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Physiological and ecological implications of ocean deoxygenation for vision in marine organisms

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Climate change has induced ocean deoxygenation and exacerbated eutrophication-driven hypoxia in recent decades, affecting the physiology, behaviour and ecology of marine organisms. The high oxygen demand of visual tissues and the known inhibitory effects of hypoxia on human vision raise the questions if and how ocean deoxygenation alters vision in marine organisms. This is particularly important given the rapid loss of oxygen and strong vertical gradients in oxygen concentration in many areas of the ocean. This review evaluates the potential effects of low oxygen (hypoxia) on visual function in marine animals and their implications for marine biota under current and future ocean deoxygenation based on evidence from terrestrial and a few marine organisms. Evolutionary history shows radiation of eye designs during a period of increasing ocean oxygenation. Physiological effects of hypoxia on photoreceptor function and light sensitivity, in combination with morphological changes that may occur throughout ontogeny, have the potential to alter visual behaviour and, subsequently, the ecology of marine organisms, particularly for fish, cephalopods and arthropods with 'fast' vision. Visual responses to hypoxia, including greater light requirements, offer an alternative hypothesis for observed habitat compression and shoaling vertical distributions in visual marine species subject to ocean deoxygenation, which merits further investigation.

This article is part of the themed issue 'Ocean ventilation and deoxygenation in a warming world'.

1. Introduction

(a) Global change

Ocean deoxygenation and eutrophication have become more prevalent over the last half century, primarily attributed to the effects of ocean warming [1–3] and the inputs of nutrients associated with growing human populations [4]. Oxygen is input into the ocean as a product of photosynthesis, from mixing at the surface and via thermohaline circulation, while it is removed from the water column by the respiration of plants, animals and microbes. Climate-forced ocean warming reduces oxygen solubility and creates stratification, which increases the outgassing of oxygen from the surface, decreases the mixing of oxygen from the surface to the deeper water column, and could also decrease nutrient inputs, limiting photosynthesis and the production of oxygen [5]. Globally, the ocean has experienced a 2% reduction in oxygen content since the 1960s [6]. This has been manifested as: expansion of oceanic oxygen minimum zones, mid-water features characterized by low oxygen concentrations [7]; expanded oxygen loss over broad sections of the east Pacific, tropical and subtropical oceans [8], and the Southern Ocean [9]; and exacerbated coastal hypoxia [10,11]. Of particular concern are upwelling areas (e.g. Southern California Bight [12]), where increased upwelling winds [13,14] and strengthened low-oxygen undercurrents [15] are intensifying the problem, and significant oxygen declines have already been recorded [15,16]. In many areas, ocean deoxygenation is accompanied by an increase in carbon dioxide and decrease in pH, linked to respiration [17–19].

The observed decline in oxygen concentration in the ocean has widespread effects on marine life, causing changes in the physiology of marine organisms [20–22] and habitat compression [23–25], which alter the distribution and ecological interactions of species [26–29]. For some mesopelagic species, Bianchi *et al.* [30] document major compression of diurnal vertical migration depths, with lower boundaries corresponding to the distribution of hypoxic (dissolved oxygen less than $60\,\mu\text{mol}\,\text{kg}^{-1}$) waters globally. Explanations of habitat compression for billfish [25], mesopelagic fish [31], euphausiid krill [32] and even benthic sea urchins [33] have largely been premised on physiological constraints imposed by limited oxygen tolerances. Here, we explore the possibility that ocean deoxygenation affects one of the most oxygen-demanding functions in marine organisms, vision, and examine both the physiological and ecological consequences.

(b) Oxygen requirements for vision

Vision is an essential and metabolically demanding sensory process for both terrestrial and marine organisms [34–36]. Oxygen is necessary for neurons and photoreceptors (light-sensitive cells in the eye) to function, and is used primarily in the oxidative phosphorylation process that releases energy to form the adenosine triphosphate (ATP) required for transport of ions out of cells against their electronic/concentration gradients in order to prime cells for reactivation [34,36,37]. As a result, oxygen requirements will be especially high in visual systems with high temporal resolution (‘fast’ vision), where there is an increased rate of these reactions [38]. Neurons use oxidative metabolism almost exclusively, instead of additional metabolism through glycolysis as found in other cells [39]. Consequently, visual cells, similar to brain cells, are dependent on oxygen and damage can occur even after only minutes without sufficient ATP [36,40]. In terrestrial vertebrates, the retina containing the photoreceptor cells is the tissue with the highest metabolic demand in the body [41–43]. Within the retina, the specific layer of photoreceptors in the eyes of mice was found to have an oxygen demand approximately two times greater than the other layers of the retina [44]. Retinal hypoxia has been linked to blindness and visual impairment in humans, and is involved in eye diseases, including retinal ischaemia and vein thrombosis, diabetes and glaucoma [45]. Numerous studies on humans have examined the function of the eye in high-altitude-flying pilots exposed to low oxygen and found deleterious effects [46–48], indicating that the effects of environmental oxygen concentration are as concerning as local hypoxia (i.e. in retina only). We note that animals possess visual systems with a range of structures. The majority

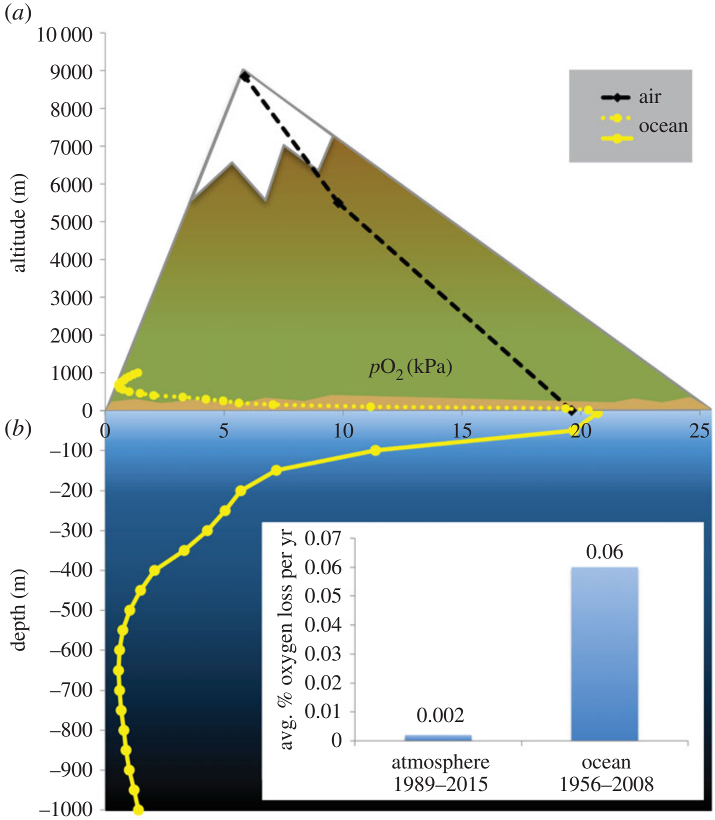

Figure 1. (*a*) Change in partial pressure of oxygen ($p0_2$) with altitude in air (black circles and dashed line) and with depth in the ocean (yellow circles and dotted line). (*b*) Ocean $p0_2$ data are shown over a 10-fold magnification in vertical distance in comparison to atmospheric data to display detail (yellow circles and solid line). Air estimates from sea level to the top of Mount Everest (8848 m) were determined using Peacock, 1998 [50]. Ocean $p0_2$ from the surface to 1000 m depth calculated from CTD (conductivity–temperature–depath) data recorded off southern California on 8 November 2015. Inset: average per cent oxygen loss in atmospheric and oceanic oxygen during the periods 1989–2015 [51] and 1956–2008 [52], respectively. (Online version in colour.)

of the approximately 2.2 million species of marine organisms [49] are without the thick retinal layer found in the vertebrate eye. However, most research studying oxygen effects on vision has targeted terrestrial vertebrates. Below, we present as many marine-specific and invertebrate examples as possible. These suggest that visual sensitivity to low oxygen is possible in most organisms and eye designs, but we acknowledge that the effects will vary among species and eye types.

