

Primer

Vision and lack of vision in the ocean

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As land-locked animals, when we visualise the ocean our mind's eye may see crashing waves or a vast blue expanse stretching to the horizon, a raft of torpedoing penguins, a glimpse of colourful coral reef fish from the shark-free safety of a sandy beach. Underwater, the crystal-clear, and in fact not at all silent, world of Jacques Cousteau, or more recently David Attenborough, is a wonderland that some cannot wait to witness first hand as divers, while others are content to see it on a screen. Spend a bit of time underwater, in the English Channel for example, and a few facts emerge. Most obviously, much of this underwater realm is visually very different to land and indeed to the cherry-picked clear waters of documentaries. It may be disappointingly murky and monochromatic. Perhaps surprisingly, therefore, on close inspection the diversity of eye designs and light sensing mechanisms that evolved in the ocean are more varied than on land, reflecting the greater range of light environments and lifestyles of the marine world. Particularly in the last ten years, the destructive influence we are having on the oceans has become visibly obvious, not just to fisheries biologists and ecologists, but to anyone returning to a favourite dive spot or reef resort. Climate change, as a resulting of burning fossil fuels, human greed and carelessness with plastic disposal are rapidly degrading entire oceanic ecosystems.

The evolution of vision underwater, as on land, is guided by what sort of light is available, the behavioural and ecological needs of each species and a balance of the best survival solutions provided by different sensory mechanisms. With these factors in mind, this primer aims to introduce aspects of vision in the ocean and comment briefly on how anthropomorphic changes to the ocean may now be impacting the visual

behaviour and survival of some marine species.

Why is vision in the ocean different and more varied than on land?

As a result of the physical constraints, optical and others, within the aquatic environment, vision is in some ways less useful in the ocean than on land. Other sensory mechanisms that we share to some degree, including hearing or olfaction (smell) become accentuated underwater, taking advantage of the greater density of this medium. A whale hunts down a giant squid in the dark by producing and analysing a sound 'image'; a salmon navigates up the already dissolved olfactory signature of its home river: both these tasks are achieved over a distance that vision would not allow. Seemingly exotic senses we lack receptors for, such as electroreception and magnetoreception, also enable aquatic animals to find food and locate home. This multisensory landscape underwater must be considered when we are surprised to find an octopus is colour blind or that some fish look mainly upwards. Colour is less important to a night-active octopus than the textural, tactile and chemosensory information provided by its eight legs. A mesopelagic fish living at a depth of 200 m de-emphasises downward and sideways vision, as there are few photons in those viewing directions, but directs its vibration-sensitive lateral line system there instead. Vision on land has become the dominant sense as air is clear, the whole of earth's atmosphere removing only 20% of light as it passes through, allowing rapid survival decisions from a distance. If evolutionary push comes to shove, considering the ocean as a whole, you may be better off there with a good nose.

This difference in overall sensory emphasis is in part derived from the fact that most of the living-space in the ocean is dark for most of the time. Sunlight does not penetrate below 1000 m in clearest ocean waters, at 200m it is dim or indeed absent altogether in more turbid waters, and 80% of the ocean ecosystem lies below this latter depth. Some deep-sea creatures produce their own light (bioluminescence), but life in the deep is sparse, specifically due to this aphotic existence that is lacking in the photosynthetic front-end of the food

chain. Both bioluminescence and life in the dim mesopelagic realm provide some fascinating visual adaptations, but most of what follows concerns life in the light-rich shallows, where vision again becomes almost indispensable. It is also biased towards coral reefs and colour vision, partly because of author-ignorance and partly because remarkable visual adaptations exist within those geographical and scientific confines.

At some point before terrestrial life emerged, the ability to use the information contained in a small region of the electromagnetic spectrum, 300–700 nm, evolved. For the visually oriented human, the obvious selective advantage for the haves over the have nots makes it surprising that some animals do not have eyes. Eyes and indeed all neural tissue are energetically expensive to maintain and vision is rapidly lost or de-emphasised where it is either not required or, as in some deep-sea animals, is less useful than other senses. Useful visual information includes: where light may be blocked (by an oncoming predator); where it emanates from (a sunny spot to display in); or where it is selectively reflected from (a colourful seaweed or fish worth eating).

The 300–700 nm wavelength band is the first physical and indeed chemically driven constraint on vision everywhere: longer than 700nm, up into the infrared, the molecule contained within photoreceptors and used to absorb light, often generically referred to as rhodopsin, suffers from signal to noise problems; below 300nm, any protein including rhodopsin absorbs light in a non-labile and therefore non-visual opaque manner, just like a rock. Given this range to work with, two other physical limitations define visual capabilities underwater: the refractive index similarities of animal tissue and water, and the rapid attenuation of light over distance. Each is discussed in turn.

Refractive index of water and animal tissue

The difference in refractive index (n) of air (close to 1.00) and of water-containing optical tissues such as cornea and lens (1.38 and 1.38–1.4, respectively, in humans) allows terrestrial eyes to focus an image on

