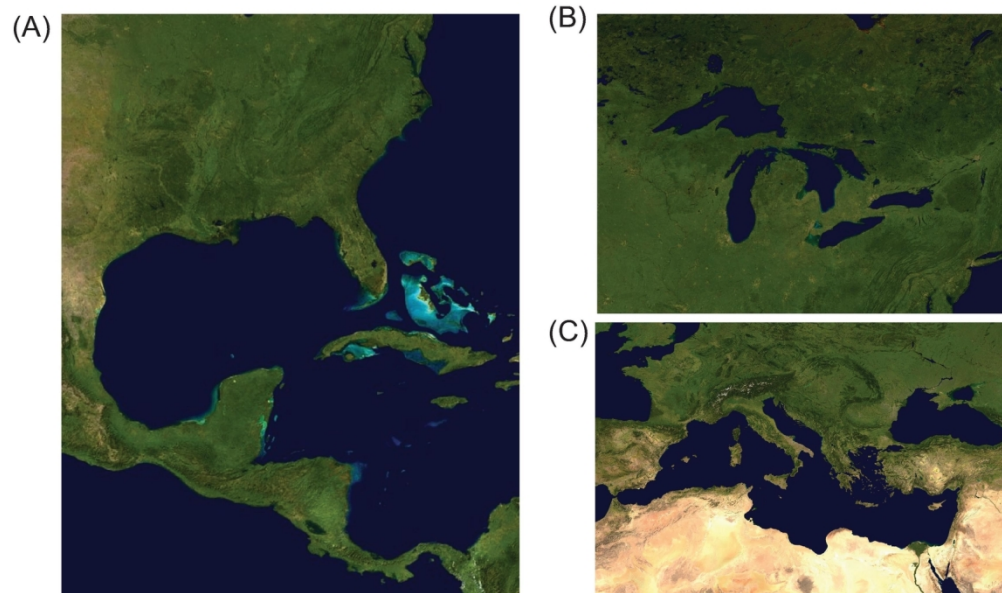


Figure 4. Species inhabiting certain geographic areas will be constrained from shifting poleward, such as those in (A) the northern Gulf of Mexico, or in east-west oriented habitats like (B) some of North America's Great Lakes or (C) the Mediterranean and Black Seas. Note that in (A), while species in the northern Gulf of Mexico cannot shift northward, those along the Atlantic coast of the United States could (as in [13]). Images from NASA/Goddard Space Flight Center.

145x86mm (300 x 300 DPI)

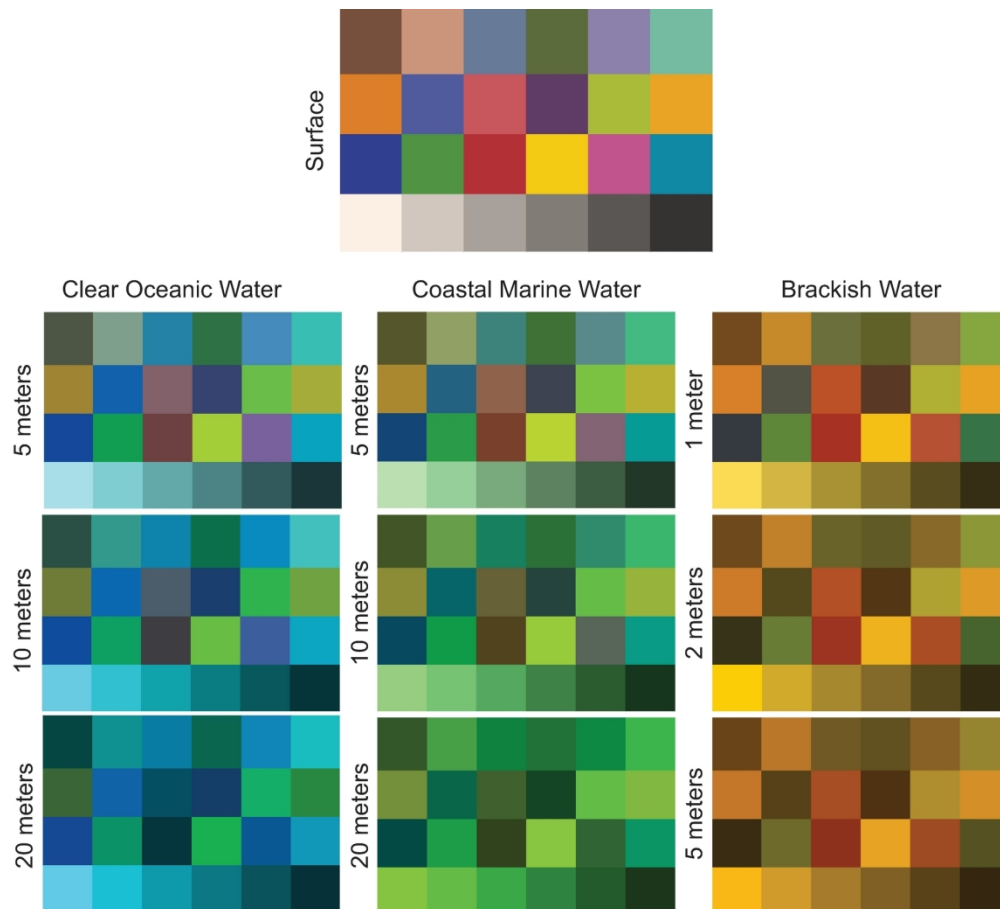


Figure 5. The effect of increased depth on the appearance of colours. Here, a GretagMacbeth ColorChecker Chart is viewed in (left) clear oceanic, (middle) coastal marine, and (right) brackish water at varying depths. The depth changes in brackish water are presented on a different scale, given how quickly 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 [32], coastal marine water about 80km east of Portsmouth, New Hampshire, USA [33], and brackish water from Waquoit Bay, Cape Cod, USA (SJ unpubl data).

178x161mm (300 x 300 DPI)