(c) Vision and oxygen in marine organisms

Oxygen effects on vision are not as well documented in marine organisms, but may be significant given the much greater range of oxygen concentrations in the ocean in comparison to the atmosphere. In air, the percentage of oxygen remains constant at 20.9%, but at high altitudes the air pressure drops, causing the partial pressure of oxygen to decrease. This decrease is linear with altitude, and at 8848 m (the summit of Mount Everest) drops to 30% of the oxygen pressure found at sea level [50] (figure 1*a*). In comparison, the percentage saturation of oxygen in the core of the oceanic oxygen minimum zone off the coast of southern California (e.g. 8.4 μmol kg^{-1} O_2 at 650 m depth and 5.6°C) is a mere 2.75% of the oxygen pressure at the surface (e.g. 226.3 µmol kg^{-1} O_2 at 5 m depth and 20.6°C) (figure 1*b*). Thus the ocean exhibits a much stronger gradient in oxygen over a much smaller vertical range than found on land (figure 1). In addition, oxygen concentrations in both the atmosphere and ocean have been steadily declining over the last few decades [1,16,51–53]. Oxygen at station P in the NE Pacific Ocean has declined by approximately 0.06% per year at the 26.5 isopycnal (constant potential density) since 1956 (0.67 µmol kg^{-1} yr^{-1} [52]); this rate of change is 30 times higher than the decrease in atmospheric oxygen (0.002% since 1989 [51]) (figure 1*b*, inset).

The high oxygen demands of vision in the marine environment are apparent when examining depth trends of metabolic rates and metabolic enzyme concentrations in marine organisms with eyes. Highly visual organisms, including fish, cephalopods and some arthropods, show large (up to 200-fold) metabolic declines with a minimum depth of occurrence [54–56]. The same trend is observed in enzyme activity for both aerobic metabolism (citrate synthase) and anaerobic metabolism (lactate and octopine dehydrogenase); highly visual fish and cephalopods residing in shallow areas of the ocean have much greater enzyme activity levels than their deeper-water counterparts [56]. These sharp declines are not observed in the metabolic rates or enzyme activity of other, less-visual pelagic organisms such as chaetognaths, pteropods or other gelatinous animals, or even in benthic fish, cephalopods or arthropods that have eyes with lower temporal resolution [54,56]. The visual interactions hypothesis [54] proposes that organisms in shallow water are highly mobile and rely on vision for frequent, high-speed predator–prey interactions, whereas the decrease in ambient light in the deep ocean reduces the need for fast vision and locomotion, and therefore reduces the metabolic needs of these organisms [54,56]. While this hypothesis includes locomotion as a key mechanism for changing metabolic rate, it also highlights the high metabolic demands of vision in marine organisms.

Eye tissues in marine organisms may therefore be highly sensitive to variations in oxygen. Despite the potential significance of this issue for visual physiology and ecology, very little research has been done to determine the full extent of the effects of low oxygen on vision in marine vertebrates and invertebrates. The specific concentration of oxygen at which eye tissues are affected is likely to be different for each species, depending on both the whole-body general metabolic demands and the complexity of their visual structures. Marine organisms have the unique challenge of regulating their internal oxygen pressure (pO_2) independent of external pO_2. The P_{crit} value, defined as the external partial pressure of oxygen below which the organism's metabolism is not able to regulate pO_2 independent of the environment [57–60], is a traditional metric used to define oxygen tolerances. However, these critical limits are most useful when they consider the specific physiological demands and ecological functions for a species [61], and the critical limit of pO_2 for visual function could be different from what is reflected in a metabolic metric such as P_{crit}. Because the eyes and associated structures require a high concentration of oxygen [41–43], 'visual hypoxia', or the oxygen concentration at which the eye is not receiving enough oxygen for normal visual function, may occur at a much higher level than traditional metabolic limits to environmental hypoxia. While this trend is suggested in existing studies [62], this hypothesis should be tested further.

The most basic requirement for an 'eye' is some form of directional photoreception (detection of light), accomplished through a photoreceptor cell. Modifications to the eye to improve its quality of detection include grouping additional photoreceptor cells and structures to achieve directionality, adding one or more lenses to form and focus an image, and/or having a pupil to control incoming light intensity [63]. Increased eye size and complexity may improve detection, but also could incur a higher oxygen demand [64]. Eyes are present to some extent in most marine animals [65], and the structure and capabilities are a reflection of both the function of vision in the organism's life history and the light quality of its environment. For example, in the marine realm, both sea stars and chitons possess light-detecting compound eyes in their bodies suitable to accomplish basic phototaxis (movement towards or away from light), despite not having traditionally structured eyes. In sea stars, these are located on modified tube feet at the end of each arm [66], and chitons have aragonite lenses over retinal photoreceptor cells built into the edges of each chitinous plate [67]. In contrast, cephalopods (the group containing squid, octopus and cuttlefish) and marine vertebrates (fish, marine mammals, etc.) have a pair of sophisticated eyes with structure and complexity comparable to those in terrestrial vertebrates [63]. These patterns can be attributed to the differences in life history of each group; sea stars use vision for phototactic responses that allow them to return to the reef or detect shadows for hiding under rocks or coral [66], whereas squid and fish are highly active predators that require an image-forming eye to detect prey and respond to the rapid changes of movement by predators and prey [68].

The spectral sensitivities of eyes in marine species are also finely tuned to the light available in their environment [69]. There is exponential decay of visible light intensity with depth in the water column and there is also a change in the intensity of specific wavelengths (quality), with higher wavelengths (red light) disappearing very quickly and middle wavelengths attenuating slightly deeper, until the only available light in the mesopelagic realm is shorter-wavelength blue light [70]. Large fluctuations can occur with time of day, turbidity and biological production, where changes in the attenuation (disappearance) of light can occur with short-term events or over seasons [71]. As a result, organisms have evolved visual systems designed to function in the specific ranges of light, and theoretically oxygen, present in their environment, and it is likely that organisms will remain in that specific range to maintain full visual function. In the ocean, this corresponds to a particular range of water depths, and probably reflects both the physiological capabilities of the organism's visual system and that of their prey and predators.

Below, we review evidence for the potential negative effects of low oxygen on vision and visual behaviours in marine organisms and assess the likely implications for their physiology, behaviour and ecology under current and future ocean deoxygenation. We first examine the evolution of eyes with respect to historical atmospheric and ocean oxygenation events. We then discuss how different eye designs and oxygenation mechanisms of eyes in vertebrates and invertebrates may play a role in determining their vulnerability to hypoxia. Previous research is reviewed to discuss potential effects on visual physiology and morphology that may subsequently alter behavioural responses of species exposed to low oxygen and change ecological interactions. Finally, potential knowledge gaps are highlighted to help articulate effective research questions for the future.