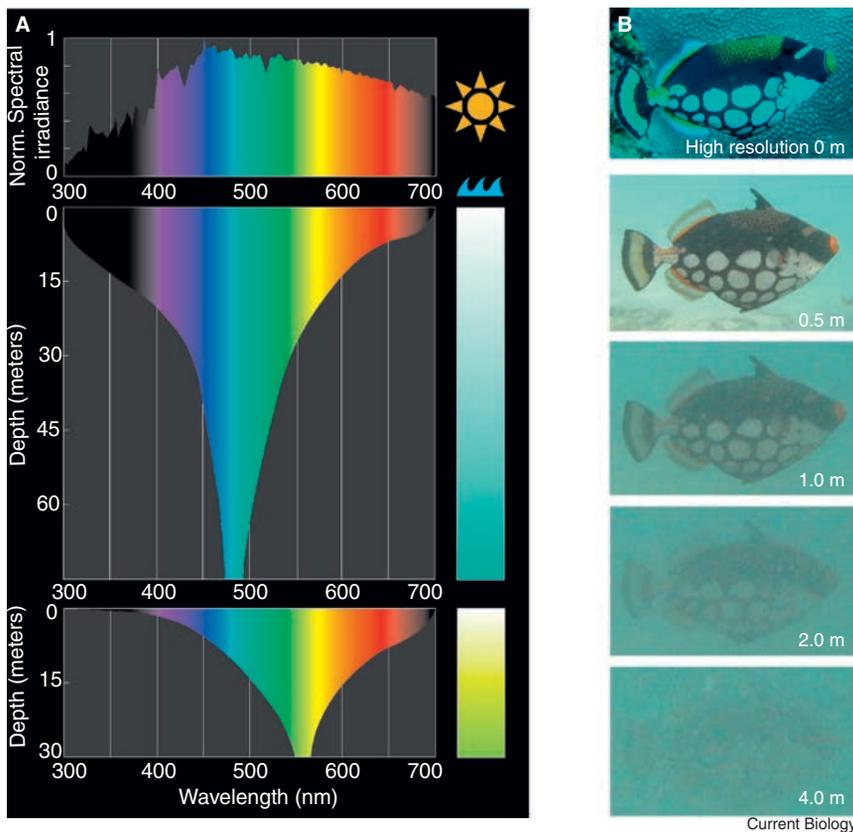


Figure 1. Light in the ocean.

(A) Modern version of the famous Levine and MacNichol representation of light underwater (courtesy of Mike Bok and adapted from original in Further reading - Levine and MacNichol 1982). Upper panel, coloured-in spectrum of light under an irradiance spectrum curve above water, full sunlight. Note ultra-violet wavelengths in black as human vision cannot colour label this range. Middle panel, attenuation of light with depth in clear oceanic water down to 75 m. Bar on left represents how water looks to us. Bottom panel, attenuation of light in green, chlorophyll and dissolved organic matter-laden coastal waters where maximal transmission is around 550 nm. Note also the more rapid reduction in luminance with equivalent depth. (B) The clown triggerfish, *Balistoides conspicillum*, photographed close up with high resolution (12 Megapixel) camera and over distance in near-shore reef water over different distances and with a lower resolution camera (4 Megapixel) that approximates to reef fish resolving power. Note the fine patterns and colours disappear rapidly and the contrasting black and white pattern and fish to background has all but vanished at 4.0 m. This water type falls between those in (A) in terms of spectral transmission (maximum at 500 nm) and overall turbidity.

the retina via diffraction, mainly at the curved corneal surface. In water, where n is 1.33, or 1.4 in the more salty ocean, this difference disappears, which is why, without the air-gap of a mask or submersible, if we open our eyes underwater objects are de-focused or blurry. One solution, notably evolved twice through convergence in both fish and the coleoid cephalopods (squid, octopus and cuttlefish), but also less successfully in cubomedusan box-jellyfish, is to forget the curved cornea and construct a graded refractive index spherical lens. In fish, the gradient proceeds from a water-like n of 1.33

on the outer surface to a high n of 1.60 at the core. Light passing through this increasing refractive index difference is bent to a sharp focus on the retina (not so sharp in jellyfish).

The fact that the phylogenetically separate vertebrates and high-end molluscs (the coleoids) independently evolved the same light-bending solution is remarkable. The ancient cephalopods, such as *Nautilus*, that live at a depth of around 200 m have dispensed with lenses altogether, making do with the poor light gathering capacity of a pin-hole camera eye and an advanced sense of smell. It may be

that, in the evolutionary past, vision was less important in more animals, especially in the ocean. There we find in animals representative of that past many half-eyes or apparently half-baked solutions to vision that seemingly could be better, and that make sense only in the light of the full context of the animal's sensory, ecological and behavioural needs. In the case of the cubomedusan lens, a blurry image is in fact preferable, acting as a low-pass filter that removes unnecessary image detail, allowing the predatory jellyfish to station-keep in the small-fish-fringe of the mangroves in which it hunts.

The now extinct but once abundant trilobites overcame the need for a high refractive index optical structure differently, by using a remarkable crystalline lens-doublet of calcite and organic material corrected for spherical aberration and, in some species, possibly bi-focal. Today, echinoderms such as brittlestars also use mineralised calcite mini-lenses to focus light and one hypothesis suggests that its star-shaped body acts like a sort of retina, sensing light from, one supposes, at least five different directions. Of all marine creatures alive today, the crustaceans perhaps display the widest variety of optical mechanisms to ensure light reaches the photoreceptors, including fibre-optic light-guiding in Hyperiid amphipods and reflective optics of several varieties in lobsters, barnacles and isopods (see Land and Nilsson, 2002).

The other result of water and bodies having a similar refractive index is that there are few(er) reflections underwater. The shiny (specular) reflections terrestrial animals may use in specific behaviours, such as water habitat location in flying water-beetles or shiny leaves to lay eggs on in butterflies, are less frequent under water. High refractive index material such as guanine ($n = 1.83$), the chemical component of shiny silvery scales in fish, can be used, but in general the colours of things underwater are more saturated as a result of the refractive index homogeneity. Where colour is used in communication underwater, on a reef for example, the colourful assemblage of fish and reef substrate is notably surface reflection free, boosting the colours and presumably their intended message. This feature

of underwater surfaces will re-appear later when we consider polarisation as a newly discovered currency of information in some marine animals.

Attenuation of light through water

The second and hardest-hitting limitation to vision in the ocean is the rapid attenuation of light over distance, mainly the result of scatter by particles small and large, from molecules to zooplankton, but also absorption of light by water and its possible dissolved contents. The physics and resulting biology dependent on these inherent optical properties of water have been described a number of times previously, in the context of the biological outcomes most notably by John Lythgoe, and more recently by Sonke Johnsen and colleagues (see Johnsen, 2012; Cronin *et al.*, 2014). Scatter of light underwater not only reduces the amount of light coming from an object, but also introduces light into the oncoming beam, essentially as light pollution or a veil obscuring the object further. In average ocean water (Jerlov, 1976 actually classifies five different oceanic and nine coastal types), object contrast to background decreases exponentially over distance (Figure 1). The result is that most animals in the ocean go about their daily routine in a visual bubble; an environment of a few centimetres or at best a few metres: imagine life in a ‘pea-souper’ fog of London in the early industrial revolution; criminals and murderers took cover behind those smoke screens and the same happens in the ocean, but involving perfectly ordinary death and deceit by innocent predators.

One of the consequences of this lifestyle also flows through to the optical design of eyes. There are no eagles underwater: the resolving power (often measured in cycles per degree, equivalent to distinguishable black and white stripes per unit angle) of fish eyes is on average ten times worse than a human, and eagles have double our resolving ability. There is simply no need for detailed resolution in the mostly close-up marine environment and small objects, unlike a mouse in a field, disappear into the background long before they are too small to see. Fish that do want to communicate as far as possible, such as the pair-bonded butterflyfish or territorial triggerfish

on the reef, often chose the highest contrast combination of bold black and white to maintain contact as far as possible (Figure 1). Further implications of resolution and colour patterns are considered later, but now I will turn to the selective attenuation of different wavelengths in the ocean.

Figure 1A is a famous illustration in ocean vision biology, modified from a Scientific American article by Levine and MacNichol (1982) on *Colour Vision in Fish*. It graphically describes how scatter and absorption in the ocean is wavelength specific: to generalise only slightly, ultra-violet and violet photons are scattered more and long-wavelength red to yellow photons absorbed more (see Johnsen, 2012 for a more thorough explanation). The combination is what makes the open ocean look blue and why coastal water such as the English Channel are a dull chlorophyll-green. Essentially the ends of the spectrum are trimmed selectively with increasing depth, the severity of the trim depending on the habitat and water type. In clear ocean, 480 nm blue light transmits best, and in coastal zones 560 nm green/yellow (Figure 1). This also holds for horizontal lines of sight and defines which colours are best to use as signals in each habitat, bearing in mind that the options become clipped with increasing depth according to the limits seen in Figure 1A.

Probably the best known example of visual ecology in action is how the colour vision of fish in different water types become tuned to sit within the envelope of available light. As championed by Lythgoe and colleagues, this principle also extends to fresh water where dominant wavelengths may be very yellow or even brown. A classic paper (Lythgoe *et al.*, 1994) examines the oceanic snapper family (Lutjanidae), describing how spectral sensitivities of different species inhabiting estuarine, coastal, reef and more open ocean habitats shift from green to blue-dominated colour vision. Following on from this, given a type of water habitat, say from 0–10 m in open ocean water, visual ecology at its purest might predict that all or most fish there would end up with the same spectral sensitivities and colour vision type; for example, a good general-purpose, short-wavelength-shifted trichromacy,

with cone photoreceptors maximally sensitive around 400 nm, 450 nm and 500 nm, just like that of the butterflyfish (Figure 2A). Trichromacy just means there are three spectral sensitivities — housed in the cones in the case of the vertebrate retina — which are compared to generate the differential colour signal required for colour vision. These receptors are selected to avoid the attenuation and lack of photons at either end of the spectrum.

This sort of correlation gave birth to the ‘sensitivity hypothesis’ of Lythgoe and others, which predicts, not surprisingly, that spectral sensitivities are generally positioned to optimise light capture. Conversely, there is no point in trying to absorb light that is not there. It mostly works for the rods, the photoreceptors that operate at night or in most deep-sea fish and that must optimally match light availability for vision to function, as there are few photons to start with. It also generally works for one of the cone types, the double cones (named as they are two cones stuck together), which may be responsible for daytime luminance vision. Some variability exists where visual systems have critical times to be active in or objects of specific interest that may be spectrally different to overall ambient illumination. Sensitivity to blue-shifted light at twilight, for example (the Purkinje-shifted ‘twilight hypothesis’), and selective sensitivity to bioluminescence of different colours in the deep sea provide variability in what matches what exactly. It is when we begin to examine the placement and number of cone photoreceptors used in oceanic colour vision, however, that such cosy correlations begin to drift away.

Running away back to land for the moment, colour vision there is comfortably conservative. Almost all birds (aside from the spectrally or intensity challenged penguins or owls), for example, possess one of two, not that different tetrachromacies: that is, four spectral sensitivities spread relatively evenly across the spectrum, sensitive to ultra-violet/violet, blue, green yellow and red. This design, or a version of it, is also found in many lizards and may have been the basal colour vision system that came onto land (for more about lungfish see Cronin *et al.*, 2014). Shallow