2. Review

(a) Effects of oxygenation on evolution of vision and eye design

Eye evolution offers substantial evidence for the influence of oxygenation on vision. The oxygenation of the atmosphere and oceans has varied greatly over the past several billion years, with major increases in oxygenation occurring approximately 2.5–2 billion years ago (bya) and 545 million years ago (mya) [72] (figure 2). The coincident timing of eye evolution and oxygenation of the ocean support the theory that ocean oxygenation allowed for the evolution of specialized eyes, enabling fast vision (as seen in marine vertebrates (fish), cephalopods and some arthropods) (figure 2). Thorough reviews detailing each step of eye evolution and eye designs and structure [63,73–75] reveal that vision has evolved multiple times independently (such as in the fan worms, chitons and bivalves), that evolution rarely follows a strictly linear path and that more complex visual structures do not always indicate recent evolution [75,76].

A complex eye is beneficial because it allows for visual acuity, spatial resolution, temporal resolution, light detection and/or colour vision [63]. There are a variety of eye designs in marine organisms, and many do not fit the traditional definition of 'complex' as characterized by the vertebrate eye [68]. The specific benefits the eye provides, however, depend on its structure. Nilsson [75] classifies eyes into four classes of function and complexity. Class I eyes show basic non-directional photoreception, often consisting of one or two photoreceptor cells that detect light intensity to maintain circadian rhythms. Class II eyes can sense light direction and can also perform basic phototaxis. The photosensitive structures of classes I and II are considered the earliest origin of eyes, such as the eyespots found in the protists that have evolved over the last 1.5 billion years [77], such as the ocelli found in the dinoflagellates in genus *Warnowia* [78] or

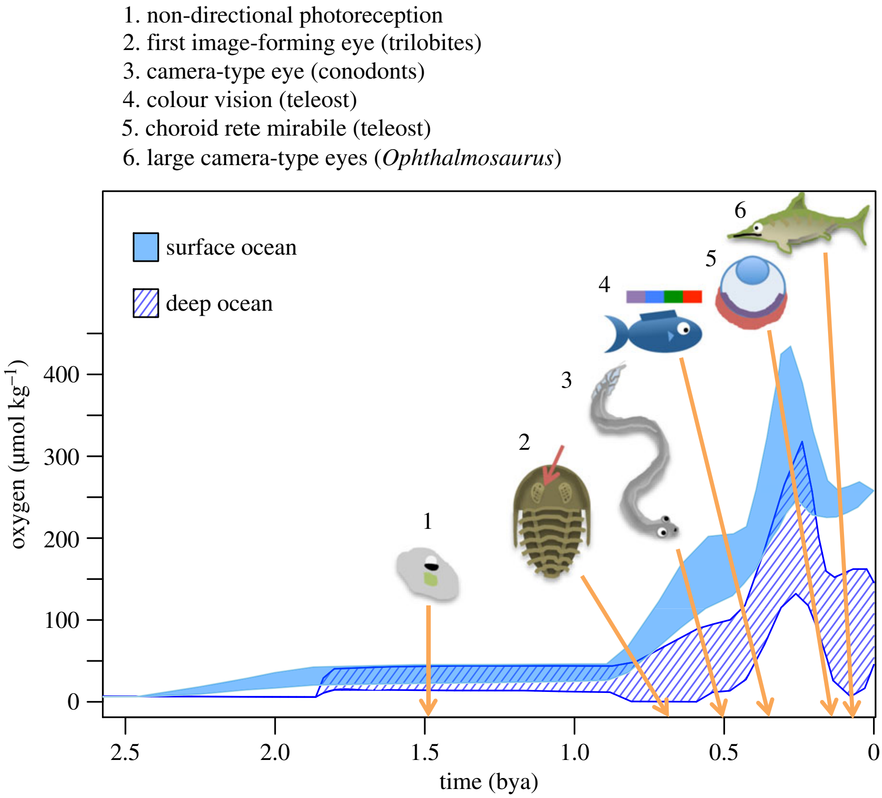

Figure 2. Evolution of ocean oxygenation and eye development. Timeline of ocean oxygenation in surface waters (light blue solid shading) and deep waters (dark blue striped shading), bounded by the minimum and maximum estimates, with key events in the evolution of eye designs added. Major steps (1–6) approach greater complexity, from basic non-directional photoreception to the development of image-forming compound and simple eyes and methods of oxygenation. Oxygen estimates modified from [72]. (Online version in colour.)

chitons [79]. An ocellus (plural ocelli) is a collection of one or more pigment cells each connected to photoreceptors, and is a primitive eye not containing any additional structures [68]. Eyespots and ocelli therefore do not have high oxygen requirements; these eye types evolved during the 'boring billion' (1.85–0.85 bya), when the atmosphere and ocean surface had a very low level of oxygen, but the deep ocean was still largely anoxic and there had been little expansion of metazoan life [72,80,81] (figure 2). Class III eyes are able to form a basic image (low-resolution vision) but have weak or no lens(es), and include the pit eye found in *Nautilus* and cup eyes in gastropod molluscs or cubozoan jellies. Class IV eyes are capable of high-resolution vision and include the camera-type eye found in fish and cephalopods [75]. Eye designs with advanced structures usually possess one to many lenses that enable the eye to focus light onto one to many photoreceptors, an aperture or migrating pigments in order to adjust the intensity of incoming light (e.g. pupil) and/or complex neural structures to transmit the electrical responses to light to the brain [68].

The large jump between class I, II and III vision (photoreceptive eyespot/ocellus or basic image-forming eye) and an eye with class IV vision (high spatial and temporal resolution capable of fast vision) that would have much higher oxygen requirements occurred around the time of the Cambrian Explosion approximately 545 mya [68]; the very first known image-forming eye was a compound eye observed in fossils from 543 mya in the trilobites [77,82]. This coincided with the end of the second and largest increase in the atmospheric and oceanic concentration of oxygen between 840 and 545 mya [72] (figure 2). Many of the animal body plans and groups that are still present today developed during the Cambrian Explosion, and the evolution of large-bodied predators and carnivory as a feeding strategy are hypothesized to be linked to increased oxygen in the atmosphere and ocean; it has even been proposed that vision was the driving force behind predator evolution [83–85]. At this time, there was a diversification of eye designs in arthropods, molluscs, annelids and, about 25 million years later, chordates [77]. For example, the first camera-type eye was found in the conodonts (eel-like early ancestors of vertebrates) [85]. The more specialized compound eye, the reflecting superposition eye design in decapod crustaceans, is thought to have developed in the Devonian/Carboniferous period (419–358 mya) [86].

During the Carboniferous period (359–299 mya), oxygen in both the atmosphere and ocean showed a large increase, although the deep ocean also showed intermittent periods of anoxia [72]. Colour vision is also hypothesized to have evolved around this time (during 400–300 mya). Photoreceptors with opsins of at least two different wavelength sensitivities are required for colour vision, and the earliest marine forms were thought to be tetra-chromats, as seen in modern-day teleosts [87]. Adding photoreceptors of different sensitivities does not necessarily add to the oxygen demand of eyes, but each photoreceptor type may show a unique oxygen limitation (see §2c). The largest camera-type eyes, perhaps also with a greater oxygen demand, were found in *Ophthalmosaurus*, a deep-sea diving reptile with a body similar to a dolphin, approximately 165 mya, when the oxygen concentration in the deep ocean had finally increased to approximately $150\,\mu\text{mol}\,\text{kg}^{-1}$ [85].

While increases in ocean oxygen concentration may have allowed for the diversification of vision, severe declines in oxygenation could promote evolution of mechanisms for coping with low oxygen in the eye. For example, the choroid rete in fish, a vascularized organ that provides oxygenation to the eye (see §2b), is thought to have evolved approximately 200 mya [88], in the same general period as a sharp decline in oxygen in the surface ocean [72]. Defining the exact periods of evolution for each eye forms is difficult; the radiation of analogous or similar eye types is thought to have occurred multiple times over the course of evolution, even within phyla, attributable to convergent evolution under similar environmental pressures and visual requirements [68,77,89]. It is probable that the evolution of sophisticated visual systems and eye designs was limited by the available oxygen concentrations, as complex visual systems and their sophisticated neural wiring have greater oxygen requirements [38].