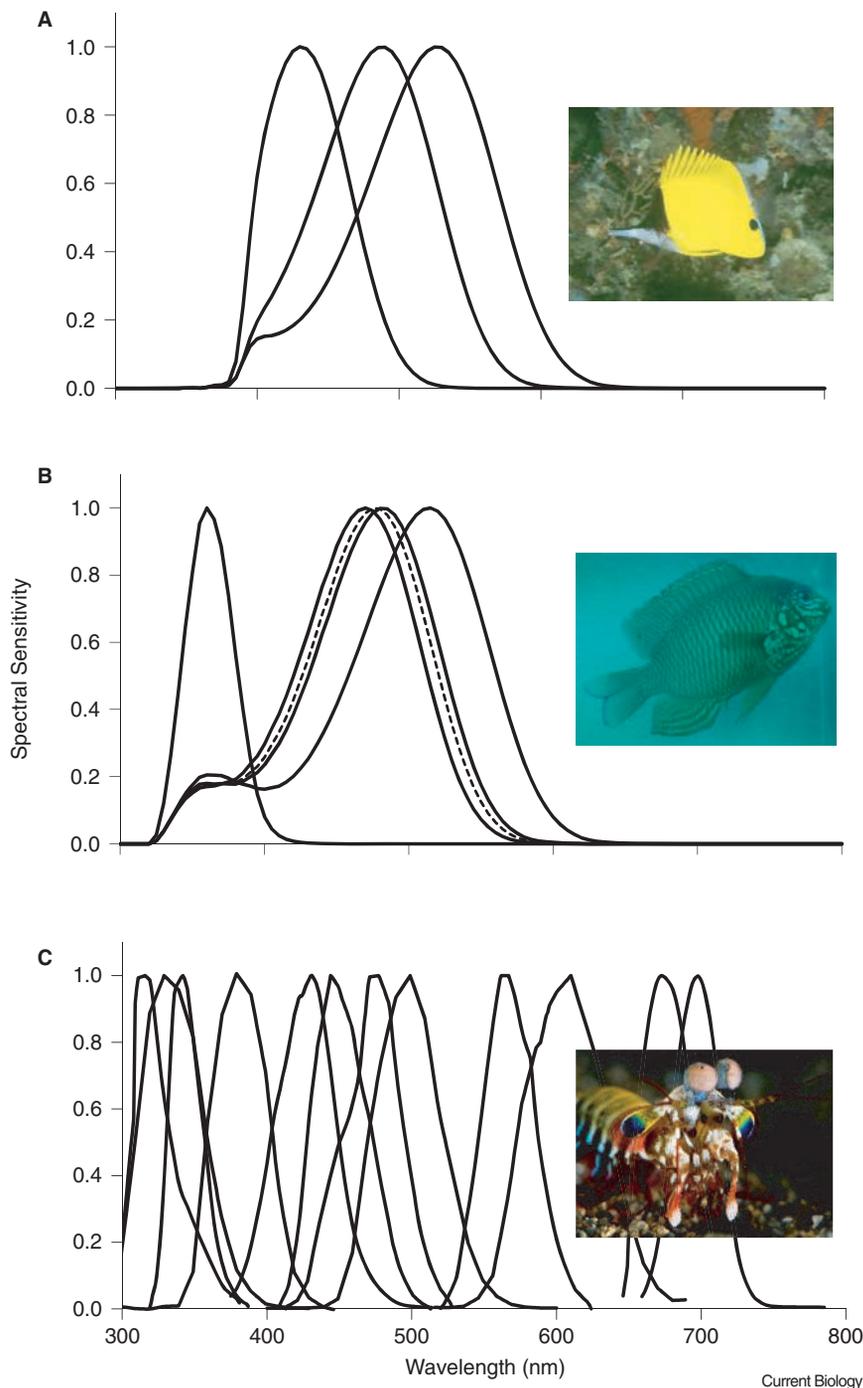


Figure 2. Different spectral sensitivities and colour vision types in the ocean.

(A) The spectral sensitivities of the long-nosed butterflyfish, *Forcipiger longirostris*, including the filtering of ocular media (cornea and lens). The rod sensitivity exactly underlies the central cone. (B) Damselfish spectral sensitivities of the ambon damsel, *Pomacentrus ambonensis*, and inset photographed through a UV sensitive (350–400 nm) camera. In full spectral photography this fish appears yellow like the butterfly fish above. Cones, solid lines; rod, dotted line. The differences in spectral sensitivity to *F. longirostris* is one example of many other differences both in cone number and placement among reef fish (Marshall *et al.* 2003). (C) Stomatopod (mantis shrimp) spectral sensitivities and inset of one of the more flamboyant species, *Odontodactylus scyllarus*, the peacock mantis shrimp.

dwelling, freshwater fish, such as goldfish or guppies, also tend towards tetrachromacy and this is a good, theoretically optimal colour vision system given a 300–700 nm spectrum to work with. Many insects, such as bees or ants, have settled out on a ultra-violet, blue green trichromacy as being good enough for their needs, interestingly largely ignoring the red-end of the spectrum. Notable exceptions exist of course, including some butterflies, dragonflies and beetles, insects that specifically utilise and see red objects such as flowers or congeners.

Diversity of colour vision in the ocean

To summarise so far; colour vision design on land and in freshwater mostly makes sense from an evolutionary adaptation view and in the marine environment there are correlations discernible between envelopes of spectral availability and photoreceptor sensitivities. Adding to this the fact that cephalopods and fish converge on precisely the same optical solution for bending light onto their retinæ, why marine colour vision systems are not more alike is still a mystery. The variation we are concerned with falls within the general light-envelope trends just identified and Lythgoe and colleagues were or are well aware of this. To expand on the problem, the shallow ocean harbours more dichromats than might be predicted, seems to shy away from tetrachromacy, even in spectrally rich surface waters, and the majority of the trichromacies present are bewilderingly diverse (Figure 2A,B; see also Lythgoe, 1979, Cronin *et al.*, 2014 and Marshall *et al.*, 2003).

Fish, like birds, have single cones (cones not fused together) which complement the double cones throughout the retina, but we know little about how these cone types interact to enable colour vision in all but one species. Birds again seem more sensible, giving their double cones the job of daytime luminance vision and their four different single cones the job of colour vision, placed in a way to optimise colour information over the whole spectrum. Single cone number or spectral sensitivity placement in marine fish, on the other hand, show few discernible trends. Small fish, such as damselfish, do tend to be the ones

with a dedicated ultra-violet sensitivity, known to be used in secret social signalling and possible planktivory, but aside from this in reef fish, for example, cones may be found with sensitivity peaks anywhere from 350–560nm and in anything from one to four varieties (Figure 2 and Siebeck *et al* 2006). The job-division between doubles and singles is certainly less cut and dried.

An easy way out of this apparent confusion is to state blandly that the variability must be something to do with behavioural or microhabitat differences and dietary needs that we don't yet understand. In a study of three cardinal fish (family Apogonidae) living in the same coral head and with very similar diet and communication modes, three different trichromacies still emerged (see Cronin *et al.*, 2014, Chapter 7) and this suggests another more radical solution. Within the limits of a spectral range, it may be that sensitivities can be placed rather randomly and give the same performance for colour tasks — at least for the survival problems of today. This is an unsettling idea, going against core-values in visual ecology, but needs definitive falsification. The idea that spectral sensitivities and colour cues or signals must be precisely matched is dissipating in several areas of visual ecology, replaced by the concept of general-purpose colour vision for many tasks. If we can add to this a relaxed-selection view of spectral sensitivities, along with a need to understand individual species colour-based biology better, visual ecology of colour vision in the ocean might become more tractable. But stand by for more confusing discoveries.

Spectral sensitivities in any animal are difficult to measure, so the recently developed techniques of transcriptomics and the rapid assessment of the visual pigment complement in a species, promised to provide more data and clarify some of this variability. Instead, however, recent results, especially in fish, have thrown the dichromatic cat amongst the tetrachromatic pigeons. In short, those fish that have been well studied, and this includes mostly freshwater species such as cichlids but now several reef fish families also, seem to have more visual pigments than they need. Five classes of opsin genes arose early in fish evolution: RH1, the type found in

rods and four cone classes; SWS1, very short often UV sensitive; SWS2, short wavelength blue sensitive; RH2, medium green sensitive rod-like opsin but in cones; and LWS, long wavelength up to red sensitive opsin. In both fish and marine invertebrates, which have a similar set of opsin genes, gene deletions, substitutions and duplications alter this base set. The tiny ostracod crustaceans have eight opsins, larger stomatopod crustaceans (about which we will say more soon) express thirty-two and fish may express ten or more opsins. Why so many? And how does older research, which just measured actual photoreceptor sensitivities, fit within this new schema?

A clue to what is possibly going on here comes from recent work on reef damselfish demonstrated that varying the light environment can change the opsin complement. Fish kept in red light express different levels of different opsins than fish kept in blue light. Such variability is also found naturally between same species damselfish from different depths on the reef (Stieb *et al* 2016). What this means is that our previous estimates of spectral sensitivities (via methods such as microspectrophotometry; see Levine and MacNichol, 1982 in further reading for a good explanation of this technique) may be snap-shots of a dynamic colour vision landscape that is variable on a number of different timescales. These seemingly more confusing new results may therefore explain, but still not determine the function of, some of the observed variability. As this is a relatively new area of discovery, it is best to finish with a list of things we think we know and that may help explain the variability, both old and new.

First, an animal with multiple opsins, even if apparently expressed, may not use them all for (colour) vision. For example, some opsins are used in thermoreception or magnetoreception and other tasks in tissues other than obvious photoreceptors. Second, given a suite of expressed opsins, determining the function threshold for vision is not straightforward; that is, if five are expressed in the retina, only three may be functional at a time. Third, co-expression of different visual pigments in the same photoreceptor is now recognised in many animals, including marine species; this, and

many of the other variables listed here, makes some sort of histological photoreceptor labelling almost essential but often not attempted.

Fourth, different combinations of visual pigments may operate along different timescales: for example, that associated with a habitat change, such as migration from and to rivers, as in salmonids; or the larval to adult ontogenetic change in all marine fish where freshly hatched fish have only cones and the full photoreceptor complement emerges through to adulthood. The depth at which the animal settles in the ocean determines its visual pigment balance with both stomatopod crustaceans and now damselfish known to tune their colour vision in this way.

Fifth, on a more established evolutionary timescale, rather like the insects, there are instances of some marine fish species pushing spectral sensitivity into the red. They include: deep-sea malacosteid dragonfish and their covert red bioluminescence; hexagrammid greenlings with astonishing orange corneal filters; and now some wrasse that have chosen long-wave-sensitive visual pigments from the shelf (Phillips *et al.*, 2016). The latter two adaptations to help distinguish algae and other food items.

Sixth, visual pigment diversity from whole eye samples may cover up retinal functional subdivisions where, for example, the ventral eye looking up constructs one form of trichromacy, while the dorsal retina looking down makes a higher sensitivity dichromacy. This is not a pentachromatic animal and such within-eye divisions for different jobs are frequent in both invertebrates and vertebrates, even in humans where our fovea lacks blue cones. Seventh, some species have what is termed unconventional colour vision: this certainly encompasses the marine stomatopod crustaceans that have twelve spectral sensitivities. Such animals, including the butterflies on land, have been placed in this sub-category through processing colour information in a way that is different to the normal comparative (opponent) process.