Therefore, an organism's eye design reflects its specific visual needs, and also the environmental characteristics to which the organism is exposed, such as light quality and quantity, and, theoretically, oxygen. For example, the superposition compound eye found in moths and many deep-sea crustaceans has an array of long lenses that act as telescopes separated by a 'clear zone' that effectively creates a large pupil and large receptors to increase the eye's sensitivity to light 10- to 1000-fold in comparison to other compound eye types. These are very efficient for low light vision, but have low temporal resolution and therefore cannot detect fast-moving objects or flashes [63]. Similarly, a single-chamber eye with a movable, spherical lens has high spatial and temporal resolution and the ability to stabilize during quick movements such as swimming, but has a reduced ability to detect images at very low light levels, and several layers of oxygen-demanding tissues [43]. Naturally, organisms possess the design that meets their specific visual requirements (e.g. a fast-moving, visual predator would possess a single-chamber lens eye rather than a superposition compound eye), but also must have the capability of supporting the metabolic requirements of the structure (eyes with high temporal resolution have higher metabolic requirements) [64]. A survey was completed of the existing literature to find oxygen tolerances for marine organisms (primarily using results from [90] and [91]) and match these values with the complexity of visual tasks required for each organism (classes I–IV [75]). Organisms that adopt higher-complexity visual tasks (e.g. class III or IV) also show higher oxygen limits (and therefore lower tolerance of low oxygen) (figure 3). Although such organisms may also be active predators whose mobility also creates high oxygen demand [84], this finding is consistent with the hypothesis that eyes with advanced visual structures and fast detection capabilities require more oxygen to function (specific to marine vertebrates, cephalopods and arthropods in the ocean).

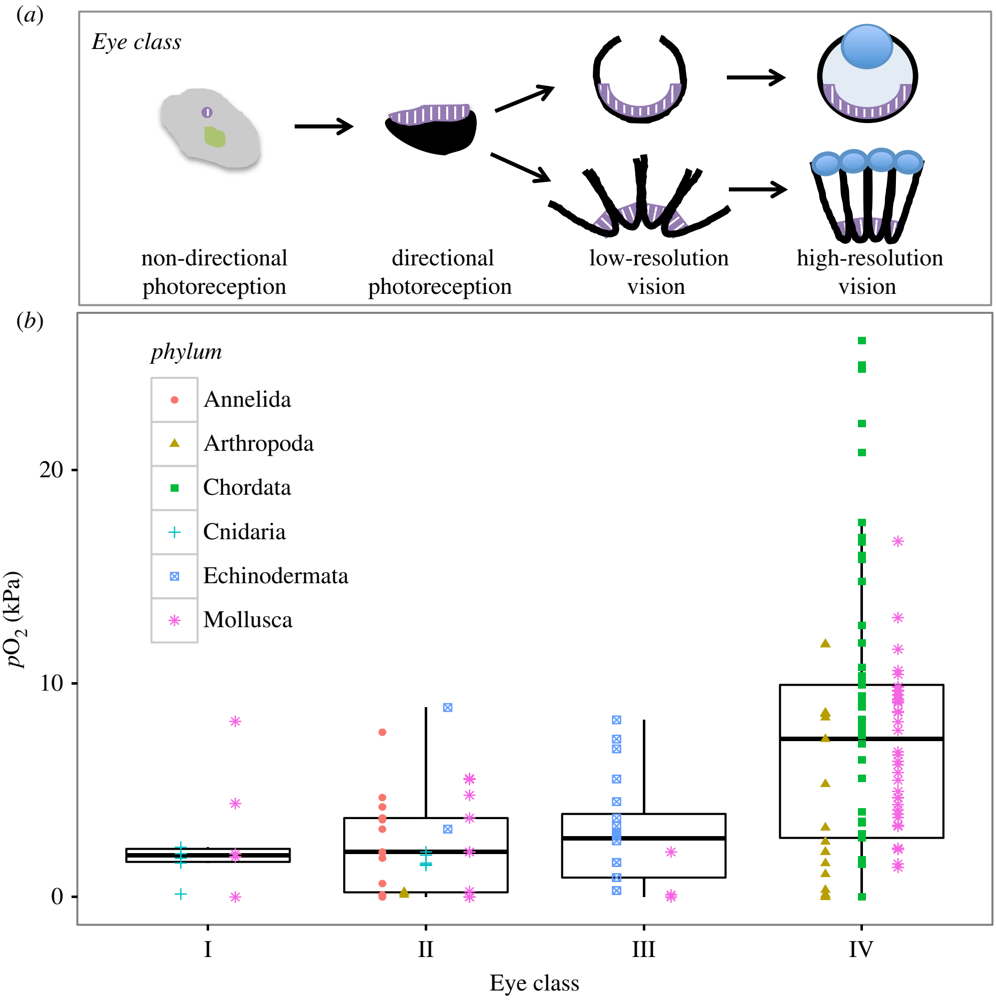

Figure 3. Oxygen tolerances as a function of visual complexity class. (*a*) Eye class (I–IV) increases in the complexity of visual structure and visual task capability. Adapted from [75]. (*b*) Oxygen tolerances (metabolic or behavioural) were obtained from [90] and [91] and then arranged by class of visual complexity as described by Nilsson [75]; details provided in electronic supplementary material. Boxes show mean values (dark midline) and first and third quartiles of oxygen tolerance data (lower and upper limits of box) for each eye class; all individual points are shown with symbols and colours designating phylum. (Online version in colour.)

(b) Mechanisms of eye oxygenation

The capability for supporting an advanced eye may be accomplished through specialized vasculature in and around the eye. General circulation required to carry oxygen to the eye may occur (i) within the haemolymph of organisms with an open circulatory system, (ii) with a combination of vessels and sinuses as found in arthropods and molluscs, or (iii) through a circulatory system such as vascularization in organisms like marine vertebrates or some polychaetes with full separate circulatory systems [92]. Organisms either can regulate their internal oxygen concentration over a range of environmental concentrations (oxygen regulators) or have metabolisms dependent on the environmental concentration of oxygen (oxygen conformers) [58].

Similarly, within the eye, a highly vascularized retina may contain local adaptations for oxygen efficiency that can buffer against external changes in conditions (e.g. an oxygen regulator), while an organism with a full body sinus may exhibit a more direct or magnified response to oxygen variation (e.g. oxygen conformer). The structures of vasculature within organisms containing a closed circulatory system can be very diverse and involve extra-ocular vascularization, intra-ocular vascularization or a combination of both [77]. Some marine organisms have developed additional, specialized tissues or vasculature for oxygenating the eye. The choroid rete mirabile in fish is known as a tissue that supplies an increased oxygen pressure to the eye, and is similar in structure and function to the rete mirabile near the swim bladder [93]. This horseshoe-shaped organ surrounds the eye, and is larger and more developed in fish that show a higher partial pressure of oxygen in the eye and rely on vision, further implying the oxygenation function of the choroid rete [94]. The oxygen-concentrating mechanism was first attributed to the counter-current capillary exchange and presence of carbonic anhydrase [95,96], but has more recently been explained by a root effect (elevating pressure of oxygen by acidifying the blood) in the tissue [43,97]. Similarly, cephalopods possess an optic (ophthalmic) sinus adjacent to each eye and optic lobe, present even in developing embryos [98]. During development in some fishes, a transient set of blood vessels and capillaries cover the eye; this forms as early as 2 days post-fertilization in zebrafish embryos, and is replaced after retinal vasculature is developed at approximately 9 days post-fertilization [99]. For animals that require visual function, but in which haemoglobin is absent or very low, such as in some Antarctic fishes, more elaborate vasculature is developed in the eye to compensate [100–102]. Oxygenation in marine invertebrates with simpler eyes, and therefore potentially a lower visual metabolic demand, may involve physiological methods (see §2c) to enable oxygenation of visual cells or organs. Both the structure and design of the eye, and also the specific methods of oxygenation employed, may influence the response of the eye to low oxygen.