Stomatopods (mantis shrimps) deserve to be almost the final word in this diversity of colour vision section. The surface-dwelling species are firmly

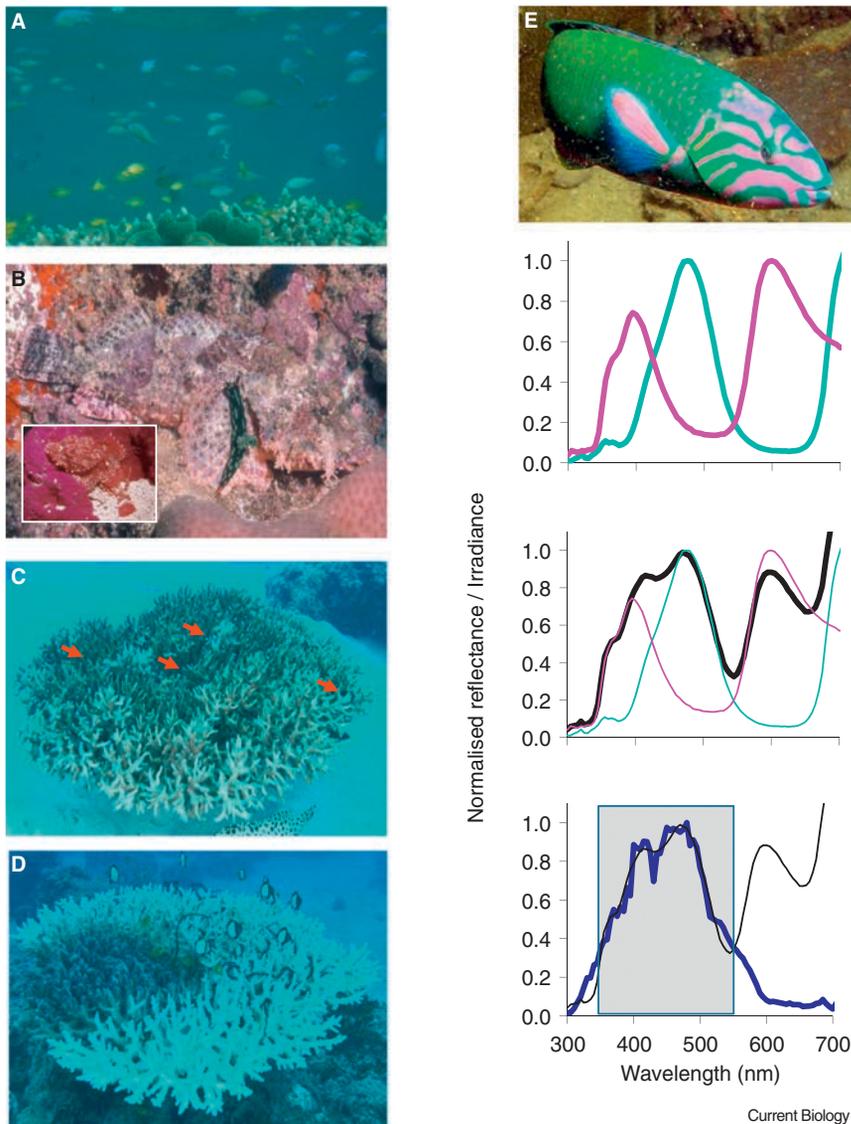


Figure 3. Communication and camouflage colours on the reef.

(A) Damselfish, *Chromis viridis* (green) and *Pomacentrus moluccensis* (yellow) over a coral head on the reef. Note general match to chosen background. (B) A scorpaenid so well camouflaged a nudibranch has mistaken it for a rock. Both background matching and edge disruptive camouflage principles are used here. Inset shows another scorpaenid species that might appear 'brightly' coloured on substrates other than an equally red sponge. (Photographs by Steve Parish). (C) Healthy branching coral (*Acropora* sp.) containing a number of different fish species camouflaged through matching or disruption (red arrows mark some fish locations). (D) Bleached *Acropora* sp. with encroaching algal overgrowth and death from left. Note how both background matching and disruptively camouflaged fish (also present in (C)) are highly conspicuous and indeed not able to use mechanical shelter in overgrown coral. (E) Colours of the moon wrasse, *Thalassoma lunare*. Top graph, normalised reflectance colours colour matched to areas measured from in photograph above. Middle graph, black line shows additive colour from mixing highly contrasting turquoise and pink colours, as would occur at a distance from fish. Bottom graph, overlay of combined colour and background water colour (blue curve). Shaded box indicates spectral region within which reef fish cone sensitivities lie.

in the unconventional colour vision camp, with twelve spectral sensitivities peaking at anything from 315 nm to 720 nm, and certainly use colour for communication and we assume other

tasks. In truth, exactly what they use this extraordinary colour sense for is still largely unknown. Within their sub-phylum, stomatopods are certainly unusual, as in the marine habitat

most other crustaceans, including in fact deeper-living stomatopods, are monochromats or dichromats.

Interestingly, it also seems that many larger marine animals including teleost, elasmobranchs (sharks not rays) and cetaceans, tend towards dichromacy. This is a parsimonious solution in the ocean as even at the polychromatic surface, colours may have to come through some distance of (remember very attenuating) water so the information contained can be detected by two channels. Lythgoe again came up with a hypothesis to explain this, the 'offset hypothesis', where having one spectral sensitivity matched to the spectrum of habitat light and one offset to this (but not so far as to fall outside the envelope) is a good way to maximise contrast of objects. It is worth following this through in further reading (see Lythgoe, 1979), as is the idea from Vadim Maximov who suggested that two-channel, dichromatic colour vision first evolved in the ocean to remove flicker (explained in Cronin *et al.* 2014). Essentially luminance is discounted and confusing transient brightness differences removed through signal difference subtraction. Monochromats that would suffer from this tend to be deep-living or nocturnal, both modes of life where flicker does not exist.

Ways of increasing contrast and decreasing contrast

Colour vision allows extra contrast information to be discerned and may involve both detection of objects (via object-background and within-object contrast), and discrimination between colours or patterns. These can be different tasks, the discrimination or choosing part necessarily coming after detection. Having located an apple tree, which apples are ripe enough to eat? The former is a large colour difference (look, red apples in a green tree over there), the latter a distinction between very similar colours (that apple is redder than the others, I'll eat that one). Colour vision systems need to accomplish both discriminations, but often the lines become blurred as some objects may not 'want' to be detected, as in the case of camouflaged animals, so the detection task becomes one of fine discrimination between object and background. Coral reefs harbour more colourful creatures per unit volume

than any other place on earth and colour there helps to: assort species; define food; distinguish sex; assist in mate choice; and drive territoriality and other aggressive encounters, such as aposematic signalling. These are the same functions as for colour on land, in other marine habitats or in fresh water, but coral reef colours designed for communication and camouflage have some reef-specific idiosyncrasies worthy of note.

A flick through a coral reef coffee table book demonstrates the importance of yellow and blue as a combination of, for example, stripes within fish or whole fish just coloured all yellow and all blue. Lythgoe, again, pointed to this combination as being best in ocean water for transmitting a message: blue at 480 nm transmits furthest and yellow is a good contrast, (whereas red and green are better in fresh or dirty coastal waters), but it is also good for camouflage when reef backgrounds are considered. A blue-green fish against a blue-green water background is well camouflaged and a yellow fish against yellow coral also blends in well, especially at a distance (Figure 3A). Simple background matching such as this is one obvious mode of camouflage but yellow fish against coral is worth further thought. As primates, we are more focussed on ripening fruit colours, such as the apple tree situation just described, than the shorter-wavelength-biased reef fish colour sense (note shaded portion in Figure 3E). It is therefore likely that many of the pretty-yellow-fish on the reef that we see, while a bunch of bananas to us, are even better background-matched to many reef fish.

This relative conspicuousness of colour to different visual systems is more obvious if the colour sense, such as our own or that of larger fish species, is completely insensitive to a spectral region rather than just less sensitive to it. As Figure 2B shows, damselfish often have a dedicated ultra-violet cone and display colours in patterns that only appear (to us) when viewed with an ultra-violet-sensitive camera. Our eyes and those of larger predatory fish contain ultra-violet-absorbing lenses and indeed no ultra-violet visual pigment. Mate selection in damselfish depends on these patterns and presumably affords these little fish the opportunity to 'get it

on' while distant and ultra-violet-blind predators are oblivious to the action (Siebeck *et al.*, 2006).

Moth-wing-like drab colour camouflage is also utilised heavily in the ocean, as Figure 3B shows. Here, as well as a general background colour match, a second principle in camouflage of disruptive patterning can be seen (or not seen, from the fish's hopeful perspective). Disruptive camouflage aims to make the animal hard to distinguish with bold internal patterns and the edge line of the fish broken up, perhaps also matching background elements such as rocks or algae. The related scorpaenid species shown in inset in Figure 3B demonstrates that, what we may see as a conspicuous red, disappears very effectively against a well-chosen reef sponge. Remember also that red is one of the first colours attenuated underwater (Figure 1A) so from any distance or at depth, this fish may be less bright than it appears in the photographers flash photograph.

How colours are used in display in the marine world is an area ripe for discovery. As well as illustrating possible camouflage, in Figure 3A a yellow fish against a blue-water background or blue fish against yellow coral are highly conspicuous. Both damselfish in this situation are behaviourally aware of this background mode switch from communication to camouflage and assort themselves close to best camouflage background when a possibly predatory photographer is near. With predators or photographers at a distance, they move up in the water to feed on plankton. The yellow-blue combination is also known to be used as a within animal combination in aposematic warning displays found in toxic nudibranchs, blue-ring octopus and potentially spiky and distasteful reef fish.

Other conspicuous colour combinations include the spectrally unusual colours of wrasse and parrotfish shown in Figure 3E. These colours are complementary in the spectrum and therefore strikingly contrasting close up, a feature presumed useful in display. Just like damselfish and their private ultra-violet signals, this is an instance of communication close up and relative invisibility at a distance but utilising the

combinatorial colours rediscovered by pointillist and impressionist painters. Many reef fish, like the wrasse in Figure 3 E, use thin stripes or spots of colour that, with our high-resolution terrestrial-optics eyes, seem highly conspicuous. For the less acute eyes of ocean-dwellers, these fine patterns blur together over a few metres and make a combined blue colour that is a good match to background water colour, especially within the known colour-vision-range of reef fish. The pointillistic-parrotfish (or Monet's-moon wrasse in this example) appear something potentially worth mating with close up, but fade to (blue) shadow in the distance, thus avoiding detection.

Several areas of colour and communication in the ocean have much to reveal. Bioluminescence is worth a primer in itself and is far more than the blue-glow we associate with it. Fluorescence is now recognised as a means of boosting colour communication in a variety of species but, in fish at least, is likely to be less important than currently thought. Polarisation and polarised light is well known for its use in animal navigation or, as mentioned above, water-body location by semi-aquatic insects. Polarised reflections from specific body parts have recently been shown to be used in communication, notably between and within the otherwise largely colour-blind cephalopods and crustaceans. Stomatopod crustaceans and their obvious concern with colour are an exception, although they also use polarisation signals and have unreasonably comprehensive polarisation vision. Unique among animals, this includes the ability to signal with and receive circular polarisation in *Odontodactylus* species. Several other stomatopod species and cuttlefish construct linear polarisation reflections on appendages used in display and in at least one stomatopod, *Haptosquilla trispinosa*, some behavioural evidence exists to suggest the polarised signal is important in mate choice.