(c) Physiological responses of vision to hypoxia

The effects of low oxygen concentration on visual physiology could be an extremely important consequence of hypoxia, as physiological limits to visual function could then subsequently alter animal behaviour, distribution and species interactions. One consequence of visual hypoxia may be impaired photoreceptor function, potentially expressed as a change in sensitivity to light. While little research has been done in marine organisms, studies in vertebrates support this idea. High-altitude-flying pilots exposed to no supplemental oxygen (and therefore mild hypoxia) showed a significant reduction in night vision at a 10 000 ft (3048 m) elevation in comparison to pilots receiving 100% oxygen or ‘normal’ supplemental oxygen [46]. Additionally, the visual system of humans exposed to air with 10% oxygen had a higher threshold for light than in those exposed to air with the normal 21% oxygen concentration; essentially their eyes required a higher light level for visual detection of the same stimulus under hypoxia [103]. In the same study, colour vision sensitivity was also reduced during exposure to 10% oxygen, with a greater inhibition in cones (colour-sensitive receptors) than in the rods (low-light receptors); mammalian cones have approximately twice as many densely packed mitochondria as rods to produce the additional ATP required for cones in light [104–106].

Hypoxia appears to affect most photoreceptor types (invertebrate and vertebrate) in the same way (insufficient oxygen, and therefore ATP production, will decrease sensitivity of the photoreceptors to light), but the light level considered stressful to organisms under hypoxia may differ according to the phototransduction method (table 1). There are two primary physiological methods for phototransduction in marine organisms: rhabdomeric and ciliary. Each transduction pathway differs in the structure and kind of photoreceptor(s) (e.g. rhodopsin for rhabdomeric or rods and cones for ciliary), the proteins and biochemical cascade for signal transduction, and the direction of the response in ion channel action and membrane potential [87] (table 1).

While the oxygen consumptions of each of the three photoreceptor species identified here are essentially similar in dark conditions, the ATP demand (and therefore oxygen consumption) increases in rhabdomeric transduction pathways upon exposure to light and decreases or remains neutral in ciliary phototransduction [106–108]. For example, the oxygen demand of the retina in

Table 1. Oxygen demand and visual stress for each transduction pathway in vertebrates and invertebrates. ATP demand (+++ > ++ > +) indicates a relative change and does not indicate a numerical value; based on information from [106].

	invertebrate	vertebrate	
transduction pathway	rhabdomeric	ciliary (rod)	ciliary (cone)
light stimulus			
ion channels	open	close	close
membrane potential	depolarize	hyperpolarize	hyperpolarize
ATP demand			
dark	++	++	++
light	+++	+	++
stressful light level under hypoxia	high	low	neutral

mice increased by 24% under dark adaptation, indicating a higher metabolic demand at low light levels for vertebrates (which have a ciliary receptor type) [44]. This is a result of the constant influx of sodium into the photoreceptor cells to maintain a voltage of −40 mV (dark current) [109]. In rabbits, the electrical response of the retina to light was severely reduced, and that of the optic nerve eliminated without oxygen and glucose; these results were reversible with short exposure times and return to 100% oxygen [110]. Similarly, intracellular recordings of photoreceptors in the squid *Loligo pealii* (rhabdomeric receptor type) showed a depolarization of the cellular current and reduced magnitude of response to light at 140 mmHg oxygen in comparison to 740 mmHg oxygen, presumably also as a consequence of insufficient ATP production to maintain ionic gradients [111]. Both photoreceptor types appear to show a reduced response to light under low oxygen. However, a difference between these photoreceptor types is expected in the light level considered 'stressful' (i.e. when the oxygen demand is highest); this would occur in the dark for ciliary photoreceptors (primarily vertebrates) and in the light for rhabdomeric photoreceptors (primarily invertebrates).

Another effect of low oxygen concentration that could affect vision may be decreased neurological function. In many organisms, there is an increase in the production of inhibitory neurotransmitters such as γ-amino butyric acid (GABA) and/or adenosine in the brain during exposure to hypoxia [112]. GABA depresses neuronal action, which is required for the transmission of visual signals, and the increase in production of this neurotransmitter is an adaptation observed in hypoxia-/anoxia-tolerant species. As an extreme example, the crucian carp (*Carassius carassius*) is known for both its resistance to low oxygen and its unique ability to maintain its activity level during long periods of exposure to anoxia. Other species, such as freshwater turtles of the genera *Trachemys* and *Chrysemys*, are considered hypoxia- or anoxia-tolerant, but enter a semi-comatose state and have very reduced brain function under hypoxia [113]. Among other mechanisms for hypoxia tolerance, one adaptation employed by *C. carassius* is metabolic modulation, where the visual system is selectively shut off to reduce metabolic demand. A reduction in electrical response of the eye to light flashes of up to 90% was observed in the retina and optic tectum (visual portion of the brain) of the carp after only one hour of exposure to anoxia; this process is completely reversed after conditions return to normoxia [114]. The horizontal cells and amacrine cells of the retina in *C. carassius* are GABAergic [115,116], indicating that GABA may play a function in the inhibition of visual responses during anoxia [114]. Decreased neurological function in other marine organisms less tolerant to low oxygen than *C. carassius* could significantly inhibit the transmission of visual signals to and within the brain, but this has yet to be documented. Little is known about visual adaptation in other oxygen-stressed marine environments such as the deep-water fluid emergence sites of hydrothermal vents and seeps. Although there is limited or no light in these environments, the shrimp *Rimicaris exoculata* does show a very interesting modified compound eye that is used to detect the very small amounts of light emitted from the vents themselves [117]. However, its oxygen demand is unknown.

Exposure to low oxygen additionally affects the regeneration of the visual pigments in terrestrial vertebrates. Mouse photoreceptors exposed to low and 'zero' oxygen concentrations were unable to regenerate rhodopsin [118]. This effect was also reversible after perfusion with 100% oxygen, even in exposures lasting greater than three hours. Evidence for a more metabolically efficient pigment regeneration pathway in cones has been found in *C. carassius*, suggesting further physiological adaptation to low oxygen [119]. In addition to the lack of electrical function in photoreceptors required to recognize light stimulus, a reduced or ceased regeneration would inhibit response to light signals and chronic exposure to hypoxia. For marine organisms, these responses could prevent proper visual function during exposure to hypoxia, even if the responses are reversible upon return to normoxia.

In reviewing general physiological adaptations of marine organisms to hypoxia [120], several whole-body physiological responses emerge that may affect visual tissue. These include a change in the affinity of the blood respiratory pigment to allow for a greater uptake of oxygen, such as observed in high-altitude-flying birds [121,122], altering the charge of myoglobin molecules in the blood of deep-diving mammals [123], or an increase in transcription factors such as hypoxia-inducible factor 1 (HIF-1 [120]). HIF-1 regulates a multitude of genes that enable the organism to adapt to hypoxia; it has been found in human eyes experiencing hypoxia from retinal ischaemia and glaucoma [124], and is responsible for activating the vascular endothelial growth factor (VEGF) that induces neovascularization (development of new blood vessels) in visual tissue in mice [125]. General upregulation of HIF-1 has been observed in low-oxygen conditions in mammalian cells [126], but whether HIF-1 has a similar function in the eyes of marine animals is unknown.

(d) Morphological and developmental responses of eyes to hypoxia

Morphological responses of the eye to hypoxia are also not well studied in marine organisms, and probably depend on the time frame of exposure to low oxygen. For example, in organisms developing under hypoxia, small changes in capillary structure can occur over shorter time periods (30–80 days [127]) than more permanent changes such as eye size, but both are potentially a result of chronic exposure to low oxygen. In human eyes, choroidal neovascularization, the development of new blood vessels in the choroid layer, occurs as a result of diseases like diabetes, retinopathy of prematurity (incomplete eye vascularization at birth) and macular degeneration with age causing local hypoxia [128]. While not all marine organisms have vasculature near the eye (see §2b), the expansion of sinuses, vessels or other specialized tissues that increase the oxygen concentration around the eye, such as the choroid rete mirabile found in fish [96], may indicate visual adaptation to hypoxia and would be a response similar to neovascularization in terrestrial vertebrates [128].

Local effects may also occur at the cellular level of visual cells or surrounding tissue. Mitochondria are the organelles responsible for cellular respiration and energy production (oxidative metabolism), and the oxidation capacity of the cell is directly related to the volume of its mitochondria [129]. Thus, a cell rich in mitochondria has the capacity to produce more energy, but also requires more oxygen [105]. Original studies of humans in high-altitude areas predicted an increase in the oxidative capacity of muscles in response to lower oxygen [130], but more recent work shows a decrease in mitochondria in skeletal muscle with a change in altitude, indicating that the opposite effect actually occurs [131,132]. Similarly, visual tissue normally contains densely packed mitochondria, and a reduction in oxidative capacity could be expressed as a smaller size or lower density of these organelles.

Morphological changes in the eye induced by low oxygen could also be attributed to new environmental stresses linked to behavioural or ecological responses to hypoxia. In the aquatic realm, there are changes in wavelength (= quality) and intensity (= quantity) of light with water depth, and these influence the structure and visual capabilities of each species [69]. For example, the wavelength sensitivity (i.e. $\lambda_{\max}$) of an eye in a coastal, nearshore environment will be different from the sensitivity of a deep-sea organism as a result of the difference in light quality in their respective environments [64].

If the vertical (depth) distribution of an organism is shifted or compressed as a result of oxygen stress, a subsequent change in the spectral sensitivity of the eye may occur. While this has not yet been observed in diel vertical migrators after a climate-induced change in the depth of migration (*sensu* [31]), ontogenetic changes in the spectral sensitivity ($\lambda_{\max}$) or type of opsin in the eye are known to occur during development that reflect the change in the spectral characteristics of different habitats, such as river versus ocean waters. This occurs in fish that are anadromous (ocean to river migration), including the lamprey (*Petromyzon marinus* [133]) and the salmon (*Salmo salar* [134]), and catadromous (river to ocean migration), such as the eel (*Anguilla anguilla* [133,135]). Additional changes in $\lambda_{\max}$ or the proportion of opsin types occur seasonally in some species of fish [134]. In the rudd (*Scardinius erythrophthalmus*), a freshwater fish, the proportion of porphyropsin, a short-wavelength-sensitive opsin, to the longer-wavelength rhodopsin increases in winter, whereas in summer the proportion decreases [136]. This was reproduced in the laboratory by exposing *S. erythrophthalmus* to different light intensities; fish exposed to low-intensity light (mimicking winter conditions) showed an increase in rhodopsin, while exposure to high-intensity light (summer) resulted in an increase in porphyropsin, and the effect was reversed when light/dark conditions were switched [136]. The existing plasticity of the spectral sensitivity in marine organisms indicates that a switch in opsin type or change in opsin sensitivity ($\lambda_{\max}$) could occur as an adaptation in species compressed vertically in the water column by physiological oxygen limitation, causing them to occupy a different spectral niche. These shifts may not be a direct effect of low oxygen, but could help to maintain visual function in a changing environment, and therefore be critical to fitness.

More permanent changes in visual development could occur when organisms are exposed to low oxygen during embryogenesis. Developing organisms typically have higher mass-specific metabolic requirements than adults, and as such are particularly at risk of low-oxygen stress [22]. Gas exchange is a challenge, particularly when eggs are embedded in a gelatinous mass or capsule, as is common in gastropod or cephalopod molluscs [137–139]. Embryonic visual development is vital to survival upon hatching; for example, some cephalopods develop the ability to discern contrast or learn to identify copepod prey during embryogenesis [140,141]. Hypoxia is known to cause developmental delays, mortality and/or morphological deformities in frogs [142], gastropods [138], abalone [143], brachyuran crabs [144] and squid [145,146]. Hypoxia-induced impairments to visual system development in marine organisms include a reduction in the size of the eyespot in the mussel (*Mytilus edulis* [147]) and eye deformities in hatched squid paralarvae *(Sepioteuthis australis),* potentially from lower oxygen found in capsules at the centre of egg clusters in comparison to those on the outside of the group [148]. Visual abnormalities in developing zebrafish (*Danio rerio*) occurred when different stages of development were exposed to hypoxia (approx. $6.9\,\mu\mathrm{mol\,l^{-1}}\ \mathrm{O_2}$) [149]. Out of 1161 hatched larvae, 18% exhibited anophthalmia (absence of eyes), 14% showed microphthalmia (small size of one or both eyes) and 31% showed cyclopia (only one eye present).

A change in eye size may be one morphological adaptation that occurs in marine organisms developing under low-oxygen conditions. In general, large eyes and pupils have a greater ability to detect light [64], but have poor spatial resolution and acuity (i.e. poor image quality) in comparison to small eyes. Eye design and eye size in comparison to body size is then a trade-off between the ability to capture photons, the quality of the image and the increased metabolic demands of a larger eye [64]. In mesopelagic fishes, eye size generally increases with depth, conferring a greater ability to detect photons to accommodate the exponential decay of light intensity. This increase in eye size continues with depth, and the corresponding decrease of oxygen concentration, until the bathypelagic (greater than 1000 m), where eye size is then dictated by metabolic requirements constrained by a lower food supply [65]. Eye size may be limited by the high oxygen requirements of a large eye. Embryos developing in unusually low-oxygen conditions may have smaller eyes than those developing in normal-oxygen conditions to reduce the metabolic demand on the body.

In addition, low oxygen may indirectly affect visual development of embryos if adults change the depth (and therefore light exposure) of benthic egg or capsule placement as a response to environmental conditions [150]. Changes in light intensity, quality and photoperiod are known to alter hatching success, development time and visual development in fish [151]. Development in low-oxygen or varied light conditions could therefore cause a change in morphological body plan and/or a reduction in success upon hatching due to an impairment of vision from either low oxygen and/or altered light intensity.

(e) Vision-mediated behavioural responses to hypoxia

If hypoxia causes the visual system to be compromised, organisms will probably demonstrate altered behaviour as a result. One major behaviour that could be significantly changed by visual hypoxia is phototaxis, defined as movement towards light (positive phototaxis) or away from light (negative phototaxis). The basic process of phototaxis is essential to a majority of marine organisms; it is used in diel vertical migration [152], larval settlement [153], mate recognition [154] and/or predator avoidance [155]. The cue responsible for this behaviour can be a simple change in the light environment (e.g. shadow of a predator), or a response that is initiated at a particular light level or age [156]. Regardless of the cue for initiation, a hypoxia-compromised visual system that has a lower sensitivity to light or lower ability to discern rapid changes in light could cause an organism to delay its response or miss the cue entirely.