On land, butterflies also determine mate choice using polarised wings and this is an area of vision and signalling, both in the ocean and elsewhere, that we are just beginning to uncover as, without cameras or filters, rather like the ultra-violet, the information is invisible

to us. The lack of shiny and polarised reflections from surfaces underwater — as noted previously, the result of refractive index similarity between water and water-based living tissue — provides a background polarisation noise-free environment in the marine world. Both this and the fact that polarised information does not suffer spectral attenuation underwater make polarised objects conspicuous to those who can see them. A polarised signal is still attenuated within very short distances underwater so the signal would remain local.

Polarisation sensitivity among the cephalopods and the crustaceans is often a two-channel system, sensitive to vertical and horizontal polarised light, perhaps mirroring the preponderance of dichromacy in colour vision systems. It is tempting to speculate this may provide the same flicker subtraction solution to intensity ambiguity that we imagine the shallow oceans of early life delivered and that, as mentioned above, Vadim Maximov proposed as the starting point for colour vision on earth. A two-channel orthogonal polarisation analyser can also remove intervening scattered light as this light is necessarily polarised by the scattering process (see Cronin *et al.*, 2014). Being able to lift the veil of light pollution between object and observer increases sighting distance underwater and may be another driving force behind evolving such systems.

Other recent speculation suggests that as well as polarisation signals, polarisation camouflage may exist in the ocean. Initially attractive as a natural parallel to the world of colour, enough physical differences exist in water to make this unlikely. One of these is the refractive index difference outlined above, which makes reflecting polarised light underwater difficult. The polarising signals evolved by crustaceans and cephalopods are remarkable photonic structures that break light into its constituent e-vectors — that is, polarise it — via a number of unique scattering and molecular-mechanisms. The guanine-containing silvery-sides of pelagic fish are thought a potential evolutionary target for the polarisation-detecting vision of cephalopods. Recent photonic and quantitative evidence suggests that intensity matching is more important in silvery fish camouflage

and that guanine crystals do not have the right photonic characteristics to reflect polarised light and provide what has been termed ‘polarocrypsis’ the assumed evolutionary arms-race response to attack by squid (Marshall *et al.*, 2014; Johnsen *et al.*, 2016).

The changing colours of the oceans

Other articles in this special issue have provided more detail on how the ocean environment is changing as a direct result of anthropogenic influences, including global climate change, local increases in shipping and dredging (with resulting turbidity increase) and careless plastic disposal. Behavioural evidence exists in freshwater systems to indicate that turbidity change and increased light attenuation in some of the African rift lakes has broken down colour-assorted speciation among cichlid fish. A pioneer in animal behaviour, Konrad Lorenz, was the first to notice the importance of the colours of reef fish in speciation and it is possible we will see similar vision-based effects there or indeed in other marine ecosystems. More troubling however is that reefs are changing background colour through coral bleaching, a direct result of ocean temperatures remaining 1–2 degrees above normal for extended periods. Figure 3D shows a bleached coral head and the resulting increase in conspicuousness of the fish normally seeking shelter and camouflage within the healthy coral (Figure 3C). A colourful fish against a white coral is an obvious meal for a predator but the longer-lasting effects of habitat loss are more serious. Many fish and crustaceans are specifically coloured to match and rely on healthy coral for cover and food (Figure 3C). When corals die after bleaching, they are rapidly colonised by an overgrowth of macro-algae (Figure 3D). In terms of background colour and mechanical protection, as well as food loss, these changes are catastrophic and because of their scale are now resulting in ecosystem-scale shifts or collapse.

In 2016, close to one quarter of the corals on the Great Barrier Reef died after its worse and third mass bleaching and globally fewer than 50% of reefs remain in good condition. For the Great Barrier Reef, the 2016 loss is on a baseline of having lost 50% of coral cover over the last 30 years and, as I

write this, another large-scale bleaching event is starting to accelerate. The first time this reef system, the world’s largest, has bleached two years in a row. Coral is now second on the animal-type endangered list after frogs, with losses of coral species recorded every year. All too often forgotten about, the reef fish, reef invertebrates, including crustaceans and cephalopods, and the other animals that rely on corals are being lost at an alarming rate along with their remarkable visual systems.

Conclusions

The design of visual systems in the ocean is more diverse than on land, the variability driven by a greater range of light habitats. This includes a variety of unique optical mechanisms to optimise light capture at various light levels and in various light habitats. While most animals in the ocean as a whole are colour blind monochromats, just because of the volume of habitat, colour vision systems up to the twelve-channel stomatopod retina exist. Even in surface waters, however, many species including the dominant fish and crustaceans are dichromatic, probably reflecting the rapid and wavelength-specific attenuation of light and therefore information over any distance. Two channel systems may also be useful in flicker reduction and reduce intensity ambiguity that a monochromat suffers from.

Fish colour vision systems on the reef, and in the ocean in general, are remarkably variable with number and peak sensitivity placement of cones following few discernible trends other than staying within light availability windows. Smaller fish do tend to have ultra-violet-dedicated spectral sensitivities while the larger predators are often ultra-violet-insensitive dichromats. There are specific colour-codes for both communication and camouflage in the ocean, again reflecting light availability and driven by wavelength selective attenuation in this habitat.

Polarisation vision and specific body reflections are a new currency of information transfer while fluorescent signalling in fish and ‘polarocrypsis’ require further evidence. Perhaps the largest unknown, aside from trying to find trends or rules within fish colour vision, is what information is passed

(or hidden) by particular colours or indeed polarisation reflections? Is one fish that is yellower or redder than the next more viable as a mate as some freshwater systems suggest? For many reasons, including keeping a watchful eye on our oceans and their crumbling ecosystems, it is time we returned to the ocean to actually see what is in the sea.

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