A change in phototactic behaviour was observed in the walleye (*Stizostedion vitrium vitrium*) upon exposure to low oxygen concentrations [157]. Under normal dissolved oxygen (more than $6\,\mathrm{mg\,l^{-1}}$), *S. vitrium vitrium* displays negative phototaxis and moves to the bottom of the tank; this species has a well-developed tapetum lucidum (reflective layer behind the retina) and specializes in low-light vision. Under graded reductions of oxygen, beginning at $2\text{–}4\,\mathrm{mg\,l^{-1}}$ O_2, individuals increase their movement into lit areas; beyond approximately $1\text{–}2\,\mathrm{mg\,l^{-1}}$, the individuals show a reversal in phototactic response and swim upwards [157].

Feeding behaviour may also be altered by a change in light requirements or reduced visual capabilities. This could be manifested as a reduction in successful attack attempts, lack of ability to detect prey that are normally within visual range or a change in the time of day when the light is suitable for feeding. It is challenging to attribute changes in feeding behaviour directly to visual impairment. For example, reduced predation under hypoxia is commonly attributed to the organism trying to conserve energy by reducing movement [114,158] or to a lower appetite [159], but the changes could also be due to a decrease in visual system function such as acuity or sensitivity to motion. Visual acuity is the ability to discern details from a distance, while sensitivity to motion is related to the temporal resolution of the eye, usually measured by examining the flicker fusion response (ability of the eye to respond to repeated fast light stimuli [160]). Several studies in humans have shown negative effects of hypoxia on visual response time [161], visual acuity, flicker fusion and ocular muscle control [162]. While much less studied in marine organisms, this type of response to oxygen stress may explain changes in predation or feeding; a reduction in any one of these visual functions would have significant consequences for success in prey capture and swimming manoeuvrability. Although impaired vision has not been investigated as a cause, a reduction in feeding (among other processes) occurs with chronic exposure to hypoxia in many species. Among invertebrates, hypoxia reduces feeding in juvenile and adult blue crabs (*Callinectes sapidus*), juvenile lesser blue crabs (*Callinectes similus*) and the adult oyster drill (*Stramonita haemastoma*) [163,164], although predation in these species is not entirely reliant on vision [165,166]. Among vertebrates, a decrease in feeding under hypoxic conditions was seen in the European sea bass (*Dicentrarchus labrax*) [159], which is considered a highly visual predator [167]. The visual acuity in snapper (*Pagrus auratus*) was reduced beginning at oxygen concentrations of 40% air-saturated seawater, and severely compromised when the level was decreased to 25%, approaching the critical oxygen tension (P_{crit}) of this species [62].

Similarly, juveniles of the flounder (*Platichthys flesus*) showed a 64% reduction in predation success when exposed to 20–30% oxygen saturation [168], and plaice (*Pleuronectes platessa*) exposed to 30% oxygen saturation showed reduced feeding in comparison to those in 50–100% oxygen saturation [169]. These flatfish are known to be visual predators [170], and it is possible that visual impairment was causing these responses.

Other visual behaviours, such as response to visual signalling by both conspecifics and other species, ability to camouflage correctly, and/or mate selection, may be compromised, with hypoxia-impaired vision for similar reasons. However, changes in these behaviours as a result of low oxygen have not yet been directly associated with impaired vision [28,171,172]. Indirect effects of oxygen-compromised visual behaviour can subsequently lead to changes in the phenology of feeding, mating or breeding if animals are limited by the light levels (e.g. intensity and photoperiodicity) required for each action.

(f) Effects of hypoxia on visual ecology

Recently, documented changes in the ecology of marine organisms have been attributed to ocean deoxygenation [8,173]. Many pelagic marine organisms undergo a large, daily migration through the water column known as diel vertical migration (DVM), where they remain deeper during the day to avoid visual predators and then ascend to near-surface waters at night to feed [174,175], or show the reverse trend [176]. The movement of large aggregations of these organisms at particular depths, known as deep scattering layers, is often measured by mapping their acoustic signature [30,31,177]. Oxygen concentration can be a predictor of the extent and lower depth of DVM [30,178], and the current depths of vertical migration have already shoaled in comparison to previous years in areas that are experiencing ocean deoxygenation, such as the Southern California Bight (SCB) [31]. Wishner *et al.* [179] found that the upper depth of vertical migration in zooplankton corresponded to oxygen concentration; organisms needed to ascend to a shallower depth to ‘repay’ their oxygen debt; this repayment may also be necessary after organisms descend into low-oxygen areas in pursuit of prey [178]. As a result, habitat compression from physiological limitations attributed to low oxygen concentration has been documented or is expected to occur in many taxa, including billfish [23–25], benthic, small pelagic and mesopelagic fish [27,28,180], krill [32] and squid [178,181]. An additional concern is that the concentrated consumption of oxygen by migrating pelagic organisms in highly stratified and poorly ventilated areas of the ocean (i.e. limiting zones directly above the oxygen minimum zones) will further intensify oxygen depletion in areas that are already low in oxygen [30], potentially exacerbating these effects.

There are potential indirect effects of the responses discussed above. If prey distributions (e.g. fish and crustaceans) shoal under hypoxia, then predators may follow them into shallower waters. This is one possible explanation for the shoaling of billfish [25]. Concurrently, species with shallower distributions may become more vulnerable to predation due to increased light availability. Koslow *et al.* [28] documented major declines in the abundance of mid-water fishes of the SCB during a 9-year period of shoaling oxyclines (1999–2008) and proposed increased visual predation on these species as one explanation for their decline.

Indeed, light intensity is also a factor in determining the boundaries of vertical migration or distribution [182–184], as the organisms involved are performing the migration and distribute themselves to avoid visual predators [175]. Both metabolically driven and vision/light-driven changes in vertical distribution as a result of oxygen stress could therefore lead to increased predation risk [26], or a change in prey selection because of increased or decreased visibility from altered light availability. This has been observed in lake fish populations, where trout selectively preyed on a large species of the cladoceran *Daphnia pulex* until winter deoxygenation at the bottom of the lake created oxygen conditions below the physiological tolerance of the fish, and caused the fish to reduce their depth distribution. Because there was a greater light intensity at shallower depths, the fish were able to switch prey species and feed on a smaller copepod [185]. Thus oxygen stress has the potential to change trophic dynamics of the visual predators and their ability to feed, and also the dynamics of the prey species or lower trophic levels. Visual predation has been

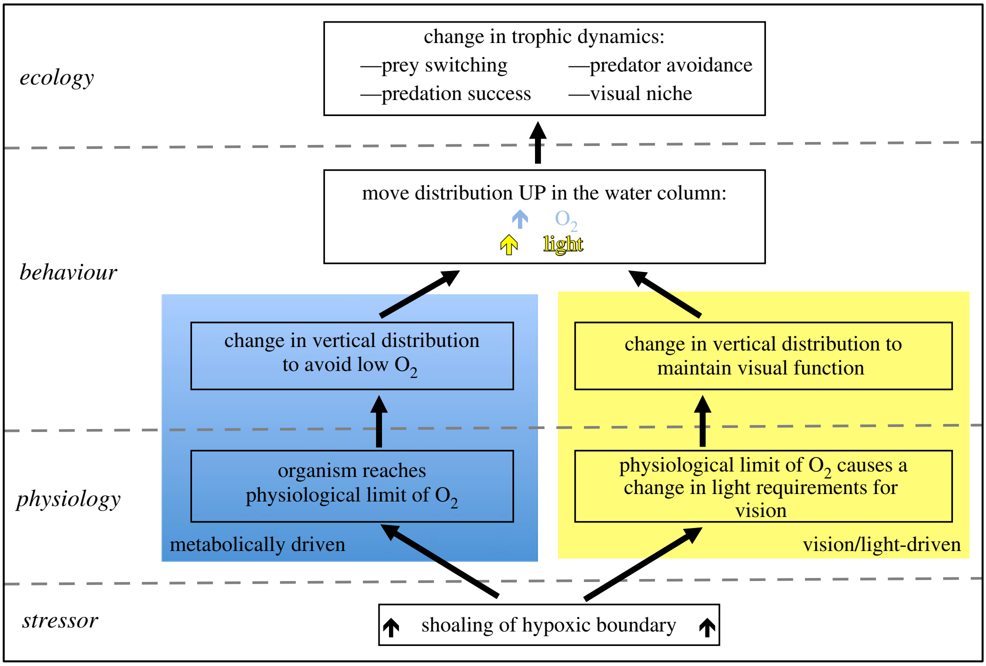

Figure 4. Dual mechanisms potentially underlying shoaling distributions as a result of hypoxia. Both metabolically driven tolerances (left, blue box) and vision/light-driven requirements (right, yellow box) may explain changes in distribution and vertical compression in the water column. (Online version in colour.)

recognized as an important driver of trophic dynamics in the marine environment [186], and implies that, even under the current hypothesis of metabolically driven movement of animals higher in the water column, direct or indirect effects of oxygen on vision play an important role (figure 4).

Current studies have not recognized limits to visual physiology as a potential cause for changes in species distribution or migration patterns in the open ocean. The effects of low oxygen on visual physiology and behaviour reviewed here offer an alternative or additional hypothesis to explain ecological responses to hypoxia (figure 4). For example, if low oxygen causes a change in the light required for vision (due to a decrease in sensitivity to light), organisms may ascend in the water column to an area where there is sufficient light for visual function. Similarly, if phototaxis behaviour is reduced, organisms may not be able to respond to visual cues and behaviours, such that the extent of DVM may be expressed differently. Both vision/light-driven scenarios yield shoaling vertical distributions in the water column, and would result in similar distributions in response to metabolically driven constraints (figure 4).

Changes in vertical distribution and compression are not only changing species interactions and trophic dynamics [187], but also exposing the organisms to light regimes that may be outside of their normal exposures (e.g. higher intensity with upward vertical motion), potentially inducing additional (light) stress on their visual systems. This may be particularly stressful for invertebrates that have a greater visual metabolic demand at higher light levels (table 1). Even a small change in depth can result in an entirely different light field with respect to intensity and spectral quality [70]. Fluctuations in the light field can occur as a result of primary production, induced by the upwelling or run-off of nutrients, or by weather patterns, and these natural light variations can be more important than abundance of prey for feeding success [188]. For example, seasonal variation in the nitracline depth, which is inversely correlated to the attenuation (dissipation) of light, consistently changes the optical properties of the water column on a yearly basis [71]. It then becomes important to examine both the oxygen and light conditions when determining the effects of oxygen stress on the visual system, as eyes with different mechanisms of phototransduction may find different light conditions stressful under low oxygen (e.g. invertebrates versus vertebrates; table 1).

(g) A note on multiple stressors

Most observed changes in the ecology of marine organisms under deoxygenation are likely to result from a combination of environmental alterations that are tightly linked, e.g. light, nutrients, carbon dioxide (CO_2) and temperature [18,189]. We highlight here the importance of vision and light as mediators when discussing climate change impacts on distributions, behaviour and fitness of marine species. Each of the stressors mentioned above can impact vision directly or in combination with oxygen loss. Low oxygen rarely occurs without a simultaneous increase in CO_2 and decrease in pH caused by enhanced respiration linked to nutrient input from eutrophication or upwelling [17–19,190,191]. The additional stress of environmental hypercapnia can exacerbate or otherwise change the effects of low oxygen on the physiology of marine organisms [192–194], and has the potential to impact or contribute to the visual responses presented here. For example, recent work by Miller and colleagues [195] has shown that acidification exacerbates the effects of hypoxia; silversides (*Menidia menidia* and *M. beryllina*) exhibit greater mortality, increased surface respiration and reduced gill movements when exposed to both low pH and low dissolved oxygen in comparison to those exposed to only low oxygen. One cause of this may be a dampened protective physiological response to hypoxia (which allows the organism to acclimate or otherwise cope with reduced oxygen concentration) in the presence of environmental hypercapnia, which causes the effects of hypoxia to be exacerbated, as seen in the Pacific whiteleg shrimp (*Litopenaeus vannamei*) [196,197]. A similar effect (reduced adaptive response to hypoxia, and therefore exacerbation of effects) has been observed with temperature; the number of larval *Fundulus heteroclitus* showing visual defects after exposure to both hypoxia and high temperatures during development increased 8-fold in comparison to those exposed to only hypoxia [149]. Negative effects of low pH and high CO_2 on vision and other sensory systems have already been documented in marine organisms [198–200]. Organisms possessing a choroid rete, an organ that relies on using a change in pH to change the affinity of blood to oxygen (root effect), may be particularly vulnerable to the combined effects of environmental hypercapnia and hypoxia. For example, in addition to the effects of a graded reduction in oxygen, Scherer [157] showed that the phototactic reaction in the walleye (a species with a choroid rete) was also reduced under the combined effects of low oxygen and low pH. In contrast, two-spotted gobies, *Gobiusculus flavescens*, that developed under high-CO_2 conditions showed an increase in phototaxis behaviour (greater number of larvae moving towards light and faster swimming speed) after hatching in comparison to those developed in normal conditions [201]. Thus, testing effects of ocean deoxygenation with multiple stressors may be necessary to accurately resolve physiological and ecological effects on vision and visual function.

3. Conclusion and future directions

Ocean deoxygenation has the potential to impair visual function in marine organisms, and has probably done so for over a billion years. Anthropogenic influences have accelerated rates of oxygen loss in the ocean through ocean deoxygenation caused by warming and eutrophication. Oxygen stress may induce a change in the light environment from habitat compression or cause a physiological change in light requirements that could alter the behaviour and distribution of visual marine organisms, and increase their vulnerability to predators or their feeding success. Changes in the physiology, morphology, behaviour and ecology of marine animals have already been observed in response to ocean deoxygenation, but it is unclear to what extent visual limitations are driving these changes. Organisms that live full time in the oxygen minimum or oxygen-limiting zones (*sensu* [173]) may already employ adaptations to maintain visual function, whereas transient species or those that avoid areas with reduced oxygen (and are probably less tolerant to these conditions) may be particularly at risk for a decline in visual function. This review details the importance of oxygen for visual function, and presents the case for varied and serious consequences in visual marine organisms exposed to low oxygen resulting from climate change. The effect of low oxygen on vision has been studied in humans and terrestrial animals, but is a novel theme that merits further exploration in marine organisms. Care should be taken to study visual responses in both vertebrates and invertebrates, as the effects will probably reflect the many differences in visual physiology within each group. We hypothesize that marine organisms possessing visual systems with high temporal resolution, such as fish, cephalopods and arthropods, many of which support large coastal fisheries, will be particularly at risk. Further research could help determine which specific taxa will be most susceptible to these effects, whether adaptations to lower oxygen occur on acute or chronic time scales and whether these adaptations can maintain ecosystem integrity in a future ocean subject to deoxygenation.

Data accessibility. The data for figure 3 and associated references can be found in electronic supplementary material, Supplement 1.

Authors' contributions. L.R.M. conceived the basic premise of the paper, conducted the literature review and wrote the manuscript. L.A.L. placed the work in the context of ocean deoxygenation, helped refine concepts and edited the manuscript.

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